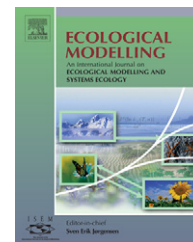


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Preliminary trophic model of the Antarctic Peninsula Ecosystem (Sub-area CCAMLR 48.1)

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ABSTRACT

Species, biomasses, production rates, distribution and other aspects of the community structure have been studied in the Antarctic Ecosystem; however there are no integrated models that explain mass transfer at the spatial mesoscale.

Even though the Antarctic Ecosystem as a whole has been identified as a functional unit, subsystems could be identified and characterized, among which, the Antarctic Peninsula stands out for its particular geography, oceanography and trophic web.

The aim of this work is to construct a mass balanced model describing the main trophic interactions of this community. The model is built using the software Ecopath with Ecosim 5.0, which yields a representation of the trophic web and estimations of global ecosystem properties.

Phytoplankton, zooplankton and krill accounted for most of the mass flow. Flows to the trophic level II (TL II; detritivores and herbivores) were attributed to zooplanktonic and benthic organisms mainly. Flows to the TL III were explained by fish, birds (flying birds and penguins), *Balaenoptera acutorostrata* and baleen whales. Flows to the TL IV were dominated by some fish, birds (flying birds and penguins) and mammals. Finally, in TL VI, the flows were dominated by *Orcinus orca*. *O. orca* was the top predator in the ecosystem with a TL of 4.88, followed by *Physeter catodon* (4.63) and *Hydrurga leptonyx* (4.62). Krill was found at the intermediate TL (2.33). Resulting ecosystem indexes (e.g. total transfer efficiency, connectance index, etc.) were consistent and characteristic of ecosystems of high temporal and spatial variability.

The model gives a comprehensive description of the food web dominated by phytoplankton–krill–top predators chain, and complemented with alternative food pathways (e.g. through *Electrona antarctica*), which together gives an enhanced complexity to the system. Despite the limitations of the model in data gaps, particularly for winter season, grouping of functional groups, steady state assumptions, etc., it improves the description of the trophic structure and ecosystem functioning of the Antarctic Peninsula and highlights gaps in knowledge.

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1. Introduction

The study of ecosystems based on the behaviour and dynamic of biological components, could result in a better description of its trophic structure or food web. A trophic web, understood as the web of interactions that occur among the components of the community, presumes dependence between predators and preys, as well as competition between two or more predators for a common, limiting food resource (Connell, 1961; Stiling, 1996; Ricklefs and Miller, 2000). A correct representation of predation–competition interaction processes allows the prediction of the behaviour of each component and the dynamic of the whole community when changes in any of its components occur.

The ecosystem structure, its functioning, interactions among species and its biological sustainability (Odum, 1972) can be described by the Ecopath mass balance model (Christensen and Pauly, 1995) based on the assumption that predation and competition are significant factors in the community structure.

The Antarctic Ecosystem as a whole is a complex ecosystem, whose food web is centered around a krill species (*Euphausia superba*; Laws, 1985; Verity and Smetacek, 1996; Reid, 2001), a keystone prey item of a wide range of organisms such as birds, fish and whales (Hardy and Gunther, 1936; Marr, 1962; Croll and Tershy, 1998; Tinan, 1998). Nevertheless, sub-zones and subsystems have been identified in the Antarctic Circumpolar region based on oceanographic characteristics (Knox, 1994) and trophic webs (Hempel, 1985). The Antarctic Peninsula stands out by its particular oceanography, geography (Knox, 1994), trophic web (Hempel, 1985), large and constant amount of krill over time (Nicol and Endo, 1999; CCAMLR, 2000), and for being the principal area of spawning and feeding of krill (Marr, 1962). It is also the area where industrial krill fishing has been concentrated since 1970 (CCAMLR, 2000). This study concentrates on the identification of the main trophic interactions of the trophic web for this unique sector of the Antarctic, where mass balance models are still needed.

The study intends to synthesize extensive literature information ranging from phytoplankton to detritivorous up to penguins and whales, in order to improve the understanding of the interactions between the principal biological components. It aims as well, to obtain information on the global properties and trophic structure of the ecosystem, in order to predict eventual changes resulting from natural modifications (e.g. regime shifts, global climatic change, etc.) and human activities (fisheries, pollution, etc.).

2. Methodology

2.1. Mass balanced ecosystem model with ecopath

The Ecopath model was developed to estimate biomass and food consumption of the various components (species or groups of species) of aquatic ecosystems, and after improvements derived from theoretical approaches (e.g. Ulanowicz, 1986 fide Christensen et al., 2000) is utilized to examine

trophic flows between compartments. Instead of adopting the original steady state assumption of mass balance, parameterization is based over an arbitrary time period (usually 1 year).

The first Ecopath equation describes how the production term for each group (*i*) can be split in components (Christensen et al., 2000):

$$\begin{aligned} \text{production} = & \text{catches} + \text{predation mortality} \\ & + \text{biomass accumulation} + \text{net migration} \\ & + \text{other mortality} \end{aligned} \quad (1)$$

This conceptual model could be partially expressed in the following equation, which was used in this study

$$B_i \left(\frac{P}{B} \right)_i EE_i = Y_i + \sum_{j=1}^n B_j \left(\frac{Q}{B} \right)_j DC_{ij} \quad (2)$$

where B_i and B_j are biomasses (of the prey *i* and predator *j*), P/B is the biomass production rate, equivalent to the total mortality rate (Z ; Allen, 1971), EE_i is the proportion of the group production *i* which is consumed, Y_i is the total fishery catch rate of *i* ($Y = FB$; where F is the mortality rate for fishing), Q/B is the food consumed by a biomass unit of *j*, and DC_{ij} is the contribution of *i* in the diet of *j* in mass terms. In this equation biomass accumulation and net migration are ignored.

The inputs of the model varied according to the availability and quality of data.

For the functional groups with reliable sources of biomass (B) data (e.g. benthic epifauna, squids, marine mammals), the model inputs were (beside the biomass), the contribution of all items of the diet of each functional group *i* (Table 1), the production/biomass ratio (P/B) and the consumption/biomass ratio (Q/B). The outputs of the model for these groups were ecotrophic efficiency (EE), production/consumption ratio (P/Q) and omnivory index (OI), all defined in Table 2.

For the functional groups lacking estimates of biomass data, or when those were inconsistent in the literature, the chosen inputs were the Q/B ratio, P/Q ratio and EE instead of B and P/B . The outputs of the model, for these functional groups therefore were biomasses, P/B ratios and OI .

