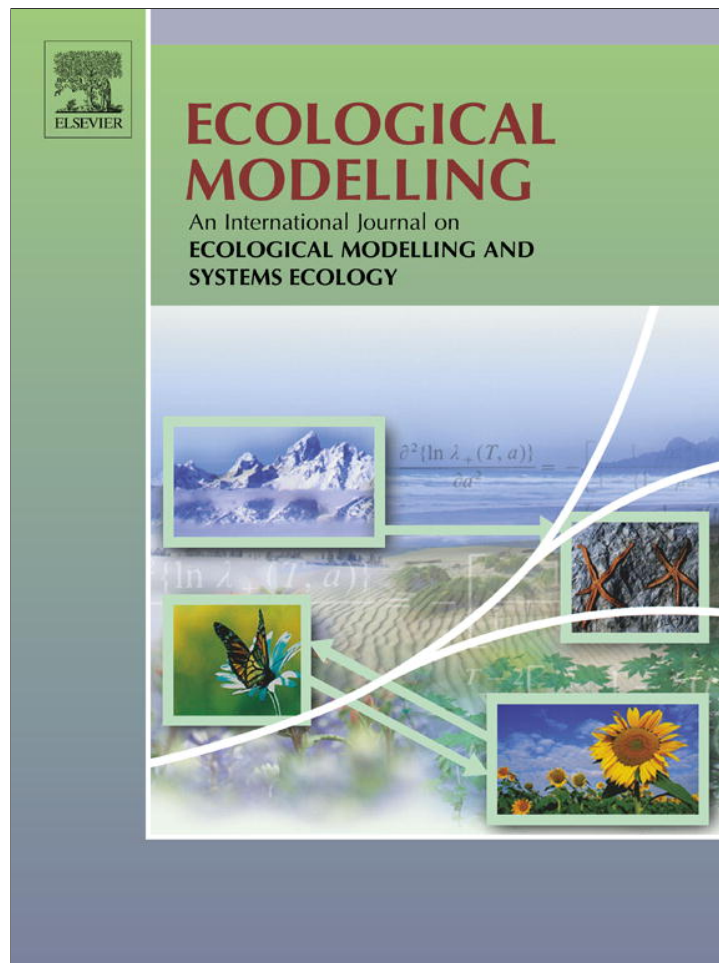


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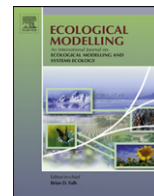
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# Ecological Modelling

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## Network properties and keystone assessment in different intertidal communities dominated by two ecosystem engineer species (SE Pacific coast): A comparative analysis

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### ARTICLE INFO

#### Article history:

Received 7 July 2012

Received in revised form 13 October 2012

Accepted 19 October 2012

#### Keywords:

*Lessonia nigrescens*

*Pyura praeputialis*

Ecopath

Ecosim

Loop Analysis model keystone indices

### ABSTRACT

Multispecies quantitative and qualitative models of the kelp *Lessonia nigrescens* and the tunicate *Pyura praeputialis* were constructed for intertidal areas of northern Chile (SE Pacific). Information on biomass, *P/B* ratios, catches, food spectrum, consumption and dynamics of commercial and non-commercial species was obtained and examined using *Ecopath* with *Ecosim* and *Loop Analysis* theoretical frameworks. The biomass of *L. nigrescens* and *P. praeputialis* constituted the most important compartments, exceeding 97% of the total biomass in each model system. Based on *Pp/R*, the system of *P. praeputialis* appeared to be the most developed. However, according to *Pp/B*, *A/C*, *A<sub>i</sub>/C<sub>i</sub>*, and redundancy, the *L. nigrescens* system was the most developed and, in turn, the least resistant to disturbances. The results obtained using *mixed trophic impacts (MTI)*, *Ecosim* simulations, and *system recovery time (SRT)* showed different response patterns. The tunicate species propagated higher effects on the remaining species, whereas the kelp species presented the longest *SRT* (as a resilience measure). The model keystone species indices suggested that each model system contained a core of ecologically related species. In the *L. nigrescens* system, core was made up of the filter feeders *Semimytilus algosus*, barnacles, and small epifauna herbivores (SEH) and the predators *Concholepas concholepas* and *Heliaster helianthus*. In the *P. praeputialis* system, the core consisted of phytoplankton, zooplankton, other filter feeders and the predators *C. concholepas*, *H. helianthus*, other starfish, and large epifauna. The outcomes obtained in the current work did not indicate that the alien tunicate *P. praeputialis* was a better or superior bio-engineer when compared to the system constructed by the kelp *L. nigrescens*. Rather, each species was relevant and relied on different ecological mechanisms.

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### 1. Introduction

The search for unique species or groups of related species whose main purpose is to sustain – in part – the properties and dynamics of communities and ecosystems has been one of the most researched areas in ecology (Wilson, 1987; Dufrene and Legendre, 1987; Padani and Csányi, 2010). These investigations reported: (1) the contribution of the ecological system, in which species or functional groups with greater biomass play a fundamental role in the structure and dynamics of the ecosystems and their emergent properties (Ulanowicz, 1986, 1997); (2) thanks to the development of

experimental ecology at the end of the 1960s, certain less abundant species were also found to play an important role in the structure, dynamics, and functioning of communities and ecosystems, leading to the concept of *keystone species* (Paine, 1969) and its later applications (Paine, 1992; Wootton, 1994; Power et al., 1996; Berlow, 1999); (3) another 30 years later, the new concept of *bio-engineer* (Lawton, 1994) or *ecosystem engineer species* (Jones et al., 1994, 1997) was defined and applied to those species that create, modify, and/or increment the heterogeneity of the habitat, thereby allowing the maintenance of high species richness locally and regionally (Takeshi and Romero, 1995; Cerda and Castilla, 2001; Thiel and Ulrich, 2002; Roff et al., 2003); and (4) parallel to the research lines described above, Lewontin (1983) and Levins and Lewontin (1985) proposed a process that would explain the properties of certain species, that is, those dynamic and permanent

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organisms that, through their metabolism and different activities, select, define, partially create, and destroy their own niches. This led to the proposal of the concept of *niche construction*, which has not yet been widely accepted within contemporary evolutionary theory (Lewontin, 1983; Odling-Smee, 1988; Odling-Smee et al., 1996; Laland et al., 1996, 2001).

Intertidal communities have received much attention from ecologists around the planet. In the case of the SE Pacific coast, numerous investigations have been done in all areas of biology, with notable studies of the kelp communities dominated by the native brown algae *Lessonia nigrescens* (Vasquez and Santelices, 1984) and later works done in San Jorge Bay (Antofagasta) with communities dominated by the alien tunicate *Pyura praeputialis* (Cerdeña and Castilla, 2001). In both communities, the importance of these organisms as *bio-engineers* or *ecosystem engineer species* (Lawton, 1994; Jones et al., 1994, 1997) or *niche constructors* (after Odling-Smee et al., 1996) has been described and evaluated. Both species offer specific conditions of protection for numerous other invertebrate species, particularly for their juvenile stages (Vasquez and Santelices, 1984; Cerdeña and Castilla, 2001; Castilla et al., 2004).

Cerdeña and Castilla (2001) relied exclusively on estimators of species diversity and richness when proposing that *P. praeputialis* constructs a more complex and diverse ecological community than does *L. nigrescens*. Although this study is an interesting exploration intending to discriminate the importance of one species or another in their respective communities, it is limited, as it fails to include the interspecific relationships based on network analysis and does not allow estimates of the emergent properties related to the state of growth and development of such systems. These properties include: *ascendency*, *redundancy*, *ascendency/capacity* ratio, *system recovery time* (as a measure of resilience), propagation of higher order effects, and quantitative and qualitative model keystone-ness in both ecological systems.

