

Trophodynamic effects of climate change-induced alterations to primary production along the western Antarctic Peninsula

Paul Mark Suprenand^{1,2,*}, Cameron H. Ainsworth¹

¹University of South Florida, College of Marine Science, 140 7th Avenue South, St. Petersburg, FL 33701, USA

²Mote Marine Laboratory, 1600 Ken Thompson Parkway, Sarasota, FL 34236, USA

ABSTRACT: Under climate change, alterations in primary production and concomitant changes in community dynamics are expected in many marine ecosystems. We used an Ecopath with Ecosim (EwE) marine ecosystem model of the western Antarctic Peninsula to simulate effects on the food web based on proposed changes in the primary production regime expected as a result of climate change. Scenarios for trophic modeling are based on published results from coupled high-resolution regional ocean sea-ice and ice-shelf models, which consider alterations in water circulation from westerly wind intensification, increases in circumpolar deep water upwelling, iron upwelling, and decreases in sea-ice extent. Modeling scenarios included 6, 15, and 41 % increases in phytoplankton production with equivalent percentage decreases in ice algal production, and 1 scenario with 15 % increase for phytoplankton with no change for ice algae. These scenarios were achieved through linear forcing functions within the EwE software. We framed ecosystem changes in terms of biomass, species diversity, mean trophic level, trophodynamics, and network metrics. Simulations revealed that in each scenario, mean trophic level increased, species diversity generally decreased, and energetic pathways were reorganized. Modeled changes in the planktonic invertebrate assemblage include changes in 2 key competitors, krill and salps. For example, model results predict declines in krill biomass with concomitant increases in salp biomass. In all scenarios that assumed a negative change in ice-algae production rates due to sea-ice habitat loss, whale, seal, and penguin populations were negatively affected. Changes in ecosystem structure in this sensitive region may serve as an indicator of changes expected in the Southern Ocean.

KEY WORDS: Antarctic warming · Trophodynamics · Climate change · Antarctic Peninsula · Ecosystem model · Ecopath with Ecosim

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INTRODUCTION

The western Antarctic Peninsula (WAP) region is among the fastest-warming regions in the world (Meredith & King 2005) as a result of a combination of atmospheric and oceanic changes. Atmospheric changes include an intensification of westerly winds around the continent (Shindell & Schmidt 2004, Schiermeier 2009). This leads to increased upwelling of warmer sub-Antarctic Circumpolar Deep Water (CDW) from the Antarctic Circumpolar Current (ACC)

and a consequential reduction in the annual mean sea-ice extent (Smith et al. 1999, Parkinson 2002, Martinson 2012). Atmospheric and oceanic changes of this magnitude will likely affect regional community structure, as the life cycles of many WAP marine organisms depend on the Antarctic sea-ice or on low, stable water temperatures (e.g. Atkinson et al. 2004, Moline et al. 2004, McClintock et al. 2008, Suprenand et al. 2015a).

Distributions of krill along the WAP have already been observed to be shifting southward (Lawson et al. 2008), as have the distributions of their notothe-

noid predator, Antarctic silverfish *Pleuragramma antarcticum* (Ducklow et al. 2007, Parker 2012), as well as Adélie penguins *Pygoscelis adeliae* (Ducklow et al. 2007) and the foundation of the food web, phytoplankton (Moline et al. 2004, Montes-Hugo et al. 2009, Schofield et al. 2010). Simultaneously, the atmospheric and oceanic changes have also increased the abundances of ice-intolerant shallow-water sponges and deeper water (200–400 m) bryozoans (Barnes et al. 2006, ASOC 2008, Barnes & Griffiths 2008). Southward shifts of cold-adapted taxa could alter trophodynamics (e.g. Croxall et al. 1999, Moline et al. 2004). As changes in biomass occur in species at the lower end of the food web (e.g. pteropods, Loeb & Santora 2013, Suprenand et al. 2015a,b), we could expect consequences for predators through bottom-up drivers (Hunt et al. 2008).

Marine ecosystem models can be used to predict the responses of upper trophic levels to changes in the primary or secondary production regime mediated by the loss of sea-ice. Ecopath with Ecosim (EwE) has been used in this regard for the Antarctic Peninsula (e.g. Hoover et al. 2012). EwE (Christensen & Pauly 1992, Walters et al. 1997) is a mass-balance trophodynamic box model that can simulate food web responses to natural and anthropogenic drivers. Climatological effects can be incorporated by means of forcing functions (Christensen et al. 2005, Koenigstein et al. 2016), which can alter the productivity of species or their vulnerability to predators.

In the present study, we developed 4 climate change-related scenarios to describe a range of potential changes in the primary production regime and ice cover over the next 40 yr. Primary production scenarios are based on the predictions of coupled high-resolution (4 km) regional ocean, sea-ice, and ice shelf models of the WAP's shelf waters (Diniman et al. 2012). These models consider a range of alterations in water circulation from westerly wind intensification, resulting increases in circumpolar deep water upwelling, nutrient upwelling, and decreases in sea-ice extent. In each scenario, we monitored changes to functional group biomass, species diversity (Q90 and Shannon Index), mean trophic level (TL), and trophodynamics (prey functional group cluster) in the year 2050. We hypothesized that our scenarios describing changes in primary production rates would simulate observed and predicted changes in populations, species diversity, and regime shifts, and therefore provide insights into potential structural changes in the food webs of the WAP and the Southern Ocean in the coming decades.

MATERIALS AND METHODS

Ecopath with Ecosim

EwE organizes individual species, multi-stanza (or multiple age classes) species, and aggregated groups of species into functional groups. The model acts like a thermodynamic accounting system, tracking material flows through the ecosystem and functional groups according to the constraints of mass-balance and conservation of energy. Ecopath represents an instantaneous 'snap-shot' of material fluxes in the ecosystem (Christensen & Pauly 1992), while Ecosim adds a temporal dimension, predicting biomass change for primary producers and consumers according to Eqs. (1) and (2), respectively, based on equations from Walters et al. (1997):

$$\frac{dB_i}{dt} = cB_i \left(\frac{P}{B} \right)_i EE_i - \sum_{j=1}^n f(B_i, B_j) - M_i B_i \quad (1)$$

$$\frac{dB_j}{dt} = cg_j \sum_{i=1}^n f(B_j, B_i) - \sum_{j=1}^n f(B_i, B_j) + I_j - B_j (M_j + F_j + E_j) \quad (2)$$

where B_i and B_j are biomasses of prey (i) and predator (j), P is production rate, EE is ecotrophic efficiency, f is a relationship predicting consumption, I is immigration, M and F are natural and fishing mortality, E is emigration, g is growth efficiency, and n is the number of functional groups. The scalar c is used in this article to introduce forcing functions on productivity (described below), and EE is the proportion of the production that does not flow directly to detritus owing to death or senescence. Biomass is measured in metric tons (t) km⁻² wet weight. Natural mortality, fishing mortality, emigration, and production/biomass are instantaneous rates of unit yr⁻¹. Ecotrophic efficiency and growth efficiency are unitless.

Our current EwE model (EwE 6.4) considers the WAP, Sub-area 48.1, as defined by the Food and Agriculture Organization of the United Nations (FAO) and adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR; Fig. 1). It is based on the work of Hoover et al. (2012), which included data fitted to time series. The only change we made to the model of Hoover et al. (2012) is that Antarctic monophagous gymnosome pteropods *Spongiobranchaea australis* and *Clione antarctica* and their thecosome pteropod prey *Clio pyramidata* and *Limacina antarctica*, respectively, are appended as individual functional groups rather than amassed within micro- and macrozooplankton groups, respectively. Separate treatment of the pteropod groups allows investigation of pteropods as

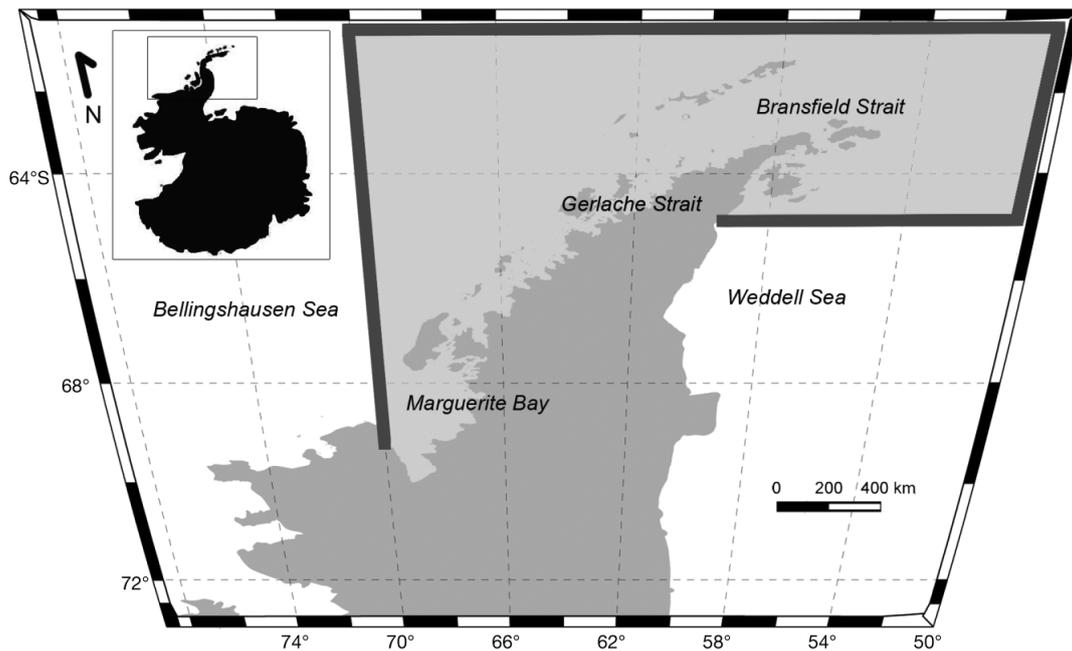


Fig. 1. Conservation of Antarctic Marine Living Resources (CCAMLR) Sub-area 48.1 along the western Antarctic Peninsula indicated by the light gray area within the dark gray border lines (adapted from fao.org)

indicators of trophic shifts under climate change, as hypothesized in other climate-related, high-latitude studies (e.g. Fabry et al. 2008). Additionally, our approach in addressing climate change scenarios differs from that of Hoover et al. (2012) in that we integrate model-predicted changes in primary productivity directly (discussed below), which has allowed us to forgo IPCC scenario challenges related to data access and model output reliability. Table 1 lists functional groups in the model. The groups are based on single species, aggregated sets of species, or linked age classes (for krill only). Species contained within aggregate functional groups are detailed in Table 2. Diet connectivity is provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m569p037_supp.pdf.