The Ecopath model provides several other indexes to characterize the ecosystem structure, functioning and stability. Among those are the total system throughput, total primary production and connectance index (Table 2). Furthermore, definition of trophic levels could be fractional, according to the proportion of items consumed (e.g. plants versus animal items; Table 2).

The Ecopath model was adjusted to the Antarctic Peninsula by choosing and defining functional groups according to their behaviour similarities, by selecting data according to availability and reliability of the sources, and by assuming no biomass accumulation, no fishing mortality and nor in-, nor out-migration. The mass balance was computed for parameters averaged over a year.

Table 1 – Matrix of diet composition (DC) of principal components of the Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model

No.	Prey	PREDATOR																									
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1	Phytoplankton	(0.90)	(0.80)	(0.70)	(0.90)	0.05	(0.11)	–	–	–	–	(0.10)	(0.09)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Zooplankton	(0.10)	(0.20)	0.30	(0.1)	(0.01)	–	(0.19)	(0.48)	(0.22)	0.09	(0.10)	(0.16)	(0.20)	(<0.01)	(0.15)	(0.02)	–	(0.02)	–	(<0.01)	–	(0.01)	(0.01)	(0.02)	–	–
3	Krill larvae	–	–	–	(<0.01)	(<0.01)	–	(0.16)	(0.10)	(0.01)	(0.10)	(0.38)	(0.20)	0.11	(0.02)	(0.05)	(0.03)	–	(<0.01)	–	(0.01)	(0.25)	0.06	(0.02)	0.08	–	–
4	Krill adult	–	–	–	–	(<0.01)	–	(0.23)	(0.21)	(0.23)	(0.24)	(0.41)	(0.41)	(0.61)	0.09	(0.23)	(0.17)	–	(0.27)	–	(0.03)	(0.66)	(0.54)	(0.37)	(0.16)	–	–
5	Salps	–	–	–	–	(<0.01)	–	(0.02)	(0.02)	(<0.01)	(0.10)	(0.02)	–	–	–	–	(0.03)	–	(0.04)	–	(<0.01)	–	(0.01)	(0.10)	(0.03)	–	–
6	Benthic infauna	–	–	–	–	(<0.01)	(<0.01)	–	(0.09)	0.07	(0.01)	–	(0.3)	–	(<0.01)	(0.02)	–	(<0.01)	(<0.01)	–	(0.01)	–	–	–	–	(<0.01)	–
7	Benthic epifauna	–	–	–	–	–	(0.02)	–	(0.09)	(0.12)	(0.21)	–	(<0.01)	(0.05)	0.08	–	–	(<0.01)	(<0.01)	–	(0.01)	–	–	–	–	(<0.01)	–
8	<i>Notothenia rossii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(0.06)	0.13	(0.02)	0.10	–	–	–	(0.02)	(0.06)	0.04
9	Small demersals	–	–	–	–	–	–	(0.18)	–	(0.10)	(0.21)	–	(0.04)	(0.01)	(0.27)	–	(0.19)	(0.06)	–	(0.06)	(0.04)	(0.02)	(0.04)	(0.03)	(0.02)	(0.06)	0.04
10	Medium demersals	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(0.04)	(0.06)	0.13	(0.02)	(0.10)	(0.02)	(0.04)	(0.01)	–	(0.06)	0.04
11	Large demersals	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(0.04)	(0.06)	0.13	(0.02)	0.10	–	–	(0.01)	–	–	0.04
12	<i>Electrona antarctica</i>	–	–	–	–	–	–	–	–	0.13	–	–	(0.04)	(0.01)	(0.27)	(0.51)	(0.18)	(0.06)	–	(0.06)	(0.04)	(0.02)	(0.04)	(0.22)	(0.27)	(0.04)	0.04
13	Small pelagics	–	–	–	–	–	–	(0.22)	–	(0.10)	(0.21)	–	(0.04)	(0.01)	(0.27)	–	(0.19)	(0.06)	–	(0.06)	(0.04)	(0.02)	(0.04)	(0.22)	(0.27)	(0.04)	0.04
14	Medium pelagics	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(0.04)	(0.06)	0.13	(0.1)	(0.10)	(0.01)	(0.02)	(0.01)	(0.01)	(0.04)	0.04
15	Large pelagics	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(0.04)	(0.06)	(0.14)	0.10	0.10	(0.01)	(0.01)	(0.01)	(0.01)	(0.04)	(0.04)
16	Cephalopods	–	–	–	–	–	–	–	–	<0.01	(<0.01)	–	–	–	(<0.01)	(0.04)	(0.02)	(0.53)	(0.01)	(0.60)	(0.28)	(<0.01)	(0.20)	–	0.12	(0.66)	(0.04)
17	<i>A. gazella</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.06
18	<i>Mirounga leonina</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08
19	<i>L. carcinophagus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08
20	<i>Hydrurga leptonyx</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08
21	<i>L. weddellii</i> + <i>O. Rossii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.08
22	Penguins	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(<0.01)	–	–	(<0.01)	–	–	–	–	–	–	0.10
23	Birds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(<0.01)	–	–	(<0.01)	–	–	–	–	–	–	(0.08)
24	<i>B. acutorostrata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25	Baleen whales	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26	<i>P. macrocephalus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
27	<i>O. orca</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
28	Detritus	–	–	–	–	(0.93)	(0.86)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Values in parenthesis were modified in order to balance the model (–, no trophic interaction). The references are presented in Table 4.

Table 2 – Definition of ecosystem properties and descriptors of functional groups as in Christensen et al. (2000)

Descriptor	Definition
Biomass (B) t km ⁻²	Average value that can be used to represent the biomass of each group
Connectance index (CI)	Ratio of the number of actual links to the number of possible links. Feeding on detritus (by detritivores) is included in the count. The number of possible links in an Ecopath model can be estimated as $(N - 1)^2$, where N is the number of living groups
Consumption/biomass ratio (Q/B) year	Intake of food by a group over a given time period
Ecotrophic efficiency (EE)	Fraction of the production that is used in the system
Finn's cycling index (FCI)	Fraction of ecosystem throughput that is recycled
Mean path length (MPL)	Total number of trophic links divided by the number of pathways
Net system production (NSP) t km ⁻² year ⁻¹	Difference between total primary production and total respiration. The NSP is large in immature systems and close to zero in mature ones
Omnivory index (OI)	Variance of the trophic level of the group of preys of a given consumer. The square root of OI is the standard error of the fractional trophic level
Production/biomass ratio (P/B) year ⁻¹	Equivalent to the instantaneous rate of total mortality used by fisheries biologists
Production/consumption ratio (P/Q)	Is a measure of gross food conversion efficiency
Total primary production (TPP) t km ⁻² year ⁻¹	Summed primary production from all producers
Total system throughput (TST): t km ⁻² year ⁻¹	Sum of all flows in the system. It represents the size of the entire ecosystem (in flows terms; Ulanowicz, 1986). It is estimated as the sum of four flow components: TST = Tot. consumption + Tot. export + Tot. respiration + Tot. flows to detritus
Trophic level (TL)	It refers to its position in a food chain. It is given in integers being TL 1 producers, TL2 herbivores, TL3 carnivores, and so on. In Ecopath fractional TL are used, as suggested by Odum and Heald (1975). Producers and detritus are assigned to TL1 and a TL 1 + [the weighted average of the preys' trophic level] to consumers

2.2. Functional groups

Functional groups were made of individual species, or could integrate developmental stages of a species or

several species. Twenty-eight functional groups were identified (Table 3) within phytoplankton, zooplankton, benthos, fish, cephalopods, pinnipeds, birds, whales and detritus.