Multispecies modelling offers a way to deal with some of the difficulties in the experimental identification of relevant species. It also allows the estimation of the ecosystem macrodescriptors. The application of network theory has proven to be a useful tool for evaluating and describing system properties, dynamics, and the overall health of ecosystems (Costanza and Mageau, 1999), as well as for predicting the propagation of direct and indirect effects on system recovery times in response to disturbances (e.g. Monaco and Ulanowicz, 1997; Ortiz and Wolff, 2002a,b; Arias-González et al., 2004; Pinnegar and Polunin, 2004; Patrício and Marques, 2006; Ortiz, 2008a,b, 2010). Besides, quantitative trophic models have permitted estimates of the strength of the interactions between model species or functional groups by identifying the presence of topological keystone species that occupy key positions in trophic interaction networks (Jordán et al., 1999; Jordán and Scheuring, 2004). Likewise, keystone-ness can also be identified using qualitative loop models in which the topological key position of a species is a consequence of changes in its self-dynamics (density-dependent or density-independent of growth rates), modifying the balance (prevalence) of positive and negative feedbacks and, therefore, the local stability of the network.

Therefore, in the current work, we have attempted to construct quantitative and qualitative models of intertidal benthic ecological subsystems dominated by *L. nigrescens* and *P. praeputialis*. The quantitative trophic model was built using *Ecopath* with *Ecosim* software package v.5.1 (Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997; Christensen and Walters, 2004) and the qualitative version was based on *Loop Analysis* (Levins, 1998). These models were used to estimate the macrodescriptors of each subsystem and try to determine: (1) the biomass distribution and biomass flow structure in each system type; (2) the principal benthic predators in each system; (3) the possibility for recognizing and quantifying redundancy, i.e. if several species played similar

trophic roles (Lawton, 1994) in the systems; (4) which species or functional groups were most likely to be affected by different disturbance scenarios; (5) the resistance to disturbances and resilience time of each ecological subsystem as a response to disturbances; and (6) the model keystone species.

## 2. Materials and methods

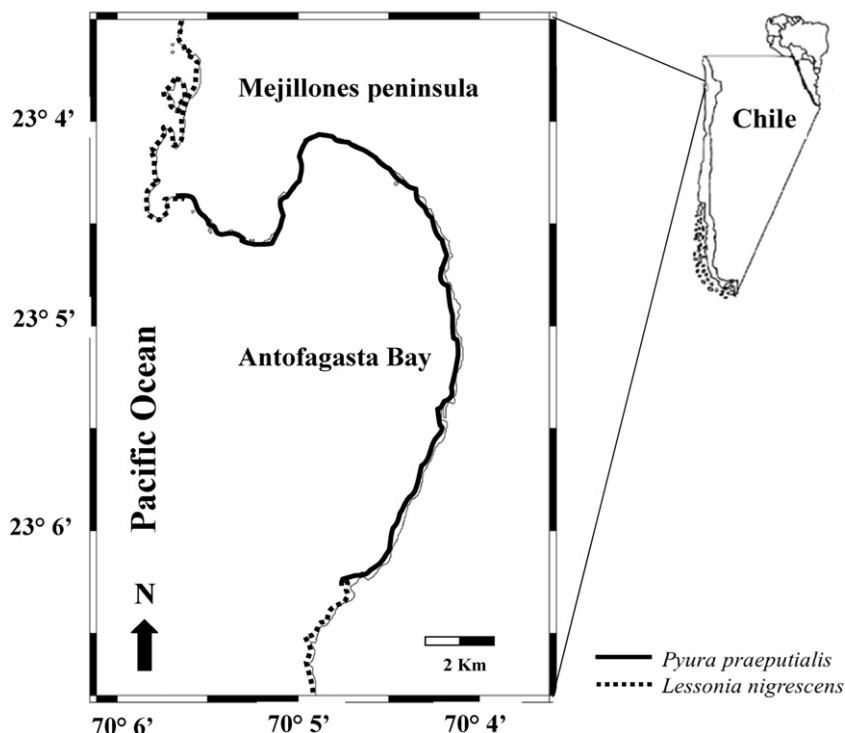
### 2.1. Habitat characteristics

#### *L. nigrescens* beds and *P. praeputialis* matrices

In general terms, the beds of *L. nigrescens* constitute a band between the intertidal and the subtidal over rocky shelves and large boulders, normally exposed to the waves and the wind, which blows predominantly from the south-west (for more details, see Vasquez and Santelices, 1984; Vasquez et al., 1998). Aggregations of *P. praeputialis* develop in the normally protected intertidal sectors of Antofagasta Bay, characterized by flat, rocky shelves with a coastal slope of less than 20°. The vertical amplitude of *P. praeputialis* beds in the intertidal fluctuates between 1 and 7 m (for more details, see Cerdeña and Castilla, 2001). It is important to note that aggregations of *P. praeputialis* are restricted only along Antofagasta Bay, limited on the north and south of their distribution by the macroalgae, *L. nigrescens* (Fig. 1).

### 2.2. Selection of model compartments and data sources

The species and functional groups selected for the construction of the quantitative and qualitative trophic models were based on studies describing communities dominated by *L. nigrescens* (Vasquez and Santelices, 1984; Vasquez et al., 1998) and *P. praeputialis* (Cerdeña and Castilla, 2001). The biomass (*B*), catches (*Ca*), turnover rates (*P/B*), consumption rates (*Q/B*), and food items for the variables selected were obtained from the literature. Appendix A1 shows the source data for each of the compartments selected for both ecological subsystems. Although most of the model compartments represent individual species, it was necessary to consider functional groups, which included different species. In order to make the following comparison of the macrodescriptors that emerged from the network analysis more robust, these were constructed with the same number of compartments ( $n=20$ ), sharing most of them except the macroalgae *L. nigrescens*, the tunicate *P. praeputialis*, the sea urchin *Loxechinus albus*, and the functional group small epifauna carnivore (SEC). The remaining compartments included the sea urchin *Tetrapigus niger*, the mytilid *Semimytilus algosus*, the muricidea *Concholepa concholepa*, the seastar *Heliaster helianthus*, and the limpets *Fissurella* spp. The following functional groups were established: the macroalgae compartment, including plants belonging to the Chlorophyta (*Ulva* sp., *Enteromorpha* sp., and *Chaetomorpha* sp.), Rhodophyta (*Chondrus* sp., *Corallina* sp., and *Gelidium* sp.), and other Phaeophyta (*Glossophora* sp., *Colpomenia* sp., and *Enderachne* sp.); the mesograzers, including different gastropod herbivores (*Tegula* spp., *Scurria scurra*, *Crepidatella dilatata*, *Chiton* spp., among others); the other filter feeders (*Petrolisthes tuberculatus*, *P. violaceus*, *Allopetrolisthes puntatus*, and *Pachycheles grosimani*); the barnacles (*Austromegabalanus psittacus*, *Balanus flosculus*, and *Chthamalus scabrosus*); the worms belonging to the classes Polychaeta and Nemertina; the Cnidaria (*Phymactis clematis* and *Anthothoe chilensis*); the bivalves (*Brachidontes granulata* and *Aulacomya ater*); other starfish (*Patiria chilensis* and *Stichaster striatus*); small epifauna herbivores (SEH), consisting of *S. scurra*, *S. araucana*, *Tegula atra*, *Acanthopleura echinata*, *Chaetopleura peruviana*; small epifauna carnivores (SEC), which contain the snails *Thais* spp.; and the large epifauna (LE), made up of specimens from the class Crustacea



**Fig. 1.** Study area of Antofagasta Bay (SE Pacific coast), northern Chile. The symbols along the coast describe the type of ecological subsystem (*Pyura praeputialis* and *Lessonia nigrescens*).

(*Talipeus dentatus*, *Homalaspis plana*, *Gaudichaudia gaudichaudia*, among others), phytoplankton, zooplankton, and detritus. The diet and qualitative interaction matrices for each of the systems are shown in Appendix A2. All the compartments are trophically linked by detritus, primarily as microbial film since diverse studies have emphasized the importance of bacteria as food for various species of molluscs (e.g. Grossmann and Reichardt, 1991; Plante and Mayer, 1994; Epstein, 1997; Plante and Shriver, 1998), zooplankton (Epstein, 1997), and echinodermata (Findlay and White, 1983).

