



FRDC

FISHERIES RESEARCH &
DEVELOPMENT CORPORATION

Adaptive management of temperate reefs to minimise effects of climate change: Developing new effective approaches for ecological monitoring and predictive modelling

Neville Barrett, Amanda Bates, Maria Beger, Rick Stuart-Smith, Craig Syms, Neil Holbrook, Nathan Knott, David Booth, Brendan Kellaher, Stefan Howe, Colin Buxton, and Graham Edgar.

September 2014

FRDC Project No **2010/506**

© 2014 Fisheries Research and Development Corporation.
All rights reserved.

ISBN 978-1-86295-770-1

Adaptive management of temperate reefs to minimise effects of climate change: Developing new effective approaches for ecological monitoring and predictive modelling]
Project No. 2010/506 2014

Ownership of Intellectual property rights

Unless otherwise noted, copyright (and any other intellectual property rights, if any) in this publication is owned by the Fisheries Research and Development Corporation and the University of Tasmania.

This publication (and any information sourced from it) should be attributed to **Barrett, N., Bates, A., Beger, M., Syms, C., Holbrook, N., Knott, N., Booth, D., Kellaher, B., Howe, S., Buxton, C. and Edgar, G. University of Tasmania, Institute for Marine and Antarctic Studies, 2014, Adaptive management of temperate reefs to minimise effects of climate change: Developing new effective approaches for ecological monitoring and predictive modelling, Hobart, May.**

Creative Commons licence

All material in this publication is licensed under a Creative Commons Attribution 3.0 Australia Licence, save for content supplied by third parties, logos and the Commonwealth Coat of Arms.



Creative Commons Attribution 3.0 Australia Licence is a standard form licence agreement that allows you to copy, distribute, transmit and adapt this publication provided you attribute the work. A summary of the licence terms is available from creativecommons.org/licenses/by/3.0/au/deed.en. The full licence terms are available from creativecommons.org/licenses/by/3.0/au/legalcode.

Inquiries regarding the licence and any use of this document should be sent to: frdc@frdc.gov.au.

Disclaimer

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

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

Researcher Contact Details

Name: Neville Barrett
Address: IMAS, Uni of Tas, Locked Bag 49, Hobart 7001
Phone: 03 62277210
Fax: 0362278035
Email: Neville.barrett@utas.edu.au

FRDC Contact Details

Address: 25 Geils Court
Deakin ACT 2600
Phone: 02 6285 0400
Fax: 02 6285 0499
Email: frdc@frdc.com.au
Web: www.frdc.com.au

In submitting this report, the researcher has agreed to FRDC publishing this material in its edited form.

Contents

Contents	2
Acknowledgments	5
Executive Summary	6
Introduction	10
Objectives	12
Report Structure	13
Methods	14
Methods for Objective 1	14
Methods for Objective 2	17
Methods for Objective 3	17
Methods for Objective 4	19
Extension	20
Results	21
Objective 1	21
Objective 2:	31
Objective 3:	39
Objective 4	50
Discussion	94
Conclusion	100
Implications	101
Recommendations	103
Extension and Adoption	105
Project coverage	108
References	109
Project materials developed	114
Appendices*	115
Appendix i. Ecological traits and climate velocity explain range shifts in an ocean warming hotspot	115
Appendix ii. Resilience and signatures of tropicalization in protected reef fish communities.....	132
Appendix iii Statistical solutions for error and bias in global citizen science datasets	168

Appendix iv. Distinguishing geographic range shifts from artefacts of detectability and sampling effort.	198
Appendix v. Report from initial project workshop. August 2011.....	216

Tables

Table 1. Predicted current per site abundance of fish species from LTTRMP and RLS data.

Table 2 Predicted current per site abundance of mobile invertebrate species from LTTRMP and RLS data.

Table 3. Summary of the central issues currently arising in SE Australia in response to a warming climate, potential management responses, and the information/monitoring requirements necessary to support these.

Figures

Figure 1. Sites surveyed by the LTTRMP and RLS surveys between 1992 and 1013. Does not include additional sites surveyed by the Victorian MPA monitoring program (identical methods) or the South Australian reef health survey (identical for fish and mobile invertebrates) that further increase the spatial coverage in those states.

Figure 2. Invertebrate abundances (n/200 m²) of common species at sites within the Jervis Bay Marine Park in NSW during surveys between 2003-2007.

Figure 3. Oceanographic variables, obtained from CSIRO's long-term observing station, driving reef assemblage change at Maria Island. a, Mean annual silicate and b, salinity, and c-d, extreme surface temperatures.

Figure 4. Predictors of abundance-weighted species diversity. Species diversity (SDa) related negatively to the abundance of *Trachinops caudimaculatus* abundance in the reserve and reference sites, and positively to nitrate and silicate; see Appendix ii, Figures 1d and S1 for the y-axis dimensions of nitrate and silicate concentrations.

Figure 5 Community weighted biological trait values calculated based on biomass. a, Proportion herbivores kg⁻¹; b, maximum body length kg⁻¹ and c, thermal affinity kg⁻¹ biomass. Regression slopes (dotted lines) and 95% confidence intervals (shading) are in colour when a significant difference between the reference and reserve sites was observed, predicted from linear mixed effects models.

Figure 6. The log abundance, through time, of herbivorous fishes within the Maria Island marine reserve (green circles) and adjacent fished reference sites (open circles). Warm affinity herbivours increasing through time include *O. cyanomelas*, *G. zebra* and *P. microlepis*.

Figure 7. Species and functional diversity at Maria Island over 20 years. a–f, Species and functional richness (a,b), SDa and FDa (c,d) and SDb and FDb in reserve (nD6) and reference sites (nD6; e,f). Regression slopes (dashed lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table 2). A single regression line indicates similar mean values for reserve and reference sites.

Figure 8. Annual change in richness and diversity metrics. Mean (s.e.) year-to-year differences in species richness (SR), functional richness (FR), SDa and FDa, and SDb and FDb in reserve (nD6) and reference sites (nD6) for the 20-year study period. Generalized linearmixed effects model results are in Supplementary Table 3. Values were scaled before differencing.

Figure 9. Species displaying trends related to changes in the community weighted mean functional traits. a-b, Changes in the abundance of herbivores (*Girella zebra* and *Olisthops cyanomelas*), c-d, large-bodied fish (*Latridopsis forsteri* and *Cepaloscyllium laticeps*) and e, warm-water species typical of Maria Island (*Parma microlepis*) in reserve and reference sites. f, Four species atypical of Maria Island and thought to be extending their range were sighted in reference sites only (*Chromis hypsilepis*, *Heterodontus portusjacksoni*, *Hypoplectrodes maccullochi* and *Sphyræna novaehollandiae*).

Figure 10. Trends in key site attached resident fish within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/2000m²), for fishes in each size category (greater than 250 and 300 mm total length).

Figure 11. Trends in warm affinity reef associated fish within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/2000m²).

Figure 12. Trends in Southern rock lobster (*Jasus edwardsii*) abundance (n/200m²) and biomass (g/1200m²) within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection.

Figure 13 a. Trends in reef associated mobile invertebrates within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/200m²).

Figure 13 b. Trends in reef associated mobile invertebrates within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/200m²).

Figure 14. Matching current SST and future (2060's) predicted SST for inshore regions of SE Australia based on Oliver et al. (2014) and used to derive species future latitudinal (thermal) relationships based on current latitudinal (thermal) relationships.

Figure 15. Modelled species distributions of fishes with potential SE Australian range.

Figure 16. Fish abundance records by Latitude & site (n/2000m²) from LTPMP and RLS data.

Figure 17. Modelled species distributions of mobile invertebrates with potential SE Australian range.

Figure 18. Mobile invertebrate abundance records by Lat. & site (n/2000m²) from LTPMP and RLS.

Figure 19. Current (blue) and predicted (red-2060's) abundance (n= y axis) by latitude south (x axis) and transect (500m²) for typical fishes on Temperate SE Australian reefs based on modelled species distributions and predicted future thermal distributions (from Oliver et al. 2014).

Figure 20. Current (blue) and predicted (red-2060's) abundance (n= y axis) by latitude south (x axis) and transect (500m²) for typical mobile macroinvertebrate species on Temperate SE Australian reefs based on modelled species distributions and predicted future thermal distributions (from Oliver et al. 2014).

Acknowledgments

We would like to thank a range of organisations and people for their contributions to this research.

Firstly we thank FRDC and the Department of Climate Change and Energy Efficiency (DCCEE) for the grant that under-pinned this research as well as other funding agencies that supported a range of collaborations that built upon this. An ANNiMS grant assisted in leveraging this work with collaboration from Jennifer Sunday, and several grants from ARC facilitated further collaboration with Tom Bird, and, through the Super Science program, the contribution of Eric Oliver with respect to physical data collation. Colin Creighton from FRDC provided valuable feedback to improve the structure and clarity of the report. We also thank CSIRO for contributing physical data via BRAN and from the Maria Island long-term monitoring station, and Peter Thompson for his efforts on allowing access to the most recent versions of that. Andre Belo-Couto assisted with initial attempts at gathering appropriate physical data from BRAN, and a wide range of people assisted with collecting the initial biological data that contributed to the analysis, too many to thank individually, but their contribution is very much appreciated. Finally we thank Just Berghout for database development necessary to access and merge the multiple datasets used in this analysis, Antonia Cooper and Justin Hulls for technical support, and all our collaborating agencies from the Temperate Australian States who assisted in collection of the biological data, and in the case of Victoria, contributed data collected as part of their monitoring programs. Reef Life Survey also contributed a substantial component of the data analysed, and we thank all their volunteers for the tremendous effort they have put into this program, as well as Rick Stuart-Smith, for facilitating much of the RLS survey work and contributing to interpretation of many of the results presented here.

Executive Summary

Waters along Australia's most densely populated south-east coast are warming at 3.8 times the global average rate, the most rapid change in the Southern Hemisphere. Ecosystems in this region are therefore likely to be severely impacted by climate change and significant biodiversity change is expected. The rapid nature of these ecosystem changes requires science-based decisions about where, how and when to apply adaptive management interventions. Well informed predictive models are needed to estimate likely ecological changes and inform management actions such as spatial closures to protect vulnerable habitats, translocation of key predators, or direct manipulation of abundances of threatening and or threatened species. Our study addressed these challenges using a mix of long-term (up to 20-yr) monitoring records of fishes, invertebrates and macro-algae in, and adjacent to marine reserves in the region undertaken as part of University and/or State agency research programs. This was coupled with spatially extensive species abundance data derived from the Reef life Survey citizen science program (<http://reeflifesurvey.com/>) to examine past, and predict future ecological responses to warming, including assemblage changes, kelp decline and predator-prey relationships.

In the initial phase of the study we focussed on examining temporal patterns in species abundance and the relationship with physical drivers such as temperature. For many species there was no clear relationship evident, as the time-series of observations were, as yet, generally insufficient through time to detect relationships with changing environmental variables such as mean monthly temperature. The 20 year dataset from Maria Island proved to be the most meaningful in this context, and could readily be matched with oceanographical variables derived from a nearby CSIRO monitoring station. While few individual species in this dataset could be clearly determined to be responding to climate signals through time, a range of community level metrics did show significant trends when examined for the fish assemblage. Signatures of a warming trend could be seen in metrics such as functional trait richness, and functional diversity, reflecting increasing abundances of warm affinity species and species traits such as herbivory. It is this latter trait that may have one of the largest initial impacts in the SE region of Australia, as, prior to recent warming, herbivorous fishes were relatively rare in the cool temperate zone, thus their increasing biomass may reflect a significant change in system function through time.

One notable feature was that in some metrics, such as thermal affinity, there was a differing response to warming between the unfished sites in the Maria Island marine reserve and adjacent fished reference sites. These differences reflect "resilience" of the reserve to some aspects of climate change. The primary mechanism underlying this appears to be related to increased top down control of sea urchins within the reserve (via lobster predation) reducing the extent of urchin barren formation that in turn provides habitat for many warmer affinity species. The message from this is that MPAs can provide increased "resilience" to climate change effects, particularly when these are driven by an ecosystem engineer such as the Long spined urchin *Centrostephanus rodgersii*. However, this resilience is context dependent, as in many areas such lobster/urchin interactions may not be the primary drivers of ecosystem function on reefs, or where they are, resilience can, and should, be enhanced in off reserve areas as well, by appropriate changes in fishery management. Ultimately this management needs to be informed by long-term studies examining differences between fished and protected areas at representative locations along our coastline, building on existing studies to extend that time series over future years of warming.

In the second phase of the study we modelled the latitudinal species abundance curves of a wide range of fish and mobile invertebrate species in order to identify the current shape of the curves and their abundance centres, and use these distributions to predict both likely future distributions and the relative contributions of individual species under possible climate change scenarios. The use of Reef Life Survey (RLS) data was essential for this modelling, as existing data from MPA and reef health monitoring programs was too sparse to identify both core abundance areas and the spatial extent of rarer abundances in the tails of species distributions. In addition, in many cases, knowing the upper thermal limit of distributions is important for refining models and examining likely losses at northern extent of ranges, and the RLS dataset was unique in providing abundance data across that range. Overall, the modelled distributions are invaluable for estimating the extent that some species will extend their central maximum

abundance distributions into parts of SE Australia, or to the south of Tasmania and hence be lost, or simply increase/decrease marginally in influence if the distribution has a long tail around a central peak. The predicted likely emergent community at any location is clearly dependent on site (exposure regime etc), likely temperature increase through time, and the time for communities to come to equilibrium. Recent research suggests there will be a 2 degree Celsius increase in temperature in the SE region by 2060, under the A1B scenario of the IPCC (Oliver et al. 2014). Under that basis we can determine likely assemblages based on our distribution data, and use that to inform discussions by the biological and resource management community as to future adaptation options, both with respect to conservation and fishery management outcomes. We have some confidence that our species distribution models are likely to predict the general species distribution following warming, as an additional study undertaken as part of this project determined that during the previous period of warming in this region, the range expansion of many species closely tracked the climate warming velocity. That change was surprisingly irrespective of individual species traits, such as dispersal capability via adult or larval movement.

The species distribution models predict significant changes in the assemblages of fishes and mobile invertebrate species in the SE region, although for many regional species this change was not at an order of magnitude level, and the influx of warmer water species meant that overall levels of diversity would increase. Few species were predicted to be lost, and with one exception (the Real bastard trumpeter), all were introduced species with a localised distribution. The major predicted change of consequence to ecosystem function was a doubling of *Centrostephanus* abundance in eastern Tasmanian waters, and extending to the south coast in significant numbers. This was coupled with a predicted decline in Southern rock lobster numbers in this region (in the order of 20%), such that the key predator of *Centrostephanus* will be declining at a time when increasing numbers are needed to arrest likely barren formation.

Recommendations

1. It is recommended that long-term monitoring initiatives with national scale and consistency in methods be continued/established/supported for providing the essential knowledge on rates and impacts of climate change such that this can best inform adaptive management and the success of management measures once implemented. In principle support for such initiatives via acknowledgement of this as a priority area in marine policy development is an important first step.

Context: Long-term monitoring is essential for detecting and describing change, as well as informing appropriate management responses, thus appropriate monitoring programs need to be in place for informing adaptive management of temperate reef systems. Additionally, such monitoring needs to involve MPAs as reference areas to understand the extent that fishing and other human activities interact with climate change, such that off-reserve management may adapt to prevent adverse effects where/if possible. Such monitoring could readily and cost-effectively include and build upon current MPA/biodiversity/reef health programs in temperate WA, SA, Vic, Tas and NSW that utilize a common methodology, and, based on existing MPA networks, provide a good spatial framework for detecting and understanding regional trends, as well as national ones. As these programs are spatially isolated, and often constrained to particular habitats, further monitoring by cost-effective programs such as RLS are essential to adequately describe changing abundances over the ranges of key species, as well as documenting changes in habitats and depths not adequately surveyed by current government based monitoring programs.

2. It is recommended that the current MPA network in SE Australia form the basis of any regionally based monitoring, with monitoring sites within MPAs matched by similar sites in fished habitats. This framework will inform management of changes as they occur, and if significant differences arise between fished and protected coastal regions, the extent that management adaptation via fishery related measures may be effective in preventing change where this is seen to be adversely damaging to fishery or biodiversity values.

Context: Well-established and adequately protected MPAs are an essential component of a monitoring framework that untangles fishing and other human impacts from climate change, allowing magnitudes of impacts and resilience to be determined and management options to be evaluated realistically against “natural” benchmarks. While our evidence suggests no-take MPAs can provide resilience to change, such resilience can take decade scales or more to establish, hence, MPAs need to be established with the long-term reference and resilience goal in mind. Flexible “adaptive” MPAs are unlikely to be an option for adaptive management due to the time required for resilience to develop. Additional “scientific reference” MPAs are needed in SE Australia (and other regions in general) given that not all typical coastal reef ecosystems are included, or adequately protected in the existing framework throughout the region, hence adaptive management may not be adequately/fully informed by the current configuration.

Specific reference areas of significant value to such a monitoring program are Jervis Bay Marine Park, Batemans Marine Park (NSW parks), Cape Howe Marine National Park, Point Hicks Marine National Park, Wilsons Promontory Marine National Park, Bunurong Marine National Park, Port Phillip Heads Marine National Park (Vic), Kent Group Marine Nature Reserve, Governor Island Marine Nature Reserve, Maria Island Marine Nature Reserve, Tinderbox Marine Nature Reserve and Port Davey Marine Nature Reserve. All these areas have no-take areas suitable for a reference role, existing long-term data and monitoring available (at least a minimum of ten years for most) and adjacent fished habitat that is representative of the coastal region and is also monitored as part of existing programs. Their spacing within the SE region of Australia is at approximately 100 km scale, giving a good regional spread to both represent regional variability in ecosystem function, and latitudinal gradients in biogeographical trends, including the current and future range of species. The main significant gaps include far NE Tasmania where a monitoring location is needed to maintain the 100 km regional scale of observations, and exposed coast reef systems at Jervis Bay that are under-represented in the current monitoring program. Monitoring must occur at these spatial and biogeographical scales if changes are to be detected (including species range changes and ecosystem changes) and this knowledge interpreted in the context of regionally specific system function. The data collected needs to be informative of changes in the variety of species that represent biodiversity, key fishery species, key system drivers and key impacts of system change. Hence, it needs to be comprehensive in species coverage and include habitat forming species such as macroalgae and endemic species at risk of loss. The current methodology in use for MPA and reef health monitoring in the temperate Australian states is appropriate to this task and provides a sound baseline from which to detect further change. Ideally such monitoring would occur on an annual basis to establish baseline variability, however, recognising that resources are limited, such monitoring would need to be at a maximum of five year periods to allow for temporal trends to be detected and reported as part of an integrated reporting framework incorporating climate change metrics into the State of Environment reporting. To provide improved range edge detection within the 100 km scale of MPA related surveys, additional surveys at regular spatial scales (ten km scale) undertaken by Reef Life Survey or state agencies would also need to be undertaken at 5 year time scales. Reporting metrics include the velocity of species movement, loss of endemic species within their range, changes in key ecosystem species such as urchins and lobsters, and habitat metrics such as kelp cover and algal diversity. Ideally reporting would be guided by the a regional management group (recommendation 3) and on the basis of a national standard database for sharing data across jurisdictions, with funding from all agencies involved in climate change adaptation and State of Environment reporting.

The extent that MPAs can further contribute to climate change adaptation as a management response to protecting biodiversity in their own right depends upon the extent that off-reserve resource management can adapt quickly enough and sufficiently to counter negative impacts such as *Centrostephanus* barren formation, via reestablishment of essential ecosystem function. Ultimately this is a policy/social/ political issue that can only be informed by adequate monitoring such as that arising from the focus on Maria Island over the past two decades.

3. It is recommended that given recent predictions indicate warming will continue rapidly in the SE over the next 50 years, a regional committee with representation by fishery/conservation management and research be established to review changes documented by monitoring programs and predictions, and to develop and coordinate adaptation responses, (both management and research).

Context: Species distribution models are now available for a wide range of temperate reef species, along with future temperature predictions. The overall intersection with predicted species abundances and the community structure that follows after warming is something that requires further expert evaluation, establishment/refinement of conceptual models, and on-going discussions about the overall implications and potential for adaptive management. A workshop will be held following the completion of this study to begin this process, but it will need to be an ongoing one over the remainder of this century, and a clear recommendation is that a regional committee be established and meet regularly to review new information as changes evolve, and to examine potential adaptation options for resource managers. If, as the predictions of Oliver et al. (2014) are correct, and we can expect a further 2C increase in SST in inshore waters of SE Australia within 60 years from now, our models suggest many Tasmanian endemic species will contract their range to southern Tasmania or be lost entirely. The overall community structure in NE Tasmania will also be vastly different with assemblages dominated by many “typically” southern NSW species and the likelihood that *Centrostephanus* barren formation will be widespread. Our initial workshop, examining possible management options, indicated there were very few clear options available for management. For endemic species at risk of loss for example, the Tasmanian Government is unlikely to be able to deal with a small subset of the range of terrestrial species, much less marine species that might need to be maintained artificially in aquaria. For protection against widespread habitat loss via mechanisms such as *Centrostephanus* barren formation, rebuilding of natural predator stocks is one of the few clear options, and this is currently being implemented by management via changes to lobster fishing effort. Monitoring of the effectiveness of this, and future adaptive measures, will be a critical part of the evaluation and feedback process.

Introduction

Waters along Australia's most densely populated east coast are currently warming at 3.8 times the global average rate (Hobday et al. 2007), the most rapid change in the Southern Hemisphere. As this regional warming is predicted to continue throughout the 21st century (Oliver et al. 2014), ecosystems in this region are likely to be severely impacted by climate change, and significant biodiversity responses are expected. These changes are expected to be widespread, influencing both our fishery and our biodiversity assets, and likely require informed management responses from fishery and conservation management alike, at least in circumstances where adaptive management responses are available. Significant climate mediated changes have already become apparent in locations such as NE Tasmania, where the Long-spined urchin *Centrostephanus rodgersii* has extended its range following warming of over 1 degree Celsius in this area since the late 1970's (Johnson et al. 2011, Last et al. 2011), with these barren areas causing a substantial decline in the productive algal communities that support import and inshore fisheries such as Southern rock lobster and abalone. The barren areas also cause a significant loss of biodiversity, at least at the scale of the barrens (Ling, 2008), a loss that will become increasingly significant if barrens increase to the extent that they are found in NSW within the central part of their distribution. In that area barrens form up to 50% of rocky reef systems between 5-20 m depth (Andrew and O'Neil, 2000). Current studies in NE Tasmania have found that barrens constitute approximately 5% of rocky reef cover at depths between 15-50 m, with these extending substantially deeper than those found in NSW (Perkins et al, in review). That increased depth distribution is of significant concern, as it means such barrens may impact over a significant area of the reef systems that currently support the lobster fishery in this region, and into the high biodiversity sponge-garden habitats, previously thought to be relatively immune to loss through barren formation.

The rapid nature of likely ecosystem changes will require science-based information to inform decisions about where, how and when to apply adaptive management interventions. Clearly monitoring of on-ground changes as they occur is one approach to providing this information, and monitoring programs are underway at a wide range of locations throughout temperate Australian waters. A clear need exists to continually observe temperate reefs in our region to provide the necessary feedback for management agencies to both detect and understand the nature and magnitude of changes occurring, to develop adaptive management strategies to respond to changes as they occur, and to monitor the success of such strategies. Having an appropriate monitoring strategy in place is indeed an adaptive strategy in itself. Given that such monitoring programs can be expensive, and are currently often targeted at different outcomes (such as MPA management) they need to be refined with respect to providing cost-effective yet robust detection of biotic responses to climate change. Fortunately, several monitoring programs are underway in the temperate Australian waters, allowing evaluation of the benefits that they provide for informing climate mediated patterns. While they are not specifically funded for (or focussed on) informing climate change adaptation, the time series they provide is ideal for detecting temperature-mediated responses. At the habitat and biodiversity level they are often associated with monitoring of Marine Parks (e.g. Barrett et al. 2007, 2009 for Maria Island, Barrett et al. (1998-Port Davey), Barrett et al. (2005-Jervis Bay), Edgar et al. (2005-Jurien Bay), Edgar et al (2005-Encounter Bay, SA), e.g. Edmunds et al. (2004-an example of many Victorian reports), or on understanding overall reef health (Turner et al. (2008) and Collings et al. (2008) for South Australia, Edgar et al. (1997) and Stuart-Smith et al. (2008, 2011) for Tasmania). The marine park focus has been ideal for untangling climate responses from those due to fishing pressure, and the potential interaction between the two factors.

In more recent years, a move towards more community engagement has led to the establishment of the Reef Life Survey program, that has provided a framework for regularly monitoring coastal locations in temperate Australian waters ranging from the Abrohlos Islands in WA through to the Solitary Islands and Lord Howe Island in NSW

(http://reeflifesurvey.com/files/2013/11/RLSF_AnnualReport_2013_WEB.pdf). This program has already quantified a number of climate related changes of concern to the broader community, including coral bleaching and kelp loss at the Abrohlos as part of the marine heatwave (http://reeflifesurvey.com/files/2013/11/RLSF_AnnualReport_2013_WEB.pdf), coral bleaching at Lord Howe Island (Edgar et al. 2010) and *Centrostephanus* barren formation at Beware reef in NE Vic (http://reeflifesurvey.com/files/2013/11/RLSF_AnnualReport_2013_WEB.pdf). Finally, such monitoring programs, capable of tracking climate responses through time series, have been supplemented by once-off studies that describe current patterns and/or biological interactions that produce these patterns, such as the *Centrostephanus* study of Johnson et al (2005) in NE Tasmania, which described the distribution of barrens as well as, through transplant experiments with lobsters, the possible mechanisms by which barrens may be restored to kelp communities.

While ongoing monitoring and process studies are a critical component of adaptive management, if we are to make informed decisions about likely future changes, the development of predictive models is the other essential approach to ensuring management is well informed of likely future change. However, such biologically-based models often have high uncertainty when extrapolated into new conditions, as do the matching physical Climate Change scenario models (e.g. Oliver et al. 2014). Despite this, unless protocols for tracking and predicting ecological changes are well informed, the remote nature of marine habitats, with associated difficulties and expense when mapping biodiversity assets, will inevitably translate to sub-optimal management interventions. For example potential management interventions could include targeted spatial closures to protect vulnerable habitats, targeted translocation or rebuilding of stocks of key predators, direct manipulation of abundances of threatening and or threatened species. Such interventions have already begin in SE Australia, including the protection of Blue grouper in Vic waters as a potential urchin predator (<http://www.dpi.vic.gov.au/fisheries/recreational-fishing/catch-limits-and-closed-seasons/marine-and-estuarine-scale-fish/Blue-Groper>) and measures to rebuild lobster stocks in NE Tasmanian waters (<http://dpipwe.tas.gov.au/sea-fishing-aquaculture/commercial-fishing/rock-lobster-fishery/east-coast-catch-cap>), again, as a measure to rebuild predator numbers to keep *Centrostephanus* urchin numbers under control. Yet undertaking such significant intervention needs to be based on the best possible information, to ensure that any predictive models are well supported by proven quantitative relationships.

Our project addresses these challenges using Australia's south east coast as a focus, as it is the region of greatest change and hence under the most imminent threat. Using the longest available worldwide (20-yr) ecological reef data record of fishes and mobile invertebrates in, and adjacent to, marine reserves (from the Long-Term Temperate Reef Monitoring Program, LTTRMP), we identify thresholds in ecological responses such as significant assemblage shifts, potential kelp decline, predator-prey relationships and the resilience of natural systems to climate mediated change. The LTTRMP data is matched with similar data obtained by the Reef Life Survey program, that while lacking extensive temporal replication, provides a broader spatial coverage that compliments the more clumped LTTRMP survey data outside of Tasmanian waters. Together, these datasets allowed species distribution models to be developed, based on quantitative data that often extended over the entire distribution of species ranges. These distribution models are subsequently used to predict likely future distributions based on relationships with current temperatures at each survey location, and predicted future temperatures under a central CC scenario (from Oliver, et al. 2014). From that, likely future assemblage structures are identified with respect to increases or decreases in species abundances at a range of latitudes throughout the SE region, along with likely major system function shifts.

Future species distributions based on models derived from current thermal envelopes alone, run the risk that many species may not track the rate (velocity) of warm water expansion southward, with species characteristics (traits) such as limited adult and larval dispersal potentially restricting rates of migration and hence producing lags in thermal responses. We therefore examined these relationships to examine whether our future predictions needed to be adjusted to account for such lags. We also examined the extent that relatively sparse survey data in the tails of species distributions can influence Species Distribution Models (SDMs) and current estimates of range expansion, the importance of

abundance data vs presence/absence data, and how these factors could be accounted for in models. In addition, we examined and developed statistical solutions for dealing with the non-perfect knowledge, error and bias associated with citizen science and similar datasets, that are often clumped, and contain artefacts relating to data from individual divers that ideally need to be detected and accounted for within descriptive models.

These outputs, combined with future climate scenarios, will empower state management and NRM agencies with improved capacity to build ecosystem resilience through spatial management actions. The project was funded via DCCEE and its agent FRDC and therefore specifically addresses three National Climate Change Adaptation Research Plan (NARP) priority questions by: (3.1) identifying priority ecosystems and species most vulnerable in this globally significant warming hotspot; (2.1) identifying vulnerable inshore reef species of commercial fisheries importance (including Southern rock lobster, abalone, and temperate wrasses) and priority locations for adaptive management; and (3.2) clarifying management benefits from one intervention strategy – MPAs – for enhancing resilience of temperate ecosystems.

The approach to these priority NARP questions was to (1) quantitatively relate spatial and temporal variation in the distribution of inshore species to key oceanographic metrics of climate variability using a uniquely long marine species record collected along Australia's east coast, and matching spatial data from Reef Life Survey; (2) develop predictive models of the sensitivity (and hence potential impact) of temperate reef marine biota to exposure from scenarios of climate variability and change; and (3) identify appropriate adaptive strategies to minimise impacts of change on inshore temperate biodiversity, with particular emphasis on species of importance to the commercial and recreational fishing sectors.

Through collaboration with government agencies, the ultimate aim of the project is to provide the necessary biodiversity level information necessary to develop climate change strategies within management frameworks, thereby enhancing local adaptation to climate change. In the initial phase of the project a workshop was held with management agencies and stakeholder groups to introduce the project and to explore the possible range of management options available to respond to climate change in the marine environment, and it is proposed that a follow-up workshop be held to discuss the extent that the results of this study may further inform these management strategies.

Objectives

- 1 To collate and analyse the long-term marine ecological data records for southeast Australian reefs and use these to quantitatively describe relationships between species' distribution and abundance and changes in ocean temperature, salinity and EAC position as key drivers of climate change;
- 2 To identify optimal locations and species for monitoring programs (including Reef Life Survey – a cost-effective, ecological monitoring program using trained recreational divers – and comparable agency-based programs) to best inform adaptive management via delivery of up-to-date relevant information
- 3 To assess the costs and benefits of existing temperate Marine Protected Areas for biodiversity-conservation management in response to CC and evaluate the robustness of adaptive management frameworks given uncertainty in predictions; and
- 4 To develop models that quantify and predict the impacts of climate change on inshore reef communities of fishes, invertebrates and macroalgae across the southeast Australian region so that potential responses to change can be identified, considered and developed appropriately.

Report Structure

The nature of this study involves a number of substantial cross-overs between the four key objectives with respect to the individual analyses undertaken, which often inform a number of objectives. In addition, the research undertaken here was leveraged through collaborative studies involving co-investigators on related projects such as the Springboard program, and PhD projects. As these studies were prepared as research papers for publication, and some have currently been published, they are attached in the appendices rather than appearing in the body of the report, and will instead be referred to where appropriate in the results and discussion. The body of this report is therefore broken up into an objective specific approach, allowing the applicable components of each study to be referred to, discussed and built upon, without including all the content in each individual section.

For example, Objective 1 focussed on quantitatively describing relationships between species distributions and abundances, and changes in ocean temperature, salinity and EAC position as key drivers of climate change. This work was informed by the Sunday et al. (Appendix ii) study examining climate velocity vs rate of species migration, and provided the grounding that allowed us to understand the direct nature of coupling between ocean temperature and species distribution. It was also informed by the study of Bird et al. (2013) that examined the statistical issues associated with various forms of biological data available to make predictions on species distributions, and how to deal with these. The study of Bates et al. (in review) complimented that by simulating patterns in empirically derived assemblage range shift data from two regional-scale (100s km) field studies, one on Western Australian Kelps (Wernberg et al. 2011), and the other on SE Australian fish species (from the database assembled for this report). This work found that even with a well-designed sampling regime, accurate estimation of range edges are difficult to obtain for many species, due to the often sparse nature of data from these edges. One way of dealing with that is to apply time-to-extinction models to spatial distribution data to provide species-specific confidence limits for range edges. Ultimately, this informed the study by Bates et al. (2013) that examined the extent that physical drivers related to climate change have influenced species distribution, abundance and diversity within the Maria Island region of Eastern Tasmania, as a case study of climate driven changes in diversity.

Overall, the results/discussion component of the report is divided into four main sections that deal with each of the key objectives individually, followed by a broader summary of the implications and recommendations. The methods section shown here, gives a broad overview of the approach taken to individual components of the study, however, the more detailed description of the methods supporting each of the individual studies that make up this report is found within each study description in the appendices.

Methods

Methods for Objective 1: To collate and analyse the long-term marine ecological data records for southeast Australian reefs and use these to quantitatively describe relationships between species' distribution and abundance and changes in ocean temperature, salinity and EAC position as key drivers of climate change;

Datasets: Central to the project is the spatial and temporal analysis of a globally unique dataset compiled by the Investigators since 1992, involving quantitative surveys of reef fishes, macro-algae, coral, urchins, abalone, rock lobsters and other macro-invertebrates at more than 600 sites off southeast Australia. The survey methodology involves quantitative counts of the abundance and size distribution of fishes on four replicate 500 m² transects at 5 to ten metres depth at each site. These are matched by four 50m² quantitative counts of the abundance of mobile invertebrate and cryptic fish species. Algal quadrats are replicated twenty times along these transects, with the percentage cover of each algal species recorded under 50 points within a 0.25m² quadrat. A more detailed description of this methodology is given in Edgar and Barrett (1997).

Data include long-term series at MPAs along the latitudinal gradient from NSW to southern Tasmania, undertaken as part of the Long Term Temperate Reef Monitoring Program (LTTRMP). The survey locations of these time series include (Jervis Bay 1996-2012, 12 annual surveys, 30 sites in fished and protected zones repeatedly studied; Lord Howe Island 2006-2012, 5 surveys, 33 sites; Batemans Bay 2005-2012, 7 surveys, 36 sites; Cape Howe 2001-2010, 5 surveys, 12 sites; Wilsons Promontory 1999-2002, 4 surveys; 28 sites; Port Phillip Heads, 1998-2009, 8 surveys, 15 sites; Kent Group 1992-2012, 9 surveys, 20 sites; Bicheno 1993-2012, 11, surveys, 8 sites; Maria Island 1992-2012, 24 surveys, 12 sites; D'Entrecasteaux Channel 1992-2012, 23 surveys, 7 sites; Port Davey 1993-2012, 10 surveys, 30 sites). This represents the longest ecological monitoring record worldwide designed to contrast marine community changes within no-take zones in a regional MPA network with controls at typical fished locations. For analysis of broader spatial patterns, a range of extra sites that utilise this methodology were also available throughout this region, including more than 100 sites around Tasmania surveyed as part of bioregional biodiversity surveys (Edgar et al. 1997) and reef health studies (e.g. Stewart-Smith et al., 2008, 2010).

In addition, an extensive number of extra survey locations have been surveyed by the Reef Life Survey (RLS) program between southern Queensland and southern Tasmania. The RLS program was initially funded by a CERF major project grant, and has subsequently been supported by a range of grants, including ARC and NRM-based funding. This has allowed sites to be actively targeted in locations not otherwise covered by the long-term monitoring programs, thus filling in the spatial gaps between long-term monitoring sites. Major locations surveyed include Morton Island (Qld), Cape Byron, the Solitary Islands, Port Stephens, Sydney Harbour, Eden, Cape Howe, Beware Reef (Vic), Port Philip Bay, in addition to an number of locations in-between. The combined distribution of sites included in this project and subsequent analysis is shown in Figure 1. The RLS methodology is essentially a subset of the LTTRMP protocols, with replicate fish transects at 250 m² instead of 500m², identical mobile invertebrate transects, and with algal quadrats instead replaced by photoquadrats taken every 5 m along each 50 m replicate transect. This latter approach limited our ability to combine algal datasets other than for the few dominant cover species, and as subsequent modelling needed the full distribution of sites to obtain good species distribution models, analysis of algal species distributions was not pursued further. Sites surveyed by the LTTPMP and RLS are shown in Figure 1.

Both the LTTRMP data and the RLS data were transferred into SQL databases as part of this project, with this being a significant task and a significant outcome. This database has allowed multiple datasets to be merged in one accessible location, and to be readily queried through a simple front-end

linking to an Excel pivot table function. Related tables in the database allow individual species characteristics to be recorded and used in subsequent analysis. These include a range of life-history traits such length-weight relationships (body size), dietary group, range, depth distribution, larval dispersal, adult mobility etc). Many of these were derived from Fishbase, and where they could not be sourced for an individual species they were taken from the nearest species or genus.

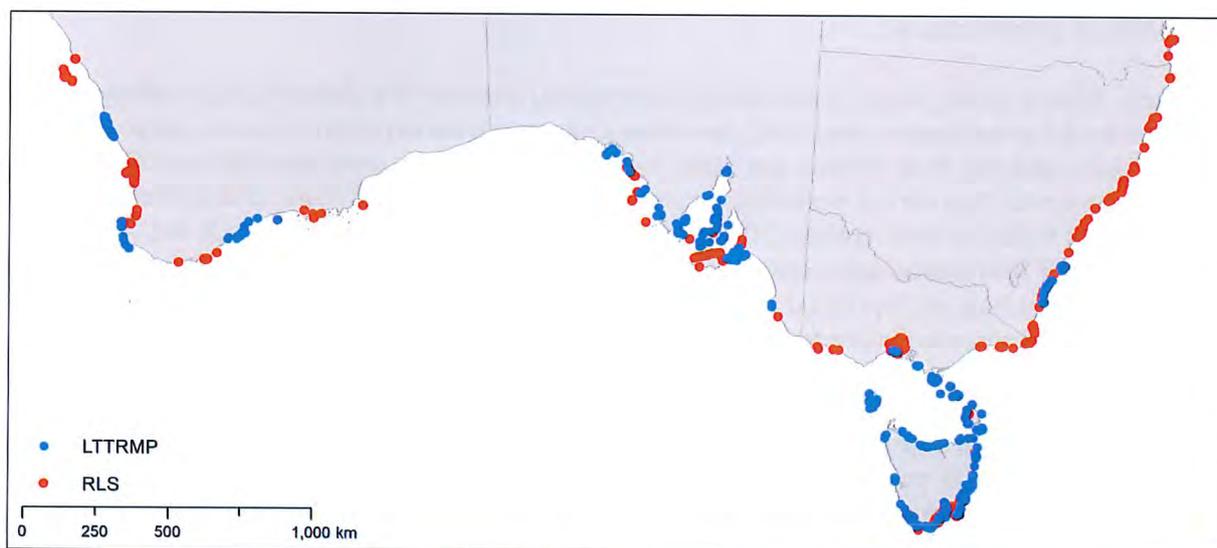


Figure 1. Sites surveyed by the LTRMP and RLS surveys between 1992 and 2013. Does not include additional sites surveyed by the Victorian MPA monitoring program (identical methods) or the South Australian reef health survey (identical for fish and mobile invertebrates) that further increase the spatial coverage in those states.

Physical data from which to derive climate-based relationships within models, were derived from a range of sources. The first of these was the CARS dataset of CSIRO and Geoscience Australia that provides a 0.1 degree gridded dataset of a range of averaged physical parameters, including nutrients, salinity and a range of temperature derivatives. However, this dataset is a static one, so cannot provide temporal data from which to determine time-based relationships, and is also based on offshore data that is often remote from our inshore sites. Our second available dataset was the BLUElink reanalysis (BRAN) ocean temperature and salinity data available from 1992 to 2008 on a 1/10 degree (~10km) grid. This dataset takes available satellite derived data (with gaps due to cloud formation etc), and using a model-based approach, recalculates expected daily means such that each grid point has a daily value, with no missing datapoints. A significant component of our initial work on this project (a six month position) involved an oceanographer (Andre Belo Couto) matching the nearest neighbour grid data from BRAN for each of our survey sites and developing a range of physical products that could be used to explain patterns in the biological datasets. These include daily values, and monthly, seasonally and yearly averages maximum and minimums. This was primarily for temperature, as nutrients are not available from satellite data.

Subsequent to this analysis, a postdoc on a related project (supervised by CI's Holbrook and Barrett), developed an approach to apply a coastal correction to BRAN data (derived offshore) such that it more realistically matches true coastal conditions (Oliver et al. 2014). This data has been used in all model development relating to the species distribution component of this study. It is available upon request for other researchers, but as it is derived from BRAN, a CSIRO product, it can't be accessed automatically from a repository such as AODN at this stage.

For analysis of the long-time series of data available at Maria Island and vicinity, additional physical data was derived from the nearby Maria Island monitoring station maintained by CSIRO. At this station monthly records of temperature, salinity, nutrients and chlorophyll have been collected since the late 1940's, allowing close coupling to be made between physical and biological patterns in this region. That dataset had the additional advantage of extending a time series past 2008, the nearest time point available from the BRAN at the time. An updated BRAN (version3) has just been released (March 2014), but was available too late for this study.

Time series analysis. Correlations between biological and physical drivers: A range of methodologies were explored by both our initial postdoc (Maria Beger) and our subsequent postdoc (Craig Syms) to explore possible correlations between patterns in the physical and biological data. It was determined that in all but the SE Tasmanian datasets, even using the data from species with the greatest abundances and likely temporal patterns, the available time series was either too short or sufficiently punctuated by gaps in years where surveys were not undertaken, to be able to develop models that showed a statistically valid trend. Subsequently, the SE dataset became the focus of this work. Our initial approach for this was to use a Generalized Model to isolate different scales of temporal change. This involved fitting a smoother of 10 years, and smoothed 5 year, and annual deviations from the 10 year mean with the aim of minimising collinearity and decomposing the series into different windows of trends. Lags between biological and physical data were compared at different time intervals, from annual cycles up to years on a 3 month smoother. This because there is likely to be a window over which fish can recruit and grow through to a size that they are observed on surveys. A range of windows were examined to find the best resolution. Latitude, Longitude and their interaction were also used as spatial predictors. As each site was likely to have its own peculiarities, site was included as a random effect – so this is a random intercepts model. Additionally, as fish can be long-lived, an autoregressive term (AR1) was also included to take this into account and not overestimate the site effect. Only those sites that had a long enough time series for lags to be calculated were included in the analysis. Species selection was based on occurrence (number of sites) on the condition they were not exclusive to one area as this would have caused problems with estimating the correlation with the range of BRAN data. While this approach provided models that describe the variability in the data, no clear pattern was found in individual species relationships with the temperature signal.

As most datasets were found to lack the temporal continuity necessary to find correlations with climate signals, the last part of our research into these patterns focussed exclusively on the long time series available for Maria Island and adjacent coastline where data was available on an annual basis over a twenty year period, with additional sampling on a six monthly basis during some time steps. This was able to be related to physical data derived from the CSIRO monitoring station located nearby (as discussed above). The analysis is described in detail in Bates et al. (2014) and in Appendix ii, but essentially related to examining trends in several fish species abundances (restricted to short lived species such as the Blotch-tailed hulafish *Trachinops caudimaculatus* and the Toothbrush leatherjacket *Acanthaluteres vittiger*) most likely to show climate driven signals due to the lack of intergenerational storage in their populations. In addition, a range of community metrics on the fish assemblage were also examined, including average temperature affinity, trophic level, species richness, species diversity, functional trait diversity and functional trait richness. These were compared against a range of physical variables, including Nitrate, Silicate, salinity, extreme sea surface temperatures, monthly temperature values, and the southern oscillation index (SOI). The analysis was constrained to the fish component of the data at Maria Island due to overall time constraints in the analysis and publication stages, with fish likely to be a good surrogate for similar changes occurring in the invertebrate and macroalgal populations.

Changing spatial distributions: One analysis central to understanding the likely rate of responses to warming, including validation of predictions based on thermal envelope models, is the extent that range shifts follow or lag climate velocity and how this relates to life history traits of species. This analysis was undertaken as a joint project between this study and one funded by ANNiMS. The methodology, including model structure, is detailed in full in Appendix iii, but essentially involves

comparing a range of available datasets (including the LTTRMP and RLS datasets described previously) to match the extent that individual species have tracked temperature changes over a 20-50 year period. As detailed for the database development discussed previously, species traits were analysed along with range changes for individual species to determine the extent that the rate of these changes correlated with specific traits. The traits examined included dispersal ability, retention ability, maximum body size, trophic level, latitudinal range size, water column position, and habitat generalisation.

Dealing with sampling artefacts and sampling effort when detecting range shifts: Depending on the shape of individual species abundance by latitude curves, range shifts may be difficult to detect during early phases of colonisation due to low abundance in the tails of these distributions. Hence sampling effort and the nature of sampling may be critical to determining the magnitude and extent of species redistributions, as well as using the most appropriate models to describe and interpret sampling data. To address this we compared empirically derived assemblage range shift data from two case study areas, the LTTRMP data from Tasmania (described earlier), and macroalgal data from SE Western Australia, with simulated patterns to identify the best modelling approach. This analysis was undertaken as a joint project between this study and one funded by ANNiMS. The full details of the methodology are given in Appendix iv.

Correcting for error and bias in global citizen science datasets. All datasets collected by “observers” are likely to have some form of error and bias associated with them due to the nature of individual subjective variability between observers during collection of data on surveys. In addition, such datasets can often have spatio-temporal clustering that influences the way that the information can be interpolated more generally. Modern analytical approaches can account for many types of error and bias typical of citizen science datasets such as the RLS dataset. As this dataset formed a significant component of the data available to our study, we applied a range of these approaches to (1) examine how pseudo-replicated sampling influences the overall variability in response data using mixed-effects modelling, (2) integrate data to explicitly model the sampling process and account for bias using a hierarchical modelling framework, and (3) examine the relative influence of many different or related explanatory factors using machine learning tools. The information from these modelling approaches was then used to inform how we predict species distributions in Objective 4. The detailed methodology behind this analysis is documented in Bird et al. (2014) and included in Appendix v in this report.

Methods for Objective 2: To identify optimal locations and species for monitoring programs (including Reef Life Survey – a cost-effective, ecological monitoring program using trained recreational divers – and comparable agency-based programs) to best inform adaptive management via delivery of up-to-date relevant information.

While on-going observation of biological patterns associated with climate change was not included as part of this proposal, a clear need exists to continually observe temperate reefs in our region to provide the necessary feedback for management agencies to both detect and understand the nature and magnitude of changes occurring, to develop adaptive management strategies to respond to changes as they occur, and to monitor the success of such strategies. Analyses undertaken for Objectives 1, 3 and 4 have identified the locations, species subsets, monitoring frequency and replication that have provided the strongest signal so far. These outputs, along with the gaps that they identify, were used to qualitatively generate recommendations about future observing protocols to guide funding bodies and management agencies to determine potential monitoring priorities.

Methods for Objective 3: To assess the costs and benefits of existing temperate Marine Protected Areas for biodiversity-conservation management in response to climate change and evaluate the robustness of adaptive management frameworks given uncertainty in predictions.

The main focus of this analysis was on examining relationships of species and indicators of management interest between MPAs and climatic anomalies. Long-term biological data surveyed in and adjacent to a range of east/southeast-coast MPAs were analysed using multiple statistical approaches (ANOVA, PERMANOVA, GLMs, GAMs) to identify ecological changes associated with: (i) the marine physical condition during years of extreme climatic anomalies (El Niño and La Niña), (ii) protection from fishing, and (iii) interactions between these major two factors. The latter was particularly important in identifying whether fishing and climate change interact synergistically, additively or antagonistically with each other or with other threats (particularly invasive species), and which components of biodiversity are most resilient to the effects of fishing. Response variables investigated in these analyses will include densities of commercially-important species such as rock lobster and abalone, flagship species such as eastern blue groper, climate change indicator species such as those with warmer water affinities and habitat-modifying species such as the invasive Long spined urchin *Centrostephanus rodgersii*. In order for results to be generalised across other regions, life-history traits (e.g. size, dispersal capacity) of species showing high and low resilience to climate change were identified.

An initial focus, utilising ARC funding, allowed an investigation of five MPAs that were distributed around the southern half of the Australian continent and subject to monitoring by the LTRMP over their duration of protection, to be investigated for evidence of responses in fish populations related to protection. These MPAs were (i) the Jurien Bay Marine Park, (ii) the Jervis Bay Marine Park, (iii) the Kent Group National Park, (iv) Maria Island National Park and (v) Port Davey National Park. Three of these MPAs are multi-zoned (Table 1), with multiple no-take sanctuary zones interspersed with general use zones and restricted fishing zones. This analysis, published as Edgar and Barrett (2013) indicated there was little response to protection at the individual species level except for Bastard trumpeter (*Latridopsis forsteri*) at Maria Island and Red morwong (*Cheilodactylus fuscus*) at Jervis Bay. This overall lack of response was attributed to the short period of protection of many of these MPAs, coupled with low levels of fishing effort in some relatively remote area locations (Kent Group and Port Davey), and in places, small sanctuary zone size relative to fish movement patterns. This study complimented a related meta-analysis study undertaken by Edgar et al. (2009) that indicated changes in current Australian MPAs accumulate slowly following protection, and it takes decades for more significant changes to accumulate.

These results, followed by an initial examination of climate related trends from a range of SE MPAs as part of the analysis undertaken for Objective 1, indicated that if we wanted to tease out interactions between MPA protection and climate change, we needed to focus on a location with a sufficiently long time series to detect climate related responses, and where sanctuary zones were known to be sufficiently large to be effective. Hence we focussed our analysis on Maria Island as a case study of the types of responses that may be expected elsewhere as the age of protected areas increased.

This analysis is fully described in detail in Bates et al. (2014) and in Appendix ii, as well as outlined in the methods for Objective 1 (above). The component of this study undertaken for Objective 3 that differentiates it from the climate change signal analysis outlined in Objective 1 is the additional focus on the interaction between MPA protection and the response to climate change, including the reference area role of MPAs for ecosystem monitoring and the extent that MPAs may provide additional resilience to tropicalisation during climate change. Several of the variables examined were specifically targeted at metrics that may become evident if there was an interaction between levels of protection and climate change. These included species diversity and species richness, functional trait diversity and richness, large fish biomass and thermal affinity. Where patterns in the traits and diversity based approaches were found to be significant, these were decomposed to identify the components making the most significant contributions to differences detected.

In addition to this analysis, overall patterns in the abundance of numerically common species of fishes and mobile invertebrates within and adjacent to the Maria Island marine reserve were also examined

for their responses over the twenty years of protection of this reserve. This analysis was undertaken to visualise key responses to protection that may underpin the interpretation of the analysis above, as well as to highlight the extent that such monitoring programs can inform changes in species assemblages generally.

Evaluation of management frameworks, an additional component of this objective, is based on an overall assessment of the performance of current MPAs for biodiversity conservation (as examined above) in light of a changing climate, the model predictions from Objective 4, and off-reserve management options. This was not intended to be a rigorous quantitative analysis, rather an interpretation of the results of our studies above, intersected with forecast changes and the range of management options available.

Methods for Objective 4. To develop models that quantify and predict the impacts of climate change on inshore reef communities of fishes, invertebrates and macroalgae across the southeast Australian region so that potential responses to change can be identified, considered and developed appropriately.

Species distribution models (SDMs) were used to statistically estimate relationships between species abundance records and their latitudinal/thermal distribution. SDMs were primarily developed using regression methods that include generalised additive models. The models used biological data from SE Australia derived from both the LTTRMP and the RLS datasets collated in Objective 1. For each site, the latest time point in the time series was utilised in situations where multiple replicate surveys were available through time. The SDMs were developed for fish and mobile invertebrate distributions but not for macroalgae. In making the SDMs, the RLS component was an essential input into each model to ensure distributions were fully informed across the entire range of each species latitudinal distribution where possible. This meant that for algal species there was generally insufficient information available to make appropriate models, as the RLS photoquadrat methodology was only able to examine the canopy species, unlike the full quadrat method of the LTTRMP dataset. Temperature relationships for each site were established from the 0.1 degree nearest neighbour point available from the near-shore corrected BRAN dataset supplied by Eric Oliver (discussed in Objective 1). Estimation of the likely change in abundance of a wide range of fish and mobile abundance was made for theoretical assemblages at one degree intervals from 38 south to 43 south, based on predicted changes in abundance relating to a latitudinal shift of 2C, the predicted IPCC climate scenario A1B for the 2060's (Oliver et al. 2014). These changes in abundance were then interpreted for their likely ecological significance on the basis of "expert knowledge", with these interpretations requiring further assessment in follow-up workshops with stakeholders.

The reliability of the use of simple SDM's for future predictions based on likely latitudinal shifts, was validated by the range shift vs climate velocity vs ecological traits study outlined in Objective 1 methods and presented in Appendix i. This indicated that generally, most species distributions in this region do closely track thermal gradients, irrespective of life history characteristics.

Data

Average transect abundance (fishes: 500 m² and invertebrates: 50 m²) was calculated for each fish and invertebrate species for 1665 locations south of 35.2 °S and east of 140 °E between 1992 and 2013 using visual census methods (described earlier in the methods for Objective 2). Species with latitudinal range breadths less than 2 ° of latitude or those observed at fewer than 5 locations were excluded from the analysis (in being restricted to a specific geographic location, such as Lord Howe, or rare in terms of occupancy), as were species that are difficult to identify underwater returning 280 fish and 215 invertebrate species.

Geographic abundance curves: a tool for prediction

For each species the absolute minimum (equatorward range edge) and maximum (poleward range edge) were calculated. We then modelled the geographic abundance curve using a generalized additive model (function “gam”: Hastie, 2013; R Development Core Team, 2013). In this case, the gam model is fitted iteratively using weighted additive models and backfitting (the algorithm is a Gauss-Seidel method for fitting additive models by iteratively smoothing partial residuals, as described in the function description in R). We used a loess smoothing function with family equal to “poisson”, and the link function equal to log, across all locations where the species of interest was observed. Thus, the abundance curve is an average across seasons and depths for any given species, representing geographic locations where the species is expected to be present. The tails to the abundance distribution were modelled by also including all locations outside the species geographic range that fell within 5° of latitude of the range edges, which brings modelled abundance to zero outside where each species was observed.

To create a warming scenario of a plus 2°C in southeast Australia, we calculated the average annual SST temperature for each surveyed location from 1992 to 2008 based on the Bluelink ocean model data, and then plotted the median SST value for each latitude and described this relationship using a lowess smoothing function with f equal to 1/5th (Figure 14). We extrapolated temperature by assuming a 1°C increase at 35°S and a 2°C increase at 43°S, with intermediate values interpolated based on the observed curve. This approach captures the higher rate of warming that has been detected in the region in recent decades and is expected to continue for the region. To estimate changes in the future distributions and abundances of each species, we assumed the abundance curve for each species will retain a similar shape, allowing us to make species-specific predictions at a regional scale that will be useful for management decisions, rather than site-level predictions that are challenging to make with high confidence due to the likelihood of small-scale abiotic and biotic processes influencing community dynamics.

Extension

We proposed to undertake two workshops with representatives from relevant management agencies, research bodies, and stakeholders. The first workshop was held in Hobart in March 2011 and discussed the potential realistic suite of management strategies that may be used to address a range of climate change scenarios and introduced the project. Strategies discussed included a broad range of options from small scale closures to distinct fishery controls to direct manipulation of abundances of key ecological species. The workshop report is included as Appendix v. A second workshop was proposed following the availability of results from Objectives 3 and 4 such that adaptation options could be discussed and evaluated in light of the new knowledge available. Delays in this project mean that this workshop will now be held after finalisation of this report, if sufficient stakeholder interest is indicated.

Results

Objective 1: To collate and analyse the long-term marine ecological data records for southeast Australian reefs and use these to quantitatively describe relationships between species' distribution and abundance and changes in ocean temperature, salinity and EAC position as key drivers of climate change.

Databases.

A significant component of this project in the initial stages involved collation of dispersed biological survey datasets into a single database that would pool all available data from surveys in the SE of Australia (and more broadly) into one central location for analysis. This was undertaken using the Microsoft SQL system, and a single SQL database was established for each of the LTTRMP and the RLS datasets. In addition to establishing database structures to store and access the basic data, additional matching tables were developed to allow individual characteristics of each species to be attributed, including a wide range of species traits (as listed in the Methods section). For fishes, this included length/weight relationships so biomass patterns could also be readily determined. As well as providing a framework for the various analysis undertaken in this study, and related studies that are building on these, the databases allow ready access by regional researchers and management agencies to these valuable datasets via a simple query front-end. It is anticipated that both databases would be readily available to agencies through the future, so that up to date information on individual species abundances, distributions and survey locations are readily accessed and able to be monitored.

The physical data collated as part of this project primarily consisted of 0.1 degree BRAN data from (CSIRO) that was subsequently corrected for near-shore factors by correction protocols developed by Oliver et al. (2013). As this is essentially an extension of BRAN (a CSIRO product), this near-shore corrected product is available from the author (Oliver) on request. The BRAN data available for our analysis was only available up until 2008, however a new version of BRAN has now been released, with time series until 2012. Near-shore corrections will be made for this as well, and may be available on request once completed.

Relationships between species distributions and physical processes.

The analyses in this component of our study was broken into three main components as we explored various approaches to tackling these relationships, in addition to ensuring the fundamental issues regarding using the survey data in this context were well understood and addressed. These components were (1) examining available biological time series at a range of locations with long-term data to establish the extent that long-term trends could be explained by physical processes, (2) focusing on the long-term dataset from Maria Island to more specifically examine a case study where the longest comprehensive biological dataset is available, and able to be matched with similar long-term physical data from a nearby CSIRO monitoring site, (3) looking more widely across SE Australian datasets to examine the rates that species range extensions matched climate velocity over 20-50 year time spans, and the influence that species traits may have on these relationships, and (4) examining the extent that artefacts in survey data can influence predictions of range shifts, determining appropriate models to deal effectively with the uncertainty associated with such data, and statistical approaches to further refine the applicability of citizen science datasets to such problems. The results of each of these components are examined and discussed below.

1. Time series trends throughout SE Australian monitoring datasets.

Correlations between biological and physical drivers: A range of methodologies were explored to explore possible correlations between patterns in the physical and biological data. They centred around the use of generalised linear models to match biological trends with the temporal physical signal from BRAN data from nearest neighbour grid cells. The extensive analyses and outputs are not presented here as all involve quite a degree of complexity to present and explain, but also because no clear patterns were evident from this analysis at most locations. Our initial approach examined trends over multiple time scales, including direct comparison of physical and biological data as well as the addition of temporal smoothing and offsets in time increments that may compensate for clear lags in the relationship between conditions suitable for successful larval development and settlement, and the size that fish or mobile invertebrate species become visible to divers during a visual census. In addition, particularly warm summers or winters may increase survival of vagrant species that become more evident in subsequent years surveys, and offsets are necessary to detect this.

Despite extensive pattern exploration, and trials of a number of alternative modelling approaches, few clear patterns emerged from this approach, and subsequent analysis focussed exclusively on data from Maria Island where the richest time series was available (discussed in the next section). A number of independent but important issues contributed to this inability to detect patterns, even where some distinct patterns were evident, such as the decline of common invertebrate species at Jervis Bay (Figure 2) or Maria Island through time (Figure 14a-b). These issues collectively provide important insights into what is needed in the future if we are to effectively track changes related to significant variation in environmental variables, and partition out the components due to climate change.

The first of these was related to both the duration of a time series and also the extent that it was punctuated by gaps in the continuity. For locations such as Wilsons Promontory or Jervis Bay, the extent of time covered by monitoring programs was around ten years, and in the case of Jervis Bay, that was punctuated by occasional gaps in the time series for years when funding programs were not available. Analysis of long-term time series elsewhere, e.g. Hawkins et al. (2009), examining changes in intertidal assemblages in the UK, suggests that routine time-series of forty years is the typical length of time necessary to determine climate relationships from such datasets, and that indeed, the monitoring does need to also span enough variations in the strength of the environmental signal for patterns to be statistically valid. This is the second issue to arise in our analysis.

For the more eastern locations such as Jervis Bay, no temperature increase or significant variation was encountered over the temporal extent of the survey series there, so despite some clear trends such as the decline in invertebrate abundances shown in Figure 2, were not able to be related to changes in physical processes in that region. The lesson from this is that it is imperative that any specific biological monitoring programs targeted at informing climate related relationships are able to continue across time periods over which biologically meaningful warming may be expected to occur. This pattern was evident from a study examining bioregional level change over a decade scale on Tasmanian reef systems between the mid 1990's and mid 2000's. No significant biological change was detected over this period as it corresponded with a relative stable temperature regime following a significant increase of around 1 degree Celsius in the previous decade (Stuart-Smith et al. 2008, 2011), yet had the study been undertaken a decade earlier it may have documented the almost complete loss of Giant kelp (*Macrocystis pyrifera*) on the Tasmanian east coast (Edyvane, 2003) and changes in kelp associated assemblages.

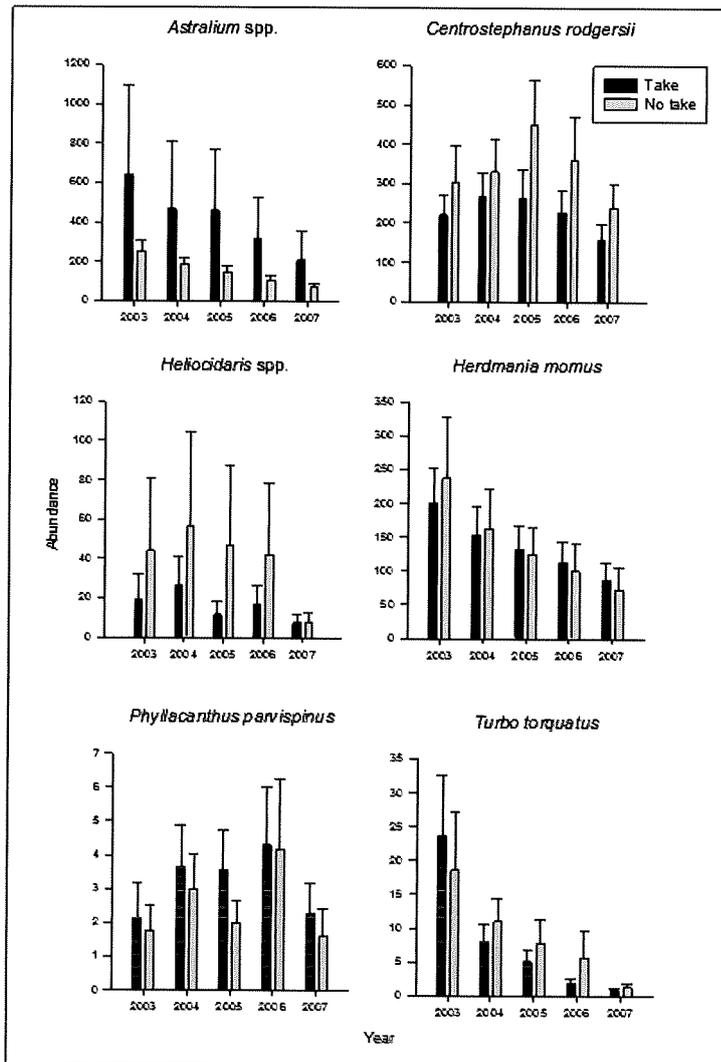


Figure 2. Invertebrate abundances (n/200 m²) of common species at sites within the Jervis Bay Marine Park in NSW during surveys between 2003-2007.

Finally, many of the changes that do appear to be evident in our datasets relate to vagrant species that respond to periods of warming and cooling. These tend to be low in abundance, and variable temporally, hence requiring additional replication or targeted sampling such as that of Figueira and Booth et al. (2010) in southern NSW, where climate vagrants are specifically and actively targeted in annual monitoring surveys. An alternative approach to enhance statistical power is to study these changes at a higher level such as changes in overall species thermal affinities, overall species diversity, and changes in the types and diversity of biological traits, and this is examined in the following section.

2. Climate related patterns derived from high density biological and physical data from eastern Tasmania (Maria Island and surrounding coast).

As discussed above, initial examination of the available data indicated that only surveys from the Maria Island region and related early Tasmanian MPA study areas in smaller reserves (Tinderbox, Ninepin Point and Governor Island (Bicheno)) had sufficient temporal data to fully explore physical relationships and so analysis in this area has focussed on these. Moreover, as replication at the site level was lower in the smaller reserves, and these had a number of missing years, the final analysis centred on the Maria Island dataset as a case study of what could be examined with the best available

data. The analysis focussed on two aspects of change, the regional trends associated with climatic variability, and the interaction between these and MPA protection. This latter component is described later in the section dealing with Objective 3. The overall analysis has been published in Nature Climate Change (Bates et al. 2014), and the majority of this work is documented here as Appendix ii. The results and discussion presented here are a selected overview of this work. Due to time constraints, the study focussed entirely on the fish assemblages, other than a brief examination of the response of *Centrostephanus rodgersii* urchins in this region through time, as these are related to some of the patterns observed.

Our focus was on analysis of community metrics such as species richness, diversity and functional traits within the temperate reef fish communities of this region over the 20 years of monitoring data availability, within what is acknowledged as a global warming hotspot. In addition, to conventional diversity-based approaches, our analysis included a range of potential indicators of change that extend beyond the simple abundance of key species. For example, a novel species traits-based approach was developed, allowing traits such as thermal niche to be quantified. The establishment of a traits-based approach here has allowed the population of variables such as latitudinal range, trophic level, mobility, maximum age etc to be included into our database structure, and utilised for a wide range of future analyses and applications, including the climate velocity vs life history analysis presented in the next section. One key trait that was developed here was the thermal niche of each species. This was developed empirically as part of the species distribution modelling (SDM's) and thermal relationships produced for Objective 4 in this study. This information allows us to readily characterise species, not only on their widest geographical range (e.g. on the basis of museum collections) but also on their main centre of thermal comfort.

A key regional finding from this work was that species richness and diversity oscillated strongly at the decadal scale, with long-term warming signatures also identified, and present as increasing functional trait richness and functional diversity, driven in part by a general increase in herbivores. Figure 3 illustrates the types of physical variability over this period of time, including large changes in minimum and maximum temperatures from year to year, as well silicate levels (that determine phytoplankton availability) and a general increase in salinity, reflecting increasing influence of the EAC. Additional patterns in physical variability, such as the southern oscillation index (SOI), average monthly temperatures, and nitrate levels are shown in Appendix ii. When these relationships were explored in detail, significant correlations were found with both changes in nutrients and the southern oscillation index, with species richness, species diversity and functional diversity being correlated with this physical variability. One large contributor to this variability was the short-lived reef attached planktivore, the Blotch-tailed hulafish *Trachinops caudimaculatus*. This species underwent an order of magnitude in variation in abundance over the period of the study (Figure 4) with this evidently being driven by the physical processes that underpin planktonic food availability, such as the availability of nitrogen and silicate.

Over longer time periods, there was a clear signature of tropicalisation, with a significant temporal trend relating to an increase in average temperature and SOI values, being evident in functional richness and diversity, and thermal affinity. This longer-term trend in functional richness and diversity appears to be mostly related to an increase in both the number of herbivorous species being observed, as well as the overall biomass of herbivores (Figures 5&6). To some degree such an increase is to be expected as warming-related poleward extensions of herbivorous fishes at high latitudes are likely to be related to the temperature-dependence of metabolic rates of plant material digestion vs metabolic requirements (Floeter et al., 2005). It is likely that such changes will be one of the most significant with respect to fish assemblages in cooler latitudes in the early stages of any future warming. Given that increases in the abundance of large bodied resident herbivorous fishes such as the Herring gale *Olisthops odax* (Figure 6) also reflect a significant increase in overall biomass, it is likely that such changes may also have a marked impact on community function as changes accumulate, especially as more mobile herbivores such as the Zebrafish *Girella zebra* (Figure 6) also migrate further south during summer warm periods.

The increase in diversity and thermal affinity over the longer-term related to the increase in a range of species with warmer water affinity, such as White-ear *Parma microlepis*, Mado sweep *Atypichthys strigatus*, One-spot puller *Chromis hypsilepis*, and Herring cale *Olisthops odax*. The changing abundance of many of these species is shown in Figure 11 in the results for Objective 3. Many of these species were most conspicuous in *Centrostephanus* barrens, or similar barrens formed by the Common urchin *Heliocidaris erythrogramma* (Barrett, pers. obs.) and therefore represent a response that is somewhat mediated by habitat affinity and availability. In the core part of their range, these species appear to closely track the availability of urchin barren or turfing habitat (Barrett per. obs.). As *Centrostephanus* barrens become more established in this region, this habitat facilitation is expected to therefore further enhance the abundance of such warmer affinity species (as expected under the invasion meltdown hypothesis of Simberloff and Von Holle, 1999).

Overall, the main messages from this component of the study were that while it was very difficult to detect patterns at the individual species level, even with our best available long-term datasets, appropriate ecological metrics such as those based on biological traits could be used as effective indicators of change. In addition, some individual species, that are numerically abundant and short lived (such as *Trachinops caudimaculatus* and *Acanthaluteres vittiger*) and show marked changes in abundance through time, may show good correlations with physical variables, but for most species, significantly greater replication (to reduce noise and increase detectability) would be required to detect clear patterns, with the cost of this extra replication generally being prohibitive. The changes detected by these “indicators” include greater influence of herbivours, and warm affinity species, so these metrics seem appropriate for longer term monitoring, and suggest the broad multi-species approach to monitoring undertaken so far may be more informative than single species targeted monitoring, particularly if the chosen “indicator” species are found to be inappropriate in the future, or at least not important drivers of changing ecosystem function.

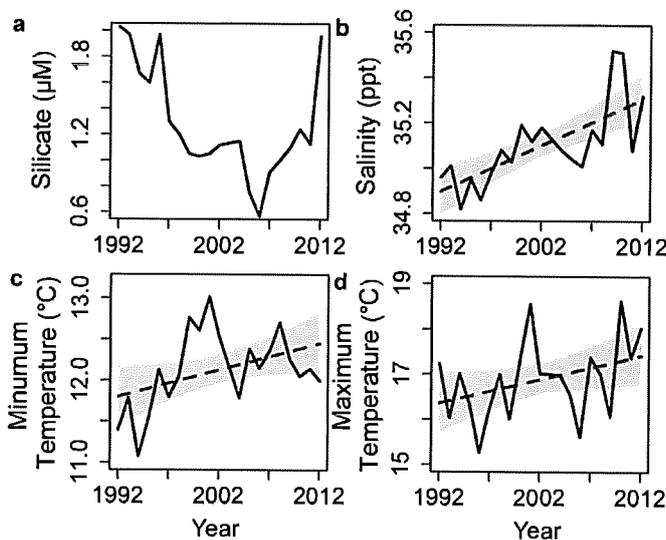


Figure 3. Oceanographic variables, obtained from CSIRO’s long-term observing station, driving reef assemblage change at Maria Island. a, Mean annual silicate and b, salinity, and c-d, extreme surface temperatures.

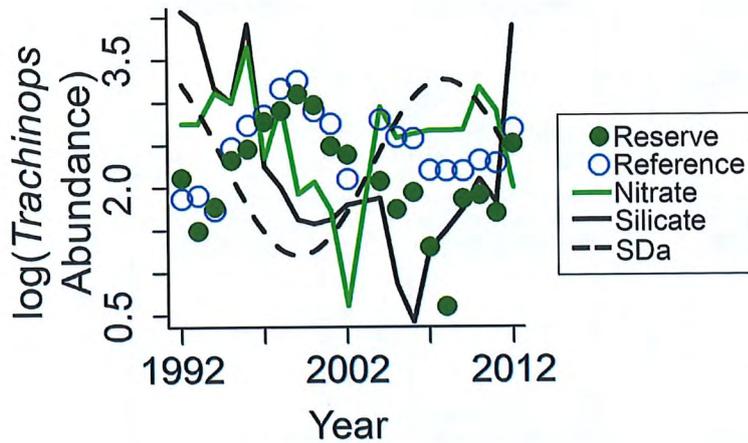


Figure 4. Predictors of abundance-weighted species diversity. Species diversity (SDa) related negatively to the abundance of Blotch-tail hulafish *Trachinops caudimaculatus* abundance in the reserve and reference sites, and positively to nitrate and silicate; see Appendix ii, Figures 1d and S1 for the y-axis dimensions of nitrate and silicate concentrations.

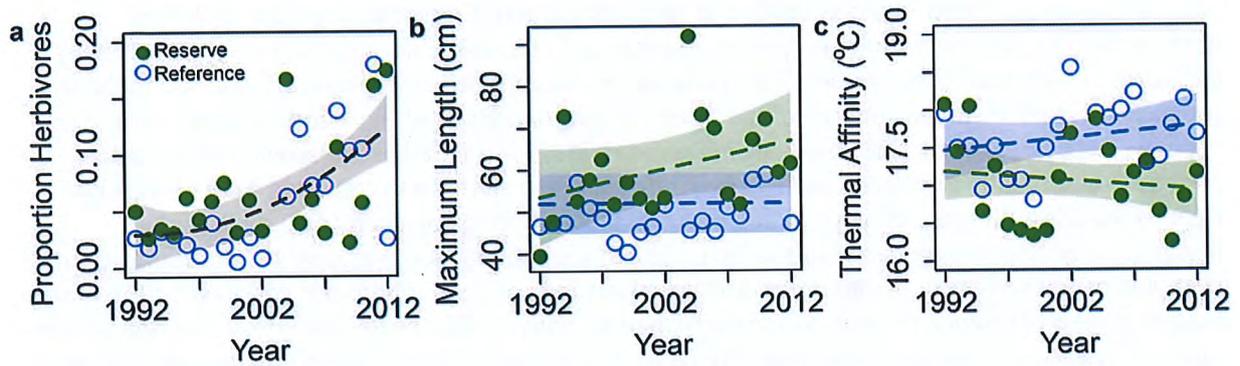


Figure 5 Community weighted biological trait values calculated based on biomass. a, Proportion herbivores kg-1; b, maximum body length kg-1 and c, thermal affinity kg-1 biomass. Regression slopes (dotted lines) and 95% confidence intervals (shading) are in colour when a significant difference between the reference and reserve sites was observed, predicted from linear mixed effects models.

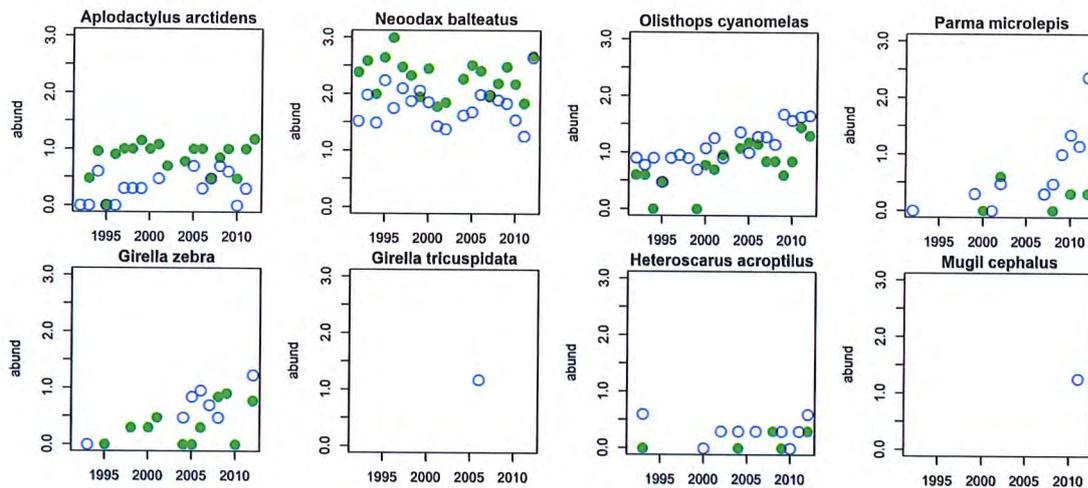


Figure 6. The log abundance, through time, of herbivorous fishes within the Maria Island marine reserve (green circles) and adjacent fished reference sites (open circles). Warm affinity herbivours increasing through time include *O. cyanomelas*, *G. zebra* and *P. microlepis*.

The overall patterns with species distributions and abundance curves and their relationship with physical drivers such as temperature are currently being modelled and described. This work is now well advanced and required incorporation of all available quantitative survey data, including ReefLifeSurvey data, to enable the species abundance by latitude curves to be developed for many of the warm to cool temperate species. This information was utilised to populate the thermal niche traits for each fish species in the analysis of the Maria Island time series in the Nature Climate Change paper as well. Some early indications from this work are that it is rather important to have cost-effective sampling by a program such as ReefLifeSurvey in addition to our Long Term Temperate Reef Monitoring Program surveys, as the development of species by abundance by latitude distribution curves requires good quantitative data at multiple locations across the latitudinal gradient occupied by each species. Without this, species extensions or contractions are very difficult to detect. Simple presence/absence records, as typically used in many studies of CC patterns, can often produce quite misleading results due to detectability issues (i.e. failure to detect doesn't always mean a species is absent), and range centres of "temperate" species often require sampling that extends into tropical regions to detect the upper tails of thermal distributions. As part of this analysis, issues relating to detectability have been explored in collaboration with other researchers and these have either been published such as "Statistical solutions for error and bias in global citizen science datasets" attached here, have been submitted for review such as "Distinguishing geographic range shifts from artefacts of detectability and sampling effort" which is also attached here, or are in preparation, such as an intended publication looking at range-shift rates and how these relate to species traits. The final papers/s from this analysis will deal with species distributions, their traits and how these may be projected forward to allow us the estimate likely assemblages under future warming scenario's.

Relating range shifts to climate velocity and ecological traits.

A significant piece of information necessary to fully inform predictions of future biological communities under warming scenarios, is the rate that species move in response to warming and the extent that different species may do this due to their particular life history attributes. This information is critical to determining whether the species distribution models produced for Objective 4 are appropriate if just based on thermal responses alone, or if they should be adjusted to take into account life history attributes.

To examine this, multiple biological data sets were examined from SE Australia, to see the extent that rates of migration of species matched climate changes recorded over recent time scales of 20-50 years. This included the LTTMP datasets spanning that time frame, both for fish and invertebrate species. The major results from that analysis are presented in Appendix i, in the form of a paper in the final stages of preparation, with the major points summarised here.

Although many marine species have moved to higher latitudes as a response to climate warming, there is little information on species' ecological traits which may explain the vast variation in species responses to date. Therefore we have utilised the species traits database prepared for the analysis presented previously, and relate these to the compiled range shifts of marine coastal species in this region, obtained from our own, or published data. This has enabled us to identify species traits that may explain variation in rates of range expansions over the last half-century. We found that species-specific climate velocity explains the vast majority of variation in the data, rather than specific characteristics that might have a-priori been expected to explain this variation. Among fishes, expansion rate was also positively related to latitudinal range size, and negatively related to trophic level. Hence the patterns seen for herbivorous fish that are detailed in the previous section of this report may be an indication of a ubiquitous response throughout this cool temperate region. In addition to the relationship with thermal control over rates of digestion, the role of fish herbivory is essentially a vacant niche in southern regions, so there is less potential for inter-specific competition or resource limitation to limit population expansion.

Patterns in invertebrates were similar to those noted for the fish species, although with greater overall uncertainty. Remarkably, for both fish and invertebrates, dispersal potential had a low ability to explain range expansion rates, with low-dispersal species among those with the greatest expansion rates. Species-ecosystem interactions thus appear to be most important in predicting range shifts in southeastern Australia. There are a number of clear implications of these results. Firstly in a conservation sense, range-limited species may be a subset of the fish and invertebrate community to focus planned conservation measures on, rather than species with limited dispersal capacity. Secondly, the results bode well for using climate velocities to generally predict range shifts responses in marine organisms, given that most species distributions tracked thermal gradients, thus validating our application of this approach in our analysis for Objective 4. Finally, the results suggest that many marine species may have an inherent capacity for adaptation to changing environmental conditions, with populations able to track current rates of change. Clearly though, this only applies to species where available niches exist further south, rather than to species such as the Red handfish, only found in southern Tasmania, which have no ability to move further south in response to warming.

