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Climate-change induced tropicalisation of marine communities in Western Australia

William W. L. Cheung[A,F], *Jessica J. Meeuwig*[B,C], *Ming Feng*[D],
Euan Harvey[B,E], *Vicky W. Y. Lam*[A], *Tim Langlois*[B,E], *Dirk Slawinski*[C],
Chaojiao Sun[D] *and Daniel Pauly*[A]

[A]Fisheries Centre, AERL, 2202 Main Mall, The University of British Columbia, BC, Canada, V6T 1Z4.
[B]Ocean Institute, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[C]Centre for Marine Futures, Oceans Institute and School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[D]CSIRO Marine and Atmospheric Research, Centre for Environment and Life Sciences, Underwood Avenue, Floreat, WA 6014, Australia.
[E]School of Plant Science, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia.
[F]Corresponding author. Email: w.cheung@fisheries.ubc.ca

Abstract. A major observed and predicted impact of climate change on marine species is the poleward shift in their distributions and the resulting changes in community structure. Here, we used a Dynamic Bioclimate Envelope Model to project range shift of exploited marine fishes and invertebrates in Western Australia. We combined published data and expert knowledge to predict current species distributions for 30 tropical, sub-tropical and temperate species that occur along the coast of Western Australia. Using outputs from both a Regional Oceanographic Model and a Global Circulation Model, we simulated change in the distribution of each species. Our study shows that under the SRES (Special Report for Emission Scenarios) A1B scenario, the median rate of distribution shift is around 19 km decade^{-1} towards higher latitudes and 9 m deeper decade^{-1} by 2055 relative to 2005. As a result, species gains and losses are expected along the south coast and north coast of Western Australia, respectively. Also, the coast of Western Australia is expected to experience a 'tropicalisation' of the marine community in the future, with increasing dominance of warmer-water species. Such changes in species assemblages may have large ecological and socio-economic implications through shifts in fishing grounds and unexpected trophic effects.

Additional keywords: distribution shift, dynamic bioclimate envelope model, marine climate change, Western Australia.

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Introduction

Anthropogenic climate change is modifying oceanographic conditions more rapidly than ever before. With substantial increase in the heat content of the ocean, the world's oceans have warmed substantially on average since 1955, with regional variations (Belkin 2009); this increase is likely to be more rapid in the future (IPCC 2007). Other major oceanographic effects of increased anthropogenic CO_2 emissions include changes in salinity, reduction in sea-ice extent, shifts in ocean currents (IPCC 2007), acidification (Doney *et al.* 2009) and expansion of oxygen minimum zones (Stramma *et al.* 2008). In Australia, average surface temperature has increased by more than 0.7°C since 1910, which is consistent with the global trend (Collins 2000). Recent evidence suggests that warming is occurring faster than the global average along the west coast of Australia (Pearce and Feng 2007), with the lower west coast of Australia being the area with the greatest increase in sea surface temperature (SST) in the Indian Ocean (0.02°C year^{-1}) over the last 50 years (Pearce and Feng 2007), and a higher rate of increase in autumn–winter temperatures (Caputi *et al.* 2009).

The above types of changes in oceanographic conditions have caused considerable modifications to the biology and ecology of marine species (Perry *et al.* 2005; Richardson 2008; Cheung *et al.* 2009). Shifts in distribution of marine populations are the most commonly reported changes in relation to shifting oceanographic conditions (Perry *et al.* 2005; Dulvy *et al.* 2008). For instance, nearly two-thirds of exploited marine fishes in the North Sea shifted in mean latitude or depth or both over 25 years as sea temperature increased (Perry *et al.* 2005; Dulvy *et al.* 2008). In Australia, 45 marine species off the south-eastern coast (around Tasmania) were found to display major shifts in distribution from the late 1800s to the present, which may be linked to climate change (Pitt *et al.* 2010; Last *et al.* 2011). The distribution of the sea urchin *Centrostephanus rodgersii* shifted from the south of mainland Australia to Tasmania, a phenomenon also interpreted as climate change related (Ling *et al.* 2009).

Projections from models suggest that distributions of marine fish and shellfish will continue to shift in the coming decades (Cheung *et al.* 2009; Hobday 2010). Using the 'dynamic bioclimate envelope model' (Cheung *et al.* 2008*b*), Cheung *et al.* (2009) examined the potential global shift in distribution of 1066 exploited marine fish and shellfishes. This model simulates changes in habitat suitability, larval transport, adult migration and population growth of marine animals as modified by ocean conditions predicted by global circulation model (Cheung *et al.* 2008*b*). Cheung *et al.* (2009) found that species distributions are projected to shift towards the pole at an average rate of around 40 km decade^{-1}. These projected shifts in distribution are likely to result in high rates of species invasion in the high-latitude regions and local extinctions along the tropics and in semi-enclosed seas. This is consistent with regional projections for 14 species of pelagic fishes (tunas and billfishes) off the coast of Australia which suggests that distributions of these species would shift southward by year 2050 at an average rate of 40 km decade^{-1} (Hobday 2010).

There is much interest in understanding the potential impacts of climate change on fish populations in Western Australia so that marine conservation and fisheries management plans that are adaptive to climate change can be developed (Cheung *et al.* 2011*a*). Geographically, Western Australia extends from 15°S to 35°S, bordering the Indian Ocean in the west and the Southern Ocean in the south. Fish assemblages along the coast of Western Australia are heavily influenced by the Leeuwin Current (Ayvazian and Hyndes 1995) and there is a continuum of tropical to temperate fish communities from north to south (Hutchins 1994). The Western Australian coast is generally oligotrophic and its subtropical and temperate fish communities are characterised by high diversity, low abundance and endemism. Changes in distribution of marine species may affect the vulnerability of marine species to human impacts (e.g. through increase in range overlap between by-catch and targeted species under climate change) and the effectiveness of marine spatial planning. Potential climate-induced impacts on commercially valuable species such as the Western rock lobster (*Panulirus cygnus*), Australia's most valuable single species wild capture fishery, are also of significant interest. For instance, an empirical study suggests that Western rock lobster has shown a decline in size at maturity and size of migrating lobsters from shallow to deep water, with an increase in abundance of lobsters in deep water relative to shallow water and shifts in catch to deep water that may be related to oceanographic changes (Caputi *et al.* 2010).

To understand the potential effects of climate change on the Western Australian marine fish communities it is important to incorporate species and physical dynamics that are regionally representative. Cheung *et al.* (2011*a*) proposed that such regional analysis could be conducted by incorporating locally important ecological and physical dynamics into a previously tested global model. This involves examination of regionally important species, use of outputs from regional oceanographic models and incorporation of local expert knowledge to improve regional representation of species distributions (Jones *et al.* 2012).

In this study, we examined the effects of climate change on marine fish and invertebrate distributions along the Western Australian coast. The hypothesis was that species distributions would be projected to shift southward, with distribution extension along the south coast and distribution contraction along the north coast. This would then result in the increased dominance of tropical or subtropical communities along the coast. We used a simulation model to project changes in distribution of 30 exploited fish and invertebrates by 2055 to test the above hypothesis. We also examined the sensitivity of our projections to oceanographic forcing from regional and global models. Here we discuss the implications of such changes for marine conservation planning and fisheries management.

Materials and methods

Sample of species and their current distributions

This study focuses on a sample of 30 tropical, subtropical and temperate marine species, including 23 species of fishes and seven species of invertebrates occurring in Western Australia (Table 1). These are commercially important species in the region, of which several are endemic to Australia. Exploited species were chosen as they are generally abundant and better studied, with more available biological and distributional data, as well as being of socio-economic importance.