### 2.3. Ecopath, Ecosim (v.5.0) and Loop Analysis modelling approaches

This work uses *Ecopath with Ecosim* software ([www.Ecopath.org](http://www.Ecopath.org)) to construct trophic mass-balance models. *Ecopath* was first developed by Polovina (1984) and further extended by Christensen and Pauly (1992) and Walters et al. (1997). *Ecopath* 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 locations, and complexities (Monaco and Ulanowicz, 1997; Christensen and Walters, 2004; Guénette et al., 2008; Griffiths et al., 2010; Arias-González et al., 2011). For more details, see Appendix A3.

*Loop Analysis* is based on the correspondence among differential equations near equilibrium, matrices, and their loop diagrams. *Loop Analysis* (Levins, 1998) is a useful technique for estimating the local stability (sustainability) of systems and assessing the propagation of direct and indirect effects as a response to external perturbations (Ramsey and Veltman, 2005). This approach has been applied widely in different fields of the natural sciences (Briand and

McCauley, 1978; Levins and Vandermeer, 1990; Lane, 1998; Hulot et al., 2000; Ortiz and Wolff, 2002c, 2008; Ortiz, 2008b; Ortiz and Stotz, 2007; Dambacher et al., 2009; Ortiz and Levins, 2011). For more details of the modelling assumptions and basic equations, see Appendix A3.

### 2.4. Network properties (macrodescriptors)

*Ecopath* modelling combines the approach of Polovina (1984) to estimate the biomass and food consumption of the ecosystem variables or functional groups with Odum's (1969) and Ulanowicz's (1986, 1997) ecosystem and network analyses of flows between model compartments of the system for the calculation of ecosystem macrodescriptors. These descriptors are the *primary production/community respiration (Pp/R) ratio*, *primary production/biomass (Pp/B) ratio*, *total system throughput (T)*, *ascendency (A)*, *development capacity (C)*, and *A/C ratio*. *Throughput* describes the vigour or size of a system, and this descriptor represents a measure of the system's metabolism. *Ascendency* integrates both the size and organization of the system. *Organization* refers to the number and diversity of interactions between the system components. The *development capacity* quantifies the upper limit to *ascendency*, and the *A/C ratio* describes the degree of maximum specialization that is actually achieved in the system (maturity index) (e.g. Baird and Ulanowicz, 1993; Costanza and Mageau, 1999). This ratio can also be used as the system's ability to withstand disturbance (Ulanowicz, 1986, 1997). All these macrodescriptors have been widely used to describe and compare a variety of ecosystems of different spatial sizes, geographical locations, and complexities (e.g. Monaco and Ulanowicz, 1997; Jarre-Teichmann and Christensen, 1998; Niquil et al., 1999; Heymans and Baird, 2000; Wolff et al., 2000; Ortiz and Wolff, 2002a; Arias-González et al., 2004; Patrício and Marques, 2006; Patrício et al., 2006; Ortiz, 2008a; Ortiz et al., 2009; Yunkai et al., 2009; Kaufman and Borrett, 2010; Li and Yang, 2011).

**Table 1**  
Parameter values entered (in bold) and estimated by *Ecopath II* software for *P. praeputialis* (A) and *L. nigrescens* system (B). (Note: TL=trophic level, Ca=catches (g wet weight m<sup>-2</sup> year<sup>-1</sup>), B=biomass (g ww m<sup>-2</sup>), P/B=turnover rate (year<sup>-1</sup>), Q/B=consumption rate (year<sup>-1</sup>), and EE=ecotrophic efficiency.

Compartments						
Species/functional groups	TL	Ca	B	P/B	Q/B	EE
<b>A. <i>Pyura praeputialis</i> system</b>						
(1) <i>Pyura praeputialis</i>	2.1	<b>3681.00</b>	<b>36,810.0</b>	<b>3.2</b>	<b>7.0</b>	0.03
(2) <i>Fissurella</i> spp.	2.0	<b>0.51</b>	<b>15.4</b>	<b>1.4</b>	<b>9.9</b>	0.71
(3) <i>Tetrapigus niger</i>	2.0		<b>13.5</b>	<b>1.3</b>	<b>6.7</b>	0.58
(4) SEH	2.0		<b>29.5</b>	<b>2.3</b>	<b>7.0</b>	0.98
(5) Mesograzers	2.0		<b>9.9</b>	<b>4.3</b>	<b>12.5</b>	0.72
(6) Bivalvia	2.1		<b>18.3</b>	<b>2.5</b>	<b>7.0</b>	0.95
(7) <i>Semimytilus algosus</i>	2.1		<b>12.0</b>	<b>1.7</b>	<b>7.0</b>	0.90
(8) Barnacles	2.1		<b>16.6</b>	<b>3.2</b>	<b>7.0</b>	0.99
(9) Other filter feeders	2.1		<b>14.7</b>	<b>1.7</b>	<b>7.0</b>	0.38
(10) <i>Concholepas concholepas</i>	3.1	<b>2.95</b>	<b>29.5</b>	<b>0.8</b>	<b>4.3</b>	0.19
(11) SEC	2.9		<b>9.6</b>	<b>2.4</b>	<b>4.7</b>	0.90
(12) LE	3.1		<b>13.8</b>	<b>1.5</b>	<b>9.7</b>	0.93
(13) <i>Heliaster helianthus</i>	3.3		<b>17.1</b>	<b>0.6</b>	<b>2.3</b>	0.04
(14) Other Starfish	2.5		<b>6.0</b>	<b>0.9</b>	<b>2.3</b>	0.07
(15) Worms	2.1		<b>31.7</b>	<b>2.2</b>	<b>14.0</b>	0.96
(16) Cnidaria	2.4		<b>10.1</b>	<b>1.6</b>	<b>5.0</b>	0.09
(17) Macroalgae	1.0		69.4	<b>7.5</b>	–	0.89
(18) Zooplankton	2.0		216.0	480.0	1280.0	0.25
(19) Phytoplankton	1.0		336.0	3000.0	–	0.41
(20) Detritus	1.0		100.0	–	–	0.10
<b>B. <i>Lessonia nigrescens</i> system</b>						
(1) <i>Lessonia nigrescens</i>	1.0	<b>2004.00</b>	<b>20,400.0</b>	<b>9.0</b>	–	0.01
(2) <i>Fissurella</i> spp.	2.0	<b>0.09</b>	<b>0.9</b>	<b>1.1</b>	<b>9.9</b>	0.72
(3) <i>Tetrapigus niger</i>	2.0		<b>0.4</b>	<b>3.1</b>	<b>6.7</b>	0.91
(4) <i>Loxechinus albus</i>	2.0	<b>0.04</b>	<b>0.2</b>	<b>0.8</b>	<b>6.7</b>	0.31
(5) SEH	2.0		<b>3.7</b>	<b>1.7</b>	<b>7.0</b>	0.98
(6) Mesograzers	2.0		<b>1.9</b>	<b>3.6</b>	<b>12.5</b>	0.99
(7) Bivalvia	2.1		<b>8.4</b>	<b>2.2</b>	<b>7.0</b>	0.19
(8) <i>Semimytilus algosus</i>	2.1		<b>20.2</b>	<b>2.2</b>	<b>7.0</b>	0.03
(9) Barnacles	2.1		<b>3.5</b>	<b>2.1</b>	<b>7.0</b>	0.75
(10) Other filter feeders	2.1		<b>7.7</b>	<b>1.3</b>	<b>7.0</b>	0.10
(11) <i>Concholepas concholepas</i>	3.1	<b>0.02</b>	<b>3.1</b>	<b>0.5</b>	<b>4.3</b>	0.10
(12) LE	2.9		<b>1.5</b>	<b>1.4</b>	<b>9.7</b>	0.83
(13) <i>Heliaster helianthus</i>	3.2		<b>0.2</b>	<b>0.8</b>	<b>2.3</b>	0.03
(14) Other Starfish	3.2		<b>0.2</b>	<b>0.9</b>	<b>2.3</b>	0.05
(15) Worms	2.1		<b>3.4</b>	<b>1.8</b>	<b>14.0</b>	0.90
(16) Cnidaria	2.4		<b>5.0</b>	<b>2.4</b>	<b>5.0</b>	0.01
(17) Macroalgae	1.0		<b>17.4</b>	<b>7.5</b>	–	0.21
(18) Zooplankton	2.0		<b>18.0</b>	<b>40.0</b>	<b>160.0</b>	0.04
(19) Phytoplankton	1.0		<b>28.0</b>	<b>250.0</b>	–	0.42
(20) Detritus	1.0		<b>100.0</b>	–	–	0.00

