

1 Productivity and Linkages of the Food Web  
2 of the Southern Region of the Western Antarctic Peninsula  
3 Continental Shelf  
4

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34 **Abstract**

35 The productivity and linkages in the food web of the southern region of the west Antarctic  
36 Peninsula continental shelf were investigated using a multi-trophic level mass balance model.  
37 Data collected during the Southern Ocean Global Ocean Ecosystem Dynamics field program  
38 were combined with data from the literature on the abundance and diet composition of  
39 zooplankton, fish, seabirds and marine mammals to calculate energy flows in the food web  
40 and to infer the overall food web structure at the annual level. Sensitivity analyses  
41 investigated the effects of variability in growth and biomass of Antarctic krill (*Euphausia*  
42 *superba*) and in the biomass of Antarctic krill predators on the structure and energy fluxes in  
43 the food web. Scenario simulations provided insights into the potential responses of the food  
44 web to a reduced contribution of large phytoplankton (diatom) production to total primary  
45 production, and to reduced consumption of primary production by Antarctic krill and  
46 mesozooplankton coincident with increased consumption by microzooplankton and salps.  
47 Model-derived estimates of primary production were  $187 - 207 \text{ g C m}^{-2} \text{ y}^{-1}$ , which are  
48 consistent with observed values ( $47\text{-}351 \text{ g C m}^{-2} \text{ y}^{-1}$ ). Simulations showed that Antarctic krill  
49 provide the majority of energy needed to sustain seabird and marine mammal production,  
50 thereby exerting a bottom-up control on higher trophic level predators. Energy transfer to top  
51 predators via mesozooplankton was a less efficient pathway, and salps were a production loss  
52 pathway because little of the primary production they consumed was passed to higher trophic  
53 levels. Increased predominance of small phytoplankton (nanoflagellates and cryptophytes)  
54 reduced the production of Antarctic krill and of its predators, including seabirds and seals

55 **Key words:** Antarctic krill; climate change; donor-controlled model; food web; mass balance  
56 model; Southern Ocean.

57

## 58 **1. Introduction**

59         The traditional view of Southern Ocean food webs is that of a simple system  
60 dominated by Antarctic krill (*Euphausia superba*) that links diatom-based primary production  
61 with higher trophic levels in short efficient food chains (Everson, 1977; Laws, 1984; Murphy  
62 et al., 2012). However, this conceptual food web is not the dominant structure for many  
63 regions of the Southern Ocean where other zooplankton, such as copepods and crystal krill  
64 (*Euphausia crystallorophias*), as well as Antarctic silverfish (*Pleuragramma antarcticum*),  
65 provide the linkage between primary producers and higher trophic levels (Murphy et al.,  
66 2007; Ducklow et al., 2007; Smith et al., 2007, 2012; Murphy et al., 2012). Even within the  
67 same region, the food web structure can vary in response to physical (circulation, sea ice) and  
68 chemical (micro and macro-nutrient supply) processes, which alter primary production,  
69 phytoplankton composition, the relative abundance of zooplankton species, and predator  
70 foraging dynamics (Murphy et al., 2007; Smith et al., 2007, 2012; Atkinson et al., 2008).  
71 Superimposed on regional and seasonal variability are the effects of climate-induced changes  
72 and harvesting of resources, which also produce perturbations to food web structure (e.g.,  
73 Pakhomov et al., 2002; Atkinson et al., 2004; Smetacek and Nicol, 2005; Ballance et al.,  
74 2006; Ainley and Blight, 2009; Murphy et al., 2012).

75         Descriptions of Southern Ocean food webs initially focused on qualitative  
76 descriptions of linkages in particular areas, such as the open ocean, sea ice, or coastal regions  
77 (Everson, 1977; Laws, 1984). Studies done during the past three decades provide the basis for  
78 quantification of food web models. Detailed analysis of food webs that are based on mass  
79 balance constraints, which require that predator consumption of a prey group does not exceed  
80 prey production, have been developed for the Ross Sea (Pinkerton et al., 2010), the Antarctic  
81 Peninsula-Scotia Sea (Cornejo-Donoso and Antezana, 2008) and the South Georgia shelf in  
82 the Scotia Sea (Hill et al., 2012). These modeling studies compiled and analyzed extensive

83 and disparate data sets, which allowed identification and analysis of important trophic groups  
84 and interactions. The analysis of the Ross Sea food web was focused on the production of  
85 Antarctic toothfish (*Dissostichus mawsoni*) and the consequences of harvesting this species  
86 for its predators. The Antarctic Peninsula-Scotia Sea and South Georgia food webs showed  
87 that Antarctic krill was the primary link between low and high trophic levels, and also  
88 showed that alternative trophic pathways through other zooplankton species, benthic  
89 organisms, and fish provided support for the upper trophic levels.

90         The Antarctic Peninsula (Fig. 1a) is warming faster than most other regions on Earth,  
91 and is undergoing a transition from a maritime-Antarctic climate to a warmer sub-Antarctic–  
92 type climate (Montes-Hugo et al., 2009). Since the 1950s the western Antarctic Peninsula  
93 shelf has experienced significant increases in average air and sea water temperature (Turner  
94 et al., 2005; Meredith and King, 2005; review in Ducklow et al., 2007) associated with  
95 increased heat transport and glacial meltwater input and decreased sea ice extent and duration  
96 (Stammerjohn et al., 2008; Meredith et al., 2013).

97         In the northern part of the western Antarctic Peninsula, these changes in the physical  
98 environment have affected various components of the food web (Ducklow et al., 2007;  
99 Schofield et al., 2010). In particular, reductions in sea ice extent have been linked to observed  
100 changes in the composition of phytoplankton assemblages (Moline et al., 2004; Montes-Hugo  
101 et al., 2009), to reduced recruitment of intermediate trophic levels such as Antarctic krill and  
102 Antarctic silverfish that use the under ice habitat as a nursery (Atkinson et al., 2004; Ducklow  
103 et al., 2007; Chapman et al., 2011), and to reduced populations of vertebrate predators such as  
104 the Adélie penguin (*Pygoscelis adeliae*) that use the sea ice habitat (Ainley, 2002). Changes  
105 in the hydrography and reduction of sea ice cover have also been associated with the  
106 increased occurrence of the tunicate *Salpa thompsoni*, which may compete with Antarctic  
107 krill for food (Loeb et al. 1997). Unusually high abundances of salps have been observed in

108 the northern part the western Antarctic Peninsula, and were associated with intrusions of  
109 oceanic water masses close to the Antarctic shelf (Pakhomov et al. 2002; Pakhomov 2004).

110 As the warming trend along the western Antarctic Peninsula continues, changes in the  
111 ecosystem are expected to occur in the southern portion of the western Antarctic Peninsula in  
112 response to reduction of winter sea ice extent and duration (Dinniman et al. 2012), increased  
113 glacial meltwater and changes in hydrography (Clarke et al., 2008; Meredith et al., 2013).  
114 These changes may result in ecosystem trends for the southern region that are similar to those  
115 now occurring along the northern part of the western Antarctic Peninsula, such as an  
116 increased presence of salps (Pakhomov et al. 2002; Pakhomov 2004). Currently, however, the  
117 ecosystems of the southern and northern portions of the Antarctic Peninsula are behaving  
118 differently. For example, Adélie penguin colonies are increasing in size in the south (Lynch  
119 et al., 2012), as the reduction in sea ice concentration and sea ice cover is facilitating penguin  
120 travel and foraging, and Antarctic silverfish are still present in the south although they have  
121 already largely disappeared from the northern areas (Schofield et al., 2010).

122 The U.S. Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC)  
123 Program, which was focused around Marguerite Bay in the southwestern Antarctic Peninsula  
124 (sWAP) continental shelf (Fig. 1), was designed to investigate the physical and biological  
125 factors that influence growth, reproduction, recruitment, and overwintering survival of  
126 Antarctic krill (Hofmann et al., 2004). Important target species from all trophic levels,  
127 including other zooplankton, fish, seabirds, and marine mammals, were the focus of extensive  
128 ecological and physiological studies that were coincident with studies of habitat structure. As  
129 a result, quantitative measures of species abundance, distribution, and vital rates are now  
130 available for many components of the food web of this region. The SO GLOBEC data,  
131 collected during the austral fall and winter of 2001 and 2002, combined with data sets from  
132 the austral fall and spring (e.g. Palmer Station Long-term Ecological Research (LTER)

133 program), provide the basis for development of a food web model for the sWAP continental  
134 shelf.

135 The three objectives of this study are to: 1) develop a mass balance food web model to  
136 quantify the energy flows and identify the dominant trophic pathways from primary  
137 producers to top predators in the sWAP food web; 2) perform sensitivity analyses to  
138 investigate the role of Antarctic krill in energy transfer in the sWAP food web; 3) and  
139 investigate potential changes in the productivity of seabirds and marine mammals in response  
140 to changes in the relative abundance of plankton groups that might occur in the future as a  
141 response to climate change in the sWAP region.

142

## 143 **2. Methods**

### 144 *2.1 Southwestern Antarctic Peninsula food web model*

145 The food web model for the sWAP continental shelf consists of 24 trophic groups that  
146 represent the pelagic, benthic and microbial components (Fig. 2, Table 1). The species  
147 represented within the trophic groups correspond to those observed during SO GLOBEC and  
148 to species reported from previous studies in the sWAP. Some trophic groups are composed of  
149 a single species (e.g., Antarctic krill and Adélie penguin), while other trophic groups are  
150 composed of more than one species (Table A.1). Primary producers are represented by three  
151 microbial groups, small phytoplankton (nanoflagellates and cryptophytes, < 20µm), large  
152 phytoplankton (diatoms, > 20µm) and ice algae. The intermediate trophic groups consist of  
153 micro-, meso- and macrozooplankton, Antarctic krill, and benthic invertebrates. The pelagic  
154 fish assemblage along the sWAP is dominated by two species, Antarctic silverfish and lantern  
155 fish (*Electrona antarctica*) (Donnelly and Torres, 2008). Cephalopods and benthic fish are  
156 consumers of intermediate trophic level production and also are prey for top predators (e.g.  
157 Kock, 1987; Barrera-Oro, 2002). The top predators are the Adélie penguin, a group of several

158 species of flying seabirds, seals, and cetaceans. These predators constitute the majority of  
 159 upper trophic level biomass along the sWAP (Chapman et al., 2004; Thiele et al., 2004; Ribic  
 160 et al., 2008, 2011).

161 In the mass balance food web model (ECOPATH-type, based on Christensen et al.,  
 162 2004) developed for the sWAP region, production of prey species is determined by predator  
 163 consumption (i.e., top down control). The average annual energy flux budget ( $\text{g C m}^{-2} \text{y}^{-1}$ )  
 164 through the food web was obtained using:

$$165 \quad P_p = M2_p B_p + M0_p B_p \quad (1)$$

166 where the production,  $P_p$ , of each producer group,  $p$ , is calculated as the sum of removal of  
 167 its biomass,  $B_p$ , by predation mortality,  $M2_p$ , and by non-predation mortality,  $M0_p$ . The model  
 168 assumes no loss to fisheries and a steady state food web so that biomass accumulation and  
 169 emigration/immigration are zero.

170 Predation mortality is given by

$$171 \quad M2_p = \sum_{c=1}^n \frac{Q_c DC_{pc}}{B_p}, \quad (2)$$

172 which is the sum of consumption by all consumer groups,  $c$ , feeding on the producer group,  
 173  $p$ . For each consumer group,  $Q_c$  is the total consumption rate and  $DC_p$  is the fraction of the  
 174 consumer group's diet that is composed of the producer group. The non-predation mortality  
 175 is given by

$$176 \quad M0_p = (1 - EE_p) (P_p / B_p), \quad (3)$$

177 where  $EE_p$  is the ecotrophic efficiency, which indicates the fraction of the total production of  
 178 a trophic group,  $p$ , that is consumed by its predators,  $c$ , and  $P_p/B_p$  is the ratio of production  
 179 ( $P_p$ ) of a species/group to its biomass ( $B_p$ ). The system of linear equations (Eq. 1) allows  
 180 calculation of the food web mass balance based on specified diet interactions (Eq. 2), and the  
 181  $EE_p$  of each group (from Eq. 3). The food web model is balanced if  $EE_p$  is  $<1$  for each trophic

182 group.

183 Because the above food web model assumes top-down control, assessing the effect of  
184 a reduction in prey production and biomass on predator production and biomass is difficult  
185 (Steele, 2009). Thus, the second part of the modeling study was to use the approach of Steele  
186 (2009) and Steele and Ruzicka (2011) that allows the linear equations in the above model to  
187 be transposed into a set of equations in which the production of a predator ( $P_c$ ) is controlled  
188 by the production of its prey ( $P_p$ ) (i.e. bottom-up control):

$$189 \quad P_c = P_p / Q_p \sum_p A_{cp} E E_p P_p \quad (4)$$

190 where  $P_p/Q_p$  is the predator production to consumption ratio (equivalent to gross growth  
191 efficiency) and  $A_{cp}$  is the partitioning of the production of each prey ( $P_p$ ) among their  
192 predators ( $P_c$ ) (Steele, 2009; Steele and Ruzicka, 2011). The production matrix  $A_{cp}$  is  
193 calculated from the system of equations:

$$194 \quad Q_{pc} = DC_{pc} Q_c \quad DC_{pc} \geq 0 \quad (\text{top-down approach}) \quad (5)$$

$$195 \quad Q_{pc} = A_{cp} P_p \quad A_{cp} \geq 0 \quad (\text{bottom up approach}), \quad (6)$$

196 where  $Q_{pc}$  is the rate at which the prey biomass,  $B_p$ , is consumed by the predator biomass,  $B_c$ .  
197 The terms  $DC_{pc}$ ,  $Q_{pc}$ , and  $P_p$  are obtained from the top-down model and used to calculate the  
198 production matrix,  $A_{cp}$ .

199 The top-down (Eq. 1) and bottom-up (Eq. 4) models both require estimates of  
200 spatially-averaged biomass, estimates of production and consumption, as well as specification  
201 of diet composition for each trophic group. Details of how these were obtained follow.

202

## 203 **2.2 Specification of model parameters**

### 204 **2.2.1 Carbon biomass estimates**

205 The initial biomass values used for each trophic group in the sWAP food web model



206 (Table 1) did not include a biomass estimate for the primary producer group. The biomass for  
207 this group corresponds to the direct demand for primary production by consumer groups, and  
208 was calculated using Eq. 1. Passive sinking for the primary producer groups and non-  
209 predation mortality for the consumer groups were not included in the mass balance model.  
210 Spatial averages of biomass ( $\text{g C m}^{-2} \text{ y}^{-1}$ ) for the sWAP model consumer groups were  
211 computed using data from the SO GLOBEC cruises and from the literature. Climatological  
212 estimates of the average number of sea ice days in a year (Stammerjohn et al., 2008) were  
213 used to divide the sWAP shelf into two regions: shelf (162 sea ice days  $\text{y}^{-1}$ ) and inner  
214 Marguerite Bay (208 sea ice days  $\text{y}^{-1}$ ; Fig. 1b). For those trophic groups that include species  
215 that have different densities in open water (*DOW*) and in the pack ice (*DPI*), the fraction of  
216 the annual sea ice days in the shelf (*sh*) and inner Marguerite Bay (*mb*) regions was used to  
217 scale their annual density (*AD*) as:

$$218 \quad AD = sh \text{ DOW} + mb \text{ DPI} \quad (7)$$

219 where  $sh = 0.44$  and  $mb = 0.57$ .