In ecosystems with low data availability, such as the WAP, it is not practical to calibrate model parameters against observational data. Nevertheless, trophic vulnerabilities, the main tuning parameters in Ecosim, can be set using one of several common

Table 1. Balanced western Antarctic Peninsula (WAP) Ecopath model parameters. TL: trophic level, B: biomass (fresh mass in $\text{t km}^{-2} \text{yr}^{-1}$); P/B: production/biomass ratio (yr^{-1}); Q/B: consumption/biomass ratio (yr^{-1}). Ecotrophic efficiency (EE) and production/consumption (P/Q) ratios are dimensionless. B, P/B, and Q/B values are model inputs, and EE are calculations in Ecopath. The only exception is for flying birds, for which Ecopath estimated P/B

Functional group	TL	B	P/B	Q/B	EE	P/Q
Killer whales	4.554	0.001	0.05	11	0	0.005
Leopard seals	4.092	0.039	0.12	3.5	0.235	0.034
Ross seals	4.117	0.004	0.28	12	0.767	0.023
Weddell seals	3.971	0.036	0.17	13.88	0.622	0.012
Crabeater seals	3.393	0.281	0.09	15.86	0.46	0.006
Antarctic fur seals	3.668	0.028	0.175	25	0.897	0.007
Southern elephant seals	4.258	0.006	0.25	10.37	0.843	0.024
Sperm whales	4.226	0.005	0.034	7.33	0	0.005
Blue whales	3.371	0.001	0.032	3.53	0.683	0.009
Fin whales	3.305	0.003	0.035	4.12	0.524	0.008
Minke whales	3.256	0.065	0.064	6.34	0.91	0.01
Humpback whales	3.38	0.02	0.04	4.12	0.963	0.01
Emperor penguins	3.841	0.005	0.15	28.69	0.91	0.005
Gentoo penguins	3.951	0.007	0.25	29	0.908	0.009
Chinstrap penguins	3.936	0.005	0.33	34	0.906	0.01
Macaroni penguins	3.645	0.014	0.3	30	0.701	0.01
Adélie penguins	3.483	0.034	0.29	30	0.996	0.01
Flying birds	3.701	0.19	0.36	14.88	0.95	0.024
Cephalopods	3.418	2.49	0.95	2	0.672	0.475
Other icefish	3.709	0.337	0.38	1.57	0.754	0.242
Toothfish	4.255	0.046	0.165	0.77	0.627	0.214
Large Nototheniidae	3.222	0.59	0.37	1.95	0.523	0.19
Small Nototheniidae	3.393	0.341	0.65	2.2	0.911	0.295
Shallow demersals	3.497	0.031	0.75	4.125	0.4	0.182
Deep demersals - large	3.705	0.042	0.29	2.18	0.856	0.133

(Table continued on next page)

Table 1 (continued)

Functional group	TL	B	P/B	Q/B	EE	P/Q
Deep demersals - small	3.726	0.08	0.65	2.7	0.863	0.241
Myctophids	3.259	0.185	1.35	3.73	0.898	0.362
Other pelagics	3.733	0.49	0.55	2.02	0.825	0.272
<i>Chamsocephalus gunnari</i>	3.365	0.29	0.48	1.8	0.52	0.267
<i>Pleuragramma antarcticum</i>	3.223	1.25	1.1	3.55	0.656	0.31
<i>Notothenia gibberifrons</i>	3.261	0.81	0.41	1.55	0.669	0.265
Mollusca	2.13	9.5	0.639	2.556	0.526	0.25
Salps	2.504	2	3	12	0.263	0.25
Urochordata	2.13	5.05	0.234	1	0.554	0.234
Porifera	2	12.719	0.159	0.795	0.815	0.2
Hemichordata	2	0.045	0.375	2	0.534	0.188
Brachiopoda	2.32	0.028	0.898	4.5	0.59	0.2
Bryozoa	2.15	0.491	0.475	1.75	0.95	0.271
Cnidaria	2.959	1.531	0.25	1	0.979	0.25
Arthropod Crustacea	2.533	3.613	1.05	4.2	0.826	0.25
Arthropod - other	2.951	1.01	0.616	3.326	0.964	0.185
Worms	2.467	12	0.7	3.2	0.82	0.219
Echinoidea	2.743	4.33	0.116	0.464	0.774	0.25
Crinoidea	2.442	0.164	0.125	0.8	0.523	0.156
Ophiuroidea	2.489	6.76	0.45	1.8	0.551	0.25
Asteroidea	2.351	1.778	0.231	0.924	0.774	0.25
Holothuroidea	2	5.45	0.316	1.1	0.938	0.287
Krill adult	2.465	9.08		33	0.797	0.045
Krill sub-adult	2.234	25.893		51.643	0.867	0.017
Krill juvenile	2	0.013		356.132	0.795	0.007
Krill larvae	2	0.003		698.506	0.461	0.011
<i>Spongiobranchaea australis</i>	3.321	0.194	5.8	7.3	0.99	0.795
<i>Clione antarctica</i>	2.95	0.175	5.3	7.7	0.99	0.688
Macrozooplankton	2.199	8.17	9.216	30.719	0.882	0.3
<i>Clio pyramidata</i>	2.39	0.179	9.3	35	0.99	0.266
<i>Limacina antarctica</i>	2	3.2	12	65	0.99	0.185
Microzooplankton	2	2.08	27.066	90.221	0.979	0.3
Cryptophytes	1	1.8	75		0.957	
Copepods	2	21.88	16.56	90	0.943	0.184
Diatoms	1	20.88	90.51		0.936	
Ice algae	1	26.69	45		0.948	
Other phytoplankton	1	2.93	86		0.889	
Detritus	1	3.43			0.314	

'short-cut' methods that often provide plausible model behavior (Ainsworth 2006, Ainsworth et al. 2008). These methods are: (1) all functional groups receive a global vulnerability value, (2) prey vulnerability values are scaled proportionately to the TL of their predator (predator control hypothesis), or (3) predator vulnerability values are scaled proportionately to the TL of their prey (prey control hypothesis). As a form of sensitivity analysis, we examined WAP ecosystem responses determined using each of these assumptions. We used global vulnerability values of 2 and 10 (bottom-up and top-down trophic control, respectively) and scaled vulnerability values between 2 and 10 and between 10 and 50 linearly with predator (or prey) TL under the predator (or prey) control hypotheses. Similar to the model calibration,

we validated our current EwE model parameters using a broader approach, because limited spatial-temporal data are disparate across functional groups, and the present study focused on forecasting changes in the ecosystem. However, vulnerability estimates are not a suitable replacement for time-series fitting, if data are available.

Our broader approach evaluates our current Ecopath model using the PREBAL methods outlined by Link (2010). Diagnostics include biomass (B), vital rates, and vital rate ratios per functional group, as well as biomass and vital rate ratios among taxa. For functional group vital rates, we examined ratios of respiration to biomass (R/B), consumption to biomass (Q/B), and production to biomass (P/B). For vital rate ratios per functional group, we examined biomass and productivity relative to primary production (PP), as well as production to consumption (P/Q) and production to respiration (P/R). Lastly, we examined biomass ratios among taxa.

Environmental forcing functions

Our Ecosim simulations were run for a duration of 40 yr (2010–2050). We conducted simulations based on 4 assumptions of primary production changes over this period. In all cases, we used linear environmental forcing

functions that gradually change the rate of primary productivity. We refer to climate change-related scenarios as 'primary production scenarios,' which might result from westerly wind intensification and nutrient upwelling, increases in Upper CDW (UCDW) upwelling, and decreases in sea-ice extent. Changes in primary production relate strongly to changes in the flux rate of dissolved iron into the upper 100 m of the water column through UCDW intrusions onto the peninsula from the ACC. Estimates of temporal changes in primary production along the WAP are based on ocean sea-ice and ice-shelf models (Dinniman et al. 2012) that use the Regional Ocean Modeling System (ROMS; Haidvogel et al. 2008, Shchepetkin & McWilliams 2009) and a coupled dynamic sea-ice model (Budgell 2005). This allows us to

Table 2. Functional groups comprising several species

Functional group	Organisms included
Toothfish	<i>Dissostichus eleginoides</i> and <i>Dissostichus mawsoni</i>
Large Nototheniidae	<i>Notothenia coriiceps</i> , <i>Notothenia (Notothenia) neglecta</i> , <i>Notothenia rossii</i> , <i>Notothenia squamifrons</i> , <i>Lepidonotothen kempfi</i> , and <i>Trematomus hansonii</i>
Small Nototheniidae	<i>Cryothenia peninsulae</i> , <i>Notothenia (Lepidonotothen) larseni</i> , <i>Notothenia (Lepidonotothen) nudifrons</i> , <i>Trematomis loennbergi</i> , <i>Pagothenia (Trematomus) bernacchii</i> , <i>Trematomus newnesi</i> , <i>Trematomus scotti</i> , <i>Trematomus eulepidotus</i> , and <i>Trematomus centronotus</i>
Shallow demersals	<i>Artedidraco skottsbergi</i> , <i>Harpagifer antarcticus</i> , and <i>Harpagifer bispinis</i>
Deep demersals - large	<i>Chionobathyscus dewitti</i> , <i>Paradiplospinus antarcticus</i> , <i>Parachaenichthys charcoti</i> , <i>Gymnodraco acuticeps</i> , <i>Mancopsetta maculate</i> , <i>Muraenolepis microps</i> , <i>Pachycara brachycephalum</i> , <i>Ophthalmolycus amberensi</i> , <i>Bathyraja eatonii</i> , and <i>Bathyraja maccaini</i>
Deep demersals - small	<i>Pogonophryne marmorata</i> , <i>Prionodraco evansii</i> , <i>Psilodraco breviceps</i> , and <i>Paraliparis antarcticus</i>
Myctophids	<i>Electrona antarctica</i> , <i>Gymnoscopelus braueri</i> , <i>Gymnoscopelus nicholsi</i> , <i>Gymnoscopelus opisthopterus</i> , and <i>Protomyctophum bolini</i>
Other pelagics	<i>Anotopterus pharaoh</i> , <i>Bathylagus antarcticus</i> , <i>Lampris immaculatus</i> , <i>Paradiplospinus gracilis</i> , and <i>Paradiplospinus antarcticus</i>
Mollusca	Bivalves, opisthobranchs, prosobranchs, Schaphopoda, Solenogastra, and most gastropods
Salps	<i>Salpa thompsoni</i>
Urochordata	Ascidiacea but not salps
Porifera	All sponges
Bryozoans	Lophotrochozoa
Cnidaria	Anthozoa, Hydrozoa, Actiniaria, and Gorgonaria
Arthropod Crustacea	Amphipods, cumaceans, isopods, ostracods, and tanaidaceans
Arthropod - other	Acari and Pycnogonidians
Worms	Turbellaria (Platyhelminthes), Nemertini (Nemertea), Sipuncula (Sipuncula), Nematoda (Nematoda), Polychaeta (Annelida), Oligochaeta (Annelida), Hirudinea (Annelida), Sipunculoidea (Sipuncula), and Priapulida (Priapulida)
Echinoidea	Echinoderms