2.5. Balancing and calibration of the quantitative models

The first step in balancing the models was to determine the feasibility of the model outputs, that is, checking if all *ecotrophic efficiencies (EE)* of the compartments were <1.0 (Ricker, 1968). If any deviation was detected, the biomass values (averages) were slightly changed within the confidence limits (standard deviation) obtained from the literature. For Rhodophyta and Chlorophyta, *P/B* values were also adjusted using *Ecopath* software. It was not necessary to modify the diet matrixes when balancing the models. As a second step, Gross Efficiency (*GE*) values were checked for consistency by comparing them with data from the literature (Christensen and Pauly, 1993).

2.6. Mixed trophic impacts, Ecosim simulations and system recovery time

The *mixed trophic impacts (MTI)* (Ulanowicz and Puccia, 1990) routine of *Ecopath* was used to make a preliminary evaluation of the propagation of direct and indirect effects in response to disturbances affecting species of commercial interest. *Ecosim* simulations were used to assess the propagation of instantaneous direct and indirect effects and the *system recovery time (SRT)* – as an

internal stability measure – in response to increased total mortality ( $Z=M+F$ ) equivalent to 30% more total production ( $P=B \times Z$ ). This procedure was done between the first and second year of simulation for all species or functional groups of each model. The propagation of instantaneous effects was determined by evaluating the changes of biomass in the remaining variables in the third year of simulation. Because of the lack of time-series of landings for the variables, all the dynamic simulations were carried out using the following flow control mechanisms ( $v_{ij}$ ): (1) bottom-up, (2) mixed, and (3) top-down. It is important to indicate that the *mixed trophic impacts* and *Ecosim* simulations shown up to ~60% certainty under short-term dynamics in benthic system in northern Chile (Ortiz, 2008b).

2.7. Functional, topological-structural and qualitative keystone indices

Once the trophic model was balanced, the functional index (*KS*) developed by Libralato et al. (2006) was used. This index is an extension of the *mixed trophic impacts (MTI)* (Ulanowicz and Puccia, 1990). Additionally, the results of higher order effects and *system recovery time (SRT)* magnitudes estimated by *Ecosim* were treated in the same way as were those obtained with *MTI* in order to

obtain two additional functional keystone indices. All these indices revealed, as did the  $KS_i$  (Libralato et al., 2006), that high values of keystone indices corresponded to variables with low biomass and a high overall effect. For more details of procedure see Appendix A3.

The structural keystone index ( $K_i$ ) developed by Jordán et al. (1999) and Jordán (2001) was also used in this work. Jordán's index considers direct and indirect interactions in both directions (i.e. bottom-up and top-down). It is important to note that 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 different flow control mechanisms. For a detailed description of the basic equation and assumptions, see Appendix A3.

Finally, two keystone indices based on a qualitative loop model were also calculated. Once the stabilized matrix with  $F_n < 0$  was obtained, the self-dynamics of each variable, corresponding to the principal diagonal of the qualitative interaction matrix (Appendix A1), were modified in order to estimate a new perturbed magnitude of local stability  $F_p$ . Due to the qualitative character of *Loop Analysis*, the prey–predator interaction is simulated as a mixed mechanism. For more details see Appendix A3.

### 3. Results

First of all, special mention should be made of the balancing process for both trophic models. In the case of the *L. nigrescens* model, the balancing was relatively simple to adjust  $EE < 1$ , modifying just the biomass of SEH, mesograzers, and barnacles (Table 1). A different situation occurred with the model for *P. praeputialis* given the high biomass and filter-feeding behaviour of this tunicate species. In this case, the biomass and productivity of phytoplankton and zooplankton had to be increased ~10 times more than the values described for the Chilean and Peruvian coast (Wolff, 1994; Taylor et al., 2008). This large modification also meant changes in other compartments such as *Fisurella* spp., SE, Bivalvia, *S. algosus*, barnacles, SEC, LE, worms, and macroalgae (Table 1).

The phaeophyta *L. nigrescens* and the alien ascidian *P. praeputialis* concentrated by far the greatest magnitudes of biomass in their systems, reaching 98.9% and 97.4% of the total system biomass, respectively (Table 1) (Fig. 2). With regard to the system structure and properties, both ecological models presented higher values of the  $Pp/R$  ratio, with the *P. praeputialis* model having the lowest magnitude. With regard to the  $Pp/B$  ratio, the *L. nigrescens* model showed the lowest value (Table 2). The *P. praeputialis* model had the highest magnitude of system throughput ( $T$ ) (2,434,316 g wet weight  $m^{-2} year^{-1}$ ), being one order of magnitude greater than that calculated for the *L. nigrescens* model (380,441 g wet weight  $m^{-2} year^{-1}$ ) (Table 2).

In both ecological systems, the mean trophic level of the fishery was different. Whereas that in the *P. praeputialis* system was equal to 2.1, which showed that harvesting was done almost exclusively on secondary producers, in the *L. nigrescens* system, the fishery operated over primary producers (Table 2). Although the *P. praeputialis* model system presented the highest values of *development capacity* ( $C = 6,829,259.1$  Flowbits) and *ascendency* ( $A = 2,520,195.4$  Flowbits) ( $A/C$  ratio = 36.9%), the *L. nigrescens* model was the most developed and least stable based on the  $A/C$  ratio (82.8%). Based on the system *redundancy* and  $A/C$  ratio, the *P. praeputialis* model was the most resistant to perturbations (Table 2). The large decrease in  $A_i/C_i$  ratio in relation to  $A/C$  ratio for the *P. praeputialis* model could indicate a strong dependency of this system on few dominant external connections (sensu Baird et al., 1991) (Table 2). According to the contribution of each compartment to *ascendency*, used to assess the relative importance of each group on the overall structure and function of the system (sensu Ulanowicz,

**Table 2**

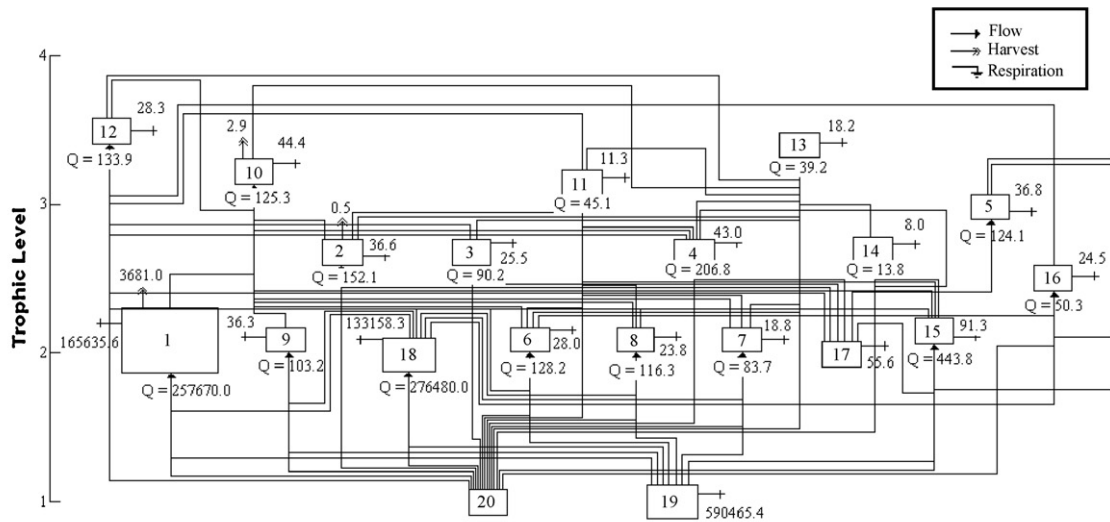
Summary statistics after mass-balance process by *Ecopath* II, and network flow indices. The units are in g wet weight and Flowbit is the product of flow (g wet weight  $m^{-2} year^{-1}$ ) and bits.

