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Productivity and linkages of the food web of the southern region of the western Antarctic Peninsula continental shelf

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ABSTRACT

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

1. Introduction

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

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Descriptions of Southern Ocean food webs initially focused on qualitative descriptions of linkages in particular areas, such as the open ocean, sea ice, or coastal regions (Everson, 1977; Laws, 1984). Studies done during the past three decades provide the basis for quantification of food web models. Detailed analysis of food webs that are based on mass balance constraints, which require that predator consumption of a prey group does not exceed prey production, have been developed for the Ross Sea (Pinkerton et al., 2010), the Antarctic Peninsula-Scotia Sea (Cornejo-Donoso and Antezana, 2008) and the South Georgia shelf in the Scotia Sea (Hill et al., 2012). These modeling studies compiled and analyzed extensive and disparate data sets, which allowed identification and analysis of important trophic groups and interactions. The analysis of the Ross Sea food web was focused on the production of Antarctic toothfish (*Dissostichus mawsoni*) and the consequences of harvesting this species for its predators. The Antarctic Peninsula-Scotia Sea and South Georgia food webs showed that Antarctic krill was the primary link between low and high trophic levels, and also showed that alternative trophic pathways through other zooplankton species, benthic organisms, and fish provided support for the upper trophic levels.

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

In the northern part of the western Antarctic Peninsula, these changes in the physical environment have affected various components of the food web (Ducklow et al., 2007; Schofield et al., 2010). In particular, reductions in sea ice extent have been linked to observed changes in the composition of phytoplankton assemblages (Moline et al., 2004; Montes-Hugo et al., 2009), to reduced recruitment of intermediate trophic levels such as Antarctic krill and Antarctic silverfish that use the under ice habitat as a nursery (Atkinson et al., 2004; Ducklow et al., 2007; Chapman et al., 2011), and to reduced populations of vertebrate predators such as the Adélie penguin (*Pygoscelis adeliae*) that use the sea ice

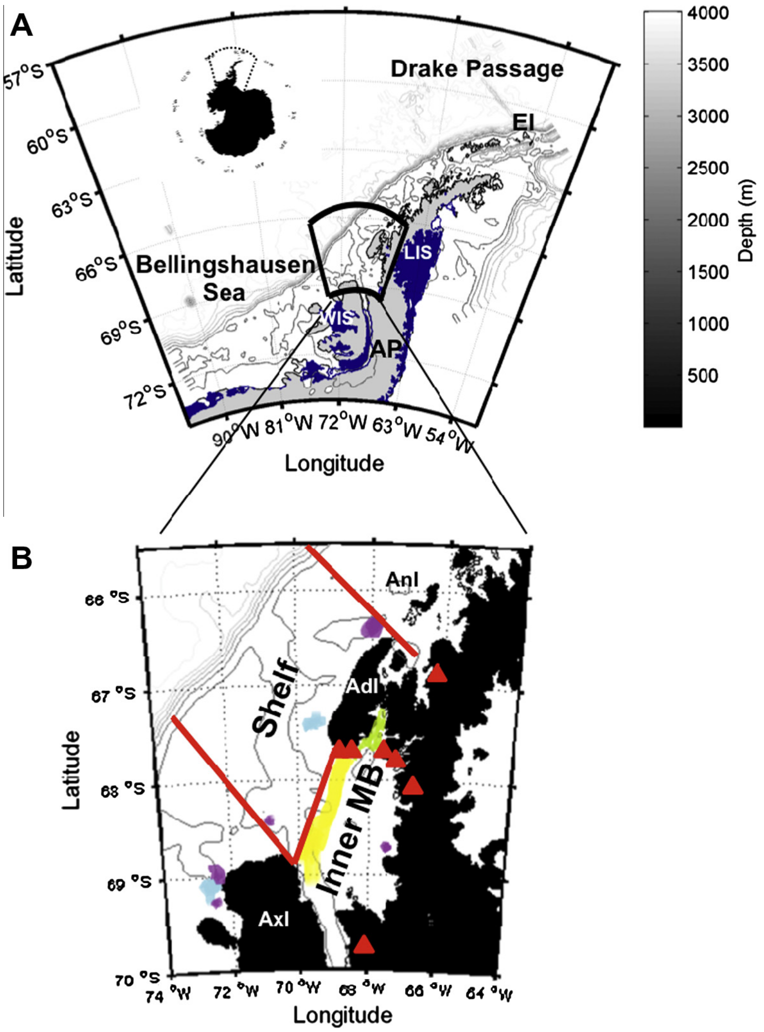

Fig. 1. Map of the Antarctic Peninsula (A) showing the SO GLOBEC study region and the partitioning of this region used for calculating inputs to the food web model (B, heavy black lines). Regions of enhanced concentrations of pelagic fish (green), seabirds (light blue), crabeater seals (purple) and baleen whales (yellow) that were observed during the SO GLOBEC survey cruises (Costa et al., 2007) are indicated. The location of Adélie penguin colonies (Ainley, 2002) is also indicated (triangles). Geographic features are identified as: Adelaide Island-AdI, Alexander Island-AxI, Anvers Island-AnI, Elephant Island-EI, George VI Ice Shelf-GVIIS, Marguerite Bay-MB, Marguerite Trough-MT, and Wilkins Ice Shelf-WIS. Bathymetric contours are in meters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

habitat (Ainley, 2002). Changes in the hydrography and reduction of sea ice cover have also been associated with the increased occurrence of the tunicate *Salpa thompsoni*, which may compete with Antarctic krill for food (Loeb et al., 1997). Unusually high abundances of salps have been observed in the northern part the western Antarctic Peninsula, and were associated with intrusions of oceanic water masses close to the Antarctic shelf (Pakhomov et al., 2002; Pakhomov, 2004).

