

Quantifying keystone species complexes: Ecosystem-based conservation management in the King George Island (Antarctic Peninsula)



Marco Ortiz^{a,*,1}, Brenda Hermosillo-Nuñez^{a,b,2}, Jorge González^{a,b,2},
Fabián Rodríguez-Zaragoza^{c,2}, Iván Gómez^{d,e,2}, Ferenc Jordán^{f,g,1}

^a Instituto Antofagasta, Instituto de Ciencias Naturales AvH, Facultad de Recursos del Mar, Universidad de Antofagasta, Antofagasta, Chile

^b Programa de Doctorado en Ciencias Aplicadas: mención Sistemas Marinos Costeros, Universidad de Antofagasta, Chile

^c Laboratorio de Ecosistemas Marinos y Acuicultura (LEMA), Departamento de Ecología, CUCBA, Universidad de Guadalajara, Carretera Guadalajara-Nogales Km. 15.5, Las Agujas Nextipac, Zapopan, 45110 Jalisco, Mexico

^d Instituto de Ciencias Marinas y Limnológicas, Universidad Austral de Chile, Casilla 567, Valdivia, Chile

^e Centro FONDAP de Investigaciones de Ecosistemas Marinos de Altas Latitudes (IDEAL), Chile

^f MTA Centre for Ecological Research, Danube Research Institute, Karolina ut 29, Budapest 1113, Hungary

^g Stazione Zoologica Anton Dohrn, Napoli, Italy

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ABSTRACT

A *keystone species complex (KSC)* is a small set of interacting species that play an outstandingly important role in community organization. Two KSC indices are suggested and have been calculated in the coastal benthic/pelagic ecosystem of Fildes Bay, King George Island (Antarctica). These indices of keystoneity emerge after considering: (1) functional indices based on steady-state and dynamic quantitative trophic models (using bottom-up, mixed and top-down control flow mechanisms); (2) structural indices including bottom-up and top-down control mechanisms, (3) semi-quantitative (qualitative) keystone indices using *loop analysis* (under mixed control); and (4) topological key player indices based on the centrality of node sets in the network. The models constructed and analyzed describe the interactions of the most abundant species and functional groups inhabiting the coastal ecological systems of Fildes Bay. Although our results only represent the transient dynamics of these ecological systems, the KSC indices identified the following trophically connected common core of components: the functional groups of Seastars (top-predators), the herbivorous sea urchin species *Sterechinus neumayeri* and the Phytoplankton (primary producers). The KSC indices for Fildes Bay could facilitate the design and assessment of conservation monitoring, especially when the Antarctic ecosystems are being severely stressed by the direct effects of global warming and UV radiation. A more holistic view of conservation remains difficult because the traditional view is based principally on single species. This imposes an even greater challenge, for global changes accompany the network of interacting species, co-varying with the variables of the natural system.

1. Introduction

The coastal marine ecosystems of the Antarctic Peninsula and South Shetland Islands are inhabited by a rich and dense flora and fauna that are physiologically adapted to colder waters and low-light conditions (Clarke et al., 2004; Gómez et al., 2009). Despite the Antarctic being the largest protected environment on the planet (sensu the *Antarctic Environmental Protocol*), in the past 20 years this continent has indirectly been impacted by global changes, increasing the average air temperature by 4–5 °C along the Antarctic Peninsula (Stark, 1994). This environmental change could have long-term consequences for sea and

land ice dynamics (e.g., glacial melting) (Vaughan and Doake, 1996; Smith and Stammerjohn, 2001), modifying the time of direct light exposure on macroalgae and other organisms. At the same time, ultraviolet (UV) radiation has become another perturbation factor due to the ozone hole in the Antarctic, a consequence of anthropogenic release of atmospheric pollutants (Pessoa, 2012). For these reasons, the Antarctic coastal marine ecosystems are being severely stressed by the direct effects of global warming, which could facilitate biological invasions and reduce the growth of macroalgae species (Richter et al., 2008).

The ecological concept of *keystone species*, introduced by Paine (1969), has become a key issue in numerous research programs in

* Corresponding author.

E-mail addresses: marco.ortiz@uantof.cl, mortizmaoh@gmail.com (M. Ortiz).

¹ MO and FJ wrote the first draft.

² These authors contributed ideas and revisions.