test a range of climate-induced changes in primary production rates in 4 different scenarios, and we assume that the UCDW, a primary source of nutrients and heat to the WAP, mixes with waters within the marine ecosystem (Moffat et al. 2009, Martinson & McKee 2012). Percent changes in primary production rates are calculated by changing $g(C) m^{-2} yr^{-1}$ re-

ported by Dinniman et al. (2012) to g fresh mass $m^{-2} yr^{-1}$. Primary production scenario 1, referred to as '+6 Phyto' ('Base+' from Dinniman et al. 2012), simulates an estimated 6% increase in primary production of cryptophytes, diatoms, and other phytoplankton and a 6% decrease in primary production for ice algae in the present EwE model by the year 2050. The latter method assumes that increases in the productivity of cryptophytes, diatoms, and other phytoplankton, with decreases in sea-ice extent, would have an equal but inverse impact on ice-algae productivity due to the loss of the cryosphere and limitation of total production by nutrients. This is considered a mild change in primary production. Scenario 2, referred to as '+15 Phyto' ('1.2K+' from Dinniman et al. 2012), simulates an estimated 15% increase in primary production for cryptophytes, diatoms, and other phytoplankton and a 15% decrease in primary production for ice algae. This is considered the most likely change in primary production by the year 2050. Scenario 3, referred to as '+41 Phyto' ('1.5M' from Dinniman et al. 2012), simulates an estimated 41% increase in primary production for cryptophytes, diatoms, and other phytoplankton and a 41% decrease in primary production for ice algae. This is considered an extreme change in primary production by the year 2050. Scenario 4, referred to as '+15 Phyto-Ice Algae' simulates an increase of primary production for cryptophytes, diatoms, and other phytoplankton according to Scenario 2, but assumes no habitat loss for ice algae or reduction in productivity.

As the intensity of climate change increases from the +6 Phyto to +41 Phyto scenarios (Base+ to 1.5M), a different vertical mixing scheme corre-

sponds to each primary production scenario. The +6 Phyto scenario refers to a modified vertical mixing scheme of Large et al. (1994), the +15 Phyto scenario refers to the standard scheme of Large et al. (1994), and the +41 Phyto scenario refers to a combination of the Mellor & Yamada (1982) and the standard Large et al. (1994) mixing schemes. At the end of each

Ecosim run, biomass outputs were compared to a reference ecosystem, run without primary production forcing, at the year 2050 to assess relative differences in functional group biomass.

Trophic level and species diversity

Mean TL changes are monitored in each scenario and compared to the reference ecosystem in the year 2050 to understand relative ecosystem shifts towards producers (lower mean TL) or predators (higher mean TL). Changes in species diversity are monitored in each scenario's output using the species diversity statistic Q90 (Ainsworth & Pitcher 2006). This index is a variant of Kempton's Q Index (Kempton & Taylor 1976). It represents the interdecile slope of the cumulative species abundance curve, with each functional group in the food web network equivalent to a species, and it measures changes in trophic group richness as well as evenness. The Shannon species diversity index was also used (Shannon 1948). In applying this to an ecosystem model, the total number of species (i.e. model functional groups, n) is fixed, which reduces this metric to an evenness measure. Every sample results in n species, and we are only concerned with the distribution of biomass across that fixed number of species. We apply the Shannon Index H as follows:

$$H = -\sum_{i=1}^k p_i \ln(p_i) \quad (3)$$

where k is fixed at the number of functional groups in the model (63) and p_i is the biomass in the i^{th} group as a proportion of total system biomass.

Statistical analyses

For assessing trophodynamic changes in each scenario, the similarities between prey functional groups, in terms of the proportions they comprise in the diets of predators, are analyzed using the approach described by Clarke et al. (2008). This approach describes a series of similarity profile routine (SIMPROF) tests, dissimilarity profile analyses (DISPROF; Jones 2015), and Euclidean distance and unconstrained agglomerative, Unweighted Pair Group Method with Arithmetic Mean (UPGMA) clustering methods. The analysis produces significant ($p < 0.05$) and unique clusters of individual prey taxa according to the predators that eat them

and the dietary proportion they provide to the predators.

For each primary production scenario, the SIMPROF clusters of prey are then compared to the clusters produced by the reference simulation and each other using binary connectivity matrices (Jones 2015). This reveals the percent of congruency between prey clusters. A high percent of congruency between clusters indicates that overall trophodynamics throughout the WAP marine ecosystem remain unchanged among primary production scenarios. Congruence of 100% indicates identical clustering of prey by their predators and the number of cluster groups produced; thus primary production scenarios have little impact on trophodynamics. Lower congruency indicates greater divergence as a result of the different scenarios, and the lower the percent congruency, the greater the impact on trophodynamics.

Lastly, we try to identify the indicator predator functional group for each prey cluster according to Dufrêne & Legendre (1997). An indicator predator functional group is the most significant predator for the prey functional groups found within a cluster, and we report its indicator value (IV). The IV for an indicator predator functional group can range from 0 to 100%. The IV is maximum (100%) for the predator functional group when it eats only prey found within the cluster, and eats all of the prey within that cluster. A change in the significant indicator predator functional group for a prey cluster, when making comparisons between scenarios, indicates significant changes in the predators' diets. Additionally, if an indicator predator functional group remains the same for a prey cluster, the change in the IV will also indicate whether a predator is eating more (higher IV) or less (lower IV) of the prey within its cluster.

To further understand WAP ecological changes with each climate change scenario, relationships among functional group biomasses and species diversity statistics are plotted as radar plots. Radar plots are used to display multivariate data in 2-dimensional illustrations; each spoke of the radar plot represents a particular ecosystem characteristic. Spoke length is proportional to the magnitude of the variable and is presented relative to the maximum magnitude of that variable observed across all simulations. We present the data in relative terms in this way so that we may examine several metrics of very different units and achieve a rounded impression of the simulation results. Functional group biomasses presented as variables in the radar plots include those from important functional groups significant to ecosystem structure and behavior. For example,

increased bryozoan biomass has changed benthic community structure (Barnes et al. 2006), Adélie penguin distributions are shifting along the WAP (Ducklow et al. 2007), krill and salps represent inverse food-web energetic pathways (Flores et al. 2012), and the Q90 species diversity index provides insights into whole-ecosystem structural changes.

RESULTS

Ecopath with Ecosim

In sensitivity analyses, we found that predictions of the model concerning fish biomass under the climate change scenarios were largely insensitive to the vulnerability hypothesis, and minor changes in biomass were observed (e.g. Fig. 2). However, a donor-controlled scheme may be more appropriate considering that the WAP is dominated by open-ocean areas with few refugia, and microhabitats can occur even without physical structure (Walters & Martell 2004). Therefore, we use vulnerabilities between 2 and 10 scaled proportionately to prey TL. TLs of groups are reported in Table 1.

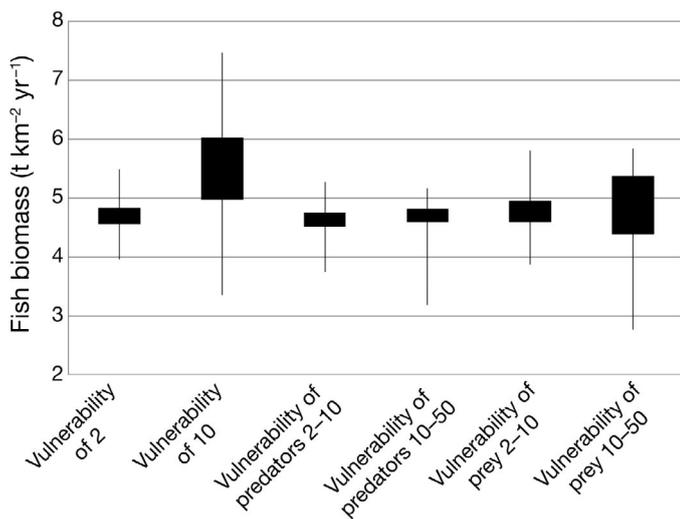


Fig. 2. Mean, maximum, and minimum biomass values for all fish groups, for all primary production scenarios, and according to methods to identify vulnerability by setting all functional group vulnerability values to 2 (Vulnerability of 2), 10 (Vulnerability of 10), between 2 and 10 using the predator control hypothesis (Vulnerability of Predators 2–10), between 10 and 50 using the predator control hypothesis (Vulnerability of Predators 10–50), between 2 and 10 using the prey control hypothesis (Vulnerability of Prey 2–10) and between 10 and 50 using the prey control hypothesis (Vulnerability of Prey 10–50). Biomass values reflect the output after the 40 yr model run period

Biomass of individual trophic groups in the current Ecopath model spans 6 orders of magnitude, with a 10.3% decline in biomass with increasing TL, as illustrated in Fig. S1 in the Supplement. Vital rates of R/B, C/B, and P/B generally decline from lowest to highest TL (Fig. S1; birds, seals, and whales [homeotherms] omitted as per Link 2010). Vital rates disproportionately above the slope-line (Fig. S2) include the multi-stanza functional groups of krill as well as pteropods, although all functional group biomass values are relative to primary production biomass (Fig. S3a) and biomass ratios among taxa are <1 (Fig. S4). Functional group vital rate ratios of productivity relative to primary productivity, P/Q, and P/R are also largely <1 (Fig. S3a,b), with the exception of the P/R vital rates for pteropods. The R/B vital rate is interpreted as an expression of functional group activity, whereas the P/R vital rate ratio expresses the fate of assimilated food. Pteropods have a high metabolic activity compared to euphausiids (Ikeda & Mitchell 1982, Suprenand et al. 2015b), and can be monophagous predators with highly efficient food assimilation (Lalli & Gilmer 1989). Overall, we conclude that the current EwE model is robust, indicating valid model structure and data quality.

