



Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): Comparative network structure and assessment of human impacts



Marco Ortiz^{a,*}, Fernando Berrios^{a,b}, Leonardo Campos^{a,b}, Roberto Uribe^{a,b}, Alejandro Ramirez^{a,b}, Brenda Hermsillo-Núñez^{a,b}, Jorge González^{a,b}, Fabián Rodríguez-Zaragoza^c

^a Instituto de Antofagasta (IA), Instituto de Ciencias Naturales AvH, Facultad de Ciencias del Mar & Recursos Biológicos, Universidad de Antofagasta, PO Box 170, Antofagasta, Chile

^b Programa de Doctorado en Ciencias Aplicadas, mención sistemas marinos costeros, Universidad de Antofagasta, Antofagasta, Chile

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

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ABSTRACT

Mass-balanced and dynamical multispecies trophic models were constructed for benthic systems of Mejillones and Antofagasta bays. We analysed data on biomass, P/B ratios, catches, food spectra, and the consumption and dynamics of commercial and non-commercial species or functional groups using the *Ecopath* with *Ecosim* framework. The biomass of the Rhodophyta group, which contributed 25.5% of the total system biomass, was the most abundant compartment in Mejillones bay, whilst the bivalve *Tranzenella pannosa* recorded the highest biomass (~39%) in Antofagasta bay. Amongst the carnivores, the commercial gastropod *Tais chocolata* (~2%) and the sea star *Luidia magallanica* (~4%) were the compartment containing the highest biomass in Mejillones Bay and Antofagasta Bay, respectively. Based on the magnitudes of Pp/R , *Relative Ascendency* (A/C), *Relative Overhead* (Ov/C), *Redundancy*, *Finn's cycling index* and the system recovery time (*SRT*), the benthic system of Antofagasta Bay was more developed or mature and, in turn, less resistant against perturbations compared to Mejillones Bay. The outcomes of the mixed trophic impacts (*MTI*) indicate that the small epifauna carnivore (*SEC*) and the phytoplankton propagate the highest magnitudes of direct and indirect effects on the remaining compartments in the Mejillones and Antofagasta bays, respectively. According to the *Ecosim* short-term simulations (increasing 10, 30 and 50% the mortality by fishing and/or toxic substances) the snail *Tegula* spp. had the highest impact on the other compartments in Mejillones Bay, whilst the bivalve *T. pannosa* exhibited the highest impacts in Antofagasta Bay. Based on our results, we suggest that environmental studies should not only aim to promote and ensure the quality of physical components of nature, but should also consider the ecosystem properties and dynamics that emerge from complex networks.

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1. Introduction

In coastal northern Chile (SE Pacific coast), a notable geological structure called Mejillones Peninsula separates the two most important bay systems of this area: Mejillones Bay and Antofagasta Bay (Fig. 1). Both bays have been historically impacted by various human activities, principally those related to the mining industry

(loading of mineral concentrates of Cu, Zn, Pb and Hg), thermoelectric plants, acid transfer plants, port operations, artisanal fisheries and the sewage treatment of human settlements, amongst others. It has been recently accepted that the port operations related to mineral transport have enriched the bottom sediments and seawater of both bays with Cu, Pb, and Zn (Valdés and Sifeddine, 2009). As a result, it has suggested that the current Chilean Environmental Legislation is not an efficient tool for the protection of these marine ecosystems (Valdés et al., 2010, 2011). However, we claim that this legislation is additionally biased because it only considers the chemical loading of the physical environment (seawater and

* Corresponding author. Tel.: +56 552637866; fax: +56 552637804.