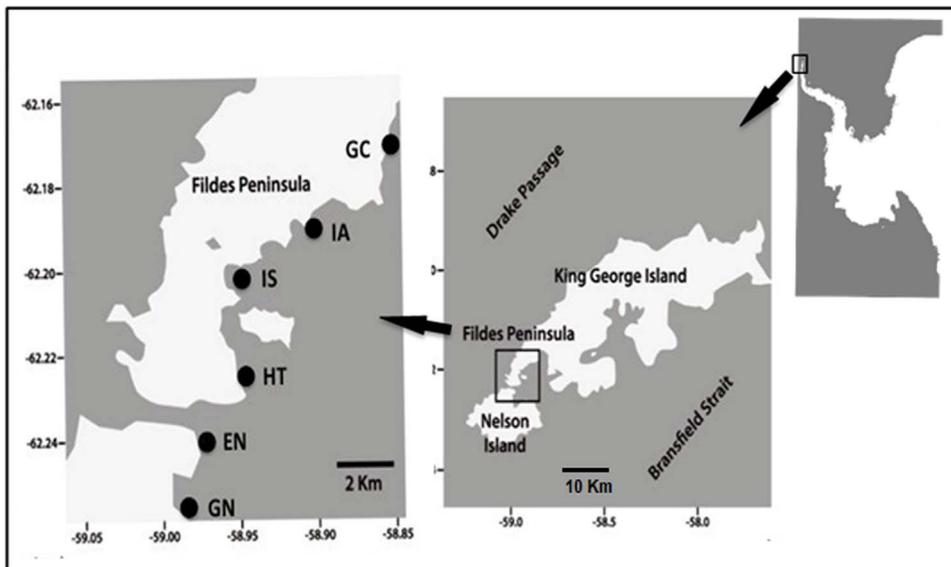


Fig. 1. Study area and sampling stations at Fildes Bay (King George Island, Antarctica) (GC = Glacier Collins, IA = Island Artigas; IS, Island Shoa, HT = Half Three, EN = Estrecho Nelson, and GN = Glacier Nelson).

different communities and ecosystems around the planet (Mills et al., 1993; Power et al., 1996), especially given its direct use in the design and application of conservation management and monitoring measures (Payton et al., 2002; Barua, 2011; Ortiz et al., 2013a,b). Of all the definitions given for *keystone species*, the most widespread and the simplest was proposed by Power et al. (1996): “a species whose effect is large, and disproportionately large relative to its abundance”. Although the concept seems to be sufficiently clear, its determination in communities and ecosystems is not, requiring observations and experiments that include different spatio-temporal scales, levels of organization, and taxonomic groups (Power et al., 1996; Libralato et al., 2006). Even though studies based on field experiments have quantified the strength of interactions by assessing the impacts propagated into networks when the abundance of a single species in a community changes (Paine, 1992; Berlow, 1999), these studies are necessarily limited to a few species, possibly causing an inevitable bias in the identification of *keystone species* (Wootton, 1994; Libralato et al., 2006). At the same time, such external factors as the level of exposure to coastal waves and environmental heterogeneity could result in high variability of the density of *keystone species* in different habitats, calling for better understanding the context-dependency of the keystone role. In turn, some purely experimental studies (Pace et al., 1999) have omitted the propagation of direct and indirect effects, despite the recognized ecological importance of these processes (Wootton, 1994; Patten, 1997; Yodzis, 2001).

Many studies have determined the role that different species play in their ecological systems by using different network indices (Jordán et al., 2007; Luczkovich et al., 2003; Jordán and Scheuring, 2004; Allesina and Bodini, 2005; Libralato et al., 2006; Benedek et al., 2007; Ortiz et al., 2013a; Valls et al., 2015). Such analysis offers a complementary way to address some of the limitations in the experimental identification of key groups. Quantitative trophic models permit estimations of the strength of interactions between species or functional groups by identifying the presence of *keystone species*, which occupy key positions in the networks (Jordán and Scheuring, 2004). At the same time, keystone species can also be determined using semi-quantitative or qualitative loop network analysis. In this case, the key position of a species is a consequence of changes in its self-dynamics, modifying the balance (prevalence) of positive and negative feedbacks, and in turn, the local stability of the network (Ortiz et al., 2013a).

Following field observations (Daily et al., 1993), two independent contributions have proposed methodological extensions towards multispecies approaches to keystones. One was given by Benedek et al. (2007) which is based on the centrality of node sets, and the other proposed by Ortiz et al. (2013a) based on quantitative and semi-

quantitative multispecies trophic models. In both cases, the keystone species complexes (KSCs) consist of a core of species and/or functional groups linked by strong inter-specific interactions. These more holistic concepts could facilitate the design of conservation and monitoring programs in ecosystems since it is not guaranteed that always a single species plays the key role. It is also relevant to mention that over the last few years, multispecies modelling has gained ground due to growing interest in the evaluation, quantification, and prediction of the changes that human activities produce in ecosystems' properties (Ulanowicz, 1997; Pickitch et al., 2004; Benedek et al., 2007; Crowder et al., 2008).

The aim of this work is to determine the *keystone species complex indices* (KSC_i) in the coastal benthic/pelagic ecological systems of Fildes Bay, King George Island (Antarctica) using quantitative and semi-quantitative (qualitative) multispecies trophic models. This holistic index of keystone species emerges after using: (1) functional indices based on quantitative models (using *Ecopath with Ecosim* v. 5.0) considering bottom-up, mixed and top-down control mechanisms; (2) structural indices including bottom-up and top-down controls; (3) a semi-quantitative (qualitative) index based on *Loop Analysis* (mixed control) (Ortiz et al., 2013a), and (4) topological keystone species indices based on the centrality of *n* nodes in the network (Benedek et al., 2007). The identification of keystone species in the Antarctic benthic/pelagic network systems complements existing information describing other attributes of such ecosystems, thereby contributing to conservation ecology, especially when these ecosystems are being stressed by global change.