The current distributions of these 30 focal species, representing the average pattern of relative abundance in recent decades (i.e. 1980–2000), were produced using an algorithm developed by the *Sea Around Us* Project (Close *et al.* 2006). This algorithm predicts probability of occurrence of a species on a 30′ latitude × 30′ longitude grid based on the species' depth range, latitudinal range and polygons encompassing their known occurrence regions. The distributions were further refined by assigning habitat preferences to each species, such as affinity to shelf (inner, outer), estuaries and coral reefs. Such information was initially obtained from FishBase (www.fishbase.org, accessed 3 May 2011) for fish and SeaLifeBase for other taxa (www.sealifebase.org, accessed 3 May 2011). We presented the first iteration of the distribution maps generated from the above algorithm to scientists with expert knowledge on the focal species, and asked them to comment on the accuracy of the predicted distribution maps by correcting the input distributional data (e.g. latitudinal range, depth limits and associated habitats), identifying regional important habitat types that we did not include initially (e.g. limestone reefs) and drawing possible range boundaries. We then revised the input parameters and data and generated a revised set of predicted distribution maps. The experts were asked to review the maps again and these assessments were used to generate a final set of distribution maps for the simulation model.

Table 1. Projected shift (latitudinal and longitudinal) in distribution centroid (km) of 2055 relative to present (2005), for each of the 30 species of fish and shellfish included in this study under the SRES A1B scenario, based on outputs from the CSIRO/OFAM model

Species with an asterisk (*) are endemic to Australia

Scientific name	Common name	Climate	Centroid shift (km)
Invertebrates			
*Amusium balloti**	Western saucer scallop	Tropical	192
*Chaceon bicolor**	Crystal crab	Temperate	17
*Panulirus cygnus**	Western rock lobster	Subtropical	77
*Penaeus latisulcatus**	Western king prawn	Tropical	108
Portunus pelagicus	Blue swimmer crab	Tropical	205
*Haliotis laevigata**	Greenlip abalone	Temperate	320
*Haliotis roei**	Roe's abalone	Temperate	151
Fish			
*Arripis georgianus**	Australian herring	Temperate	818
*Arripis truttacea**	Western Australian salmon	Temperate	187
Carcharhinus obscurus	Dusky shark	Subtropical	31
Carcharhinus plumbeus	Sandbar shark	Subtropical	111
*Centroberyx gerrardi**	Bright redfish	Temperate	111
Centroberyx lineatus	Swallowtail	Temperate	55
*Choerodon rubescens**	Baldchin groper	Subtropical	78
*Epinephelides armatus**	Breaksea Cod	Temperate	95
*Furgaleus macki**	Whiskery shark	Temperate	182
*Glaucosoma hebraicum**	West Australian dhufish	Subtropical	110
*Hyperlophus vittatus**	Sandy sprat	Temperate	427
Lethrinus miniatus	Redthroat emperor	Tropical	72
Lethrinus nebulosus	Spangled emperor	Tropical	20
*Mustelus antarcticus**	Gummy shark	Temperate	597
Pagrus auratus	Snapper	Subtropical	132
Plectropomus leopardus	Common coral trout	Tropical	74
Pristipomoides filamentosus	Rosy snapper	Tropical	31
Pristipomoides multidens	Goldbanded snapper	Tropical	82
Sardinella lemuru	Scaly Mackerel	Tropical	319
Sardinops sagax	Australian sardine	Subtropical	192
Seriola hippos	Samsonfish	Temperate	157
*Sillaginodes punctate**	King George whiting	Temperate	276
*Spratelloides robustus**	Blue sprat	Temperate	741

Projecting change in species distributions

Using the dynamic bioclimate envelope model, we projected changes in distribution of the 30 species of fishes and invertebrates under different climate change scenarios. The modelled species' preferences for environmental conditions were defined by sea water temperature (bottom and surface), salinity and habitat types (coral reef, estuaries, limestone reefs). Suitability, represented by the relative density of the species under environmental conditions and by habitat type, was calculated by overlaying environmental data with maps of relative abundance of the species.

Species' environmental preferences were linked to the expected carrying capacity in a population dynamics model in which growth, mortality and spatial dynamics of adult movement and larval dispersal along ocean currents were explicitly represented (Cheung *et al.* 2008*b*, 2009). The model simulated changes in relative abundance of a species by:

$$\frac{dA_i}{dt} = \sum_{j=1}^{N} G_i + L_{ji} + I_{ji}, \qquad (1)$$

where A_i is the relative abundance of a $30' \times 30'$ cell i, G is the intrinsic population growth and L_{ji} and I_{ji} are settled larvae and net migrated adults from surrounding cells j respectively.

Population growth is modelled by a logistic equation:

$$G_i = r \bullet A_t \bullet \left(1 - \frac{A_i}{KC_i}\right), \qquad (2)$$

where r is the intrinsic rate of population increase, and A_i and KC_i are the relative abundance and population carrying capacity at cell i, respectively. The model assumes that carrying capacity varies positively with habitat suitability of each spatial cell and habitat suitability is dependent on the species' preference profiles to the environmental conditions (e.g. temperature) in each cell. Parameter values of r were obtained from the published literature, FishBase, SealifeBase or personal communications with local experts on the focal species. The distance and direction of larval dispersal are a function of the predicted pelagic larval duration estimated based on an empirical equation (O'Connor *et al.* 2007). The model calculates dispersal of pelagic larvae over time through diffusion and advection as these are important factors determining dispersal of pelagic larvae of marine organisms (Gaines *et al.* 2003). The temporal and spatial patterns of pelagic larval dispersal were modelled by a two-dimensional advection-diffusion equation (Sibert *et al.* 1999; Gaylord and Gaines 2000):

$$\frac{\partial Lav}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial Lav}{\partial x}\right) + \frac{\partial}{\partial y}\left(D\frac{\partial Lav}{\partial y}\right) - \frac{\partial}{\partial x}(u \cdot Lav) - \frac{\partial}{\partial y}(v \cdot N) - \lambda \cdot Lav, \quad (3)$$

where change in relative larvae abundance over time ($\partial Lav/\partial t$) is determined by diffusion (i.e. the first two terms on the right-hand side of Eqn 3) and current-driven movements (i.e. the third and fourth terms of Eqn 3). Diffusion is characterised by a diffusion parameter D, whereas advection is characterised by the two current velocity parameters (u, v) which describe the east–west and north–south current movement. The partial differential equation (Eqn 3) was solved numerically using the implicit alternating direction method (Press *et al.* 1988; Sibert and Fournier 1993) with a daily time step.

In addition, animals are assumed to migrate along the calculated gradient of habitat suitability. Thus, changes in habitat suitability in each cell, determined by ocean conditions, lead to changes in the species' carrying capacity, population growth, net migration, and thus, relative abundance in each cell (Cheung *et al.* 2008*b*, 2009).

Using data from the National Oceanographic and Atmospheric Administration (NOAA) Geophysical Fluid Dynamic Laboratory (GFDL) atmosphere-ocean coupled model (CM) 2.1 and the Commonwealth Scientific and Industrial Research Organisation (CSIRO)'s Ocean Forecasting Australia Model (OFAM) (Fig. 1), we simulated changes in relative abundance of the 30 focal species by 2055 relative to year 2005. The model is driven by changes in ocean conditions and advection fields from projection from two classes of models. First, we used projections from OFAM developed by CSIRO (Sun *et al.* 2012). This model provides high- resolution (10 km) dynamically downscaled predicted ocean conditions for climatological ocean conditions for the 1990s and 2060s forced with the CSIRO Mk3.5 climate model (bias-corrected) under the SRES A1B scenario (CO_2 concentration is stabilised at 720 ppm by 2100). We re-gridded the model outputs into $30'$ latitude × $30'$ longitude cells. Moreover, since time-series ocean condition data were needed, we assumed that the physical parameters change linearly from the means of 1994–2004 to 2062–2064. In addition, we used projections from the NOAA/GFDL CM 2.1 (Delworth *et al.* 2006). Projected physical variables include sea temperature, salinity and advection under different climate change scenarios from 2000 to 2060. In addition to projections under the SRES A1B from both models, we used the scenario with CO_2 concentration stabilised at 2000 level (360 ppm). We re-gridded the original data onto a $30'$ latitude × $30'$ longitude grid using a bilinear interpolation method. This study focused on coastal and shelf of Western Australian waters because most of the 30 species considered here are coastal, at least in part of their life history. However, the NOAA/GFDL CM2.1 resolves the topography and dynamics of the coastal shelf poorly because of its relatively coarse resolution. Thus, the bottom temperature projected for the Western Australia coast from the model may not be representative, so we tested the sensitivity of our model outputs by running the model using sea surface temperature from the NOAA/GFDL instead of bottom temperature.