The study also highlighted the necessity for the uncertainty in species ranges, and hence rates of thermally mediated migration, to be better addressed by biological surveys that inform the likelihood of species to be present in the tails of their distribution, particularly at the most distant extremes. A better understanding of this is critical for informing management of the extent of responses as they accumulate under the warming predicted over the next 50 years. The following two components of the work undertaken for this objective attempt to deal with some of the uncertainties provided by such data where it is imperfect, including modelling and statistical approaches.

Detecting geographic range shifts from artefacts of detectability and sampling effort.

As noted above, the redistribution of species with climate change is well-documented, and we are able to make some predictions about the rates of change based on observational data. Even so, it remains unknown exactly what proportion of apparent shifts in species ranges reflect real change due to ecological processes, and which are simply artefacts of variable detectability. This difference in detectability can come from a wide range of sources, including the spatial and temporal extent of sampling, the search effort per species or location, and whether data collected presences, presence/absence, or quantitative estimates of abundance. In addition there are potentially errors associated with sampling protocols (e.g. species identification issues or abundance estimates derived

from citizen science sources), however, these more specific issues are addressed in the following section. For this component of our study, we use simulations under scenarios of varying abundance-related occupancy and sampling effort to describe the null expectation of patterns in the magnitude and variability of range shifts. We compared simulated patterns to empirically derived assemblage range shift data from two regional-scale (100s km) field studies (a Western Australian algal distribution study and a comprehensive Tasmanian reef health study within the LTTRMP dataset) and find that even with a well-designed sampling regime, accurate estimation of range edges are difficult to obtain for many species. The results from this analysis are presented in detail in Appendix ii, a manuscript in revision for *Diversity and Distributions*, with the highlights and overall implications discussed here. The results illustrated that a time-to-extinction model can be applied to spatial distribution data to provide species-specific confidence limits for range edges. These simulation and modelling approaches are particularly valuable for studies of marine species, where observations are typically few and patchy. However, the best model fits, as expected, applied to species where there were still regular occurrences in datasets towards the range edges. For species with low detectability on surveys, if the aim is at least in part to inform the extent of range edge changes, sampling needs to include additional spatial or within survey replication, to ensure detectability for such rare species is fully accounted for, particularly in areas known to be potential range boundaries for species of interest. Previous sampling programs have not been designed with this aim in mind, so a clear recommendation is that in future programs, informing climate change focussed management becomes a central focus of regional surveys, and particular effort be focussed on detecting the presence of species likely to be at the extent of their range. For RLS and LTTPMP surveys, that extra effort could be in the form of recording off-transect sightings of expected rare species, and/or additional off-transect searching for regional species of interest. The second recommendation is that given the uncertainty in species distributional limits, time-to-extinction models be applied in model based approaches to monitor and describe future changes to account for this. Attempts to estimate null expectations of assemblage-level range shifts in the marine environment, and assigning confidence in the values obtained for particular species, represent important steps in advancing our understanding of global change.

Statistical solutions for error and bias in global citizen science datasets

Survey data in general can suffer from a range of error and bias, and ideally these should be accounted for when utilising such datasets that can have a range of subjective biases due to individual observer variability, or simply uneven geographical distribution of sampling locations due to clumping in the dispersal of sampling sites, which is often determined by site suitability. The RLS dataset formed a core component of our data available for development of species distribution models, and therefore we explored biases associated with the use of such data and statistical approaches to overcoming these biases where possible, so that the results had greatest reliability. More generally, given the cost effectiveness of RLS, citizen science (CS) programs have the potential to observe biodiversity and species distribution patterns through time in Australian waters, proving an important component of a future integrated approach to monitoring biological change and range expansion. Yet the adoption of such datasets in conservation science and resource management is hindered by a perception that the data are of low quality. This perception likely stems from the propensity of data generated by CS to contain greater levels of variability (e.g., measurement error) or bias (e.g., spatio-temporal clustering) in comparison to data collected by scientists or instruments. We explored the global extent of data available in the RLS dataset using a range of modern analytical approaches to see if they could account for many types of error and bias typical of CS datasets. The detailed results of this analysis are given in Appendix iii, and form the basis of a manuscript published in *Biological Conservation* (Bird et al., 2014). In summary, it was found that it is possible to (1) describe how pseudo-replication in sampling influences the overall variability in response data using mixed-effects modelling, (2) integrate data to explicitly model the sampling process and account for bias using a hierarchical modelling framework, and (3) examine the relative influence of many different or related explanatory factors using machine learning tools. Information from these modelling approaches can be used to significantly improve the prediction of species distributions and the estimation of patterns of

biodiversity. Even so, achieving the full potential from CS projects such as RLS requires meta-data describing the sampling process, reference data to allow for standardization, and insightful modelling suitable to the question of interest.

Recommendations arising from this analysis include working with both statisticians and volunteers to identify likely constraints around sampling quality, and major sources of error. Given the broad array of possible modelling approaches available, it is important to consider the main issues with the dataset, how they will affect the question being asked and then to choose the best method to deal with those issues. Ideally researchers using CS datasets would design their sampling program to collect the appropriate metadata needed to account for such issues ahead of time. At the same time, the design of CS studies must meet the needs of the question being asked, while acknowledging trade-offs between data quality and quantity that are likely to occur with CS data.

Once the critical metadata components are identified, it is vital to record these during survey execution (such as observer i.d., water quality) so they can be accounted for in model-based corrections of outlying results. While standardized data collection procedures will help ensure that volunteers are, to the best of their abilities, collecting data in the same way, true uniformity in sampling is unlikely. Recording meta-data can also help account for pseudo-replication due to clustered sampling. Finally, where measurement bias is a potential issue, useful procedures include additional re-sampling of areas with known quantities of species of interest, using training datasets, or performing multiple-observer surveys.

In summary and recommendation,

Many of the monitoring programs currently in place on temperate reef systems in SE Australia are still in their infancy as far as the extent that they span time periods over which the thermal climate has changed sufficiently to be able to detect long-term trends or significant correlations with inter annual variability in physical drivers. Despite this, where there is a significant time series available, ecological metrics such as those based on biological traits appear to be effective indicators of change. The changes detected by these “indicators” include greater influence of herbivours, and warm affinity species, so these metrics seem appropriate for longer term monitoring, and suggest the broad multi-species approach to monitoring undertaken so far may be more informative than single species targeted monitoring, particularly if the chosen “indicator” species are found to be inappropriate in the future, or at least not important drivers of changing ecosystem function. Given that repeated sampling at the annual time steps required to detect such changes is likely to be too expensive to continue in the long term, ideally such monitoring would be in place for at least a 5 year period at regionally representative locations (the MPAs and representative coastal areas indicated in Objective 2) to establish benchmark understanding of inter-annual variability, and then subsequently at 5 year periods. Without the annual time series available to make inference of bio-physical coupling in observed patterns there will be little capacity to infer detailed relationships with physical drivers of variability, however, longer-term trends will be detected where/when more directional change in parameters such as SST occurs. Given the urgency of informing management of potential changes responding to the physical predictions of Oliver et al (2014) for warming in the SE region, ideally the regional MPA focussed sampling and reef health bases sampling at locations in-between (e.g. Lap of Tas or RLS approach) would be undertaken at 5 year intervals to inform management of related biological changes. A 5 year time period matches the State of Environment reporting cycle, and ideally reporting on climate related changes on temperate reef systems would be incorporated as a core component of that, using the above metrics of change as indicators to report against. Developing nationally utilised databases to share and exchange this monitoring data will be a key need to facilitate analysis and reporting at SE region to national scales, as will acceptance in marine policy that such information gathering, analysis and reporting is of central importance to state and commonwealth

governments if we intend to be prepared with the information required to mitigate adverse impacts of future climate change via adaptive management.

Finally, given that one documented change from the long-term data from the Maria Island region was a marked increase in the biomass of herbivorous fish, this is likely to reflect a more general response throughout the region and one that will increase with future warming. The extent that this will cause significant change to algal productivity is a significant unknown, and warrants targeted research into grazing rates, target algal species, predicted increases in herbivore biomass and modelling of likely consequences.

Objective 2: To identify optimal species and locations for monitoring programs (including Reef Life Survey – a cost-effective, ecological monitoring program using trained recreational divers – and comparable agency-based programs) to best inform adaptive management via delivery of up-to-date relevant information.

The results from this objective are essentially an interpretation of lessons learned from the results and analyses in objective's 1, 3 & 4, including an overview of what worked, what significant gaps were detected, and what are the likely future needs of management that monitoring programs can adequately address. This interpretation is particularly with respect to species distributions and identification of species with life-history traits that make them potential “indicator” species of change, and hence targets for focussed monitoring programs.

Survey methods. Any future monitoring program is going to have to address the need to collect information across a broad range of species to properly understand how they respond to a warming climate, such that adaptive management processes can be well informed. The results from the analysis at Maria Island, utilising our best available long-term dataset, indicated that two of the key responses to warming were at the level of thermal traits and trophic level (herbivores), both of which required monitoring of multi-species assemblages rather than individual “indicator” species. However, at the same time, where major climate indicator species (such as *Centrostephanus*) do occur, monitoring does need to ensure that these are also adequately detected and described, particularly in the outer tails of their distribution. This latter requirement was highlighted in the analysis for Objective 1 examining the importance of detectability at range limits, and while appropriate choice of models may account for imperfect knowledge, an increased focus on improving knowledge in the tails of species distributions is recognised.

The current reef monitoring protocol in place in temperate WA, Temperate NSW, Tasmania, Victoria and South Australia is a nationally accepted methodology that has been demonstrated here and elsewhere (e.g. Barrett et al., 2007; 2009; Edgar and Barrett, 2013) to return practical, cost effective and informative results for management applications, allowing comparison of species distributions and patterns across state borders and regional gradients. The core protocols are broadly identical in all states (except a minor modification for algal cover in the “Reef Health” program in SA), based on diver observations of fish and mobile invertebrates abundances, and the percentage cover of macroalgae and sessile invertebrates. These protocols, described in detail in Edgar and Barrett (2007), and further below, yield robust abundance data on most species of interest, and can be supplemented by additional targeted surveys for particular species (both of identical methodology or complimentary alternatives such off-transect timed swims targeted at species of interest, or non-diver based methods such as Baited Underwater Video (BUV), or simply by additional replication if the focus is to improve the power of detection of trends in climate change species at their range edges where detections are imperfect due to lower abundances.

In addition, these identical protocols have generally been in use as part of monitoring programs examining changes in MPAs following or prior to declaration (WA, SA, Vic, Tas, NSW, or as part of

programs documenting changes in reef health (The SA Reef Health Program (Turner et al., 2008), the Lap of Tassie program (Stuart-Smith et al., 2008; 2011)) so they allow detection of any interaction of fishing with CC species and their abundances (as is the case for *Centrostephanus* in Tasmania for example). They currently have the support of a range of management agencies (conservation, fisheries and NRM) in many of these states, and staff experienced in their implementation. Furthermore, these methods provide quantitative abundance data, such that changes in abundance can be described through time, and are therefore more reliable than presence/absence data obtained by other methods. Perhaps most importantly still, the methods have been in widespread use from as early as 1992 in Tasmania (Maria Island, Tinderbox, Ninepin Point and Governor Island- e.g. Edgar and Barrett, 1997), 1993 for a full “reef health” bioregionalisation of Tasmania (Edgar et al., 1997), 1996 in NSW (Jervis Bay-Barrett et al., 2005, 2007) and Western Australia (Esperance to Albany Coast), 1997 in Victoria (Port Phillip Heads- Barrett and Edgar 1997), 1999 in Western Australia (Jurien Bay- in Edgar et al., 2005) and Victoria (Wilsons promontory - in Buxton et al., 2006) and 2002 in South Australia (Flurieu Peninsula- in Edgar et al., 2005). Many of these surveys have been repeatedly added to through time, providing a critical time series, and new locations and regions have been added, including Port Davey in SW Tasmania- Barrett et al. 2007a, Kent Group in Bass Strait – Barrett et al. 2007b, Batemans Bay region in NSW- Barrett et al. 2008), numerous locations in South Australia from Ceduna to Robe and a wide range of locations in Victorian MPAs from 1999 onwards as part of the Victorian government commitment to performance evaluation of their MPA network (e.g. Lindsay et al 2006, but there are many in this report series, available from Parks Victoria on request). That program continued on an annual basis for a decade providing a broad framework by which regional changes could be assessed. It was reviewed in 2007 by Keough et al. (2007) and Power and Boxall (2007), and subsequently continued with a lower rate of temporal replication to address budgetary constraints.

This legacy of very broad national coverage, coupled with a standardised protocol, and a long historical record in many locations, including time series data, does make it the most logical framework for the development of a more specific application to inform climate change adaptation management. Clearly the focus of such programs up until now has been on understanding reef health, describing biogeographic patterns in species distributions, conservation planning, monitoring MPA networks, and informing ecosystem-based fishery management. This framework now needs to be further evaluated and potentially adjusted to meet the additional requirements necessary to meet climate management needs.

Overall, the current MPA network in temperate Australia does provide reasonable spatial coverage to detect climate-related changes and trends, and when coupled with similar replication of surveys in adjacent fished areas (as is the case in the current programs), will allow good description and understanding of regionally specific processes associated with differing species assemblages. For example the Kent Group in Bass Strait has very low Southern rock lobster abundances naturally due to low settlement, so here *Centrostephanus* barrans, which are extensive in this area, may never be controlled by lobster predation. This is contrasted by results from Governor Island or Maria Island in eastern Tasmania, which show lobsters to be abundant and key predators, capable of regulating *Centrostephanus* numbers. It is really important to understand and describe this regional variation and responses, as many “paradigms” are not generalizable and it is a mistake to assume they are.

A recent FRDC project examined the potential application and development of indicators for informing spatial management in SE Australia, utilising a range of datasets, including the Victorian MPA monitoring data and our regional LTTRMP data (Smith et al. 2010, Johnson et al. 2011). That report found that despite many areas having a range of species in common, there were very few responses that could be generalised to the extent that specific indicators would be applicable generally. The models demonstrated that while processes operating within individual MPA regions could be described, they were not transferrable between these regions, so it is imperative to provide a monitoring framework that accounts for regionally specific responses in ecological communities.

Clearly then, there are several aspects to a climate driven need in a monitoring framework that need to be addressed in any future programs. The first of these is the extent of spatio-temporal coverage of species ranges and abundance distributions, especially at the margins of species ranges. This has been relatively well addressed by the mix of State agency programs (including the LTTRMP) and the RLS-based projects, and will be addressed later in this section with respect to refinement. The second component is the long-term monitoring of MPAs and adjacent fished areas, where such areas can offer the necessary regional level understanding of ecosystem function and the extent that individual species contribute, as well as a fuller understanding of the interaction between climate related impacts and fishing activities. The work undertaken to inform Objectives 1 and 3, indicate that long-time series are necessary to both detect changes related to climate drivers (particularly as warming trends are accumulated over decade scales), and to adequately untangle the interactions between fishing activities and climate driven changes in biological assemblages and processes. This latter component is critical, as in many cases, understanding this interaction is the basis of developing adaptive management responses, given that controlling fishing effort, either spatially through closures, or via effort controls, is one of the few levers available for management to provide a response.

Overall there is moderate coverage of the temperate Australian coastline with MPAs that have some form of monitoring programs in place. Fortunately most of these are based on a BACI design, with “before” data available to ensure observed changes are in response to protection, or temporal responses, rather than inherent differences between zones or sites. Temperate water examples of the spatial distribution of these include, from Western Australian, Jurien Bay and the Capes (Cape Naturaliste to Cape Leeuwin) MPAs, as well as protected areas at The Abrohlos and Rottnest Island. South eastern Australian examples include MPAs at Port Stephens, Jervis Bay, Batemans Bay (NSW), Cape Howe, Wilsons Promontory, Bunnerong and Port Phillip Heads (Vic), and The Kent Group, Governor Island, Maria Island, Tinderbox, and Port Davey MPAs (Tas).

There are some gaps in the physical distribution of these MPAs within SE Australia from the viewpoint of their use as scientific reference locations by which to assess the impacts of climate change and fishery interaction. These primarily relate to typical coastal habitats subject to some degree of fishing pressure (such as far NE Tasmania), however the current MPA framework in NSW and Victoria within this region does appear to provide the necessary spatial coverage to describe regional variation in responses, and minor additions within Tasmania would help provide a robust spatial framework for monitoring of the SE region. Within that framework though, there are still zones within some MPAs where the current no-take MPA configuration is not ideal for scientific reference area function, and this is something that requires further discussion, and a common approach to its solution, with FRDC, state management agencies and other stakeholders. These primarily relate to either the size of a MPA, or the no-take zones within it, where the effectiveness of no-take reference areas are compromised by either an inadequate area of protection relative to the movement patterns of the species they are intended to protect, or poorly functioning boundaries, such as those situated on continuous reef habitat, where cross boundary movement causes a significant edge effect. An example of this is the Governor Island MPA in Bicheno, Tasmania, where the northern boundary of this small MPA (less than 1 km coastline) is situated on continuous reef and is heavily potted for lobsters and netted for fish. This results in this otherwise well positioned MPA being less than ideal as a reference area for examining lobster/*Centrostephanus* interactions, despite being otherwise ideally located.

With respect to species distributions, and determining changes in these through time (a central focus of our work against Objectives 1 and 4), one big hole in the State agency/MPA reference focus, was that the distribution by abundance curves of many species were not adequately described. There were multiple reasons for this, including (1) significant gaps in-between reference areas (for example between Jervis Bay and Port Stephens), (2) habitat related gaps, for example where MPAs are predominantly in sheltered waters, whereas particular species of interest are in exposed waters, (3) depth related gaps, where the bulk of MPA monitoring has been at 5-10 m, but significant habitat related change, or important indicator species may be more evident at greater depths, (4) missing values at the mid to extremes of species ranges, especially to the north of the current MPA monitoring

focus. In these instances, data from Reef Life Survey (RLS) has been invaluable in our current analysis in providing many additional data points over species ranges to help understand current patterns, and potentially detect future changes in these, particularly in the “tails” of distributions. We could not, for example, have completed the species distribution work (Objective 4) without RLS data, particularly allowing northern range limits and range shapes to be described.

As described in the methods section, the RLS methodology is very similar for fishes and mobile invertebrates to the other reef monitoring protocols in place, allowing data comparisons to be made as identical areas are searched by these methods when replicates are pooled to give the same area coverage. It does differ in the methodology used to examine algal cover though, as volunteers lack the necessary skills to determining a broad range of algal species, and therefore the methodology is based on a photo-quadrat method, that allows dominant algal cover to be described and monitored, but not the overall compliment of algal species often present at these sites. For fishes and invertebrates, RLS surveys are a cost-effective approach to obtaining essential distributional data, particularly at the distributional limits of species ranges. Many of the species distribution models developed for Objective 4 heavily relied on RLS data from sites extending up into Queensland to properly describe the shape of species distribution curves, and this was particularly important to establish given that these curves often related to widely distributed warm-temperate species most likely to influence assemblage changes in the SE region over the next 50 years.

The extent of replication available through RLS also meant that a wider range of habitats were able to be surveyed, thus minimising any region by habitat interactions (e.g. sheltered habitats dominating in Jervis Bay vs exposed habitats at Batemans Bay) in the data that may have confounded the analysis in Objective 4 otherwise. In time, this approach should also yield appropriate temporal patterns in locations and habitats that are not covered by established monitoring studies in fixed locations such as Jervis Bay or Maria Island, or where state agency-based approaches are not able to provide the temporal replication through time necessary to detect changes with environmental variables.

In that respect, in addition to continuing with a state-agency approach to monitoring coastal reefs within current MPA monitoring frameworks, we suggest that given the complimentary nature of the RLS approach, continuation an RLS style program is an essential and integral component of climate change monitoring for adaptive management. It is essential to both fill-in gaps in biological ranges and latitudinal site locations, and to provide a cost-effective solution to maintaining time-series when government agencies are not able to do so. This could be supplemented by occasional state agency initiatives such as the South Australian and Tasmanian reef health projects, which may be repeated at temporal scales that match expected scales of biological change (decade scale). One priority action is to undertake a region-wide macroalgal survey that utilises the conventional quadrat method to supplement the RLS fish and invertebrate data from locations in the tails of distributions in particular. The lack of adequate algal data precluded our analysis if this in objectives 1 and 4 for SE Australia, yet many algal species show restricted thermal distributions and may form a significant component of regional diversity at threat from warming related impacts.

Specific recommendations regarding monitoring locations and analysis/reporting protocols in SE Australia for identifying biodiversity responses to climate change, potential management adaptation measures, and describing the effectiveness of these.

To supplement the above discussion of monitoring frameworks, there are a number of specific reference areas of significant value to our long-term understanding where monitoring should be continued/established as a top priority. These locations include Jervis Bay Marine Park, Batemans Marine Park (NSW parks), Cape Howe Marine National Park, Point Hicks Marine National Park, Wilsons Promontory Marine National Park, Bunurong Marine National Park, Port Phillip Heads Marine National Park (Vic), Kent Group Marine Nature Reserve, Governor Island Marine Nature Reserve, Maria Island Marine Nature Reserve, Tinderbox Marine Nature Reserve and Port Davey Marine Nature Reserve (Tas). All these areas have no-take areas suitable for a reference role, existing

long-term data and monitoring available (at least a minimum of ten years for most) and adjacent fished habitat that is representative of the coastal region and is also monitored as part of existing programs. Their spacing within the SE region of Australia is at approximately 100 km scale, giving a good regional spread to both represent regional variability in ecosystem function, and latitudinal gradients in biogeographical trends, including the current and future range of species.

The main significant gaps include far NE Tasmania where a monitoring location is needed to maintain the 100 km regional scale of observations, and exposed coast reef systems at Jervis Bay that are under-represented in the current monitoring program. These gaps should be filled as a top priority. Monitoring must occur at these spatial and biogeographical scales if changes are to be detected (including species range changes and ecosystem changes) and this knowledge interpreted in the context of regionally specific system function. The data collected needs to be informative of changes in the variety of species that represent biodiversity, key fishery species, key system drivers and key impacts of system change. Hence, it needs to be comprehensive in species coverage and include habitat forming species such as macroalgae and endemic species at risk of loss. The current methodology in use for MPA and reef health monitoring in the temperate Australian states is appropriate to this task and provides a sound baseline from which to detect further change. This methodology is described in detail in a section below. Ideally such monitoring would occur on an annual basis to establish baseline variability, however, recognising that resources are limited, such monitoring would need to be at a maximum of five year periods to allow for temporal trends to be detected and reported as part of an integrated reporting framework incorporating climate change metrics into the State of Environment reporting.

To provide improved range edge detection within the 100 km scale of MPA related surveys, additional surveys at regular spatial scales (ten km scale) undertaken by Reef Life Survey or state agencies would also need to be undertaken at 5 year time scales, given the urgency of our need to understand the consequences of climate change on marine systems and to be able to implement adaptive measures in a timely way.

One final essential gap that needs to be addressed as a top priority is to undertake a comprehensive survey of macroalgal species abundance by latitude to allow range/abundance envelopes to be fully developed for algae in addition to the fish and invertebrate analysis undertaken for Objective 4. Our ability to do this here was significantly constrained outside of Tasmanian waters (where spatial coverage is comprehensive) as such data was only available for the major MPA locations mentioned above. Information both from gaps in-between locations, and from locations north of Jervis Bay towards the northern range limits of temperate algal species is necessary to describe range/abundance envelopes and predict consequences of warming. Developing this understanding further is particularly needed given the enhanced vulnerability of macroalgal species to future warming due their high level of endemism in the cool temperate zone and restricted ranges, relative to many other phyla.

For analysis of information collected as part of this integrated monitoring framework, an essential component is the development of a common database format, enabling shared access to data between state agencies, and the ability to provide regular reporting. Much of this reporting can be automated, as occurs for Victorian MPA surveys, and readily adapted to incorporate specific reporting for climate induced patterns, including changes in indicator species. Typical outputs would simply be reports of the extent of change in species abundances by latitude through time (including northern range contractions as well as southerly extensions), and identification of system level changes and interactions with levels of protection (e.g. MPAs). These could either be incorporated into routine MPA reporting, or specifically tailored towards climate response management needs, including input into regional plans and stock assessments. Apart from reporting of clear ecological changes associated with warming processes, this process could include the data analysis protocols developed for Objectives 1 and 4 in this report, as well as tracking indicators of change identified in Objectives 1 and 3. Further improvement in our knowledge of species abundances at range edges will increase our understanding of rates of change via extinction models, our species distribution curves used for future

range predictions, while indicators such as functional trait richness and functional diversity will assist in detecting overall assemblage change in response to warming.

Reporting metrics include the velocity of species movement, loss of endemic species within their range, changes in key ecosystem species such as urchins and lobsters, and habitat metrics such as kelp cover and algal diversity. Ideally reporting would be guided by the a regional management group and on the basis of a national standard database for sharing data across jurisdictions, with funding from all agencies involved in climate change adaption and State of Environment reporting. The metrics above should provide most of the knowledge needs of management agencies with respect to habitat loss, changes in key species abundances following management intervention, and benchmarks of ecosystem condition and the status of threatened species.

Costs: Given that the MPAs in NSW, Victoria and Tasmania (e.g. Port Stephens, Jervis Bay, Batemans Bay, Cape Howe, Kent Group, Wilsons Prom, Maria Island, Governor Island, Port Davey, Port Phillip Heads) can be accessed and surveyed by relatively small dive teams, the actual cost on an annual basis, of a SE Australian climate-focussed monitoring program can be estimated with regards to maintaining an adequate level of replication. The review of Keough et al. (2007) suggested that following an initial time period to obtain estimates of natural variability, MPA monitoring in Victorian waters would be well informed by a rotating series of bi-annual surveys. Under that assumption, and that a climate change program would have similar requirements, costs can be roughly estimated. The average field program is two weeks (ten field days) for large MPA for monitoring, resulting in twenty weeks of time in total (equivalent to eighty staff (FTE) weeks of fieldwork, \$190k), plus data entry time (80k), and field costs for vessels, vehicles and accommodation. This would be estimated at a similar cost (\$1000 per day for vessel and vehicle costs, \$500 per day for field accommodation and meals), with a total of approximately \$150k for field costs. That would equate to \$420k across SE Australia for a typical bi-annual survey with sufficient spatial and temporal replication, excluding costs associated with reporting. In addition that would be ideally matched by the decade scale “reef health” projects such as the 2005/6 Tasmanian project, with a budget of \$330k to undertake a more comprehensive spatial coverage of reef systems. Similar costings would apply to both Victorian and NSW projects if matching spatial surveys were planned to provide extensive coverage for the SE region of these States. Reef Life Survey costs are more difficult to assess, however, it is anticipated that they would be approximately half the cost of state agency based surveys, and provide the additional spatial coverage necessary to track range edges.

In that sense, we have a good indication of the costs of current monitoring programs (both Government and RLS). Clearly this work is synergistic with current research focussed on MPA and biodiversity management in a range of Temperate Australian states. In that respect such monitoring programs are a shared responsibility between a range of state and commonwealth agencies, which will hopefully mean, that if they are identified as priority areas to support, a range of synergies can be found, and cost savings made. One of these relates to analysis protocols. We would suggest that a common database across temperate states be maintained, from which particular species abundances could be extracted and tracked through time by management agencies and their associates research staff. The IMAS SQL database structure, species lists, traits tables etc are available to any interested agencies as a framework, and hopefully will assist in establishment of a common framework.

Detailed description of standard survey methods.

The underwater visual census methods described here are those currently in use in Tasmania, Victoria, New South Wales, South Australia and Western Australia for assessing population structure and biodiversity on temperate reef systems. The methods were originally developed for assessing the effectiveness of Tasmanian MPAs (Edgar and Barrett 1997, 1999), and based on commonly used techniques (e.g. Russell, 1997; McCormick and Choat, 1987; Lincoln Smith, 1988, 1989) to ensure

compatibility of datasets within Australasia. The suitability of this methodology for assessing the magnitude of biotic change in temperate MPAs was an objective of this study and the subject of a FRDC sponsored workshop in 1999 (Barrett and Buxton 2002) and has been further reviewed by the Victorian government Department of Natural Resources and the Environment (NRE) as part of their commitment to long-term monitoring of Victorian MPAs (Keough et al. 2007; and Power and Boxall, 2007). Both the FRDC workshop and the NRE review found these methods to be appropriate for the purposes discussed above. The methods described here have been developed within the framework of being non-destructive (for use in MPAs) and gathering as much data as possible on a wide range of species, including fishes, invertebrates and macroalgae. This broad census of biota allows changes to be examined at the species level (for fished, bycatch or key species) and more widely at the biodiversity and ecosystem levels. As information was required on the abundance of fish, invertebrates and macroalgae, three different census methods were used to obtain reliable quantitative abundance estimates on these widely differing groups. At each reef site, the abundance and size structure of large fish, the abundance of cryptic fishes and benthic invertebrates, and the percentage cover of macroalgae were censused separately.

Suprabenthic Fishes

The densities and sizes of suprabenthic fishes are estimated at each site by laying four 50m transect lines along the 5m depth contour and recording on waterproof paper the number and estimated size of fish observed by a diver while slowly swimming above the algal canopy along the centre of a 5m wide swathe up one side and then down the other side of the line. A total of 4 x 500m² transects are thus censused for large fish at each site. Fish sizes are recorded in size categories: 25, 50, 75, 100, 125, 150, 200, 250, 300, 350, 375, 400, 500, 625, 750, 875 and 1000+ mm. Calibration of size estimates is based on comparison of observed fish lengths with a scale-bar on the underwater slates carried by divers. Care is taken to minimise the duplicate counting of individuals, especially fishes obviously attracted to the divers.

Invertebrates and cryptic fishes

Invertebrates and cryptic fish are censused along the same transect lines (four 50m lines) established for the suprabenthic fish surveys. A diver thoroughly searches the seabed for a distance of 1 m from the transect line, investigating all visible crevices and overhangs but not overturning boulders. The distance of 1m is measured by a 1m length section of conduit carried by each diver. This also aided in the capture of lobsters. Macroalgae are swept away from the transect to obtain a clear view of the

substrate. Most mobile megafaunal (approximately >20 mm length) invertebrates are counted, including decapod crustaceans (crabs, rock lobster and hermit crabs, but excluding shrimps), large gastropods (whelks, tritons, abalone), selected mobile bivalves (scallops, excluding mussels and oysters), octopus, crinoids (feather stars), asteroids (seastars), echinoids (sea urchins) and holothurians (sea cucumbers). Other invertebrates such as annelids (worms), polyplacophorans (chitons), shrimps and ophiuroids (brittle stars) were not counted as they were mostly cryptic and too numerous to be properly counted in the time available per survey. For abalone the maximum shell length of each animal is measured in situ to the nearest mm with callipers, until at least 20 abalone have been measured on each 50 m transect. The carapace length of lobsters is also measured where possible. Measurements are restricted to lobsters greater than 30 mm carapace length and to situations where the animal could be captured and handled without damage. Where lobsters cannot be captured, estimates of carapace length are obtained by holding callipers as close to the lobsters as possible.

Macroalgae

The percentage cover of macroalgal species and encrusting invertebrates (sponges, ascidians, octocorals, bryozoans) are quantified by placing a 0.5 x 0.5m quadrat at 10 m intervals along the four 50m transect lines and estimating the percent cover of the all plant species in each quadrat. Twenty quadrats were thus sampled per site. The quadrat is divided into a grid of 7 x 7 perpendicular wires, giving 50 points (including one corner) per sample position, under each of which the cover of each species present is recorded. Initially the cover or overstorey species is recorded, and then these

are swept aside exposing the understorey species for counting. Point-counts are recorded for each lowest identifiable taxon, usually to species level. Unknown or unidentifiable species are assigned functional categories including: 'unidentified structural reds', 'unidentified erect corallines', 'encrusting corallines', 'unidentified filamentous reds', 'unidentified filamentous browns' and 'unidentified small browns'. The percentage cover of sessile invertebrates is also counted (at Phyla level, e.g. ascidians, sponges) as well as the nature of substrate cover (e.g. encrusting sponge, bare rock). Where bare rock is clearly caused by urchin grazing and quadrats return zero counts of algae, they are scored as Urchin Barrens.

Site protocols

The location of each site is recorded and determined by GPS and depth sounder, once a suitable extent of reef (usually at least 200 m in length) is located. The boat anchor is usually used to mark the position of the site. Starting at the anchor a diver then swims out a 100m transect line in each direction along the 5m depth contour, thus a 200m length of transect line is established which is subdivided into four 50 m segments for the purposes of the census. After the transect is established the diver swims away from the line for 10 minutes to minimise interaction with fishes attracted to the disturbance, then counts fishes as described previously. Once the fish counts are completed, transects are searched for invertebrates and cryptic fish, with the algal census usually being conducted concurrently by separate divers. Using this method, between two and three sites can be surveyed each day.

In Summary,

The optimal, and most cost-effective approach for monitoring programs to best inform adaptive management via delivery of up-to-date relevant information, is to build upon current initiatives for MPA and biodiversity monitoring within the SE Australian, and more broadly in temperate Australia. These programs are currently in place in many jurisdictions, use a common monitoring methodology, have appropriate spatial coverage to inform changes occurring at regional scales, and allow regional differences in ecosystem function to be accounted for. Moreover, they also often include a pre-existing time series to allow earlier recognition of climate induced changes, and have contrasting fished and protected sampling designs to detect fishing and climate interactions where present, such that management responses may be informed and implemented if such interactions are deleterious. With a clear need to incorporate results from multiple regions and states into a common climate reporting framework, linking results of monitoring programs through a common database structure may significantly facilitate analysis and reporting of changes as they occur.

In that sense, the locations to best base monitoring programs are the regionally significant MPAs, as these offer multiple benefits from such programs, and engage multiple management agencies, linking conservation and resource management in a common framework for responding to climate change. Additional sampling via identical methods (as utilised by RLS for fishes and mobile invertebrates) is needed at a range of spatially distributed locations between, and to the north of the extent of the MPA

locations, to describe, and track, changes in species distributions. There are no identical sites for these, only that sites chosen encompass the range of habitats typical of our coastal systems. Ideally these would include comprehensive quadrat-based algal surveys, as algal abundance by latitude data is not comprehensive for this region, despite the algal diversity richness and endemism that may place many species at risk in the future.

No clear species arise with respect to indicators to track other than *Centrostephanus*, but rather an optimal approach is to focus on describing the overall assemblage at each location, detecting changes via community indicators based on ecological traits. This more broad brush approach also allows regionally specific responses to be described and detected without picking winners that might not prove to be the case. However, the regional (latitudinal) predictions of likely future changes in abundance produced for Objective 4 give guidance to the likely set of individual species that would be reported against in future outputs of climate-related monitoring programs.

The likely application of these approaches to management includes:

1. Improved detection of range shifting species,
2. Description of functional change in ecosystems that may arise from such species changes,
3. An indication of the rates of change that occur through time,
4. An indication of the spatial distribution of changes, likely changes, and the mechanisms underpinning this (e.g. Kent Group responding very differently to *Centrostephanus* than Wilsons Promontory or Maria Island),
5. An indication of the extent that these changes might impact on current fisheries and adaptation towards developing new fisheries,
6. An indication of the extent that fishing or other human activities interact with climate change, such that fisheries and conservation agencies can develop adaptive responses towards maintaining healthy ecosystem function and productivity if such interactions are deemed to be deleterious and preventable (e.g *Centrostephanus barrens* in NE Tas).

Objective 3: To assess the costs and benefits of existing temperate Marine Protected Areas for biodiversity-conservation management in response to Climate Change and evaluate the robustness of adaptive management frameworks given uncertainty in predictions.

This objective was approached from a number of perspectives. We initially explored changes through time in a range of temperate SE Australian MPAs. However, as with Objective 1, we required a lengthy and continuous time-series to be able to document species relationships with climate, and to untangle interactions with fishing activities to the extent that relationships with biodiversity could be effectively explored and described. The analysis undertaken for Objective 1 indicated that at this stage in time, Maria Island was the only dataset of sufficient length and temporal replication to allow clear patterns to be determined. So one clear point, even at the early stage of analysis, was that we cannot fully evaluate the benefits of MPAs for biodiversity management without a matching long-term monitoring program in many of these, and the patient continuation of these programs to allow this evaluation to be made at some point in the future (a typical minimum time may be twenty years in many cases).

Ecological changes arising in MPAs are often slow, but do accumulate through time, as documented in a range of recent studies and analysis from a wide range of short to long term MPAs (e.g. Babcock et al., 2010; Edgar et al., 2009; and Edgar and Barrett, 2012). This waiting period is a real “cost” of

utilising the MPA approach to evaluating ecological relationships, but the flipside is that the benefits include that it is the only way of effectively untangling fishing related relationships with biodiversity under a changing climate. Unfortunately, as most of the no-take MPAs in the SE Australian region have only recently been proclaimed, monitoring in these rarely exceeds ten years following protection, and for many this is even less.

To that extent, we focussed the majority of our analysis on the one available long-term dataset (the data-rich Maria Island dataset) as a model case study approach. This analysis examined to what extent a fishing-related interaction with biodiversity could be detected fish assemblages in a well-established MPA, and what lessons could be learned with respect to the role MPAs might play in both informing adaptive management strategies, as well as MPAs themselves being a part of such strategies through spatial management. The bulk of this analysis has been published in Nature Climate Change Paper (Bates et al., 2014) and the associated extensive analysis that went with that is published as supplementary material. Much of the analysis and discussion of this are presented in Appendix ii of this report, and therefore are simply summarised here in this section.

This analysis made a number of important discoveries. Firstly it documented that at least in this case study, fully protected areas can have some resilience to climate change when contrasted with adjacent fished coastlines. It is therefore the first “marine diversity” focussed study to demonstrate the otherwise theoretical understanding that no-take MPAs should offer some “resilience” to climate change related tropicalisation. Reserve sites were distinguished from fished sites by displaying greater stability in some aspects of biodiversity, recovery of large-bodied temperate species, resistance to colonization by subtropical vagrants, and less pronounced increases in the community-averaged temperature affinity.

The study quantified changes in community structure using six metrics of richness and diversity. These include the traditional approaches of species richness and abundance-weighted diversity but, in a novel approach, also considered the richness and diversity of functional traits among individuals, to illustrate new aspects of diversity. This trait-based approach is discussed in Objective 1, and is a unique application in the context of long-term community change. In addition, because increasing individual body size is a well-documented reserve effect, we also calculated biomass-weighted species (SDb) and functional diversity (FDb). The functional metrics we developed and tested are based on ten traits, representing thermal physiology, life history strategy, feeding ecology, behaviour, habitat use and geographic range breadth. For each metric, we tested for differences between reserve and reference sites in mean values and patterns of variability that may reflect physical parameters associated with climate variability and long-term change. Overall, mean species richness and functional richness were higher in the reserve, although not significantly so (Appendix ii, Table S2). Diversity values (all metrics: Figure 7) were generally comparable in reserve and reference communities. Hence, although fishing has the potential to alter the ratio of trophic groups present (such as by targeting of higher order predators) and alter the complement of species present, we found no evidence for the establishment of a significant difference in the variety of species or functions in the time period (20 years) following the implementation of the Maria Island Marine Reserve.

However, we did detect relationships between biodiversity and climate variability. Although richness and diversity values were similar in the reserve and reference sites, reserve communities displayed greater temporal stability on both annual and decadal scales. First, the magnitude of successive year-to-year changes in diversity at individual sites was lower in the reserve (significantly so for SDa, FDa and SDb; Figure 8). Second, the amplitude of the decadal oscillation in mean species richness and SDb was dampened in the reserve versus reference sites (Figure. 8).

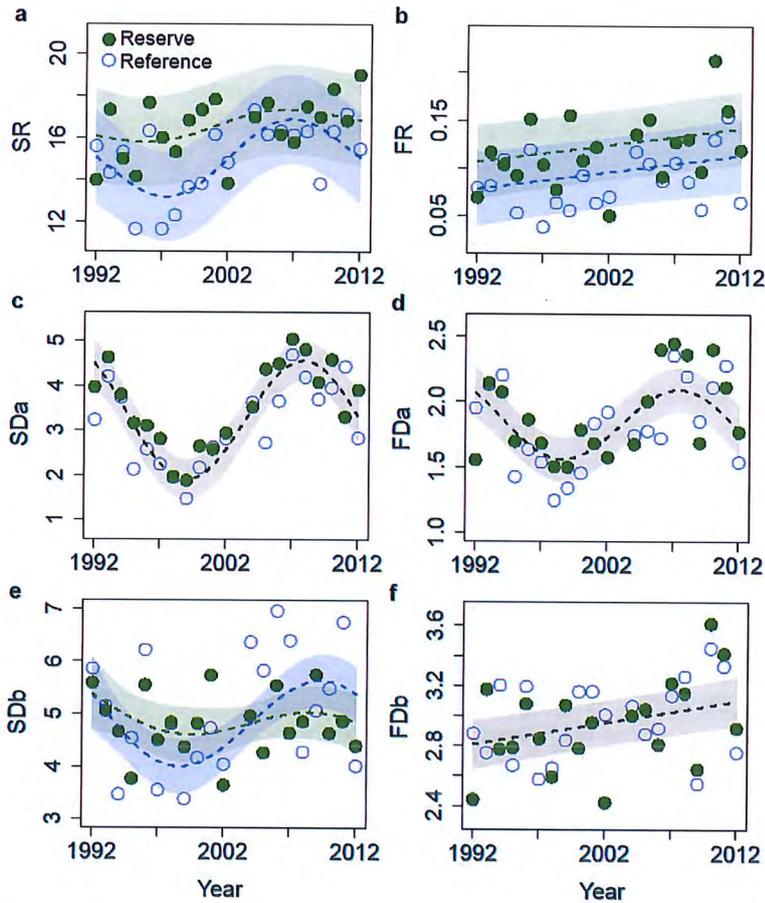


Figure 7. Species and functional diversity at Maria Island over 20 years. a–f, Species and functional richness (a,b), SDa and FDa (c,d) and SDb and FDb in reserve (nD6) and reference sites (nD6; e,f). Regression slopes (dashed lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table 2). A single regression line indicates similar mean values for reserve and reference sites.

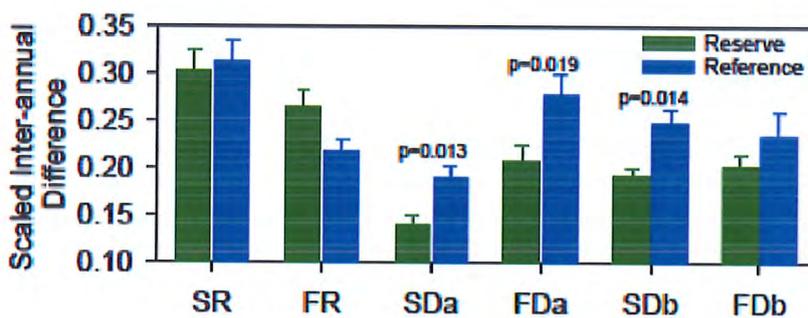


Figure 8. Annual change in richness and diversity metrics. Mean (s.e.) year-to-year differences in species richness (SR), functional richness (FR), SDa and FDa, and SDb and FDb in reserve (nD6) and reference sites (nD6) for the 20-year study period. Generalized linearmixed effects model results are in Supplementary Table 3. Values were scaled before differencing.

We further analysed independent trends in species traits in the reserve and fished communities to ascertain whether increasing functional richness and diversity were underpinned by the same mechanisms. We found the proportion of species with a large maximum body size increased over the study duration, contributing to increases in functional richness and presumably FDb. However, this

trend was limited to sites in the reserve where, in particular, several large-bodied carnivorous species increased following protection (Figure 9), leading to an increase in the mean maximum body size of species present. Recovery of large-bodied species inside the reserve apparently represents an important ecological response to protection, in addition to the better-documented biological responses of increasing biomass, individual body size and density in protected versus fished communities.

Community thermal affinity, measured as the upper realized temperature niche averaged across all species present, gradually rose, consistent with the tropicalisation hypothesis. Even so, the increase in thermal affinity was not as strong in reserve sites (0:08 C per decade) in comparison with fished sites (0:20 C per decade). In fact, community thermal affinity in the reserve declined when weighted by biomass, due to the recovery of large bodied temperate species following protection from fishing. Conversely, the steep increase in thermal affinity in the reference communities can be attributed to increasing colonization by warm-water species. An exponential increase in the abundance of some warm-water species occurred over the 20-year observation period at the reference sites (Figure 9). Furthermore, four range-shifting species (One-spot puller *Chromis hypsilepis*, Port Jackson shark *Heterodontus portusjacksoni*, Halfbanded seaperch *Hypoplectrodes maccullochi* and Sea pike *Sphyræna novaehollandiae*: species from lower latitudes and atypical of Maria Island) were detected at reference locations, whereas none were recorded within the reserve boundary (Figure 9).

There are a number of mechanisms that may be underpinning the differing responses of fished and protected assemblages to climate variability in this region. Two possible explanations are given for this. First, as higher predation rates can result in biotic resistance to colonization (Sax et al., 2007), the larger individuals within the reserve had the potential to even out fluctuations in the abundance of new recruits via increased predation rate (Sax et al, 2007; Wanger et al., 2011). Indeed, many of the warm-water recruits that were relatively abundant in the reference locations were small in size and thus vulnerable to predation (for example, White ear *Parma microlepis*, Figure 9). An alternative explanation, particularly relating to metrics such as the proportion of subtropical vagrants and community-averaged thermal affinities, is that biogenic habitat differences resulting from cascading effects of protection may provide different settlement cues for warm-affinity fish outside the reserve. For example, the urchin *Centrostephanus rogersii* (also counted but excluded from the analyses of fish community diversity) is a range-extending urchin, limited from reserve communities due to predation by lobsters, has substantially increased in abundance in the reference sites (Figure 13) forming barren patches of reef. These barren patches were observed to facilitate colonization by warm-affinity fish (Barrett, pers. obs.), perhaps representing a form of invasional meltdown (Simberloff and Von Holle, 1999). Whether warm-affinity species are associated with urchin barrens presents an important line of research to advance understanding of colonization differences between the reserve and reference communities.

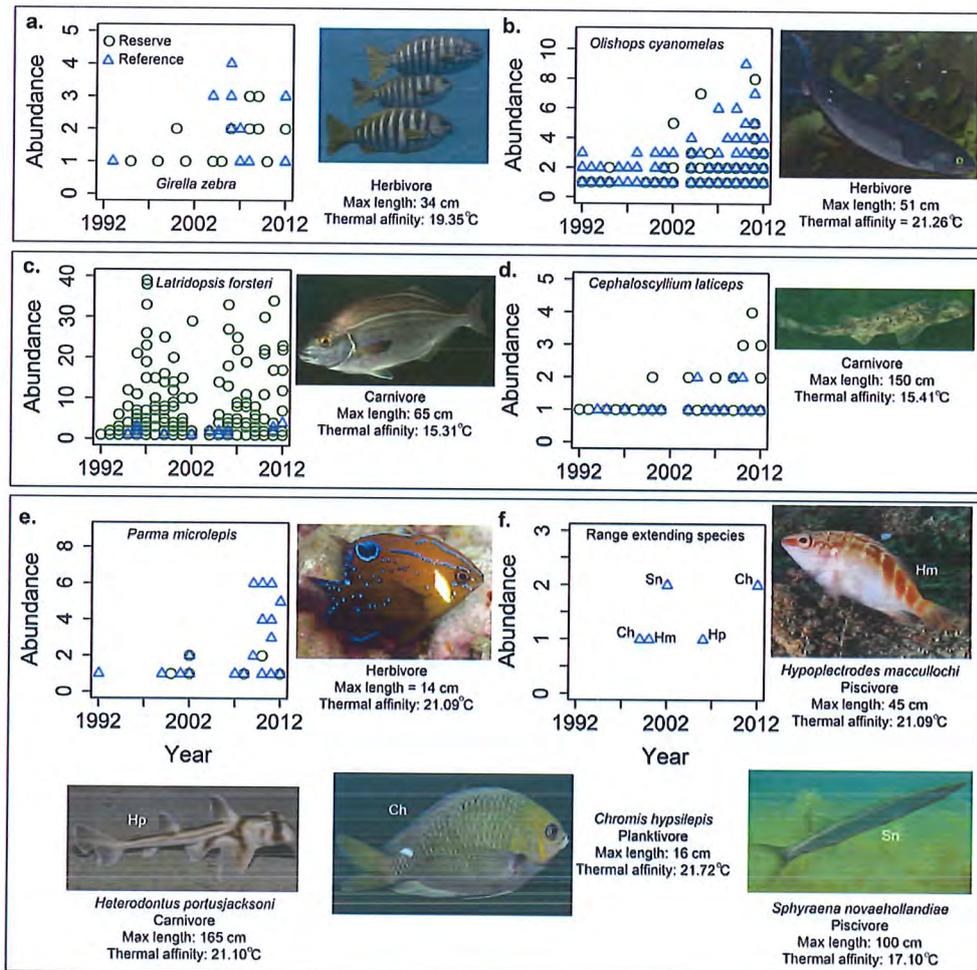


Figure 9. Species displaying trends related to changes in the community weighted mean functional traits. a-b, Changes in the abundance of herbivores (*Girella zebra* and *Olisthops cyanomelas*), c-d, large-bodied fish (*Latridopsis forsteri* and *Cepaloscyllium laticeps*) and e, warm-water species typical of Maria Island (*Parma microlepis*) in reserve and reference sites. f, Four species atypical of Maria Island and thought to be extending their range were sighted in reference sites only (*Chromis hypsilepis*, *Heterodontus portusjacksoni*, *Hypoplectrodes maccullochi* and *Sphyræna novaehollandiae*).

In summary, it appears that in a long-term, well protected MPA such as Maria Island, marine communities protected from fishing can, to some degree, buffer climate-related biological variability and resist colonization by warm-affinity species. In the context of climate change, protected areas therefore have the potential to build community resilience through a number of mechanisms to promote species and functional stability, and resist the initial stages of tropicalisation. However, this aspect of our analysis only focussed on the fish assemblage, and while links were made between the arrival of some tropical species and the development of urchin barrens in the region, the role that invertebrate interactions were playing with respect to resilience was not fully explored due to time constraints.

A second component of our study focussed on examining trends in the abundance of a range of key species within the Maria Island reserve and adjacent reference locations, to provide context to the study above, and examine patterns in the invertebrate community, which through processes such as resilience to *Centrostephanus* invasion, may further inform the above patterns and the extent that invertebrate communities are also responding to a changing climate.

While many changes were noted in the fish assemblage in this region, there were very few that showed a marked response to a varying climate, with these being explored for such patterns in the analysis presented in Objective 1. The most notable of these was the tenfold cycle in abundance in *Trachinops caudimaculatus*, shown previously in Figure 4. The overall component that displayed a clear pattern to MPA protection itself (other than the biodiversity metrics presented in the previous section), was the abundance of large reef resident fish species, in the size class (> 300 mm), a size range most subject to fishing pressure, being both vulnerable to capture in nets, and usually above minimum legal size limits that protect a proportion of the population. These went up threefold over the duration of the study within the reserve (Figure 10), with the most significant to this being the contribution of the Bastard trumpeter *Latridopsis forsteri*, a schooling reef resident species that is particularly vulnerable to gillnetting effort (Figure 10). Another contribution to this change was the abundance of large Blue-throated wrasse *Notolabrus tetricus*, although less distinct (Figure 10), with the remainder being contributed by less abundant large bodied species such as Long-snouted boarfish, Banded morwong and Marblefish. One other notable feature of these results was the increase in large fishes in the off-reserve control sites in the last few years (Figure 10), which corresponds with the introduction of management changes banning the setting of recreational gillnets at night, suggesting these new measures are having a demonstrable and positive effect on reef fish stocks.

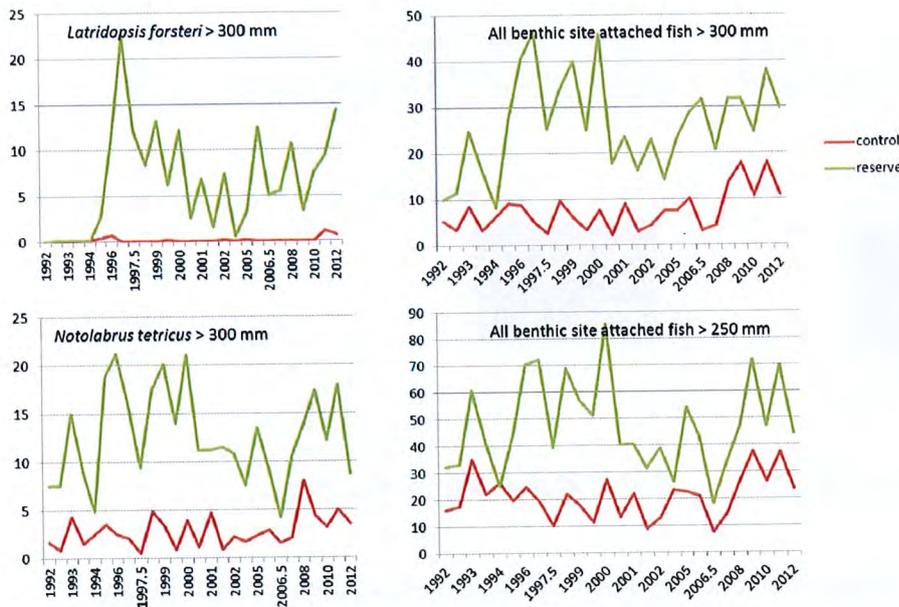


Figure 10. Trends in key site attached resident fish within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/2000m²), for fishes in each size category (greater than 250 and 300 mm total length).

The other notable feature within the fish assemblage at Maria Island was the clear increase through time of warm affinity species that were either absent when the study began in 1992, or were just occasional vagrants. The monitoring has recorded an ongoing increase in the presence and abundance of these, with some of the key species shown in Figure 11. *Parma microlepis* numbers have increased markedly in recent years, and seem to have followed a sequence of good recruitment years and the availability of preferred habitat. These are most commonly sighted in bare patches of reef that have been created by urchin grazing, with such barren areas increasing markedly in abundance at a number

of external reference sites over this time. This same pattern and habitat relationship appears for *Atypichthys strigatus* (Figure 11) and *Chromis hypsilepis* (not shown). The patterns for the two herbivores *Odax cyanomelas* and *Girella zebra* was not related to barren formation, with these becoming more abundant at a widespread range of locations. The increase in *O. cyanomelas*, a species now resident year round in this region, represents a major shift in the trophic function of fish assemblages in this region, as these are large-bodied fish representing a significant biomass. As discussed in the results for Objective 1, the increase in herbivorous fish biomass may be one of the most significant process-related responses of fish assemblages in this region in response to warming, although more research is needed into the likely consequences of this for influencing algal abundance or community structure.

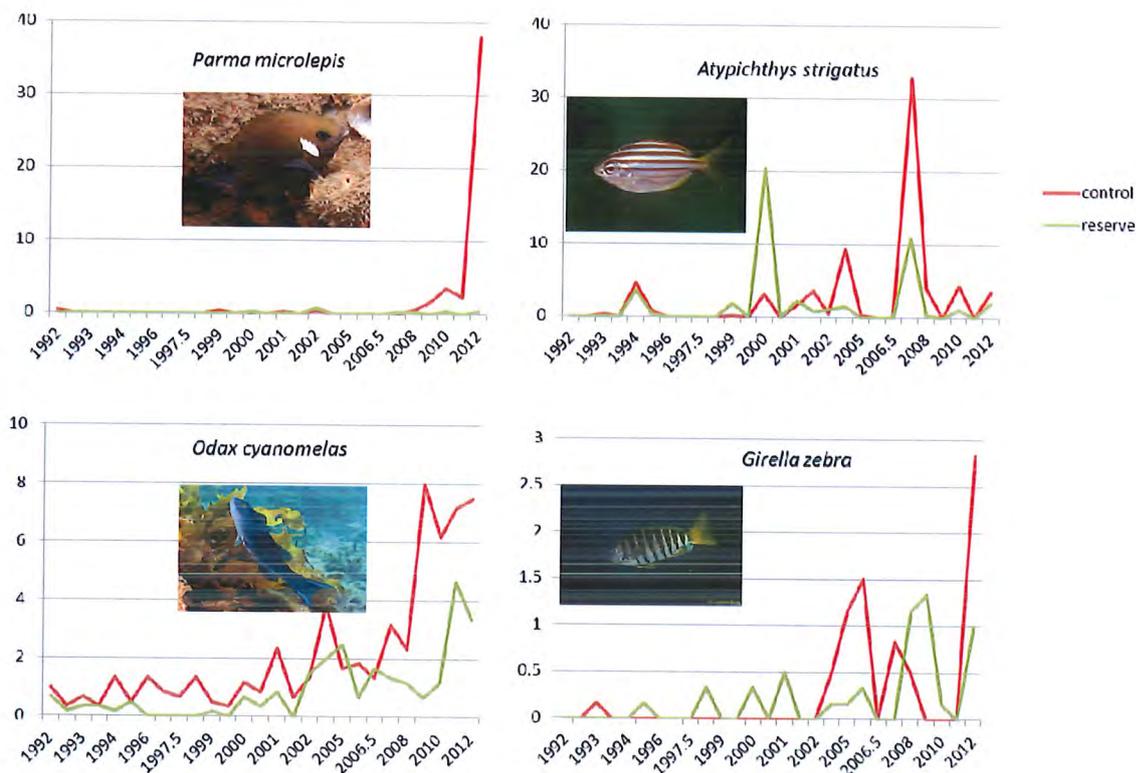


Figure 11. Trends in warm affinity reef associated fish within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/2000m²).

For invertebrates, the change with the most ecological significance was likely to be the increase in lobster biomass. This has increased significantly through time of protection with in the reserve, and at twenty years had nearly doubled the value reported for ten years post protection (Barrett et al., 2007; 2009), representing more than a tenfold increase over the period 1992-2012 (Figure 12). This increase was not as clearly represented in the simple abundance data (Fig 13) where numbers were strongly influenced by inter annual recruitment variation and were dominated by the number of sub-legal sized animals in the population, that while contributing to abundance values, did not overly influence the biomass as most of these were quite small.

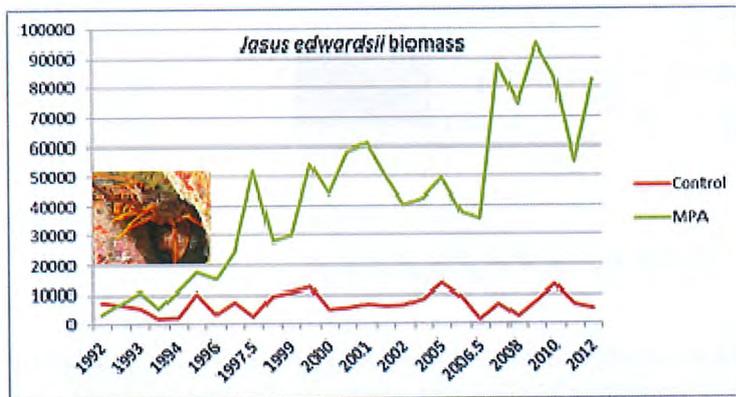
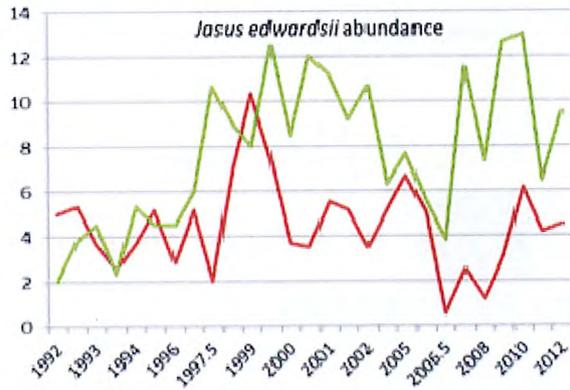


Figure 12. Trends in Southern rock lobster (*Jasus edwardsii*) abundance (n/200m²) and biomass (g/1200m²) within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection.

Matching the lobster biomass increase in the reserve was a correlated decrease in the abundance of a number of prey species, including Blacklip abalone (*Haliotis rubra*), Common urchins (*Heliocidaris erythrogramma*), and Pencil urchins *Goniocidaris tubaria* (Figure 13a). These declines were not evident at sites outside the reserve. While declines in common urchins and abalone were noted after ten years of protection (Barett et al, 2007) this decline has continued markedly over the subsequent decade with urchins, the numerically dominant large invertebrate species on these reef systems, with numbers within the reserve declining to 25% of original values. Likewise, for abalone, at the ten year post-protection stage, numbers had declined substantially but only for smaller abalone around the size of emergence (Barrett et al 2007) and it was unclear whether this decline was real, or a result of increased crypsis of juvenile abalone in response to increased numbers of predators (Pedderon et al., 2008). However, these numbers have continued to decline, and many of the large abalone have now been consumed as well, resulting in a greater than tenfold reduction within the reserve over the twenty years of protection (Figure 13a), while numbers outside the reserve have remained constant, albeit with significant year to year variability. Many broken shells of large abalone have been sighted

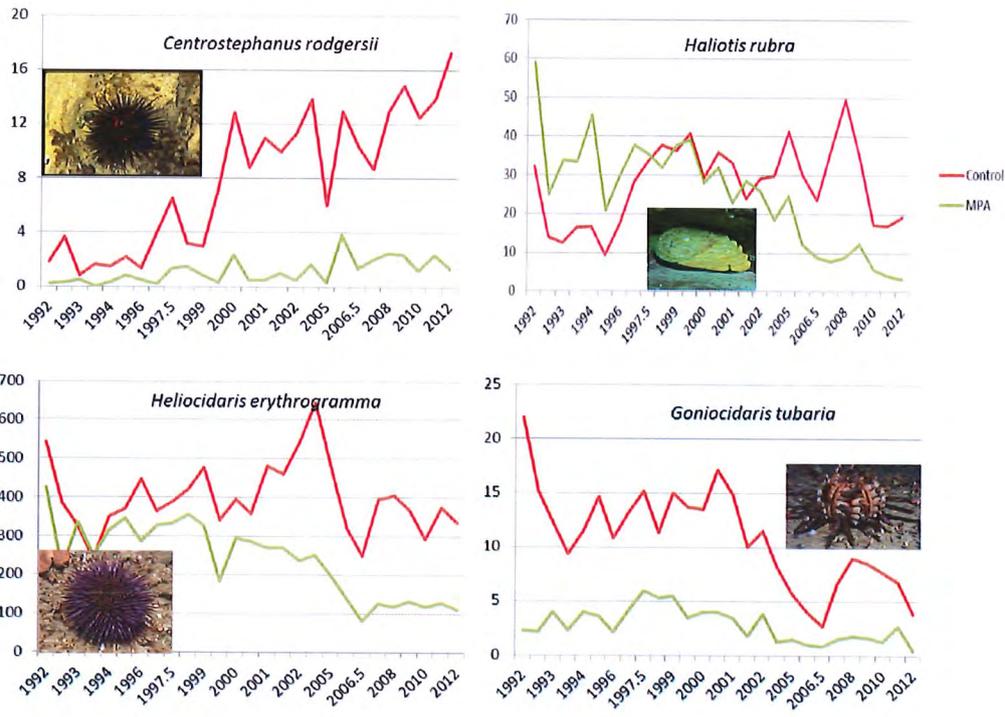


Figure 13 a. Trends in reef associated mobile invertebrates within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/200m²).

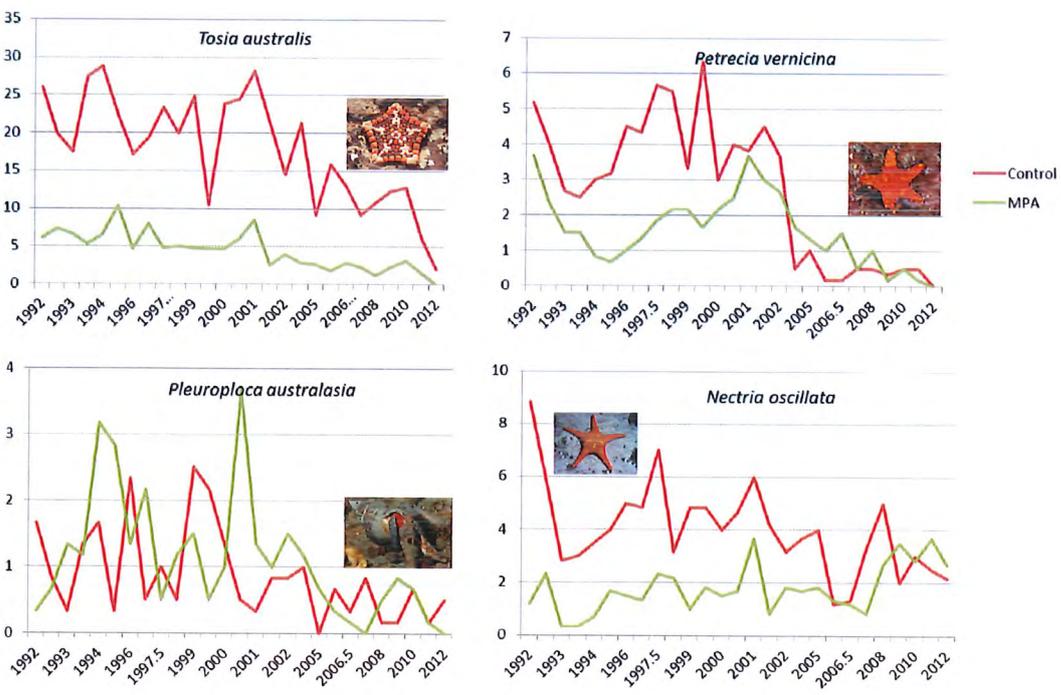


Figure 13 b. Trends in reef associated mobile invertebrates within, and adjacent to, the Maria Island Marine Reserve over the first twenty years of protection. Abundance values are the per-site means (n/200m²).

outside the dens of large lobsters, indicating that while once free from such predation due to reaching “escape size”, this relationship has altered once lobsters reached large-post legal sizes, restoring an ecological function now absent from eastern Tasmanian waters.

Numbers of the long-spined urchin *Centrostephanus rogersii* increased significantly over the twenty year period of this study, representing a tenfold increase at reference sites outside the reserve (Figure 13a). These are now present at three of the six reference sites, and are ecologically significant at one of these (Isle du Nord) where barren patches are now forming. Within the reserve numbers have been kept in check by the lobster population, with this species being present, but not at numbers that cause loss of kelp to the extent that barrens are evident. This is perhaps the most significant climate related result of our study as it demonstrates marked resilience of a well-protected, long-term no-take reserve to invasion by this significant ecosystem engineer. It demonstrates empirically that lobster populations, at what may be assumed to be natural levels of abundance and naturally distributed size structure, can resist *Centrostephanus* invasion and barren formation in the face of climate change, that otherwise would result in eventual widespread barren formation and habitat loss.

Clearly there are widespread implications of these results. It demonstrates empirically the relationship between lobster numbers and *Centrostephanus* numbers, such that management agencies can be confident that this relationship is more than theoretical, and that a range of management responses may be available if the spread of urchin barrens is deemed to be an issue that needs addressing. There is also the strong interaction between lobster numbers and abalone numbers to take into account in this response, as rebuilding resilience via lobster numbers will have a negative impact on abalone numbers as well. However, in the case of abalone, the decision process is a complicated one and requires a careful response to optimise the worst case loss of habitat by barren formation vs the potential to be consumed by the lobsters as populations, and perhaps more importantly natural size structures, rebuild.

Finally, for invertebrates, there was a pattern of ongoing decline in many of the common mobile invertebrate species over the period of the study (Figure 13b). This included the Ocellate seastar (*Nectria ocellata*), the Velvet seastar (*Petricia vernicina*), the Biscuit star (*Nectria ocellata*) and the predatory whelk (*Pleuroplocha australasia*). The response of these common invertebrates, coupled with a range of other species recorded but not shown, was not related in any way to MPA protection, but rather part of a more general regional response to changing environmental conditions. While not statistically significant, this pattern clearly matched the observed increase in average sea surface temperature over this period, and indeed could represent a lagged response to the larger increases that occurred prior to commencement of this study, reflecting the importance of long-term datasets to better determine bio-physical relationships. Regardless of the ultimate cause, this significant decline in common species, is of concern, and an indication of likely future climate mediated responses. When these declines were examined in relation to predictions made for each of these species in the models presented in Objective 4 under a 2C warming scenario, all were predicted to decline in this region, thus the observed decline does at least match the predicted direction of change for these in the future.

Regional implications: While this work was clearly a case study given Maria Island was the only MPA with a significantly long enough time series to be able to determine likely MPA related changes and their interaction with climate change, it does allow us to make some generalisations that may apply more broadly, and how MPAs may play a role in addressing these.

At a biodiversity and even fishery productivity level, the emergence of urchin barrens (regardless of the species responsible) represents the most significant management issue to address, as barrens represent both a loss of productive habitat as well as a loss of the biodiversity that relies on such habitat availability. Current work examining *Centrostephanus* barren distribution in eastern Tas (Perkins et al.-in prep), indicates that in this region they extend much deeper than in NSW, and thus represent a threat, not only to the algal assemblages to a depth of 20 m (as in NSW) but also to

sponge-garden assemblages in waters to at least 70 m depth. Thus, for south-eastern Australia, these represent by far the most significant threat to biodiversity in the region, and the fish and fishery stocks that rely on the habitats at threat from urchin grazing.

In areas where lobsters are naturally common to abundant in this region, rebuilding lobster stocks represents the one most realistic potential management response, given that they are demonstrably the key urchin predator in this region, and management capacity exists by which fishing pressure can be altered. This capacity was recognised and identified by management agencies in our initial workshop (Appendix v), with initial stages of this response now under way in Tasmania with a move towards a regional quota for NE Tasmanian waters to allow a degree of stock rebuilding. Certainly the role that MPAs can play in this process is one that needs much further discussion, a need suggested in our discussion of objective 1 results. Ideally, following release of this report (and matching NARP reports) a follow-up workshop would be held to initiate this process. One topic of discussion is that any MPAs within this region, if intended to provide resilience to climate change and protect representative examples of habitats and species, need to have long-term protection if these benefits are to be realised. Our results have demonstrated that this resilience builds up over multi-decade scales, and does not happen immediately. Thus, an initial suggestion about the possibility that MPAs may be mobile and adjusted to meet changing biodiversity protection needs under a changing climate, now appears to be quite inappropriate, as long-term stability is the key requirement of MPAs if they are to be effective in a conservation role.

Given that there are spatially (bio-regionally) representative MPAs in NSW and Victoria that represent this region, and include approximately 5% of this coast in no-take MPAs, there needs to be ongoing discussion about what extent that this is appropriate for habitat and biodiversity conservation under climate change scenarios, an emerging management role for which they were not initially designed. This ultimately depends on if, and to what extent, off-reserve adaptive management strategies can address the necessary level of stock and size structure rebuilding necessary to ensure numbers are adequate to prevent significant loss of habitat. If such management is able to respond in a biologically meaningful way and in an appropriate time-frame, then the current MPA network (with exception for Tasmania where bioregional representation is incomplete) may be adequate for both protecting representative examples of diversity and in acting in a scientific reference role to allow for the ongoing evaluation of climate change impacts on a regional basis, and the extent that these interact with fishing related pressures. However, the message from this current work is clear, it takes significant rebuilding of both lobster abundances and population size structure before urchin numbers can be controlled. The recent manipulative studies of Ling and Johnson (2012) also indicate that prevention is much easier than cure, and that once barrens are established it takes greater lobster numbers to ultimately control them. Thus, there is a strong interaction between decisiveness and ecological response, and responses need to be soon and substantial.

Ultimately management responses need to balance the probability that off-reserve actions will be adequate for conservation purposes, and the costs of these, with the alternative strategy of increasing the extent of MPAs or similar spatially managed areas where rebuilding of lobster stocks is integral to also maintaining conservation values and outcomes. Studies such as ours, can identify the mechanisms underpinning biological changes, and the time frames involved, but cannot inform the ultimately social choices of which action is most appropriate, or what an optimal mix will be. Particularly when it is confounded by further interactions with abalone fishery productivity (as demonstrated here), and regional differences in the extent that lobster predation is likely to be the dominant control mechanism for *Centrostephanus*.

A specific recommendation arising from this is that given no-take areas are critical to untangling climate and fishing related interactions, and potentially other climate and human use interactions where these are able to be regulated by MPAs, future climate change monitoring programs need to incorporate MPA sites as an integral component. The regional distribution of the current MPA network in SE Australia provides an ideal framework of reference sites to compare changes occurring

more widely within each region, with these changes being recorded at nearby representative locations as part of the integrated MPA-based monitoring or more widely, as part of broader reef-health monitoring programs by state agencies or RLS. The value of this monitoring and the information it yields with respect to ecosystem function and resilience in the face of climate change will significantly increase through time as regional MPAs mature and natural processes become re-established. This value will also be significantly enhanced if regional gaps in the MPA network such as that in far NE Tasmania are filled, either by functional MPAs or specially established no-take reference areas for CC and wider ecosystem monitoring. Ultimately, a well-protected network of reference areas, coupled with routine monitoring that feeds back into an effective adaptive management framework should provide the best mechanism by which biodiversity and fishery productivity values are able to meet the challenges ahead.

□

Objective 4: To develop models that quantify and predict the impacts of climate change on inshore reef communities of fishes, invertebrates and macroalgae across the southeast Australian region so that potential responses to change can be identified, considered and developed appropriately.

This objective has been addressed from several perspectives in our attempts to develop appropriate modelling approaches to predicting future species distributions on temperate reefs throughout SE Australia.

One of these approaches, “thermal happiness” has been to examine the available data in the context of the identified thermal tolerances in a range of reef species based on both spatial and temporal datasets. This approach looks at both range/abundance expansions and contractions in response to varying thermal conditions, to identify the thermal window in which individual species are constrained ecologically. This approach is ongoing, undertaken by Maria Beger, and while not as yet at a stage to present here, will be developed into a formal publication throughout the year.

An alternative approach, pursued by Amanda Bates, has been to examine species distributions and abundance/latitudinal distribution range shape relationships and use these to predict likely future abundance and range relationships based on predicted changes in future temperatures. These predictions were based on a recent analysis by Oliver et al (2014) who predicted probable temperature scenario’s for coastal regions of SE Australia for the 2060’s and we used these to inform our initial predictions of likely future change as a basis for our discussion here. Figure 14 shows predicted thermal values by latitude in SE Australia and the current thermal distribution by latitude. Using this relationship, we can determine the equivalent latitude that corresponds to predicted future temperature values for a set of representative SE Australian latitudes and then extrapolate likely future abundances of a range of species for these. Clearly the analysis and interpretation presented here is simply a starting point for further work, refinement and discussion, as future predictions are likely to change with further information, as are our current species distributions, and indeed modelling approaches as this field matures.

Our initial model outputs are presented as Figures 15 and 17 for fishes and mobile invertebrates respectively. These species distribution models (SDMs) are based on general additive models with poisson smoothing and are derived from the underlying extensive RLS and LLTRPM abundance data presented as Figures 16 and 18 for completeness and to indicate the extent that each model is usually underpinned by extensive spatial survey effort. The modelled distributions had a broad variety of range distribution “shapes” and these clearly indicate the extent that a particular species may respond to temperature change at a particular location. Here we are basing this on the assumption, from the work presented in Chapter 1 and Appendix i, that species distributions will likely follow climate velocity, irrespective of their biological traits, and that their current distribution/abundance “shape” will remain the same.

For fishes (including sharks and rays), species such as the Toothbrush leatherjacket *Acanthaluteres vittiger* or Draughboard shark *Cephaloscyllium laticeps* (Figure 15) had ranges whose “peak” in abundance was currently predicted to be the south of Tasmania, so the model appears as a sharply truncated, steeply sloped line on the left. Similarly, some species were present in SE Australia in the tail of their distribution, but whose peak in abundance was predicted to be at lower latitudes than 15 degrees S, so had a similar right truncated distribution. In general, many of the typical temperate species had the majority of their distribution represented within the latitudinal range shown, although the shape of the curve varied widely between species, both in the extent of width of the central area of abundance, and to the extent that tails of distributions dropped off slowly or sharply. For example Yellowfin bream *Acanthopagrus australis* (Figure 15) had a broad distribution, with broad area of central abundance, yet truncated sharply at approximately 36 degrees S, whereas Blue warehou *Seriola lalandi* had a much sharper distribution, reflecting an exclusive Tasmanian distribution within our dataset. These distributions indicate that not only do species have individual thermal preferences, but also that their response to these is highly individual, and needs to be taken into account in and quantitative predictions of likely abundance in the future under climate change scenarios. A contrast to *S. lalandi* is the Common bullseye *Pempheris multiradiata*, a species with no clear “bell” shaped distribution, but rather a very long tail extending from southern Tasmania into central NSW with essentially a linear decline in abundance over this latitudinal scale.

A wide range of species are presented in Figures 15 to 18, primarily representing the subset of species encountered on surveys over the SE Australian region where species were either common (represented at more than 5 sites) or had moderate abundances at several sites, to the extent that they may be ecologically significant in some way. In that respect, some species are shown here for completeness although we recognise that they may be pelagic species which are stochastically encountered on transects as they pass (e.g. Jack Mackerel *Trachurus declivis*), or more soft-sediment or seagrass species that are occasionally encountered on reefs, or on sand or seagrass patches interspersed with the reef surveyed (e.g. Flathead *Platycephalus* species). Likewise, there may be latitudinally related changes in depth or habitat preference or habitat ecotones such as reef to seagrass that can influence apparent species distributions in our datasets, and these need to be accounted for carefully in any interpretation.

Keeping this in mind, the current curves were used to make predictions of future distributions and abundances based on the regional temperature predictions for the 2060's by Oliver et al. (2014) and matched with current latitudinal temperature relationships (Fig 14) to determine latitudinal equivalents to match with the models in Figures 15 and 17. The predictions are presented in Table 1 for fishes and Table 2 for the mobile invertebrates, and for a representative sample of species, as Figures 19 and 20 for fishes and invertebrates respectively. In the tables the modelled current abundances per transect (200m² for fishes and 50 m² for invertebrates) are shown at a wide range of representative latitudes, and this is contrasted with the predicted abundance of each species at a selected representative set of latitudes. The percentage that this represents an increase or decrease from current values at these latitudes is also shown in order to put many of these changes in perspective where this is possible (i.e. where a species currently exists or will remain within these latitudes). For a representative range of fish and invertebrate species, the current and predicted abundances (derived from the values listed in Tables 1 and 2) at a set of representative latitudes in the SE Australian region is shown to better illustrate common patterns of change.

For fishes, there are clearly many changes expected, and the changes for a number of example latitudes are shown in tables 1 and 2. While the models are capable of making predictions at any latitude and expected temperature change, we needed to present a case study for discussion and evaluation here. However, the models are available upon request for further evaluation by individual jurisdictions and management agencies and clearly can be used to make predictions against a range of alternative future temperature scenarios.

Not surprisingly, for fishes, our results (Table 1, Figure 19) indicate that there will be a general influx of species into the SE region, adding substantially to the overall diversity. However, in most cases this influx will be represented by low abundances of “new” species, such that they are unlikely to significantly alter ecosystem function. Examples include Western blue grouper *Achoerodus gouldii* and Eastern blue grouper *Achoerodus viridis* (Figure 19) which are both predicted to be present in Tasmanian waters, but at low abundances such as 2.1 per site (2000m²) at 40.5 S for *A. viridis* and 1.1 per site for *A. gouldii*. While this species was speculated to be a potential controlling predator for *Centrostephanus* urchins, these abundances will likely still be well short of that necessary to be effective in this role. Other similar species include Red morwong *Cheilodactylus fuscus* (Figure 19) and Crimson banded wrasse *Notolabrus gymnogenis* (Table 1) predicted to be present and at densities of 3.5 and 3.7 per site respectively. Some schooling planktivores are predicted to be present in moderate numbers, including Mado sweep *Atypichthys strigatus* and the Eastern hulafish *Trachinops taeniatus* (Figure 19) and Jack Mackerel *Trachurus novaezelandiae* (Table 1) at 208 and 51 individuals respectively, and that while unlikely to contribute to a significant functional shift in themselves, will be amongst the visually most conspicuous changes to the fish assemblages present.