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

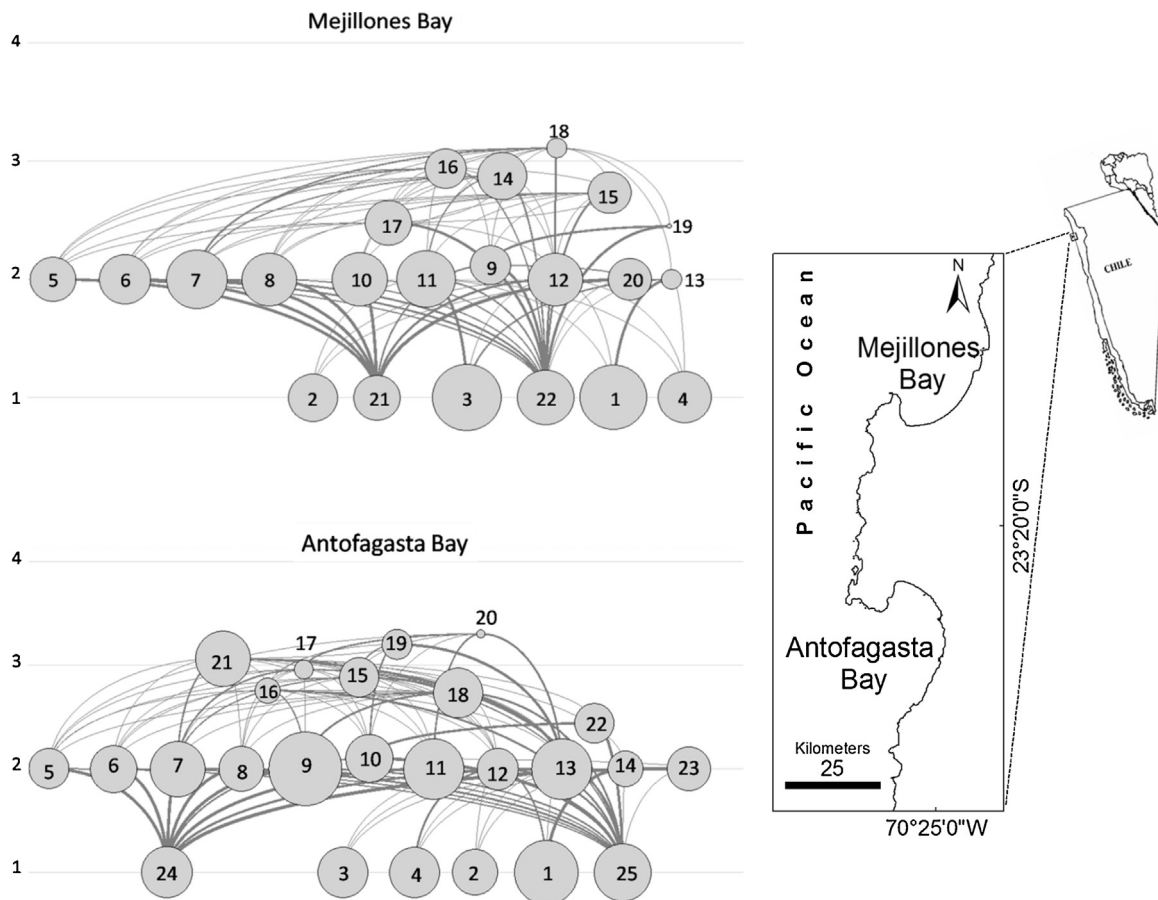


Fig. 1. Study area of Mejillones and Antofagasta bays (SE Pacific coast), northern Chile. Trophic model for the benthic ecological system of Mejillones and Antofagasta bays. Vertical position approximates trophic level. The circle size is proportional to the compartment (populations and/or functional groups) biomass ($\text{g wet weight m}^{-2}$). The number in circle corresponds to the species or functional groups (for details see Table 1).

sediments), without considering the living components, and supposes the ecosystems as homogenous and replicable units. This reductionist view is also shared by numerous fisheries studies, which are based solely on population analysis for simulating and predicting the responses of exploited species (Walters et al., 1999; Scotti et al., 2007; Ortiz, 2010; Ortiz and Levins, 2011; Ortiz et al., 2013a). Additionally, it is important to mention that several species that inhabit the shallow benthic habitats of Mejillones and Antofagasta bays are exploited for human consumption.

Alternatively, a more holistic view is needed for the study of Mejillones and Antofagasta bays. However, this view implies a consideration of the links amongst the chemical and physical compartments with the organisms present, which, in turn, directly modify their immediate environments through their structures and activities (Levins and Lewontin, 1985) and also actively participate (by predation) in the flow of energy and/or matter through their trophic networks (Odum, 1969; Ulanowicz, 1986). Therefore, the impacts of natural or anthropogenic disturbances can be propagated through these trophic networks, buffered along some pathways or amplified along others. Meanwhile, human interventions are often not constant over time; that is, humans act on the system but also respond to it. Hence, human interventions are co-variables with the variables of the natural systems, and they introduce uncertainties (Ortiz and Levins, 2011).

Despite the numerous studies conducted in Mejillones and Antofagasta bays, most notably, studies examining oceanographic conditions (Escribano and Hidalgo, 2001; Escribano et al., 2004; Dávila et al., 2014), primary production (Escribano and McLaren, 1999; Escribano et al., 2004), heavy metal contents in coastal waters

and sediments (Valdés and Sifeddine, 2009; Valdés et al., 2010, 2011), benthic communities (Laudien et al., 2007; Pacheco et al., 2012), and local benthic modelling (Ortiz et al., 2010), to date, few efforts have focused on ecologically integrating the benthic species that inhabit these two bays. For this reason, it is necessary to apply other complementary theoretical frameworks that allow the integration of a finite set of “core” variables that represent and describe the dynamics and structures of ecosystems to which they belong (Robinson and Frid, 2003; Hawkins, 2004; Francis et al., 2007). The application of network analyses based on multispecies or ecosystem models provides complementary strategies to the classic isolated-reductionist models for those cases in which the goals are to analyse the emergent properties (macrodescriptors) of ecosystems (Ulanowicz, 1986, 1997), the overall health (Costanza and Mageau, 1999) and to assess the propagation of direct and indirect effects within complex ecological systems (Levins, 1974, 1998a; Hawkins, 2004).

Multispecies trophic models based on *Ecopath II* (Christensen and Pauly, 1992) and *Ecosim* (Walters et al., 1997) have been widely employed for describing trophic webs and predicting the effects produced by the application of different exploitation scenarios in different marine ecosystems (Christensen and Pauly, 1992; Ortiz and Wolff, 2002; Ortiz, 2008a, 2010; Ortiz et al., 2009, 2010; Preikshot et al., 2013; Pinkerton and Bradford-Grieve, 2014). The main objective of this work was to build trophic models that represent the interspecific relationships (prey–predator) in the benthic systems of the Mejillones and Antofagasta bays, including the putative effects produced by the artisanal fisheries and industrial activities on the mortality rates of the benthic species, using

Ecopath with the *Ecosim* software package (Walters et al., 1997). Supported by these models and the associated network analyses, the following attributes were investigated: (1) the biomass distribution and energy flow in each benthic ecological system; (2) the main benthic predators in each system, their consumption rates, and their prey; (3) the network properties (macrodescriptors) of benthic systems of the two bays, based on the Odum (1969) and Ulanowicz (1986, 1997) theoretical frameworks; (4) redundancy, which would be defined as the existence of functional groups of species with similar trophic functions in the systems (sensu Lawton, 1994); (5) the degree of resistance to disturbances and the resilience of these ecological systems in response to different human perturbation scenarios; and (6) the species and functional groups most affected by human interventions.

2. Materials and methods

2.1. Study area and bay characteristics

Mejillones and Antofagasta bays are oriented to the north and south, respectively. Both bays belong to the Humboldt Current System (Escribano et al., 2004). They are influenced by two coastal upwelling centres, which supply nutrients to the ecosystems (Letelier et al., 2012) (Fig. 1). Additional studies have revealed that both bays are affected by an oxygen-minimum layer (Escribano and Hidalgo, 2000).

2.2. *Ecopath* and *Ecosim* (v.5.0) modelling approaches

This work analyses the trophic models produced using the *Ecopath* with *Ecosim* software (www.Ecopath.org). *Ecopath* was first developed by Polovina (1984) and further extended by Christensen and Pauly (1992) and Walters et al. (1997). The *Ecopath* 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 for 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 emergent properties of ecosystems (Odum, 1969; Ulanowicz, 1986, 1997) of varying spatial sizes, geographic locations, and complexities (e.g., Wolff, 1994; Monaco and Ulanowicz, 1997; Ortiz and Wolff, 2002; Christensen and Walters, 2004; Guénette et al., 2008; Ortiz, 2008a; Ortiz et al., 2010; Arias-González et al., 2011; Ortiz et al., 2013b). For more details of *Ecopath* and *Ecosim* frameworks see Appendix A.

