

# Effects of climate-driven primary production change on marine food webs: implications for fisheries and conservation

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## Abstract

Climate change is altering the rate and distribution of primary production in the world's oceans. Primary production is critical to maintaining biodiversity and supporting fishery catches, but predicting the response of populations to primary production change is complicated by predation and competition interactions. We simulated the effects of change in primary production on diverse marine ecosystems across a wide latitudinal range in Australia using the marine food web model Ecosim. We link models of primary production of lower trophic levels (phytoplankton and benthic producers) under climate change with Ecosim to predict changes in fishery catch, fishery value, biomass of animals of conservation interest, and indicators of community composition. Under a plausible climate change scenario, primary production will increase around Australia and generally this benefits fisheries catch and value and leads to increased biomass of threatened marine animals such as turtles and sharks. However, community composition is not strongly affected. Sensitivity analyses indicate overall positive linear responses of functional groups to primary production change. Responses are robust to the ecosystem type and the complexity of the model used. However, model formulations with more complex predation and competition interactions can reverse the expected responses for some species, resulting in catch declines for some fished species and localized declines of turtle and marine mammal populations under primary productivity increases. We conclude that climate-driven primary production change needs to be considered by marine ecosystem managers and more specifically, that production increases can simultaneously benefit fisheries and conservation. Greater focus on incorporating predation and competition interactions into models will significantly improve the ability to identify species and industries most at risk from climate change.

*Keywords:* climate change, ecological interactions, fisheries, food web model, marine biodiversity

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## Introduction

Climate change is the most widespread anthropogenic threat that ocean ecosystems face (Halpern *et al.*, 2008). Globally, oceans are warming, becoming more acidic

(IPCC, 2007a) and have altered nutrient conditions (Behrenfeld *et al.*, 2006). These environmental changes will directly affect the physiology of ocean organisms (Portner & Farrell, 2008) and hence their population dynamics (Harley *et al.*, 2006). Changes in biomass of a species alter ecological interactions and have indirect effects throughout entire marine food webs (Scheffer *et al.*, 2005). Climate change will thus affect all ocean organisms, change the composition of marine communities, and alter ecosystem function. A key requirement for preserving biodiversity and supporting sustainable fishing in the future is to understand the ecosystem effects of climate change on marine food webs.

One of the largest effects of climate change on marine ecosystems will be changes in the rate and distribution of primary production, because primary production plays a fundamental role in structuring marine food webs (Hunt & McKinnell, 2006; Shurin *et al.*, 2006). Climate change has already been observed to strongly influence the distribution and abundance of ocean primary production (Richardson & Schoeman, 2004; Behrenfeld *et al.*, 2006) and these changes have been linked to changes in higher trophic level organisms (Richardson & Schoeman, 2004; Beaugrand *et al.*, 2008). Furthermore, primary producers, particularly phytoplankton, are likely to show the most rapid response to climate change due to their small size and fast population turnover (Hays *et al.*, 2005). Effects of primary production change on marine ecosystems will have important implications for conservation of marine biodiversity and sustainable fisheries management (Cury *et al.*, 2008).

Effects of climate-driven production change on marine ecosystems and fisheries can be explored using food web models that incorporate ecological interactions such as predation and competition (Cury *et al.*, 2008). For instance, Watters *et al.* (2003) demonstrated that cyclic changes in annual primary production driven by El Niño oscillations may affect lower trophic levels more than higher trophic levels. Watters *et al.* (2003) used a single food web model, but the predicted response of biodiversity and fisheries to climate-driven primary production change may vary for different ecosystems and may be confounded by model design. Mackinson *et al.* (2008) used dynamic food web models of different ecosystems to demonstrate that including primary production change improved the fit of those models to observed biomass time-series. Modelling historical patterns provides a means for understanding the drivers of change in marine ecosystems. However, anthropogenic climate change will pose new threats to marine biodiversity and new challenges to management of marine ecosystems. Advanced warning of these threats and challenges may be provided by using

climate forced food web models to predict species and fisheries most likely to be negatively affected by climate change.

The goal of the present study is to investigate effects of predicted primary production change on biodiversity and fisheries in a broad range of Australian marine ecosystems. We used 12 existing food web models of different Australian marine ecosystems, from tropical to temperate regions, to investigate effects of changing primary production on fishery catch, fishery value, biomass of species with conservation importance and indices of community composition that may indicate system-wide change. We present results of future primary productivity changes under climate change and investigate the ecosystem response to alternative productivity changes in sensitivity analyses. We also consider how food web model design complexity and specification of predator-prey interactions affect the ecosystems' responses. In this study, we focus only on primary production driven changes and leave the more complex parameterization of temperature effects on physiology (Portner & Farrell, 2008) for subsequent work. Given the magnitude of predicted changes in production in the world's oceans (up to 400% over 50 years, Sarmiento *et al.*, 2004), there are likely to be major ramifications for marine biodiversity and fisheries.

## Materials and methods

### Overview of the approach

We used 12 existing Ecopath with Ecosim (EwE) dynamic marine food web models to describe different Australian marine ecosystems (see Table 1 for key model details and Fig. 1 for the model regions). The EwE software has been under development since the 1980s (Christensen & Walters, 2004a) and there are ~200 models developed worldwide (Fulton, 2009). The EwE equations are grounded in general ecological theory and have proved capable of capturing real ecosystem dynamics in a variety of different ecosystems (e.g. Walters *et al.*, 2005). This success stems in part from the large amounts of data, ranging from dietary information to biomass estimates that any single EwE model integrates into a consistent representation of a marine food web (Christensen & Walters, 2004a). We used EwE models to investigate the response of ecosystems to primary production change by forcing a linear change in the rate of primary production over 50 year simulations in each of the 12 Australian models. We divided these simulations into three sections. First, we present predictions from models of climate-driven production change, second we use these predictions to force EwE models to predict changes in higher trophic levels, and

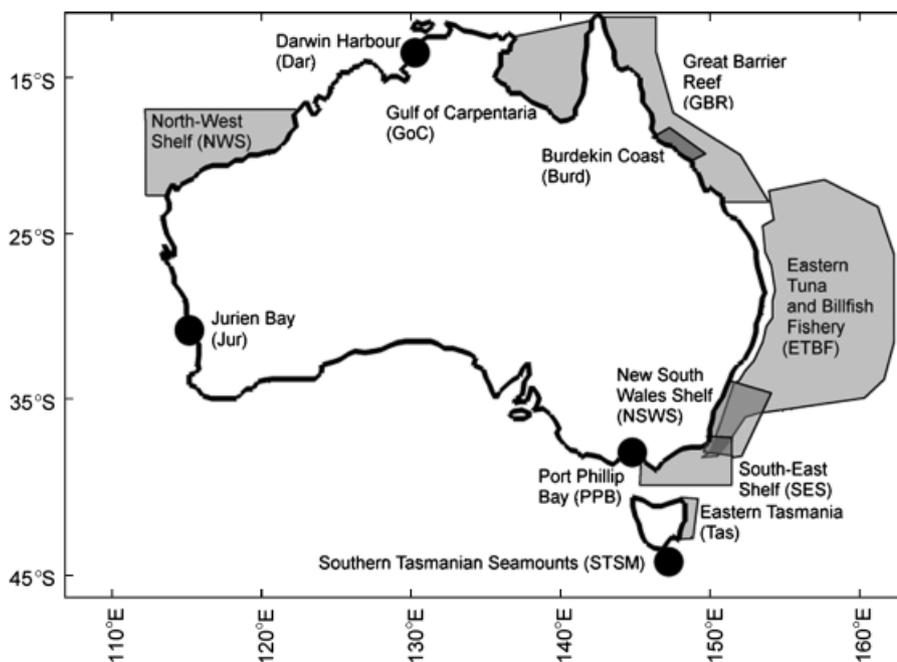
Table 1 Description of Australian Ecopath with Ecosim models used in the analyses

Model (abbreviation)	Reference and institution	Purposes for development	Area (km <sup>2</sup> )	No. living groups	Fitting to time-series data*	Primary producer groups (*habitat mediator for juvenile groups)	% of primary production	Production model predicted % change in primary production over 50 years (± 95% CI)
Burdekin coast	Gehrke (2007), CSIRO	Effect of reducing nutrient content of river outflow on coastal fisheries	987	18	Y (16 years, 7 groups)	Phytoplankton Seagrass Benthic microalgae Macroalgae Mangroves	73 20 5.8 0.88 0.25	24 -10 (0.01) 10 (1 × 10 <sup>-6</sup> ) 10 (0.01) -10
Great Barrier Reef	Gribble (2003), Queensland Department of Primary Industries	Impact of reef fisheries on by-catch species and food webs; trophic links between coastal and reef ecosystems	3.5 × 10 <sup>5</sup>	25	N	Benthic autotrophs Phytoplankton	82 19	10 (1 × 10 <sup>-6</sup> ) 22
Gulf of Carpentaria, Benthic	S. Griffiths, R. Bustamante (unpublished), CSIRO	Ecological effects of prawn trawl fishery	3.7 × 10 <sup>4</sup>	51	Y (36 years, 1 group)	Benthic micro-algae Phytoplankton Macroalgae* Seagrass*	51 45 3.4 0.12	7 (1 × 10 <sup>-6</sup> ) 30 7 (0.007) -7 (0.008)
Darwin Harbour	Martin (2005), Charles Darwin University	Predicting consequences of mangrove habitat loss to fish species	200	20	N	Mangroves Phytoplankton Benthic producers	60 34 6.8	-10 25 9 (4 × 10 <sup>-7</sup> )
Port Phillip Bay	Fulton & Smith (2004), CSIRO, University of Tasmania	Comparison of models of different complexity; impact of nutrient input and fishing policies on the ecosystem and fisheries	1930	33	N	Phytoplankton Benthic microalgae Macroalgae* Seagrass*	62 26 12 0.20	2 4 (2 × 10 <sup>-4</sup> ) 4 (0.004) -4 (0.2)
Jurien Bay	Loneragan <i>et al.</i> (2008), CSIRO, Murdoch University	Ecological and fishery implications of new marine protected areas	823	72	Y (32 years, 9 groups)	Ecklonia Sargassum Low algae Turfs Corraline algae Ephemeral seagrasses	0.77 5.7 19 1.9 7.4 5.3	7 (0.01) 7 (0.01) 9 (0.01) 9 (0.01) 9 (0.01) -9 (0.01)