Environmental forcing functions

In climate change scenarios in our model that assume negative impacts to ice algae with the loss of sea-ice habitat, whole-ecosystem biomass is reduced by a minimum of 1.4% (+6 Phyto) to a maximum of 9.0% (+41 Phyto; Table 3). Only in the +15 Phyto-Ice Algae scenario, operating on the assumption of no negative impacts to ice algae with projected loss of sea-ice habitat, does the whole-ecosystem biomass increase. Additionally, inverse biomass relationships in scenarios +6 Phyto, +15 Phyto, and +41 Phyto are revealed, such as those in the pelagic (e.g. salp versus total krill biomass), and benthic (e.g. bryozoan versus asteroidean biomass) realms (Table 3). In general, Scenarios +6 Phyto, +15 Phyto, and +41 Phyto reveal that the greatest potential for negative effects is predicted for whales, seals, penguins, flying birds, *Champtocephalus gunnari*, other icefish, krill, and ice algae (Table 3). Positive effects are predicted for many fish and invertebrates, with large nototheniids, myctophids, salps, brachiopods, bryozoans, cnidarians, pteropods, microzooplankton, and copepods benefiting the most from changes in primary productivity. Effects on other functional groups are less impactful and sometimes more variable. For instance, leopard seals are adversely

Table 3. Biomass percent changes per functional group in the year 2050 when compared to the reference model. Percent changes $> \pm 5$ are in **bold**. Percent changes are compared to the reference model. Primary production scenarios +6 Phyto, +15 Phyto, and +41 Phyto describe a 6, 15, and 41% increase in all primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) by 2050, respectively, with equivalent decreases in ice-algae production. The +15 Phyto-Ice Algae describes a 15% increase in primary production with no decrease in ice-algae production

Functional group	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae	Functional group	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae
Killer whales	-0.1	-0.2	0.0	5.1	Porifera	-0.8	-2.0	-6.1	4.8
Leopard seals	-0.2	0.3	6.8	13.3	Hemichordata	1.7	4.0	10.0	11.3
Ross seals	-3.6	-8.2	-19.3	7.9	Brachiopoda	8.1	19.2	50.6	16.9
Weddell seals	-3.1	-7.0	-16.2	8.9	Bryozoa	2.3	5.5	14.8	7.9
Crabeater seals	-5.2	-11.9	-29.0	1.9	Cnidaria	3.5	8.5	25.0	8.3
Antarctic fur seals	-5.2	-11.9	-28.8	2.5	Arthropod Crustacea	0.6	1.4	4.7	8.8
Southern elephant seals	-4.0	-9.1	-22.0	7.2	Arthropod - other	-0.1	-0.5	-3.7	6.1
Sperm whales	-0.4	-0.9	-1.6	5.3	Worms	0.7	1.8	5.2	10.1
Blue whales	-1.9	-4.4	-10.5	3.1	Echinoidea	0.4	1.1	2.9	6.4
Fin whales	-1.6	-3.7	-8.6	3.4	Crinoidea	0.1	0.3	0.8	7.8
Minke whales	-3.3	-7.4	-16.5	6.0	Ophiuroidea	0.0	0.0	-0.3	9.5
Humpback whales	-2.9	-6.6	-15.6	3.8	Asteroidea	-0.2	-0.3	-0.6	6.8
Emperor penguins	-4.2	-9.6	-23.4	4.0	Holothuroidea	-0.9	-2.3	-6.7	4.6
Gentoo penguins	-3.9	-9.0	-22.0	5.2	Krill adult	-4.0	-9.7	-26.5	-3.1
Chinstrap penguins	-3.9	-9.1	-22.2	5.7	Krill sub-adult	-6.3	-14.8	-37.1	2.2
Macaroni penguins	-5.5	-12.6	-30.4	2.9	Krill juvenile	-15.7	-35.9	-83.8	-5.1
Adélie penguins	-5.0	-11.7	-29.0	0.3	Krill larvae	-15.7	-36.0	-84.3	-4.0
Flying birds	-1.7	-3.8	-8.2	8.9	<i>S. australis</i>	2.4	6.0	19.5	7.1
Cephalopods	-0.9	-1.8	-1.9	10.9	<i>C. antarctica</i>	3.7	16.7	101.1	-2.5
Other icefish	-2.9	-6.7	-16.2	5.8	Macrozooplankton	-1.2	-2.6	-5.0	8.3
Toothfish	-0.6	-1.2	-1.9	9.5	<i>C. pyramidata</i>	9.1	21.3	56.6	16.7
Large Nototheniidae	5.5	13.5	39.4	13.6	<i>L. antarctica</i>	10.2	24.1	62.4	14.3
Small Nototheniidae	0.7	1.4	2.5	10.8	Microzooplankton	2.6	6.6	19.9	11.0
Shallow demersals	-0.7	-1.6	-4.1	12.0	Cryptophytes	10.7	25.7	71.2	15.9
Deep demersals - large	-0.9	-2.2	-5.2	9.2	Copepods	4.8	11.3	29.1	15.4
Deep demersals - small	0.8	2.1	6.3	11.8	Diatoms	3.4	7.8	17.8	7.0
Myctophids	8.4	20.3	56.9	18.6	Ice algae	-14.3	-34.1	-90.8	-8.3
Other pelagics	-0.8	-1.8	-3.1	9.0	Other phytoplankton	6.0	13.9	33.9	10.5
<i>Chamsocephalus gunnari</i>	-7.4	-17.2	-43.0	-0.4	Detritus	-0.3	-0.7	-2.6	7.9
<i>Pleuragramma antarcticum</i>	4.7	11.9	37.4	15.3	Ecosystem	-1.4	-3.4	-9.0	6.6
<i>Notothenia gibberifrons</i>	-1.6	-3.9	-10.8	7.0	Average % change per functional group	-0.4	-0.5	0.9	7.5
Mollusca	-1.3	-3.1	-9.3	7.4					
Salps	17.7	43.1	120.6	24.6					
Urochordata	1.8	4.1	9.4	6.6					

influenced in the +6 Phyto scenario, but positively influenced by the +15 Phyto and +41 Phyto scenarios. In the +15 Phyto-Ice Algae scenario, the biomass increases in the majority of functional groups, with the exceptions of *C. gunnari* (-0.4%), most krill groups (mean -3%), the pteropod *Clione antarctica* (-3%), and ice algae (-8%). The largest increase in biomass is observed for salps (+25%), and the greatest loss in biomass is observed in ice algae.

Trophic level and species diversity

More extreme climate change scenarios result in a slightly higher mean TL of the ecosystem. The mean

TL increases from 2.201 in the reference case, to 2.203 for +6 Phyto, 2.205 for +15 Phyto, and 2.215 for +41 Phyto, and is 2.205 for +15 Phyto-Ice Algae. TL ranges, as detailed in Fig. 3, illustrate that the majority of biomass is concentrated in the TL range 2.0 to 2.5, with major contributors being sub-adult krill, macrozooplankton, Mollusca, Urochordata, and salps, as well as the TL range 1.5 to 2.0 with major contributors being copepods, microzooplankton, Porifera, and the thecosome *Limacina antarctica*. Changes to TL range per forcing function scenario are shown as biomass departures from the reference ecosystem's biomass in Fig. 4a,b. The change in mean TL is the result of changes in the TL at which functional groups feed (Table 4) and also changes in biomass

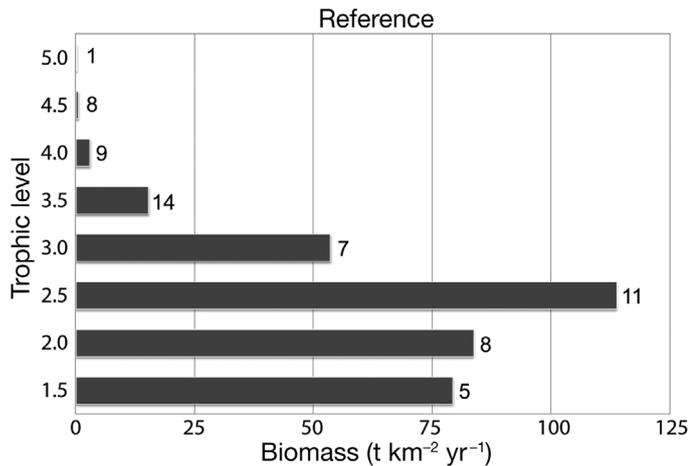


Fig. 3. Biomass by trophic level for the reference ecosystem in the year 2050. Numbers on black bars indicate the number of functional groups within that trophic level range

proportions of functional groups (Table 3). TL increases for the following groups are observed in the +6 Phyto, +15 Phyto, and +41 Phyto primary production scenarios: killer whales *Orcinus orca*, crabeater seals *Lobodon carcinophagus*, Antarctic fur seal *Arctocephalus gazella*, blue whales *Balaenoptera musculus*, humpback whales *Megaptera novaeangliae*, emperor penguins *Aptenodytes forsteri*, macaroni penguins *Eudyptes chrysolophus*, cephalopods, shallow demersals, *Chamsocephalus gunnari*, cnidarians, other arthropods, and adult krill (e.g. *Euphausia superba*). Overall, salp TL decreases as primary production increases along the WAP (Table 4). In the +15 Phyto-Ice Algae scenario, TL increases are observed for all functional groups with the exception

of salps. In scenarios assuming a negative impact on ice algae with a reduction in sea-ice extent, the Q90 Index reveals a decrease in total WAP ecosystem species diversity in all primary production scenarios, and the Shannon Index reveals an increase in ecosystem evenness (Table 5). This trend is similar in the +15 Phyto-Ice Algae scenario, with the exception of fish and krill, which have increased species diversity (Table 5).

Statistical analyses

Trophodynamic structures, when compared to the reference scenario, are altered in each primary productivity scenario. SIMPROF analyses produce 13 prey clusters in the reference model, 13 prey clusters in the +6 Phyto scenario, 14 prey clusters in the +15 Phyto scenario, 16 prey clusters in the +41 Phyto scenario, and 13 in the +15 Phyto-Ice Algae scenario (Fig. 5). Overall, the reference, +6 Phyto, and +15 Phyto-Ice Algae scenario's prey clusters, congruency (Table 6), indicator predator functional groups, and percent similarity of the indicator predator functional groups within prey clusters are very similar (Fig. 5). Only small changes in the percent similarities of the indicator predator functional groups are observed, with the exception that copepods increased consumption of primary producers in the +15 Phyto-Ice Algae scenario. Structural changes in trophodynamics are most evident in the +15 Phyto and +41 Phyto scenarios when compared to the reference model. This includes changes in predator diets indicated by

