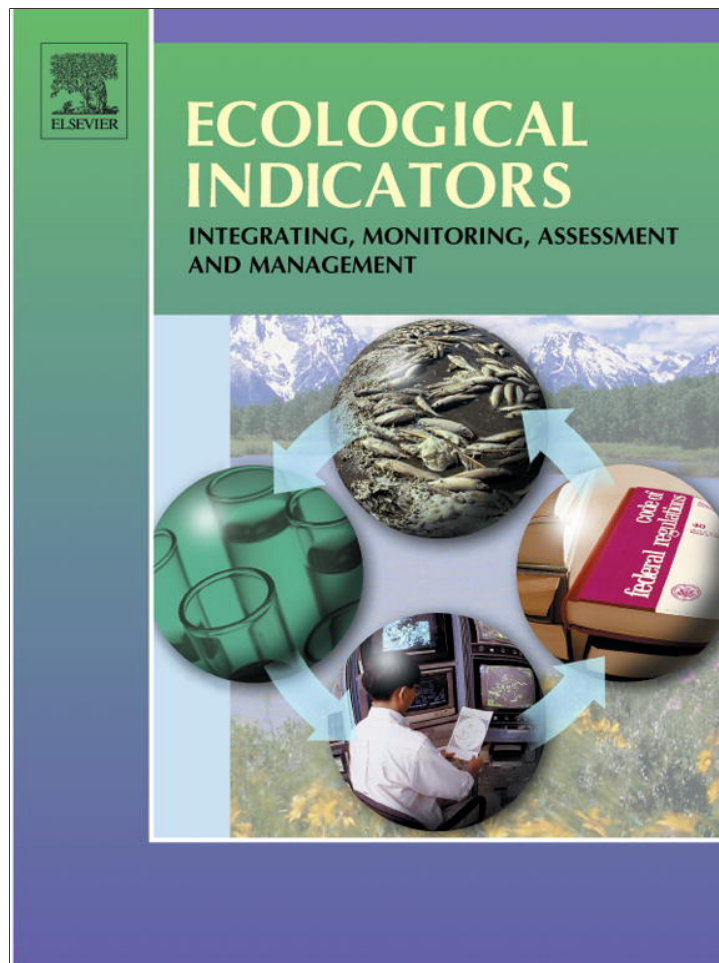


Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

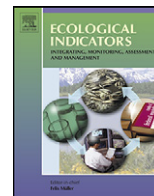
Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://www.elsevier.com/locate/locate/ecolind)

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Identifying keystone trophic groups in benthic ecosystems: Implications for fisheries management

Marco Ortiz^{a,*}, Richard Levins^b, Leonardo Campos^{a,e}, Fernando Berrios^{a,e}, Fernando Campos^a, Ferenc Jordán^c, Brenda Hermosillo^{a,e}, Jorge Gonzalez^{a,e}, Fabián Rodríguez^d

^a Instituto Antofagasta, Instituto de Investigaciones Oceanológicas, Facultad de Recursos del Mar, Universidad de Antofagasta, P.O. Box 170, Antofagasta, Chile

^b Department of Global Health and Population, Harvard School of Public Health, Harvard University, 665 Huntington Avenue, Boston, MA 02115, USA

^c The Microsoft Research – University of Trento Centre for Computational and Systems Biology, Piazza Manifattura 1, Rovereto, TN, Italy

^d 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

^e Programa de Doctorado en Ciencias Aplicadas, Mención Sistemas Marinos Costeros, Facultad de Recursos del Mar, Universidad de Antofagasta, Antofagasta, Chile

ARTICLE INFO

Article history:

Received 26 June 2012

Received in revised form 15 August 2012

Accepted 28 August 2012

Keywords:

Keystone species complex
Multispecies modelling
Coastal ecosystems
SE Pacific

ABSTRACT

Many species inhabiting the benthic marine ecosystems of the central and northern Chilean coast have been intensively harvested and this exploitation has increased considerably in recent years. Despite this harvest pressure, few studies have attempted to establish a more holistic, systems-based management plan. On the contrary, research continues to rely on population models in which the species of interest are isolated from their ecological context. This work offers several keystone indices in order to help multispecies fisheries management. The indices used are: (1) functional indices based on steady-state and dynamic trophic models; (2) structural indices based on bottom-up and top-down control mechanisms; and (3) qualitative keystone species indices using loop models (mixed control). The quantitative trophic models were constructed using *Ecopath with Ecosim* (EwE; v. 5.0) software, and the qualitative model was analysed using *Loop Analysis*. All models describe the interactions of the most representative species and functional groups inhabiting the benthic ecosystems of Tongoy Bay, La Rinconada Marine Reserve (Antofagasta Bay), and the kelp forest of Mejillones Peninsula (Antofagasta). Even though our results only represent the short-term dynamics of these systems, we have found keystone properties of several species and functional groups, including primary producers, herbivores, and top predators. Despite this wide variability of groups, we detected a different core set of species or functional groups, each of which contained prey–predator and plant–herbivore relationships. Because the traditional keystone concept of a single species is difficult to apply, we suggest shifting away from this view towards a more holistic alternative such as that of a *keystone species complex*. This kind of approach would facilitate the design and assessment of sustainable management strategies for ecological marine ecosystems. Despite the ecological relevance of our results, further experimental studies and modelling using other theoretical frameworks should be performed.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Ever since Paine (1969) introduced the concept of keystone species to ecology, it has been the “cornerstone” for the development of numerous investigations in different communities and ecosystems (Mills et al., 1993; Power et al., 1996), especially given its direct and immediate use in the design and application of conservation management programs (Payton et al., 2002). Of all the definitions proposed for keystone species, the most widespread and the simplest was given 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, since this requires observations and studies that incorporate different spatio-temporal scales, levels of organization, and taxonomic groups (Power et al., 1996; Libralato et al., 2006).

Although numerous studies based on field experiments have quantified the strength of interactions by evaluating the impacts propagated on remainder species when the abundance of one species in a community changes (Paine, 1992; Berlow, 1999), these studies necessarily focused on a few species, excluding other “uninteresting” species from the experiment and possibly causing an inevitable bias in the identification of keystone species (Wootton, 1994; Libralato et al., 2006). Likewise, other external factors (i.e.,

* Corresponding author.

E-mail address: mortiz@uantof.cl (M. Ortiz).

