# Ecosystem model of Tasmanian waters explores impacts of climate-change induced changes in primary productivity

Reg A. Watson [a,b,*], Gabrielle B. Nowara [c], Sean R. Tracey [a], Elizabeth A. Fulton [d], Cathy M. Bulman [d], Graham J. Edgar [a], Neville S. Barrett [a], Jeremy M. Lyle [a], Stewart D. Frusher [a], Colin D. Buxton [a]

[a] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia
[b] Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada
[c] Ecomarine Metaresearch, PO Box 1086, Sandy Bay, TAS 7006, Australia
[d] Commonwealth Scientific and Industrial Research Organization (CSIRO) Marine and Atmospheric Research, General PO Box 1538, Hobart, TAS 7001, Australia

## ARTICLE INFO

## ABSTRACT

An Ecopath with Ecosim (EwE) model was developed that represents the marine shelf environment surrounding the island state of Tasmania (south of mainland Australia). Climate change scenarios representing a range of potential impacts (30% increase or decrease over a century) on marine primary productivity were investigated. Temperature changes and other impacts were not investigated. This analysis uncovered an asymmetric set of system responses. Modeled increases in primary productivity predict increases in the biomass of most groups, especially shallow filter-feeders (which includes oysters), fished macrozoobenthos which includes rock lobsters (*Jasus edwardsii*) and octopus. In contrast the group of unfished macrozoobenthos (sea stars, whelks) decreased their relative biomass as primary productivity increased. All modeled fisheries responded to varying primary production levels. The most responsive modeled fisheries were for flathead (Platycephalidae) and for those offshore. Of the groups of special conservation interest (marine mammals and seabirds) the most responsive was the dolphin group – though all responded.

© 2012 Elsevier B.V. All rights reserved.

## 1. Introduction

Tasmania is an island state of Australia at 39–43° south latitude. The value of wild fishery production in Tasmania in 2007–08 was A\$157M, comprised mainly of rock lobster and abalone catches (ABARE, 2009). Many Tasmanian coastal towns rely substantially on fishing for their livelihood, and fishing activities also provide a major source of recreation. Like the south-eastern coast of mainland Australia to the north, Tasmania is considered a climate-change hotspot where warming over the last 50 years has exceeded the global average, and which is subject to the invasion of species from the north as their ranges undergo a pole-ward range expansion (Poloczanska et al., 2007; Pitt et al., 2010; Last et al., 2011).

Cheung et al. (2010) considered that the expected response of fisheries production to climate-change induced oceanographic changes around Tasmania would be mixed. In their global analysis, high latitude regions (except the Antarctic) were projected to gain in catch potential while many regions in the tropics suffered from losses. For Australia they found that under the SRESA1B scenario (GFDL's CM 2.1; Delworth et al., 2006) there would be a slight increase in catch potential from within Australia's declared Exclusive Economic Zone waters, but with a scenario that models "stabilization at the 2000 level" this potential decreased slightly. Their work was based on broad changes to the catch potential of commercial species based on expected climate-change forcing of oceanographic parameters, but the effects of ecological interactions were not considered.

Besides oceanographic features, climate-change induced alterations in primary productivity levels are expected to have major impacts on marine ecosystems. Through a metastudy of ecosystem models of Australia's marine environment, Brown et al. (2010) demonstrated significant change in the biomass of fished and unfished groups in response to predicted changes of primary productivity. Based on the IPCC A2 emission scenario (Nakicenovic and Swart, 2000), driving nutrient–phytoplankton–zooplankton–detritus model predictions, they showed a wide range of impacts on primary productivity predicted along the Tasmanian coast. Consequently, the overall impact on the Tasmanian system is uncertain, especially since they also demonstrated that the outcomes to modeled groups were dependent on local trophic interactions.

* Corresponding author at: PO Box 1086, Sandy Bay, Tasmania, 7006 Australia.
E-mail address: rwatson@ecomarres.com (R.A. Watson).

Although there is a degree of uncertainty associated with the impacts of climate change on marine primary productivity, usual projections predict the increased flow of warmer northern waters southward along the eastern Tasmanian coast (Cresswell and Golding, 1980; Harris et al., 1987, 1991; Johnson et al., 2011a). These intrusions have been found to be relatively low in nutrients compared to the cooler waters that influence the coast in periodic upwellings (Harris et al., 1991). In years of strong westerlies, however, phytoplankton biomass and productivity increases and the spring bloom lasts longer (Clementson et al., 1989). Harris et al. (1987) describe the phytoplankton biomass on the east coast of Tasmania as a complex function of seasonal and episodic events. Some predictions suggest that such nutrient rich upwellings may actually occur less frequently. The impact of currents from the south of Australia (including the Bonny upwelling) may increase with global warming, so increasing productivity. Thompson et al. (2009), however, found that the western Tasman Sea experienced a ∼50% decline in the growth rate and biomass of the spring bloom from 1997 to 2007. Taken together there is considerable uncertainty about what impact any global warming scenario could have on nutrient loading and hence marine primary productivity. Faced with this situation we believed that we should model a range of both positive and negative changes in primary productivity of algal groups to investigate how climate change might impact the modeled ecosystem, its components and fisheries.

Our study was designed to develop, parameterize and use an ecosystem model of Tasmanian waters to investigate the potential impacts of climate-change induced primary productivity changes on marine organisms including those fished commercially and those of special conservation significance.

## 2. Materials and methods

Methods and the structure of the Ecopath with Ecosim (EwE) modeling framework were described in detail by Christensen and Pauly (1992), Walters et al. (1997), and Pauly et al. (2000), and are only summarized here (after Frisk et al., 2010). Normally, a mass-balanced Ecopath network of trophically linked biomass pools is developed first. Biomass pools or functional groups used in EwE typically consist of either a single species or a group of species representing an ecological guild. These pools are created for all major components of the ecosystem, including detritus and those at lower trophic levels such as plankton and invertebrates. The principal equation describing the flow of biomass into and out of each pool can be written as:

$$B_i \left(\frac{P}{B}\right)_i EE_i = BA_i + E_i + Y_i + \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j DC_{ji}, \quad (1)$$

where subscripts refer to different trophic groups, with $i$ being the prey group and $j$ referring to its predators. In Eq. (1), $B$ is biomass, $(P{:}B)$ is the production-to-biomass ratio, which is equivalent to the total mortality rate in most instances (Allen, 1973), $EE$ is the ecotrophic efficiency, or the fraction of the total mortality that is utilized within the modeled system, $BA$ is the biomass accumulation rate, $E$ is the net migration rate (emigration–immigration), $Y$ is the fisheries catch; $(Q{:}B)$ is the consumption-to-biomass ratio, and $DC$ is the average fraction (typically by mass) of prey in the diet. Initial parameter estimates of standing stocks and flows usually result in an unbalanced network. Thus an important step is balancing the network – i.e. matter must be preserved and not created. This is ensured when all $EE_i$ values are ≤1. A systematic process of adjusting various input values was carried out to ensure all $EE_i$ values were ≤1 and the model mass balanced. Input values with the greatest uncertainty were adjusted first.

To progress past a representative static model, a time-dynamic simulation model, Ecosim, which re-expresses the static mass-balanced equations inherent to Ecopath as a system of coupled differential equations (Walters et al., 1997, 2000) was developed. In the modeling framework, Ecopath represents the initial states for Ecosim and is also used to derive parameters that determine overall growth efficiencies and predator–prey functional responses based on additional user-specified parameters in Ecosim. This system of equations is used to represent the spatially aggregated dynamics of entire ecosystems. Ecosim uses coupled differential equations to link a series of linear equations representing production for each group with the following equation (Walters et al., 1997, 2000; Christensen and Walters, 2004):

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^{n} Q_{ji} - \sum_{j=1}^{n} Q_{ji} + I_j - (M_i + F_i + e_i)B_i, \quad (2)$$

where subscripts are as before and $g$ is growth efficiency of prey pool $i$, $Q_{ji}$ is the consumption by (prey) biomass pool $i$ of all other pools $j$, $Q_{ij}$ is the consumption of biomass pool $i$ by other pools $j$, $I$ is the rate of immigration, $M$ is the instantaneous natural mortality, $F$ is the instantaneous fishing mortality, $e$ is the rate of emigration. Together, Eq. (2) and the underlying delay-difference equations representing age/size-structure, represent the dynamics of an ecosystem (Walters and Martell, 2004). The link between predator and prey is a key element in Ecosim and is expressed in the consumption or "flow" rates among linked biomass pools. Consumption of prey $i$ by predator $j$ is based on foraging arena theory (Walters and Juanes, 1993), and this is represented in Ecosim as:

$$Q_{ij}(B_i, B_j) = \frac{a_{ij} v_{ij} B_i B_j}{2 v_{ij} + a_{ij} B_j}, \quad (3)$$

where $a$ is the rate of effective search for prey $i$ and $v$ is the behavioral exchange rate between vulnerable and invulnerable prey pools. Conditional estimates of $a_{ij}$ are obtained by solving Eq. (3) using input values of $B_i$, $B_j$, and $QB_{ij}$ from Ecopath. The estimates of $a_{ij}$ are conditional on the user-specified value of $v_{ij}$, and this parameter essentially determines the shape of the predator–prey functional response; high values of $v_{ij}$ ($v_{ij} > 10$) imply a top-down control or mass-action consumption rates, whereas lower values of $v_{ij}$ ($1.0 < v_{ij} < 10$) imply a donor control or type-II functional response. Without adjustment, vulnerability settings default to 2.0. Our values were set using procedures within the Ecosim modeling framework to fit to fisheries catch and effort time series data.

### 2.1. Scope of model

The model was designed to represent the coastal shelf area of Tasmania incorporating the majority of Bass Strait to the north which separates Tasmania from mainland Australia (Fig. 1). The modeled area ranged from 38.33° to 44.34°S latitude and from 142.68° to 149°E longitude, and represents a total area of nearly 137,000 km$^2$. The model boundaries were designed to coordinate with other existing and planned ecosystem models which stretch down the south-east of Australia and include the east coast of Tasmania (Smith et al., 2011; Johnson et al., 2011b).

### 2.2. Description of data used (map)

The static Ecopath model was parameterized based on biomass estimates from surveys completed between 1993 and 2007 and from fisheries statistics averaged from 2001 to 2008. All habitats within the model area (nearly 137,000 km$^2$) were included. Of that an estimated 2300 km$^2$ were temperate reef, and 91% was less than 200 m in depth.
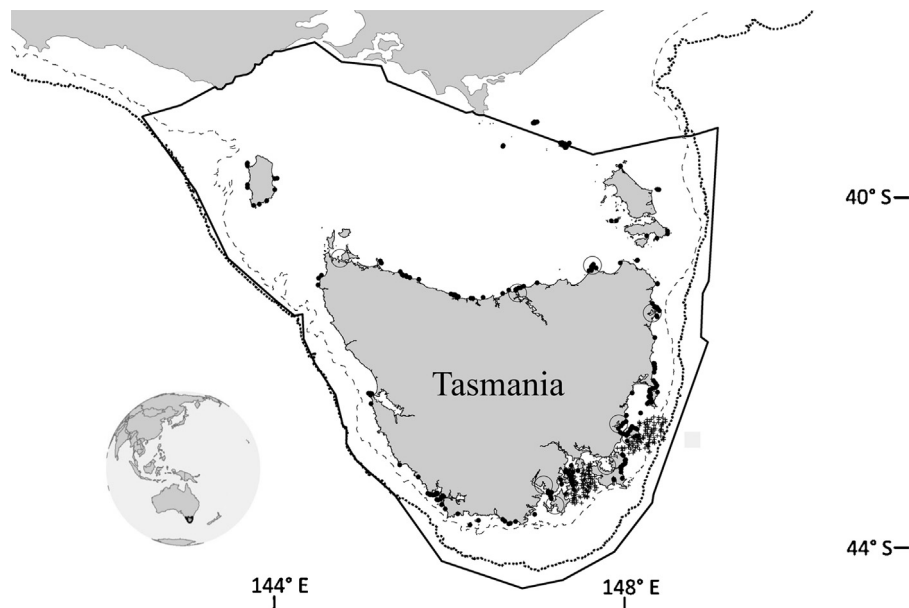
**Fig. 1.** Map showing the modeled area (outlined with a solid black line) nearly 137,000 km$^2$, the location of beam trawl samples (open circles), trawl survey samples (crosses) and temperate reef dive survey sites (filled circles) used in biomass estimates of functional groups. The 100 m (faint dashed line) and 300 m (bold dashed line) depth contours are shown.