Using the projected changes in species distributions, we estimated the rate of species' distribution expansion and contraction and turnover in waters adjacent to the coast of Western Australia. Here, rates of species' species gain (or invasion) and loss (or local extinction) were measured, for each cell, by the number of species newly occurring in or disappearing from the cells relative to its original distribution, respectively. Also, we calculated the rate of species turnover, represented by the total number of newly occurring and disappearing species in each cell. Additionally, we calculated the rate of shift in distribution, measured by the latitudinal, longitudinal and depth movement of the centroid of the species distribution within the Exclusive Economic Zones of Australia. For each species, the distribution centroid (DC) was calculated by:

$$\mathrm{DC} = \frac{\sum_{i=1}^{n} L_i \bullet Abd_i}{\sum_{i=1}^{n} Abd_i}, \quad (4)$$

where L_i and Abd_i are the latitudinal or longitudinal coordinates or mean depth of a cell, and species' relative abundance at the centre of cell i respectively. Then, n is the total number of cells within the Australian Exclusive Economic Zone.

We examined shift in assemblage structure in the Western Australian region by calculating a 'tropicalisation index' representing the change in the assemblage of tropical (TP), subtropical (STP) and temperate (TEM) species in each cell. Species are categorised as TP, STP or TEM according to FishBase (as above) and SeaLifeBase (as above) (Table 1). We defined an arbitrary threshold of 'observable' change in relative abundance as 30% increase or decrease relative to the original value in the cell. If a cell was not occupied by the species initially, but was occupied later because of distribution shift, we included this as an 'observable' change as well. Each initially occurring species had a score of 1, 0.5 and −1 for TP, STP and TEMP respectively. An 'observable' increase in relative abundance led to a doubling of the scores whereas a decrease turned the score to 0. For example, initial occurrence of redthroat emperor (*Lethrinus miniatus*), as a tropical species, in a given area will have a score of 1. If the relative abundance of redthroat emperor in that area is projected to increase over 30%, the score will be increased to 2. In contrast, if its relative abundance is reduced by 30% or more, the score became 0. The tropicalisation index is the sum of the scores for all occurring species in each time step (year). Thus, assemblages with a higher tropicalisation index are more tropical than assemblages with lower or negative tropicalisation index. We calculated the tropicalisation index for eight locations across longitude along the coast of Western Australia.

Results

Projected change in species distribution

Under the SRES A1B scenario projected from the CSIRO/OFAM, the majority of species were projected to shift southward and to deeper water (see Fig. S1, available as Supplementary

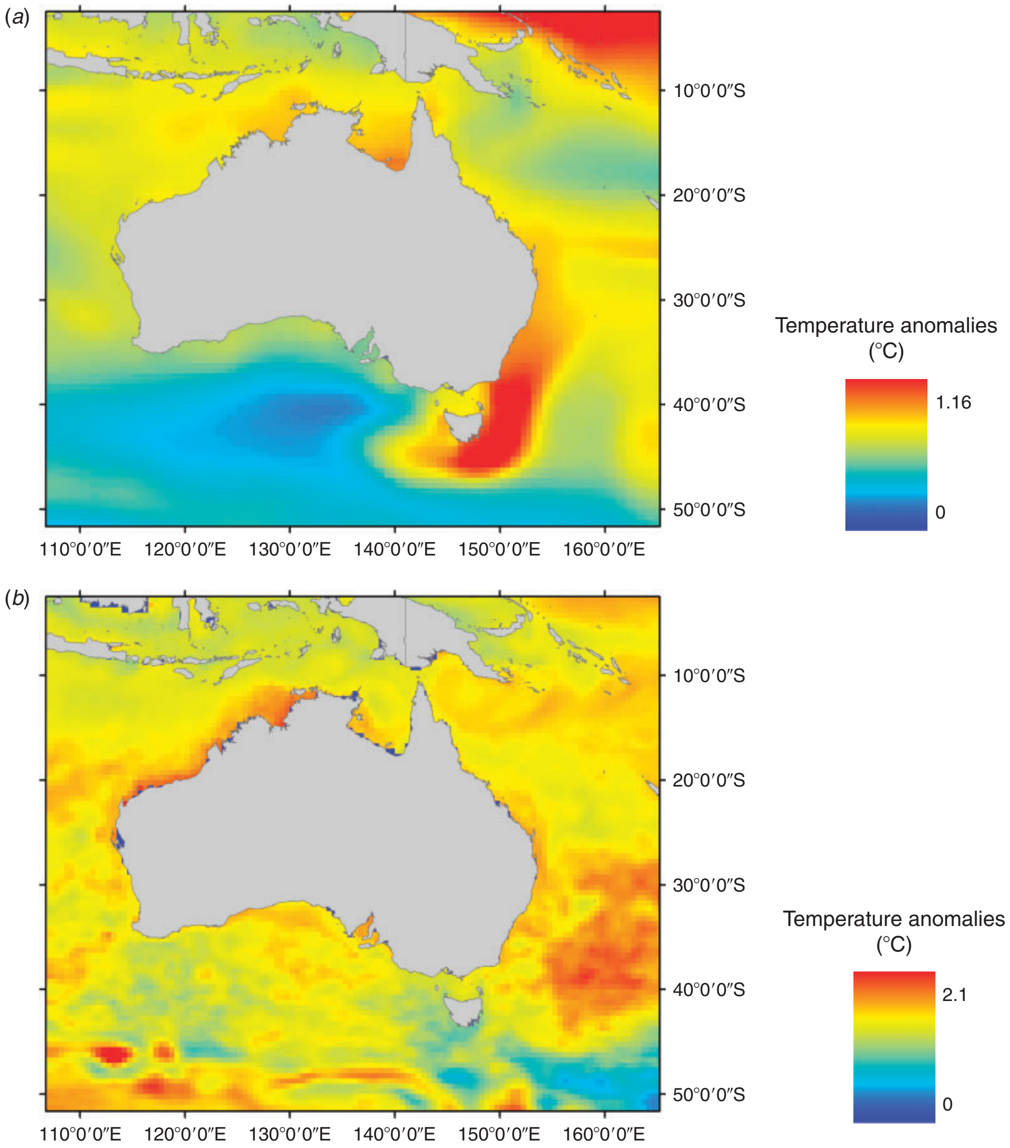

Fig. 1. Projected sea surface temperature (SST) anomalies from the (*a*) National Oceanographic and Atmospheric Administration/Geophysical Fluid Dynamic Laboratory Coupled Model 2.1 and (*b*) Commonwealth Scientific and Industrial Research Organisation (CSIRO)'s Ocean Forecasting Australia Model (by 2055 relative to 2005) under the SRES (Special Report for Emission Scenarios) A1B scenario.

Material to this paper). Around 80% of the distribution centroids of the focal species in Western Australia were projected to shift southward towards higher latitude (Figs 2, 3). The median rate of distribution shift is around 96 km southward by 2055 relative to 2005 (10-year average) or around 19 km decade^{-1} towards the high-latitude region. In contrast, 20% of the species showed no distribution shift or shifted towards lower latitudes (north). Moreover, the model projected the depth-centroid of the distribution of demersal species ($N = 24$) to shift at a rate of 9 m decade^{-1}.

Besides latitudinal shift, distributional centroids were projected to shift eastward under the higher greenhouse gas emission scenario (Fig. 3; Table 1). Distributions were projected to shift by over 144 km eastward (or 29 km decade^{-1}) by 2055 relative to 2005, based on outputs from the CSIRO/OFAM model. The longitudinal distribution shifts resulting from the eastward distribution extension occurred mainly along the south coast of Australia. The combined latitudinal and longitudinal shifts in extension and contraction of distribution resulted in an average shift of over 170 km of the distribution centroids by 2055.