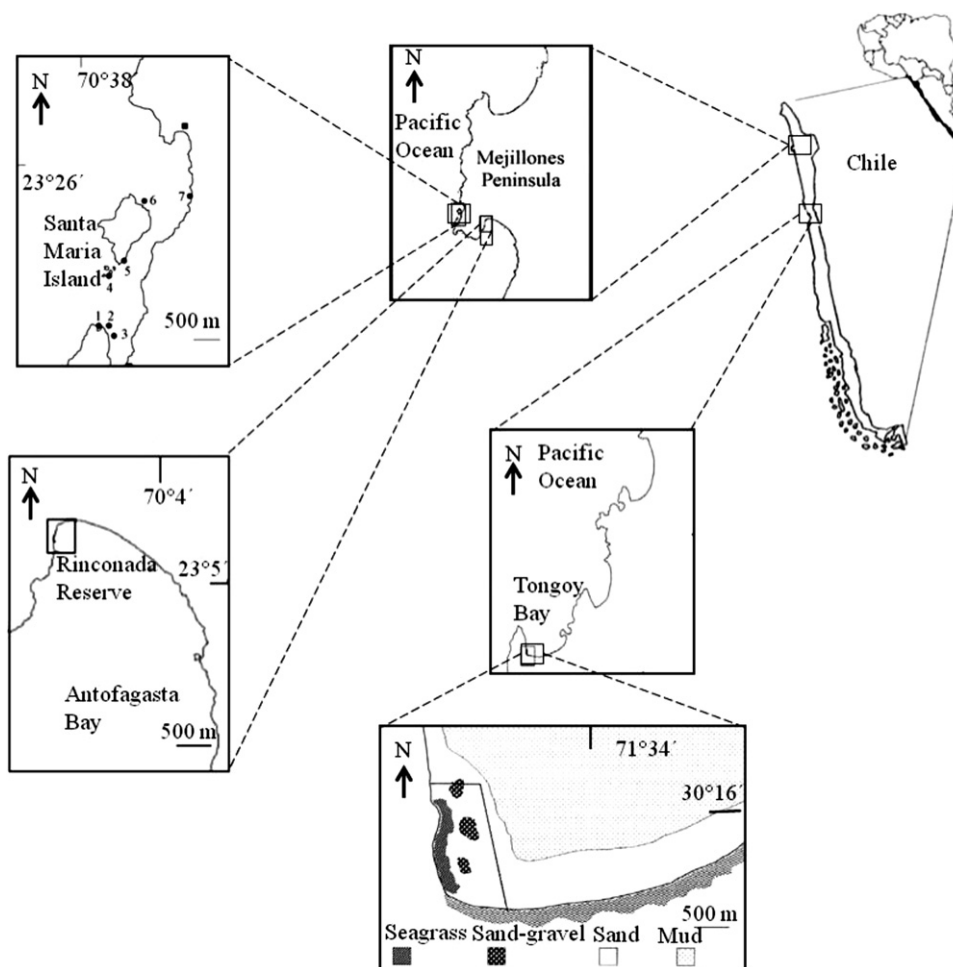


Fig. 1. Locations of the study areas in central and northern Chile: (1) Tongoy Bay, (2) La Rinconada Marine Reserve, and (3) the Mejillones Peninsula kelp forest.

level of exposure to coastal waves, environmental heterogeneity, harvest) may cause the density of the species of interest to vary in different habitats, thereby hindering the necessary replication of studies and the determination of keystone species. Finally, some purely experimental studies (Pace et al., 1999) have omitted the propagation of higher-order effects – which are buffered along some pathways and amplified along others – despite the recognized importance of this phenomenon (Wootton, 1994; Patten, 1997; Yodzis, 2001).

Many studies have suggested characterizing the role that different species play in their ecological systems by using different network indices (Jordán et al., 1999, 2007; Dunne et al., 2002; Luczkovich et al., 2003; Jordán and Scheuring, 2004; Allesina and Bodini, 2005; Brose et al., 2005; Eklöf and Ebenman, 2006; Libralato et al., 2006). Such multispecies modelling offers a complementary way to deal with some of the limitations in the experimental identification of key groups. Quantitative trophic models permit estimations of the strength of interactions between model species or functional groups by identifying the presence of keystone species, which occupy key positions in the networks (Jordán et al., 1999; Jordán and Scheuring, 2004). Keystone species can also be determined using qualitative loop models, in which 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, thus, the local stability of the network.

Over the last few years, the multispecies modelling approach has gained ground due to growing interest in the evaluation, quantification, and prediction of the changes that fisheries produce in

an ecosystem's properties (Hall, 1999a,b; Robinson and Frid, 2003; Hawkins, 2004; Pickett et al., 2004; Francis et al., 2007; Scotti et al., 2007; Crowder et al., 2008). Thus, multispecies models could be used for pre-screening, determining the core set of variables that should be considered in subsequent field experiments.

The aim of this work is to use pre-screening to identify keystone species based on: (1) functional indices using quantitative models (using EwE v. 5.0), (2) structural indices including bottom-up and top-down control mechanisms, and (3) qualitative indices based on Loop Analysis (mixed control). All trophic models represent interspecific relationships (prey–predator) taking place in the benthic communities of Tongoy Bay (Ortiz and Wolff, 2002a), La Rinconada Marine Reserve (SE Pacific coast) (Ortiz et al., 2010), and the kelp forest of Mejillones Peninsula (Antofagasta) (Ortiz, 2008a), all of which are intensively exploited. The identification of keystone species in these benthic networks would complement the existing information describing other attributes of such ecosystems (Ortiz and Wolff, 2002a; Ortiz, 2008b, 2010; Ortiz et al., 2010; Ortiz and Levins, 2011), thereby contributing to both conservation ecology and the design and implementation of sustainable multispecies fisheries management.

2. Materials and methods

2.1. Study areas

Three study areas are used herein. (1) Four habitats were modelled in Tongoy Bay: seagrass meadows at depths of 0–4 m;

sand-gravel between 4 and 10 m; sand between 10 and 14 m, and mud bottoms at >14 m depth (Fig. 1). (2) La Rinconada Marine Reserve is located in the northern part of Antofagasta Bay (Mejillones Peninsula, Chile). At depths of 8–15 m, sand and gravel dominate the physical benthos and two ecological subsystems host clearly different species aggregates (Fig. 1). (3) The benthic communities of the kelp forest adjacent to Santa Maria Island off Mejillones Peninsula were used. All kelp bed studies occupied rocky bottoms made up of boulders and platforms with varying exposure to the prevalent waves. An important upwelling centre near all the benthic communities supplies nutrients to the coastal ecosystems (Daneri et al., 2000; Escribano et al., 2004). It is important to indicate that all ecological systems modelled are intensively intervened (harvested) by local artisanal fishermen (Table 1).

2.2. Ecopath, Ecosim (v. 5.0) and Loop Analysis: theoretical frameworks

It is important to mention that the model compartments (species and/or functional groups) were selected and defined using information on direct trophic interactions between the target species and other relevant macrofauna species in the systems. For more detailed information, please see Ortiz and Wolff (2002a), Ortiz (2008a), and Ortiz et al. (2010). These contributions used Ecopath with Ecosim software (v. 5.0) (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). 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 locations, and complexities (Monaco and Ulanowicz, 1997; Christensen and Walters, 2004; Guénette et al., 2008; Griffiths et al., 2010; Arias et al., 2011). For more details, see Appendix A.

Table 1 shows the parameters entered into and estimated by Ecopath software for each benthic system studied. The diet and the qualitative interaction matrices for all benthic systems are shown in Appendix B.

In qualitative loop models (based on Loop Analysis), relationships are shown as a sign that indicates the type of influence each variable has upon another (i.e., positive, negative, or zero) (see Table 2). For instance, in ecological relationships (+, -) denotes a predator-prey or parasite-host interaction (-, -) represents competition between two species, and (+, +), (+, 0), and (-, 0) represent mutualism, commensalism, and amensalism, respectively. Each variable is shown as a large circle, the edges of which represent the directions and types of its interactions, i.e., an arrow at one end indicates a positive effect; a circle means the effect is negative; and the lack of a symbol shows a null effect.