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

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

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

2. Methods

2.1. Southwestern Antarctic Peninsula food web model

The food web model for the sWAP continental shelf consists of 24 trophic groups that represent the pelagic, benthic and microbial components (Fig. 2, Table 1). The species represented within the trophic groups correspond to those observed during SO GLOBEC and to species reported from previous studies in the sWAP. Some trophic groups are composed of a single species (e.g., Antarctic krill and Adélie penguin), while other trophic groups are composed of more than one species (Table A.1). Primary producers are represented by three microbial groups, small phytoplankton (nanoflagellates and cryptophytes, <20 μm), large phytoplankton (diatoms, >20 μm) and ice algae. The intermediate trophic groups consist of micro-, meso- and macrozooplankton, Antarctic krill, and benthic invertebrates. The pelagic fish assemblage along the sWAP is dominated by two species, Antarctic silverfish and lantern fish (*Electrona antarctica*) (Donnelly and Torres, 2008). Cephalopods and benthic fish are consumers of intermediate trophic level production and also are prey for top predators (e.g. Kock, 1987; Barrera-Oro, 2002). The top predators are the Adélie penguin, a group of several species of flying seabirds, seals, and cetaceans. These predators constitute the majority of upper trophic level biomass along the sWAP (Chapman et al., 2004; Thiele et al., 2004; Ribic et al., 2008, 2011).

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

$$P_p = M2_pB_p + M0_pB_p \tag{1}$$

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

Predation mortality is given by

$$M2_p = \sum_{c=1}^{n} \frac{Q_cDC_{pc}}{B_p}, \tag{2}$$

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

$$M0_p = (1 - EE_p)(P_p/B_p) \tag{3}$$

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

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

$$P_c = P_p/Q_p \sum_p A_{cp}EE_pP_p \tag{4}$$

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

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

$$Q_{pc} = A_{cp}P_p \quad A_{cp} \geqslant 0 \quad \text{(bottom up approach)} \tag{6}$$

where Q_{pc} is the rate at which the prey biomass, B_p, is consumed by the predator biomass, B_c. The terms DC_{pc}, Q_{pc}, and P_p are obtained

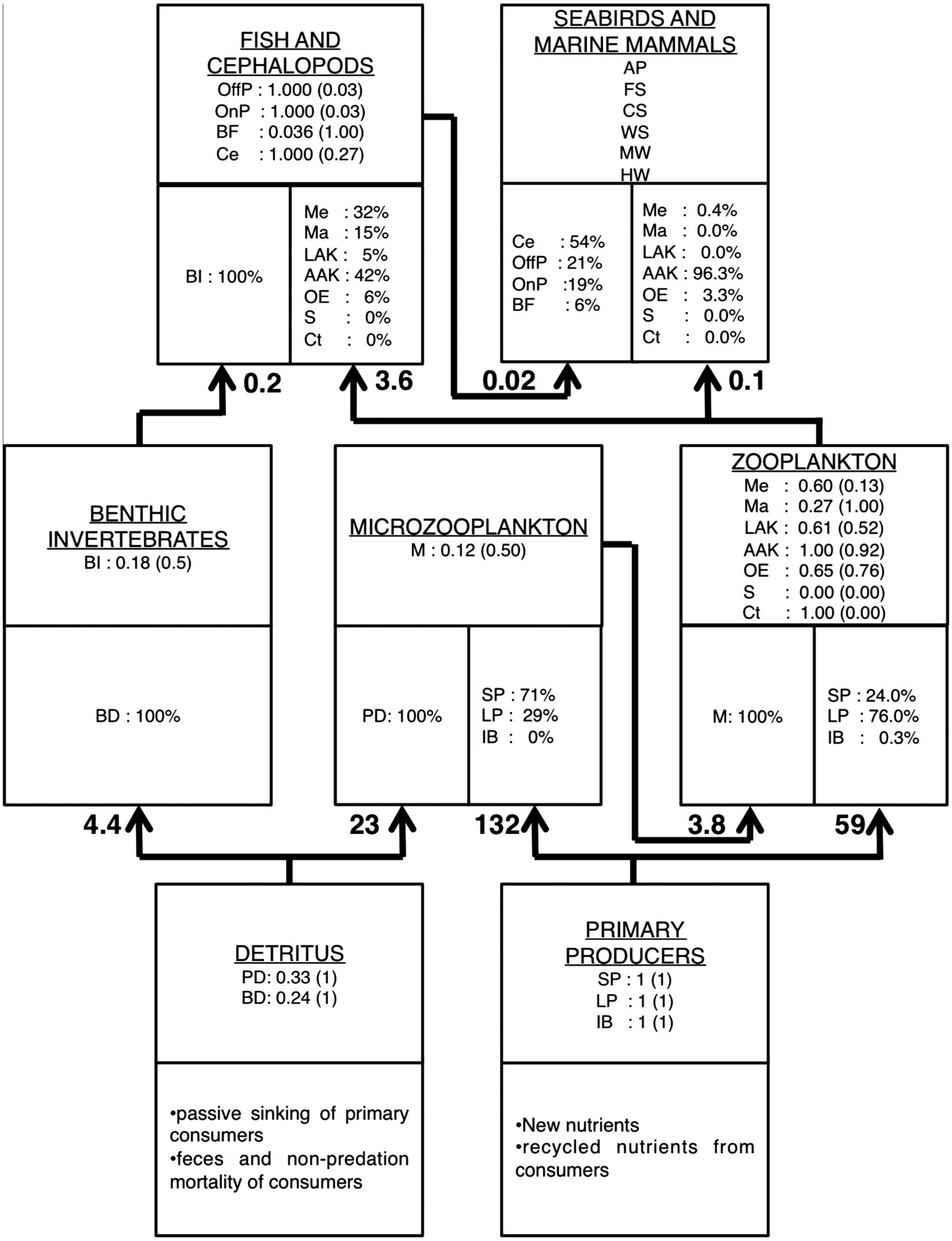

Fig. 2. Summary of the energy flows in the southwestern Antarctic Peninsula (sWAP) food web model. The 24 food web model groups are grouped into 7 compartments that correspond to primary producers, detritus, zooplankton, microzooplankton, benthic invertebrates, fish and cephalopods (intermediate predators),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

from the top-down model and used to calculate the production matrix, A_{cp}.