2.3. Selection of model compartments, sampling programs and data sources

Two intensive field studies were conducted between 2005 and 2012 at Mejillones and Antofagasta bays to identify the biological components (species or functional groups) of each system bay and to estimate the average biomass (B), average catch (C), turnover rate (P/B), consumption rate (Q/B), and food sources of the selected components. Seasonal sampling was performed to directly estimate the average biomass and density of macro benthic species (± 10 m depth) along the bays. To estimate the turnover rates (P/B), we obtained ten length frequencies, which were used to estimate the initial growth parameters (K and L_{∞}), adjusted to the von Bertalanffy growth function. Once the growth parameters were calculated, the instantaneous rate of total mortality (Z) was estimated using the length-converted catch equation (Sparre and Venema, 1997). It is important to note that Z is an approximation to P/B (after Allen, 1971). The consumption rate was calculated for a 24-h cycle following the procedure described by Cerda and Wolff (1993). To determine the food spectra of the principal benthic species,

the stomach and gut were extracted and the gut contents were classified to the lowest possible taxonomic level; the frequency of occurrence of each food item was then calculated. Appendix B lists the source data for each of the biological compartments selected for the current work, which represent the most important species inhabiting the benthic communities of Mejillones and Antofagasta bays. Models were constructed for each bay considering compartments represented both by individual species and by functional groups, which include multiple species. The models for the two bays share the majority of the compartments, except for the muricid *Concholepas concholepas*, the bivalves *Gari solida* and *Protothaca thaca*, and the cephalopod *Octopus vulgaris*. Although the majority of the remaining compartments represent individual species (for the kelp species *Lessonia trabeculata*, the scallop *Argopecten purpuratus*, the bivalves *Tagelus dombeii*, *Transannella pannosa*, *Aulacomya ater*, *G. solida*, *Choromytilus chorus*, and *P. thaca*, the carnivorous snail *T. chocolata*, and the sea star *L. magallanica*), it was also necessary to include functional groups as compartments that included multiple species. The Chlorophyta, Rhodophyta, and Phaeophyta groups included multiple species of green (e.g., *Ulva* sp.), red (e.g., *Rhodomenia* sp.), and brown (e.g., *Glossophora* sp.) algae, respectively. The *Cancer* spp. compartment contains the crabs *Cancer coronatus*, *C. polyodon*, *C. edwardsi* and *C. porteri*. The large epifauna (LE) group includes the crabs *Pagurus edwardsi*, *Taliepus dentatus*, *Hepatus chilensis*, and *Eurypanopeus crenatus*. The small epifauna herbivore (SEH) is constituted by the molluscs *Calyptrea trochiformis*, *Fissurella* sp., *Mitrella* sp., *Chiton* sp. and *Colisella* sp. The small epifauna carnivore (SEC) is composed of the molluscs *Aeneator fontanei*, *Nassarius gayi*, *Cancellaria* sp., *Oliva* sp., *Crassilabrum* sp., *Priene* sp., *Xanthochorus* sp., *Trigonostoma* sp., and *Nucula* sp. The *Tegula* spp. group includes *T. luctuosa*, *T. tridentata*, *T. atra* and *T. euryamphala*. The other filter feeders (OFF) group is primarily formed by *Petrolisthes* sp., *Allopetrolisthes* sp., *Actinia* sp., *Phymactis* sp., and *Polydora* sp. The other sea star species (OSS) group includes *Heliaster helianthus*, *Patiria chilensis*, *Megenaster gelatinosus*, and *Stichaster striatus*. Finally, the group of sea urchin species (SUS) is constituted by *Loxechinus albus*, *Tetrapigius niger* and *H. espatilegera*.

All of the compartments are trophically related to feeding on detritus, which is considered as a complex of microbial films and organic matter, because several studies have emphasised 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). The interaction matrices for each of the benthic systems are shown in Appendix C. Notably, the models were constructed to capture the trophic relationships for the most important species or functional groups (commercial resources) inhabiting the benthic communities of both bay systems, excluding the energy flows from epiphytes and the microphytobenthos as well as those leading to seals and birds because of insufficient scientific information. Although this reduces the realism of the model configuration, the most relevant interdependencies and energy flows are reflected. Furthermore, such a systemic error should not impede a comparative analysis amongst ecological systems under similar limitations.

2.4. Macrodescriptors and network properties

The trophic models based on *Ecopath* combine 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 emergent properties of ecosystems. These descriptors are the Primary Production/Total Respiration (Pp/TR) ratio, Primary Production/Total Biomass (Pp/TB) ratio, Total System Throughput (TST),

Total Biomass/Total System Throughput (TB/TST) ratio, Ascendency (A), Overhead (Ov), Development Capacity (C), A/C and Ov/C ratios. The Pp/TR , Pp/TB , and TB/TST ratios are used to indicate different states of system maturity (Odum, 1969; Christensen, 1995). The Total System Throughput describes the vigour or size of a system, and this descriptor represents a measure of a system's metabolism. Ascendency integrates both the size and organisation of a system. Organisation (complexity) refers to the number and diversity of weighted interactions amongst the system components. Ascendency and Overhead have been related to system stability (Christensen, 1995; Cropp and Gabric, 2002) and maturity (Ulanowicz and Abarca-Arenas, 1997; Perez-Espana and Arreguin-Sanchez, 2001; Fath et al., 2001; Cropp and Gabric, 2002). Overhead is the difference between Ascendency and the Development Capacity, and indicates the multiplicity of information pathways, which may closely relate to the capacity to withstand perturbations (Christensen, 1995; Angelini and Petrere, 2000). The Development Capacity quantifies the upper limit to Ascendency, and the A/C ratio describes the network efficiency (used as maturity index) (e.g., Baird and Ulanowicz, 1993; Costanza and Mageau, 1999). The A/C and Ov/C ratios can also be used as indicators of ecosystem development (Kaufman and Borrett, 2010) and a system's ability to resist disturbances (Ulanowicz, 1986, 1997). All these macro-descriptors have been widely used to describe and compare a variety of ecosystems of varying spatial sizes, geographic locations, and complexities (e.g., Monaco and Ulanowicz, 1997; Niquil et al., 1999; Heymans and Baird, 2000; Wolff et al., 2000; Ortiz and Wolff, 2002; Arias-González et al., 2004; Patrício and Marques, 2006; Ortiz, 2008a; Panikkar and Khan, 2008; Ortiz et al., 2009, 2013b; Yunkai-Li et al., 2009; Kaufman and Borrett, 2010; Li and Yang, 2011; Díaz-Urbe et al., 2012; Bayle-Sempere et al., 2013).