Loop Analysis is based on the correspondence between 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, 2002b, 2008; Ortiz, 2008b; Ortiz and Stotz, 2007; Darmbacher et al., 2009; Ortiz and Levins, 2011). For more details of the modelling assumptions and basic equations, see Appendix A.

Table 1

Parameter values entered into (bold) and estimated by (standard) Ecopath software (TL=trophic level, C=catches, B=biomass, P/B=turnover rate, Q/B=consumption rate, EE=ecotrophic efficiency) for seagrass, sand-gravel, sand, and mud habitats, and the whole model in Tongoy Bay, La Rinconada Marine Reserve, and the kelp forest ecosystem.

Seagrass model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. gelatinosus</i>	20.5		1.2	5.0	3.2	0.09
(2) <i>H. helianthus</i>	0.5		0.6	2.3	3.5	0.35
(3) <i>L. magallanica</i>	0.6		0.7	3.0	3.1	0.24
(4) <i>C. polyodon</i>	10.0	0.2	1.1	9.5	3.4	0.88
(5) <i>P. barbiger</i>	1.6		2.0	9.9	3.3	0.96
(6) <i>Taliepus</i> sp.	1.3		1.5	9.5	3.0	0.97
(7) Large Epifauna	2.2		1.3	9.5	3.2	0.96
(8) <i>A. purpuratus</i>	90.0	7.5	2.1	9.9	2.0	0.81
(9) Small Epifauna	29.5		3.7	12.5	2.8	0.94
(10) Infauna	65.0		4.4	14.7	2.2	0.85
(11) <i>H. tasmanica</i>	450.0		1.5		1.0	0.09
(12) <i>Ch. chamissoi</i>	5.5	0.01	6.0		1.0	0.25
(13) Rodophyta	6.0		5.5		1.0	0.25
(14) <i>Ulva</i> sp.	5.0		6.0		1.0	0.28
(15) Zooplankton	18.0		40.0	160.0	2.0	0.23
(16) Phytoplankton	28.0		250.0		1.0	0.52
(17) Detritus	100.0				1.0	0.16
Sand-gravel model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. gelatinosus</i>	46.8		1.2	5.0	3.1	0.09
(2) <i>H. helianthus</i>	2.0		1.1	2.3	3.1	0.22
(3) <i>L. magallanica</i>	4.0		1.1	3.0	3.0	0.53
(4) <i>C. polyodon</i>	25.6	0.2	1.1	9.5	3.3	0.70
(5) <i>P. barbiger</i>	29.3		2.0	9.9	3.0	0.85
(6) <i>Taliepus</i> sp.	1.7		1.5	9.5	2.1	0.95
(7) Large Epifauna	7.5		2.2	9.5	3.2	0.99
(8) <i>A. purpuratus</i>	71.5	7.5	2.1	9.9	2.0	0.86
(9) <i>C. trochiformis</i>	90.0		0.8	9.9	2.0	0.93
(10) <i>Tegula</i> sp.	150.0		2.2	9.9	2.0	0.77
(11) <i>Pyura chilensis</i>	70.0		3.2	11.0	2.4	0.64
(12) Small Epifauna	20.0		3.7	12.5	2.8	0.93
(13) Infauna	60.0		4.4	14.7	2.2	0.93
(14) <i>Ch. chamissoi</i>	564.8	113.9	6.0		1.0	0.26
(15) Rodophyta	230.0		5.5		1.0	0.37
(16) <i>Ulva</i> sp.	70.0		6.0		1.0	0.22
(17) Zooplankton	19.0		40.0	160.00	2.0	0.54
(18) Phytoplankton	36		250		1.0	0.53
(19) Detritus	100				1.0	0.14
Sand model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. gelatinosus</i>	17.3		1.2	5.0	3.1	0.13
(2) <i>L. magallanica</i>	0.6		0.6	2.3	2.0	0.24
(3) <i>C. polyodon</i>	17.5	0.1	1.1	9.5	3.2	0.95
(4) <i>C. coronatus</i>	6.4		1.8	9.5	2.9	0.94
(5) Large Epifauna	6.0		1.3	9.5	3.1	0.97
(6) <i>X. cassidiformis</i>	9.7	0.6	1.5	5.5	2.0	0.97
(7) <i>A. purpuratus</i>	40.0	0.99	2.1	9.9	2.0	0.82
(8) <i>Mulinia</i> sp.	150.0		1.2	9.9	2.1	0.54
(9) Small Epifauna	43.0		3.7	12.5	2.2	0.97
(10) Infauna	150.0		7.0	14.7	1.0	0.95
(11) <i>Ch. chamissoi</i>	3.0		6.0		1.0	0.83
(12) Rodophyta	6.0		5.5		1.0	0.68
(13) <i>Ulva</i> sp.	3.0		6.0		1.0	0.83
(14) Zooplankton	18.0		40.0	160.0	2.0	0.22
(15) Phytoplankton	34.0		250.0		1.0	0.39
(16) Detritus	100.0				1.0	0.12
Mud model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. gelatinosus</i>	1.1		1.2	5.0	3.2	0.08
(2) <i>L. magallanica</i>	0.6		0.7	2.3	3.1	0.13
(3) <i>C. polyodon</i>	7.4	0.1	1.1	9.5	3.5	0.87
(4) <i>C. porteri</i>	23.7		0.5	4.5	3.0	0.90
(5) <i>C. coronatus</i>	6.4		1.8	9.5	3.2	0.94

Table 1 (Continued)

Mud model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(6) Large Epifauna	15.0		1.3	9.5	3.3	0.95
(7) <i>A. purpuratus</i>	4.0	0.01	2.1	9.9	2.0	0.82
(8) Small Epifauna	21.0		3.7	12.5	2.9	0.99
(9) Infauna	96.0		4.4	14.7	2.2	0.97
(10) Zooplankton	18.0		40.0	160.0	2.0	0.34
(11) Phytoplankton	28.0		250.0		1.0	0.43
(12) Detritus	100.0				1.0	0.22

Whole model

Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. gelatinosus</i>	21.6		1.2	5.0	3.1	0.15
(2) <i>H. helianthus</i>	1.1		0.6	2.3	3.2	0.17
(3) <i>L. magallanica</i>	1.3		0.7	3.0	3.1	0.12
(4) <i>X. cassidiformis</i>	2.3	0.6	1.5	5.5	3.1	0.99
(5) <i>C. polyodon</i>	10.0	0.4	101.0	9.5	3.4	0.92
(6) <i>C. porteri</i>	3.5		0.5	4.5	3.3	0.91
(7) <i>C. coronatus</i>	2.5		108.0	9.5	3.4	0.96
(8) <i>P. barbiger</i>	4.0		2.0	9.9	2.9	0.83
(9) Large Epifauna	5.5		1.3	9.5	3.5	0.91
(10) <i>A. purpuratus</i>	55.0	16	2.1	9.9	2.0	0.81
(11) <i>Taliopus</i> sp.	0.7		1.5	9.5	2.2	0.99
(12) <i>Mulinia</i> sp.	24.0		1.2	9.9	2.0	0.80
(13) <i>C. trochiformis</i>	37.0		0.8	9.9	2.0	0.75
(14) <i>Tegula</i> sp.	38.0		2.2	9.9	2.0	0.70
(15) <i>Pyura chilensis</i>	20.0		3.2	11.0	2.4	0.73
(16) Small Epifauna	18.0		3.7	12.5	2.8	0.81
(17) Infauna	60.0		4.4	14.70	2.2	0.86
(18) <i>H. tasmanica</i>	110.0		1.5		1.0	0.48
(19) <i>Ch. chamissoi</i>	78.6	114	6		1.0	0.38
(20) Rodophyta	110.0		5.5		1.0	0.32
(21) <i>Ulva</i> sp.	50		6		1.0	0.32
(22) Zooplankton	18		40	160	2.0	0.54
(23) Phytoplankton	28		250		1.0	0.57
(24) Detritus					1.0	0.16