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

2.2. Specification of model parameters

2.2.1. Carbon biomass estimates

The initial biomass values used for each trophic group in the sWAP food web model (Table 1) did not include a biomass estimate for the primary producer group. The biomass for this group corresponds to the direct demand for primary production by consumer

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

Trophic group	Symbol	B ($g\,C\,m^{-2}$)	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

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

$$AD = sh\ DOW + mb\ DPI \qquad (7)$$

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

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

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

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

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

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

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

The combined juvenile and adult Antarctic krill net-derived abundances from 2001 and 2002 were vertically and spatially-averaged and converted to carbon biomass to obtain the annual biomass estimate for the adult Antarctic krill group in the sWAP food web model. A similar approach was used to obtain annual biomass for the other euphausiids group. The density and biomass of salps in a part of the Antarctic shelf partially overlapping with the SO GLOBEC study area was measured in early fall 2001 as part of the German SO GLOBEC field program (Pakhomov et al., 2006). The earlier timing of the German cruise placed it before sea ice developed and salps were still present. The measured biomass value of 0.0173 g C m^{-2} was applied to the shelf sub-region and the spatially averaged biomass is 0.009 g C m^{-2}. However, the salps observed on the Antarctic Peninsula shelf in fall 2001 were likely the result of an advective event, which can provide considerable variability in their mean density and distribution (Pakhomov et al., 2006). Thus, the values used in the food web model, while representative of observed conditions for one season, may not reflect conditions at other times. The density and biomass in the inner Marguerite Bay sub-region was set to zero as suggested by observations (Marrari et al., 2011).

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

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

Adélie penguin biomass was estimated using summer density values from breeding colonies in the Marguerite Bay region and then doubled to account for non-breeders (Ainley, 2002). The summer density was spatially-averaged using the model domain area (83,670 km^2) to obtain a density of 2.38 ind km^{-2}. Telemetry data from Adélie penguins tagged in Marguerite Bay during SO GLOBEC (Erdmann et al., 2011) showed that the flux of penguins into/out of this region was relatively balanced. Individual body weight for penguins in the month of October was set at 8 kg for breeding and 6 kg for non-breeding birds (Penney, 1967). Penguin body mass used for the other months was 4.5 kg (Ribic et al., 2011). The mean annual wet weight biomass was obtained by averaging the monthly values and was converted to carbon biomass using a carbon-to-wet-weight conversion of 0.2 (Burger and Schreiber, 2001).

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

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

Weddell seals (*Leptonychotes weddellii*) prefer fast ice and dense pack ice (Siniff et al., 2008) and the SO GLOBEC cruises did not extend into these regions. As a result, the winter encounter rates for Weddell seals were so low that density estimates were unreliable (Chapman et al., 2004). Thus, an indirect estimate of their abundance was obtained by scaling their number with respect to the number of crabeater seals. A study of seal relative abundance (Erickson and Hanson, 1990) showed that Weddell seal abundance is about 3% of crabeater seal abundance. This percent was used to scale crabeater seal abundance to Weddell Sea abundance. This implies a Weddell Sea density of 0.03 ind km^{-1}. An individual average weight of 450 kg (Proffitt et al., 2007) gave an annual wet biomass of 12.3 kg km^{-2}, which was converted to carbon biomass (Table 1) using the wet and dry weight ratios used for crabeater seals.

Minke whale (*Balaenoptera bonaerensis*) abundance along the sWAP for December to February has been estimated to be 0.014 ind km^{-2} (Branch, 2006). Seasonal variation in minke whale density was estimated from cetacean observations made during the SO GLOBEC fall and winter cruises as well as during SO GLOBEC mooring deployment cruises in late summer (Thiele et al., 2004). The maximum abundance value observed during each SO GLOBEC cruise was used to calculate minke whale abundance for March–May, June–August, and December–February. These values were used to calculate abundance ratios for the fall and winter and the ratios were used to scale the summer density values from Branch (2006) to obtain an annual density estimate of 0.008 ind km^{-2}. Annual wet weight biomass was calculated assuming a demographic structure (female:male, mature:immature) and the corresponding average individual body mass as reported in Konishi et al. (2008) and Tamura and Konishi (2009). The wet biomass (0.0517 t km^{-2}) was converted to carbon biomass (Table 1) using a wet weight to dry weight ratio of 0.35 and a dry weight to carbon weight ratio of 0.5. Similarly, the abundance of humpback whales (*Megaptera novaeangliae*) along the sWAP from December to February was estimated as 0.0014 ind km^{-2} (Branch, 2007). Seasonal variability in humpback whale density was determined from the SO GLOBEC cetacean sightings data (Thiele et al., 2004) and the abundance ratios were used to scale the abundance estimates from Branch (2006) to obtain seasonal density estimates, which were averaged to obtain an annual density estimate of 0.0007 ind km^{-2}. The average individual body mass for a humpback whale (26,924 kg, Reilly et al., 2004) was used to estimate wet biomass (0.0517 t km^{-2}), which was converted to carbon biomass using the same conversions as used for minke whales.

2.2.2. Production/biomass ratios

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

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

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

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

For top predators, the P/B ratio was assumed to be the value that balanced annual adult mortality (Banse and Mosher, 1980). For Adélie penguins the annual adult survival is estimated to be 0.85 (Ballerini et al., 2009), which gives a P/B ratio of 0.15. Annual adult survival rates have been estimated for several Antarctic seabirds (e.g., 0.94 for snow petrel *Pagodroma nivea*, Jenouvrier et al., 2005b; 0.92 for Antarctic fulmar *Fulmarus glacialoides*, Jenouvrier et al., 2005a; 0.96 for south polar skua *Stercorarius maccormicki*, Ratcliffe et al., 2002), and these were averaged to obtain a biomass-weighted survival of 0.94 and a P/B ratio of 0.06 for the seabird group.

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

$$le = \frac{1}{-\log s} \tag{9}$$

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

2.2.3. Gross growth efficiency and consumption rates

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

$$Q/B = \frac{P/B}{P/Q} \tag{10}$$

where the P/Q ratio corresponds to the gross growth efficiency, which is the product of the assimilation efficiency (AE) and production efficiency (PE). Using the gross growth efficiency to obtain the P/Q ratio allows explicit calculation of unassimilated ingestion (1-AE) that goes to the detrital pool and of energy lost to metabolic processes (e.g., respiration, 1-PE), and thus ensures consistency between the assumed consumption and production rates for each trophic group in the food web model (Link, 2010). The assimilation and production efficiency values used to calculate the gross growth efficiency for the sWAP trophic groups (Table 1) were obtained from Townsend et al. (2003), with the exception of the assimilation efficiency value for larval Antarctic krill that was taken from Meyer et al. (2003). The reconstructed gross growth efficiency values are consistent with values used in other Southern Ocean food web models (Banse, 1995; Priddle et al., 1998). These values and the P/B ratios given above were used to calculate the Q/B ratio for each trophic group.