2.5. Balance of trophic models

The first step in balancing the models was to determine if the model outputs were realistic, that is, to determine if the Ecotrophic Efficiency (EE) was <1.0 for all the variables or compartments (Ricker, 1968). If any inconsistency was detected, the biomass values (average) were slightly changed within the standard deviation (± 1 SD) obtained from field studies. Nevertheless, for the Rhodophyta, Chlorophyta and Phaeophyta, the turnover rates (P/B) were also estimated using the *Ecopath* software. It was not necessary to modify the diet matrices when balancing the models. As a second step, the magnitudes of the Gross Efficiency (GE) were between 0.1 and 0.3 for all compartments (Christensen and Pauly, 1993; Christensen et al., 2004).

2.6. Mixed trophic impacts, short-term Ecosim simulations and system recovery times

Ecopath's mixed trophic impacts (MTI) routine (Ulanowicz and Puccia, 1990) was employed to perform a preliminary evaluation of the propagations of direct and indirect effects in response to disturbances affecting each species or functional group. Short-term *Ecosim* simulations were used to evaluate the propagation of instantaneous direct and indirect effects and the magnitudes in system recovery time (SRT , an internal stability measure) in response to an increase of total mortality of each compartment ($Z = M + F$) equivalent to 10%, 30% and 50% ($P = B \times Z$). These three scenarios (magnitudes) were set for prediction purposes (as measure of confidence). This procedure was applied between the first and second year of simulation for each species or functional group of both models (bays). The propagation of short-term responses was determined by evaluating the biomasses of all the components of both bay systems in the third year of the simulation, that is, one year after the increase in fishing mortality (sensu Ortiz et al., 2009). Because

of the low reliability of the time-series of landings for the variables that inhabit inside both bays, all the dynamic simulations were accomplished using a mixed-flow control mechanism, which is considered to be more realistic, than bottom-up or top-down (e.g., Hunter and Price, 1992; Krebs et al., 1995; Levins, 1998b; Masterson et al., 2008; Muhly et al., 2013). Furthermore, the use of mixed control (both bottom-up and top-down) has recently been demonstrated to produce the highest certainties in predictions (Thompson et al., 2004; Ortiz, 2008b). It is important to note that the mixed trophic impacts and *Ecosim* simulations under short-term dynamics shown up to $\sim 60\%$ certainty using mixed flow control mechanism in a benthic system in northern Chile (Ortiz, 2008b).

3. Results

The Rhodophyta functional group produced the highest biomass (478.08 g wet weight [ww] m^{-2}), accounting for 25.5% of total system biomass in Mejillones Bay. Meanwhile, in Antofagasta Bay, the bivalve mollusc *T. pannosa* was the most abundant species/group (787.57 g ww m^{-2}), contributing 39.8% of the total system biomass (Table 1). Amongst the principal benthic predators, the group of small epifauna carnivore (SEC) and the seastar *Luidia magallanica* dominated the abundances in Mejillones and Antofagasta bays, respectively (Table 1). In regards to the system structure and network properties, both ecological models produced high magnitudes of the Pp/R ratio (>1), with a relatively lower value for the Antofagasta model. In the case of the Pp/B ratio, the Mejillones system had the lower value (Table 2). The Antofagasta benthic model had higher magnitudes of Total System Throughput (TST) (37,539.8 g ww $m^{-2} year^{-1}$), Development Capacity ($C = 170,237$ Flowbits), Ascendency ($A = 48,574.3$ Flowbits) and the A/C ratio (28.5%) compared to the Mejillones model (Table 2). In contrast, the Mejillones model had the highest values of Ov/C and Redundancy. The large difference between the A/C ratio and the A_i/C_i ratio for the Antofagasta model may indicate a strong dependency of this system on only a few external connections (sensu Baird et al., 1991). With regards to the contribution of each compartment to the whole-model Ascendency, for both benthic models, the detritus and phytoplankton reached magnitudes greater than 48%, followed by Rhodophyta (11.7%) and *T. pannosa* (18.3%) in Mejillones and Antofagasta bays, respectively. Additionally, the group of other sea star species and the cephalopod *O. vulgaris* were the components that accounted for the complexity (lowest % of AMI) of Mejillones and Antofagasta model systems respectively (Table 2). In regards to Finn's cycling index (FCI), the Antofagasta model produced a higher value compared to the Mejillones system (Table 2). Both systems were characterised by similar magnitudes of food web connectance, Omnivory index (OI), and Finn's mean path length (FPL) (Table 2).

The propagations of direct and indirect effects estimated using the Mixed Trophic Impacts (MTI) and short-term *Ecosim* simulations indicate, in general terms, the quantitative and qualitative differences between both ecological systems, and even between shared compartments (Fig. 2). Notably, we only selected the ten species or functional groups that exhibited the largest quantitative global changes in the remaining compartments. The MTI results for the Mejillones ecological system indicate that the group of small epifauna carnivore (SEC) propagated higher-order effects in the remaining compartments. In contrast, the group of phytoplankton propagated the strongest effects in the Antofagasta model (Fig. 2). The short-term dynamic simulations using *Ecosim* (using the three scenarios of mortality) revealed that the herbivorous snail *Tegula* sp. and *T. pannosa* propagated the strongest effects through the Mejillones and Antofagasta models, respectively (Fig. 3a and b). Within the ten compartments that propagated

Table 1Parameter values entered (in bold) and estimated (standard) by *Ecopath II* programme for the benthic ecological systems of Mejillones and Antofagasta bays.