Habitat information was based on Barrett et al. (2001) which primarily dealt with inshore areas (less than 40 m). Spatial Analysis routines in ArcMap (ESRI version 9.3.1) using an inverse distance weighted model were used to extrapolate these results to the entire model areas. For temperate reef habitat a local depth-based attrition rate was used such that most reef habitat was assumed to occur within the shallow inshore areas. It was assumed for temperate reef habitat that there was complete extinction at 60 m for the north and east coasts of Tasmania with this extended to 100 m for the west coast from 41°S round to 147°E (pers. comm., Dr Caleb Gardner, Institute for Marine and Antarctic Studies, UTAS, 2009) and a linear reduction was assumed.

Biomass estimates were based primarily on three sources: shelf trawl surveys (January 1993 to January 1995), temperate reef dive surveys (March 2006 to April 2007) and inshore beam trawl surveys (June 1995 to March 1996).

The shelf trawl surveys were conducted on the continental shelf of eastern and southeastern Tasmania (Lyle and Ford, 1993; Jordan, 1997) using a random design from a standardized vessel (FRV Challenger) and demersal trawl gear. The temperate reef dive surveys used diver transects (Stuart-Smith et al., 2009). The basic unit monitored was a 200-m long transect line, subdivided into four 50-m lengths, set along a defined depth contour. The beam trawl surveys (Jordan et al., 1998) consisted of samples of demersal fish fauna sampled at each site with a beam trawl with an opening of 2 m × 0.9 m. The trawl consisted of a 2.0 m aluminum beam (with skids and ground chain) with a 5 m long net with the following specifications: headline length 2.6 m, panel mesh 13 mm, and codend liner mesh 7 mm. At each site three non-overlapping 3 min trawls were conducted at a tow speed of 2 knots. All sampling was conducted within 2 h of high tide. Beam trawl catch rates were calculated as the number of fish per tow.

Survey locations are shown in Fig. 1. The biomass values extrapolated from survey data using kriging (ArcMap ESRI version 9.3.1) representing average levels within the last decade were used to parameterize the static Ecopath model. Production to Biomass ratios from similar groups from existing Ecopath models were used to guide estimates (Table 1) predominately from Metcalf (2009) and the associated Ecopath model. Parameter sources and subsequent modifications are recorded internally within our Ecopath model. Some parameters were estimated by the model to preserve mass balance. The diets of groups were initially parameterized from literature reports but as these were largely mostly qualitative or at best rank-order in nature, it was therefore considered that the proportions that functional groups form of the diet of predator groups would be adjusted as a priority while the model was being balanced (V. Christensen in Okey and Mahmoudi, 2002). Sources of initial diet breakdown included for birds (Montague and Cullen, 1988; Weimerskirch and Cherel, 1998; Hedd and Gales, 2001), for mammals (Gales and Pemberton, 1994; Gales et al., 1992), for fishes (Blaber and Bulman, 1987; Choat and Clements, 1992; Edgar and Shaw, 1995; Young et al., 1997; Shepherd and Clarkson, 2001; Bulman et al., 2001, 2002; Williams et al., 2001; Braccini, 2008) and for invertebrates (Shepherd, 1975; O'Sullivan and Cullen, 1983; Fenton, 1996; Grubert, 1996; Jackson and Pecl, 2003).

The proportion of biomass input from outside the modeled area (adjacent offshore areas) was adjusted to comply with expectations associated with the modeled groups in a model comprised principally of coastal shelf area (<300 m in depth). Most groups were constrained to only a portion of the model area because of their habitat (e.g. reef associated) or depth range limitations (Table 2).

Point or transect area biomass estimates were extrapolated to the model area based on Spatial Analysis (ArcMap) using an inverse distance weighted model. The model biomass estimates of reef-associated or shallow-water groups were prorated accordingly. The method for balancing the Ecopath model was similar to that used by Bulman et al. (2006).

### 2.3. Description of functional groups and fisheries

Functional groups were decided after several rounds of consultation with fisheries, seabird and marine mammal scientists and with those representing fisheries management in Tasmanian waters. There was a compromise in the selection of functional groups which involved weighing the importance of taxonomic, feeding/life history behavior and commercial groupings (Table 2) with considerations of optimum model complexity (Fulton et al., 2003; Metcalf et al., 2008).

The choice of fisheries included in the model was a compromise between the dynamic multi-gear fishing fleets active within

**Table 1**

Biomass estimates (t km$^{-2}$ total weight) and other functional group parameters in the Ecopath model. Bold numbers were provided to Ecopath which in turn estimated the other parameters through its mass-balance equations. Abbreviations (carn = carnivore, coast = coastal, dem = demersal, herb = herbivore, mic = microcarnivorous, mig = migratory, omn = omnivore, pel = pelagic, pisc = piscivore, plk = planktivore, sch = schooling, soft = soft sediment, telo = teleost).

| No. | Group name | Trophic level | Habitat area (fraction) | Biomass in habitat (t km$^{-2}$) | Biomass (t km$^{-2}$) | P/B (yr$^{-1}$) | C/B (yr$^{-1}$) | Ecotrophic efficiency | P/C |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Large phytoplankton | **1.000** | **1.000** | 8.520 | 8.520 | **50.000** | | **0.400** | |
| 2 | Small phytoplankton | **1.000** | **1.000** | 5.113 | 5.113 | **45.000** | | **0.400** | |
| 3 | Gelatinous zooplankton | 2.210 | **1.000** | 4.773 | 4.773 | **9.200** | **10.000** | **0.800** | 0.920 |
| 4 | Large zooplankton | 2.339 | **1.000** | 5.675 | 5.675 | **5.000** | **32.000** | **0.800** | 0.156 |
| 5 | Mesoplankton | 2.482 | **1.000** | 1.485 | 1.485 | **18.315** | **40.000** | **0.800** | 0.458 |
| 6 | Small zooplankton | 2.337 | **1.000** | 1.994 | 1.994 | **20.000** | **42.620** | **0.800** | 0.469 |
| 7 | Benthic carnivores | 2.361 | **0.100** | 5.245 | 0.525 | **10.000** | **25.544** | **0.800** | 0.391 |
| 8 | Benthic deposit filter feeders | 2.000 | **1.000** | 0.924 | 0.924 | **4.500** | **22.000** | **0.800** | 0.205 |
| 9 | Deep benthic filter feeders | 2.001 | **0.270** | 0.927 | 0.250 | **3.200** | **11.800** | **0.950** | 0.271 |
| 10 | Shallow filter feeders | 2.367 | **0.730** | 1.271 | 0.928 | **3.600** | **11.800** | **0.800** | 0.305 |
| 11 | Urchins | 2.268 | **0.017** | 7.934 | 0.135 | **2.500** | **11.800** | **0.970** | 0.212 |
| 12 | Reef mesograzers | 2.141 | **0.017** | 3.827 | 0.065 | **3.600** | **11.680** | **0.950** | 0.308 |
| 13 | Abalone | 2.000 | **0.011** | **32.000** | **0.352** | 2.000 | 12.410 | 0.932 | 0.154 |
| 14 | Macrozoobenthos herb | 2.000 | **0.730** | **1.850** | **1.350** | 2.200 | 11.680 | 0.736 | 0.188 |
| 15 | Macrozoobenthos | 2.311 | **0.017** | **2.000** | **0.034** | 2.700 | 12.000 | 0.881 | 0.225 |
| 16 | Macrozoobenthos fished | 2.601 | **0.017** | **4.325** | **0.074** | 2.000 | 7.400 | 0.810 | 0.270 |
| 17 | Meiobenthos | 2.877 | **1.000** | 0.570 | 0.570 | **2.500** | **11.100** | **0.950** | 0.225 |
| 18 | Macroalgae | **1.000** | **0.020** | 124.494 | 2.490 | **20.000** | | **0.300** | |
| 19 | Seagrass | **1.000** | **0.010** | 33.199 | 0.332 | **20.000** | | **0.300** | |
| 20 | Coastal squid fished | 3.713 | **0.180** | 0.648 | 0.117 | **1.5** | **8.000** | **0.950** | 0.188 |
| 21 | Transitory squid fished | 3.730 | **1.000** | 0.268 | 0.268 | **1.530** | **8.000** | **0.950** | 0.191 |
| 22 | Octopus | 3.370 | **1.000** | 0.030 | 0.030 | **1.369** | **8.000** | 0.828 | 0.171 |
| 23 | Coast soft micro carn telo | 3.253 | **1.000** | 0.001 | 0.001 | **1.200** | **10.000** | 0.307 | 0.120 |
| 24 | Coast dem reef herb telo fished | 2.000 | **0.017** | **5.880** | **0.100** | **0.900** | **15.000** | 0.837 | 0.060 |
| 25 | Coast small dem reef plk telo | 3.373 | **0.017** | **19.650** | **0.334** | **1.500** | **5.000** | 0.765 | 0.300 |
| 26 | Coast dem reef carn telo fished | 3.072 | **0.017** | **44.800** | **0.762** | **0.360** | **7.600** | 0.548 | 0.047 |
| 27 | Trans dem reef carn telo fished | 3.234 | **0.020** | **3.390** | **0.068** | **0.418** | **2.500** | 0.685 | 0.167 |
| 28 | Shelf carn telo fished | 3.390 | **0.983** | **1.326** | **1.326** | **0.320** | **2.737** | 0.627 | 0.117 |
| 29 | Coast pisc fished | 3.938 | **1.000** | **0.025** | **0.025** | 0.333 | **2.500** | **0.950** | 0.133 |
| 30 | Coast sch omn pel telo fished | 3.013 | **0.180** | **0.200** | **0.036** | 0.280 | **2.500** | 0.735 | 0.112 |
| 31 | Coast sch carn pel telo fished | 3.328 | **0.270** | **0.036** | **0.070** | 0.418 | **2.500** | 0.474 | 0.167 |
| 32 | Oceanic plk | 3.349 | **1.000** | 2.934 | 2.934 | **0.300** | **2.400** | **0.965** | 0.125 |
| 33 | Oceanic pisc | 3.403 | **1.000** | 3.526 | 3.526 | **0.418** | **2.500** | 0.628 | 0.167 |
| 34 | Small pel plk telo | 3.429 | **1.000** | 0.126 | 0.126 | **1.500** | **5.000** | 0.637 | 0.300 |
| 35 | Small pel carn telo fished | 3.371 | **1.000** | 0.212 | 0.212 | **1.000** | **4.500** | 0.911 | 0.222 |
| 36 | Offsh carn telo fished | 4.049 | **0.270** | **0.900** | **0.243** | 0.418 | **2.500** | 0.317 | 0.167 |
| 37 | Mig mesopelagics | 3.277 | **1.000** | 0.962 | 0.962 | **0.395** | **2.400** | 0.513 | 0.165 |
| 38 | Shelf-associated dem sharks | 3.834 | **1.000** | 0.106 | 0.106 | **0.270** | **5.500** | 0.119 | 0.049 |
| 39 | Offshore dem sharks | 4.088 | **0.270** | 0.330 | 0.089 | **0.270** | **5.500** | 0.0004 | 0.049 |
| 40 | Pelagic sharks | 4.523 | **1.000** | **0.0004** | **0.0004** | **0.260** | **1.433** | 0.891 | 0.181 |
| 41 | Skates and rays | 3.282 | **1.000** | **0.384** | **0.384** | **0.350** | **3.500** | 0.475 | 0.100 |
| 42 | Dolphins | 4.669 | **1.000** | **0.002** | **0.002** | **1.000** | **15.000** | 0.0008 | 0.077 |
| 43 | Fur seal | 3.967 | **1.000** | **0.045** | **0.045** | **1.158** | **15.000** | 0.001 | 0.005 |
| 44 | Little penguin and shearwaters | 3.841 | **1.000** | **0.088** | **0.088** | **1.000** | **15.000** | 0.017 | 0.067 |
| 45 | Sea birds | 4.171 | **1.000** | **0.075** | **0.075** | **1.000** | **15.000** | 0.0006 | 0.067 |
| 46 | Discards | **1.000** | **1.000** | **0.001** | **0.001** | | | 0.048 | |
| 47 | Detritus | **1.000** | **1.000** | **100.000** | **100.000** | | | 0.070 | |

Tasmanian waters, and the type and focus of commercial fisheries time series data that was available for fitting or tuning the model (see below) (Table 3).