2.2.4. Diet composition

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

Salps feed efficiently on a wide range of particles (1–1000 μm) (Pakhomov et al., 2006) and the diet for this group accounts for this, with most of the consumption focused on smaller particles (Table 2). The ctenophore diet was based on observations that show that ctenophores feed on calanoid copepods, amphipods, and larval Antarctic krill (Ju et al., 2004; Scolardi et al., 2006).

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

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

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

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

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

krill make up about 50% of the constructed Adélie penguin annual diet.

The flying seabird diet composition was constructed from observations of the diets of snow petrels, Antarctic fulmars and cape petrels (*Daption capense*) (Ainley et al., 1992), south polar skuas (Ainley et al., 1984), and black-browed albatross (*Thalassarche melanophrys*) (Xavier et al., 2003). Snow petrels are associated with areas with sea ice, whereas the other species are associated with open water, and the diet composition reflects the species differences in the two regions. The ice- and open-water associated diets were used to construct an annual average diet for seabirds (Table 2), which is based primarily on cephalopods and pelagic fish.

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

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

2.3. Food web balance

The sWAP food web model was implemented using the parameter values and diet compositions given in Tables 1 and 2. Mass balance is achieved when all of the ecotrophic efficiency values, EE_p in Eq. (3), are less than 1. An unbalanced model can be resolved by modifying predator diets and consumption rates, physiological efficiencies, or prey biomass. For the sWAP food web model, the approach used was to increase the biomass of the prey by setting their $EE = 1$ (similar to Hill et al., 2012). For the initial implementation of the sWAP food web model, three groups (ctenophores, on-shelf pelagic fish and on-shelf pelagic fish) had $EE > 1$, which indicated that the estimated production rate for these groups was too low to support the estimated consumption by their predators. The

Table 3
Biomass (*B*), annual production (*P*), annual consumption (*Q*), trophic level (*TL*) and ecotrophic efficiency (*EE*) for each trophic group in the southwestern Antarctic Peninsula (sWAP) food web model after the model was mass balanced.

Species/group	*B* (g C m^{-2})	*P* (g C m^{-2})	*Q* (g C m^{-2})	TL	EE
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

biomass for these three groups was increased, but was still within the variability of observed biomasses for these groups (Table 3). Increasing the biomass of the pelagic fish groups led to higher consumption of adult Antarctic krill, and produced an *EE* for this group > 1. Therefore, the adult Antarctic krill biomass was also mass balanced by setting its *EE* = 1. The revised biomass estimate was within the variability of biomass estimates for Antarctic krill obtained from acoustic surveys in the study area (Lawson et al., 2008a).

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

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

2.4. Model analysis and metrics

The mass balance model implemented with the data summarized in Tables 1 and 2 was used to obtain a baseline simulation for the sWAP food web that provided an estimate of the primary production required by the food web and an estimate of the energy flows between trophic groups. The diet composition of the baseline simulation was used to calculate the trophic level of the sWAP model groups. The baseline simulation also provided a reference for comparison for the sensitivity analyses and environmental change scenario simulations.

2.4.1. Sensitivity analysis – role of Antarctic krill in energy transfer

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

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

The third set of simulations investigated the effects of the assumed biomass of fish, seabirds, and marine mammals on the estimates of adult Antarctic krill biomass that is consumed in the sWAP baseline model. The estimated proportion of the production of a prey species that is consumed (i.e. the *EE* of the prey) depends on the assumed prey parameters and on the assumed consumption rates of its predators. The predator consumption rates, in turn, are related to the assumed predator biomass, which for many of the trophic groups included in the sWAP food web model is poorly constrained (see Hill et al., 2005; Laws, 1977; Woehler and Croxall, 1997; Southwell et al., 2008). Therefore, the biomass of the trophic groups that consume adult Antarctic krill was doubled with respect to the baseline simulation and the resulting demand on Antarctic krill production (i.e. the adult Antarctic krill *EE*) was calculated. These simulations also compared adult Antarctic krill biomass derived from net-tows and acoustic estimates.

2.4.2. Environmental change scenarios

Five environmental change scenarios were implemented with the bottom-up model (Eq. (4)) to simulate the effects of altered plankton assemblage composition on the production of vertebrate predators in the sWAP food web model. The scenarios were selected based on observed or expected changes in the relative abundance of phytoplankton and zooplankton groups that may result from changes in hydrographic conditions and/or sea ice extent changes linked to the warming trend in the western Antarctic Peninsula. The simulations were done by altering the entries in the production matrix, A_{cp} (Table 8), and redirecting 50% of a prey source from one consumer group to another. All simulations were implemented with constant primary production and did not allow for prey switching. The effects of the different perturbations were expressed in terms of the fractional change in productivity relative to the productivity in the bottom-up model derived from the baseline sWAP mass balance model.

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

The second scenario tested the consequences of reducing the secondary production of large zooplankton (mesozooplankton, macrozooplankton, larval and adult Antarctic krill, other euphausiids, and salps) by 50% and compensating with an equivalent increase in microzooplankton secondary production. This scenario was based on the prediction that warmer sea water temperature will increase the metabolic rates of zooplankton groups. Since the microzooplankton have faster turnover rates that the other zooplankton groups, their biomass is expected to become predominant (Richardson, 2008). Scenarios 1 and 2 were implemented with the bottom-up model derived from the baseline sWAP mass balance model and from a bottom-up model derived from a mass balance model in which the diet of the adult Antarctic krill group included a larger fraction of microzooplankton (45%, same Antarctic krill diet used by Hill et al. (2012)).