Compartments							
Species/functional groups	TL	Ca	B	P/B	Q/B	EE	GE
A. Mejillones bay							
(1) <i>Lessonia trabeculata</i>	1.0	13.61	372.5	2.0		0.51	
(2) Chlorophyta	1.0		42.0	5.0		0.89	
(3) Rhodophyta	1.0		478.1	5.0		0.67	
(4) Phaeophyta	1.0		66.0	5.0		0.99	
(5) <i>Argopecten purpuratus</i>	2.0	12.94	27.88	2.7	9.9	0.95	0.27
(6) <i>Aulacomya ater</i>	2.0	0.03	54.0	1.8	9.9	0.87	0.18
(7) <i>Tagelus dombeii</i>	2.0	0.01	168.0	2.0	9.9	0.44	0.20
(8) <i>Choromytilus chorus</i>	2.0	4.8	80.0	1.8	9.9	0.66	0.18
(9) Other Filter Feeders (OFF)	2.1	0.0014	14.0	1.2	5.0	0.66	0.24
(10) <i>Gari solida</i>	2.0	1.83	88.0	0.9	9.9	0.8	0.09
(11) <i>Tegula</i> spp.	2.0		138.2	4.0	20.0	0.14	0.2
(12) Small Epifauna Herbivore (SEH)	2.0	0.0084	84.0	1.1	9.9	0.88	0.11
(13) Sea urchin species (SUS)	2.0		1.0	1.3	6.7	0.12	0.19
(14) Small Epifauna Carnivore (SEC)	2.9		41.58	2.0	10.4	0.21	0.19
(15) Large Epifauna (LE)	2.7		20.0	1.9	9.2	0.7	0.21
(16) <i>Cancer</i> spp.	2.9	0.0015	15.06	1.9	9.5	0.01	0.20
(17) <i>Thais chocolata</i>	2.5	0.19	37.0	2.0	7.2	0.81	0.28
(18) <i>Luidia magallanica</i>	3.1		1.02	0.5	3.0	0.06	0.17
(19) Other Sea Star Species (OSS)	2.4		0.05	1.7	7.0	0.36	0.24
(20) Zooplankton	2.0		20.0	40.0	160.0	0.01	0.25
(21) Phytoplankton	1.0		30.0	250.0		0.87	
(22) Detritus	1.0		100.0			0.37	
B. Antofagasta bay							
(1) <i>Lessonia trabeculata</i>	1.0	21.1	232.83	2.0		0.63	
(2) Chlorophyta	1.0		25.0	5.0		0.8	
(3) Rhodophyta	1.0		44.0	5.0		0.8	
(4) Phaeophyta	1.0		44.26	5.0		0.88	
(5) <i>Argopecten purpuratus</i>	2.0	5.5	13.0	2.7	9.9	0.94	0.27
(6) <i>Aulacomya ater</i>	2.0		30.0	1.8	9.9	0.95	0.18
(7) <i>Tagelus dombeii</i>	2.0	0.02	81.38	2.0	9.9	0.68	0.20
(8) <i>Choromytilus chorus</i>	2.0	0.9	24.0	1.8	9.9	0.99	0.18
(9) <i>Transennella pannosa</i>	2.0	11	787.57	2.8	9.9	0.05	0.28
(10) Other Filter Feeders (OFF)	2.1	0.003	33.0	1.5	5.0	0.95	0.30
(11) <i>Protothaca thaca</i>	2.0	16	160.51	0.85	9.9	0.31	0.09
(12) <i>Tegula</i> spp.	2.0		15.64	4.0	20.0	0.79	0.2
(13) Small Epifauna Herbivore (SEH)	2.0	0.02	162.20	1.1	9.9	0.70	0.11
(14) Sea urchin species (SUS)	2.0		7.0	1.3	6.67	0.78	0.19
(15) Small Epifauna Carnivore (SEC)	2.9		12.0	2.0	10.4	0.99	0.19
(16) Large Epifauna (LE)	2.8		2.0	1.9	9.2	0.75	0.21
(17) <i>Cancer</i> spp.	2.9	0.0008	0.85	1.9	9.5	0.12	0.2
(18) <i>Thais chocolata</i>	2.7	3.6	40.99	2.0	7.2	0.27	0.28
(19) <i>Concholepas concholepas</i>	3.2	0.3	3.66	2.8	9.9	0.53	0.28
(20) <i>Octopus vulgaris</i>	3.3	0.04	0.14	0.7	3.2	0.45	0.22
(21) <i>Luidia magallanica</i>	3.1		78.89	0.5	3.0	0.06	0.17
(22) Other Sea Star Species (OSS)	2.4		12.14	1.7	7.2	0.11	0.24
(23) Zooplankton	2.0		20.0	40.0	160.0	0.02	0.25
(24) Phytoplankton	1.0		50.0	250.0		0.99	
(25) Detritus	1.0		100.0			0.46	

TL: trophic level; B: biomass (g wet weight m⁻²); Ca: catch; P/B: turnover rate; Q/B: annual food consumption; EE: ecotrophic efficiency; GE: gross efficiency.

the highest impacts on the remaining groups, exploited species were also identified, including the carnivorous gastropod *T. chocolata*, the crab *Cancer* spp., the herbivore *T. dombeii* and the kelp species *L. trabeculata*. The outcomes obtained for the system recovery time (SRT) – used as a measure of resilience – for both model systems are summarised in Table 3. In the modelled Mejillones system, a perturbation on the groups of small epifauna herbivore (SEH) and Rhodophyta would take the longest time to return to its initial condition. In contrast, the compartments of phytoplankton, large epifauna (LE) and the bivalve *T. dombeii* would provoke the highest SRTs in the Antofagasta system (Table 3). Additionally, the global average of the SRT values (considering the three scenarios of mortality) indicate that the Antofagasta Bay benthic system requires a longer time (SRT=8.29 years) to return to its steady-state initial condition than the Mejillones model (SRT=7.20 years) (Table 3). Both systems are characterised by similar magnitudes of the mean trophic level of the fishery (Table 2).

4. Discussion

A notable difference between the two modelled benthic systems was detected in regards to the accumulation of biomass. Whilst the Mejillones benthic system was principally dominated by a primary producer (Rhodophyta group), a secondary producer (*T. pannosa* bivalve) presented the greatest amount of biomass in the Antofagasta model. In terms of the network and ecosystem structure, the benthic communities of the Mejillones and Antofagasta bays have constructed different ecological systems. For the majority of the ecosystem properties, such as Pp/R, A/C and Ov/C ratios, and Redundancy, the Antofagasta Bay benthic system represents a more developed system that is, in turn, less resistant to disturbance compared to Mejillones Bay (*sensu* Christensen, 1995; Cropp and Gabric, 2002). This outcome may be explained, primarily, because Mejillones Bay is negatively affected by (1) the seasonal influence of the oxygen minimum zone, to a depth of 20 m, which constrains the respiration of organisms belonging to benthic communities

Table 2
Summary statistics after mass-balance process by *Ecopath II*, and network flow indices for benthic ecological systems of Mejillones and Antofagasta bays. The units are in g wet weight and Flowbits is the product of flow (g wet weight m⁻² year⁻¹) and bits.