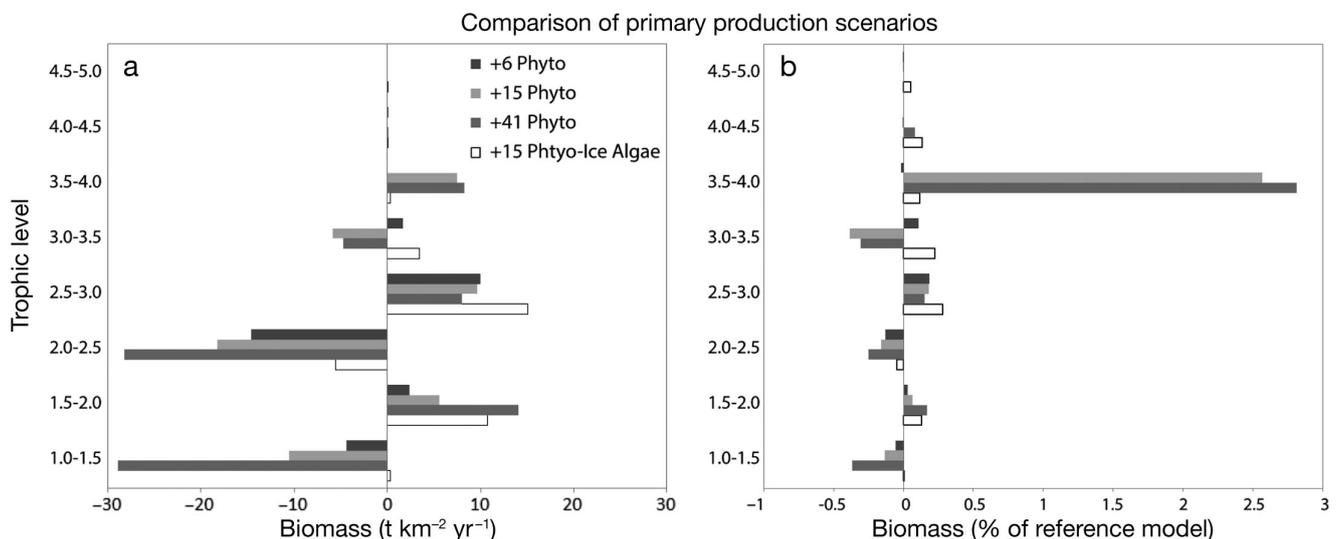


Fig. 4. Comparison of model outputs from primary production scenarios (see Table 3 for details) to reference model outputs in the year 2050. (a) Biomass excursions per trophic level range when compared to the reference model; (b) percent change in biomass when compared to the reference model (Fig. 3)

Table 4. Trophic level (TL) change in each functional group by the year 2050 for 5 different scenarios (see Table 3 for details). Changes in TL that are different from the reference model are shown in **bold**

Functional group	Ref.	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae	Functional group	Ref.	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae
Killer whales	4.792	4.826	4.874	5.018	4.861	Urochordata	2.140	2.144	2.151	2.174	2.149
Leopard seals	4.254	4.294	4.349	4.493	4.317	Porifera	2.000	2.000	2.000	2.000	2.000
Ross seals	4.224	4.243	4.269	4.339	4.257	Hemichordata	2.000	2.000	2.000	2.000	2.000
Weddell seals	4.055	4.073	4.100	4.177	4.088	Brachiopoda	2.328	2.329	2.332	2.348	2.337
Crabeater seals	3.419	3.449	3.494	3.634	3.459	Bryozoa	2.153	2.159	2.167	2.193	2.163
Antarctic fur seals	3.815	3.853	3.908	4.085	3.875	Cnidaria	2.998	3.012	3.033	3.093	3.021
Southern elephant seals	4.345	4.366	4.395	4.477	4.378	Arthropod Crustacea	2.536	2.545	2.557	2.600	2.548
Sperm whales	4.334	4.355	4.384	4.465	4.369	Arthropod - other	2.979	2.984	2.991	3.017	2.986
Blue whales	3.381	3.407	3.445	3.557	3.416	Worms	2.509	2.514	2.522	2.550	2.517
Fin whales	3.324	3.343	3.370	3.446	3.352	Echinoidea	2.783	2.789	2.796	2.823	2.793
Minke whales	3.264	3.278	3.297	3.351	3.282	Crinoidea	2.442	2.447	2.455	2.481	2.448
Humpback whales	3.383	3.410	3.450	3.570	3.416	Ophiuroidea	2.563	2.565	2.568	2.579	2.569
Emperor penguins	3.972	4.008	4.058	4.203	4.032	Asteroidea	2.408	2.414	2.422	2.448	2.417
Gentoo penguins	4.107	4.125	4.151	4.223	4.146	Holothuroidea	2.000	2.000	2.000	2.000	2.000
Chinstrap penguins	4.111	4.129	4.155	4.229	4.150	Krill adult	2.499	2.534	2.583	2.738	2.546
Macaroni penguins	3.759	3.797	3.851	4.023	3.817	Krill sub-adult	2.243	2.268	2.306	2.439	2.276
Adélie penguins	3.529	3.559	3.601	3.733	3.573	Krill juvenile	2.000	2.000	2.000	2.000	2.000
Flying birds	3.834	3.856	3.885	3.965	3.875	Krill larvae	2.000	2.000	2.000	2.000	2.000
Cephalopods	3.450	3.472	3.503	3.589	3.481	<i>S. australis</i>	3.373	3.389	3.410	3.477	3.407
Other icefish	3.781	3.801	3.828	3.901	3.811	<i>C. antarctica</i>	2.926	2.934	2.943	2.961	2.932
Toothfish	4.340	4.355	4.377	4.433	4.366	Macrozooplankton	2.235	2.245	2.261	2.321	2.251
Large Nototheniidae	3.266	3.278	3.294	3.336	3.286	<i>C. pyramidata</i>	2.439	2.450	2.467	2.525	2.470
Small Nototheniidae	3.392	3.402	3.417	3.461	3.405	<i>L. antarctica</i>	2.000	2.000	2.000	2.000	2.000
Shallow demersals	3.489	3.499	3.513	3.556	3.502	Microzooplankton	2.000	2.000	2.000	2.000	2.000
Deep demersals - large	3.796	3.813	3.837	3.908	3.828	Cryptophytes	1.000	1.000	1.000	1.000	1.000
Deep demersals - small	3.783	3.797	3.818	3.878	3.809	Copepods	2.000	2.000	2.000	2.000	2.000
Myctophids	3.251	3.255	3.260	3.269	3.254	Diatoms	1.000	1.000	1.000	1.000	1.000
Other pelagics	3.866	3.886	3.915	3.994	3.905	Ice algae	1.000	1.000	1.000	1.000	1.000
<i>Chamsocephalus gunnari</i>	3.361	3.390	3.431	3.558	3.395	Other phytoplankton	1.000	1.000	1.000	1.000	1.000
<i>Pleuragramma antarcticum</i>	3.254	3.259	3.266	3.275	3.264	Detritus	1.000	1.000	1.000	1.000	1.000
<i>Notothenia gibberifrons</i>	3.278	3.294	3.318	3.389	3.301	Ecosystem mean	2.974	2.987	3.006	3.063	2.995
Mollusca	2.149	2.151	2.155	2.167	2.154						
Salps	2.481	2.464	2.447	2.423	2.465						

the re-clustering of prey, percent similarity of the indicator predator functional groups within a prey cluster, and/or changes in the indicator predator for a prey cluster. For example, copepods, ice algae, diatoms, other phytoplankton, cryptophytes, and microzooplankton are clustered together in the reference and +6 Phyto scenarios, and salps are identified as indicator predators. In the +15 Phyto and +41 Phyto scenarios, copepods and microzooplankton are removed from the prey cluster they occupied in the reference and +6 Phyto scenarios. This leaves just the primary producers in a prey cluster. Copepods and microzooplankton cluster with salps, where they are eaten primarily by cnidarians.

The changes in prey clusters that occur in scenarios +15 Phyto and +41 Phyto indicate changes in the predators' diets (Fig. 5) to include higher TL prey

(Table 4). This is particularly evident in the prey cluster that once included primary producers, copepods, and microzooplankton. Initially, in the reference scenario, the most representative predators were salps, but in the climate change scenarios, it becomes juvenile krill. The microzooplankton and copepods, preyed upon largely by salps in the reference and +6 Phyto scenarios, are preyed upon more by cnidarians in the more intense (+15 Phyto and +41 Phyto) climate change scenarios. For salps, this indicates a drop in TL as the climate changes, which is due to a reduction in their consumption of higher TL prey items (e.g. *Spongiobranchea australis* and macrozooplankton) and an increase in their consumption of lower TL prey items (e.g. cryptophytes and copepods). This trophodynamic restructuring ultimately decreases the biomass of ice algae, far more than

Table 5. Species diversity of important western Antarctic Peninsula (WAP) groups per forcing function scenario using Q90 and Shannon Indices (SI). Reference model (Ref.) ecosystem species diversity indices compared to the WAP primary production scenarios +6 Phyto, +15 Phyto, and +41 Phyto leading to a 6, 15, and 41% increase in all primary production ($\text{gC m}^{-2} \text{yr}^{-1}$) by the year 2050, respectively, with equivalent decreases in ice-algae production. The +15 Phyto-Ice Algae describes a 15% increase in primary production without an equivalent decrease in ice-algae production. The plankton group includes phytoplankton and zooplankton, and all krill life stages are treated as a separate group. Cephalopods and salps are included in the invertebrate groups with benthic invertebrates

	Ref.	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae
Ecosystem SI	2.886	2.909	2.934	2.941	2.904
Ecosystem Q90	7.311	6.631	6.926	6.477	6.631
Whale SI	0.951	0.958	0.968	0.990	0.994
Whale Q90	1.414	1.414	1.414	1.444	1.414
Seal SI	1.127	1.136	1.147	1.178	1.151
Seal Q90	1.748	1.748	1.748	1.796	1.748
Penguin SI	1.420	1.423	1.428	1.443	1.432
Penguin Q90	4.068	4.068	4.068	4.068	4.068
Fish SI	2.111	2.105	2.093	2.035	2.104
Fish Q90	4.176	4.350	4.350	4.176	4.350
Krill life stages SI	0.487	0.492	0.498	0.518	0.475
Krill life stages Q90	0.579	0.572	0.558	0.500	0.572
Invertebrate SI	2.347	2.356	2.367	2.392	2.353
Invertebrate Q90	3.796	3.796	3.796	3.559	3.796
Plankton SI	1.661	1.683	1.700	1.600	1.673
Plankton Q90	2.274	2.063	2.318	1.977	2.109

Table 6. Congruency matrix of hierarchical clustering of prey. Matrix indicates the percent similarity between the reference and scenario clusters, as well as among scenario clusters. See Table 3 for details of the scenarios

(%)	Ref.	+6 Phyto	+15 Phyto	+41 Phyto	+15 Phyto- Ice Algae
Reference	100	100	87	41	89
+6 Phyto	100	100	87	41	89
+15 Phyto	87	87	100	54	75
+41 Phyto	41	41	54	100	33
+15 Phyto-Ice Algae	89	89	75	33	100