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

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

3. Results

3.1. Food web structure and carbon flows in the baseline sWAP simulation

3.1.1. Trophic levels and trophic pathways

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

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

3.1.2. Consumption by food web components and carbon flows

The direct estimate of annual primary production required to sustain the food web with the sWAP baseline simulations is 191 $g\,C\,m^{-2}\,y^{-1}$ (Fig. 2). The majority of this (132 $g\,C\,m^{-2}\,y^{-1}$, 69%) is consumed by microzooplankton; the other seven zooplankton groups consume the remainder. Small phytoplankton production contributes 71% of the consumption by microzooplankton (Fig. 2), while large phytoplankton production is the largest contribution (76%) to the primary production that is grazed by the other zooplankton groups (Fig. 2).

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

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

Microzooplankton and mesozooplankton consume 155 $g\,C\,m^{-2}\,y^{-1}$ and 58 $g\,C\,m^{-2}\,y^{-1}$, respectively (Table 3), and account for 89% of the annual carbon consumption by secondary producers. Most of this carbon is provided by primary production (86%) with the remaining 14% coming from detritus. Microzooplankton are the principal grazers of both small (87% of total consumption) and large phytoplankton (45% of total consumption) production. Mesozooplankton are the second most important grazers of large phytoplankton production (45%, Fig. 3). Consumption of primary and secondary production by other zooplankton groups is 1–2 orders of magnitude smaller than that of microzooplankton and mesozooplankton (Table 3). Adult Antarctic krill consume 88% less primary and secondary production than do mesozooplankton (Fig. 3).

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

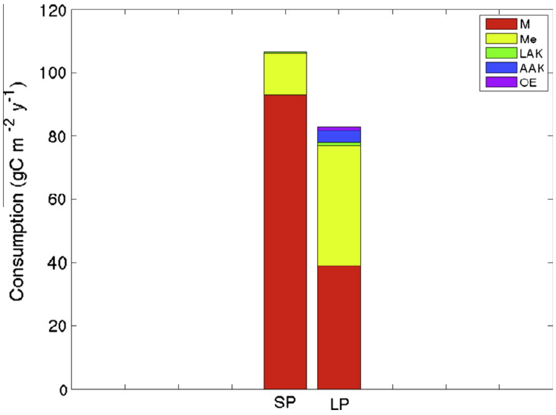

Fig. 3. Annual consumption ($g\,C\,m^{-2}\,y^{-1}$) of large and small phytoplankton primary production by zooplankton groups obtained from the southwestern Antarctic Peninsula (sWAP) mass balance food web model. Phytoplankton groups are indicated as: small phytoplankton-SP and large phytoplankton-LP. Zooplankton groups are indicated as: mesozooplankton-Me; larval Antarctic krill-LAK; adult Antarctic krill-AAK; other euphasiids-OE.

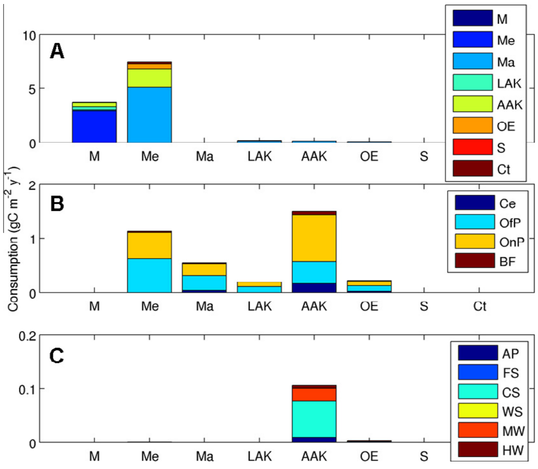

Fig. 4. Annual consumption ($g\,C\,m^{-2}\,y^{-1}$) of zooplankton and benthic invertebrates by (A) zooplankton predators, (B) intermediate predators and (C) top predators calculated from the sWAP food web model. The species/groups are defined in Table 1.

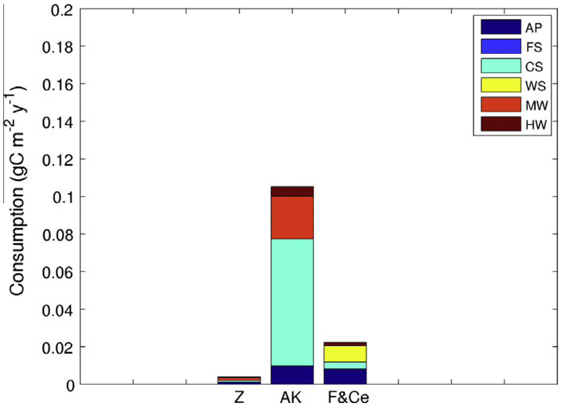

Fig. 5. Annual consumption (g C m^{-2} y^{-1}) of zooplankton and intermediate predators by top predators calculated from the southwestern Antarctic Peninsula (sWAP) food web model. Zooplankton (Z) prey include herbivorous zooplankton, carnivorous zooplankton and other euphasiids. Antarctic krill (AK)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

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

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

3.2. Sensitivity analyses

3.2.1. Changes in Antarctic krill biomass and estimates of primary production

The primary production required for consumption by the food web groups was 187–207 g C m^{-2} y^{-1}, depending on adult Antarctic krill biomass, diet and P/B ratio (simulations 1–6, Table 4). Acoustically-derived estimates of euphausiid biomass (assumed to be primarily Antarctic krill, Lascara et al., 1999) are about double that of net-derived biomass estimates (Table 1). Supporting the higher biomass estimate required an increase between 3% and 10% in annual primary production for a 100% herbivorous diet and a 100% carnivorous krill diet, respectively, relative to the primary production estimate from the baseline simulation (Table 4). The annual primary production required for other simulations that use a herbivorous diet for adult Antarctic krill is on average 31% lower than that required for a carnivorous diet (Table 4).