	Subsystems	
	<i>P. praeputialis</i>	<i>L. nigrescens</i>
(A) Summary statistics		
Sum of all consumption (g $m^{-2} year^{-1}$ )	536,006	3322.344
Sum of all exports (g $m^{-2} year^{-1}$ )	801,649.9	188,503
Sum of all respiratory flows (g $m^{-2} year^{-1}$ )	206,870.5	1819.5
Sum of all flows into detritus (g $m^{-2} year^{-1}$ )	889,789.5	186,795.8
Total system throughput (g $m^{-2} year^{-1}$ )	2,434,316	380,441
Sum of all production (g $m^{-2} year^{-1}$ )	1,230,457	191,160
Mean trophic level of the catch	2.1	1.0
Gross efficiency of the fisheries (catch/net pp, %)	0.004	0.011
Total net primary production (g $m^{-2} year^{-1}$ )	1,008,521	190,322.4
Total primary production/total respiration	4.9	104.6
Net system production (g $m^{-2} year^{-1}$ )	801,650	188,503
Total primary production/total biomass (year <sup>-1</sup> )	26.766	9.273
Total biomass/total throughput (year)	0.015	0.054
Total biomass (exc. detritus) (g $m^{-2} year^{-1}$ )	37,679.1	20,523.67
Total catches (g $m^{-2} year^{-1}$ )	3684.461	2004.1
(B) Network flow indices		
Ascendency (total) (flowbits)	2,520,195.4	401,490.8
Overhead (total) (flowbits)	4,309,063.7	68,172.1
Capacity (total) (flowbits)	6,829,259.1	484,830.4
Pathway redundancy (of overhead) (%)	53.1	12.7
$A/C$ (%)	36.9	82.8
$A_i/C_i$ (%)	20.9	76.5
Throughput cycled (exc. detritus) (g $m^{-2} year^{-1}$ )	17.1	1.8
Throughput cycled (inc. detritus) (g $m^{-2} year^{-1}$ )	74,611.8	0.03
Finn's cycling index (FCI) (%)	3.07	0.03
Average path length (APL)	2.4	2.0
Food web connectance	0.2	0.2
Omnivory index (OI)	0.1	0.1

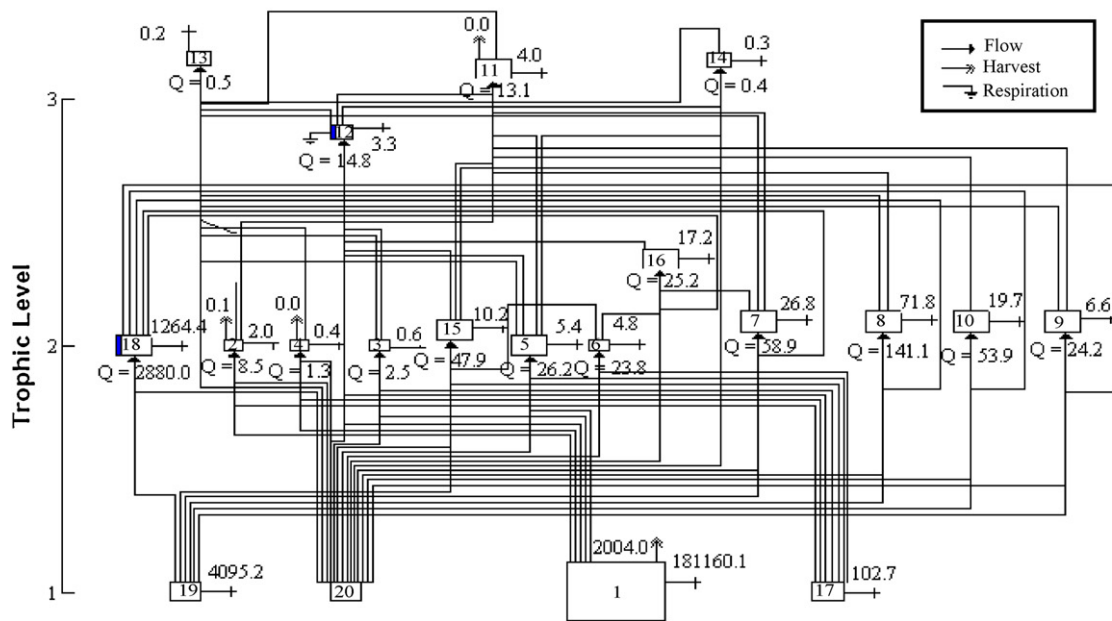
1997), in both models detritus was the most important, reaching 46.8% and 43.3% for the *L. nigrescens* and *P. praeputialis* systems, respectively. It is important to note that in the *L. nigrescens* model, this kelp species occupied second place in terms of relevance, with 45.5%, followed by phyto-zooplankton, with 7%. However, in the *P. praeputialis* model, detritus was followed in importance by phyto-zooplankton, with 44.4%, and later by the tunicate species, with 11.5%. Both ecological systems had a similar magnitude of *food web connectance*, *omnivory index (OI)*, and *average path length (APL)*, indicating that the two model systems had a comparable topological structure (Table 2).

In order to assess the propagated direct and indirect effects in both ecological systems (based on *MTI* and *Ecosim* simulations), we selected only the results obtained for *L. nigrescens*, *P. praeputialis*, the two commercial species (*C. concholepas* and *Fisurella* spp.) and *H. helianthus* (seastar top predator). The outcomes obtained using the *mixed trophic impacts (MTI)* affecting the muricidae *C. concholepas* and the seastar *H. helianthus* showed that both ecological systems presented a similar qualitative pattern. The principal differences were observed when *P. praeputialis*, *L. nigrescens*, and *Fisurella* spp. were impacted (Fig. 3). From a quantitative point of view, the *P. praeputialis* model propagated higher-order effects in the remaining compartments than did the *L. nigrescens* model (Fig. 3). With regard to the *Ecosim* simulations, the *P. praeputialis* model propagated higher direct and indirect effects than the other variables, especially if the disturbance (e.g. harvest) entered the system via *P. praeputialis*, *C. concholepas*, and *H. helianthus* (Fig. 4). Unfortunately, the outcomes obtained for the *system recovery time (SRT)* for both model systems did not allow us to construct a profound analysis, since many oscillations appeared using mixed and top-down control mechanisms (Table 3). However, the

*Pyura praeputialis* system



*Lessonia nigrescens* system



**Fig. 2.** Trophic model for the *P. praeputialis* (a) and for *L. nigrescens* subsystem (b). Vertical position approximates trophic level. The box size is proportional to the compartment (populations and/or functional groups) biomass (g wet weight m<sup>-2</sup>). Simple arrows represent the flow of matter among variables, double arrows mean flow to fisheries, and vertical arrow is flow to detritus. The number in the box corresponds to the species or functional groups (for details see Table 1).

disturbances simulated in the *P. praeputialis* model clearly provoked more oscillatory responses than did the similar disturbances in the *L. nigrescens* system. If we consider only the results obtained under bottom-up flow control mechanisms, *L. nigrescens* would take the longest time to return to its initial condition after disturbance (SRT = 10.5 years), whereas the *P. praeputialis* model needed 7.2 years to return to its initial steady-state biomass value. It is important to indicate that, in the *P. praeputialis* model, the other starfish compartment obtained the longest SRT value (Table 3). If the disturbance simultaneously impacted 19 compartments in both models, the *P. praeputialis* system would take a longer time (SRT = 19.7 years) than the *L. nigrescens* system (SRT = 14.7 years) to return to its initial condition (Table 3).