220 Microzooplankton biomass for the sWAP food web model was derived from  
221 measurements of heterotrophic microplankton carbon weight collected in the Bellingshausen  
222 Sea (Edwards et al., 1998) and close to Anvers Island (Moreau et al., 2010) to the west and  
223 north of the SO GLOBEC study area, respectively. The data from the Bellingshausen Sea  
224 were collected in spring at the marginal ice zone and include samples from open water, ice  
225 edge and pack ice. These data show that microplankton abundance in the open water was up  
226 to six times higher than in the pack-ice zone. The data from Anvers Island were collected in  
227 early spring and in late fall/winter and showed that the early spring biomass was twice that of  
228 the late fall/winter. To account for this variability in biomass in both regions, carbon biomass  
229 estimates for the open water in the Bellingshausen Sea were used for the no-sea-ice period  
230 and were scaled by seasonal factors derived from the Anvers Island study for the days with

231 sea ice. These estimates were then space and time averaged to get an annual carbon biomass  
232 estimate for the microzooplankton group in the sWAP model.

233 Vertical distributions of the abundance of meso- and macrozooplankton were obtained  
234 from sequential net tows using a Multiple Opening Closing Net Environmental Sensing  
235 System (MOCNESS) during the fall and winter 2001 and 2002 SO GLOBEC cruises  
236 (Ashjian et al., 2004, 2008; Marrari et al., 2011). The sampling locations inside the shelf  
237 break were apportioned into the two sub-regions and water column integrated abundances ( $A$ ,  
238 ind m<sup>-2</sup>) were calculated for each taxa as:

$$A = \sum_{i=1}^8 n_i z_i \quad (8)$$

239  
240 where  $n$  is abundance (ind m<sup>-3</sup>) in net  $i$  (a total of 8 nets at each sampling location), and  $z$  is  
241 the depth interval (m) of the stratum sampled by net  $i$ . For sample locations with multiple net  
242 tows, the integrated abundances of zooplankton obtained from the different net tows were  
243 averaged. The integrated abundances from different stations were then averaged to obtain  
244 biomass estimates for the inner Marguerite Bay and shelf regions.

245 The zooplankton taxa that were identified in the net tows were aggregated into the  
246 groups used in the food web model. The averages obtained from the SO GLOBEC data were  
247 extended to obtain an annual estimate by assuming that the measured values were  
248 representative of a winter season of 7 months (April-October). The summer biomass for the  
249 remaining 5 months (November-March) was obtained using a scaling factor of 2.18, which  
250 was derived from an analysis of seasonal changes in the abundance of calanoid copepods in  
251 the Weddell Sea (Schnack-Schiel et al., 1998). Species-specific conversion factors or  
252 conversion factors from similar species (Table S.1) were used to convert the biomass  
253 estimates to carbon. The annual carbon estimates for the meso- and macrozooplankton were  
254 then obtained from the weighted average of the winter and summer biomass estimates. A

255 similar approach was used to obtain annual carbon values for macrozooplankton.

256 Vertically-integrated abundances of Antarctic krill larvae obtained from net tow  
257 measurements during the SO GLOBEC cruises were converted to carbon biomass using a  
258 regression developed for larval Antarctic krill (Daly, 2004). Antarctic krill larvae biomass in  
259 fall 2001 ( $1.21 \text{ g C m}^{-2}$ ) was nine times higher than in fall 2002 ( $0.129 \text{ g C m}^{-2}$ ). The high  
260 larval krill biomass of 2001 likely occurred in response to a large phytoplankton bloom and  
261 to warmer than average water temperature that year (Marrari et al., 2008). High larval krill  
262 recruitment is thought to occur about once every seven years (i.e. with a probability of  $1/7 =$   
263  $0.143$ ; Daly, unpublished data). To account for this variability, the larval Antarctic krill  
264 biomass estimate for the sWAP food web model was calculated as the weighted average  
265 between the unusual high biomass of 2001 (with a weight of  $0.143$ ) and the more normal  
266 biomass of 2002 (with a weight equal to  $1 - 0.143 = 0.857$ ). This yielded an estimated  
267 average biomass of  $0.284 \text{ g C m}^{-2} \text{ y}^{-1}$ .

268 The combined juvenile and adult Antarctic krill net-derived abundances from 2001  
269 and 2002 were vertically and spatially-averaged and converted to carbon biomass to obtain  
270 the annual biomass estimate for the adult Antarctic krill group in the sWAP food web model.  
271 A similar approach was used to obtain annual biomass for the other euphausiids group. The  
272 density and biomass of salps in a part of the Antarctic shelf partially overlapping with the SO  
273 GLOBEC study area was measured in early fall 2001 as part of the German SO GLOBEC  
274 field program (Pakhomov et al., 2006). The earlier timing of the German cruise placed it  
275 before sea ice developed and salps were still present. The measured biomass value of  $0.0173$   
276  $\text{g C m}^{-2}$  was applied to the shelf sub-region and the spatially averaged biomass is  $0.009 \text{ g C}$   
277  $\text{m}^{-2}$ . However, the salps observed on the Antarctic Peninsula shelf in fall 2001 were likely  
278 the result of an advective event, which can provide considerable variability in their mean  
279 density and distribution (Pakhomov et al., 2006). Thus, the values used in the food web

280 model, while representative of observed conditions for one season, may not reflect conditions  
281 at other times. The density and biomass in the inner Marguerite Bay sub-region was set to  
282 zero as suggested by observations (Marrari et al., 2011).

283 Ctenophore abundance was measured during the SO GLOBEC cruises (Scolardi, et al.  
284 2006) and was converted to carbon biomass using the conversion relationships given in  
285 Scolardi et al., (2006). These observations were assumed to apply over a year.

286 No data on cephalopods are available for the SO GLOBEC region; therefore, their  
287 biomass was estimated with the top-down mass balance model (Eq. 1). Antarctic silverfish  
288 and lantern fish biomass measured during the SO GLOBEC cruises (Donnelly and Torres,  
289 2008) provided the estimates for the on-shelf and off-shelf pelagic fish groups, respectively.  
290 Other pelagic fish species were apportioned into the two pelagic fish groups based on their  
291 relative abundances in the shelf and inner Marguerite Bay regions. Carbon biomass was  
292 obtained assuming a carbon-to-wet-weight ratio of 0.1. No data are available for the sWAP  
293 benthic fish community. Therefore, data presented in Donnelly et al. (2004) for the Ross Sea  
294 benthic fish community were used to obtain carbon biomass for a representative benthic fish  
295 community. Benthic invertebrate biomass was not measured during SO GLOBEC; therefore,  
296 the biomass of this group was taken from an earlier study (Smith et al., 2006) and converted  
297 to carbon biomass using a carbon-to-dry-weight ratio of 0.4.

298 Adélie penguin biomass was estimated using summer density values from breeding  
299 colonies in the Marguerite Bay region and then doubled to account for non-breeders (Ainley,  
300 2002). The summer density was spatially-averaged using the model domain area (83,670  
301 km<sup>2</sup>) to obtain a density of 2.38 ind km<sup>-2</sup>. Telemetry data from Adélie penguins tagged in  
302 Marguerite Bay during SO GLOBEC (Erdmann et al., 2011) showed that the flux of penguins  
303 into/out of this region was relatively balanced. Individual body weight for penguins in the  
304 month of October was set at 8 kg for breeding and 6 kg for non-breeding birds (Penney,

305 1967). Penguin body mass used for the other months was 4.5 kg (Ribic et al., 2011). The  
306 mean annual wet weight biomass was obtained by averaging the monthly values and was  
307 converted to carbon biomass using a carbon-to-wet-weight conversion of 0.2 (Burger and  
308 Schreiber, 2001).

309         Densities of several species of flying seabirds were measured during the SO  
310 GLOBEC cruises (Ribic et al., 2011) and these were combined with data from the literature  
311 to obtain average densities for the sWAP region (Ribic et al., 2011). The annual densities in  
312 the shelf and inner Marguerite Bay regions were calculated based on the number of sea ice  
313 days in each region. Average body mass of individual species (Table S.2) was used to obtain  
314 a total seabird biomass, which was then converted to carbon biomass using a carbon-to-wet-  
315 weight conversion of 0.2 (Burger and Schreiber, 2001).

316         The average density of crabeater seals in ice-covered ( $1.31 \text{ ind km}^{-2}$ ) and open water  
317 ( $0.16 \text{ ind km}^{-2}$ ) areas in the Marguerite Bay region was obtained from SO GLOBEC surveys  
318 (Chapman et al., 2004; Ribic et al., 2008). An annual density for the shelf and inner  
319 Marguerite Bay regions was calculated for the time that the two regions have sea ice. The  
320 density for the overall region ( $0.74 \text{ ind km}^{-2}$ ) was obtained as a spatially-weighted average  
321 between the shelf and inner Marguerite Bay. Wet biomass was obtained using an average  
322 individual mass ( $250 \text{ kg ind}^{-1}$ ; Nørdoy et al., 1995; McDonald et al., 2008) and converted to  
323 carbon biomass assuming conversions of 0.35 and 0.5 for wet weight to dry weight and dry  
324 weight to carbon, respectively.

325         Weddell seals (*Leptonychotes weddellii*) prefer fast ice and dense pack ice (Siniff et  
326 al., 2008) and the SO GLOBEC cruises did not extend into these regions. As a result, the  
327 winter encounter rates for Weddell seals were so low that density estimates were unreliable  
328 (Chapman et al., 2004). Thus, an indirect estimate of their abundance was obtained by scaling  
329 their number with respect to the number of crabeater seals. A study of seal relative abundance

330 (Erikson and Hanson, 1990) showed that Weddell seal abundance is about 3% of crabeater  
331 seal abundance. This percent was used to scale crabeater seal abundance to Weddell Sea  
332 abundance. This implies a Weddell Sea density of  $0.03 \text{ ind km}^{-1}$ . An individual average  
333 weight of 450 kg (Proffitt et al., 2007) gave an annual wet biomass of  $12.3 \text{ kg km}^{-2}$ , which  
334 was converted to carbon biomass (Table 1) using the wet and dry weight ratios used for  
335 crabeater seals.

336 Minke whale (*Balaenoptera bonaerensis*) abundance along the sWAP for December  
337 to February has been estimated to be  $0.014 \text{ ind km}^{-2}$  (Branch, 2006). Seasonal variation in  
338 minke whale density was estimated from cetacean observations made during the SO  
339 GLOBEC fall and winter cruises as well as during SO GLOBEC mooring deployment cruises  
340 in late summer (Thiele et al., 2004). The maximum abundance value observed during each  
341 SO GLOBEC cruise was used to calculate minke whale abundance for March-May, June-  
342 August, and December-February. These values were used to calculate abundance ratios for  
343 the fall and winter and the ratios were used to scale the summer density values from Branch  
344 (2006) to obtain an annual density estimate of  $0.008 \text{ ind km}^{-2}$ . Annual wet weight biomass  
345 was calculated assuming a demographic structure (female:male, mature:immature) and the  
346 corresponding average individual body mass as reported in Konishi et al. (2008) and Tamura  
347 and Konishi (2009). The wet biomass ( $0.0517 \text{ t km}^{-2}$ ) was converted to carbon biomass  
348 (Table 1) using a wet weight to dry weight ratio of 0.35 and a dry weight to carbon weight  
349 ratio of 0.5. Similarly, the abundance of humpback whales (*Megaptera novaeangliae*) along  
350 the sWAP from December to February was estimated as  $0.0014 \text{ ind km}^{-2}$  (Branch, 2007).  
351 Seasonal variability in humpback whale density was determined from the SO GLOBEC  
352 cetacean sightings data (Thiele et al., 2004) and the abundance ratios were used to scale the  
353 abundance estimates from Branch (2006) to obtain seasonal density estimates, which were  
354 averaged to obtain an annual density estimate of  $0.0007 \text{ ind km}^{-2}$ . The average individual

355 body mass for a humpback whale (26,924 kg, Reilly et al., 2004) was used to estimate wet  
356 biomass (0.0517 t km<sup>-2</sup>), which was converted to carbon biomass using the same conversions  
357 as used for minke whales.

### 358 2.2.2 Production/Biomass ratios

359 The rate at which a species or trophic group replaces itself, the turnover rate, can be  
360 expressed by its production per unit biomass. In the mass balance model the production to  
361 biomass ratio ( $P/B$ ) provides an estimate of the annual growth for each of the food web  
362 components (Table 1).

363 The  $P/B$  ratio for the primary producer groups was derived from satellite estimates of  
364 primary production and chlorophyll a concentration in the study area during the period 1998-  
365 2007. The microzooplankton  $P/B$  ratio is consistent with values that can be calculated from  
366 data given in Hansen et al. (1997). For the zooplankton groups included in the sWAP food  
367 web model,  $P/B$  ratios were taken from previous studies (Table A.1). For the fish groups, the  
368  $P/B$  ratios were obtained from the regression given in Banse and Mosher (1980), which  
369 relates the  $P/B$  ratio to mass at maturity ( $Mm$ ) as:

$$370 \quad \log\left(\frac{P}{B}\right) = a + b\log(Mm) \quad (8)$$

371 where  $a$  is 0.44 and  $b$  is -0.23. The values of the coefficients in Eq. (8) were derived from a  
372 meta-analysis of fish species in temperate and tropical regions and did not include organisms  
373 that inhabit cold environments. Therefore, the  $P/B$  values obtained from Eq. (8) were reduced  
374 by 20% for the off-shelf pelagic fish and by 25% for the on-shelf pelagic fish (Greely et al.,  
375 1999; J. Torres, pers. comm.) to account for the slower turnover rate in colder waters.

376 For top predators, the  $P/B$  ratio was assumed to be the value that balanced annual  
377 adult mortality (Banse and Mosher, 1980). For Adélie penguins the annual adult survival is  
378 estimated to be 0.85 (Ballerini et al., 2009), which gives a  $P/B$  ratio of 0.15. Annual adult  
379 survival rates have been estimated for several Antarctic seabirds (e.g., 0.94 for snow petrel

380 *Pagodroma nivea*, Jenouvrier et al., 2005b; 0.92 for Antarctic fulmar *Fulmarus glacialisoides*,  
381 Jenouvrier et al., 2005a; 0.96 for south polar skua *Stercorarius maccormicki*, Ratcliffe et al.,  
382 2002), and these were averaged to obtain a biomass-weighted survival of 0.94 and a *P/B* ratio  
383 of 0.06 for the seabird group.

384 For crabeater seals, annual adult survival (*s*) was calculated from mean life  
385 expectancy (*le*) using the relationship:

$$386 \quad le = \frac{1}{-\log s} \quad (9)$$

387 where *le* was 34.5 years (Bengston and Siniff, 1981; Efran and Pitcher, 2005). This gives an  
388 annual survival of 0.935 and a *P/B* ratio of 0.065. Average annual survival for Weddell seals  
389 is estimated to be 0.92 (Rotella et al., 2009), which gives a *P/B* ratio of 0.08. The annual  
390 survival for minke whales and humpback whales was calculated using Eq. (9) with average  
391 life expectancies of 50 and 75 years, respectively (Ohsumi, 1979a,b), and used to obtain *P/B*  
392 ratios (Table 1).