As noted from the patterns currently observed at Maria Island (Chapter 1), one of the most marked changes that could result in a functional shift to local ecosystems may be in the abundance and biomass of herbivorous fishes. However, at 40.5 S for example, while herbivorous species are forecast to increase in number, none are likely to do so explosively. Many of these are unlikely to increase beyond a doubling of current values (Table 1, Figure 19) although increases in large-bodied species such as Rock Cale *Aplodactylus lophodon*, Ludderick *Girella tricuspidata*, Zebrafish *G. zebra*, Sydney drummer *Kyphosus sydneyanus* and Herring cale *Olisthops cyanomelas* will presumably result in a combined increase in total herbivorous biomass to a level that may impact on algal cover. More work is needed to convert these abundance predictions to biomass values and relate these to our current knowledge of consumption rates of such herbivours.

With warming, some species with southerly distributions are at risk of significantly declining in range and abundance, and perhaps becoming extinct. Our results flagged a number of these (100% or near, Table 1), although they represented a minor contribution to the overall assemblage. Several reflected artefacts of data collection rather than potential real losses through time, whereas others reflected the limited range of introduced species. For example the Variable triplefin *Forsterygion varium* is an introduced species restricted to SE Tasmania, and the Wide-bodied pipefish *Stigmatopora nigra* and the Barracouta *Thyrsites atun* (‘Couta’) represent common species that are rarely seen on transects, as they are not reef-resident species, and where they are, it is in geographically restricted locations rather than throughout their wider range. For *S. nigra* this is locations where seagrass abuts reef systems, and for *T. atun* this is where exposed, deep coastal water adjoins reef locations in southern Tasmania. Likewise, *Seriolella brama* and Southern garfish *Hyporhamphus melanochir* are mobile pelagic species that are more commonly found in Tasmanian reef surveys, thus influencing their apparent distribution. Although in the case of *S. brama* this distribution may well represent the central area of abundance of this species, and hence a potential major future decline.

Other species are intermediate in their level of confidence (Table 1), such as Jackass morwong *Nemadactylus macropterus*, (Figure 19) an epi-benthic species generally preferring deeper reef and sediment systems and Southern Sand Flathead *Platycephalus bassensis*, a sand associated species. In both cases, the results predict major declines in their abundance with warming, but their known distributions extend to around 35S and 30S respectively, so this decline may be relative to their sightings on shallow reef systems, rather than reflecting a more significant offshore range.

Other species predicted to have a major decline in this region (Table 1) include Red cod *Pseudophycis bachus*, Bearded cod *P. barbata*, Degens leatherjacket *Thamnaconus degeni*, Blotch-tailed trachinops *Trachinops caudimaculatus* (Figure 19), Banded stingaree *Urolophus cruciatus* and Red velvetfish *Gnathanacanthus goetzei*. Of these, the reef-resident cods *P. bachus* and *P. barbata* represent a likely significant contraction due to their conspicuous presence on reef systems during surveys.

Likewise, *T. caudimaculatus* is a highly conspicuous reef resident that is range restricted, and likely to undergo a major decline. The Red velvetfish *Gnathanacanthus goetzei* ranges across southern Australia, and into Tasmanian waters where it is most commonly encountered on reef surveys. The rarity of this species makes future predictions difficult to interpret, however as Tasmania represents the core region of the current abundance, future warming does present a major likely decline in the population of this species. The final species likely to show a major decline, if not overall loss is the Real bastard trumpeter *Mendosoma lineatum* (Table 1, Figure 19). In Australia, this species is only found in south eastern to south western Tasmania, and is rarely encountered except in selected habits adjacent to exposed headlands and islands. It was examined separately as it was only found at a small number of sites and therefore could not be appropriately modelled (but given its current range would be expected to become locally extinct under current our 2060's scenario). However, this species is also found in New Zealand, and would be expected to be under no threat in the cooler south Island waters.

Overall, for fishes, the likely changes to the fish assemblages in the SE region are likely to be substantial by the 2060's under our current future scenario. However, these changes relate more to alteration in overall levels of diversity and the relative abundance of many species, rather than major system shifts or loss of individual species. The potential loss of *M. lineatum* represents the most significant "impact" to the Tasmanian fish fauna from the perspective of biodiversity values, although countered by the species likely survival in New Zealand where it is also found. Our results reflect patterns for the subset of shallow reef associated or incidental pelagic or benthic species encountered on dive surveys only, and not more broadly for the SE Australian fish fauna. In that sense they are indicative of overall patterns of change, but not a complete review of likely changes in the region. For example several handfish species, rare and endemic to SE Tasmania have never been detected on our surveys so are not discussed here, yet clearly these species will be highly endangered by future warming scenarios and will likely become extinct without intervention.

For the mobile invertebrates, the results from a wide range of species are presented in Figures 17 and 18 to make the widest amount of current information available for interpretation and discussion of likely key species to focus on in future analysis, in monitoring and for reporting. In that sense many of these species will not be discussed further here, other than for their general contribution to biodiversity values. As with the fish surveys, many species are encountered on biodiversity related dive surveys, however few of these are abundant enough to play a significant functional role in the reef ecosystems of which they are part, with the majority present a only one or two individuals per site. They do contribute to overall diversity values though, and as for fish, the general trend was for an increase in overall diversity in the Tasmanian region with future warming (Table 2).

Most species predicted in the modelling to have 100% declines or similar within the Tasmanian sector, were found to be introduced species (Table 2). These include the Seven arm seastar *Astrostele scaber*, *Metacarcinus novaezelandiae*, Pie crust crab *Maoricolpus roseus* and European shore crab *Carcinus maenas*, species which either have their current core distribution in Tasmania due to introduction there or have increased rapidly there following recent invasion (in the case of *Carcinus maenus*). The additional species were the triton *Sassia subdistorta*, Pencil urchin *Goniocidaris tubaria* and the top shell *Clanaculus undatus*. In the first two species this pattern may be more related to species identification than a real pattern, and for *Clanaculus*, this may relate to the small size of this species, which means it may not be included in all surveys due to minimum size cut offs. There is no indication that any of these species should decline by 100% in Tasmanian waters based on their more widespread distribution.

From an ecological perspective there are a number of species predicted to undergo sufficient change to alter community structure and system function. Clearly the one of most concern is the abundance of *Centrostephanus rodgersii* given its capacity to form urchin barrens. The predictions suggested that in

NE Tasmania numbers were expected to double on average per site (Table 2, Figure 20), increasing from 31 per site by an additional 28. Even in far SE Tasmania at 43.5 S, numbers were predicted to increase from near zero to 49 per site. Given that barrens are forming currently in SE Tasmania, these predictions would suggest the same may be expected to extent throughout all Tasmanian waters by the 2060's in suitable habitats.

This increase will be somewhat counter balanced in Tasmanian waters by a 20-30% decline in the Common urchin *Heliocidaris erythrogramma* (Figure 20), species numerically dominant at many sites,, although there is often little overlap in habitat between these urchin species as *Heliocidaris erythrogramma* prefers more sheltered habitats than *Centrostephanus*. Compounding the increase in *Centrostephanus* is a predicted 35-53% decline in its main predator, the Southern rock lobster *Jasus edwardsii*, from NE to southern Tasmania (Figure 20). This decline will not only influence the extent that *Centrostephanus* can be contained by adaptive management measures, but it will also have clear fishery management implications in general. Again, counter balancing the decline of *Jasus edwardsii* will be an increase in the Eastern rock lobster *Jasus verreauxii*, although at southern latitudes, not at similar levels to numerically compensate for the decline in southern rock lobsters (Figure 20). At 39.5S the increase in *Jasus verreauxii* is predicted to be close to the predicted decline in *Jasus edwardsii*, so there is the possibility of some ecological replacement occurring, at least on deeper reefs given the described preference of *J. verreauxii* for such habitat. This effectiveness of this replacement will also depend on the extent that the rapid growth rate of *J. edwardsii* is matched by *J. verreauxii* at the southern end of its range.

Significant changes in the filter feeding Southern featerstar *Comanthus trichoptera* are also expected, with this species declining by up to 50% in the NE (Table 2, Figure 20). While the ecological role of this numerically abundant species is not clear, this decline represents a significant alteration to the abundance weighted diversity of these systems. Another species expected to change substantially is the Tall-ribbed limpet *Patelloida alticostata* which is numerically very dominant in the central portion of its range in NSW. This range is expected to extend into NE Tasmania with abundances up to 14000 per site (200m²), typical densities found in *Centrostephanus* barrens within its range. This species is a grazer that is likely dependent on initial *Centrostephanus* barren formation, but then applies additional and significant grazing pressure on turfing and encrusting algae. It is also likely to help maintain barrens in areas once they are established, adding additional hysteresis to the potential to restore barrens back to vegetated areas once established.

The final expected changes of some significant interest to resource management are the likely increase in abalone and calamari squid numbers throughout the Tasmanian region (Figure 20). The Greenlip abalone *Haliotis laevis* is predicted to extend to southern Tasmania in moderate numbers (clearly subject to habitat availability), while *H. rubra* is also predicted to increase, at least based on current distribution models. The extent to which that will be modified by loss of habitat through barren formation is yet to be determined, however the possibility that abalone fisheries may not be adversely impacted is one source of optimism for the future of Tasmanian fisheries (ignoring growth rate/temperature interactions). An additional source of optimism is likely increases in the abundance of calamari squid *Sepioteuthis australis* which is expected to increase markedly, including a range extension into the far south of Tasmania.

Overall, for mobile invertebrates, the likely changes to their assemblages in the SE region are likely to be substantial by the 2060's under our current future scenario. Unlike the fish assemblages however, these changes relate to not only to alteration in overall levels of diversity and the relative abundance of many species, but also to major system shifts, most notably mediated by significant increases and extended range of *Centrostephanus*, and the expected decline of its key predator, the lobster *Jasus edwardsii*. This will be further mediated by a large increase in the abundance of the limpet *Patelloida alticostata* which may add to the stability of barrens by grazing the turfing algae that replace the algal canopy.

As for the fish predictions, these results are indicative of overall patterns of change, but not a complete review of likely changes in the region. Despite not finding any invertebrate species at likely risk of extinction in Tasmanian waters, this does not mean there are not any. There are for example, a number of seastars endemic to SE Tasmania that are found in the intertidal zone and therefore not recorded from our subtidally focussed surveys. Like the endemic fish, these species will be highly endangered by future warming scenarios and will likely become extinct without intervention.

For the combined fish and invertebrate analysis, our analysis did not extend to developing qualitative/conceptual models of the strength of species interactions that are likely to occur, based on the numerical predictions of changes in abundance made in this study. However, our work does provide the groundwork necessary to inform this next stage, or indeed more quantitative ecosystem models developed for reef systems in this region. Such models would ideally incorporate estimates of biomass level changes in factors such as trophic levels of fish (from herbivores to urchin predators) as well as growth rates of key species to determine the time frames under which species such as lobsters or blue grouper can transition to sizes capable of consuming large urchins.

Finally, the results presented here do need to be interpreted carefully, due to sampling artefacts and the necessary assumptions made in model-based predictions. However, they provide a first attempt at examining such patterns in this region, and a starting point for further development and refinement. They also provide a reference to guide further discussions on whether future sampling should target individual indicator species, and the extent that monitoring effort in the form of replication and spatially distributed sampling is needed to do this. There is no specific recommendation here as to appropriate “indicator species”, with instead, the combined data utilised in analysis presented in order for future discussions to determine the most appropriate path. Clearly information on the key ecosystem driving species will be critical, such that robust information on urchin, lobster, and top predatory fishes will be a central part of this. As discussed in previous chapters, the current monitoring framework in many of the temperate states is appropriate for providing this information, as is the use of RLS style surveys to fill in geographical gaps not otherwise able to be filled by state-based monitoring programs. The analysis and modelling presented here relied heavily on RLS surveys to fill in the tails and even central portions of the range of many species, and this would not have been possible without this data. However, there are still many species where the information is still inadequate to make confident predictions, and this can only be informed by additional targeted surveys across the range of these species, coupled with refinement of modelling approaches to maximise the accuracy of predictions based on this data.

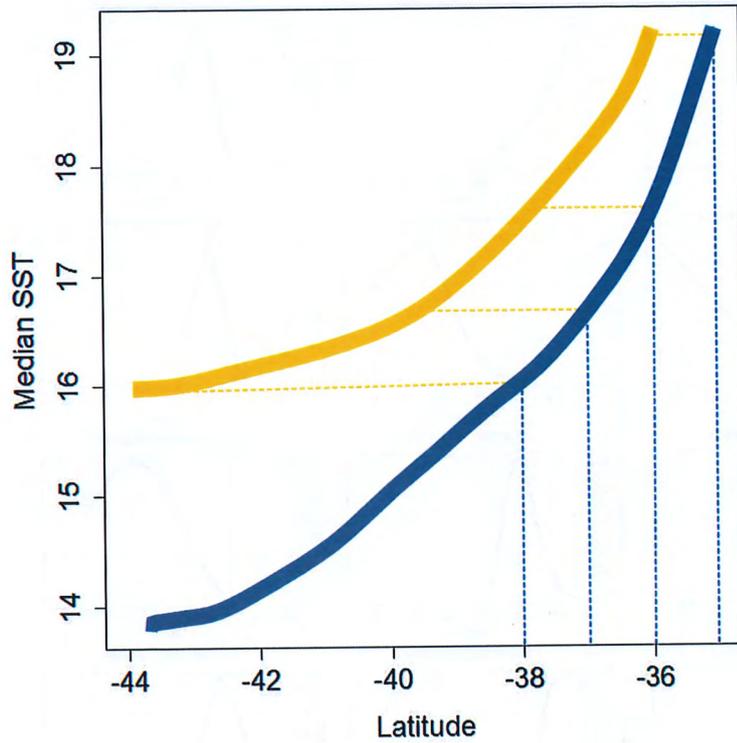


Figure 14. Matching current SST and future (2060's) predicted SST for inshore regions of SE Australia based on Oliver et al. (2014) and used to derive species future latitudinal (thermal) relationships based on current latitudinal (thermal) relationships.

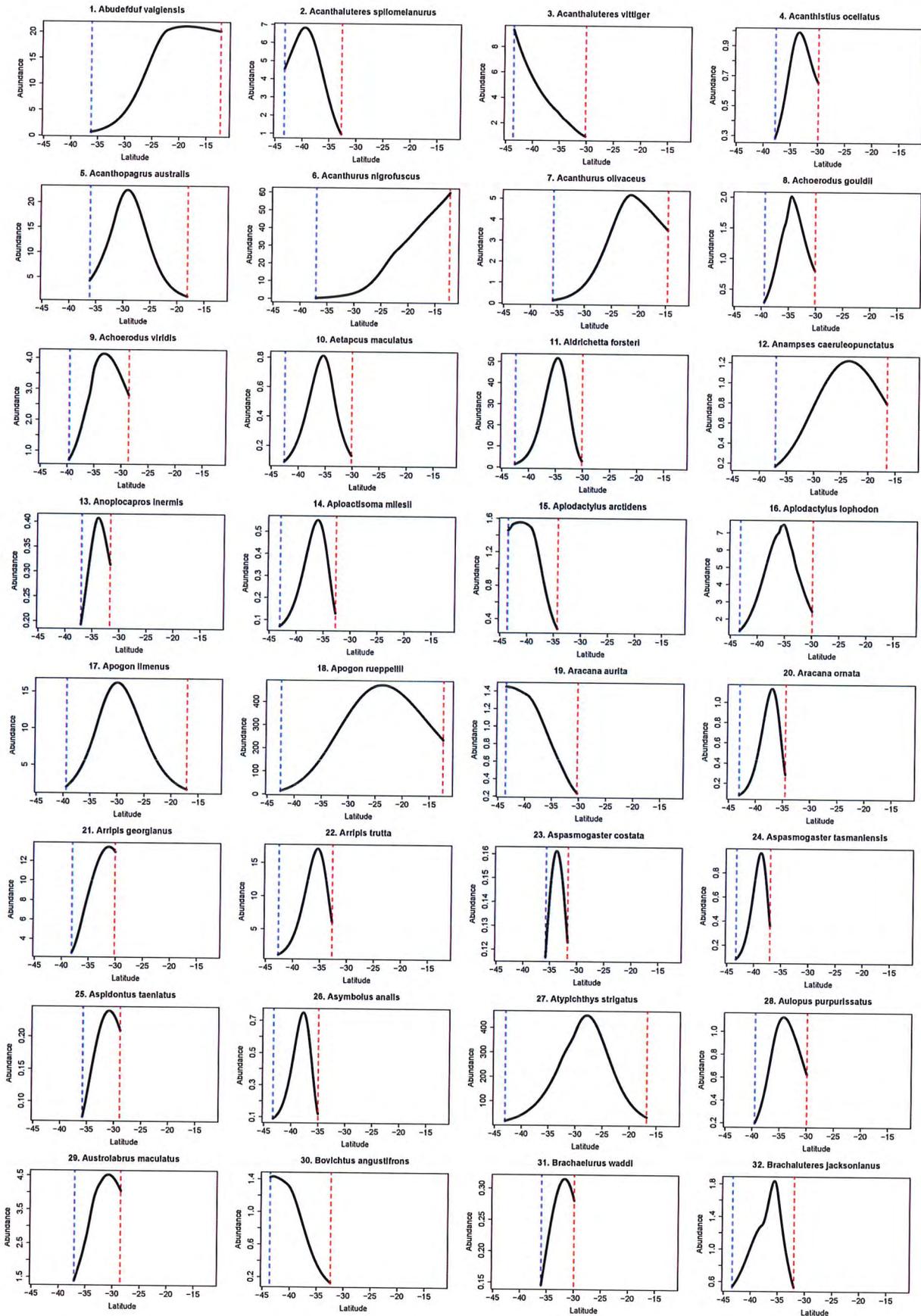


Figure 15. Modelled species distributions of fishes with a SE Australian range ($n/500m^2$). Models are derived from quantitative LTRMP data and RLS data at sites distributed over the latitudinal range.

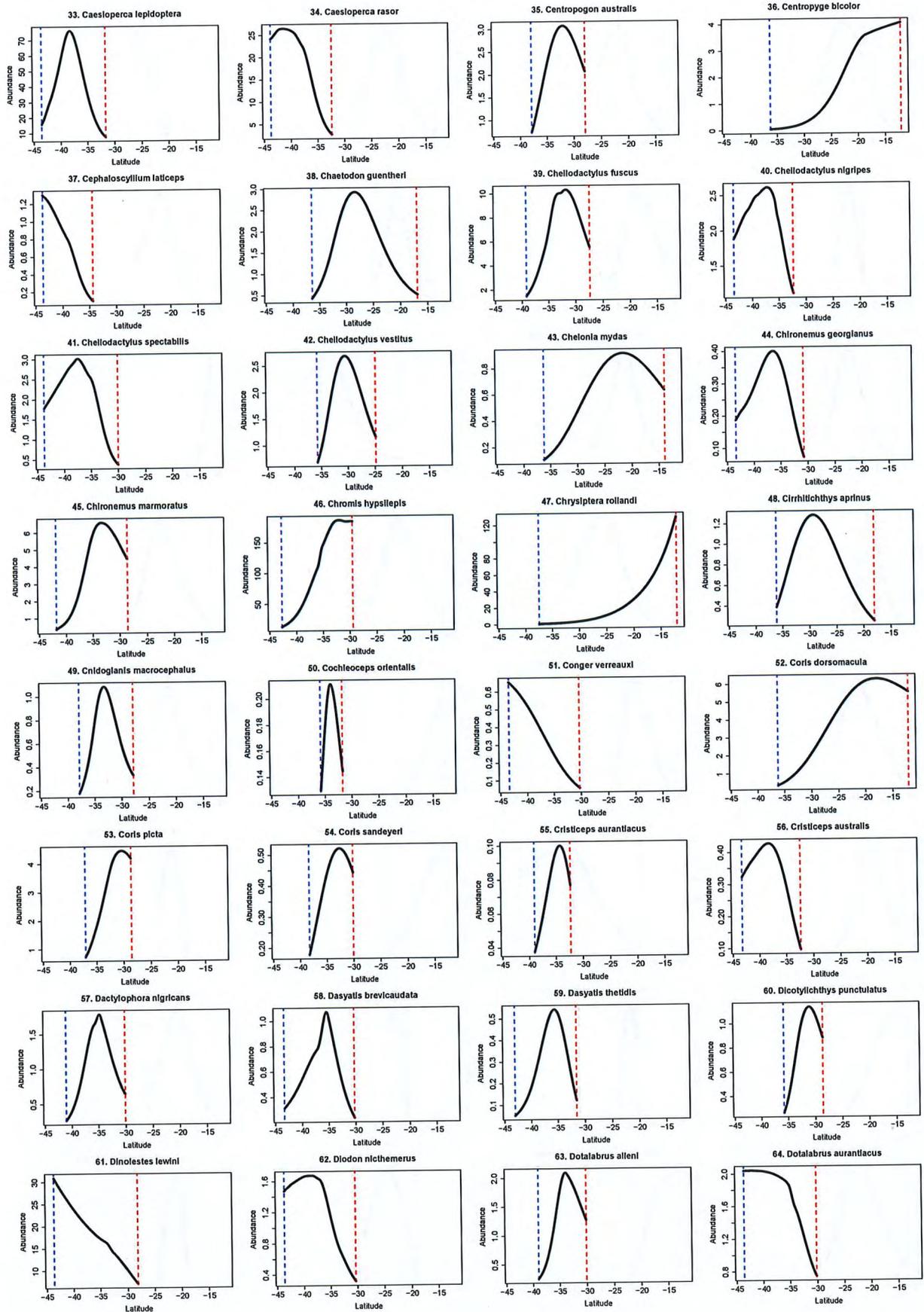


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range (n/500m²).

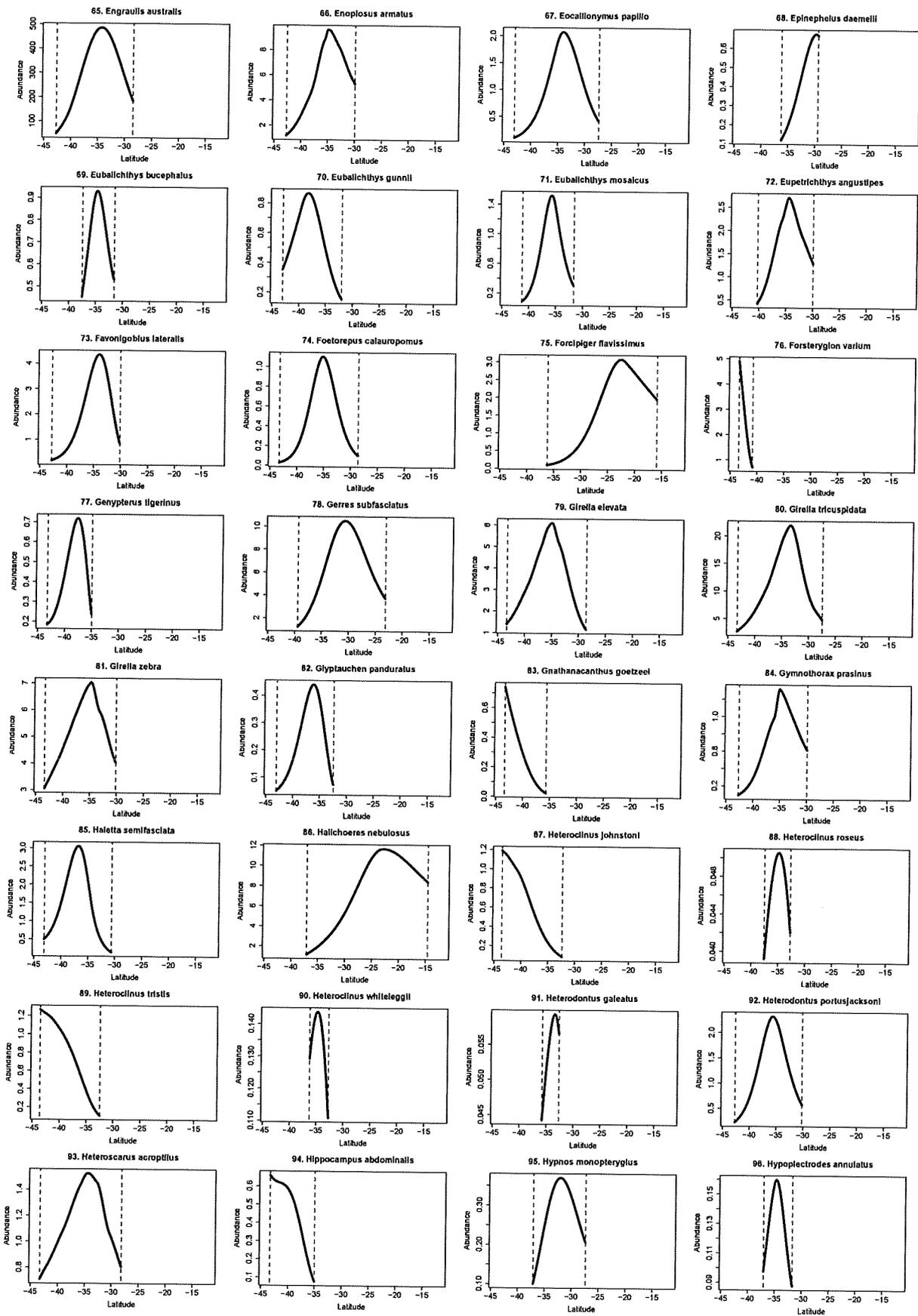


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range (n/500m²).

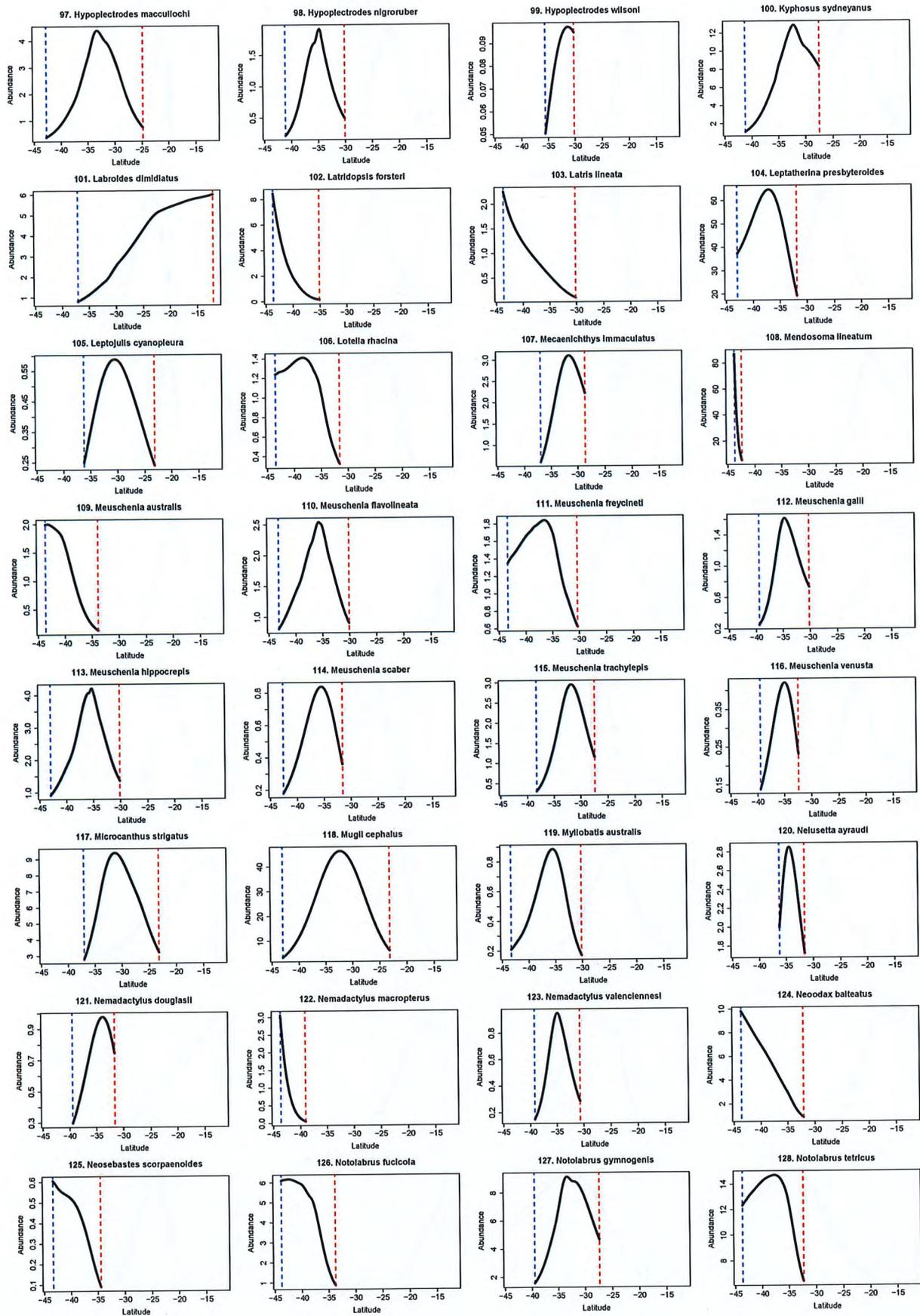


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range (n/500m²).

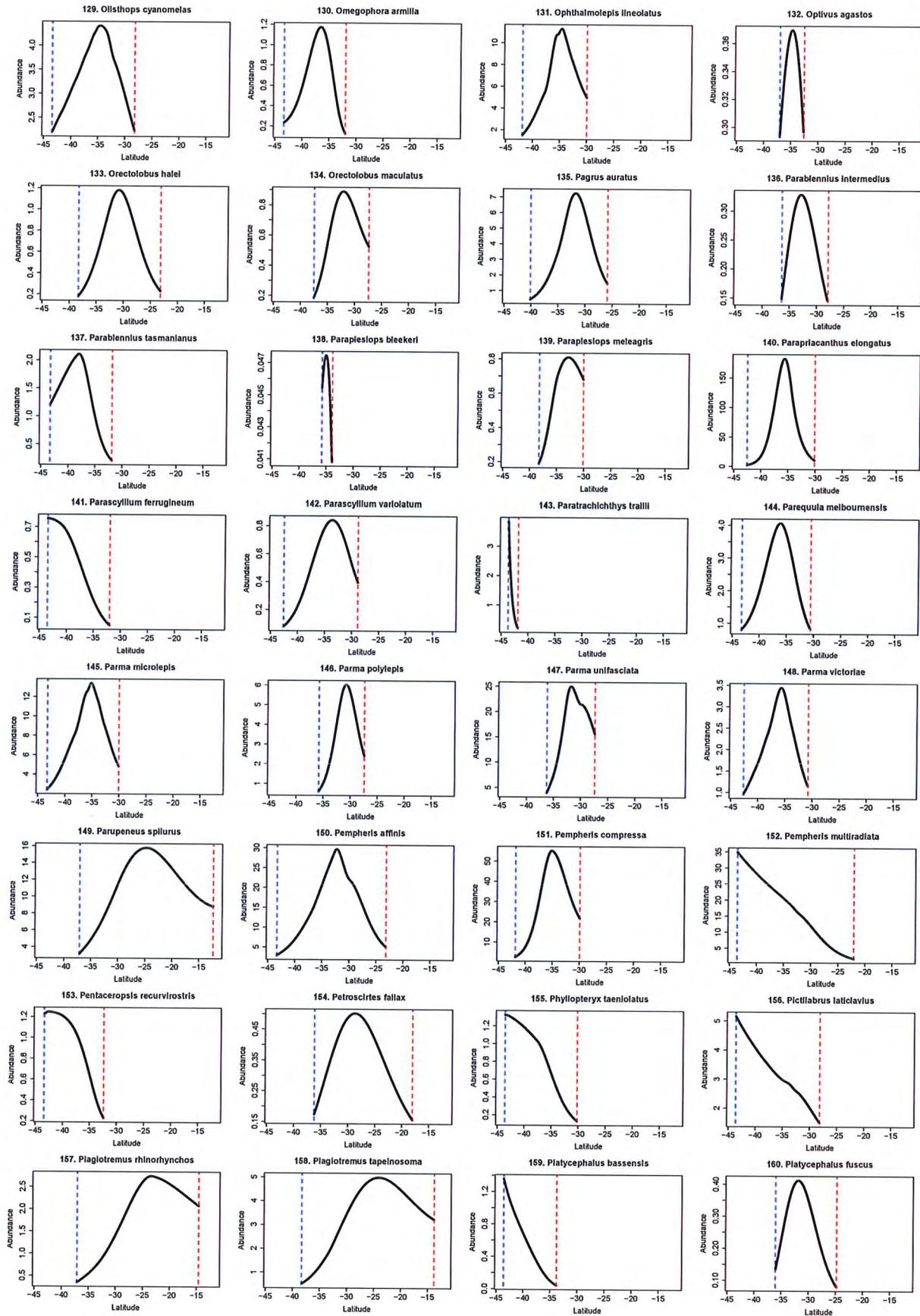


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range ($n/500m^2$).

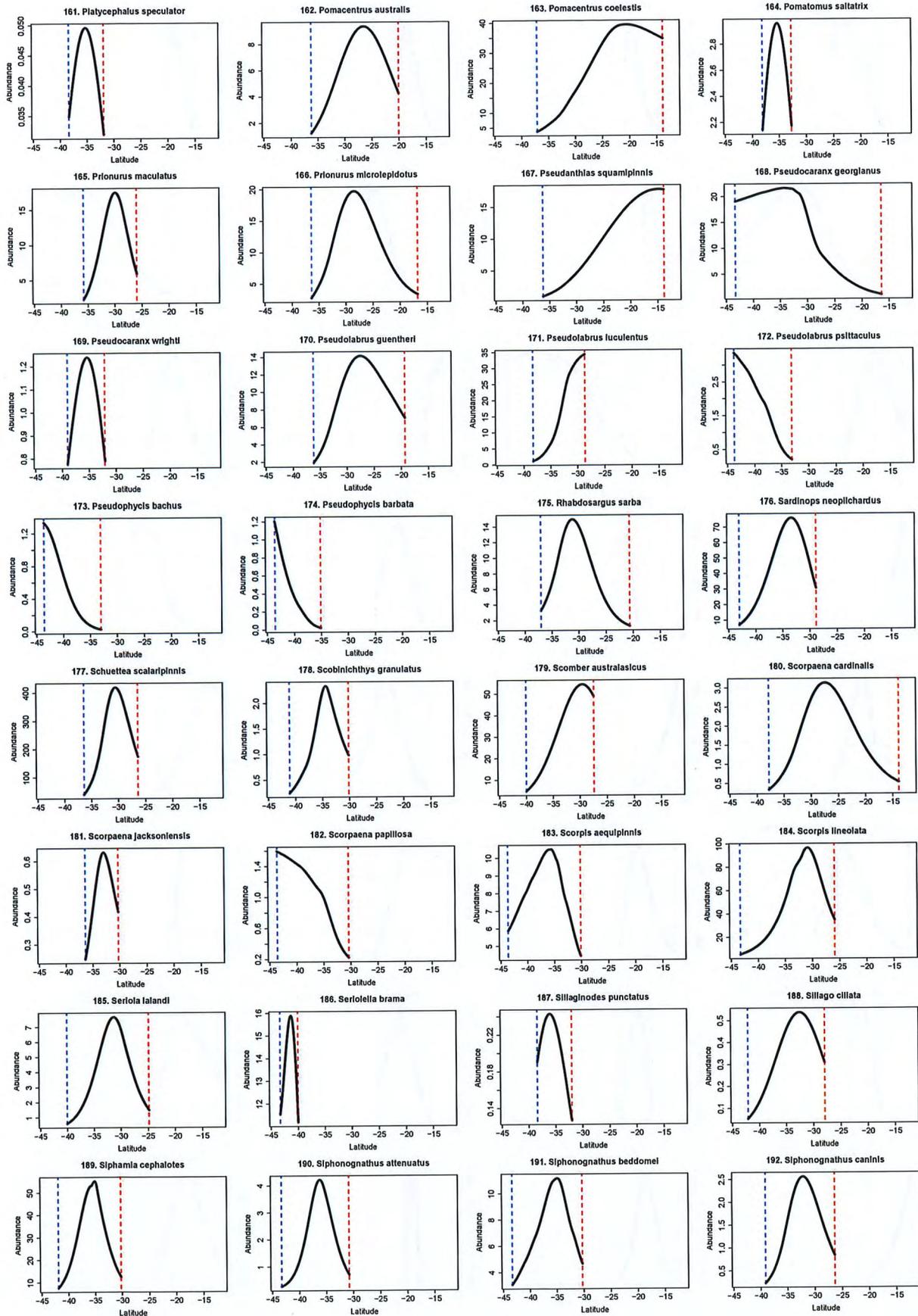


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range ($n/500m^2$).

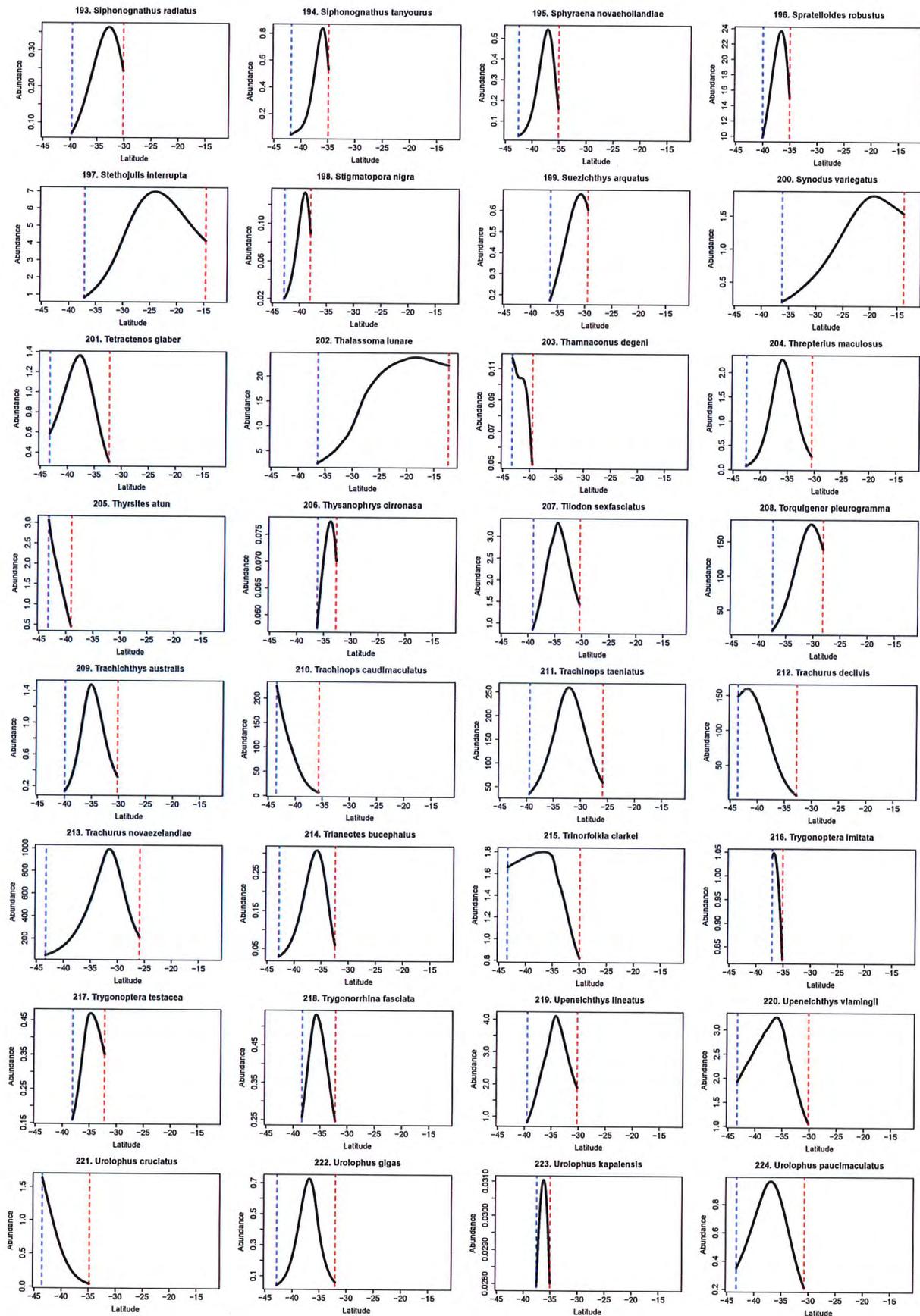


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range (n/500m2).

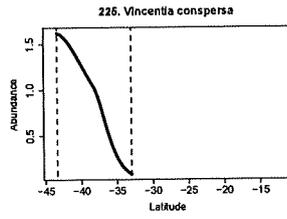


Figure 15 (Cont.). Modelled species distributions of fishes with a SE Australian range (n/500m²).

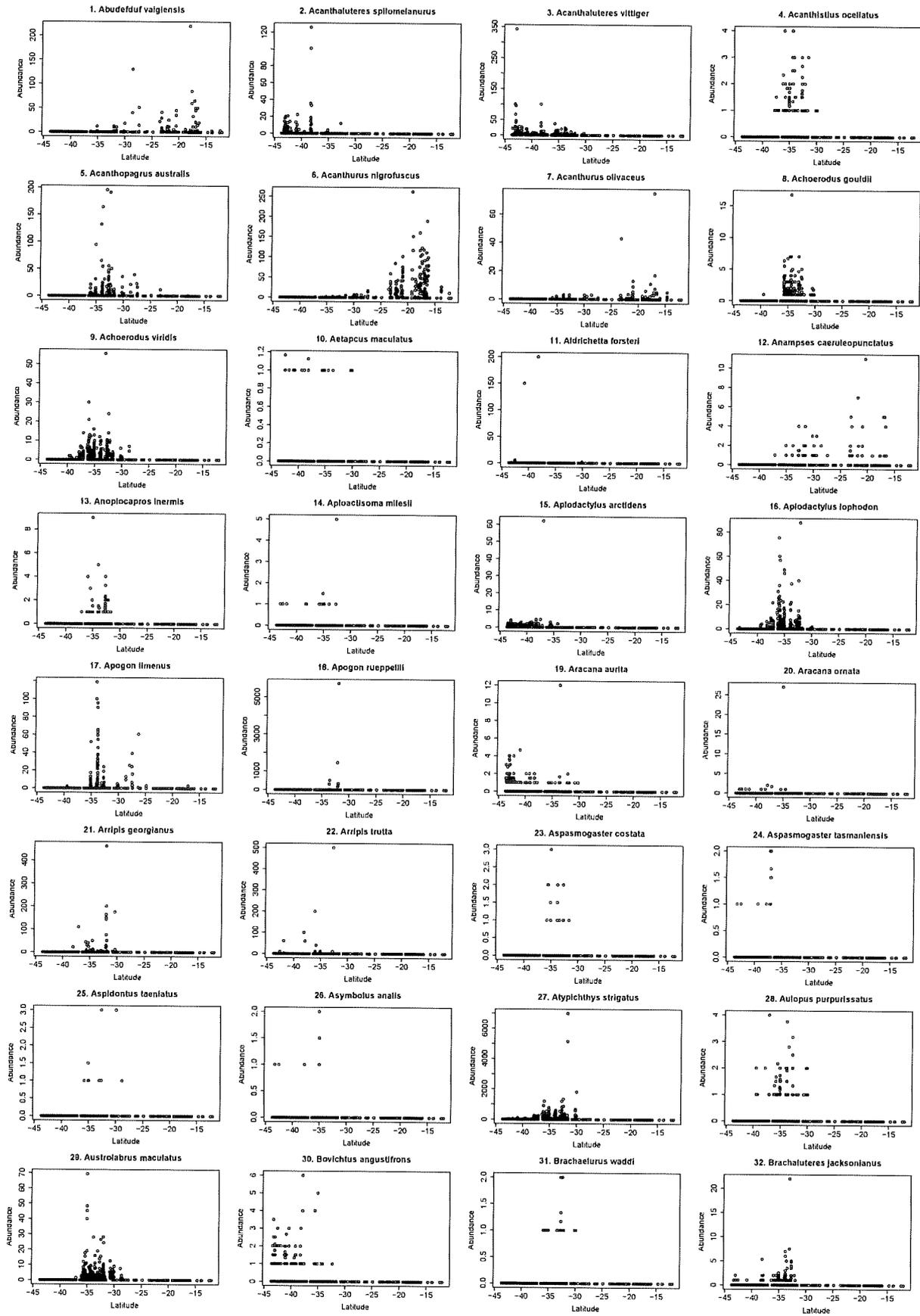


Figure 16. Fish abundance records by Latitude & site ($n/500m^2$) from LTPMP and RLS data.

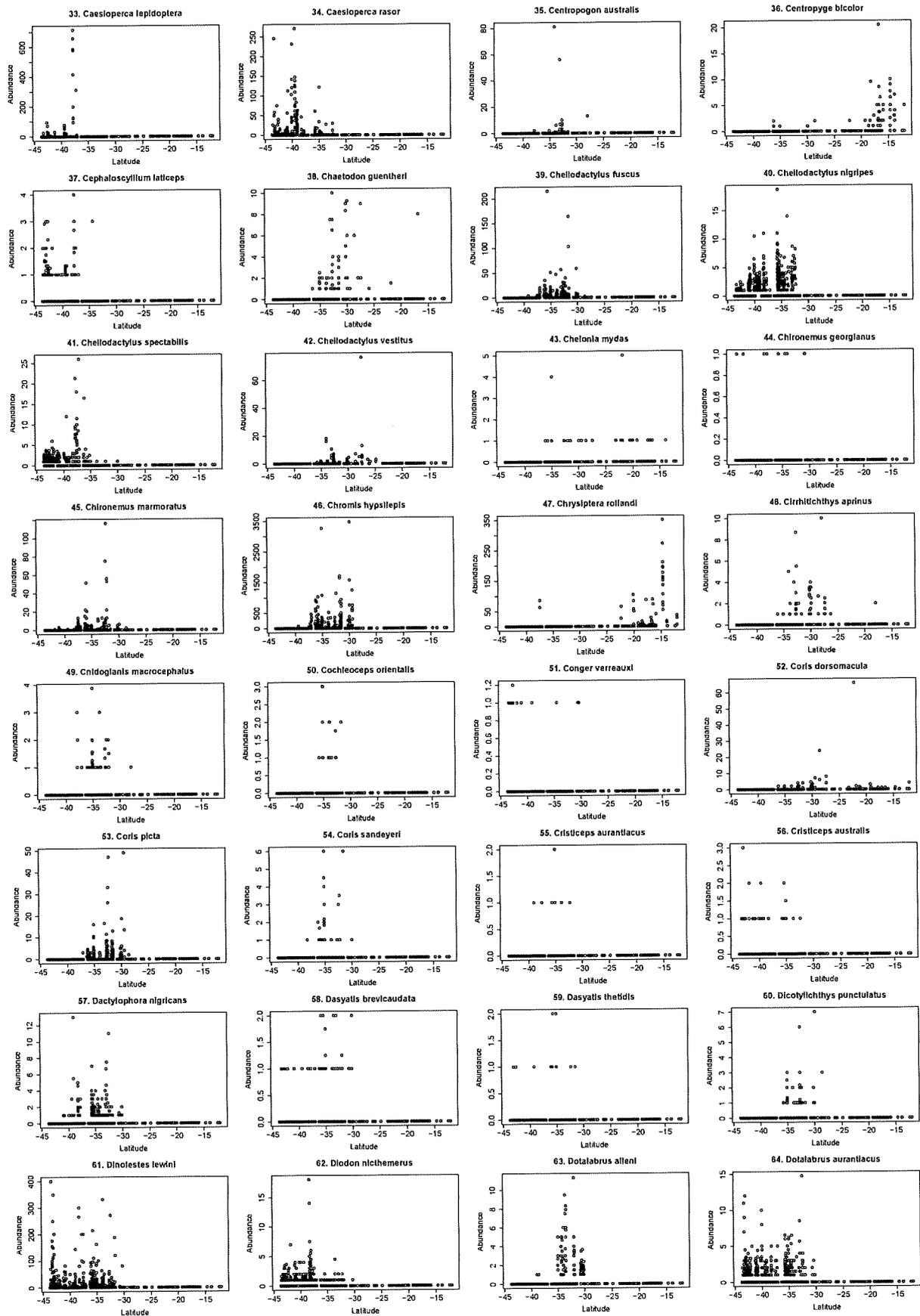


Figure 16 (Cont.). Fish abundance records by Lat. & site ($n/500m^2$) from LTPMP and RLS data.

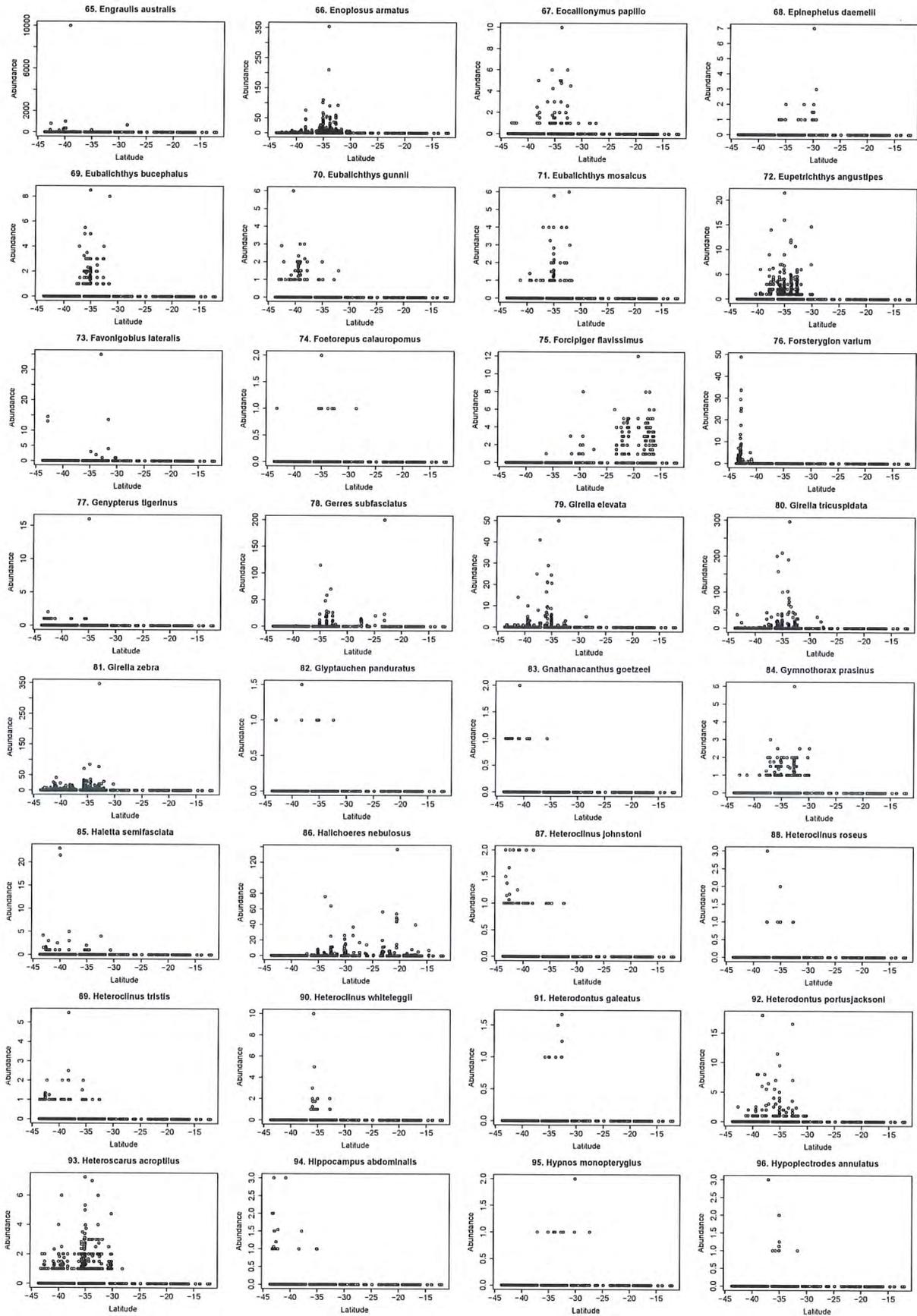


Figure 16 (Cont.). Fish abundance records by Lat. & site (n/500m²) from LTPMP and RLS data.

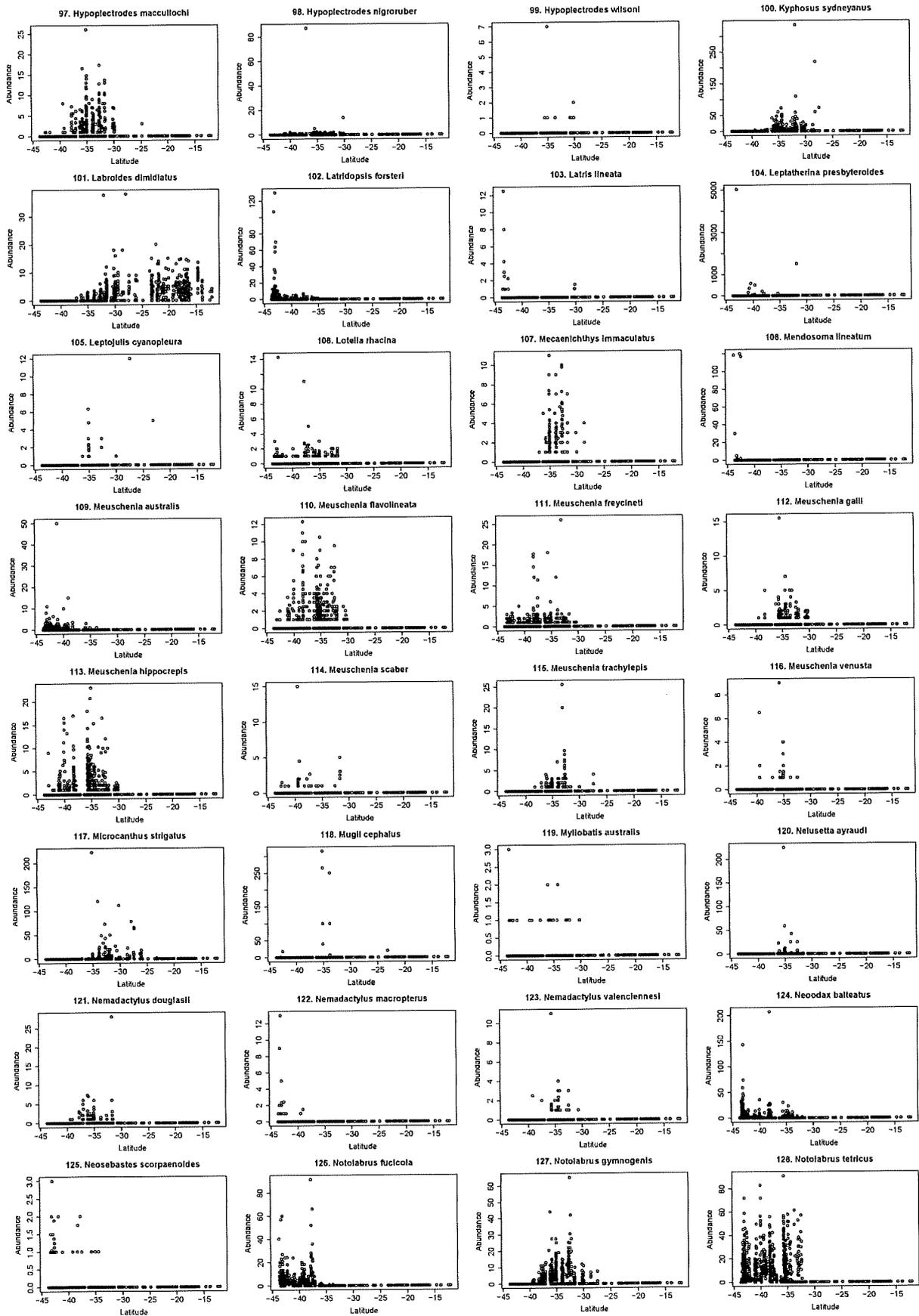


Figure 16 (Cont.). Fish abundance records by Lat. & site (n/500m²) from LTPMP and RLS data.

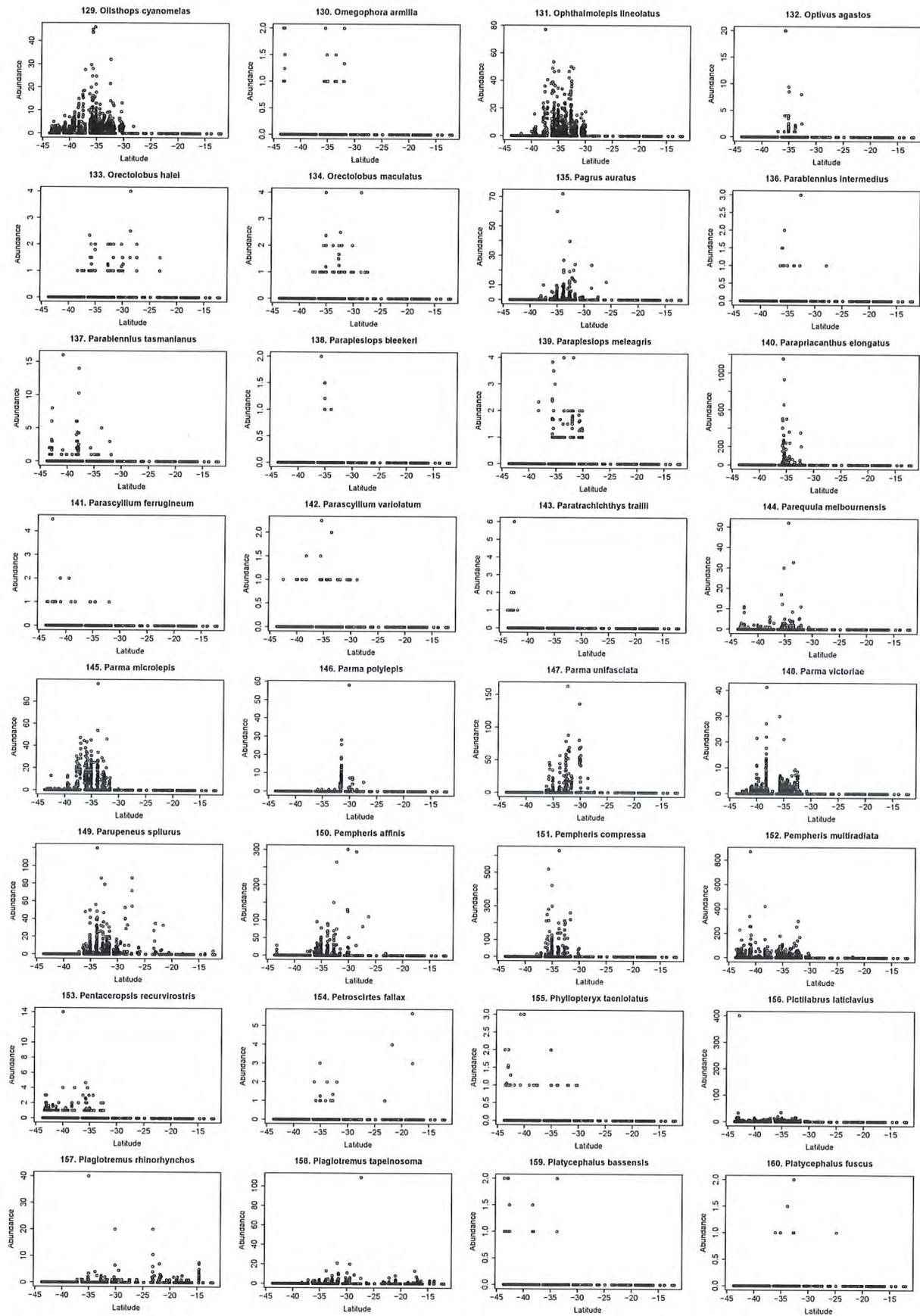


Figure 16 (Cont.). Fish abundance records by Lat. & site (n/500m²) from LTPMP and RLS data.

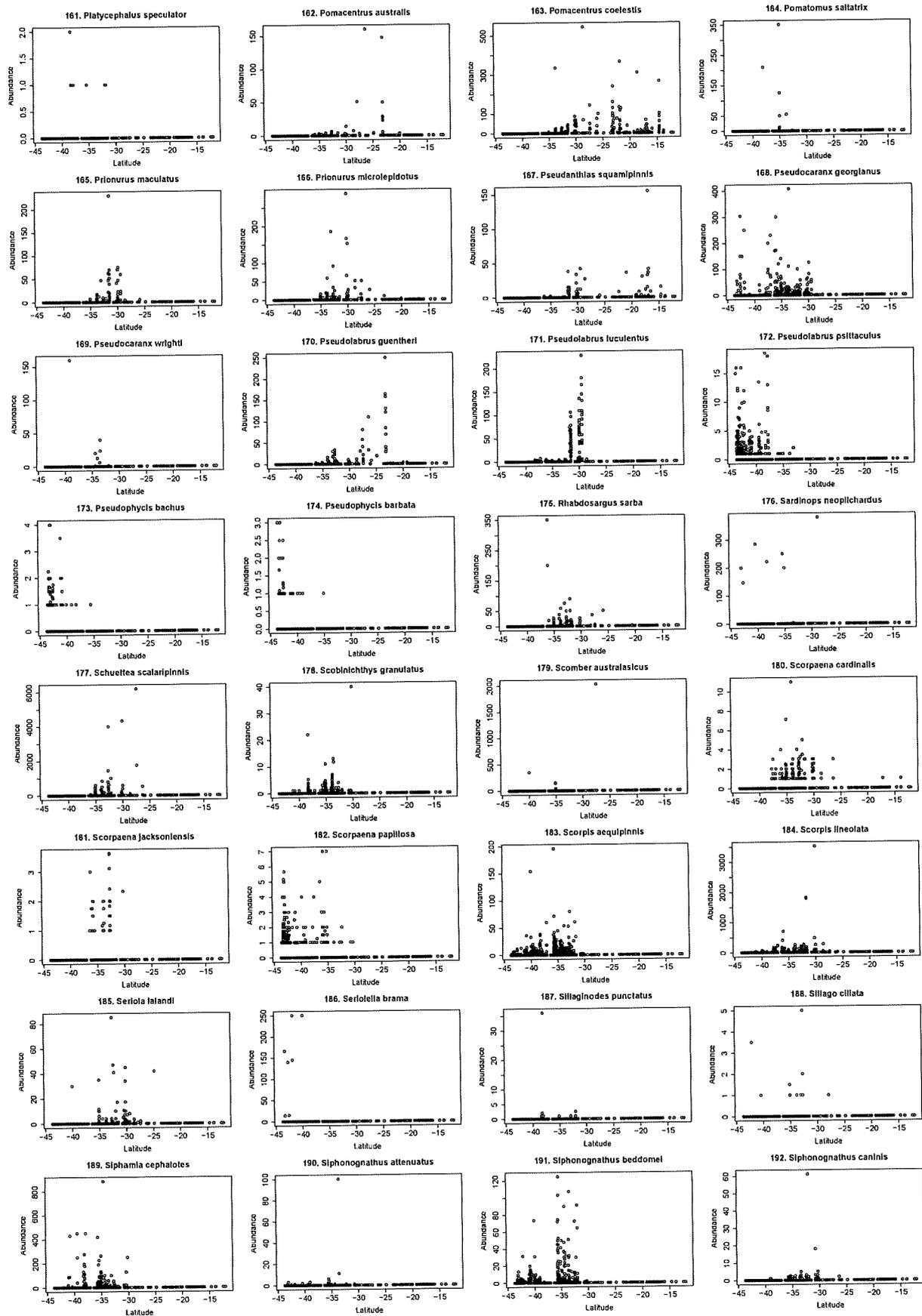


Figure 16 (Cont.). Fish abundance records by Lat. & site ($n/500m^2$) from LTPMP and RLS data.

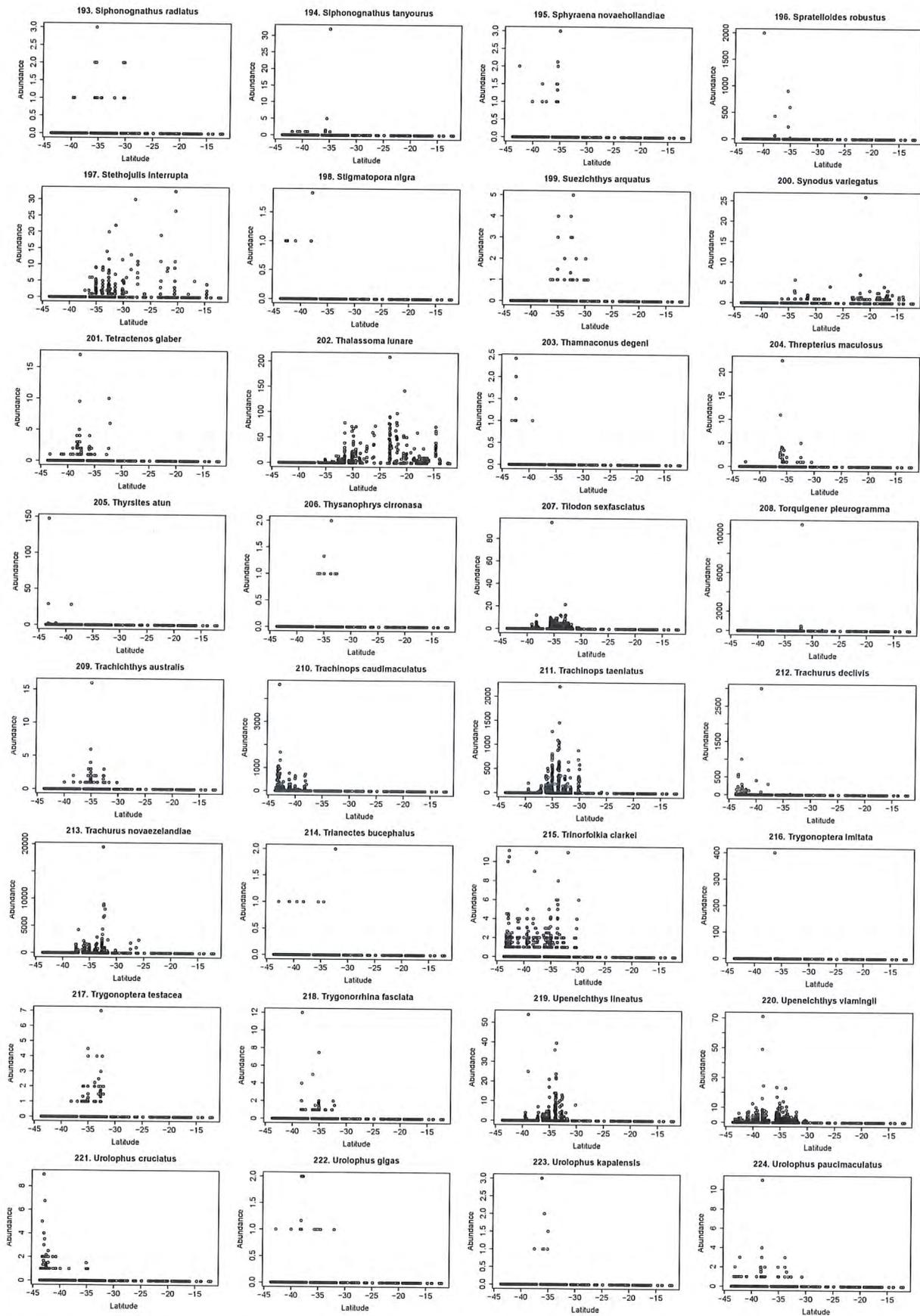


Figure 16 (Cont.). Fish abundance records by Lat. & site (n/500m²) from LTPMP and RLS data.

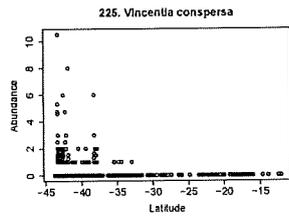


Figure 16 (Cont.). Fish abundance records by Lat. & site (n/500m²) from LTPMP and RLS data.

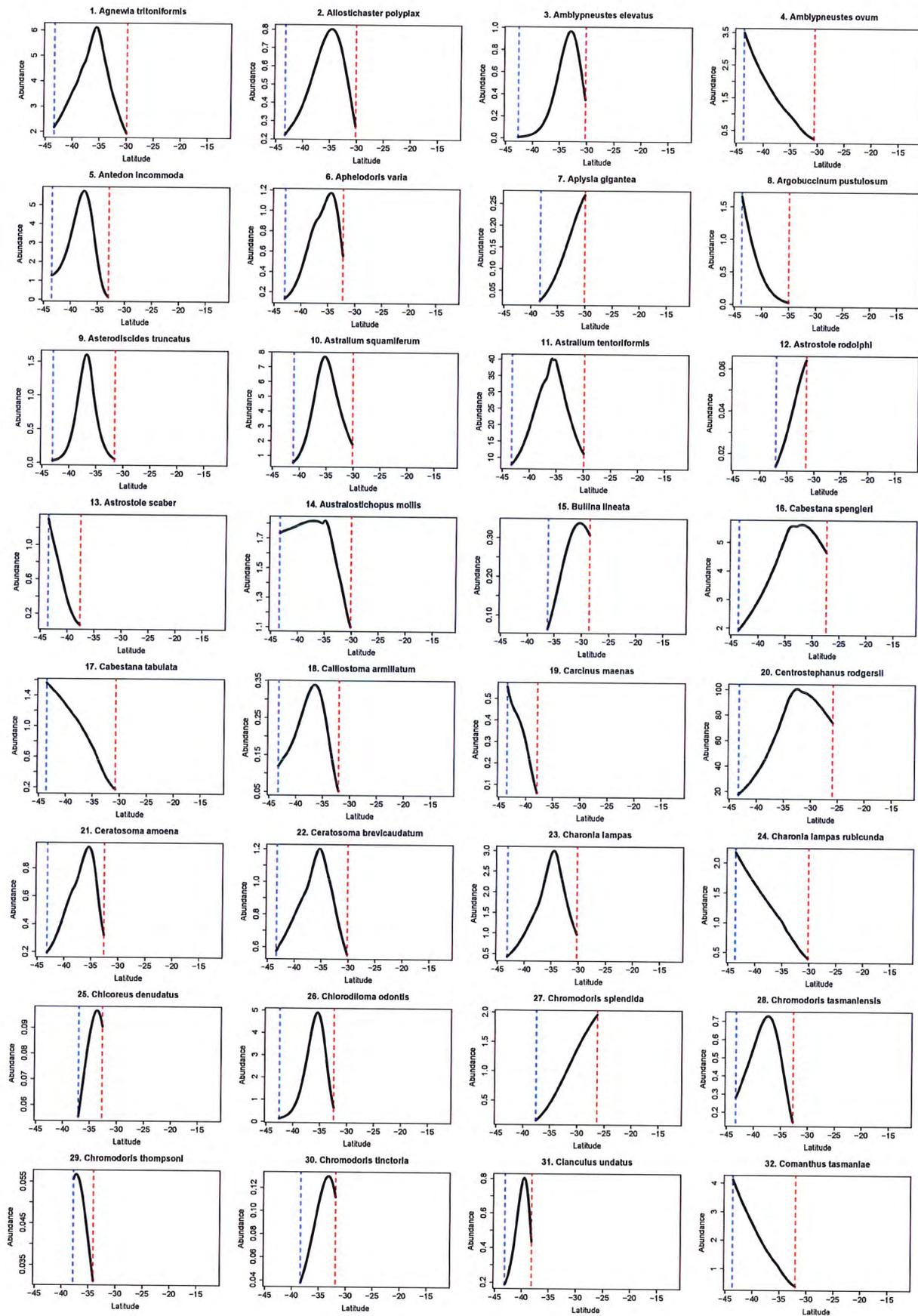


Figure 17. Modelled species distributions of mobile invertebrates with a SE Aust. range ($n/50m^2$).

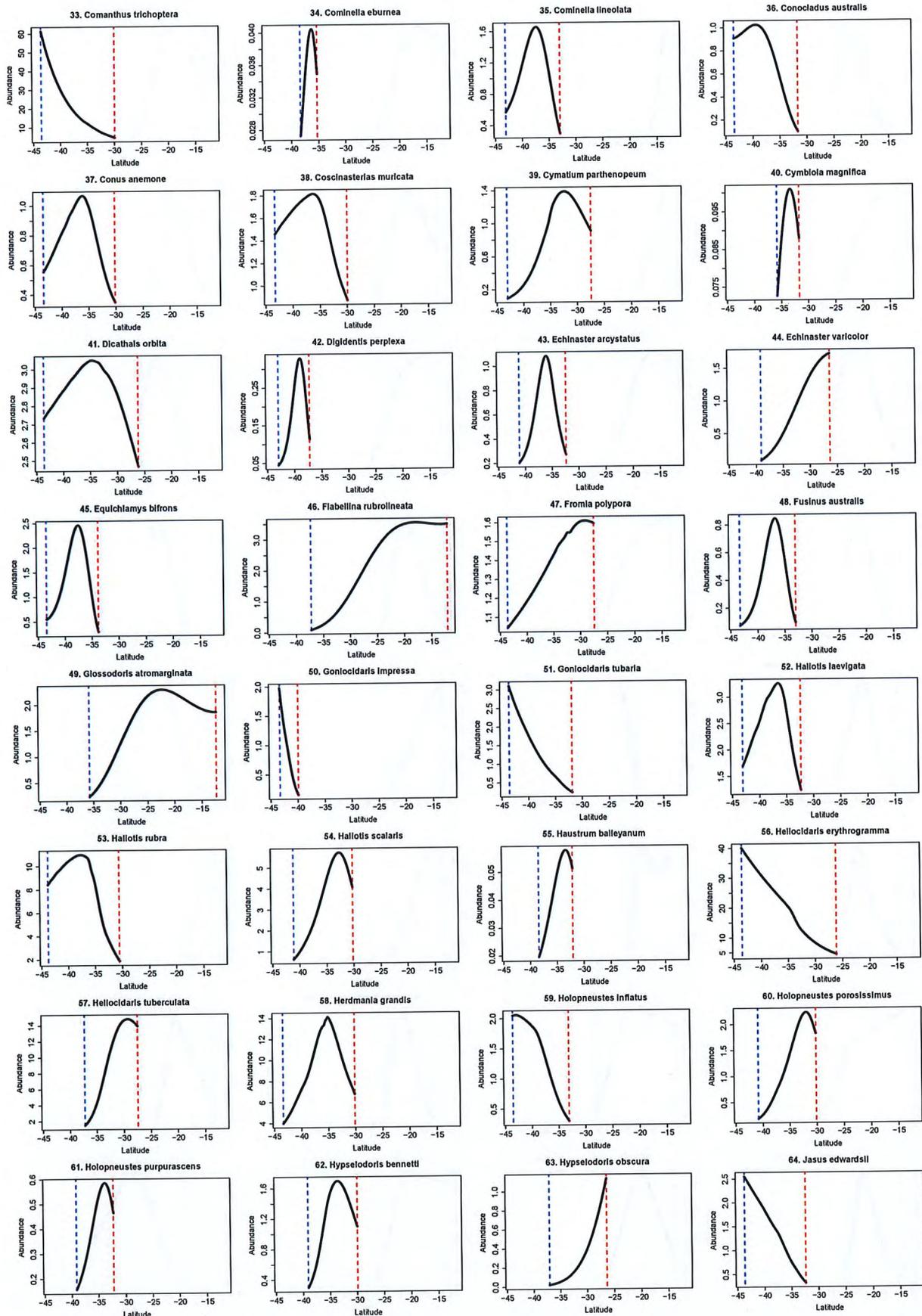


Figure 17 (Cont.). Modelled species distributions of mobile inverts with a SE Aust. range ($n/50m^2$).

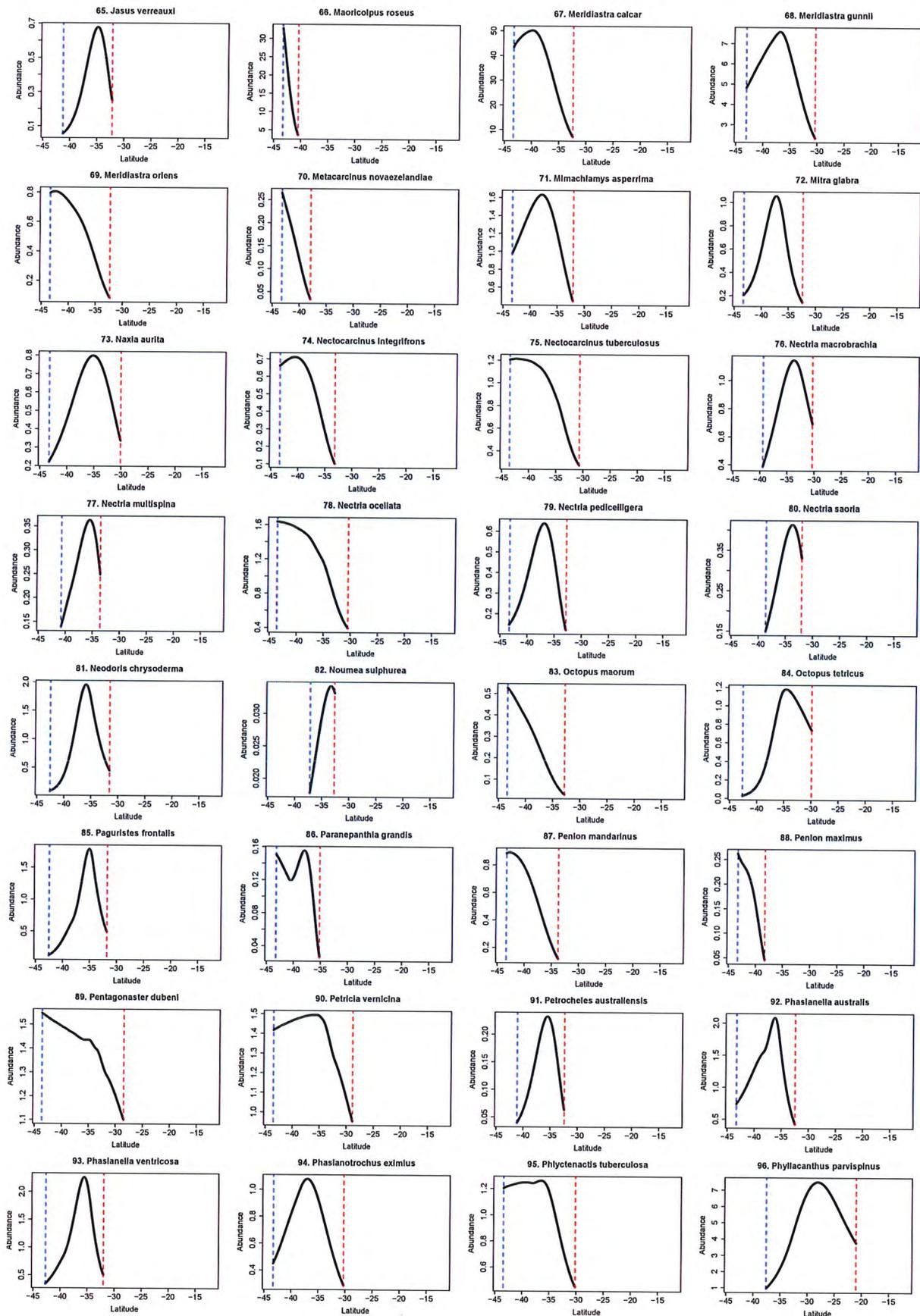


Figure 17(Cont.). Modelled species distributions of mobile inverts with potential SE Australian range.