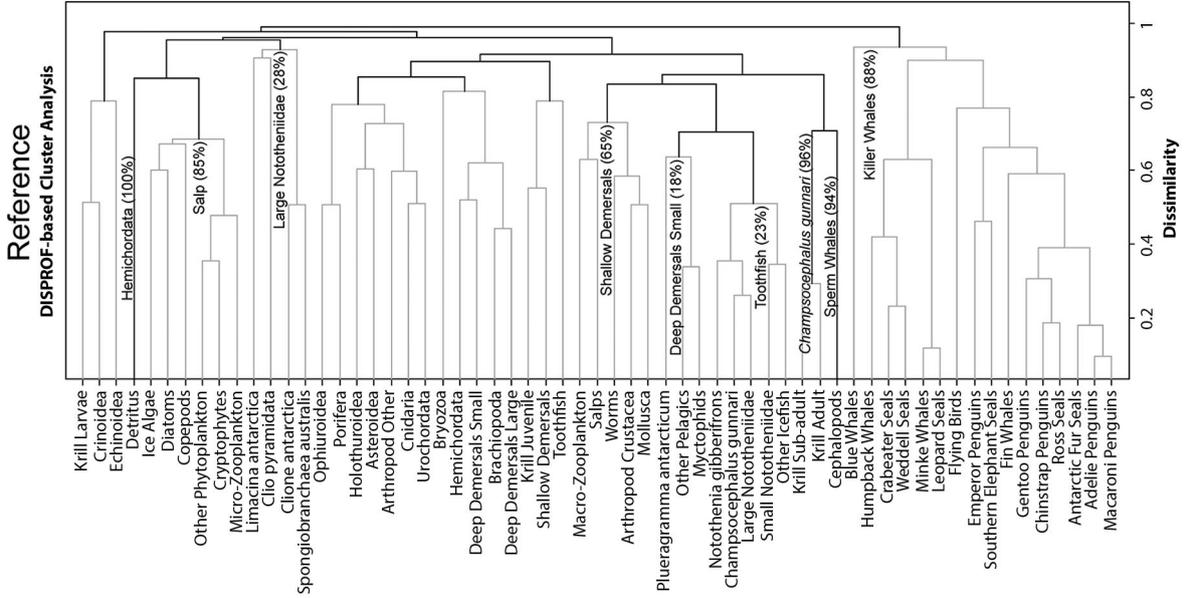
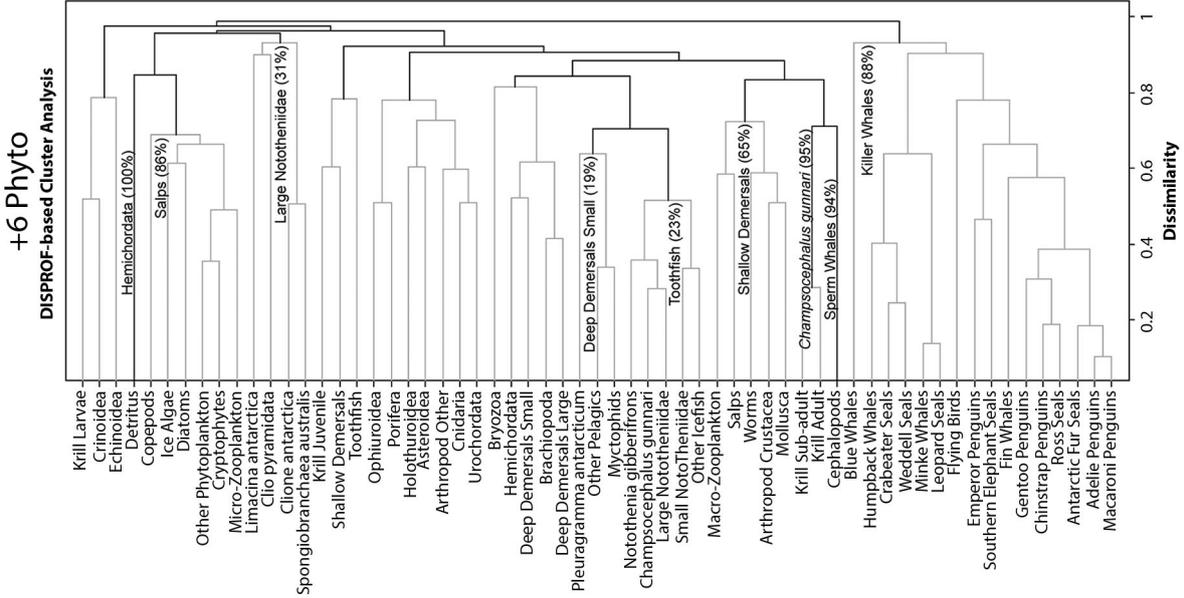
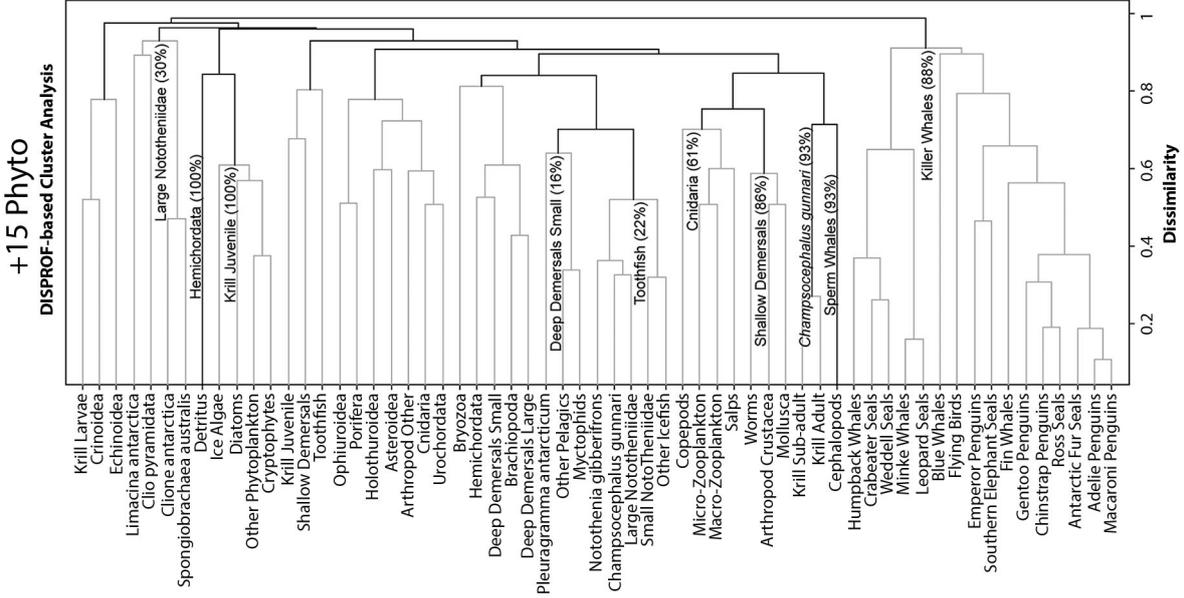
imposed in any of the primary production scenarios, and, as krill depend on ice algae, their biomass is negatively impacted. This is revealed in Fig. 6, which illustrates the importance of ice algae to all krill life stages, as well as the direct trophodynamic links of krill to every functional group above TL 3.0, with the exception of killer whales.

Based on the changes in TL, Q90, biomass, and SIMPROF analyses, potential indicator functional groups are identified, then plotted as radar plots (Fig. 7a,b). When comparing scenarios that consider impacts to primary producers and ice algae (all except +15 Phyto-Ice Algae Fig. 7a), radar plots re-

veal a monotonic positive influence with the increasing effects of climate change for worms, salps, and bryozoans, as well as small increases in the mean TL of the ecosystem. These radar plots reveal negative influences for mammals, Adélie penguins, krill, ice algae, macrozooplankton, and Asteroidea. Non-monotonic influences were observed in fish species diversity (using Q90), and whole-ecosystem species diversity (Q90). When basal TL productivity is increased (+15 Phyto-Ice Algae) and compared to the reference model (Fig. 7b) this generally translates into increased productivity for the whole marine ecosystem at the expense of species diversity. Bioindicator radar plots generally reveal the sensitivity of groups to each of the primary production scenarios.

DISCUSSION

Analysis of the changes in TL, Q90, Shannon Index, biomass, and prey clusters due to primary production scenarios, when compared to the balanced reference model, reveal significant influences to the WAP ecosystem, particularly in the most likely scenario (+15 Phyto). Model predictions include a small increase in the WAP's mean TL, a decrease in whole-ecosystem species diversity and biomass (except in the +15 Phyto-Ice Algae scenario), and trophodynamic restructuring occurring primarily in the highest biomass functional groups. The trophodynamic restructuring includes an increase in salp biomass, with concomitant decreases in energy exchanged from lower to higher TLs, as well as synergistic decreases in the biomass of ice algae, far more than imposed in any of the primary production scenarios. This point is most clearly revealed when examining the +15 Phyto-Ice Algae scenario, as its biomass still decreases with no direct forcing, and the biomass of almost every other functional group increases. A loss of ice algae biomass leads to large reductions in krill biomass, large increases in salp biomass, and overall biomass reductions in mammals and birds. The latter occurs