2. Material and methods

2.1. Study area

Fildes Bay is located at King George Island (South Shetland Islands), off the coast of the Antarctic Peninsula (Fig. 1). During austral winter (July–September), the surface of this bay and the coastal areas regularly freeze. After late October, the sea begins cracking and floating ice reaches the shore. During austral summer of 2013, 2014 and 2015 were carried out field studies to assess the richness, diversity and the community structure of subtidal benthic habitats. Six subtidal sites within Fildes Bay were sampled from 5 to 30 m depth using 8 quadrats of 0.5 × 0.5 m. This sampling allowed directly estimating the average biomass, density and food sources of the macrobenthic species (Fig. 1). The subtidal benthic communities are dominated by the brown macroalgae *Himmantothallus grandifolius* and *Desmarestia anceps*, the red algae *Gigartina skottsbergii*, *Trematocarpus antarcticus* and *Plocamium*

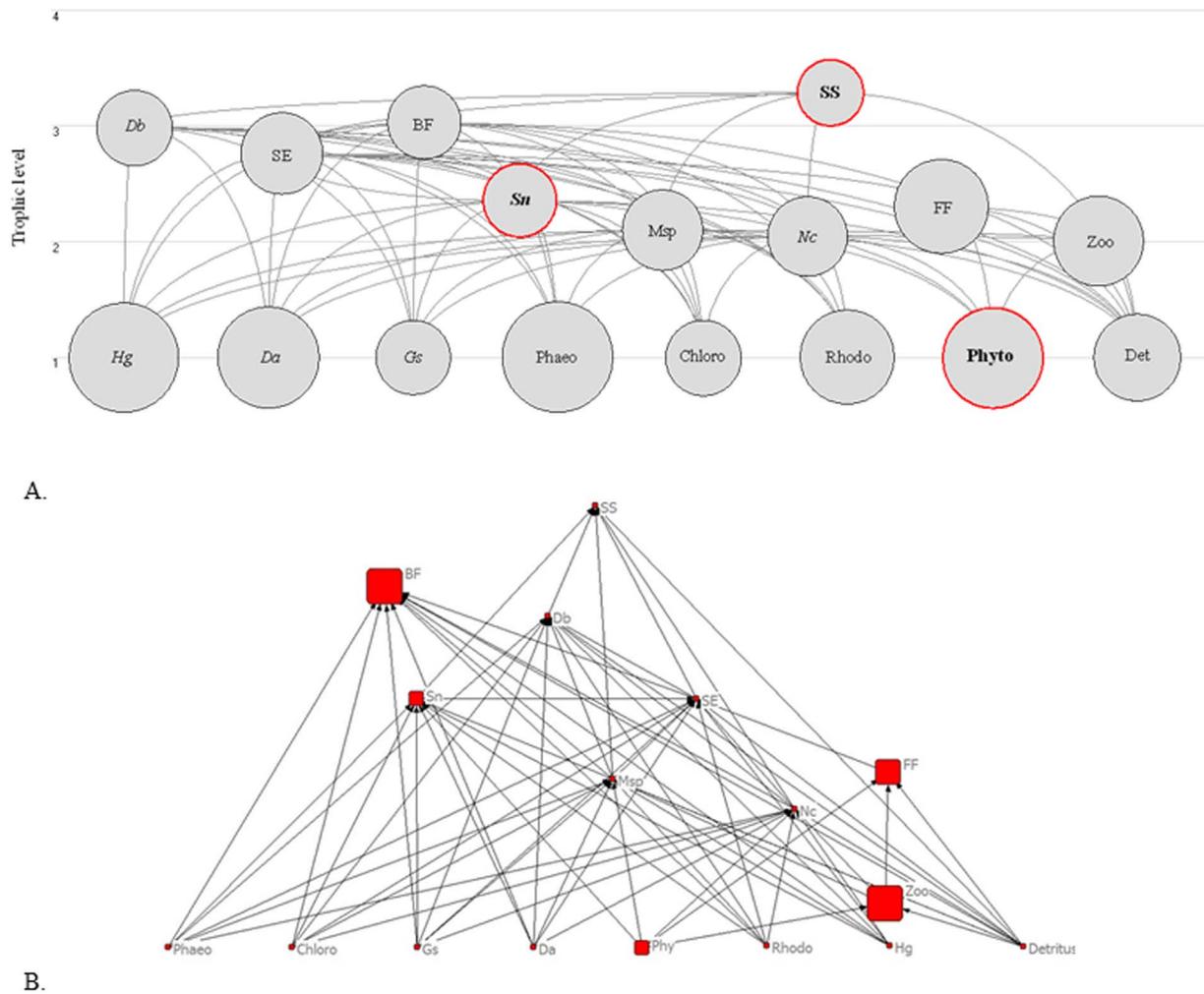


Fig. 2. Flow trophic diagram based on KSC index. The circle size is proportional to compartment biomass ($\text{g wet weight m}^{-2}$) and the vertical position approximates trophic level (for details see Appendix D in Supplementary materials) (A); and KSC index given by Borgatti (2003a) (KeyPlayer) procedures (B).

cartilagineum, the grazer *Nacella concinna*, the asteroid predator *Diplasterias brucei*, and different species of fishes, sponges, bryozoans and ascidians (Valdivia et al., 2014).