3.2.2. Changes in gross growth efficiency values and estimates of primary production

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

3.2.3. Predator biomass and fate of Antarctic krill production

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

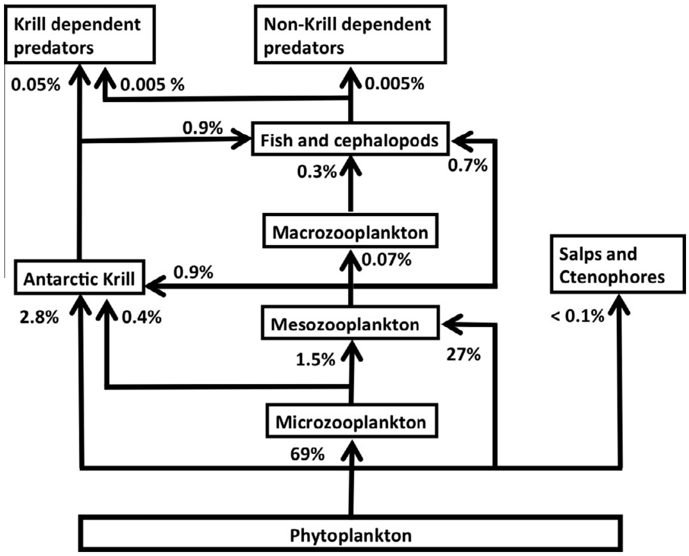

Fig. 6. Summary of the percent transfer of primary production between the pelagic components of the sWAP food web model.

Table 4

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

Simulation GGE	*P*/*B*	Biomass (g C m^{-2})	Diet	EE	PP (g C m^{-2} y^{-1})	Detritus inputs (g C m^{-2} y^{-1})
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
Q/*B*	2.4	1.6	H	0.661	312.3	99
Q/*B*	2.4	1.6	C	0.661	451.5	159
Q/*B*	2.4	3.2	H	0.033	361.7	118
Q/*B*	2.4	3.2	C	0.033	640.1	238

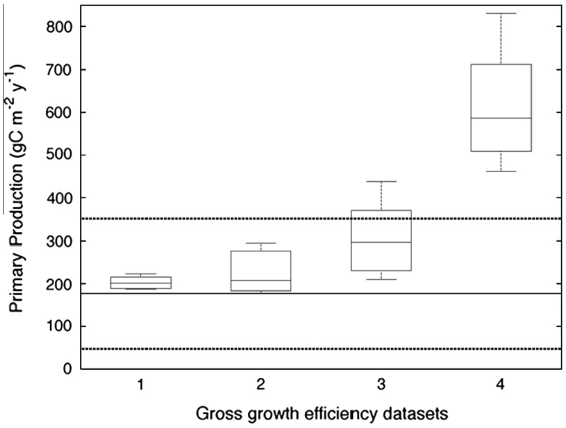

Fig. 7. Simulated estimates of primary production needed to support the south-western Antarctic Peninsula (sWAP) food web obtained using gross growth efficiency values; (1) calculated from production and assimilation efficiencies given in Table 1, (2) given in Banse (1995), (3) given in Priddle et al. (1998), and (4) derived from daily consumption rates (Table A.2). The boxes represent the range of the primary production estimates obtained from all of the simulations that used the indicated gross growth efficiencies. The median (horizontal line) and 25 and 75 percentiles (lower and upper vertical lines) are shown. The average (177 g C m^{-2} y^{-1}, solid line) and minimum and maximum (47 and 351 g C m^{-2} y^{-1}, dashed lines) primary production values estimated from field observations made on the sWAP continental shelf (Ducklow et al., 2007) are shown for comparison.

Table 5

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

Biomass (g C m^{-2})	Predator group with doubled biomass	Surplus/deficit production (%)
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

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

3.3. Environmental change scenarios

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

Redirection of primary production from the adult Antarctic krill to the mesozooplankton group (scenario 3) or to the salps group (scenario 4) also resulted in decreased carbon flow to upper trophic levels, but the response was smaller than in the previous scenarios (Fig. 8e and f). In both scenarios, the largest impacts were on predators with diets consisting primarily of adult Antarctic krill, such as crabeater seals. However, a redirection of adult Antarctic krill consumption to salps resulted in an increase in the production of the benthic invertebrate group, due to a larger flux to the benthic detritus group via sinking fecal material and dead organisms (Table 1).

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

4. Discussion

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

4.1. Southwestern Antarctic Peninsula food web structure

Early studies on the functioning of Southern Ocean marine ecosystems showed that only a small fraction of primary production is converted to biomass of upper trophic level predators (Hempel, 1985; Hill et al., 2006). Estimates of energy flow from the sWAP food web model are consistent with this observation, with only a small fraction of primary production passed to seabirds and marine mammals and the majority of energy remaining as unconsumed production at the lower trophic levels. Microzooplankton and mesozooplankton consume the majority of primary production but only a small fraction of their secondary production is consumed and transferred to higher trophic levels. Similarly, in a Ross Sea food web model, microzooplankton consumed about 90% of water column primary production (Pinkerton et al., 2010). A low *EE* value for groups with high biomass and low trophic level (e.g., the micro, meso and macrozooplankton groups in the sWAP model) could indicate that the modeled ecosystem is far from its

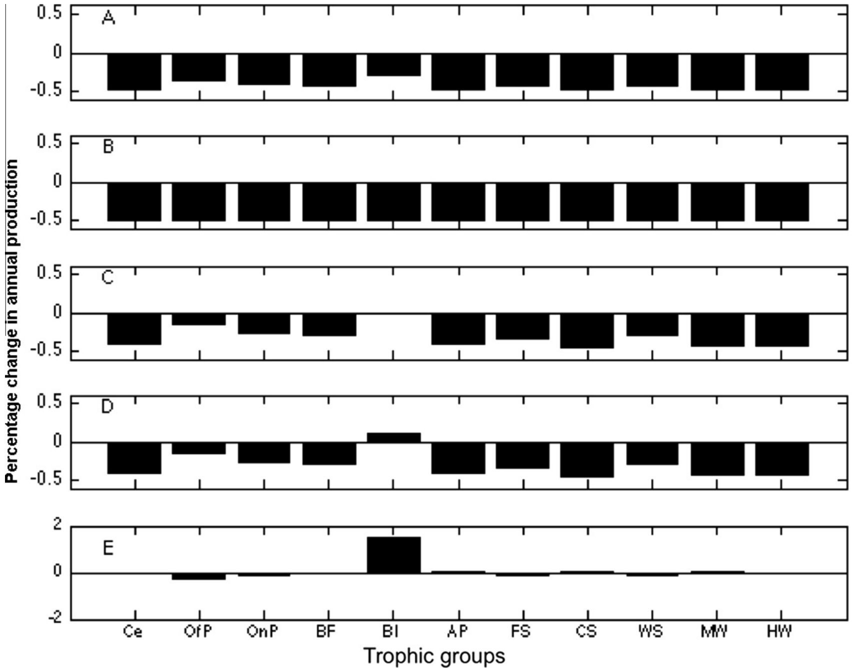

Fig. 8. Change in productivity, estimated relative to the reference simulation, of the southwestern Antarctic Peninsula (sWAP) higher trophic level components for (A) a 50% reduction in annual production of large phytoplankton; (B) a re-direction of 50% of small and large phytoplankton production from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

carrying capacity. Mesozooplankton and macrozooplankton groups also had high biomass but low *EE* values in a model for the South Georgia food web (Hill et al., 2012).

