



Conservation management and sustainable harvest quotas are sensitive to choice of climate modelling approach for two marine gastropods

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ABSTRACT

Aim To establish the robustness of two alternative methods for predicting the future ranges and abundances for two wild-harvested abalone species (*Haliotis rubra* Donovan 1808 and *H. laevigata* Leach 1814): single atmosphere–ocean general circulation model (GCM) or ensemble-averaged GCM forecasts.

Location South Australia.

Methods We assessed the ability of 20 GCMs to simulate observed seasonal sea surface temperature (SST) between 1980–1999, globally, and regionally for the Indian and Pacific Oceans south of the Equator. We used model rankings to characterize a set of representative climate futures, using three different-sized GCM ensembles and two individual GCMs (the Parallel Climate Model and the Community Climate System Model, version 3.0). Ecological niche models were then coupled to physiological information to compare forecast changes in area of occupancy, population size and harvest area based on forecasts using the various GCM selection methods, as well as different greenhouse gas emission scenarios and climate sensitivities.

Results We show that: (1) the skill with which climate models reproduce recent SST records varies considerably amongst GCMs, with multimodel ensemble averages showing closer agreement to observations than single models; (2) choice of GCM, and the decision on whether or not to use ensemble-averaged climate forecasts, can strongly influence spatiotemporal predictions of range, abundance and fishing potential; and (3) comparable hindcasting skill does not necessarily guarantee that GCM forecasts and ecological and evolutionary responses to these forecast changes, will be similar amongst closely ranked models.

Conclusion By averaging across an ensemble of seven highly ranked skilful GCMs, inherent uncertainties stemming from GCM differences are incorporated into forecasts of change in species range, abundance and sustainable fishing area. Our results highlight the need to make informed and explicit decisions on GCM choice, model sensitivity and emission scenarios when exploring conservation options for marine species and the sustainability of future harvests using ecological niche models.

Keywords

Abalone range movement, atmosphere–ocean general circulation model, ecological niche model, ensemble-averaged climate change predictions, extinction risk, marine species distribution models.

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INTRODUCTION

Marine species found in areas close to their upper thermal-tolerance limits are potentially susceptible to local extinctions, abundance declines, range contractions and trophic cascades due to global climate change (Harley *et al.*, 2006). The conservation of threatened species and sustainable management of exploited marine populations would thus benefit substantially from models that yield robust predictions of climate-induced changes in species distributions and abundances (Pereira *et al.*, 2010). Such models need to be able to account adequately for changes in the physical environments encountered by marine fishes and invertebrates, and ideally, capture their ecological and evolutionary responses to these changes (Cheung *et al.*, 2011).

Confidence in future climate change projections will depend substantially on the predictive capacity of atmosphere–ocean general circulation models (GCMs) because it is from these that broad-scale physical environments are predicted (Stock *et al.*, 2011). However, GCM uncertainties and intermodel differences can result in vastly different predicted spatial patterns of climate change (Perkins & Pitman, 2009; Fordham *et al.*, 2011). Therefore, accounting for these uncertainties and differences when making species range and abundance predictions requires rigorous climate model evaluation. GCM uncertainties, however, have only recently been considered in ecological studies (Beaumont *et al.*, 2008), despite the potential benefits and relative ease of doing so (Fordham *et al.*, 2012a). For example, climate model evaluation may be beneficial where:

1. Ecological niche models that incorporate population dynamics are used to forecast changes in the range, abundance and catch potential of exploited marine fishes and invertebrates in response to anticipated climate change (Cheung *et al.*, 2009, 2010).
2. Downscaled climate change data are used to modify site-specific ecological models that predict how species' phenology, recruitment and population dynamics will respond to global warming (Clark *et al.*, 2003; Edwards & Richardson, 2004; Hollowed *et al.*, 2009).
3. Modelling spatio-temporal frequencies of catastrophic events, such as coral bleaching and the formation of dead zones (Donner *et al.*, 2005; Brewer & Peltzer, 2009), is of interest.

In each of these examples, potential GCM uncertainties can cascade through to forecasts of species abundances, richness and range movements (Buisson *et al.*, 2010), and influence predictions of phenology and population dynamics. If ecological forecasts, dependent on GCMs, are to be robust, climate model uncertainty must be accounted for appropriately by evaluating retrospective skill with which GCMs reproduce recent climate (Fordham *et al.*, 2011) and exploring a representative set of climate futures (Whetton *et al.*, 2012).

The skill with which GCMs reproduce current climate and past changes varies considerably amongst models. For recent generations of climate models, multimodel ensemble averages

tend to agree better with observations of present-day climate than do single models (Murphy *et al.*, 2004; Reichler & Kim, 2008), at least at global scales (Fordham *et al.*, 2011). Ensemble-averaged climate forecasts are now commonly used to account for variation between different GCM predictions in climate science research (Pierce *et al.*, 2009; Santer *et al.*, 2009); however, this approach has rarely been taken in studies of climate change impacts on marine resources (but see Durner *et al.*, 2009; Hollowed *et al.*, 2009; Hare *et al.*, 2010). Although it is reasonable to assume that the uncertainty of GCMs will affect ecological predictions (Beaumont *et al.*, 2008) and adaptation assessments under global climate change (Dessai *et al.*, 2009), the potential advantages of evaluating the hindcasting skill of GCMs, and using this information to generate a set of possible climate futures for investigating ecological responses to climate change, has not been formally investigated for marine or terrestrial organisms.

To begin to address this gap, we examine the effects of GCM uncertainty on spatio-temporal predictions of geographical range, abundance and sustainable fishing area for two commercially exploited molluscs: greenlip and blacklip abalone (*Haliotis rubra* and *H. laevisgata*) in South Australia (Fig. 1) for the period 2000–2100. The South Australian abalone industry is worth more than AU\$12 million annually (Mayfield *et al.*, 2011), and its management requires robust forecasts of sea surface temperature (SST) (Russell *et al.*, 2012). We compare GCM predictive performance for SST by ranking twenty GCMs according to their skill in reproducing observed patterns of regional (Indian and Pacific Oceans) and global SST, and assess their consistency with other GCMs. We examine the relative influence of hindcasting skill on forecast areas of occupancy, population sizes and harvest areas, for different-sized GCM ensemble suites and individual GCMs. We also compare the influence of choice of climate sensitivity (the primary determinant of overall climate change; Meehl *et al.*, 2007) and greenhouse gas emission scenario on these ecological predictions. We show that the choice of GCM, and whether or not to use ensemble-averaged climate forecasts, will strongly influence predictions of future abalone ranges and abundances, thereby substantially shaping the required response from resource managers.