	Benthic systems	
	Mejillones bay	Antofagasta bay
A. Summary statistics		
Sum of all consumption (g ww m ⁻² year ⁻¹)	12,038.62	16,992.39
Sum of all exports (g ww m ⁻² year ⁻¹)	3963.847	3856.144
Sum of all respiratory flows (g ww m ⁻² year ⁻¹)	7211.554	9675.816
Sum of all flows into detritus (g ww m ⁻² year ⁻¹)	6215.834	7015.464
Total system throughput (g ww m ⁻² year ⁻¹)	29,429.86	37,539.81
Sum of all production (g ww m ⁻² year ⁻¹)	13,594.74	17,450.05
Mean trophic level of the catch	1595	1.692
Gross efficiency (catch/net p.p., %)	0.003	0.004
Total net primary production (g ww m ⁻² year ⁻¹)	11,175.4	13,531.96
Total primary production/total respiration	1549	1.399
Net system production (g ww m ⁻² year ⁻¹)	3963.847	3856.144
Total primary production/total biomass	6284	7.194
Total biomass/total system throughput (year ⁻¹)	0.06	0.05
Total biomass (excluding detritus) (g ww m ⁻² year ⁻¹)	1778.37	1881.06
Total catches (g ww m ⁻² year ⁻¹)	33.41	58.56
B. Network flow indices		
Ascendency (A) (flowbits)	34,395.1	48,574.3
Overhead (Ov) (flowbits)	108,353.1	121,434.8
Development Capacity (C) (flowbits)	142,897.9	170,237.0
AMI (Average Mutual Information)	1371	1.294
Sea star species accounting for the lowest % of AMI	0.00001	
<i>O. vulgaris</i> accounting for the lowest % of AMI		0.000009
Pathway redundancy (of overhead) (%)	53.1	49.2
A/C (%)	24.1	28.5
Ai/Ci (%)	16.0	16.7
Ov/C (%)	75.8	71.3
Throughput cycled (exc. Detritus) (g ww m ⁻² year ⁻¹)	11.56	7.18
Throughput cycled (inc. Detritus) (g ww m ⁻² year ⁻¹)	1355.05	2260.56
Finn's cycling index (FCI) (%)	4.88	6.02
Finn's mean path length (dimensionless)	2915	2.774
Food web connectance (dimensionless)	0.198	0.184
Omnivory index (OI) (dimensionless)	0.074	0.069

Table 3
Summary of the system recovery time (SRT) for each benthic ecological system of Mejillones and Antofagasta bays using mixed control mechanism (ν), and three increments of mortality (10%, 30%, and 50%).

System recovery time (years)							
Mixed flow control ($\nu=2.0$)							
	Increase in production			Increase in production			
	10%	30%	50%	10%	30%	50%	
A. Mejillones bay				B. Antofagasta bay			
(1) <i>Lessonia trabeculata</i>	4.5	7.5	8.5	(1) <i>Lessonia trabeculata</i>	6.0	8.25	9.25
(2) Chlorophyta	3.25	5.5	5.5	(2) Chlorophyta	5.25	8.75	8.25
(3) Rhodophyta	8.25	8.25	7.5	(3) Rhodophyta	7.0	8.50	8.25
(4) Phaeophyta	5.5	5.5	5.25	(4) Phaeophyta	7.5	10.0	7.5
(5) <i>Argopecten purpuratus</i>	4.5	6.75	9.25	(5) <i>Argopecten purpuratus</i>	6.0	7.75	11.25
(6) <i>Aulacomya ater</i>	4.75	9.0	6.5	(6) <i>Aulacomya ater</i>	6.25	8.0	9.75
(7) <i>Tagelus dombeii</i>	5.25	6.75	8.25	(7) <i>Tagelus dombeii</i>	7.0	11.0	10.0
(8) <i>Choromytilus chorus</i>	4.25	7.0	7.25	(8) <i>Choromytilus chorus</i>	4.75	9.25	7.0
(9) Filter feeders	6.25	10.0	9.25	(9) <i>Transennella pannosa</i>	8.5	10.25	12.25
(10) <i>Gari solida</i>	5.0	8.75	7.25	(10) Filter feeders	6.75	9.75	8.5
(11) <i>Tegula</i> spp.	5.25	11.0	9.75	(11) <i>Protothaca thaca</i>	6.0	9.25	10.25
(12) SEH	7.0	13.25	11.0	(12) <i>Tegula</i> spp.	5.75	8.0	9.5
(13) Sea urchin species	4.25	10.0	7.5	(13) SEH	7.25	10.25	11.25
(14) SEC	6.0	9.25	8.0	(14) Sea urchin species	5.25	8.0	7.25
(15) LE	4.75	7.25	8.0	(15) SEC	6.25	7.5	10.5
(16) <i>Cancer</i> spp.	4.75	6.75	7.75	(16) LE	4.75	11.0	10.75
(17) <i>Thais chocolata</i>	4.25	9.0	7.5	(17) <i>Cancer</i> spp.	5.0	8.5	9.0
(18) <i>Luidia magallanica</i>	6.75	12.75	10.25	(18) <i>Thais chocolata</i>	6.0	8.75	9.25
(19) Seastars	4.0	7.0	5.25	(19) <i>Concholepas concholepas</i>	5.25	7.5	7.75
(20) Zooplakton	4.5	7.5	7.25	(20) <i>Octopus vulgaris</i>	5.5	10.25	11.25
(21) Phytoplankton	5.75	9.25	10.25	(21) <i>Luidia magallanica</i>	7.0	10.0	10.0
(22) Detritus	-	-	-	(22) Seastars	5.75	8.0	9.5
Average	5.18	8.47	7.95	(23) Zooplakton	6.25	8	9.25
Global average	7.20			(24) Phytoplankton	8.75	10.75	12.3
				(25) Detritus	-	-	-
				Average	6.24	9.05	9.57
				Global average	8.29		