Table 4 summarizes the magnitudes obtained on all keystone species indices applied in the current work. In the case of the *L. nigrescens* model, the core of species (ecologically related) conformed by the filter-feeding *S. algosus* ( $KS_{iEcosim1}$  and  $KQ_{iLA1}$ ) and barnacles ( $KS_{iEcosim2}$  under mixed flow control and  $KQ_{iLA2}$ ), the small epifauna herbivores (SEH) ( $KS_{iEcosim2}$  under bottom-up control), and the predators *C. concholepas* ( $KS_i$ ) and *H. helianthus* ( $K_i$ ) would have keystone properties, reaching < 0.15% of the total system biomass. In the *P. praeputialis* model, the indices also coincided in a core of ecologically related groups constituted by the phytoplankton ( $KS_{iEcosim1}$  under mixed control), zooplankton ( $KS_{iEcosim1}$  under top-down control), other filter feeders ( $KQ_{iLA1}$  and  $KQ_{iLA2}$ ), the predators *H. helianthus* ( $K_i$ ), the other starfish ( $KS_{iEcosim2}$  under

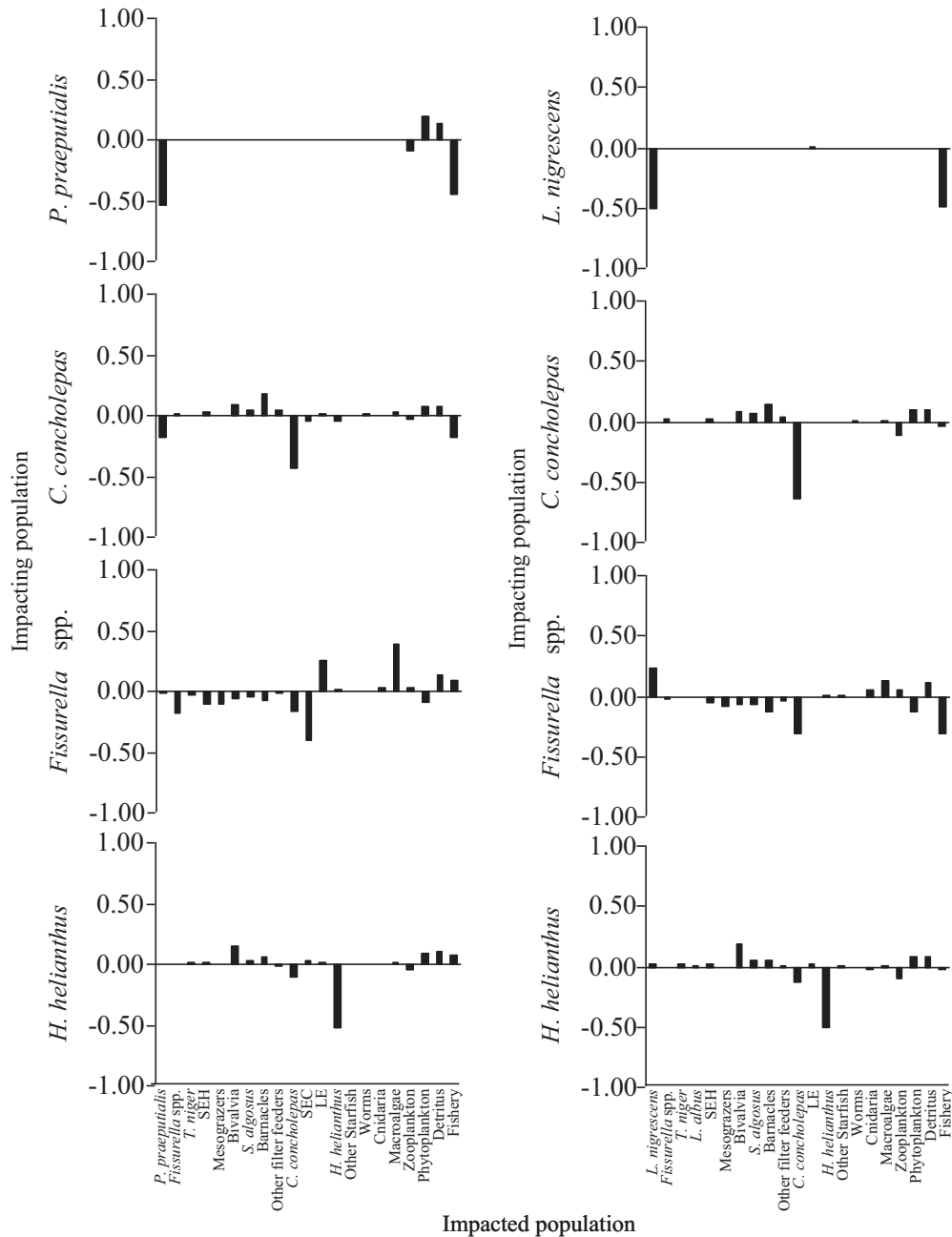


Fig. 3. Mixed trophic impacts (MTI) (direct and indirect) in response to impacting *P. praeputialis*, *L. nigrescens*, *C. concholepas*, *Fissurella* spp. and *H. helianthus*.

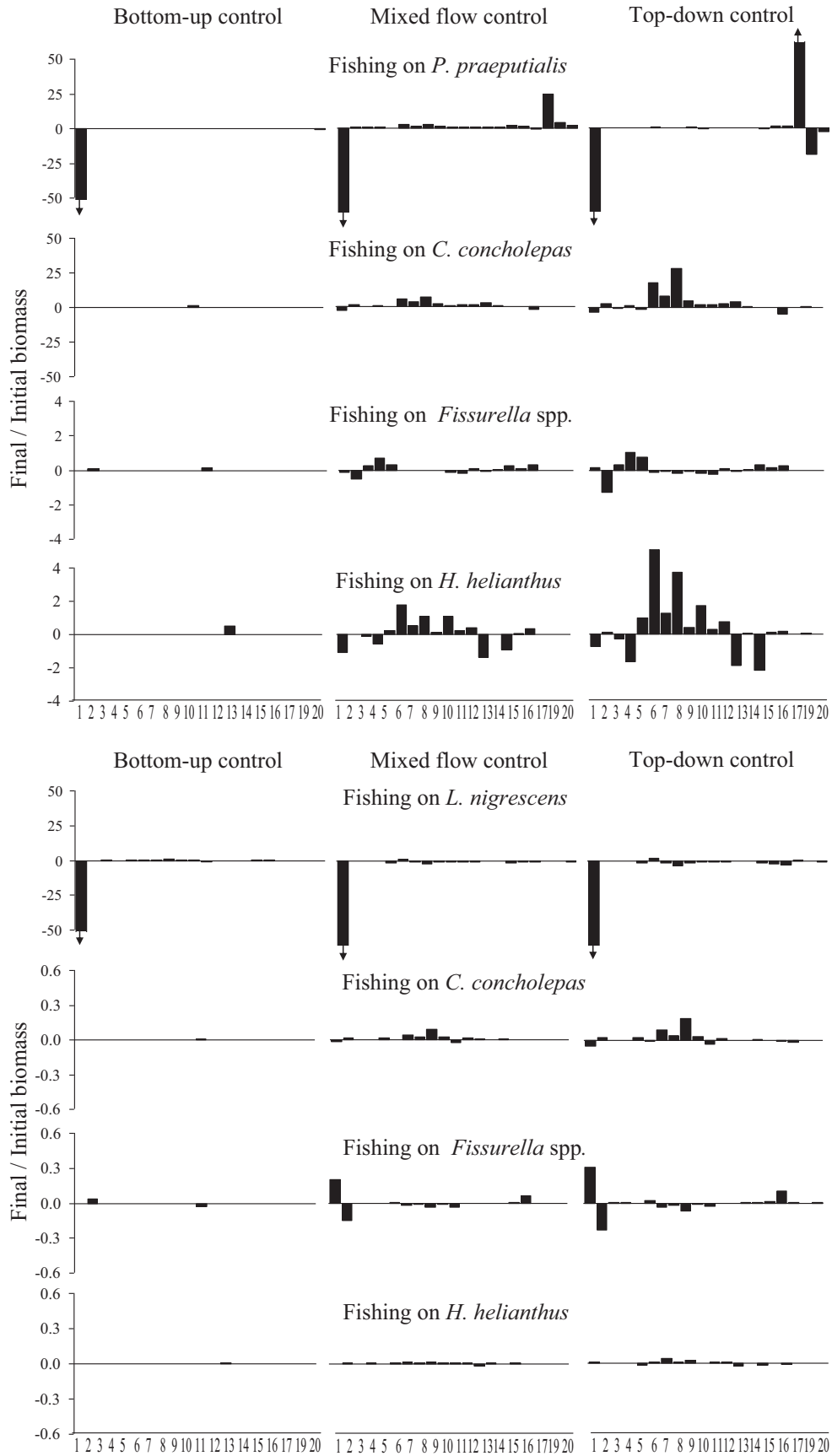
bottom-up flow control), the large epifauna (LE) ( $KS_i$ ), and *C. concholepas* ( $KS_{iEcosim1}$  under bottom-up control) (Table 4). This core of species and functional groups with keystone properties represented <1.7% of the total system biomass. It is important to indicate that *P. praeputialis* appeared as a keystone species using the  $KS_{iEcosim1}$  (under bottom-up and top-down controls). However, it was not considered to be a keystone because this tunicate represents ~97.4% of the total system biomass.