### 393 2.2.3 Gross growth efficiency and consumption rates

394 The mass balance food web model (Eqs. 1 and 2) requires estimates of the  
395 consumption (*Q*) of each trophic group per unit biomass (*Q/B*). This ratio can be estimated  
396 from daily feeding rates (expressed as kg of meal per kg of body weight) or can be calculated  
397 as:

$$398 \quad Q/B = \frac{P/B}{P/Q} \quad (10)$$

399 where the *P/Q* ratio corresponds to the gross growth efficiency, which is the product of the  
400 assimilation efficiency (*AE*) and production efficiency (*PE*). Using the gross growth  
401 efficiency to obtain the *P/Q* ratio allows explicit calculation of unassimilated ingestion (*I-*  
402 *AE*) that goes to the detrital pool and of energy lost to metabolic processes (e.g., respiration,  
403 *I-PE*), and thus ensures consistency between the assumed consumption and production rates



404 for each trophic group in the food web model (Link, 2010). The assimilation and production  
405 efficiency values used to calculate the gross growth efficiency for the sWAP trophic groups  
406 (Table 1) were obtained from Townsend et al. (2003), with the exception of the assimilation  
407 efficiency value for larval Antarctic krill that was taken from Meyer et al. (2003). The  
408 reconstructed gross growth efficiency values are consistent with values used in other  
409 Southern Ocean food web models (Banse, 1995; Priddle et al., 1998). These values and the  
410  $P/B$  ratios given above were used to calculate the  $Q/B$  ratio for each trophic group.

#### 411 *2.2.4 Diet composition*

412 Each trophic group in the sWAP food web has an associated diet, which determines  
413 the transfer of energy in the food web (Table 2). The percent composition of prey in the diets  
414 of many of the sWAP trophic groups was based on observations (Table A.1); for some groups  
415 (mesozooplankton, macrozooplankton, larval and adult Antarctic krill and other euphausiids)  
416 sufficient data were available to construct monthly or seasonal diets (Tables S.3-S.11), which  
417 were averaged to obtain an annual diet. Allowing cannibalism can result in an unstable set of  
418 linear equations (Steele and Ruzicka, 2011); therefore, the specified diet composition of the  
419 microzooplankton and benthic invertebrate groups included only primary producers or  
420 detritus (Table 2) and the intra-guild predation (i.e., consumption of heterotrophic material)  
421 in these groups was taken into account by reducing their assumed gross growth efficiency by  
422 50% (Table 1). The result is that the microzooplankton diet is composed only of autotrophic  
423 material (Table 2). The microzooplankton community during the fall SO GLOBEC cruises  
424 was dominated by phaeodarian radiolarians and the ciliate, *Mesodinium* sp., (Daly, 2004),  
425 both of which eat a range of particle sizes that are consistent with the specified diet  
426 (Froneman and Perissimotto, 1996).

427 Salps feed efficiently on a wide range of particles (1 to 1000  $\mu\text{m}$ ) (Pakhomov et al.,  
428 2006) and the diet for this group accounts for this, with most of the consumption focused on

429 smaller particles (Table 2). The ctenophore diet was based on observations that show that  
430 ctenophores feed on calanoid copepods, amphipods, and larval Antarctic krill (Ju et al., 2004;  
431 Scolardi, 2006).

432 Cephalopods are opportunistic feeders (Rodhouse and Nigmatullin, 1996) and feed on  
433 crustaceans and fish (Collins and Rodhouse, 2006). The diet specified for this group was  
434 equally divided between fish and zooplankton, with most of the zooplankton being Antarctic  
435 krill (Table 2).

436 The diets of the off-shelf and on-shelf pelagic fish groups were based on the diets of  
437 lantern fish and of Antarctic silverfish, respectively, which feed on meso- and  
438 macrozooplankton, Antarctic krill, and other euphausiids (Kock, 1987). The relative  
439 abundance of each of the zooplankton groups in the diets was used to specify the annual diets  
440 of the off- and on-shelf pelagic fish groups, with most of the consumption being  
441 mesozooplankton and adult Antarctic krill (Table 2). Observations show that the diet of  
442 benthic fish consists of benthic invertebrates, Antarctic silverfish, and Antarctic krill, with  
443 smaller contributions from other zooplankton, lantern fish, and cephalopods. The diet  
444 constructed for benthic fish was apportioned across these prey items (Table 2).

445 Adélie penguins consume primarily Antarctic krill and fish, including lantern fish (in  
446 winter, Ainley et al., 1992) and Antarctic silverfish, with some consumption of other  
447 euphausiids and cephalopods (Volkman et al., 1980; Ainley, 2002; Ainley et al., 2003; Fraser  
448 and Hofmann, 2003). The annual diet constructed for Adélie penguins accounted for  
449 variations in the relative abundance of these prey in the diet between summer, when Antarctic  
450 krill dominate, and winter, when the diet is more varied. Adult Antarctic krill make up about  
451 50% of the constructed Adélie penguin annual diet.

452 The flying seabird diet composition was constructed from observations of the diets of  
453 snow petrels, Antarctic fulmars and cape petrels (*Daption capense*) (Ainley et al., 1992),

454 south polar skuas (Ainley et al., 1984), and black-browed albatross (*Thalassarche*  
455 *melanophrys*) (Xavier et al., 2003). Snow petrels are associated with areas with sea ice,  
456 whereas the other species are associated with open water, and the diet composition reflects  
457 the species differences in the two regions. The ice- and open-water associated diets were used  
458 to construct an annual average diet for seabirds (Table 2), which is based primarily on  
459 cephalopods and pelagic fish.

460 Crabeater seals eat mostly Antarctic krill (Siniff et al., 2008) with small contributions  
461 from cephalopods and fish (Øristland, 1977). Thus, the annual diet consists primarily of  
462 Antarctic krill (Table 2). The diet for Weddell seals is more varied, consisting of cephalopods  
463 and fish, with the most common fish being Antarctic silverfish (Green and Burton, 1987;  
464 Ponganis and Stockard, 2007; Ainley and Siniff, 2009). The annual diet for Weddell seals  
465 was split evenly between cephalopods and fish, and within the fish it was evenly apportioned  
466 among the three fish groups in the food web model (Table 2).

467 The diet of Antarctic minke whales is primarily Antarctic krill (Ichii and Kato, 1991;  
468 Ichii et al., 1998) and this is reflected in the annual diet specified for this species (Table 2).  
469 Humpback whales also feed predominately on Antarctic krill (Kawamura, 1980), but with  
470 some contribution from fish. Thus, the specified diet for this trophic group consisted mostly  
471 of adult Antarctic krill with smaller contributions from on-shelf and off-shelf pelagic fish,  
472 cephalopods and mesozooplankton.

### 473 *2.3 Food web balance*

474 The sWAP food web model was implemented using the parameter values and diet  
475 compositions given in Tables 1 and 2. Mass balance is achieved when all of the ecotrophic  
476 efficiency values,  $EE_p$  in Eq. 3, are less than 1. An unbalanced model can be resolved by  
477 modifying predator diets and consumption rates, physiological efficiencies, or prey biomass.  
478 For the sWAP food web model, the approach used was to increase the biomass of the prey by

479 setting their  $EE = 1$  (similar to Hill et al., 2012). For the initial implementation of the sWAP  
480 food web model, three groups (ctenophores, on-shelf pelagic fish and on-shelf pelagic fish)  
481 had  $EE > 1$ , which indicated that the estimated production rate for these groups was too low  
482 to support the estimated consumption by their predators. The biomass for these three groups  
483 was increased, but was still within the variability of observed biomasses for these groups  
484 (Table 3). Increasing the biomass of the pelagic fish groups led to higher consumption of  
485 adult Antarctic krill, and produced an  $EE$  for this group  $> 1$ . Therefore, the adult Antarctic  
486 krill biomass was also mass balanced by setting its  $EE = 1$ . The revised biomass estimate was  
487 within the variability of biomass estimates for Antarctic krill obtained from acoustic surveys  
488 in the study area (Lawson et al., 2008a).

489 Inputs to the pelagic and benthic detritus groups are from feces and non-predation  
490 mortality of consumer groups (Table 1). The unbalanced primary producer and consumer  
491 groups were balanced using  $EE = 1$ , which does not allow for passive sinking and non-  
492 predation mortality losses. Messy feeding by zooplankton is also not included in the model.  
493 Thus the estimated detrital fluxes from the sWAP food web model represent lower bounds.

494 Results from the sWAP mass balance baseline simulations were used in Eqs. 5 and 6  
495 to create the bottom-up model (Eq. 4) and to calculate the production matrix  $A_{cp}$  (Table A.3).  
496 The production matrix was used in simulations that addressed possible outcomes of  
497 environmental changes (see Section 2.4.2).

#### 498 *2.4 Model analysis and metrics*

499 The mass balance model implemented with the data summarized in Tables 1 and 2  
500 was used to obtain a baseline simulation for the sWAP food web that provided an estimate of  
501 the primary production required by the food web and an estimate of the energy flows between  
502 trophic groups. The diet composition of the baseline simulation was used to calculate the  
503 trophic level of the sWAP model groups. The baseline simulation also provided a reference

504 for comparison for the sensitivity analyses and environmental change scenario simulations.

#### 505 2.4.1 Sensitivity analysis - role of Antarctic krill in energy transfer

506 The sWAP food web model is focused on a main target species, Antarctic krill, with  
507 decreasing resolution up and down the trophic scale from this species, i.e. a rhomboid model  
508 structure (de Young et al., 2004). Therefore, sensitivity analyses were designed to investigate  
509 changes that result from modifications to the inputs and outputs that affect Antarctic krill and  
510 the effect of this species on other trophic levels.

511 The first set of simulations focused on estimates of primary production required to  
512 sustain the food web by modifying the biomass,  $P/B$  ratio, and diet composition of the adult  
513 Antarctic krill. The second set of simulations compared the estimates of primary production  
514 from the baseline sWAP simulation with three alternative implementations that included  
515 modified values of gross growth efficiencies for all trophic groups that were derived from  
516 earlier modeling studies of Southern Ocean food webs (Banse, 1995; Priddle et al., 1998) and  
517 those derived from daily feeding rates (Table A.2). These simulations included the variability  
518 in adult Antarctic krill parameters used in the first set of sensitivity analyses.

519 The third set of simulations investigated the effects of the assumed biomass of fish,  
520 seabirds, and marine mammals on the estimates of adult Antarctic krill biomass that is  
521 consumed in the sWAP baseline model. The estimated proportion of the production of a prey  
522 species that is consumed (i.e. the  $EE$  of the prey) depends on the assumed prey parameters  
523 and on the assumed consumption rates of its predators. The predator consumption rates, in  
524 turn, are related to the assumed predator biomass, which for many of the trophic groups  
525 included in the sWAP food web model is poorly constrained (see Hill et al., 2005; Laws,  
526 1977; Woehler and Croxall, 1997; Southwell et al., 2008). Therefore, the biomass of the  
527 trophic groups that consume adult Antarctic krill was doubled with respect to the baseline  
528 simulation and the resulting demand on Antarctic krill production (i.e. the adult Antarctic

529 krill *EE*) was calculated. These simulations also compared adult Antarctic krill biomass  
530 derived from net-tows and acoustic estimates.

#### 531 *2.4.2 Environmental change scenarios*

532 Five environmental change scenarios were implemented with the bottom-up model  
533 (Eq. 4) to simulate the effects of altered plankton assemblage composition on the production  
534 of vertebrate predators in the sWAP food web model. The scenarios were selected based on  
535 observed or expected changes in the relative abundance of phytoplankton and zooplankton  
536 groups that may result from changes in hydrographic conditions and/or sea ice extent changes  
537 linked to the warming trend in the western Antarctic Peninsula. The simulations were done  
538 by altering the entries in the production matrix,  $A_{cp}$  (Table A.3), and redirecting 50% of a  
539 prey source from one consumer group to another. All simulations were implemented with  
540 constant primary production and did not allow for prey switching. The effects of the different  
541 perturbations were expressed in terms of the fractional change in productivity relative to the  
542 productivity in the bottom-up model derived from the baseline sWAP mass balance model.

543 The first scenario simulated a 50% decrease in the contribution of large phytoplankton  
544 to total primary production with a compensatory increase in the production of the small  
545 phytoplankton group. This scenario was based on the observation that in the region to the  
546 north of the sWAP study area, in the past 30 years, the phytoplankton composition has  
547 undergone a shift to smaller flagellates (Montes-Hugo et al., 2009). A similar shift from large  
548 diatoms to smaller cryptophytes has been observed in near shore coastal waters influenced by  
549 glacial meltwater (Moline et al., 2004).

550 The second scenario tested the consequences of reducing the secondary production of  
551 large zooplankton (mesozooplankton, macrozooplankton, larval and adult Antarctic krill,  
552 other euphausiids, and salps) by 50% and compensating with an equivalent increase in  
553 microzooplankton secondary production. This scenario was based on the prediction that

554 warmer sea water temperature will increase the metabolic rates of zooplankton groups. Since  
555 the microzooplankton have faster turnover rates than the other zooplankton groups, their  
556 biomass is expected to become predominant (Russell, 2008). Scenarios 1 and 2 were  
557 implemented with the bottom-up model derived from the baseline sWAP mass balance model  
558 and from a bottom-up model derived from a mass balance model in which the diet of the  
559 adult Antarctic krill group included a larger fraction of microzooplankton (45%, same  
560 Antarctic krill diet used by Hill et al., 2012).

561         The third and fourth scenarios tested the effects of a 50% reduction in adult Antarctic  
562 krill production that was compensated for by equal increases in mesozooplankton and salp  
563 production. These scenarios were based on observed correlations between reduced sea ice  
564 extent and reduced Antarctic krill recruitment (Fraser and Hofmann, 2003) and increased salp  
565 abundance (Loeb et al., 1997), and on observations of increased occurrences of salps in some  
566 regions of the Antarctic (Atkinson et al., 2004). Antarctic krill larvae and juveniles use sea  
567 ice as an overwintering habitat (Daly, 1990; Daly and Macaulay, 1991) and both larval and  
568 juvenile Antarctic krill feed on the under-ice microbial communities, especially in late winter  
569 and spring (Hamner et al., 1983; Daly and Macaulay, 1988; Marschall, 1988). Reductions in  
570 sea ice will, therefore, affect krill recruitment.

571         The final scenario considered a 50% reduction in the mesozooplankton production  
572 that was compensated by the same increase in salp production. This scenario determined if a  
573 reduction in the mesozooplankton group had the same effect as a reduction in the adult  
574 Antarctic krill group.

### 575 **3. Results**

#### 576 *3.1 Food web structure and carbon flows in the baseline sWAP simulation*

##### 577 *3.1.1 Trophic levels and trophic pathways*

578         The structure of the modeled food web is determined by the specified diet

579 composition and annual consumption rates for each model group (Tables 1, 2). The primary  
580 producers and the detrital groups have trophic level 1, while the trophic level of the consumer  
581 groups is calculated according to the percentage of autotrophic and heterotrophic material in  
582 their diet (Table 3). The calculated trophic level for the microzooplankton and benthic  
583 invertebrate groups is 2, given the assumptions made about their diet. The trophic level of the  
584 other seven zooplankton groups ranges between 2 and 3, while the trophic level of the  
585 vertebrate predators ranges between 3 and 5. Crabeater seals and minke whales have the  
586 lowest trophic level among the top predators because their assumed diet is composed mainly  
587 of adult Antarctic krill; the flying seabirds and Weddell seal groups have a higher trophic  
588 level because their diets consist primarily of pelagic and benthic fish.