The magnitude of distribution shift varied substantially between different sets of oceanographic projections. Under the SRES A1B scenario, the rates of species range shift calculated from simulations forced by outputs from the NOAA/GFDL CM2.1 (using sea bottom temperature for demersal species) were considerably lower (13 km decade^{-1}) than those projected using outputs from the CSIRO/OFAM, largely due to the fact that the global coupled model does not resolve the continental shelf well. When only SST was used, the rates of range shift more than doubled compared to those projected using outputs

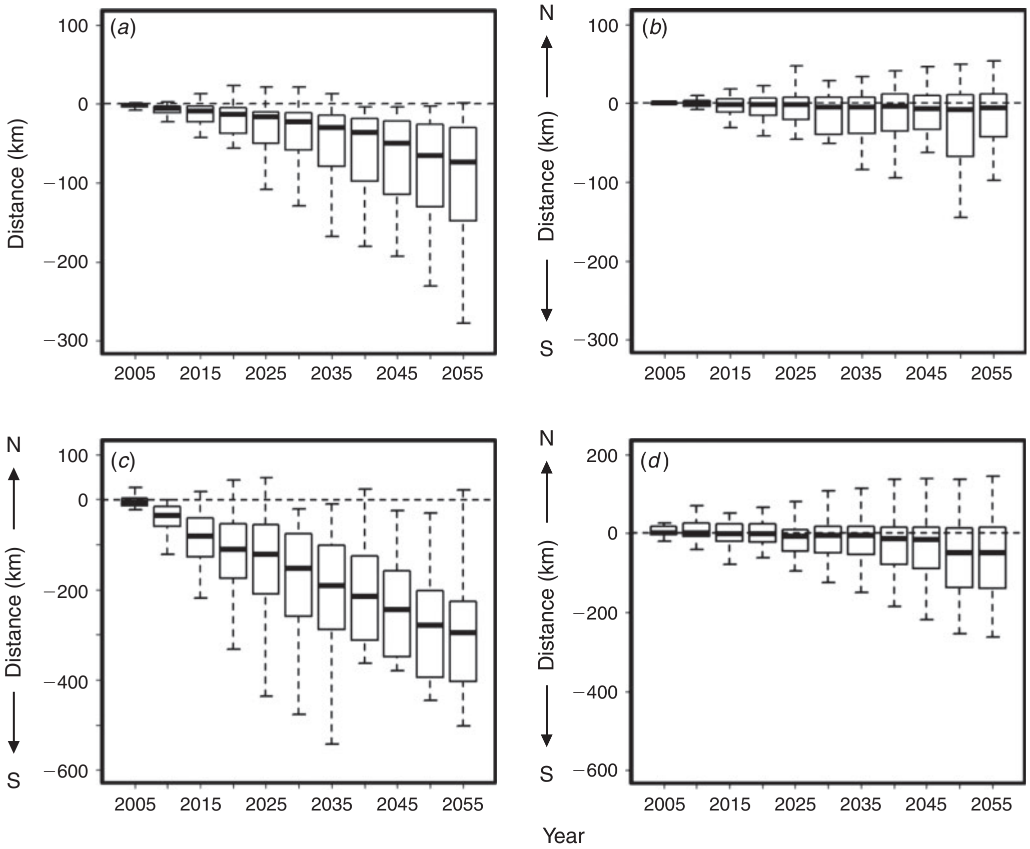

Fig. 2. Projected median shift in distance in the latitudinal centroids of 30 species of fish and invertebrates in Western Australia relative to 2005 under the scenario SRES A1B predicted from: (*a*) CSIRO/OFAM; (*b*) NOAA/GFDL CM2.1; (*c*) NOAA/GFDL CM2.1 (using sea surface temperature only); and (*d*) under the scenario with greenhouse gas concentration stabilised at year 2000 level from NOAA/GFDL CM2.1. Note that the OFAM simulation has been linearly interpolated in the time dimension.

from CSIRO/OFAM (Fig. 2). With a lower-range climate change scenario (stabilisation of CO_2 concentration at year 2000 level) and applying SST instead of sea bottom temperature, the projected range shift is small (Fig. 2*d*).

Changes in species richness

As a result of the distribution shifts, our model projected a higher frequency of species gains and losses along the south coast and north coast of Western Australia, respectively (Fig. 4). Under the SRES A1B scenario, species gains were projected to be more extensive in the south coast, in the area east of Albany. Moreover, species gains were mainly in areas further away from the coast. In contrast, species losses were projected to be highest in the north coast, in the area between Port Hedland and the Kimberly, and concentrated along the coast. Overall, the pattern of species turnover was higher in the south coast of Western Australia, followed by the west coast.

Change in species assemblages

Projections from the CSIRO/OFAM (SRES A1B) resulted in slight decreases in the tropicalisation index in locations along the north coast (A, B and C) and considerable increases along the south-east (D and E) and south coast (F–H) (Fig. 5). There was a latitudinal gradient (from A to H) of the initial tropicalisation index, which ranged from positive in the north to negative in the south. In the north coast (Stations A and B), the tropicalisation index decreased from 10 to 9, suggesting an ‘observable’ decrease in tropical species assemblages that are included in this study. Station C, dominated initially by tropical species (index of 10), did not exhibit many observable changes in the number of tropical or temperate species. Along the south-west and south coast (D–H), all stations were projected to have observable increases in tropical species or decreases in temperate species. The stations with the largest increase in the tropicalisation index occurred along the south coast (F–H).

Projected changes in the tropicalisation index using outputs from the NOAA/GFDL CM2.1 showed similar trends to the index calculated from using the CSIRO/OFAM model, although the magnitude of changes varied considerably depending on whether sea surface or bottom temperatures were used (under the same emission scenario). When sea bottom temperature for the NOAA/GFDL model was used, changes in tropicalisation index were consistently smaller relative to those calculated from CSIRO/OFAM, except in station H. However, when sea surface temperature from the NOAA/GFDL model was used, the

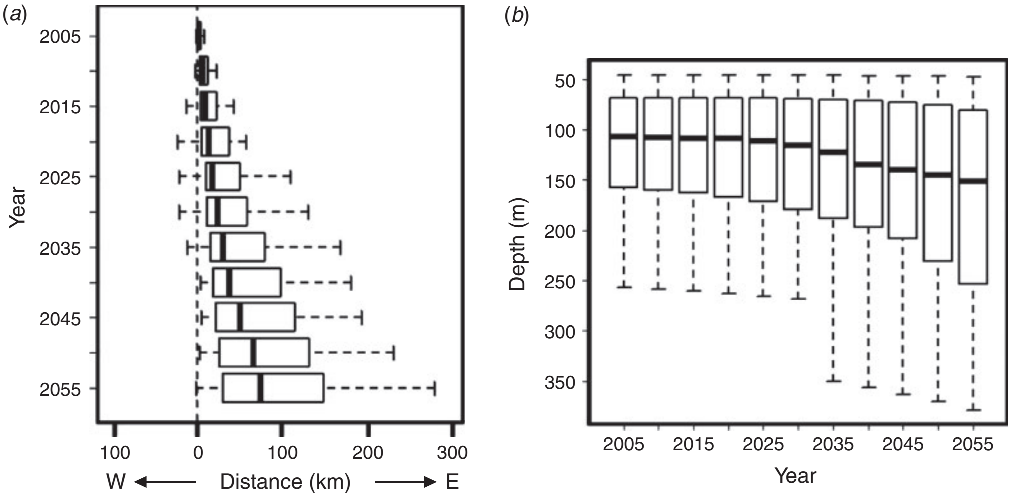

Fig. 3. Projected shift in (*a*) longitudinal and (*b*) depth centroid of 30 species of marine fishes and invertebrates from 2005 to 2055 under the SRES A1B scenario from the CSIRO/OFAM model.

model projected greater community changes than those derived from CSIRO/OFAM or NOAA/GFDL based on sea bottom temperature.