METHODS

We modelled spatially explicit abundance patterns of *H. rubra* and *H. laevisgata* separately for each species across their ranges (north of latitude 39.5° S) using an ensemble ecological niche modelling approach that combined likelihood-based generalized linear models and boosted regression trees. For each modelling technique, a two-step procedure was used to predict (at $\sim 1 \times 1$ km grid cell resolution): (1) the current probability of presence, followed by (2) current abundance conditional on presence (Mellin *et al.*, 2012). Previous work showed that the best primary predictors of abundance were mean coolest monthly (August) SST and, to a lesser extent, its standard deviation. A positive linear

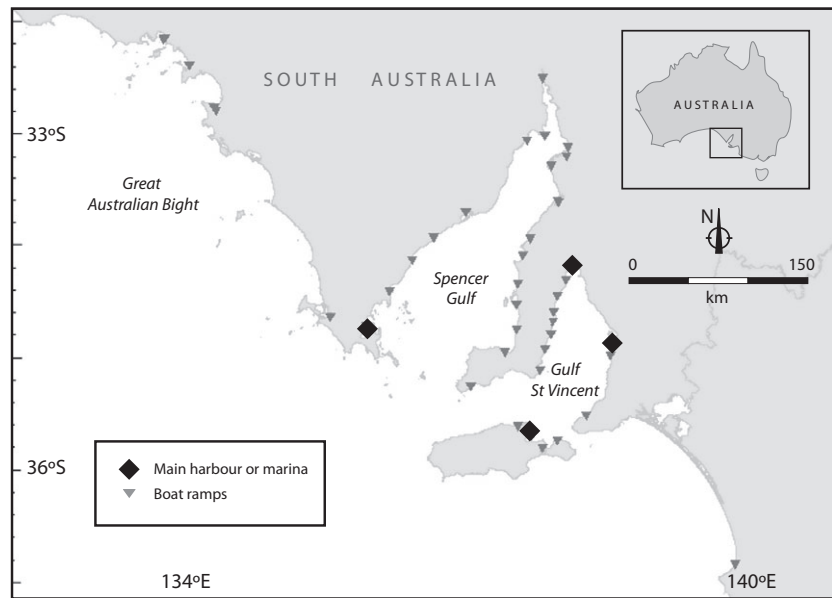


Figure 1 Extent of the South Australian abalone management area, showing key fishing harbours and boat ramps.

correlation between August SST and *H. rubra* abundance explained 34% of model structural deviance; a positive quadratic relationship for *H. laevisgata* explained 17% of deviance (Mellin *et al.*, 2012). Harvest intensity, water depth and distance from the nearest boat launching point were also important predictors. Collectively all predictors accounted for up to 55 and 45% of deviance explained in the abundance of *H. rubra* and *H. laevisgata*, respectively (Mellin *et al.*, 2012). Predicted abundance estimates for each species across the seascape accounted for the proportion of each grid cell expected to encompass rocky reef habitats (based on Watts *et al.*, 2011). This is because the presence of *H. rubra* and *H. laevisgata* is restricted to rocky reefs (McShane & Smith, 1991; Shepherd, 1998).

We used MAGICC/SCENGEN 5.3 (www.cgd.ucar.edu/cas/wigley/magicc/) to assess the ability of twenty CMIP3 GCMs [Coupled Model Intercomparison Project 3 GCM database (www-pcmdi.llnl.gov)] to simulate observed seasonal (December–February; March–May; June–August; September–November) SST (1980–1999), globally and for the Indian and Pacific Oceans (south of the Equator and north of latitude -52.5°). MAGICC/SCENGEN 5.3 is a freely available software package for the Windows operating system that allows: (1) the full suite of GCMs used for the Fourth Assessment Report (AR4) of the Intergovernmental Panel on Climate Change (IPCC) to be directly ranked according to their ability to simulate historical climate conditions over regional and global domains; (2) multimodel ensemble-averaged forecasts of surface temperature and precipitation (and mean sea level pressure), for any given year up to 2100, to be generated using a user-defined subset of GCMs; and (3) results to be produced for matched reference and policy emissions scenarios (Fordham *et al.*, 2012a). We chose SST because physiological studies and field-based surveys (1980–2009) indicate a strong biophysical response to SST, through

recruitment and mortality (Russell *et al.*, 2012; also see below). We did not assess the ability of IPCC Fifth Assessment Report (AR5) GCMs because not all modelling groups have submitted data to the CMIP5 database, meaning that a full assessment of AR5 models is not yet possible – however, the same approach will be applicable to AR5 models once they all have been released.

Because all GCM skill (or validation) metrics have strengths and weaknesses, we considered six alternatives which are described in detail elsewhere (Fordham *et al.*, 2011). These were model bias (i.e. the difference between model and observed spatial means averaged over a user-specified area), pattern correlation, standard and centred root-mean-square error and comparison indices devised by Reichler and Kim (Reichler & Kim, 2008) and Taylor (Taylor, 2001). We ranked GCMs according to each statistic and calculated the seasonal and annual cumulative rank. We separately standardized the annual and seasonal cumulative ranks by dividing them by the smallest cumulative rank for a given time period. We used model rankings to produce three different-sized model ensembles (5-model, 7-model and 10-model) based on regional and global retrospective skill with which GCMs reproduce recent SST (the method is described in detail in Appendix S1).

To generate the 7-model average, we first chose four models with good global skill. We then chose an additional three models with good regional skill (Appendix S1). We limited the number of flux adjusted models to one, because flux adjustment can give models an advantage when using hindcasting validation procedures (Fordham *et al.*, 2011). To generate the 5-model ensemble, we started with the 7-model case and eliminated one model from the global assessment and one from the regional assessment. For the 10-model case, we used six models from the global assessment and four models from the regional assessment; and relaxed the rule regarding flux adjustment

to include two flux adjusted models. We limited ensemble model sets to 10-model averages because ensemble-averaged climate forecasts based on large numbers of models are relatively insensitive to the choice of models used to generate projections (Pierce *et al.*, 2009; Santer *et al.*, 2009). We also used model rankings to choose two individual GCMs – the Parallel Climate Model (PCM; Washington *et al.*, 2000) and the Community Climate System Model, version 3.0 (CCSM-3; Collins *et al.*, 2006) – commonly used in marine ecological studies (e.g. Boyd & Doney, 2002; Donner *et al.*, 2005), and with contrasting skill in simulating SST over the reference period (Appendix S1). We modelled greenhouse-gas emissions for individual GCMs and ensembles of GCMs according to a no-climate-policy reference scenario (MiniCAM Ref.) (Clarke *et al.*, 2007) with a best-estimate climate sensitivity of 3 °C (Meehl *et al.*, 2007). Climate sensitivity is the equilibrium warming resulting from a doubling of CO₂ and, through its effect on global-mean temperature, is the primary determinant of overall climate change (Meehl *et al.*, 2007).