### 2.4. Climate change scenarios

Given the general uncertainty about the environmental changes expected in the marine environment around Tasmania under a range of possible future greenhouse gas abatement scenarios, we decided to concentrate on changes to primary productivity in planktonic algal groups (i.e. exclude changes to macroalgae and seagrasses), and their impact on the other functional groups in the modeled system and its fisheries. To ensure that we covered the ranges that have been previously predicted we simulated a range of change from −30% to +30% in primary productivity from current model static values over a century. The primary productivity levels for large and small phytoplankton were both modified from base levels as shown in Fig. 2. The statistics reported for the simulations were collected as the average values from years 100 to 120 while primary productivity levels were held constant.
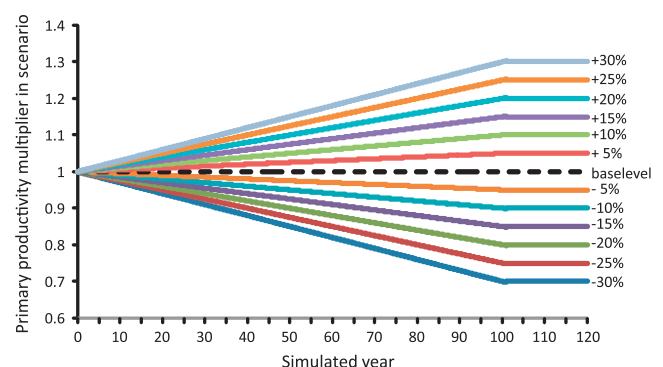


**Fig. 2.** The primary production values used in simulation scenarios (the base level is shown as the central dashed line). Values were ramped up or down in a linear fashion for a simulated 100-years then left static for the simulation of the following 20 years for which the average statistics were collected.

**Table 2**
Functional groups used in the Ecopath model in marine shelf waters surrounding Tasmania.

| No. | Group name | Range | Members |
|---|---|---|---|
| 1 | Large phytoplankton | All | Large plankton (diatoms) |
| 2 | Small phytoplankton | All | Picophytoplankton |
| 3 | Gelatinous zooplankton | All | Salps (pryosomes), coelentrates |
| 4 | Large zooplankton | All | Krill (also chaetognaths, etc.) |
| 5 | Mesozooplankton | All | Copepods |
| 6 | Small zooplankton | All | Heterotrophic flagellates |
| 7 | Soft sediment small benthic carnivores | 10% | Shrimps, small crabs, carnivorous polychaetes |
| 8 | Benthic deposit feeders | All | Polychaetes, some echinoderms incl holothurians (on shelf), infaunal bivalves |
| 9 | Deep benthic filter feeders | >100 m depth | Sponges, corals, crinoids, bivalves, bryozoa |
| 10 | Shallow filter feeders | <100 m depth | Oysters, other shallow filter feeders (e.g. corals and sponges), ascidians |
| 11 | Urchins | Reef | Including *Centrostephanus rodgersii* |
| 12 | Reef mesograzers | Reef | Amphipods, errant polychaetes, microgastropods |
| 13 | Benthic grazers fished (Abalone) | <30 m reef | Blacklip abalone, greenlip abalone (*Haliotis* spp.) |
| 14 | Herbivorous macrozoobenthos | <100 m depth | Gastropods (including *Turbo* spp.) |
| 15 | Carnivorous macrozoobenthos | Reef | Sea stars, dog whelks |
| 16 | Carnivorous macrozoobenthos fished | <200 m reef | Southern rock lobster (*Jasus edwardsii*), velvet crabs, giant crabs (*Pseudocarcinus gigas*) |
| 17 | Meiobenthos | All | Nematodes, copepods, ostracods |
| 18 | Macroalgae | Reef + drift areas | Kelp |
| 19 | Seagrass | Some reefs | Seagrass |
| 20 | Coastal squid fished | <50 m depth | Southern calamari (*Sepioteuthis australis*) |
| 21 | Transitory squid fished | All | Gould's squid (*Nototodarus gouldi*) |
| 22 | Octopus fished | All | *Octopus maorum*, *Octopus pallidus* |
| 23 | Coastal soft sediment microcarnivorous teleost | All | Gobies, pipefish, seahorse |
| 24 | Coastal demersal reef herbivorous teleost fished | Reef | Herring cale, marblefish, luderick |
| 25 | Coastal small demersal reef planktivore teleost | Reef | Southern hulafish, damselfish, cardinalfish, bullseyes, barber perch, butterfly perch |
| 26 | Coastal demersal reef carnivorous teleost fished | Reef | Magpie perch, leatherjacket, long snouted boarfish, purple wrasse, blue throat wrasse, banded morwong, bastard trumpeter |
| 27 | Transitory demersal reef carnivorous teleost fished | Reef + nearby | Striped trumpeter, jackass morwong |
| 28 | Shelf associated carnivorous teleost fished | Non-reef | Flounder, flatheads, stargazers, gurnard, latchet, rock cod, dories, whitings |
| 29 | Coastal piscivores fished | All | Barracouta, Australian salmon, pike |
| 30 | Coastal schooling omnivorous pelagic teleosts fished | <50 m depth | Mullets, sea garfish |
| 31 | Coastal schooling carnivorous pelagic teleosts fished | <100 m depth | Blue warehou, silver trevally |
| 32 | Oceanic planktivores | All | Sauries, flying fish |
| 33 | Oceanic piscivores fished | All | Tunas, swordfish, billfish |
| 34 | Small pelagic planktivorous teleost | All | Sardine, pilchard, herring, sprats, anchovy |
| 35 | Small pelagics carnivorous teleost fished | All | Redbait, yellowtail scad, jack mackerel, blue mackerel |
| 36 | Offshore demersal carnivorous teleosts fished | >100 m depth | Blue-eye trevalla, ling, blue grenadier, hapuka, whiptails, cardinalfish |
| 37 | Migratory mesopelagics | All | Myctophids, frostfish, lancetfish, hatchetfish |
| 38 | Shelf associated demersal sharks | All | Gummy shark, draughtboard shark, Port Jackson shark, saw shark, inshore dog sharks, school shark |
| 39 | Offshore demersal sharks | >100 m depth | Deepwater dogsharks (Owstons dogfish, golden dogfish, Plunket's dogfish, etc.) |
| 40 | Pelagic sharks | All | Bronze whaler, dusky whaler, blue shark, mako, white pointer, 7-gill shark |
| 41 | Skates and rays | All | Angel shark, stingray, stingaree, fiddler, Tasmanian numbfish, skate |
| 42 | Dolphins | All | Dolphins: longfin pilot whale *Globicephala melaena*, killer whale *Orcinus orca*, false killer whale *Pseudorca crassidens*, common dolphin *Delphinus delphis*, bottlenose dolphin *Tursiops truncatus* |
| 43 | Fur seal | All | Australian fur seal (*Arctocephalus pusillus*) and New Zealand fur seal (*A. forsteri*) |
| 44 | Little penguin, mutton birds | All | Little penguin (*Eudpyptula minor*), short-tailed shearwater (*Puffinus tenuirostris*) |
| 45 | Sea birds | All | Shy albatross (*Thalassarche cauta cauta*), gannets, storm petrels, fairy prions |
| 46 | Detritus | All | |

## 2.5. Time series and vulnerability parameter fitting

Both relative fishing effort and relative catch per unit of effort (based on gear units and relative to the starting value in 1995) were extracted for a range of Tasmanian fisheries (Table 3) from 1995 to 2007 from Zeigler and Lyle (2009). Data on the commercial landings of sharks in the model area were obtained from the Australian Fisheries Management Authority (Canberra, Australia) under a deed of confidentiality.

Sensitivity analysis was conducted exploring the impact of a wide range of assumed prey biomass "vulnerability" rates on the response of modeled groups and fisheries to climate change scenarios. EwE has a routine for maximizing the goodness of fit between biomass estimates made by the model using time series data. This required relative fishing effort and the biomass estimates (in our case relative catch per unit of effort) data. We provided both for most fisheries and their principal target biomass groups for the period 1995–2006 inclusive (Table 3). The general approach is described by Christensen and Walters (2011). The fitting process uses time series of catch per unit of effort data (cpue). This was indexed on the first year (1995) because the fitting process in Ecosim uses relative cpue data. The fitting process attempts to match the change in relative cpue data in the modeled fishery (representing biomass changes in the impacted groups in t km$^{-2}$) based

**Table 3**

Fisheries included in the Ecopath model. Groups fished refer to functional groups in Table 1. Catch per unit (cpue) was available for some fisheries for a 13-year period (1995–2006). This was converted from various measures to relative cpue indexed on the first year (1995). SS refers to the sum of squares value in absolute units when fitting biomass pool vulnerabilities. The fitting process attempts to match the change in relative cpue in the modeled fishery (representing biomass changes in the impacted groups in t km$^{-2}$) based on the vulnerabilities being tested with the cpue in the time series (as a biomass measure) provided from the actual fisheries statistics.

| Fishery no. | 'Fleet' name | Groups fished | SS | Years |
|---|---|---|---|---|
| 1 | Rock lobster commercial (southern rock lobster *Jasus edwardsii*) | 16 | 0.02 | 1995–2006 |
| 2 | Rock lobster recreational (southern rock lobster *Jasus edwardsii*) | 16 | | |
| 3 | Abalone (blacklip and greenlip) (*Haliotis*) | 13 | | |
| 4 | Giant crab (*Pseudocarcinus gigas*) | 16 | | |
| 5 | Recreational finfish | 24,26–31,33,35,38 | | |
| 6 | Shearwater harvest (*Puffinus tenuirostris*) | 44 | | |
| 7 | Southern calamari (*Sepioteuthis australis*) | 20 | 1.84 | 1995–2006 |
| 8 | Reef-associated | 26,27 | 0.62 | 1995–2006 |
| 9 | Coastal transitory finfish | 29–31 | 3.12 | 1995–2006 |
| 10 | Flathead (Platycephalidae) | 28 | 0.17 | 1995–2006 |
| 11 | Gould's squid (*Nototodarus gouldi*) | 21 | 12.5 | 1995–2006 |
| 12 | Small pelagics | 34,35 | 2.9 | 1995–2006 |
| 13 | Shark | 38,40 | 5.19 | 1995–2006 |
| 14 | Octopus (*Octopus maorum, Octopus pallidus*) | 22 | | |
| 15 | Coastal demersal | 24 | | |
| 16 | Offshore fishery | 36 | | |

on the vulnerabilities being tested, with the relative cpue in the time series (as a biomass measure) provided from the actual fisheries statistics. Vulnerability settings obtained in this way were used to substitute for default values initially assigned by EwE.