589 As a result of the diet composition, the sWAP food web model has two principal  
590 trophic pathways for energy transfer from primary producers to air-breathing predators. The  
591 first trophic pathway goes from primary producers to Adélie penguins, crabeater seals and  
592 baleen whales. The diet of these predators has a large contribution (52 - 94%) from Antarctic  
593 krill (Table 2) and thus, despite their large body size, they have a relatively low trophic level  
594 (between 3 and 4), which is similar to the trophic level of fish and cephalopods (Table 3).  
595 The second trophic pathway goes from primary producers to the flying seabirds and Weddell  
596 seals groups. The diets of these two groups are composed principally of fish and cephalopods  
597 (Table 2), leading to a trophic level between 4 and 5 (Table 3).

### 598 *3.1.2 Consumption by food web components and carbon flows*

599 The direct estimate of annual primary production required to sustain the food web  
600 with the sWAP baseline simulations is  $191 \text{ g C m}^{-2} \text{ y}^{-1}$  (Fig. 2). The majority of this ( $132 \text{ g C}$   
601  $\text{m}^{-2} \text{ y}^{-1}$ , 69%) is consumed by microzooplankton; the other seven zooplankton groups  
602 consume the remainder. Small phytoplankton production contributes 71% of the consumption  
603 by microzooplankton (Fig. 2), while large phytoplankton production is the largest



604 contribution (76%) to the primary production that is grazed by the other zooplankton groups  
605 (Fig. 2).

606 In the sWAP baseline simulation a relatively small amount of microzooplankton  
607 production ( $EE = 0.12$ ) is consumed by other zooplankton groups (Fig. 2, Table 3).  
608 Mesozooplankton and macrozooplankton production contributes 32% and 15% of the  
609 consumption by fish and cephalopods, respectively, but is a minimal contribution to the  
610 consumption by seabirds and marine mammals (Fig. 2). Antarctic krill production contributes  
611 46% of consumption by fish and cephalopods and 96.3% of consumption by seabirds and  
612 marine mammals. Only small fractions of macrozooplankton ( $EE = 0.27$ ), benthic  
613 invertebrates ( $EE = 0.18$ ) and benthic fish ( $EE = 0.036$ ) production are consumed by seabirds  
614 and marine mammals (Fig. 2). Salps and ctenophores are not consumed by fish and  
615 cephalopods, only infrequently by seabirds (Ainley et al., 1992), and not by marine mammals  
616 (Fig. 2).

617 Consumption of zooplankton by fish and cephalopods is 36 times higher than  
618 consumption by seabirds and marine mammals ( $3.6 \text{ g C m}^{-1} \text{ y}^{-1}$  and  $0.1 \text{ g C m}^{-2} \text{ y}^{-1}$ ,  
619 respectively). Seabirds and marine mammals also consume fish and cephalopods ( $0.02 \text{ g C m}^{-2}$   
620  $\text{y}^{-1}$ ), which represent 20% of their total consumption (Fig. 2).

621 Microzooplankton and mesozooplankton consume  $155 \text{ g C m}^{-2} \text{ y}^{-1}$  and  $58 \text{ g C m}^{-2} \text{ y}^{-1}$ ,  
622 respectively (Table 3), and account for 89% of the annual carbon consumption by secondary  
623 producers. Most of this carbon is provided by primary production (86%) with the remaining  
624 14% coming from detritus. Microzooplankton are the principal grazers of both small (87% of  
625 total consumption) and large phytoplankton (45% of total consumption) production.  
626 Mesozooplankton are the second most important grazers of large phytoplankton production  
627 (45%, Fig. 3). Consumption of primary and secondary production by other zooplankton  
628 groups is 1 to 2 orders of magnitude smaller than that of microzooplankton and

629 mesozooplankton (Table 3). Adult Antarctic krill consume 88% less primary and secondary  
630 production than do mesozooplankton (Fig. 3).

631 Microzooplankton and mesozooplankton are the most consumed diet items by other  
632 zooplankton groups, with 78% of microzooplankton consumed by mesozooplankton and 59%  
633 of mesozooplankton consumed by macrozooplankton (Fig. 4a). The consumption of adult  
634 Antarctic krill by fish and cephalopods is larger than the consumption of mesozooplankton  
635 (86% and 13% respectively; Fig. 4b).

636 The biomass and consumption rates of seabirds and marine mammals (Table 3) are 16  
637 and 31 times, respectively, lower than the biomass of fish and cephalopods (Table 3). Among  
638 seabirds and marine mammals, the crabeater seal has the largest biomass (65% of the total)  
639 and the highest annual consumption rate (55% of the total). Despite differences in diets  
640 (Table 2), the air-breathing predators collectively consume more adult Antarctic krill ( $0.11 \text{ g}$   
641  $\text{C m}^{-2} \text{ y}^{-1}$ ) than fish and cephalopods ( $0.02 \text{ g C m}^{-2} \text{ y}^{-1}$ ) or other zooplankton groups (Fig. 5).  
642 Consumption of adult Antarctic krill by fish and cephalopods (Fig. 4b) is 14 times higher  
643 than by seabirds and marine mammals (Fig. 4c).

644 Only 0.06% of the primary production reaches the air-breathing predators (seabirds  
645 and marine mammals) (Fig. 6). Overall, Adélie penguins, crabeater seals and baleen whales  
646 receive 0.055% of the annual primary production, 92% of which is provided by consumption  
647 of Antarctic krill (Fig. 6). The portion of primary production that supports flying seabirds and  
648 Weddell seals is 10 times smaller (0.005%), and a large part of it is obtained from  
649 consumption of fish and cephalopods (Fig. 6).

## 650 **3.2 Sensitivity analyses**

### 651 *3.2.1 Changes in Antarctic krill biomass and estimates of primary production*

652 The primary production required for consumption by the food web groups was 187 -  
653  $207 \text{ g C m}^{-2} \text{ y}^{-1}$ , depending on adult Antarctic krill biomass, diet and *P/B* ratio (simulations 1-

654 6, Table 4). Acoustically-derived estimates of euphausiid biomass (assumed to be primarily  
655 Antarctic krill, Lascara et al., 1999) are about double that of net-derived biomass estimates  
656 (Table 1). Supporting the higher biomass estimate required an increase between 3 and 10% in  
657 annual primary production for a 100% herbivorous diet and a 100% carnivorous krill diet,  
658 respectively, relative to the primary production estimate from the baseline simulation (Table  
659 4). The annual primary production required for other simulations that use a herbivorous diet  
660 for adult Antarctic krill is on average 31% lower than that required for a carnivorous diet  
661 (Table 4).

### 662 *3.2.2 Changes in gross growth efficiency values and estimates of primary production*

663 The annual primary production estimates using the gross growth efficiency values  
664 from Banse (1995) were similar to the estimates obtained from the gross growth efficiency  
665 used in the baseline simulation (Table 4, Fig. 7). The gross growth efficiencies used by  
666 Priddle et al. (1998) are higher than those used in the baseline simulation because of the  
667 assumed higher rates of respiration and feces production (Table A.2). As a result, the annual  
668 primary production estimates obtained using the values of Priddle et al. (1998) are on average  
669 1.7 times larger than that obtained with the baseline simulation (Fig. 7). The annual primary  
670 production estimates obtained with the gross growth efficiency values derived from daily  
671 feeding rates are higher than all other estimates (Table 4, Fig. 7).

### 672 *3.2.2 Predator biomass and fate of Antarctic krill production*

673 In the baseline simulation, annual production of adult Antarctic krill estimated from  
674 net-derived values of biomass (Table 3) is 9% lower than the estimated consumption of adult  
675 Antarctic krill by its predators (Table 5). Conversely, annual production of adult Antarctic  
676 krill obtained using the acoustically-derived biomass results in a 46% surplus in krill  
677 production (Table 5), which is potentially unconsumed or available for export to other areas.  
678 The percentage of surplus adult Antarctic krill production decreased in response to increases

679 in the biomass of cephalopods, off-shelf and on-shelf pelagic fish, and benthic fish groups.  
680 Doubling the biomass of the benthic fish resulted in the largest decrease in surplus krill  
681 production (Table 5). Doubling the biomass of these four groups simultaneously resulted in a  
682 small deficit (-1%) in adult Antarctic krill production. Doubling the biomass of all seabird  
683 and marine mammal groups reduced the krill surplus production by an amount equivalent to  
684 that obtained by doubling the biomass of the off-shelf pelagic fish group alone (Table 5).  
685 Doubling the biomass of all krill predator groups produced a 5% deficit in adult Antarctic  
686 krill production.

### 687 *3.3 Environmental change scenarios*

688 The 50% reduction in the contribution of the large phytoplankton group (compensated  
689 by an increase in the small phytoplankton group) to total primary production (scenario 1)  
690 resulted in a nearly uniform decrease in the production of fish, cephalopods, seabirds and  
691 marine mammals for both the adult Antarctic krill diet in the baseline sWAP simulation and  
692 the adult Antarctic krill diet that included a larger percentage of microzooplankton (Figs.  
693 8a,b). A similar uniform reduction in all predator groups' production occurred for the scenario  
694 in which 50% of the primary production consumed by the large zooplankton groups was  
695 redirected to the microzooplankton (scenario 2, Figs. 8c,d). The benthic invertebrates group  
696 was affected indirectly via changes in the benthic detritus group (Fig. 2).

697 Redirection of primary production from the adult Antarctic krill to the  
698 mesozooplankton group (scenario 3) or to the salps group (scenario 4) also resulted in  
699 decreased carbon flow to upper trophic levels, but the response was smaller than in the  
700 previous scenarios (Figs. 8e,f). In both scenarios, the largest impacts were on predators with  
701 diets consisting primarily of adult Antarctic krill, such as crabeater seals. However, a  
702 redirection of adult Antarctic krill consumption to salps resulted in an increase in the  
703 production of the benthic invertebrate group, due to a larger flux to the benthic detritus group

704 via sinking fecal material and dead organisms (Table 1).

705         Redirection of primary production from the mesozooplankton group to the salps  
706 group (scenario 5), but keeping the amount of primary production to the adult Antarctic krill  
707 group the same, had little effect on upper trophic level production (Fig. 8g). The linkage  
708 between the mesozooplankton group and upper trophic level predators is weaker than the link  
709 between adult Antarctic krill and upper trophic level predators (Fig. 2). Salps are not  
710 important components of the diet of fish, cephalopods, seabirds, and marine mammals. Thus,  
711 the only consequence of an increase in salps production was an increase in the benthic  
712 invertebrate production through increases in the benthic detritus group as in scenario 4 (Table  
713 1).

#### 714 **4. Discussion**

715         The mass balance model developed for the sWAP provided quantitative estimates of  
716 energy flows in the food web. This model provides a framework for comparing the sWAP  
717 food web with other Southern Ocean marine ecosystems, evaluating the effects of data  
718 uncertainty, and for making inferences about possible changes in the sWAP food web that  
719 might arise in response to environmental change.

##### 720 *4.1 Southwestern Antarctic Peninsula food web structure*

721         Early studies on the functioning of Southern Ocean marine ecosystems showed that  
722 only a small fraction of primary production is converted to biomass of upper trophic level  
723 predators (Hempel, 1985; Hill et al., 2006). Estimates of energy flow from the sWAP food  
724 web model are consistent with this observation, with only a small fraction of primary  
725 production passed to seabirds and marine mammals and the majority of energy remaining as  
726 unconsumed production at the lower trophic levels. Microzooplankton and mesozooplankton  
727 consume the majority of primary production but only a small fraction of their secondary  
728 production is consumed and transferred to higher trophic levels. Similarly, in a Ross Sea food

729 web model, microzooplankton consumed about 90% of water column primary production  
730 (Pinkerton et al., 2010). A low *EE* value for groups with high biomass and low trophic level  
731 (e.g., the micro, meso and macrozooplankton groups in the sWAP model) could indicate that  
732 the modeled ecosystem is far from its carrying capacity. Mesozooplankton and  
733 macrozooplankton groups also had high biomass but low *EE* values in a model for the South  
734 Georgia food web (Hill et al., 2012).

735         In the sWAP region mesozooplankton can account for the majority of the herbivorous  
736 grazer biomass (not considering the microzooplankton) at various times and locations  
737 (Ashjian et al., 2004; Marrari et al., 2011). The sWAP mass balance model shows that the  
738 mean annual production by the mesozooplankton (and fish groups) is potentially sufficient to  
739 replace the estimated consumption of adult Antarctic krill by its predators. However, the  
740 spatial distribution of food web groups and timing of occurrence in peaks of primary and  
741 secondary production may alter this result.

742         Consumption of primary and secondary production by the adult Antarctic krill in the  
743 sWAP model is small in comparison to the other zooplankton groups. However, most of the  
744 energy flow to higher trophic levels is through adult Antarctic krill, which therefore exert a  
745 bottom-up control on the most abundant seabirds and marine mammals. The model-derived  
746 estimates of the consumption of Antarctic krill production by pelagic fish, benthic fish and  
747 cephalopods indicate the potential importance of these little studied species/groups, similar to  
748 the results of other modeling studies of Antarctic food webs (Pinkerton et al., 2010; Hill et  
749 al., 2012). Antarctic krill control production of upper trophic level predators at South Georgia  
750 (Hill et al., 2012) and in the open ocean regions of the Southern Ocean (Smetacek and Nicol,  
751 2005). In the Ross Sea shelf ecosystem, crystal krill and Antarctic silverfish provide the  
752 transfer of energy from primary producers to top predators (Pinkerton et al. 2010). The  
753 structure of these Southern Ocean food webs is similar to the ‘wasp-waist’ ecosystem

754 structure that has been hypothesized for marine ecosystems characterized by low taxonomic  
755 diversity in the mid-trophic levels where few species of small planktivorous fish control the  
756 transfer of energy to higher trophic levels (Rice, 1995; Bakun, 2006). As in the classic wasp-  
757 waist ecosystem structure, the dependence on only one or two species at the intermediate  
758 trophic levels, makes the sWAP food web and the other Southern Ocean food webs  
759 vulnerable to changes in the biomass of these species.

#### 760 *4.2 Implications of model assumptions and data uncertainty*

761 A challenge for food web models is assessing the effect of uncertainty in the data on  
762 the representation and parameterization of ecological processes. For models with many  
763 potential sources of uncertainty, sensitivity analyses are typically done in terms of key  
764 parameters or processes. For this study, parameters and processes that affect biomass and  
765 production of the target species, Antarctic krill, were the focus of the sensitivity analyses.  
766 This provides a tractable assessment of model sensitivity, allows identification of processes  
767 that require further study, and highlights data needs for model development and evaluation  
768 (de Young et al., 2004).