#### 4. Discussion

The results obtained for the distribution of abundances in both systems clearly show that the kelp *L. nigrescens* and the tunicate *P. praeputialis* largely dominate, exceeding 97% of the total system biomass in their respective communities. These are followed at a

distance by the mytilid *S. algalis* and other macroalga species in the *L. nigrescens* model and by the muricea *C. concholepas* and small epifauna herbivores (SEH) in the *P. praeputialis* system. Based on the wide difference between the estimated  $Pp/R$  and  $Pp/B$  ratios, system throughput ( $T$ ),  $A/C$  ratios, and development capacity ( $C$ ), it is clear that *L. nigrescens* and *P. praeputialis* build different ecological systems. Unfortunately, in terms of establishing which system is more developed, the indices calculated do not show a similar tendency. Based on the  $Pp/R$  ratio, the *P. praeputialis* system appears to be the most developed, whereas the  $Pp/B$ ,  $A/C$  ratios and redundancy indicate that the *L. nigrescens* system is the most developed and, in turn, the least resistant to disturbances. It should be noted that conclusions based on  $A/C$  ratios should be taken cautiously due to the negative correlation between *Ascendency* and maturity described by Christensen (1995). Although it would be inappropriate to compare the magnitudes of  $T$  and the  $A/C$  ratio calculated in





**Fig. 4.** Dynamical responses of *P. praeputialis*, *L. nigrescens*, *C. concholepas*, *Fissurella* spp. and *H. helianthus* subject to one year of increased fishing mortality (between year 1 and 2 of the simulation) under three control mechanisms using *Ecosim*. The biomass responses were obtained for the third year of the simulation. (Note: the numbers on the x-axis correspond to the species or functional groups of Table 1.)

**Table 3**Summary of the system recovery time (SRT) for each ecological subsystem using bottom-up, mixed and top-down control mechanisms ( $\nu$ ).

Ecological subsystem	Bottom-up control ( $\nu = 1.0$ ) SRT (year)	Mixed flow control ( $\nu = 2.0$ )	Top down control ( $\nu = 6.0$ )
<i>Pyura praeputialis</i>			
Harvest on			
(1) <i>Pyura praeputialis</i>	7.2	Oscillations	Oscillations
(2) <i>Fissurella</i> spp.	6.2	Oscillations	Oscillations
(3) <i>Tetrapigus niger</i>	7.2	Oscillations	Oscillations
(4) SEH	8.2	Oscillations	Oscillations
(5) Mesograzers	8	Oscillations	Oscillations
(6) Bivalvia	7.5	Oscillations	Oscillations
(7) <i>Semimytilus algosus</i>	7	Oscillations	Oscillations
(8) Barnacles	5.7	Oscillations	Oscillations
(9) Other filter feeders	7.2	Oscillations	Oscillations
(10) <i>Concholepas concholepas</i>	6.5	Oscillations	Oscillations
(11) SEC	6.2	Oscillations	Oscillations
(12) LE	5.7	Oscillations	Oscillations
(13) <i>Heliaster helianthus</i>	6.7	Oscillations	Oscillations
(14) Other Starfish	8.5	Oscillations	Oscillations
(15) Worms	6.7	9	Oscillations
(16) Cnidaria	7	Oscillations	Oscillations
(17) Macroalgae	6.7	Oscillations	Oscillations
(18) Zooplankton	5.5	Oscillations	Oscillations
(19) Phytoplankton	8.2	24.7	Oscillations
(20) All	19.7	–	–
<i>Lessonia nigrescens</i>			
Harvest on			
(1) <i>Lessonia nigrescens</i>	10.5	35.3	Oscillations
(2) <i>Fissurella</i> spp.	6	17	Oscillations
(3) <i>Tetrapigus niger</i>	7	15.5	Oscillations
(4) <i>Loxechinus albus</i>	6.7	13.2	Oscillations
(5) SEH	9.2	24.5	Oscillations
(6) Mesograzers	5.7	8	Oscillations
(7) Bivalvia	6.5	20	Oscillations
(8) <i>Semimytilus algosus</i>	6.5	18.2	Oscillations
(9) Barnacles	6.5	35.7	Oscillations
(10) Other filter feeders	7.5	11.5	Oscillations
(11) <i>Concholepas concholepas</i>	3.7	14.5	Oscillations
(12) LE	6.5	15.5	Oscillations
(13) <i>Heliaster helianthus</i>	6.5	15.5	Oscillations
(14) Other Starfish	8	14.2	Oscillations
(15) Worms	7	15.2	Oscillations
(16) Cnidaria	6.2	8	Oscillations
(17) Macroalgae	6.5	9.5	Oscillations
(18) Zooplankton	5.5	15.2	Oscillations
(19) Phytoplankton	8	24.7	Oscillations
(20) All	14.7	–	–

the present work with those described in the literature given the spatial scale and geographic distribution of the *L. nigrescens* and *P. praeputialis* systems, we can state that the magnitude of system throughput ( $T$ ) and the  $A/C$  ratio obtained for the *P. praeputialis* and *L. nigrescens* models, respectively, are much higher than those described for other intertidal systems (Baird et al., 2004; Leguerrier et al., 2007; Xu et al., 2011) and subtidal ecological systems along the Chilean coast (Ortiz, 2008b; Ortiz et al., 2009). Although for both model systems,  $A_i/C_i < A/C$ , the *P. praeputialis* model seems to have a stronger dependency on external connections than the *L. nigrescens* model (sensu Baird et al., 1991), which could be explained by flows to fishes and birds that are not included in our models. It is important to indicate that the comparison among macrodescriptors (absolute values) of both model systems should be taken with a degree of caution as the tunicate species *P. praeputialis* required a relevant increment of production during the balancing process, and these maturity estimates are sensitive to changes in the input values.