Eastern Tuna and Billfish Fishery	Young <i>et al.</i> (2009), CSIRO	Past ecosystem effects of fishing; future effects of new management policy	$2.6 \times 10^6$	43	Y (3 groups, 55 years)	Perennial seagrasses Seagrass epiphytes Benthic micro-algae Small phytoplankton Large phytoplankton Phytoplankton	26 2.7 2.4 26 3.5 100	-9 (0.01) 9 (0.01) 9 (0.01) 4 4 33
North-West shelf	Bulman (2007), CSIRO	Define trophic structure of the system	$7 \times 10^4$	43	N	Phytoplankton Benthic producers Benthic micro-algae	86 8.2 5.9	6 $8 (1 \times 10^{-6})$ $8 (1 \times 10^{-6})$
New South Wales Shelf	Forrest (2008), University of British Columbia	Effects of fishing on shark species	$4.8 \times 10^4$	56	Y (21 years, 19 groups)	Phytoplankton Macroalgae	87 13	22 6 (0.007)
South-east Shelf	Bulman <i>et al.</i> (2006), CSIRO	Assess impact of variability in primary production on fisheries; potential impact of increasing seals on fisheries; ecosystem effects of fishery discards	$3 \times 10^4$	55	Y (10 years, 42 groups)	Phytoplankton	100	19
Eastern Tasmania	Metcalf (2009), University of Tasmania	Suitability of new quotas for the banded morwong fishery; trophic cascades caused by introduced species; compare qualitative and quantitative ecosystem models	350	27	N	Phytoplankton Red algae Brown algae* Green algae Crustose algae	70 17 7.6 2.0 3.1	4 2 (0.01) 2 (0.01) 2 (0.01) 2 (0.01)
Southern Tasmanian Seamounts	Bulman <i>et al.</i> (2002), CSIRO	Effects of hypothetical re-introduction of pelagic fishing on deep sea benthic marine protected area	370	24	N	Phytoplankton	100	-1

Listed are the model's name, key reference and the main purpose for which it was created. Also included are some key model variables: the area they cover, the number of living groups, details of the time-series data used to estimate the vulnerability parameters and primary producer groups in each model with the percentage each contributes to system primary productivity (estimated from the model). The final column shows prediction for change in relative primary production rate (see Results).

\*Not all groups have data for every year.



**Fig. 1** Map of Australian Ecopath with Ecosim model regions. Filled circles indicate models that represent bays or small regions and grey shapes are larger regional model domains. Model acronyms used for subsequent figures are given in brackets.

third we investigate the sensitivity of EwE models to different rates of change in primary production.

To predict effects of climate change on marine ecosystems, we linked an ocean general circulation model (GCM) to primary production models that drive production in EwE models. The three types of models (GCM, primary production and EwE) operate on different spatial and temporal scales and differ in their levels of biological complexity. EwE models represent discrete ecosystems with no spatial structure. They capture complex ecological interactions between groups of functionally equivalent species, but have limited input of physical environmental conditions, such as nutrient concentration.

GCMs provide global coverage of physical changes in environmental variables driven by projected greenhouse gas emissions. We use the physical environmental conditions from the GCM under a plausible emissions scenario to force a range of primary production models for coastal primary producers (benthic algae, seagrass, macroalgae and mangroves) and to drive a nutrient-phytoplankton-zooplankton-detritus (NPZD) model for phytoplankton productivity. The spatial resolution of the GCM means it has limited ability to accurately represent local and shelf processes that are important for primary productivity; however, we have used output from this model to illustrate predicted effects, pending further development of models at a finer spatial scale. Other approaches have been used to project primary production responses to global

warming (e.g. Sarmiento *et al.*, 2004) and we acknowledge that there still is no clear consensus on how global warming will affect primary production globally. A comprehensive list of model caveats and how they were addressed is provided in Appendix S1.

#### *EWE food web models*

Ecopath provides a static description of energy or mass flow in a food web over an arbitrary time period and Ecosim is its dynamic counterpart. The EwE approach is described in detail in Christensen & Walters (2004a), so only a brief description follows. An Ecopath model consists of a number of compartments, each of which represents the biomass of a group of functionally equivalent species (or more rarely a single species). Flows of biomass between the different groups are captured through predator-prey interactions and death to detritus. Ecopath models normally have greater taxonomic resolution for higher trophic levels, because these are usually the groups of interest for fisheries and conservation. Species of interest may also be further split into different life history stages. Different fishery types can also be represented and remove biomass from the system. During model development, biomass flows within groups are mass-balanced, such that consumption by a group is sufficient to account for its respiratory losses, biomass growth or decline and biomass production. Flows between groups are also balanced so that

each group's biomass production is sufficient to account for consumption by its predators and fishery catches.

The Ecopath model is the starting point for temporal simulations of biomass and food web dynamics in Ecosim. In Ecopath, the biomass of an autotrophic group changes over time according to its primary production rate and the consumption rate of its herbivores. The biomass of each consumer group changes according to the biomass of its prey and consumption by its predators. A key conceptual aspect of the Ecosim approach is foraging arena theory, which partitions the availability of a prey group's biomass to each predator group into vulnerable and refuge states (Walters & Martell, 2004). Foraging arena theory is implemented in Ecosim using the vulnerability parameter, which determines the maximum increase in mortality rate that a predator can exert on a prey group. Higher values of this parameter mean that predator consumption can control prey biomass (top-down control), whereas lower values mean prey biomass can control predator biomass (bottom-up control). These parameters also affect competition; for instance if two predators consume the same prey group in equal proportions, the predator to which the prey is more vulnerable will be the superior competitor. The vulnerability parameters can be estimated using a nonlinear procedure that fits predicted Ecosim biomass time-series to observed biomass time-series (Walters & Martell, 2004). Table 1 gives details about the EwE models in our study that had fitted vulnerability parameters.

#### *Ocean GCM and primary production*

The GCM model we used to project ocean conditions into the future is the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Mark 3.5 coupled atmosphere-ocean GCM (Hirst *et al.*, 2000; Gordon *et al.*, 2002). This model is an improved version of the Mark 3.0 model that was included in the latest Intergovernmental Panel on Climate report (IPCC, 2007b). The ocean model has global coverage, a spatial resolution of 1.875° longitude by 0.84° latitude, operates on a 15 minute time-step and has 31 ocean depth levels.

Climate conditions in GCMs are forced by projections of greenhouse gas emissions provided by the IPCC (Nakicenovic & Swart, 2000). Changes in future global greenhouse gas emissions are uncertain and differences in possible emissions scenarios contribute significantly to divergence in climate model predictions on time-scales beyond 40 years into the future (IPCC, 2007a). We used predictions under the standard IPCC emission scenario A2. This scenario was devised as a high emission scenario (Nakicenovic & Swart, 2000), although recent observations suggest climate change is occurring

more rapidly than this scenario predicts (Rahmstorf *et al.*, 2007). IPCC emissions scenarios have not yet been updated (<http://www.ipcc.ch>), so we consider the A2 scenario as a mid-range scenario and explore the effect of alternative climate change scenarios indirectly in sensitivity analyses.

To project the effect of climate change on phytoplankton production, we linked the output from the GCM to a NPZD model. The NPZD primary production model has the same spatial and temporal resolution as the GCM. It describes the flux of nitrogen between inorganic and organic dissolved states, including nitrogen uptake by phytoplankton, the consumption of phytoplankton by zooplankton, the remineralization of nitrogen from plankton egestion, excretion and mortality.

Such models represent the major climate-driven processes that impact oceanic phytoplankton production (Sarmiento *et al.*, 2004). In these models, phytoplankton production is directly impacted by ocean warming and light availability driven by changes in cloud cover, wind and the depth of the mixed layer. The models also capture the process of enhanced ocean stratification caused by surface waters heating faster than at depth. This impacts availability of nutrients in surface waters where light is available for photosynthesis. Changes in broad-scale oceanographic processes, such as basin-scale circulation patterns, also affect supply of nutrients to surface waters.

The linked GCM-NPZD simulation predicts primary production of phytoplankton only, so we employ models to predict production rate in benthic primary producers including macroalgae, seagrass and benthic microalgae (e.g. Murray & Parslow, 1999; Aveytua-Alcazar *et al.*, 2008, see Appendix S2 for details and equations). Monthly intervals were used because the Ecosim food web models that we force with primary production estimates operate on monthly forcing functions. Our 12 EwE models did not resolve particular primary producer species, but rather primary producer functional groups (for instance phytoplankton, seagrass, macroalgae, benthic microalgae, mangroves). Primary production models were run for functional groups of primary producers using light, temperature and nutrient concentration for each EwE model region. Given the scope of the area covered by the benthic primary production models vs. the level of available data on climate-related primary productivity impacts, the models have not been parameterized specifically for the Ecosim model regions. Sensitivity of the primary production models to alternative parameterizations was investigated using Monte-Carlo simulations of production rate with random combinations of parameters selected from uniform distributions. The range of the parameter distributions for seagrass, macroalgae and

benthic microalgae was taken from the literature search of possible values for that functional group conducted by Murray & Parslow (1999, their parameters given in Table B1). Results were not sensitive to alternative parameterizations, so production change from the mean of the Monte-Carlo simulations was used in this study. Because EwE uses primary producer functional groups and not individual species, the approach assumes that primary producer species that go locally extinct due to their specific environmental tolerances will be replaced by other species within each functional group.

We were unable to find a simple mechanistic model of mangrove primary production rate in the published literature. Mangroves will be affected by a range of processes under climate change and a review by Gilman *et al.* (2008) suggests that sea-level rise will cause large-scale loss of mangrove habitat. To simulate this in the Ecosim models, we assumed a 10% decline in mangrove primary production rate over 50 years, which was comparable to the magnitude of change for other primary producers, and investigated the influence of this assumption in the sensitivity analysis.