2.2. Quantitative and loop trophic models

The model compartments (species and/or functional groups) were selected and defined using information on direct trophic interactions between the abundant species and other relevant species that inhabit the coastal system. The quantitative trophic model was constructed using the *Ecopath with Ecosim* software (v. 5.0) (www.Ecopath.org). *Ecopath* was first developed by Polovina (1984) and further extended by Christensen and Pauly (1992) and Walters et al. (1997). The *Ecopath* model permits a steady-state description of the matter/energy flow within an ecosystem at a particular time, whereas *Ecosim* enables dynamic simulations based on an *Ecopath* model, allowing the estimation of ecosystem changes as a consequence of a set of perturbations. *Ecopath* and *Ecosim* models have been widely used to describe and compare a variety of ecosystems of different spatial sizes, geographical loc (Monaco and Ulanowicz, 1997; Christensen and Walters, 2004; Guénette et al., 2008; Ortiz, 2008a; Griffiths et al., 2010; Pinkerton and Bradford-Grieve, 2014; Ortiz et al., 2015a, 2016; Rodríguez-Zaragoza et al., 2016). For more details of the modelling assumptions and basic equations see Appendix A in Supplementary material. The trophic model was balanced following the six rules given by Heymans et al. (2016) in order to fulfill the laws of thermodynamics. The first step was

to check if the ecotrophic efficiency (EE) was < 1.0 for all compartments. If inconsistencies were detected, the biomass values (averages) were slightly adjusted within the confidence limits (± 1 standard deviation) obtained during field studies. Appendix B in Supplementary material summarizes the six rules calculated during the model balancing.

In the case of semi-quantitative or qualitative loop model (based on *Loop Analysis*), is based on the correspondence between differential equations near equilibrium, matrixes and their loop diagram. This approach has been applied widely in different fields of the natural sciences (Briand and McCauley, 1978; Lane, 1998; Hulot et al., 2000; Darmbacher et al., 2009; Ortiz and Levins, 2011, 2017; Ortiz et al., 2015b; Reum et al., 2015). The community matrix (sensu Levins, 1968) that represents this Antarctic coastal system was constructed by a_{ij} 's elements which describe the effect of variable j on the growth variable i . Whether the link from j to i is positive, negative or zero, then the matrix was constituted by $+1$, -1 or 0 , respectively. Using *Loop Analysis*, the local stability of any community matrix (Levins, 1968) can be determined by the Routh-Hurwitz criteria (Porter, 1968), which means that the following conditions must be satisfied:

Condition 1. All $F_k < 0$ for all k ; i.e. F_k corresponds to the negative feedback on every level (k) that must exceed the positive feedback.

Condition 2. Negative feedback on higher levels cannot be too great compared to the negative feedback on lower levels in order to conserve the qualitative stability properties of the systems. This second condition was calculated by using the expansion of the Hurwitz determinants in

Table 1

Mean path length and food web connectance of the coastal benthic/pelagic ecological system of Fildes Bay (Antarctica) compared to other system along the Chilean coast (A), and with other locations around the globe (B), (Note: both indices were calculated using Ecospath II software).

Coastal Marine Ecosystems	Network properties	
	Path length	Food web connectance
A. Fildes Bay and SE Pacific coast		
Benthic/pelagic coastal ecological system of Fildes Bay ^a	2.37	0.28
Kelp ecological system dominated by <i>M. pyrifera</i> , Antofagasta Peninsula ^b	2.10	0.30
Kelp ecological system dominated by <i>L. trabeculata</i> , Antofagasta Peninsula ^b	2.60	0.30
Seagrass habitat ecological system of Tongoy Bay ^c	2.41	0.23
Mud habita ecological system of Tongoy Bay ^c	2.49	0.32
Benthic/pelagic ecological system of Tongoy Bay ^d	2.34	0.20
La Rinconada Marine Reserve coastal ecological system, Antofagasta Bay ^e	2.60	0.20
Mejillones benthic/pelagic ecological system of Mejillones Bay ^f	2.92	0.20
Antofagasta benthic/pelagic ecological system of Antofagasta Bay ^f	2.77	0.18
B. Around the world		
Coral reef ecosystem, Chinchorro Bank, México ^g	7.69	0.23
Mangrove estuary of Caeté, Brazil ^h	3.40	–
Ems estuary in The Netherlands ⁱ	3.42	–
Benguela upwelling ecosystem, Namibia ^j	2.90	–
Bay of Bengal, Bangladesh ^k	2.58	0.42

^a Current study.

^b Ortiz (2008a).

^c Ortiz and Wolff (2002).

^d Wolff (1994).

^e Ortiz et al. (2010).

^f Ortiz et al. (2015a).

^g Rodríguez-Zaragoza et al. (2016).

^h Wolff et al. (2000).

ⁱ Baird and Ulanowicz (1993).

^j Heymans and Baird (2000).