Table 3 – Definition of functional groups

No.	Functional group	Components
1	Phytoplankton	Diatoms and dinoflagellates mainly
2	Zooplankton	All zooplankters excluding krill (<i>E. superba</i>) adult and larvae
3	Krill larvae (<i>Euphausia superba</i>)	All developmental stages of krill
4	Krill adult	Adult krill
5	Saps	<i>Salpa thompsoni</i> mainly
6	Benthic infauna	Annelida, mollusca, crustacea and others
7	Benthic epifauna	Echinodermata, crustacea, porifera, cnidaria and others
8	<i>Notothenia rossii</i>	<i>Notothenia rossii</i>
9	Small demersals	Demersal fishes with an asymptotic weight (<i>Winf</i>) less than 100 g
10	Medium demersals	Demersal fishes with <i>Winf</i> between 150 and 4000 g
11	Large demersals	Demersal fishes with <i>Winf</i> more than 8000 g
12	<i>Electrona antarctica</i>	<i>Electrona antarctica</i>
13	Small pelagics	Pelagic fishes with <i>Winf</i> less than 100 g
14	Medium pelagics	Pelagic fishes with <i>Winf</i> between 100 and 1000 g
15	Large pelagics	Pelagic fishes with <i>Winf</i> more than 1000 g
16	Cephalopods	Squids (e.g. <i>Moreoteuthis</i> spp. and <i>Kondakovia</i> spp.)
17	<i>Archtocephalus gazella</i>	<i>Archtocephalus gazella</i>
18	<i>Mirounga leonina</i>	<i>Mirounga leonina</i>
19	<i>Lobodon carcinophagus</i>	<i>Lobodon carcinophagus</i>
20	<i>Hydrurga leptonyx</i>	<i>Hydrurga leptonyx</i>
21	<i>Leptonychotes weddellii</i> and <i>Ommatophoca rossii</i>	<i>Leptonychotes weddellii</i> and <i>Ommatophoca rossii</i>
22	Penguins	<i>Aptenodites forsteri</i> , <i>A. patagonica</i> , <i>Pygoscelis adeliae</i> , <i>P. papua</i> , <i>P. antarctica</i> and <i>Eudyptes chrysolophus</i>
23	Birds	Birds whose distributions or colonies were found in the Antarctic Peninsula
24	<i>Balaenoptera acutorostrata</i>	<i>Balaenoptera acutorostrata</i>
25	Baleen whales	<i>B. borealis</i> , <i>B. musculus</i> , <i>B. physalus</i> and <i>Megaptera novaeangliae</i>
26	<i>Physeter macrocephalus</i>	<i>Physeter macrocephalus</i>
27	<i>Orcinus orca</i>	<i>Orcinus orca</i>
28	Detritus	All organic matter not included in the other functional groups

Table 4 – References used for the construction of the diet matrix of the Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model

Group	References
Zooplankton	(Hopkins, 1985a,b; Hopkins et al., 1993; Croxall et al., 1999; Pakhomov et al., 1999)
Krill	(Hopkins, 1985a,b; Schnack, 1985; Miller and Hampton, 1989; Hopkins et al., 1993; Hill et al., 1996; Kawaguchi and Takahashi, 1996; Opalinski et al., 1997; Perissinotto et al., 1997; Croxall et al., 1999; Cripps and Atkinson, 2000; Perissinotto et al., 2000)
Salps	(Hopkins, 1985a; Hopkins et al., 1993; Perissinotto and Pakhomov, 1998a; Perissinotto and Pakhomov, 1998b)
Benthos	(Hopkins, 1985a; Jarre-Teichmann et al., 1997)
Penguins	(Boveng et al., 1991; Veit et al., 1995; Hill et al., 1996; Reid et al., 1996; Bost et al., 1997; Croll and Tershy, 1998; Croxall et al., 1999; Reid and Croxall, 2001)
Birds	(Veit et al., 1995; Reid et al., 1996; Coria, 1997; Casaux et al., 1998b; Cherel and Kooyman, 1998; Hahn, 1998; Lorentsen et al., 1998; Croxall et al., 1999; Reid and Croxall, 2001)
Cephalopods	(Nemoto et al., 1988; Kozlov, 1995; Croxall et al., 1999; Phillips et al., 2001)
Fish	(Duhamel and Hureau, 1985; Hopkins, 1985a; Barrera-Oro and Casaux, 1990; Hopkins et al., 1993; Kozlov, 1995; Daneri, 1996; Takahashi and Iwami, 1997; Casaux, 1998; Pakhomov, 1998; Pakhomov et al., 1999; Vacchi et al., 2000)
Pinnipeds	(Doidge and Croxall, 1985; Todd, 1988; Boyd et al., 1994; Daneri, 1996; Reid et al., 1996; Cherel et al., 1997; Burns et al., 1998; Casaux et al., 1998a; Cherel and Kooyman, 1998; Croll and Tershy, 1998; Klages and Bester, 1998; Pauly et al., 1998; Brown et al., 1999; Daneri and Carlini, 1999; Daneri et al., 2000; Reid and Croxall, 2001)
Whales and Orca	(Nemoto et al., 1988; Pauly et al., 1998)

2.3. Data sources

The biomasses, production rates, consumptions, diets, P/B ratios and Q/B ratios were obtained directly or computed from literature sources (Tables 4 and 5). P/B ratios for the fish groups were calculated through Pauly's (1980; $P/B = Z = k^{0.65} L_{\infty}^{-0.279} T_c^{0.463}$) general equation relating natural mortality

(Z), growth parameters (k , L_{∞}) and temperature (T_c). Available data were inputs of the model and are marked in parenthesis in Table 6, whereas outputs of the model are depicted without parenthesis.