#### *Applying changes in primary production to Ecosim*

Ecosim uses a forcing function on the monthly rate of primary production to specify temporal changes in primary production that are driven by physical processes. For both climate-driven primary production change and sensitivity analyses, we used linear forcing functions over 50-year periods. For the climate-driven production change scenarios, mean production trends for each primary producer were calculated for each EwE model region using regression of time against monthly production predictions from the primary production models. The GCM and NPZD resolutions were not sufficiently fine to resolve the EwE models for Darwin Harbour and Port Phillip Bay, so we took the mean across model cells adjacent to these bays. Trends in primary production rate were calculated by taking the slope of primary production across all years from 2000 to 2050 in the primary production models and standardizing the trend to the mean for years 2000–2004. While seasonal and interannual variability in future primary production may also affect marine ecosystems, we used trends to simplify interpretation of results.

#### *Sensitivity analysis of primary production*

Prediction of changes in primary production is a major source of uncertainty in our results. To address this and to investigate the sensitivity of marine ecosystems to primary production trends, we considered alternative production change scenarios in each Ecosim model to

investigate the sensitivity of marine ecosystems to primary production trends. For each Ecosim model, we simulated six primary production change scenarios where primary production rate by all autotroph groups in each model changed linearly by –40%, –20% –10%, 10%, 20% or 40% over 50 years. To further explore differences in response to climate change by different types of producers, we considered two additional scenarios for models with benthic and pelagic producers; one with benthic primary producers alone declining linearly by 10% over 50 years, and the other with pelagic primary producers (phytoplankton) alone declining by 10% over 50 years.

#### *Sensitivity analyses of vulnerability formulations*

Each Ecosim model's representation of an ecosystem is a function of the hypothesis it was developed to explore, the data available, and the developer's expertise (Table 1), all of which contribute to uncertainty in our predictions. By comparing results among 12 different Ecosim models we could simultaneously consider effects of ecosystems properties and effects of model design.

We also considered the effect of different Ecosim vulnerability formulations on the robustness of predictions. The first vulnerability formulation had all vulnerability parameters in all models set to a moderate level, whereby consumption rate of a predator group could at most double (Mackinson *et al.*, 2003). The second uses the fitted vulnerability estimates for each model where time-series data were available. In this formulation vulnerability parameters could vary substantially across functional groups and be of greater magnitude, with the high values reflecting potential for strong top-down control of prey biomasses by predators. The third formulation represented a top-down ecosystem, where higher trophic levels can exert stronger predation pressures on their prey. We achieved this by assuming that the vulnerability of prey was a positive linear relationship with each consumer's trophic level (trophic level formulation). Values were scaled such that consumption rates of the lowest trophic level consumers were constant and consumption rates of the highest trophic level predators could increase four times. For details of sensitivity of results to nontrophic interactions see Appendix S3. For all models we excluded formulations that produced numerical instability, indicated by cyclic oscillations in biomass trends of unrealistic magnitude.

#### *Ecological indicators of climate change effects on fisheries and biodiversity*

To assess the impact of climate-driven changes in primary production on marine ecosystems, we analysed the difference in ecosystem state in the 50th year of

Ecosim simulations with and without primary production forcing. Note that fishing effort was held constant for all simulations. Thus, in simulations without primary production forcing, trends in the biomasses of groups did not differ from those in the initial conditions specified by the model's author. Effects of climate change on marine ecosystem biodiversity, fisheries, and community composition were measured using six ecological indicators for each Ecosim model. The first was wet weight of fishery landings (except the Tasmanian Seamount model, because this region has been declared a protected area and has no current fishing). The second indicator was the value of fishery landings because the composition of fisheries catch might also change in the future. Prices per kilogram for each functional group in each model region during the 2005–2006 financial year were used to estimate value of catches (Australian Bureau of Agriculture and Resource Economics, 2008). This calculation assumes the relative value and costs of each fishery was constant through time and we did not consider changes in the costs of fishing. The third indicator was the change in biomass of functional groups with conservation interest, including sharks, turtles, seabirds and marine mammals.

The final three indices used reflect effects of climate change on community composition, that is, the relative abundance of different functional groups. The fourth indicator, mean biomass longevity, was used to measure changes in the prevalence of functional groups with slow biomass turnover. Biomass longevity of a functional group was calculated as the inverse of its Ecopath production per unit biomass rate and the mean for each model was calculated by weighting longevity values by the relative biomass of each group (Christensen & Walters, 2004b). The fifth indicator, mean trophic level, is a useful indicator of the effects of fishing on ecosystems (Fulton *et al.*, 2005). Ecopath calculates trophic level on a continuous scale for each functional group, based on its dietary composition. Changes in mean biomass longevity and mean trophic level indicate that some groups of particular biomass longevity or trophic level benefit from trends in primary production more than others. The last indicator was community biomass evenness of all groups in an Ecosim model and was measured using the Kempton index, which is the slope of the cumulative biomass curve (Ainsworth & Pitcher, 2006). A decrease in the slope under production change would indicate that a small number of groups dominate under the new environmental conditions.

## Results

The first section of the Results describes predicted climate-driven primary production change under the A2

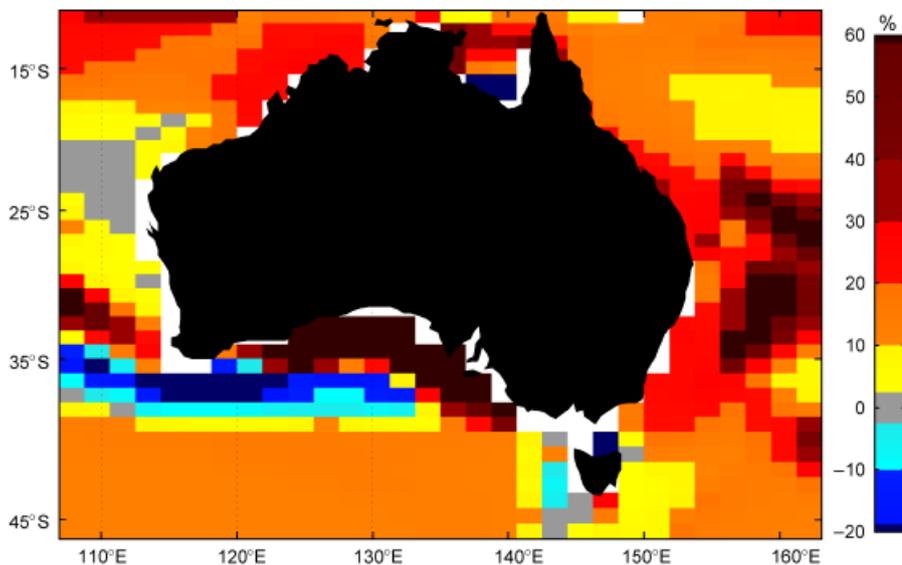
emission scenario, the second section details the impact of these changes on the ecosystems using the Ecosim models, and the third section is a sensitivity analysis that considers the effect of uncertainty in primary production trends and Ecosim model formulation.

### *Predicted primary production change*

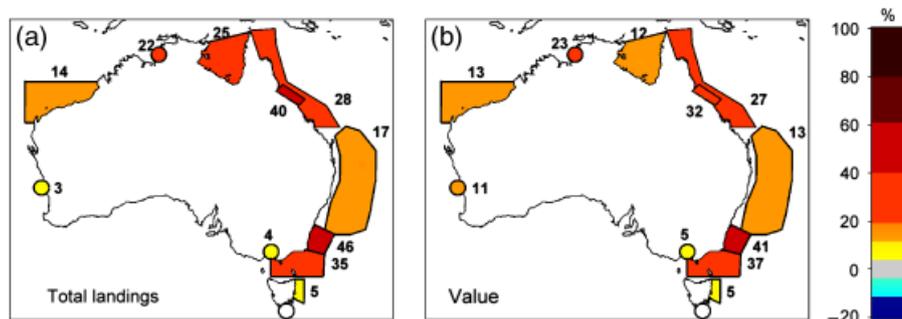
Under the IPCC A2 emission scenario, the NPZD model predicted a small increase of nutrients (generally <10%) in most of the Australian Ecosim model regions. This increase in nutrients caused increases in phytoplankton production rate in most areas (Fig. 2). In coastal models, increased nutrient availability and temperatures also increased the primary production rate of macroalgae and benthic microalgae, but decreased primary production of seagrasses (see Table 1 for magnitudes), due to enhanced epiphyte growth on photosynthetic seagrass blades. There was considerable spatial variation in primary production rate change around Australia. Increases were largest on the east coast of Australia, where the NPZD model predicted phytoplankton production rate to increase by >60% for some grid cells. This means high primary production rate increases for east coast Ecosim models, up to 33% over 50 years in the Eastern Tuna and Billfish fishery model. Changes in the far south-east (Tasmania, Port Phillip Bay and Seamounts models) and west coast (Jurien Bay and North-West Shelf models) were much smaller and negative in some cases. In the North, within the Gulf of Carpentaria Ecosim region there were areas of large increases and decreases. However, the mean production trend was for increases in phytoplankton, benthic microalgae and macroalgae and decreases in seagrass. The Darwin Harbour Ecosim model region also showed increases in phytoplankton and benthic microalgae production.

### *Effects of projected production change on fisheries and marine ecosystems*

Over 50 years, total fishery landings and the value of landings increased due to increasing primary productivity (Fig. 3a and b). Landings and biomass increases were small in regions with small increases in primary productivity (Port Phillip Bay and Tasmania) and larger in regions with large productivity increases (Gulf of Carpentaria and the Eastern Tuna and Billfish Fishery, Fig. 3a and b). Fishery value increased at a slower rate than fishery landings in the Gulf of Carpentaria, Burdekin coast, Eastern Tuna and Billfish Fishery and New South Wales shelf models, because lower value species replaced higher value species in catches. Vulnerability fitting in these three models contributed to



**Fig. 2** Predicted relative percent change in phytoplankton production rate from the 2000–2004 mean to 2050 for the Australasian region. The CSIRO Mk 3.5 global climate model (GCM) was used to force a nutrient-phytoplankton-zooplankton submodel under the A2 emission scenario. Phytoplankton production rate is predicted to generally increase around Australia. The pixel size indicates the resolution of the NPZD and land (white spaces) has been overlaid with a high-resolution map.