These five GCM scenarios characterize a small set of representative climate futures (Whetton *et al.*, 2012), with the PCM predicting the lowest increase in summer (March) SST and the highest increase in winter (August) SST, and the model averaged predictions providing intermediate forecasts between those given by the PCM and CCSM-3 for March SST (Fig. S1). To compare the influence of model choice with other common decisions faced by natural resource managers, such as choice of greenhouse gas emission scenario or climate sensitivity, we also did a comparative analysis using the 7-model ensemble. Using the 7-model ensemble, we simulated a highly contrasting (strong mitigation) emission scenario (LEV1), designed to stabilize at an equivalent CO₂ concentration of 450 ppm (Wigley *et al.*, 2009), and the 90th percentiles of the range in expected climate sensitivity for GCMs in the AR4/CMIP3 database [i.e. 1.5 (low sensitivity, LS) and 6 °C (high sensitivity, HS)] (Wigley *et al.*, 2009).

We forecast change in average monthly SST using MAGICC/SCENGEN for the coolest and warmest months of the year (August and March) at decadal time slices (2000–2100) under each of the eight climate model scenarios. By working within the MAGICC/SCENGEN framework, we isolated climate sensitivity effects and modelled a more distinct anthropogenic climate change signal by averaging across individual runs of GCMs, a procedure that helps to isolate the signal from internally generated noise (Fordham *et al.*, 2012a). In this way, intermodel differences in future climate forecasts were studied without being confounded by intermodel differences in climate sensitivity.

We downscaled our SST projections by first applying bilinear interpolation to reduce discontinuities in the perturbed climate at the GCM grid-box boundaries (~ 50 × 50 km latitude/longitude). We then added the forecast climate anomaly (change in SST since 1994) directly to a high-resolution (~ 1 × 1 km) average monthly climatology (1985–2004) (following Russell *et al.*, 2012).

We compared predicted area of occupancy, population size and spatial patterns of abundance across the eight climate model scenarios to explore how choice of GCM, model sensitivity and emissions scenario influenced predicted abalone abundance and sustainable fishing areas in South Australia (Fig. 1). We used the minimum adult density needed to maintain the rates of recruitment required to sustain commercial harvests of *H. rubra* and *H. laevisgata* (20 individuals 100 m⁻²; Shepherd & Partington, 1995) to define a sustainable fishing area.

We restricted forecast abundance to grid cells with SST below species-specific, upper thermal-tolerance levels, based on the following evidence: (1) optimal temperatures for *H. rubra* and *H. laevisgata* are 17.0 and 18.3 °C, respectively (Gilroy & Edwards, 1998) and relative abundance declines with SST above these thermal bounds (Fig. S2); (2) temperatures > 18–20 °C affect juvenile recruitment and growth negatively (Shepherd & Breen, 1992; Harris *et al.*, 2005); (3) temperatures > 21 °C (*H. rubra*) and 22.5 °C (*H. laevisgata*) cause a detrimental behavioural response in adults, inhibiting feeding and growth (Gilroy & Edwards, 1998); (4) the critical thermal maxima (i.e. temperature at which 50% of animals die) is approximately 27 °C, but temperature-related deaths can occur at temperatures as low as 24.5 °C for some individuals (Gilroy & Edwards, 1998). Considering that population recruitment would be impossible, or severely dampened, at temperatures greater than 21 °C for *H. rubra* and 22.5 °C for *H. laevisgata*, and that a 1 °C buffer is needed to account for the mean difference between sea surface and seabed temperatures (Fig. S3), we set the upper thermal tolerance to a SST of 22 °C for *H. rubra* and 23.5 °C for *H. laevisgata*.

We contrasted the effects of GCM and ecological-niche-model uncertainty on the mean predicted abundance of *H. rubra* and *H. laevisgata* using a representative set of possible climate futures based on the 7-model average, CCSM-3, PCM (See Fig. S1). For each species, we predicted abundances in 2100 in each grid cell (~ 1 × 1 km) according to each of the three climate model scenarios and calculated average cell abundance across scenarios. We then calculated the deviation (% difference) from this average predicted abundance per grid cell for each individual climate model scenario. We then calculated mean deviation (%) across all cells in the study region to generate, for each species, an estimate of mean prediction error resulting from the application of this range of climate models. We compared these estimates of prediction error to the mean prediction error from ecological niche models estimated using 10-fold cross-validation (Franklin, 2009) and reported in Mellin *et al.* (2012).

RESULTS

For most of the model performance metrics, the 7-model ensemble average outperformed single models in its ability to hindcast recently observed seasonal SST at global and regional scales (Table 1). Only the model bias metric and the Reichler-Kim metric (Reichler & Kim, 2008) indicated that

Table 1 Climate model skill (atmosphere–ocean general circulation model; GCM) in simulating observed sea surface temperature in summer (1 Dec–28 Feb), autumn (1 Mar–31 May), winter (1 Jun–31 Aug) and spring (1 Sep–30 Nov) over the reference period (1980–1999) for the 7-model ensemble average (7-mod) and for CCSM-3 and PCM, according to a range of comparison metrics and two geographic extents (*Global* and *Regional*). Climate model scenarios are ordered by the sum of model ranks (i.e. across the six metrics) divided by the smallest observed cumulative rank for 20 GCMs in the AR4/CMIP3 database (*Relative Sum Rank*)