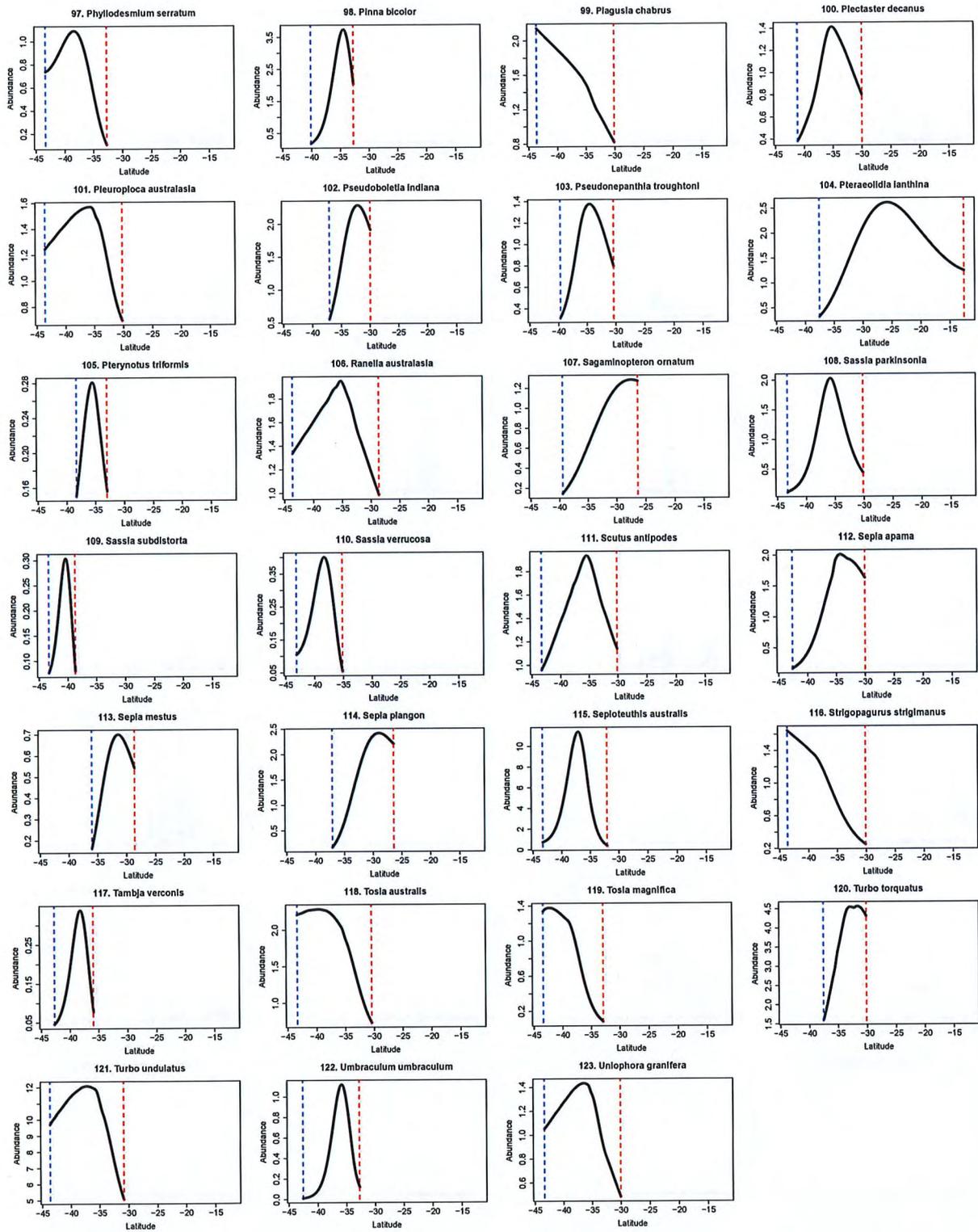


Figure 17(Cont.). Modelled species distributions of mobile inverts with potential SE Australian range.

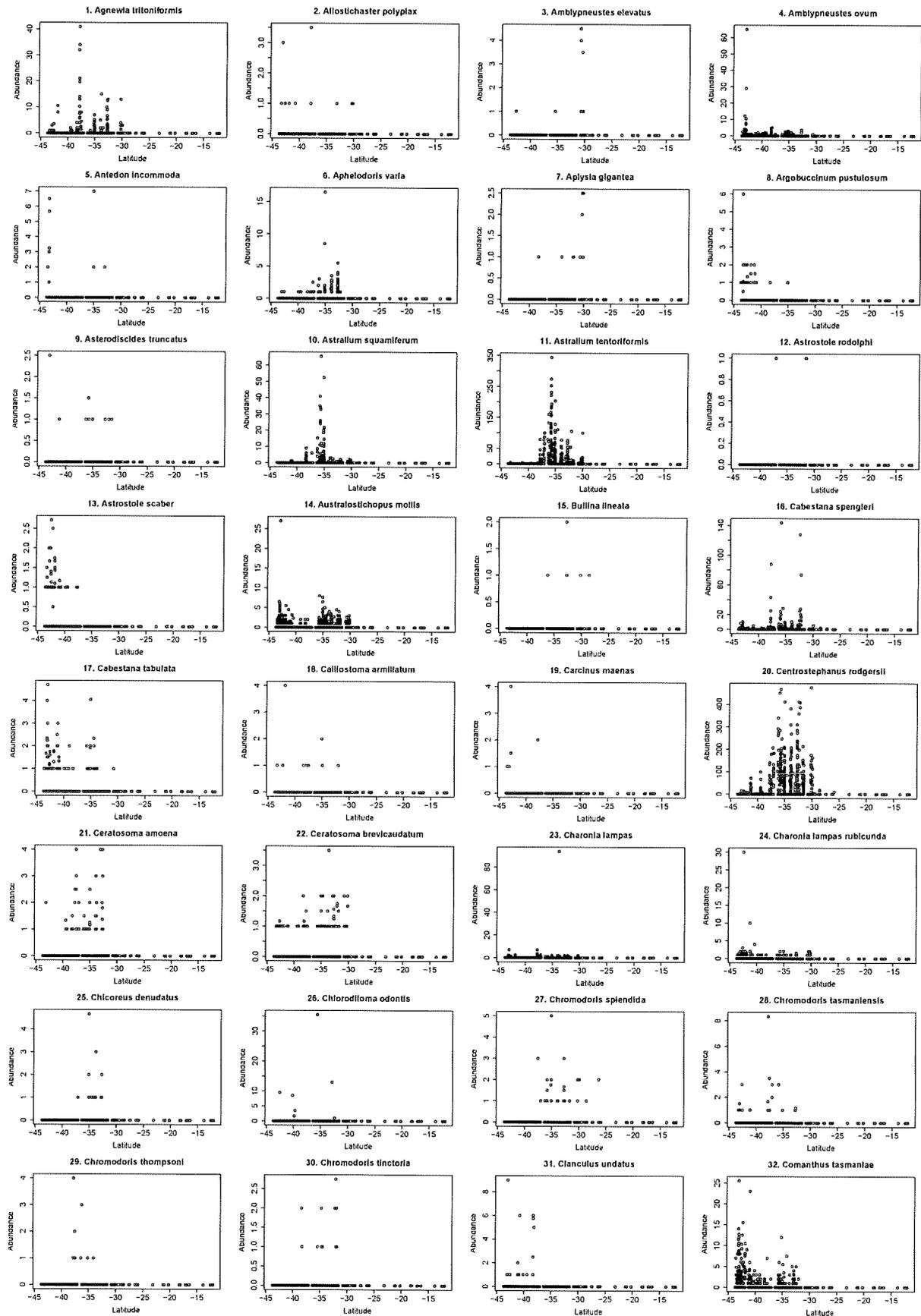


Figure 18. Mobile invertebrate abundance records by Lat. & site ($n/50m^2$) from LTPMP and RLS.

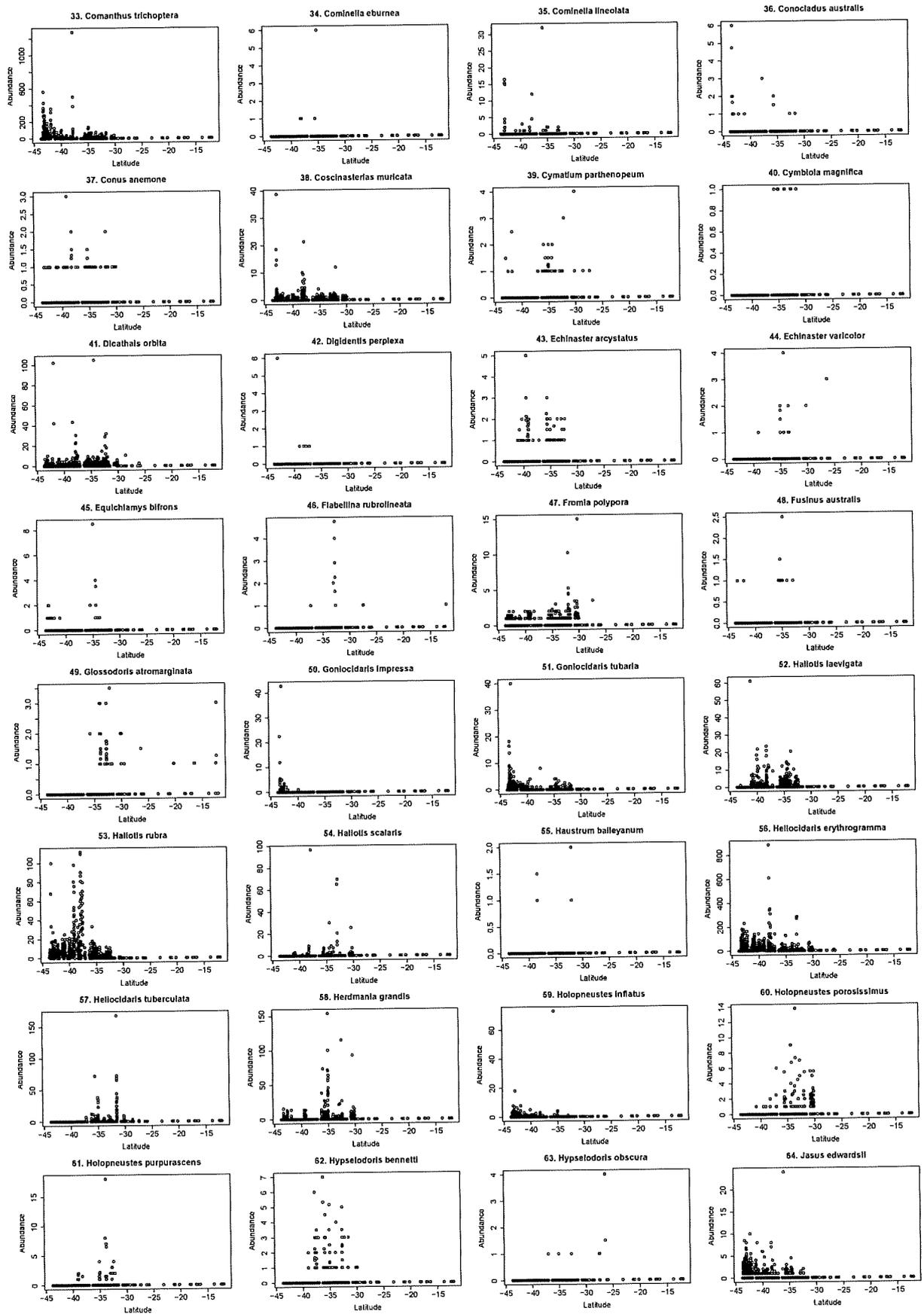


Fig. 18(Cont). Mobile invert. abundance records by Lat. & site ($n/50m^2$) from LTPMP and RLS.

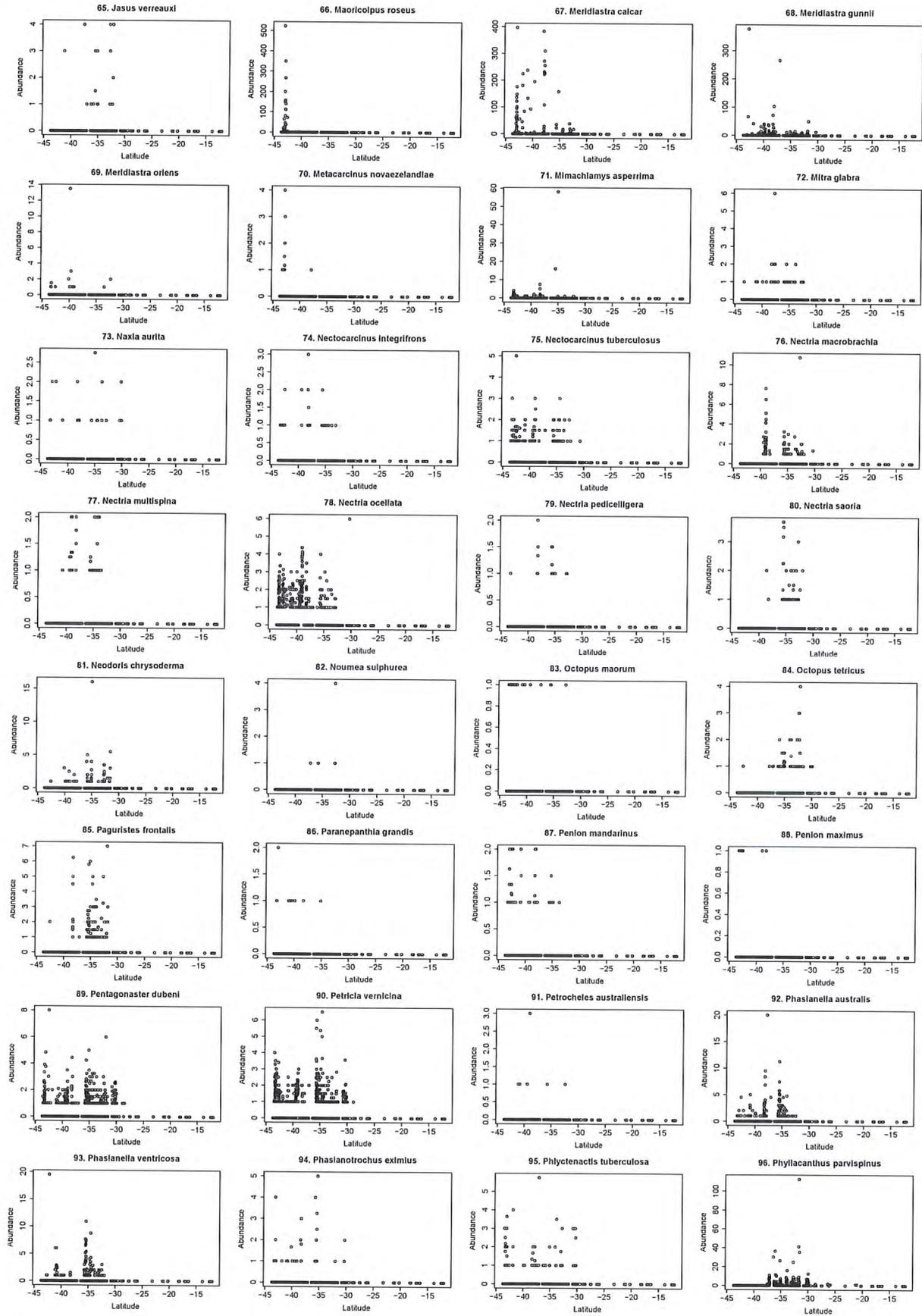


Fig. 18(Cont). Mobile invert. abundance records by Lat. & site ($n/50m^2$) from LTPMP and RLS.

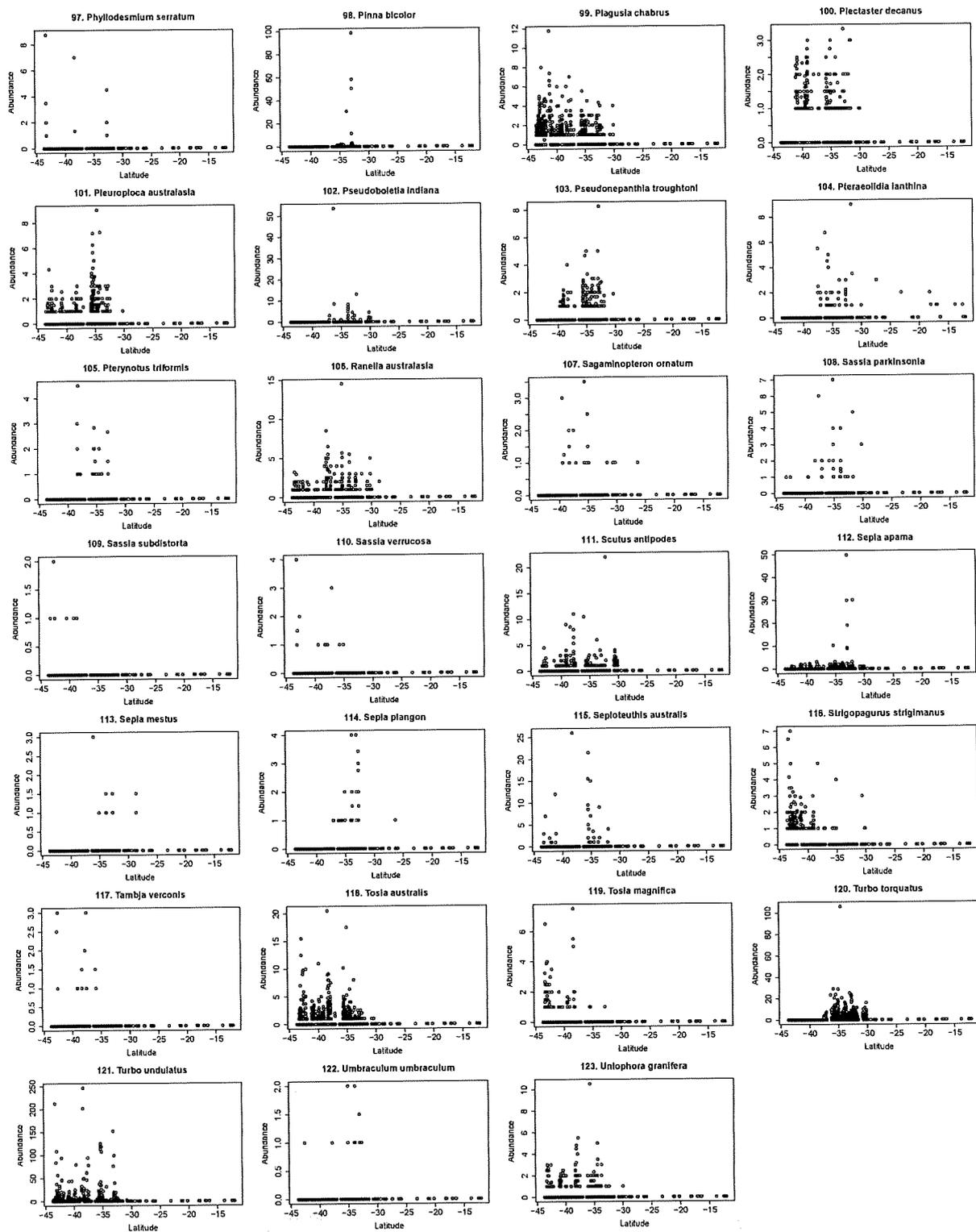


Fig. 18(Cont). Mobile invert. abundance records by Lat. & site ($n/50m^2$) from LTPMP and RLS.

Table 1 (cont.). Predicted latitudinal distribution of current and future per transect abundance (n/500m2) of fish species from LTTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																	ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT										
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward	poleward range	Δ-43.5*	Δ-42.5*	Δ-41.5*	Δ-40.5*	Δ-39.5*	-43.5	-42.5	-41.5	-40.5	-39.5					
	range edge	edge	1.1	0.9	0.8	0.5	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-24.8	0.0	0.0	0.0	0.0	0.0	59.5	43.7	33.6	21.1	7.4				
41. Cheilodactylus spectabilis	2.5	2.6	2.8	2.9	3.0	3.0	2.9	2.9	2.8	2.7	2.6	2.5	2.4	2.2	2.2	2.0	1.9	1.8	-43.7	-30.0	1.1	0.9	0.8	0.5	0.2	-	-	-	-	-	-	-	-	-	
42. Cheilodactylus vestitus	1.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-14.0	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
43. Chelonia mydas	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.4	-30.8	0.4	0.2	0.1	0.1	0.1	-	72.0	61.6	46.4	29.4	-	-	-	-	-
44. Chironemus georgianus	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3	0.3	0.3	0.3	0.2	0.2	0.2	0.2	0.0	0.0	-41.9	-28.6	2.1	2.1	2.2	2.5	2.8	-	-	492.6	382.5	270.5	-	-	-	-	-
45. Chironemus marmoratus	5.8	5.3	4.6	3.8	3.1	2.6	2.1	1.6	1.3	1.0	0.8	0.6	0.6	0.4	0.0	0.0	0.0	0.0	-42.7	-29.4	64.5	50.4	56.8	60.0	57.8	-	355.9	296.7	215.3	148.0	-	-	-	-	-
46. Chromis hypsilepis	143.8	128.8	108.3	96.9	87.9	75.9	64.5	54.2	47.2	39.1	32.2	27.9	23.0	19.1	16.0	14.2	0.0	0.0	-37.5	-12.1	0.0	0.0	0.6	0.7	0.8	-	-	-	-	-	-	-	-	-	
47. Chrysiptera rollandi	1.1	1.0	0.9	0.8	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.1	-18.0	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
48. Crrhitichthys aprinus	0.6	0.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.9	-27.9	0.0	0.0	0.2	0.3	0.4	-	-	-	-	-	-	-	-	-	
49. Cnidoglanis macrocephalus	0.8	0.6	0.5	0.4	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-31.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
50. Cochleoceps orientalis	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.4	-30.3	0.4	-0.2	-0.2	-0.2	-0.2	-	-33.5	-34.9	-33.9	-33.2	-	-	-	-	-
51. Conger verreauxi	0.2	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.0	0.0	-36.2	-12.1	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
52. Coris dorsomacula	0.5	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-28.6	0.0	0.0	0.0	0.8	1.0	-	-	-	-	-	-	-	-	-	-
53. Coris picta	1.8	1.5	1.2	1.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-30.0	0.2	0.2	0.2	0.3	0.3	-	-	-	-	-	-	-	-	-	
54. Coris sandeyeri	0.4	0.4	0.4	0.3	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.0	-32.3	0.1	0.1	0.1	0.1	0.1	-	-	-	-	-	-	-	-	-	
55. Cristiceps aurantiacus	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.3	-32.4	0.4	0.1	0.1	0.0	0.0	-	23.9	13.7	4.8	-5.6	-	-	-	-	-
56. Cristiceps australis	0.3	0.3	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3	0.0	0.0	-41.1	-30.1	0.9	0.9	1.1	1.0	1.0	-	-	-	304.7	199.8	-	-	-	-	
57. Dactylophora nigricans	1.8	1.7	1.6	1.5	1.3	1.1	0.9	0.7	0.6	0.5	0.4	0.3	0.3	0.0	0.0	0.0	0.0	0.0	-43.3	-30.2	0.7	0.4	0.3	0.3	0.3	-	101.4	77.5	58.4	44.1	-	-	-	-	-
58. Dasyatis brevicaudata	1.0	1.1	1.0	0.9	0.8	0.8	0.7	0.7	0.6	0.6	0.5	0.5	0.4	0.4	0.4	0.3	0.0	0.0	-43.1	-31.5	0.4	0.3	0.3	0.3	0.3	-	451.1	340.3	214.5	123.4	-	-	-	-	-
59. Dasyatis thetidis	0.5	0.5	0.5	0.5	0.5	0.4	0.4	0.3	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.0	0.0	-35.8	-28.6	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
60. Dicotylichthys punctulatus	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.6	-28.2	-9.7	-7.8	-6.3	-5.5	-4.2	-31.9	-27.3	-23.9	-22.1	-18.3	-	-	-	-	-
61. Dinolestes lewini	17.2	17.7	18.2	18.7	19.3	20.2	20.8	21.5	22.2	22.9	24.0	24.8	25.6	26.5	27.4	28.6	29.6	30.5	-43.6	-30.3	0.2	0.1	0.0	0.0	-0.1	12.2	7.8	2.6	-1.0	-6.1	-	-	-	-	-
62. Diodon nictemerus	1.2	1.3	1.4	1.6	1.6	1.6	1.7	1.7	1.7	1.7	1.7	1.6	1.6	1.6	1.5	1.5	1.5	0.0	-39.0	-30.1	0.4	0.4	0.6	0.7	0.9	-	-	-	-	-	-	-	-	-	
63. Dotalabrus alleni	1.8	1.5	1.2	0.9	0.7	0.6	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.6	-30.2	0.0	0.0	-0.1	-0.1	-0.1	-2.1	-2.2	-2.7	-3.5	-4.2	-	-	-	-	-
64. Dotalabrus aurantiacus	1.8	1.9	1.9	1.9	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	2.0	0.0	-42.7	-28.5	312.1	255.3	262.5	261.6	226.7	449.3	315.3	207.3	119.8	-	-	-	-	-	
65. Engraulis australis	481.0	465.4	447.3	416.0	387.8	345.8	312.1	266.3	232.4	189.3	159.4	126.2	105.8	83.3	69.1	56.8	0.0	0.0	-42.7	-30.0	4.8	3.5	3.9	4.0	4.2	272.7	230.9	168.9	128.8	-	-	-	-	-	
66. Enoplosus armatus	9.6	9.0	8.4	7.5	6.4	5.6	4.8	4.3	3.8	3.3	2.8	2.4	2.0	1.7	1.5	1.3	0.0	0.0	-43.0	-27.4	0.8	0.7	0.8	0.8	0.9	547.7	395.2	292.6	207.2	-	-	-	-	-	
67. Eocallionymus papilio	1.9	1.8	1.6	1.3	1.1	0.9	0.8	0.7	0.5	0.4	0.3	0.3	0.2	0.2	0.1	0.1	0.0	0.0	-36.2	-29.4	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
68. Epinephelus daemeli	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.6	-31.6	0.0	0.0	0.5	0.6	0.7	-	-	-	-	-	-	-	-	-	
69. Eubalichthys bucephalus	0.9	0.9	0.8	0.7	0.6	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.1	-32.0	0.9	0.5	0.3	0.1	-0.1	110.5	57.7	19.4	-10.1	-	-	-	-	-	
70. Eubalichthys gunnii	0.5	0.6	0.6	0.7	0.8	0.8	0.9	0.9	0.8	0.8	0.7	0.7	0.6	0.5	0.5	0.4	0.4	0.0	-41.2	-31.7	0.8	0.8	1.0	1.1	1.1	-	-	742.0	400.3	-	-	-	-	-	-
71. Eubalichthys mosaicus	1.3	1.5	1.5	1.4	1.2	1.0	0.8	0.5	0.4	0.3	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	-40.3	-30.0	1.1	1.1	1.4	1.7	1.3	-	-	-	218.5	-	-	-	-	-	
72. Eupetrichthys angustipes	2.6	2.3	2.2	1.9	1.7	1.4	1.1	0.9	0.7	0.6	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-42.8	-30.2	1.6	1.4	1.7	1.9	2.0	673.7	572.8	415.7	260.1	-	-	-	-	-	
73. Favonigobius lateralis	4.0	3.7	3.2	2.7	2.4	2.0	1.6	1.2	1.0	0.8	0.6	0.5	0.4	0.3	0.2	0.2	0.0	0.0	-43.3	-28.6	0.5	0.5	0.6	0.7	0.7	1211.2	807.0	510.8	275.4	-	-	-	-	-	
74. Foetorepus calauropomus	1.1	1.1	1.0	0.9	0.8	0.7	0.5	0.4	0.3	0.3	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	-36.2	-16.0	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	
75. Forcipiger flavissimus	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.4	-40.8	0.0	-3.1	-1.4	0.0	0.0	-100.0	-100.0	-	-	-	-	-	-	-	
76. Forsterygion varium	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	1.4	2.2	3.1	4.0	0.0	-43.3	-35.0	0.7	0.5	0.4	0.3	0.1	244.8	167.5	80.9	14.5	-	-	-	-	-	
77. Genypterus tigerinus	0.0	0.4	0.5	0.6	0.7	0.7	0.7	0.7	0.6	0.5	0.4	0.4	0.3	0.3	0.2	0.2	0.2	0.0	-39.5	-23.2	2.1	2.1	2.5	2.9	3.5	-	-	-	-	-	-	-	-	-	
78. Gerres subfasciatus	5.5	4.8	4.1	3.5	2.9	2.5	2.1	1.7	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.4	-28.6	4.3	2.6	2.5	2.5	2.2	153.4	116.8	94.2	70.3	-	-	-	-	-	
79. Girella elevata	6.1	6.0	5.8	5.4	5.1	4.6	4.3	3.9	3.5	3.2	2.9	2.6	2.4	2.1	1.9	1.7	1.5	0.0	-43.4	-28.6	4.3	2.6	2.5	2.5	2.2	208.7	166.2	129.6	100.4	-	-	-	-	-	
80. Girella tricuspidata	19.2	17.7	16.2	14.7	13.2	11.3	10.2	9.2	8.2	7.3	6.5	5.7	5.0	4.3	3.8	3.3	2.9	0.0	-43.3	-27.5	10.2	6.9	7.1	7.4	7.4	-	-	-	-	-	-	-	-	-	

Table 1 (cont.). Predicted latitudinal distribution of current and future per transect abundance (n/500m2) of fish species from LTTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																			ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT				
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward range edge	poleward range edge	Δ-43.5°	Δ-42.5°	Δ-41.5°	Δ-40.5°	Δ-39.5°	-43.5	-42.5	-41.5	-40.5	-39.5	
81. <i>Girella zebra</i>	7.0	6.9	6.7	6.5	6.2	5.9	5.6	5.4	5.1	4.8	4.6	4.3	4.1	3.8	3.7	3.4	3.2	0.0	-43.4	-30.2	5.6	2.2	2.1	1.9	1.6	-	64.1	53.8	43.3	34.2	
82. <i>Glyptauchen panduratus</i>	0.4	0.4	0.4	0.4	0.4	0.4	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.0	-43.1	-32.4	0.3	0.3	0.3	0.3	0.2	-	436.8	327.0	213.9	110.4	
83. <i>Gnathanacanthus goetzei</i>	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.2	0.2	0.2	0.3	0.3	0.4	0.5	0.5	0.6	0.7	0.0	-43.4	-35.7	0.1	-0.5	-0.4	-0.3	-0.2	-	-81.0	-81.3	-82.0	-81.7	
84. <i>Gymnothorax prasinus</i>	1.3	1.2	1.0	0.9	0.8	0.7	0.7	0.5	0.4	0.4	0.3	0.2	0.2	0.1	0.1	0.1	0.0	0.0	-42.7	-29.9	0.7	0.5	0.6	0.6	0.6	-	532.6	403.0	269.4	160.5	
85. <i>Halletta semifasciata</i>	2.1	2.5	2.8	3.0	3.0	3.0	2.8	2.5	2.2	1.8	1.5	1.3	1.0	0.9	0.7	0.6	0.5	0.0	-43.1	-30.6	2.8	2.2	2.1	1.8	1.2	-	360.2	245.9	141.4	63.5	
86. <i>Halichoeres nebulosus</i>	1.9	1.7	1.5	1.4	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-14.7	0.0	0.0	0.0	1.3	1.4	-	-	-	-	-	
87. <i>Heteroclinus johnstoni</i>	0.2	0.3	0.3	0.4	0.5	0.5	0.6	0.7	0.8	0.8	0.9	1.0	1.0	1.1	1.1	1.2	1.2	1.2	-43.6	-32.4	-0.6	-0.5	-0.5	-0.5	-0.5	-	-49.6	-47.0	-49.4	-51.4	
88. <i>Heteroclinus roseus</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.6	-32.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	
89. <i>Heteroclinus tristis</i>	0.4	0.5	0.5	0.6	0.7	0.8	0.8	0.9	1.0	1.0	1.1	1.1	1.1	1.2	1.2	1.2	1.2	1.3	-43.6	-32.5	-0.4	-0.4	-0.4	-0.4	-0.4	-	-33.3	-31.1	-34.8	-36.4	
90. <i>Heteroclinus whiteleggii</i>	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.3	-32.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	
91. <i>Heterodontus galeatus</i>	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-32.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	
92. <i>Heterodontus portusjacksoni</i>	2.2	2.3	2.3	2.2	2.0	1.8	1.5	1.3	1.1	0.9	0.7	0.6	0.5	0.4	0.3	0.3	0.0	0.0	-42.7	-30.2	1.5	1.3	1.4	1.4	1.3	-	508.5	374.5	245.0	155.7	
93. <i>Heteroscarus acropitilus</i>	1.5	1.5	1.4	1.4	1.3	1.3	1.2	1.1	1.1	1.0	1.0	0.9	0.9	0.9	0.8	0.8	0.7	0.0	-43.3	-28.2	1.2	0.4	0.4	0.4	0.3	-	55.5	46.8	39.5	32.4	
94. <i>Hippocampus abdominalis</i>	0.0	0.1	0.2	0.2	0.3	0.4	0.4	0.5	0.5	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.0	-43.3	-35.0	0.4	-0.2	-0.3	-0.3	-0.3	-	-32.9	-41.6	-50.9	-58.8	
95. <i>Hypnos monopterygius</i>	0.3	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-27.4	0.0	0.0	0.0	0.1	0.1	-	-	-	-	-	
96. <i>Hypoplectrodes annulatus</i>	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-31.7	0.0	0.0	0.0	0.1	0.1	-	-	-	-	-	
97. <i>Hypoplectrodes maccullochi</i>	3.4	3.0	2.6	2.2	2.0	1.7	1.5	1.3	1.2	1.0	0.9	0.7	0.7	0.6	0.5	0.4	0.0	0.0	-42.7	-24.8	1.5	1.1	1.2	1.3	1.2	-	272.6	210.9	174.8	120.3	
98. <i>Hypoplectrodes nigroruber</i>	1.9	1.7	1.7	1.6	1.4	1.2	1.0	0.8	0.6	0.5	0.4	0.3	0.2	0.0	0.0	0.0	0.0	0.0	-41.1	-30.1	1.0	1.0	1.2	1.1	1.1	-	-	367.6	223.4	-	-
99. <i>Hypoplectrodes wilsoni</i>	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.6	-30.1	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	
100. <i>Kyphosus sydneyanus</i>	8.3	6.9	6.2	5.4	4.8	4.0	3.3	2.9	2.4	2.1	1.7	1.4	1.2	0.0	0.0	0.0	0.0	0.0	-41.3	-27.5	3.3	3.3	4.0	3.4	3.3	-	-	239.0	158.8	-	-
101. <i>Labroides dimidiatus</i>	1.1	1.0	1.0	0.9	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-12.1	0.0	0.0	0.0	0.8	0.9	-	-	239.0	158.8	-	-
102. <i>Latridopsis forsteri</i>	0.0	0.2	0.2	0.3	0.4	0.6	0.7	1.0	1.2	1.6	1.9	2.3	2.9	3.6	4.4	5.5	6.7	7.9	-43.6	-35.1	-7.2	-4.8	-3.0	-1.9	-1.3	-	-90.9	-86.9	-84.4	-82.4	
103. <i>Latris lineata</i>	0.5	0.6	0.7	0.7	0.8	0.9	0.9	1.0	1.1	1.2	1.2	1.3	1.4	1.5	1.7	1.8	2.0	2.2	-43.6	-30.2	-1.3	-0.9	-0.7	-0.5	-0.4	-	-57.5	-48.8	-43.4	-40.2	
104. <i>Leptatherina presbyteroides</i>	55.4	59.0	62.3	63.9	64.6	64.3	62.8	61.1	58.3	55.7	53.0	49.6	46.9	43.8	41.5	39.0	0.0	0.0	-43.0	-31.9	62.8	23.9	20.5	15.0	8.2	-	61.2	46.8	30.3	14.7	
105. <i>Leptojulius cyanopleura</i>	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-23.2	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	
106. <i>Lotella rhacina</i>	1.0	1.2	1.2	1.3	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.3	1.3	1.3	1.3	1.3	0.0	-43.5	-31.6	1.4	0.1	0.1	0.0	-0.1	-	10.9	7.7	1.2	-5.7	
107. <i>Mecaenichthys immaculatus</i>	1.6	1.3	1.0	0.8	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.0	-28.6	0.0	0.0	0.0	0.6	0.8	-	-	-	-	-	
108. <i>Mendosoma lineatum</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.5	18.5	52.5	-43.7	-42.4	-52.5	-6.5	0.0	0.0	-	-100.0	-100.0	-	-	
109. <i>Meuschenia australis</i>	0.2	0.3	0.4	0.5	0.6	0.7	0.9	1.1	1.3	1.5	1.6	1.8	1.8	1.9	1.9	2.0	2.0	2.0	-43.6	-33.8	-1.1	-1.1	-1.2	-1.2	-1.0	-	-54.2	-53.9	-60.8	-66.0	
110. <i>Meuschenia flavolineata</i>	2.5	2.5	2.5	2.4	2.2	2.1	1.9	1.7	1.6	1.5	1.4	1.3	1.2	1.1	1.0	0.9	0.8	0.0	-43.2	-30.1	1.9	1.0	1.0	0.9	0.8	-	113.3	91.2	71.0	56.4	
111. <i>Meuschenia freycineti</i>	1.7	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.7	1.7	1.6	1.6	1.6	1.5	1.4	1.4	0.0	0.0	-43.3	-30.3	1.8	0.4	0.3	0.2	0.2	-	25.0	19.1	13.5	9.3	
112. <i>Meuschenia galii</i>	1.6	1.4	1.2	1.0	0.8	0.6	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.5	-30.2	0.5	0.5	0.6	0.8	1.0	-	-	-	-	-	
113. <i>Meuschenia hippocrepis</i>	4.2	4.2	4.1	3.9	3.5	3.2	2.8	2.4	2.2	2.0	1.8	1.6	1.4	1.3	1.2	1.0	0.0	0.0	-43.0	-30.1	2.8	1.7	1.9	1.9	1.9	-	169.8	149.1	120.0	95.1	
114. <i>Meuschenia scaber</i>	0.8	0.8	0.8	0.8	0.7	0.7	0.6	0.6	0.5	0.5	0.4	0.3	0.3	0.3	0.2	0.2	0.0	0.0	-42.6	-31.6	0.6	0.4	0.4	0.4	0.3	-	239.8	176.9	119.2	76.4	
115. <i>Meuschenia trachylepis</i>	1.4	1.2	0.9	0.7	0.6	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-27.4	0.4	0.4	0.4	0.6	0.7	-	-	-	-	-	
116. <i>Meuschenia venusta</i>	0.4	0.4	0.4	0.3	0.3	0.3	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.5	-32.4	0.2	0.2	0.3	0.3	0.3	-	-	-	-	-	
117. <i>Microcanthus strigatus</i>	5.2	4.5	3.9	3.3	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-23.2	0.0	0.0	0.0	2.8	3.3	-	-	-	-	-	
118. <i>Mugil cephalus</i>	38.6	35.4	33.1	29.5	27.1	23.6	21.3	18.0	16.0	13.2	11.5	9.2	7.9	6.2	5.2	4.0	0.0	0.0	-43.0	-23.2	21.3	17.3	17.4	17.9	16.4	-	431.1	279.5	193.6	124.0	
119. <i>Myliobatis australis</i>	0.9	0.9	0.9	0.8	0.8	0.7	0.7	0.6	0.5	0.5	0.4	0.4	0.3	0.3	0.3	0.2	0.2	0.0	-43.3	-30.1	0.7	0.4	0.4	0.4	0.4	-	168.8	141.4	110.0	74.4	
120. <i>Nelusetta ayraudi</i>	2.7	2.5	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.3	-31.6	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	

Table 1 (cont.). Predicted latitudinal distribution of current and future per transect abundance (n/500m2) of fish species from LTTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																	ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT					
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	equatorward range edge	poleward range edge	Δ-43.5*	Δ-42.5*	Δ-41.5*	Δ-40.5*	Δ-39.5*	-43.5	-42.5	-41.5	-40.5	-39.5	
	0.9	0.8	0.8	0.7	0.6	0.5	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.4	-31.6	0.5	0.5	0.5	0.6	0.7	-100.0	-100.0	-100.0	-100.0	-100.0	
121. <i>Nemadactylus douglasii</i>	0.9	0.8	0.8	0.7	0.6	0.5	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.4	-31.6	0.5	0.5	0.5	0.6	0.7	-100.0	-100.0	-100.0	-100.0	-100.0	
122. <i>Nemadactylus macropterus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.4	0.6	0.8	1.3	1.9	2.8	-43.6	-39.1	-2.8	-1.3	-0.6	-0.2	-0.1	-	-	-	-	-
123. <i>Nemadactylus valenciennesi</i>	0.9	0.9	0.8	0.6	0.5	0.4	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.2	-30.7	0.3	0.3	0.4	0.5	0.6	-	-	-	-	-	
124. <i>Neodax balteatus</i>	2.9	3.4	3.8	4.2	4.6	5.1	5.5	5.9	6.3	6.7	7.0	7.3	7.8	8.2	8.5	9.0	9.3	9.7	-43.6	-32.1	-4.2	-3.5	-3.1	-2.8	-2.5	-43.5	-39.1	-37.6	-37.5	-37.2
125. <i>Neosebastes scorpaenoides</i>	0.1	0.2	0.2	0.3	0.3	0.4	0.4	0.5	0.5	0.5	0.5	0.5	0.5	0.6	0.6	0.6	0.6	0.0	-43.3	-34.4	0.4	-0.2	-0.2	-0.2	-0.2	-	-26.3	-30.9	-36.6	-44.3
126. <i>Notolabrus fucicola</i>	1.6	2.1	2.7	3.4	4.0	4.7	5.1	5.3	5.5	5.8	5.9	6.0	6.1	6.1	6.2	6.2	6.1	6.1	-43.7	-33.8	-1.0	-1.0	-1.4	-1.9	-2.4	-16.3	-17.0	-23.6	-32.4	-41.7
127. <i>Notolabrus gymnogenis</i>	6.8	5.9	5.2	4.5	3.7	3.1	2.6	2.2	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.5	-27.4	2.6	2.6	3.1	3.7	4.5	-	-	-	-	-
128. <i>Notolabrus tetricus</i>	12.3	13.4	14.0	14.4	14.6	14.7	14.6	14.5	14.4	14.2	13.9	13.7	13.5	13.2	13.0	12.7	12.4	12.4	-43.6	-32.3	2.3	1.7	1.2	0.7	0.1	18.3	12.8	8.6	4.7	0.4
129. <i>Olisthops cyanomelas</i>	4.4	4.3	4.2	4.0	3.9	3.7	3.6	3.5	3.3	3.2	3.0	2.9	2.8	2.6	2.5	2.4	2.3	0.0	-43.4	-28.2	3.6	1.2	1.1	1.0	0.9	-	48.3	41.6	33.6	27.1
130. <i>Omegophora armilla</i>	0.9	1.1	1.1	1.2	1.2	1.1	1.0	0.9	0.8	0.7	0.6	0.5	0.4	0.4	0.3	0.3	0.2	0.0	-43.3	-32.0	1.0	0.7	0.7	0.7	0.5	-	267.3	206.3	131.0	74.3
131. <i>Ophthalmolepis lineolatus</i>	11.1	10.8	10.2	8.7	7.2	5.7	5.1	4.6	4.0	3.5	3.0	2.4	2.0	1.7	0.0	0.0	0.0	0.0	-41.9	-30.0	5.1	5.1	4.0	4.8	5.3	-	-	233.9	199.2	152.5
132. <i>Optivus agastos</i>	0.4	0.4	0.3	0.3	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.0	-32.6	0.0	0.0	0.0	0.3	0.3	-	-	-	-	-
133. <i>Orectolobus halei</i>	0.6	0.5	0.4	0.3	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-23.2	0.2	0.2	0.2	0.3	0.3	-	-	-	-	-
134. <i>Orectolobus maculatus</i>	0.6	0.5	0.4	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.5	-27.4	0.0	0.0	0.0	0.2	0.3	-	-	-	-	-
135. <i>Pagrus auratus</i>	3.6	3.0	2.6	2.1	1.7	1.4	1.1	0.9	0.7	0.6	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.1	-25.9	1.1	1.1	1.4	1.7	1.5	-	-	-	-	261.9
136. <i>Parablennius intermedius</i>	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.4	-27.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-
137. <i>Parablennius tasmanianus</i>	1.0	1.2	1.5	1.7	1.9	2.1	2.1	2.1	2.0	1.9	1.9	1.8	1.7	1.6	1.5	1.4	1.3	0.0	-43.3	-31.9	2.1	0.7	0.5	0.1	-0.3	-	54.9	30.6	6.9	-13.4
138. <i>Paraplesiops bleekeri</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-33.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-
139. <i>Paraplesiops meleagris</i>	0.7	0.6	0.5	0.4	0.3	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-30.1	0.2	0.2	0.3	0.3	0.4	-	-	-	-	-
140. <i>Parapriacanthus elongatus</i>	167.5	182.0	179.1	161.5	134.8	105.3	77.8	55.0	37.5	25.1	16.5	10.9	7.2	4.9	3.4	2.5	0.0	0.0	-42.6	-30.1	77.8	75.3	100.4	123.9	136.4	-	3010.1	2046.3	1138.3	544.2
141. <i>Parascyllium ferrugineum</i>	0.2	0.3	0.3	0.4	0.4	0.4	0.5	0.5	0.6	0.6	0.7	0.7	0.7	0.7	0.7	0.8	0.8	0.8	-43.5	-32.0	-0.2	-0.2	-0.3	-0.3	-0.3	-32.9	-32.2	-38.4	-42.0	-43.4
142. <i>Parascyllium variolatum</i>	0.8	0.7	0.7	0.6	0.6	0.5	0.4	0.4	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.0	0.0	-42.6	-28.9	0.4	0.4	0.4	0.4	0.4	-	415.9	310.6	210.3	141.9
143. <i>Paratrachichthys trailli</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	1.3	2.7	-43.7	-41.9	-2.7	-0.6	0.0	0.0	0.0	-100.0	-100.0	-	-	-
144. <i>Parequula melbournensis</i>	3.7	3.9	4.1	4.0	3.9	3.6	3.3	3.0	2.6	2.3	2.0	1.7	1.5	1.3	1.1	1.0	0.9	0.0	-43.3	-30.6	3.3	2.4	2.4	2.2	1.7	-	247.1	188.7	126.7	73.3
145. <i>Parma microlepis</i>	13.2	13.1	12.5	12.0	10.8	9.4	8.4	7.8	7.1	6.3	5.7	5.0	4.3	3.8	3.4	2.9	2.6	0.0	-43.3	-30.0	8.4	5.4	5.7	5.8	5.7	-	184.7	151.2	114.9	89.5
146. <i>Parma polylepis</i>	1.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-27.4	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-
147. <i>Parma unifasciata</i>	7.5	6.0	4.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-42.7	-30.8	2.5	1.5	1.4	1.4	1.4	-	148.6	114.6	92.7	74.6
148. <i>Parma victoriae</i>	3.2	3.4	3.4	3.2	3.0	2.7	2.5	2.3	2.0	1.8	1.7	1.5	1.4	1.3	1.1	1.0	0.0	0.0	-37.1	-12.4	0.0	0.0	0.0	3.2	3.5	-	-	-	-	-
149. <i>Parupeneus spilurus</i>	4.7	4.3	3.9	3.5	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-12.4	11.1	7.5	7.9	7.6	7.7	-	205.0	167.8	123.2	96.5
150. <i>Pempheris affinis</i>	20.8	18.6	17.1	15.6	13.7	12.6	11.1	10.1	8.8	7.9	6.8	6.1	5.2	4.7	4.2	3.6	3.3	0.0	-43.3	-23.2	11.1	7.5	7.9	7.6	7.7	-	-	848.6	589.7	343.4
151. <i>Pempheris compressa</i>	55.1	54.7	51.2	45.6	37.0	30.0	23.6	18.2	13.7	10.3	7.7	5.4	4.1	3.2	0.0	0.0	0.0	0.0	-41.9	-29.9	23.6	23.6	26.8	31.6	35.3	-	-	-	-	-
152. <i>Pempheris multiradiata</i>	20.5	21.4	22.0	22.7	23.6	24.3	24.9	25.9	26.6	27.3	28.1	29.2	29.9	30.7	31.9	32.8	33.6	34.9	-43.6	-22.1	-10.0	-7.8	-6.5	-5.6	-4.7	-28.7	-23.9	-21.0	-19.1	-17.1
153. <i>Pentaceroptis recurvirostris</i>	0.6	0.7	0.8	0.9	1.0	1.0	1.1	1.1	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	0.0	-43.4	-32.4	1.1	-0.2	-0.2	-0.2	-0.3	-	-13.1	-16.1	-20.4	-23.5
154. <i>Petroscirtes fallax</i>	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-18.0	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-
155. <i>Phyllopteryx taeniolatus</i>	0.7	0.7	0.8	0.9	1.0	1.0	1.1	1.1	1.1	1.2	1.2	1.2	1.3	1.3	1.3	1.3	1.3	1.3	-43.6	-30.2	-0.3	-0.2	-0.2	-0.2	-0.3	-19.6	-18.2	-18.3	-19.6	-22.2
156. <i>Pictilabrus laticlavus</i>	3.0	3.1	3.1	3.2	3.3	3.5	3.6	3.7	3.8	3.9	4.1	4.2	4.3	4.5	4.6	4.8	4.9	5.1	-43.6	-28.2	-1.5	-1.2	-1.0	-0.9	-0.7	-29.9	-25.4	-22.3	-20.8	-17.5
157. <i>Plagiotremus rhinorhynchus</i>	0.5	0.5	0.4	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-14.6	0.0	0.0	0.0	0.4	0.4	-	-	-	-	-
158. <i>Plagiotremus tapeinosoma</i>	1.2	1.1	0.9	0.8	0.7	0.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-13.9	0.6	0.6	0.6	0.6	0.8	-	-	-	-	-
159. <i>Platycephalus bassensis</i>	0.1	0.1	0.2	0.2	0.3	0.3	0.4	0.5	0.5	0.6	0.7	0.8	0.8	0.9	1.0	1.1	1.2	1.3	-43.6	-33.8	-0.9	-0.7	-0.6	-0.5	-0.4	-69.4	-63.1	-62.3	-62.6	-62.6
160. <i>Platycephalus fuscus</i>	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.1	-24.8	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-

Table 1 (cont.). Predicted latitudinal distribution of current and future per transect abundance (n/500m2) of fish species from LTTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																	ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT											
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward range edge	poleward range edge	Δ-43.5*	Δ-42.5*	Δ-41.5*	Δ-40.5*	Δ-39.5*	-43.5	-42.5	-41.5	-40.5	-39.5						
161. <i>Platycephalus speculator</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.4	-31.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
162. <i>Pomacentrus australis</i>	2.1	1.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-20.1	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
163. <i>Pomacentrus coelestis</i>	6.1	5.5	4.9	4.4	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-13.9	0.0	0.0	0.0	3.8	4.4	-	-	-	-	-	-	-	-	-	-	
164. <i>Pomatomus saltatrix</i>	2.9	3.0	2.9	2.8	2.6	2.4	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.1	-32.7	2.2	2.2	2.4	2.6	2.8	-	-	-	-	-	-	-	-	-	-	
165. <i>Prionurus maculatus</i>	3.5	2.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-35.8	-25.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
166. <i>Prionurus microlepidotus</i>	4.7	4.1	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.4	-16.8	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
167. <i>Pseudanthias squamipinnis</i>	1.4	1.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-13.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
168. <i>Pseudocaranx georgianus</i>	21.5	21.4	21.3	21.2	21.0	20.9	20.8	20.7	20.5	20.3	20.1	20.0	19.8	19.7	19.5	19.3	19.1	0.0	-43.3	-16.4	20.8	1.5	1.2	1.1	0.8	-	7.9	6.2	5.3	4.1	-	-	-	-	-	
169. <i>Pseudocaranx wrighti</i>	1.2	1.2	1.2	1.2	1.1	1.1	1.0	0.9	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.0	-32.0	1.0	1.0	1.1	1.1	1.2	-	-	-	-	-	-	-	-	-	-	
170. <i>Pseudolabrus guentheri</i>	3.0	2.5	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-19.3	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
171. <i>Pseudolabrus luculentus</i>	6.7	5.4	4.0	3.1	2.3	1.8	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-28.6	1.3	1.3	1.8	2.3	3.1	-	-	-	-	-	-	-	-	-	-	
172. <i>Pseudolabrus psittaculus</i>	0.6	0.7	0.9	1.2	1.4	1.6	1.8	2.0	2.1	2.3	2.4	2.6	2.8	2.9	3.0	3.1	3.2	3.3	-43.7	-33.1	-1.5	-1.3	-1.3	-1.2	-1.1	-44.4	-41.1	-43.7	-47.8	-49.5	-	-	-	-	-	
173. <i>Pseudophycis bachus</i>	0.1	0.1	0.1	0.2	0.2	0.3	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0	1.1	1.2	1.3	1.3	-43.6	-33.0	-1.0	-0.9	-0.8	-0.6	-0.4	-75.5	-73.6	-75.3	-75.6	-73.1	-	-	-	-	-	
174. <i>Pseudophycis barbata</i>	0.0	0.0	0.0	0.1	0.1	0.1	0.2	0.2	0.3	0.3	0.4	0.4	0.5	0.6	0.8	0.9	1.0	1.2	-43.6	-35.1	-1.0	-0.7	-0.5	-0.4	-0.2	-86.9	-82.5	-82.3	-81.6	-79.8	-	-	-	-	-	
175. <i>Rhabdosargus sarba</i>	6.6	5.5	4.6	3.9	3.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-20.6	0.0	0.0	0.0	3.3	3.9	-	-	-	-	-	-	-	-	-	-	
176. <i>Sardinops neopilchardus</i>	68.3	64.6	58.9	54.3	48.0	43.3	37.3	33.1	27.9	24.4	20.2	17.5	14.4	12.3	10.1	8.6	7.0	0.0	-43.1	-28.9	37.3	28.7	30.9	30.5	29.9	-	332.7	250.7	174.0	122.5	-	-	-	-	-	
177. <i>Schuettea scalaripinnis</i>	85.9	66.2	50.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.4	-26.4	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
178. <i>Scobinichthys granulatus</i>	2.2	2.0	1.7	1.4	1.1	0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.3	0.0	0.0	0.0	0.0	0.0	-41.1	-30.1	0.8	0.8	0.9	0.8	0.9	-	-	-	-	-	-	251.5	193.5	-	-	
179. <i>Scomber australasicus</i>	26.5	23.3	20.2	18.0	15.4	13.0	10.8	9.0	7.4	6.0	4.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.0	-27.4	10.8	10.8	13.0	15.4	12.0	-	-	-	-	-	-	-	-	200.1	-	
180. <i>Scorpaena cardinalis</i>	0.8	0.7	0.6	0.5	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.8	-13.9	0.0	0.0	0.4	0.4	0.5	-	-	-	-	-	-	-	-	-	-	
181. <i>Scorpaena jacksoniensis</i>	0.4	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.4	-30.2	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
182. <i>Scorpaena papillosa</i>	1.0	1.1	1.1	1.2	1.2	1.2	1.3	1.3	1.4	1.4	1.4	1.5	1.5	1.5	1.5	1.6	1.6	1.6	-43.6	-30.3	-0.3	-0.3	-0.3	-0.3	-0.3	-18.4	-16.5	-17.4	-17.4	-17.9	-	-	-	-	-	
183. <i>Scorpius aequipinnis</i>	10.3	10.5	10.5	10.3	10.2	9.8	9.5	9.2	8.9	8.5	8.2	7.9	7.6	7.3	6.9	6.5	6.3	5.9	-43.6	-30.1	3.5	2.9	2.5	2.2	1.8	59.2	45.0	34.7	28.2	21.1	-	-	-	-	-	
184. <i>Scorpius lineolata</i>	51.0	44.2	40.1	34.8	30.1	26.0	22.4	19.3	17.6	15.2	13.2	11.4	9.9	8.5	7.4	6.7	5.8	0.0	-43.3	-25.9	22.4	15.7	17.5	18.7	19.6	-	233.4	204.2	164.3	129.1	-	-	-	-	-	
185. <i>Seriola lalandi</i>	3.9	3.2	2.7	2.3	1.9	1.5	1.3	1.1	0.9	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.0	-24.8	1.3	1.3	1.5	1.9	1.6	-	-	-	-	-	-	-	-	-	225.6	
186. <i>Seriola lalandi</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.1	15.7	15.8	14.9	13.6	12.2	0.0	-43.3	-40.0	0.0	-13.6	-15.8	-14.1	0.0	-	-100.0	-100.0	-100.0	-	-	-	-	-	-	
187. <i>Sillaginodes punctatus</i>	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.4	-32.0	0.2	0.2	0.2	0.2	0.2	-	-	-	-	-	-	-	-	-	-	
188. <i>Sillago ciliata</i>	0.5	0.4	0.4	0.4	0.3	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	-42.1	-27.9	0.3	0.3	0.2	0.2	0.2	-	-	-	-	-	-	310.5	207.8	131.5	-	
189. <i>Siphamia cephalotes</i>	55.0	53.7	52.6	49.5	45.4	40.3	34.9	29.6	23.6	19.5	16.0	13.1	10.3	8.6	0.0	0.0	0.0	0.0	-41.9	-30.2	34.9	34.9	31.7	32.2	30.0	-	-	-	-	-	-	-	-	-	-	
190. <i>Siphonognathus attenuatus</i>	3.7	4.0	4.2	4.2	3.9	3.5	3.0	2.5	2.0	1.6	1.2	0.9	0.7	0.6	0.4	0.3	0.0	0.0	-43.3	-30.8	3.0	2.6	2.9	3.0	2.6	-	748.7	525.1	317.6	165.7	-	-	-	-	-	-
191. <i>Siphonognathus beddomei</i>	11.1	11.0	10.8	10.2	9.5	8.7	7.9	7.4	6.8	6.2	5.7	5.1	4.8	4.4	4.0	3.6	3.2	0.0	-43.3	-30.3	7.9	4.3	4.3	4.3	4.0	-	121.7	97.9	84.3	63.8	-	-	-	-	-	-
192. <i>Siphonognathus caninis</i>	1.6	1.3	1.1	0.8	0.7	0.5	0.4	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.1	-26.4	0.4	0.4	0.5	0.7	0.8	-	-	-	-	-	-	-	-	-	-	
193. <i>Siphonognathus radiatus</i>	0.3	0.3	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.7	-30.2	0.1	0.1	0.2	0.2	0.1	-	-	-	-	-	-	-	-	-	172.1	
194. <i>Siphonognathus tanyourus</i>	0.6	0.7	0.8	0.8	0.7	0.5	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	-41.9	-34.9	0.4	0.4	0.5	0.6	0.7	-	-	-	-	-	-	855.6	747.8	517.0	-	
195. <i>Sphyraena novaehollandiae</i>	0.0	0.3	0.4	0.5	0.5	0.5	0.5	0.4	0.3	0.2	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.0	-42.6	-35.1	0.5	0.4	0.5	0.4	0.3	-	1488.8	932.8	420.0	132.7	-	-	-	-	-	-
196. <i>Spratelloides robustus</i>	0.0	18.4	21.7	23.5	23.5	22.0	19.7	17.0	14.3	11.9	10.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.1	-35.1	19.7	19.7	22.0	23.5	11.5	-	-	-	-	-	-	-	-	-	96.7	
197. <i>Stethojulis interrupta</i>	1.4	1.2	1.1	1.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-14.6	0.0	0.0	0.0	0.9	1.0	-	-	-	-	-	-	-	-	-	-	
198. <i>Stigmatopora nigra</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	-42.9	-38.0	0.1	0.1	0.0	-0.1	-0.1	-	290.0	-100.0	-100.0	-100.0	-	-	-	-	-	-
199. <i>Suezichthys arquatus</i>	0.3	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.4	-29.4	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
200. <i>Synodus variegatus</i>	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-13.9	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-	
201. <i>Tetractenos glaber</i>	0.9	1.0	1.1	1.2	1.3	1.4	1.4	1.3	1.3	1.2	1.1	1.0	0.9	0.8	0.8	0.7	0.6	0.0	-43.3	-32.2	1.4	0.7	0.5	0.3	0.0	-	-	-	-	-	-	-	-	-	-	
202. <i>Thalassoma lunare</i>	3.5	3.2	2.8	0.0	0.0	0.0																														

Table 1 (cont.). Predicted latitudinal distribution of current and future per transect abundance (n/500m2) of fish species from LTTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																	ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT							
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward range edge	poleward range edge	Δ-43.5*	Δ-42.5*	Δ-41.5*	Δ-40.5*	Δ-39.5*	-43.5	-42.5	-41.5	-40.5	-39.5		
	0.9	1.0	1.1	1.2	1.3	1.4	1.4	1.3	1.3	1.2	1.1	1.0	0.9	0.8	0.8	0.7	0.6	0.0	-43.3	-32.2	1.4	0.7	0.5	0.3	0.0	-	101.0	63.2	29.9	-	2.6	
201. Tetractenos glaber	0.9	1.0	1.1	1.2	1.3	1.4	1.4	1.3	1.3	1.2	1.1	1.0	0.9	0.8	0.8	0.7	0.6	0.0	-36.4	-12.4	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-
202. Thalassoma lunare	3.5	3.2	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.3	-39.4	0.0	-0.1	-0.1	-0.1	-0.1	-	-100.0	-100.0	-100.0	-100.0	-	
203. Thamnaconus degeni	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	-42.6	-30.5	1.4	1.3	1.6	1.7	1.6	-	1517.3	1005.4	573.8	257.9	-	
204. Threpterus maculosus	2.1	2.2	2.3	2.2	2.0	1.7	1.4	1.1	0.8	0.6	0.4	0.3	0.2	0.2	0.1	0.1	0.0	0.0	-43.3	-39.0	0.0	-2.4	-1.8	-1.2	-0.7	-	-100.0	-100.0	-100.0	-100.0	-	
205. Thyrsites atun	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.2	-32.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-
206. Thysanophrys cirronasa	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.1	-30.4	1.4	1.4	1.7	2.0	2.4	-	-	-	-	-	-	
207. Tilodon sexfasciatus	3.2	2.9	2.7	2.4	2.0	1.7	1.4	1.1	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.5	-28.2	0.0	0.0	20.7	25.7	33.2	-	-	-	-	-	-	
208. Torquigener pleurogramma	62.8	49.9	40.8	33.2	25.7	20.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.0	-30.2	0.5	0.5	0.7	0.9	0.9	-	-	-	-	-	488.6	
209. Trachichthys australis	1.5	1.4	1.3	1.1	0.9	0.7	0.5	0.4	0.3	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.6	-35.7	-193.5	-138.1	-103.3	-73.3	-48.3	-87.8	-83.7	-83.5	-82.6	-81.4		
210. Trachinops caudimaculatus	0.0	0.0	8.3	11.1	15.4	20.5	27.0	35.1	47.1	59.4	73.4	88.7	107.1	123.8	143.2	165.1	193.8	220.5	-39.5	-25.9	59.6	59.6	72.7	84.3	102.1	-	-	-	-	-		
211. Trachinops taeniatus	162.3	139.0	117.1	102.1	84.3	72.7	59.6	49.0	42.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.6	-32.7	-56.5	-64.6	-79.5	-79.0	-72.5	-37.8	-41.0	-50.2	-53.6	-56.5		
212. Trachurus declivis	29.7	36.7	46.7	55.8	68.3	79.1	93.0	104.3	118.1	128.3	139.8	147.3	154.5	158.6	159.6	157.6	154.4	149.5	-43.3	-25.9	241.5	175.3	195.6	208.7	215.0	-	265.1	229.8	179.5	134.8		
213. Trachurus novaezelandiae	540.1	469.9	428.9	374.4	325.0	280.7	241.5	207.0	186.6	159.5	136.2	116.3	99.4	85.1	73.1	66.1	56.9	0.0	-42.9	-32.4	0.2	0.2	0.2	0.2	0.2	-	523.3	419.9	273.9	161.2		
214. Trianectes bucephalus	0.3	0.3	0.3	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	-43.4	-29.9	1.8	0.1	0.1	0.1	0.0	-	6.2	5.0	3.3	2.0		
215. Trinorfolkia clarkei	1.7	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.8	1.7	1.7	1.7	1.7	1.7	1.7	1.7	-37.1	-35.1	0.0	0.0	0.0	1.0	1.0	-	-	-	-	-		
216. Trygonoptera imitata	0.0	0.9	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.2	-32.2	0.2	0.2	0.2	0.3	0.3	-	-	-	-	-		
217. Trygonoptera testacea	0.5	0.4	0.4	0.3	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.4	-32.2	0.3	0.3	0.4	0.4	0.5	-	-	-	-	-		
218. Trygonorrhina fasciata	0.5	0.5	0.5	0.5	0.4	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.5	-30.2	1.6	1.6	1.9	2.3	2.6	-	-	-	-	-		
219. Upeneichthys lineatus	3.7	3.4	2.9	2.6	2.3	1.9	1.6	1.3	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.3	-30.1	3.0	0.9	0.8	0.7	0.5	-	43.3	33.3	26.8	19.0		
220. Upeneichthys viamingii	3.1	3.2	3.3	3.2	3.2	3.1	3.0	2.9	2.8	2.7	2.6	2.5	2.4	2.3	2.2	2.1	2.0	0.0	-43.6	-34.8	-1.4	-1.1	-0.8	-0.5	-0.3	-85.8	-82.2	-81.5	-79.2	-76.6		
221. Urolophus cruciatus	0.0	0.1	0.1	0.1	0.1	0.2	0.2	0.3	0.4	0.5	0.6	0.7	0.8	1.0	1.1	1.3	1.4	1.6	-42.9	-32.0	0.6	0.5	0.6	0.6	0.4	-	1131.8	657.5	329.9	131.0		
222. Urolophus gigas	0.4	0.5	0.6	0.7	0.7	0.7	0.6	0.5	0.4	0.3	0.2	0.2	0.1	0.1	0.1	0.0	0.0	0.0	-37.6	-35.1	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-		
223. Urolophus kapalensis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-43.3	-30.7	0.9	0.5	0.4	0.3	0.2	-	122.3	85.4	53.0	27.1		
224. Urolophus paucimaculatus	0.8	0.9	0.9	1.0	1.0	1.0	0.9	0.9	0.8	0.8	0.7	0.6	0.6	0.5	0.5	0.4	0.4	0.0	-43.4	-33.0	1.0	-0.6	-0.6	-0.6	-0.6	-	-37.3	-40.8	-46.0	-49.1		
225. Vincentia conspersa	0.3	0.4	0.5	0.6	0.7	0.9	1.0	1.1	1.1	1.2	1.3	1.3	1.4	1.5	1.5	1.6	1.6	0.0	-	-	-	-	-	-	-	-	-	-	-	-		

Table 2 (Cont.). Predicted latitudinal distribution of current and future per transect abundance (n/50m2) of invertebrate species from LTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE															ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT												
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward range edge	poleward range edge	Δ-43.5*	Δ-42.5*	Δ-41.5*	Δ-40.5*	Δ-39.5*	-43.5	-42.5	-41.5	-40.5	-39.5					
81. Neodoris chrysoiderma	1.7	1.9	2.0	1.9	1.7	1.5	1.2	0.9	0.7	0.5	0.4	0.3	0.2	0.2	0.1	0.1	0.0	0.0	-42.6	-31.6	1.2	1.1	1.3	1.4	1.4	-	-	-	-	-	-	1189.3	870.5	509.0	264.1
82. Nourmea sulphurea	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.2	-32.7	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-
83. Octopus maorum	0.1	0.1	0.2	0.2	0.2	0.2	0.3	0.3	0.3	0.4	0.4	0.4	0.4	0.5	0.5	0.5	0.5	0.0	-43.4	-32.9	0.3	-0.2	-0.2	-0.2	-0.2	-	-	-	-	-	-	-	-	-	-
84. Octopus tetricus	1.2	1.1	1.0	0.9	0.7	0.6	0.4	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	-42.7	-29.9	0.4	0.4	0.5	0.6	0.7	-	-	-	-	-	-	-	-	-	-
85. Paguristes frontalis	1.8	1.7	1.5	1.3	1.0	0.9	0.7	0.6	0.5	0.4	0.4	0.3	0.2	0.2	0.2	0.1	0.0	0.0	-42.6	-31.8	0.7	0.6	0.7	0.7	0.9	-	-	-	-	-	-	-	-	-	-
86. Parapanthia grandis	0.0	0.0	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	-43.3	-35.2	0.2	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-
87. Penion mandarinus	0.2	0.3	0.3	0.4	0.5	0.5	0.6	0.6	0.7	0.7	0.8	0.8	0.8	0.9	0.9	0.9	0.9	0.0	-43.4	-33.8	0.6	-0.3	-0.4	-0.4	-0.3	-	-	-	-	-	-	-	-	-	-
88. Penion maximus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	-43.3	-38.3	0.0	-0.2	-0.2	-0.2	-0.1	-	-	-	-	-	-	-	-	-	-
89. Pentagonaster dubeni	1.4	1.4	1.4	1.4	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	0.0	-43.6	-28.5	-0.1	-0.1	-0.1	-0.1	0.0	-	-	-	-	-	-	-	-	-	-
90. Petricia vernicina	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.5	1.4	1.4	1.4	1.4	0.0	-43.5	-28.9	0.1	0.1	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-
91. Petrocheles australiensis	0.2	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	-41.1	-32.4	0.1	0.1	0.2	0.1	0.1	-	-	-	-	-	-	-	-	-	-
92. Phasianella australis	1.5	1.8	2.0	2.1	1.9	1.7	1.6	1.5	1.5	1.4	1.3	1.2	1.1	1.0	0.9	0.8	0.8	0.0	-43.3	-32.5	1.6	0.8	0.8	0.7	0.7	-	-	-	-	-	-	-	-	-	-
93. Phasianella ventricosa	2.1	2.3	2.2	2.1	1.8	1.5	1.3	1.1	0.9	0.8	0.7	0.7	0.6	0.5	0.4	0.4	0.0	0.0	-42.7	-32.0	1.3	0.9	1.0	1.2	1.2	-	-	-	-	-	-	-	-	-	-
94. Phasianotrochus eximius	0.9	1.0	1.0	1.1	1.1	1.1	1.0	1.0	0.9	0.9	0.8	0.8	0.7	0.6	0.5	0.5	0.0	0.0	-43.3	-30.3	1.0	0.5	0.4	0.3	0.2	-	-	-	-	-	-	-	-	-	-
95. Phlyctenactis tuberculosa	1.2	1.2	1.3	1.3	1.3	1.3	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	1.2	0.0	0.0	-43.5	-30.2	1.2	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-
96. Phyllacanthus parvispinus	2.2	1.9	1.6	1.4	1.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.6	-21.0	0.0	0.0	1.0	1.2	1.4	-	-	-	-	-	-	-	-	-	-
97. Phylloidesmium serratum	0.5	0.7	0.8	0.9	1.0	1.1	1.1	1.1	1.1	1.0	1.0	1.0	0.9	0.8	0.8	0.8	0.7	0.0	-43.4	-32.7	1.1	0.3	0.2	0.0	-0.1	-	-	-	-	-	-	-	-	-	-
98. Pinna bicolor	3.5	3.1	2.6	2.0	1.5	1.1	0.8	0.5	0.4	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-40.1	-32.7	0.8	0.8	1.1	1.5	1.7	-	-	-	-	-	-	-	-	-	-
99. Plagusia chabrus	1.5	1.5	1.6	1.6	1.7	1.7	1.8	1.8	1.8	1.9	1.9	1.9	2.0	2.0	2.0	2.1	2.1	2.1	-43.6	-30.1	-0.4	-0.3	-0.3	-0.3	-0.2	-	-	-	-	-	-	-	-	-	-
100. Plectaster decanus	1.4	1.4	1.3	1.2	1.1	0.9	0.8	0.7	0.6	0.5	0.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	-41.2	-30.0	0.8	0.8	0.9	0.7	0.6	-	-	-	-	-	-	-	-	-	-
101. Pleuroploca australasia	1.5	1.6	1.6	1.6	1.6	1.5	1.5	1.5	1.5	1.5	1.4	1.4	1.4	1.3	1.3	1.3	1.3	0.0	-43.6	-30.2	0.3	0.2	0.2	0.1	0.1	-	-	-	-	-	-	-	-	-	-
102. Pseudoboletia indiana	1.4	1.2	0.9	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-29.9	0.0	0.0	0.0	0.6	0.7	-	-	-	-	-	-	-	-	-	-
103. Pseudonepanthia troughoni	1.4	1.3	1.2	1.1	0.9	0.7	0.6	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.7	-30.3	0.6	0.6	0.7	0.9	0.7	-	-	-	-	-	-	-	-	-	-
104. Pteraeolidia ianthina	0.8	0.7	0.6	0.5	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.6	-12.6	0.0	0.0	0.3	0.4	0.5	-	-	-	-	-	-	-	-	-	-
105. Pterynotus triformis	0.3	0.3	0.3	0.3	0.2	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-38.3	-33.0	0.2	0.2	0.2	0.2	0.3	-	-	-	-	-	-	-	-	-	-
106. Ranella australasia	1.9	1.9	1.9	1.9	1.8	1.8	1.8	1.7	1.7	1.6	1.6	1.6	1.5	1.5	1.5	1.4	1.4	1.3	-43.6	-28.6	0.4	0.3	0.3	0.3	0.2	-	-	-	-	-	-	-	-	-	-
107. Sagaminopteron ornatum	0.6	0.6	0.5	0.4	0.4	0.3	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-39.5	-26.4	0.3	0.3	0.3	0.4	0.4	-	-	-	-	-	-	-	-	-	-
108. Sassa parkinsonia	1.9	2.0	2.0	1.9	1.7	1.5	1.2	1.0	0.8	0.6	0.5	0.4	0.3	0.2	0.2	0.2	0.1	0.0	-43.3	-30.2	1.2	1.1	1.3	1.3	1.3	-	-	-	-	-	-	-	-	-	-
109. Sassa subdistorta	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.3	0.3	0.3	0.3	0.2	0.2	0.1	0.1	-43.3	-38.7	0.0	-0.1	-0.2	-0.3	-0.2	-	-	-	-	-	-	-	-	-	-
110. Sassa verrucosa	0.0	0.1	0.2	0.2	0.3	0.4	0.4	0.4	0.4	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.1	0.0	-43.1	-35.1	0.4	0.3	0.2	0.1	-0.1	-	-	-	-	-	-	-	-	-	-
111. Scutus antipodes	1.9	1.9	1.9	1.8	1.8	1.7	1.6	1.6	1.5	1.4	1.4	1.3	1.2	1.2	1.1	1.0	1.0	0.0	-43.3	-30.1	1.6	0.6	0.5	0.5	0.4	-	-	-	-	-	-	-	-	-	-
112. Sepia apama	1.9	1.7	1.6	1.4	1.2	1.0	0.9	0.7	0.6	0.5	0.4	0.4	0.3	0.2	0.2	0.2	0.0	0.0	-42.6	-30.0	0.9	0.7	0.8	0.9	0.9	-	-	-	-	-	-	-	-	-	-
113. Sepia mestus	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-36.0	-28.6	0.0	0.0	0.0	0.0	0.0	-	-	-	-	-	-	-	-	-	-
114. Sepia plangon	0.7	0.5	0.4	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.1	-26.4	0.0	0.0	0.0	0.2	0.3	-	-	-	-	-	-	-	-	-	-
115. Sepioteuthis australis	4.8	6.7	9.2	10.6	11.4	11.1	10.1	8.4	6.9	5.1	3.9	3.0	2.1	1.6	1.3	1.0	0.8	0.0	-43.3	-32.0	10.1	9.1	9.4	8.4	5.5	-	-	-	-	-	-	-	-	-	-
116. Strigopagurus strigimanus	0.8	0.8	0.9	1.0	1.1	1.2	1.3	1.3	1.4	1.4	1.4	1.4	1.5	1.5	1.5	1.6	1.6	1.6	-43.6	-30.1	-0.4	-0.3	-0.3	-0.4	-0.4	-	-	-	-	-	-	-	-	-	-
117. Tambja verconis	0.0	0.0	0.1	0.2	0.2	0.3	0.3	0.3	0.3	0.2	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	-42.7	-35.9	0.3	0.3	0.2	0.1	-0.1	-	-	-	-	-	-	-	-	-	-
118. Tosia australis	1.9	2.0	2.1	2.1	2.2	2.2	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.3	2.2	2.2	2.2	0.0	-43.4	-30.4	2.3	0.0	0.0	0.1	-0.2	-	-	-	-	-	-	-	-	-	-
119. Tosia magnifica	0.3	0.4	0.5	0.6	0.7	0.9	1.1	1.2	1.2	1.3	1.3	1.3	1.3	1.4	1.4	1.4	1.4	0.0	-43.4	-32.9	1.1	-0.3	-0.5	-0.6	-0.6	-	-	-	-	-	-	-	-	-	-
120. Turbo torquatus	3.5	3.1	2.7	2.3	2.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-37.6	-30.1	0.0	0.0	1.6	2.0	2.3	-	-	-	-	-	-	-	-	-	-

Table 2 (Cont.). Predicted latitudinal distribution of current and future per transect abundance (n/50m2) of invertebrate species from LTRMP and RLS data.

SPECIES NAME	ABUNDANCE IN SOUTHEAST AUSTRALIA BY LATITUDE																	ABSOLUTE RANGE EDGES		PREDICTED CHANGE IN ABUNDANCE					% INCREASE/DECREASE FROM CURRENT					
	-35	-35.5	-36	-36.5	-37	-37.5	-38	-38.5	-39	-39.5	-40	-40.5	-41	-41.5	-42	-42.5	-43	-43.5	equatorward range edge	poleward range edge	Δ -43.5°	Δ -42.5°	Δ -41.5°	Δ -40.5°	Δ -39.5°	-43.5	-42.5	-41.5	-40.5	-39.5
121. Turbo undulatus	11.1	11.8	11.9	12.0	12.1	12.1	12.0	11.9	11.8	11.6	11.4	11.2	11.0	10.7	10.6	10.3	10.1	9.8	-43.6	-30.8	2.2	1.7	1.3	0.9	0.4	22.8	16.4	12.3	7.6	3.6
122. Umbraculum umbraculum	1.0	1.1	1.1	1.0	0.9	0.7	0.5	0.3	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	-42.6	-32.7	0.5	0.5	0.6	0.8	0.9	-	3387.4	2393.6	1316.4	600.9
123. Uniophora granifera	1.3	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.3	1.3	1.3	1.2	1.2	1.2	1.1	1.1	1.1	0.0	-43.4	-30.0	1.4	0.3	0.2	0.2	0.1	-	26.2	19.7	15.3	9.8

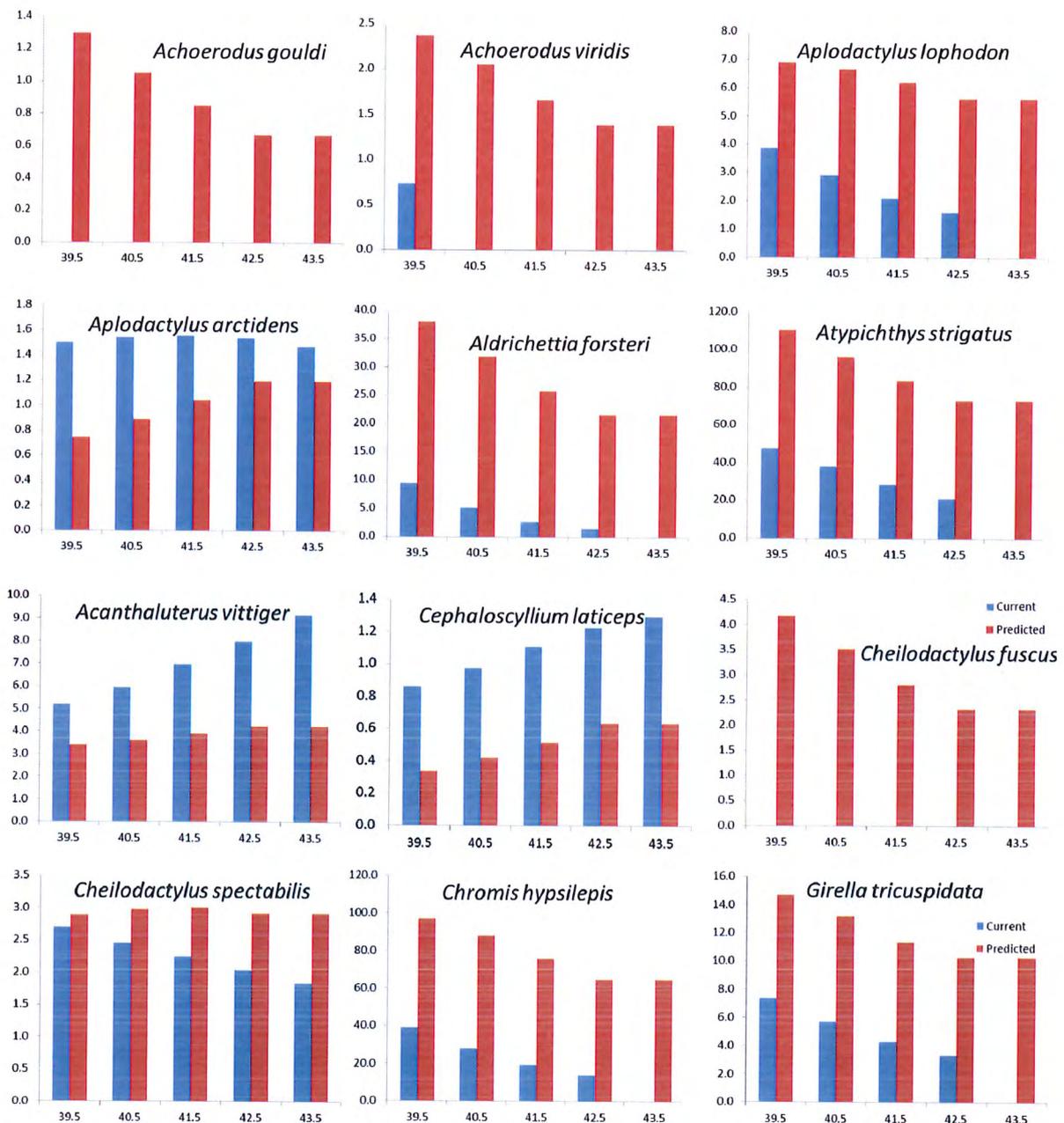


Figure 19. Current (blue) and predicted (red-2060's) abundance (n= y axis) by latitude south (x axis) and transect (500m2) for typical fishes on Temperate SE Australian reefs based on modelled species distributions and predicted future thermal distributions (from Oliver et al. 2014).