In order to balance the model, input data for each functional group as depicted in Table 6, had to be adjusted (within the range of values given in the literature), until outputs fell

Table 5 – References used for the input data matrix of the Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model

Group	References
Phytoplankton	(El-sayed, 1987; Kottmeier and Sullivan, 1987; El-Sayed, 1988; Holm-Hansen et al., 1989; Walker and Smith, 1990; Holm-Hansen and Mitchell, 1991; Villafañe et al., 1992; Holm-Hansen and Villafañe, 1993; Villafañe and Holm-Hansen, 1993; Figueiras et al., 1994; Priddle et al., 1994; Kang and Lee, 1995; Villafañe et al., 1995; Villafañe et al., 1996; Dubischar and Bathmann, 1997; Froneman et al., 1997; Priddle et al., 1998; Smith et al., 1998a; Smith et al., 1998b; Kelley et al., 1999; Dierssen et al., 2000)
Zooplankton	(Voronina et al., 1981; Duhamel and Hureau, 1985; Hopkins, 1985a,b; Boysen-Ennen et al., 1991; Wormuth et al., 1992; Schnack-Schiel and Mujica, 1994; Rudjakov, 1996; Siegel and Harm, 1996; Dubischar and Bathmann, 1997; Alcaraz et al., 1998; Hernández-León et al., 1999; Pakhomov et al., 1999; Ward and Shreeve, 1999)
Salps	(Dubischar and Bathmann, 1997; Alcaraz et al., 1998; Le Fèvre et al., 1998; Perissinotto and Pakhomov, 1998b; Perissinotto and Pakhomov, 1998a; Chiba et al., 1999)
<i>E. superba</i>	(Ivanov, 1970; Hampton, 1985; Everson, 1988; Daly, 1990; Everson and Goss, 1991; Siegel, 1991; Agnew, 1992; Hewitt and Demer, 1992; Trathan et al., 1992; Wormuth et al., 1992; Agnew and Marín, 1994; Schnack-Schiel and Mujica, 1994; Buchholz et al., 1996; Kawaguchi and Takahashi, 1996; Brierley et al., 1997; Brierley et al., 1999a; Brierley et al., 1999b; Lascara et al., 1999; Brierley and Watkins, 2000; CCAMLR, 2000; Cruzin-Roudy, 2000; Reid, 2001)
Benthos	(Gallardo and Castillo, 1969; Jazdzewski et al., 1986; Gallardo, 1987; Arntz et al., 1992; Galéron et al., 1992; Gerdes et al., 1992; Arntz and Gallardo, 1994; Barnes, 1995a,b; Brey and Gerdes, 1997; Jarre-Teichmann et al., 1997; Arnaud et al., 1998; Gutt and Starman, 1998; Fabiano and Danovaro, 1999)
Cephalopods	(Nemoto et al., 1988; Cherel and Weimerskirch, 1999; Gröger et al., 2000)
Fish	(Pauly, 1980; Duhamel and Hureau, 1985; Kellermann and Kock, 1988; Barrera-Oro and Casaux, 1990; Bax, 1991; Kozlov, 1995; Coggan, 1997b; Coggan, 1997a; Kock, 1998; Lourdes et al., 1998; Palomares and Pauly, 1998; Greely et al., 1999; Barrera-Oro et al., 2000)
Birds	(Croxall and Prince, 1979; Croxall, 1984; Ainley, 1985; Bengtson et al., 1991; Croll et al., 1991; Croll et al., 1992; Bengtson and Jansen, 1993; Veit et al., 1993; Bengtson and Boveng, 1994; Orgeira, 1994; Kooyman et al., 1995; Ichii et al., 1996; Trathan et al., 1996; Bost et al., 1997; Croll and Tershy, 1998; Barbraud et al., 1999; Berrow et al., 2000; Gonzalez-Solis et al., 2000; Quillfeldt and Pans-Ulrich, 2000; Burns and Kooyman, 2001; Wilson et al., 2001; Forero et al., 2002)
Pinnipeds	(FAO, 1978; De Master, 1979; Laws, 1979; Bonner, 1982; Ainley, 1985; Doidge and Croxall, 1985; Testa and Siniff, 1987; Bengtson et al., 1991; Boveng et al., 1991; Bengtson and Jansen, 1993; Bengtson and Boveng, 1994; Bester and Wilkinson, 1994; Boyd et al., 1994; Laws, 1994; Boyd et al., 1997a,b; Hofmeyr et al., 1997; Croll and Tershy, 1998; Trites and Pauly, 1998; Boyd, 1999; Bornemann et al., 2000; Guinet et al., 2000; McMahon et al., 2000; Burns and Kooyman, 2001)
Cetaceans	(FAO, 1978; Gambell, 1981; Gulland, 1981; Watson, 1981; Ainley, 1985; Gill and Thiele, 1997; Kasamatsu et al., 1998; Trites and Pauly, 1998; Chaloupka et al., 1999; Perry et al., 1999; Thiele and Gill, 1999; Thiele et al., 2000; Branch and Butterworth, 2001)

Table 6 – Principal outputs of the balanced Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model

No.	Group	TL	B	P/B	Q/B	EE	P/Q	OI
1	Phytoplankton	1.00	(300.00)	(17.58)	–	0.27	–	–
2	Zooplankton	2.11	68.68	(4.50)	15.00	(0.95)	(0.30)	0.11
3	Krill larvae	2.22	14.14	(4.00)	13.33	(0.95)	(0.30)	0.20
4	Krill adult	2.33	105.35	(1.00)	4.00	(0.95)	(0.25)	0.26
5	Salps	2.11	(1.00)	3.60	(12.00)	0.48	(0.30)	0.11
6	Benthic infauna	2.02	6.00	(0.60)	2.40	(0.95)	(0.25)	0.02
7	Benthic epifauna	2.02	(30.00)	(0.40)	2.00	0.38	(0.20)	0.02
8	<i>Notothenia rossii</i>	3.62	0.23	0.32	(2.11)	(0.95)	(0.15)	0.23
9	Small demersals	3.15	3.35	1.33	(5.31)	(0.95)	(0.25)	0.01
10	Medium demersals	3.51	2.08	0.66	(3.32)	(0.95)	(0.20)	0.24
11	Large demersals	3.61	0.25	0.29	(1.94)	(0.95)	(0.15)	0.27
12	<i>Electrona antarctica</i>	3.13	10.25	1.97	(7.17)	(0.95)	(0.28)	0.15
13	Small pelagics	3.24	3.76	1.25	(5.00)	(0.95)	(0.25)	0.25
14	Medium pelagics	3.29	1.15	0.61	(3.05)	(0.95)	(0.20)	0.04
15	Large pelagics	3.98	2.76	0.25	(1.68)	(0.95)	(0.15)	0.16
16	Cephalopods	3.74	(2.79)	(3.10)	10.33	0.18	(0.30)	0.24
17	<i>A. gazella</i>	4.03	(0.05)	0.90	(9.00)	0.01	(0.10)	0.23
18	<i>M. leonina</i>	4.60	(0.00)	0.70	(7.00)	0.14	(0.10)	0.07
19	<i>L. carcinophagus</i>	4.16	(0.04)	0.90	(9.00)	0.01	(0.10)	0.43
20	<i>H. leptonyx</i>	4.62	(0.01)	0.70	(7.00)	0.08	(0.10)	0.07
21	<i>L. weddellii</i> + <i>O. rossii</i>	4.50	(0.00)	0.90	(9.00)	0.16	(0.10)	0.17
22	Penguins	3.39	(5.53)	1.29	(12.85)	0.00	(0.10)	0.09
23	Birds	3.78	(0.08)	1.00	(10.00)	0.02	(0.10)	0.37
24	<i>B. acutorostrata</i>	3.76	(0.00)	(0.09)	(6.29)	0.05	0.01	0.24
25	Baleen whales	4.01	(0.17)	(0.09)	(5.03)	0.02	0.02	0.26
26	<i>P. macrocephalus</i>	4.63	(0.01)	(0.05)	(4.07)	0.00	0.01	0.06
27	<i>O. orca</i>	4.88	(0.00)	(0.05)	(7.76)	0.00	0.01	0.22
28	Detritus	1.00	(2.00)	–	–	0.01	–	0.25