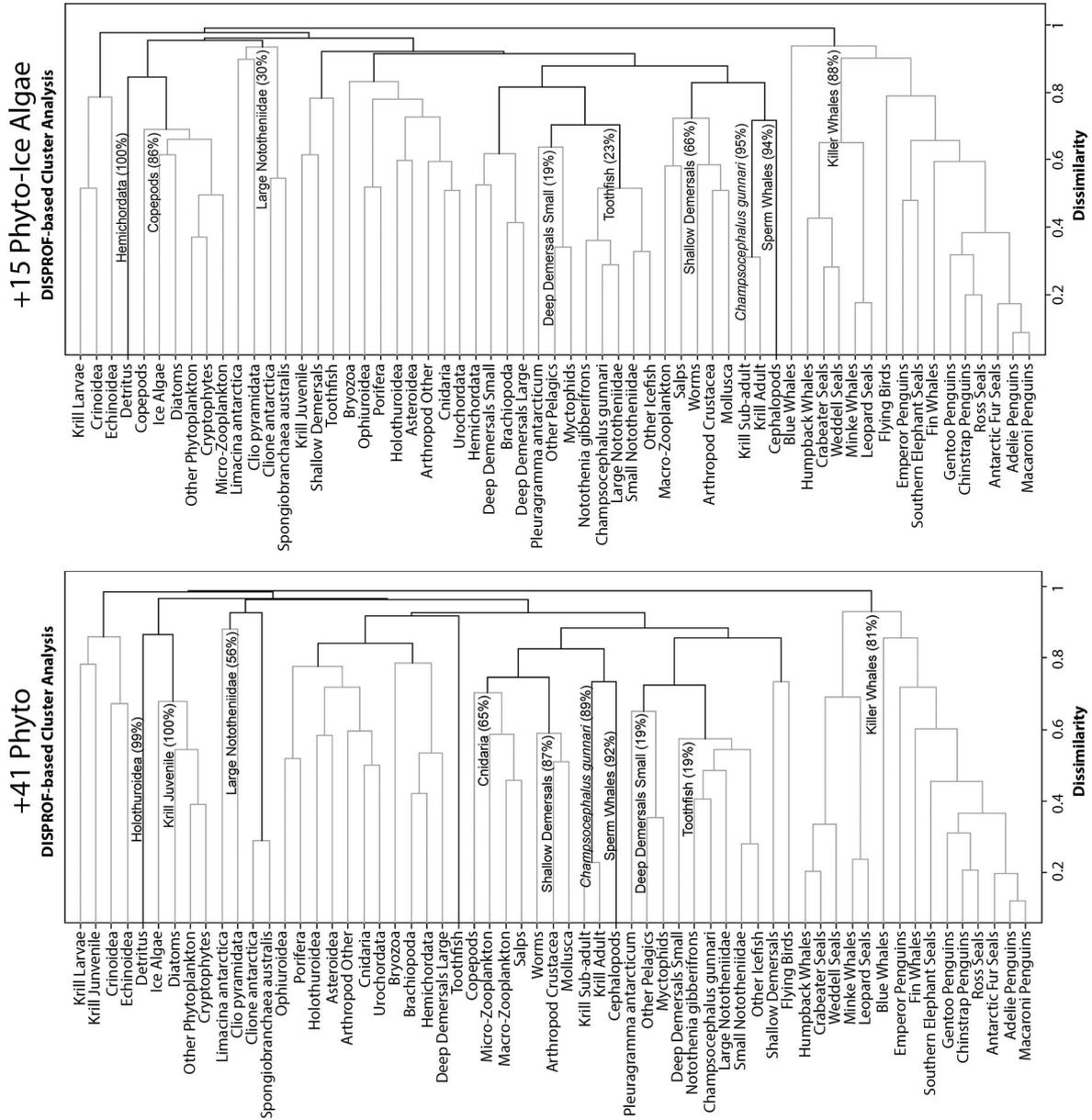


Fig. 5. Results of similarity profile routine (SIMPROF) tests, dissimilarity profile analyses (DISPROF), and Euclidean distance and unconstrained agglomerative (UPGMA) clustering methods to produce significant ($p < 0.05$) aggregations of prey groups as hierarchical clusters according to similarities in predators who prey upon them. Prey clusters are based on diet percentages of each predator in the year 2050, and for each scenario (see Table 3 for details). Functional groups listed within clustering hierarchies corresponded to indicator predator functional groups determined to be the most characteristic predator for a prey cluster based on its similar predatory pressure among all prey within that cluster if $p < 0.05$ (100% equals total similarity). Percent similarity for the predator functional is reported (%)

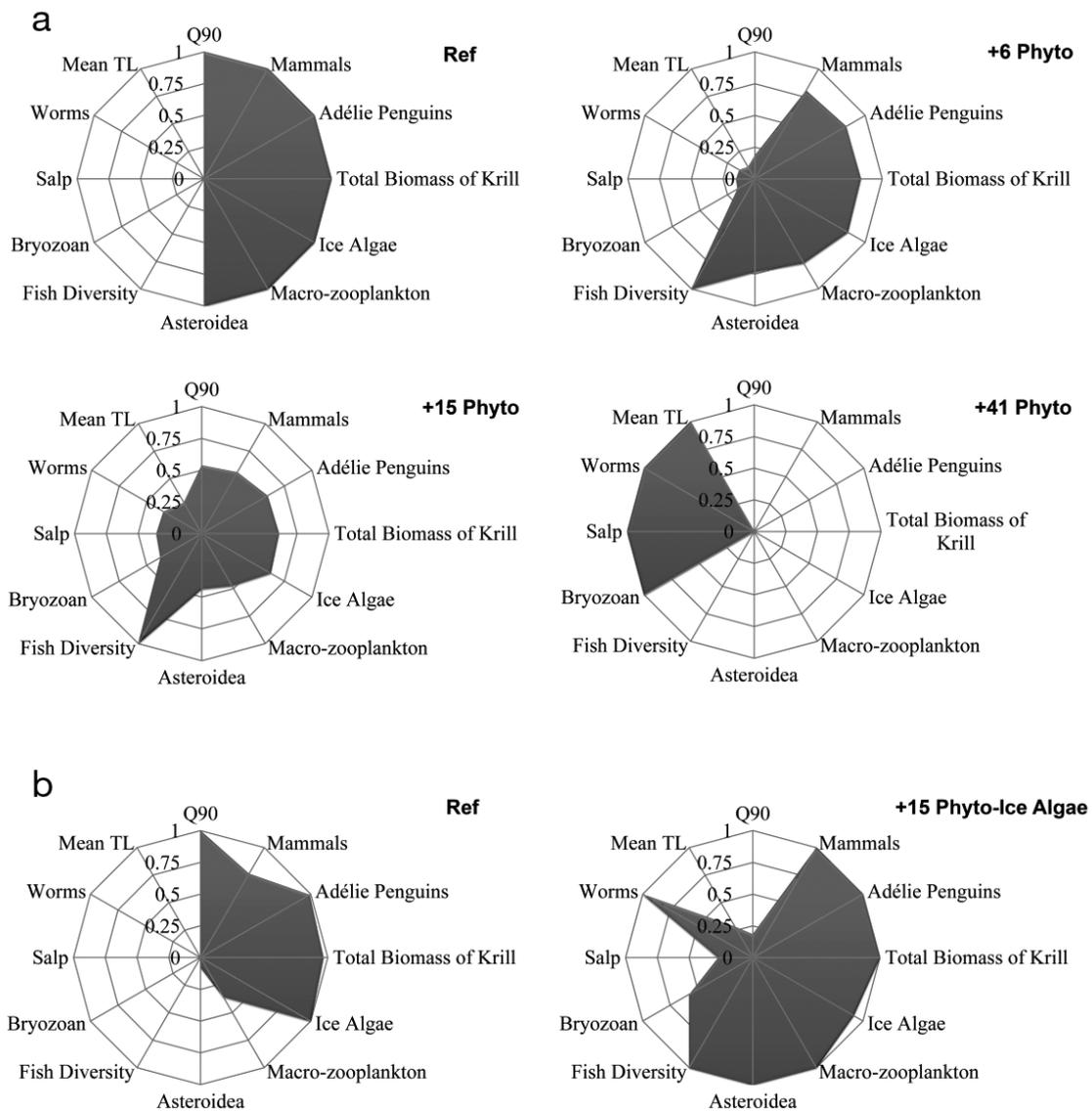


Fig. 7. Relative changes in guild biomass and ecological indicators between climate change scenarios (see Table 3 for details) affecting (a) all primary producers and (b) all primary producers except ice algae. Spoke length is proportional to the magnitude of the output and is relative to the maximum magnitude of that variable observed across all scenarios

because large biomass increases in some mid-TL functional groups, which eat lower TL prey, truncate the energy exchange between primary producers and higher trophic functional groups such as birds, penguins, seals, and whales. As an example of such an energetic impasse, salps significantly increase in biomass yet are rarely consumed by high TL functional groups.

The majority of functional groups that the model predicts to experience adverse trophodynamic effects are directly linked by diet to the vitality of adult and sub-adult krill. For instance, the majority of

whale, seal, and penguin functional groups all have diets largely comprising krill. These distressed functional groups also have significant proportions of their diets consisting of cephalopods, another functional group that decreases with decreasing primary productivity. Therefore, the reduction in krill biomass reduces the energetic contribution to higher TL predators, and this might only be overcome when increasing whole-ecosystem productivity (+15 Phyto-Ice Algae) under the assumption that ice-algae productivity does not decrease with reductions in sea-ice extent.

The largest and most important dietary component for all krill age classes is ice algae. Ice algae comprise the functional group predicted by our EwE model to be the most adversely affected by the primary production scenarios representing alterations in water circulation from westerly wind intensification, nutrient circumpolar deepwater upwelling, increased ambient temperatures, and decreases in sea-ice extent. As the intensity of the primary productivity scenarios increases, krill diets contain less ice algae and more copepods, diatoms, and cryptophytes. Unfortunately, the groups positively affected by climate change such as Urochordata, Brachiopoda, Bryozoa, Echinoidea, macrozooplankton, and microzooplankton have small proportions of krill in their diets, and also consume diatoms, copepods, cryptophytes, and ice algae. This further exacerbates the population decrease in krill.

The increased reliance of krill on higher TL prey is observed in TL changes. This likely causes TL shifts throughout the entire WAP food web and consequently reduces the ecosystem's species diversity. Disagreements in species diversity indices in the +6 Phyto, +15 Phyto, and +41 Phyto scenarios happen when low biomass groups increase in biomass proportionately more than high biomass groups or, as is the case here, when high biomass groups lose biomass faster than low biomass groups. This loss is driven by changes in the planktonic assemblage. Considering species diversity within taxonomic guilds, whale and seal species diversity is largely unchanged until the +41 Phyto primary production scenario, whereas krill and plankton species diversity is impacted in all primary productivity scenarios. This suggests that food web shifts increasingly propagate to higher TLs under stronger changes in primary productivity.

Ultimately, a reduction in krill biomass diminishes energetic transfers throughout the WAP food web. This is congruent with observations of ecological shifts in the WAP ecosystem (e.g. Moline et al. 2004, Ducklow et al. 2007, Lawson et al. 2008, Montes-Hugo et al. 2009, Schofield et al. 2010, Parker 2012, Suprenand et al. 2015b). In the most likely scenario (+15 Phyto), the WAP marine ecosystem's species diversity is predicted to decrease by the year 2050. Likewise, the biomasses of whales, Adélie penguins, and shallow demersals are predicted to decrease in similar proportions to the impact to krill biomass. In the continuum of change described in the series of primary production scenarios, it is evident that salps become a clear winner in WAP climate change. This coincides with field observations (Flores et al. 2012 and references therein).

Ecological studies considering climate change along the WAP support observed trends in our climate change scenarios that consider impacts to ice algae. For instance, declines in krill populations are coincident with reductions in sea-ice extent, which results in an increase in salp abundance and range (Atkinson et al. 2004, Ross et al. 2008). This is due to the reliance of krill on sea-ice for refuge and feeding habitat (e.g. Quetin & Ross 2003), and an increase in salp abundance may impact krill survival (Loeb et al. 1997). Our model simulations also predict reductions in all penguin functional groups, similar to observations over the last 2 decades (Steinberg et al. 2012 and references therein), as well as likely impacts to higher TL predators like seals (Croxall et al. 1999) and whales (Mori & Butterworth 2005). This indicates that physical drivers and the resulting community composition of primary producers control energy flows to the majority of higher TL predators through krill (Ducklow et al. 2006). Thus, a reduction in krill likely impoverishes the WAP food web.