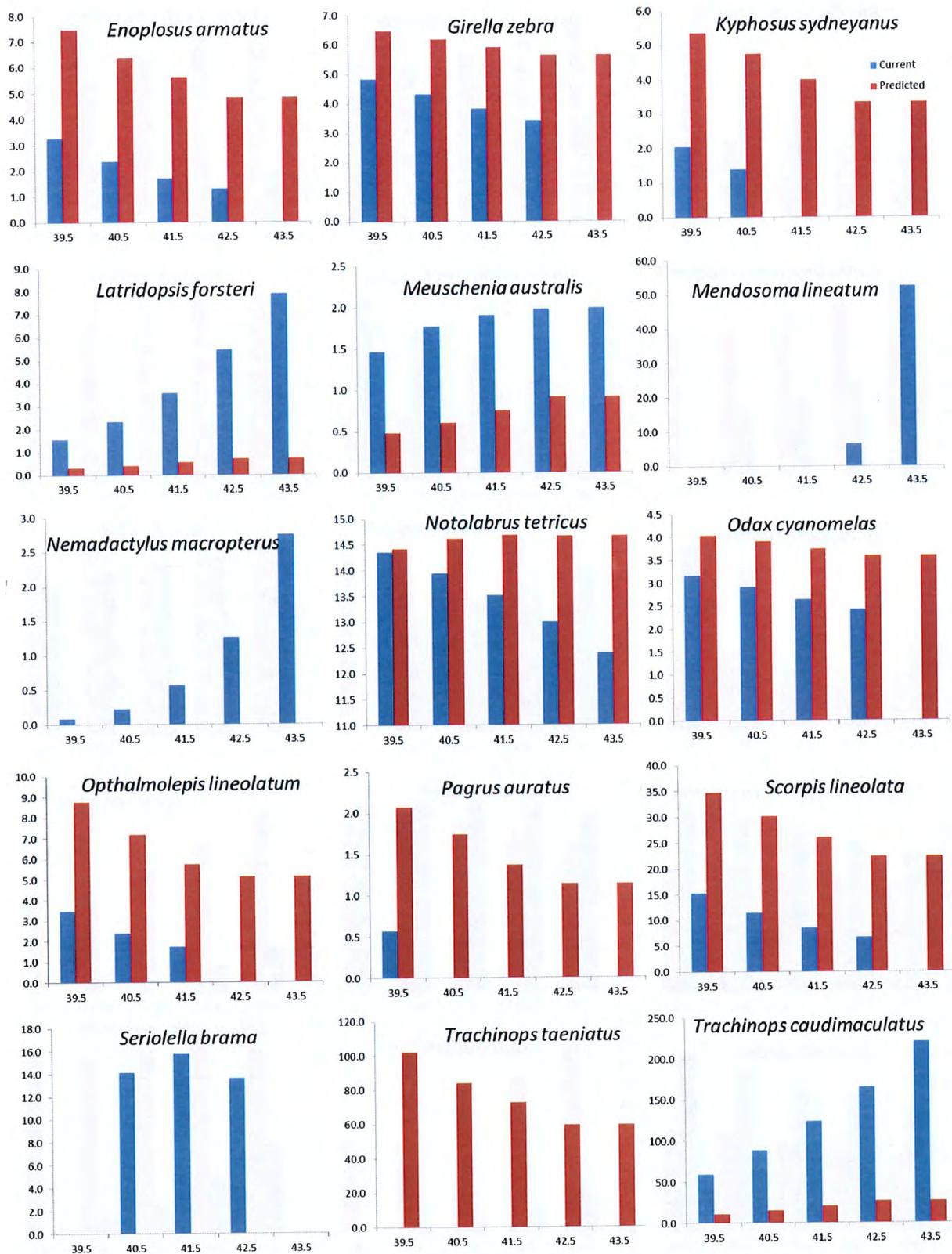


Figure 19 (cont.). Current (blue) and predicted (red-2060's) abundance (n= y axis) by latitude south (x axis) and transect (500m²) for typical fishes on Temperate SE Australian reefs based on modelled species distributions and predicted future thermal distributions (from Oliver et al. 2014).

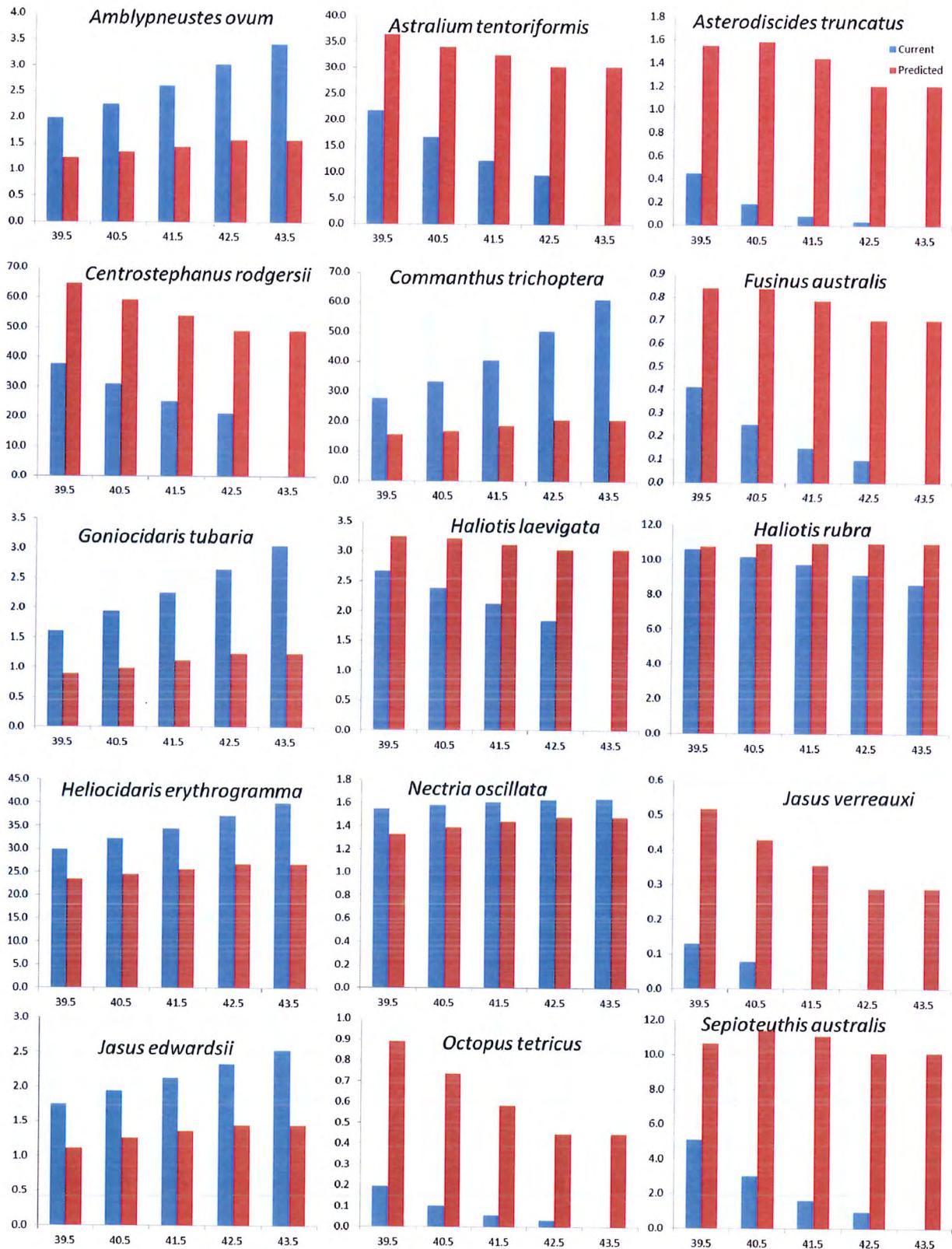


Figure 20. Current (blue) and predicted (red-2060's) abundance (n= y axis) by latitude south (x axis) and transect (500m2) for typical mobile macroinvertebrate species on Temperate SE Australian reefs based on modelled species distributions and predicted future thermal distributions (from Oliver et al. 2014).

Discussion

Many of the key points within this study are discussed in detail within the results section as part of a combined results/discussion relative to each of the individual objectives. The discussion here therefore provides more of an overview, linking these individual components. It must be stated upfront, that as this work focusses on monitoring climate change and informing adaptive management responses, there are two strongly related components, overall monitoring of temperate reef systems, and linking this to MPAs, by which changes in typical coastal systems can be compared with corresponding changes in those with a degree of protection to anthropogenic impacts. This is a deliberate approach, as while there may be a number of processes that interact with climate change, potential management levers to influence such change are rather limited. These are likely to be mediated via fishery management (where there is a clear interaction between fishing effects and climate driven processes, and this is demonstrated by contrasts of fished vs MPA habitats), or broader conservation related intervention where patterns are widespread and deleterious, irrespective of current spatial management arrangements.

Overall this project was successful in bringing together a range of matching biological datasets for the analysis of current and possible future patterns and distributions under a changing climate. In parts the analysis was limited by the extent of available time series from which to examine correlations with physical processes, however, this first examination of existing datasets in the light of needing to inform climate change adaptation, was particularly informative in highlighting gaps in current biological datasets and monitoring programs, as well as related gaps in the availability of physical data. The work indicated that to make valid correlations, long time series of data are needed, extending over periods of at least twenty years, during which physical processes may also change sufficiently to detect bio-physical coupling. Many current monitoring programs are MPA performance focussed, with multiple year gaps between consecutive surveys. While this approach may be suitable for that role (as reviewed by Keough et al., 2007), it is less suitable for informing climate-change relationships, at least where the aim is to develop statistically valid correlations between biological patterns and physical processes. Thus, at least part of an integrated approach to informing this space in SE Australia and elsewhere, would involve increasing the frequency of monitoring at a range of key reference locations within the region.

Some specific gaps to fill in this space include annual monitoring at a set of core reference locations to establish a better understanding of biophysical relationships and the key drivers of variability. Clearly the Maria Island region forms one of these given the continuity of data from that area and the close coupling with CSIRO's nearby reference station. Similar programs would ideally be established at Jervis Bay (adding value by continuing the existing time series), and NE Victoria (Cape Howe), with matching physical data collection to allow biophysical relationships to be determined where they occur.

Analysis of the one existing long-term dataset at Maria Island did show a range of climate driven responses, including fluctuations in various diversity metrics as some species distributions changed in response to warmer and cooler years. Another key response was the increasing influence of herbivorous fish as presumably warmer conditions aided digestion of algal material in their diet. This response may be one of the biggest functional changes associated with fish assemblages in the cool temperate zone, and requires further investigation through experimental and modelling approaches to determine the extent that this extra grazing pressure might influence algal assemblages (discussed later). A further outcome of this work was the detection of an interaction between the protected MPA and areas open to fishing, with greater resilience to inter-annual variability in diversity metrics being found within the MPA. This relates in a greater part to fluctuations in the abundance of warm affinity species that occupy urchin barren areas that have formed at a number of locations in the region. Hence, much of the resilience pattern appears to be related to the greater ability of the MPA to resist urchin invasion and barren development. Clearly this finding is just one from the case study at Maria

Island, and not replicated elsewhere due to the overall lack of other long term studies throughout the region, and certainly system responses may well vary from region to region depending on the relative natural abundances of key species that drive these responses. However, some generality is provided for the eastern Tasmanian region where an AUV-based study contrasting the extent of urchin barrens from inside the Governor Island (Bicheno) marine reserve with adjacent fished areas has documented a similar pattern of less barrens in that reserve (Perkins et al.-submitted manuscript). As longer-term monitoring continues at key locations throughout this region, the extent of this generality will be more readily tested empirically.

We suggest, given the evidence of increasing barren formation in places such as Cape Howe and Beware Reef (RLS data), that mechanism is likely to be the greatest factor driving change in biodiversity patterns in SE Australia. Hence continued monitoring of changes in the biological assemblages of this area is needed to fully inform adaptive management and the effectiveness of management actions. The current MPA framework in the region, based on a bioregional approach, appears to be the most appropriate basis for continuing and expanding monitoring programs focused on informing climate based management responses, given the need to untangle fishing and climate related responses as demonstrated at Maria Island. Where gaps in this framework exist, either through inadequately protected reference locations or missing bioregionally-based key habitats, these could readily be addressed by creating “scientific reference areas” as an additional spatial management response. When matched with existing or enhanced monitoring programs, and coupled with appropriate reference sites in fished locations, the overall information provided would inform climate change adaptation, EBFM, and MPA management as an integrated approach.

The largest existing gap is centred around NE Tasmania where there is currently no MPA or long-term observing program. Establishing a regional reference area, with associated monitoring of representative coastal sites is recommended as a high priority to not only complete an adequate SE Australian network, but to also track changes occurring in one of the regional areas most significantly influenced by recent warming and the associated influx of warmer affinity species.

During our analysis, another clear gap in our knowledge that became evident was the spatial distribution (by abundance) of many species outside of their central range, and particularly towards range edges. The Reef Life Survey dataset was particularly informative in filling these gaps for the analysis undertaken here, however, to improve our quantitative knowledge and to improve future predictions, this information gathering needs to be continued, not just in time but in space. This work particularly needs to target latitudinal gaps in the current distribution of sites within the region, and sites with anomalous abundances that can influence overall averages and hence predictions. Specific recommendations are to undertake a targeted research program to ensure, where possible, the eastern Australian coastline is represented by sites at the ten km spatial scale to allow more precise detection of range edges and prediction of species/abundance distributions. Such a program would infill the current distribution of sites and provide a comprehensive baseline from which to measure future change. Site distributions at this scale already exist in Tasmanian waters (as part of reef health and bioregional studies) and are readily achievable with cost effective methods such as RLS, and would ideally be repeated at the decade time scale to compliment more frequent sampling at the core reference locations distributed throughout the SE region.

To address limitations in the available data we explored model-based approaches to deal with sparse data towards range edges, and statistical approaches to deal with uncertainties in the quality of citizen science data such as RLS, and these approaches can form the basis of future work in this space that incorporates such datasets. Hence, along with compiling existing datasets into a readily manageable and available database, we have developed analytical frameworks to improve the value of this data for future analysis. One component of that framework has been the development of a database that may form the basis of a communally utilised data repository for all temperate reef monitoring programs ranging from WA to NSW, allowing spatial and temporal information on a wide range of species to be examined on a regular basis with the aim of informing adaptive management as timely as possible of

significant changes. That database could then be linked to the analytical tools discussed above to produce a range of tailored outputs, including current status of species distributions, as well as revised predictions of future distributions as more information comes available.

The ideal goal would be establishment of a common database within the IMOS and AODN framework with linked automated analysis tools that flagged changes in the abundance of key species such as urchins, lobsters and abalone, indicator fish species and species groupings (e.g. herbivores or herbivore biomass), the extent of urchin barrens, algal cover, and characteristics such as the mean thermal affinity of fish/invertebrate populations. We now have sufficient quantitative data to establish and test such a structure, allowing the knowledge obtained to flow into an integrated reporting process such as the 5 year SOE reporting for the marine environment, where a climate change focussed output could be an output for management review.

Our modelling was a first attempt in this field, bringing together all of the regionally available matching quantitative data to make predictions of future change. We are aware that the models are simply that, they are not perfect predictions, and are certainly even less so for species with limited information available. However, by presenting much of our available data here, and our initial approach to analysis, we hope to stimulate discussion of how we move forward by improving available data, by improving our modelling methods, and linking these with conceptual and quantitative ecosystem models to provide a further and fuller understanding of likely functional processes that can additionally alter abundances of individual species as well as ecosystem function. Certainly our future predictions are based on thermal/latitudinal distributions only at this stage, yet species also respond to gradients in exposure, depth, habitat complexity and inter-specific interactions, as well as broader oceanographic processes that alter levels of recruitment at a regional scale. Future modelling needs to incorporate this extra complexity where possible, and to identify any important gaps in current knowledge of species distributions with respect to their relationships with physical factors.

Despite the limitations discussed above, our species distribution modelling allowed predictions to be made relating to the likely future distributions of many fish and invertebrate species under the IPCC A1B scenario addressed by Oliver et al. (2014) when predicting inshore SST for the SE Australian region. The typical response for both fishes and invertebrates was a general increase in species richness and diversity in the NE Tasmanian region, with many of the cooler adapted species undergoing declines in abundance. However, there were few cases where these declines were extreme, and where they were predicted to be so, they were either for introduced species, or the cool temperate fish *Mendosoma lineatum* (Real bastard trumpeter). This species is likely to become extinct in Tasmanian waters under the scenario examined, however it is also found in southern New Zealand, so has a climate refuge there. It needs to be re-stated though, that this analysis only applies to species detected on our surveys, and not to all fishes and mobile invertebrates on reefs within the study area. There are a number of cryptic and rare species, including intertidal seastars, that are only found in the SE region of Tasmania for example, and these will most certainly become extinct under the A1B scenario. Hence, while we found no urgent conservation priority species in our analysis, several are certainly in that category within the region, and will likely need to be conserved in aquaria in the future if their survival is a conservation priority.

While for fishes and many mobile invertebrates the extent of regional change was not predicted to have a significant impact on system function under the A1B scenario, this was not the case for invertebrate species such as the Long-spined urchin *Centrostephanus rodgersii* or the Southern rock lobster *Jasus edwardsii*. By the 2060's, *Centrostephanus* numbers were forecast to double in abundance in NE Tasmania, in an area where problematic barrens are developing currently, and this can only get worse with increasing numbers. Moderate numbers were also forecast to extend to southern Tasmania, extending potential barren formation throughout all Tasmanian waters where suitable habitat exists. This would likely be exacerbated by a concurrent predicted decline in the abundance of lobsters, the main controlling predator of *Centrostephanus* in many locations. Coupled with the likely loss of some cool-temperate fish and invertebrate species (and algal species not able to

be included in our analysis), it is this likely significant alteration to ecosystem function that contributes the major challenge to adaptive management in the future, both with respect to conservation values and fishery management. Predictions of the likely future abundance of other potential urchin predators, such as the Eastern blue grouper *Achoerodus viridis*, or the Eastern rock lobster *Jasus verreauxii*, suggest that their numbers, while increasing in the region, will still be at sufficiently low levels to not influence overall prey numbers significantly. Initial indications are that *J. verreauxii* numbers in the NE of Tasmania may increase sufficiently in far NE Tasmania (e.g. 39.5 S) to almost offset the loss of *J. edwardsii* at that latitude, although it is not clear to the extent that *J. verreauxii* will occupy shallow reef systems (as it is currently predominantly found on deep reef systems in NSW), or that similar numbers will translate into similar biomass given the possibility of differential growth rates between species at the upper and lower limits of their range.

For the major problem of habitat loss via barren formation, the optimal adaptive management (as discussed in the results for Objective 4) is to ensure lobster stocks (of both species) are managed in a regional approach to rebuild resilience to barren formation via adequate abundances and size structures of this key predator. This would ideally be coupled with an MPA network appropriately configured to perform a scientific reference area role, such that well planned monitoring programs, undertaken in areas selected by management agencies with a consensual approach to identifying these gaps and remedying them, are able to inform adaptive responses in a timely way. Given that there will be regional variation in the species/abundance mix, such as that recorded between surveys at The Kent Group and Maria Island in Tasmania, and that ecosystem function can change over relatively small spatial scales, management responses may well need to be tailored to these scales. Hence the need for regionally focussed monitoring networks. The robustness of adaptive management is only as good as the information available, and obtaining this information is key to improving our adaptive capacity, regardless of which management strategies are ultimately applied.

One somewhat unknown future change on cool temperate reefs is the increase in herbivorous fishes that arises as conditions become more favourable for algal digestion and related metabolic processes. The long term patterns detected within the Maria Island region suggest that this may be a significant functional shift that has potential to alter the distribution of algal productivity into the food chain, and such changes may be widespread in cool temperate systems. For SE Australia the future implications of this need further exploration. Currently the ecological role/influence of fish herbivory is poorly understood in temperate Australia and this knowledge gap needs addressing if we are to be able to more effectively predict changes in ecosystem function in the future. A research priority is to better understand the extent that key herbivores such as the herring cale (*Olisthops cyanomelas*), Sydney drummer (*Kyphosus sydneyanus*), Zebra fish (*Girella zebra*) and Ludderick (*Girella tricuspidata*) influence algal productivity and community structure across their current gradient of abundance. If such species do have the capacity to substantially alter system function in the future, resilience could be enhanced by direct manipulation of their overall abundances through targeted fishing or similar activities.

Our analysis precluded predictions of algal distributions in the future due to a lack of spatially distributed quantitative data on algal species cover over the range of the study region. This information needs addressing as part of future programs to better inform our knowledge of the latitudinal distribution of species, particularly as temperate Australia is a hotspot of endemism and algal diversity, and unlike the fish and invertebrate assemblages, diversity within this region would likely decline with future warming rather than increase. Moreover, there are a number of algal species only recorded in SE Tasmanian waters and all would be expected to become extinct under the 2060's warming scenario. In addition, several algal species that are key habitat species, including the Bull kelp *Durvillaea potatorum* and the Strap-weed *Lessonia corrugata*, would be expected to decline significantly, causing a major alteration to the shallow (0-5 m) habitats in which they often dominate. Further work is urgently needed to understand the longer-term implications of this. Therefore a specific recommendation is to implement a targeted quantitative survey of the distribution of algal species throughout eastern Australian temperate waters as an initial baseline from which to adequately

describe range edges, abundance/latitudinal distributions and to act as a long-term baseline from which to measure future change. Knowledge at this scale is already available in Tasmanian waters, while in Victoria and NSW it is available from MPA monitoring programs but not at locations in-between. In these states an infill program would ideally be undertaken as part of spatial gap-filling surveys discussed previously, and act as a solid baseline from which to detect future changes and prioritise conservation issues.

Overall, the key to good adaptive management is to have the information necessary from which to base decisions. Ultimately, the necessary management decisions will flow naturally from this. The optimal, and most cost-effective approach for monitoring programs to best inform adaptive management via delivery of up-to-date relevant information, is to build upon current initiatives for MPA and biodiversity monitoring within the SE Australian, and more broadly in temperate Australia. These programs are currently in place in many jurisdictions, use a common monitoring methodology, have appropriate spatial coverage to inform changes occurring at regional scales, and allow regional differences in ecosystem function to be accounted for. Moreover, they also often include a pre-existing time series to allow earlier recognition of climate induced changes, and have contrasting fished and protected sampling designs to detect fishing and climate interactions where present, such that management responses may be informed and implemented if such interactions are deleterious. With a clear need to incorporate results from multiple regions and states into a common climate reporting framework, linking results of monitoring programs through a common database structure may significantly facilitate analysis and reporting of changes as they occur.

Clearly the current system of MPA-based regional monitoring will not necessarily cover all the vectors / stressors of change. It will not detect change on deep reefs for example, beyond diving depths, or in shallow reef systems within estuarine areas that may be under strong physical influence of rainfall/introduced pests or nitrification/siltation. However, given the approximately 100 km spatial spacing of the current MPA network and monitoring programs, and the spatial distribution of external monitoring sites outside of no-take areas, these locations do provide the capacity to adequately represent the typical inshore coastal reef habitats in the SE Australian region and the threats to them. For deeper reef systems below diving depths, the advent of baited underwater video systems is allowing a more comprehensive knowledge to be developed, again with a central reference to existing MPAs particularly in NSW and Victoria. Further emphasis may be required on the development of such programs to compliment the inshore monitoring, however, in a biodiversity sense, techniques such as this are constrained by the much smaller overall set of phyla and species able to be surveyed by this approach.

In the sense that a regional approach to climate change monitoring is warranted and necessary at informative (100 km) scales, the locations to best base monitoring programs are the regionally significant MPAs and associated coasts (discussed in detail in Objective 2), as they offer multiple benefits from such programs, and such programs should engage multiple management agencies, linking conservation and resource management in a common framework for responding to climate change. No specific species or indicators are recommended as the focus of such programs, rather the broad biodiversity approach currently used in many locations, as that is robust for the species of significant interest (e.g. *Centrostephanus*, lobsters, blue grouper, abalone), and additionally provides the more broadly needed information on extent of change in diversity patterns and shifts in system function.

Finally, the monitoring requirements for climate change adaptation, the issues they address and the management responses/levers that they relate to are summarised in Table 3. While this is not necessarily a comprehensive coverage of all likely CC mediated issues (for example the effects of a changing climate on the influence of toxic dinoflagellates), it does summarise the link between many of the major issues, likely management levers (which as discussed in our initial workshop and presented in Appendix 5, are very limited) and the monitoring, analysis and reporting frameworks necessary to inform these. We hope that our work, and the summary in Table 3, provides a framework

for further discussions such that this can be refined, and incorporated into the future management and monitoring response for climate change adaptation and understanding.

Table 3. Summary of the central issues currently arising in SE Australia in response to a warming climate, potential management responses, and the information/monitoring requirements necessary to support these.

Priority	Issue	Management response	Monitoring/information requirement
H	<i>Centrostephanus</i> expansion/Habitat loss	Mitigate <i>Centrostephanus</i> numbers by Increasing lobster predation via rebuilding of biomass and size structures in critical regions Protection or manipulation of alternative predators (e.g. Blue grouper) Culling urchins No take areas	<i>Centrostephanus</i> abundance Lobster abundance Habitat loss (kelp cover, sponge cover, loss of diversity) Predator abundance
M	Expansion of fish herbivores	Understand ecological implications of potential impacts on algal productivity to inform adaptive measures.	Monitoring of changing herbivore abundances and targeted research to understand likely consequences of this additional grazing.
M	Loss of endemic species	Protection of critical habitat, translocation to refuge areas, long-term protection of priority species in aquaria.	Improve knowledge of range by abundance distribution of cool temperate endemic species, particularly algal species where the current knowledge gap is greatest. Refine modelling approaches such as species extinction models to better predict current and future range edges and abundance distributions.
M	Inform management an public of rates of change and emerging issues	Policy support for current and future monitoring programs, fund and develop a common database and reporting structure and link climate change reporting to the State of Environment process as a key reporting measure.	Develop a common monitoring and reporting framework between state agencies, continue and expand monitoring using current broadly-based protocols, improve spatial coverage of reference areas via establishing areas in large spatial gaps and infilling of species/abundance/range edge relationship at finer scales via RLS or similar state-based surveys at 5 year reporting scales.
M	Marine Protected areas. Are these an essential direct component of climate change management for biodiversity protection, or an indirect component via their reference area role?	Continue to evaluate the effectiveness of off-reserve management measures in place or being developed by reference to no-take areas (best strategy is to manage the whole coast effectively). Consider appropriate spatial management to protect representative examples of biodiversity if other measures fail.	Continue monitoring based evaluation of the current MPA network over appropriate time scales (20 years) to establish regional patterns in the extent that no-take areas can or cannot provide increased resilience to adverse climate change impacts.

Conclusion

In conclusion, we have successfully collated and analysed a range of long-term marine ecological data records for southeast Australian reefs and used these to quantitatively describe relationships between species distributions and abundances and changes in the physical environment through time, location and relationship with processes such as temperature and nutrients. We have found that long-term datasets are critical to understanding biological relationships with climate-related physical processes. Few datasets with the necessary time-span exist, and remedying this situation is critical to understanding climate related patterns into the future. However, where such datasets exist (such as the Maria Island monitoring program), some clear patterns are detectable, and that these often show an interaction with no-take protection within MPAs.

This MPA interaction suggests both that such areas can offer some degree of resilience to climate mediated change, and that by adapting fishery management practices, such resilience may also be rebuilt in off-reserve areas. In that sense, the existing MPA network in SE Australia offers a significant benefit to biodiversity-conservation management in response to CC, as well as an important reference role for informing adequate off-reserve management responses. Information from monitoring programs utilising this reference role thus improve the robustness of adaptive management frameworks by providing feedback on the effectiveness of alternative management responses.

We found that the current MPA network in SE Australia offers optimal locations and the mix of species necessary for monitoring programs to best inform adaptive management via delivery of up-to-date relevant information. However, some bioregional gaps still exist, and not all MPAs have no-take areas of sufficient size or configuration to act as unbiased scientific reference areas. Remedying that gap, and matching it with suitably designed monitoring programs will significantly improve the flow of information required to optimise adaptive management responses. Understanding temporal patterns from such programs also needs to be informed by an improved knowledge of the quantitative spatial distribution of individual species. Data acquired from RLS was critical to informing the distributions of many species, particularly towards range edges, and further surveys of a similar nature will improve predictions of future distributions, as well as our capacity to detect such changes as they occur.

Our models developed to quantify and predict the impacts of climate change across reefs in the southeast Australian region suggest that the relative abundance of many species will change over the next 50 years. For most reef communities this will not involve order of magnitude changes in abundance of many core species, but rather, subtle changes of most species (due to their broad latitudinal/abundance distribution in this region), with an increase in diversity reflecting an influx of warmer species to the mix. Few of these are predicted to significantly alter community structure, with the exception of *Centrostephanus rodgersii*, as increasing numbers of this ecosystem engineer are likely to precipitate increased urchin barren formation, and resultant loss of habitat and biodiversity. There are a range of potential responses to this problem, and we have demonstrated that resilience to barren formation is possible using one spatial management tool (MPAs) to rebuild urchin predator populations. At Maria Island, the lobster population and its natural size structure was the key factor responsible for urchin decline. Modelling of likely future species distributions indicates that this will continue to be the case over the next 50 years in the SE, with alternative predators such as blue grouper predicted to increase, but not to ecologically meaningful numbers. Overall, rebuilding region-wide resilience to barren formation is the most important adaptive management response needed for the SE temperate reef system over the next 50 years, and the approaches to undertaking this, or exploring alternatives if that approach is not feasible, are going to be some of the greatest adaptation challenges in the immediate future.

Implications

There are several implications of this work for end users such as management and industry.

The first of these is that as long-term monitoring programs are necessary and invaluable in providing the quantitative information of on ground changes and the responses of marine communities to differing management initiatives, these programs need to be supported and funded within a sustainable fisheries and climate change adaptation framework, in addition to the current MPA-related funding focus and objectives. Agencies and programs such as FRDC and IMOS would ideally recognise the value of this, and work with research providers to ensure that a reef monitoring framework was in place and optimised to meet a broad range of management needs and objectives. In the past, funding for such work has been ad-hoc, with funding primarily being grant-based (with the exception of Victoria), including ARC, NHT, NRM, FRDC, CERF, but with little continuity. If marine management agencies within Temperate Australia do want to be adequately informed of climate related changes on Temperate reefs into the future, then the ad-hoc nature of the current approach needs to be addressed.

The second of these is that marine protected areas are effective in providing some resilience to climate change and offer one approach to minimising climate-related impacts to marine communities. Certainly many changes are anticipated in response to a warming climate, as our predictive modelling of species abundance and distribution changes suggests. Many of these will be general changes that do not necessarily interact with human induced pressures and will simply be adapted to in a passive acceptance of change. In that sense, the monitoring approaches suggested here will be effective in monitoring such changes so they can be understood, accepted and acted on where possible. However, in the case of urchin barren formation, such changes are deleterious to both productivity and biodiversity values, hence the need to build resilience to barren formation where possible

In our case study, and likely in many parts of SE Australia, this resilience is primarily mediated through resistance to *Centrostephanus* population increases that result in barren formation. Investment is needed to further test the generality of these observations on a regional basis, through longer-term observing of processes occurring in regional MPA relative to adjacent fished areas, as well as manipulative experiments to mimic natural predator/prey levels. However, as the abundance and size structure of lobster populations is the most likely key to controlling *Centrostephanus* numbers in habitats where lobsters are common, an adaptive response to climate change is possible via management actions that restore lobster populations. There will though, be locations such as the Kent Group in Bass Strait, where lobster numbers are naturally low due to a lack of larval supply (recruitment limitation), and in such locations predator mediated control of urchins may not be possible. Whether restoring urchin predators is mediated via spatial management, rebuilding of critical lobster biomass more regionally, or some combination of both, finding a solution is going to be a major management issue over the next decade. Ideally the optimal solution is to rebuild lobster stocks as widely as possible to prevent urchin barren formation to the greatest extent possible. Alternative approaches to *Centrostephanus* control are currently being trialled, including development of a fishery for *Centrostephanus* and planned culling by divers. However, while potentially successful in reducing urchin numbers in shallower diving depths, they are unlikely to be able to prevent barren formation at depths below 15 m due to decompression limits on divers, yet evidence suggests most barren formation in Tasmanian waters is in depths below 15 m (Perkins et al. –submitted MS) so control via natural predators remains the most likely viable option at this stage.

Following on from this, there is a clear intersection between MPAs and developing our understanding of fishing-related changes to coastal ecosystems, including changes that may be mediated by climate change. In many locations MPAs have been chosen on a bioregional basis (e.g. Victoria and NSW) and do represent typical coastal and fishery habitats within them, thus forming an adequate reference network by which to monitor change and inform management responses. However, not all coastal

regions are adequately covered (Tasmania has yet to complete a bioregionally-based network), and some MPAs lack adequately protected no-take areas of sufficient size to be deemed appropriate reference areas. Ideally these gaps would be addressed with the wide support of conservation and fisheries management agencies and communities, to ensure monitoring programs were effective, and management agencies were adequately informed of changes as they occur, and the degree that these vary on a regional basis. This will allow us to track marine biodiversity and productivity shifts due to a wide range of stressors in general (warming waters, changing ocean chemistry, loss of habitat, changing fishing pressure etc) with a reference network that is representative of our open coast reef systems. Thus providing an integrated monitoring system that informs all levels of management and potential management responses to improve resilience and productivity.

Recommendations

Support the existing monitoring framework on rocky reefs within Temperate Australia, but to adapt it such that the focus is an integrated monitoring program to inform integrated management, meeting the needs of climate change adaptation, EBFM and MPA evaluation. The no-take MPA framework is essential as part of this, to untangle fishing vs climate interactions where they occur.

Maintain a realistic time series in key locations (Jervis Bay, Cape Howe, Maria Island) to ensure trends can be detected adequately, particularly if the intent is to match climate variability with biological variability. This time series is ideally continued annually at multi-decade time scales. At 100 km scales (maintain a minimum of 5 yearly surveys to track change at regional scales and within regionally differing systems).

Additional surveys encompassing a wide range of habitats (depths, exposures etc) and geographical range, are needed to provide adequate information about the abundance of species in the tails of their distribution, and in habitats not well represented in MPAs. Ideally at 10 km scale to adequately describe range edges. These need to include quantitative algal biodiversity data wherever possible to allow better predictions for algae to be developed. Repeated surveys at decade time scales supplement patterns detected in recommendation 2, and inform extent and rate of range changes through time.

As a framework is currently in place, across multiple states and using a common methodology, it is sensible to both support this framework and extend it where possible such that it is adequate for informing CC focussed adaptive management. The Reef Life Survey volunteer program provides a cost-effective way of supplementing state agency based monitoring programs, and, with the notable exception of provision of algal diversity data, provides an otherwise ideal way of providing the additional spatial coverage currently lacking in the MPA-focussed state programs.

Adopt a standard database format such that programs in all states and by all agencies (including RLS) are able to communally access up-to-date species abundance and distribution information for the wide range of species that transition across state boundaries. Ideally integrated within IMOS and the AODN, with automated analytical and reporting tools. This would be suitable for state-of-the-environment reporting, as well as for regularly updating information for management addressing CC issues.

Utilise the common database framework to provide regular climate-based updates and assessments of biological changes occurring. Ideally this would be on a 5 year basis and aligned with SOMER reporting. As part of this, continue to refine species distribution models with the necessary quantitative abundance information needed within the tails of the distribution of key species of interest.

Where clear (bioregional) spatial gaps exist in the current MPA network (such as NE and northern Tasmania), or in the availability of no-take reference areas within current MPAs, address these gaps with suitably placed MPAs (or any other form of spatial closure that is appropriate) designed to be adequate reference areas for informing future CC related changes and responses to management initiatives. These need to be in typical coastal “representative” habitats. As no-take areas need to be in place for many years to be effective as reference areas, these locations need to be fixed.

If MPAs or similar spatial management options are included as an adaptation response to managing biodiversity values, they do need to be long-term and stable to build resilience. The concept of moving MPAs to protect hotspots as they emerge is not likely to be viable given the time frame necessary to build resilience.

The biggest future change to reef systems in SE Australia that management activities can meaningfully address is most likely to be mediated via increasing abundance of *Centrostephanus rodgersii* and the associated barrens that form when this species is present in large numbers and unregulated by predation. Addressing barren formation is therefore likely to be the central issue for climate change adaptation in this time frame if we are to minimise impacts on fishery habitat and the biodiversity it supports. We know that this is an issue that can be addressed, with a range of management options including spatial closures and rebuilding of lobster numbers and size structures, and recommend that management agencies and all stakeholders work together to ensure that a working outcome is achieved that minimises overall habitat loss.

As herbivorous fishes are both shown and predicted to increase with warming, the implications of this are unclear but need to be determined through targeted research to better understand grazing rates, target species, and the extent that fish herbivory may alter algal assemblages and productivity into the future.

Extension and Adoption

The project was communicated to end users in an initial project workshop with invited stakeholders (workshop report is given as Appendix v), and then via a second workshop facilitated by Gretta Pecl at IMAS, on Nov 4th 2011, hosting key researchers working on major climate change projects and initiatives, to maximise the awareness of projects between researchers and stakeholders. In addition, a project flier was produced to communicate the project to the wider community (shown below). Since that time, our focus has been on developing our analysis to the stage of reporting and publication, so that we had a product from which to base further discussions. The current publications, and additional analysis reported here, now form both a mechanism for communicating this work to all stakeholders, and a basis from which we intend to hold a workshop to begin discussions about the implications of this work for future adaptive management. Ultimately, coupled with the outputs from a range of related Climate Change projects, this work will lead to the adoption of management measures that are appropriate for the management of marine conservation values into the future.

Adaptive management of temperate reefs for climate change: New approaches for ecological monitoring and predictive modelling

Climate change necessitates management adaptation on temperate reefs in Australia

Waters along Australia's most densely populated east coast are warming at 3.8 times the global average – the most rapid change in the Southern Hemisphere. Ecosystems in this region are severely threatened and significant biodiversity changes are anticipated, including loss of diversity in places. Ecosystem changes associated with climate change will require wise decisions about where, how and when to apply particular adaptive management interventions.

Theoretical frameworks and laboratory experiments dominate climate change adaptation science, but the associated simplification of complex social and ecological processes means that potential adaptive management decisions still lack a scientific foundation underpinned by in situ measurements. This project combines long-term and spatial ecological datasets from temperate reefs with remotely sensed environmental characteristics to determine climate forced signals in ecological responses, to better inform predictions of likely future changes and the practical adaptive management responses that may build resilience to such change. Unless protocols for tracking and predicting ecological changes are well informed, the remote nature of marine habitats, with associated difficulties and expense when mapping biodiversity assets, will inevitably translate to poorly-conditioned management response.



Photo: Maria Beger, 2010

Objectives of the project

Goal

1. To build a database of remotely-sensed and other physical environmental data that corresponds to locations included in long-term Marine Protected Area and Reef Life Survey monitoring programs
2. To identify climate change impacts on inshore communities and also environmental predictors of those impacts that are relevant to managers
3. To identify indicator species/ groups for monitoring that respond measurably to the climate
4. To engage with stakeholders to develop adaptive management of temperate reefs to manage climate change impacts, and assess the monitoring requirements

Benefit

- ➔ enable easy access to ecological and environmental databases for temperate reefs
- ➔ benchmark changes to the environment, and to enable an assessment of possible adaptive responses
- ➔ identify triggers to inform the need to adapt management
- ➔ develop practical frameworks for managers that integrates scientific information and managerial constraints

Contact:
Neville Barrett Neville.Barrett@utas.edu.au or
Maria Beger m.beger@uq.edu.au



Private Bag 49 Hobart
Tasmania 7001 Australia
Ph + 61 3 62277277





20 year quantitative reef surveys and environmental data explain past changes

Central to the project is the spatial and temporal analysis of a unique dataset compiled by IMAS dating back to 1992, involving quantitative surveys of reef fishes, macro-algae, coral, urchins, abalone, rock lobsters and other macro-invertebrates at >600 sites off southeast Australia. Data include long-term series at Marine Protected Area (MPA) locations along the latitudinal gradient from NSW to southern Tasmania. This represents one of the longest ecological monitoring records worldwide for contrasting ecological changes within a regional MPA network with controls at fished locations in a region subject to prolonged warming over the past 60 years. Thus, when coupled with environmental data, the ecological datasets will allow an unprecedented analysis of marine species' distributional change over the past two decades. Broad-scale environmental data (sea-surface temperature, salinity, wave exposure) will be related to the marine ecological record across all sites to identify ecological changes associated with: (i) the marine physical condition during years of significant climatic anomalies (e.g., El Niño and La Niña), (ii) protection from fishing, and (iii) interactions between these two factors. The latter will be particularly important in identifying how fishing and climate changes interact.

Modelling sensitive species and robust locations to inform monitoring for climate

Species distribution models serve to statistically estimate relationships between species abundance records and environmental predictors. The usual assumptions that ecological interactions between species can be ignored in models, and that distributional responses to climatic shifts are rapid, will be tested by cross-validating climatic envelope models developed on the basis of latitudinal distributional patterns (and associated SST clines) with measurements of temporal ecological change at sites surveyed in anomalously hot and cold years. Underpinning the need to continually observe temperate reefs in our region to provide the necessary feedback for management agencies to both detect and understand the nature and magnitude of changes occurring, the projects' findings aim to inform monitoring. Given that such monitoring programs are expensive, and often have specific objectives (such as MPA management) they need to be refined with respect to providing cost-effective yet robust detection of biotic responses to climate change. This project will identify the locations, species subsets, monitoring frequency and replication that have provided the strongest signal so far, and be used to make recommendations about future observing protocols to guide funding bodies and management agencies.

Alternative management recommendations

Where increased protection from fishing is shown to increase/decrease resilience or resistance to climate change, the ecological benefits/costs of the existing MPA network in SE Australia will be contrasted with alternative adaptive management strategies, including alterations to catch rates of key species, and increased spatial management, either via MPAs or other spatially based fishery management controls. In all determinations of potential future adaptive management arrangements, possible options will be scoped with State biodiversity conservation and fisheries management agencies, to ensure options are realistic and feasible.



People on the project:

Neville Barrett, Graham Edgar, Neil Holbrook, Maria Beger, David Booth, Steffan Howe, Brendan Kelaher, Nathan Knott, Colin Buxton, André Couto

Contact: Neville Barrett Neville.Barrett@utas.edu.au or Maria Beger m.beger@uq.edu.au

Project coverage

A range of media articles followed the release of our Nature Climate Change paper, including a very small piece in The Mercury (cut and used out of context from our press release),

An article requested by The Conversation (which again, was sub-edited out of context) which appears as

<http://theconversation.com/marine-reserves-help-fish-resist-climate-change-invaders-20960>

An article in the New Your Times

http://www.nytimes.com/2013/12/04/opinion/sustaining-resilience-at-sea.html?hp&_r=1&_ga=2.111111111.111111111.111111111-111111111-111111111

and matching articles in the Sydney Morning Herald and The Age.

In addition, the article resulted in two on-air interviews with 7ZR ABC local radio in Hobart, and 7 NT in Launceston.

Delays within the project meant that insufficient time was available for further forms of communication, with the focus being on completing the analysis for predictions of likely future change. It is anticipated that those results will be communicated via a range of forums, including a follow-up workshop, scientific publications, and media articles.

References

- Andrew, N. & O'Neill, T. (2000). Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. *Journal of Marine & Freshwater Research* **51**: 255-263.
- Babcock, R.C., Alcala, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., Shears, N.T. (2010). Decadal Trends in Marine Reserves: differential rates of change for direct and indirect effects. *Proceedings of the National Academy of Sciences*. **107**: 18256-61
- Barrett, N.S., Edgar, G.J. & Mooney, P. (1998). A preliminary investigation of the distribution, range and extent of reef habitats and communities in Port Davey. Report to the Tasmanian parks and Wildlife Service. 26p.
- Barrett, N and Edgar, G. (1999). A survey of the proposed Port Phillip Heads Marine Park. Report to the Victorian Department of Sustainability and Environment. 35p.
- Barrett, N.S & Wilcox, S. (2000). Biological surveys and habitat mapping of proposed Marine Protected Areas on the Tasmanian North and North-eastern coasts. Tasmanian Aquaculture and Fisheries Technical Report Series. No. 6, 56p.
- Barrett, N.S. & Buxton, C. (2002). Examining underwater visual census techniques for the assessment of population structure and biodiversity in temperate coastal marine protected areas. *Tasmanian Aquaculture and Fisheries Technical Report Series*. No. 11, 114p.
- Barrett N.S, Edgar G.J. & Morton, A. (2002). Monitoring of Tasmanian inshore reef ecosystems. An assessment of the potential for volunteer monitoring programs and summary of changes within the Maria Island Marine Reserve from 1992-2001. *Tasmanian Aquaculture and Fisheries Technical Report Series*. No. 10, 50p.
- Barrett, N., Polacheck, A., Lynch, T., Clements, F., & Edgar, G. (2005). Ecosystem Monitoring of Subtidal Reefs in the Jervis Bay Marine Park 1996-2005. *TAFI Internal Report*. Jan 2006.
- Barrett, N., Edgar, G., Buxton, C. & Haddon, M (2007). . Changes in fish assemblages following ten years of protection in Tasmanian marine protected areas. *Journal of Experimental Marine Biology and Ecology* **345**:141-157.
- Barrett, N., Edgar, G. and Polacheck, A. (2007a). Baseline Surveys of Subtidal Reefs in the South West National Park Marine Nature Reserve 2004-2005. TAFI internal report to the Tasmanian Parks and Wildlife Service. 36p.
- Barrett, N., Edgar, G. and Polacheck, A. (2007b). Baseline Surveys of the Subtidal Reef Biota of the Kent Group Marine Nature Reserve, 2004-2006. TAFI internal report to the Tasmanian Parks and Wildlife Service. 45p.
- Barrett, N., Edgar, G., Polacheck, A., Lynch, T. and Clements, C. (2007). Ecosystem Monitoring of Subtidal Reefs in the Jervis Bay Marine Park 1996-2007. TAFI internal report to the NSW Marine Parks Authority. 54p.
- Barrett, N., Stuart-Smith, R., Zagal, C., Polacheck, A., Lynch, T., Edgar, G., & Clements, F. (2008). Baseline Surveys of the Subtidal Reef Biota of the Batemans Bay Marine Park 2005-2007. TAFI internal report to the NSW Marine Parks Authority. 30p.

- Barrett, N.S., Buxton, C.D. & Edgar, G.J. (2009). Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *Journal of Experimental Marine Biology and Ecology* **370**: 104–119.
- Barrett, N.S. & Edgar, G.J. (2010). Distribution of benthic communities in the Bathurst Channel estuarine protected area, southwestern Tasmania, a globally anomalous fjord-like ecosystem. *Aquatic Conservation* **20**: 397-406.
- Barrett, N, Edgar, G, Zagal, C, Oh, E, and Jones, D (2012) Surveys of intertidal and subtidal biota of the Derwent Estuary. (2010). *Institute for Marine and Antarctic Studies Technical Report*. University of Tasmania, Hobart, Tasmania.
- Barrett, N. Buxton, C., Gardner, C. (2009). Rock lobster movement patterns and population structure within a Tasmanian Marine Protected Area inform fishery and conservation management. *Marine and Freshwater Research* **60**: 417–425
- Bates A, Barrett, N, Stuart-Smith, R, Holbrook, N, Thompson, P, Edgar, G. (2014). Resilience and signatures of tropicalization in protected reef fish communities. *Nature Climate Change*. **4**: 62-67
- Bird, T, Bates, A, Lefcheck, J, Hill, N, Thomson, R, Edgar, G, Stuart-Smith, R, Wotherspoon, Krkosek, M, Stuart-Smith, J, Pecl, G, Barrett, N, Frusher, S. (In Press). Statistical solutions for error and bias in global citizen science datasets *Biological Conservation* (<http://www.sciencedirect.com/science/article/pii/S0006320713002693>)
- Buxton, C, Barrett, N, Haddon, M., Gardner, C. & Edgar, G. (2006). Evaluating the effectiveness of Marine Protected Areas as a fisheries management tool. Tasmanian Aquaculture and Fisheries Report to FRDC. Project Examining the health of subtidal reef environments in
- Collings, G., Bryars, S., Turner, D., Brook, J and Theil, M. (2008). Assessment of community reef monitoring and status of selected South Australian reefs based on the results of the 2007 surveys. SARDI Publication Number F2008/000511-1 no. 1999/162. 395.
- Edgar, G.J., Moverley, J., Barrett, N., Peters, D. & Reed, C. (1997). The conservation-related benefits of a systematic marine biological sampling program: the Tasmanian reef bioregionalisation as a case study. *Biological Conservation* **79**: 227-240.
- Edgar, G.J. & Barrett, N.S. (1997). Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology* **213**: 261-279.
- Edgar, G.J. & Barrett, N.S. (1999). Effects of declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* **242**: 107-144.
- Edgar, G.J. and Barrett, N.S. (2000). Impact of the Iron Baron oil spill on subtidal reef assemblages in Tasmania. *Marine Pollution Bulletin* **40**: 36-49.
- Edgar, G.J., Barrett, N.S., Bancroft, K, Brook, J. & Crane, K. (2005). Ecosystem monitoring in different management zones within the Jurien Bay Marine Park - results of 2004 surveys. *TAFI Internal Report*. June 2005.
- Edgar, G., Barrett, N., Brook, J., McDonald, B., & Bloomfield, A. (2005) Ecosystem monitoring inside and outside Sanctuary Zones within the Encounter Marine Park- 2005 baseline surveys. *TAFI Internal Report*. July 2006.

- Edgar, G., Barrett, N. and Stuart-Smith, R. (2009). Exploited reefs protected within marine reserves transform over decades into conservation features not otherwise present in the seascape. *Ecological Applications* **19**: 1967-74.
- Edgar, G. and Stuart-Smith, R. (2009). Ecological effects of marine protected areas on rocky reef communities: A continental-scale analysis. *Marine Ecology Progress Series* **388**: 51-62.
- Edgar, G. and Barrett, N. (2010). Biotic affinities of rocky reef fishes, invertebrates and macroalgae in different zones of the Port Davey marine protected area, south-western Tasmania. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 282-296.
- Edgar, Graham J; Davey, Adam; Kelly, Geoff; Mawbey, Ron B; Parsons, Karen. (2010). Biogeographical and ecological context for managing threats to coral and rocky reef communities in the Lord Howe Island Marine Park, south-western Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems* **20**: 378-396.
- Edgar, G. and Barrett, N (2012). An assessment of population responses of common inshore fishes and invertebrates following declaration of five Australian marine protected areas, *Environmental Conservation*, **39**: 271-281.
- Edmunds M, Hart S, Elias J and Power B (2004). Victorian Intertidal Reef Monitoring Program: The Reef Biota in the Central Victoria and Port Phillip Bay Marine Sanctuaries. *Parks Victoria Technical Series* No. 11. Parks Victoria, Melbourne.
- Edyvane, K. 2003, Conservation, monitoring and recovery of Threatened Giant Kelp (*Macrocystis pyrifera*) beds in Tasmania - Final Report, Natural Heritage Trust project final report to Environment Australia, Published by Department of Primary Industries, Water and Environment, Hobart.
- Figueria, W. and Booth, D. (2010). Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters. *Global Change Biology* **16**: 506-516.
- Floeter, S., Behrens, M., Ferreira, M., Paddock, C. and Horn, M. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology* **147**: 1435-47.
- Frusher, S., Buxton, C., Barrett, N., Tarbath, D., Redd, K., Semmens, J., Pederson, H., Valentine, J., Guest, M. (2010). Towards integrated multi-species management of Australia's SE reef fisheries: A Tasmanian example. *Report to Fisheries research and Development Corporation*. No 2004/013. Tasmanian Aquaculture and Fisheries Institute, Tasmania. 236p.
- Gardner, C, Barrett, N., Haddon, M. & Buxton, C. (2006). Spatial variation in size at onset of maturity of southern rock lobster *Jasus edwardsii*, around Tasmania, Australia. *Scientia Marina* **70**: 423-30.
- Hawkins, S., Sugden, H., Mieszkowska, N., Moore, P., Poloczanska, E., Leaper, R., Herbert, R., Genner, M., Moschella, P., Thompson, R., Southward, A. and Burrows, M. (2009). Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series* **396**: 245-59.
- Hastie, T. (2013). gam: Generalized Additive Models. R package version 1.08. <http://CRAN.R-project.org/package=gam>
- Hobday, A., Okey, T., Poloczanska, E., Kunz, T. & Richardson, A. (2007). Impacts of climate change on Australian marine life. CSIRO Marine and Atmospheric Research. *Report to the Australian Greenhouse Office*, Canberra, Australia. September 2006

- Johnson, C., Ling, S., Ross, J., Shepherd, S. & Miller, K. 2005. Establishment of the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania: first assessment of potential threat to fisheries. . *Final Report to Fisheries Research and Development Corporation*, Hobart, Australia. Hobart.
- Johnson, C., Banks, S., Barrett, N., Cazassus, F., Dunstan, P., Edgar, G., Frusher, S., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K., Holbrook, N., Hosie, G., Last, P., Ling, S., Melbourne-Thomas, J., Miller, K., Pecl, G., Richardson, A., Ridgway, K., Rintoul, S., Ritz, D., Ross, D., Sanderson, J., Shepherd, S., Slotwinski, A., Swadling, K., Taw, N. (2011). Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology* **400**: 17–32.
- Johnson, P., Fulton, E., Smith, D., Jenkins, G. and Barrett, N. (2011). The use of telescoping spatial scales to capture inshore to slope dynamics in marine ecosystem modelling. *Natural Resource Modeling* **34**: 335-364.
- Keough, M., Ross, D. and Knott, N. (2007). Ecological performance measures for Victorian Marine Protected Areas: Review of the existing biological sampling program. *Parks Victoria Technical Series* No 51. Parks Victoria, Melbourne.
- Last, P., William, W., Gledhill, D., Hobday, A., Brown, R., Edgar, G., Pecl, G. (2011). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography* **20**: 58-72.
- Lincoln-Smith, M. (1988). Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages. *Marine Ecology Progress Series* **43**: 223-31
- Lincoln-Smith, M. (1989). Improving multi-species rocky reef fish censuses by counting different groups of species using different procedures. *Environmental Biology of Fishes*. **266**: 29-37.
- Lindsay M, Edmunds M, Gilmour P, Bryant C and Williams J (2006). Victorian Subtidal Reef Monitoring Program: The Reef Biota at Port Phillip Heads Marine National Park. *Parks Victoria Technical Series* No. 32. Parks Victoria, Melbourne.
- Ling, S. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia*: **156**: 883-94.
- Ling, S. and Johnson, C. (2012). Marine reserves reduce risk of climate-driven phase shift by reinstating size- and habitat-specific trophic interactions. *Ecological Applications* **22**: 1232-45.
- McCormick, m. and Choat, H. ((1984). Estimating total abundance of a large temperate fish using strip transects. *Marine Ecology Progress Series* **43**: 232-41.
- Oksanen, J., Blanchet, R., Kindt, P., Legendre, P., Minchin, R., O'Hara, G., Simpson, P., Solymos, M., Hen, Stevens, H. and Wagner, H. (2013). vegan: Community Ecology Package. R package version 2.0-7. <http://CRAN.R-project.org/package=vegan>
- Oliver, E., Holbrook, N. (2013). A Statistical Method for Improving Continental Shelf and Nearshore Marine Climate Predictions. *Journal of Atmospheric and Oceanic Technology* **31**: 216-32
- Oliver, E., Wotherspoon, S., Chaimberlain, M., Holbrook, N. (2014). Projected Tasman Sea Extremes in Sea Surface Temperature through the Twenty-First Century. *Journal of Climate* **27**: 1980-87
- Pederson, H., Barrett, N., Frusher, S., Buxton, C. (2008) Effect of predator-prey and competitive interactions on size at emergence in the black-lip abalone *Haliotis rubra* in a Tasmanian MPA. *Marine Ecology Progress Series* **366**: 91-98.

- Perkins, H, Barrett, N, Hill, N. (in review). Altered niche of an ecologically significant species, *Centrostephanus rodgersii*, in its extended range revealed using an Autonomous Underwater Vehicle.
- Power, B and Boxshall, A. (2007). Marine National Park and Sanctuary Monitoring Plan 2007-2012. *Parks Victoria Technical Series* No. 54. Parks Victoria, Melbourne.
- Russell, B. (1997). Population and standing crop estimates for rocky reef fishes of north eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* **11**: 23-26.
- R Development CT. (2013). A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Sax, D, Stachowicz, F., Brown, J., Bruno, J., Dawson, M., Gaines, S., Grosberg, R. and Hastings, A. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution* **22**: 465-471
- Shepherd, S., Edgar, G. and Barrett, N. (2005). Reef Fishes of the Althorpe Islands and Adjacent Coasts of Central South Australia. *Transactions of the Royal Society of South Australia* **129**: 183-92.
- Simberloff D. & Von Holle B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* **1**: 21-32.
- Smith, D.C., Fulton, B., Johnson, P., Jenkins, G., Barrett, N., Buxton, C., Edgar, G. (2010). Developing integrated performance measures for spatial management of marine systems. *Final Report to FRDC*. Project No 2004/005.
- Stuart-Smith, R., Barrett, N., Crawford, C., Edgar, G. & Frusher, S. (2008). Condition of rocky reef communities: A key marine habitat around Tasmania. *NRM/NHT Report, Tasmanian Aquaculture and Fisheries Institute*, 31p.
- Stuart-Smith, R., Barrett, N.S., Stevenson, D.S. & Edgar, G. J. (2010). Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology* **16**: 122-34.
- Turner D, Kildea T and Westphalen G. (2007). Examining the health of subtidal reef environments in South Australia, Part 2: Status of selected South Australian reefs based on the results of the 2005 surveys. South Australian Research and Development Institute (Aquatic Sciences), Adelaide, 97pp. SARDI Publication Number RD03/0252-6.
- Wanger, T. C. Wielgoss, A., Motzke, I., Clough, Y., Brook, B, Sodhi, N. and Tschardtke, T. (2011). Endemic predators, invasive prey and native diversity. *Proceedings of the Royal Society B: Biological Sciences*. **278**: 690-694).
- Wernberg, T.; Bayden, R., Moore, P., Ling, S. and Smale, D. (2011). Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology* **400**: 7-16.

Project materials developed

If the project creates any products such as books, scientific papers, factsheets, images these should be outlined in this section outline and attach them where possible.

Two scientific papers were published arising in full or in part from this project at the time of this report, with two additional publications underway, one being resubmitted following review, and the other in final draft for submission.

In addition a fact sheet was produced as part of the NCCARF series, as shown in the Extension section above.

Appendices

Appendix i. Ecological traits and climate velocity explain range shifts in an ocean warming hotspot

This work has been submitted for possible publication in *Ecology Letters*. Please cite the published version of this research in any future reference, once it is available.

Ecological traits and climate velocity explain range shifts in an ocean warming hotspot

Jennifer Sunday^{1,2*}, Amanda E. Bates², Gretta T. Pecl², Stewart Frusher², Alistair J. Hobday³, Nicole Hill², Neil J. Holbrook², Graham J. Edgar², Rick Stuart-Smith, Neville Barrett, Thomas Wernberg^{4,5}, Reg A. Watson², Dan A. Smale^{4,6}, Elizabeth A. Fulton², Dirk Slawinski⁷, Ming Feng⁷, Ben T. Radford^{4,5,11}, Peter A. Thompson³, Peter Last

¹Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby V5A 1S6, Canada

²Institute for Marine and Antarctic Studies, University of Tasmania, Hobart 7001, Australia

³Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, Hobart 7001, Australia

⁴School of Plant Biology & UWA Oceans Institute, The University of Western Australia, Crawley 6009, Australia

⁵Australian Institute of Marine Science, 39 Fairway, Crawley 6009, Western Australia

⁶The Marine Biological Association of the United Kingdom, The Laboratory, Plymouth PL1 2PB, UK

⁷Wealth from Oceans National Research Flagship, CSIRO Marine and Atmospheric Research, Perth 6913, Australia

⁸School of Earth and Environment, The University of Western Australia, Crawley 6009, Western Australia

*Corresponding author: sunday@biodiversity.ubc.ca

Abstract (150 words)

Many marine species have shifted to higher latitudes in response to ocean warming. Despite the pervasiveness of this pattern, there has also been great variation in species responses and we currently have a very poor understanding of why this is. Here we identify possible causes of variation in rates of range extensions over the last five decades, using data on range shifts, climate velocity, and ecological traits of coastal marine species in one of the fastest warming regions in the world. Range boundaries on average tracked the expectation based on mean isotherm shift, but species traits usefully explained further variation...Specifically, range boundary shifts in fishes were positively related to latitudinal range size, and negatively related to trophic level, while for invertebrates, omnivores extended their ranges faster than herbivores. Using a separate dataset, we also found that fish species with smaller ranges underfill their potential thermal latitudinal ranges. Remarkably, dispersal potential explained only a small proportion of variation in range extension rates, with low-dispersing species among those

with the greatest extension rates. Fish species with smaller ranges that are intrinsically more vulnerable to extinction may thus be in double-jeopardy, as they have a poorer ability to escape warming by colonizing new regions.

Introduction

Changes in the distribution of organisms are being reported around the world as a broadly acknowledged fingerprint of global climate change (Parmesan & Yohe 2003; Poloczanska *et al.* 2013). However, the growing record of range shifts indicates that responses have been extremely variable among species, both on land and in the ocean. Even within regions where the rate of warming has been relatively uniform, some species have expanded rapidly into newly available habitats, while others have moved to a lesser extent, and yet others have moved in the opposite direction to predictions (Parmesan & Yohe 2003; Poloczanska *et al.* 2013; Lenoir *et al.* 2013). Variation in responses might be due to differences in the distance of isotherm movement associated with warming ('climate velocity', Loary *et al.*, Burrows, Pinsky), the relative role of temperature in setting range boundaries (see Brown, Sexton for reviews), or to differences in species' intrinsic or extrinsic propensities to respond to warming. Identifying the mechanism(s) of response variation is critical if we are to predict future ecological change and to manage proactively for changes in resource-based human livelihoods and to meet conservation objectives (Pinsky & Fogarty 2012) (Pecl *et al.* in prep).

Although results have been mixed among terrestrial species (Poyry *et al.* 2009, Angert *et al.* 2011, Betzholtz *et al.* 2013), there are reasons to expect stronger predictive relationships among species traits and range shifts in marine species. First, species range shifts have been faster in the ocean (Perry *et al.* 2005; Sorte *et al.* 2010; Pinsky *et al.* 2013; Poloczanska *et al.* 2013), which may be due in part to greater climate velocities in the ocean at temperate latitudes (Burrows *et al.* 2011) where most range shifts have been observed (Parmesan & Yohe 2003; Sunday *et al.* 2012; Poloczanska *et al.* 2013). This faster rate of change provides greater detection and analytical power for understanding the variation among species. Second, present-day species distributions in the ocean appear to be more closely tied to thermal tolerance limits of marine compared to terrestrial species (Sunday *et al.* 2012). This suggests that marine geographic ranges are more strongly linked to temperature gradients than terrestrial species, and are less influenced by other abiotic or biotic factors.

In the North Sea, fishes with smaller body sizes, faster maturation rates, and smaller sizes at maturity were found to have significantly greater range shifts, suggesting the importance of population growth rate in promoting faster range responses (Perry *et al.* 2005; Dulvy *et al.* 2008). Although species traits had poor explanatory power in some large-scale analyses of marine range shifts (Pinsky *et al.*, Przeskowski *et al.*), these were done in regions with relatively low climate velocities (Pinsky *et al.*) or did not take climate velocity into account (Przeskowski *et al.*). Intrinsic ability to respond to moving isotherms is more likely to have been expressed where climate velocity has been greatest.

Here we examined the extent to which intrinsic ecological traits explain variation in range extensions among marine taxa in a region of rapid climate warming. We compiled range-shift records from the Tasman Sea, where the recent multi-decadal rate of upper ocean warming has been 3-4 times greater than the global average (Holbrook and Bindoff 1997; Ridgway 2007) because the increased strength of the East Australian Current brings warmer eddies further south (Ridgway 2007; Hill *et al.* 2008; Hobday and Pecl 2013). We tested the influence of species traits, while accounting for the climate velocities experienced by each species at their range edge. We focussed on extensions at species' poleward range boundaries, or 'leading edges', based on the direct predictions provided by invasion theory (as opposed to contracting edges which would be better predicted by extinction theory; Bates *et al.* in review GEC). We used broadly-available morphological, distributional, and life-history traits (reproductive mode, maximum body size, trophic level, latitudinal range size, and water column position) to understand range shift variation in 121 fish and invertebrate species. We hypothesized that traits related to dispersal potential, population growth rate, and ecological generalization will be important in explaining variation among species' range shifts (Kinlan & Hastings 2005; Dunstan and

Bax, 2007, Hill *et al.* 2001; Warren *et al.* 2001; Poyry *et al.* 2009; Angert *et al.* 2011).

Materials and Methods

Range shift estimates

We compiled range shift data from all published studies reporting range shifts in coastal animal species in the Tasman Sea (Pitt 2010; Stuart-Smith *et al.* 2010; Poloczanska *et al.* 2011; Last *et al.* 2010), and added new underwater visual census data from the Reef Life Survey database (RLS data; Edgar and Stuart-Smith, 2009) and compatible long-term temperate reef monitoring program (LTTRMP – Edgar and Barrett, 2012). We filtered these data to only include records with two observational time-points that span 20 years or greater, or (for RLS and LTTRMP data, see below) for which we had multiple observations across 11 years. This seemed appropriate given the very high variability in range shifts inferred from short-term studies with only two-time points of observation (see Fig. S1). In most of these records (Pitt 2010, Poloczanska *et al.* 2011, and the RLS and LTTRMP datasets), historic systematic surveys of coastal species were conducted across a range of latitudes and repeated at one or multiple a later times. For each species, the southern-most survey site in which the species was observed was taken as the southern (poleward) range boundary. While this estimate might inaccurately represent the location of the southern-most reproductive population, the consistency across time points yields a meaningful change in the location of the southern-most observable adult individuals. From the RLS and LTTRMP data, we extracted records of species' southern-most location observed across 4 or 5 time points between 1996 and 2013, and ran a simple linear regression through these data (see Fig.S2). In Last *et al.* 2010 (Last *et al.* 2010), present-day species ranges were compared to those in the 1980s based on extensive presence-only records from fishing competitions and scientific surveys. We extracted only species for which historical and present-day range edges could be assigned to an approximate landmark from Appendix S2 of Last *et al.* (2010), so that a distance of range-boundary shift could be estimated, thus we excluded observations of changes in abundance at range edges). Because this dataset only included species with apparent range shifts, we also obtained a list of species (n=8) for which the same sources showed no range change, from the primary author (Last, *personal communication*). Finally, we included data from a single-species study for the sea urchin *Centrostephanus rodgersii* because of the more substantial historical information on the range boundary of this species (Ling *et al.* 2009). For studies in which the first time period spanned several years, we used the median year as the first time point. We used the distance of range shift (km) as our response variable.

For some species (14 fish and 13 invertebrates), range boundaries moved towards the equator. This type of change may represent (i) inaccuracy of our estimates of poleward range edges, (ii) inherent variability in poleward range edges, or (iii) indirect ecological responses to warming or other aspects of environmental change. Regardless of the underlying mechanism(s), we assumed that the factor(s) leading to these equatorward-movements were equally influential across the entire dataset and random with respect to species' intrinsic propensity for range extension, and therefore kept these reverse-moving species in our analysis as a means to best model the residual error. When these equatorward-movers were removed from the analyses, results were quantitatively similar, but model assumptions of heteroscedasticity were violated.

Climate expectation

To better isolate the contributions of species traits from extrinsic processes in determining the extension of southern range boundaries, we calculated and accounted for an expected distance of range boundary shift for each species based on climate velocity, the time period of the study, and the

hard boundary introduced by the continental edge of southern Tasmania. For climate velocity, we used isotherm movement meridionally (across latitudes in the north-south direction) throughout the study region (Fig. 1), using isotherms of mean annual sea surface temperature summarized across one degree of latitude and 100 km offshore. For each species, we calculated the latitudinal distance moved by the isotherm at the original poleward range boundary across the time period of study. For species in which the isotherm moved beyond the southern edge of Tasmania during the time period of study ($n=21$), we cropped the expected distance at that hard latitudinal boundary (43.639°S), beyond which coastally-surveyed species could not exist or could not be observed. However, the latitude of new mean isotherms were not far beyond this boundary (all within 0.4° latitude from this hard limit), and therefore results were similar whether or not we cropped the expected distance at the southern edge of Tasmania.

Species traits

We considered the effect of eight species traits on range shifts, for which data were broadly obtainable across the dataset: dispersal ability, retention ability, maximum body size, trophic level, latitudinal range size, water column position, habitat generalization. We established predictions for the effect of each trait on range shift rates, which we develop below. We separated our data into fish and invertebrate datasets for a more straightforward analysis.

Dispersal score: We predicted that species with greater dispersal abilities would have greater rates of range extensions (Feary *et al.*, 2013). We categorized species by their life-histories, into live-bearers, egg-layers, and those with lecithotrophic and planktotrophic larval development, respectively. Based on these life-history characteristics we assigned dispersal ability scores of 1 (egg-layers and live-bearers), 2 (lecithotrophic larvae; representing pelagic durations that are typically short, on the order of hours to several days), and 3 (planktotrophic larvae, representing longer pelagic durations). Species that brood or lay eggs and also release larvae for planktonic development (e.g. the lobster, *Jasus edwardsii*, and the warratah anemone *Actinia tenebrosa*), were given the greater dispersal ability score (3) based on their most dispersive (planktotrophic) stage.

Colonization score: If a species that broods or lays eggs arrives already fertilized, it has a greater chance to overcome allee effects and therefore colonize a new area (). Likewise, a species with short dispersive phases may better colonize a suitable habitat patch (). We therefore assigned a 'colonization score' to represent this aspect of life-history, which may counteract the role of arrival potential. We assigned a colonization score of 1 (planktotrophic larvae), 2 (lecithotrophic larvae), and 3 (brooders, egg-layers, live-bearers). This metric varied from the dispersal score because species that have a high colonization ability (brooding or laying eggs) and also release larvae for planktonic development (see examples above) were given the maximum colonization score (3) based on their ability to arrive as gravid adults.

Maximum body size: Maximum body size is typically correlated with many life-history traits (Roff 1992; Stearns 1992). For example, the maximum body size of fish may approximate intrinsic rates of population growth, with smaller-bodied fish having younger ages of first reproduction (Denney *et al.* 2002). On this premise, we predicted smaller-bodied fish to have faster rates of range extension. For marine invertebrates, a similar relationship between body size and generation time is not known, but body size correlates positively with fecundity (Jablonski 1996), and larger-bodied bivalves have been found to have more unstable range limits through historical climate change (Roy *et al.* 2001). Hence, we expected larger-bodied invertebrates to have greater rates of range extension.

Maximum body size estimates were based on data in FishBase (Froese and Pauly), cross-referenced where possible with values in the primary literature, the CSIRO, and from the RLS database used by Stuart-Smith *et al.* 2013). Total length was used for fishes, anterior-to-posterior length was used for most invertebrates, diameter was used for radially symmetrical taxa, and ray-length was used for sea stars.

Trophic level: Lower trophic level species might require fewer other species to be present before they can colonize a new area, assuming that diet speciality is equal across trophic levels. Thus we predicted that species at lower trophic levels would expand their ranges faster. Trophic level estimates were based on data in Fishbase, values from the primary literature, or based on descriptions of species' diets in the literature. When based on diet description, the following proxies were used: herbivore (2), detritivore (2), filter feeder (2.5), predators all had trophic levels from 3-5 ().

Latitudinal range size: Species with broader latitudinal ranges typically experience a broader range of biotic and abiotic conditions. We therefore predicted that species with larger ranges would have greater rates of range extension with warming (Angert *et al.* 2011; Feary *et al.*, 2013). Latitudinal range size estimates were based on information in FishBase, cross-referenced with information from the Global Biodiversity Information System and values from the primary literature. Importantly, these data were independent from estimates of range boundaries within our range-shift studies, and most variation in latitudinal range size was correlated to the northern extent of species' ranges (r^2 between latitudinal range size and northern range boundary: 0.93) and not the southern range boundary (r^2 between latitudinal range size and southern range boundary: 0.16).

Water column position: We assumed that pelagic species would have fewer specific habitat associations compared with benthic and demersal species, and therefore have faster range extensions. Pelagic vs. demersal water column position was collected based on CSIRO information on habitat use, cross-referenced with information in FishBase and the authors' knowledge of the species. All of the invertebrates in our dataset were benthic.

Habitat specificity: We predicted that species with narrower habitat requirements would have slower range extensions. We used expert knowledge (authors SF and GE) to identify species that were known habitat specialists, however only 3 specialist fish species were identified: *Aplodactylus lophodon*, *Kyphosus sydneyanus*, and *Olisthops cyanomelas*.

Analysis

We used multi-model averaging of mixed-effects linear models using maximum likelihood estimation to test for ecological traits that explain variability in latitudinal changes in southern range boundaries. We started with a global model, fitting the latitudinal changes in southern range boundaries to the climate expectation, species' dispersal score, colonization score, body size, trophic level, range size, water column position (fishes only), ecological specialization (fishes only), and intertidal height (invertebrates only). We included interactions between each trait variable and the climate expectation, to allow for differences in the rate of responses to climate forcing (slope) among trait levels. We subset the data to include only species for which we had information on every trait variable, and we lacked data of dispersal scores for 13 fishes and 8 invertebrates, and colonization scores for 9 fishes and 4 invertebrates. We therefore reran models with and without these variables to increase the sample size when these variables had low importance scores. For each data subset, we normalized all continuous variables around zero with a standard deviation of one. We tested for collinearity between explanatory variables, and removed intertidal height from the invertebrate dataset because of a high correlation between intertidal height and climate. For fishes, dispersal and colonization score were positively collinear (variance inflation factor >2; Zuur *et al.* 2010), so we ran separate models using one or the other variable only. All other variables had variance inflation factors below 2 (see Table S1). Although phylogenetic relationships were not available for the wide sample of taxa within these datasets, we accounted for non-random sampling across taxonomic groups by including taxonomic position as a hierarchical random effect on the intercept (from Class to Genus for fishes, and from Phylum to Genus for invertebrates; Ricotta *et al.*, 2012). We included all levels of taxonomic hierarchy as a closest reflection of the evolutionary relationships among groups.

Initial analyses showed that residual variability increased as a function of the duration of the study, with short-duration studies having greater variability in range shifts. We first identified 5 outliers from

the shortest-duration study (RLS/LTRMP datasets), in which range extensions were greater than 250 km within 14 years. Removal of these outliers improved heteroscedasticity of residual variation. With the remaining data, we included a weighting factor in which the variance structure was modelled as a function of study duration. This improved model AIC scores (fishes model delta AIC =1; invertebrate model delta AIC=7.1) and heteroscedasticity of residual variation.

From our global model including all ecological traits and their interactions with climate expectation, we ran all possible subsidiary models, setting the maximum number of variables within any model as less than one-tenth of the sample size (5 for the fishes dataset $n=59$, and 4 for the invertebrate dataset $n=48$). We included climate expectation within all models, as we expected it to be an important covariate. However, results were identical if we did not force its inclusion, indicating that expected distance was an heuristically important explanatory variable. From these models, we identified the confidence set of models as those comprising the top 95% of model weights using the Akaike Information Criterion adjusted for small sample sizes, and used these to calculate the model-averaged parameter values and variable importance for each ecological trait using the MuMIn package in R (Barton 2012). In addition, we extracted the results of the model with no species traits, using only climate expectation as a predictor on range shift rates. Because dispersal and colonization scores both had low relative variable importance ($RVI < 0.05$) and including them limited the sample size of our complete dataset, we reran the modelling process without these two variables.

Relationship between latitudinal range size and potential thermal-niche filling

We investigated the relationship between latitudinal range size and the extent to which species occupy their potential thermal niche, using a separate dataset on thermal tolerance and range size (Sunday *et al.*, 2012). For 33 marine fish and one marine invertebrate, we extracted the *underfilling* metric from Sunday *et al.* (2012), representing the extent to which species occupy a smaller latitudinal range than would be predicted based on their thermal tolerance. We regressed this underfilling metric as a function of latitudinal range, considering cold and warm range boundaries separately, using a generalized linear model with a Poisson error distribution (using the lmer package in R). If species overfilled their ranges (ie. had ranges that extended to more extreme latitudes than would be predicted based on their thermal tolerance), we cropped their underfilling at zero, but results were similar if we allowed overfilling (without cropping at zero, data not shown).

Results

Polewards range boundaries shifted on average towards higher latitudes, with high variation in shift rates (mean range shift = 82.8 ± 195 s.d. km South; Fig. 1), which generally matched the distance of mean isotherm movement (67.1 ± 65.5 km, cropped at Tasmania). This climate expectation explained some of the variation in range shifts among species (model with only expected distance explained 38% of variation in fishes, 13% in invertebrates). However, much of the remaining variation could be explained by species traits – the best model with species traits explained an additional 18% of variation in fishes, and an additional 42% of variation in invertebrates, Table 1.

Among fishes, latitudinal range size and trophic level were the most important species traits for predicting rates of range shifts (Fig. 2, Table 1). Latitudinal range size was the most important single predictor, and there was a positive interaction between latitudinal range size and expected distance; species with larger latitudinal ranges had the greatest range shifts and were best able to track mean isotherms (Fig. 2a-c). Given the influence of range size, species with lower trophic levels responded faster than those at higher trophic levels (Fig. 2a,c). Other traits in fishes had variable effects, and point-estimates were not in the directions predicted (Fig. 2).

For invertebrates, trophic level was the most important species trait and had a positive interaction with climate expectation. The effect of trophic level in invertebrates was opposite to that in fishes – species at higher trophic levels had the greatest range shifts and were best able to track mean isotherms (Fig. 2d-e, Table 1). However, this finding is highly influenced by large range shifts in two barnacles

(omnivores with trophic level 2.5), compared to six herbivores (trophic level 2) (Fig. 2e). When these two barnacle species were removed, the effect of all species traits, including trophic level, was variable in the final model.

Dispersal ability did not have a strong effect on the rate of range shifts in either fishes or invertebrates, and there was high variation in responses within each reproductive mode (Fig. 3). Some live-bearing and egg-laying species, which had low dispersal ability scores, expanded their ranges as fast as species with planktotrophic larvae (Fig. 3). Nor did species with high colonization scores (greater offspring retention upon arrival) have greater range shifts. Instead, there was a bimodal distribution in range shift rates across almost all dispersal groups, showing that species either expanded rapidly or slowly relative to the climate velocity without an explanation from the variables researched here.

Marine species with smaller latitudinal ranges in the dataset of Sunday *et al.*, 2012 had a greater a distance between their potential and realized thermal niche (Fig.4). Although this relationship was only significant at species' warm range boundaries (warm range boundary, $p < 0.001$; cold range boundary, $p = 0.17$), the trends were similar at both range boundaries, indicating that fish species with smaller range sizes are more likely to be restricted by factors other than temperature and thermal tolerance.