LRMR model

Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>A. purpuratus</i>	162.8	271.0	2.7	9.9	2.0	0.70
(2) <i>sA. purpuratus</i>	50.0	5.0	2.0	9.9	2.0	0.05
(3) <i>T. dombeii</i>	159.7	0.2	2.0	9.9	2.0	0.18
(4) <i>T. pannosa</i>	35.0	0.2	2.8	9.9	2.0	0.96
(5) <i>A. ater</i>	20.0	0.2	1.8	9.9	2.0	0.88
(6) <i>T. chocolata</i>	31.5	0.7	2.7	7.2	2.5	0.35
(7) <i>L. magallanica</i>	0.4		0.5	3.0	3.1	0.06
(8) <i>Cancer</i> spp.	5.3		1.9	9.5	3.0	0.10
(9) SEH	30.0		2.5	11.7	2.0	0.79
(10) SEC	20.0		2.0	10.4	2.8	0.72
(11) LE	12.0		1.9	9.2	2.8	0.60
(12) Chlorophyta	15.0		5.0		1.0	0.70
(13) Rhodophyta	169.3		5.0		1.0	0.01
(14) Phaeophyta	30.0		5.0		1.0	0.94
(15) Zooplankton	20.0		40.0	160.0	2.0	0.01
(16) Phytoplankton	30.0		250.0		1.0	0.86
(17) Detritus	100.0				1.0	0.28

Kelp forest model

Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(1) <i>M. integrifolia</i>	1448.0	80.0	10.30		1.0	0.13
(2) <i>L. trabeculata</i>	2646.0	160.0	3.40		1.0	0.25
(3) Mesophylum	40.0		15.0		1.0	0.80
(4) Rhodophyta	687.70		5.0		1.0	0.57
(5) Chlorophyta	111.90		25.0		1.0	0.86
(6) <i>H. helianthus</i>	56.42		1.20	2.50	3.3	0.06
(7) <i>M. gelatinosus</i>	28.72		0.60	5.0	3.1	0.25
(8) Other Seastar	2.77		1.50	3.0	3.2	0.71
(9) <i>T. niger</i>	284.83		2.90	10.0	2.0	0.61
(10) <i>Tegula</i> sp.	90.0		4.0	20.0	2.0	0.91
(11) <i>Turritella</i> sp.	425.19		3.92	8.0	2.0	0.31
(12) Large Epifauna	200.0		1.50	9.50	2.8	0.31

Table 1 (Continued)

Kelp forest model						
Species/functional groups	B	C	P/B	Q/B	TL ^a	EE ^a
(13) Small Epifauna	150.0		6.0	12.50	2.3	0.61
(14) <i>P. chilensis</i>	12.47	10.0	2.10	4.50	3.4	0.38
(15) <i>Ch. variegatus</i>	17.72	10.0	2.05	6.0	3.2	0.28
(16) Zooplankton	20.0		40.0	160.0	2.0	0.47
(17) Phytoplankton	30.0		250.0		1.0	0.46
(18) Detritus	100.0				1.0	0.03

^a Parameter calculated by Ecopath II.

2.3. Mixed trophic impacts 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 evaluate the propagation of instantaneous direct and indirect effects and the system recovery time (SRT) in response to increased total mortality ($Z=M+F$) equivalent to 30% more total production ($P=B \times Z$). This was done between the first and second year of simulation for all species and functional groups considered in the model. Since the models studied represent only their short-term dynamics, the propagation of instantaneous effects was determined by evaluating the changes of biomass in the remainder variables in the third year of simulation. Due to the lack of experimental accuracy and time-series of landings for the variables, all dynamic simulations by Ecosim were carried out using the following flow control mechanisms (v_{ij}): (1) bottom-up, (2) mixed, and (3) top-down.

2.4. Functional keystone indices

Once the trophic model was balanced, the functional index (KS_i) developed by Libralato et al. (2006) was used. This is an extension of the MTI (Ulanowicz and Puccia, 1990). Since 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 relationship:

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2} \tag{1}$$

where m_{ij} corresponds to the elements of the MTI matrix and quantifies the direct and indirect impacts that each (impacting) species or group i has on any (impacted) group j of the food web. However, the effect of the change in 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 food web was estimated using the following relationship:

$$p_i = \frac{B_i}{\sum_k^n B_k} \tag{2}$$

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, in order to balance the overall effect and biomass, we established the keystone index (KS_i) for each species or functional group, integrating Eqs. (1) and (2) as follows:

$$KS_i = \log[\varepsilon_i(1 - p_i)] \tag{3}$$

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 were those obtained with *MTI* in order to obtain two additional functional keystone indices. Eqs. (1)–(3) were used to obtain one keystone species index related to the propagation of effects ($KS_{iEcosim1}$), and Eqs. (2) and (3) were used to obtain another functional keystone species index related to *SRT* values ($KS_{iEcosim2}$). Both indices revealed, as did the KS_i index (Libralato et al., 2006), that high values of keystone-ness corresponded to variables with low biomass and a high overall effect.

2.5. Topological-structural keystone index

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 vertical directions (i.e., bottom-up and top-down). The keystone index of the *i*th species or functional group (K_i) is calculated as follows:

$$K_i = \sum_{c=1}^n \frac{1}{d_c} (1 + K_{bc}) + \sum_{e=1}^n \frac{1}{f_e} (1 + K_{te}) \quad (4)$$

where *n* is the number of predators 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 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 et al. (1999), Jordán (2001), and Vasas et al. (2007). 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 different flow control mechanisms.

2.6. Qualitative keystone index

Keystone-ness indices based on qualitative loop models were also calculated. Once the stabilized matrix with $F_n < 0$ was obtained, the self-dynamics of each variable corresponding to the principal diagonal (Appendix B) were modified in order to estimate a new perturbed magnitude of local stability F_p . Based on the distance between F_n and F_p , $\Delta = |F_n - F_p|$, it was possible to determine the change provoked by each variable on initial stability (F_n), thereby obtaining a first qualitative keystone species index (KQ_{iLA1}). Since *Loop Analysis* does not consider the abundance of the variables, the difference (Δ) was used in Eq. (3) to obtain an additional keystone index (KQ_{iLA2}) in which high values of keystone-ness corresponded to variables with low biomass and a high overall effect. Due to the qualitative character of *Loop Analysis*, the prey–predator interaction was captured as a mixed control mechanism.