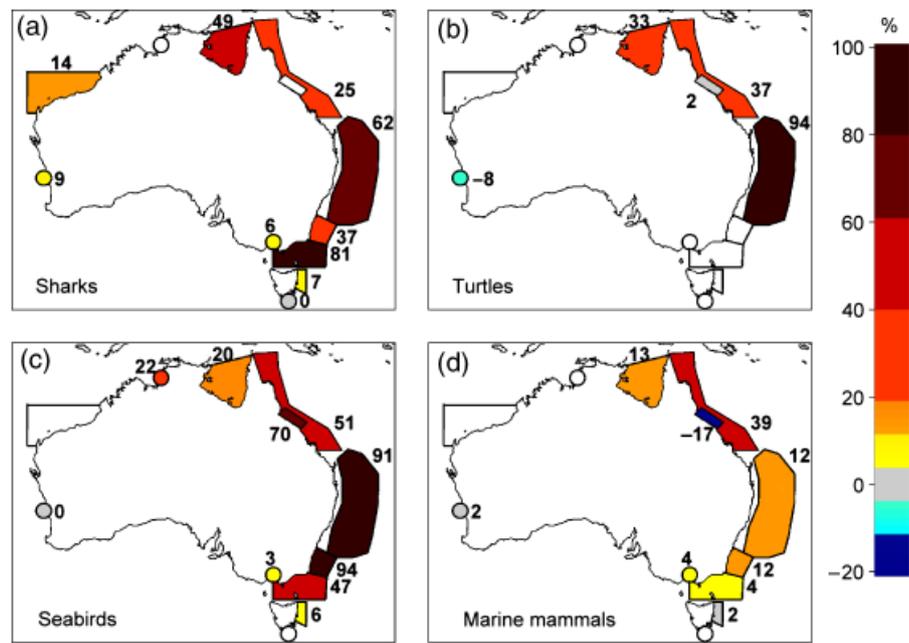
**Fig. 3** Change in fisheries landings (a, %) and value of landings (b, %) over 50 years for the Australian Ecosim model regions under the A2 greenhouse gas emission scenario. Regions shown on the maps are representative of the model regions only. Results are relative to simulations with no climate change.

non-linear changes in fishery value by allowing for higher predation rates and strong competition interactions. For example in the Eastern Tuna and Billfish Fishery, the climate-driven increase in shark predation on juvenile tuna reduced catches of high value adult tuna ( $-9\%$  compared with increases in catches for other groups of over  $40\%$ ) and catches of the small predators functional group declined in the South-East Shelf model due to increasing predation by rays ( $-6\%$  compared with increases in catches for other groups of over  $30\%$ ).

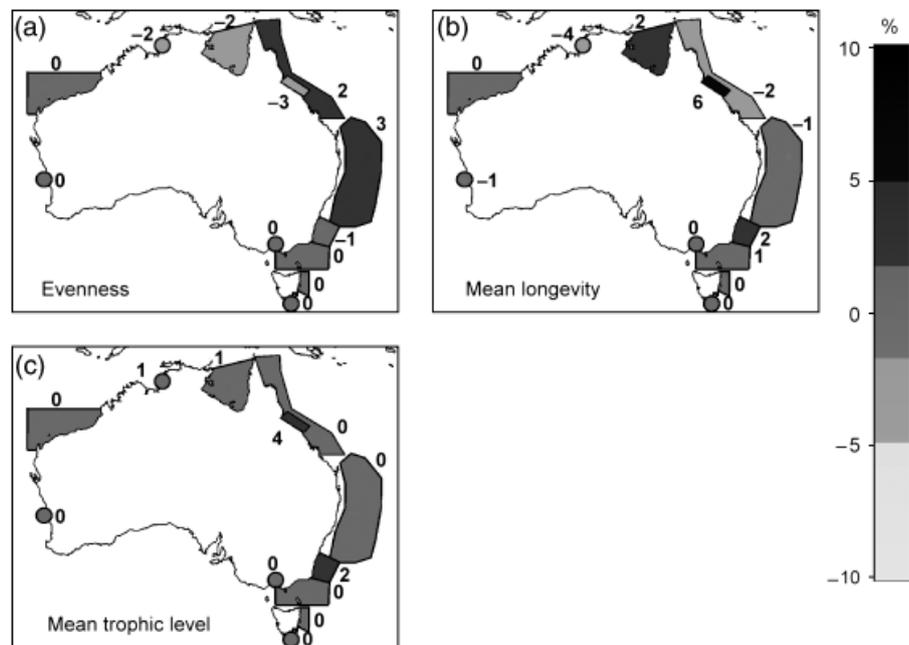
Biomass of functional groups of conservation interest also generally increased (Fig. 4), although turtles declined in the Jurien Bay model and marine mammals (dugongs) declined in the Burdekin coast model, due to seagrass declines. Strong competition between marine

mammals and fast growing fish species contributed to the decline in the Burdekin coast model (Fig. 4b and d). Increases in the biomass of marine mammals in the other models were generally smaller than those of other groups (Fig. 4d). Turtles showed large increase in the Eastern Tuna and Billfish Fishery and Gulf of Carpentaria models, despite concurrent increases in biomass of sharks which are a major predator of turtles (Fig. 4b).

Changes in community composition (captured by community biomass evenness, mean biomass longevity of each system, and mean trophic level) were small for most regions (Fig. 5). The Burdekin coast model showed the greatest change for all indices of compositional change. Vulnerability fitting of this model allowed for strong top-down control and nonlinear changes in



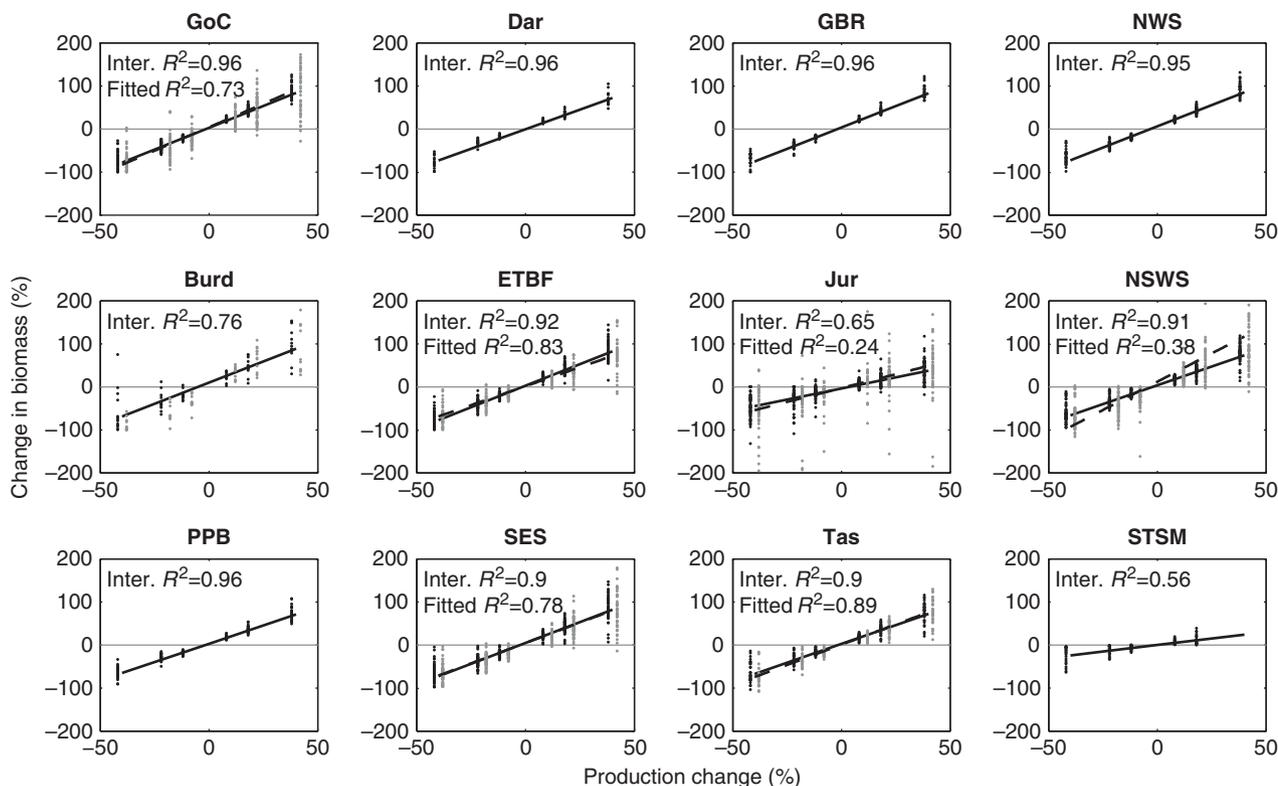
**Fig. 4** Change in biomass abundance of conservation interest functional groups (%) over 50 years for the Australian Ecosim model regions under the A2 greenhouse gas emission scenario. Shown are change relative to no climate effects simulations for biomass of sharks (a), turtles (b), seabirds (c) and marine mammals (d). Regions shown on the maps are representative of the model regions only. Note that not all functional groups occur in all models.



**Fig. 5** Change in community biomass evenness (a, %), mean biomass longevity (b, %) and mean trophic level (c, %) over 50 years for the Australian Ecosim model regions under the A2 greenhouse gas emission scenario. Regions shown on the maps are representative of the model regions only. Note that not all functional groups occur in all models. Results are relative to simulations with no climate change.

community composition. The small number of functional groups in this model (due to a high degree of aggregation of species) also contributed to the nonlinear changes in community composition. Interestingly, even

though total primary productivity increased, evenness declined for this model and the Darwin Harbour and Gulf of Carpentaria models, indicating that interactions between declines in seagrass or mangroves and



**Fig. 6** Change in the biomass of all consumer groups (%) for change in primary production rates of all primary producers over 50 years for each Ecosim model. Shown are results for intermediate (black points, solid regression line) and fitted (grey points, dashed regression line) vulnerability scenarios. Values are offset on the horizontal axis for visualization.  $R^2$  values indicate the proportion of variance in groups responses explained by primary production change for intermediate and fitted scenarios. See Fig. 1 for model acronyms. All vertical axes are scaled between  $-200$  and  $+200$ , two outlying groups in the Great Barrier Reef coast and New South Wales models are not shown. One outlier (herbivorous fish) was removed from the analysis for the Burdekin coast model because it biased variance estimates to values unrepresentative of the general trend.

increases in phytoplankton can have large effects on community composition in these ecosystems.