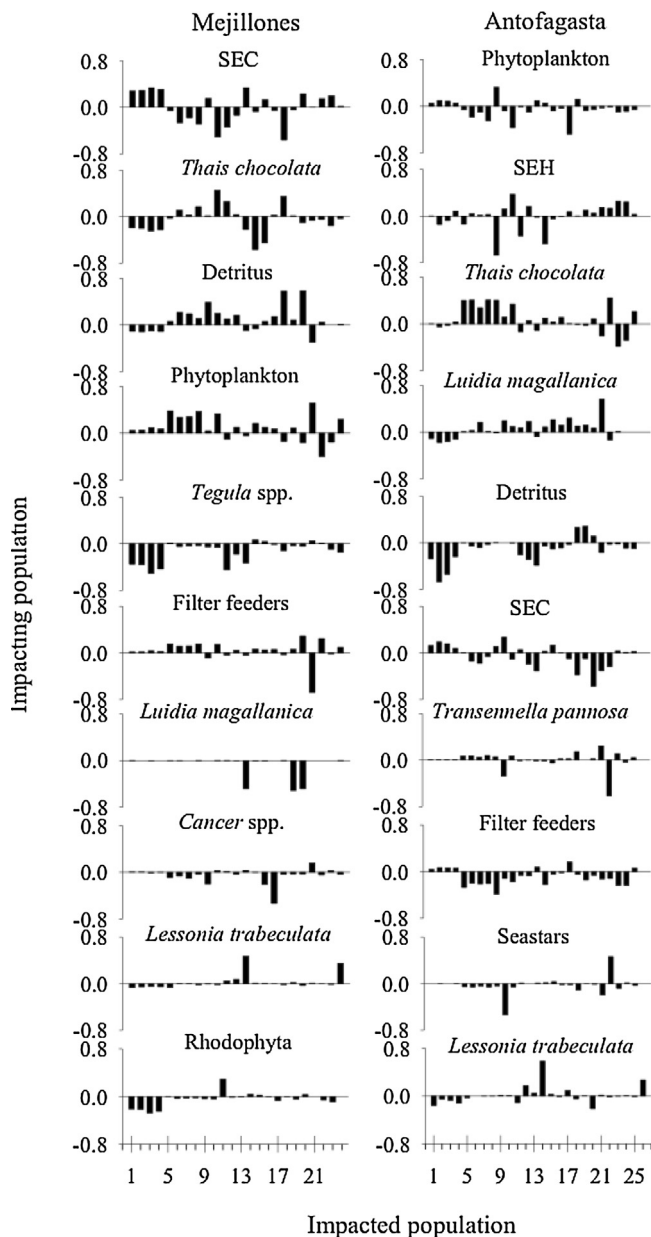


Fig. 2. Ten most relevant propagated direct and indirect effects using Mixed Trophic Impacts (MTI) (direct and indirect) in the benthic model systems of Mejillones and Antofagasta bays. (Note: the numbers on the x-axis correspond to the species or functional groups of Table 1).

(Escribano and Hidalgo, 2000) and by (2) the discharge of sewage from fishmeal industries, the impacts of thermoelectric plants, the greater loading of heavy metals as consequence of mining activities, and the impacts from the acid transfer plant and port operations (Valdés and Sifeddine, 2009).

The magnitudes of the estimated *Total System Throughput* (T), *Ascendency* (A), *Capacity* (C) and A/C ratio for the benthic systems of Mejillones and Antofagasta bays are lower than those described for subtidal and intertidal systems dominated by kelp forests located in the same geographical region (Ortiz, 2008a; Ortiz et al., 2013b). This difference could be a consequence of the omission of flows to the pelagic system in the current models and because the rocky bottoms dominated by kelp forest are highly productive and present greater habitat heterogeneity, allowing for greater abundances of other algae and invertebrate species (Duggins et al., 1989; Tala and Edding, 2005; Ortiz, 2008a). In contrast, the ecosystem parameters

calculated in the present work were similar to those calculated for the benthic communities in Tongoy Bay (Ortiz and Wolff, 2002), potentially because the benthic habitats are similar, that is, dominated by soft bottoms (sand, gravel, and mud). In addition, the values of the *Total System Throughput* (T) (as a measure of a system's size or vigour) estimated for the two ecological systems were also higher than those described for other ecosystem models, such as estuaries, lakes, bays and mangroves (Wolff et al., 2000; Vega-Cendejas and Arreguin-Sanchez, 2001; Patricio and Marques, 2006; Patricio and Marques, 2006; Liu et al., 2007; Yunkai-Li et al., 2009; Jia et al., 2012; Ullah et al., 2012), but lower than those obtained for various coral reef ecosystems (Arias-González et al., 2004). The Finn's cycling index values, which correspond to the amount of the flow in a system that is recycled in respect to the *Total System Throughput* (Finn, 1976), suggests that the Antofagasta Bay benthic system presents a higher degree of system maturity compared to Mejillones Bay (sensu Odum, 1969), coinciding with the above-described results for other macrodescriptors. The benthic models produced similar magnitudes of the omnivory index (OI) and Finn's mean path length (FPL), demonstrating that the benthic systems were characterised by a similar topological structure. Likewise, the similarity in the magnitudes of the mean trophic level of the fishery estimated for the two benthic systems indicates that the harvest pressure operates on primary and secondary producers.

One of the most relevant results obtained in terms of the propagated impacts, using *MTI* and short-term *Ecosim* simulations (under three levels of mortality) was that the compartments (species or functional groups) shared amongst the two benthic systems produced different response patterns throughout their networks. With the exception of the phytoplankton, *MTI* and *Ecosim* simulations for the Mejillones and Antofagasta bays showed that the groups of small epifauna carnivore (*SEC*), the herbivorous *Tegula* spp. and *T. pannosa* propagated the highest impacts on the other remaining compartments. In addition, *T. chocolate*, *T. dombeii*, *L. trabeculata*, and *Cancer* spp. were identified as exploited species and amongst the ten compartments that propagated the highest impacts on the other remaining groups. These outcomes are relevant because Valdés et al. (2014) recently described several of these exploited species within a process of bio-transference and bio-magnification of heavy metals (Cu, Pb and Zn) in Antofagasta Bay. Likewise, the other sea star species group and the cephalopod *O. vulgaris* (inhabiting the Mejillones and Antofagasta benthic systems, respectively) should also be taken under consideration because both components play a relevant role in promoting the complexity (in terms of flow) of these systems. The average *SRT* was greater for the benthic system of Antofagasta Bay, which suggests that this system is less resilient to disturbance than Mejillones Bay. This finding is consistent with the results obtained using the A/C and Ov/C ratio, *Redundancy* and Finn's cycling values. All of these outcomes are relevant because they demonstrate that both benthic systems build different trophic networks in terms of their structure, size, complexity and dynamics, regardless of their similarities in terms of shared species or compartments.