769 Some comparisons between model results and observational data can be made that  
770 allow evaluations of the sWAP food web model. Primary production places a system-wide  
771 constraint on the sWAP food web and hence provides an indirect evaluation of the values  
772 chosen for model parameters. Primary production estimates have been made for the western  
773 Antarctic Peninsula region for almost 50 years and in all seasons (see Table 2 in Smith et al.,  
774 1996; Prézelin et al., 2004; Ducklow et al., 2007) and thus provide a consistent metric for  
775 assessing the sWAP food web model. The estimates of annual primary production derived  
776 from the sWAP model ( $187\text{-}207 \text{ g C m}^{-2} \text{ y}^{-1}$ ) fall within the range of observed values of  
777 primary production measured on the northern part of the western Antarctic Peninsula in  
778 summer ( $47\text{-}351 \text{ g C m}^{-2}$  from October to March/April; Ducklow et al., 2007). In addition,

779 Weston et al. (2013) reported a mean summer primary productivity value of  $239 \text{ g C m}^{-2} \text{ y}^{-1}$   
780 for the northern Marguerite Bay for 2005 to 2007. The annual average obtained from the food  
781 web model ( $191 \text{ g C m}^{-2} \text{ y}^{-1}$ ) is about 80% lower than the observed mean value for the  
782 northern Marguerite Bay (Weston et al., 2013) and 43% lower than the maximum observed  
783 value ( $351 \text{ g C m}^{-2} \text{ y}^{-1}$ ; Ducklow et al., 2007) in the northern part of the west Antarctic  
784 Peninsula shelf. However, it is about 10% higher than the average observed value ( $177 \text{ g C}$   
785  $\text{m}^{-2} \text{ y}^{-1}$ ) from the northern part of the west Antarctic Peninsula shelf. Differences between the  
786 observed values and the model-estimated values may be explained by the different time  
787 periods included in the estimates. For example, the sWAP food web model estimate is based  
788 on annual consumption needs; whereas, the observed primary production values are primarily  
789 from the summer. Differences in observed and simulated primary production estimates may  
790 also arise because the spatial variability in actual primary production and passive sinking of  
791 phytoplankton, which can be important at particular times and locations on the western  
792 Antarctic Peninsula shelf (Smith et al., 2006), are not included in the model.

793 The magnitude of the reconstructed flows through the food web results from the  
794 choices made for parameter values such as gross growth efficiency and  $P/B$  ratios. The gross  
795 growth efficiencies chosen for the sWAP food web model produced annual primary  
796 production estimates that were similar to those obtained using lower values of gross growth  
797 efficiency from other Southern Ocean food web modeling studies (e.g. Banse, 1995; Priddle  
798 et al., 1998), but all were within the range of observed values. The gross growth efficiency  
799 values derived from daily feeding rates produced primary production estimates that exceeded  
800 measured values, which highlights the need for consistent measurements for food web  
801 processes.

802 The  $EE$  values of the zooplankton groups calculated with the sWAP model are poorly  
803 constrained because of large uncertainties in the biomass/consumption rates of zooplankton



804 predators and because zooplankton migration inside/outside the study area was not taken into  
805 account. Data are not usually available on non-predation mortality rates in natural  
806 populations and these parameters are usually estimated by models. The low *EE* values of the  
807 zooplankton groups indicate of the uncertainty of the data for these important food web  
808 groups. This uncertainty affects the accuracy of the reconstructed energy flows in the sWAP  
809 food web. Low *EE* values for the zooplankton groups were also calculated in the mass  
810 balance model for the South Georgia shelf (Hill et al., 2012), highlighting a similar  
811 uncertainty in the magnitude of these trophic flows. The sensitivity of the food web models to  
812 the choices made for the zooplankton groups highlights the need for process studies to  
813 investigate the space and time variability of their population dynamics, predator-prey  
814 interactions, and to assess their ecological roles in energy flows. Non-predation mortality is  
815 also potentially an important input to the detrital pools. The use of the food web model to  
816 estimate direct demand for primary production results in underestimates of flows via the  
817 detrital pools, which is potentially important for coupling the benthic and pelagic systems of  
818 the west Antarctic Peninsula continental shelf (Smith et al., 2012).

819         Similarly, the food web model results are sensitive to biomass estimates. The net-  
820 based estimates of Antarctic krill biomass were insufficient to support the consumption needs  
821 of top predators; whereas, the acoustically-derived biomass estimates provided a surplus of  
822 Antarctic krill after the consumption demands by predators were satisfied. The accurate  
823 estimation of krill biomass depends on estimates of density and on correct specification of the  
824 Antarctic krill spatial range (Nicol et al., 2000). The krill densities used to convert acoustic  
825 backscatter measurements to biomass were based on estimates made specifically for the  
826 region included in the sWAP food web model and an analysis of the error introduced by  
827 uncertainties showed that the values were within the range of other reported biomass values  
828 (Lawson et al., 2008b). These biomass estimates average over krill aggregations because

829 Antarctic krill were assumed to be present throughout the model region. Acoustic surveys in  
830 the region around Marguerite Bay showed that Antarctic krill biomass tended to be  
831 concentrated along the shelf break and the inner shelf regions (consistent with Atkinson et al.,  
832 2008), and that a few large swarms accounted for a disproportionate amount of the total  
833 biomass (Lascara et al., 1999; Lawson et al., 2008a). Therefore, the effective spatial range for  
834 Antarctic krill is likely less than the model region. Accurate biomass estimates, especially for  
835 species or groups that exert a primary control on system productivity, are a priority for food  
836 web models such as the one used in this study.

837 The type of uncertainty associated with the sWAP model is common to other  
838 ECOPATH-type implementations (e.g. Pauly et al., 2000; Fulton, 2010; Steele and Ruzicka,  
839 2011). However, the sWAP model does allow understanding of the direction of change that  
840 might occur in the food web for changes in specified model parameters (as in the case of the  
841 sensitivity analyses) and investigating the indirect effects in the food web (such as in the  
842 scenario simulations). The simulation results reveal something about the current processes in  
843 the ecosystem and about processes that might occur with changes in the relative abundance of  
844 food web components.

#### 845 *4.3 Possible future changes in food web structure – model implications*

846 The western Antarctic Peninsula region is undergoing rapid climate change, the  
847 manifestations of which are warming ocean temperatures (Meredith and King, 2005),  
848 reduction in sea ice extent (Smith and Stammerjohn, 2001; Stammerjohn et al., 2008), and  
849 shortening of sea ice duration (Stammerjohn et al., 2008). The relative abundance of salps  
850 and Antarctic krill has been correlated with winter sea ice extent, with salps replacing krill  
851 during times of reduced sea ice (Loeb et al., 1997). The increase in the abundance of  
852 chinstrap penguins (*Pygoscelis antarcticus*) relative to Adélie penguins along the northern  
853 portion of the western Antarctic Peninsula has been linked to changes in the availability of

854 their primary prey species, Antarctic krill and Antarctic silverfish (Schofield et al., 2010;  
855 Trivelpiece et al., 2011). However, Lynch et al. (2012) show that the changes are more  
856 complex and in fact Adélie penguin numbers have been growing in the sWAP, seemingly in  
857 response to loosening of the pack ice and increased availability of suitable nesting habitat as  
858 glaciers retreat, a prediction of Ainley et al. (2010).

859         The sWAP food web model provides insights into the potential consequences of  
860 modified abundances of particular species/groups and changes in consumption. The  
861 simulations showed that a reduction in Antarctic krill biomass reduces the overall energy flux  
862 to top predators. A potentially significant change suggested by the sWAP food web  
863 simulations comes from a reduction in the average cell size of phytoplankton, which reduces  
864 Antarctic krill production and hence production of the top trophic levels. Although the diet of  
865 top predators such as Adélie penguins and crabeater seals potentially comprises important  
866 contributions of alternate prey like the Antarctic silverfish (Volkman et al. 1980; Lowry et  
867 al., 1987; Klages and Cockcroft, 1990; Chapman et al. 2010; 2011), the sWAP model  
868 suggests that there may be limited scope for Antarctic silverfish to support the consumption  
869 of these top predators. In fact, a significant part of the diet of the fish groups is also composed  
870 of Antarctic krill, and if Antarctic krill is reduced or disappears, maintaining or increasing the  
871 biomass of the fish groups will require an increase in the availability and biomass of other  
872 zooplankton groups. In addition, the declining trend in Antarctic silverfish abundance  
873 observed in the northern portions of the western Antarctic Peninsula (Ducklow et al., 2007;  
874 Schofield et al., 2010) may occur in the future also in the sWAP region if sea ice continues to  
875 decrease.

876         In simulations that reduced the production of Antarctic krill by redirecting primary  
877 production to microzooplankton and salps (which are not consumed by top predators) a  
878 proportionate decrease in the production of fish, cephalopods, seabirds and marine mammals

879 occurred, indicating that this trophic pathway is not effective in channeling energy to upper  
880 trophic levels. Thus, a reduction in Antarctic krill biomass and/or changes in the relative  
881 abundance of phytoplankton may result in a reorganization of the sWAP food web that favors  
882 top predators that can take advantage of open water, such as chinstrap penguins (Trivelpiece  
883 et al., 2011) and southern elephant seals (*Mirounga leonine*) (Costa et al., 2010).

## 884 **5. Summary and Conclusions**

885 The mass balance model developed for the sWAP region represented general patterns  
886 of the overall food web structure and provided a basis for qualitative (Murphy et al., 2013)  
887 and quantitative comparisons with other Southern Ocean ecosystems. The strength of this  
888 modeling approach is that it quantified energy flow pathways through the food web while  
889 highlighting uncertainties in data, which are potentially useful for indicating where  
890 measurements are needed. The modeling approach also allowed investigation of possible  
891 changes in the structure of the sWAP food web that might arise in response to changes in the  
892 relative abundance of plankton components that may occur as a result of climate-induced  
893 changes.

894 The simulated sWAP food web sustains the top predator biomass primarily by  
895 consumption of a single prey species, Antarctic krill. Trophic pathways through alternative  
896 zooplankton groups and through fish provide a significantly smaller contribution to the  
897 production of seabirds and marine mammals. The dependence of the upper trophic level  
898 predators on a single prey makes the current sWAP food web vulnerable to changes in this  
899 food source. Antarctic krill are long-lived (4-7 years, Ikeda and Thomas, 1987) and, as a  
900 result, respond to environmental cycles with scales beyond seasonal (Smetacek and Nicol,  
901 2005). The cumulative effects of longer-term environmental changes, particularly decreasing  
902 sea ice, exert controls on the distribution and availability of this important prey and predator  
903 in the sWAP food web. For this system, the additive effects of bottom-up resource control

904 through changes in phytoplankton assemblages (Antarctic krill prey) and the top down effects  
905 of consumers of Antarctic krill may amplify the effects of climate change on the sWAP food  
906 web. Thus, end-to-end models that include food web interactions, biogeochemical cycling,  
907 and environmental controls are the next step in developing scenarios for projections of the  
908 future state of the sWAP ecosystem.

909

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919

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1424 **Figure Legends**

1425 **Figure 1.** Map of the Antarctic Peninsula (A) showing the SO GLOBEC study region and the  
1426 partitioning of this region used for calculating inputs to the food web model (B, heavy black  
1427 lines). Regions of enhanced concentrations of pelagic fish (green), seabirds (light blue),  
1428 crabeater seals (purple) and baleen whales (yellow) that were observed during the SO  
1429 GLOBEC survey cruises (Costa et al., 2007) are indicated. The location of Adélie penguin  
1430 colonies (Ainley, 2000) is also indicated (triangles). Geographic features are identified as:  
1431 Adelaide Island-AdI, Alexander Island-AxI, Anvers Island-AnI, Elephant Island-EI, George  
1432 VI Ice Shelf-GVIIS, Marguerite Bay-MB, Marguerite Trough-MT, and Wilkins Ice Shelf-  
1433 WIS. Bathymetric contours are in meters.

1434  
1435 **Figure 2.** Summary of the energy flows in the southwestern Antarctic Peninsula (sWAP)  
1436 food web model. The 24 food web model groups are grouped into 7 compartments that  
1437 correspond to primary producers, detritus, zooplankton, microzooplankton, benthic  
1438 invertebrates, fish and cephalopods (intermediate predators), seabirds and marine mammals  
1439 (top predators). Arrows indicate the transfer of energy between compartments ( $\text{g C m}^{-2} \text{y}^{-1}$ );  
1440 the percentage contribution of model groups to these energy fluxes is indicated (bottom part  
1441 of each box). For each model group, the overall proportion of annual production consumed in  
1442 the food web (ecotrophic efficiency, first number, upper part of box) and the fraction of this  
1443 proportion that is consumed outside the compartment (number in parentheses, upper part of  
1444 box) is given. The species/groups are defined in Table 1.

1445  
1446 **Figure 3.** Annual consumption ( $\text{g C m}^{-2} \text{y}^{-1}$ ) of large and small phytoplankton primary  
1447 production by zooplankton groups obtained from the southwestern Antarctic Peninsula  
1448 (sWAP) mass balance food web model. Phytoplankton groups are indicated as: small  
1449 phytoplankton-SP and large phytoplankton-LP. Zooplankton groups are indicated as:

1450 mesozooplankton-Me; larval Antarctic krill-LAK; adult Antarctic krill-AAK; other  
1451 euphasiids-OE.

1452  
1453 **Figure 4.** Annual consumption ( $\text{g C m}^{-2}\text{y}^{-1}$ ) of zooplankton and benthic invertebrates by A)  
1454 zooplankton predators, B) intermediate predators and C) top predators calculated from the  
1455 sWAP food web model. The species/groups are defined in Table 1.

1456  
1457 **Figure 5.** Annual consumption ( $\text{g C m}^{-2}\text{y}^{-1}$ ) of zooplankton and intermediate predators by top  
1458 predators calculated from the southwestern Antarctic Peninsula (sWAP) food web model.  
1459 Zooplankton (Z) prey include herbivorous zooplankton, carnivorous zooplankton and other  
1460 euphasiids. Antarctic krill (AK) prey includes larvae and adults. Intermediate predators  
1461 (F&Ce) include cephalopods, off- and on-shelf pelagic fish, and benthic fish.

1462  
1463 **Figure 6.** Summary of the percent transfer of primary production between the pelagic  
1464 components of the sWAP food web model.

1465  
1466 **Figure 7.** Simulated estimates of primary production needed to support the southwestern  
1467 Antarctic Peninsula (sWAP) food web obtained using gross growth efficiency values; (1)  
1468 calculated from production and assimilation efficiencies given in Table 1, (2) given in Banse  
1469 (1995), (3) given in Priddle et al., (1989), and (4) derived from daily feeding rates (Table  
1470 A.4). The boxes represent the range of the primary production estimates obtained from all of  
1471 the simulations that used the indicated gross growth efficiencies. The median (horizontal line)  
1472 and 25 and 75 percentiles (lower and upper vertical lines) are shown. The average ( $177 \text{ g C}$   
1473  $\text{m}^{-2} \text{y}^{-1}$ , solid line) and minimum and maximum ( $47$  and  $351 \text{ g C m}^{-2} \text{y}^{-1}$ , dashed lines)  
1474 primary production values estimated from field observations made on the sWAP continental  
1475 shelf (Ducklow et al. 2007) are shown for comparison.