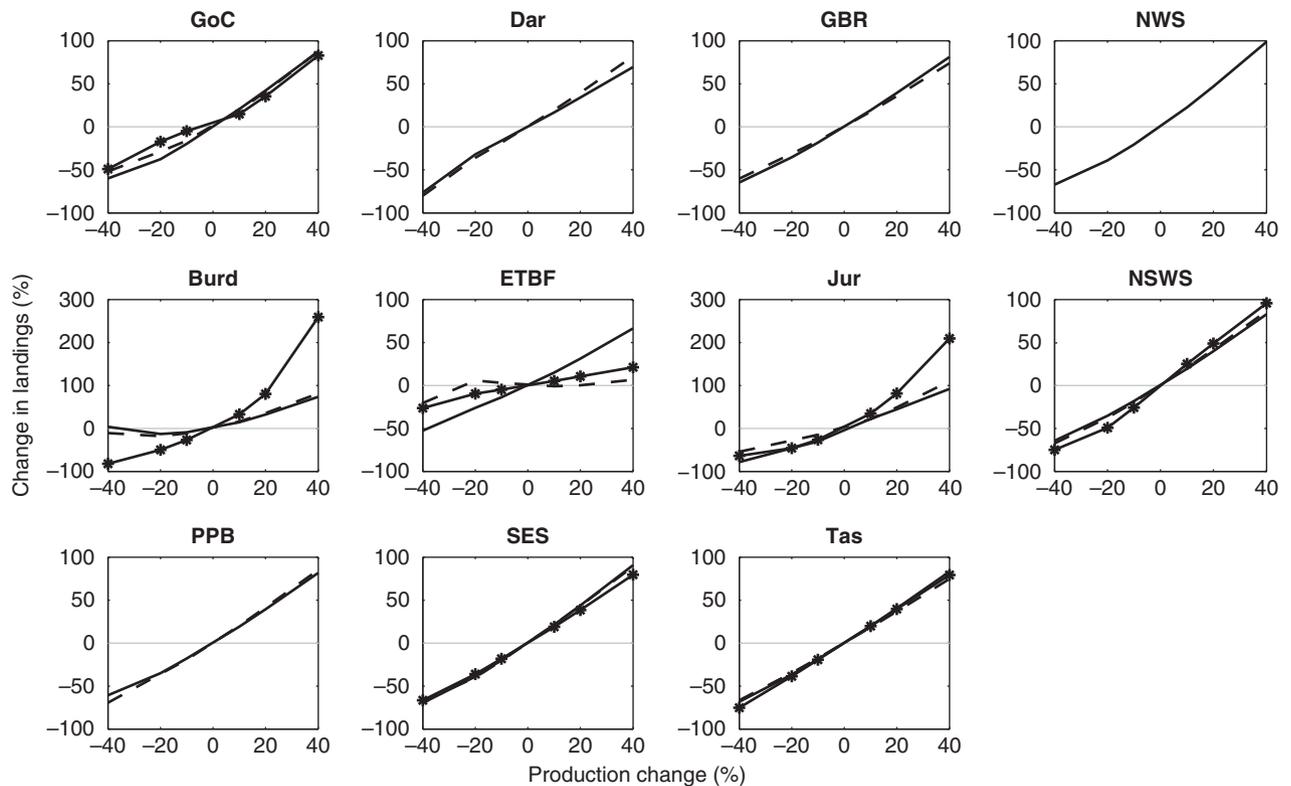
#### *Sensitivity of Ecosim models to different primary production trends*

We conducted model experiments where production rate of all primary producers was changed linearly at the same rate over 50 years for each model and for different vulnerability formulations. The general trend of all functional groups was for primary productivity increases (decreases) to cause the biomass of higher trophic levels to increase (decrease, Fig. 6). These groups included most of those caught by fisheries and groups with conservation interest, including sharks, turtles, seabirds, and marine mammals.

While this mean response of functional group biomasses to primary production change was similar for fitted and moderate vulnerability formulations, there was considerable variability among the magnitude of group responses to productivity change. Fitted vulner-

ability formulations always had greater variance in the response of groups to primary production change than moderate vulnerability formulations (Fig. 6). This can be attributed to greater variability and magnitude of vulnerability parameters, which allows for stronger top-down control of functional group biomasses in fitted formulations when compared with moderate formulations.

Models that had vulnerability parameters fitted to more time-series data (Gulf of Carpentaria, Jurien Bay, South East Shelf and New South Wales Shelf, Table 1) tended to show greater variability. For some functional groups this variability was manifest as a reversal of the expected response, due to high predation rates or strong competition with other functional groups, with increases in primary productivity causing biomass declines. Groups showing such reversals include tiger prawns in the Gulf of Carpentaria model and yellowfin tuna in the Eastern Tuna and Billfish Fishery model. These groups have sufficient time-series data available to estimate the Ecosim vulnerability parameters using



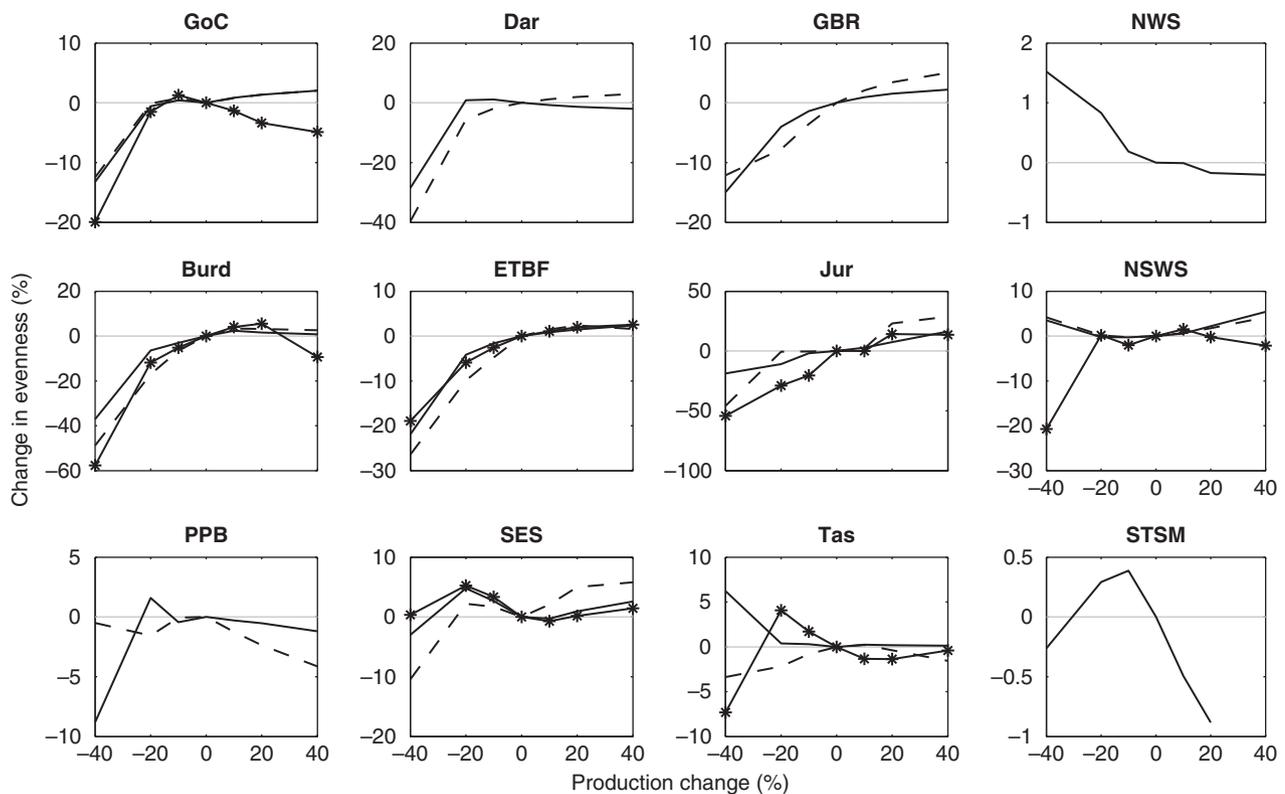
**Fig. 7** Change in fishery landings for change in primary production rates for all primary producers (%) over 50 years for each model with moderate (solid line), fitted (starred line) and trophic level (dashed line) vulnerability formulations. See Fig. 1 for model acronyms. Results are relative to simulations with no climate change and simulations that showed numerical instability are not shown.

real biomass trends, which provides some confidence in the simulated response.

Increases in biomass of most functional groups caused fishery landings to increase (Fig. 7). The response was generally linear, although larger and more variable vulnerability parameters in vulnerability fitted models could cause nonlinear responses. For instance, in the fitted vulnerability formulation of the Eastern Tuna and Billfish fishery model, increases in primary production led to increases in predation on juvenile yellowfin tuna by sharks, which led to declines in the yellowfin biomass. Yellowfin tuna makes up a relatively large proportion of the catch, so declines in this species led to smaller catch gains overall than in the moderate vulnerability formulation. In the South-East Shelf model, gemfish biomass and thus gemfish catch, increased more slowly in fitted vulnerability formulations, due to competition for prey with other species. However, changes in total catch for the South-East Shelf model were linearly related to production change, because fisheries in this model catch a large number of other functional groups. Nonlinear trends in catch were more pronounced in the Eastern Tuna and Billfish fishery and Burdekin coast models than other models, where fisheries caught fewer functional groups.

Changes in indices of community composition were nonlinear and tended to show greater changes when primary production declined, compared with when production increased. Production declines caused greater changes because as a group approaches extinction, dependent predator species must feed more heavily on other prey species or go extinct. Evenness tended to decrease for reductions in primary production but remain relatively constant for production increases. This indicates that fewer functional groups dominate under lower productivity environments and that the relative biomasses of all functional groups remain constant under higher productivity environments (Fig. 8).