^k Ullah et al. (2012).

terms of feedbacks or loops (Puccia and Levins, 1985). It is relevant to indicate that the feedback for each level can also be calculated by estimating the characteristic polynomial related to the Jacobian-Levins interaction community matrix, in which the polynomial now can be written in terms of the feedback notation as follows (Eq. (1)):

$$F_0\lambda^n + F_1\lambda^{n-1} + F_2\lambda^{n-2} + \dots + F_{n-1}\lambda^1 + F_n\lambda^0 = 0 \quad (1)$$

where $F_0 \equiv -1$ and the F_n is the feedback of the whole system (n = total number of variables in the system) (Puccia and Levins, 1985). It is assumed that the system is locally stable when F_n is negative (Levins 1998). The stronger the negative feedback (F_n) becomes, the greater the resistance will be to external change (Levins, 1998). Based on this local stability criterion, it is possible to estimate the degree of resistance to perturbations (as a measure of sustainability) of the system and, simultaneously, to explore strategies to increase this resistance. A detailed description of the basic equations and modelling assumptions are shown in Appendix A in Supplementary material.

2.3. Determination of functional keystone indices

Once the trophic model was balanced following the rules given by Heymans et al. (2016), the functional index (KS_i) developed by Libralato et al. (2006) was used. This index is an extension of the mixed trophic impacts (MTI) (Ulanowicz and Puccia, 1990). Because every impact can be quantitatively positive or negative, a new measure of the

overall effect must be determined for each species or functional group (ε_i) using the following mathematical Eq. (2):

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2} \quad (2)$$

where m_{ij} corresponds to the elements of the MTI matrix and quantifies the direct and indirect effects that each (affecting) species or group i has on any (affected) group j of the food web. However, the effect of the change in a group's biomass on the group itself (i.e., m_{ii}) is not included. The contribution of biomass from every species or functional group with respect to the total biomass of the network was estimated using the following Eq. (3):

$$p_i = \frac{B_i}{\sum_i^n B_k} \quad (3)$$

where p_i is the proportion of biomass of each species B_i with respect to the sum of the total biomass B_k . Therefore, to balance the overall effect and the biomass, the keystone index (KS_i) for each species or functional group was established using Eq. (4), which integrates the Eqs. (2) and (3) as follows:

$$KS_i = \log [\varepsilon_i * (1 - p_i)] \quad (4)$$

This index assigns high values of functional keystone to those variables (species) or functional groups that have low biomass and a high overall effect.

The propagation of direct and indirect effects and system recovery time (SRT) magnitudes estimated by *Ecosim* were treated in the same way as those obtained with MTI in order to obtain two additional functional keystone indices. The *Ecosim* simulations were used to evaluate the propagation of instantaneous direct and indirect effects and the system recovery time (SRT) (as a system resilience measure) in response to a steady increase in the total mortality (Z) of all compartments (see Eqs. (5) and (6)) which was set equivalent to 10%, 30% and 50%. This procedure was done between the first and second year of simulation for all components considered in the model. These three magnitudes (scenarios) were set for prediction purposes as a measure of confidence. As the models studied represent only short-term (transient) dynamics, the propagation of instantaneous effects was determined by evaluating the changes of biomass in the remainder variables in the third year of simulation. All dynamic simulations by *Ecosim* were carried out using the following vulnerabilities (flow control) (v_{ij}): (1) bottom-up (prey controls the flow), (2) top-down (predator controls the flow), and (3) mixed (both prey and predator controls the flow), and (3).

$$Z = M \text{ (natural mortality)} + F \text{ (fishing mortality)} \quad (5)$$

$$\text{Production (P)} = \text{Biomass(B)} * Z \quad (6)$$

After that, the Eqs. (2)–(4) were used to obtain one keystone species index related to the propagation of direct and indirect effects ($KS_{iEcosim1}$), and Eqs. (2) and (3) were used to obtain another functional keystone species index related to SRT magnitudes ($KS_{iEcosim2}$). Both of these indices have the property, as does the KS_i index (Libralato et al., 2006), that high values of keystone correspond to compartments with low biomass and a high overall effect.

2.4. A topological keystone index

The structural keystone index (K_i) developed by Jordán et al. (1999) and Jordán (2001), following Harary (1961), was also used in this work. This index is applicable for trophic hierarchies (directed acyclic trophic networks) and considers direct and indirect interactions in vertical directions (i.e., bottom-up and top-down). The structural keystone index of the i^{th} species or functional group (K_i) is calculated using the following Eq. (7):