1476

1477 **Figure 8.** Change in productivity, estimated relative to the reference simulation, of the  
1478 southwestern Antarctic Peninsula (sWAP) higher trophic level components for A) a 50%  
1479 reduction in annual production of large phytoplankton; B) a re-direction of 50% of small and  
1480 large phytoplankton production from mesozooplankton, larval Antarctic krill, adult Antarctic  
1481 krill, other euphysiids and salps to microzooplankton; C) a redirection of 50% of large  
1482 phytoplankton production from adult Antarctic krill to mesozooplankton; D) a redirection of  
1483 50% of large phytoplankton production from adult Antarctic krill to salps; E) a redirection of  
1484 50% of small and large phytoplankton production from mesozooplankton to salps. The bars  
1485 (left to right) indicate changes in intermediate predators (cephalopods-Ce, off-shelf pelagic  
1486 fish-OfP, on-shelf pelagic fish-OnP, benthic fish-BF), benthic invertebrates-BI, and top  
1487 predators (Adélie penguin-AP, flying seabirds-FS, crabeater seals-CS, Weddell seals-WS,  
1488 minke whales-MW, humpback whales-HW).

1489

1490 **TABLES**

1491 **Table 1.** Biomass, production to biomass ratio ( $P/B$ ), assimilation efficiency ( $AE$ ), production  
 1492 efficiency ( $PE$ ) and the fractional contribution of fecal material and non-predation mortality  
 1493 to pelagic and benthic detritus used as input to the southwestern Antarctic Peninsula (sWAP)  
 1494 food web model. References for the sources used to obtain the  $P/B$  ratios are given in Table  
 1495 A.1. Biomass estimates obtained from the mass balance model are indicated by \* and detrital  
 1496 flows that were set to zero are indicated by \*\*.

1497

Trophic group	Symbol	Biomass (g C m <sup>-2</sup> )	P/B	AE	PE	Pelagic detritus	Benthic detritus
Small Phytoplankton	SP	*	75.00	1.00	1.00	**	**
Large Phytoplankton	LP	*	75.00	1.00	1.00	**	**
Ice Biota	IB	*	75.00	1.00	1.00	**	**
Microzooplankton	M	0.57	55.00	0.80	0.25	1.0	0.0
Mesozooplankton	Me	2.97	4.81	0.70	0.35	0.5	0.5
Macrozooplankton	Ma	0.79	2.50	0.80	0.35	0.5	0.5
Antarctic krill larvae	AKL	0.30	2.00	0.84	0.35	0.5	0.5
Antarctic krill adults	AAK	1.60	1.00	0.70	0.35	0.5	0.5
Other euphausiids	OE	0.30	1.50	0.70	0.35	0.5	0.5
Salps	S	0.01	3.00	0.70	0.35	0.0	1.0
Ctenophores	Ct	0.0003	3.00	0.80	0.35	0.0	1.0
Cephalopods	Ce	*	3.20	0.80	0.13	0.0	1.0
Off-shelf pelagic fish	Off-P	0.12	1.27	0.80	0.13	0.0	1.0
On-shelf pelagic fish	On-P	0.06	0.40	0.80	0.13	0.0	1.0
Benthic fish	BF	0.20	0.20	0.80	0.13	0.0	1.0
Benthic invertebrates	BI	2.00	0.44	0.58	0.35	0.0	1.0
Adélie penguin	AP	0.01	0.15	0.83	0.02	0.0	1.0
Flying seabirds	FS	0.0002	0.06	0.90	0.02	0.0	1.0
Crabeater seal	CS	0.03	0.06	0.85	0.02	0.0	1.0
Weddell seal	WS	0.0024	0.05	0.87	0.02	0.0	1.0
Minke whale	MW	0.01	0.05	0.93	0.02	0.0	1.0
Humpback whale	HW	0.0034	0.01	0.93	0.02	0.0	1.0
Pelagic detritus	PD	2.30	1.00	1.00	1.00	0.0	1.0
Benthic detritus	BD	4.70	1.00	1.00	1.00	0.0	1.0

1498

1499

1500 **Table 2.** Diet composition (%) specified for each trophic group included in the southwestern  
 1501 Antarctic Peninsula (sWAP) food web model. The values represent the fractional contribution  
 1502 of each producer group (rows) to the diet of the consumer group (columns). References for  
 1503 the percent diet composition used for each model group are given in Table A.1. The symbols  
 1504 used to identify the species/groups are defined in Table 1.

		Consumers																		
Producers		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<b>1</b>	SP	60	23	1	23	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0
<b>2</b>	LP	25	65	10	46	53	60	20	0	0	0	0	0	0	0	0	0	0	0	0
<b>3</b>	IB	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>4</b>	M	0	5	1	15	6	0	30	0	0	0	0	0	0	0	0	0	0	0	0
<b>5</b>	Me	0	0	72	0	24	24	5	88	0	41	28	5	0	0	2	0	0	0	5
<b>6</b>	Ma	0	0	0	0	0	0	0	0	9	18	12	5	0	0	0	0	0	0	0
<b>7</b>	AKL	0	0	2	0	0	0	5	12	0	7	5	0	0	0	0	0	0	0	0
<b>8</b>	AAK	0	0	2	0	0	0	0	0	37	27	50	15	0	52	10	94	0	94	70
<b>9</b>	OE	0	0	1	0	0	0	0	0	4	7	5	2	0	7	0	1	0	6	0
<b>10</b>	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>11</b>	Ct	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>12</b>	Ce	0	0	0	0	0	0	0	0	0	0	0	8	0	30	30	2	50	0	5
<b>13</b>	Off-P	0	0	0	0	0	0	0	0	25	0	0	10	0	8	32	1	18	0	10
<b>14</b>	On-P	0	0	0	0	0	0	0	0	25	0	0	15	0	3	20	2	16	0	10
<b>15</b>	BF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	16	0	0
<b>16</b>	BI	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0
<b>17</b>	AP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>18</b>	FS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>19</b>	CS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>20</b>	WS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>21</b>	MW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>22</b>	HW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>23</b>	PD	15	7	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<b>24</b>	BD	0	0	10	0	16	16	0	0	0	0	0	0	100	0	0	0	0	0	0

1505

1506

1507 **Table 3.** Biomass after the southwestern Antarctic Peninsula (sWAP) food web model was  
 1508 mass balanced (*B*), annual production (*P*), annual consumption (*Q*), trophic level (*TL*) and  
 1509 ecotrophic efficiency (*EE*) for each species/group. Annual consumption of the primary  
 1510 producer groups and annual production and consumption of pelagic and benthic detritus were  
 1511 estimated from the simulation (-).

Species/group	<b>B</b> (g C m <sup>-2</sup> )	<b>P</b> (g C m <sup>-2</sup> )	<b>Q</b> (g C m <sup>-2</sup> )	<b>TL</b>	<b>EE</b>
Small Phytoplankton	1.43	107.39	-	1.00	1.00
Large Phytoplankton	1.11	83.35	-	1.00	1.00
Ice Biota	0.003	0.185	-	1.00	1.00
Microzooplankton	0.57	31.13	155.65	2.00	0.12
Mesozooplankton	2.97	14.29	58.30	2.05	0.60
Macrozooplankton	0.79	1.98	7.06	2.85	0.27
Antarctic krill larvae	0.30	0.60	2.05	2.15	0.61
Antarctic krill adults	1.74	1.74	7.11	2.31	1.00
Other euphausiids	0.30	0.45	1.84	2.25	0.65
Salps	0.009	0.027	0.110	2.41	0.00
Ctenophores	0.024	0.071	0.252	3.06	1.00
Cephalopods	0.014	0.044	0.435	3.85	1.00
Off-shelf pelagic fish	0.12	0.15	1.53	3.29	1.00
On-shelf pelagic fish	0.43	0.17	1.73	3.29	1.00
Benthic fish	0.20	0.04	0.4	3.57	0.04
Benthic invertebrates	2.00	0.88	4.38	2.00	0.18
Adélie penguin	0.002	0.0003	0.0185	3.88	0.00
Flying seabirds	0.0002	0.00000	0.00067	4.35	0.00
Crabeater seal	0.032	0.0014	0.0720	3.37	0.00
Weddell seal	0.0024	0.0002	0.0086	4.61	0.00
Minke whale	0.009	0.0005	0.0242	3.31	0.00
Humpback whale	0.0034	0.0001	0.0073	3.57	0.00
Pelagic detritus	2.30	-	-	1.00	0.38
Benthic detritus	4.70	-	-	1.00	0.35

1512  
 1513



1514 **Table 4.** Total net primary production (PP) and total detrital inputs (pelagic and benthic  
1515 detritus) obtained from simulations that used gross growth efficiency (GGE) values from the  
1516 baseline food web model (sWAP), from Banse (1995) (B) and Priddle et al. (1998) (P), and  
1517 GGE values derived from daily feeding rates ( $Q/B$ ). The simulations also considered different  
1518 production biomass ratios ( $P/B$ ), biomass, and diet composition (H-herbivorous, including  
1519 100% large phytoplankton, C-carnivorous, including 100% mesozooplankton) for adult  
1520 Antarctic krill. The resulting ecotrophic efficiency ( $EE$ ) of the adult Antarctic krill group is  
1521 shown for each simulation.

1522

Simulation GGE	P/B	Biomass (g C m <sup>-2</sup> )	Diet	EE	PP (g C m <sup>-2</sup> y <sup>-1</sup> )	Detritus inputs (g C m <sup>-2</sup> y <sup>-1</sup> )
sWAP	1	1.6	H	1.100	194.3	94
sWAP	1	1.6	C	1.100	187.5	87
sWAP	1	3.2	H	0.545	200.2	96
sWAP	1	3.2	C	0.545	207.4	95
sWAP	2.4	1.6	H	0.454	190.1	93
sWAP	2.4	1.6	C	0.454	193.7	96
sWAP	2.4	3.2	H	0.227	200.2	102
sWAP	2.4	3.2	C	0.227	207.4	100
B	1	1.6	H	1.100	137.9	73
B	1	1.6	C	1.100	197.7	93
B	1	3.2	H	0.550	146.4	77
B	1	3.2	H	0.550	255.0	113
B	2.4	1.6	H	0.458	200.0	100
B	2.4	1.6	C	0.458	280.5	122
B	2.4	3.2	H	0.229	222.7	111
B	2.4	3.2	C	0.229	433.4	176
P	1	1.6	H	1.220	202.0	93
P	1	1.6	C	1.220	305.3	127
P	1	3.2	H	0.612	212.4	96
P	1	3.2	C	0.612	381.3	152
P	2.4	1.6	H	0.510	217.7	97
P	2.4	1.6	C	0.510	420.4	166
P	2.4	3.2	H	0.255	294.7	113
P	2.4	3.2	C	0.255	655.0	247
$Q/B$	1	1.6	H	1.586	341.2	106
$Q/B$	1	1.6	C	1.586	562.0	202
$Q/B$	1	3.2	H	0.793	361.7	113
$Q/B$	1	3.2	C	0.793	640.1	234

<i>Q/B</i>	2.4	1.6	H	0.661	312.3	99
<i>Q/B</i>	2.4	1.6	C	0.661	451.5	159
<i>Q/B</i>	2.4	3.2	H	0.033	361.7	118
<i>Q/B</i>	2.4	3.2	C	0.033	640.1	238

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1523

1524 **Table 5.** Summary of simulations used to assess the effects of the biomass of fish,  
 1525 cephalopods, seabirds and marine mammals on the amount of adult Antarctic krill production  
 1526 that is consumed in the sWAP food web. All simulations used an omnivorous diet (Table 2)  
 1527 and a *P/B* ratio of 1 for adult Antarctic krill. The net-derived annual adult Antarctic krill  
 1528 biomass (1.6 g C m<sup>-2</sup>) was used for the reference simulation; the annual acoustically-derived  
 1529 biomass (3.2 g C m<sup>-2</sup>) was used for all other simulations. The biomass of the indicated  
 1530 predator groups was doubled from the value used in the reference simulation (Table 1), the  
 1531 food web model was mass balanced, and the percent (%) surplus (+) or deficit (-) in adult  
 1532 Antarctic krill production were calculated as  $(1-EE)/100$ , where *EE* is the ecotrophic  
 1533 efficiency of adult Antarctic krill for a particular simulation.

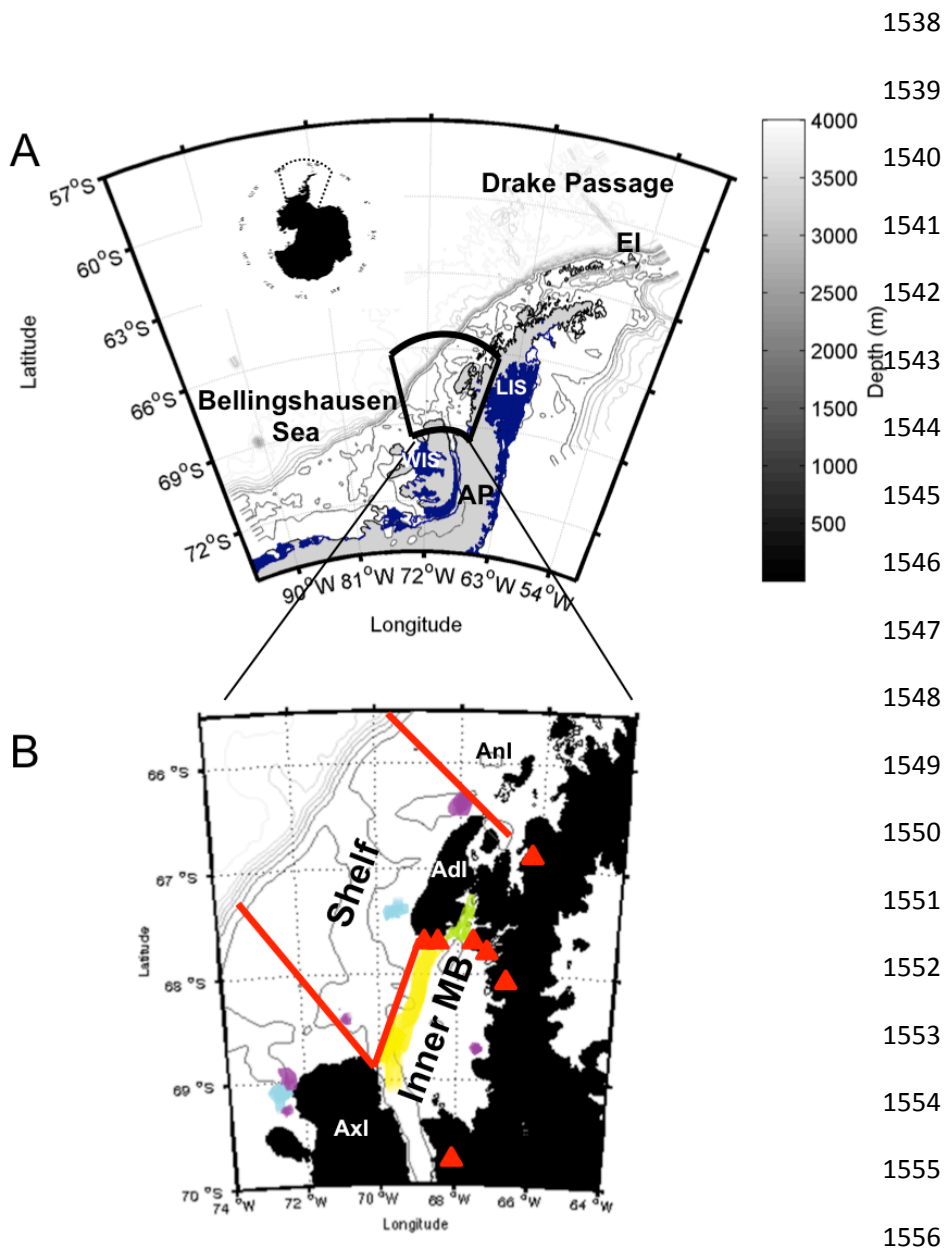
1534

<b>Biomass (g C m<sup>-2</sup>)</b>	<b>Predator group with doubled biomass</b>	<b>Surplus/deficit production (%)</b>
1.6	Initial values in Table 1	-9
3.2	Initial values in Table 1	+46
3.2	Cephalopods	+14
3.2	Off-shelf pelagic fish	+33
3.2	On-shelf pelagic fish	+19
3.2	Benthic fish	+8
3.2	All fish and cephalopods	-1
3.2	All seabirds and marine mammals	+33
3.2	All fish, cephalopods, seabirds and marine mammals	-5