Discussion

Robustness of the future projections

Our results support our hypothesis that substantial shifts in the exploited species assemblage along the coast of Western Australia would occur by 2055, resulting in the 'tropicalisation' of the subtropical and temperate parts of the zones, with 'tropicalisation' referring to the increased dominance of tropical species in the assemblage. Our results also agree with previous global or regional model projections and observations on shifts in species distribution (Perry *et al.* 2005; Cheung *et al.* 2009, 2011*a*; Hobday 2010). For example, the observed poleward range extension of the sea urchin *Centrostephanus rodgersii* from mainland Australia to Tasmania is suggested to reflect climate change (Ling *et al.* 2009). This study suggests that such changes in the distribution of major commercial species are likely to be observed in the Western Australia region in the next 10–20 years. This is also consistent with recent observations suggesting that fish species that are normally restricted to the north coast of Western Australia now occur further south, which may be related to increases in sea temperature (Langlois *et al.* in press). The distribution of western rock lobster in the region is also shown to have shifted to deeper waters (Caputi *et al.* 2010).

Although variations in projected changes in ocean conditions may affect the predicted species distribution shift, we obtained similar patterns of change in species distributions using the two oceanographic models with different resolution. However, their magnitude is sensitive to the physical variables. The CSIRO/OFAM is a regional downscaling model, and has higher resolution in its predictions, designed to better represent coastal and continental shelf dynamics of Western Australia. In contrast, the NOAA/GFDL coupled model has coarse resolution and is poor in its representation of coastal and shelf dynamics and the bottom topography of the Western Australia coast. For instance, this model predicts colder sea bottom temperature with smaller degree of changes in the coastal cells compared to the outputs from CSIRO/OFAM. This contributes to the difference in magnitude of the projected changes when the same environmental variables from both models were used. This highlights the potential limitations of using IPCC-class global circulation model to assess regional changes in marine ecosystems, particularly in coastal and shelf waters and the need to use better spatially resolved climate and oceanographic projections (e.g. regional oceanographic models) in regional assessments (Stock *et al.* 2011).

Long-term (decadal) records of the focal species in the regions would be useful to test the accuracy of the model. The modelling approach attempts to capture key physiological preferences and population dynamics that affect species distribution. However, it did not consider factors such as biogeochemistry of the seas (e.g. pH, oxygen content) and species interactions, which are important factors affecting species distributions (Guisan and Thuiller 2005; Pörtner and Farrell 2008; Pauly 2010). Also, some species may adapt to changing ocean conditions. For example, it is suggested that some level of adaptation to increased temperature may largely reduce the impacts of coral bleaching caused by ocean warming on coral reefs (Donner 2009; Pandolfi *et al.* 2011). Evidence from studies of terrestrial animals suggests that species may adapt to climate change by favouring individuals that have greater dispersal ability (Thomas *et al.* 2001). Some fishes are able to acclimatise to increased temperature (Hutchinson and Maness 1979; Donelson *et al.* 2009), although the long-term effects on the organisms and populations are uncertain. In either case, the degree of adaptation to the changing ocean conditions would depend on the generation time of the species and the diversity of life history traits and environmental tolerance in the existing gene pool. Currently, we have little empirical knowledge of the rate of adaptation to climate change in fish and shellfish, which limits incorporating this factor into our model.

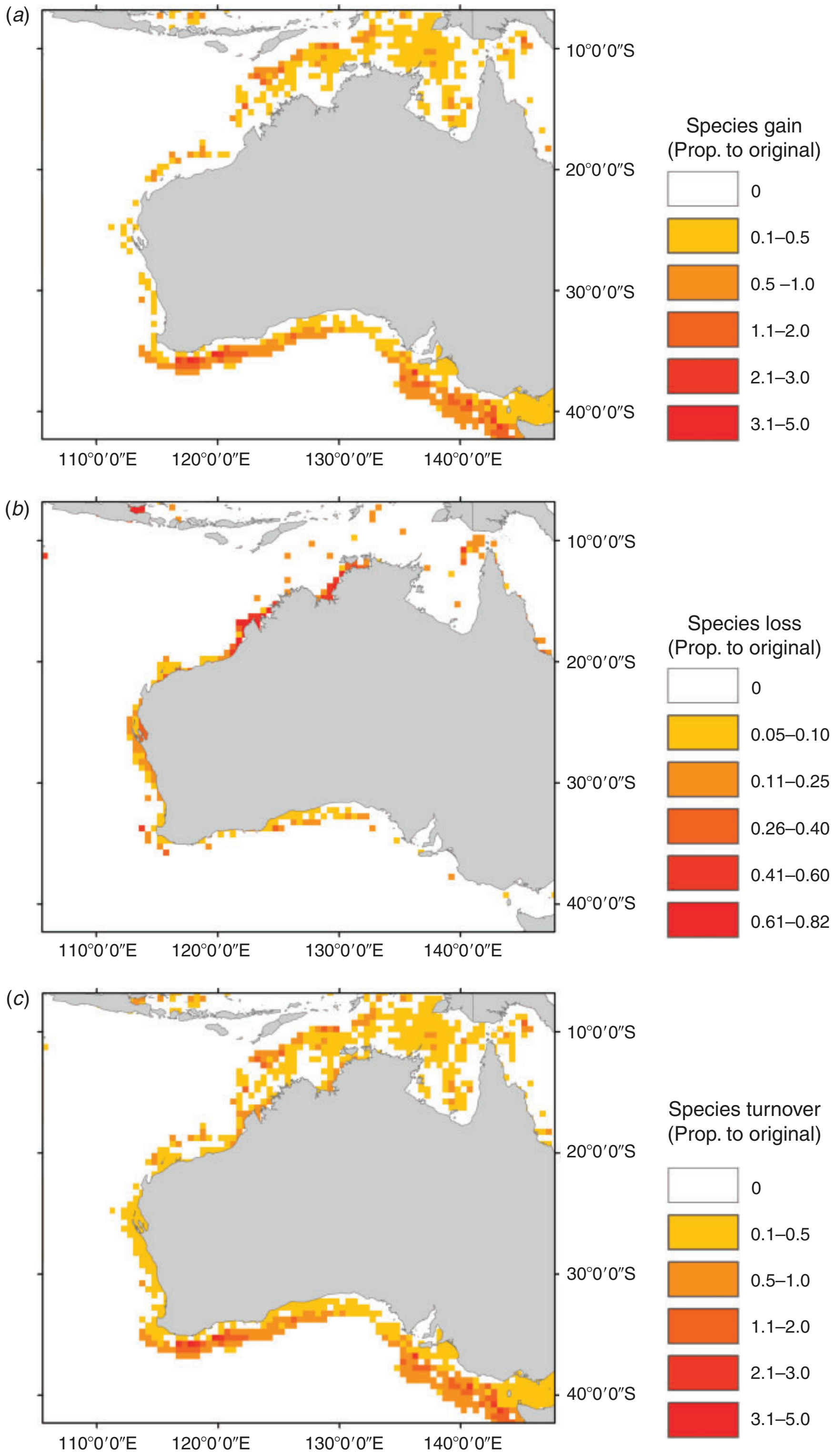

Fig. 4. Projected change in species richness in the Western Australian region between 2005 and 2055 under the SRES A1B from the CSIRO/OFAM model. Change in species richness was measured by (*a*) rate of species gain (or invasion); (*b*) rate of species loss (or local extinction); and (*c*) rate of species turnover. Total number of species examined is 30.