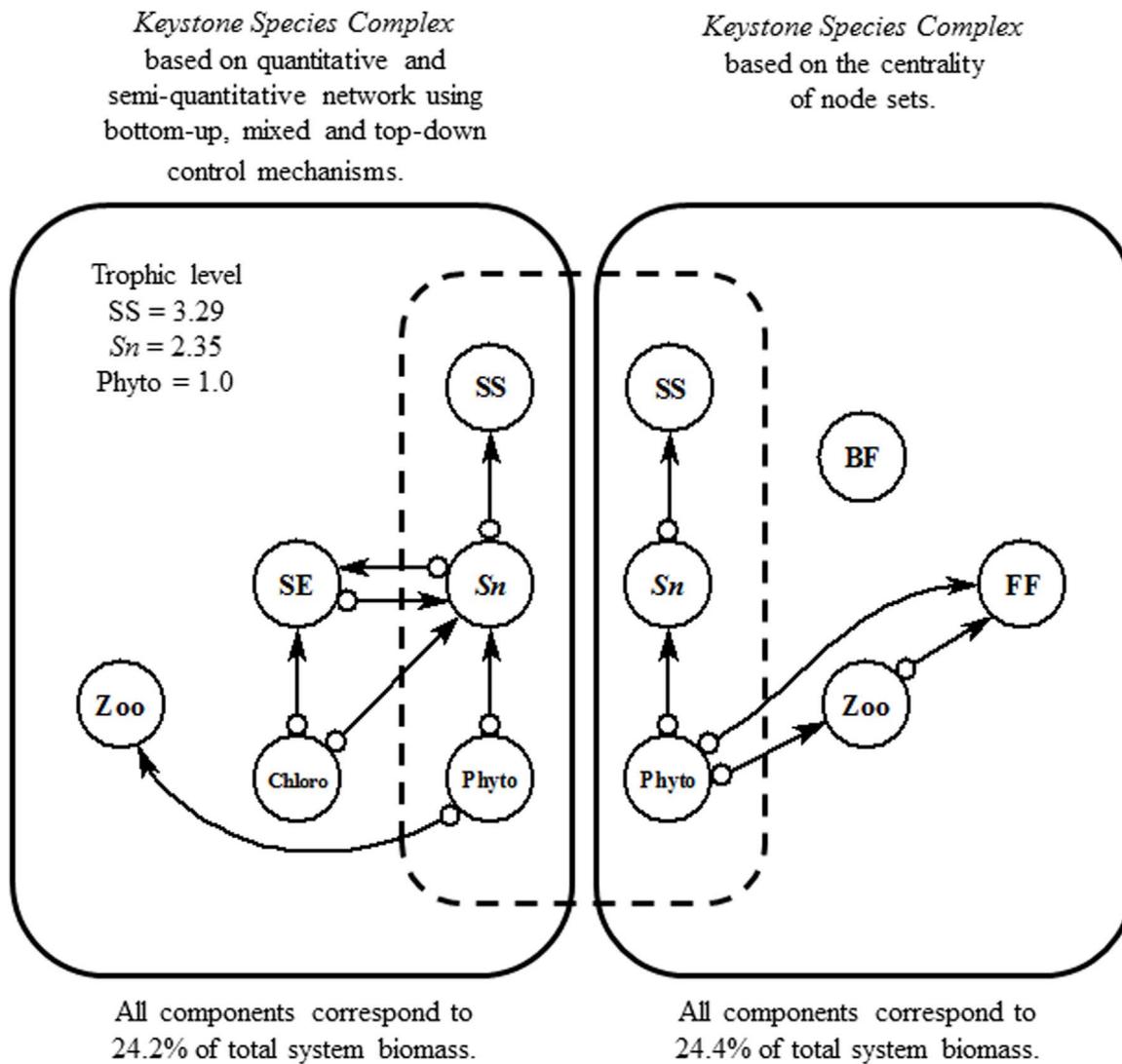


Fig. 3. Core of species and functional groups with keystone properties based on Ortiz et al. (2013a) and Borgatti (2003a) procedures. The shared groups are highlighted. (Note: the arrow and circle mean positive and negative effect respectively).

$$K_i = \sum_{c=1}^n \frac{1}{d_c} (1 + K_{bc}) + \sum_{e=1}^n \frac{1}{f_e} (1 + K_{te}) \quad (7)$$

where n is the number of predator species eating species i , d_c is the number of prey of the c^{th} predator, K_{bc} is the bottom-up keystone index of the c^{th} predator, and symmetrically we have m as the number of prey species eaten by species i , f_e as the number of predators of its e^{th} prey, and K_{te} as the top-down keystone index of the e^{th} prey. Within this index, the first and second components represent the bottom-up (K_{bc}) and top-down (K_{te}) effects, respectively. Finally, the keystone index (K_i) corresponds to the highest value as a product of the addition of bottom-up (K_{bc}) and top-down (K_{te}) components. For more details on this method, see Jordán (2001) and Vasas et al. (2007). The K index has been shown to be one of the most robust centrality indices (Fedor and Vasas, 2009). It is important to indicate that only bottom-up and top-down components of K_i were used in the current work as a way to compare functional indices obtained using *Ecosim* simulations under comparable flow control mechanisms.

2.5. Semi-quantitative keystone index

A keystone index based on qualitative or semi-quantitative loop models was also calculated. Once the stabilized trophic matrix with $F_n < 0$ was obtained, the self-dynamics of each variable corresponding

to the principal diagonal (Appendix B in Supplementary material) were modified to estimate two new perturbed magnitudes of local stability F_p . Based on the distance (Δ) between F_n and F_p as shown in Eq. (8).

$$\Delta = |F_n - F_p| \quad (8)$$

Based on it was possible to determine the change provoked by each variable on initial stability (F_n), thereby obtaining a first qualitative keystone species index (K_{QILA1}) (selecting only the largest change by variable). Because *Loop Analysis* does not consider the abundance of the components, the difference (Δ) was treated in similar way to Eq. (4) to obtain an additional keystone index (K_{QILA2}) in which high values of keystone index corresponded to variables with low biomass and a high overall effect. Appendix C in Supplementary material describes the procedure for estimation of both qualitative keystone indices. Due to the qualitative-dialectic character of *Loop Analysis*, the prey-predator interaction is captured as a mixed control mechanism.