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

Consumption of primary and secondary production by the adult Antarctic krill in the sWAP model is small in comparison to the other zooplankton groups. However, most of the energy flow to higher trophic levels is through adult Antarctic krill, which therefore exert a bottom-up control on the most abundant seabirds and marine mammals. The model-derived estimates of the consumption of Antarctic krill production by pelagic fish, benthic fish and cephalopods indicate the potential importance of these little studied species/groups, similar to the results of other modeling studies of Antarctic food webs (Pinkerton et al., 2010; Hill et al., 2012). Antarctic krill control production of upper trophic level predators at South Georgia (Hill et al., 2012) and in the open ocean regions of the Southern Ocean (Smetacek and Nicol, 2005). In the Ross Sea shelf ecosystem, crystal krill and Antarctic silverfish provide the transfer of energy from primary producers to top predators (Pinkerton et al., 2010). The structure of these Southern Ocean food webs is similar to the 'wasp-waist' ecosystem structure that has been hypothesized for marine ecosystems characterized by low taxonomic diversity in the mid-trophic levels where few species of small planktivorous fish control the transfer of energy to higher trophic levels (Rice, 1995; Bakun, 2006). As in the classic wasp-waist ecosystem structure, the dependence on only one or two species at the intermediate trophic levels, makes the sWAP food web and the other Southern Ocean food webs vulnerable to changes in the biomass of these species.

4.2. Implications of model assumptions and data uncertainty

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

Some comparisons between model results and observational data can be made that allow evaluations of the sWAP food web model. Primary production places a system-wide constraint on the sWAP food web and hence provides an indirect evaluation of the values chosen for model parameters. Primary production estimates have been made for the western Antarctic Peninsula region for almost 50 years and in all seasons (see Table 2 in Smith et al., 1996; Prézelin et al., 2004; Ducklow et al., 2007) and thus provide a consistent metric for assessing the sWAP food web model. The estimates of annual primary production derived from the sWAP model (187–207 g C m^{-2} y^{-1}) fall within the range of observed values of primary production measured on the northern part of the western Antarctic Peninsula in summer (47–351 g C m^{-2} from October to March/April; Ducklow et al., 2007). In addition, Weston et al. (2013) reported a mean summer primary productivity value of 239 g C m^{-2} y^{-1} for the northern Marguerite Bay for 2005–2007. The annual average obtained from the food web model (191 g C m^{-2} y^{-1}) is about 80% lower than the observed mean value for the northern Marguerite Bay (Weston et al., 2013) and 43% lower than the maximum observed value (351 g C m^{-2} y^{-1}; Ducklow et al., 2007) in the northern part of the west Antarctic Peninsula shelf. However, it is about 10% higher than the average observed value (177 g C m^{-2} y^{-1}) from the northern part of the west Antarctic Peninsula shelf. Differences between the observed values and the model-estimated values may be explained by the different time periods included in the estimates. For example, the sWAP food web model estimate is based on annual consumption needs; whereas, the observed primary production values are primarily from the summer. Differences in observed and simulated primary production estimates may also arise because the spatial variability in actual primary production and passive sinking of phytoplankton, which can be important at particular times and locations on the western Antarctic Peninsula shelf (Smith et al., 2006), are not included in the model.

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

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

Similarly, the food web model results are sensitive to biomass estimates. The net-based estimates of Antarctic krill biomass were insufficient to support the consumption needs of top predators; whereas, the acoustically-derived biomass estimates provided a surplus of Antarctic krill after the consumption demands by predators were satisfied. The accurate estimation of krill biomass depends on estimates of density and on correct specification of the Antarctic krill spatial range (Nicol et al., 2000). The krill densities used to convert acoustic backscatter measurements to biomass were based on estimates made specifically for the region included in the sWAP food web model and an analysis of the error introduced by uncertainties showed that the values were within the range of other reported biomass values (Lawson et al., 2008b). These biomass estimates average over krill aggregations because Antarctic krill were assumed to be present throughout the model region. Acoustic surveys in the region around Marguerite Bay showed that Antarctic krill biomass tended to be concentrated along the shelf break and the inner shelf regions (consistent with Atkinson et al., 2008), and that a few large swarms accounted for a disproportionate amount of the total biomass (Lascara et al., 1999; Lawson et al., 2008a). Therefore, the effective spatial range for Antarctic krill is likely less than the model region. Accurate biomass estimates, especially for species or groups that exert a primary control on system productivity, are a priority for food web models such as the one used in this study.

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

4.3. Possible future changes in food web structure – model implications

The western Antarctic Peninsula region is undergoing rapid climate change, the manifestations of which are warming ocean temperatures (Meredith and King, 2005), reduction in sea ice extent (Smith and Stammerjohn, 2001; Stammerjohn et al., 2008), and shortening of sea ice duration (Stammerjohn et al., 2008). The relative abundance of salps and Antarctic krill has been correlated with winter sea ice extent, with salps replacing krill during times of reduced sea ice (Loeb et al., 1997). The increase in the abundance of chinstrap penguins (*Pygoscelis antarcticus*) relative to Adélie penguins along the northern portion of the western Antarctic Peninsula has been linked to changes in the availability of their primary prey species, Antarctic krill and Antarctic silverfish (Schofield et al., 2010; Trivelpiece et al., 2011). However, Lynch et al. (2012) show that the changes are more complex and in fact Adélie penguin numbers have been growing in the sWAP, seemingly in response to loosening of the pack ice and increased availability of suitable nesting habitat as glaciers retreat, a prediction of Ainley et al. (2010).