### 2.6. Baseline Ecopath model and climate change Ecosim simulations

The resulting parameterized and balanced Ecopath model is illustrated in Fig. 3 which shows the major flows of the biomass through the food relationships. Fished groups (those with a shaded background) appear at all levels of the food web from abalone (trophic level = 2) to the harvest of piscivorous shearwaters (diving seabirds) on the coast (3.8) and pelagic sharks (4.5). Including detritus, there were 46 groups represented. After the model was balanced the diets of the groups within the balanced model were examined and were found to be similar to those used to set initial, usually rank-order estimates. The diets used in the balanced model were examined and found to be broadly similar to that used in an existing Ecopath model of the Eastern Bass Strait shelf area (just to the north of our modeled area) (Bulman et al., 2006).
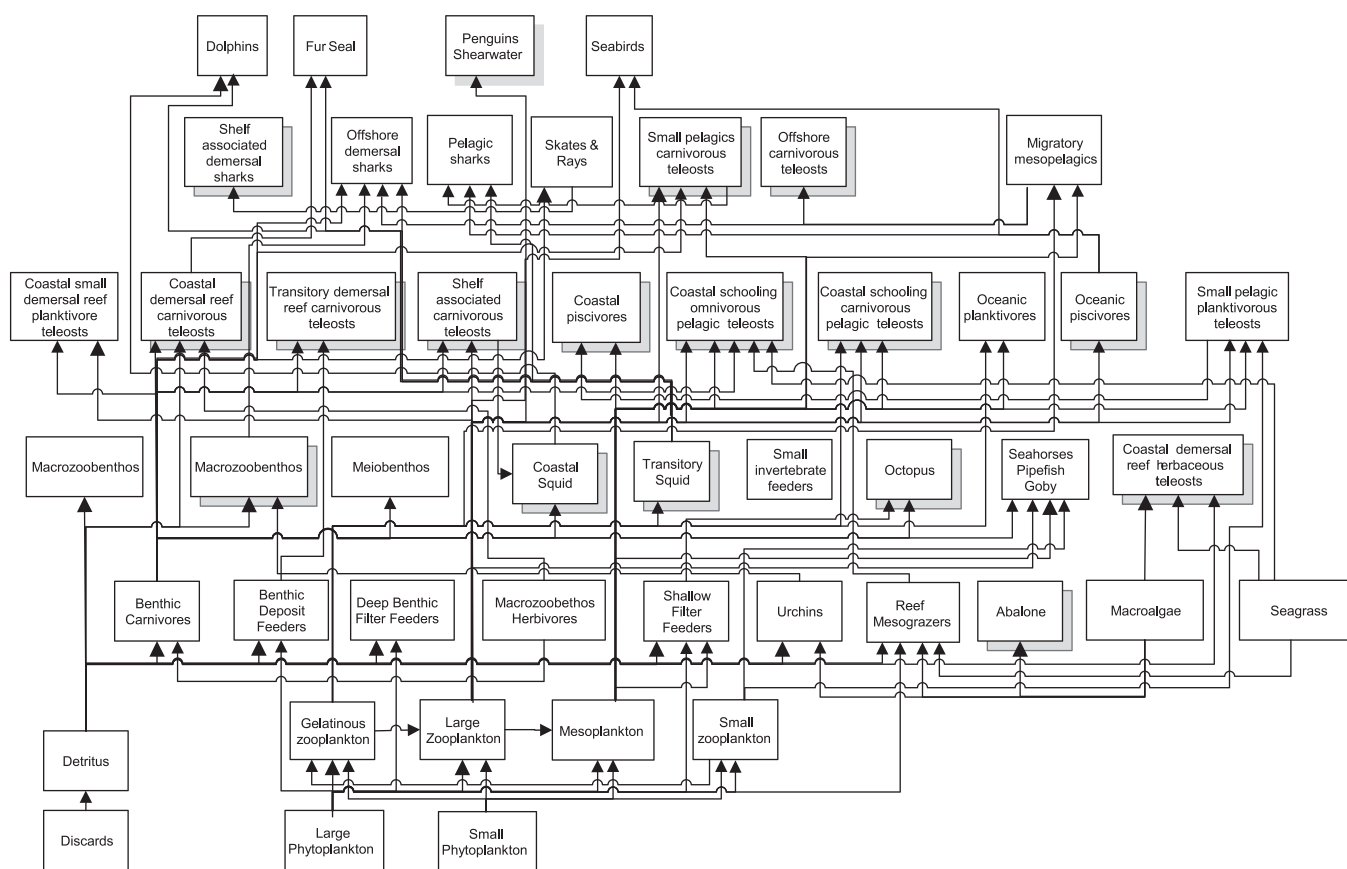


**Fig. 3.** A simplified diagram of the modeled food web with thick connection lines representing > 40% biomass flows to a functional group (into a box), while thinner lines represent smaller flows. For clarity flows of <10% are not shown. The size of boxes does not represent biomass. Shaded boxed represent fished groups.

**Table 4**

Ecosystem statistics describing the Tasmanian coastal ecosystem structure.

| Parameter | Value | Units |
|---|---|---|
| Sum of all consumption | 493.135 | t km$^{-2}$ yr$^{-1}$ |
| Sum of all exports | 525.695 | t km$^{-2}$ yr$^{-1}$ |
| Sum of all respiratory flows | 230.159 | t km$^{-2}$ yr$^{-1}$ |
| Sum of all flows into detritus | 564.940 | t km$^{-2}$ yr$^{-1}$ |
| Total system throughput | 1813.929 | t km$^{-2}$ yr$^{-1}$ |
| Sum of all production | 876.898 | t km$^{-2}$ yr$^{-1}$ |
| Mean trophic level of the catch | 3.088 | |
| Gross efficiency (catch/net p.p.) | 0.00017 | |
| Calculated total net primary production | 712.538 | t km$^{-2}$ yr$^{-1}$ |
| Total primary production/total respiration | 3.096 | |
| Net system production | 482.378 | t km$^{-2}$ yr$^{-1}$ |
| Total primary production/total biomass | 14.996 | |
| Total biomass/total throughput | 0.026 | |
| Total biomass (excluding detritus) | 47.514 | t km$^{-2}$ |
| Total catches | 0.120 | t km$^{-2}$ yr$^{-1}$ |
| Connectance index | 0.165 | |
| System omnivory index | 0.458 | |

The model can be seen summarized in Table 4 which shows commonly compared ecosystem statistics. These statistics are based on theoretical ecology and can be used to summarise aspects of the potential system function. Here we present those commonly presented for Ecopath models in the literature as a basis of comparison with other modeled systems.

The model describes a system with modest demands by fishing on primary production. This is partially because the model extends to the coastal shelf limits – much of which is not fished intensely. The spatial range of the model was extended to the shelf limits so that the areas where climate change impacts expected on marine mammals would be included. Because of this, the overall density of catch was modest at 0.12 tonnes km$^{-2}$.

The time dynamic extrapolations were performed using the balanced Ecopath model for a simulated period one century after the static period modeled (circa 2008). It was confirmed that projections were sensitive to vulnerability settings, therefore those fitted from time series data were used. Vulnerability settings fitted by the minimum sum of squares between modeled and observed biomass (where times series data was available) appear in Table 5. The sum of squares for each of the fisheries with time series catch available is shown in Table 3.

In this study only the impacts of changes on primary productivity induced by climate-change were modeled. As described above, there was considerable uncertainty about the magnitude, and even the direction of change in primary production induced through changes in currents, water temperature and relative frequency of storm events. Global primary production is projected to increase by 0.7–8.1% by 2050 but with wide regional differences (Sarmiento et al., 2004). Therefore a series of scenarios was modeled; each scenario simulated an increase or decrease of 5% in the biomass of the small and large phytoplankton groups from the static Ecopath levels. Both small and large phytoplankton groups were changed in the same way. In total a range of −30% to +30% gradual linear change over the course of 100-years was simulated (Fig. 2). After that, a further 20-year period was simulated without further changes to primary production. The average biomass levels and fisheries landings for this last 20-year period were used for scenario comparisons.

## 3. Results

### 3.1. Ecosim modeling

The degree of fit was variable, with the best achieved for the commercial rock lobster fishery but for others the catch per unit of effort (cpue) trends in the data available did not fit the modeled

**Table 5**

Fitted vulnerability settings used for model groups. Values above 10 have little additional impact of model outcomes. Values near 1.0 represent bottom-up interactions with predators near carrying capacity while those greater than 2 (the model default) represent top-down interactions which are typically less stable. Abbreviations (carn = carnivore, coast = coastal, dem = demersal, herb = herbivore, mic = microcarnivorous, mig = migratory, omn = omnivore, pel = pelagic, pisc = piscivore, plk = planktivore, sch = schooling, soft = soft sediment, telo = teleost).

| No. | Group name | Vulnerability |
|---|---|---|
| 3 | Gelatinous zooplankton | 1.0 |
| 4 | Large zooplankton | >10 |
| 5 | Mesoplankton | 1.0 |
| 6 | Small zooplankton | >10 |
| 7 | Benthic carnivores | >10 |
| 8 | Benthic deposit filter feeders | 2.0 |
| 9 | Deep benthic filter feeders | 1.0 |
| 10 | Shallow filter feeders | 1.0 |
| 11 | Urchins | 2.0 |
| 12 | Reef mesograzers | 2.0 |
| 13 | Abalone | 5.1 |
| 14 | Macrozoobenthos herb | 2.0 |
| 15 | Macrozoobenthos | >10 |
| 16 | Macrozoobenthos fished | 1.0 |
| 17 | Meiobenthos | 1.2 |
| 20 | Coastal squid fished | 1.3 |
| 21 | Transitory squid fished | >10 |
| 22 | Octopus | >10 |
| 23 | Coast soft micro carn telo | 2 |
| 24 | Coast dem reef herb telo fished | 2 |
| 25 | Coast small dem reef plk telo | 1 |
| 26 | Coast dem reef carn telo fished | >10 |
| 27 | Trans dem reef carn telo fished | >10 |
| 28 | Shelf carn telo fished | >10 |
| 29 | Coast pisc fished | 1.0 |
| 30 | Coast sch omn pel telo fished | 3.8 |
| 31 | Coast sch carn pel telo fished | 1.0 |
| 32 | Oceanic plk | >10 |
| 33 | Oceanic pisc | 2.0 |
| 34 | Small pel plk telo | 2.0 |
| 35 | Small pel carn telo fished | 1.0 |
| 36 | Offsh carn telo fished | >10 |
| 37 | Mig mesopelagics | 1.0 |
| 38 | Shelf-associated dem sharks | 1.0 |
| 39 | Offshore dem sharks | 1.0 |
| 40 | Pelagic sharks | 2.0 |
| 41 | Skates and rays | 2.0 |
| 42 | Dolphins | 1.0 |
| 43 | Fur seal | >10 |
| 44 | Little penguin and shearwaters | 2.0 |
| 45 | Sea birds | >10 |

biomass as well. Fitting cpue trends for fisheries to biomass trends for specific groups is difficult as fisheries often target unrelated groups – that is biomass groups that have different diets and life-histories so cannot be easily combined. In addition, cpue trends do not always track biomass changes well in general. When the base level of primary production was used (that is the starting biomass of large and small algal groups were at the static 'balanced' Ecopath model) the biomass of most of the 46 biomass groups stabilized within 100 years (Fig. 4) and most did so at near the starting biomass level. Three groups appeared to diverge from this pattern, and these were the macrozoobenthos (both unfished and commercially fished) and the reef mesograzers. Of those the commercially fished macrozoobenthos reached a stable biomass level, up from the starting level. Considering these results it was decided to use a 20-year average biomass value following year 100 for scenario comparisons.