Geographic extent	Season	Model	Correl	RMSE (mm day ⁻¹)	Bias (mm day ⁻¹)	CRMSE (mm day ⁻¹)	RK index	T index	Relative sum rank	
Global	Summer	7-mod	0.997 (1)	1.205 (1)	0.748 (9)	0.945 (1)	0.997 (1)	2.5 (7)	1.053	
		CCSM-3	0.993 (5)	1.422 (3)	0.25 (2)	1.4 (4)	0.980 (12)	1.713 (2)	1.474	
	Autumn	PCM	0.979 (18)	2.776 (20)	1.317 (14)	2.443 (18)	0.981 (11)	4.612 (20)	5.316	
		7-mod	0.996 (1)	1.361 (1)	0.905 (9)	1.016 (1)	0.998 (1)	2.872 (8)	1.105	
	Winter	CCSM-3	0.992 (5)	1.593 (3)	0.535 (5)	1.501 (5)	0.978 (14)	2.068 (1)	1.737	
		PCM	0.988 (10)	2.828 (17)	2.124 (20)	1.868 (11)	0.994 (3)	5.261 (20)	4.263	
	Spring	7-mod	0.997 (1)	1.239 (1)	0.771 (9)	0.97 (1)	0.996 (3)	3.014 (7)	1.294	
		CCSM-3	0.994 (5)	1.349 (2)	0.06 (1)	1.347 (3)	0.987 (7)	1.911 (2)	1.176	
	Regional	Summer	PCM	0.979 (19)	3.315 (20)	1.469 (16)	2.971 (20)	0.962 (15)	4.563 (13)	6.059
			7-mod	0.997 (1)	1.225 (1)	0.879 (8)	0.854 (1)	0.995 (1)	2.83 (8)	1.000
	Regional	Summer	CCSM-3	0.994 (2)	1.289 (2)	0.229 (2)	1.269 (2)	0.979 (12)	1.838 (2)	1.100
			PCM	0.991 (10)	2.248 (11)	1.648 (16)	1.528 (8)	0.995 (2)	4.514 (17)	3.200
Autumn		7-mod	0.997 (2)	0.797 (3)	0.566 (10)	0.562 (1)	0.998 (2)	2.481 (7)	2.083	
		CCSM-3	0.996 (4)	0.72 (2)	0.028 (1)	0.72 (3)	0.945 (15)	1.44 (2)	2.250	
Winter		PCM	0.986 (16)	1.234 (8)	0.063 (2)	1.232 (14)	0.992 (6)	2.868 (9)	4.583	
		7-mod	0.997 (1)	0.674 (1)	0.397 (7)	0.544 (1)	0.999 (1)	1.926 (6)	1.000	
Spring		CCSM-3	0.996 (4)	0.719 (2)	0.168 (5)	0.699 (3)	0.940 (18)	1.213 (1)	1.941	
		PCM	0.975 (21)	1.755 (17)	0.055 (2)	1.754 (21)	0.987 (8)	3.447 (17)	5.059	
Regional		Summer	7-mod	0.997 (1)	0.772 (1)	0.462 (8)	0.618 (1)	0.997 (2)	2.249 (9)	1.048
			CCSM-3	0.995 (2)	0.774 (2)	0.171 (3)	0.755 (3)	0.967 (13)	1.421 (1)	1.143
Regional		Autumn	PCM	0.988 (19)	2.451 (20)	2.141 (20)	1.192 (18)	0.993 (8)	5.751 (20)	5.000
			7-mod	0.995 (3)	0.824 (1)	0.033 (2)	0.824 (3)	0.950 (13)	1.479 (1)	1.000
Regional	Winter	CCSM-3	0.997 (1)	0.928 (3)	0.667 (10)	0.645 (1)	0.998 (1)	2.52 (9)	1.087	
		PCM	0.991 (12)	2.262 (20)	1.994 (20)	1.068 (11)	0.995 (3)	5.445 (20)	3.739	

The comparison metrics are model bias (*Bias*), pattern correlation (*Correl*), standard (*RMSE*) and centred root-mean-square errors (*CRMSE*), and comparison indices suggested by Reichler & Kim (2008) (*RK index*) and Taylor (2001) (*T index*). The regional scale is the Pacific and Indian Oceans (south of the equator and north of latitude -52.5°). Numbers in parenthesis indicate the relative ranking of the 7-model average and single GCMs based on a suite of AR4/CMIP3 GCMs (see Methods for further details).

the 7-model ensemble was outperformed; nonetheless, the 7-model ensemble was always ranked in the top 50% of alternative model combinations across all metrics, geographical extents and seasons. The CCSM-3 had superior retrospective skill in reproducing recent SST compared to the PCM (Table 1).

Total abundance for both *H. rubra* and *H. laevigata* was forecast to increase in response to increased SSTs in cool months of the year. Concordantly, initial area of occupancy was predicted to decrease due to increased SSTs in warm months of the year, which in some areas are expected to exceed thermal tolerances that limit population recruitment, adult growth and survival (Fig. S4). However, the severity of forecast change in population size and area of occupancy was highly variable and depended on choices of GCM, climate sensitivity and emission scenario (Figs 2 & 3).

For *H. rubra*, ensemble-averaged climate forecasts (5-, 7- and 10-model ensembles) predict an intermediate rate of contraction in area of occupancy (61–72% reduction in extent of occurrence by 2100) compared to either more pessimistic (CCSM-3) or more optimistic (PCM) forecasts from single GCMs (Fig. 2). According to CCSM-3, *H. rubra* stocks

will experience a faster rate of contraction (85% reduction in extent of occurrence by 2100) when compared to ensemble-averaged climate forecasts, modelled under an identical emission scenario and with the same climate sensitivity of 3 °C. The velocity of reduction in area of occupancy for *H. rubra* according to CCSM-3 was most similar to that forecast using the 7-model ensemble with climate sensitivity set at the upper 90th percentiles of the range in expected climate sensitivity (6 °C) (89% by 2100). In contrast, the PCM forecast a much slower rate of contraction in area of occupancy (50% by 2100) compared to ensemble-averaged climate forecasts with a similar climate sensitivity and emissions scenario (Fig. 2). The PCM predicted a much more rapid rate of population growth than the ensemble-averaged climate forecasts and CCSM-3: +94% compared to a +24–58% increase in population size between 2000 and 2100 (Fig. 2). The rate of change in area of occupancy and population size for the PCM was most similar to the 7-model ensemble with climate sensitivity set at the lower 90th percentiles of the range in expected climate sensitivity (1.5 °C) (Fig. 3). The influence of model choice on population size for *H. laevigata* was similar to predictions for *H. rubra*, but differed for area of occupancy (Figs 2 & 3). Namely, area of occupancy for the PCM,