Discussion

The expected distance of range expansions based on climate velocity and a coastal habitat barrier was the most important single predictor of range shift distance in the marine climate change hotspot of southeastern Australia. This bodes well for using climate velocities to generally predict range shift responses in marine organisms, and conforms to previous findings in North American fishes (Pinsky *et al.* 2013) and marine species globally (Polozcanska *et al.*, 2013). However, we also identified species traits that improve upon our ability to explain variation in range shifts.

Fishes with the greatest latitudinal ranges – such as the widespread Queensland groper (*Epinephelus lanceolatus*), tiger shark (*Galeocerdo cuvier*), yellowtail jack (*Seriola lalandi*), and Maori wrasse (*Cheilinus undulatus*) – responded fastest to warming. This suggests that widespread species are better able to move into newly-available regions. Species with larger ranges are likely to have broader ecological niches, fewer range-limiting associations with particular habitats and other species, and range boundaries that are limited by climate (Brown, 1996; Lester *et al.*, 2007). Indeed, marine species with larger latitudinal ranges were more likely have range boundaries that matched their temperature tolerance (Fig. 4). Species with larger ranges also tend to have greater local abundance (Lawton 1999; Roughgarden 2009), and greater body sizes, although the wide-ranging species listed above have notably low local abundance (RSS, personal communication), and body size had low explanatory power in our models. The importance of range size on range extensions is also supported by a global analysis of tropical fishes that have been observed in temperate waters (tropical vagrants). Tropical vagrancy was positively related to latitudinal range size, and although it was positively related to other traits in univariate analyses (e.g. body size, swimming velocity, larval duration, and size at larval settlement), latitudinal range size was the only significant variable in multivariate analyses (Feary *et al.* 2013). Hence, latitudinal range size appears to be a useful proximate trait related to greater arrival of adults beyond to regions outside their historical ranges.

Among species with smaller latitudinal ranges, it was those at lower trophic levels that responded fastest. Herbivores such as the black drummer, silver drummer, zebrafish, and rock cule extended faster than omnivores and predators with similar-sized latitudinal ranges. However, trophic level was only important in our models if range size was also included, hence among species with moderate ranges (spanning 1000-2000 km North-South) herbivores were better able to colonize new areas than predatory species. Such a finding may result if herbivores are less specialized, or if their (algal) resources are more broadly distributed polewards of their current distributions. Indeed, the

common algal resource *Ecklonia sp.* is broadly distributed from northern New South Wales to the southern tip of Tasmania (T. Wernberg).

By contrast, among invertebrates, species at higher trophic levels had greater range extensions relative to the expected rate. This finding was driven by two filter-feeding barnacles with large reported range extensions relative to six herbivorous snails within a long time-spanning dataset (Polozcanska et al.). Therefore, the robustness of the pattern has yet to be tested, but suggests that filter-feeding (or omnivorous) invertebrates may respond most quickly to warming.

Although dispersal ability has been considered as a generally important predictor for range shift responses to climate change on land (e.g. Brooker *et al.* 2007; Barton et al, 2012), our analysis does not support this hypothesis for the marine environment.

Dispersal potential was also unimportant as a univariate predictor of range shifts in a previous global study (Przeslawski *et al.* 2012). Although we based dispersal potential on the relatively coarse metric of dispersal mode, higher resolution data using planktonic duration would not likely improve this relationship, as even brooding and egg-laying taxa (with zero time in the plankton) were among the fastest to extend their ranges. Indeed, pelagic larval duration was unrelated to spread rates of introduced marine species (Kinlan & Hastings 2005), and to the occurrence of tropical species observed in temperate waters (Feary et al, 2013). Recent theoretical work suggests that propagule pressure (Clark and Johnston, 2009; Hedge *et al.*, 2012) or rare long-distance dispersal (Clark *et al.* 2001; Kinlan & Hastings 2005) is a better predictor of invader success than average dispersal distance (or dispersal mode). The contrasting relationships between dispersal and colonization potential may obscure relationships between life-history modes with range extensions: a brooding or egg-laying species might have low mean expected dispersal potential, but in the rare case of long-distance transport via rafting or human-mediated transport of a fertilized female or an egg mass, such a species may readily colonize and start a new population (*The Paradox of Rockall*, Johannesson 1988). Such rare transport events might increase in frequency with climate warming (Macreadie *et al.* 2011), and may in part explain the bimodal distribution of range shift rates observed among dispersive categories (Fig. 3).

Two aspects of the present analysis may explain why species traits were useful predictors of range shifts in fish and invertebrates of southeastern Australia but not in North American fishes (Pinsky et al, 2013) or other previous studies. First, southeastern Australia is a climate-warming hotspot, in which climate velocity was over 10 times faster than in the North American sites investigated by Pinsky *et al.* 2013 (maximum climate velocity in the present study was 4.6° latitude year⁻¹, compared to $\sim 0.15^{\circ}$ latitude year⁻¹ in Pinsky *et al.* 2013). This greater climate pressure might allow trait-mediated differences in range-expansion potentials to be expressed. Second, we focused on range extension fronts rather than species range centroids (Pinsky *et al.* 2013). Because different ecological factors govern range extensions vs. range contractions or changes in the centre of abundance, the importance of species traits on each response should also differ. For example, while habitat generalists or species with fast generation times may be expected to expand into newly-available habitats more quickly, they are not expected to be the fastest to recede or go locally extinct (Bates et al GEC, in press). In a global synthesis of range shifts in marine algae, fishes, and invertebrates, variation in range extensions could not be explained by adult mobility, water column position, dispersal potential, or trophic level, but could be explained by habitat type, with intertidal and near-shore subtidal species moving faster than shelf fauna (Przeslawski *et al.* 2012). However, the two variables that best explained range shifts in our dataset - range size and climate expectation - were not included, and species traits were only investigated in univariate models (Przeslawski *et al.* 2012). In North Sea fishes, polewards range shifts were detected in species with smaller body sizes (Perry et al), and further analysis revealed that more widespread fishes had more northerly shifts (based on spatial extent of occurrence; Dulvy *et al.* 2008).

Although the distance of mean isotherm shifts was a significant predictor of range shifts in both fishes

and invertebrates, there was large and equal spread both above and below expected rates of shifts (Fig. 3), with about half of the species in the dataset moving faster than mean isotherms. High variation above and below the expectation was reported in other large-scale studies of range shifts and climate velocity (Pinsky *et al.* 2013; Poloczanska *et al.* 2013), and might be attributed to three factors. First, the aspects of climate regime that limit species distributions may be finer in temporal and geographic scale than the relatively coarse scale used here (Poloczanska *et al.* 2013), especially in the coastal zone for which remotely sensed temperature estimates are less accurate (Smale *et al.*, 2009). Cold range margins may be set by a minimal number of warm summer days needed for successful reproduction, for example, or by a maximal number of cold days tolerable in the winter. In our analysis, the poleward range boundary of the sea urchin *Centrostephanus rodgersii*, moved faster than the mean temperature isotherm, but matches expectations based on the 12°C winter threshold temperature needed for larval development (Ling *et al.* 2008; Johnson *et al.* 2011). Second, range-limiting factors other than temperature, such as habitat availability or biotic interactions, may have previously constrained southern range boundaries such that they respond to temperature change non-linearly. Finally, observation and sampling error based on low abundances, low detectability, or non-continuous sampling along the coastline is expected to generate noise in range boundary estimates, and error in the original range limits could lead to overestimates of range shifts. More information on historical and present-day species distributions is needed to more robustly estimate range edges, particularly if the aim is to use mean isotherm distance for predicting range shifts (Stafford *et al.* 2013; Bates *et al.* in review).

Remaining variation in range extensions might be explained with more intrinsic species traits, such as fecundity, generation time, diet breadth, or aggressiveness (Carere and Gherardi 2013), or extrinsic factors, such as availability of required habitats, biotic interactions, or population growth history (Phillips, 2012). Information on species-specific habitat associations and careful mapping of coastal geomorphologies may be useful for identifying particular habitat limitations. Species may be limited by the presence of other species to facilitate their invasion (Hillerislambers *et al.*, 2013; Pigot A and Tobias J, 2013). For example, the extension of the habitat-modifying sea urchin *Centrostephanus rodgersii* into Tasmanian waters (southwest Tasman Sea) may facilitate further invasion of urchin-barren associated taxa. This process would be analogous to the ‘invasional meltdown’ hypotheses for species invasion success, where the presence of invasive species in an ecosystem facilitates invasion by additional species (Simberloff & Von Holle 1999), recently supported through meta-analysis (Jeschke *et al.* 2012), and may therefore be important for redistribution patterns as well. To the extent that natural communities are hierarchically organized (Bruno *et al.* 2003), identifying groups of species that are associated with early responders through facilitation may help to explain variation in range shifts, and lead to useful predictions.

Conclusion

We found that species traits in combination with climate velocity improved our ability to explain range shift extensions in eastern Australian marine fauna. Our most compelling finding was a positive relationship between range extensions and latitudinal range size in fishes: species that are already broadly distributed appear to have moved more easily into newly available regions (Feary *et al.*, 2013). A positive global relationship between latitudinal range size and the extent to which species fill their potential latitudinal range suggests a mechanism for why larger-range species would respond faster to warming - species with larger latitudinal ranges are more likely to be limited by temperature and not by other factors. The conservation implications are potentially immense and deserve further investigation across systems and regions. Because small range-size species also face a greater risk of extinction (Roberts and Hawkins, 1999), particularly in response to climate fluctuations (Davies *et al.*, 2009), small-range size fish are in double jeopardy: they are intrinsically more vulnerable to extinction and are less able to escape via colonizing new latitudes.

Acknowledgements

We acknowledge the assistance of Peter Last, Jessica Melbourne-Thomas, Stats-beers group at Simon Fraser University, ANNiMs, and the Australian Government Fisheries Research and Development Corporation and Department of Climate Change and Energy Efficiency grant. Reef Life Survey and IMAS divers who helped collect data. Australian Research Council supported TW

References

- Angert A.L., Crozier L.G., Rissler L.J., Gilman S.E., Tewksbury J.J. & Chunco A.J. (2011). Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, 14, 677-689.
- Barton K. (2012). MuMIn: Multi-model inference. R package version 1.7.12. <http://CRAN.R-project.org/package=MuMIn>.
- Barton K, Hovestadt T, Phillips B, Travis J (2012) Risky movement increases the rate of range extension. *Proceedings Biological sciences / The Royal Society* 279:1194–202. doi:10.1098/rspb.2011.1254
- Brooker R.W., Travis J.M.J., Clark E.J. & Dytham C. (2007). Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of theoretical biology*, 245, 59–65.
- Brown J.H., Stevens G.C. & Kaufman D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597-623.
- Bruno J.F., Stachowicz J.J. & Bertness M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18, 119-125.
- Burrows M.T., Schoeman D.S., Buckley L.B., Moore P., Poloczanska E.S., Brander K.M., Brown C., Bruno J.F., Duarte C.M., Halpern B.S., Holding J., Kappel C.V., Kiessling W., O'Connor M.I., Pandolfi J.M., Parmesan C., Schwing F.B., Sydeman W.J. & Richardson A.J. (2011). The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science*, 334, 652-655.
- Chen I.C., Hill J.K., Ohlemuller R., Roy D.B. & Thomas C.D. (2011). Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, 333, 1024-1026.
- Clark J.S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist*, 152, 204–224.
- Clark J.S., Lewis M. & Horvath L. (2001). Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, 157, 537–554.
- Clark GF & **Johnston EL** (2009) Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. *OIKOS* 118:1679-1686
- Denney N.H., Jennings S. & Reynolds J.D. (2002). Life history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 269, 2229-2237.

- Dulvy N.K., Rogers S.I., Jennings S., Stelzenmuller V., Dye S.R. & Skjoldal H.R. (2008). Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45, 1029-1039.
- Dunstan, P.K., Bax, N.J., 2007. How far can marine species go? Influence of population biology and larval movement on future range limits. *Marine Ecology- Progress Series* 344, 15e28.
- Edgar, G. J. & Stuart-Smith, R. D. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Mar. Ecol. Prog. Ser.* **388**, 51-62 (2009)
- Froese, R. & Pauly, D. (Ed.) 2000. *FishBase 2000: concepts, design and data sources*. ICLARM Contribution 1594, ICLARM: Los Baños
- Frusher SD, Hobday AJ, Jennings SM, Creighton C, D'Silva D, Haward M, Holbrook NJ, Nursey-Bray M, Pecl GT, Putten EI (2013) The short history of research in a marine climate change hotspot: from anecdote to adaptation in south-east Australia. *Reviews in Fish Biology and Fisheries*. doi:10.1007/s11160-013-9325-7
- Hedge LH, WA O'Connor, **Johnston EL** (2012) The intrinsic parameters of invasive propagule pressure: arrival frequency, not size, increases invader colonisation. *Ecosphere*. 36(6). Article 48.
- Hillerislambers J, Harsch M, Ettinger A, Ford K, Theobald E (2013) How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*. doi:10.1111/nyas.12182
- Hill J.K., Collingham Y.C., Thomas C.D., Blakeley D.S., Fox R., Moss D. & Huntley B. (2001). Impacts of landscape structure on butterfly range extension. *Ecology Letters*, 4, 313-321.
- Hill K.L., Rintoul S.R., Coleman R. & Ridgway K.R. (2008). Wind forced low frequency variability of the East Australia Current. *Geophysical Research Letters*, 35.
- Holbrook NJ and NL Bindoff, 1997: Interannual and decadal temperature variability in the southwest Pacific Ocean between 1955 and 1988. *Journal of Climate*, **10**, 1035-1049.
- Jablonski D. (1996). Body size and macroevolution. In: *Evolutionary Paleobiology* (ed. Jablonski D). University of Chicago Press Chicago, pp. 256-289.
- Jeschke J.M., Aparicio L.G., Haider S., Heger T., Lortie C.J., Pyšek P. & Strayer D.L. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, 14, 1–20.
- Johannesson K. (1988). The paradox of Roekall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology*, 99, 507-513.
- Johnson C.R., Banks S.C., Barrett N.S., Cazassus F., Dunstan P.K., Edgar G.J., Frusher S.D., Gardner C., Haddon M., Helidoniotis F., Hill K.L., Holbrook N.J., Hosie G.W., Last P.R., Ling S.D., Melbourne-Thomas J., Miller K., Pecl G.T., Richardson A.J., Ridgway K.R., Rintoul S.R., Ritz D.A., Ross D.J., Sanderson J.C., Shepherd S.A., Slotvinski A., Swadling K.M. & Taw N. (2011). Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, 400, 17-32.

- Kinlan B. & Hastings A. (2005). Rates of population spread and geographic range extension. What exotic species tell us. In: *Species invasions: insights into ecology, evolution, and biogeography*. (eds. Sax D, Stachowicz J & Gaines S). Sinauer Associates Sunderland.
- Last P.R., White W.T., Gledhill D.C., Hobday A.J., Brown R., Edgar G.J. & Pecl G. (2010). Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. *Global Ecology and Biogeography*, 20, 58-72.
- Ling S., Johnson C., Ridgway K., Hobday A. & Haddon M. (2009). Climate driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology*, 15, 719-731.
- Ling S.D., Johnson C.R., Frusher S. & King C.K. (2008). Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology*, 14, 907-915.
- Macreadie P.I., Bishop M.J. & Booth D.J. (2011). Implications of climate change for macrophytic rafts and their hitchhikers. *Marine Ecology Progress Series*, 443, 285-292.
- Parmesan C. & Yohe G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.
- Perry A.L., Low P.J., Ellis J.R. & Reynolds J.D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308, 1912-1915.
- Pigot A, Tobias J (2013) Species interactions constrain geographic range expansion over evolutionary time. *Ecology letters* 16:330–8. doi:10.1111/ele.12043
- Phillips BL (2012) Range shift promotes the formation of stable range edges. *Journal of Biogeography* 39. doi:10.1111/j.1365-2699.2011.02597.x
- Pinsky M. & Fogarty M. (2012). Lagged social-ecological responses to climate and range shifts in fisheries. *Climatic change*, 115, 883-891.
- Pinsky M.L., Worm B., Fogarty M.J., Sarmiento J.L. & Levin S.A. (2013). Marine taxa track local climate velocities. *Science*, 341, 1239-1242.
- Pitt N.R., E.S. Poloczanska and A.J. Hobday (2010). Climate-driven range changes in Tasmanian intertidal fauna. *Marine and Freshwater Research*, 61, 963-970.
- Poloczanska E.S., Brown C.J., Sydeman W.J., Kiessling W., Schoeman D.S., Moore P.J., Brander K., Bruno J.F., Buckley L.B., Burrows M.T., Duarte C.M., Halpern B.S., Holding J., Kappel C.V., O'Connor M.I., Pandolfi J.M., Parmesan C., Schwing F., Thompson S.A. & Richardson A.J. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, early online doi:10.1038/nclimate1958.
- Poloczanska E.S., Smith S., Fauconnet L., Healy J., Tibbetts I.R., Burrows M.T. & Richardson A.J. (2011). Little change in the distribution of rocky shore faunal communities on the Australian east coast after 50 years of rapid warming. *Journal of Experimental Marine Biology and Ecology*, 400, 145-154.
- Poyry J., Luoto M., Heikkinen R.K., Kuussaari M. & Saarinen K. (2009). Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15, 732-743.

- Przeslawski R., Falkner I., Ashcroft M. & Hutchings P. (2012). Using rigorous selection criteria to investigate marine range shifts. *Estuarine Coastal & Shelf Science*, 113, 205-212.
- Ridgway K.R. (2007). Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters*, 34.
- Roff D.A. (1992). *Evolution of life histories: theory and analysis*. Chapman and Hall, New York.
- Roy K., Jablonski D. & Valentine J.W. (2001). Climate change, species range limits and body size in marine bivalves. *Ecology Letters*, 4, 366-370.
- Simberloff D. & Von Holle B. (1999). Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, 1, 21-32.
- Sorte C.J.B., Williams S.L. & Carlton J.T. (2010). Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography*, 19, 303-316.
- Stearns S. (1992). *The Evolution of Life Histories*. Oxford University Press, London.
- Stuart-Smith R.D., Barrett N.S., Stevenson D.G. & Edgar G.J. (2010). Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology*, 16, 122-134.
- Sunday J.M., Bates A.E. & Dulvy N.K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Clim. Change*, 2, 686-690.
- Warren M.S., Hill J.K., Thomas J.A., Asher J., Fox R., Huntley B., Roy D.B., Telfer M.G., Jeffcoate S., Harding P., Jeffcoate G., Willis S.G., Greatorex-Davies J.N., Moss D. & Thomas C.D. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, 414, 65-69.
- Zuur A.F., E.N. I. & C.S. E. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology & Evolution*, 1, 3-14.

Table 1. Models explaining the rate (km/decade) of latitudinal shifts in fishes and invertebrates. Relative variable importance (summed Akaike weight of variables across all models in which it is included, RVI) is reported for each variable in the final average model. Model coefficients and 95% confidence limits (CL) from multimodel average (*average model*) are shown, as well as model coefficients from the most parsimonious single model (with lowest Akaike information criterion; *best model*) and the model including only climate expectation (*climate expect. only model*). AIC corrected for small sample sizes (AICc), r^2 , and Akaike weight are also shown for singular models.

Explanatory variable	multimodel average				best model	climate expect. only model
	RVI	coef.	Lower Cl	Upper Cl	coef.	coef.
Fishes (n=56)						
climate expectation	1	0.239	-0.002	0.480	0.6359	0.6269
log range size	1	-0.114	-0.501	0.273	0.1646	
log range size x climate expectation	0.92	0.414	0.163	0.664	0.3772	
trophic level	0.62	-0.260	-0.490	-0.031	-0.3017	
ecological	0.22	0.405	-0.571	1.380		
water column position	0.18	0.199	-1.175	1.573		
log body size	0.05	0.089	-0.251	0.430		
trophic level x climate expectation	0.02	-0.016	-0.235	0.203		
r^2					0.620	0.356
AICc					129	134
Akaike weight					0.205	0.018
Invertebrates (n=51)						
climate expectation	1	0.86	0.60	1.12	0.855	0.204
trophic level	1	0.46	0.19	0.72	0.462	
trophic level x climate	1	1.09	0.77	1.41	1.10	
body size	0.12	-0.162	-0.542	0.218		
r^2					0.522	0.116
AICc					143	161
Akaike weight					0.81	<0.0001

Figure legends

Fig. 1. Poleward range boundary extensions and latitudinal changes in mean annual temperature isotherms over study period.

Fig. 2. Traits explaining variation in range shifts of fishes (a-c) and invertebrates (d-e). (a,d) Multi-model average parameter estimates for each species trait; lines indicate 95% confidence intervals; units are in standard deviations of each trait upon standard deviation of range shifts. (b) Range shifts in fishes as a function of climate expectation, greyscale represents range size: 400-1000km (black), 1000-2600 km (dark grey), and 2600-6400 km (light grey). (c) Range shifts in fishes as a function of log latitudinal range size, greyscale represents trophic level: 2-2.85 (black), 2.85-3.69 (dark grey), and 3.69-4.54 (light grey). Lines in (b,c) represent multi-model average coefficients and point size represents duration of each study from 14 (smallest point) to 29 years. (e) Range shifts in invertebrates as a function of climate expectation; greyscale represents trophic position of 2 (black), 2.5 (dark grey) and 3-3.5 (light grey). Lines represent multi-model average coefficients; point size represents duration study from 12 (smallest point) to 62 years.

Fig. 4. Rate of range shift relative to climate velocity for different reproductive modes of fishes (a) and invertebrates (b), showing high variability within groups and no strong pattern across groups.

Fig. 5. Underfilling of the potential thermal latitudinal range as a function of latitudinal range size in fish. Species with larger latitudinal ranges are more likely to fill their full potentials based on thermal tolerance, and hence are limited by factors other than temperature. A single invertebrate was included in the analysis, denoted by a circle. Grey lines represent best-fit linear model regressions using a poisson error distribution.

Fig. 1.

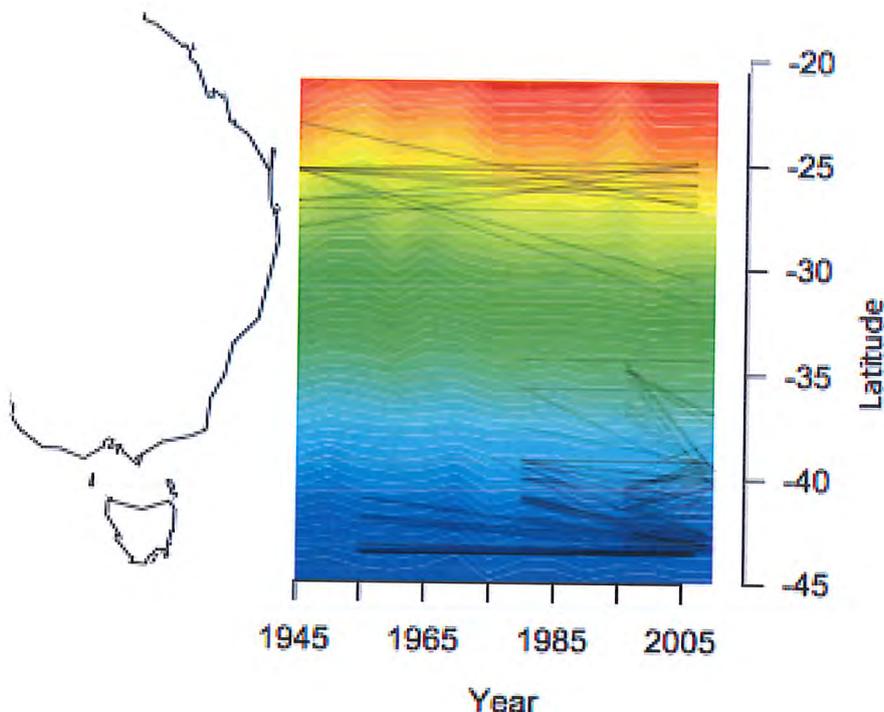


Fig. 2

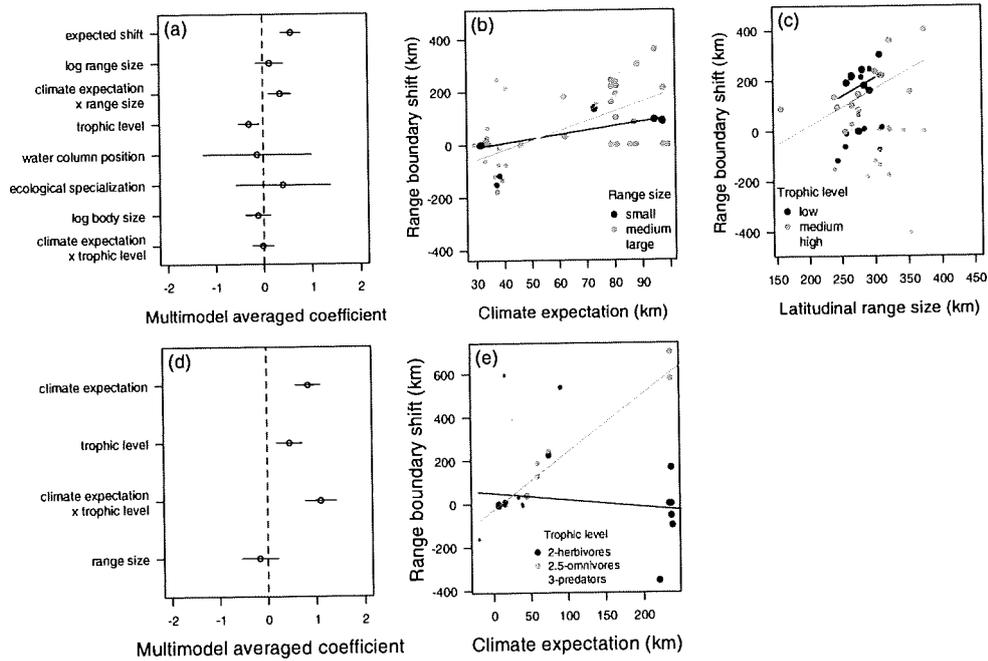


Fig. 4.

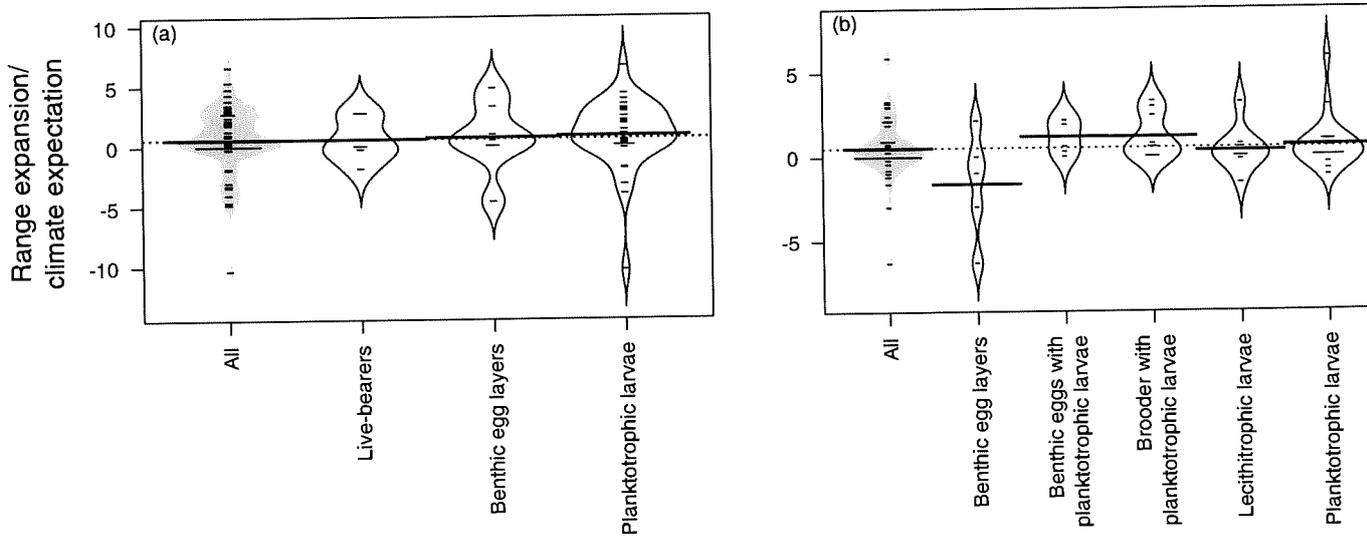
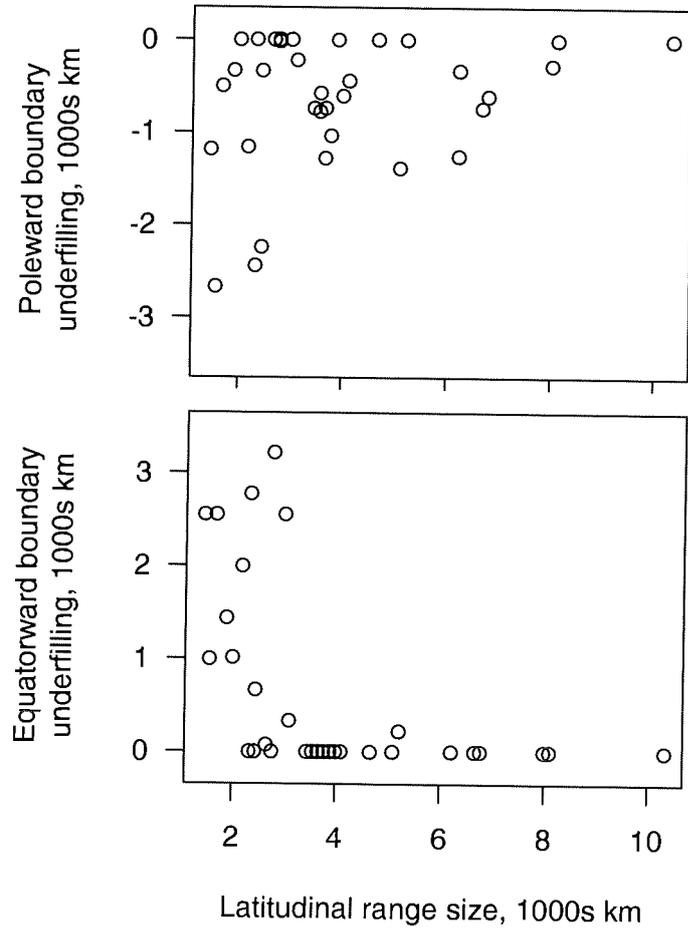


Fig. 5.



Appendix ii. Resilience and signatures of tropicalization in protected reef fish communities.

This work, in a revised format, has been published in the journal Nature Climate Change. Please cite this publication in any reference to it. It can be found at:
<http://www.nature.com/nclimate/journal/v4/n1/full/nclimate2062.html>

Resilience and signatures of tropicalization in protected reef fish communities

Amanda E. Bates^{1*}, Neville S. Barrett¹, Rick D. Stuart-Smith¹, Neil J. Holbrook^{1,2}, Peter A. Thompson³, Graham J. Edgar¹

¹Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, Australia²Australian Research Council Centre of Excellence for Climate System Science³CSIRO Marine and Atmospheric Research, Climate Adaptation Flagship, Hobart, Tasmania, Australia

*Corresponding author: A.E.Bates@soton.ac.uk
National Oceanography Centre
University of Southampton Waterfront Campus
Southampton SO14 3ZH
United Kingdom
Tel: +44 (0)23 8059 6666
Summary

Marine reserves may resist community change through supporting intact trophic webs and large-bodied individuals¹⁻³ and even alter colonization patterns as species shift polewards⁴. Here we test for community-wide responses to climate cycles and warming over 20 years, by analyzing species richness, diversity and functional traits in a marine reserve situated in a global warming hotspot. We find that both species richness and species diversity oscillate strongly at the decadal scale, underpinning ecological change. Warming signatures are also present as increasing functional trait richness and functional diversity, driven in part by a general increase in herbivores. Nevertheless, protected communities are distinguished from fished communities by displaying: (1) greater stability in some aspects of biodiversity, (2) recovery of large-bodied temperate species, (3) resistance to colonization by subtropical vagrants, and (4) less pronounced increases in the community-averaged temperature affinity. We empirically demonstrate that protection from fishing has buffered fluctuations in biodiversity and provided resistance to the initial stages of tropicalization.

Communities protected from exploitation and other human activities are thought to possess greater resilience to climate impacts - the capacity to resist and recover from the effects of climate-related variability⁵. Mechanisms conferring resilience include a greater potential to buffer changes in community structure due to higher species diversity, where a diverse community is more likely to functionally compensate if some species are lost⁵. Moreover, the set of functional traits present in reserves may differ from fished communities, including greater variety of functions, which may also enhance community resilience^{1,5,6}. Community dynamics are therefore expected to be more stable in reserves versus fished communities. In addition to climate variability, long-term climate change trends further impact biological systems^{7,8}. Abundance and geographic shifts related to climate change are driving the "tropicalization" of temperate systems as species from more equatorial latitudes with relatively warmer thermal affinities replace those living closer to the poles^{9,10}. An unanswered question is how protection from fishing will influence community resilience under the scenarios of both climate variability and ocean warming.

Empirical evidence to understand long-term climate change responses in marine reserves is limited. In particular, identity and abundance data for entire communities are scarce in rapidly warming regions. Moreover, disentangling short- and long-term biological responses requires adequate spatial and temporal replication at sites amenable for comparison of protected and fished areas. Here we take advantage of a 20-year data series initiated in 1992 of shallow reef fish abundance in temperate Australia, including quantitative underwater visual surveys of reef fishes in a marine reserve (protected) and nearby reference areas (fished)¹¹. This data set provides the unique opportunity to assess whether marine reserves facilitate resilience under environmental variability where ocean temperatures have risen by ~ 1.5 °C (Fig. 1)¹².

We assess changes in community composition using six metrics of richness and diversity. These include the traditional approaches of species richness and abundance-weighted diversity. Additionally, we consider the richness and diversity of functional traits amongst individuals, which can illustrate new aspects of diversity^{13,14}, a unique application in the context of long-term community change. Moreover, because increasing individual body size is a well-documented reserve effect^{15,16}, we also calculate biomass-weighted species and functional diversity. Our functional metrics are based on 10 traits representing thermal physiology, life history strategy, feeding ecology, behaviour, habitat use and geographic range breadth. For each metric, we test for differences between reserve and reference sites in patterns of variability mean values that may relate to physical parameters associated with climate variability and long-term change (Fig. 1, Supplementary Fig. S1 and Table S1).

Overall, species richness (SR) and functional richness (FR) were higher in the reserve, although not significantly so (Supplementary Table S2). Diversity values (all metrics: Fig. 2) were also comparable in reserve and reference communities. Hence, while fishing can lead to the removal of entire trophic groups and alter the complement of species present, and consequently the taxonomic and functional richness and diversity of the community⁶, we found no evidence for a difference in the variety of species or functions following the implementation of the Maria Island reserve.

However, we did detect relationships between biodiversity and climate variability. Significant fluctuations in species richness were apparent that corresponded with changes in nutrients and the Southern Oscillation index (SOI, Supplementary Table S2) – a commonly used metric for the timing of the dominant El Niño – Southern Oscillation climate mode. Abundance-weighted species diversity (SDa) and functional diversity (FDa) also fluctuated through time (Fig. 2c-d). Trends in abundance-weighted diversity therefore required careful interpretation when assessing reserve effects, as SDa and FDa were sensitive to order-of-magnitude changes in numbers of a numerically dominant species *Trachinops caudimaculatus* (e.g., SDa: Supplementary Table S2 and Fig. S2). In comparison, weighting diversity measures by biomass (SDb and FDb) produced values that were less variable through time. Biomass-weighted diversity metrics more closely resembled richness patterns (Fig. 2e-f), and, even though overall biomass was higher in the reserve¹¹, indicate a similar distribution of biomass among species and functional groups in the reserve and reference communities. Our results demonstrate the value of long-term monitoring for understanding how climate cycles can influence communities following protection, but also caution on the sensitivity of diversity metrics used to report community change to patterns in single species.

While richness and diversity values were similar in the reserve and reference communities, the reserve displayed greater temporal stability at both annual and decadal scales. First, the magnitude of successive year-to-year changes in diversity at individual sites was lower in the reserve versus fished areas (significantly so for SDa, FDa and SDb) (Fig. 3, Supplementary Table S3). Second, the amplitude of the decadal oscillation in mean SR and SDb was dampened in the reserve versus reference sites (Fig. 2, Supplementary Table S2). Greater stability in the reserve cannot be explained by higher richness and diversity, which would be expected to increase community resilience to climate variability due to functional redundancy ('insurance hypothesis'¹⁷). An alternate explanation lies in greater stability in the population abundances of species in the reserve¹⁸, where the community

shifted from smaller, more abundant fishes to larger, less abundant fishes following protection (Supplementary Fig. S3 and Table S4). In fact, the year-to-year differences in the abundance of two dominant small-bodied species were significantly less in the reserve (Supplementary Table S3). Increased predation may limit natural cycles in abundance of prey species, essentially forming a feedback mechanism to promote stability^{18,19}. Greater short-term stability would also contribute to the long-term dampening of decadal cyclic patterns observed inside the reserve, but it is likely that long-term trends have also been facilitated by cascading changes in trophic interactions following protection^{19,20}. Our results consequently support the contention that direct and indirect effects are playing out at different timescales¹⁹, effectively increasing community resistance to both inter-annual climate variability and decadal-scale changes.

While resistance to climate variability was apparent in the reserve, an increase in species and functional richness (SR, FR) and biomass-weighted functional diversity (FDb) over the study period were common to the reserve and reference communities (Fig. 2, Supplementary Table S2). These patterns track the warming trend (Fig. 1c, Supplementary Fig. S1), suggesting that the signature of longer-term climate change was more detectable in diversity metrics that incorporated functional traits, in comparison to traditional taxonomic diversity measures. However, direct comparisons of functional richness and diversity between communities are challenged because both are multi-metric indices - identical values can represent different underlying trait combinations. Thus, we further analysed independent trends in species traits in the reserve and fished communities to ascertain whether increasing functional richness and diversity were underpinned by the same mechanisms.

The increase in functional richness and diversity can at least partially be attributed to an increase in herbivorous species over the study period. Both the proportion of herbivorous species present in the community and biomass attributable to herbivores increased, exponentially in the case of biomass (Fig. 4, Supplementary Fig. S4 and Table S5). This response is unlikely due to a general decrease in predation intensity, as the abundances of larger fish in both the reserve and reference did not decline (Supplementary Fig. S3). Instead, warming-related poleward extension and increases in the abundances of herbivorous fish at high latitudes are expected because the digestion of algal and plant material is temperature-dependent, thereby limiting herbivorous fish from occupying temperate latitudes where waters are relatively cold²¹. Our results suggest that increases in herbivores will be an important signature of tropicalization in temperate reef communities, as has been observed in subtropical systems²², and an important potential mechanism of ecological and functional community change.

The proportion of species with a large maximum body size also increased over the study duration, contributing to increases in functional richness, and presumably also biomass-weighted functional diversity. However, this trend was limited to sites in the reserve where, in particular, several large-bodied carnivorous species increased following protection (see species examples in Supplementary Fig. S5), leading to an increase in the mean maximum body size of species present by 2.5 cm decade⁻¹ (Fig. 4b, Supplementary Fig. S4 and Table S5). Recovery of large species inside the reserve apparently represents an important response to protection, in addition to the better-documented biological responses of increasing biomass, individual body size and density in protected versus fished areas^{15,16}.

Community thermal affinity, measured as the upper realized temperature niche averaged across all species present, gradually rose, consistent with the tropicalization hypothesis (Fig. 4c). Even so, the increase in thermal affinity was not as strong in reserve sites (0.08 °C decade⁻¹) in comparison to fished sites (0.20 °C decade⁻¹, Supplementary Table S5), and was also lower than the rate of 0.19 °C reported at the global scale for the mean temperature preference of fisheries catch¹⁰. In fact, community thermal affinity in the reserve declined when weighted by biomass (Supplementary Fig. S4). This buffering effect is due to the recovery of large-bodied temperate species following protection from fishing. Conversely, the steep increase in thermal affinity in the reference communities can be attributed to increasing colonization by warm-water species. An exponential

increase in the abundance of some warm-water species occurred over the 20-year observation period at the reference sites (Supplementary Fig. S5). Additionally, four range-shifting species (i.e., *Chromis hypsilepis*, *Heterodontus portusjacksoni*, *Hypoplectrodes maccullochi* and *Sphyaena novaehollandiae*: species atypical of Maria Island from lower latitudes) were detected at reference locations, while none were recorded within the reserve boundary (Supplementary Fig. S5).

Hence both communities displayed an increase in herbivores, which presumably contributed to the overall increase in species and functional richness, and biomass-weighted functional diversity. However, the reference sites further displayed greater invasion by warm-water species, while large-bodied species increased in the reserve. These results imply an interaction between warming and recovery following from protection that has reshaped community structure and function inside the reserve.

We consider two hypotheses that provide mechanisms for the observed resistance to warm-water species in the reserve. First, higher predation rates can result in ‘biotic resistance’ to colonization²³. Averaged over the 20-year study period, large individuals (> 25 cm) were more abundant in the reserve (by 41%) while small individuals (< 10 cm) were less abundant (Supplementary Fig. S3 and Table S4). The potential for decreased survival of recruits, and thus colonization success, certainly exists due to greater predation intensity inside the reserve^{24,25}. Indeed, many of the warm water recruits that were relatively abundant in the reference locations were small in size and thus vulnerable to predation (e.g., *Parma microlepis*, Supplementary Fig. S5). Second, a range-extending urchin, *Centrostephanus rodgersii*, also counted during the fish surveys but excluded from analyses, was more abundant in the reference sites (Supplementary Fig. S6 and Table S6). Marine reserves in southeast Tasmania have permitted lobsters to reach large sizes, and in turn, these larger animals predate on urchins. Areas protected from fishing thereby resist establishment by urchins and their poleward spread²⁶. The presence of urchins may facilitate further colonization of subtropical species (‘invasional meltdown’²⁷) through habitat modification¹², such as if warm-water species prefer barrens, suggesting an important line of investigation for future studies.

Intact marine communities protected from fishing therefore have the potential to buffer climate-related biological variability, including range shifts. In addition, reserves may also offer suitable habitat for some species to establish⁴, and are also important conservation tools for habitat-limited species. In the context of climate change, static protected areas have potential to build community resilience through a number of mechanisms to promote species and functional stability, and resistance to initial stages of tropicalization.

Methods

Field Surveys

The Maria Island Marine Reserve (east coast of Tasmania, Fig. 1a) was established in 1991 and stretches along a 7 km length of coastline. Fish communities were surveyed annually from 1992 to 2012 (except 2003) using standardized visual census methods at six sites within the reserve and six external sites selected for their similarity¹¹. All surveys were undertaken in the austral summer to autumn (February–April), and involved recording the species, number and size-class of all fishes observed within 5 m of each side of a 200 m long transect along the 5-m isobath. Size-classes were in 2.5 cm increments to 15 cm, 5 cm increments from 15 cm to 40 cm, and then 10 cm increments. Approximately 65% of the data were collected by NSB and GJE, and other divers were distributed as evenly as possible between reserve and reference sites. Biomass was estimated by incorporating data on the abundance and size structure of each species on transects and species-specific coefficients for the associated length-weight relationship from FishBase²⁸. A correction factor was first applied to size data to account for bias in size estimates from divers²⁵. In addition, abundance data for the habitat-modifying urchin, *Centrostephanus rodgersii*, were collected in 1-m wide bands along

transects at the same time as the fish surveys. These data were excluded during calculations of the diversity metrics but are reported in the Supplementary Information.

Richness and Diversity Calculations

Diversity is a function of the number of species present (richness: mean species density survey-1) and how evenly species abundance or biomass are distributed across a community. To calculate species and functional diversity we used the function `divc` (Rao's quadratic entropy, Q29), which incorporates the relative abundance (numbers of individuals) or biomass (kg) of each species per 1000 m², using the `FD` package in R30. All values were converted to effective numbers (as in 14). For species diversity, the distances between all species were assumed to be one (where effective Q is mathematically equivalent to the Inverse Simpson index), while the Gower dissimilarity matrix (ultrametric conversion was with generalized least squares methods) was used for functional diversity, based on the trait matrix (described below). In addition, functional richness (convex hull volume, `FRic30`) and the community weighted mean trait values were calculated.

We selected 10 traits: maximum body length, longitudinal range breadth, thermal affinity, trophic breadth, trophic group, water column position, diel activity pattern, gregariousness, macrophyte association and substratum preference (Supplementary Table S7). To calculate thermal affinity, we selected an upper percentile of the realized temperature distribution for each species. This statistic allows comparison of Australian temperate species, many of which might otherwise live further poleward but are constrained by the southern edge of the continent, to subtropical species, which can fully achieve their fundamental thermal niche in Australia (Supplementary Methods). Water column position and macrophyte association contributed most of the variability in functional diversity (Supplementary Table S8).

Statistical Models

We used fixed and mixed effects models fitted using maximum likelihood (ML). Where appropriate, the random effect of site or year was included to control for variation in the response variable due to repeated sampling. We tested for differences in community stability by modelling the oscillation in biological responses (using the sine and cosine function) and interactions between the reserve and reference sites. We also tested for an increase through time (SOI and temperature displayed a positive trend over the study period: Fig. 1b-c). Additionally, to explore shorter-term patterns with environmental parameters, we tested for significant relationships with oceanographic variables. Salinity was highly correlated with the different sea surface temperature measures (mean, minimum and maximum); silicate and nitrate were also correlated (Supplementary Fig. S1). We therefore included the following de-trended physical and chemical data as predictors (year was included in all models to test for trends through time, expected in response to warming): SOI, summer mean sea surface temperature, and nitrate concentration, in addition to the interaction between year and protection from fishing. The best model was selected based on AIC, or in cases where models with different predictors had similar AIC values we used multi-model inference to produce model-averaged parameter estimates and unconditional standard errors. The 70% confidence model set was calculated with the package "MuMIn" in each case, with the function `model.avg`, and component models reported in combination with the results summary table in the Supplementary Information where applicable. Before executing each model, we conducted collinearity diagnostics by calculating generalized variance inflation factors (GVIF) for the fixed effects; variables with GVIF values that exceeded 2.5 were excluded.

The model fit and residual behaviour were visually inspected to ensure that the test assumptions were met, and error structures (site-level variance and autocorrelation structure) were applied to normalize the residuals if required or when significant time lags were present. Alpha was adjusted to 0.025 to control for the increased probability of making a Type I error.

See Supplementary Information for full methods.

Correspondence and requests for materials should be addressed to A.E.B.

Acknowledgements. We are grateful for the contributions of the many field technicians that assisted with diving surveys over the 20-year monitoring period, to A. Schaap for initiating the monitoring program, to C. Buxton for continuing lab support, and to J. Lefcheck for insightful discussions on the topic of functional diversity. AEB was supported by an Australian Government Fisheries Research and Development Corporation and Department of Climate Change and Energy Efficiency grant. Salary for RDSS was provided by an Australian Research Council Postdoctoral Fellowship. Biological monitoring was funded in parts by the Australian and Tasmanian Governments (Australian Research Council; Natural Heritage Trust; National Resource Management; Fisheries Research and Development Corporation; and Department of Primary Industries, Parks, Water and Environment) with considerable logistic support from Tasmanian Parks and Wildlife Service. Temperature, salinity and nutrient data from 2009 to 2012 were sourced from the Integrated Marine Observing System (IMOS) - IMOS is supported by the Australian Government. The CSIRO Coastal Monitoring program provided oceanographic data prior to 2008.

Author contributions. AEB, NSB, GJE and RDS-S conceived the idea for the manuscript. NSB and GJE and others collected the fish data. AEB analysed the data and drafted the manuscript with significant input from NSB, GJE and RDS-S. NJH and PAT assisted with collating and interpreting the oceanographic data. All authors commented on manuscript drafts.

Competing financial interests. The authors declare no competing financial interests.

References

1. Behrens, M. D. & Lafferty, K. D. Effects of marine reserves and urchin disease on southern California rocky reef communities. *Mar. Ecol. Prog. Ser.* 279, 129-139, doi:10.3354/meps279129 (2004).
2. Micheli, F. et al. Evidence that marine reserves enhance resilience to climatic impacts. *PLOS ONE* 7, e40832, doi:10.1371/journal.pone.0040832 (2012).
3. Mumby, P. J., Wolff, N. H., Bozec, Y.-M., Chollett, I. & Halloran, P. Operationalizing the resilience of coral reefs in an era of climate change. *Conserv. Lett.*, advance online publication, doi:10.1111/conl.12047 (2013).
4. Thomas, C. D. et al. Protected areas facilitate species' range expansions. *Proc. Natl. Acad. Sci. USA* 109, 14063-14068, doi:10.1073/pnas.1210251109 (2012).
5. Bernhardt, J. R. & Leslie, H. M. Resilience to climate change in coastal marine ecosystems. *Annual Review of Marine Science* 5, 371-392, doi:10.1146/annurev-marine-121211-172411 (2013).
6. Villamor, A. & Becerro, M. A. Species, trophic, and functional diversity in marine protected and non-protected areas. *J. Sea Res.* 73, 109-116, doi:10.1016/j.seares.2012.07.002 (2012).

7. Poloczanska, E. S. et al. Global imprint of climate change on marine life. *Nature Clim. Change* 3, 919-925, doi:10.1038/nclimate1958 (2013).
8. Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37-42, doi:10.1038/nature01286 (2003).
9. Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of animals. *Nature Clim. Change* 2, 686-690, doi:10.1038/nclimate1539 (2012).
10. Cheung, W. W. L., Watson, R. & Pauly, D. Signature of ocean warming in global fisheries catch. *Nature* 497, 365-368, doi:10.1038/nature12156 (2013).
11. Barrett, N. S., Edgar, G. J., Buxton, C. D. & Haddon, M. Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *J. Exp. Mar. Biol. Ecol.* 345, 141-157, doi:10.1016/j.jembe.2007.02.007 (2007).
12. Johnson, C. R. et al. Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J. Exp. Mar. Biol. Ecol.* 400, 17-32, doi:10.1016/j.jembe.2011.02.032 (2011).
13. Halpern, B.S. & Floeter, S.R. Functional diversity responses to changing species richness in reef fish communities. *Mar. Ecol. Prog. Ser.* 364, 147-156, doi:10.3354/meps07553 (2008).
14. Stuart-Smith, R. D. et al. Integrating abundance and functional traits reveals new global hotspots of fish diversity *Nature* 501, 539-542, doi:10.1038/nature12529 (2013).
15. Halpern, B. S. The impact of marine reserves: do reserves work and does reserve size matter? *Ecol. Appl.* 13, 117-137, doi:10.1890/1051-0761 (2003).
16. SE, L. et al. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33-46, doi:10.3354/meps08029 (2009).
17. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Nat. Acad. Sci. USA* 96, 1463-1468, doi: 10.1073/pnas.96.4.1463 (1999).
18. MacArthur, R. Fluctuations of Animal Populations and a Measure of Community Stability. *Ecology* 36, 533-536 (1955).
19. Babcock, R. C. et al. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci. USA* 107, 18256-18261, doi:10.1073/pnas.0908012107 (2010).
20. Edgar, G. J., Barrett, N. S. & Stuart-Smith, R. D. Exploited reefs protected from fishing transform over decades into conservation features otherwise absent from seascapes. *Ecol. Appl.* 19, 1967-1974, doi:10.1890/09-0610.1 (2009).
21. Floeter, S. R., Behrens, M. D., Ferreira, M. J., Paddock, C. E. L. & Horn, M. H. Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar. Biol.* 147, 1435-1447 (2005).
22. Vergas, A. et al. Role of fish herbivory in structuring the vertical distribution of canopy algae *Cystoseira* spp. in the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 375, 1-11, doi:10.3354/meps07778 (2009).
23. Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., Grosberg, R. K., Hasting, S. A., Holt, R. D., Mayfield, M. M., O'Connor, M. I. & Rice, W. R.

Ecological and evolutionary insights from species invasions. *Trends Ecol. Evol.* 22, 465-471, doi:10.1016/j.tree.2007.06.009 (2007).

24. Edgar, G. J. & Stuart-Smith, R. D. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Mar. Ecol. Prog. Ser.* 388, 51-62, doi:10.3354/meps08149 (2009).

25. Wanger, T. C. et al. Endemic predators, invasive prey and native diversity. *Proc. Biol. Sci.* 278, 690–694, doi:10.1098/rspb.2010.1512 (2011).

26. Ling, S. D. & Johnson, C. R. Marine reserves reduce risk of climate-driven phase shift by reinstating size- and habitat-specific trophic interactions. *Ecol. Appl.* 22, 1232-1245, doi:10.1890/11-1587.1 (2012).

27. Simberloff D. & Von Holle B. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Inv.* 1, 21-32, doi:10.1023/A:1010086329619 (1999).

28. FishBase; available at www.fishbase.org.

29. Botta-Dukát, Z. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16, 533-540, doi:10.1111/j.1654-1103.2005.tb02393.x (2005).

30. Laliberté, E. & Legendre, P. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299-305, doi:10.1890/08-2244.1 (2010).

Figure Legends

Figure 1| Geographic and oceanographic setting of the Maria Island Marine Reserve. The East Australian Current (EAC) brings warm tropical waters polewards. While the majority of flow turns abruptly at ~32°S, a small portion continues south towards Maria Island, driving regional warming. Increases in primary productivity on the southeast coast are the result of EAC activity uplifting nutrient-rich slope water onto the shelf. a, Map showing distribution of survey sites along the eastern Tasmanian coast. Six sites were surveyed annually from 1992-2012 within the reserve, while external reference sites fall outside reserve boundaries. b-d, Variability and trends in the Southern Oscillation index (SOI) – an indicator of El Niño (low values) or La Niña (high values) events, sea surface temperature, and nitrate concentration, respectively, over the study period (Supplementary Methods provide details). Regression (dotted line) and 95% confidence limits (shaded) are from linear mixed effects models (Supplementary Table S1).

Figure 2| Species and functional diversity at Maria Island over 20 years. a-b, Species (SR) and functional richness (FR), c-d, abundance-weighted species (SDa) and functional diversity (FDa) and e-f, biomass-weighted species (SDb) and functional diversity (FDb) in reserve (n = 6) and reference sites (n = 6). Regression slopes (dotted lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table S2). A single black regression line indicates similar mean values for reserve and reference sites.

Figure 3| Annual change in richness and diversity metrics. Mean (± 1 SE) year-to-year differences in species (SR) and functional richness (FR), abundance-weighted species (SDa) and functional diversity (FDa), and biomass-weighted species (SDb) and functional diversity (FDb) in reserve (n = 6)

and reference sites (n = 6) for the 20-year study period. Model results are in Supplementary Table S3. Values were scaled prior to differencing.

Figure 4| Community averaged functional trait values. a, Proportion of fish species which are herbivorous, b, maximum body length and c, thermal affinity averaged across all species recorded on a survey. Regression slopes (dotted lines) and 95% confidence intervals (shading) are predicted from linear mixed effects models (Supplementary Table S5). A single black regression line indicates similar mean values for reserve and reference sites.

Fig. 1.

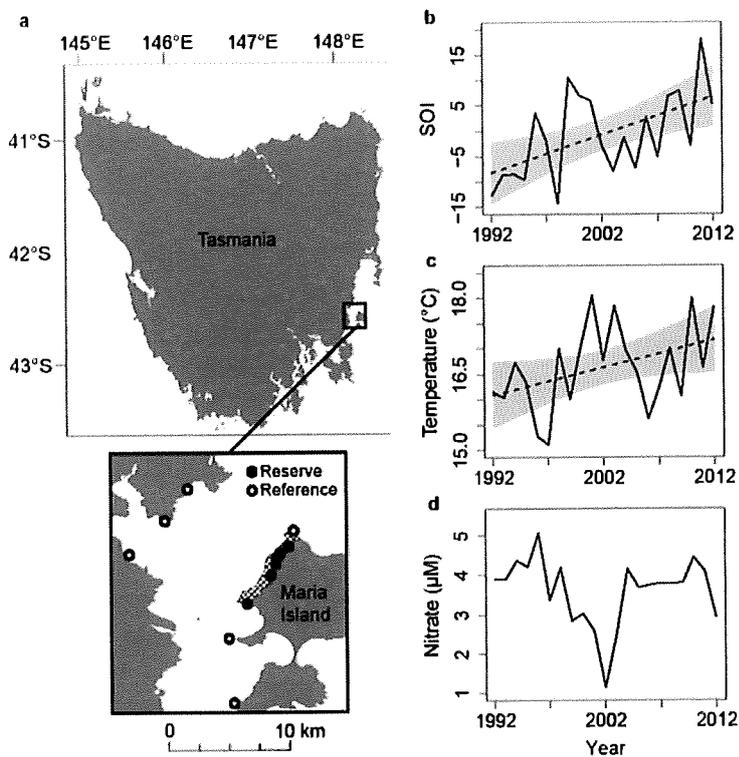


Fig. 2.

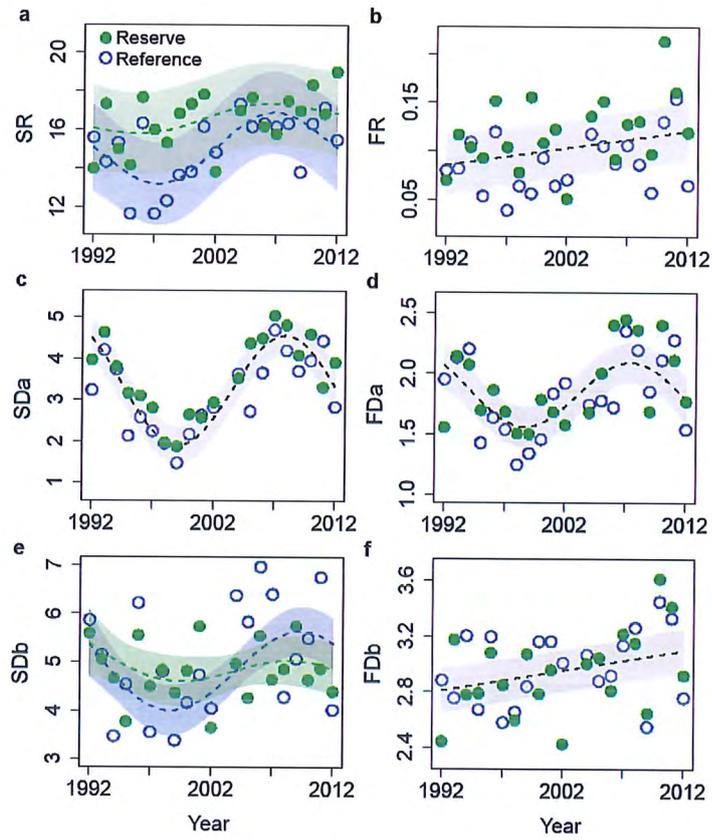


Fig. 3.

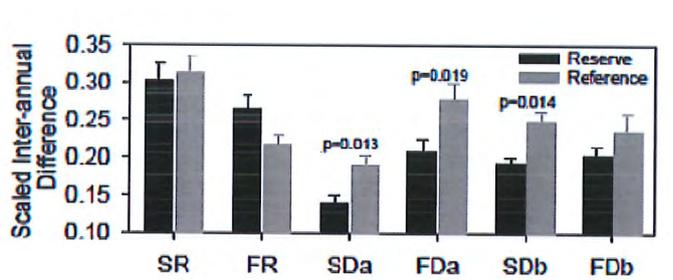
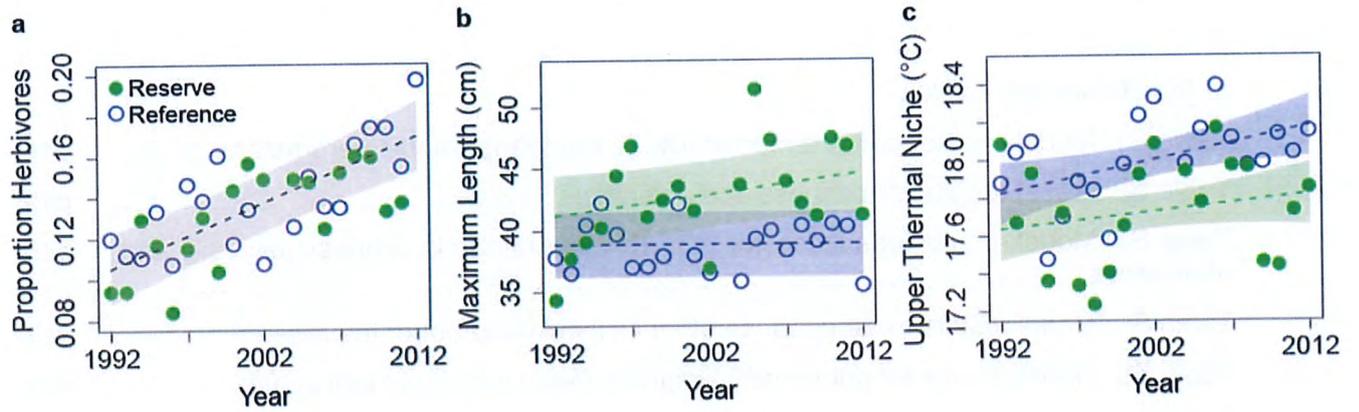


Fig. 4.



Supplementary Information

Reef fish communities protected from fishing resist tropicalization

Amanda E. Bates, Neville S. Barrett, Rick D. Stuart-Smith, Neil J. Holbrook, Peter A. Thompson, Graham J. Edgar

1. Supplementary Methods

Functional traits.....	p2
Oceanographic data.....	p2

2. Supplementary Figures

Figure S1. Additional oceanographic variables of interest at Maria Island.....	p4
Figure S2. Predictors of abundance-weighted species diversity.....	p5
Figure S3. Abundance of large and small fish in the reserve and reference sites	p6
.....	
Figure S4. Community weighted biological trait values calculated based on	p7

biomass....

Figure S5. Species displaying trends related to changes in the community weighted mean functional traits p8

.....

Figure S6. Abundance of the range extending urchin in the reserve and reference sites over time p9

.....

3. Supplementary Tables

Table S1. Model results for the temporal trends in oceanographic parameters..... p10

Table S2. Model results for richness and diversity..... p12

Table S3. Model results for successive year-to-year change in richness, diversity and abundance..... p15

Table S4. Model results for abundance of small fish in and out of the reserve p17

Table S5. Model results for community weighted mean functional trait values..... p18

Table S6. Model results for abundance of a range extending urchin in and out of the reserve..... p21

...

Table S7. Functional traits of fishes used in estimation of functional diversity..... p22

Table S8. Relative contributions of the different traits to biomass-weighted functional diversity..... p23

.

4. Supplementary References

1. Supplementary Methods

1.1 Functional Traits

Selected traits (Table S7) represent the functional roles of fish within a community: life history, trophic position, behaviour, habitat associations, ecological generality and physiology. Data for eight functional traits were subset from a global dataset described fully in¹: maximum body length, trophic breadth, trophic group, water column position, diel activity pattern, gregariousness, macrophyte association, and substratum preference. We add longitudinal range breadth (sourced from FishBase⁴) as an indicator of ecological generality and dispersal potential. We further calculate a physiological trait expected to change with ocean warming - thermal affinity. To infer the upper thermal preference for species we first extracted each occurrence record for all 97 species occurring at Maria Island in the high-resolution Reef Life Survey dataset for Australia (<http://reeflifesurvey.com>)⁵ and matched mean SST for each site provided by Bio-ORACLE at a spatial resolution of 9.2 km (www.bio-oracle.ugent.be)⁶. We quantified the 95th percentile of the temperature distribution for each species because the distributions of temperate species in Australia are habitat limited beyond the most southern edge of Tasmania; thus a measure of upper occupied habitat temperatures allows for direct comparisons between the temperate and subtropical fishes in the dataset. Prior to analyses, numeric traits (body length, trophic breadth, and longitudinal range breadth) were scaled, and gregariousness (1 to 3), was ordered as a factor. All other traits were coded as unordered factors and functional richness and diversity metrics quantified as described in the main text methods.

To evaluate the relative contributions of individual traits to variability in functional diversity we used the approach of Stuart-Smith et al.¹ (Table S8). Briefly, we removed each trait from the full trait matrix and re-calculated functional diversity ten times. We used linear regression to estimate the relationship of each of the ten functional diversity estimates where one trait was removed to functional diversity calculated using all traits. In cases where traits had minimal influence on functional diversity, dropping the traits led to a small change in functional diversity consequently a higher R^2 value. We ranked the traits based on the relative change in R^2 resulting from the removal of each trait, where lower R^2 values indicated a higher contribution to the overall functional diversity, but not necessarily differences between the reserve and reference.

1.2 Oceanographic Data

The Southern Oscillation index (SOI) was sourced from the Australian Bureau Meteorology (<http://www.bom.gov.au/climate/glossary/soi.shtml>) using Troup SOI - the standardised anomaly of the Mean Sea Level Pressure difference between Tahiti and Darwin². Mean annual SOI was calculated on the basis of the austral seasonal year (i.e., from July of the previous calendar year to June of the successive year).

Time-series of oceanographic data collected by the CSIRO Division of Marine and Atmospheric Research (Hobart, Tasmania) was from the coastal station monitored by the near Maria Island (42°36'S, 148°14'E). Monitoring at the coastal station has been ongoing under the CSIRO Coastal Monitoring Programme since the 1940s at intervals of one to several weeks. Sea surface temperature and salinity were measured at regular intervals, while nitrate and silicate have been at less regular intervals since April 2009, and are stored on-line as part of the CMAR hydrology archive in Hobart and available via the CMAR Data Trawler (http://www.cmar.csiro.au/trawler/dataset.cfm?survey=CS-MAI-ALL&data_type=hydro), as described in³. From 2009, sampling has been by the Integrated Marine Observing System, IMOS, currently available via the IMOS portal (<http://imos.aodn.org.au/webportal/>). The IMOS sampling includes additional biological data

and temperature data taken from the CTD on the IMOS mooring instead of reversing thermometers. Because the sampling resolution and methodology changed seasonally and through time, we calculated the mean sea surface temperature for the austral summer (January – March), maximum annual nitrate, and average annual silicate and average annual salinity.

2. Supplementary Figures

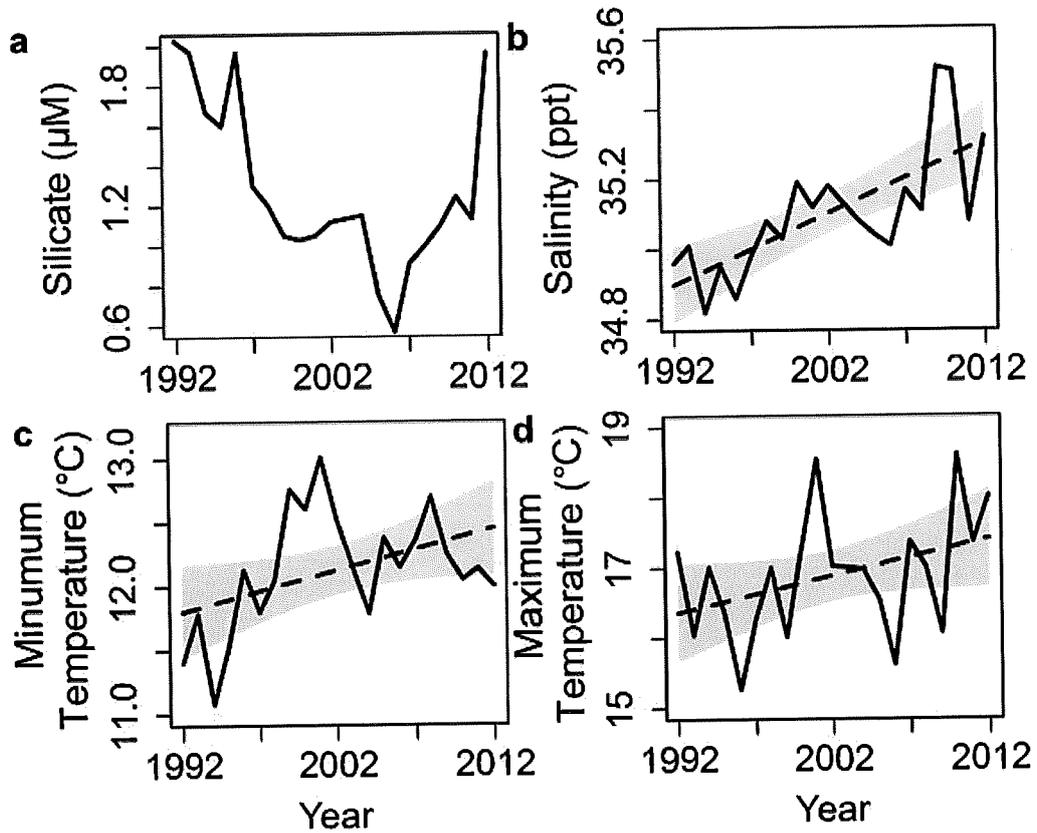


Figure S1. Additional oceanographic variables of interest at Maria Island. a, Mean annual silicate and **b,** salinity, and **c-d,** extreme sea surface temperatures.

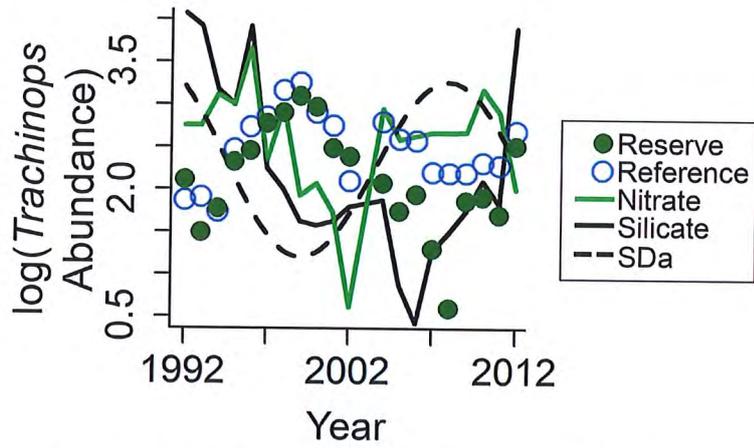


Figure S2. Predictors of abundance-weighted species diversity. Species diversity (SDa) related negatively to the abundance of *Trachinops caudimaculatus* abundance in the reserve and reference sites, and positively to nitrate and silicate; see Figures 1d and S1 for the y-axis dimensions of nitrate and silicate concentrations.

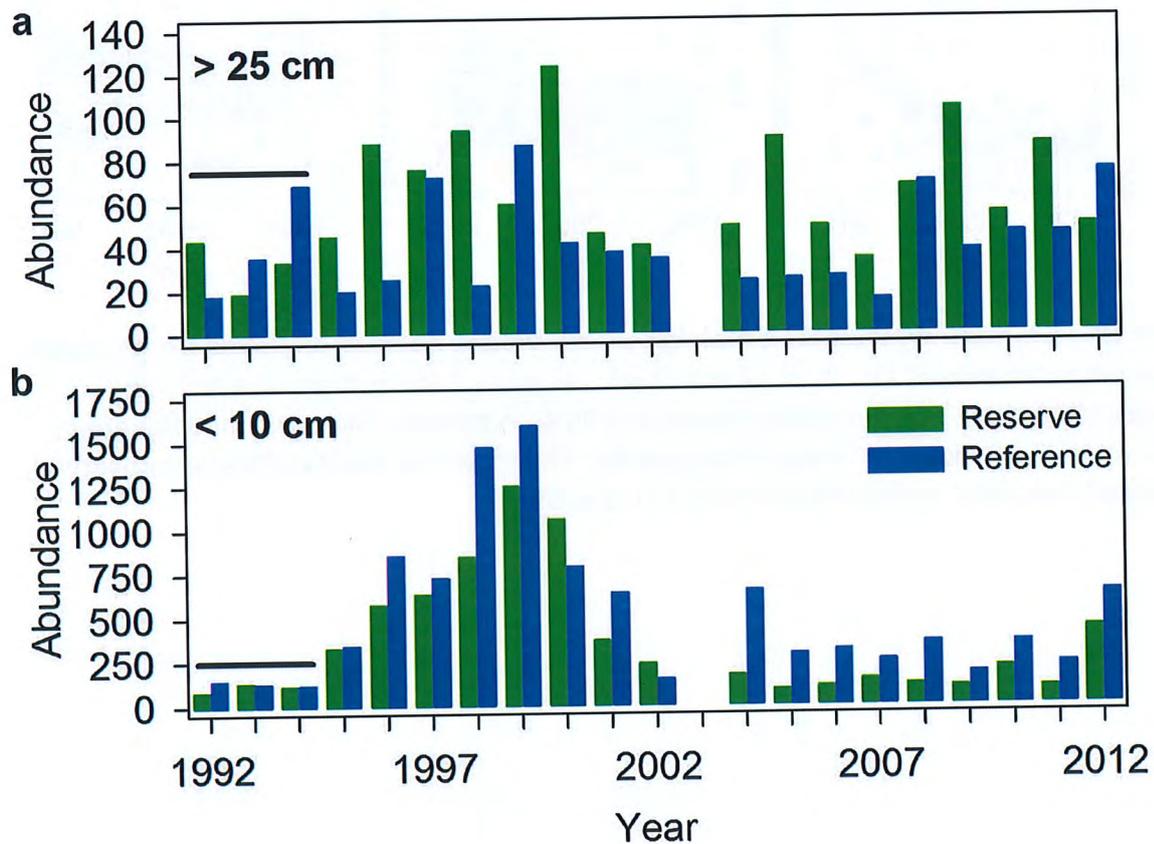


Figure S3. Abundance of small fish in the reserve and reference sites over time. Mean abundance (± 1 SE) of fish **a**, greater than 25 cm and **b**, less than 10 cm in length ($n = 6$ sites) from 1992 to 2012; abundance in both size groups did not differ between the reserve and reference sites for the the first three years following implementation of the reserve, indicated by a black line. Generalized linear mixed model results are reported in Table S4.

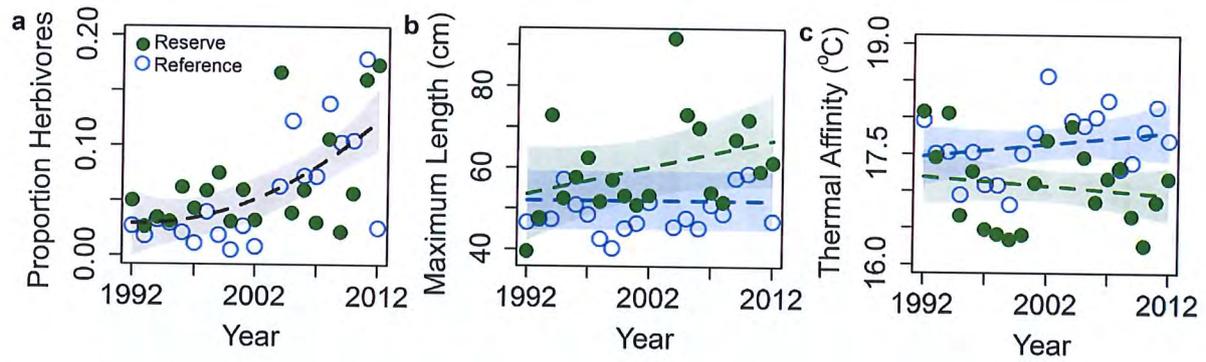


Figure S4. Community weighted biological trait values calculated based on biomass. **a**, Proportion herbivores kg⁻¹; **b**, maximum body length kg⁻¹ and **c**, thermal affinity kg⁻¹ biomass. Regression slopes (dotted lines) and 95% confidence intervals (shading) are in colour when a significant difference between the reference and reserve sites was observed, predicted from linear mixed effects models (Table S5).

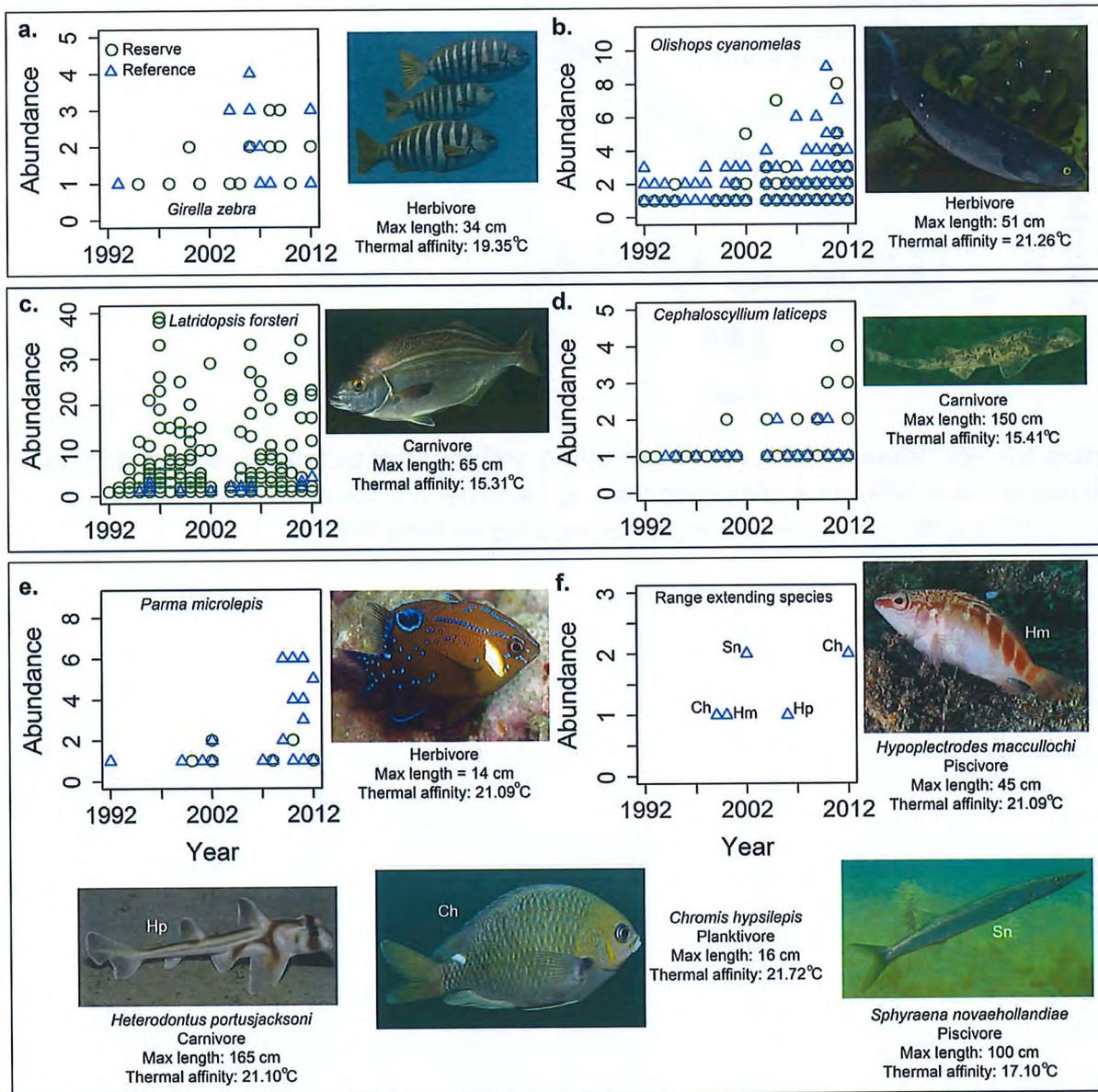


Figure S5. Species displaying trends related to changes in the community weighted mean functional traits. a-b, Changes in the abundance of herbivores (*Girella zebra* and *Olisthops cyanomelas*), c-d, large-bodied fish (*Latridopsis forsteri* and *Cephaloscyllium laticeps*) and e, warm-water species typical of Maria Island (*Parma microlepis*) in reserve and reference sites. f, Four species atypical of Maria Island and thought to be extending their range were sighted in reference sites only (*Chromis hypsilepis*, *Heterodontus portusjacksoni*, *Hypoplectrodes maccullochi* and *Sphyraena novaehollandiae*).