### 3.2. Climate change primary productivity forcing

The relative biomass response of all groups relative to the base line (primary production not impacted by climate change) is shown
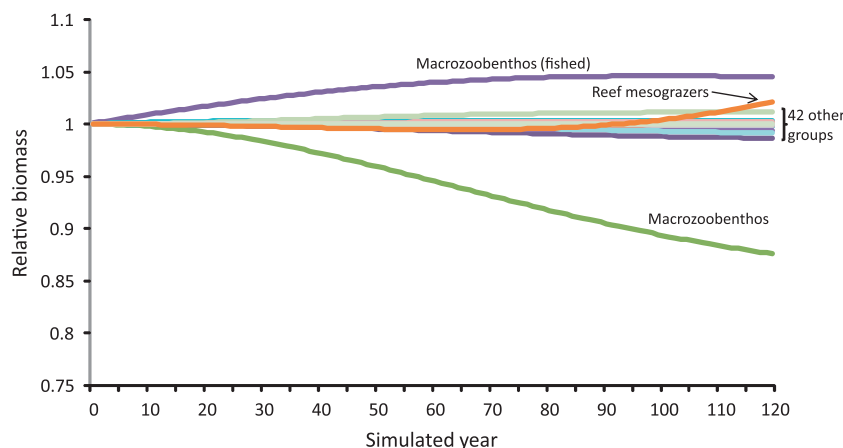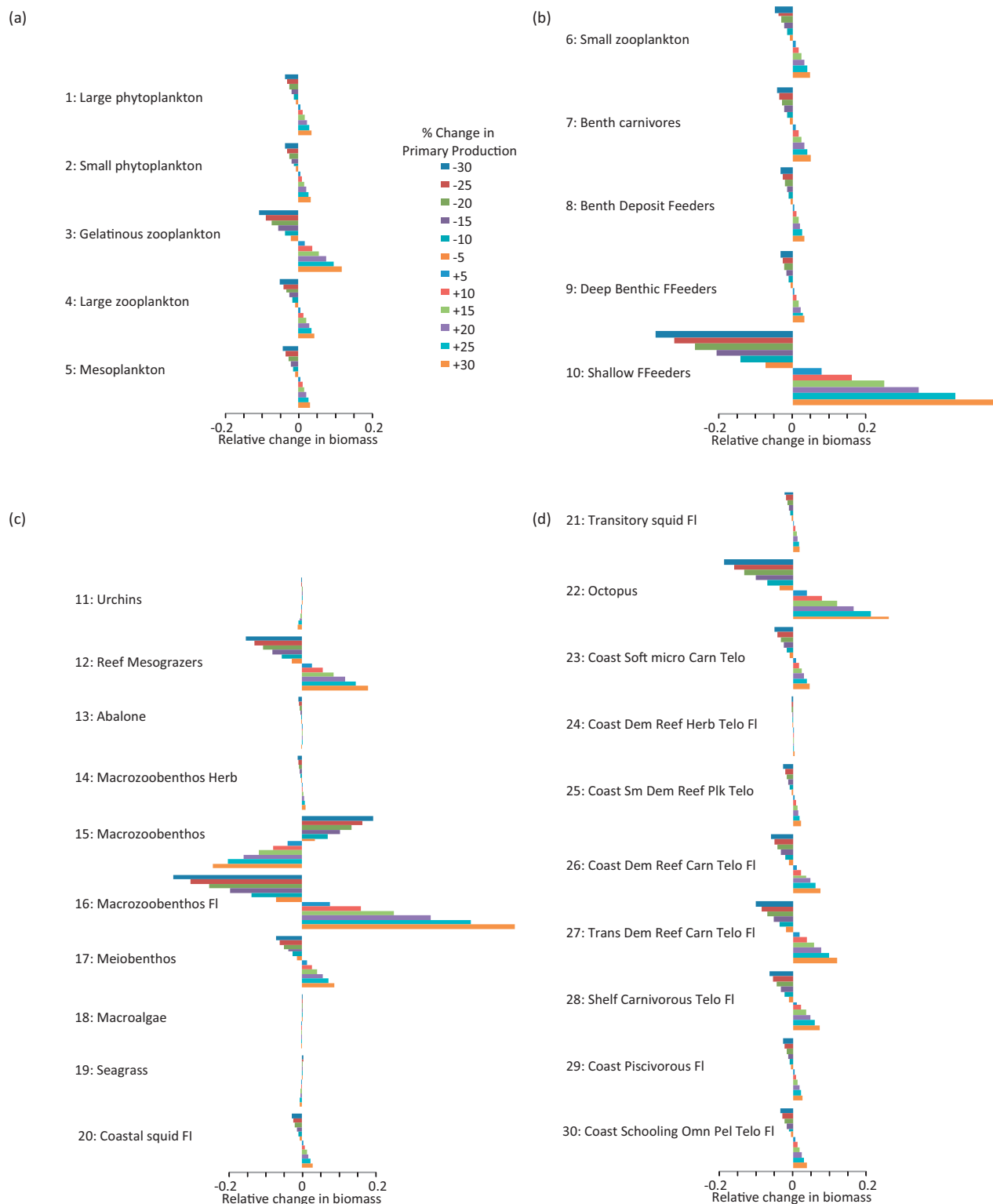
**Fig. 4.** Trajectories of the 45 modeled biomass groups in the Ecosim model relative to those resulting from baseline levels of primary productivity (that is in scenarios using the original biomass levels of large and small algae groups). Relative values represent the average for a 20-year period after a simulation of a 100-year period during which primary production rates were altered in each scenario (see Fig. 2 for details).
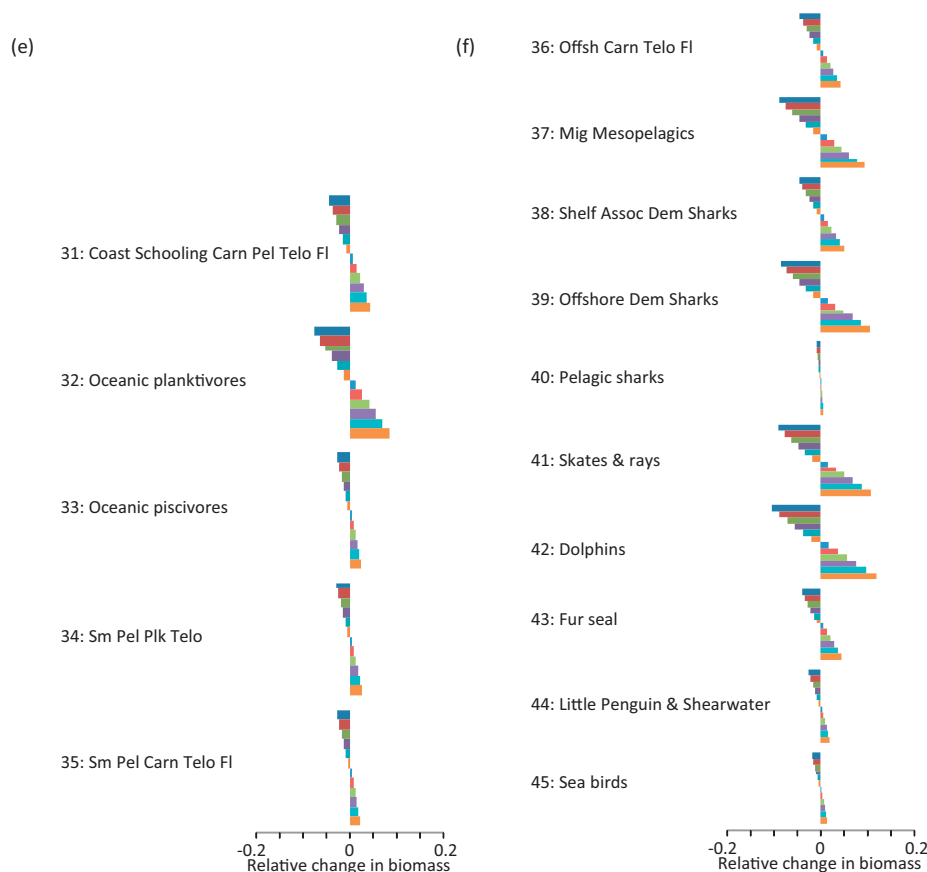
in Fig. 5. Of these groups, 10 (shallow filter-feeders) (Fig. 5b), 15 and 16 (unfished and commercially fished macrozoobenthos respectively) (Fig. 5c) and 22 (Octopus) (Fig. 5d) showed the largest relative biomass responses. Most groups increased with increasing primary productivity to varying degrees in a positive way except for group 15 (unfished macrozoobenthos) (Fig. 5c) which increased with decreasing primary productivity and vice versa.

All of the modeled fisheries increased their landings with primary productivity increase and decreased with decreasing primary productivity. The biggest positive responses were in the flathead (Platycephalidae) and the offshore fisheries (Fig. 6). Though the relative change in the flathead and offshore fisheries was the greatest these fisheries are much smaller in catch densities (tonnes removed per sq km) than most of the others. In fact, though there was only a slight increase in the biomass of the abalone group this translated to the 2nd largest increase in predicted fishery tonnage. The recreational fishery is predicted to have the largest absolute catch increase of 745 tonnes for the entire modeled area. With catch levels predicted to diminish to zero or near zero with maximal reduction in primary productivity, Fig. 6 does make it obvious that the modeled fisheries would be expected to greatly decline and possibly cease if the greatest reductions in primary productivity were realized.

Of those groups with special conservation interest, that is marine mammals and seabirds, the dolphins were the most responsive, increasing their relative biomass as primary production increased. Other groups were much less responsive (Fig. 5).

It should be noted that the model relates the consumption of a predator to the available prey biomass (especially for top-down relationships) as per Eq. (3). The explanation for most of the increases in biomass and fisheries catch with increased primary production typically therefore results from more biomass available at the lower end of the food web, which moves up and expands the biomass of upper tropic levels. From Fig. 5b we can see a strong response of the group shallow filter feeders (10), which feed at least partially directly on large and small algae (the groups whose biomass we modified to simulate climate change impacts). Once the biomass of filter feeders increased, this biomass was available for the fished macrozoobenthos (16) which eats them and this group consequently increased in biomass. The octopus group (22) preys upon both the shallow filter feeders (10) and the fished macrozoobenthos (16) and its biomass subsequently increased. There is some evidence for the decreased primary productivity releasing groups from predation. This seems to be the dominant impact on the unfished macrozoobenthos (15) which increased

their biomass from baseline levels only when primary production decreased thereby reducing the biomass of their predators including the fished macrozoobenthos group (16).

The impacts of each functional group and fishery upon each other (both positive and negative) in the Ecopath model is shown in Fig. 7. We can see, for example, that the biomass or functional group of Macrozoobenthos (fished) (group 16) which represents southern rock lobster (*Jasus edwardsii*), velvet crabs, giant crabs (*Pseudocarcinus gigas*) impacted positively on the fisheries for Rock Lobster (commercial) (F1), Rock Lobster (recreational) (F2) and Giant Crab (F4) as would be expected as these fisheries target species in this group. The group of coastal squid (fished) (20) which represented Southern calamari (*Sepioteuthis australis*) had a positive impact on dolphins (42) but had a negative impact on the coastal schooling omnivorous pelagic teleosts (fished) (30) which represented mullets and sea garfish.

## 4. Discussion

The goals of this study for the participating agencies were to bring together fisheries and survey data into a single model with representative biomass groupings that would describe the entire coastal waters of Tasmania, and to parameterize it with time series data so that various impacts induced by climate change could be investigated. In this paper we have described the impacts of changes in the biomass of algal groups that would be expected to respond to a range of changes in currents, nutrient levels and storm frequency. These impacts include changes to landings of existing fisheries and to the biomass of seabirds and marine mammals. In a previous meta-analysis by Brown et al. (2010), which looked at primary productivity impacts on Australian marine ecosystems, Tasmania was represented by a single model (Metcalf, 2009) representing only a small area off the mid eastern coast, which is primarily reef habitat. This model had not fitted vulnerability settings to relevant fisheries time series data and, as Brown et al. (2010) showed, this reduces the reliability we can place in a model's predictive abilities as predictions are sensitive to these settings. We have addressed these two issues in our model.

The EwE model constructed and examined here covered a vast area (nearly 137,000 km²) surrounding the whole island, and represents the coastal areas of Tasmania down to about 300 m of depth. As such, the biomass of many groups, even those only utilizing a relatively small fraction of the whole modeled area is quite large. For example, reef-only groups used about 1.7% of the total area but still this amounted to 2300 km². This is a large area compared to some

EwE models and it means that commercial landings used in the model accounted for only relatively low biomass extraction densities in most cases. Often fishing mortalities were not high compared to calculated natural mortality rates. This can cause problems when fitting time series data. In this procedure, fishing effort data is used to model fishing mortality relative to initial levels while EwE compares the resulting biomass estimates of impacted groups with user-provided relative catch per unit effort data (a proxy for relative biomass) over the same time period. If fishing mortality is not a significant part of the total mortality then in situations where there are only slight changes in relative fishing effort over the time series (such as in most tightly managed fisheries) it does not perturb the



**Fig. 5.** Biomass levels of modeled groups in the Ecosim model relative to those resulting from baseline levels of primary productivity (that is in scenarios using the original biomass levels of large and small algae groups). Relative values represent the average for a 20-year period after a simulation of a 100-year period during which primary production rates were altered in each scenario (see Fig. 2 for details).

(e)

31: Coast Schooling Carn Pel Telo Fl

32: Oceanic planktivores

33: Oceanic piscivores

34: Sm Pel Plk Telo

35: Sm Pel Carn Telo Fl

-0.2    0    0.2
Relative change in biomass

(f)

36: Offsh Carn Telo Fl

37: Mig Mesopelagics

38: Shelf Assoc Dem Sharks

39: Offshore Dem Sharks

40: Pelagic sharks

41: Skates & rays

42: Dolphins

43: Fur seal

44: Little Penguin & Shearwater

45: Sea birds

-0.2    0    0.2
Relative change in biomass

**Fig. 5.** (*Continued*).

modeled system much and induce much change in biomass. This is a consequence of the large area modeled and also the lack of a strong signal that some fisheries time series data provides to fitting routines. It must be said, however, that situations where fisheries are highly impacted by natural mortality are exactly where ecosystem models are most valuable because of the insights they provide that are outside of traditional stock assessment practices (Gaichas et al., 2010). The dynamics of fisheries that are completely dominated by fishing mortality are perhaps well served by standard single-species stock assessments.

When we compare the summary statistics of Table 4 with other models we found that the high value of primary production/total respiration (which is >1.0) is typical of an immature system, suggesting the system is under stress or frequently perturbed (either naturally or via anthropogenic pressure). The ratio of total primary production/total biomass also suggests the system may be relatively immature (Christensen, 1995) – the value is below the average value (approximately 19.0) of this indicator across known systems, but is well above the minimum values (3.9) associated with the most mature systems in Christensen (1992). In contrast the low levels of net and total primary production are much lower than typically seen in immature systems – it is an order of magnitude lower than for highly productive systems like the Benguela (which have values of 7000 or more, Heymans et al., 2004). Another feature that sets this system apart is the degree of connectivity–the system omnivory index (0.462) is high compared to many other modeled systems (e.g. maximum in Christensen and Pauly, 1992 is 0.35). This indicates that the model led system has a high level of interaction diversity and should be reasonably stable in its current form.