3. Results

Table 2 summarizes the results obtained from all the keystone indices applied (only the top ranking group). These indices indicated keystone-ness properties for a variety of different species and functional groups, coinciding in only some of them. In general terms, keystone-ness properties were detected for species of different trophic levels, from primary producers to herbivores (filter feeders) to top predators. Fig. 2 shows the different core sets of species for each model. The core sets of species contain from 14.4 to 44.5% of the total system biomass.

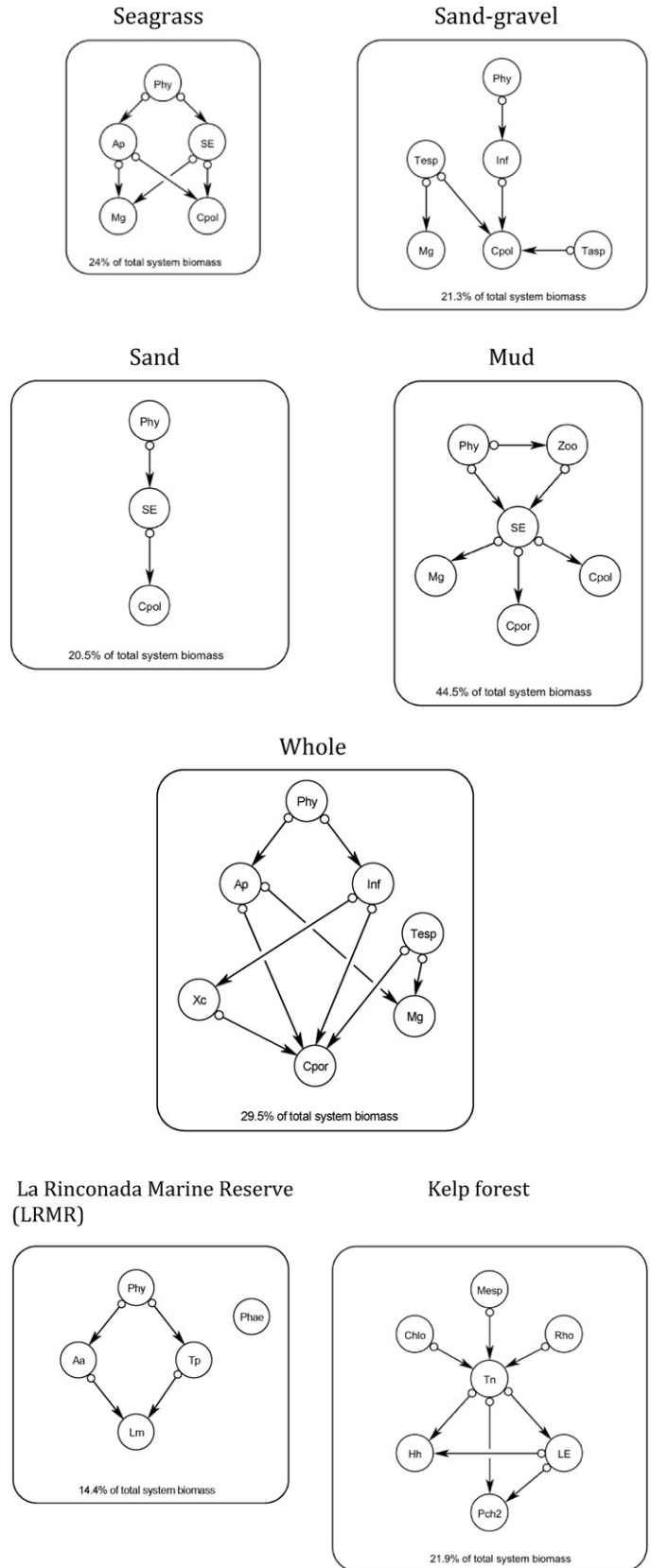


Fig. 2. Core set of species with keystone properties (*keystone species complex*) in each ecological system studied (Note: species names are listed in Table 2. The small circles and arrows represent negative and positive effects, respectively).

Table 2
Key species or groups identified by different keystone species indices in each ecological system modelled (for details, see Section 2).

Model keystone indexes	Species and/or functional groups						
	Ecological model systems						
	Seagrass	Sand-gravel	Sand	Mud	Whole	LRMR	Kelp forest
K_i	<i>C. polyodon</i> (Cpol)	<i>C. polyodon</i> (Cpol)	<i>C. polyodon</i> (Cpol)	<i>C. polyodon</i> (Cpol)	<i>C. polyodon</i> (Cpol)	Phytoplankton (Phy)	<i>H. helianthus</i> (Hh)
KS_i	Small Epifauna (SE)	<i>Tegula</i> sp. (Tesp)	Small Epifauna (SE)	Zooplankton (Zoo)	<i>Tegula</i> sp. (Tesp)	Phytoplankton (Phy)	Chlorophyta (Chlo)
$KS_{iEcosim1}$ (bottom-up)	<i>A. purpuratus</i> (Ap)	<i>M. gelatinosus</i> (Mg)	<i>C. polyodon</i> (Cpol)	<i>C. porteri</i> (Cpor)	<i>M. gelatinosus</i> (Mg)	<i>T. pannosa</i> (Tp)	Large Epifauna (LE)
$KS_{iEcosim1}$ (mixed)	<i>M. gelatinosus</i> (Mg)	<i>Tegula</i> sp. (Tesp)	Small Epifauna (SE)	<i>C. porteri</i> (Cpor)	Infauna (Inf)	Phaeophyta (Phae)	Rhodophyta (Rho)
$KS_{iEcosim1}$ (top-down)	<i>A. purpuratus</i> (Ap)	Infauna (Inf)	Small Epifauna (SE)	Small Epifauna (SE)	Infauna (Inf)	Phaeophyta (Phae)	Rhodophyta (Rho)
$KS_{iEcosim2}$ (bottom-up)	<i>A. purpuratus</i> (Ap)	Phytoplankton (Phy)	Phytoplankton (Phy)	Phytoplankton (Phy)	Phytoplankton (Phy)	<i>L. magallanica</i> (Lm)	<i>Mesophylum</i> sp. (Mesp)
$KS_{iEcosim2}$ (mixed)	Phytoplankton (Phy)	Phytoplankton (Phy)	Phytoplankton (Phy)	Small Epifauna (SE)	<i>A. purpuratus</i> (Ap)	<i>L. magallanica</i> (Lm)	<i>P. chilensis</i> ² (Pch2)
$KS_{iEcosim2}$ (top-down)	<i>M. gelatinosus</i> (Mg)	Phytoplankton (Phy)	–	Small Epifauna (SE)	Phytoplankton (Phy)	–	<i>H. helianthus</i> (Hh)
KQ_{iLA1} (mixed)	Phytoplankton (Phy)	<i>Taliepus</i> sp. (Tasp)	Phytoplankton (Phy)	<i>M. gelatinosus</i> (Mg)	<i>X. cassidiformis</i> (Xc)	<i>A. ater</i> (Aa)	<i>T. niger</i> (Tn)
KQ_{iLA2} (mixed)	Phytoplankton (Phy)	<i>Taliepus</i> sp. (Tasp)	Phytoplankton (Phy)	<i>M. gelatinosus</i> (Mg)	<i>X. cassidiformis</i> (Xc)	<i>A. ater</i> (Aa)	Large Epifauna (LE)

In the seagrass model (Tongoy Bay), just five species or functional groups were detected with keystone properties. According to the structural index K_i , the carnivorous crab *Cancer polyodon* was keystone, whereas the functional indices $KS_{iEcosim1}$ and $KS_{iEcosim2}$ showed the seastar *Meyenaster gelatinosus* to occupy this position. The functional index KS_i indicated that the group Small Epifauna (SE) was keystone; $KS_{iEcosim1}$ and $KS_{iEcosim2}$ showed the scallop *Argopecten purpuratus* to be keystone; and according to the functional $KS_{iEcosim2}$ index and the qualitative indices KQ_{iLA1} , and KQ_{iLA2} , Phytoplankton was keystone.