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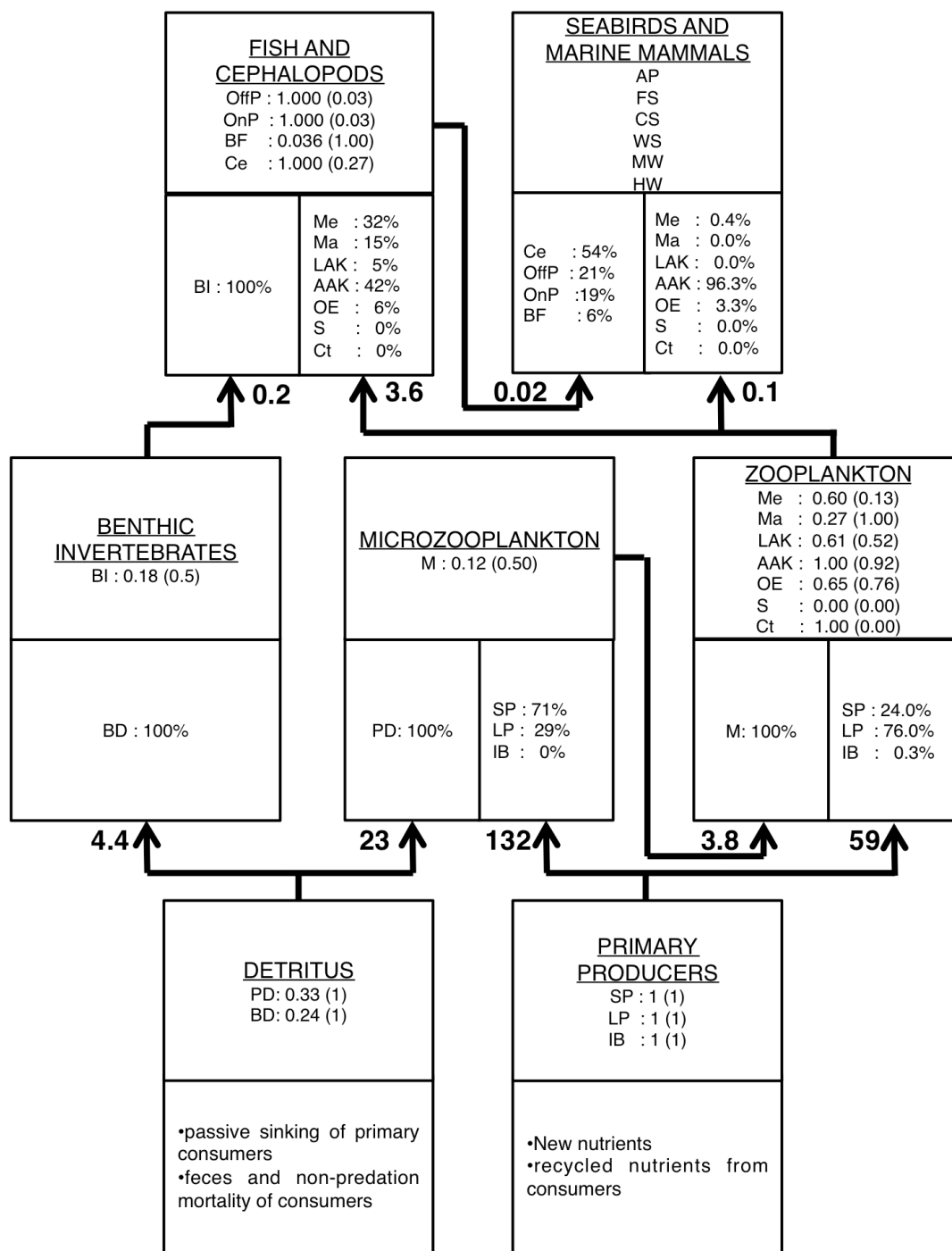
1556

1557 **Figure 1**

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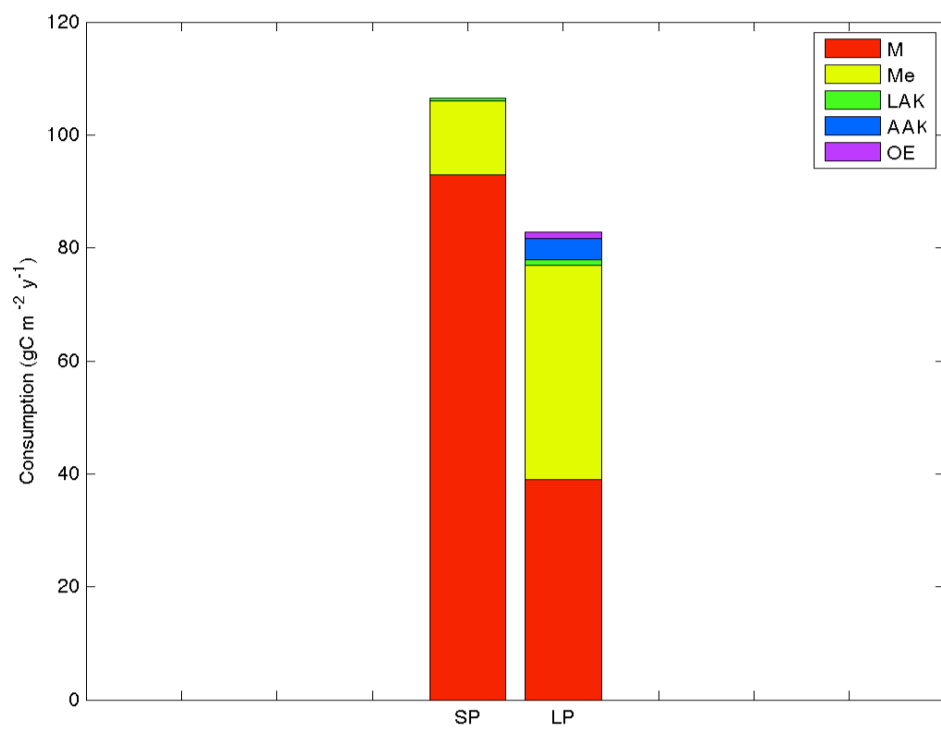


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1562

1563 **Figure 2.**

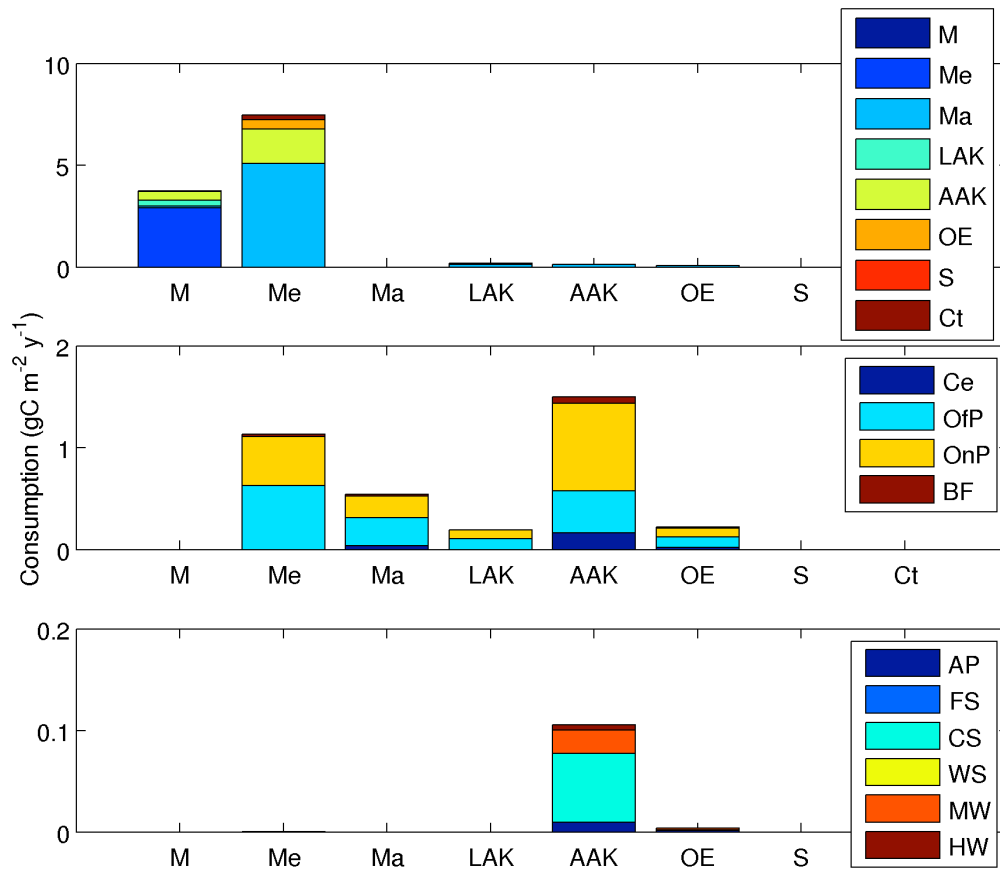
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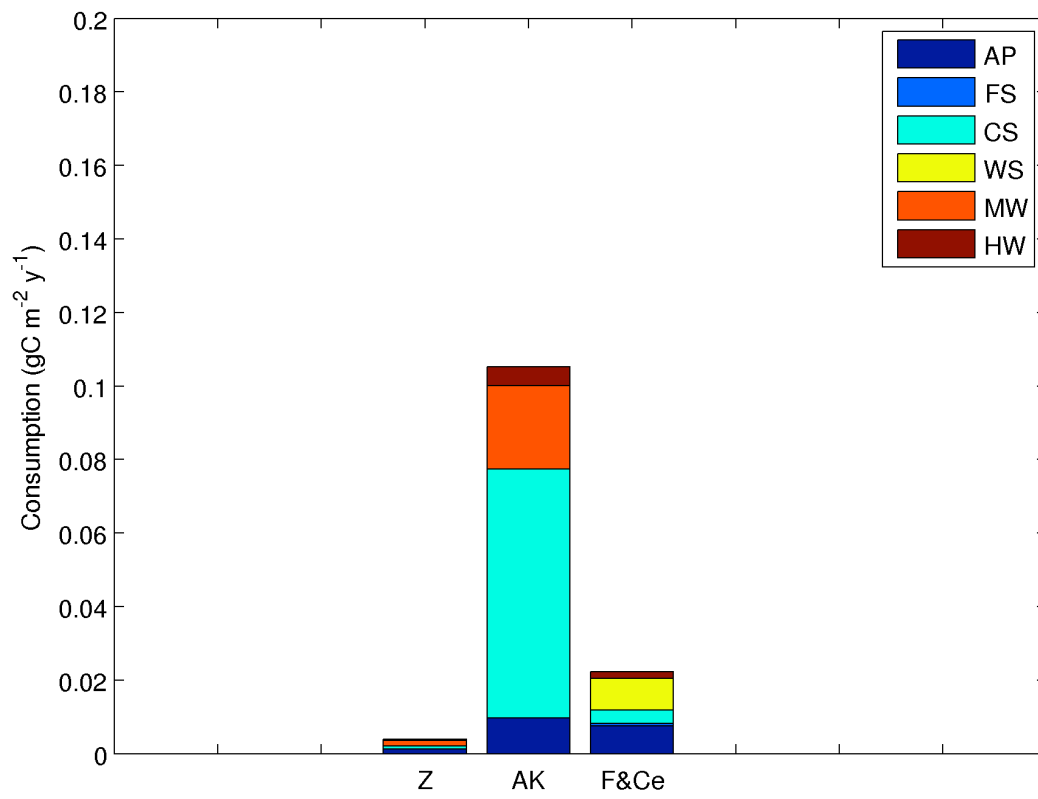
1566 **Figure 3**