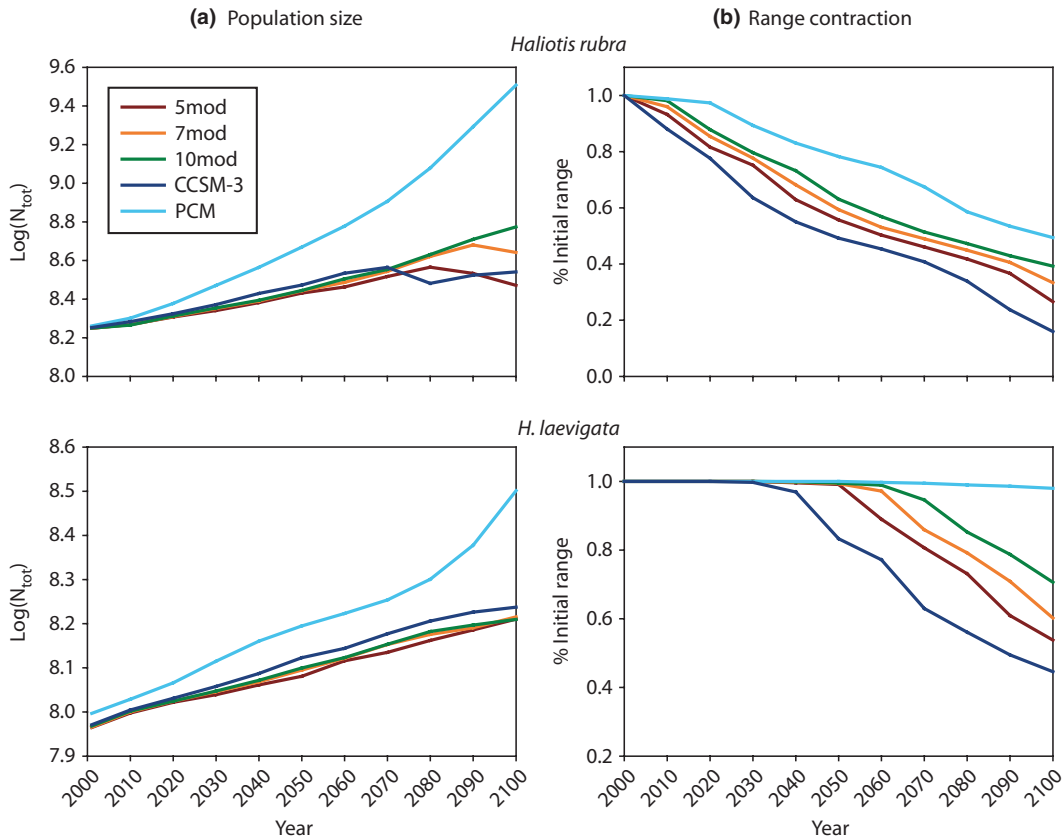


Figure 2 Forecast total population size [$\text{Log}(N_{\text{tot}})$] and change in area of occupancy (% Initial range) for *H. rubra* and *H. laevigata* between 2000 and 2100 according to different-sized model ensembles [5-model (5-mod), 7-model (7-mod) and 10-model (10-mod)], and two individual GCMs that are commonly used in published ecological applications (CCSM-3 and PCM). Emissions are modelled according to a no-climate-policy reference scenario (MiniCAM Ref.) and a climate sensitivity of 3 °C.

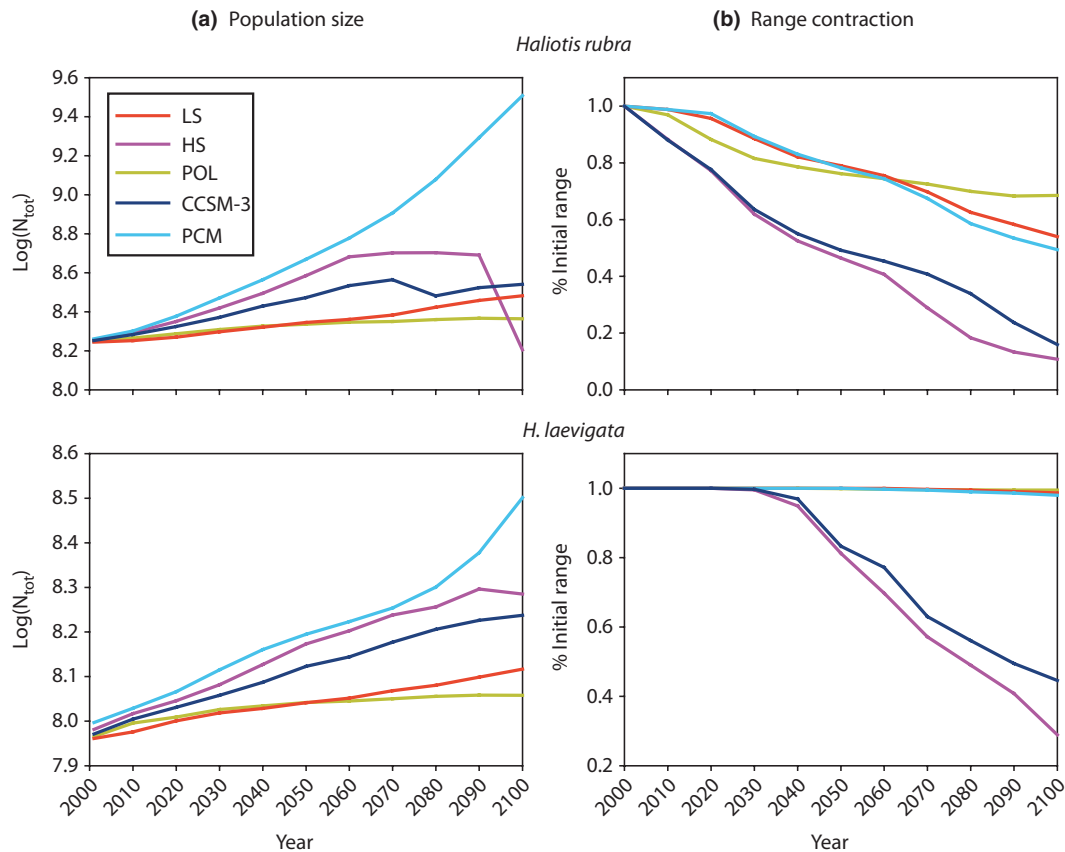


Figure 3 Forecast total population size [$\text{Log}(N_{\text{tot}})$] and change in area of occupancy (% Initial range) for *H. rubra* and *H. laevisgata* between 2000 and 2100 for the 7-model ensemble for the extremes of the range in expected climate sensitivity [$1.5\text{ }^{\circ}\text{C}$ (LS) and $6\text{ }^{\circ}\text{C}$ (HS)] according to a no-climate-policy reference scenario (MiniCAM Ref.). We also show population size and change in area of occupancy for the 7-model ensemble according to the LEV1 policy (strong greenhouse gas mitigation) emission scenario (POL) and a climate sensitivity of $3\text{ }^{\circ}\text{C}$, and the CCSM-3 and PCM models with parameters as described in Fig. 2.

7-model ensemble with climate sensitivity set at $1.5\text{ }^{\circ}\text{C}$ and 7-model ensemble Policy emission scenario was predicted to remain relatively stable for *H. laevisgata*.

General circulation model choice affected the location and size of productive *H. rubra* and *H. laevisgata* fishing areas in South Australia in 2100 in similar ways (Figs 4 & 5, Figs S5–S7). The hindcasting skill of CCSM-3 ranked a close second to the 7-model ensemble (Table 1); however, spatial patterns of forecast change in abundance (i.e. total population size and area of occupancy) differed markedly from most of the ensemble-based predictions (Figs 4 & 5, Fig. S5–S7). The CCSM-3 forecasts were most similar to the 7-model ensemble climate scenario with high climate sensitivity (Figs 4 & 5). Thus ranking GCMs using model skill in simulating reference conditions does not guarantee that forecasts will be similar amongst closely ranked models.