We can further compare the summary statistics describing our Ecopath model (Table 4) to those from another Ecopath model describing the Eastern Bass Strait (EBS) (just to the north of our modeled area) (Bulman et al., 2006). Our net system production was 482 t km$^{-1}$ year$^{-1}$, which was much lower than the 1694 reported for the EBS model, however, those authors described their system production as relatively high compared to most other systems citing Christensen and Pauly (1993) and Trites et al. (1999). Compared to the EBS model the one we describe was a less productive system with less flows. We found the gross efficiency of the fisheries (catch divided by net primary production) was similar to the EBS model and indeed at 0.00017 it was close to the weighted global average of 0.0002 (Christensen et al., 2005). Freire et al. (2008) found that their system off northeastern Brazil had total extractions (catches) of 0.13 t km$^{-1}$ year which they cited as comparable to the southeastern U.S., Yucatan, and Grenada and the Grenadines. Our extractions were similar at 0.12. Our modeled system had a mean trophic catch of 3.1 compared to 3.95 for the EBS model, partially because the EBS model captured more of the offshore fisheries. Bulman et al. (2006) described their EBS system as probably the most severely disturbed on the east coast of Australia. The EBS was also described as a 'large' system described by a total throughput of 15,806 t km$^{-1}$ year, larger than many others cited by Trites et al. (1999) so as expected, it was far larger in throughput than that for our system (1813). The total biomass/total throughput ratio should increase as a system approaches maturity (Christensen, 1995). Our fitted model's ratio was 0.026 compared to 0.012 for that of the EBS.

Bulman et al. (2006) described their EBS Ecosim model as having many groups with relatively low vulnerabilities consistent with an assertion by Bax and Williams (2000) that this area was predominantly a bottom-up system. Heavily exploited stocks were usually
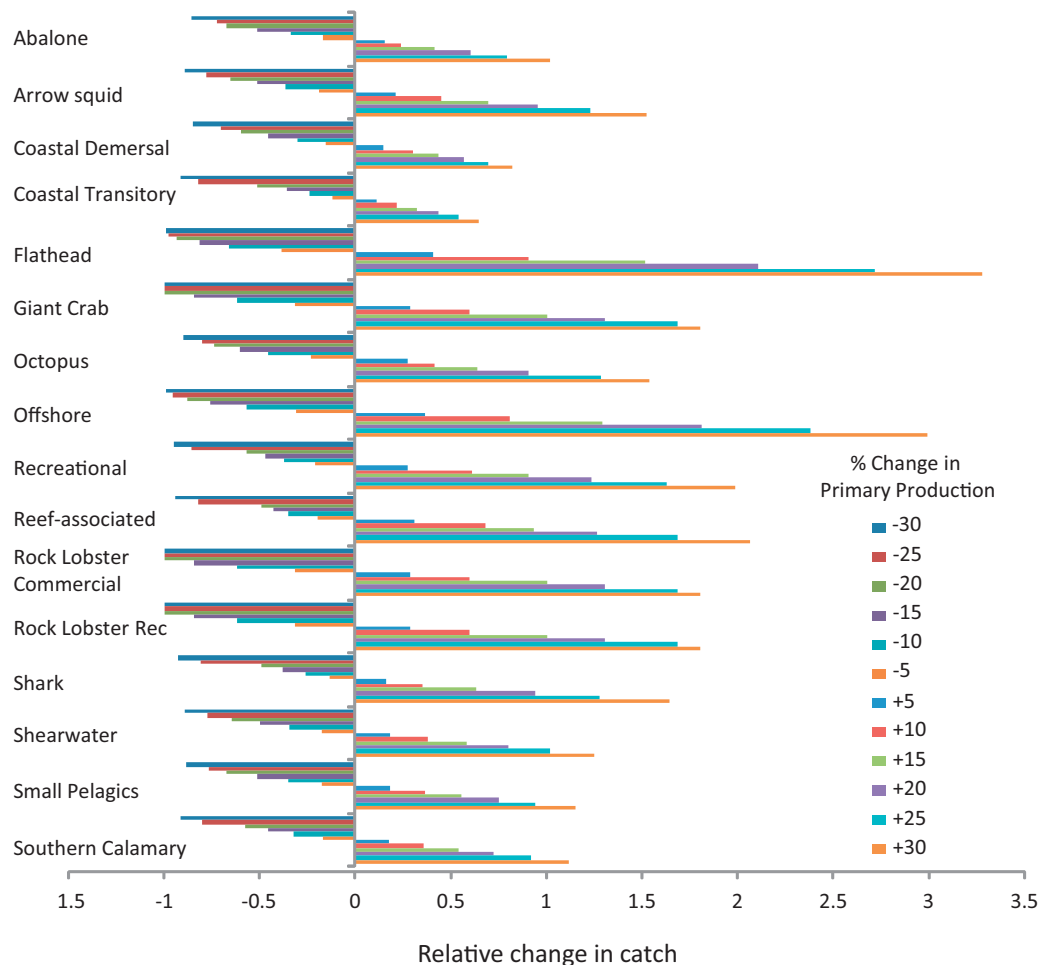
**Fig. 6.** Projected fisheries landings in the Ecosim model relative to those resulting from baseline levels of primary productivity (that is in scenarios using the original biomass levels of large and small algae groups). Relative values represent the average for a 20-year period after a simulation of a 100-year period during which primary production rates were altered in each scenario (see Fig. 2 for details).

given a very low vulnerability, indicating that in their depleted state relatively fewer predator–prey interactions occur (Bulman et al., 2006). Our model also has many groups with low vulnerabilities, however, there are several groups which did not have low vulnerabilities. We believe interpretations of these values should only proceed with great caution. We found that fitting the vulnerabilities (Table 5) was challenging. Finding biomass time-series data, especially for non-fished groups was extremely difficult, therefore our fitting was dependent on those that were fished and surveyed (at least with respect to catch per unit of fishing effort expended). Discussions with experts in the use of the Ecopath/Ecosim modeling framework (Christensen and Walters, 2011) indicated that this is a relatively new area, and many published ecosystem models do not as yet attempt to address how much of the prey biomass is available to predators. Though this ratio would be expected to have some functional-group similarities between models, it is also expected that individual models could vary considerably depending on the ability of prey groups to use protective habitat. In using Ecosim's inbuilt functions, we tried multiple starting points, and grouped functional groups in various ways in an effort to examine how this would influence vulnerability estimates. As expected, those vulnerability estimates most directly associated with our provided biomass time series data were the most robust. In our model there were examples of both top-down and bottom-up predator–prey interactions though we believe that without further biomass time series data, these estimates are only provisional in nature,

nevertheless they do play an important role in shaping modeled outcomes (as demonstrated by Okey and Wright, 2004).

Christensen and Walters (2011) provide a report card for model uncertainty on the status quo of using models to address ecosystem management questions. Clearly there are still deficiencies in the areas associated with vulnerabilities as grades assigned here ranked from C through to a failing F. One important bottom-up effect involves the ability of predators to find and use alternative food sources as their more typical prey are fished, and hence reduced in biomass and availability. Difficulties in capturing uncertainty about this dynamic in modeling frameworks makes prescribed diets in ecological models challenging.

We found that the fisheries represented in our model increased their landings with increases in primary productivity. Brown et al. (2010) also found that most marine EwE models available for Australian waters showed positive linear responses under these conditions, but that this was not always the case. They did, however, conclude that production increases can simultaneously benefit fisheries and conservation. Bulman et al. (2006) did examine reductions in primary productivity in their EBS model. They included two scenarios; in which, over the last 40 years of a 50-year simulation, the mean productivity decreased to 60% or 80% of initial levels. This was to simulate strengthening of the Eastern Australia Current which would be expected to carry more of the warm low nutrient water into the EBS area and reduce primary productivity levels. They found that these scenarios caused ubiquitous declines
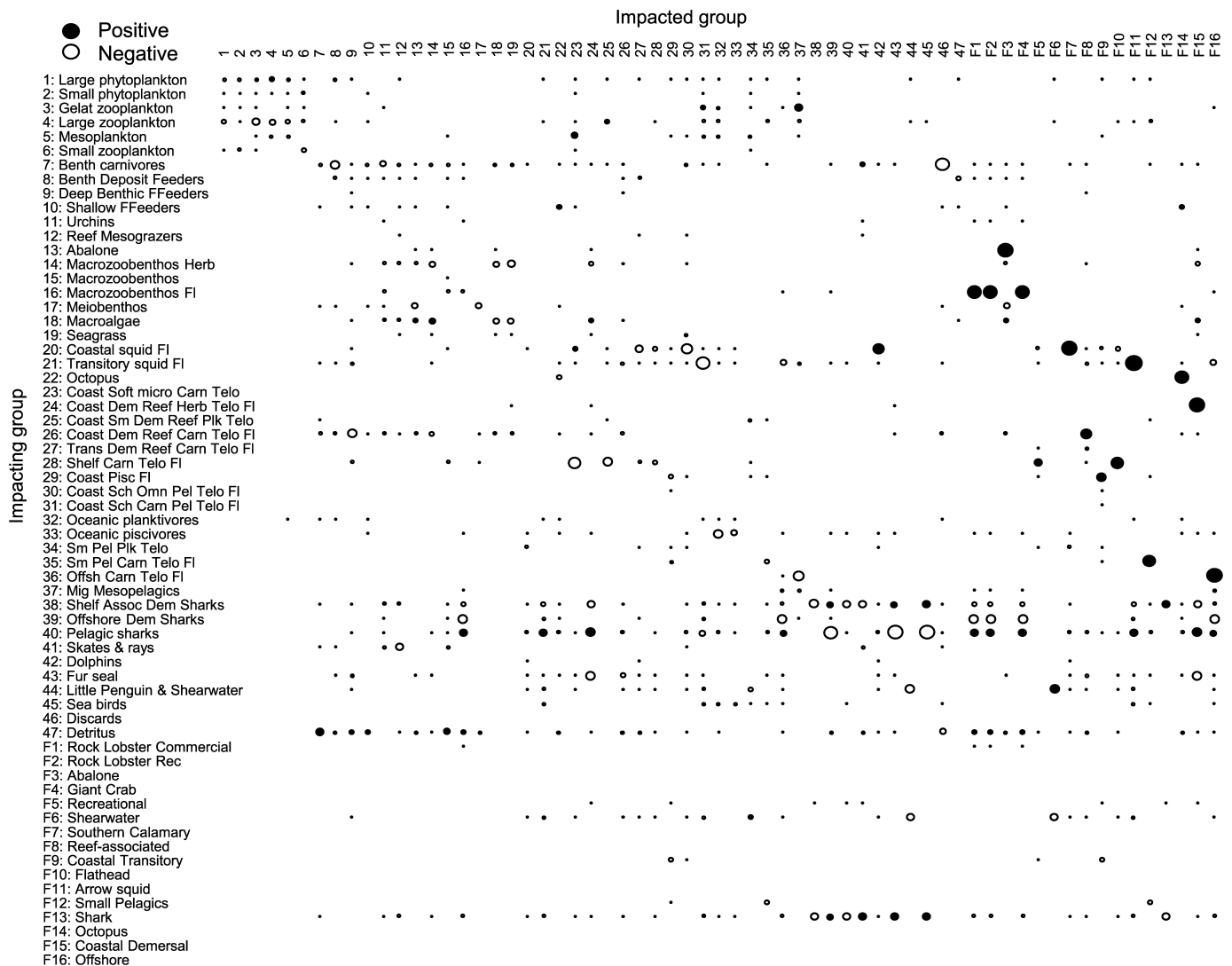
**Fig. 7.** Relative impact of the biomass of each modeled group on the biomass of other modeled groups in the Ecopath model (filled circles are positive and hollow circles are negative impacts).

in their modeled system. Only seals and the pelagic sharks that prey on them increased in biomass in their model with decreasing primary production.