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1569 **Figure 4**

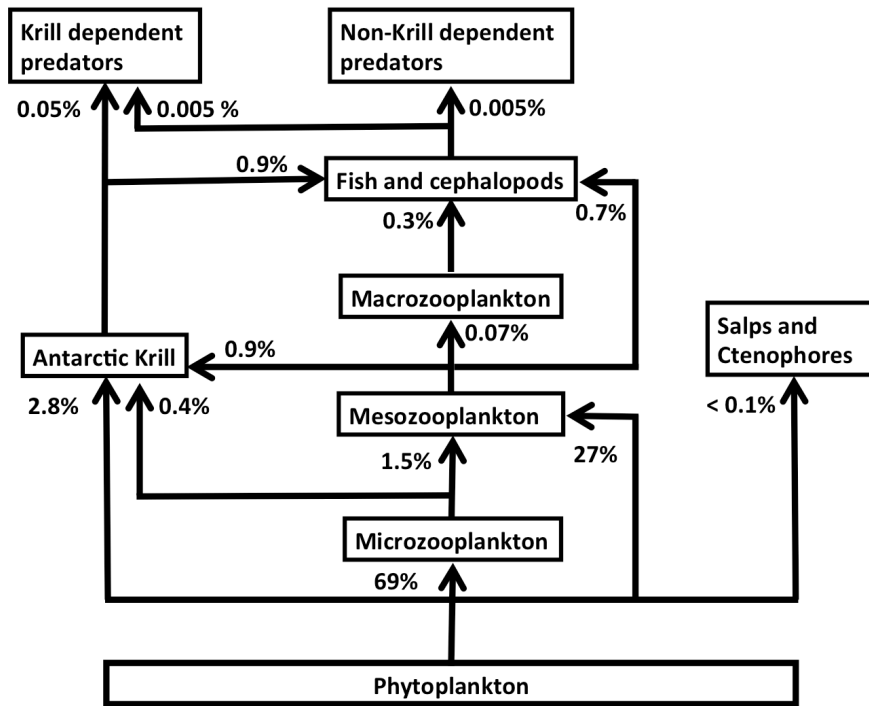


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1571 **Figure 5**



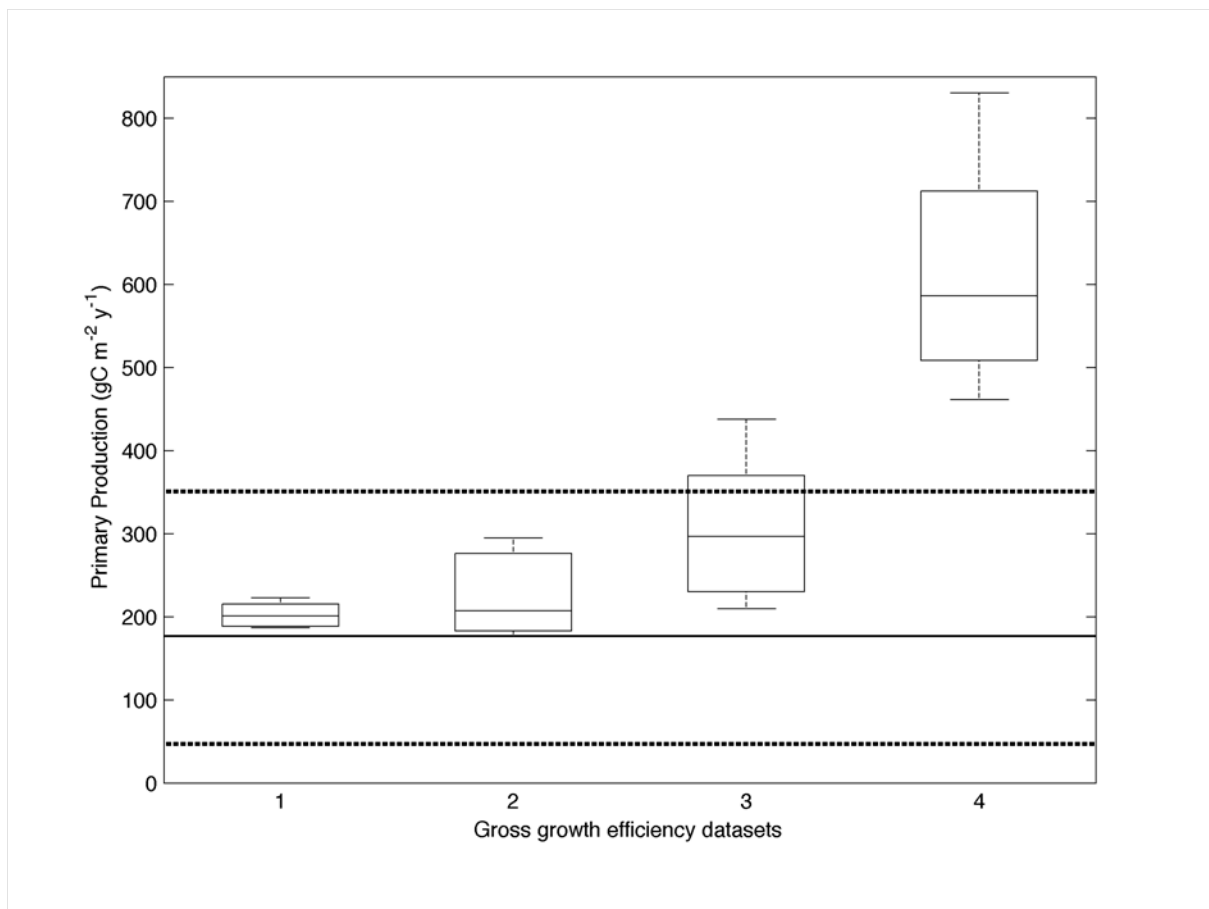
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1573 **Figure 6**

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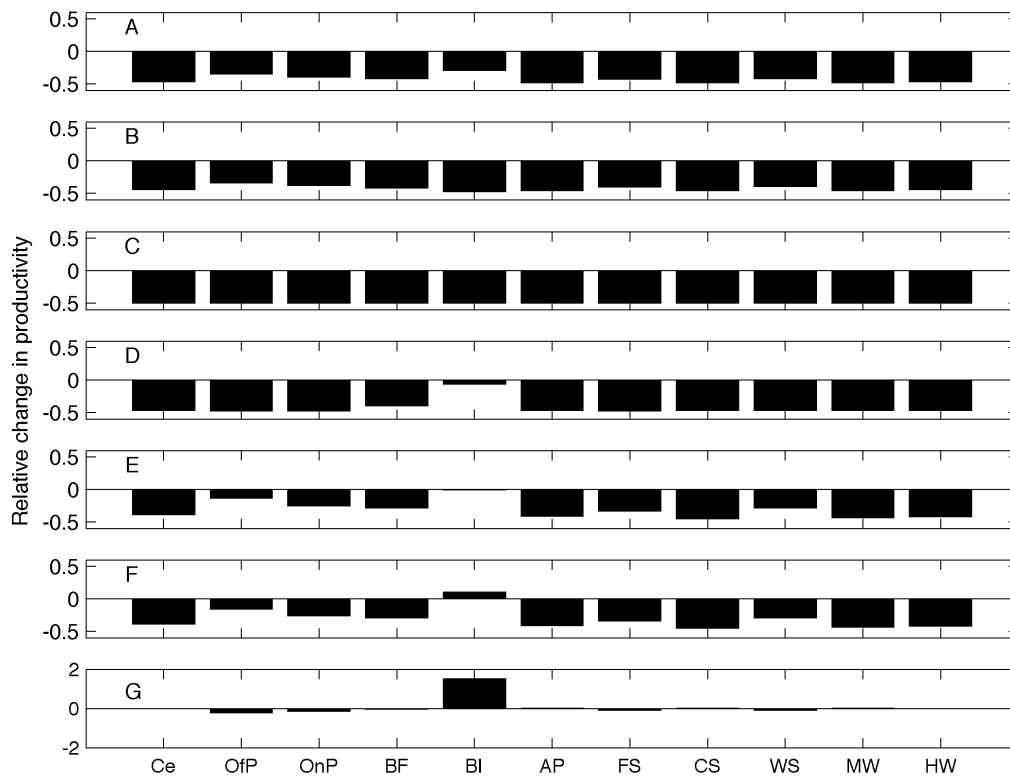
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1577 **Figure 7**

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1580 **Figure 8**

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1582 **APPENDIX A**

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1584 **Table A.1.** Summary of the species and groups included in the sWAP food web model. The1585 references used to obtain the production to biomass ratios (*P/B*) and the diet compositions are

1586 given.

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<b>Trophic group</b>	<b>Species/group</b>	<b>P/B References</b>	<b>Diet References</b>
Microzooplankton	Dinoflagellates, aloricate oligotrichs, tintinnids, other ciliates and sarcodine	S.Strom, pers.comm.	S. Strom, pers. comm.; Froneman and Perissinotto, 1996
Mesozooplankton	<i>Calanoides acutus</i> , <i>Calanus propinquus</i> , <i>Metridia gerachei</i> , <i>Ctenocalanus sp</i>	Voronina et al., 1980 a,b	Hopkins, 1985; Pakhomov et al., 1997; Pasternak and Schnack-Schiel, 2001
Macrozooplankton	<i>Paraeucheta sp.</i> , Ostracods	Voronina et al., 1980a; Fransz and Gonzalez, 1995	Pakhomov and Froneman, 2004; Hopkins, 1985; Oresland and Ward, 1993; Oresland, 1995; Pakhomov and Perissinotto, 1996
Antarctic krill larvae	<i>Euphausia superba</i>	Taki, 2006	Ross et al., 2000; Meyer et al., 2003, 2009; Ju et al., 2004a; Daly, 2004; Töbe et al., 2009
Antarctic krill adults	<i>Euphausia superba</i> > 15 mm	Taki, 2006	Kawaguchi et al., 1986; Tanoue and Hara, 1986; Price et al., 1988; Kopczyńska, 1992; Atkinson and Snýder, 1997; Perissinotto et al., 1997, 2000; Ligowski, 2000; Moline et al., 2004; Atkinson et al., 2006; Schmidt et al., 2006; Clarke and Tyler, 2008
Other euphausiids	<i>Euphausia crystallorophias</i> ; <i>Tyssanoessa macrura</i>	Taki, 2006	Hopkins, 1995
Salps	<i>Salpa thompsoni</i>	Pakhomov et al., 2002	Hopkins, 1995; Pakhomov et al., 2006
Ctenophores	<i>Callianira antarctica</i>	Pakhomov et al., 2002	Ju et al, 2004b; Moline et al., 2004; Scolardi et al., 2006;
Cephalopods	Glacial squid ( <i>Psychroteuthis glacialis</i> )	Aydin et al., 2007	Rodhouse and White, 1995; Rodhouse and Nigmatullin, 1996; Phillips et al., 2001; Collins and Rodhouse, 2006
Off-shelf pelagic fish	<i>Electrona antarctica</i>	Greely et al., 1999	Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov, 1997; Barrera-Oro, 2003; La Mesa et al., 2004; Pusch et al., 2004; Bushula et al., 2005

On-shelf pelagic fish	<i>Pleuragramma antarcticum</i> , <i>Trematomus eulepidotus</i> , <i>Trematomus scotti</i> , <i>Chaenodraco wilsoni</i> , <i>Bathyraja maccaini</i> , <i>Trematomus loennbergii</i>	Hubold, 1992	Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov, 1997; Barrera-Oro, 2003; La Mesa et al., 2004; Pusch et al., 2004; Bushula et al., 2005
Benthic Fish	Nototheniidae, Channictidae, Bathyracnidae, Rajidae, Arctedraconidae, Zoarcidae		Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov, 1997; Barrera-Oro, 2003; La Mesa et al., 2004; Pusch et al., 2004; Bushula et al., 2005
Benthic Invertebrates	HOLOTUROIDEA; ASTEROIDEA: <i>Odonaster validus</i> , <i>Acodontaster conspicus</i> ; OPHIUROIDEA: <i>Ophloceres incipens</i> , <i>Ophionotus victoriae</i> ; POLYCHAETA	Jarre- Tiechmann et al., 1997	Jarre-Tiechmann et al., 1997
Adelie penguin	<i>Pygoscelis adeliae</i>	Ballerini et al., 2009	Ainley et al., 1992; Ainley, 2002; Ainley et al., 2003; Fraser and Hofmann, 2003; Volkman et al., 1980
Flying seabirds	Snow petrel ( <i>Pagodroma nivea</i> ), Antarctic fulmar ( <i>Fulmarus glacialis</i> ), cape petrel ( <i>Daption capense</i> ), south polar skua ( <i>Catharacta maccormicki</i> ), black-browed albatross ( <i>Diomedea melanophris</i> )	Ratcliffe et al., 2002; Jenouvrier et al., 2003; Rolland et al., 2010	Ainley et al. 1992; Xavier et al., 2003
Crabeater seal	<i>Lobodon carcinophagus</i>	Bengston and Siniff, 1981	Oritsland, 1977; Siniff et al., 2008
Weddell seal	<i>Leptonychotes weddellii</i>	Hadley et al., 2007	Green and Burton, 1987; Ponganis and Stockard, 2007; Ainley and Siniff, 2009
Minke Whale	<i>Balaenoptera acutorostrata</i>	Ohsumi, 1979a,b	Leatherwood et al., 1983; Ichii and Kato, 1991, Ichii et al., 1998
Humpback Whale	<i>Megaptera novaeangliae</i>	Ohsumi, 1979a,b	Kawamura, 1980

1588 **Table A.2.** Summary of annual consumption to biomass ratios ( $Q/B$ ) and gross growth  
1589 efficiencies (GGE, in parentheses) used in the sWAP food web model. The  $Q/B$  ratios were  
1590 obtained from GGEs that are: 1) calculated from the assimilation efficiency ( $AE$ ) and  
1591 production efficiency ( $PE$ ) values given Table 1, 2) given in Banse (1995), 3) given in  
1592 Priddle et al. (1998), and 4) calculated from daily consumption rates (DCR), expressed as a  
1593 percentage of body size for each species/group, and the component biomass. The trophic  
1594 group GGE not represented in the Banse (1995) and Priddle et al. (1998) analysis are  
1595 indicated by NA.

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Species/group	Q/B AE and PE	Q/B Banse (1995)	Q/B Priddle et al. (1998)	Q/B DCR
Microzooplankton	275.00 (0.200)	157.14 (0.350)	137.50 (0.400)	275.00
Meso zooplankton	19.63 (0.245)	37.00 (0.130)	40.08 (0.120)	16.80
Macrozooplankton	8.93 (0.280)	8.33 (0.300)	20.83 (0.120)	35.30
Antarctic krill larvae	6.80 (0.294)	11.76 (0.170)	16.67 (0.120)	113.25
Antarctic krill adults	4.08 (0.245)	5.88 (0.170)	8.83 (0.120)	30.90
Other Euphasiids	6.12 (0.245)	8.82 (0.170)	12.50 (0.120)	30.09
Salps	12.24 (0.245)	20.00 (0.150)	25.00 (0.120)	91.00
Ctenophores	10.71 (0.280)	20.00 (0.150)	25.00 (0.120)	83.95
Cephalopods	32.00 (0.100)	32.00 (0.100)	32.00 (0.100)	16.30
Off-shelf pelagic fish	12.70 (0.100)	12.70 (0.100)	12.70 (0.100)	8.76
On-shelf pelagic fish	4.00 (0.100)	4.00 (0.100)	4.00 (0.100)	3.32
Benthic fish	2.00 (0.100)	2.00 (0.100)	2.00 (0.100)	2.00
Benthic Invertebrates	2.19 (0.201)	NA	NA	2.19
Adélie penguin	8.82 (0.017)	8.82 (0.017)	4.29 (0.035)	31.99
Flying seabirds	3.33 (0.018)	3.53 (0.017)	1.71 (0.035)	149.65
Crabeater Seal	3.00 (0.020)	3.53 (0.017)	1.71 (0.035)	25.55
Weddell Seal	2.87 (0.017)	2.94 (0.017)	1.43 (0.035)	4.50
Minke whale	2.69 (0.0189)	2.94 (0.017)	1.43 (0.035)	5.10
Humpback whale	2.15 (0.019)	2.35 (0.017)	1.14 (0.035)	7.30

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1599 **Table A.3.** Production matrix,  $A_{cp}$ , for the baseline bottom-up model obtained by  
1600 transposing the mass balance model that used the adult Antarctic krill diet given in Table 2.  
1601 The contribution (%) of each producer (columns) to each consumer (rows) is shown for each  
1602 group in the southwestern Antarctic Peninsula (sWAP) model.

		Producers																		
Consumers		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	SP	60	23	1	23	0	0	40	0	0	0	0	0	0	0	0	0	0	0	0
2	LP	25	65	10	46	53	60	20	0	0	0	0	0	0	0	0	0	0	0	0
3	IB	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	M	0	5	1	15	6	0	30	0	0	0	0	0	0	0	0	0	0	0	0
5	Me	0	0	72	0	24	24	5	88	0	41	28	5	0	0	2	0	0	0	5
6	Ma	0	0	0	0	0	0	0	0	9	18	12	5	0	0	0	0	0	0	0
7	AKL	0	0	2	0	0	0	5	12	0	7	5	0	0	0	0	0	0	0	0
8	AAK	0	0	2	0	0	0	0	0	37	27	50	15	0	52	10	94	0	94	70
9	OE	0	0	1	0	0	0	0	0	4	7	5	2	0	7	0	1	0	6	0
10	S	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	Ct	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	Ce	0	0	0	0	0	0	0	0	0	0	0	8	0	30	30	2	50	0	5
13	Off-P	0	0	0	0	0	0	0	0	25	0	0	10	0	8	32	1	18	0	10
14	On-P	0	0	0	0	0	0	0	0	25	0	0	15	0	3	20	2	16	0	10
15	BF	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	16	0	0
16	BI	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	0
17	AP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	FS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	CS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	WS	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	MW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	HW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	PD	15	7	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	BD	0	0	10	0	16	16	0	0	0	0	0	0	100	0	0	0	0	0	0

1603