Uncertainty arising from variation in choice of climate model (7-model ensemble, CCSM-3, PCM) had a larger effect on error in abundance estimates for *H. rubra* than for *H. laevisgata*, resulting in a mean prediction error of 65 and 25%, respectively. In comparison, ecological niche model-related errors were 37 and 47% for *H. rubra* and *H. laevisgata*,

respectively. These results show that abundance predictions of *H. rubra* were more sensitive to GCM uncertainty, whereas those of *H. laevisgata* were influenced more by ecological-niche-model uncertainty; nonetheless, the influence of climate model choice was still large enough to cause large variation in spatial abundance patterns (Fig. 5).

DISCUSSION

Until now, ecological evidence for incorporating ensemble-averaged climate forecasts into sets of representative climate futures for use in predicting climate change impacts and developing conservation and management strategies has been missing (Cook *et al.*, 2010). We show that choice of GCM, and the decision of whether to use ensemble-averaged or single-model climate forecasts, can strongly influence spatio-temporal projections of future location and population size of marine species under climate change. We demonstrate that although single models can display similar retrospective (hindcasting) skill to the ensemble in predicting past climates, they can generate very different forecasts of spatial abundance patterns.

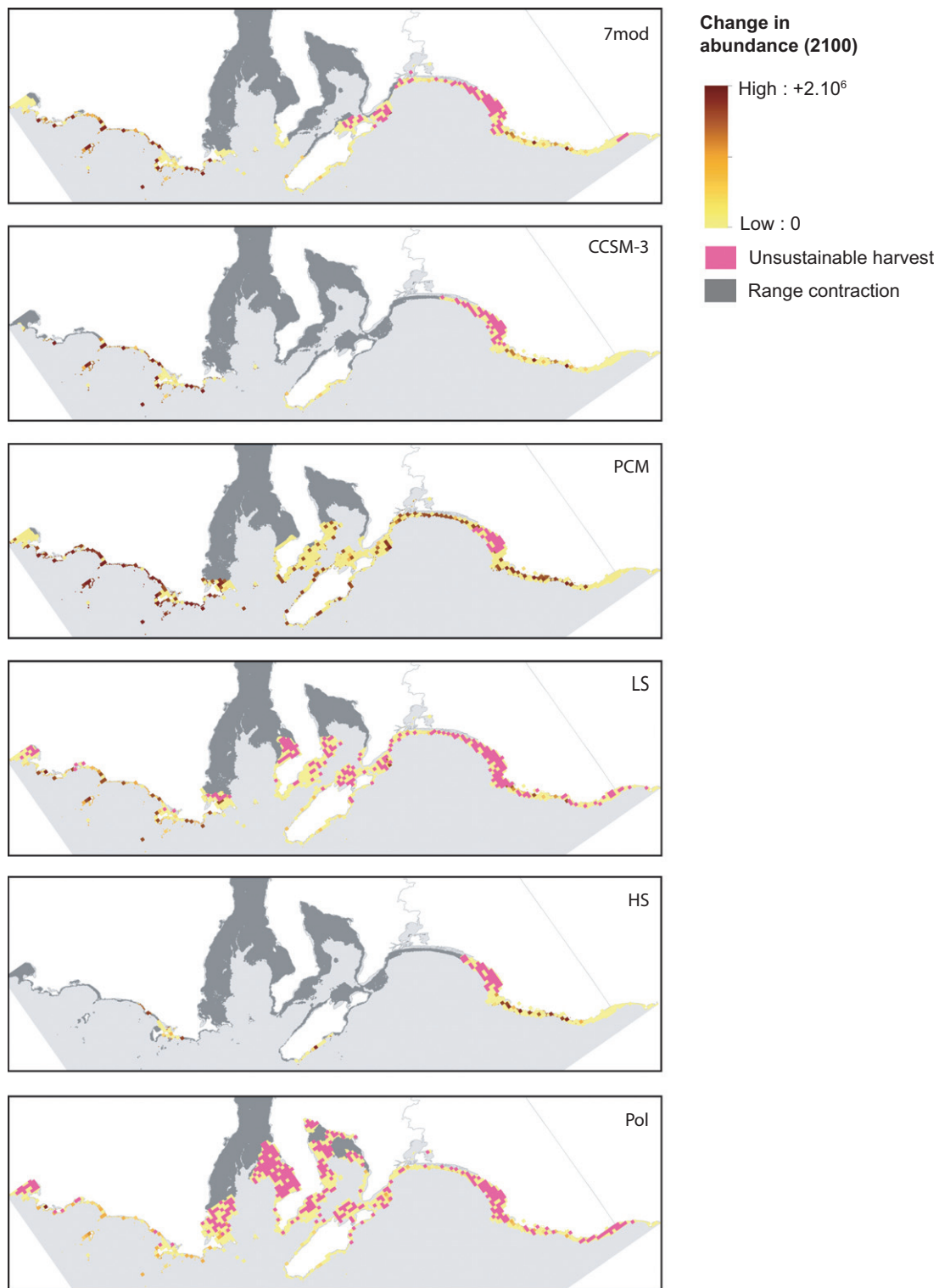


Figure 4 Change in area of occupancy and spatial abundance for *H. rubra* in 2100 (number of individuals 100 km^{-2}) in South Australia. Change in abundance is mapped for the 7-model ensemble (7-mod) and for two commonly used GCMs (CCSM-3 and PCM) – modelled according to a no-climate-policy reference scenario (MiniCAM Ref.) and a likely climate sensitivity of 3°C . We also show change in abundance for the 7-model ensemble for the extremes of the range in expected climate sensitivity [1.5°C (LS) and 6°C (HS)] and according to the LEV1 policy emission scenario (POL). Range contraction shows areas where *H. rubra* is predicted to experience local extinctions by 2100. Unsustainable harvest shows areas where abalone abundance is forecast to be < 20 individuals 100 m^{-2} – the minimum density needed to maintain the rates of recruitment required to sustain any fisheries catches. Mapped *H. rubra* abundance for the year 2000 is available as supplementary material (Fig. S5).