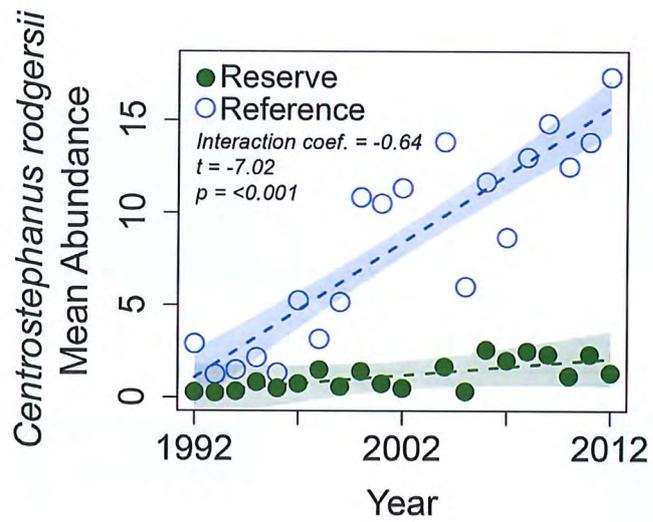


Figure S6. Abundance of the range extending urchin, *Centrostephanus rodgersii*, in the reserve and reference sites over time. a, Mean abundance of urchins (n = 6 sites) from 1992 to 2002. Linear model results are reported in Table S6.

3. Supplementary Tables

Table S1. Model results for climate trends from 1992 to 2012. Models were generalized least squares fit by maximum likelihood (ML). The empirical autocorrelation structure of the residuals was modelled when significant lags were present (assessed using the function “ACF” in the package nlme⁷) by competing models with moving average and first-order autoregressive terms⁸. Silicate, salinity and extreme temperature values were excluded from subsequent analyses due to high generalized variance inflation factors (GVIF of 2 or greater)⁹. Standard error = SE; Akaike information criterion = AIC.

a. Southern Oscillation Index (results are relevant to Fig. 1b in the main text)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-1520.037	522.419	-2.909	0.009
Year	0.759	0.261	2.908	0.009
AIC	139.814			
Residual standard error	6.865			

b. Sea Surface Temperature (results are relevant to Fig. 1c in the main text)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-89.239	54.851	-1.627	0.121
Year	0.053	0.027	1.929	0.069
AIC	49.660			
Residual standard error	0.721			

c. Nitrate (results are relevant to Fig. 1d in the main manuscript)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	33.868	61.982	0.547	0.592
Year	-0.015	0.031	-0.487	0.632
AIC	54.549			

d. Silicate (results are relevant to Fig. S1a)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	37.498	58.474	0.641	0.529
Year	-0.018	0.029	-0.617	0.545
AIC	15.797			
Residual standard error	0.426			
Correlation structure, AR(1)				
Phi	0.737			

e. Salinity (results are relevation to Fig. S1b)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-5.776	9.483	-0.609	0.550
Year	0.021	0.005	4.310	0.001
AIC	-20.543			
Residual standard error	0.124			

f. Minimum Sea Surface Temperature (results are relevation to Fig. S1c)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-49.257	46.995	-1.048	0.308
Year	0.031	0.023	1.305	0.058
AIC	25.907			
Residual standard error	0.423			
Correlation structure, AR1()				
Phi	0.457			

g. Maximum Sea Surface Temperature (results are relevation to Fig. S1d)

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-96.560	38.810	-2.488	0.023
Year	0.057	0.019	2.923	0.009
AIC	51.667			
Residual standard error	0.839			
Correlation structure, ARMA(4,0)				
Phi	0.191	-0.206	0.272	-0.694

Table S2. Model results for richness and diversity. The reference (intercept) represents the fished sites and MPA is the reserve. A correlation structure of form $\sim 1|Site$ was included as weight using the function “varIdent” in the following models. When a model averaging approach was used, the component models are listed, otherwise results for the best model are shown. Standard error = SE.; Standard deviation = SD; Confidence interval = ci; Akaike information criterion = AIC.

a. Species richness (results are relevant to Fig. 2a in the main manuscript). Component models terms: 1. $\cos(\pi/9*Year)$, 2. MPA, 3. Temperature (detrended), 4. Nitrate, 5. SOI (detrended), 6. $\sin(\pi/9*Year)$, 7. Year, 8. $MPA:\cos(\pi/9*Year)$.

Random-effects, $\sim 1 Site$		SD					
Site		2.43					
Residual		2.19					
Component modes		df	AICc	Delta	Weight		
2,3,4,5,6,7,8		21	1180.15	0.00	0.44		
1,2,3,4,5,6,7,8		22	1181.68	1.53	0.20		
1,2,3,4,5,6,8		21	1181.84	1.68	0.19		
2,3,4,5,6,8		20	1182.00	1.85	0.17		
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	14.732	1.112	13.185	<0.001	12.542	16.922	
$\cos(\pi/9*Year)$	0.383	0.307	1.243	0.213	-0.221	0.987	
MPA	1.463	1.468	0.877	0.381	-1.807	4.734	
Temperature (detrended)	0.661	0.247	2.662	0.008	0.174	1.478	
Nitrate	0.762	0.242	3.128	0.001	0.284	1.239	
SOI (detrended)	0.088	0.028	3.145	0.002	0.033	0.143	
$\sin(\pi/9*Year)$	-1.709	0.397	4.288	<0.001	-2.491	-0.928	
Year	0.063	0.032	2.600	0.050	0.001	0.127	
$MPA:\cos(\pi/9*Year)$	1.251	0.479	2.600	0.009	0.308	2.195	

b. Functional richness (results are relevant to Fig. 2b in the main manuscript). Component models terms: 1. MPA, 2. Temperature (detrended), 3. Nitrate, 4. SOI (detrended), 5. Year.

Random-effects, $\sim 1 Site$		SD					
Site		0.05					
Residual		0.08					
Component modes		df	AICc	Delta	Weight		
3,5		16	-626.23	0.00	0.25		
2,3,4,5		18	-626.07	0.16	0.23		
2,3,5		17	-625.98	0.25	0.22		
1,3,5		17	-625.23	1.00	0.15		
3,4,5		17	-625.09	1.14	0.14		
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	0.088	0.017	5.086	<0.001	0.054	0.123	
MPA	0.032	0.028	1.026	0.305	-0.003	0.094	

Temperature (detrended)	0.008	0.005	1.669	0.089	-0.001	0.018
Nitrate	0.018	0.004	4.233	<0.001	0.009	0.026
SOI (detrended) SOI	0.001	0.001	1.384	0.166	-0.001	0.002
Year	0.001	0.001	2.007	0.040	0.001	0.002

c. Abundance-weighted species diversity (results are relevant to Fig. 2c in the main text)

Random-effects, ~1 Site		SD					
Site		0.64					
Residual		1.02					
Fixed-effects	Estimate	SE	t-value	p-value	2.5%ci	97.5%ci	
Intercept	3.424	0.240	14.246	<0.001	2.954	3.893	
Year	-0.017	0.013	-1.295	0.196	-0.042	0.009	
sin(pi/9*Year)	-0.914	0.116	-7.862	<0.001	-1.141	-0.687	
cos(pi/9*Year)	1.067	0.097	-11.016	<0.001	0.877	-1.256	
AIC	763.849						

d. Abundance-weighted functional diversity (results are relevant to Fig. 2d in the main text)

Random-effects, ~1 Site		SD					
Site		0.24					
Residual		0.57					
Fixed-effects	Estimate	SE	t-value	p-value	2.5%ci	97.5%ci	
Intercept	1.878	0.087	21.217	<0.001	1.705	2.051	
Year	-0.005	0.004	-1.142	0.255	-0.013	0.003	
cos(pi/9*Year)	0.187	0.032	5.939	<0.001	0.126	0.249	
sin(pi/9*Year)	-0.217	0.037	-5.695	<0.001	-0.291	-0.142	
AIC	324.560						

e. Abundance-weighted species diversity predicted by the abundance of *Trachinops caudimaculatus* and nitrate (results are relevant to Fig. S2)

Random-effects, ~1 Site		SD					
Site		0.40					
Residual		1.47					
Fixed-effects	Estimate	SE	t-value	p-value	2.5%ci	97.5%ci	
Intercept	-3.751	0.148	25.327	<0.001	3.461	4.041	
<i>Trachinops</i> abundance	-0.011	0.001	-9.080	<0.001	-0.014	-0.001	
Nitrate	0.209	0.091	2.293	0.023	0.030	0.387	
AIC	790.012						

f. Biomass-weighted species diversity (results are relevant to Fig. 2d in the main manuscript). Terms for component models are: 1. Temperature (detrended), 2. Nitrate, 3. SOI (detrended), 4. $\sin(\pi/12 \cdot \text{Year})$, 5. MPA: $\sin(\pi/12 \cdot \text{Year})$.

Random-effects, ~1 Site		SD					
	Site	0.45					
	Residual	1.77					
Component modes		df	AICc	Delta	Weight		
	1,2,4,5	18	949.76	0.00	0.42		
	2,4,5	17	950.33	0.58	0.31		
	2,3,4,5	18	950.65	0.89	0.27		
Fixed-effects		Estimate	SE	z-value	p-value	2.5%ci	97.5%ci
	Intercept	4.852	0.174	27.761	<0.001	4.509	5.194
	Temperature (detrended)	-0.244	0.136	1.776	0.076	-0.513	0.025
	Nitrate	0.364	0.128	2.839	0.005	0.113	0.615
	SOI (detrended)	0.021	0.015	1.454	0.146	-0.007	0.050
	$\sin(\pi/12 \cdot \text{Year})$	-0.678	0.186	3.644	0.003	-1.043	-0.313
	MPA: $\sin(\pi/12 \cdot \text{Year})$	0.647	0.261	2.470	0.013	0.133	1.160

g. Biomass-weighted functional diversity (results are relevant to Fig. 2e in the main manuscript). Terms for component models are: 1. Nitrate, 2. SOI (detrended), 3. Year

Random-effects, ~1 Site		SD					
	Site	0.34					
	Residual	0.61					
Component modes		df	AICc	Delta	Weight		
	1,2,3	17	839.86	0.00	0.56		
	1,3	16	840.31	0.45	0.44		
Fixed-effects		Estimate	SE	z-value	p-value	2.5%ci	97.5%ci
	Intercept	2.057	0.119	17.236	<0.001	-1.823	2.291
	Nitrate	0.111	0.041	2.667	0.007	0.029	0.484
	SOI (detrended)	0.010	0.005	1.996	0.046	0.001	0.019
	Year	0.020	0.005	3.623	<0.001	0.009	0.031

Table S3. Model results for successive year-to-year change in richness, diversity and abundance. Results are relevant to Fig. 3 in the main text). The reference (intercept) represents the fished sites and MPA is the reserve. Diversity values were scaled prior to analyses. The random effect of year indicates cases where inclusion of year produced the best model. The best-fit model for abundance responses was a general linear mixed effects model (family = negative binomial). Standard error = SE.; Standard deviation = SD; Akaike information criterion = AIC.

a. Species richness

Random-effects, ~1 Year		SD			
	Year	0.24			
	Residual	0.96			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	0.017	0.136	0.124	0.901
	MPA	-0.034	0.192	-0.176	0.864
	AIC	646.484			

b. Functional richness

Random-effects, ~1 Year		SD			
	Year	0.37			
	Residual	0.92			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	-0.122	0.174	-0.697	0.486
	MPA	0.246	0.247	0.995	0.343
	AIC	630.329			

c. Abundance-weighted species diversity

Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	0.165	0.093	1.776	0.077
	MPA	-0.330	0.131	-2.517	0.013
	AIC	642.892			

d. Abundance-weighted functional diversity

Random-effects, ~1 Year		SD			
	Year	0.01			
	Residual	0.98			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	0.154	0.093	1.663	0.098

MPA	-0.309	0.131	-2.357	0.019
AIC	645.657			

e. Biomass-weighted species diversity

Random-effects, ~1 Year		SD			
Year		0.01			
Residual		0.98			
Fixed-effects	Estimate	SE	t-value	p-value	
Intercept	0.162	0.093	1.754	0.081	
MPA	-0.326	0.131	-2.486	0.014	
AIC	643.045				

f. Biomass-weighted functional diversity

Random-effects, ~1 Year		SD			
Year		0.03			
Residual		0.99			
Fixed-effects	Estimate	SE	t-value	p-value	
Intercept	0.088	0.094	0.937	0.350	
MPA	-0.178	0.133	-1.327	0.113	
AIC	649.399				

g. *Trachinops caudimaculatus* abundance

Random-effects, ~1 Year		SD			
Year		0.30			
Residual		0.55			
Fixed-effects	Estimate	SE	t-value	p-value	
Intercept	5.691	0.225	25.260	<0.001	
MPA	-0.572	0.176	-3.250	0.001	
AIC	2767.13				

h. *Acanthaluteres vittiger* abundance

Random-effects, ~1 Year		SD			
Year		0.35			
Residual		0.57			
Fixed-effects	Estimate	SE	t-value	p-value	
Intercept	3.603	0.169	21.362	<0.001	
MPA	-0.549	0.167	-3.294	0.002	
AIC	1914.30				

Table S4. Model results for abundance of large and small fish in and out of the reserve for the different time periods. a,b the entire monitoring (1992 to 2012): Fig. S3, and **c,d** the first three years of monitoring (1992 to 1995). The reference (intercept) represents the fished sites and MPA is the reserve. Model results are returned from a generalized linear mixed model with multivariate normal random effects (using Penalized Quasi-Likelihood (PQL) and family = poisson). Standard error = SE.; Standard deviation = SD.

a. 1992-2012: > 25 cm size classes

Random-effects, ~1 Year		SD			
	Year	0.43			
	Residual	12.05			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	1.088	0.148	7.311	<0.001
	MPA	0.342	0.191	2.794	0.007

b. 1992-2012: < 10 cm size classes

Random-effects, ~1 Year		SD			
	Year	0.83			
	Residual	21.83			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	5.837	0.217	26.927	<0.001
	MPA	-0.495	0.151	-3.272	0.001

c. 1992-1994: > 25 cm size classes

Random-effects, ~1 Year		SD			
	Year	0.02			
	Residual	7.61			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	0.888	0.248	3.584	<0.001
	MPA	0.423	0.314	1.671	0.151

d. 1992-1994: < 10 cm size classes

Random-effects, ~1 Year		SD			
	Year	0.44			
	Residual	12.21			
Fixed-effects	Estimate	SE	t-value	p-value	
	Intercept	4.251	0.365	11.657	<0.001
	MPA	-0.049	0.530	-0.092	0.926

Table S5. Model results for community weighted mean trait values (CWM) based on species present and biomass. The reference (intercept) represents the fished sites and MPA is the reserve. A correlation structure of form $\sim 1|Site$ was included as weight using the function “varIdent”. The empirical autocorrelation structure of the residuals was modelled when significant lags were present (assessed using the function “ACF” in the package nlme⁷) by competing models with moving average and first-order autoregressive terms⁸. Standard error = SE.; Standard deviation = SD; degrees of freedom = df; Akaike information criterion corrected for finite sample sizes = AICc.

a. CWM herbivores (results are relevant to Fig. 4a in the main text). Terms for component models are: 1. Temperature (detrended), 2. Nitrate, 3. Year.

Random-effects, $\sim 1 Site$		SD					
Site		0.022					
Residual		0.048					
Component modes	df	AICc	Delta	Weight			
1,3	16	-729.72	0.00	0.38			
2,3	16	-729.41	0.32	0.32			
1,2,3	17	-729.23	0.30	0.30			
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	0.103	0.009	11.943	<0.001	0.086	0.119	
Temperature (detrended)	0.007	0.004	1.653	0.098	-0.001	0.015	
Year	0.003	0.001	7.292	<0.001	0.002	0.004	
Nitrate	-0.006	0.004	1.585	0.113	-0.012	-0.001	

b. CWM herbivores based on biomass (results are relevant to Fig. S4a). Terms for component models are: 1. Temperature (detrended), 2. Nitrate, 3. Year².

Random-effects, $\sim 1 Site$		SD					
Site		0.021					
Residual		0.051					
Component modes	df	AICc	Delta	Weight			
3,4	16	-734.23	0.00	0.50			
2,3,4	17	-733.46	0.77	0.34			
1,3,4	17	-732.04	2.19	0.17			
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	0.113	0.008	13.721	<0.001	0.097	0.130	
Temperature (detrended)	0.005	0.004	1.275	0.202	-0.003	0.013	
Year ²	2e-4	2e-5	7.830	<0.001	1e-4	3e-4	
Nitrate	-0.006	0.003	1.585	0.113	-0.015	-0.002	

c. CWM maximum length (results are relevant to Fig. 4b in the main text). Terms for component models are: 1. MPA, 2. Nitrate, 3. SOI (detrended), 4. MPA:Year.

Random-effects, ~1 Site		SD					
	Site	2.73					
	Residual	4.46					
Component modes		df	AICc	Delta	Weight		
	1,2,4	19	1523.20	0.00	0.57		
	1,2,3,4	20	1523.77	0.57	0.43		
Fixed-effects		Estimate	SE	z-value	p-value	2.5%ci	97.5%ci
	Intercept	38.431	1.228	31.135	<0.001	36.011	40.850
	MPA	1.902	1.909	0.877	0.381	-2.351	6.157
	Nitrate	0.762	0.375	2.021	0.043	0.023	1.501
	SOI (detrended)	0.062	0.044	1.401	0.161	-0.025	0.149
	MPA:Year	0.236	0.075	3.122	0.002	0.088	0.384
Correlation ARMA(2,0)							
	Phi	0.122	-0.129				

d. CWM maximum length based on biomass (results are relevant to Fig. S4b). Terms for component models are: 1. Nitrate, 2. SOI (detrended), 3. Year, 4. MPA:Year.

Random-effects, ~1 Site		SD					
	Site	3.04					
	Residual	4.59					
Component modes		df	AICc	Delta	Weight		
	1,2,3,4	19	1569.35	0.00	0.37		
	1,2,4	20	1569.49	0.15	0.35		
	1,2,3	18	1569.02	0.57	0.28		
Fixed-effects		Estimate	SE	z-value	p-value	2.5%ci	97.5%ci
	Intercept	38.796	1.419	27.191	<0.001	35.999	41.592
	MPA	2.810	2.317	1.081	0.279	-2.284	7.902
	Nitrate	1.087	0.429	2.522	0.012	0.242	1.931
	SOI (detrended)	0.078	0.048	1.607	0.108	-0.017	0.172
	MPA:Year	0.174	0.098	1.769	0.066	-0.002	0.367
Correlation AR1(1)							
	Phi	0.142					

e. CWM thermal affinity (results are relevant to Fig. 4c in the main text). Terms for component models are: 1. Nitrate, 2. SOI (detrended), 3. Year, 4. MPA:Year.

Random-effects, ~1 Site		SD					
Site		0.05					
Residual		0.43					
Component modes		df	AICc	Delta	Weight		
1,3,4		11	267.25	0.00	0.73		
1,2,3,4		12	269.23	1.98	0.27		
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	17.732	0.607	290.082	<0.001	35.999	41.592	
Nitrate	-0.087	0.030	2.870	0.004	-2.284	7.902	
SOI (detrended)	0.002	0.004	0.505	0.613	0.242	1.931	
Year	0.020	0.006	4.209	<0.001	-0.017	0.172	
MPA:Year	-0.012	0.003	3.915	<0.001	-0.002	0.367	
Correlation AR1(1)							
Phi		0.27	-0.11	-0.13	-0.22		

f. CWM thermal affinity based on biomass (results are relevant to Fig. S4c) Terms for component models are: 1. Nitrate, 2. Temperature (detrended), 3. Year, 4. MPA:Year.

Random-effects, ~1 Site		SD					
Site		0.09					
Residual		0.42					
Component modes		df	AICc	Delta	Weight		
2,3,4		11	268.75	0.00	0.75		
1,2,3,4		12	270.95	2.19	0.25		
Fixed-effects	Estimate	SE	z-value	p-value	2.5%ci	97.5%ci	
Intercept	17.73222	0.607	304.205	<0.001	17.610	17.836	
Nitrate	-0.105	0.030	3.423	0.001	-0.166	-0.045	
Temperature (detrended)	-0.007	0.035	0.164	0.869	-0.075	0.063	
Year	0.024	0.005	4.616	<0.001	0.014	0.035	
MPA:Year	-0.013	0.056	3.080	<0.001	-0.028	-0.006	
Correlation AR1(1)							
Phi		0.16	-0.13	-0.11	-0.23		

Table S6. Model results for abundance of *Centrostephanus rodgersii* in and out of the reserve over time. Results are relevant to Fig. S6. Linear model results for a difference in mean urchin abundance (n = 6 sites) in the reserve and reference. The reference (intercept) represents the fished sites and MPA is the reserve. Standard error = SE.; Standard deviation = SD; degrees of freedom = df.

Fixed-effects	Estimate	SE	t-value	p-value
Intercept	-1454.144	129.873	-11.267	<0.001
Year	0.759	0.644	11.332	<0.001
MPA	1270.534	182.202	6.989	<0.001
Year*MPA	-0.641	0.001	-7.028	<0.001
R ²	0.890			
Residual standard error	1.787			
df	36			

Table S7. The following traits were parameterized for species observed at Maria Island from 1992-2012 (n = 96 species) and used to calculate functional diversity and richness. Data from Fishbase⁴ are indicated with an asterix.

Functional trait	Category	Units
1. Maximum length*	body size	total length (cm)
2. Trophic breadth	trophic niche	number of prey phyla consumed, described fully in ¹
3. Trophic group*	trophic niche	herbivore, benthic invertivore, carnivore, omnivore, planktivore, piscivore
4. Water column position	behaviour	benthic, demersal, site-attached pelagic, roaming pelagic
5. Gregariousness	behaviour	index from 1-3 indicating solitary to schooling species
6. Diel activity pattern	behaviour	diurnal, nocturnal
7. Preferred substrate	habitat use	hard substrate, soft sediment
8. Macrophyte association	habitat use	low, macroalgae, seagrass
9. Longitudinal range breadth*	ecological generality and dispersal capacity	degrees longitude occupied
10. Thermal affinity	physiology	95 th percentile of the upper occupied temperature distribution, °C

Table S8. Rank order of the ten traits by their relative influence on abundance-weighted functional diversity (FDa). Data sets traits are ranked by the magnitude of change in functional diversity following their removal, as assessed by R^2 (also described in Stuart-Smith et al.¹).

Functional trait rank for relative change in FDa	R^2
Water column position	0.5333
Macrophyte association	0.6163
Preferred substrate	0.8979
Diel activity pattern	0.9011
Gregariousness	0.9211
Trophic breadth	0.9262
Longitudinal range breadth	0.9269
Maximum length	0.9271
Thermal affinity	0.9293
Trophic group	0.9446

4. Supplementary References

1. Stuart-Smith, R. D. *et al.* Integrating abundance and functional traits reveals new global hotspots of fish diversity *Nature* (in press).
2. Troop, A. J. Southern oscillation. *Quart J Royal Metero Soc* **91**, 490-506 (1965).
3. Thompson, P. A., Baird, M. E., Ingleton, T. & Doblin, M. A. Long-term changes in temperate Australian coastal waters: implications for phytoplankton. *Mar. Ecol. Prog. Ser.* **394**, 1 – 19 (2009).
4. Froese, R. & Pauly, D. (World Wide Web electronic publication, 2011).
5. Edgar, G. J. & Stuart-Smith, R. D. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Mar. Ecol. Prog. Ser.* **388**, 51-62, (2009).
6. Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**, 231-259 (2006).
7. nlme: Linear and Nonlinear Mixed Effects Models (R package version 3.1-96, 2009).
8. Crawley, M. J. *The R Book*. (John Wiley & Sons Ltd, 2007).
9. Zuur, A. F., E.N., I. & C.S., E. A protocol for data exploration to avoid common statistical problems. *Meth. Ecol. Evol.* **1**, 3-14 (2010).

Appendix iii Statistical solutions for error and bias in global citizen science datasets

This work in a revised format has been published in the journal *Biological Conservation*. Please cite this article in any reference to it. The reference is: Tomas J. Bird, Amanda E. Bates, Jonathan S. Lefcheck, Nicole A. Hill, Russell J. Thomson, Graham J. Edgar, Rick D. Stuart-Smith, Simon Wotherspoon, Martin Krkosek, Jemina F. Stuart-Smith, Gretta T. Pecl, Neville Barrett, Stewart Frusher (2014). Statistical solutions for error and bias in global citizen science datasets *Biological Conservation* **173**:144–154.

Statistical solutions for error and bias in global citizen science datasets

Tomas J. Bird^{1,2,*}, Amanda E. Bates¹, Jonathan S. Lefcheck³, Nicole Hill¹, Russell J. Thomson¹, Graham J. Edgar¹, Rick D. Stuart-Smith¹, Simon Wotherspoon¹, Martin Krkosek⁴, Jemina F. Stuart-Smith¹, Gretta Pecl¹, Neville Barrett¹, Stewart Frusher¹

¹School of Botany, University of Melbourne, Parkville, Victoria, 3010 Australia

²Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001 Australia

³Virginia Institute of Marine Science, College of William & Mary, PO Box 1346, Gloucester Point, Virginia, 23062-1346, USA

⁴Department of Ecology and Evolutionary Biology, Ramsay Wright Zoological Laboratories, University of Toronto, 25 Harbord St, Toronto, ON, M5S 3G5, Canada

*Corresponding author: tbird@student.unimelb.edu.au

PO Box 49, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001 Australia

phone: +61 4 0949 6340

Abstract

Networks of citizen scientists (CS) have the potential to observe biodiversity and species distributions at global scales. Yet the adoption of such datasets in conservation science may be hindered by a perception that the data are of low quality. This perception likely stems from the propensity of data generated by CS to contain greater levels of variability (e.g., measurement error) or bias (e.g., spatio-temporal clustering) in comparison to data collected by scientists or instruments. Modern analytical approaches can account for many types of error and bias typical of CS datasets. It is possible to (1) describe how pseudo-replication in sampling influences the overall variability in response data using mixed-effects modeling, (2) integrate data to explicitly model the sampling process and account for bias using a hierarchical modeling framework, and (3) examine the relative influence of many different or related explanatory factors using machine learning tools. Information from these modeling approaches can be used to predict species distributions and to estimate biodiversity. Even so, achieving the full potential from CS projects requires meta-data describing the sampling process, reference data to allow for standardization, and insightful modeling suitable to the question of interest.

Keywords: Volunteer data, statistical analysis, experimental design, linear models, additive models, species distribution models, biodiversity

1. Introduction

Evaluating global changes in the distribution and diversity of Earth's biota requires datasets of ambitious proportions where effort is shared over hundreds, or even thousands of individuals (Silvertown, 2009). In recent decades, volunteers, often labeled as 'citizen scientists' (CS), have been central to the collection of broad-scale databases, allowing the scientific community to address questions that would otherwise be logistically or financially unfeasible, even for the most dedicated scientific team (Dickinson et al., 2010). Consequently, volunteer networks provide an opportunity to answer conservation-related questions on the broad temporal and spatial scales that are relevant to understanding global biodiversity patterns. As proof of this concept, long-running volunteer monitoring programs have generated thousands of peer-reviewed papers (Sullivan et al., 2009) and can thus offer models for the development of similar programs in novel systems (Bonney et al., 2009).

As well as providing a practical means of addressing large-scale questions in ecology, involving citizens in the collection of data has a number of benefits to conservation-related projects. By being inclusive and engaging large numbers of people, CS projects can bring important publicity and discourse on conservation issues, and provide opportunities for the public to take an active role in management and conservation (Pattengill-Semmens and Semmens, 2003). Additionally, CS projects can often afford to be more exploratory than more regimented monitoring programs, making observations of rare events possible with sightings from large networks of volunteers that span broad spatial scales. Given these advantages, the capacity for addressing global-scale conservation may well rest in the realm of citizen science (Silvertown, 2009).

In spite of the proven success and potential for using CS datasets to address pressing global issues, there has been intense debate over the utility of such data in a scientific framework. Detractors suggest that involving large numbers of individuals with varying skill and commitment will lead to decreased precision in measurements such as in the identification or counting of species. Moreover, significant sources of bias may be present in the data, such as under-detection of species or the non-random distribution of effort (Crall et al., 2011). Such concerns have motivated CS projects to maximize the quality of data collected through improved sampling protocols and training (Edgar and Stuart-Smith, 2009), database management (Crall et al., 2011), and filtering or subsampling data to deal with error and uneven effort (Wiggins and Crowston, 2011; Wiggins et al., 2011). However, in many broadly distributed databases it may be impossible to implement rigid protocols or to eliminate all sources of error and bias. Thus, global CS data sets will likely violate the basic assumptions of some statistical analyses.

Fortunately, the issues of error and bias that are often present in CS data are not unique and analogous problems exist in datasets across a wide variety of disciplines and can be addressed using a suite of analytical approaches. In many cases, CS databases resemble the data collected for meta-analytical and landscape ecology syntheses where methods for accurately estimating and incorporating within-study or within-observer variability are key to drawing conclusions from the data (Hedges et al., 2010). For complex datasets, machine learning (ML) approaches are available that can examine the relative importance of large numbers of predictive variables in explaining the response data (Fink and Hochachka, 2012; Olden et al., 2008). Moreover, custom hierarchical analyses can recognize and account for the variable and clustered nature of CS data (Hochachka et al., 2012).

Here, our overall objective is to promote the use of CS data in conservation ecology and policy by highlighting how issues of data quality can be addressed using a suite of relatively new statistical tools. We first provide context by describing the main considerations for identifying and quantifying data quality issues present in CS data. Second, we explore a number of modeling approaches

available for use with CS data with case examples to illustrate how specific issues of error and bias can alter understanding of biological patterns when left unaccounted for. Our perspective is that CS data has the potential to describe global patterns in biodiversity and the mechanisms driving change in ecosystems, communities and species. The inferential capacity to do so rests on the continued development and use of modeling approaches to identify and correct for data quality issues.

2. Contextualizing the quality issues present in citizen science data

Most CS projects recognize the potential issues of error and bias present when using large numbers of volunteers to collect data. Volunteer training, data standardization, validation and filtering procedures reduce potential sources of error and bias before, during and after the data are collected (Bonter and Cooper, 2012; Wiggins et al., 2011). In fact, studies comparing data generated by skilled volunteers versus experts often show comparable estimates (e.g. Delaney et al., 2008; Edgar and Stuart-Smith, 2009). In spite of the best efforts of volunteers and researchers, two primary quality issues may still remain. First, CS data may still be prone to greater variability, or error, due to differences in the skills, dedication, and training of volunteer participants. Second, CS data may contain persistent bias. To address these quality issues, it is necessary to carefully consider the type of response data collected and how potential sources of error and bias might have been introduced during sampling.

2.1. Types of Response Data

Central to the design of CS studies is the consideration of what kind of data to collect, as this will influence the kinds of questions that can be asked, what statistical tools are appropriate, and what additional information should be collected with each response data point for analyses (Wiggins and Crowston, 2011; Wiggins et al., 2011). At the same time, survey design and analysis also should acknowledge the limitations of data collection. For applications of CS data to conservation-related issues, inference is generally focused on describing changes in the locations and abundance of species, populations, and their associated habitats. Thus, response data in CS studies generally fall into the categories of presence, presence-absence, or some measure of quantity (such as abundance, percent cover or biomass), all recorded over time and space. Which kind of data is collected will depend on the scope of the study and the challenges associated with collecting the data.

Presence-only data require minimal effort to collect, and are therefore amenable to many CS applications that aim to recruit greater numbers of volunteers. However, the lack of information on where species were absent constrains what questions can be answered and the types of analyses available (Pearce and Boyce, 2006). Most significantly, presence-only samples are not representative of where the species (or event) was not found, which limits the predictive power of inference. For example, consider a walking club that is recruited to report sightings of a species of bird. In general walkers are more likely to go to aesthetically interesting locations. Thus, the inferred distribution of bird species based solely on presence data will be concentrated at sites preferred by humans, when in fact the real distribution might be uniform in space. As well, because the amount of effort put into sampling is often directly tied to the distribution of reported presences, any changes in effort may be interpreted as a change in the true distribution of a species.

By contrast, presence-absence (or occupancy) data provide information on the spatial and/or temporal distribution of a species, allowing for comparison of a species' occupancy status between different areas or time, such as for documenting range contractions associated with population declines (Tulloch et al., 2013). Similarly, abundance (or other measures of quantity) data are required to detect changes in the size of a population. However, presence-absence and abundance data have their limitations as well: in many cases, it is difficult to distinguish imperfect detections (i.e., failing to observe a species that is actually present) from true absences. Similarly, reported abundances often provide an underestimate of the true number of individuals present at a location. We discuss approaches to dealing with error in each of these kinds of data in section 3.

2.2. Random Error in Citizen Science Datasets

The aim of much of ecological inference is to attribute variation in the response data to one or more explanatory variables. Random error is the variability in the response that cannot be described in terms of explanatory variables. While some of this error may be due to predictors of interest, sampling-related variability can contribute a large portion of the overall variability. In the context of CS data, random error is often introduced when observers differ in their ability to detect, identify and quantify species or events. Mistakes can be introduced directly in the observation process, through measuring and recording covariate data (such as associated environmental data), or through variable execution of sampling protocols. If these sources of variation are not accounted for in a model, then they are included in the overall random error, which may obscure trends of interest. Large amounts of random error may not be an issue if the trend of interest is strong, but more usually results in more data being required to detect patterns. Fortunately, the increased quantity of data from CS programs can sometimes offset this issue, in contrast to the sometimes-limited quantity of data from more formal surveys.

Accounting for sources of random error requires measurements of both meta-data and covariates. Meta-data are measurements or classifiers related to sampling which help describe variation in how sampling was performed. As a start, each observation should be attributed an observer identifier. This identifier can then be used to relate metrics (such as observer training, frequency of involvement, or outside experience) to the response data and consequently quantify the overall effectiveness of a particular observer (Snäll et al., 2011). Measures of the effort spent conducting each survey are also useful for standardizing abundance or detection data (Bray and Schramm, 2001; Maunder and Punt, 2004). Covariates, on the other hand, include factors that are outside the realm of survey design, but which might still have significant impacts on the success of sampling. For instance, underwater visibility can greatly affect visual surveys undertaken by SCUBA, regardless of whether undertaken by experts or novices (Edgar and Stuart-Smith, 2009).

2.3. Bias

Random error can be biased or unbiased. In unbiased data, the random error is centered around zero. Bias occurs when this random error is consistently above or below zero due to some flaw in the data collection or estimation process, resulting in over- or under-estimates of the mean. There are many different ways bias can be introduced to a data set, and identifying the processes which contribute bias is central to deciding what analytical approach to take. Here we differentiate systematic and sampling biases.

Systematic bias occurs when repeated measures of the same process provide consistent over or under-estimates of the true value. Imperfect detection in presence-absence data and species misidentification are examples of bias particularly common with CS data and they typically lead to incorrect estimates of species abundance and occurrence (Royle et al., 2007). Such biases can be non-intuitive. For example, in a survey in which volunteers identified birds from their calls, volunteers that self-identified as experts were more likely to falsely identify rare species than moderately skilled observers (Farmer et al., 2012). Another example of measurement bias occurs when divers are asked to estimate fish size. Typically, the size of small individuals are underestimated while the size of large individuals are overestimated, according to magnification and other factors affecting perception of size underwater. Either attempting to reduce the occurrence of such bias in data collection and/or calibration of data prior to analyses can be used to account for measurement bias. For example, in the case of size estimation by divers, divers can be trained through practice with objects of known size, and/or size data can be transformed using known relationships between true and estimated sizes (Edgar et al., 2004).

By contrast, sampling bias occurs when some aspects of the process of interest are more likely to be sampled than others, so that the mean is overly influenced by these samples. One common source of bias for datasets collected by multiple observers is variability among observers in their sampling effectiveness. While on average, the mean of measurements made by observers may be centered on the true value; some observers may contribute more samples than others. In cases where observations

are consistently over- or under-estimated by a particular observer, then considering each observation as an independent sample has the potential to bias the overall estimate of a mean or trend. Also, clustered sampling of a process that is auto-correlated in space or time (i.e., closely spaced observations are more alike than more distant observations) can introduce bias, as eventual understanding of the underlying process is dominated by information from the clustered areas that may tend to be more similar than if sampling was regular in spacing (Boakes et al., 2010). For example, bird surveys are often clumped near areas that are more accessible, such as sites near roads, which may in turn be associated with habitats preferable to certain species or population subsets (Lawler and O'Connor, 2004; Tulloch and Szabo, 2012). Volunteer effort may change over time due to seasonal windows or declining commitment, making it difficult to distinguish seasonal patterns from those due to effort expended (Ahrends et al., 2011; Seys et al. 2002).

3.0 Modeling approaches

Modern statistical tools present options for accounting for many types of error and biases. In the following sections, we describe a variety of such techniques that may be particularly relevant to CS data. We aim to indicate where and why one might use each tool, to describe the different approaches and illustrate applications by drawing on examples from the literature. Table 1 provides examples of freely available statistical packages for implementing many of the approaches we describe in the open-source program R (R Core Team, 2013). As well, we provide examples for how error and bias can be accounted for using selected subsets of the detailed global marine biodiversity dataset generated through the Reef Life Survey program (RLS, Edgar and Stuart-Smith, 2009). RLS uses intensively trained volunteer divers to quantify the abundance and diversity of fish and invertebrate species on replicate 50 x 5 m transects on rocky and coral reefs, using standardized visual census methods (details provided in the supplementary materials).

3.1. Linear and Generalized Linear Models and extensions

Linear models and their extensions are some of the more widely used tools for quantifying random error in ecological data. The basic premise behind their use is that changes in the response data can be described as a linear function of predictors of interest, covariates or meta-data, called 'fixed-effects'. Additive models extend linear models by allowing non-linear relationships between predictors and response data through the use of smoothing functions with multiple degrees of freedom (Hastie and Tibshirani, 1990). Put another way, a simple linear model with a single predictor and multiple covariates asks how much a change in that predictor would influence the response data if all other covariates were held constant. The strength of the relationship between two variables is summarized as a parameter. Thus, linear models and their extensions are often used in CS studies to control for sampling-related covariates when estimating the effects of predictors of interest (Table 2).

Often, a large amount of variation in the response data can be described using simple relationships. However, the response data are rarely fully explained by available predictors and covariates. Any variation that cannot be accounted for using parameters is modeled as though it were the result of a random process that can be described using a probability distribution. The goodness-of-fit of a model can then be described based on this remaining, or residual, variation in the data using likelihood based methods such as Akaike's Information Criterion (AIC).

Basic linear and additive models assume that the response data follow a normal or Gaussian distribution, which are suited to specific kinds of measurement data, but may not be suitable for other kinds of response data. Generalized linear and additive models (GLMs and GAMs) further extend linear and additive models to allow for other kinds of distributions, such as a Poisson or negative binomial regression for count data, or the logistic regression for binary data (Zuur et al., 2007). Many CS ecological datasets contain a large number of zero counts, which can violate the assumptions of the Poisson or negative binomial distributions. In this case, zero-inflated models can be useful for analyzing CS data (Arab et al., 2012). As well, autoregressive regression models, which model the change in similarity between more distant data points, can be used where closely-spaced samples are more likely to be similar to one another than those that are more distant (Legendre et al., 2002).

To show how different types of data can be accommodated using linear modeling, we present a subset of RLS data on sightings of the urchin genus *Holopneustes* along the east coast of Australia (Fig. 1A). We used the counts data from the RLS data first as presence-only data (ignoring sites in which the genus was absent), second as presence-absence data (ignoring counts of the species within sites) and third as abundance data. We related each of these three kinds of response data, to the maximum sea-surface temperature at each site to describe the range of temperatures occupied by *Holopneustes* spp. Using presence-only data, we find that the range occupied by the genus was between 17 and 25 °C (Fig. 1B). In comparison, using presence-absence data in a logistic regression model, we find that the probability of the genus occupying a site decreases as the sea-surface temperature increases, reflecting its increasing prevalence at more southern sites in Australia (Fig. 1C). Incorporating abundance data in a zero-inflated Poisson model shows that the temperature distribution of the genus displays two distinct peaks, likely corresponding to the gap between the core ranges of the two main species in the *Holopneustes* genus (Fig. 1D).

While attractive for their conceptual simplicity and broad applicability, GLMs and GAMs have limitations in terms of the numbers of predictors and covariates they can accommodate simultaneously. Thus, an important part of inference using linear or additive models (and their extensions, section 3.2) is the process of determining which model provides the best fit with as few parameters as possible (Zuur, 2007). Where large numbers of predictors and covariates may be in play, ML approaches may be more suitable for inference (section 3.4). As well, linear and additive models are generally not suitable for presence-only data, unless used in the context of species distribution models (SDMs; section 3.5), an important consideration for the context of citizen-generated data. GLMs and GAMs are generally unreliable when the data are heteroscedastic, that is, the variance within the data is uneven across samples. To account for sampling bias in predictive models, tools such as mixed effects or hierarchical models are required.

3.2. Mixed-effects models

Where CS data are subject to sampling bias, mixed-effects models can be a powerful tool. Mixed-effects models include fixed effects used in linear or additive models with ‘random-effects’ that estimate the influence of predictors (often groups) that increase variability in the data but do not affect the mean response. For example, some observers in a study may have differing sampling efficiency—i.e., some over and some under-estimating a true value. A mixed-effects model would assume that if each observer contributed one sample, the mean of these observations would be centered on the true mean (Zuur, 2009). However, if some observers contribute more samples than others, the contribution of these observers would skew the overall average, an effect that must be accounted for as with pseudoreplication in controlled experiments. Thus, we could use the observer identifiers as an index to model observer-to-observer variability before estimating the effects of other predictors in the model.

To demonstrate how sampling bias can influence inference and one way that this bias may be accounted for using linear mixed-effects modeling, we provide an example of a dataset with high variability among sampling sites and patchy sampling across latitude. In our example we plot species richness data of reef fish against latitude for a subset of the RLS dataset (selected purposely to illustrate uneven variance among groups of samples and differences in the means among sites). In Fig. 2A, we show a dataset that is clustered at two spatial scales; the bulk of the data are from lower latitudes and there is significant site-level pseudo-replication. Applying a linear model to the data (the *nlme* package in R, (Table 1) using the function “*lme*” and fitted using maximum likelihood) provides a fit (AIC = 3472) with narrow confidence intervals around the model prediction. However, this narrow interval is largely an artifact of the large sample size; examination of the residuals shows a large discrepancy between the variance in different regions, violating the assumption of equal variance required for linear models (Fig. 2B). Including a random effect at the site level gives a marginally better fit (Fig. 2C, AIC = 3470), broader confidence intervals and centers the model predictions (Fig. 2D), however, there is still uneven variance between the high and low latitude sites

that were sampled. Finally by using a variance-weighting model that accounts for the error structure among the four dominant regions of the data (Temperate Northern Pacific, Eastern Indo-Pacific, Temperate Northern Atlantic and Tropical Eastern Pacific), we arrive at a better-fitting model (Fig. 2E, AIC = 3381) that does not require the polynomial relationship between latitude and richness and that properly reflects the amount of variability in each region (Fig. 2F). We have therefore improved model fit by taking into account the clustered nature of the data collection and met the assumptions of the approach.

As extensions of GLMs and GAMs, generalized linear and additive mixed models (GLMMs and GAMMs) have proven extremely useful in ecological studies due to their flexibility and predictive power (Bolker et al., 2009). Thus, GLMMs and GAMMs have been used in CS data to accommodate observer bias and spatial clustering (Table 2). However as in GLMs and GAMs, the number of predictors that can be included in models is limited by the amount of response data available and estimating the influence of random factors can require a great deal of replication within each factor level.

Thus, to avoid over-parameterizing the model, inference using mixed-effects models should include model selection using some measure of model fit such as AIC (Zuur, 2009). Finally, the assumption that random effects influence the variance but not the mean of the data ignores the possibility of measurement bias. We also note that while our example has shown how mixed-effects models can account for some kinds of sampling bias, systematic bias must be dealt with using other approaches. Hierarchical models may therefore be required to deal with sources of bias that cannot be accounted for with fixed or random-effects models.

3.3. Hierarchical models

Hierarchical models are a good choice for modeling CS data when the sampling design has some element of systematic bias that can be measured with data. Hierarchical models are similar to the models described above in that they are used to estimate parameters describing the relationship between predictor and response data using linear (or other) models. However, in hierarchical models the parameters themselves may be described as a function of other predictor variables (Royle and Dorazio, 2008). For example, in the previous section, we saw how sampling variability could be modeled separately between regions. As such, mixed-effects models represent a kind of hierarchical model and many other kinds of models can be adapted to match the specifics of CS surveys. Examples of ways to deal with systematic bias include models for imperfect detection, false-positives, and species misidentification (Table 2). As well, hierarchical Bayesian approaches are available to deal explicitly with spatially or temporally clustered data (Wikle, 2003). Hierarchical models, however, usually require specific sampling designs to accurately describe the sampling process (Royle and Dorazio, 2008).

Here, we show how not accounting for imperfect detection in sampling can result in drastic underestimates of species occurrence. Again, we subsample from the RLS data to investigate how the presence or absence of the urchin genus *Echinostrephus* relates to maximum sea-surface temperature (Max_SST) on the east coast of Australia. A logistic regression estimates the influence of temperature on the probability of *Echinostrephus* occurring at a site, which is highest (~60%) at lower temperatures (Fig. 3).

However, this model ignores the possibility that the urchin may have gone undetected in some transects. *Echinostrephus* species are small, burrow, and are patchily distributed at local scales, meaning that patches of few individuals may easily be overlooked. Our hierarchical model takes advantage of the fact that multiple transects were laid at some sites and employs an occupancy-detection model (MacKenzie, 2006) to estimate the probability of detecting the urchin. We do so by assuming that the site-level occupancy of *Echinostrephus* is known to be 1 if it is found at one transect within a site. From this assumption and the known number of transects used within a site, we can estimate the probability of observing the urchin given that it is present. Thus, the observed data at

each site now becomes the outcome of two attempts to find the urchin, with the number of successes determined by both the product of the probability of occurrence (which we still assume is related to temperature) and the probability of detecting the urchin. We fit this model using Markov-chain Monte-Carlo (MCMC) sampling in the WinBUGS programming language (Lunn et al., 2000), and find that by accounting for low detection rates, the occupancy rate of *Echinostrephus* is almost double that estimated by the logistic regression (Fig. 3, dashed line).

We note here that in the case of *Echinostrephus* spp. the detection rate that we are estimating at the site-level is confounded with the patchiness of the genus. Thus our example shows how replication can be used to build a hierarchical model, but also demonstrates how different kinds of error can be additive. In our case, site-level replication allows for explicit modeling of the observation process, resulting in a more realistic modeling approach. Statistical packages are available to perform hierarchical analyses using similar syntax to well-known linear and additive models (Table 1), and the development of more complex models can be accommodated using the WinBUGS programming language.

3.4. Machine Learning

In cases where many predictor variables are of interest and may be correlated, ML approaches can be particularly useful (De'ath and Fabricius, 2000). In CS data, there can be many competing factors influencing the response data and there is a risk of building models with more parameters than can be supported by the data. Some ML approaches bypass many of the assumptions required by the models described in sections 3.1 to 3.3, by ignoring the need for the response data to fit any particular probability distribution, though, options such as Boosted regression trees (BRT) may use different algorithms (and perform better) for different kinds of response data.

Machine learning approaches use heuristic algorithms to learn about the most likely relationship between predictors and response data (Olden, 2008). For example, a classification tree might split the proportions of observed presences in presence/absence data based on whether the observer was experienced or novice. Because these rules are not based on rigid probabilistic assumptions about the distribution of the response, ML approaches may be more suited to CS data that were collected under a sampling design that might violate the assumptions of classical experimental design.

Applications of ML are available for presence-only, presence-absence, abundance and other data types (Table 1). As well, many ML approaches do not assume that the relationships between responses and predictors are linear (or even smooth). Many available methods have been applied in an ecological setting, including classification and regression trees (CART, De'ath, 2000), boosted regression trees (BRT, Elith et al., 2008), random forests (Cutler et al., 2007), artificial neural networks, and genetic algorithms (Olden et al., 2008).

In our example, we use a random forests (RF) approach to predict the global presence/absence of sharks using RLS data. The worldwide RLS data set has surveys nested within sites, which are nested within eco-regions. The unmodified RF procedure assumes all observations are independent, ignoring possible bias due to within-site pseudo-replication. It is possible to account for non-independence in the data by aggregating observations up to a higher level (Fig. 4). The Receiver-Operator Curves (ROC) shown in Fig. 4 show how aggregating observations at different levels improve model performance, with curves that have a greater area under curve (AUC - a measure of the discriminatory power of the model) providing greater predictive power. In our case model performance is greatest when samples are grouped at the site-level, albeit with a reduction in sample size. Details of the RF approaches and ROC curves used in Fig. 4 are available in the SOM.

The ROC curves in Fig. 4 were obtained from a cross-validation technique that is part of the RF method, so that predictions at a survey are independent from the models developed using a particular survey. However, predictions at a survey location could be based on nearby surveys, which could introduce a spatial bias. Consequently the performance of non-aggregated methods could be over-

estimated. In spite of this, the RF method used here shows how site aggregation can be used to remove pseudo-replication.

A drawback of ML approaches is that they generally do not provide easy ways to deal explicitly with uncertainty in the model, data or parameters. As such, it can be difficult to determine the reliability of results derived by ML methods that do not provide confidence intervals or standard errors. Boosted regression tree approaches have been developed to allow a more probabilistic style of inference using ML (Elith *et al.*, 2008). Several novel approaches for dealing with bias are also being developed, including mixed-effects regression tree (which allows for hierarchical clustering of the response data) (Sela and Simnoff, 2012). Another novel approach to dealing with clustered data is a spatio-temporal exploratory model (STEM) framework which breaks the data into discrete but overlapping spatial and temporal units that are modeled locally (using bagged trees in this instance) and then aggregated (Fink *et al.*, 2010). Alternatively, pseudo-replication can be accounted for by altering the bootstrapping step in random forests, so that the bootstrap sampling is at a higher level (Karpievitch *et al.*, 2009). Interestingly, when this method was used on a data set that was cluster-correlated as CS data often are, Karpievitch *et al.* found no difference in classification accuracy over the unmodified random forest model, but a significant improvement in predictive ability, a result that highlights the importance of checking whether particular approaches are suitable to each dataset.

3.5. Estimating Biodiversity

One common aim in many large-scale CS projects is to compare different habitats in terms of their species composition. Biodiversity indices describe species (and functional/phylogenetic) diversity within ecological communities. Numerous indices are available ranging from species richness (the number of species in a site or sample), to more complicated indices incorporating information on species' relative abundances (e.g., Shannon or Simpson), functional traits (Petchey *et al.*, 2006) or phylogenetic relationships (e.g., Cadotte *et al.*, 2010).

Some species are more cryptic than others and as a consequence biodiversity indices can be heavily influenced by variation in sampling and detectability. To account for error and bias in biodiversity measures, the calculated indices can be treated as response data, as in Fig. 2, and analyzed using approaches such as linear modeling. Alternatively, error and bias correction measures can be applied at the species level in a hierarchical model (such as by using a detection-occupancy model) and the diversity indices calculated as a derived parameter (Gelfand *et al.*, 2005; Holt *et al.*, 2013; Kery *et al.*, 2010a).

Various diversity indices also emphasize the contributions of rare species differently, and the choice of index used may also help minimize issues of detectability, and a simple solution is to choose a metric that emphasizes abundant species (e.g., Simpson index) to down-weight the influence of rare or poorly detected species. Additionally, rarefaction is often used on biodiversity data to account for uneven sampling effort. Traditional rarefaction generates species accumulation curves, and then reduces the largest samples until they are equivalent in size to the smallest (Gotelli and Colwell, 2001).

New methods employ what is called “shareholder quorum subsampling” (Alroy, 2010) or “fixed coverage subsampling” (Chao and Jost, 2012), which extrapolate richness outwards and then scale back based on a measure of sample ‘completeness.’ These methods are less biased, have ideal mathematical properties, and minimize the amount of discarded data and sampling effort. Recent work has extended this framework to include effective numbers, which are increasingly being used to compare different dimensions of biodiversity (Chao *et al.*, 2013).

In Fig. 5, we present species richness of fish aggregated within two RLS sites in New Zealand. The Shortland Bluff site has much greater richness ($S=54$) compared to the Goat Island site ($S=18$, Fig. 5A). Taking the traditional rarefaction approach, we scale richness back to the fewest number of observed individuals: 68, in the Goat Island sample. In this case, the estimated richness for the

Shortland Bluff site is approximately equal to that in the Goat Island Site: $S=22$ vs 18 , respectively. Taking a coverage-based approach, we first extrapolate outwards (dashed line, Fig. 5A) and calculate the coverage, or proportion of individuals in the sample that belong to species in the sample. Subtracting the coverage from unity yields the probability that a new species would be found if an additional individual was sampled, and is equivalent to the final slope of the rarefaction curve in Fig. 5A. Scaling back to the lowest degree of coverage (approximately 93%, Fig. 5B), we see that the estimated richness for Shortland Bluff is now twice that of Goat Island: $S=39$ vs $S=18$, respectively. Using the coverage-based approach, we have used more of the available data, and provided a less biased interpretation of the difference in richness between the two sites.

3.6. Species Distribution Models

Species distribution models (SDMs) use spatial occurrence or abundance datasets to describe or predict species' distributions in unsampled space. The basic premise is to use one of the modeling approaches described above to characterize the relationship between species data and a series of environmental predictor variables. This model can then be used to predict the likely distribution of species (or communities) in unsampled space or time (Elith et al., 2006; Ferrier and Guisan, 2006; Franklin, 2009). A broad range of modeling techniques are applied to SDMs, including many of the parametric and ML methods discussed above. Large and broad-scale datasets such as those collected by citizen science programs are a natural place to use SDMs as they can be compared against extensive geographical data sets using GIS. As a consequence SDMs are gaining popularity in conservation ecology (Ashcroft et al., 2012; Sarda-Palomera et al., 2012).

Given that most SDMs use linear, additive or ML models to make predictions into unsampled space, it is possible to address random error and bias appropriate for each method using meta-data and covariates where possible. However, this approach may be limited for use in predictive SDMs because the sampling-related fixed and random effects may not be defined in the space for which predictions are being made. Occupancy or abundance predictions can be made by 1) averaging across values for each sampling-related effect (representing, for example, predictions across the typical observer or survey period), 2) omitting them (random effects only) or 3) a combination of the two (Welham, 2004). In practice, however, random error of the kind encountered in CS data is often reduced as much as possible by screening the data before analysis. Detection-occupancy modeling has been used successfully within SDMs (Kery et al., 2010b) to account for imperfect detection rates where repeat observations are available. Additional research is needed on how best to account for observation errors in SDMs where the underlying data do not have repeat observations (Monk, 2013).

Approaches for dealing with sampling biases in CS data for SDM applications have focused on addressing uneven spatial and temporal sampling effort, and include subsampling to reduce the overall variability in sampling effort (Segurado et al., 2006), potentially at the expense of large amounts of data, or down-weighting heavily sampled areas to reduce their influence in models (Dudík et al., 2005). Alternatively, autoregressive models and other spatially explicit models may be useful for dealing with these biases (Dormann et al., 2007). Similarly, hierarchical models can incorporate spatial structures and extensions of detection/occupancy models are possible to simultaneously account for both observation error and spatial and/or temporal bias (Gelfand, 2005; Latimer et al., 2006).

Predictive SDM models are also available to deal with presence-only data through programs such as BIOCLIM (Busby, 1991) and HABITAT (Walker & Cocks, 1991), which calculate the likely environmental limits of a species. Alternatively, SDMs based on presence-only data have used entropy modeling (MAXENT, Phillips et al., 2006) or maximum likelihood (MAXLIKE, Royle et al., 2012) to generate pseudo-absences to compare against observed presences in something like a logistic regression. Highly clustered presence-only data, which are particularly prone to bias, have received recent attention in SDMs. Presence-only methods such as MAXENT are particularly sensitive to sampling bias (Yackulic et al., 2013). Recent work suggests that generating pseudo-absence data that are spatiotemporally biased in the same way as the observation data may improve the performance of

predictive models (Barbet-Massin et al., 2012; Phillips et al., 2009). However, care needs to be taken when interpreting the outputs of presence-only models as unless additional data on prevalence are available, then models represent relative (rather than absolute) probability of presence. (Phillips and Elith, 2013).

In Fig. 6 we use boosted regression trees to predict the occurrence of a common shallow, rocky-reef fish, *Parma unifasciata* on the East coast of Australia based on environmental covariates (Table S1). We take RLS data and create three modeling scenarios; one where we have presence-absence data (PA), another where we keep only the presence data (PO) and randomly select pseudo-absences from all available sites in the study region (random background) and the third where we use PO data and weight our random selection of pseudo-absences using an additional model that describes the likelihood that a site is sampled (targeted background), thus simulating the biases present in the original dataset (following Phillips et al., 2009). We generated 100 datasets for each PO modeling scenario (Fig. S1) and evaluated each against 30% of the data set aside for validation. Using both AUC and correlations between predicted and observed presence-absence data, we found that the presence-absence model performs the best, followed by the PO model with a targeted selection of background pseudo-absences, although the values for both PO scenarios are similar and lower than the PA scenario (Table S2). Maps of the predicted distribution of *P. unifasciata* show that it is most likely to occur in the center of the study region in all models (Fig. 6). Probability of occurrence is also relatively high in the PA model at several northern sites (Fig. 6A), which, relatively speaking, is captured better by the targeted background PO model (Fig. 6B), and may account for more of the original bias in sampling site distribution than the PO random background model (Fig. 6C).

4. Recommendations

There is great potential for the use of CS data as a mainstream tool to address the important ecological and conservation questions of our time. However, in order to do so, researchers will need to consider some basic principles of data collection, management and analysis. Taking an overview of recent techniques used in research based on citizen-science data (Table 2) and incorporating the advice found in Zuur (2010), we have extracted a few recommendations.

First, working with both statisticians and volunteers will help build an understanding of the likely constraints around sampling, and may require some trial and error. Given the broad array of possible modeling approaches available, it is important to consider the main issues with the dataset, how they will affect the question being asked and then to choose the best method to deal with those issues. Ideally researchers using CS datasets would design their sampling program to collect that data needed to account for such issues ahead of time. At the same time, the design of CS studies must meet the needs of the question being asked, while acknowledging tradeoffs between data quality and quantity that are likely to occur with CS data.

Next, it is vital to record data on aspects of the environment or survey execution (such as observer i.d.) that are likely to influence the results. While standardized data collection procedures will help ensure that volunteers are, to the best of their abilities, collecting data in the same way, true uniformity in sampling is unlikely. Recording meta-data can also help account for pseudo-replication due to clustered sampling.

Finally, where measurement bias is a potential issue, it is important to consider whether it is possible to collect data that will allow characterization of this bias. Using such data, it may be possible to use validation approaches within data collection, or hierarchical modeling to correct or account for such bias. Useful procedures might include re-sampling areas with known quantities, using training datasets, or performing multiple-observer surveys.

In closing, the challenges associated with analyzing CS databases present an exciting opportunity for collaboration between statisticians and conservation scientists. We anticipate the development of

novel statistical approaches and survey designs that will break new ground in overcoming some of the problems we have outlined in this paper.

Acknowledgments

T.J.B. was supported by an Australian Research Council Linkage doctoral fellowship and the Australian Research Council Center for Excellence in Environmental Decisions. Salary for A.E.B was by the Fisheries Research Development Corporation, the National Climate Change Adaptation Facility, and the Australian National Network in Marine Science (a collaborative funding initiative between James Cook University, the University of Tasmania, and the University of Western Australia). Development of the RLS dataset was supported by the former Commonwealth Environment Research Facilities Program, while analyses of this dataset were supported by the Marine Biodiversity Hub, a collaborative partnership supported through the Australian Government's National Environmental Research Program. In addition, we thank the many Reef Life Survey volunteers who contributed their time and energy to collecting these data, as well as several anonymous reviewers for their thoughtful comments

References

- Ahrends, A., Fanning, E., Rahbek, C., Burgess, N.D., Gereau, R.E., Marchant, R., Bulling, M.T., Lovett, J.C., Platts, P.J., Wilkins Kindemba, V., Owen, N., 2011. Funding begets biodiversity. *Diversity and Distributions* 17, 191-200.
- Alroy, J., 2010. Geographical, environmental and intrinsic biotic controls on Phanerozoic marine diversification. *Palaeontology* 53:6, 1211-1235
- Amano, T., Okamura, H., Carrizo, S.F., Sutherland, W.J., 2012. Hierarchical models for smoothed population indices: the importance of considering variations in trends of count data among sites. *Ecological Indicators* 13, 243-252.
- Arab, A., Wildhaber, M. L., Wikle, C. K., Gentry, C. N. 2008. Zero-inflated modeling of fish catch per unit area resulting from multiple gears: application to channel catfish and shovelnose sturgeon in the Missouri River. *N. A. J. of Fish. Manag.* 28:4, 1044-1058.
- Ashcroft, M.B., Gollan, J.R., Batley, M., 2012. Combining citizen science, bioclimatic envelope models and observed habitat preferences to determine the distribution of an inconspicuous, recently detected introduced bee (*Halictus smaragdulus* Vachal Hymenoptera: Halictidae) in Australia. *Biological Invasions* 14, 515-527.
- Barbet-Massin, M., Jiguet, F. Elbert, C.H., Thuiller, W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3, 327-338.
- Boakes, E.H., McGowan, P.J.K., Fuller, R.A., Chang-qing, D., Clark, N.E., O'Connor, K., Mace, G.M., 2010. Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS biology* 8, e1000385.
- Bolker, B., M., Brooks, M., E. , Clark, M., Connie, J., Geange, S., W. , Poulsen, J., R. , Stevens, H.H., White, J.-S., S., 2009. Review: Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24, 127-135.
- Bonney, R., Cooper, C.B., Dickinson, J., Kelling, S., Phillips, T., Rosenberg, K.V., Shirk, J., 2009. Citizen Science: a developing tool for expanding science knowledge and scientific literacy. *BioScience* 59, 977-984.

- Bonter, N. D., Cooper, C. B., 2012. Data validation in citizen science: a case study from Project FeederWatch. *Frontiers in Ecology and the Environment*, 10:6, 305–307.
- Bray, B.S., Schramm, J.L. Jr., 2001. Evaluation of a statewide volunteer angler diary program for use as a fishery assessment tool. *North American Journal of Fisheries Management*, 21:3, 606-615.
- Brunsdon, C., Comber, L., 2012. Assessing the changing flowering date of the common lilac in North America: a random coefficient model approach. *Geoinformatica*, 16, 675-690.
- Busby, J.R., 1991. BIOCLIM — A Bioclimate Analysis and Prediction System. *Nature Conservation: Cost effective biological surveys and data analysis*. Nature conservation (ed. by C.R. Margules and M.P. Austin), pp. 64–68. CSIRO, Melbourne.
- Butt, N., Slade, E., Thompson, J., Malhi, Y., Riutta, T., 2013. Quantifying the sampling error in tree census measurements by volunteers and its effect on carbon stock estimates. *Ecological Applications*, 23:4, 936-943
- Cadotte, M. W., Davies, J. T., Regetz, J., Kembel, S. W., Cleland, E., & Oakley, T. H. 2010. Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. *Ecology Letters*, 13:1, 96–105
- Chao, A., Gotelli, N., Hsieh, T. C., Sander, E., Ma, K. H., Colwell, R. K., & Ellison, A. M., 2013. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*.
- Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93, 2533-2547.
- Crall A.W., G. Newman, T.J. Stohlgren, K.A. Holfelder, J. Graham, Waller, D.M., 2011. Assessing citizen science data quality: a case study. *Conservation Letters*, 4:433-442.
- Comber, A., See, L., Fritz, S., Van der Velde, M., Perger, C., Foody, G., 2013. Using control data to determine the reliability of volunteered geographic information about land cover. *International Journal of Applied Earth Observation and Geoinformation* 23:0, 37-48.
- Conn, P., McClintock, B.T., Cameron, M., Johnson, D.S., Moreland, E., Boveng, P.L., 2013. Accommodating species identification errors in transect surveys. *Ecology preprint*.
- Cox, T.E., Philippoff, J., Baumgartner, E., Smith, C.M., 2012. Expert variability provides perspectives on the strengths and weaknesses of citizen-driven intertidal monitoring program. *Ecological Applications* 22:4, 1201-1212.
- Cutler, A., Cutler, D.R., Edwards, T.C., Beard, K.H., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. *Ecology* 88, 2783-2792.
- De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178-3192.
- deSolla, S.R., Shirose, L.J., Fernie, K.J., Barrett, G.C., Brousseau, C.S., Bishop, C.A., 2005. Effect of sampling effort and species detectability on volunteer based anuran monitoring programs. *Biological Conservation* 121, 585-594.
- Delaney, D., Sperling, C., Adams, C., Leung, B., 2008. Marine invasive species: validation of citizen science and implications for national monitoring networks. *Biological Invasions* 10, 117-128.

- Dickinson, J.L., Zuckerberg, B., Bonter, D.N., 2010. Citizen science as an ecological research tool: challenges and benefits. *Annual of Ecology, Evolution and Systematics* 41, 149-172.
- Dormann, F.D., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Gudrun, C., Davies, R.G., Hirzel, A., Jetz, W., Kissling, D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., 2007. Methods to account for spatial autocorrelation in the analysis of species distribution data: a review. *Ecography*, 30, 609-628.
- Dudík, M., Phillips, S.J., Schapire, R.E., 2005. Correcting sample selection bias in maximum entropy density estimation., In *Advances in neural information processing systems*. pp. 323-330. MIT Press, Cambridge, Massachusetts, USA.
- Edgar, G.J., Stuart-Smith, R.D., 2009. Ecological effects of marine protected areas on rocky reef communities; a continental-scale analysis. *Marine Ecology Progress Series* 388, 51-62.
- Edgar, G. J., Barrett, N.S., Morton A.J., 2004. Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. *Journal of Experimental Marine Biology and Ecology*, 308.2, 269-290.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *Journal of Animal Ecology*, 802.
- Elith, J., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Peterson, A.T., Phillips, S.J., Graham, C.H., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M.S., Zimmermann, N.E., Araujo, M., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129-151.
- Farmer, R.G., Leonard, M.L., Horn, A.G., 2012. Observer effects and avian-call-count survey quality: rare-species biases and overconfidence/ Effets des observateurs et qualite des inventaires par le denombrement des chants: biais sur les especes rares et exces de confiance. *The Auk* 129, 76.
- Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology* 43, 393-404.
- Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R., Wilson, J.D., 2000. Analysis of population trends for farmland birds using generalized additive models. *Ecology* 81, 1970-19.
- Fink, D., Hochachka, W.M., 2012. Using data mining to discover biological patterns in citizen science observations. In *Citizen Science: Public Participation in Environmental Research*. Dickinson, J.L. and Bonney, R., eds. Comstock Publishing Associates.
- Fink, D., Hochachka, W.M., Zuckerberg, B., Winkler, D.W., Shaby, B., Munson, M.A., Hooker, G., Riedewald, M., Sheldon, D., Kelling, S., 2010. Spatiotemporal exploratory models for broad-scale survey data. *Ecological Applications* 20, 2131-2147.
- Franklin, J., 2009. Mapping species distributions. Cambridge University Press, New York.
- Gelfand, A.E., Schmidt, A.M., Wu, S., Silander, J.A., Latimer, A., Rebelo, A.G., 2005. Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* 54, 1-20.
- Gotelli, N.J., Colwell, R.J., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4, 379-391.
- Hastie, T., Tibshirani, R.J., 1990. Generalized additive models. Chapman and Hall, London.

- Hedges, L.V., Tipton, E., Johnson, M.C., 2010. Robust variance estimation in meta-regression with dependent effect size estimates. *Research Synthesis Methods* 1, 39-65.
- Hochachka, W.M., Fink, D., Hutchinson, R.A., Sheldon, D., Wong, W.-K., Kelling, S., 2012. Data-intensive science applied to broad-scale citizen science. *Trends in Ecology & Evolution (Personal edition)* 27, 130-137.
- Holt, B.G., Rioja-Nieto, R., MacNeil, M.A., Lupton, J., Rahbek, C., 2013. Comparing diversity data collected using a protocol designed for volunteers with results from a professional alternative. *Methods in Ecology and Evolution*, 4:4, 383 – 392.
- Karpievitch, Y.V., Hill, E.G., Leclerc, A.P., Dabney, A.R., Almeida, J.S., 2009. An introspective comparison of random forest-based classifiers for the analysis of cluster-correlated data by way of RF++. *PLoS One*. 2009 Sep 18, 4:9.
- Kery, M., Gardner, B., Monnerat, C., 2010a. Predicting species distributions from checklist data using site-occupancy models. *Journal of Biogeography* 37, 1851-1862.
- Kery, M., Royle, J.A., Schmid, H., Schaub, M., Volet, B., Hafliger, G., Zbinden, N., 2010b. Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conservation Biology* 24, 1388-1397.
- Latimer, A.M., Wu, S., Gelfand, A.E., Silander, J.J.A., 2006. Building statistical models to analyze species distributions. *Ecological Applications* 16, 33-50.
- Lawler, J.L., O'Connor, R.R., 2004. How well do consistently monitored breeding bird survey routes represent the environments of the conterminous United States? *The Condor* 106:801–814
- Legendre, P., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601-615.
- Lunn, D.J., Thomas, T. Best, N., Spiegelhalter, D. WinBUGS – a Bayesian modeling framework: concepts, structure, and extensibility. *Statistics and computing*, 10:4, 325-337
- MacKenzie, D.I., 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier, Burlington, MA.
- Mateo, R.G., Felicísimo, Á.M., Muñoz, J., 2010. Effects of the number of presences on reliability and stability of MARS species distribution models: the importance of regional niche variation and ecological heterogeneity. *Journal of Vegetation Science* 21, 908-922.
- Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. *Fisheries Research* 70, 141-159.
- Miller, D.A., Nichols, J.D., McClintock, B.T., Grant, E.H.C., Bailey, L.L., Weir, L.A., 2011. Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology* 92:7, 1422-1428.
- Monk, J., 2013. How long should we ignore imperfect detection of species in the marine environment when modelling their distribution? *Fish and Fisheries*, 1467-2979.
- Olden, Julian D., Lawler, Joshua J., Poff, N.L., 2008. Machine learning methods without tears: a primer for ecologists. *The Quarterly Review of Biology*, 171.
- Pattengill-Semmens, C.V., Semmens, B.X., 2003. Conservation and management applications of the reef volunteer fish monitoring program. *Environmental Monitoring and Assessment* 81, 43-50.

- Parsons, B., Short, J., Roberts, D.D., 2009. Using community observations to predict occurrence of malleefowl (*Leipoa ocellata*) in the Western Australian wheatbelt. *Biological Conservation* 142, 364-374.
- Pearce, J.L., Boyce, M.S., 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, 43:3, 405-412.
- Petchey, O. L., Gaston, K. J., 2006. Functional diversity: back to basics and looking forward. *Ecology Letters*, 9, 741–758
- Phillips, S.J., Elith, J., 2013. On estimating probability of presence from use–availability or presence–background data. *Ecology* 94:6, 1409-1419.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias for presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications* 19:1, 181-197.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190, 231-259.
- R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Royle, J. A., Chandler, R. B., Yackulic, R. B., Nichols, J. D., 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. *Methods in Ecology and Evolution*, 3:3, 545-554.
- Royle, J.A., Dorazio, R.M., 2008. Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Amsterdam; Boston: Academic, 2008. 1st ed.
- Royle, J.A., Kéry, M., Gautier, R., Schmid, H., 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs*, 77:3, 465-481.
- Sarda-Palomera, F., Brotons, L., Villero, D., Sierdsema, H., Newson, S.E., Jiguet, F., 2012. Mapping from heterogeneous biodiversity monitoring data sources. *Biodiversity and Conservation* 21, 2927-2948.
- Sela, S.J., Simnoff, J.S., 2012. RE-EM trees: a data mining approach for longitudinal and clustered data. *Machine Learning*, 86: 169-207.
- Segurado, P., Araújo, M.B., Kunin, W.E., 2006. Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology*, 43, 433-444.
- Seys, J., Offringa, H., Van Waeyenberge, J., Meire, P., Kuijken, E., 2002. An evaluation of beached bird monitoring approaches. *Marine pollution bulletin* 44, 322-333.
- Silvertown, J., 2009. A new dawn for citizen science. *Trends in ecology & evolution (Personal edition)* 24, 467-471.
- Snäll, T., Kindvall, O., Nilsson, J., Pärt, T., 2011. Evaluating citizen-based presence data for bird monitoring. *Biological Conservation* 144, 804-810.
- Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142, 2282-2292.

Sunde, P., Jesson, L., 2013. It counts who counts: an experimental evaluation of the importance of observer effects on spotlight count estimates. *European Journal of Wildlife Research*, 1612-4642, 1-9.

Tulloch, A. I. T., Possingham, H.P., Joseph, L.N., Szabo, J., Martin, T.G., 2013. Realizing the full potential of citizen science monitoring schemes. *Biological Conservation*, 165, 128-138.

Tulloch, A. I. T., Szabo, J. T., 2012. A behavioral ecology approach to understand volunteer surveying for citizen science datasets. *Emu*, 112, 313-335.

Walker, P.A., Cocks, K.D. (1991) HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters*, 1, 108-118.

Welham, S., Cullis, B., Gogel, B., Gilmour, A., Thompson, R., 2004. Prediction in linear models. *Australia and New Zealand Journal of Statistics*. 46:3, 325-347.

Wikle, C. K., 2003. Hierarchical Bayesian models for predicting the spread of ecological processes. *Ecology*, 84:6, 1382-1394.

Wiggins, A., Crowston, K., 2011. From conservation to crowdsourcing: a typology of citizen science, In *System Sciences (HICSS)*, 2011 44th Hawaii International Conference on. pp. 1-10.

Wiggins, A., Newman, G., Stevenson, R.D., Crowston, K., 2011b. Mechanisms for data quality and validation in citizen science, In *e-Science Workshops (eScienceW)*, 2011 IEEE Seventh International Conference on. pp. 14-19.

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., Veran, S. (2013), Presence-only modelling using MAXENT: when can we trust the inferences?. *Methods in Ecology and Evolution*

Zuur, A.F., Elena, N.I., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1.1, 3-14.

Zuur, A.F., 2009. *Mixed effects models and extensions in ecology with R*. Springer New York, New York.

Figure Captions:

Fig. 1. A) Occurrence of the urchin genus *Holopneustes spp.* along the east coast of Australia in RLS surveys. B) The temperature range occupied by these species lies between 17 and 26 degrees. C) These species occupied 49 of 2008 surveys, leading to low predicted occupancy rates across the range of temperatures examined. D) The number found per site is generally low, to a maximum of 18 individuals, resulting in low predicted numbers per site.

Fig. 2. Species richness of fish in the northern Pacific decreases with increasing latitude: Analysis by using linear model with the package “nlme” in R (A), linear regression with random effects at the site level (B) and with variance weighting (C). Predicted richness values (black line) and 95% confidence intervals (grey) are shown for each model. Residuals of the fitted values for each of the three models are shown in D-F. Points are 30% transparent to show areas of high data density.

Fig. 3. Relationships between estimated occupancy rates and maximum sea-surface temperature for the sea urchin genus *Echinostrephus spp.* found in RLS surveys along the east coast of Australia.

Solid line indicates an estimate based on a logistic regression (LR) between Max SST and occupancy, while the dashed line is the estimated probability of occupancy from a detection-occupancy (DO) model which takes into account failure to detect the genus given that it was present at a site. Grey shading indicates 95% Bayesian credible intervals around the estimated trend. Points indicate temperatures at which the urchin was (o) or was not (+) found.

Fig. 4. Receiver Operator Characteristic (ROC) curves for estimated presence/absence of sharks found in RLS sites worldwide using random forests (RF) at different scales. A) Regression RF on the average presence at an eco-region, area under the curve (AUC, (95% CI*) = 0.649 (0.62-0.67)). B) regression RF on the average presence at a site (AUC = 0.814 (0.80-0.83)). C) classification RF on the presence/absence at a site, where one survey (with depth closest to 6 m) is sampled for each site (AUC = 0.78 (0.76-0.8)). D) classification RF on the presence/absence at a survey (AUC = 0.809 (0.79-0.83)).

Fig. 5. Estimated species richness for two sites from the Reef Life Survey: Goat Island and Shortland Bluff. (A) Traditional rarefaction scales estimates back to number of individuals in the smallest sample (vertical dotted line). Dashed lines indicate extrapolated richness (i.e., species accumulation curves). (B) Coverage-based rarefaction scales estimates back to the lowest level of sample coverage (vertical dotted line). In both panels, shaded areas represent 95% confidence intervals.

Fig. 6. Predicted probability (and likelihood in the case of presence-only models) of occurrence of *P. unifasciata* using three different modelling scenarios; A) presence-absence data, B) presence-only data with pseudo-absences drawn from the study region at random (random background), C) presence-only data with pseudo-absences drawn from the study region weighted by their probability of being sampled based on the distribution of sampled sites (targeted background). Arrow indicates north, and figures have been rotated to optimize space usage.

Table 1. Statistical approaches and software packages available for dealing with error and bias in citizen science data.

Method	R package	Package reference ^a
GLM	base	R core team, 2012
GLMM	MCMCglmm	Hadfield, 2010
	lme4	Bates et al., 2012
	glmmADMB	Skaug et al., 2011
GAMM	mgcv	Wood, 2011
	gammSlice	Pham and Wand, 2012
GWR	spgwr	Bivand, 2013
Spatio- temporal Models	stem	Cameletti, 2009
Detection-Occupancy	unmarked	Fiske, 2011
Capture-Recapture	unmarked	
Bayesian hierarchical	R2WinBUGS,	Sturtz et al., 2005
	R2jags	Su and Yajima, 2012
Multiple ML approaches	RWeka	Hornik et al., 2009
Mixed-effects trees	REEMtree	Sela and Simonoff,

	longRPart	(2012) Stewart and Abdoell, 2008
Boosted Regression Tree	gbm	Ridgeway, 2013
CART	tree	Ripley, 2012
	rpart	Therneau, 2012
Neural networks	nnet	Venables and Ripley, 2002
Richness and other indices	vegan	Oksanen (2012)
Ordination (NMDS, CCA, RDA)	vegan	Oksanen (2012)
Indicator species analysis	indicspecies	De Caceres and Legendre, P., 2009
Modeling detectability	mrds	Laake et al., 2012
Species Distribution Models	Biomod2	Thuiller, et al., 2013
BioClim	dismo	Hijmans, et al., 2012
Bayesian Hierarchical SDM	hSDM	Vieilledent, et al., 2012
BRT and Random Forest Mapped Predictions	ModelMap	Freeman (2012)

^bR package citations are available in the supplementary reference material

Table 2: Examples of CS studies that have used methods described in the text. For each study, the general class of method is listed, along with the source of the data (CS or otherwise), type of data and a description of the general class of issue addressed with the modeling approach. We also briefly summarize how the analysis helped inform the study results.