2.6. Centrality of node sets

Field studies suggest that in some situations, a small group of species behave as keystones and they form a keystone species complex (Daily et al., 1993). The importance of this group is typically realized through their inter-specific interaction network, so a network approach

to better understand multi-species keystone complexes is reasonable. A particular measure was suggested by Borgatti (2003a) in order to find the most central set of k nodes in a network. According to this, a topological keystone species complex is defined as a solution of the KeyPlayer Problem (KPP) (sensu Borgatti, 2003a). The software KeyPlayer 1.44 (Borgatti, 2003b) was used to compute the importance of species combinations in maintaining the integrity of a network. The importance of a set of nodes can be calculated by considering either their fragmentation effect (KPP1) or their reachability effect (KPP2). In the first case, we identify which k nodes should be deleted from the network of n nodes in order to maximally increase its fragmentation. In the second case, we identify from which k nodes the largest proportion of the other $n-k$ nodes are reachable within a certain distance.

Based on fragmentation (F of KPP1), the best set of the deleted k nodes can maximally increase the fragmentation of the network. This means an increase of the number of components and a larger average distance generated within individual components. We used $k = 1, 2$ and 3 with 10,000 simulations for each.

We also consider the distance-based reachability approach (R^d of KPP2). We simply count the number of nodes that are reachable within a given distance of $m = 1$ step from a given set of k nodes. We have chosen $m = 2$ steps and increased the size of the KP-set from $k = 1$ to $k = 3$. We applied 10,000 runs for each simulation. The outcome was three sets of nodes (for $k = 1, 2, 3$) for each network, containing species codes. For each k , the software presents the percentage of nodes outside the KP-set but reachable from it in 1 step. If this percentage reaches 100%, then the whole network is reachable from the KP-set and we cannot create larger KP-sets.

3. Results

The mean path length of the coastal ecological system model for Fildes Bay (Fig. 2a) was of intermediate magnitude compared to other model systems along the Chilean coast (Table 1), being higher than kelp forests dominated by *Macrocystis pyrifera* and lower than those dominated by *Lessonia trabeculata*. However, all ecosystems along the Chilean coast and Fildes Bay presented lower magnitudes of path length compared to coral reef, mangrove and estuary systems. Regarding food web connectance, the model for Fildes Bay was also intermediate, being lower in connectance than was estimated for kelp forest (Table 1).

The outcomes obtained from all the keystone indices used are summarized in Fig. 3 (Appendix D in Supplementary material). These indices indicated keystone species for a variety of different species and functional groups, with some agreement. In general terms, keystone properties were detected for species of all different trophic levels, including primary producers, herbivores and top predators. Notably, the topological-structural (K_i) and the functional (KS_i) indices both identified Seastars (SS) as keystone species even though they are based on different algorithms. Similarly, both the qualitative and semi-quantitative keystone indices (KQ_{ILA1} and KQ_{ILA2}) identified Small Epifauna (SE) to have keystone properties. Regarding the functional indices based on *Ecosim* dynamical simulations (under three mortality levels and three types of flow control mechanisms), $KS_{IECOSIM1}$ and $KS_{IECOSIM2}$ both identified the group of Chlorophyta (Chloro), Phytoplankton (Phyto), Zooplankton (Zoo), the Small Epifauna (SE) and the species *S. neumayeri* (Sn) (grazers) as having keystone properties (Appendix D in Supplementary material). It is important to mention that it was not possible to determine species or functional groups with keystone properties based on the functional $KS_{IECOSIM2}$ index under a 30% increased mortality and using a top-down flow control mechanism because the model system does not return to initial steady-state conditions, instead oscillating persistently. Fig. 3 shows the core species as indicated by the keystone species complex index (KSC_i) for the coastal ecological system of Fildes Bay, which contains 24.2% of the total system biomass. Importantly, the KSC includes species and functional groups that make up an ecological path clearly representing three trophic levels.

The composition of the KeyPlayer sets is nested: for $F_{k=1}$ the key group is Phytoplankton (Phyto), $F_{k=2}$ the key groups are Phyto and benthic fishes (BF) and for $F_{k=3}$ the key groups are Phyto, BF and the Seastars (SS). For $R_{k=1}^d$ the key group is Phyto, for $R_{k=2}^d$ the key groups are Phyto and BF, and for $R_{k=3}^d$ the key groups are Phyto, BF and *S. neumayeri* (Sn). This means that the Phyto-Sn-SS chain as well as BF together composes a core of species in this community (Figs. 2 b, 3). The keystone species complex obtained by multinode centrality represents 24.4% of the total system biomass, a value quite similar to the previous approach.

4. Discussion

Although the quantitative trophic and semi-quantitative loop models constructed and analyzed in the current work correspond to a partial representation of the components and ecological relationships underlying the dynamics of the coastal benthic/pelagic ecological system of Fildes Bay (Antarctica), the core species and functional groups that constituted the two keystone species complexes (KSCs) in the coastal ecological systems at Fildes Bay coincides with those groups and species identified as keystones in experimental studies using variations of the original keystone species concept (Menge et al., 1994; Estes et al., 1998; Bond, 2001). Several species or functional groups from different trophic levels could have keystone properties. This result should not be considered as ambiguous because populations inhabit heterogeneous and changing environments (Levins, 1968). This insight would support the design of putative conservation strategies in the Antarctic Peninsula, including a core of species or functional groups linked trophically, which could supplement the unique species with keystone properties or those species considered as *niche constructors* (sensu Lewontin and Levins, 2007) or *bio-engineers* (sensu Jones et al., 1994). Therefore, we suggest – in general terms – that some efforts should be focused on multispecies conservation in coastal ecosystems with particular focus on the core species of the KSC.