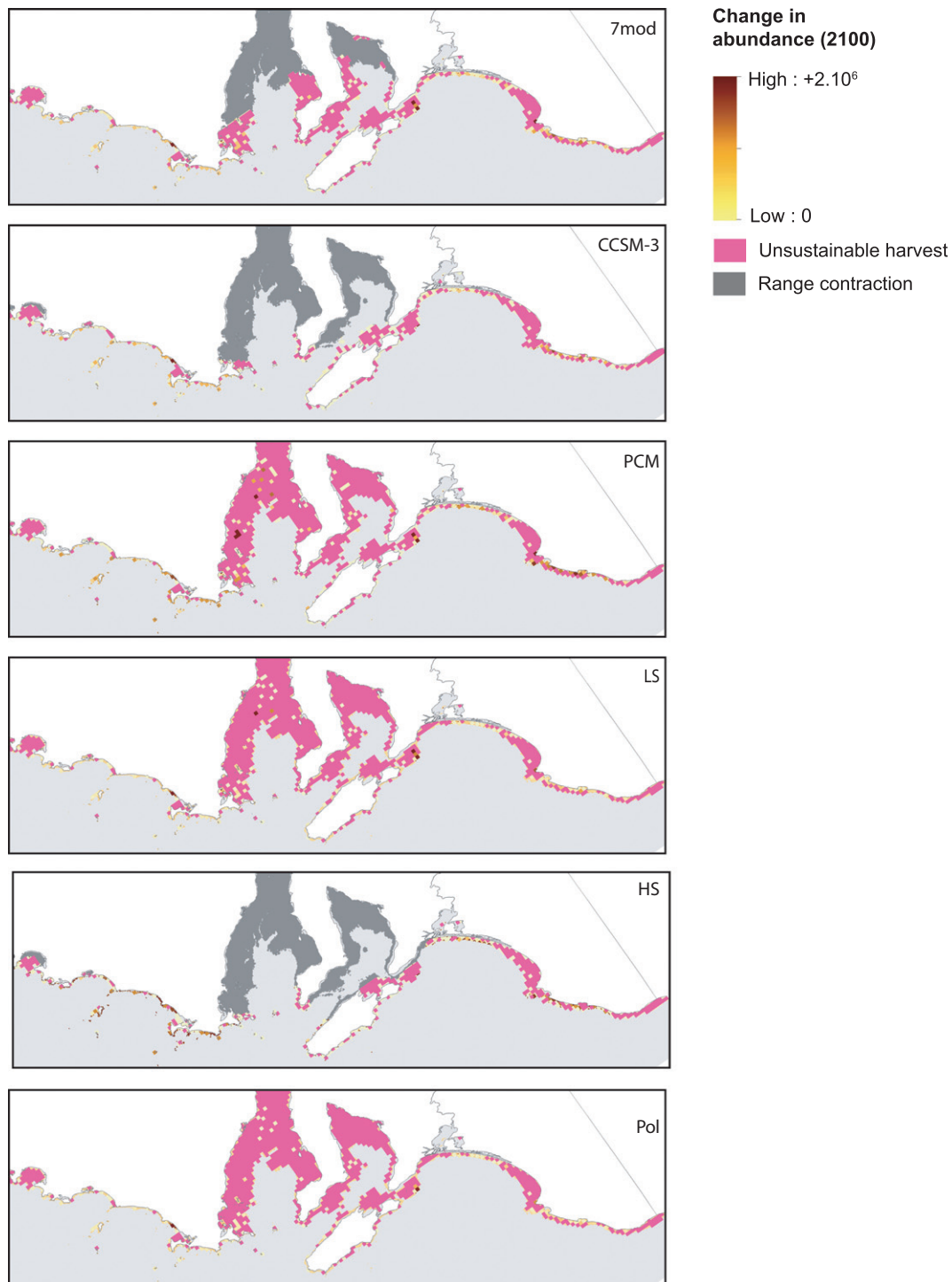


Figure 5 Change in area of occupancy and spatial abundance for *H. laevigata* (number of individuals 100 km^{-2}) in 2100 in South Australia. All other parameters are identical to Fig. 4. Mapped *H. laevigata* abundance for the year 2000 is available as supplementary material (Fig. S5).

The range and abundance of many exploited marine species, like *H. rubra* and *H. laevigata*, are expected to be affected negatively by climate change (Stock *et al.*, 2011), and ecological niche models are increasingly important for informing the management of exploited marine fishes and

invertebrates (Cheung *et al.*, 2009, 2010). Thus, our results strongly suggest that better outcomes in marine resource management will be available through the use of sets of representative climate futures, centred around regionally and globally skilful ensemble-averaged climate forecasts, rather

than uncritical use of GCM information. Our contention here is supported by ensemble-averaged climate forecasts: (1) providing better agreement with observations of recent seasonal SST (an important climate force in conditioning ecological responses in marine systems; Chavez *et al.*, 2003; Behrenfeld *et al.*, 2006) than do single models; and (2) accounting for inherent uncertainties that result from GCM differences, which can influence forecasts of abundance and area of occurrence and sustainable fishing area.

The extent of occurrence and area of occupancy of *H. rubra* and *H. laevisgata* in South Australia are likely to decline (compared to present-day distributions) during the 21st Century, owing to increased SSTs in warmer months of the year exceeding thermal tolerances in northern regions of their current range. Indeed, our models predicted range decline in *H. rubra* even under the most optimistic of the current credible greenhouse-gas-mitigation scenarios (LEV1), which is designed to stabilize at an equivalent CO₂ concentration of 450 ppm. In contrast, we forecast that the total population sizes of *H. rubra* and *H. laevisgata* will increase, driven by warmer SSTs leading to enhanced abalone fertility and recruitment. Gonad development increases linearly with temperature up to 18 °C (Grubert & Ritar, 2004b), leading to a greater reproductive output and development of larvae (Grubert & Ritar, 2004a), thereby promoting faster settlement and increased juvenile survival (Russell *et al.*, 2012). Compared to CCSM-3 or the ensemble-averaged climate forecasts, the PCM predicted a relatively high decadal rate of increase in August SST, but a comparatively low rate of change in March SST (Fig. S1). The net results of these changes under this model scenario are large predicted population sizes for *H. rubra* and *H. laevisgata* and a slower rate of range contraction, or range stability (Fig. 2). However, populations are often limited by endogenous processes such as density feedbacks (Brook & Bradshaw, 2006). Thus, it is possible that intraspecific resource competition (a process not considered in our models) could potentially modify population abundance, dampening the predicted positive influence of SST on population size for *H. rubra* and *H. laevisgata*.

From a fisheries management perspective, our models predicted climate change will shift southwards the potential harvest areas for *H. rubra* by 2100 due to increasing SST. Currently, uninhabited and low-density habitats in the South Australian fishery will become warmer and more suitable for population establishment, growth and persistence, all else being equal. A similar, but less pronounced shift in fishing areas is expected for *H. laevisgata*. However, where fishers can expect to harvest abalone in 2100 very much depends on the climate model scenario used. Commonly used GCMs, with opposing retrospective skill in simulating recent regional and global SST, provide contrasting future predictions of the size of the potential abalone fishing area in South Australia, and the spatial distribution of harvestable sites. For instance, under the PCM, the future of the *H. rubra* industry in South Australia is encouraging, being characterized by high, contiguous

densities of abalone, reasonably close to fishing harbours and market centres. According to the CCSM-3 model, by contrast, harvestable stocks are forecast to be relatively sparse, posing management challenges for this commercially important fishery. The most plausible scenario for *H. rubra*, based on ensemble-averaged climate forecasts, suggest a more viable abalone fishery (compared to CCSM-3) with larger adjoining potential fishing areas, and where distances between fishing harbours and harvest sites are short.