In the sand-gravel model, in addition to the species named above, the herbivores *Tegula* sp. (snail) (KS_i) and *Taliepus* sp. (crab) (KQ_{iLA1} , and KQ_{iLA2}), and the Infauna ($KS_{iEcosim1}$) were keystone. In the sand habitat, Phytoplankton ($KS_{iEcosim2}$, KQ_{iLA1} , and KQ_{iLA2}), Small Epifauna (KS_i and $KS_{iEcosim1}$), and *C. polyodon* (K_i and $KS_{iEcosim1}$) were detected as keystone. Two more keystone species were found in the mud model: Zooplankton (KS_i) and the carnivorous crab *Cancer porteri* ($KS_{iEcosim1}$). The whole model, which integrates the four habitats/models described above, showed that the core set of species made up of the carnivorous snail *Xanthochorus cassidiformis* (KQ_{iLA1} , and KQ_{iLA2}), *C. polyodon* (K_i), *M. gelatinosus* ($KS_{iEcosim1}$), *Tegula* sp. (KS_i), *A. purpuratus* ($KS_{iEcosim2}$), Infauna ($KS_{iEcosim1}$), and Phytoplankton ($KS_{iEcosim2}$) were keystone (Table 2) (Fig. 2).

In La Rinconada Marine Reserve (LRMR) model, the structural K_i and functional KS_i indices showed Phytoplankton to be a topological keystone species. The Phaeophyta group also showed keystone properties when using the functional $KS_{iEcosim1}$ index. The functional $KS_{iEcosim1}$ and qualitative KQ_{iLA1} and KQ_{iLA2} indices revealed keystone properties for species and functional groups such as the clams *Transanella pannosa* and *Aulacomya ater*. However, the $KS_{iEcosim2}$ index indicated that the asteroid top predator *Luidia magallanica* was a keystone species (Table 2) (Fig. 2).

In the case of the kelp beds model, the functional KS_i , $KS_{iEcosim1}$, and $KS_{iEcosim2}$ indices showed the macroalgae Chlorophyta, Rhodophyta, and *Mesophylum* sp., respectively, to be keystone species. The structural K_i and the functional $KS_{iEcosim2}$ indices indicated keystone properties for the asteroid *H. helianthus* and the fish *Pinguipes chilensis* (Table 2). Additionally, the herbivorous sea urchin *Tetrapigus niger* and the group Large Epifauna were detected as keystone species using the qualitative KQ_{iLA1} and KQ_{iLA2} and the functional $KS_{iEcosim1}$ indices (Fig. 2).

It is important to indicate that the functional $KS_{iEcosim1}$ index in the sand-gravel model (under mixed and top-down controls) and in the whole model (under bottom-up and mixed controls) showed, respectively, Rhodophyta and *Heterozostera tasmanica* with keystone properties, each one with >15% of the total system biomass. Thus, both species were replaced by the species with the second place of keystone relevance, that is, *Tegula* sp. and Infauna for sand-gravel and *M. gelatinosus* and Infauna for the whole model (Table 2, Fig. 2).

4. Discussion

Since Paine's (1969) first definition of keystone species, variations of the original concept have emerged in response to the limitations of the experimental design and functional variations of the species over scales of time and space (Mills et al., 1993; Menge et al., 1994; Estes et al., 1998; Bond, 2001). This is not as ambiguous as it might seem at first; because populations are part of heterogeneous and changing environments (Levins, 1968), variations in functionality are to be expected. The results obtained herein coincide with the variations found in experimental studies, since – according to the functional, structural, and qualitative keystone indices – several species or functional groups from different trophic levels could have keystone properties. Although this undoubtedly would complicate the design of traditional fisheries management strategies, which are based on just those species with economic value, we suggest that some efforts should be focused on multispecies management using the core of species found herein.

Although the models analysed in the current work describe different and heterogeneous benthic systems along the Chilean coast, the indices determined keystone properties for the principal asteroid species inhabiting such habitats (*M. gelatinosus*, *H. helianthus*, *L. magallanica*). This outcome agrees partially with the observations of Gaymer and Himmelman (2008), who studied dominant seastar species in benthic communities of northern Chile, establishing *M. gelatinosus* as a keystone species in subtidal systems. Likewise, the relevance of *L. magallanica* determined in the present work coincides with the results described by Ortiz et al. (2009) regarding the highest magnitudes of model resilience obtained in response to perturbations in this starfish species. Phytoplankton was also detected as keystone in all model systems (with the exception of the kelp forest), possibly a consequence of the

influence of upwelling waters (Daneri et al., 2000; Escribano et al., 2004).

It is relevant to mention that the phytoplankton-zooplankton group supports >40% of the overall structure and function in the ecological systems of Tongoy Bay (Ortiz and Wolff, 2002a) and La Rinconada Marine Reserve (Antofagasta) (Ortiz et al., 2010). Nevertheless, the phytoplankton would be not relevant in kelp forests because the concentration of biomass and contribution of nutrients (through detritus) to the coastal ecosystems would be supported – in this case – by the kelp species (Duggins et al., 1989). In this case, the macroalgae in northern Chile (Antofagasta) would contribute 25% of the overall structure and function of the ecosystem (followed by the phyto-zooplankton group with 20%) (Ortiz, 2008a).

The whole model of Tongoy Bay shows an integration of most species and/or groups with keystone properties found by habitat, and all these species are related ecologically (Fig. 2). A similar situation appears in La Rinconada Marine Reserve (LRMR) since top predators and other species or functional groups from low and intermediate trophic levels were also determined as keystone species. These were Phaeophyta, the scallop *A. purpuratus*, and the clam *T. pannosa*. In the case of primary producers, it is possible that these indices confused structural and trophic functional properties in the system. On the other hand, the qualitative indices showed keystone properties for the mussel *A. ater*. This result is very interesting since 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 kelp model also showed a core set of species or groups with keystone properties constituted by the fish *P. chilensis*, the asteroid *H. helianthus*, Large Epifauna (predators), the sea urchin *T. niger* (herbivore), and primary producers (the algae *Mesophyllum* sp., Rhodophyta, Chlorophyta). The keystone property of the fish *P. chilensis* coincides with reports by Ortiz (2008a) that show that increased mortality of this fish species by fishing would cause the highest magnitudes of model resilience in the system. Two qualitative keystone indices based on the loop model differed from those obtained with the other indices, indicating keystone in the herbivorous sea urchin *T. niger* (intermediate trophic level) and the Large Epifauna functional group of predatory crabs (*Taliepus dentatus* and *Homalaspis plana*). The sea urchin *T. niger* deserves special attention because, as described in the kelp forests of the SE Pacific, an increased abundance of this herbivore would partially explain the reduced forests, especially of *Macrocystis integrifolia* (Steneck et al., 2002).