Even though the similar values of connectance, omnivory index ( $OI$ ), and average path length ( $APL$ ) calculated for both models indicate comparable degrees of topological structure, this could be a consequence of the strategy of model construction, which limited them to a similar number of compartments ( $=20$ ). The

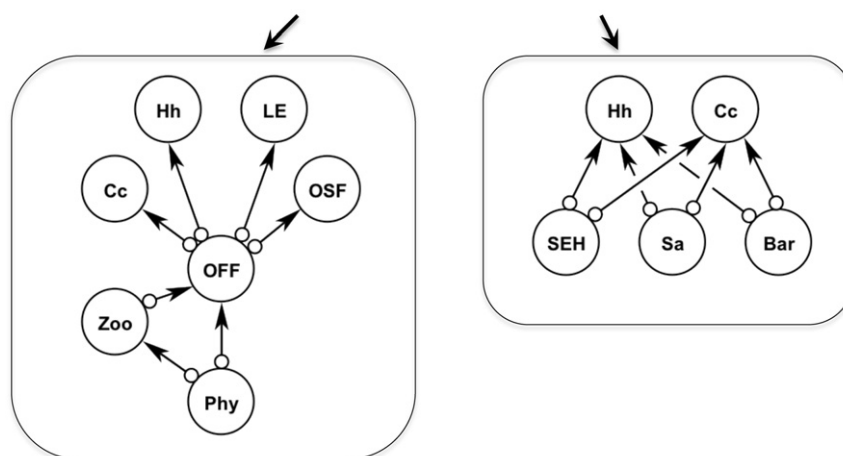
differences detected between the mean trophic levels of fishery values clearly show that which occurs in both systems: whereas in the *L. nigrescens* system, the harvest concentrates mainly on this kelp species due to its high market demand, both as raw material for the chemical industry and as food for the different species of abalone now being farmed along the northern Chilean coast, in the *P. praeputialis* model, the harvest (illegal) focuses largely on secondary producers (the muricidea *C. concholepas* and other molluscs).

Ulanowicz (1997) suggested estimating the relative ascendancy of each species and/or functional group as a way of assessing the contribution of each of the compartments to the overall structure and function of the system. In this sense, our results show that the compartments of both systems contribute in a different manner since, in the *P. praeputialis* model, relative ascendancy is supported by detritus and phyto-zooplankton, which is consistent with the permanent influence of nutrient-rich waters coming from the upwelling centre located off Antofagasta (Escribano et al., 2004). On the contrary, in the *L. nigrescens* model, relative ascendancy is supported basically by detritus and *L. nigrescens*. A similar pattern was described by Ortiz (2008a) when modelling the subtidal kelp systems dominated by *Lessonia trabeculata* and *Macrocystis integrifolia*. These results are consistent with the supposition of Duggins

**Table 4**

List of species and/or functional groups with model keystone properties. Core of species related ecologically (*keystone species complex*). (Note: large circles = species and/or functional groups, small circles = negative effect, and small arrows = positive effect.)

Model Keystone Indices	Species and/or Functional groups	
	Ecological subsystem	
	<i>P. praeputialis</i>	<i>L. nigrescens</i>
$K_i$	<i>H. Helianthus</i> (Hh)	<i>H. Helianthus</i> (Hh)
$KS_i$	Large Epifauna (LE)	<i>C. concholepas</i> (Cc)
$KS_{iEcosim1}$ (bottom-up)	<i>C. concholepas</i> (Cc)	<i>S. algalus</i> (Sa)
$KS_{iEcosim1}$ (mixed)	Phytoplankton (Phy)	<i>S. algalus</i> (Sa)
$KS_{iEcosim1}$ (top-down)	Zooplankton (Zoo)	<i>S. algalus</i> (Sa)
$KS_{iEcosim2}$ (bottom-up)	Other Starfish (OSF)	Small Epifauna Herbivore (SEH)
$KS_{iEcosim2}$ (mixed)	-	Barnacles (Bar)
$KS_{iEcosim2}$ (top-down)	-	-
$KQ_{iLA1}$ (mixed)	Other Filter Feeders (OFF)	Barnacles (Bar)
$KQ_{iLA2}$ (mixed)	Other Filter Feeders (OFF)	<i>S. algalus</i> (Sa)



et al. (1989) that the kelp species essentially concentrates biomass and contribute nutrients to coastal marine ecosystems through macroalgal detritus.

In terms of the outcomes of the direct and indirect effects estimated using *MTI* and *Ecosim* simulations and the *system recovery time (SRT)* (using *Ecosim*), different response patterns were observed. This shows that *P. praeputialis* and *L. nigrescens* are relevant in their respective communities using different mechanisms, since, on the one hand, the tunicate species propagates higher effects on the remaining variables and, on the other, the kelp species *L. nigrescens* presents the longest *system recovery time* (as a resilience measure).

The concept of keystone species has generated broad debate in terms of: (1) experimental designs, which present limitations such as considering only some species for the effect of exclusion or changes in the abundance of one species on another species in a community (Mills et al., 1993; Wootton, 1994; Libralato et al., 2006), and (2) higher order effects (indirect effects), which are normally excluded from the experimental design as they could be magnified by cascading effects (Brett and Goldman, 1996; Pace et al., 1999). Our results show a similar core of species in both ecological systems, including prey and predator species with model keystone properties. It is important to indicate that both cores of species constitute <2% of the total system biomass, conforming to the original concept of keystone given by Paine (1969). Likewise, these results coincide with that described by Ortiz et al. (2013), who proposed that we should broaden the classic concept of keystone species towards a more holistic one such as *keystone*

*species complex*. Okey (2004) arrived at a similar conclusion – keystone guilds or clusters of species with keystone properties – based on a trophic model in Alaska.

**5. Conclusions**

The *Pp/R*, *Pp/B*, and *A/C* ratios and *redundancy* do not show the tunicate *P. praeputialis* to be a superior bio-engineer as compared with the system built by the kelp *L. nigrescens*, disagreeing with the conclusions described by Cerda and Castilla (2001) and Castilla et al. (2004). The above is relevant since the field of ecology tends to place species in a hierarchy in terms of biodiversity and species richness indices (see Cerda and Castilla, 2001), without considering the different mechanisms and properties that emerge from complexity based on Odum’ and Ulanowicz’ ecosystem indices, propagations of higher order effects, and the *system recovery time*, nor when comparing a native kelp species (*L. nigrescens*) with a recently introduced-alien species such as *P. praeputialis* (sensu Castilla et al., 2002).

As described earlier, the increment in one order of magnitude of biomass and productivity of phyto-zooplankton during the procedure of balancing the *P. praeputialis* model did not agree with estimates given for the Chilean and Peruvian coastal ecosystems (Wolff, 1994; Taylor et al., 2008). This, nonetheless, could be explained not only by the upwelling centre located near Mejillones Peninsula (Escribano et al., 2004), but also could be due to internal waves or tidal bores occurring with a semidiurnal frequency,

which could be an important additional mechanism for delivering high concentrations of chlorophyll-*a* to shallow subtidal and intertidal communities dominated by filter-feeders inside Antofagasta Bay (Guiñez, personal communication). It is important to indicate that this mechanism has been previously described for a coastal ecosystem of central Chile (Vargas et al., 2004).

Finally, at least two important facts should be noted: (1) in spite of the inherent and well-known limitations and shortcomings of the *Ecopath*, *Ecosim*, and *Loop Analysis* theoretical frameworks, the models constructed and the simulations executed in the current paper represent the mechanisms underlying the system studied only when considering its short-term dynamics, and (2) the comparison among different system-development estimates (magnitudes) should be taken with care, because the *P. praeputialis* model required an important increment of the production of phytoplankton – as input value – during the balancing process.

### Acknowledgement

This contribution was partially financed by the Chilean National Foundation for Scientific and Technological Development (FONDECYT), grant no. 1040293.

### 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.ecolmodel.012.10.014>.

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