Generally, mean biomass longevity increased for reductions in primary production, indicating that functional groups with lower biomass turnover out-compete those with higher turnover in low productivity environments (Fig. 9), although this trend was reversed in the Darwin Harbour, Port Phillip Bay, and vulnerability fitted Burdekin coast models. We could not relate the different response of these models to a particular feature of the ecosystems or to model design because these models cover a range of different ecosystem types and other models with similar levels of complexity did not show the same trend (e.g. Eastern Tasmania and Great



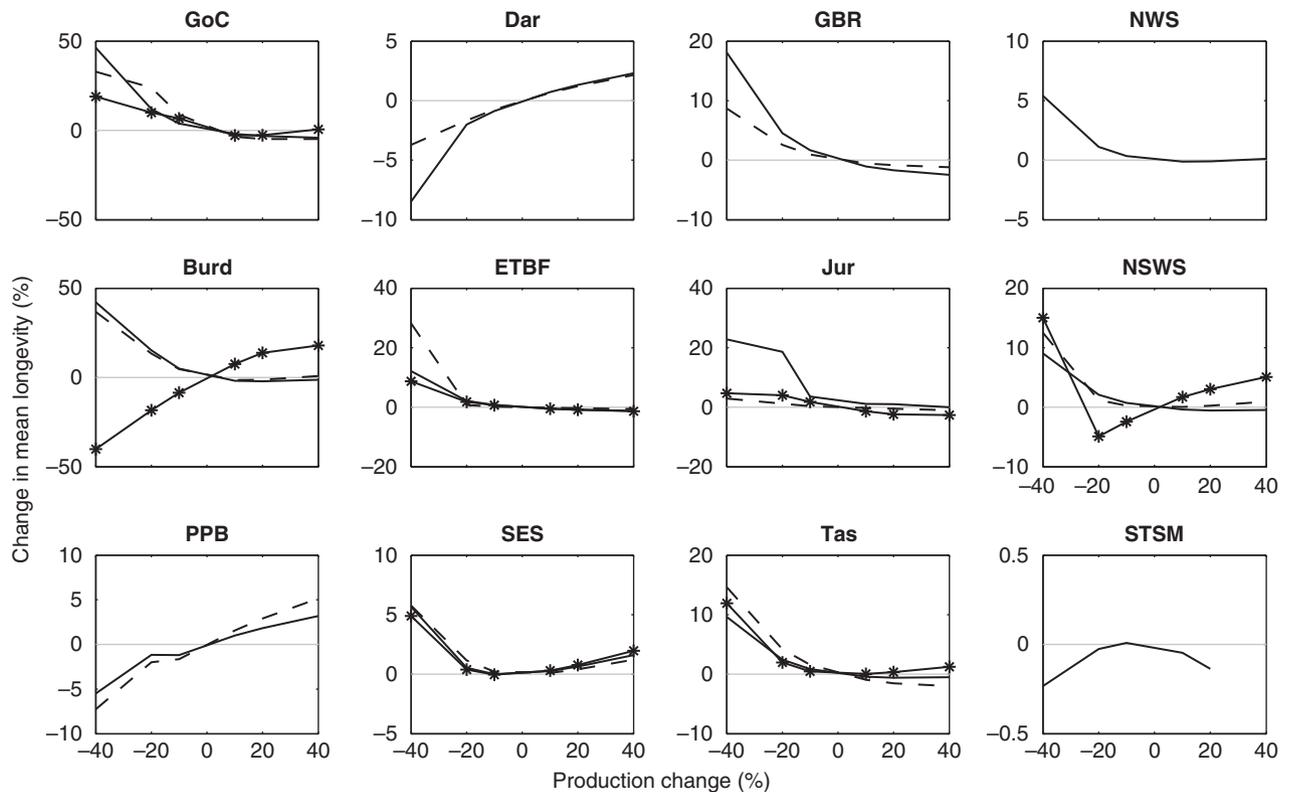
**Fig. 8** Change in community biomass evenness (%) for change in primary production rates of all primary producers over 50 years for each model with moderate (solid line), fitted (starred line) and trophic level (dashed line) vulnerability formulations. See Fig. 1 for model acronyms. Results are relative to simulations with no climate change and simulations that showed numerical instability are not shown.

Barrier Reef models). Mean biomass longevity in the southern Tasmanian Seamounts model was insensitive to production change, due to the high proportion of species with low biomass turnover rates in this ecosystem, which also accounts for the slow response of its groups to changes in primary production (Fig. 6). Mean trophic level was insensitive to primary production change in most models (Fig. 10). Qualitative trends depended upon both the model and the vulnerability formulation, suggesting that trophic level was not a strong determinant of the response of a functional group to changes in primary production. Comparisons of model structure did not shed any light on the reasons for the different responses to production change between models.

Sensitivity analysis of declines in benthic primary producers (macroalgae, seagrass, benthic micro-algae and mangroves) or pelagic production (phytoplankton) indicated the relative importance of autotrophic groups in each model (Fig. 11). Despite the relatively low contribution to total primary production (Table 1), benthic production was more important to fisheries in the Jurien Bay, Gulf of Carpentaria, Great Barrier Reef, Burdekin coast and Eastern Tasmania models, indicated

by substantial decreases in fishery landings when benthic primary producers were decreased (Fig. 11a). This is due to the importance of benthic feeding invertebrates (prawns, rock lobster and shellfish) for fisheries in these systems. Fishery landings in other models were more dependent on pelagic phytoplankton production. Landings always decreased when one or both benthic and pelagic primary producers were specified to decrease, indicating that generally fisheries are dependent on primary production from both sources.

Changes in either benthic or pelagic production had a greater effect on community composition than when benthic and pelagic production changed simultaneously for some indices and Ecosim models (Fig. 11b–d). For instance, increases in mean biomass longevity were greatest for benthic production decreases in the Gulf of Carpentaria model (Fig. 11c) and changes in benthic and pelagic production had antagonistic effects on mean trophic level in the Darwin Harbour, Great Barrier Reef, North-West Shelf, Jurien Bay and Tasmanian Coast models (Fig. 11d). These antagonistic responses of indices are caused by pelagic and benthic primary production providing for different subsets of functional groups within the models.



**Fig. 9** Change in mean biomass longevity for change in primary production (%) rates of all primary producers over 50 years for each model with moderate (solid line), fitted (starred line) and trophic level (dashed line) vulnerability formulations. See Fig. 1 for model acronyms. Results are relative to simulations with no climate change and simulations that showed numerical instability are not shown.

## Discussion

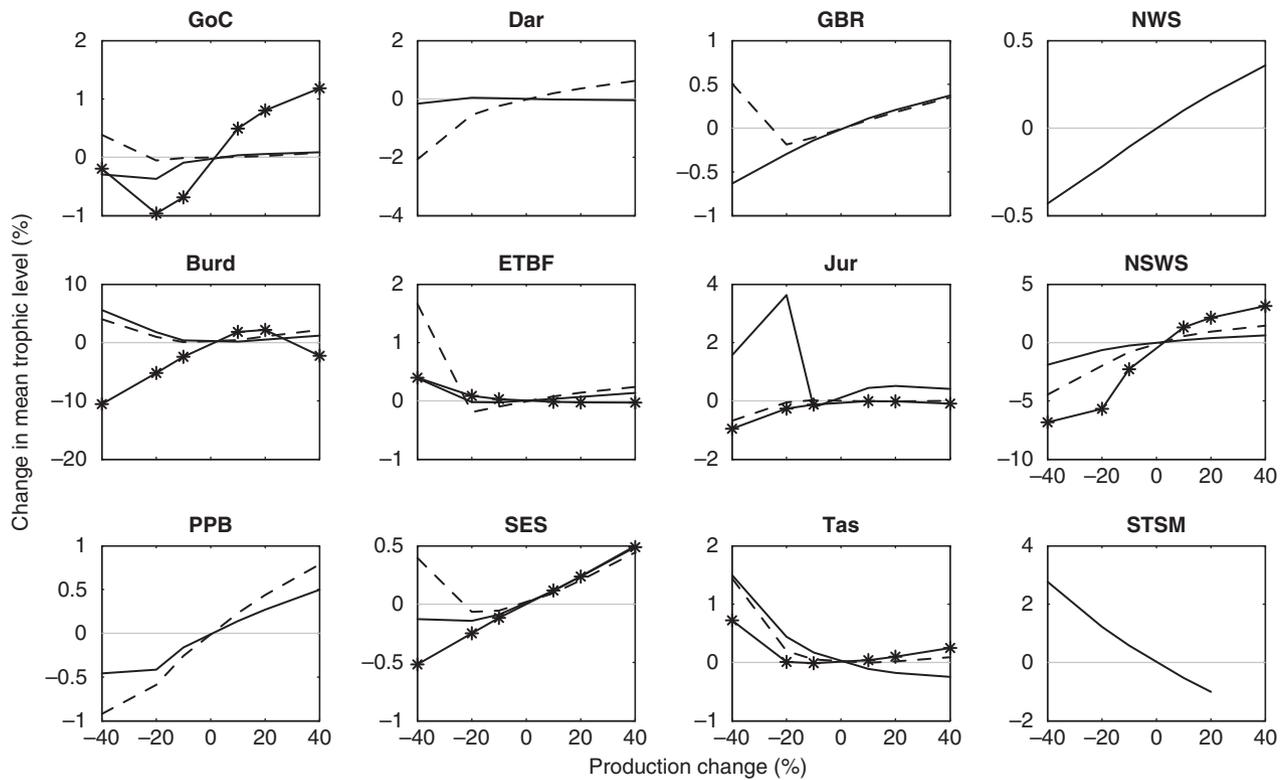
### *Effects of primary production change*

Increases in primary productivity of the magnitude predicted by the primary production models can have large effects on the biomass of marine organisms and fishery catches. For most of the 12 ecosystems examined, predicted increases in primary production in Australia's seas led to greater fisheries catch and supported higher biomasses of animals such as sharks, turtles and seabirds, which are currently threatened by human activities. This prediction is supported by empirical evidence that fishery catch is strongly controlled by primary production (Ware & Thomson, 2005). In sensitivity analyses that considered alternative rates of primary production change, the biomasses of functional groups and fishery catch showed linear responses to linear primary production rate forcing across the 12 different models used here. Designing food web models with appropriate levels of complexity that balance model tractability and generality with model realism has been the focus of much research attention, because it can have large effects on model results (Fulton *et al.*,

2003). The 12 models used here cover a range of different complexities and ecosystem types. However, the responses of these models to different rates of primary production change were broadly similar. Therefore, responses of fisheries catch and biomass of marine organisms to climate-driven primary production change may be predictable at a broad scale given reliable primary production predictions.