The values in parenthesis were input data to the model. TL = trophic level, B = biomass, P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency, P/Q = production/consumption; OI = index of omnivory. Biomass in t km^{-2} ; all others in year^{-1} (except EE and OI that are dimensionless). The references are presented in Table 5.

within the expected range. The expected values of EE are between 0 and 1, of P/Q are between 0.1 and 0.3 and expected range for P/Q varies according to the organism (Christensen et al., 2000). Average values from the literature were used at the starting point of model balancing.

Diet composition data obtained from the literature (Table 4) was organized in a matrix indicating the proportion of items contributing to the diet of every functional group. Data were also adjusted through a similar procedure until output parameters fell within the expected ranges (Table 1).

Although, the model assumed that the biomass remains unaltered over time, hence the parameters represent the annual averages, seasonality was not ignored when winter values were available. Otherwise, P/B, EE and/or P/Q were estimated using winter data from other regions of the Antarctic (i.e. krill larvae, adults, salps), as suggested in Ecopath model construction (Christensen et al., 2000: pp 46). Estimations of EE for zooplankton, krill larvae, krill adult, *Notothenia rossii*, small demersals, medium demersals, large demersals, *E. antarctica*, small pelagics, medium pelagics, large pelagics followed Christensen et al. (2000). Q/B ratios for fish were computed from mortality, food type, morphometrics, temperature and salinity following Palomares and Pauly (1998).

For a seasonally migrating functional group, and although the model assumed no in- nor out-migration, its input biomass was computed from the time proportion (over the entire year) spent in the Antarctic Peninsula.

Mortality of groups subjected to antarctic fisheries were extracted from CCAMLR Fishery Statistic Bulletin (CCAMLR, 2000).

2.4. The study area

The study area is located around the Antarctic Peninsula. Its limits have been previously defined by FAO (Food and Agriculture Organization of the United Nations) and adopted by the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) as Sub-area 48.1 (Fig. 1). The Weddell Sea, South Orkney Islands and South Georgia Island are excluded from Sub-area 48.1 since they have their own characteristics (Knox, 1994; CCAMLR, 2000).

3. Results

3.1. Trophic structure

A compartment model describing the principal trophic interactions in the study area (Fig. 2) was constructed according to the following rules (Christensen et al., 2000): (a) each compartment is located in the Y-axis according to the trophic level that it represents, (b) the area of the compartment is proportional to the biomass of the trophic group, (c) the flows leaving the compartment from the upper part or from both sides cannot split, but they can merge with flows coming from other

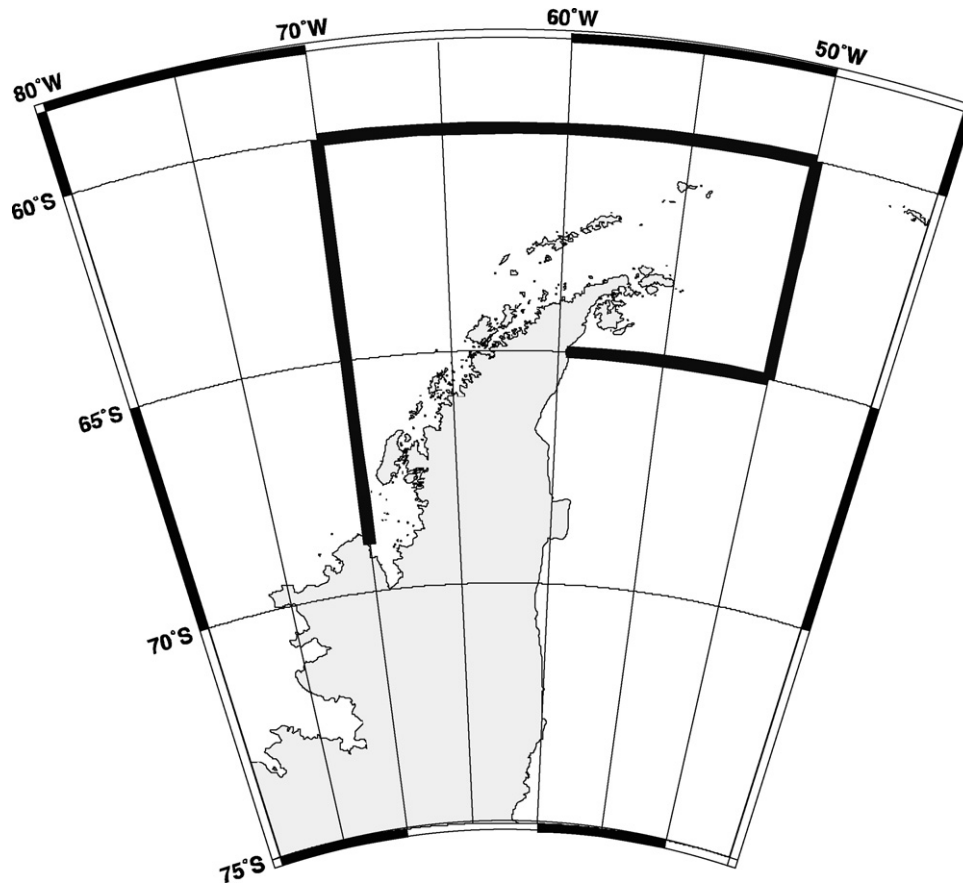


Fig. 1 – Study area, defined by FAO and adopted by the CCAMLR as Sub-area 48.1.

compartments when they have the same destination (compartment), (d) the flows enter a given compartment at its base and (e) all the compartments are balanced; the inputs are equal to the outputs, including respiration.