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

In simulations that reduced the production of Antarctic krill by redirecting primary production to microzooplankton and salps (which are not consumed by top predators) a proportionate decrease in the production of fish, cephalopods, seabirds and marine mammals occurred, indicating that this trophic pathway is not effective in channeling energy to upper trophic levels. Thus, a reduction in Antarctic krill biomass and/or changes in the relative abundance of phytoplankton may result in a reorganization of the sWAP food web that favors top predators that can take advantage of open water, such as chinstrap penguins (Trivelpiece et al., 2011) and southern elephant seals (*Mirounga leonine*) (Costa et al., 2010).

5. Summary and conclusions

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

The simulated sWAP food web sustains the top predator biomass primarily by consumption of a single prey species, Antarctic krill. Trophic pathways through alternative zooplankton groups and through fish provide a significantly smaller contribution to the production of seabirds and marine mammals. The dependence of the upper trophic level predators on a single prey makes the current sWAP food web vulnerable to changes in this food source. Antarctic krill are long-lived (4–7 years, Ikeda and Thomas, 1987) and, as a result, respond to environmental cycles with scales beyond seasonal (Smetacek and Nicol, 2005). The cumulative effects of longer-term environmental changes, particularly decreasing sea ice, exert controls on the distribution and availability of this important prey and predator in the sWAP food web. For this system, the additive effects of bottom-up resource control through changes in phytoplankton assemblages (Antarctic krill prey) and the top down effects of consumers of Antarctic krill may amplify the effects of climate change on the sWAP food web. Thus, end-to-end models that include food web interactions, biogeochemical cycling, and environmental controls are the next step in developing scenarios for projections of the future state of the sWAP ecosystem.

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Appendix A

See Tables A.1–A.3.

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

Trophic group	Species/group	P/B References	Diet References
Microzooplankton	Dinoflagellates, aloricate oligotrichs, tintinnids, other ciliates and sarcodine	S. Strom, pers. comm.	S. Strom, pers. comm.; Froneman et al., 1996; Froneman and Perissinotto, 1996
Mesozooplankton	*Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei*, *Ctenocalanus* spp.	Voronina et al., 1980a,b	Hopkins, 1985; Pakhomov et al., 1997; Pasternak and Schnack-Schiel, 2001; Swadling et al., 1997
Macrozooplankton	*Paraeucheta* spp.., Ostracods	Voronina et al., 1980a; Fransz and Gonzalez, 1995	Pakhomov and Froneman, 2004; Hopkins, 1985; Øresland and Ward, 1993; Øresland, 1995; Pakhomov and Perissinotto, 1996
Antarctic krill larvae	*Euphausia superba*	Taki, 2006	Ross et al., 2000; Meyer et al., 2003, 2009; Ju and Harvey, 2004; Daly, 2004; Töbe et al., 2010
Antarctic krill adults	*Euphausia superba* >15 mm	Taki, 2006	Kawaguchi et al., 1986; Tanoue and Hara, 1986; Price et al., 1988; Kopczynska, 1992; Atkinson and Snÿder, 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	*Euphausia crystallorophias; Tyssanoessa macrura*	Taki, 2006	Hopkins, 1985
Salps	*Salpa thompsoni*	Pakhomov et al., 2002	Hopkins, 1985; Pakhomov et al., 2006
Ctenophores	*Callianira antarctica*	Pakhomov et al., 2002	Ju et al., 2004; Moline et al., 2004; Scolardi et al., 2006;
Cephalopods	Glacial squid (*Psychroteuthis glacialis*)	Aydin et al., 2007	Rodhouse and White, 1995; Rodhouse and Nigmatullin, 1996; Phillips et al., 2001; Collins and Rodhouse, 2006
Off-shelf pelagic fish	*Electrona antarctica*	Greely et al., 1999	Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov et al., 1997; Barrera-Oro, 2002; La Mesa et al., 2004; Bushula et al., 2005
On-shelf pelagic fish	*Pleuragramma antarcticum*, *Trematomus eulepidotus*, *Trematomus scotti*, *Chaenodraco wilsoni*, *Bathyraja maccaini*, *Trematomus loennbergii*	Hubold, 1992	Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov et al., 1997; Barrera-Oro, 2002; La Mesa et al., 2004; Bushula et al., 2005
Benthic fish	Nototheniidae, Channictidae, Bathydraconidae, Rajidae, Artedraconidae, Zoarcidae		Eastman, 1985; Casaux et al., 1990; Kock, 1992; Pakhomov et al., 1997; Barrera-Oro, 2002; La Mesa et al., 2004; Bushula et al., 2005
Benthic Invertebrates	HOLOTUROIDEA; ASTEROIDEA: *Odonaster validus*, *Acodontaster conspicus*; OPHIUROIDEA: *Ophloceres incipens*, *Ophionotus victoriae*; POLYCHAETA	Jarre-Teichmann et al., 1997	Jarre-Teichmann et al., 1997
Adelie penguin	*Pygoscelis adeliae*	Ballerini et al., 2009	Ainley et al., 1992, 2003; Ainley, 2002; Fraser and Hofmann, 2003; Volkman et al., 1980
Flying seabirds	Snow petrel (*Pagodroma nivea*), Antarctic fulmar (*Fulmarus glacialoides*), cape petrel (*Daption capense*), south polar skua (*Catharacta maccormicki*), black-browed albatross (*Diomedea melanophris*)	Ratcliffe et al., 2002; Jenouvrier et al., 2003; Rolland et al., 2010	Ainley et al., 1992; Ainley et al., 1994; Xavier et al., 2003
Crabeater seal	*Lobodon carcinophagus*	Bengston and Siniff, 1981	Øristland, 1977; Siniff et al., 2008
Weddell seal	*Leptonychotes weddellii*	Hadley et al., 2007	Green and Burton, 1987; Ponganis and Stockard, 2007; Ainley and Siniff, 2009
Minke whale	*Balaenoptera acutorostrata*	Ohsumi, 1979a,b	Leatherwood and Randall, 1983; Ichii and Kato, 1991; Ichii et al., 1998
Humpback whale	*Megaptera novaeangliae*	Ohsumi, 1979a,b	Kawamura, 1980

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

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
Macroooplankton	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

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

Consumers		Producers																		
		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

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2013.11.007.

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