### *Response depends upon vulnerability formulation and data available*

Predicting species' responses to primary production change will be more challenging when predation and competition with other species strongly influences those species' biomass. Where time-series data were available for estimating vulnerability parameters, the trends in biomass of fitted groups sometimes showed the reverse response to those in moderate vulnerability formulations, due to stronger top-down control on those groups and competition with other groups. Likewise, the role of predation and competition interactions may be underestimated when data are unavailable for time-series fitting. For instance, turtle biomass increased



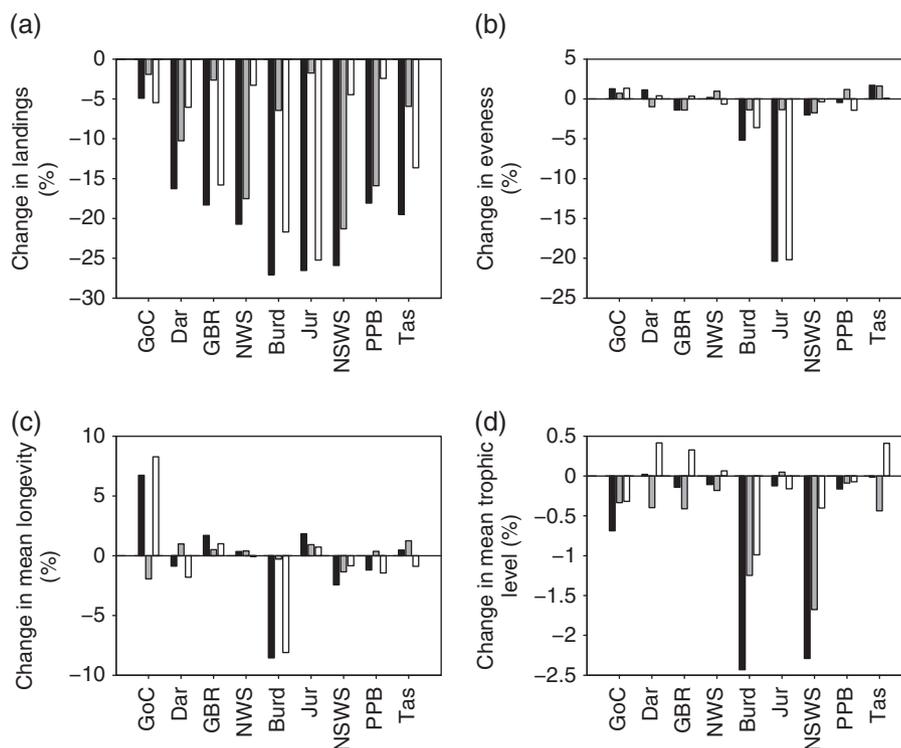
**Fig. 10** Change in mean trophic level (%) for change in primary production rates of all primary producers over 50 years for each model with unfitted (solid line), fitted (starred line) and trophic level (dashed line) vulnerability formulations. See Fig. 1 for model acronyms. Results are relative to simulations with no climate change and simulations that showed numerical instability are not shown.

concurrent with increases in sharks, but in reality large shark populations may exert strong control on turtle biomass (Heithaus *et al.*, 2008). Thus, changes in primary productivity (bottom-up effects) will cause predictable changes in the biomass of most marine organisms, but predation and competition can control the magnitude and direction of the response. Acquiring adequate time-series data to parameterize predation and competition interactions can significantly improve predictive ability of food web models under primary production change (Gu nette *et al.*, 2006; Mackinson *et al.*, 2008). Unfortunately, long-term data sets are in short supply; gathering more long-term data is an important research aim, especially given rapid anthropogenic climate change (Richardson & Poloczanska, 2008). Alternatively, other methods to estimate the interaction strength between top-down effects and environmental change need to be sought, such as meta-analysis (Gruner *et al.*, 2008) or analysis of environmental effects on diet composition (Kirkwood *et al.*, 2008).

#### *Effects of model complexity*

In order to resolve predation and competition interactions, food web models need to be designed with

appropriate levels of complexity (Metcalf *et al.*, 2008). For instance in sensitivity analysis, fishery catch showed nonlinear responses to primary production change in the vulnerability fitted Burdekin coast model. Strong top-down effects in the Burdekin coast model were further amplified by a high degree of aggregation of species into functional groups. Aggregation reduces the total number of groups in the model but increases their connectivity (Pinnegar *et al.*, 2005), thereby increasing the relative importance of each functional group for determining the model's behaviour. Thus, predation and competition interactions which strongly influence a single functional group's biomass will have large effects on other functional groups in aggregated models. By contrast, the vulnerability fitted New South Wales shelf and South-East Shelf models which are disaggregated into a larger number of species are less impacted, because biomass changes in a single group did not have as large an effect on other groups. Appropriately designed Ecosim models may be even more robust to uncertainty in the magnitude of the vulnerability parameters, for instance, model design choices can result in numerical instability under some vulnerability parameter formulations and produce unrealistic cyclic patterns in functional group biomasses.



**Fig. 11** Change in fishery landings (a), community biomass evenness (b), mean biomass longevity (c) and mean trophic level (d, %) over 50 years for  $-10\%$  change in all primary producers (black bars),  $-10\%$  change in pelagic primary producers only (grey bars), and  $-10\%$  change in benthic primary producers only (white bars). Only models with pelagic and benthic primary producers are shown. Vulnerability settings used were described in the Results section. See Fig. 1 for model acronyms. Results are relative to simulations with no climate change.

### Indices of community composition

Indices of community composition may help to identify functional groups that will be most affected by climate change. Using an Ecosim model, Watters *et al.* (2003) found lower trophic level consumers responded more to changes in primary production than higher trophic levels. We did not find the same pattern in trophic levels across the 12 models used here. This may be due to either the longer time-scale of our analysis than that of Watters *et al.* (2003), who looked at 1 year pulses in primary production, or it may be that this trend does not generally occur across a broad range of models or ecosystems, particularly those with the lower productivity levels typical of the Australian region. In our analyses and those of Pinnegar *et al.* (2005), functional groups with lower biomass turn-over tended to show smaller changes in biomass than groups with higher biomass turnover, due to their slower responses to change. This trend was manifest as increases in mean biomass longevity for decreases in primary production and was also apparent in the generally smaller changes in marine mammal biomass when compared with other groups of conservation importance. However, due to

the weak strength of these effects and inconsistency of responses across different models, we found it difficult to interpret changes in the community indices and consistently relate them to model design or real ecosystem effects. In another comparison of multiple fitted EwE models, Mackinson *et al.* (2008) also found that system level indices were inadequate for predicting effects on species. The lack of generality in these studies suggests that a species' interactions with other species are more important determinants of its response to primary production change than that species' traits, such as trophic level (Mackinson *et al.*, 2008). Quantifying the strength of predation and competition interactions should be a major focus for improving predictions of the effects of primary production change on fisheries and biodiversity.

### Caveats to predicting coastal primary production

Reliable predictions of coastal primary productivity are important for predicting the effects of climate change on coastal species and fisheries. Changes in production by the coastal primary producers, seagrass, mangroves, benthic microalgae, and macroalgae, did have large

effects on population biomasses. Furthermore, sensitivity analyses showed that community composition was more dependent on benthic than pelagic primary production in some models, because different parts of the community were dependent on different sources of primary production. However, patterns of productivity may be more complex and consequently, more difficult to predict in coastal regions than open ocean regions (Cloern & Jassby, 2008), due to land–sea interactions and dynamic feedbacks between primary producers, consumer food webs and available habitat (Murray & Parslow, 1999; Fulton *et al.*, 2004; Cloern & Jassby, 2008). A goal for the future is to integrate primary production models with food web models that fully account for feedbacks between primary producers and consumer nutrient recycling (Travers *et al.*, 2007). Further work should also consider the effects of climate change on land-based nutrient inputs to coastal regions and the potential loss of shallow water habitats under sea level rise. Currently, predicting changes in the physical environment in coastal regions is challenging because general circulation models do not resolve fine-scale oceanographic processes which can be important for coastal productivity. Developing more reliable primary production models is important because our sensitivity analyses show decreases in primary production will cause decreases in fishery catches and biomass of species which will prove challenging for management.

#### *Caveats relating to global warming*

Predictions from food web models under climate change could also be improved by incorporating the effects of global warming on consumer species. Warming temperatures that cause individual species life histories and distributions to change can have implications for community composition and ecosystem function (Hiddink & ter Hofstede 2008; Ling *et al.*, 2008). Current models of the ecological effects of global warming effects have made useful progress by studying the responses of individual species to warming (e.g. Clark *et al.*, 2003; Cheung *et al.*, 2009; Hobday 2009). Warming will also affect ecological interactions (Poloczanska *et al.*, 2008; Preston *et al.*, 2008) and we have shown that ecological interactions have an important bearing on predictions of biomass change for species. Food web models provide a useful platform for investigating the combined effects of warming, primary production change and inter-specific interactions (Watters *et al.*, 2003). For instance, spatially explicit Ecosim models (Christensen & Walters, 2004a) that include climate change effects, could capture temperature-driven shifts in species ranges and the resulting altered ecological interactions.

#### *Conclusions and recommendations*

In summary, reliable primary productivity predictions will be a necessary part of predicting ecosystem and fishery responses to climate change. However, knowledge of ecological interactions is required to predict outcomes for particular species because interactions affect the magnitude and direction of biomass changes. Analyses of food webs under climate change should take care to parameterize ecological interactions. Biomass time-series are used to parameterize interactions in Ecosim, however, alternative methods that make the most of available data should also be sought. Primary production declines may challenge management by necessitating reductions in other anthropogenic impacts on marine ecosystems to maintain sustainable fisheries and conserve biodiversity. On the other hand, primary production increases will provide opportunities to recover overfished fisheries, increase profitability of fisheries and conserve threatened biodiversity.