The biomass and magnitude of the larger flows associated with each compartment are summarized in Tables 6 and 7. Values of predation mortality of a prey by a particular predator are shown in Table 8, whereas pooled flow of biomass at each compartment by predation of all predators are shown in Table 7.

To simplify and improve the understanding of the trophic web with all its interactions between compartments, flows smaller than $0.1 \text{ (t km}^{-2} \text{ year}^{-1})$ were ignored (e.g. *O. orca*; Fig. 2). Fig. 2 includes annual values of biomass of each prey transferred to a given predator, being the sum of these values equal to values given in Table 7.

The principal flows occur at the base of the web, between the first and second TL and are explained mainly by the consumption of phytoplankton by zooplankton ($927.2 \text{ t km}^{-2} \text{ year}^{-1}$), krill larvae ($150.8 \text{ t km}^{-2} \text{ year}^{-1}$) and krill adult ($295.1 \text{ t km}^{-2} \text{ year}^{-1}$). Group predation mortality due to predators are presented in Table 8.

As a result of merging compartments of the model, nine discrete trophic levels were identified. Since the magnitude of the flows occurring in the levels higher than VI represented a small fraction of the flows, they were omitted from the analyses. Most of the flows in TL II (detritivores and herbivores)

were attributed to zooplanktonic organisms (zooplankton, krill larvae, krill adult and salps) and benthic organisms. The flows in the TL III were mainly explained by fish (all the fish groups), birds (flying birds and penguins), *B. acutorostrata* and baleen whales. In TL IV, flows were dominated by some fish (mainly large pelagics and large demersals), birds (flying birds and penguins) and mammals (pinnipeds and whales). Flows in the TL V were clearly dominated by *H. leptonyx*, *Leptonychotes weddellii* + *Ommatophoca rossii* and *Physeter macrocephalus*. Finally, in TL VI, flows were dominated by *O. orca*.

Merging compartments in discrete trophic levels determined flows between trophic levels (Fig. 3). Only ca. 25% of the total primary production ($5275.2 \text{ t km}^{-2} \text{ year}^{-1}$) was consumed by herbivores. The final fate of the remaining 75% was the detritus compartment. The primary and secondary carnivores had transfer efficiencies of 21% and 20%, respectively, which diminished to 10% for the tertiary carnivores and to 5% for the quaternary carnivores (TL VI).

Orcinus orca was the top predator of the ecosystem with a TL of 4.88, followed by *P. macrocephalus* (4.63) and *H. leptonyx* (4.62). Krill was found in an intermediate TL (2.33), separated by almost a complete TL from its closest predator (*E. antarctica*, 3.13).

The estimation of the omnivory indices (Pauly et al., 1993) showed that ca. 60% of the groups had a wide trophic spectrum.

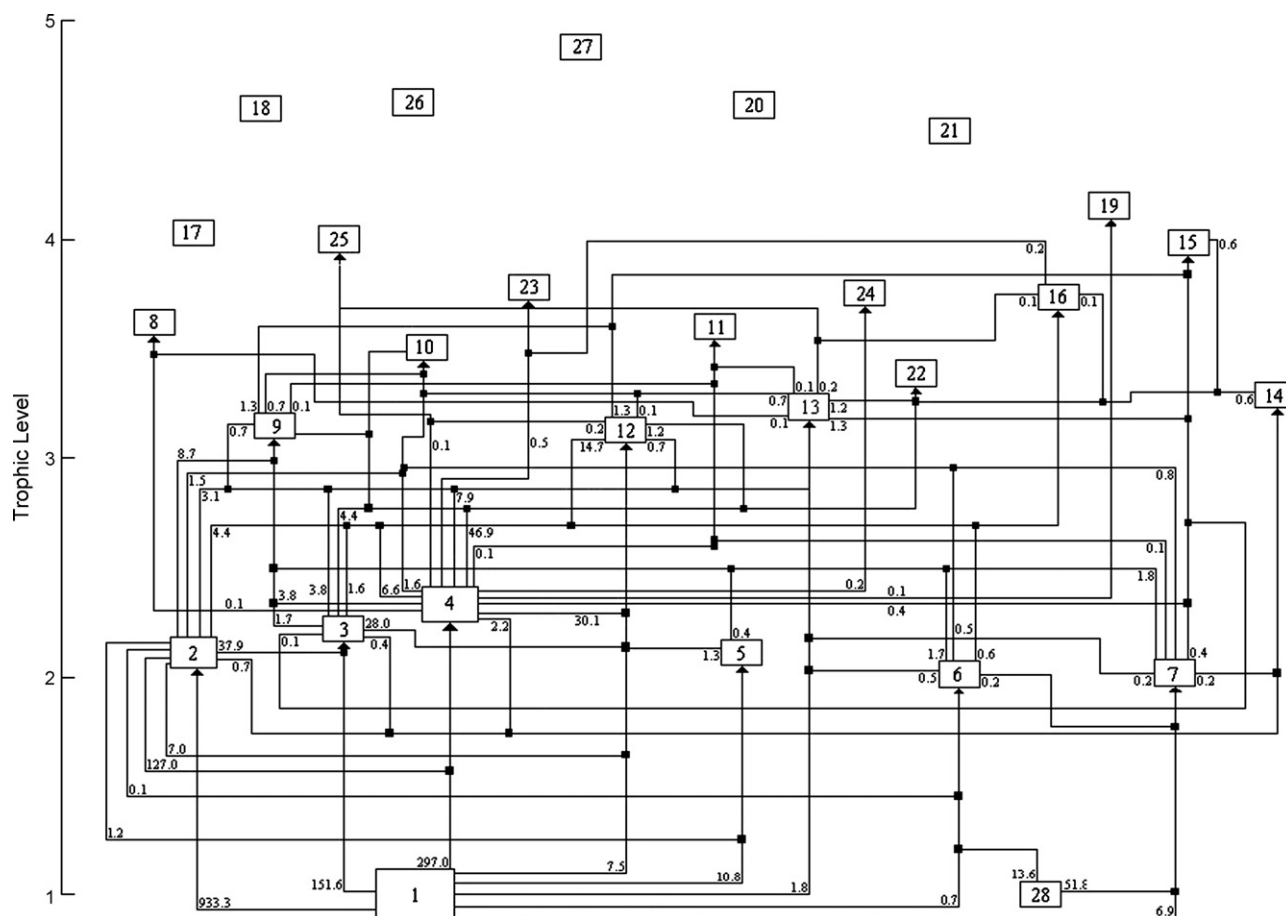


Fig. 2 – Diagram of biomass flow between the Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model's compartments. Each trophic group is represented by a number (Table 1); its position in the axis y is given by its trophic level and the compartment area is a function of the biomass (Table 6). Arrows represent the flows between compartments and the black boxes are flow connectors. Flows are given in $\text{t km}^{-2} \text{ year}^{-1}$. Flows < 0.1 are not presented in the diagram.