The keystone species complex indices (KSC_i) identified keystone species in the functional group of Seastars (SS), principal benthic predators. This outcome agrees partially with the field observations of Gaymer and Himmelman (2008), who studied dominant seastar species in benthic communities of northern Chile, establishing *Meyenaster gelatinosus* as a keystone species in subtidal systems. Likewise, Ortiz et al. (2013a) determined that most of the keystone species complexes identified by KSC indices in different ecological systems along the Chilean coast include one asteroid species as the top predator. The relevance of the seastar species determined in the present work also coincides with the results described by Ortiz et al. (2009) regarding the longest *system recovery times* (as a measure of resilience) being obtained in response to perturbations on these species. The small epifauna (SE) was detected as part of the KSCs based on $KS_{IECOSIM2}$ setting a control bottom-up, mixed and top-down (under 10%, 30%, and 50% increased total mortality), and on the two semi-quantitative loop keystone indices. This result is very interesting because loop model predictions respond with a high degree of certainty to external perturbations (Briand and McCauley, 1978; Lane and Blouin, 1985; Lane, 1986; Hulot et al., 2000; Ortiz, 2008b). The multinode approach based on the KP indices thus partly reinforces the identity of some key players (e.g. *S. neumayeri*) but also suggest new key organisms (e.g. Zooplankton). This latter result is well supported by the literature (e.g. Stibor et al., 2004; Murphy et al., 2007). That Phytoplankton was identified as a component of the KSC could be a consequence of the higher level of primary productivity in Antarctic waters (Smith et al., 2007; Cornejo-Donoso and Antezana, 2008).

The keystone species complex indices (KSC_i) determined for Fildes Bay integrates fewer components than the one determined for the kelp forest of northern Chile. However, both ecological systems share a sea urchin species (herbivore positioned at intermediate trophic level), a seastar species (top predator), and the Chlorophyta (Chloro) (primary

producers). After all, the outcomes obtained show that the components with keystone properties in the benthic-pelagic system of Fildes Bay are widely heterogeneous, coinciding with results reported for other ecosystems (Power et al., 1996; Piraino et al., 2002; Libralato et al., 2006). Furthermore, Jordán et al. (2007, 2008) reported similar findings after comparing several structural and functional keystone species indices. Despite the wide trophic heterogeneity of components with keystone properties, it is possible to observe that the core set of species and functional groups are trophically linked, independent of the path length and food web connectance (see Table 1). A similar pattern was reported for other coastal ecological systems along the Chilean coast (Ortiz et al., 2013a). Okey (2004) arrived at similar results by defining keystone guilds or clusters of species with keystone properties based on a trophic model in Alaska. Thus, we believe that the *keystone species complex* index (KSC) for coastal benthic/pelagic ecological systems of Fildes Bay would facilitate the design and assessment of conservation and monitoring measures, especially when the Antarctic coastal marine ecosystems are being severely stressed by the direct effects of the global warming and UV radiation (Richter et al., 2008; Pessoa, 2012). The above notwithstanding, it is necessary also to recognize that the use of the *keystone species complex* indices is still quite difficult because the traditional view of conservation and monitoring efforts is based principally on single species such as keystone and/or niche-constructor or bio-engineer species. This mindset, without a doubt, imposes an even greater challenge, for global changes act on networks of interacting species, co-varying with the variables of the natural system.

The multimode approaches (KPP1 and KPP2) reinforce the composition of the core group (Phyto, Sn, SS) and suggests also BF to be of key importance. The general view outlined from these analyses is that the core of this food web is a vertical set of organisms, representing different trophic levels. This is of key importance for conservation management, suggesting to consider well-selected producers, intermediate and top species at the same time.

5. Conclusions

The models constructed and analyzed herein are subject to at least the following simplifications: (1) the models represent only the austral summer condition, and ignore the annual benthic/pelagic dynamics; (2) the ecological complexity was reduced through the aggregation of several functional groups; in this respect, exceptions were made for the most abundant macroalgae, herbivores and carnivores; and (3) in addition to the inherent and well-known limitations and shortcomings of the *Ecopath*, *Ecosim*, *Loop Analysis*, and *KeyPlayer* node sets theoretical frameworks, the models constructed and the dynamical simulations performed only represent the short-term dynamics of the underlying ecosystem. In spite of these concerns, we claim that the most relevant trophic relationships and energy/matter flows are reflected. Several techniques are capable of identifying groups of keystone species and the outcome of these analyses overlap to a large extent, mutually supporting each other and suggesting the core set of key organisms for multispecies conservation management. Since this set is not identified one by one, but within a network context, we suggest that our study contributes to the development of systems-based conservation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.06.016>.

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