For *H. laevisgata*, the economically important fishing areas located in the Spencer Gulf and Gulf of St Vincent are predicted to remain unchanged, contract or disappear depending on whether climate change is simulated using the PCM, suites of GCMs or the CCSM-3, respectively. Because ensemble-averaged climate forecasts provide more robust estimates of future change (see below), the most likely scenario is that these valuable fishing areas will be lost in all but the southern sections of the Spencer Gulf and Gulf of St Vincent. Although our predictions capture key components of ocean systems and how they are likely to change in the future, they might not sufficiently capture local-upwelling (Kämpf *et al.*, 2004) and its potential influence on the range dynamics of abalone.

Resource managers often use ecological niche models to evaluate climate management options (Willis *et al.*, 2009). Therefore, the choice of climate model scenario clearly must be integral to any future industry risk analysis for an abalone fishery, an enterprise worth more than AU\$200 million annually. Because abalone are amenable to introduction and translocation (Dixon *et al.*, 2006), ecological niche models linked to robust climate forecasts could be used to assist the migration of *H. rubra* and *H. laevisgata* to future habitats predicted to be climatically suitable and stable (Fordham *et al.*, 2012c), thereby reducing the risk that the velocity of climate change will outpace dispersal and enhancing resilience and potential sustainability of the abalone fishery. These models could also be used to identify key areas to establish refugia to replenish stocks in surrounding harvest zones (Shepherd & Brown, 1993).

Beyond GCMs, there is evidence from various applications of numerical modelling to suggest that multimodel averages often yield better predictions than do single models (Johnson & Omland, 2004). In ecology, including those studies using ecological niche models (Araújo & New, 2007), weighted model averaging is now widely used to account for model uncertainty (Burnham & Anderson, 2002). Thus, because they display good skill in predicting observed conditions and they account for important intermodel uncertainties that can influence forecasts (Fordham *et al.*, 2011), ecological niche models linked to ensemble-average climate forecasts should provide fishery managers with a more realistic and robust tool for projecting the influence of climate change on abalone range and abundance. This is especially so, when treated as the 'most likely' of a set of representative climate scenarios, because adaptation planning requires consideration of a range of plausible and relevant climate futures (Whetton *et al.*, 2012).

Although CCSM-3 simulations of observed and regional seasonal SST were ranked a close second to the 7-model ensemble (Table 1), and even outperformed the ensemble average for some evaluation metrics, spatial patterns of forecast change in abundance differed markedly from most of the ensemble-based predictions (Figs 3–5, Fig. S6 and S7). The CCSM-3 forecasts were most similar to the 7-model ensemble climate scenario when climate sensitivity (the equilibrium warming resulting from a doubling of CO₂) was set to 6.0 °C, rather than the much more likely estimate of 3.0 °C (Meehl *et al.*, 2007). This observation reinforces our argument for using multimodel averaging to generate future climate projections because, through its effect on global-mean temperature, climate sensitivity is a primary determinant of overall climate change.

While our ecological niche models successfully predicted present-day spatial patterns of abalone abundance (Mellin *et al.*, 2012), they incorrectly projected abalone occurrence in some areas of the species' South Australian range. This is probably due to a combination of predictor uncertainty (Watts *et al.*, 2011) and regional environmental conditions not reflected in our model parameters. Predictor uncertainty might be reduced in future models by incorporating information on the location of soft-sediment trawl fisheries, which are now accurately tracked. Furthermore, the explicit incorporation of metapopulation processes, modified dynamically by exploitation, food availability and climate change, could improve the model's predictive performance (Fordham *et al.*, 2012b,d).

It is generally assumed that GCM skill in simulating observed conditions translates to more reliable climate projections (Perkins *et al.*, 2009; Pierce *et al.*, 2009; Santer *et al.*, 2009). However, ranking GCMs based on model skill in simulating reference conditions does not necessarily guarantee that forecasts will be similar amongst closely ranked models according to hindcasting skill (Whetton *et al.*, 2007). Such inconsistencies arise because GCMs differ in how they model complex physical processes of climate systems and their interactions (Knutti *et al.*, 2010), and these differences might only appear when used to forecast future conditions (Stock *et al.*, 2011). Better understanding of potential differences between skilful GCMs (or suites of models) is important because they transfer to ecological predictions, something which, until now, had remained unclear.

By averaging across an ensemble of highly ranked skilful GCMs, inherent uncertainties that result from GCM differences are incorporated, providing a consensus (average) forecast of change in species range, abundance and sustainable fishing area. Ideally, ecologists and resource managers should use a mixed approach, evaluating the sensitivity of their outcomes to both ensemble- and some individual-model forecasts, while acknowledging that climate model-related variability is one of a number of important sources of uncertainty in forecasts of climate impacts on marine resources. Using single-model climate forecasts based on GCMs with contrasting skill in simulating recent climates, in

combination with ensemble-averaged climate forecasts, can reduce the effort required to develop a range of plausible climate futures for the purposes of risk assessment. However, the generality of this conclusion (across taxa and systems) needs further investigation. Our abalone case study highlights the need to use user-friendly climate modelling programs, such as MAGICC/SCENGEN, to allow the ecological research community to make more informed decisions on GCM choice, model sensitivity and emissions scenarios when exploring future climate-induced changes in species' ranges, abundance and sustainable fishing areas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Global and regional analysis of GCM skill in simulating seasonal SST over the reference period 1980–1999.

Figure S1 Forecast average March and August SST across the study region according to five GCM approaches (5-mod, 7-mod, 10-mod, CCSM-3 and PCM).

Figure S2 Influence of August SST on the density of *H. rubra* and *H. laevigata*.

Figure S3 Relationship between seabed temperature, sea surface temperature (SST) and depth along the South Australian and Victorian coastlines at depths less than 30m.

Figure S4 Influence of climate model choice on forecast March SST in South Australia between 2000 and 2100.

Figure S5 Current day spatial abundance patterns for *H. rubra* and *H. laevigata* in Southern Australia.

Figure S6 Change in area of occupancy and spatial abundance for *H. rubra* in 2100 in South Australia for different-sized model ensembles suites.

Figure S7 Change in area of occupancy and spatial abundance for *H. laevigata* in 2100 in South Australia for different-sized model ensembles suites.

BIOSKETCH

This study is part of a broader project supported by the Australian Research Council (DP1096427), which is developing a quantitative understanding of the demographic mechanisms underpinning range margins and incorporating this new knowledge into spatially dynamic population-habitat models. The results will provide generalizations on how geographic range size and structure change through time in response to global change and deliver a new toolbox for exploring trade-offs inherent in conservation planning.

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