Bulman et al. (2006) in their EBS model set many of the vulnerabilities of the predator-prey interactions to low values i.e. below 2, thus creating a bottom-up control. Therefore, they believed that this increased the impact of reducing mean productivity on higher trophic levels causing quite serious detrimental effects on nearly all groups in the model, with some groups nearing collapse. They hypothesize, however, that in reality, these effects could be offset by a net migration into the system of primary and secondary production i.e. phytoplankton, zooplankton and other groups, probably through advection. Unfortunately, they conclude that this advection could be minimal and would not support the system even in its presently depleted state. In our study, many fisheries also responded strongly to changing production levels, though some had a minimum or maximum at 10–15% below current levels.

We found little impact on the bird groups in our ecosystem model, however, changes in primary productivity did have a stronger impact on the biomass of the dolphin group. Certainly the impact of these climate-induced changes on groups of special conservation interest requires more investigation.

The current study was somewhat constrained by the limited spatial compartmentalization available in the Ecopath/Ecosim framework. The large size represented in the single model was achievable through fractioning the area for each biomass pool, however, in hindsight the spatial nature of some of the fisheries could not be well represented. It is also important to consider the spatial energetics of foraging, inherent to seabirds and marine mammals, which must reach adequate food sources for their young from rookeries and nursery areas with limited time away. Though generally the model showed that impacts of changes in primary productivity had limited consequences, our model was not able to examine how much further off shore populations might be forced to search for food under each scenario. Invasive species and range shifts were not considered. This model could be further developed into a true spatial model either in Ecospace (Walters et al., 1999), the spatial version of the EwE modeling framework, or perhaps in the Atlantis modeling framework (Fulton et al., 2004) which already has a network of regional models for southeastern Australia. In this way the rich information on habitat and fisheries spatial patterns could be better utilized.

Bulman et al. (2006) found that productivity in the Eastern Bass Strait (EBS) region of Australia was higher than elsewhere in temperate regions (Harris et al., 1987). During summer, the

warm nutrient-poor waters of the East Australian Current extend as far south as Tasmania, and winds are light and variable. By autumn, the winds favor upwelling of nutrients and restrict the warm water to the north of Tasmania. The wind direction in winter (southerly) does not favor upwelling but by late winter or early spring (August–September) conditions produce a strong algal bloom. They found only a weak and species-limited correlation between peak fishery catches and ocean color (and after lags of up to 100 days). They found that in the EBS, the trophic structure may be more complex and the fisheries species further removed trophically from primary production than in the case of small pelagic fisheries. Upwellings in EBS favored diatom production feeding copepods and euphausiids, followed by planktivorous fishes then carnivorous fishes. This causes lags, and with greater trophic distance the influence on recruitment to the fishery from primary productivity diminishes. They did not find a consistent link between annual catches of even zooplankton-feeders and phytoplankton biomass. Where a link did exist, as with tiger flathead (*Neoplatycephalus richardsoni*), there was a year lag from phytoplankton bloom until a peak in catches. We also found in the current study that the flathead fishery which includes this species reacted strongly to simulated changes in primary productivity. Upwelling events have been linked to increases in Mesozooplankton abundance and biomass with impacts on fisheries (Lehodey et al., 1997; Young et al., 1996). Jack mackerel fishery (*Trachurus declivis*) increases have been associated with greater upwellings with its impacts on euphausiids (Harris et al., 1992). Mesozooplankton blooms in other systems have supported increases in small pelagics such as herring (*Clupea pallasi*) and Pacific hake (*Merluccius productus*) (Ware and McFarlane, 1994) and Pacific sardine (*Sagax sardinops*) (Ware and Thomson, 1991). In real fisheries, the link between primary production and fishery production may be primarily caused by a lagged enhancement of recruitment success (Bulman et al., 2006). In southeastern Australian waters this has been observed by increased larval survival following an upwelling event (Neira, 2005; Prince et al., 1997).

It has been generally accepted that with global warming there will be increased sea surface temperatures which will lower ocean productivity (Behrenfeld et al., 2006; Behrenfeld, 2011). Similar to our study, Chassot et al. (2007) found a strong linkage between marine productivity and fisheries production in European seas. They argue that such large-scale coupling is due to energy transfer along the food web (from phytoplankton to predators) through predation processes, primary productivity driving the production of living marine resources and their exploitation at the scale of eco-regions. Their work supports our view that reduction in primary productivity will challenge sustainable fisheries exploitation. While warning that the relationship is complex and still poorly understood, they predicted that variations in primary production in the north Atlantic, as a response to ocean warming, will strongly modify the limits of fisheries production over the next decades.

Even ignoring induced changes in primary productivity, there are predictions that the bioclimate envelope that controls the distribution and abundance of marine species will be greatly altered under all likely climate change scenarios, resulting in major shifts in marine systems such as dramatic species turnovers of over 60% of the present biodiversity, which will in turn impact the services like fisheries that they provide (Cheung et al., 2009).

The present study makes it clear that modeling scenarios of climate change, even when limited to changes in the biomass of algal groups, is challenging. Views about the response of these groups are changing. Warming may stimulate productivity through changes in plankton metabolism (Behrenfeld, 2011). For Tasmania various sources predict potential changes to ocean currents that could either increase or decrease nutrient levels seasonally. Integrating these various impacts has to be accomplished before any further

modeling can explore the subsequent biological impacts that might be expected. In this study, we had to examine a wide range of both increases and decreases in primary productivity. We simplified the scenarios by applying these changes only to two algal groups equally, and ignoring the potential impacts on macrophytes and seagrasses. Undoubtedly these groups will be impacted if nutrient levels or other oceanographic parameters change, but the direction of change is less clear. Taken together, the autophytic groups could each respond differently and in different directions with regard to their biomass levels with climate change. At present, this is simply unknown. Therefore modeling the impacts on the food web from climate change even on autophytes through shifts in nutrient regimes must be viewed as preliminary in nature. Future work requires further grounding through directed studies that integrate expected changes in nutrients, and indeed temperature, on autophytic groups in the modeled areas. This would prepare a firmer base for future ecosystem modeling.

Nevertheless, there are considerable benefits in developing ecosystem models even when future environmental changes to be simulated are not well understood or defined, as is certainly the case for climate change research. The collaborative approach required to develop ecosystem models forces high levels of cross-agency cooperation that will certainly be required to facilitate preventative action and mitigation once we fully begin to understand the direction and scale of climate change impacts. The uncertainty about even the direction of change in marine primary productivity along the Tasmanian coast required a broad-bush approach and a model that was wide in scope because the groups and fisheries that will be impacted are not yet clear. Preliminary indications are that most fisheries and groups will thrive with mild increases in primary productivity but will decline if productivity declines. Considerations of range shifts, however, will be very important when predicting the full possible impacts of climate change. Such considerations may become overriding for groups such as seabirds which though they may not suffer greatly from mild declines in primary productivity maybe be forced into a poleward shift in range which is not possible owing to the absence of land masses south of Tasmania (Chambers et al., 2011).

The model can now be further developed and applied to a range of other climate change predictions including important changes to water temperature (Neuheimer et al., 2011) and pH (Fabry et al., 2008) – all of which may be expected to act in concert. The collaborative structures are in place to facilitate this and the existing model will focus future work. Food production from global oceans is essential to human populations and projections are that it will need to increase by 50% from current levels by 2050 (Rice and Garcia, 2011). Never has it been more important to be able to understand, mitigate and prepare for our impacts on marine systems.

## Acknowledgments

## References

ABARE, 2009. Australian fisheries statistics 2008. Canberra, July, 87 pp.

Allen, K.R., 1973. The influence of random fluctuations in the stock-recruitment relationships on the economic return from salmon fisheries. Fish stocks and recruitment. Rapports et procès-verbaux des réunions/Conseil permanent international pour l'exploration de la mer 164, 350–359.

Barrett, N., Sanderson, J.C., Lawler, M., Halley, V., Jordan, A., 2001. Mapping of inshore marine habitats in south-eastern Tasmania for marine protected area planning and marine management. Tasmanian Aquaculture and Fisheries Technical Report Series 7, 74 pp.

Bax, N.J., Williams, A. (Eds.), 2000. Habitat and Fisheries Production in the Southeast Fishery Ecosystem. Project No 94/040. Final Report to the FRDC.

Behrenfeld, M., 2011. Uncertain future for ocean algae. Nature Climate Change 1, 33–34.

Behrenfeld, M., O'Malley, R.T., Siegel, D.A., McClain, C.R., Sarmiento, J.L., Feldman, G.C., Milligan, A.J., Falkowski, P.G., Letelier, R.M., Boss, E.S., 2006. Climate-driven trends in contemporary ocean productivity. Nature 444, 752–755.

Blaber, S.J.M., Bulman, C.M., 1987. Diets of fishes of the upper continental slope of eastern Tasmania: content, calorific values, dietary overlap and trophic relationships. Marine Biology 95 (3), 345–356.

Braccini, J.M., 2008. Feeding ecology of two high-order predators from south-eastern Australia: the coastal broadnose and the deepwater sharpnose sevengill sharks. Marine Ecology Progress Series 371, 273–284.

Brown, C.J., Fulton, E.A., Hobday, A.J., Matear, R., Possingham, H., Bulman, C., Christensen, V., Forrest, R., Gehrke, P., Gribble, N., Griffiths, S., Lozano-Montes, S.H., Martin, J., Metcalf, S., Okey, T., Watson, R., Richardson, A.J., 2010. Ecological interactions will determine winners and losers under climate change in marine ecosystems and fisheries. Global Change Biology 16 (4), 1194–1212.

Bulman, C.M., He, X., Koslow, J.A., 2002. Trophic ecology of the mid-slope demersal fish community off southern Tasmania, Australia. Marine and Freshwater Research 53, 59–72.

Bulman, C.M., Althaus, F., He, X., Bax, N.J., Williams, A., 2001. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. Marine and Freshwater Research 52, 537–548.

Bulman, C., Condie, S., Furlani, D., Cahill, M., Klaer, N., Goldsworthy, S., Knuckey, I., 2006. Trophic dynamics of the eastern shelf and slope of the South East Fishery: impacts of and on the fishery. Final Report for Fisheries Research and Development Corporation 2002/028, 197 pp.

Chambers, L.E., Devney, C.A., Congdon, B.C., Dunlop, N., Woehler, E.J., Dann, P., 2011. Emu 111, 235–251.

Chassot, E., Mélin, F., Le Pape, O., Gascuel, D., 2007. Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. Marine Ecology Progress Series 343, 45–55.

Cheung, W.L.W., Close, C., Lam, V.W.Y., Sarmiento, J., Kearney, K., Watson, R., Pauly, D., 2009. Projections of global marine biodiversity impacts under climate change scenarios. Fish and Fisheries 10 (1), 1–17.

Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Zeller, D., Pauly, D., 2010. Large-scale distribution of maximum catch potential in the global ocean under climate change. Global Change Biology 16 (1), 24–35.

Choat, J.H., Clements, K.D., 1992. Diet in Odacid and Aplodactylid fishes from Australia and New Zealand. Australian Journal of Marine and Freshwater Research 43, 1451–1459.

Christensen, V., 1992. Network analysis of trophic interactions in aquatic ecosystems. Royal Danish School of Pharmacy, Copenhagen, Denmark. PhD Thesis. pp. 55 + 13 Appendices.

Christensen, V., 1995. Ecosystem maturity – towards quantification. Ecological Modelling 77, 3–32.

Christensen, V., Pauly, D., 1992. Ecopath-II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61, 169–185.

Christensen, V., Pauly, D., 1993. Flow characteristics of aquatic ecosystems, pp. 338–352. In: Christensen, V., Pauly, D. (Eds.), 'Trophic models of aquatic ecosystems'. ICLARM Conference Proceedings, vol. 26. , 390 pp.

Christensen, V., Walters, C., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172, 109–139.

Christensen, V., Walters, C., Pauly, D., 2005. Ecopath with Ecosim: A User's Guide. Fisheries Centre, University of British Columbia, Vancouver, Canada.

Christensen, V., Walters, C.J., 2011. Progress in the use of ecosystem modeling for fisheries management. In: Christensen, V., Maclean, J. (Eds.), Ecosystem Approaches to Fisheries: A Global Perspective. Cambridge Univ. Press.

Clementson, L.A., Harris, G.P., Griffiths, F.B., Rimmer, D.W., 1989. Seasonal and interannual variability in chemical and biological parameters in Storm Bay, Tasmania. I. Physics, chemistry and the biomass of components of the food chain. Australian Journal of Marine and Freshwater Research 40, 25–38.

Cresswell, G.R., Golding, T.J., 1980. Observations of a south-flowing current in the southeastern Indian Ocean. Deep-Sea Research 27A, 449–466.