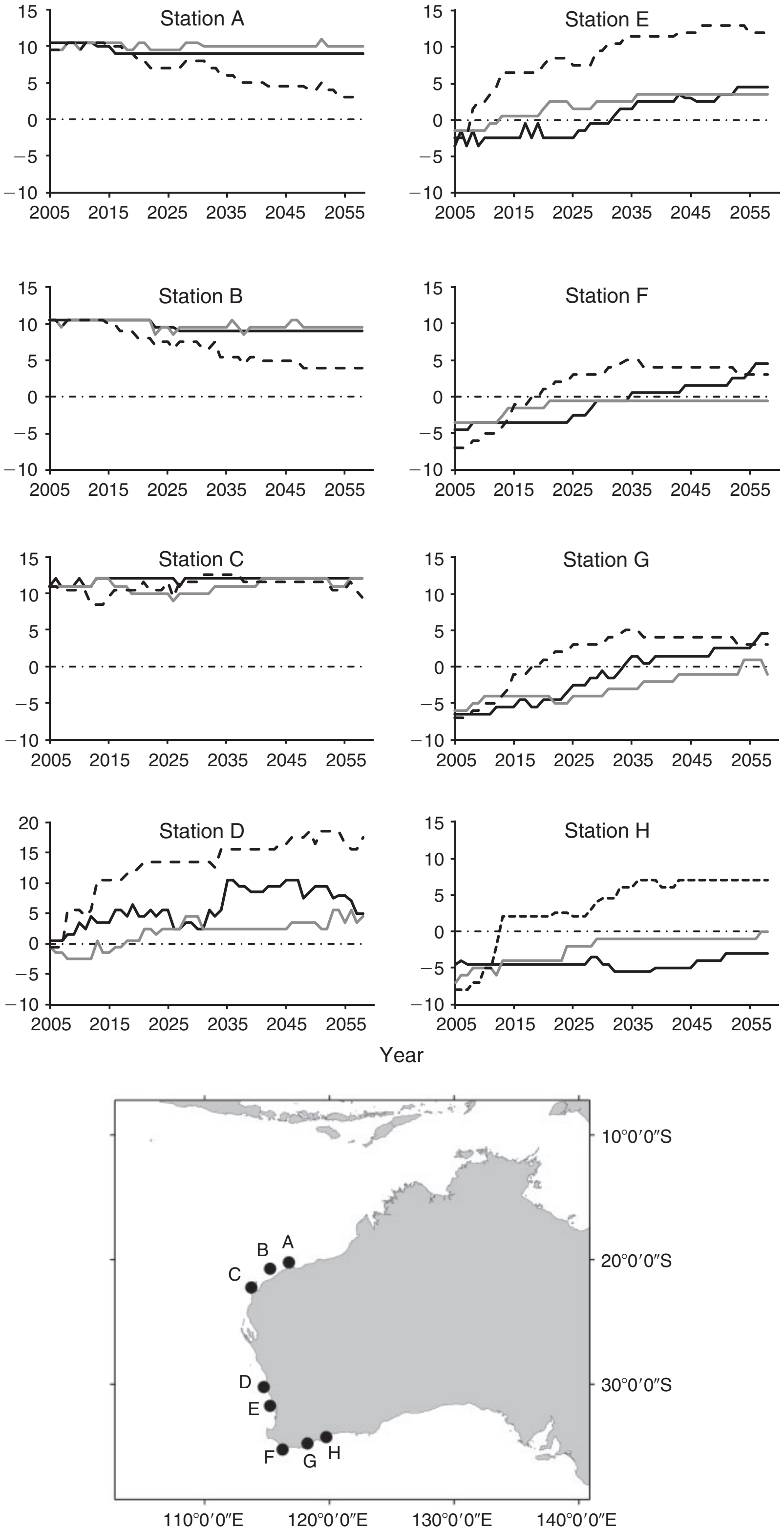

Fig. 5. Calculated tropicalisation index in eight locations across the coast of Western Australia based on the projections from CSIRO/OFAM (black line), NOAA/GFDL (using sea bottom temperature for demersal species) (grey line) and NOAA/GFDL (sea surface temperature for demersal species) (dashed line) under the SRES A1B scenario. Location of each station is shown in the lower panel. A, Dampier; B, Barrow Island; C, Ningaloo; D, Jurien Bay; E, Two Rocks; F, Broke; G, Albany; H, Point Anne; each represented by a spatial cell, a higher tropicalisation index represents a more tropical assemblage and *vice versa*.

Our projections are also based on the prediction of one particular IPCC greenhouse emission scenario. However, it is likely that we are heading towards a higher range climate change scenario (Rogelj *et al.* 2009). Thus, our results may be considered conservative. In addition, the uncertainties of the CSIRO/OFAM downscaling products due to its uncoupled nature have not been fully assessed. There have been observations of significant multi-decadal natural climate variability of the tropical Pacific affecting wind stresses, the Leeuwin Current, sea levels and other related physical conditions of the ocean (Feng *et al.* 2010), which have not been taken into account in our model simulation. Thus, our projections are more representative of the long-term (multi-decadal average) trends whereas shorter-term projections are more uncertain because of the potential confounding effects of climate variability that are not accounted for in our analysis.

Overall, projections in this study may be considered as a set of null hypotheses that should be tested with future data and observed changes in the recent past. It also highlights the potential responses of marine communities to climate change impacts. Such information is important in designing monitoring programs to detect climate change effects on marine ecosystems.

Implications of 'tropicalisation' of marine communities

The findings from this study contribute to addressing some major questions on managing marine biodiversity and fisheries resources under climate change. These questions include: What are the implications for the biodiversity and the goods and services from marine ecosystems? How should we develop conservation and fisheries management policies that are adaptive to climate change? How should we monitor changes in species distribution and community structure in the future?

The projected changes in species distributions and community structure may have substantial ecological implications. The turnover of species in each area may have consequences for food web and biodiversity. For example, the distribution extension of predatory species may increase the predation mortality of some prey species or competition with other predatory species in the area (Harley 2011). Although our understanding of the potential trophic interactions implied by different species' distribution is limited, evidence from elsewhere suggests that such ecological impacts could be large. For example, the northward expansion of the distribution of predatory squid, Humboldt squid (*Dosidicus gigas*), may have led to the reduction of groundfish species such as Pacific hake (*Merluccius productus*) (Zeidberg and Robison 2007). The explosion of jellyfish populations have been suggested to greatly reduce recruitment of commercially important fish species as their larvae are preyed on by the jellyfish (Purcell 1985; Brodeur *et al.* 2002). Moreover, climate change induced changes in distribution and abundance of predators may result in unexpected changes in species distributions, community structure and diversity of prey species (Harley 2011). These observations provide a preview of the potential ecological impacts of shifts in species distributions. Moreover, in areas with high rates of local extinction (e.g. the north coast of Australia), organisms that are dependent on these locally extinct species may be affected. It is uncertain whether the ecological niches that these species leave behind will be filled by other species that are not included in our study.

Shifts in the distributions of commercially important species will also likely affect fishing activities (Sumaila *et al.* 2011). Some commercially valuable species may shift their distributions to more remote areas in southern Australia, where existing fishing effort is relatively low because of the remoteness of the coast and distance from ports. In contrast, negative impacts are likely to occur on fisheries in the northern tropical region of the Western Australia coast as species shift southward, although some species may move into existing fishing grounds, creating new opportunities for the fishing industry. Overall, change in distribution area and primary productivity will likely lead to re-distribution of potential catch (Cheung *et al.* 2008*a*, 2009, 2011*a*; Brown *et al.* 2010) and this redistribution needs to be reflected in spatial management arrangement.

Fisheries management and conservation planning should be adaptive to climate change. Given the likely changes in species distribution, abundance and potential fisheries production, fisheries and conservation policies may become less effective in the future. Specifically, in Western Australia, zoning of the marine environment determines access for individual licence holders and catch is controlled through either input or output controls (Fletcher and Santoro 2010). The projected changes in species distributions may significantly change the resources available to fishers within a given zone, and distort the relationship between the amount of effort that can be supported by the resource (e.g. the demersal gill-net fishery) or the proportion of the resource allocated to quota (e.g. abalone). Effective ecosystem-based management of fisheries that recognises climate change will require reconsideration of zoning and controls and will be partly dependent on the projected and observed species' responses to climate change.

One of the basic approaches to manage fisheries and conserve biodiversity in the region under climate change is to increase the adaptive capacity of the marine ecosystems and fisheries. Generally, depleted populations and stressed marine organisms are more vulnerable to impacts from environmental changes (Griffith *et al.* 2011). Similarly, fisheries that under-perform economically are less adaptive to changes (Sumaila *et al.* 2011). Thus, climate change would further raise the urgency to ensure sustainable management of fisheries and marine ecosystems. Moreover, instead of assuming that the ocean is relatively stable, multiple long-term scenarios of ocean changes should be considered in designing new policies or reviewing existing management measures, and proactively increasing ocean resiliency through, for instance, the establishment of marine protected area (McLeod *et al.* 2009).