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#### **References**

- Ainsworth CH, Pitcher TJ (2006) Modifying Kempton's species diversity index for use with ecosystem simulation models. *Ecological Indicators*, **6**, 623–630.
- Australian Bureau of Agricultural and Resource Economics (2008) *Australian Fisheries Statistics*. Australian Bureau of Agricultural and Resource Economics, Canberra, Australia.
- Aveytua-Alcazar L, Camacho-Ibar VF, Souza AJ, Allen JI, Torres R (2008) Modelling *Zostera marina* and *Ulva* spp. in a coastal lagoon. *Ecological Modelling*, **218**, 354–366.
- Beaugrand G, Edwards M, Brander KM, Luczak C, Ibañez F (2008) Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*, **11**, 1157–1168.
- Behrenfeld MJ, O'Malley RT, Siegel DA *et al.* (2006) Climate-driven trends in contemporary ocean productivity. *Nature*, **444**, 752–755.
- Bulman C (2007) Trophic webs and modelling of Australia's North West Shelf. In: *North West Shelf Joint Environmental Management Study Technical Report No 9*. CSIRO Marine and Atmospheric Research, Hobart, Australia.
- Bulman C, Butler A, Condie S *et al.* (2002) *A trophodynamic model for the Tasmanian Seamounts Reserve: Links between pelagic and deepwater ecosystems*. CSIRO Marine and Atmospheric Research, Hobart, Australia.

- Bulman C, Condie S, Furlani M, Cahill M, Klaer N, Goldsworthy S, Knuckley I (2006) *Trophic dynamics of the eastern shelf and slope of the South East Fishery: impacts of and on the fishery*. CSIRO Marine and Atmospheric Research, Hobart, Australia.
- Cheung WL, Lam VW, Sarmiento JL, Kearney K, Watson R, Pauly D (2009) Projecting global biodiversity impacts under climate change scenarios. *Fish and Fisheries*, **10**, 235–251.
- Christensen V, Walters CJ (2004a) Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, **172**, 109–139.
- Christensen V, Walters CJ (2004b) Trade-offs in ecosystem-scale optimization of fisheries management policies. *Bulletin of Marine Science*, **74**, 549–562.
- Clark RA, Fox CJ, Viner D, Livermore M (2003) North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biology*, **9**, 1669–1680.
- Cloern JE, Jassby AD (2008) Complex seasonal patterns of primary producers at the land-sea interface. *Ecology Letters*, **11**, 1294–1303.
- Cury PM, Shin YJ, Planque B *et al.* (2008) Ecosystem oceanography for global change in fisheries. *Trends in Ecology & Evolution*, **23**, 338–346.
- Forrest R (2008) *Simulation models for estimating productivity and trade-offs in the data-limited fisheries of New South Wales, Australia*. Unpublished PhD thesis, University of British Columbia, 357 pp.
- Fulton EA (2009) Approaches to end to end ecosystem models. *ICES Journal of Marine Science*, in press.
- Fulton EA, Smith ADM (2004) Lessons learnt from a comparison of three ecosystem models for Port Phillip Bay, Australia. *African Journal of Marine Science*, **26**, 219–243.
- Fulton EA, Smith ADM, Johnson CR (2003) Effect of complexity on marine ecosystem models. *Marine Ecology-Progress Series*, **253**, 1–16.
- Fulton EA, Smith ADM, Johnson CR (2004) Biogeochemical marine ecosystem models I: IGBEM – a model of marine bay ecosystems. *Ecological Modelling*, **174**, 267–307.
- Fulton EA, Smith ADM, Punt AE (2005) Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science*, **62**, 540–551.
- Gehrke PC (2007) *Comparative analysis of coastal fishery food webs in the Great Barrier Reef region, Australia*. CSIRO: Water for a Healthy Country National Research Flagship, Brisbane, Australia.
- Gilman EL, Ellison J, Duke NC, Field C (2008) Threats to mangroves from climate change and adaptation options: a review. *Aquatic Botany*, **89**, 237–250.
- Gordon HB, Rotstain LD, McGregor JL *et al.* (2002) *The CSIRO Mk3 Climate System Model*. CSIRO Atmospheric Research, Hobart, Australia.
- Gribble NA (2003) GBR-prawn: modelling ecosystem impacts of changes in fisheries management of the commercial prawn (shrimp) trawl fishery in the far northern Great Barrier Reef. *Fisheries Research*, **65**, 493–506.
- Gruner DS, Smith JE, Seabloom EW *et al.* (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters*, **11**, 740–755.
- Guénette S, Heymanns SJJ, Christensen V, Trites AW (2006) Ecosystem models show combined effects of fishing, predation, competition and ocean productivity on Steller sea lions (*Eumetopias jubatus*) in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **63**, 2495–2517.
- Halpern BS, Walbridge S, Selkoe KA (2008) A global map of human impact on marine ecosystems. *Science*, **319**, 948–952.
- Harley CDG, Randall Hughes A, Hultgren KM *et al.* (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.
- Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. *Trends in Ecology & Evolution*, **20**, 337–344.
- Heithaus MR, Wirsing AJ, Thomson JA, Burkholder DA (2008) A review of lethal and non-lethal effects of predators on adult marine turtles. *Journal of Experimental Marine Biology and Ecology*, **356**, 43–51.
- Hiddink J, ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. *Global Change Biology*, **14**, 453–460.
- Hirst AC, O'Farrell SP, Gordon HB (2000) Comparison of a coupled ocean-atmosphere model with and without oceanic eddy-induced advection. Part I: ocean spinup and control integrations. *Journal of Climate*, **13**, 139–163.
- Hobday AJ (2009) Ensemble analysis of the future distribution of large pelagic fishes in Australia. *Progress in Oceanography*, in press.
- Hunt GL, McKinnell S (2006) Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. *Progress in Oceanography*, **68**, 115–124.
- IPCC (Intergovernmental Panel on Climate Change) (2007a) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland, <http://www.ipcc.ch>.
- IPCC (Intergovernmental Panel on Climate Change) (2007b) *Climate change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland, <http://www.ipcc.ch>.
- Kirkwood R, Hume F, Hindell M (2008) Sea temperature variations mediate annual changes in the diet of Australian fur seals in Bass Strait. *Marine Ecology-Progress Series*, **369**, 297–309.
- Ling SD, Johnson CR, Frusher S, King CK (2008) Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology*, **14**, 907–915.
- Loneragan N, Babcock RC, Dambacher JM, Lozano-Montes H (2008) *Evaluating how food webs and the fishery they support are affected by fishing closures in Jurien Bay, temperate Western Australia*. Murdoch University and CSIRO Marine and Atmospheric Research, Perth, Australia.
- Mackinson S, Blanchard JL, Pinnegar JK, Scott R (2003) Consequences of alternative functional response formulations in models exploring whale-fishery interactions. *Marine Mammal Science*, **19**, 661–681.
- Mackinson S, Daskalov G, Heymanns JJ *et al.* (2008) Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecological Modelling*, Online early, doi: 10.1016/j.jecolmodel.2008.10.021.
- Martin JM (2005) *The distribution, abundance and trophic ecology of the fishes of Darwin harbour mangrove habitats*. Unpublished PhD thesis, Charles Darwin University, Darwin, 291 pp.
- Metcalfe SJ (2009) *Ecosystem modelling in data-poor situations: the use of qualitative models and Ecopath to investigate the inshore reefs of Eastern Tasmania*. Unpublished PhD thesis, University of Tasmania, Hobart, 188 pp.
- Metcalfe SJ, Dambacher JM, Hobday AJ, Lyle JM (2008) Importance of trophic information, simplification and aggregation error in ecosystem models. *Marine Ecology-Progress Series*, **360**, 25–36.
- Murray AG, Parslow JS (1999) Modelling of nutrient impacts in Port Phillip Bay - a semi-enclosed marine Australian ecosystem. *Marine and Freshwater Research*, **50**, 597–611.
- Nakicenovic N, Swart R (2000) *Emissions Scenarios*. Cambridge University Press, Cambridge, UK.
- Pinnegar JK, Blanchard JL, Mackinson S, Scott RD, Duplisea DE (2005) Aggregation and removal of weak-links in food-web models: system stability and recovery. *Ecological Modelling*, **184**, 229–248.
- Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modelling the response of populations of competing species to climate change. *Ecology*, **89**, 3138–3149.
- Portner HO, Farrell AP (2008) Physiology and climate change. *Science*, **322**, 690–692.
- Preston K, Rotenberry JT, Redak RA, Allen MF (2008) Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Global Change Biology*, **14**, 2501–2515.

- Rahmstorf S, Cazenave A, Church JA, Hansen JE, Keeling RF, Parker DE, Somerville RCJ (2007) Recent climate observations compared to projections. *Science*, **316**, 709–709.
- Richardson AJ, Poloczanska ES (2008) Ocean science- under-resourced, under threat. *Science*, **320**, 1294–1295.
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, **305**, 1609–1612.
- Sarmiento JL, Slater R, Barber R *et al.* (2004) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles*, **18**, GB3003, doi: 10.1029/2003GB002134.
- Scheffer M, Carpenter S, de Young B (2005) Cascading effects of overfishing marine systems. *Trends in Ecology & Evolution*, **20**, 579–581.
- Shurin JB, Gruner DS, Hillebrand H (2006) All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1–9.
- Travers M, Shin YJ, Jennings S, Cury P (2007) Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Progress in Oceanography*, **75**, 751–770.
- Walters CJ, Christensen V, Martell SJ, Kitchell JF (2005) Possible ecosystem impacts of applying MSY policies from single-species assessment. *Ices Journal of Marine Science*, **62**, 558–568.
- Walters CJ, Martell SJ (2004) *Fisheries Ecology and Management*. Princeton University Press, Princeton.
- Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. *Science*, **308**, 1280–1284.
- Watters GM, Olson RJ, Francis RC *et al.* (2003) Physical forcing and the dynamics of the pelagic ecosystem in the eastern tropical Pacific: simulations with ENSO-scale and global-warming climate drivers. *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 1161–1175.
- Young JW, Lansdell MJ, Hobday AJ *et al.* (2009) *Determining the ecological effects of longline fishing in the Eastern Tuna and Billfish Fishery*. CSIRO Marine and Atmospheric Research, Hobart, Australia.

### Supporting Information

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

**Appendix S1.** Caveats, impacts on results and how each was addressed.

**Appendix S2.** Predicting benthic primary production rate.

**Appendix S3.** Habitat mediation.

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