The group with the highest consumption rate ($B_i \times Q_i/B_i$) was zooplankton ($193,569.8 \text{ t km}^{-2} \text{ year}^{-1}$), followed by krill adult ($37,760.5 \text{ t km}^{-2} \text{ year}^{-1}$) and krill larvae ($6468.9 \text{ t km}^{-2} \text{ year}^{-1}$). Marine mammals (pinnipeds and cetaceans) showed the minimum food intake, with rates lower than $0.1 \text{ t km}^{-2} \text{ year}^{-1}$. Respiration and Assimilation followed similar tendencies (Table 7). Among fish, the highest rates (respiration, assimilation and food intake) were accounted for by smaller organisms (firstly *E. antarctica*, followed by the small pelagics and small demersals). Lowest rates were attributed to *N. rossii* and large demersals fish. The mass flows towards the detritus compartment were dominated by phytoplankton, followed by zooplankton, krill adult and krill larvae.

3.2. Global ecosystem properties

Some global ecosystem properties (Table 2) were used in order to establish the state of the ecosystem in terms of its maturity (*sensu* Odum, 1969) and for ecosystem comparisons. The total system throughput was $11,884 \text{ (t km}^{-2} \text{ year}^{-1})$ and the net system production was $4575 \text{ (t km}^{-2} \text{ year}^{-1})$.

Approximately 6% of the total system throughput went to respiration and 39.5% to the detritus compartment. The phytoplankton, zooplankton and krill groups were the principal responsible for this flow (Table 7).

The connectance index, which corresponds to the actual number of links in the trophic web with respect to the total possible number of links (Gardner and Ashby, 1970), was 0.303.

4. Discussion

The main goal of this work was to quantitatively describe the food web of the ecosystem of the Antarctic Peninsula, by examining main trophic interactions among 28 functional groups. A vast amount of data coming from many sources was synthesized to obtain a static mass balance of the ecosystem utilizing the Ecopath model. This model is built under several assumptions as pointed out by Christensen et al. (2000).

Model construction and balancing required data adjustments to cope for information gaps. This process is considered satisfactory, as values fell within the range given in the literature. It was the case of input values used. Phytoplankton production seemed too high in the balanced model, however they layed within the recorded range for

Table 7 – Flows from each box of Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model

No.	Group	Respiration output	Predation output	Detritus output
1	Phytoplankton	–	1403.90	3864.99
2	Zooplankton	311.25	294.36	430.56
3	Krill larvae	56.86	53.79	78.66
4	Krill adult	148.51	100.12	175.02
5	Salps	3.60	1.75	6.61
6	Benthic infauna	8.00	3.44	3.09
7	Benthic epifauna	36.00	4.65	19.36
8	<i>Notothenia rossii</i>	0.31	0.09	0.10
9	Small demersals	9.90	4.26	3.83
10	Medium demersals	4.16	1.32	1.45
11	Large demersals	0.33	0.08	0.11
12	<i>Electrona antarctica</i>	38.82	19.18	15.81
13	Small pelagics	10.62	4.50	4.10
14	Medium pelagics	2.12	0.68	0.74
15	Large pelagics	3.04	0.67	0.97
16	Cephalopods	14.43	1.54	12.91
17	<i>A. gazella</i>	0.32	< 0.01	0.14
18	<i>M. leonina</i>	0.02	< 0.01	0.01
19	<i>L. carcinophagus</i>	0.26	< 0.01	0.11
20	<i>H. leptonyx</i>	0.03	< 0.01	0.01
21	<i>L. weddellii</i> + <i>O. rossii</i>	0.01	< 0.01	0.01
22	Penguins	49.74	< 0.01	21.32
23	Birds	0.59	< 0.01	0.25
24	<i>B. acutorostrata</i>	0.34	< 0.01	0.09
25	Baleen whales	0.67	< 0.01	0.19
26	<i>P. macrocephalus</i>	0.03	< 0.01	0.01
27	<i>O. orca</i>	< 0.01	< 0.01	< 0.01

Units in $\text{t km}^{-2} \text{ year}^{-1}$.

the Antarctic Peninsula Ecosystem ($0.1\text{--}4.0 \text{ gC m}^{-2} \text{ day}^{-1}$; ca. $133 \text{ t WW km}^{-2} \text{ year}^{-1}$ to $5333 \text{ km}^{-2} \text{ year}^{-1}$; Smith et al., 1998a; Knox, 1994; Dierssen et al., 2000). The P/B values of krill may also seem too high, however they layed within the range of reported values of adults (0.5; Voronina, 1998) and larval stages and adults (5.0; Siegel, 2000).

Other parameters (as krill biomass) were obtained as outputs of the balanced model since values from the literature were unreliable or inappropriate. These output values fell also within reported ones.

The definition of functional groups, presented conceptual restrictions with regard to the assumptions on similarities among the components (e.g. fish as a function of size; Christensen et al., 2000), feeding behaviour (e.g. baleen whales) or general behaviour (e.g. flying birds versus penguins). Grouping was an unavoidable trade-off constraint of data gaps in order to balance the model. Restriction on this regard, were for instance lumping all phytoplankton species in one group despite of their assumed specific metabolism and growth, and particularly merging in the same primary production compartment both phyto-, micro- and picoplankton. Similar restriction of defining groups could be raised for zooplankton species.

However, and despite of other major restrictions such as ignoring export production, biomass accumulation and fishery export of biomasses, the model could be balanced and rendered coherent and interesting outcomes.

Some features were consistent to previous knowledge, such as the relevance of krill as a keystone component in the transfer of phytoplankton to a wide diversity of top consumers.

This central position of krill in the ecosystem has been widely described in the Antarctic Ecosystem (Hardy and Gunther, 1936; Marr, 1962; Laws, 1985; Verity and Smetacek, 1996; Croll and Tershry, 1998; Tinan, 1998; Reid, 2001). As such, the trophic structure takes the typical wasp-waist shape (Curry et al., 2000), which does not necessarily means that the control of the system is from this central compartment, since both top-down and bottom-up controls may be effectively acting upon this compartment.