On monitoring future changes

The results from this study will be useful in adapting and designing existing and future monitoring program to collect data that could be used to test the hypotheses of climate change impacts on marine species and communities in Western Australia (Cheung *et al.* 2011*b*). First, predictions of regionally relevant locations where organisms are most sensitive to climate change can direct decisions with respect to the location of monitoring programs. In this study, we suggest that communities most sensitive to climate change impacts are along the north and south coasts of Western Australia. Such locations should provide an early warning of changes in marine assemblages and, by incorporating a multispecies response, they should be the first locations to signal change in an otherwise notoriously noisy environment.

Second, species that are predicted to be strongly responsive to climate change can be identified as key indicators for long-term monitoring across a range of sites. In general, pelagic fishes are projected to show the greatest shifts in distributions because of the higher rate of predicted change in ocean conditions in the surface ocean layer and the higher mobility of these species. In contrast, benthic invertebrates and deeper water fishes which are less mobile and which may experience a lower rate of changes of their physical environment may have a much slower rate of distribution shift (Caputi *et al.* 2010). A subset of the most sensitive species with different climatic associations (temperature, subtropical and temperate) and in different habitats (pelagic, coastal and deep water demersal) should be included in the monitoring program. Currently, in Western Australia, the identification of indicator species is linked to fisheries value or is an outcome of broadscale regional sampling programs such as those using stereo-baited remote video systems (Harvey *et al.* 2007). The sensitive areas and species can inform the future design of such monitoring programs to study marine climate change impacts in the regions.

Third, projections of differential responses of a wide range of exploited species to climate change help determine directional changes of community level indicators for fisheries management. Climate change confounds the expected responses of these indicators to management or changes in fisheries. Projections of changes in relative abundance and distribution of species assemblages can be taken into account to improve the interpretation of these indicators in reflecting the status, pressure, and responses of ecosystems. In addition, establishing or using existing no-take marine reserves within these locations would further allow the disentanglement of the effects of climate change and fishing on marine communities (Cheung *et al.* 2011*b*).

Conclusions

Our study shows that Western Australia coast, which extends from tropical to temperate zones, may experience a 'tropicalisation' of the marine community in the future under a business-as-usual climate change scenario. Such 'tropicalisation' is caused by the generally southward shift of species distributions around Australia. The projected changes from our model agree with large-scale projections and observations elsewhere. Such changes in species assemblages may have major ecological and socio-economic implications through unexpected trophic effects and shift in fishing grounds. The model projections provide sets of alternative hypotheses for future studies to test. It also helps identify area and species that are most sensitive to marine climate change in the region. Such information is useful for designing monitoring programs for climate change effects on marine species in Western Australia.

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References

Ayvazian, S. G., and Hyndes, G. A. (1995). Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology* **122**, 527–536. doi:10.1007/BF00350675

Belkin, I. M. (2009). Rapid warming of large marine ecosystems. *Progress in Oceanography* **81**, 207–213. doi:10.1016/J.POCEAN.2009.04.011

Brodeur, R. D., Sugisaki, J., and Hunt, G. L., Jr (2002). Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* **233**, 89–103. doi:10.3354/MEPS233089

Brown, C. J., Fulton, E. A., Hobday, A. J., Matear, R. J., Possingham, H. P., Bulman, C., Christensen, V., Forrest, R. E., Gehrke, P. C., Gribble, N. A., Griffiths, S. P., Lozano-Montes, H., Martin, J. M., Metcalf, S., Okey, T. A., Watson, R., and Richardson, A. J. (2010). Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation. *Global Change Biology* **16**, 1194–1212. doi:10.1111/J.1365-2486.2009.02046.X

Caputi, N., de Lestang, S., Feng, M., and Pearce, A. (2009). Seasonal variation in the long-term warming trend in water temperature off the Western Australian coast. *Marine and Freshwater Research* **60**, 129–139. doi:10.1071/MF08199

Caputi, N., Melville-Smith, R., de Lestang, S., Pearce, A., and Feng, M. (2010). The effect of climate change on the western rock lobster (*Panulirus cygnus*) fishery of Western Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **67**, 85–96. doi:10.1139/F09-167

Cheung, W. W. L., Close, C., Lam, V., Watson, R., and Pauly, D. (2008*a*). Application of macroecological theory to predict effects of climate change on global fisheries potential. *Marine Ecology Progress Series* **365**, 187–197. doi:10.3354/MEPS07414

Cheung, W. W. L., Lam, V. W. Y., and Pauly, D. (2008*b*) Dynamic bioclimate envelope model to predict climate-induced changes in distribution of marine fishes and invertebrates. In 'Modelling Present and Climate-shifted Distributions of Marine Fishes and Invertebrates. Vol. 16(3)'. (Eds W. W. L. Cheung, V. W. Y. Lam and D. Pauly.) pp. 5–50. (University of British Columbia: Vancouver, BC, Canada.)

Cheung, W. W. L., Lam, V. W. Y., Sarmiento, J. L., Kearney, K., Watson, R., and Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* **10**, 235–251. doi:10.1111/J.1467-2979.2008.00315.X

Cheung, W. W. L., Dunne, J., Sarmiento, J. L., and Pauly, D. (2011*a*). Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* **68**, 1008–1018. doi:10.1093/ICESJMS/FSR012

Cheung, W. W. L., Meeuwig, J. J., and Lam, V. W. Y. (2011*b*). Ecosystem-based fisheries management in the face of climate change. In 'Ecosystem Approaches to Fisheries: a Global Perspective'. (Eds V. Christensen and J. Maclean.) pp. 171–188. (Cambridge University Press: New York.)

Close, C., Cheung, W. W. L., Hodgson, S., Lam, V., Watson, D., and Pauly, D. (2006). Distribution ranges of commercial fishes and invertebrates. In 'Fishes in Databases and Ecosystems. Vol. 14(4)'. (Eds D. Palomares, K. I. Stergiou and D. Pauly.) pp. 27–37. (University of British Columbia: Vancouver, BC, Canada.)

Collins, D. (2000). Annual temperature summary: Australia records warmest decade. *Climate Change Newsletter* **12**, 6.

Delworth, T. L., Broccoli, A. J., Rosati, A., Stouffer, R. J., Balaji, V., Beesley, J. A., Cooke, W. F., Dixon, K. W., Dunne, J., Dunne, K. A., Durachta, J. W., Findell, K. L., Ginoux, P., Gnanadesikan, A., Gordon, C. T., Griffies, S. M., Gudgel, R., Harrison, M. J., Held, I. M., Hemler, R. S., Horowitz, L. W., Klein, S. A., Knutson, T. R., Kushner, P. J., Langenhorst, A. R., Lee, H.-C., Lin, S.-J., Lu, J., Malyshev, S. L., Milly, P. C. D., Ramaswamy, V., Russell, J., Schwarzkopf, M. D., Shevliakova, E., Sirutis, J. J., Spelman, M. J., Stern, W. F., Winton, M., Wittenberg, A. T., Wyman, B., Zeng, F., and Zhang, R. (2006). GFDL's CM2 global coupled climate models. Part I: Formulation and simulation characteristics. *Journal of Climate* **19**, 643–674. doi:10.1175/JCLI3629.1

Donelson, J. M., Munday, P. L., and McCormick, M. I. (2009). Parental effects on offspring life histories: when are they important? *Biology Letters* **5**, 262–265.