In general, our results coincide with those reported for ecological experiments and modelling approaches. That is, species likely to have keystone properties are widely heterogeneous. Jordán et al. (2007, 2008) reported similar findings after comparing several structural and functional keystone species indices. The heterogeneity of possible species or functional groups determined in the current contribution coincide with those described by Power et al. (1996), Piraino et al. (2002), Libralato et al. (2006), and Jordán et al. (2007, 2008), particularly concerning: (1) the difficulty in recognizing keystone species in communities and ecosystems with both experimental and modelling approaches, and (2) the lack of a general pattern between trophic levels and keystone. Despite the wide heterogeneity of species and/or functional groups with keystone properties, we were still able to observe some interesting tendencies. The core set of species and functional groups constituted by prey/algae and its natural enemies (predators/grazers) reveals a more holistic view of keystone, i.e., a *keystone species complex*, particularly in studies based on quantitative and qualitative multispecies models such as that constructed herein (see Fig. 2). Okey (2004) described similar results defining keystone guilds or clusters of species with keystone properties based

on a trophic model in Alaska. Thus, we believe that the application of this holistic view for keystone would facilitate the design and assessment of management strategies in all benthic systems analysed. However, we must also recognize that comprehensive management is still quite difficult because: (1) the traditional fisheries management is based solely on commercial species; and (2) some species within each *keystone species complex* are intensively exploited (such as the bivalves *A. purpuratus*, *A. ater*, and *T. pannosa*; the crabs *C. polyodon* and *Taliepus* sp.; the snail *X. cassidiformis*; and the fish *P. chilensis*), reducing their natural densities (this is not the case of the asteroids). This, without a doubt, imposes an even greater challenge, since human interventions accompany the network of interacting species, co-varying with the variables of the natural system.

Finally, we know that our results should be contrasted with experimental studies and other modelling approaches such as those based on artificial neural networks (Mutil and Chau, 2007) in order to increase global understanding of these matters and our capacity for prediction. Likewise, it is relevant to note that, 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 present contribution represent the processes underlying the systems studied only when considering short-term dynamics.

Acknowledgements

This contribution was supported by the Chilean National Foundation for Scientific and Technical Development (FONDECYT) (Chile) grant no. 1040293 and CORFO-INNOVA (Chile) grant no. 04CR7IPM-01.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2012.08.020.

References

- Allesina, S., Bodini, A., 2005. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. *J. Theor. Biol.* 230, 351–358.
- Arias, G., González, C., Cabrera, J., Christensen, V., 2011. Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. *Environ. Res.* 111 (7), 917–925.
- Berlow, E., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Bond, W., 2001. Keystone species – hunting the shark? *Science* 292, 63–64.
- Briand, F., McCauley, E., 1978. Cybernetic mechanisms in lake plankton systems: how to control undesirable algae. *Nature* 273, 228–230.
- Brose, U., Berlow, E., Martinez, N., 2005. Scaling up keystone effects from simple to complex ecological networks. *Ecol. Lett.* 8, 1317–1325.
- Christensen, V., Pauly, D., 1992. *Ecopath II: a software for balancing steady-state ecosystem models and calculating network characteristics*. *Ecol. Model.* 61, 169–185.
- Christensen, V., Walters, C., 2004. *Ecopath with Ecosim: methods, capabilities and limitations*. *Ecol. Model.* 172, 109–139.
- Crowder, L., Hazen, E., Avissar, N., Bjorkland, R., Latanich, C., Ogburn, M., 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. *Annu. Rev. Ecol. Syst.* 39, 259–278.
- Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P., Ulloa, O., 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. *Mar. Ecol. Prog. Ser.* 197, 41–49.
- Darmbacher, J., Guaghan, D., Rochet, M., Rossignol, P., Trenkel, V., 2009. Qualitative modelling and indicators of exploited ecosystems. *Fish and Fish.* 10, 305–322.
- Duggins, D., Simenstad, C., Estes, J., 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245, 101–115.
- Dunne, J., Williams, R., Martinez, N., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567.
- Eklöf, A., Ebenman, B., 2006. Species loss and secondary extinctions in simple and complex model communities. *J. Anim. Ecol.* 75, 239–246.
- Escribano, R., Rosales, S., Blanco, J.L., 2004. Understanding upwelling circulation off Antofagasta (northern Chile): a three-dimensional numerical-modeling approach. *Cont. Shelf Res.* 24, 37–53.