Nevertheless, some unexpected deviations outstand, as the presence of major food links, other than through adult krill. Although krill (adult and larvae together) which is located at an intermediate TL (2.33), transferred most of the primary production (58 t km^{-2}) to top consumers, *E. antarctica* (TL 3.13), which is located almost a complete TL higher than krill, becomes the second most important link to top predators as it is a consumer of krill. The model identifies penguin as the main predator of adult krill and *E. antarctica* as the main predator of krill larvae. And since krill larvae and adults were separated in two compartments, *E. antarctica* predation on krill population (larvae and adults) is higher than penguin predation. The role of *E. antarctica* has been raised according to its high density and biomass in the Antarctic (Greely et al., 1999), to be a major consumer of macrozooplankton (krill included) and a major prey of top predators (Greely et al., 1999), including birds (Casaux et al., 1998a,b; Hopkins et al., 1993).

These and other food links resulted in a higher than expected complexity of the ecosystem. Instead of the typical three-link food chain (phytoplankton–krill–top predators), the model identified nine trophic levels. Since biomass flow

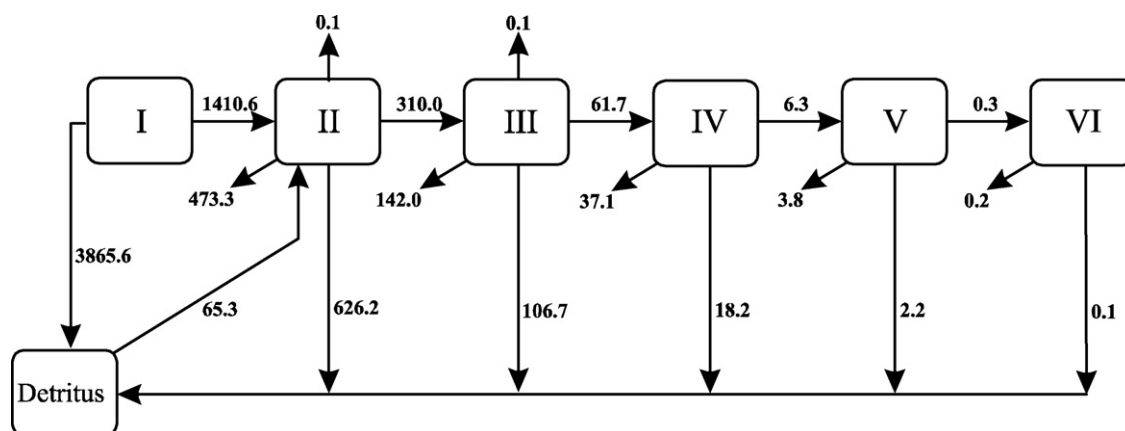


Fig. 3 – Arrangement of groups in discrete trophic levels of the Antarctic Peninsula (Sub-area CCAMLR 48.1) Ecosystem model. Mass transfer from one level to another is presented by arrows. The exportation is shown by \uparrow and the losses by respiration by \downarrow . Flows are given in $\text{t km}^{-2} \text{ year}^{-1}$.

between these TL diminished up the food chain, overall transfer efficiency was low. This is a common feature of marine ecosystems (Christensen and Pauly, 1995; Jarre-Teichmann and Christensen, 1998), and typical of immature ecosystem, in the sense of Odum (1969). Other consistent global features of the model were low connectance index (0.3), low Finn's cycling index (0.01), and high mean path length (2.3).

In immature system there is a trend to loose information, which could be represented as unutilized primary production (Margalef, 1992). The low EE of primary production found in the model indicates that only a small portion was consumed, and most of flowed via detritus and flowed to the benthic compartment. This low EE of the detritus compartment is associated to rather high level of primary production and to the construction of the model itself, which ignored other pelagic pathways of utilization of the detritus (e.g. microbial loop). It was a convenient representation of blooming conditions of the austral spring and summer.

On the other extreme of the web, the EE of marine mammals, particularly cetaceans, and birds were remarkably low, since they have no predators (Knox, 1994). This is characteristic of the top predators whose mortality is accounted for by natural mortality, added to haunting mortality by humans.

It has been widely recognized that the Antarctic Ecosystem is affected by drastic seasonal fluctuations. Trophic interactions are under the effect of drastic changes of light conditions over primary production (Knox, 1994), of ice shelf extension affecting community structure (Ainley et al., 1986; Knox, 1994; Brierley and Watkins, 2000). Although Primary Production is based on microphytoplankton during spring–summer season, nano- and picoplankton could be an important alternative biomass link during the winter season (Garrison et al., 1991). The model did not account for this feature.

Herbivorous zooplankters dominated the system in the beginning of the summer, to change to carnivores at the end of summer. In winter, the zooplankton behaviour changed drastically to: (a) omnivorous/detritivorous diet (e.g. *Calanus propinquus*, *C. simillimus*, *Metridia gerlachei*, *Euchaeta antarctica*, etc.; Oeresland, 1995; Atkinson, 1998), (b) diapause (e.g.

Calanoides acutus; Atkinson, 1998), (c) alternative life cycles associated with the sea-ice (e.g. *Paralabidocera antarctica*, *E. superba*; Kottmeier and Sullivan, 1987; Frazer, 1996; Atkinson, 1998; Cripps and Hill, 1998; Frazier et al., 2002).

Seasonal variability was not considered in detail in the model, but only to estimate average values (e.g. phytoplankton biomass) when seasonal data were available.

The assumption of steady state of this Ecopath model as a most adequate representation of the Antarctic Ecosystem is also questionable, when examining year-to-year fluctuations in ice extent, biomasses of krill, birds and other components of the community (Siegel, 1988; Knox, 1994; Croxall et al., 1999). Krill crashes and its alternations with salps (Knox, 1994; Siegel and Loeb, 1995) have not lead to a community crash. This could be explained by alternative pathways of the biomass flows, which could be examined with Ecosim routine in the future.

In summary, it is clear that this model could be improved with more and better information, and particularly for the winter period and for El Nino and other sources of mesoscale variability. Despite these limitations, it permits a comprehensive description of the general trophic structure and functioning of the Antarctic Peninsula Ecosystem. The role of krill as a keystone component of the web is emphasized, as well as the existence of other alternative food pathways, which gives the system an enhanced complexity. Several ecosystem indexes (e.g. total transfer efficiency, connectance index, etc.) are common to, and consistent with ecosystems of high temporal and spatial variability. Simulations of the EwE for varying inputs parameters including fishing pressure of krill and its top predators, and its time variability may render a better understanding of this unique ecosystem.

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