Doney, S. C., Fabry, V. J., Feely, R. A., and Kleypas, J. A. (2009). Ocean acidification: the other CO_2 problem. *Annual Review of Marine Science* **1**, 169–192. doi:10.1146/ANNUREV.MARINE.010908.163834

Donner, S. D. (2009). Coping with commitment: projected thermal stress on coral reefs under different future scenarios. *PLoS ONE* **4**, e5712. doi:10.1371/JOURNAL.PONE.0005712

Dulvy, N. K., Rogers, S. I., Jennings, S., Stelzenmüller, V., Dye, S. R., and 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. doi:10.1111/J.1365-2664.2008.01488.X

Feng, M., McPhaden, M. J., and Lee, T. (2010). Decadal variability of the Pacific subtropical cells and their influence on the southeast Indian Ocean. *Geophysical Research Letters* **37**, L09606. doi:10.1029/2010GL042796

Fletcher, W. J., and Santoro, K. (Eds) (2010). 'State of the fisheries report 2008/2009.' (Department of Fisheries, Government of Western Australia: Perth.)

Gaines, S. D., Gaylord, B., and Largier, J. L. (2003). Avoiding current oversights in marine reserve design. *Ecological Applications* **13**, 32–46. doi:10.1890/1051-0761(2003)013[0032:ACOIMR]2.0.CO;2

Gaylord, B., and Gaines, S. D. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *American Naturalist* **155**(6), 769–789. doi:10.1086/303357

Griffith, G. P., Fulton, E. A., and Richardson, A. J. (2011). Effects of fishing and acidification-related benthic mortality on the southeast Australian marine ecosystem. *Global Change Biology* **17**, 3058–3074. doi:10.1111/J.1365-2486.2011.02453.X

Guisan, A., and Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**, 993–1009. doi:10.1111/J.1461-0248.2005.00792.X

Harley, C. D. G. (2011). Climate change, keystone predation, and biodiversity loss. *Science* **334**, 1124–1127. doi:10.1126/SCIENCE.1210199

Harvey, E., Cappo, M., Butler, J., Hall, N., and Kendrick, G. (2007). Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series* **350**, 245–254. doi:10.3354/MEPS07192

Hobday, A. J. (2010). Ensemble analysis of the future distribution of large pelagic fishes off Australia. *Progress in Oceanography* **86**, 291–301. doi:10.1016/J.POCEAN.2010.04.023

Hutchins, J. B. (1994). A survey of the nearshore reef fish fauna of Western Australia's west and south coasts – the Leeuwin Province. *Records of the Western Australian Museum* **44**(Suppl.), 1–66.

Hutchinson, V. H., and Maness, J. D. (1979). The role of behavior in temperature acclimation and tolerance in ectotherms. *American Zoologist* **19**, 367–384.

IPCC (2007). Summary for policymakers. In 'Climate Change 2007: the Physical Science Basis. Working Group I Contribution to the Fourth Assessment Report of the IPCC'. (Eds S. Solomon, D. Qin and M. Manning.) pp. 1–18. (Cambridge University Press: Cambridge.)

Jones, M., Dye, S., Pinnegar, J., Warren, R., and Cheung, W. W. L. (2012). Modelling commercial fish distributions: prediction and assessment using different approaches. *Ecological Modelling* **225**, 133–145. doi:10.1016/J.ECOLMODEL.2011.11.003

Langlois, T. J., Radford, B. T., Niel, K. P. V., Meeuwig, J. J., Pearce, A. F., Rousseaux, C. S. G., Hendrick, G. A., and Harvey, E. S. (in press). Consistent abundance distributions of marine fishes in an old, climatically buffered, infertile seascape. *Global Ecology and Biogeography.*

Last, P. R., White, W. T., Gledhill, D. C., Hobday, A. J., Brown, R., Edgar, G. J., and 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. doi:10.1111/J.1466-8238.2010.00575.X

Ling, S. D., Johnson, C. R., Ridgway, K., Hobday, A. J., and 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. doi:10.1111/J.1365-2486.2008.01734.X

McLeod, E., Salm, R., Green, A., and Almany, J. (2009). Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* **7**, 362–370. doi:10.1890/070211

O'Connor, M. I., Bruno, J. F., Gaines, S. D., Halpern, B. S., Lester, S. E., Kinlan, B. P., and Weiss, J. M. (2007). Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 1266–1271. doi:10.1073/PNAS.0603422104

Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418–422. doi:10.1126/SCIENCE.1204794

Pauly, D. (2010). 'Gasping Fish and Panting Squids: Oxygen, Temperature and the Growth of Water-Breathing Animals.' (International Ecology Institute: Oldendorf, Germany.)

Pearce, A., and Feng, M. (2007). Observations of warming on the Western Australian continental shelf. *Marine and Freshwater Research* **58**, 914–920. doi:10.1071/MF07082

Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915. doi:10.1126/SCIENCE.1111322

Pitt, N. R., Poloczanska, E. S., and Hobday, A. J. (2010). Climate-driven range changes in Tasmanian intertidal fauna. *Marine and Freshwater Research* **61**, 963–970. doi:10.1071/MF09225

Pörtner, H. O., and Farrell, A. P. (2008). Physiology and climate change. *Science* **322**, 690–692. doi:10.1126/SCIENCE.1163156

Press, W. H., Flannery, B. P., Teukolsky, S. A., and Vetterling, W. T. (1988). 'Numerical Recipes in C.' (Cambridge University Press: New York.)

Purcell, J. E. (1985). Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bulletin of Marine Science* **37**, 739–755.

Richardson, A. J. (2008). In hot water: zooplankton and climate change. *ICES Journal of Marine Science: Journal du Conseil* **65**, 279–295. doi:10.1093/ICESJMS/FSN028

Rogelj, J., Hare, B., Nabel, J., Macey, K., Schaeffer, M., Markmann, K., and Meinshausen, M. (2009). Halfway to Copenhagen, no way to 2°C. *Nature Reports Climate Change* **3**, 81–83. doi:10.1038/CLIMATE.2009.57

Sibert, J. R., and Fournier, D. A. (1993). Evaluation of advection-diffusion equations for estimation of movements patterns from tag recapture data. In 'Interactions of Pacific Tuna Fisheries. Vol. 1: Summary Report and Papers on Interaction. FAO Fisheries Technical Paper, 336, Vol. 1'. (Eds R. Shomura, J. Majkowski and S. Langi.) pp. 108–121. (FAO: Rome.)

Sibert, J. R., Hampton, J., Fournier, D. A., and Bills, P. J. (1999). An advection-diffusion-reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (*Katsuwonus pelamis*). *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 925–938. doi:10.1139/CJFAS-56-6-925

Stock, C. A., Alexander, M. A., Bond, N. A., Brander, K. M., Cheung, W. W. L., Curchitser, E. N., Delworth, T. L., Dunne, J. P., Griffies, S. M., Haltuch, M. A., Hare, J. A., Hollowed, A. B., Lehodey, P., Levin, S. A., Link, J. S., Rose, K. A., Rykaczewski, R. R., Sarmiento, J. L., Stouffer, R. J., Schwing, F. B., Vecchi, G. A., and Werner, F. E. (2011). On the use of IPCC-class models to assess the impact of climate on living marine resources. *Progress in Oceanography* **88**, 1–27. doi:10.1016/J.POCEAN.2010.09.001

Stramma, L., Johnson, G. C., Sprintall, J., and Mohrholz, V. (2008). Expanding oxygen-minimum zones in the tropical oceans. *Science* **320**, 655–658. doi:10.1126/SCIENCE.1153847

Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., and Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change* **1**, 449–456. doi:10.1038/NCLIMATE1301

Sun, C., Feng, M., Matear, R. J., Chamberlain, M. A., Craig, P., Ridgway, K. R., and Schiller, A. (2012). Marine downscaling of a future climate scenario for Australian boundary currents. *Journal of Climate*, in press. doi:10.1175/JCLI-D-11-00159.1

Thomas, C. D., Bodsworth, E. J., Wilson, R. J., Simmons, A. D., Davies, Z. G., Musche, M., and Conradt, L. (2001). Ecological and evolutionary processes at expanding range margins. *Nature* **411**, 577–581. doi:10.1038/35079066

Zeidberg, L. D., and Robison, B. H. (2007). Invasive range expansion by the Humboldt squid, *Dosidicus gigas*, in the eastern North Pacific. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 12 948–12 950. doi:10.1073/PNAS.0702043104