Contrary to the environmental studies, we claim that an ecosystem health assessment should extend the boundaries of the current view towards a more holistic scope that integrates the physical, chemical, biological and ecological components of an ecosystem and their relationships. This view is especially important when the live components directly modify their surroundings through their structures and activities (Levins and Lewontin, 1985), and they are actively involved in the flows of energy and/or matter throughout the trophic networks (Ulanowicz, 1986). Likewise, environmental stakeholders should recognise that the ecosystems are heterogeneous in terms of their structure, organisation and dynamics, thus the minimum permitted concentration of toxic substances should

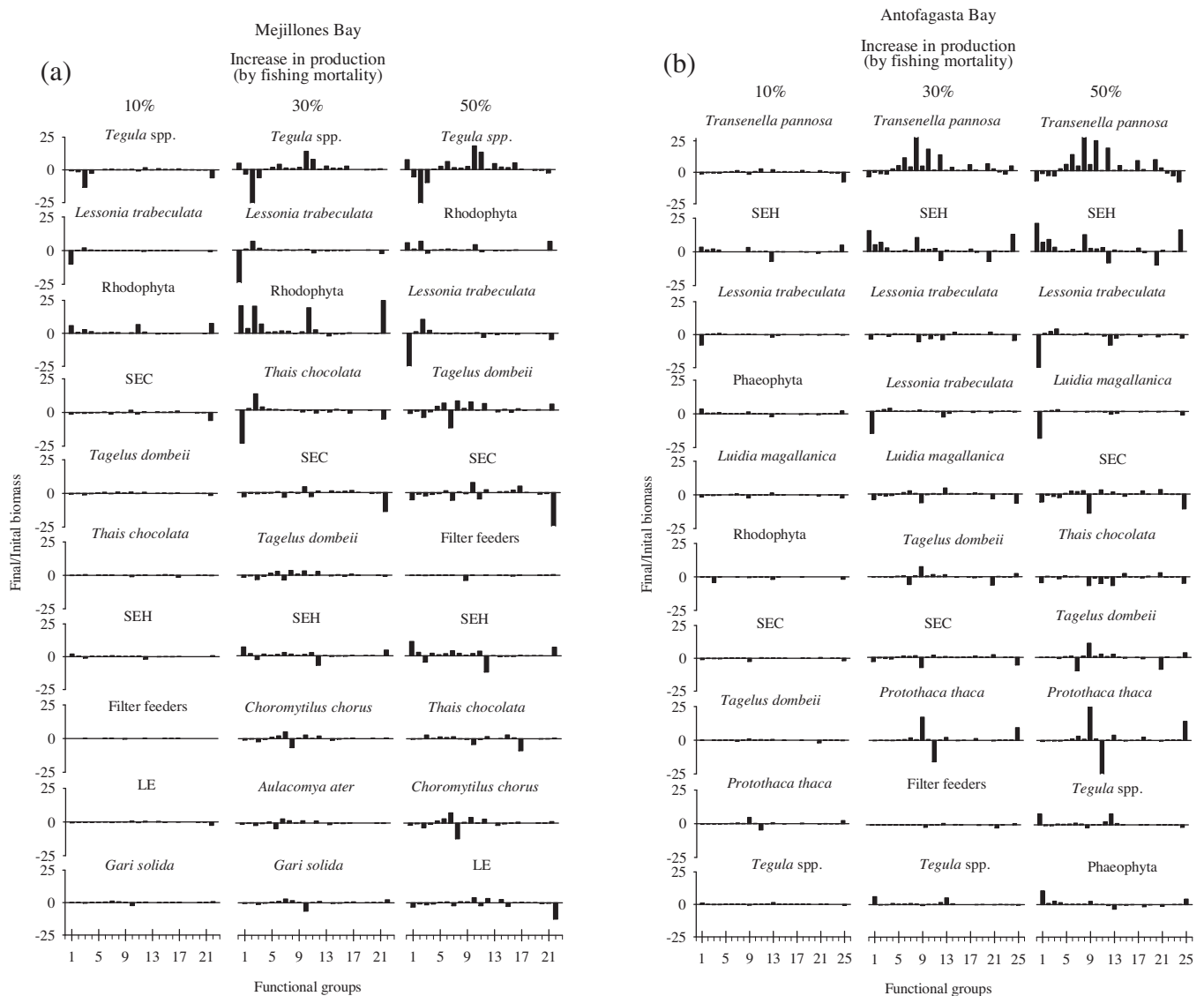


Fig. 3. Ten most relevant dynamical responses propagated using *Ecosim* under mixed control mechanism in Mejillones Bay (a) and Antofagasta Bay (b). All compartments were subject to 1 year of increased fishing mortality (10%, 30% and 50%) (between year 1 and 2 of simulation) and the responses of biomass were obtained for the third year of the simulation. (Note: the numbers on the x-axis correspond to the model compartments of Table 1).

be also according to their degree of ecosystem's development, resistance and resilience.

5. Conclusions

The majority of the ecosystem macrodescriptors (Pp/R , A/C and Ov/C ratios, *Redundancy* and Finn's cycling index) and the average system recovery times (SRT) calculated in the current work clearly show that the benthic system of Antofagasta Bay would be more developed, mature and organised but, in turn, less resistant to perturbations compared to Mejillones Bay. This result may be a consequence of negative impacts acting on Mejillones Bay, such as, the seasonal influence of the oxygen minimum zone, and the discharge of sewage from fishmeal industries, the impacts of thermoelectric plants, the greater loading of heavy metals. These two benthic systems construct networks of interacting organisms and their environments in which each species or functional group has a particular and different role. This latter is important because the protection of environment -as a whole- should not only aim to ensure the quality of water and sediments but also consider that

(1) the ecological properties and functions of ecosystems emerge from complex networks (based on the ecosystem indices of Odum and Ulanowicz); (2) any natural or anthropogenic intervention percolates through the network and directly and indirectly impacts the other components, and (3) the minimum permitted concentration of toxic substances should be defined spatial and locally, recognising the ecosystems as heterogeneous.

In the model presented here, we recognise the following sources of simplifications: (1) our models represented only the benthic communities of the two bay systems. In spite of this reduced model configuration, we believe that the most relevant energy flows are reflected; (2) both systems were analysed in an already impacted state; (3) although there is no verification of the simulations through time-series calibration, however, this latter was mitigated by comparing different scenarios based on three level of mortality; (4) regardless of the well-known limitations of the *Eco-path* and *Ecosim* theoretical frameworks, the models constructed and the dynamical simulations executed in the present work represent the processes underlying the systems analysed when only considering short-term dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2015.04.006>

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