<u>Model type</u>	<u>Source^a</u>	<u>Data^b</u>	<u>Issue</u>	<u>Study</u>	<u>Findings</u>
<u>GLM</u>	<u>CS</u>	<u>Size</u>	<u>Measurement error</u>	<u>Butt et al., 2013</u>	<u>Measurements made by volunteers were not significantly different to those made by experts, after filtering.</u>
<u>GLM</u>	<u>CS</u>	<u>PA</u>	<u>Identification</u>	<u>Delaney, 2008</u>	<u>Age and education predicted rates of false identification of invasive crabs</u>
<u>GLM</u>	<u>CS</u>	<u>A</u>	<u>Identification</u>	<u>Crall et al., 2010</u>	<u>Volunteers that were more confident performed better at species identifications</u>
<u>GLM</u>	<u>CS</u>	<u>PA</u>	<u>Detection</u>	<u>Sunde and Jessen, 2013.</u>	<u>Experienced hunters were more likely to detect rabbits in spotlight surveys.</u>
<u>GLM</u>	<u>CS</u>	<u>Size</u>	<u>Bias</u>	<u>Edgar et al., 2004</u>	<u>Volunteers consistently over-estimated the sizes of fish</u>
<u>GLMM</u>	<u>CS</u>	<u>P</u>	<u>Spatial clustering</u>	<u>Brunsdon and Comber, 2012</u>	<u>Onset of spring was shown to gradually advanced over time when continental-scale spatial clustering was accounted for</u>
<u>GAM</u>	<u>CS</u>	<u>P</u>	<u>Spatial clustering</u>	<u>Fewster et al., 2000</u>	<u>GAMMs reveal temporal trend in arrival time of bird species based on volunteer data</u>
<u>GLM</u>	<u>CS</u>	<u>P</u>	<u>Presence-only data</u>	<u>Parsons et al., 2009</u>	<u>Targeted generation of pseudo-absences resulted in presence-absence data suitable for regression modeling.</u>
<u>GWR</u>	<u>CS</u>	<u>P</u>	<u>Spatial clustering</u>	<u>Comber et al., 2013</u>	<u>Geographically-weighted regressions (GWR) and control data used to infer reliability of volunteered geographic information</u>
<u>Hierarchical</u>	<u>CS</u>	<u>PA</u>	<u>Detection</u>	<u>deSolla, 2005</u>	<u>Survey effort is related to probability of detecting rare frogs from calls</u>
<u>Hierarchical</u>	<u>CS</u>	<u>PA</u>	<u>False-positive</u>	<u>Miller et al., 2011</u>	<u>False-positive rates of bird classification by calls were related to distance, ambient noise and observer ability</u>

Table 2 continued

<u>Model type</u>	<u>Source^a</u>	<u>Data^b</u>	<u>Issue</u>	<u>Study</u>	<u>Findings</u>
<u>Hierarchical</u>	<u>CS</u>	<u>PA</u>	<u>Spatiotemporal Clustering</u>	<u>Fink, et al., 2010</u>	<u>Modeling effort and detection in space and time led to improved models of species distribution</u>
<u>Hierarchical</u>	<u>DDB</u>	<u>A</u>	<u>Site-level bias</u>	<u>Amano et al., 2012</u>	<u>Accounting for site-level effects allowed for more accurate estimation of population trends</u>
<u>Hierarchical</u>	<u>CS</u>	<u>PA</u>	<u>Detection</u>	<u>Kery, et al., 2010b</u>	<u>Accounting for detection in SDMs led a 2-fold increase in estimated site occupancy</u>
<u>Hierarchical</u>	<u>S</u>	<u>PA</u>	<u>Identification</u>	<u>Conn et al., 2013</u>	<u>Hierarchical modeling allowed for estimation of species misidentification rates in double-observer surveys.</u>
<u>Regression Tree</u>	<u>CS</u>	<u>A</u>	<u>Observer error</u>	<u>Cox, et al., 2012</u>	<u>The differences in community similarity values among data collectors were not important</u>
<u>Regression splines</u>	<u>NHC</u>	<u>P</u>	<u>Spatial Clustering</u>	<u>Mateo et al., 2010</u>	<u>Generating pseudo-absences using targeted rather than random approaches produced more accurate distribution models</u>
<u>MaxEnt</u>	<u>DDB</u>	<u>P</u>	<u>Spatial Clustering</u>	<u>Phillips et al., 2009</u>	<u>Clustering pseudo-absences at the same scale as occurrence data results in more accurate distribution models</u>
<u>Diversity</u>	<u>CS</u>	<u>P</u>	<u>P</u>	<u>Holt et al., 2013</u>	<u>Hierarchical models show that species richness estimates based on roving diver surveys were higher than those of standardized protocols.</u>

^a Data Sources include: Citizen Science (CS), Natural History Collections (NHC) and distributed sampling databases (DDB). ^b Data types include: (P), presence-absence (PA), abundance (A), biodiversity (B) or derived parameters (D). For each paper we have included a result that shows how the analysis helped improve inference.

Fig.1.

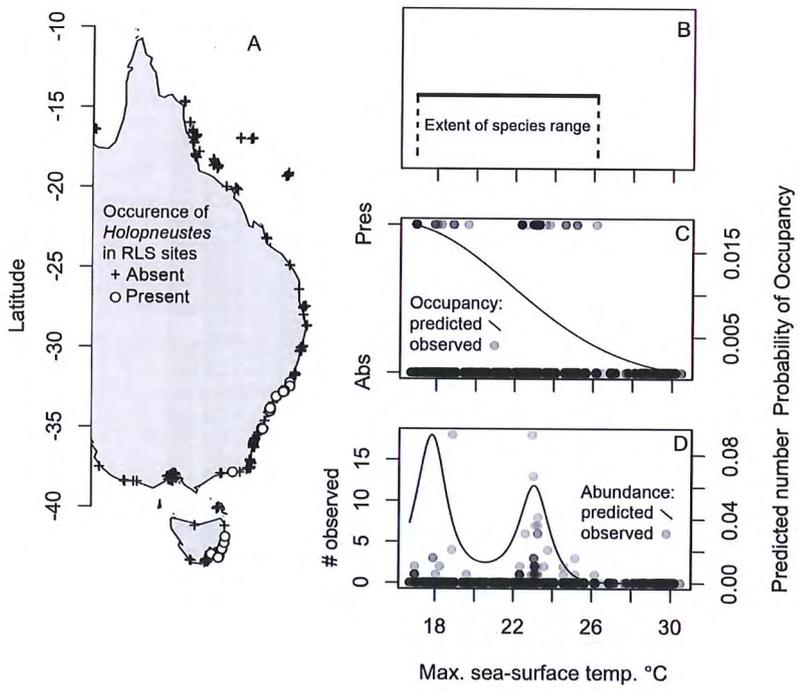


Fig. 2

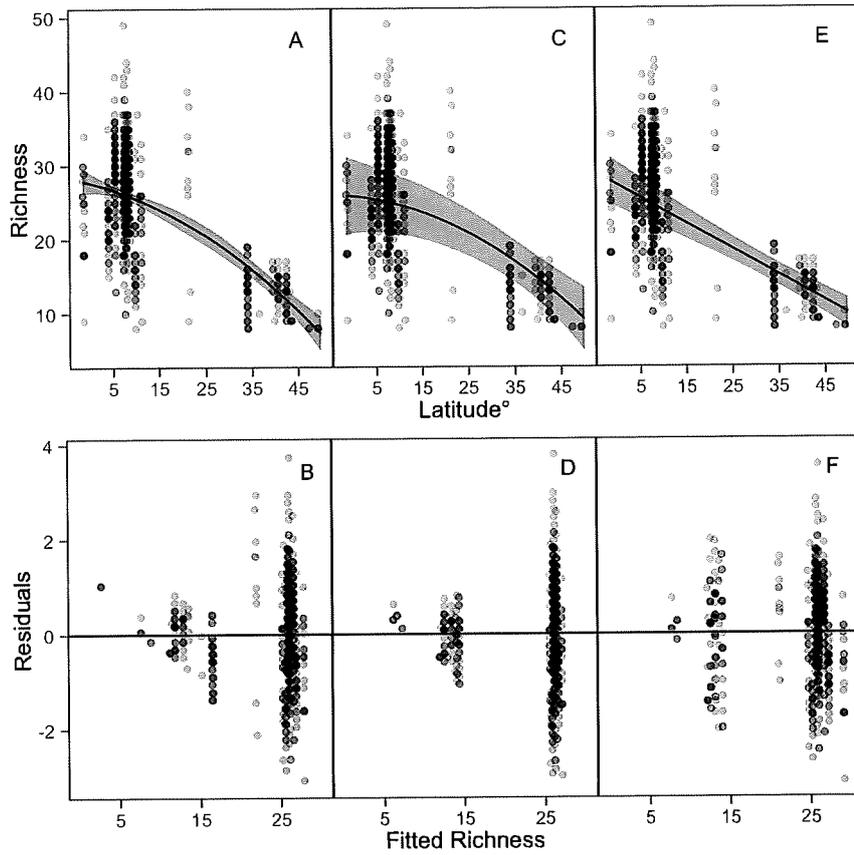


Fig. 3.

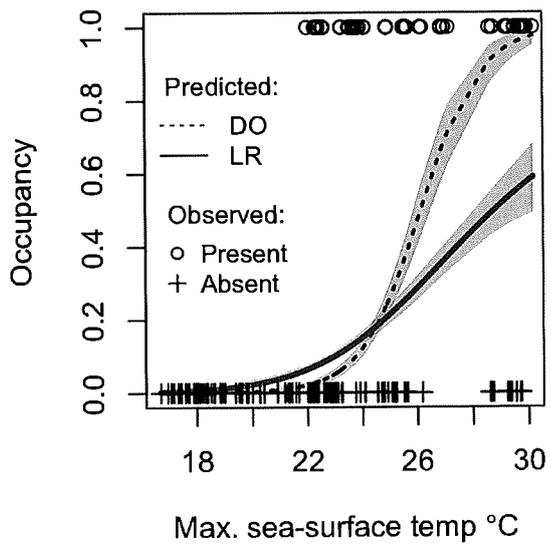


Fig. 4.

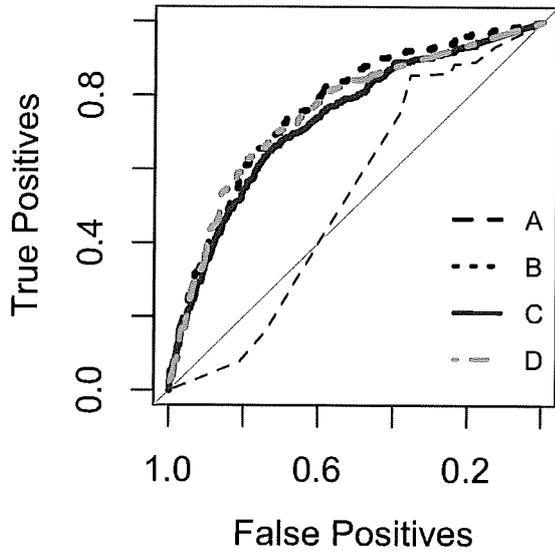


Fig. 5.

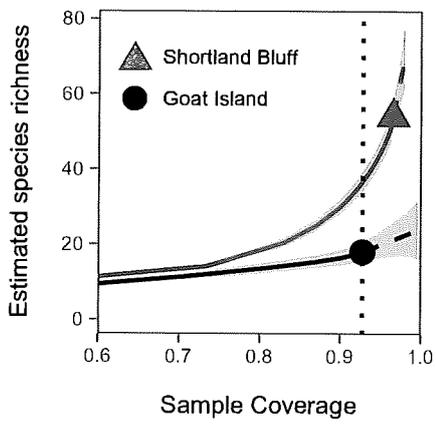
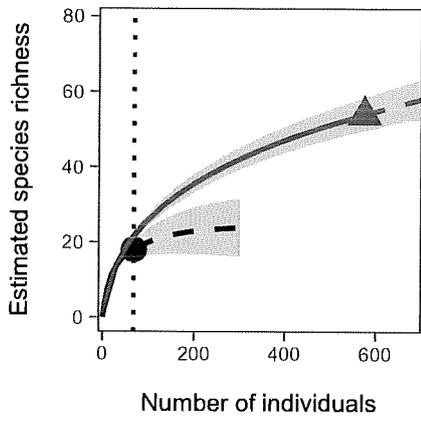
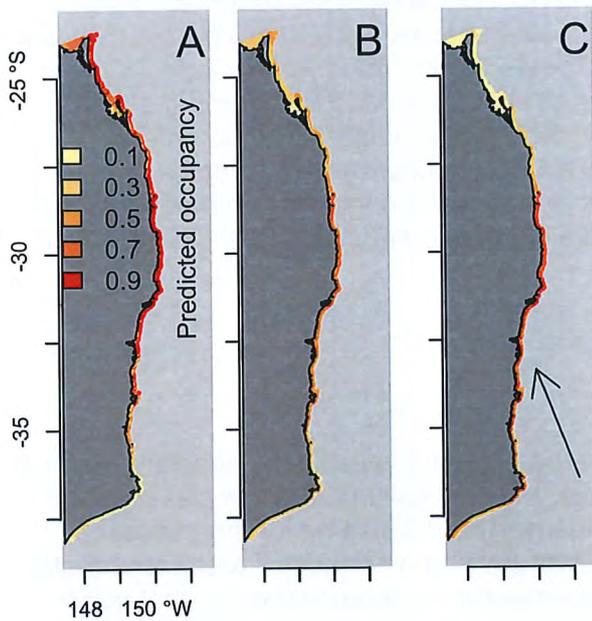


Fig. 6.



Supplementary Online Materials for:

“Statistical solutions for error and bias in global citizen science datasets”

Appendix A: Supplementary Methods

A.1 Details on Reef-life survey data collection protocols

Data used for examples in the study were subsets of the Reef Life Survey (RLS) global marine biodiversity dataset, carefully selected to demonstrate aspects of data analysis outlined in the text. Standard RLS methods involve visual census of fish and mobile invertebrate species by trained volunteer SCUBA divers along 50 m transect lines set in shallow rocky and coral reef habitats. Methods have been described in detail elsewhere (Edgar and Stuart-Smith, 2009) and can be found in an online methods manual http://reeflifesurvey.com/files/2008/09/NEW-Methods-Manual_15042013.pdf

).

The data include the identities, sizes and abundance of fishes in 5 m wide blocks, and identities and abundance of mobile invertebrates, such as sea urchins, in 1 m wide blocks, with duplicate contiguous transect blocks assessed each deployment of the transect line, and multiple depths generally surveyed at each site. To date, data have been collected from >10,000 transect blocks distributed amongst 2000 sites in 40 countries.

Data provided by trained volunteer divers have been compared to data generated by professional biologists at the same sites, and differences between these groups was found to be non-significant and trivial compared to spatial variation between regions and within and between sites (Edgar, G.J., Stuart-Smith, R.D., 2009. Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Marine Ecology Progress Series* 388, 51-62.).

Geo-referenced records of sea urchins in the genera *Holopneustes* and *Echinostrephus* from the east coast of Australia were extracted from the RLS database for analyses relating to Figures 1 and 3, while Figure 2 was based on data on the mean number of fish species observed along transects (the two contiguous blocks aggregated to represent species per 500 m²) from surveys in the Temperate Northern Pacific, Eastern Indo-Pacific, Temperate Northern Atlantic and Tropical Eastern Pacific marine realms, as identified by Spalding et al. (2007). Machine learning analyses used in Figure 4 were based on records of all species in RLS global database in the orders Carcharhiniformes, Heterodontiformes, Lamniformes and Orectolobiformes. Richness and abundance data used in Figure 5 represent aggregates of species and their abundances recorded on each transect surveyed at two sites in NZ, which were chosen to emphasize the differences in their rarefaction curves.

A.2 Random Forests methods

Classification trees or decision trees are used to predict the outcome variable, by choosing splits in the data based on the predictor variables. In our example, the first split in the shark classification tree could be based on a Longitude of 148.5°W. Then the next split would be for the subset of sites with a Longitude < 148.5°W, where the data is split on the same or another predictor variable (e.g. mean silicate > 1.1 µmol/l). Each leaf of the tree corresponds to a prediction (so that in our example those sites with Longitude < 148.5°W and silicate > 1.1 µmol/l are predicted to have sharks present).

A random forest is based on a set of multiple decision trees, each one generated from a bootstrap sample of the sites and of the set of predictor variables. By combining the predictions for each tree in the forest, we can obtain a probability of presence/absence at a site, based on the predictor variables. One could say that all sites with a probability greater than 0.5 are predicted to have sharks present. By increasing this cut-off, you can improve the true positive rate, while also increasing the false positive rate. The ROC curves are created by calculating the true and false positive rates for all possible values for this cut-off.

A.3 Species Distribution Model

Biological data (species' presences-absences) were sourced from Reef Life Survey data for a section of the east coast of Australia between -26 and -38 degrees south. Environmental data was sourced from data compiled by the NERP Marine Biodiversity Hub (www.nerpmarine.edu.au, datasets available on the Australian Ocean data Network (AODN) portal: <http://portal.aodn.org.au/aodn/>) of a range of remotely sensed and modelled environmental covariates (Table S1). These environmental data were available on a 0.01 degree point grid (approximately 900 m at this latitude) for the entire study region. Biological data were assigned to the closest environmental data grid point. Where multiple records were attributed to the same grid point, if any assigned record was a presence then that grid point (referred to as a site) and its associated environmental variables were treated as a presence (following Elith et al., 2006). This resulted in 186 sites for modelling.

The data were randomly divided into a training dataset (70%) and a semi-independent validation dataset, stratified by prevalence. The data were used to generate three modelling scenarios; modelling with presence-absence (PA) data, modelling with presence-only data (PO) and a random selection of pseudo-absences from the available background (i.e. all grid points in the study region), modelling with PO data and a targeted selection of pseudo-absences from the available background (following Phillips et al., 2009). The targeted selection of background pseudo-absences was intended to focus pseudo-absence selection towards sites that were similar to those surveyed (and hence with a similar bias). This was achieved by running a separate boosted regression tree (BRT) analysis where all 186 sites samples were treated as presences and random selection of 186 of the background were treated as absences. The model (10-fold cross-validation AUC = 0.854 +/- 0.019, fig S1) was used to predict the probability of a site being sampled and this probability was used as a weighting when selecting pseudo-absences (following Zaniewski et al., 2002). One hundred datasets were generated for each PO scenario. The

presence records from the PA training dataset were bound with the same number of pseudo-absences as absences in the training PA dataset selected as described above. The single training dataset was used for the PA scenario (as running the BRT model 100 times with the same dataset would have resulted in very little difference to model outputs).

The three scenarios were modelled using boosted regression trees, with the package `gbm` (Ridgeway, 2009) and code supplied by Elith (2008), in R. Models were run that accommodated two-way interactions (tree complexity= 2) with a learning rate (0.02-0.04) optimised to build models with 1000-2000 trees for a majority of iterations. Scenarios were evaluated by comparing the predictions made from each model with the presences and absences observed in the validation dataset. Two metrics were used for evaluation. The area under the receiver operating curve (AUC) quantifies the ability of the models to discriminate between presences and absences at sites (Franklin, 2009), where values around 0.5 indicate that the model performs no better than random and a value of 1 indicates perfect discrimination. The Pearson correlation between observed and predicted values was also calculated as a measure of the fit of the model.

Appendix B. Supplementary Tables and Figures

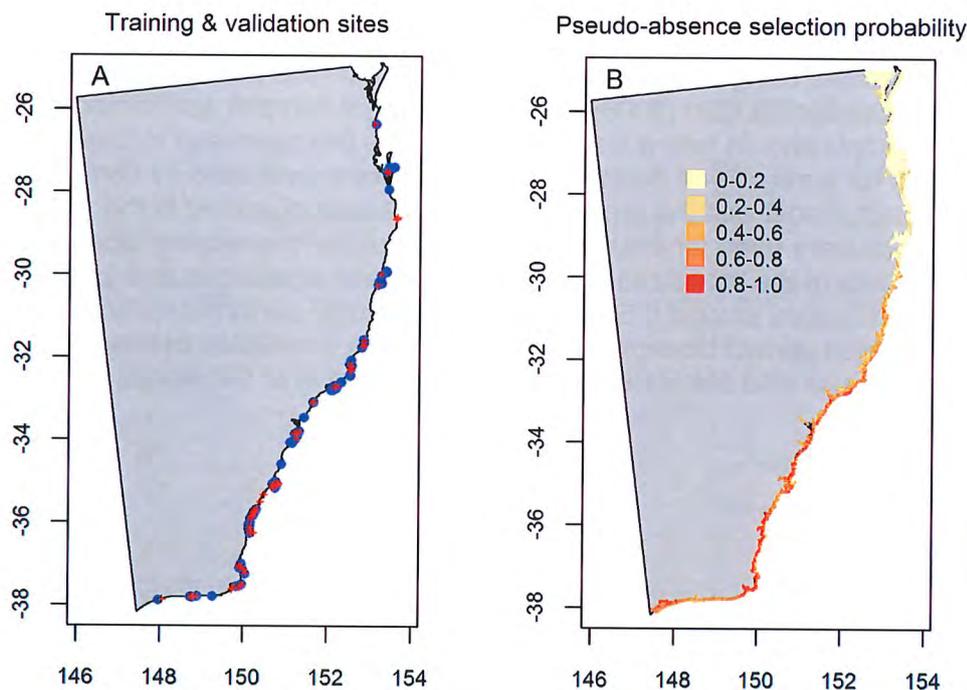


Figure S1. A) Location of training site (blue) used to build BRT models, and validation sites (red) used to test model predictions. B) Probability used to select sites for targeted pseudo-absences.

Table S1. Environmental covariates used in BRT analyses compiled by the NERP Marine Biodiversity Hub

Source	Covariate	Unit
Geoscience Australia	Bathymetry – mean	m
CSIRO Atlas of Regional Seas	Nitrate – mean	μM
CSIRO Atlas of Regional Seas	Nitrate – seasonal range	μM
CSIRO Atlas of Regional Seas	Phosphate – mean	μM
CSIRO Atlas of Regional Seas	Phosphate – seasonal range	μM
CSIRO Atlas of Regional Seas	Salinity – mean	PSU
CSIRO Atlas of Regional Seas	Salinity – seasonal range	PSU
MODIS	Chlorophyll-a – mean	$\text{mg}\cdot\text{m}^{-3}$
MODIS	Chlorophyll-a – seasonal range	$\text{mg}\cdot\text{m}^{-3}$
SeaWiFS	Sea surface temperature – mean	$^{\circ}\text{C}$
SeaWiFS	Sea surface temperature – seasonal range	$^{\circ}\text{C}$

Table S2. Evaluation statistics for the three scenarios modelled for *Parma unifasciata*. Presence-only (PO) model statistics are based on 100 randomly generated pseudo-absence datasets and values of the average and standard errors are presented.

Model	AUC (\pm s.e)	COR (\pm s.e)
Presence-absence	0.848	0.584
PO: Random Background	0.713 (0.006)	0.407 (0.009)
PO: Targeted Background	0.762 (0.005)	0.476 (0.009)

Appendix C: R package citations

- Bates, D., Maechler, M., Bolker, B., (2012). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. <http://CRAN.R-project.org/package=lme4>
- Bivand, R., Yu, D., Nakaya, T., and tricube function based on a contribution by Garcia-Lopez, M., (2013). spgwr: Geographically weighted regression. R package version 0.6-19. <http://CRAN.Rproject.org/package=spgwr>
- De Caceres, M., Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. Ecology, <http://sites.google.com/site/miqueldecaceres/>
- Cameletti, M., (2009). Stem: Spatio-temporal models in R. R package version 1.0.
- Fiske, I., Chandler, R. (2011). unmarked: An R Package for Fitting Hierarchical Models of Wildlife Occurrence and Abundance. Journal of Statistical Software, 43(10), 1-23. URL <http://www.jstatsoft.org/v43/i10/>.
- O'Connell, J., Hojsgaard, S., (2011). Hidden Semi Markov Models for Multiple Observation Sequences: The mhsmm Package for R. Journal of Statistical Software, 39(4), 1-22. URL <http://www.jstatsoft.org/v39/i04/>.
- Hadfield, J.D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. Journal of Statistical Software, 33(2), 1-22. URL <http://www.jstatsoft.org/v33/i02/>.
- Harte, D., (2012). HiddenMarkov: Hidden Markov Models. R package version 1.7-0. Statistics Research Associates, Wellington. URL: <http://cran.at.r-project.org/web/packages/HiddenMarkov>
- Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., (2013). dismo: Species distribution modeling. R package version 0.8-5. <http://CRAN.R-project.org/package=dismo>
- Himmelman, L., (2010). HMM: HMM - Hidden Markov Models. R package version 1.0. <http://CRAN.R-project.org/package=HMM>
- Hornik, K., Buchta, C., Zeileis, A., (2009) Open-Source Machine Learning: R Meets Weka. Computational Statistics, 24(2), 225-232. doi:10.1007/s00180-008-0119-7
- Laake, J., Borchers, D., Thomas, L., Miller, D., Bishop, J., (2012). mrds: Mark-Recapture Distance Sampling (mrds). R package version 2.1.0. <http://CRAN.R-project.org/package=mrds>

- Oksanen, J., Guillaume, B.F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., (2012). *vegan*: Community Ecology Package. R package version 2.0-5. <http://CRAN.R-project.org/package=vegan>
- Pham, T., Wand, M., (2012). *gammSlice*: Generalized additive mixed model analysis via slice sampling. R package version 1.2-6. <http://CRAN.R-project.org/package=gammSlice>
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Ridgeway, G., with contributions from others (2013). *gbm*: Generalized Boosted Regression Models. R package version 2.0-8. <http://CRAN.R-project.org/package=gbm>
- Ripley, B., (2012). *tree*: Classification and regression trees. R package version 1.0-33. <http://CRAN.R-project.org/package=tree>
- Sela, R.J., Simonoff, J.T., (2011), *REEMtree*: Regression Trees with Random Effects. R package version 0.90.3.
- Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., Bolker, B., (2011). *glmmADMB*: Generalized Linear Mixed Models Using AD Model Builder. R package version 0.7. <http://glmmadmb.r-forge.r-project.org>, <http://admb-project.org>
- Stewart, S., Abdoell, M., (2008). *longRPart*: Recursive partitioning of longitudinal data using mixed-effects models. R package version 1.0.
- Sturtz, S., Ligges, U., Gelman, A. (2005). *R2WinBUGS*: A Package for Running WinBUGS from R. *Journal of Statistical Software*, 12(3), 1-16.
- Su, Y., Yajima, M., (2012). *R2jags*: A Package for Running jags from R. R package version 0.03-07. <http://CRAN.R-project.org/package=R2jags>
- Therneau, T., Atkinson, B., Ripley, B., (2012). *rpart*: Recursive Partitioning. R package version 4.1-0. <http://CRAN.R-project.org/package=rpart>
- Thuiller, W., Georges, D., Engler, R., (2013). *biomod2*: Ensemble platform for species distribution modeling. R package version 2.0.0. <http://CRAN.R-project.org/package=biomod2>
- Vieilledent, G., Latimer, A.M., Gelfand, A.E., Merow, C., Wilson, A.M., Mortier, F., and Silander, J.A. Jr. (2012). *hSDM*: hierarchical Bayesian species distribution models. R package version 1.0. <http://CRAN.R-project.org/package=hSDM>
- Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* 73(1):3-36

Appendix iv. Distinguishing geographic range shifts from artefacts of detectability and sampling effort.

This work, in a revised format, has been accepted for publication and is currently in press in the journal *Diversity and Distributions*. Please cite the journal article in any reference to this work.

Distinguishing geographic range shifts from artefacts of detectability and sampling effort

Amanda E. Bates^{1*}, Tomas J. Bird^{2†}, Rick D. Stuart-Smith¹, Michael McCarthy², Thomas Wernberg³, Neville Barrett¹, Graham Edgar¹, Stewart Frusher¹, Alistair J. Hobday⁴, Gretta T. Pecl¹, Dan A. Smale^{3,5}, Jennifer M. Sunday⁶

[†] Authors contributed equally to the manuscript

Author Affiliations:

¹Institute for Marine and Antarctic Studies, University of Tasmania, PO Box 49, Hobart, Tasmania, 7001 Australia

²School of Botany, The University of Melbourne, Parkville Victoria 3010 Australia

³UWA Oceans Institute and School of Plant Biology, University of Western Australia, Crawley, Western Australia, 6009, Australia

⁴Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, Hobart, Tasmania, 7001, Australia

⁵The Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

⁶Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, V5A 1S6, Canada

*Corresponding author details:

A.E.Bates@soton.ac.uk

Earth and Ocean Sciences

National Oceanography Centre Southampton
University of Southampton Waterfront Campus
Southampton SO14 3ZH
United Kingdom
Tel: +44 (0)23 8059 6666

Keywords:

latitudinal gradient, range edge estimation, climate warming, survey methodology, species abundance, extreme value statistics

Abstract

The redistribution of species with climate change is well-documented. Even so, it remains unknown what proportion of apparent shifts in species ranges reflect real change due to ecological processes, and which are simply artefacts of variable detectability. Here, we use simulations under scenarios of varying abundance-related occupancy and sampling effort to describe the null expectation of patterns in the magnitude and variability of range shifts. We compare simulated patterns to empirically derived assemblage range shift data from two regional-scale (100s km) field studies and find that even with a well-designed sampling regime, accurate estimation of range edges are difficult to obtain for many species. We illustrate that a time-to-extinction model can be applied to spatial distribution data to provide species-specific confidence limits for range edges. These simulation and modelling approaches are particularly valuable for studies of marine species, where observations are typically few and patchy. Attempts to estimate null expectations of assemblage-level range shifts in the marine environment, and assigning confidence in the values obtained for particular species, represent important steps in advancing our understanding of global change.

Introduction

Species are tracking environmental warming by moving towards the poles through range extensions at the poleward (high-latitude) boundary and range contractions at the equatorward (low-latitude) range boundary (Chen et al. 2011, Sunday et al. 2012, Pinsky et al. 2013, Poloczanska et al. 2013). Yet even in areas experiencing rapid temperature change, the magnitude of observed biological responses differs among species (Poloczanska et al. 2013). At least some of this variation maybe due to the magnitude and spatio-temporal distribution of sampling effort, which has the potential to generate inaccurate range shift estimates. This is a particular problem for species unlikely to be observed due to low population numbers, patchy occupancy patterns, or cryptic characteristics (Dorazio and Royle 2005, Shoo et al. 2006, Blanchard et al. 2008, Hassall and Thompson 2010, McCarthy et al. 2012). Thus when entire assemblages of species are systematically surveyed with the same effort, biases or error in observed range shifts can be expected due to the abundance and occupancy patterns of different species, and their biological traits.

Difficulties in measuring species' distribution patterns are well-known and have been acknowledged in a range shift context (reviewed in Tingley and Beissinger 2009). In particular, locating the middle of species' distribution ranges can be achieved with greater accuracy than for estimates of range edges, especially for rarer species (Shoo et al. 2006, Hassall and Thompson 2010, Pinsky et al. 2013). Yet range edges may be of particular interest because, for example, range extension into new regions and contraction from previously occupied areas will ultimately drive changes in novel species interactions. It is therefore important to understand what error exists in the estimation of range edges.

Species detectability, i.e., the probability a species will be observed by a sampling protocol when it is present, differs among species in marine environments. As range shift data often encompass entire assemblages, species detectability may influence our understanding of the true scale of range expansions and contractions occurring. This is a particular problem at the edge of species' geographical range limits, where population numbers typical tail off. Quantifying the extent of uncertainty associated with species range edges will therefore be of value.

However, in most cases, the power of a particular sampling method to detect each species present within a community is unknown. Biases due to variable species detectability have been acknowledged when interpreting observed range shift patterns, but are generally not accounted for using statistical methods (Tingley and Beissinger 2009, Tanadini and Schmidt 2011, Brown et al. 2011, Monk 2013). For instance, Hassall and Thompson (2010) have suggested a range edge statistic based on a gamma frequency distribution rather than the most extreme or averaged range edge values (e.g., mean of the 10 most extreme

range records, as in Hickling et al. 2005, Thomas and Lennon 1999). Alternatively, in order to increase the probability that observed range edge shifts represent true distributional change, Jones et al. (2010) suggest considering only shifts that are greater than a threshold distance, set for example by the upper 95th percentile of the distances among survey sites. However, both of these examples assume that all species are equally likely to be detected if present (Dorazio and Glimskar 2006, Wintle et al. 2012). Indeed quantifying species detectability using distance sampling has recently been attempted for butterflies (Isaac et al. 2011), a model taxonomic group for understanding climate-driven range shifts (Parmesan et al. 1999, Sunday et al. 2012).

Evaluation of range shifts in the ocean, for pragmatic reasons, have generally ignored species detectability, indirectly assuming uniformly high detectability across species, despite the fact that detectability can vary markedly even among similar species (e.g., within reef fish assemblages, MacNeil et al. 2008). This is likely because approaches for quantifying species detectability are laborious and costly in comparison to terrestrial environments and may therefore not be not always be feasible, especially for regional-scale analyses.

In this paper, we first assert that the uncertainty in the range edges of marine species will result in biased estimates of species range shifts, in particular for species with low abundance or detectability. We use simulations (and provide R code for interested readers) to show how factors related to species detectability influence whether range shifts are observed and the variability of those estimates – even when observed change is modeled as zero. We also provide two examples that demonstrate evidence of detection-related biases as predicted by our simulations, and thus illustrate the utility of using simulations based on simple assumptions to understand underlying biases or error.

Second, we explore how occupancy information can inform uncertainty in range edge estimates. We apply a time-to-extinction model, an optimal linear estimator tool (Solow 2005), to spatial distribution data for species with geographic ranges that fall near the edge of Tasmania. Time-to-extinction models estimate the most likely date of extinction based on the timing of observations leading up to the last sighting and are commonly used in contexts related to palaeontology and conservation biology (e.g., Solow 2005). In the same way that the last sighting of an individual from a near-extinct species is unlikely to represent the very last individual of a population (except where the entire population is known), the most extreme location at which a species is observed is unlikely to represent its true range edge (except in cases such as where known habitat barriers exist). Exchanging space for time therefore estimates confidence in the tails of spatial distributions and we test the accuracy of this application using real data.

Materials and methods

Simulation of methodological artefacts

We simulated differing species abundances and levels of sampling effort to provide null expectations for the magnitude of variability in range edges that may be due to sampling error. While many factors influence whether a species will be observed in a given sample or survey, in the marine realm, species abundance is one of the more important determinants of both site occupancy and detectability (McCarthy et al. 2013). Rare or patchily distributed species will be observed in fewer samples and will have lower occupancy, while those with higher abundance and more uniform distributions will be observed more frequently with higher occupancy. Abundance is also a convenient descriptor, varies by orders of magnitude within and between species, and can be assessed as categories (i.e., rare versus common), often suitable to describe relative abundance differences between species. Moreover, at higher sampling effort, the probability of detecting species with low abundance and occupancy is expected to increase.

As range edges were of interest here, we simulated the tails of the species abundance distributions. While one or more peaks in abundance can be expected across the range of a species (McGill and Collins 2003), the shape and number of peaks in the middle of a species range are irrelevant to the present analysis. We therefore simulated an abundance distribution with a single peak and long tails in which abundance was 1–2 orders of magnitude lower than the peaks (McGill and Collins 2003). We first generating a standard normal probability density function (though different distributions were tested and produced similar patterns) centred at 10 degrees latitude and tails that extended 7.5 degrees above and below this mean. To simulate species with differing abundance levels, we then inflated the height of this distribution by values between 1 and 500, depending on the scenarios described in Table 1. To simulate a shift in range, we displaced the entire distribution by 5 degrees of latitude (Fig. 1).

Estimates of species range edges are typically based on the last observed sightings, which depend both on species detectability and sampling effort. To relate the detectability of a species within a latitudinal band to its abundance (or prevalence) at that latitude, we assumed that there were 100 available habitat spaces at each band of latitude. We then took the abundance score from the normal distribution described above and divided it by 100 to get a measure of habitat occupancy. Where the number within a degree of latitude exceeded the 100 available habitat spaces, we set the occupancy to one (Fig 1). We simulated observations of the occurrence of species within their range by modelling survey data as a series of Bernoulli trials along the latitudinal gradient, with the probability of success equal to the occupancy score. We therefore only considered the influence of abundance on species' detected presence, ignoring the role of crypsis or habitat patchiness and our simulations are intended to characterize the variability in range edge estimates that can be attributed to abundance-related sampling error alone. However, any other process that would lead to a tailed distribution in the probability of observing a species as described above would result in similar patterns.

In each simulation, characterization of a species' distribution was then achieved by randomly sampling a number of positions along the latitudinal gradient (depending on total sampling effort, summarized in Table 1). The minimum range edge for each simulation was recorded as the most extreme latitude in which the species was observed and the observed range shift was recorded as the difference between the minimum latitudes detected in the 'historical' and 'recent' distributions (Fig. 1b).

Simulation scenarios

Based on the assumption that abundance and sampling effort influence species detectability, we test how variation in these two factors, in combination with sampling stochasticity, affect range shift estimates. We first varied mean abundance, while keeping sampling effort constant, and shifted the species distribution by 5° of latitude (scenario 1). Next, we kept abundance constant, and varied sampling effort across the species range, again shifting the distribution by 5 degrees (scenario 2). Finally, we simulated observations for a variety of species abundances with no underlying shift (scenario 3); this scenario describes the level of observed change that may be expected due simply to stochasticity in sampling. For all three scenarios, we simulated 1000 datasets at each level of abundance or sampling effort and recorded the observed range change (simulation parameters are summarized in Table 1).

Real data for comparison to simulated community scenarios

We analysed two datasets to determine if the kinds of patterns identified using scenarios 1, 2 and 3 are present at the community level in the marine environment. We tested for a relationship between the two

factors, sampling effort and species' abundances, with the magnitude and direction of measured range shift estimates in two published datasets using linear models.

The first dataset comprised 45 seaweed species from the southwestern Australian coastline (Wernberg *et al.* 2011). Latitudinal displacement was determined from ~1950 (historical) to ~2000 (recent) on the basis of opportunistic collections in herbaria where sampling effort was episodic and varied among species (Wernberg *et al.* 2011). As this dataset did not contain information on the abundance of the species included, we asked experts to score each species on a qualitative scale of 1 to 5 with respect to their expected relative abundance across the region (Table S1: pooled into low (1 to 3) and high (>3) categories for presentation). Based on simulations, we expected that if abundance and sample size are important drivers of observed range changes, we should see a positive relationship between these factors and observed range changes. We tested for influences of each of these factors on the extent of macroalgal range shifts with a generalized linear model.

The second data set was limited to Tasmania, comprised of range shift responses in shallow reef fishes. In this case sampling effort was even in 1994 and 2006, spanned from -43.58°S to -39.21°S (n = 108 sites), and followed a rigorous underwater visual census protocol in which local abundances were recorded for each species (Stuart-Smith *et al.* 2010). The relationship between the measured difference in the lowest latitude at which each species was recorded in the two sampling intervals and their mean abundance was determined for 66 fish species.

Confidence in range edges using prevalence data and a time-to-extinction model

Rivadeneira *et al.* (2009) used simulated data to evaluate time-to-extinction models under varying sampling scenarios. From these models we selected "RandS" because it provides conservative estimates and does not assume even distribution of sampling effort (Roberts and Solow 2003). Briefly, the RandS model uses an optimal linear endpoint estimate based on the spacing of the k last sightings on record. Thus, in the case of range edge, S_{ci} is upper bound of the confidence interval of the range edge, S_n is the location of the sighting (1994 range edge position for southwards shifts, 2006 range edge position for northwards shifts), H is the total number of sightings, and α is alpha (0.05).

$$S_{ci} = S_n + \frac{S_n - S_{n-H+1}}{c(\alpha) - 1}$$

$$c(\alpha) = \left[\frac{-\log\left(\frac{\alpha}{2}\right)}{H} \right]^{-v}$$

$$v = \frac{1}{H-1} \sum_{i=1}^{H-2} \log \frac{S_n - S_{n-H+1}}{S_n - S_{i+1}}$$

This approach for estimating confidence in range edges is thus independent of distribution shape and considers only the shape of the tail of the range distribution, which generally matches a Weibull distribution (Roberts and Solow, 2003). Solow (2005) describes the temporal model in full, now available as an R package (Clements 2012).

Our distance-to-edge model replaces time in the RandS model with latitude to compare estimates of the range edge for different species, based on their pattern of occupancy within the study area. Occupancy was estimated with prevalence data (# sites in which a species was observed within a latitudinal band), quantified for 28 species that occurred in both sampling years and were present in at least three of the 108

sites sampled in each year. To satisfy the assumption of discrete sampling effort, we binned the occupancy data by 0.1° of latitude. The reef fish dataset offers the unique benefit of having a known geographical range limit for shallow marine species at the southern end of Tasmania (the continental margin). Whether the range edge confidence estimate from our distance-to-edge model overlapped the southern edge of Tasmania, and the precision of this estimate, could therefore be visually assessed.

Results

Range shifts and sampling design

Due to the stochastic nature of the sampling, under scenarios 1 and 2 which simulated a range shift of 5° of latitude, range shifts remained undetected in some cases. As expected, our simulations demonstrated that the proportion of observed range edge shifts increased with abundance (sigmoidal relationship, Fig. 2a) and that variability in estimates was reduced with higher sampling effort (Fig. 2c). Under scenario 3, where the range edge of species did not change, we further illustrate that range shifts in less abundant species are identified, even when the simulations did not include a latitudinal displacement in the location of the range edge. This is because range shift estimates in rarer species in the simulated community were markedly more variable than for abundant species (Fig. 3a).

These same patterns were observed in field data, where other sources of variability could conceivably swamp any variability in the detection of range edges due to abundance. First, in macroalgae, range shifts were less evident in species with relatively low abundance throughout the region (Fig. 2b). However, the measured change in the equatorward range edge of species was not significantly related to abundance when five qualitative scores were included in a generalized linear model as a predictor (Table 2). Second, less variable estimates of range change were observed for macroalgal species with more sampling (i.e. museum records, Fig. 2d, Table 2). Third, in the dataset of reef fish abundance, variability in the magnitude and direction of range change spanned from 4 to -4° latitude for species which averaged less than 2-3 individuals per site across the region, while estimates for more abundant species converge on zero. This finding supports the hypothesis that assessments for less abundant species are inaccurate and that range shifts in both directions will be observed due to sampling variability alone (Fig. 3b).

Distance-to-edge model of confidence in range edges for Tasmania reef fish data

Confidence intervals assessed for range edge estimates in the reef fish data from 2006 and 1994 substantially overlapped for most fishes (Fig. 4a). There was thus little confidence in shifts in southern range limits of fishes during the study period, with the exception of three species. One species was observed shifting southwards (*Enoplosus armatus*) and the southern range edge shifted northwards for two species (*Atypichthys strigatus* and *Upeneichthys vlamingii*). The confidence intervals for the remaining 25 species overlapped in the two time intervals. For species with low prevalence (i.e., presence at 3 to 5 sites in each of the two years), the location of the modelled range edge fell further from the location of the last observed presence and the confidence limits were wider (Fig. 4b). With increasing prevalence (occurrence at >10 sites in 1996 and 2004) the range edge estimate fell closer to the last observed location with reasonable confidence, so that we could confirm that a northward range shift occurred in *Upeneichthys vlamingii* (Fig. 4c). Moreover, the model performed well for abundant species that occurred throughout Tasmania in

predicting the range edge at a location close to the true geographic range limit with high confidence (Fig. 4d).

Discussion

While the issue of variability in detection among species is well-known in ecological studies (e.g., Tanadini *et al.* 2011), we here show how species detectability has the potential to confound our understanding of range shifts of marine species. Failure to account for non-detection leads to inaccurate and inconsistent conclusions of range shifts among species. We demonstrate the influence of abundance-related occupancy and varying sampling on accuracy in estimated range shifts using simple simulations. We further suggest that exchanging space for time in a time-to-extinction model to create a distance-to-edge model can estimate confidence in range edge locations when species distributional limits are of interest. Tools such as simulations and modeling confidence intervals will allow more realistic descriptions of range changes for individual species and entire communities, leading to better understanding of the environmental and ecological factors underpinning range-shift dynamics.

Simulations of range change provide a null expectation for species with different abundance for comparison to field data and subsequently assist in interpretation of patterns. As expected, the likelihood of observing and correctly estimating a range change is greater for more abundant species and with increasing sampling frequency in time and space (Shoo *et al.* 2006; Tanadini and Schmidt 2011).

While these sampling issues associated with detectability (not just related to abundance) are a well-known problem, the large spatial and temporal scale required to obtain accurate range edge locations presents particular challenges in marine systems (Monk 2012). Simulations indicate that even under a best-case scenario of high-resolution sampling, estimates of range-edge boundaries are highly variable for less abundant species, patterns that are also observed in regional-scale field data sets. This issue is likely to be more acute for marine than terrestrial systems, due to the sampling effort limitations imposed by logistics of collecting data underwater. Therefore, while solutions such as subsampling data to equalize sampling effort between time periods have been advised on the basis of terrestrial studies (Hill *et al.* 2002; Hassall and Thompson 2010), such solutions may be counter-productive for marine studies, where sample sizes can be much lower to start with and maximizing information is a key consideration. Moreover, subsampling techniques only exacerbate the fact that rarer species are going undetected or, if measured, are more likely to have inaccurate estimates of change in comparison to more abundant species. These results suggest that the available baseline data in marine systems is insufficient to estimate range movements of rare and inconspicuous species due to quality (e.g., museum collections: Przeslawski *et al.* 2012) or limited sampling resolution (e.g., spatial positioning of samples may not capture range changes), especially when sampling is focussed at the expected range edge.

The signatures of abundance-related occupancy and sampling effort (both of which influence species detectability) are therefore present in published data sets of marine range shifts, illustrating the importance of confidence estimates when quantifying range shifts. If we are to improve our ability to model and predict both current and future range extensions and contractions, variable detectability of species needs to be considered in analyses and monitoring efforts (Monk 2013). Unfortunately, approaches such as estimation of range statistics based on the gamma frequency distribution or the use of distance thresholds to provide a minimum cut-off for defining a level of change that constitutes a range shift (Jones *et al.* 2010) do not incorporate species detectability.

Here we show that simulations and a distance-to-edge model can be applied to identify real range shifts, approaches that can be used across both marine and terrestrial ecosystems. Our application to museum collection (macroalgae) and quantitative survey data (fishes) highlights that species with low detectability are unlikely to be observed in regional analyses of range change. For those species that are observed, range shifts estimates will be inaccurate, and issue that is of particular concern at low sample sizes.

To provide a solution for identified range shift data that is more likely to represent true distribution change, we assessed the performance of a time-to-extinction model (distinguished here as the distance-to-edge model) for species found near the southern edge of Tasmania. Doing so allowed us to assess the performance of the model where the true range edge was known. In species with higher occupancy (measured here as prevalence), the model estimated the range edge location with high precision. However, at lower occupancy, precision in the range edge position was also low, as expected. Thus we were able to assign a threshold – presence at less than 5 sites in each of the two years – for which confidence was considered too low. Moreover, the model indicated several range shifts for which the confidence intervals for the two sampled time periods did not overlap, and thus indicate a likely range change with >95% confidence. Overall, the range edge estimates between the two time periods were generally similar for most species, further supporting the original interpretation of stability in the range edges of reef fish communities for a 13 year period where warming was minimal (Stuart-Smith *et al.* 2010). We therefore suggest that further evaluation of different time-to-extinction models with data that have different sampling resolutions and spatial distribution patterns will be important. Including habitat variables (such as by using species distribution modelling approaches) in conjunction with range edge estimates based on spatial occupancy patterns has the potential to build more accurate estimates of where species are located. In addition, trait-based time-to-detection models, such as described by Garrard *et al.* (2012), may be applicable to a spatial setting.

Although confidence in the accuracy of range edge estimates is a step forward, the most fundamental issue is that baseline data are either lacking or were not collected at a spatial and temporal resolution designed for rarer species (Maxwell and Simon 2005). Statistical tools may help to account for the patchy nature of present and historical data and inherent variation in species detectability, such as hidden-Markov or Bayesian hierarchical models (Wintle *et al.* 2012). However, monitoring programs designed to detect future range shifts should be implemented now with the goal of detecting changes in species distributions for species with different detectability, in combination with robust quantitative approaches tailored for climate change ecology (Brown *et al.* 2011). Well-designed surveys will provide baseline data for comparison to the present, facilitating systematic assessments so that range change in rarer species are not going unnoticed and more accurate quantification of range edges for species with varying detectability.

ACKNOWLEDGEMENTS

K. Dixon and G. Kendrick kindly estimated the abundance of southwest Australia algal species. AEB was supported by the Australian National Network in Marine Science (a collaborative funding initiative between James Cook University, The University of Tasmania, and The University of Western Australia) and an Australian Government Fisheries Research and Development Corporation and Department of Climate Change and Energy Efficiency grant.

REFERENCES

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, 14, 677-689.

- Blanchard JL, Maxwell DL, Jennings S (2008) Power of monitoring surveys to detect abundance trends in depleted fish populations: the effects of density-dependent habitat use, patchiness, and climate change. *ICES Journal of Marine Science*, 65, 111–120.
- Booth DJ, Bond N, Macreadie P (2010) Detecting range shifts among Australian fishes in response to climate change. *Marine and Freshwater Research*, 62, 1027.
- Brown CJ, Schoeman DS, Sydeman WJ, Brander K, Buckley LB, Burrows MT, Duarte CM, Moore PJ, Pandolfi, JM, Poloczanska ES, Venables WN, Richardson AJ (2011) Quantitative approaches in climate change ecology. *Global Change Biology*, 17, 3697–3713.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, 333, 1024–1026.
- Clements C (2012) sExtinct: Calculates the historic date of extinction give a series of sighting events. R package version 1.0.0 (available at <http://CRAN.R-project.org/package=sExtinct>).
- Dorazio R, Royle JA (2005) Estimating size and composition of biological communities by modelling the occurrence of species. *Journal of the American Statistical Association*, 100, 389–398.
- Dorazio RM, Royle JA, Söderström B, Gilmskär A (2006) Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology*, 87, 842–854.
- Dulvy NK, Rogers SI, Jennings S, Stelzenmuller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, 45, 1029–1039.
- Edgar GJ, Stuart-Smith RD (2009) Ecological effects of marine protected areas on rocky reef communities: a continental-scale analysis. *Marine Ecology Progress Series*, 388, 51–62.
- Edgar GJ (1997) *Australian Marine Life: the Plants and Animals of Temperate Waters*. Reed New Holland, Sydney.
- Garrard GE, McCarthy MA, Williams NSG, Bekessy SA, Wintle BA (2012) A general model of detectability using species traits. *Methods in Ecology and Evolution*
- Hassall C, Thompson DJ (2010) Accounting for recorder effort in the detection of range shifts from historical data. *Methods in Ecology and Evolution*, 1, 343–350.
- Johnson CR, Banks SC, Barrett NS, *et al.* (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, 400, 17–32.
- Jones SJ, Lima FP, Wethey DS (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography*, 37, 2243–2259.
- Kery M, Dorazio RM, Soldaat L, van Strien A, Zuiderwijk A, Royle AJ (2009) Trend estimation in populations with imperfect detection. *Journal of Applied Ecology* 2009, 46, 1163–1172.
- Isaac NJB, Cruickshanks KL, Weddle AM *et al.* (2011) Distance sampling and the challenge of monitoring butterfly populations. *Methods in Ecology and Evolution*, 2, 585–594.
- Leigh E (1981) The average lifetime of a population in a varying environment. *Journal of Theoretical Biology*, 90, 1–239.
- Maxwell D, Simon J (2005). Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *Journal of Applied Ecology*, 42, 25–37.

- McCarthy MA, Moore JL, Morris WK, Parris KM, Garrard GE, Vesk PA, Rumpff L, Giljohann KM, Camac JS, Bau SS, Friend T, Harrison B, Yue B (2013). The influence of abundance on detectability. *Oikos*, 122, 717-726.
- McGill B, Collins C (2003) A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research*, 5, 469–492.
- Monk J (2013) How long should we ignore imperfect detection of species in the marine environment when modelling their distribution? *Fish Fisher*. doi: 10.1111/faf.12039
- Oliver T, Hill JK, Thomas CD, Brereton T, Roy DB (2009) Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters*, 12, 1091–1102.
- Page J, Schurr FM (2012) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography*, 21, 293–304.
- Parmesan C, Ryrholm N, Stefanescu C, *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579-583.
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37-42.
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science*, 308, 1912-1915.
- Poloczanska, E. S. *et al.* (2013) Global imprint of climate change on marine life. *Nature Clim. Change* 3, 919-925.
- Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) Marine Taxa Track Local Climate Velocities. *Science*, 341, 1239-1242.
- Przeslawski R., Falkner I., Ashcroft MB, Hutchings P (2012). Using rigorous selection criteria to investigate marine range shifts. *Estuarine, Coastal and Shelf Science*, 113, 205-212.
- R Development Core Team (2011). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Australia.
- Rivadeneira MM, Hunt K, Roy K (2009) The use of sighting records to infer species extinctions: an evaluation of different methods. *Ecology*, 90, 1291-300.
- Roberts DL, Solow AR (2003) Flightless birds: When did the dodo become extinct? *Nature*, 426, 245-245.
- Sagarin RD, Gaines SD (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters*, 5, 137-147.
- Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. *Annual Reviews in Ecology, Evolution and Systematics*, 40, 415-436.
- Shoo LP, Williams SE, Hero JM (2006) Detecting climate change induced range shifts: Where and how should we be looking? *Austral Ecology*, 31, 22-29.
- Solow, A. R. 2005. Inferring extinction from a sighting record. *Mathematical Biosciences* 195, 47-55.
- Stauffer HB, Ralph CJ, Miller SL (2002) Incorporating detection uncertainty into presence-absence surveys for marbled murrelet. In: *Prediction species occurrences: issues of scale and accuracy* (eds Scott JM, Heglund PJ, Morrison ML, Haufler JB, Rafael MG, Wall WA, Samson FB) pp. 357-365. Island Press, Washington, DC, USA.
- Stuart-Smith RD, Barrett NS, Stevenson DG, Edgar GJ (2010) Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. *Global Change Biology*, 16, 122-134.

- Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, 2, 686–690.
- Tanadini LG, Schmidt BR (2011) Population Size Influences Amphibian Detection Probability: Implications for Biodiversity Monitoring Programs. *Plos One*, 6, e28244.
- Taylor BL, Gerrodette T (1993) The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conservation Biology*, 7, 489-500.
- Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends in Ecology and Evolution*, 24, 625-633.

Tables

Table 1. Parameters tested in simulations of range shifts for species in a theoretical community. Sampling effort is the number of randomly allocated sites included from an array of 200 evenly spaced sites surrounding the true range edge. Abundance is the multiplier used to generate distributions of prevalence throughout the range.

Scenario	Sampling effort	Abundance	Shift (degrees latitude)
1. shifts detected: Fig. 2a	40	1 to 500	-5
2. range change: Fig. 2b	8 to 200	100	-5
3. range change: Fib. 3	40	1 to 500	0

Table 2. Model results for relationships between measured change in the latitudinal location of the range edge in macroalgae versus abundance and sample size. Negative values indicate a declining slope. In addition to the fixed effects of interest (abundance and sample size), we further included a covariate for change in sampling effort through time (as reported in Wernberg et al. 2011) which is known to influence range edge detection (Shoo et al. 2006).

	coefficient	standard error	t-value	P-value
intercept	-0.51	0.90	-0.57	0.57
abundance category	-0.40	0.26	-1.51	0.11
sample size	0.065	0.024	2.70	0.010
log(effort ratio)	-1.61	0.69	-2.35	0.024

Figures

Figure 1. Schematic diagram of a theoretical relationship between occupancy and latitude at two time periods (historical = hatched, present = filled) for a species under three abundance levels (high: purple, medium: yellow, low: green). A 'peak-and-tail' pattern is expected if range limits are set by environmental conditions (although this may include multiple peaks). More abundant species have higher occupancy because they are more likely to be both observed and present during sampling. The poleward (high latitude) and equatorward (low latitude) range boundaries are predicted to shift towards the poles (black arrow) with increasing climate warming. This leads to an extension at the poleward boundary and contraction at the equatorward boundary.

Figure 2. Relationship between abundance and sampling effort versus proportion of range shifts detected (a-b) and shift magnitude (latitudinal change; c-d) from simulations of a theoretical community and field data for macroalgae in southwest Australia (blue) (Wernberg *et al.* 2011). For all panels, range shift estimates are based on differences in minimum latitude a species was observed, or the equatorward range boundary. Details of simulations are reported in Table 1 (as scenarios 1 and 2 for plots a and c, respectively).

Figure 3. Changes in latitudinal range limit versus abundance in a simulated theoretical community (a, orange) and measured from field data on reef fishes (b, blue). The simulated range change was set to 0 degrees in latitude (scenario 3, Table 1); thus range shifts in (a) suggested in rarer species are artefacts of low detectability (due to abundance-related occupancy). Abundance data on 66 reef fish species were collected from the same 108 sites in 1994 and 2006 (Stuart-Smith *et al.* 2010).

Figure 4. (a) Range edges (symbols) and 95% confidence intervals (bars) predicted using a distance-to-edge model for 28 fish species in 1994 and 2006. Species are ranked by increasing occupancy. While range shifts were detected (filled symbols), the majority of the 2006 range edge estimates fell clearly within the 95% confidence interval (CI) of the 1994 estimate. Letters indicate example species highlighted in panels b-d. The dotted line represents the latitude of the southern edge of Tasmania (which is the southern limit of shallow marine habitat on the continent and thus limits the range edges of species and allows for comparison to the model estimates). (b-d) Latitude (sites were binned into 0.1 degrees latitude) versus prevalence (# sites occupied per latitudinal band) for three species with the true range edge estimates and 95% CIs for 1994 and 2006 (offset to the right of each panel).

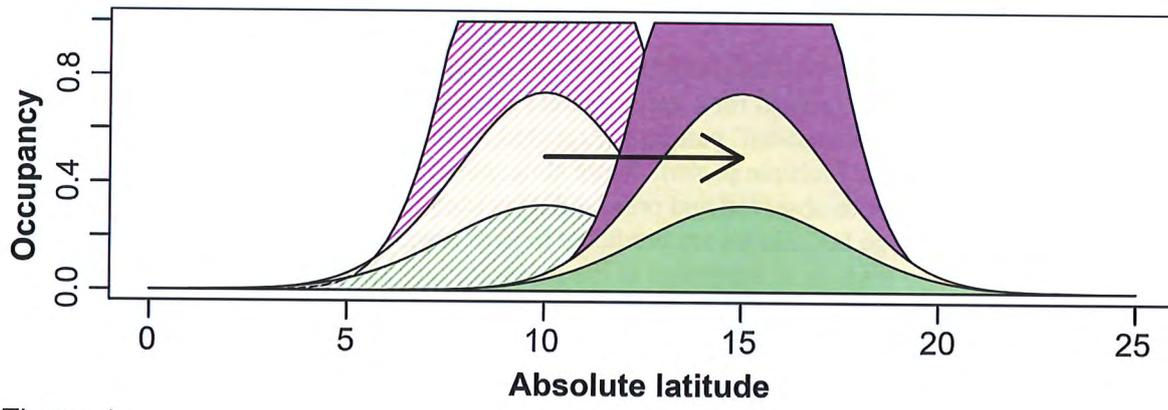


Figure 1

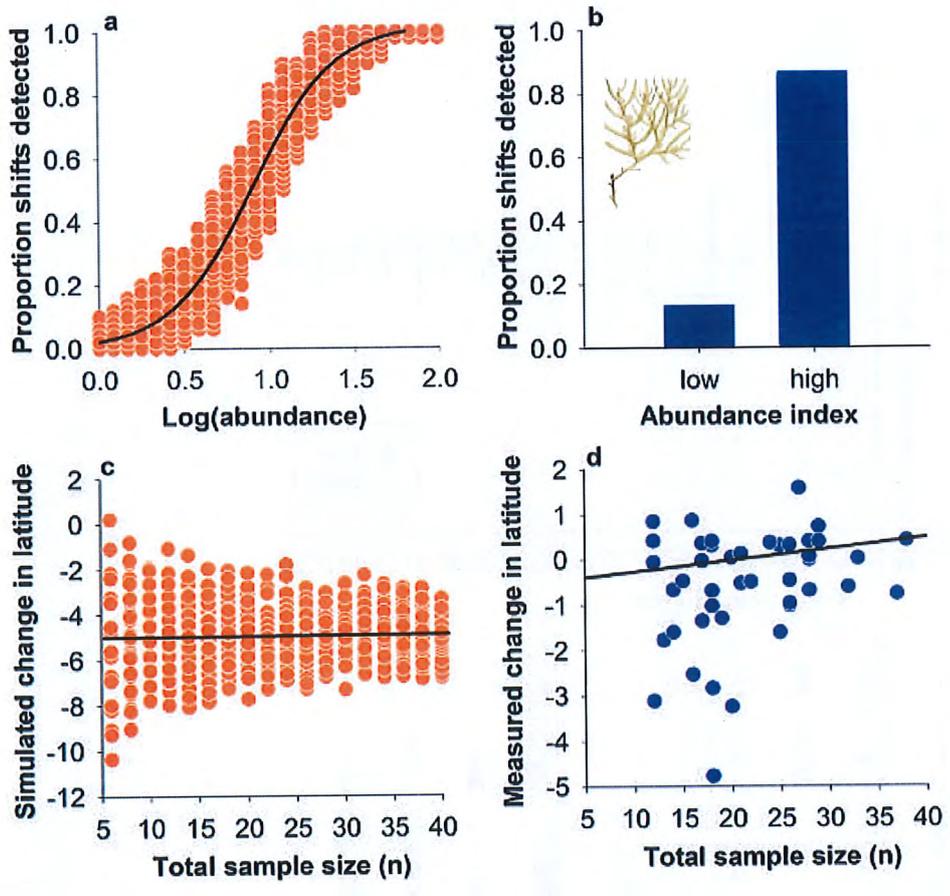


Figure 2

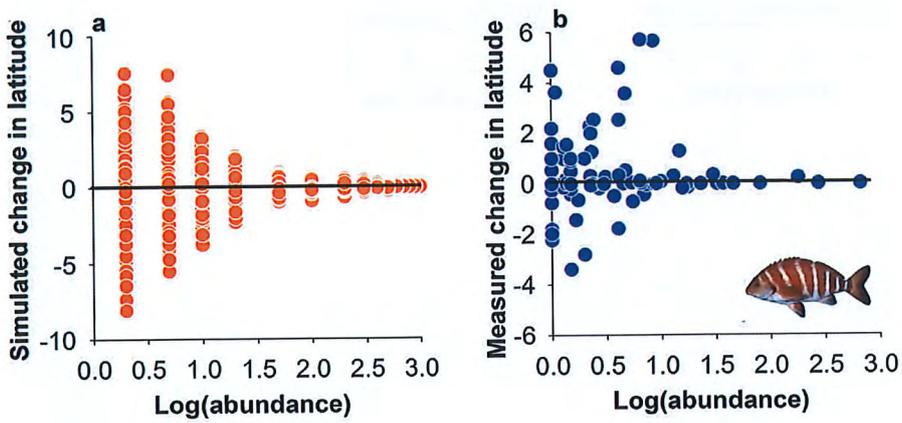


Figure 3

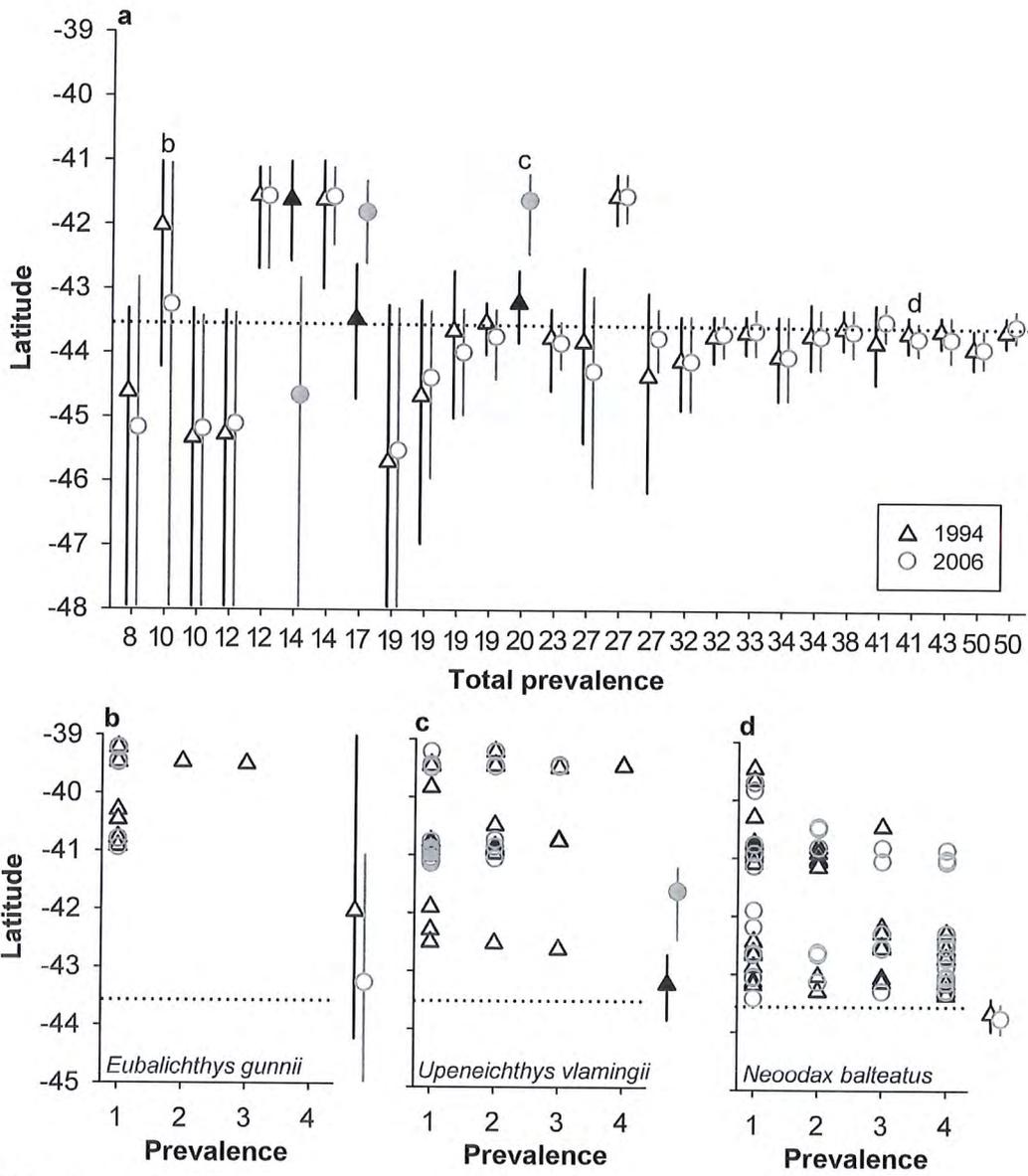


Figure 4

Supplementary Information

Table S1. Qualitative abundance of the macroalgal species estimated by experts^{1,2,3} on a qualitative scale of 1 to 5 where 1 = rare, 2 = infrequent, 3 = common but low abundance, 4 = moderately abundant, 5 = highly abundant (the three experts scored algae within 2 units in all instances). Effort ratio is the number of museum records in 1950 divided by the number of samples in 1990. Effort ratio, total sample size and change in latitude are reported in Wernberg *et al.* (2011): see main text methods.

Species	Qualitative Abundance index	Effort ratio	Total sample size	Change in latitude
<i>Bornetia binderiana</i>	3	0.9	21	-0.5
<i>Callophycus oppositifolius</i>	3	3.6	32	-0.6
<i>Carpopeltis elata</i>	3.7	2.3	20	-3.2
<i>Carpopeltis phyllophora</i>	3	0.3	14	-0.7
<i>Caulerpa flexilis</i>	4	3.2	25	-1.6
<i>Caulerpa obscura</i>	4	1.2	26	0.3
<i>Caulerpa sedoides</i>	3	2.2	16	-2.5
<i>Caulerpa simpliciuscula</i>	3.7	1.8	25	0.3
<i>Caulocystis uvifera</i>	2.5	1.9	29	0.7
<i>Ceramium puberulum</i>	2.5	1.4	12	0.9
<i>Cladurus elatus</i>	3	0.5	21	0.1
<i>Clavicolonium ovatum</i>	1.7	2.5	28	0
<i>Craspedocarpus blepharicarpus</i>	3.5	0.6	18	-1
<i>Cystophora brownii</i>	3.3	1.7	16	-4.8
<i>Dasyclonium incisum</i>	2.3	2.1	28	-0.7
<i>Dicranema revolutum</i>	2	0.5	12	0.4
<i>Dictyomenia sonderi</i>	3.7	0.9	28	0.4
<i>Dictyomenia tridens</i>	2.5	1.1	15	-0.5
<i>Dictyopteris muelleri</i>	3.5	1.3	28	0.1
<i>Dictyota fastigiata</i>	2	0.7	12	-0.1
<i>Erythroclonium muelleri</i>	3.5	1.2	13	-1.8
<i>Euptilota articulata</i>	3	1.4	26	-1
<i>Gigartina disticha</i>	1.7	2.3	26	-1
<i>Glossophora nigricans</i>	2.7	1.3	16	0.9
<i>Griffithsia teges</i>	3	0.5	12	-3.1
<i>Heterodoxia denticulata</i>	3	2.1	37	0.3
<i>Hypnea ramentacea</i>	4.3	6.6	38	0.4
<i>Kuetzingia canaliculata</i>	3.5	1.6	26	-0.5
<i>Laurencia elata</i>	4	0.9	19	-1.3
<i>Metagoniolithon chara</i>	3.5	2	18	-0.7
<i>Metagoniolithon stelliferum</i>	4	1	18	0.4

<i>Metamastophora flabellata</i>	4	1.4	29	0.4
<i>Myriodesma quercifolium</i>	3.7	3.1	33	0
<i>Nizymania conferta</i>	2.7	1.8	17	0.4
<i>Osmundaria prolifera</i>	2.5	3.7	33	0
<i>Pachydictyon paniculatum</i>	2.7	1.3	18	0.3
<i>Platythalia angustifolia</i>	2.3	1.1	17	0
<i>Plocamium preissianum</i>	3.7	1.6	18	-2.8
<i>Pollexfenia lobata</i>	3	3.4	22	-0.5
<i>Pterocladia lucida</i>	3.5	1.9	49	-1.2
<i>Scaberia agardhii</i>	3.5	3	24	0.4
<i>Scytothalia doryocarpa</i>	4.3	1.8	14	-1.6
<i>Thuretia quercifolia</i>	3	1.8	17	-1.4
<i>Vidalia spiralis</i>	3	1.9	20	0.1
<i>Zonaria turneriana</i>	3.5	0.3	27	1.6

¹ Prof. Gary Kendrick, The University of Western Australia, Australia

² Dr. Kyatt Dixon, University of New Brunswick, Canada

³ Assoc. Prof. Thomas Wernberg, The University of Western Australia, Australia

Appendix v. Report from initial project workshop. August 2011.

Workshop August 29-30th at IMAS, Taroona Campus, Hobart:

Adaptive management of temperate reefs to minimise effects of climate change: Developing new effective approaches for ecological monitoring and predictive modelling

30th August – Workshop notes /minutes

Present:

Neville Barrett – IMAS; Marine biodiversity research and monitoring

Graham Edgar – IMAS; Marine biodiversity research and monitoring

Dave Jarvis – DPIPWE, Tas, Marine Resources

Brendan Kelaher – NSW Marine Parks Authority & DPI (Fisheries)

Stephen Howe – Parks Victoria

Penny Wells – DPIPWE, Tas, Resource Management and Conservation

Stuart Frusher – IMAS

Gretta Pecl - IMAS

Amanda Bates – IMAS; Postdoc; climate change/range shifting species

David Feary – representing David Booth; University of Technology (Sydney)

Maria Beger - postdoc on project-

Neil Holbrook – IMAS; Physical Oceanography

Andre Belo Couto– IMAS; Physical Oceanography, postdoc on project

Martin Marzloff – IMAS; PhD candidate; ecological modelling

Alistair Hobday – CSIRO; Climate impacts and marine systems

Nathan Knott – NSW MPA Authority & DPI (Fisheries)

Cath Samson – Tasmanian Parks and Wildlife; marine parks officer

Colin Buxton – IMAS Director; Reef fisheries and ecology

Amelia Fowles – IMAS; PhD candidate human impacts on marine reef habitats

Alastair Morton – DPIPWE; Tas, Marine conservation

Workshop Structure:

Project Overview (Neville Barrett) and discussion

Biophysical modelling overview (Maria Beger) and discussion

Physical variables overview (Andre Belo Couto) and discussion

Related projects (SEAP) overview (Gretta Pecl) and discussion

Morning tea

Related Projects (Neville Barrett and Alistair Hobday) and discussion

Qualitative model development to inform management (Martin Marzloff)

Discussion – Potential management scenarios against possible ecological changes

Lunch

Discussion – Potential management scenarios against possible ecological changes

The workshop began with an initial overview of project and an outline of what the workshop hoped to achieve. Namely to improve awareness of the project within the research and management and stakeholder communities, and to provide opportunity for feedback from these communities on the likely range of practical management responses to climate change that might be possible given a range of climate change scenarios. This introduction was followed by discussion of progress so far by Maria Beger (lead postdoc on the project) with respect to biological data collation and preliminary analysis of patterns, followed by progress in collating oceanography by Ander Belo Couto, an oceanographer working on the project in a six month postdoc position.

Some initial discussion centred on whether all current data should be used for building of predictive models of bio-physical relationships or whether to keep some back for validation. The feeling was to use all available information initially to maximise our ability to detect correlations where they occur.

There was discussion on the need to use the outputs of these predictive models to inform monitoring programs about appropriate species to focus on, the degree of replication necessary to obtain meaningful trends, and the extent that work needs to be repeated temporally to detect patterns.

This was followed by an overview of the SEAP program by Gretta Pecl, including an indication that, in addition to SEAP, there were similar western and northern programs that we should be aware of. SEAP has multiple aspects. One initial output being a biological risk assessment using 35 species with sensitivities to climate change including profiles of factors that could be climate change influenced. Life histories and other aspects that are likely to be affected are included in this. The report has a risk assessment basis, using existing knowledge and known data gaps and provides a relative risk ranking for a large number of species of interest. Following that, the current focus of SEAP is to prepare fisheries for climate change using 4 species in the SE (Lobster, abalone, snapper and blue grenadier) as case studies. The focus of the work is on harvest strategies, not biological processes, following clear FRDC guidance.

Al Hobday outlined a project he is engaged with which is looking at the underlying biophysical implications of climate change. This utilises existing models to determine what variable and derived variables are useful for species distribution modelling and predicting future changes.

Another SEAP project involving Beth Fulton is looking at quantitatively testing fisheries management arrangements under climate change scenarios using Atlantis. In addition, it is developing and testing a national integrated cc adaptation framework.

An ANIMMS springboard project is focussing on the SE and SW Australian hotspots and a synthesis across all global hotspots to develop an understanding the global importance and implications for range shifting species. It has a fisheries focus and utilises the expertise of Amanda Bates in global meta analysis.

Peter Strutton is also looking at annual responses to temperature in terms of tracking data as part of this study.

A lot of synergies and possible overlap were identified between a range of projects in this space, so one outcome of this discussion was to plan a meeting in November to organise collaboration and to minimise stakeholder fatigue, with this meeting being facilitated by Gretta Pecl.

End of overview.

Next stage was to look at a conceptual/qualitative model of temperate reef systems to see if we could use that as a framework for discussions on potential changes to temperate reef systems in NSW, Vic and Tas (appreciating responses may differ significantly between regions), the drivers of these change, and potential adaptive management responses to mitigate against adverse change.

This was facilitated and introduced by Martin Mazelov, who gave an introduction to quantitative models and how they could be used to examine the functioning of temperate kelp communities.

The formal model building/discussion started by examining the simple version of the Vic reefs model that had been developed by DSE (Vic) with the assistance of Sarah Metcalf as a model builder and with input from a broad range of reef ecologists and biologists with experience in Victorian coastal waters.

The initial discussion indicated a number of missing trophic links between groups already recognised in the model, before ranging onto how to most effectively deal with the complexity involved in adding potential climate related changes at multiple levels and with multiple associated stressors. As well as links missing within the groups in the existing structure of the simple model, it was pointed out that important additional components includes the vulnerable offshore larval stages.

Gretta pointed out that a similar complex modelling approach had been undertaken by the Alaskan giant crab fishery where it was tackled by developing approximately 40 different versions of the base model. The discussion then focussed on identifying a number of key stressors and their likely influence on key points in the existing model.

Stressors included

Temperature

Increased *Centrostephanus* numbers, survival and growth

May increase southern lobster growth but decrease recruitment

Likely to increase octopus growth leading to increased lobster mortality

Increased eastern lobster growth and recruitment, particularly in Tas

Decreased abundance of cool water finfish species such as trumpeter (bastard, stripey and real)

Decreased plankton productivity, with consequences for filter feeders on reefs and larval survival

Extreme events-more expected

Hot days, rainfall, wind

Influencing ECL, harvest rates, mixing and sediment re-suspension

Disease outbreaks related to harmful algal blooms and other factors, including thermal stress

Changes in currents, particularly the EAC, Leeuwin currents and interaction with sub-Antarctic water. Potential for productivity associated with this to move south of Tas. Can also influence the extent of upwelling and associated Temperature and nutrient flux.

Rainfall patterns influencing salinity, pesticides and other land derived pollutants such as sewage, nutrient fluxes and sediments from rivers and the coastal zone.

pH. Potential for pH changes to alter system function, initially at least via changes in algal assemblages and productivity where species change on favour of non-calcified phytoplankton.

Human populations. Changing populations in response to warming conditions. Potential for large population pressures on cooler temperate coasts as they become the “new” northern NSW coast with respect to temperatures.

Sea level rise. Has significant implications for coastal fringing reefs in particular. Some reef habitat will be lost where geomorphology is not similar above the intertidal. Particular risk to rare seastars in immediate subtidal environments in sheltered waters where no appropriate habitat will be available with rises over 1 m.

The meeting broke for lunch after this initial discussion and it was decided that the aim of trying to integrate all these possibilities into one model for each of three regions (southern NSW, Eastern Vic and NE Tas) to underpin discussions on potential management responses to particular scenarios was overly optimistic. Discussions after lunch therefore focussed on examining a number of the more likely major drivers of change and scenarios related to adaptive management.

Temperature is seen as a major CC driver of change.

One significant issue for NE Tasmania and Eastern Vic in the near term is increasing *Centrostephanus* abundance leading to loss of ecosystem function. Possible responses include facilitation of increases on natural predators including blue grouper and lobsters. For Tasmania at least, the introduction of blue grouper would add a known urchin predator to facilitate system stability but some other interactions remain unknown. Rebuilding of lobster populations through maximum size limits and area quota caps is probably the most viable management response and is being actively looked at via management and related projects. It could be actively enhanced by reseeded barrens with large lobsters as per the current Tasmanian trial. Populations could be maintained at the margins of barrens to keep numbers below densities where barrens form, either by divers harvesting urchins or destroying them. The patch dynamics of NSW barrens can inform this management, utilising long-term NSW datasets to understand the stability/patchiness of these barrens. One further potential control of *Centrostephanus* numbers could be disease if an appropriate vector could be found.

MPAs could be utilised as effective control locations for undertaking research necessary for untangling interactions between climate change and fishing, and potentially as precautionary approaches to protect areas against barren formation and associated loss of diversity and system function if other management approaches proved difficult to implement.

Giant Kelp loss in response to increasing temperature and associated declining nutrients was also discussed. Here, a range of possibilities were considered, including translocations to future refugia habitats, spatial management to protect refugia habitats, selective breeding of adapted strains, minimising physical damage to beds, and utilising the nutrient enhancement benefits of sewage outfalls when considering refugia habitats.

Rare/endemic species included discussion on how to identify those most at risk (establish a risk analysis) to prioritise species that are at significant risk and might be saved through mechanisms such as translocations, new habitat creation (where old habitats are not present, such as sea level rise for intertidal species), maintenance in aquarium systems (arcs), and spatial management to protect against, understand and minimise synergistic threats, and manage existing threats.

Key finfish and crustaceans with vulnerable life history stages (such as extended larval duration found in lobsters, morwong, stripey and bastard trumpeter) may be particularly susceptible to CC. Spatial management may assist with protection.

Maintaining ecosystem function and biodiversity.

The discussion explored possibilities such as providing artificial reefs in areas where corridors for biodiversity/migration of species may provide the necessary connectivity for species to move in response to warming conditions. Perhaps across biogeographical barriers such as Ninety Mile beach.

At a broader focus, MPAs will provide the baseline protection and reference against the effectiveness of alternative and more novel approaches. However, we need both MPAs and off-reserve management to address CC, so we are not left with a few oases in an ecological desert. Maintaining system function is important and MPAs are needed to inform management options.

While spatial management similar to MPAs may be very important to managing CC impacts on biodiversity, the term "MPA" builds up huge divisiveness in the community. We need to move away from this terminology towards a system of management with "reference sites for cc management" as protected areas.

The discussion examined to what extent management responses can managers achieve easily and which ones would need changes to legislation? From management experience present it was felt that there were a broad range of options available under current legislation and that the important step was the complete an appropriate risk management analyses etc. The current constraints are generally resource/time issues. For example, in Tasmania, with 680 threatened species to manage currently, we cannot actively manage them all, much less in a CC framework in addition to current threats. The reality is that it is a triage process at best, with actions proportional to the risk assessment undertaken.

Overall, the workshop was highly successful in introducing the project to fisheries and conservation management in Tas, Victoria and NSW, and raising the awareness of the various research programs underway within this region that inform this space and have clear synergies. This awareness, and the clear need to collaborate wherever possible, led to the scoping of a more focussed workshop to follow up these opportunities in November, sponsored by SEAP.