Delworth, T.L., Rosati, A., Stouffer, R.J., et al., 2006. GFDL's CM2 global coupled climate models. Part I: Formulation and simulation characteristics. Journal of Climate 19, 643–674.

Edgar, G., Shaw, C., 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. II. Diets of fishes and trophic relationships between fishes and benthos at Western Port, Victoria. Journal of Experimental Marine Biology and Ecology 194, 83–106.

Fabry, V.J., Seibel, B.A., Feely, R.A., Orr, J.C., 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES Journal of Marine Science 65, 414–432.

Fenton, G.E., 1996. Diet and predators of Tenagomysis tasmaniae Fenton, Anisomysis mixta australis (Zimmer) and Paramesopodopsis rufa Fenton from south-eastern Tasmania (Crustacea: Mysidacea). Hydrobiologia 323, 31–44.

Freire, K.M.F., Christensen, V., Pauly, D., 2008. Description of the East Brazil Large Marine Ecosystem using a trophic model. Scientia Marina 72 (3), 477–491.

Frisk, M.G., Miller, T.J., Latour, R.J., Martell, S.J.D., 2010. Assessing biomass gains from marsh restoration in Delaware Bay using Ecopath with Ecosim. Ecological Modelling, http://dx.doi.org/10.1016/j.ecolmodel.2010.08.026.

Fulton, E.A., Smith, A.D.M., Johnson, C.R., 2003. Effect of complexity on marine ecosystem models. Marine Ecology-Progress Series 253, 1–16.

Fulton, E.A., Smith, A.D.M., Punt, A.E., 2004. Ecological indicators of the ecosystem effects of fishing: Final Report. Report No. R99/1546, Australian Fisheries Management Authority, Canberra, Australia.

Gaichas, S.K., Aydin, K.Y., Francis, R.C., 2010. Using food web model results to inform stock assessment estimates of mortality and production for ecosystem-based fisheries management. Canadian Journal of Fisheries and Aquatic Sciences 67, 1490–1506.

Gales, R., Pemberton, D., 1994. Diet of the Australian fur seal in Tasmania. Australian Journal of Marine and Freshwater Research 45, 653–664.

Gales, R., Pemberton, D., Clarke, M., Lu, C.C., 1992. Stomach contents of long-finned pilot whales (Globicephala melas) and bottlenose dolphins (Tursiops truncates) in Tasmania. Marine Mammal Science 8 (4), 405–413.

Grubert, M.A., 1996. The Reproductive Biology, Ecology and Diet of the Maori Octopus (Octopus maorum) in Eaglehawk Bay, south-east Tasmania. Department of Zoology, University of Tasmania, Hobart, 105 pp.

Harris, H., Nilsson, C., Clementson, L., Thomas, D., 1987. The water masses of the east coast of Tasmania: seasonal and interannual variability and the influence on phytoplankton biomass and productivity. Australian Journal of Marine and Freshwater Research 38, 569–590.

Harris, G.P., Griffiths, F.B., Clementson, L.A., 1992. Climate and fisheries off Tasmania – interactions of physics, food chains and fish. South African Journal of Marine Science 12, 107–121.

Harris, G.P., Griffiths, F.B., Clementson, L.A., Lyne, V., Van der Doe, H., 1991. Seasonal and interannual variability in physical processes, nutrient cycling and the structure of the food chain in Tasmanian shelf waters. Journal of Plankton Research 13 (Suppl.), 109–131.

Hedd, A., Gales, R., 2001. The diet of shy albatrosses (Thalassarche cauta) at Albatross Island, Tasmania. Journal of Zoology 253, 69–90.

Heymans, J.J., Shannon, L.J., Jarre, A., 2004. The Northern Benguela Ecosystem: changes over three decades (1970, 1980 and 1990). Ecological Modelling 172 (2–4), 175–196.

Jackson, G.D., Pecl, G., 2003. The dynamics of the summer-spawning population of the loliginid squid (Sepioteuthis australis) in Tasmania, Australia—a conveyor belt of recruits. ICES Journal of Marine Science 60, 290–296.

Johnson, C.R., Banks, S.C., Barrett, N.S., Cazassus, F., Dunstan, P.K., Edgar, G.J., Frusher, S.D., Gardner, C., Haddon, M., Helidoniotis, F., Hill, K.L., Holbrook, N.J., Hosie, G.W., Last, P.R., Ling, S.D., Melbourne-Thomas, J., Miller, K., Pecl, G.T., Richardson, A.J., Ridgway, K.R., Rintoul, S.R., Ritz, D.A., Ross, D.J., Sanderson, J.C., Shepherd, S.A., Slotwinski, A., Swadling, K.M., Taw, N., 2011a. Climate change cascades: shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. Journal of Experimental Marine Biology and Ecology 400, 17–32.

Johnson, P., Fulton, E.A., Smith, D.C., Jenkins, G.P., Barret, N., 2011b. The use of telescoping spatial scales to capture inshore to slope dynamics in marine ecosystem modelling. Natural Resource Modeling 24, 335–364.

Jordan, A., 1997. Demersal trawl surveys of the continental shelf of southern and eastern Tasmania 1993–95. Dept of Primary Industry and Fisheries Tasmania, Taroona, Tasmania. Tech Rept 50, 148 pp.

Jordan, A.R., Mills, D.M., Ewing, G., Lyle, J.M., 1998. Assessment of inshore habitats around Tasmania for life-history stages of commercial finfish species. FRDC Final Report (Project 94/037), 176 pp.

Last, P.R., White, W.T., Gledhill, D.C., Hobday, A.J., Brown, R., Edgar, G.J., Pecl, G., 2011. Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Global Ecology and Biogeography 20, 58–72.

Lehodey, P., Bertignac, M., Hampton, J., Lewis, A., Picaut, J., 1997. El Nino Southern Oscillation and tuna in the western Pacific. Nature 389, 715–718.

Lyle, J.M., Ford, W.B., 1993. Review of trawl research 1979–1987, with summaries of biological information for the major species. Technical Report 46, Department of Sea Fisheries, Tasmania. M.C. Reed, Government Printer, Tasmania, p. 87.

Metcalf, S., 2009. Qualitative modelling to aid ecosystem analysis for fisheries management in a data-limited situation. PhD Thesis. University of Tasmania.

Metcalf, S.J., Dambacher, J.M., Hobday, A.J., Lyle, J.M., 2008. Importance of trophic information, simplification and aggregation error in ecosystem models. Marine Ecology Progress Series 360, 25–36.

Montague, T.L., Cullen, J.M., 1988. The diet of the little penguin Eudyptula minor at Phillip Island, Victoria. Emu 88, 139–149.

Nakicenovic, N., Swart, R., 2000. Emissions Scenarios. Cambridge University Press, Cambridge, UK.

Neira, F.J., 2005. Summer and winter plankton fish assemblages around offshore oil and gas platforms in south-eastern Australia. Estuarine Coastal and Shelf Science 63, 589–604.

Neuheimer, A.B., Thresher, R.E., Lyle, J.M., Semmens, J.M., 2011. Tolerance limit for fish growth exceeded by warming waters. Nature Climate Change, http://dx.doi.org/10.1038/NCLIMATE1084.

Okey, T.A., Mahmoudi, B., 2002. An Ecosystem Model of the West Florida Shelf for Use in Fisheries Management and Ecological Research; Volume II Model Construction. Florida Marine Research Institute, St Petersburg, FA, USA.

Okey, T.A., Wright, B.A., 2004. Toward ecosystem-based extraction policies for Prince William Sound, Alaska: integrating conflicting objectives and rebuilding pinnipeds. Bulletin of Marine Science 74 (3), 727–747.

O'Sullivan, D., Cullen, J.M., 1983. Food of the squid Nototodarus gouldi in Bass Strait. Australian Journal of Marine and Freshwater Research 34 (2), 261–285.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science 57, 697–706.

Pitt, N.R., Poloczanska, E.S., Hobday, A., 2010. Climate-driven range changes in Tasmanian intertidal fauna. Marine and Freshwater Research 61, 963–970.

Poloczanska, E.S., Babcock, R.C., Butler, A., Hobday, A.J., Hoegh-Guldberg, O., Kunz, T.J., Matear, R., Milton, D.A., Okey, T.A., Richardson, A.J., 2007. Climate change and Australian marine life. Oceanography and Marine Biology: An Annual Review 45, 407–478.

Prince, J.D., Griffin, D., Diver, G., 1997. Industry survey of the 1997 eastern gemfish spawning season. FRDC Report No. 97/147.

Rice, J.C., Garcia, S.M., 2011. Fisheries, food security, climate change, and biodiversity: characteristics of the sector and perspectives on emerging issues. ICES Journal of Marine Science 68 (6), 1343–1353.

Sarmiento, J.L., Slater, R., Barber, R., Bopp, L., Doney, S.C., Hirst, A.C., Kleypas, J., Matear, R., Mikolajewicz, U., Monfray, P., Soldatov, V., Spall, S.A., Stouffer, R., 2004. Response of ocean ecosystems to climate warming. Global Biogeochemical Cycles 18, GB3003, http://dx.doi.org/10.1029/2003GB002134.

Shepherd, S.A., 1975. Distribution, habitat and feeding habits of abalone. Australian Fisheries 34, 1–4.

Shepherd, S.A., Clarkson, P.S., 2001. Diet, feeding behaviour, activity and predation of the temperate blue-throated wrasse, *Notolabrus tetricus*. Marine and Freshwater Research 52 (3), 311–322.

Smith, D.C., Fulton, E.A., Johnson, P., Jenkins, G., Barrett, N., Buxton, C., 2011. Developing integrated performance measures for spatial management of marine systems. Final Report, Project No 2004/005. Fisheries Research and Development Corporation.

Stuart-Smith, R.D., Barrett, N.S., Stevenson, D.G., Edgar, G.J., 2009. Stability in temperate reef communities over a decadal time scale despite concurrent ocean warming. Global Change Biology 16, 122–134.

Thompson, P.A., Baird, M.E., Ingleton, T., Doblin, M.A., 2009. Long-term changes in temperate Australian coastal waters: implications for phytoplankton. Marine Ecology Progress Series 394, 1–19.

Trites, A.W., Livingston, P.A., Mackinson, S., Vasconcellos, M.C., Springer, A.M., Pauly, D., 1999. Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and commercial whaling hypothesis. Fisheries Centre Research Report 7.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7, 139–172.

Walters, C., Pauly, D., Christensen, V., 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2, 539–554.

Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3, 70–83.

Walters, C.J., Juanes, F., 1993. Recruitment limitation as a consequence of natural-selection for use of restricted feeding habitats and predation risk-taking by juvenile fishes. Canadian Journal of Fisheries and Aquatic Sciences 50, 2058–2070.

Walters, C.J., Martell, S.J.D., 2004. Fisheries Ecology and Management. Princeton University Press, Princeton, NJ, p. 399.

Ware, D.M., McFarlane, G.A., 1994. Climate induced changes in hake abundance and pelagic community interactions in the Vancouver Island Upwelling System. Canadian Special Publication for Fisheries and Aquatic Science 51.

Ware, D.M., Thomson, R.E., 1991. Link between long-term variability in upwelling and fish production in the northeast Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences 48, 2296–2306.

Weimerskirch, H., Cherel, Y., 1998. Feeding ecology of Short-tailed Shearwaters breeding in Tasmania and foraging in the Antarctic. Marine Ecology Progress Series 167, 261–274.

Williams, A., Koslow, J.A., Terauds, A., Haskard, K., 2001. Feeding ecology of five fishes from the mid-slope micronekton community off southern Tasmania, Australia. Marine Biology 139, 1177–1192.

Young, J.W., Bradford, R.W., Lamb, T.D., Lyne, V.D., 1996. Biomass of zooplankton and micronekton in the southern bluefin tuna fishing grounds off eastern Tasmania, Australia. Marine Ecology Progress Series 138, 1–14.

Young, J.W., Lamb, T.D., Le, D., Brandford, R.W., Whitelaw, A.W., 1997. Feeding ecology and interannual variations in diet of southern bluefin tuna, *Thunnus maccoyii*, in relation to coastal and oceanic waters off eastern Tasmania, Australia. Environmental Biology of Fishes 50, 275–291.

Zeigler, P.E., Lyle, J.M., 2009. Tasmanian scalefish fishery 2008. Tasmanian Aquaculture and Fisheries Institute, Fishery Assessment Rep., Univ. Tasmania, Australia, 82 pp.