- Estes, J.A., Tinker, M.T., Williams, T.M., Doak, D.F., 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282, 473–476.
- Francis, R., Hixon, M., Clarke, M., Murawski, S., Ralston, S., 2007. Ten commandments for ecosystem-based fisheries scientists. *Fisheries* 32 (5), 217–233.
- Gaymer, C., Himmelman, J.H., 2008. A keystone predatory sea star in the intertidal zone is controlled by a higher-order predatory sea star in subtidal zone. *Mar. Ecol. Prog. Ser.* 370, 143–153.
- Griffiths, S., Young, J., Lansdell, M., Campbell, R., Hampton, J., Hoyle, S., Langley, A., Bromhead, D., Hinton, M., 2010. Ecological effects of longline fishing and climate change on the pelagic ecosystem off eastern Australia. *Rev. Fish Biol. Fish.* 20, 239–272.
- Guénette, S., Christensen, V., Pauly, D., 2008. Trophic modelling of the Peruvian upwelling ecosystem: towards reconciliation of multiples datasets. *Prog. Oceanogr.* 79, 326–335.
- Hall, S.J., 1999a. Managing fisheries within ecosystems: can the role of reference points be expanded? *Aquat. Conserv. Mar. Freshw. Ecosyst.* 9, 579–583.
- Hall, S.J., 1999b. The Effects of Fishing on Marine Ecosystems and Communities. Blackwell Science, Oxford.
- Hawkins, S., 2004. Scaling up. The role of species and habitat patches in functioning of coastal ecosystems. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 14, 217–219.
- Hulot, F., Lacroix, G., Lescher-Moutoué, F., Loreau, M., 2000. Functional diversity governs ecosystem response to nutrient enrichment. *Nature* 405, 340–344.
- Jordán, F., 2001. Trophic fields. *Community Ecol.* 2 (2), 181–185.
- Jordán, F., Scheuring, I., 2004. Network ecology: topological constrains on ecosystem dynamics. *Phys. Life Rev.* 1, 139–172.
- Jordán, F., Takács-Sánta, A., Molnár, I., 1999. A reliability theoretical quest for keystone species. *Oikos* 86, 453–462.
- Jordán, F., Benedek, Z., Podani, J., 2007. Quantifying positional importance in food webs: a comparison of centrality indices. *Ecol. Model.* 205, 270–275.
- Jordán, F., Okey, T., Bauer, B., Libralato, S., 2008. Identifying important species: linking structure and function in ecological networks. *Ecol. Model.* 216, 75–80.
- Lane, P., 1986. Symmetry, change, perturbation, and observing mode in natural communities. *Ecology* 67, 223–239.
- Lane, P., 1998. Assessing cumulative health effects in ecosystems. In: Rapport, D., Costanza, R., Epstein, P., Gaudet, C., Levins, R. (Eds.), *Ecosystem Health*. Blackwell Science, Oxford, pp. 129–153.
- Lane, P., Blouin, A., 1985. Qualitative analysis of the pelagic food webs of three acid impacted lakes. *Int. Rev. Ges. Hydrobiol.* 70, 203–220.
- Levins, R., 1968. *Evolution in Changing Environments*. Princeton Monographs Series. Princeton University Press, NJ.
- Levins, R., 1998. Qualitative mathematics for understanding, prediction, and interventions in complex ecosystems. In: Rapport, D., Costanza, R., Epstein, P., Gaudet, C., Levins, R. (Eds.), *Ecosystem Health*. Blackwell Science, Oxford, pp. 178–204.
- Levins, R., Vandermeer, J., 1990. The agroecosystem embedded in a complex ecological community. In: Carroll, R., Vandermeer, J., Rosset, P. (Eds.), *Agroecology*. McGraw-Hill, New York, pp. 341–362.
- Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. *Ecol. Model.* 195, 153–171.
- Luczakovich, J., Borgatti, S., Johnson, J., Everett, M., 2003. Defining and measuring trophic role similarity in food webs using regular equivalence. *J. Theor. Biol.* 220, 303–321.
- Menge, B.A., Berlow, E.L., Balchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Mills, L., Soulé, M., Doak, F., 1993. The key-stone-species concept in ecology and conservation. *Bioscience* 43, 219–224.
- Monaco, M., Ulanowicz, R., 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Mar. Ecol. Prog. Ser.* 161, 239–254.
- Muttill, N., Chau, K.W., 2007. Machine-learning paradigms for selecting ecologically significant input variables. *Eng. Appl. Artif. Intell.* 20, 735–744.
- Okey, T., 2004. Shifted community states in four marine ecosystems: some potential mechanisms. PhD Thesis, The University of British Columbia, Canada, 173 pp.
- Ortiz, M., 2008a. Mass balance and dynamic simulations of trophic models of kelp ecosystems near the Mejillones Peninsula of northern Chile (SE Pacific): comparative network structure and assessment of harvest strategies. *Ecol. Model.* 216, 31–46.
- Ortiz, M., 2008b. The effect of a crab predator (*Cancer porteri*) on secondary producers versus ecological model predictions in Tongoy Bay (south-east Pacific coast): implications for management and fisheries. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 18, 923–929.
- Ortiz, M., 2010. Dynamical and spatial models of kelp forest of *Macrocystis integrifolia* and *Lessonia trabeculata* (SE Pacific) for assessment harvest scenarios: short-term responses. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20, 494–506.
- Ortiz, M., Wolff, M., 2002a. Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and preliminary assessment of management strategies. *J. Exp. Mar. Biol. Ecol.* 268, 205–235.
- Ortiz, M., Wolff, M., 2002b. Application of loop analysis to benthic systems in northern Chile for the elaboration of sustainable management strategies. *Mar. Ecol. Prog. Ser.* 242, 15–27.
- Ortiz, M., Stotz, W., 2007. Ecological and eco-social analysis for the introduction of the abalone *Haliotis discus hannoi* into benthic systems of central-north Chile. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 17, 89–105.
- Ortiz, M., Wolff, M., 2008. Mass-balanced trophic and loop models of complex benthic systems in northern Chile (SE Pacific) to improve sustainable interventions: a comparative analysis. *Hydrobiologia* 605, 1–10.
- Ortiz, M., Levins, R., 2011. Re-stocking practices and illegal fishing in northern Chile (SE Pacific coast): a study case. *Oikos* 120, 1402–1412.
- Ortiz, M., Avendaño, M., Campos, L., Berrios, F., 2009. Spatial and mass balanced trophic models of La Rinconada Marine Reserve (SE Pacific coast), a protected benthic ecosystem: management strategy assessment. *Ecol. Model.* 220, 3413–3423.
- Ortiz, M., Avendaño, M., Cantillanez, M., Berrios, F., Campos, L., 2010. Trophic mass balanced models and dynamic simulations of benthic communities from La Rinconada Marine Reserve off northern Chile: network properties and multi-species harvest scenario assessment. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 20 (1), 58–73.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., 1999. Trophic cascades revealed in diverse ecosystems. *TREE* 14, 483–488.
- Paine, R.T., 1969. A note of tropic complexity and community stability. *Am. Nat.* 103, 91–93.
- Paine, R.T., 1992. Food-web analysis through field measurements of per capita interaction strength. *Nature* 355, 73–75.
- Patten, B., 1997. Synthesis of chaos and sustainability in a nonstationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. *Ecol. Model.* 100, 11–42.
- Payton, I., Fenner, M., Lee, W., 2002. Keystone species: the concept and its relevance for conservation management in New Zealand. *Sci. Conserv.* 203, 5–29.
- Pikitch, E., Santora, C., Babcock, E., Bakum, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J., Sainsbury, K., 2004. Ecosystem-based fishery management. *Science* 305, 346–347.
- Piraino, S., Fanelli, G., Boero, F., 2002. Variability of species roles in marine communities: changes of paradigms for conservation priorities. *Mar. Biol.* 140, 1067–1074.
- Polovina, J., 1984. Model of a coral reef ecosystem. I. ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3, 1–11.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B., Bond, W., Mills, L., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *Bioscience* 46 (8), 609–620.
- Ramsey, D., Veltman, C., 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *J. Anim. Ecol.* 74, 905–916.
- Robinson, L., Frid, C., 2003. Dynamic ecosystem models and the evaluation of ecosystem effects of fishing: can we make meaningful predictions? *Aquat. Conserv. Mar. Freshw. Ecosyst.* 13, 5–20.
- Scotti, M., Podan, J., Jordán, F., 2007. Weighting, scale dependence and indirect effects in ecological networks: a comparative study. *Ecol. Complexity* 4, 148–159.
- Steneck, R., Graham, M., Bourque, B., Corbett, D., Erlandson, J., Estes, J., Tegner, M., 2002. Kelp ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29 (4), 436–459.
- Ulanowicz, R., Puccia, Ch., 1990. Mixed trophic impacts in ecosystems. *Ceonoces* 5, 7–16.
- Vasas, V., Lancelot, C., Rousseau, V., Jordán, F., 2007. Eutrophication and overfishing in temperate nearshore pelagic food webs: a network perspective. *Mar. Ecol. Prog. Ser.* 336, 1–14.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172.
- Wootton, J.T., 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* 75, 151–165.
- Yodzis, P., 2001. Must top predators be culled for the sake of fisheries? *TREE* 16, 78–84.