In model forecasts, only krill and salps have significantly decreased and increased biomass in the year 2050, respectively, throughout every primary production scenario that considers impacts to ice algae, with the exception of *Clione antarctica*. Of the 63 functional groups in the current EwE model, only salps experienced reductions in TL throughout every primary production scenario. Other functional group TLs increased under some scenarios, although not as considerably as krill. This implies a high level of trophodynamic restructuring, as evident in prey re-clustering. This produced considerable changes in species diversity and whole-ecosystem biomass. TLs increase across the entire ecosystem (except for salps) as predation becomes more and more focused on higher TLs in each of the functional groups' diets. As salp biomass increases in primary production scenarios, and they become increasingly focused on eating lower TL organisms (which are also eaten by krill), the energy provided by those lower trophic organisms becomes lost to the food web because salps are not widely consumed. Although salps may provide energy for a few marine animals (e.g. Henschke et al. 2016), in the Antarctic they are energetically inferior when compared to krill, and are thought to be an energetic impasse that negatively impacts higher TLs. The change in the quality of prey would negatively affect predators, such as whales, pinnipeds, seabirds, penguins, and fish. An observed increase in salp biomass along the WAP could imply an energetic turning point, and that trophodynamic restructuring is near.

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LITERATURE CITED

- ✦ Ainsworth CH (2006) Strategic marine ecosystem restoration in northern British Columbia. PhD dissertation, University of British Columbia, Vancouver, BC
- Ainsworth CH, Pitcher TJ (2006) Modifying Kempton's species diversity index for use with ecosystem simulation models. *Ecol Indic* 6:623–630
- ✦ Ainsworth CH, Pitcher TJ, Heymans JJ, Vaconcellos M (2008) Reconstructing historical marine ecosystems using food web models: northern British Columbia from Pre-European contact to present. *Ecol Model* 216:354–368
- ✦ ASOC (Antarctic and Southern Ocean Coalition) (2008) Impacts of climate change on Antarctic ecosystems. XXXI ATCM, Kiev. http://www.asoc.org/storage/documents/Meetings/ATCM/XXXI/ASOC_IP_on_climate050608_final.pdf
- Atkinson A, Siegel V, Pakhomov EA, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–103
- Barnes DKA, Griffiths HJ (2008) Biodiversity and biogeography of southern temperate and polar bryozoans. *Glob Ecol Biogeogr* 17:84–89
- ✦ Barnes DKA, Webb K, Linse K (2006) Slow growth of Antarctic bryozoans increases over 20 years and is anomalously high in 2003. *Mar Ecol Prog Ser* 314:187–195
- ✦ Budgell P (2005) Numerical simulation of ice-ocean variability in the Barents Sea region towards dynamical downscaling. *Ocean Dyn* 55:370–387
- ✦ Christensen V, Pauly D (1992) ECOPATH II—a software for balancing steady-state models and calculating network characteristics. *Ecol Model* 61:169–185
- Christensen V, Walters CJ, Pauly D (2005) Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver, BC
- ✦ Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. *J Exp Mar Biol Ecol* 366:56–69
- ✦ Croxall JP, Reid K, Prince PA (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Mar Ecol Prog Ser* 177:115–131
- ✦ Dinniman MS, Klinck JM, Hofmann EE (2012) Sensitivity of Circumpolar Deep Water transport and ice shelf basal melt along the west Antarctic Peninsula to changes in the winds. *J Clim* 25:4799–4816
- ✦ Ducklow HW, Fraser W, Karl DM, Quetin LB and others (2006) Water column processes in the West Antarctic Peninsula and the Ross Sea: interannual variations and foodweb structure. *Deep Sea Res II* 53:834–852
- ✦ Ducklow HW, Baker K, Martinson DG, Quetin LB and others (2007) Marine pelagic ecosystems: the west Antarctic Peninsula. *Philos Trans R Soc Lond B Biol Sci* 362:67–94
- Dufrène M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- ✦ Fabry VJ, Seibel BA, Feely RA, Orr JC (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J Mar Sci* 65:414–432
- ✦ Flores H, Atkinson A, Kawaguchi S, Krafft BA and others (2012) Impact of climate change on Antarctic krill. *Mar Ecol Prog Ser* 458:1–19
- ✦ Haidvogel DB, Arango H, Budgell WP, Cornuelle BD and others (2008) Ocean forecasting in terrain following coordinates: formulation and skill assessment of the Regional Ocean Modeling System. *J Comput Phys* 227:3595–3624
- ✦ Henschke N, Everett JD, Richardson AJ, Suthers IM (2016) Rethinking the role of salps in the ocean. *Trends Ecol Evol* 31:720–733
- Hoover C, Pitcher T, Pakhomov E (2012) The Antarctic Peninsula marine ecosystem model and simulations: 1978–present. In: Wabnitz CCC, Hoover C (eds) *From the tropics to the poles: ecosystem models of Hudson Bay, Kalokohonokau, Hawai'i, and the Antarctic Peninsula*. Fisheries Centre Research Reports 20(2). Fisheries Centre, University of British Columbia, Vancouver, BC, p 108–182
- ✦ Hunt BPV, Pakhomov EA, Hosie GW, Siegel V, Ward P, Bernard K (2008) Pteropods in Southern Ocean ecosystems. *Prog Oceanogr* 78:193–221
- ✦ Ikeda T, Mitchell AW (1982) Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. *Mar Biol* 71:283–298
- Jones DL (2015) *The fathom toolbox for Matlab: multivariate ecological and oceanographic data analysis*. College of Marine Science, University of South Florida, St. Petersburg, FL
- ✦ Kempton RA, Taylor LR (1976) Models and statistics for species diversity. *Nature* 262:818–820
- ✦ Koenigstein S, Mark FC, Göbbling-Reisemann S, Reuter H, Poertner HO (2016) Modelling climate change impacts on marine fish populations: process-based integration of ocean warming, acidification and other environmental drivers. *Fish Fish* 17:972–1004
- Lalli CM, Gilmer RW (1989) *Pelagic snails: the biology of holoplanktonic gastropod mollusks*. Stanford University Press, Stanford, CA
- ✦ Large WG, McWilliams JC, Doney SC (1994) Oceanic vertical mixing: a review and a model with nonlocal boundary layer parameterization. *Rev Geophys* 32:363–403
- ✦ Lawson GL, Wiebe PH, Ashjian CJ, Stanton TK (2008) Euphausiid distribution along the Western Antarctic Peninsula—Part B: distribution of euphausiid aggregations and biomass, and associations with environmental features. *Deep Sea Res I* 55:432–454
- ✦ Link JS (2010) Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol Model* 221:1580–1591
- ✦ Loeb VJ, Santora JA (2013) Pteropods and climate off the Antarctic Peninsula. *Prog Oceanogr* 116:31–48
- ✦ Loeb V, Siegel V, Holm-Hansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance of the Antarctic food web. *Nature* 387:897–900
- ✦ Martinson DG (2012) Antarctic circumpolar current's role in the Antarctic ice system: an overview. *Palaeogeogr Palaeoclimatol Palaeoecol* 335-336:71–74
- ✦ Martinson DG, McKee DC (2012) Transport of warm Upper Circumpolar Deep Water onto the western Antarctic Peninsula continental shelf. *Ocean Sci* 8:433–442
- ✦ McClintock J, Ducklow H, Fraser W (2008) Ecological responses to climate change on the Antarctic Peninsula. *Am Sci* 96:302–310
- ✦ Mellor GL, Yamada T (1982) Development of a turbulence

- closure model for geophysical fluid problems. *Rev Geophys Space Phys* 20:851–875
- Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys Res Lett* 32:L19604
- ✦ Moffat C, Owens B, Beardsley RC (2009) On the characteristics of Circumpolar Deep Water intrusions to the west Antarctic Peninsula continental shelf. *J Geophys Res* 114:C05017
- ✦ Moline MA, Claustre H, Frazer TK, Schofield O, Vernet M (2004) Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Glob Change Biol* 10:1973–1980
- ✦ Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323:1470–1473
- Mori M, Butterworth DS (2005) Summary of a preliminary model of the minke whale–blue whale–krill interaction in the Antarctic. In: Palomares MLD, Pruvost P, Pitcher TJ, Pauly D (eds) *Modeling Antarctic marine ecosystems*. Fisheries Centre Research Reports 13(7). Fisheries Centre, University of British Columbia, Vancouver, BC, p 28–30
- Parker ML (2012) *Micronekton and macrozooplankton of the western Antarctic Peninsula and the eastern Ross Sea: contrast between two different thermal regions*. PhD dissertation, University of South Florida, Tampa, FL
- ✦ Parkinson CL (2002) Trends in the length of the Southern Ocean sea-ice season, 1979–99. *Ann Glaciol* 34:435–440
- Ross RM, Quetin LB, Martinson DG, Iannuzzi RA, Stammerjohn SE, Smith RC (2008) Palmer LTER: Patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. *Deep Sea Res II* 55:2086–2105
- ✦ Schiermeier Q (2009) Atmospheric science: fixing the sky. *Nature* 460:792–795
- ✦ Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How do polar marine ecosystems respond to rapid climate change? *Science* 328:1520–1523
- Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423, 623–656
- ✦ Shchepetkin AF, McWilliams JC (2009) Correction and commentary for 'Ocean forecasting in terrain-following coordinates: Formulation and skill assessment of the regional ocean modeling system' by Haidvogel et al. *J. Comp. Phys.* 227, pp. 3595–3624. *J Comput Phys* 228:8985–9000
- ✦ Shindell DT, Schmidt GA (2004) Southern Hemisphere climate response to ozone changes and greenhouse gas increases. *Geophys Res Lett* 31:L18209
- ✦ Smith DA, Hofmann EE, Klinck JM, Lascara CM (1999) Hydrography and circulation of the west Antarctic Peninsula continental shelf. *Deep Sea Res I* 46:925–949
- ✦ Steinberg DK, Martinson DG, Costa DP (2012) Two decades of pelagic ecology of the Western Antarctic Peninsula. *Oceanography* 25:56–67
- ✦ Suprenand PM, Jones DL, Torres JJ (2015a) Distribution of gymnosomatous pteropods in western Antarctic Peninsula shelf water: influences of Southern Ocean water masses. *Polar Rec* 51:58–71
- ✦ Suprenand PM, Ombres EH, Torres JJ (2015b) Metabolism of gymnosomatous pteropods in waters of the western Antarctic Peninsula shelf during austral fall. *Mar Ecol Prog Ser* 518:69–83
- Walters CJ, Martell SJD (2004) *Fisheries ecology and management*. Princeton University Press, Princeton, NJ
- ✦ Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev Fish Biol Fish* 7:139–172

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