Assessment of long-term changes of ecosystem indexes in Tongoy Bay (SE Pacific coast): Based on trophic network analysis

Jorge González [a,b,*], Marco Ortiz [a,c], Fabián Rodríguez-Zaragoza [d], Robert E. Ulanowicz [e]

[a] Laboratorio de Modelamiento de Sistemas Ecológicos Complejos (LAMSEC), Instituto Antofagasta, Universidad de Antofagasta, Chile
[b] Programa de doctorado en Ciencias aplicadas mención Sistemas marinos costeros, Universidad de Antofagasta, Chile
[c] Instituto de Ciencias naturales Alexander Humboldt, Universidad de Antofagasta, Chile
[d] Laboratorio de Ecosistemas Marinos y Acuicultura (LEMA), Departamento de Ecología, CUCBA, Universidad de Guadalajara, Mexico
[e] Department of Zoology, University of Florida, 110 Bartram Hall, Gainesville, FL 32611-8525, USA

ARTICLE INFO

ABSTRACT

Quantitative macroscopic's indexes have been used to compare three trophic models of the exploited benthic ecosystem of Tongoy Bay. In this system the primary productivity and benthic invertebrates are more important in the cycling of biomass. The models were built with a similar number of compartments for the years 1992, 2002 and 2012, using *Ecopath with Ecosim* (*EwE*). Odum and Ulanowicz's frameworks and ecological network analysis were then used to estimate the levels of maturity, growth and development of the system. Likewise, "keystoneness" indexes – at each time – were also estimated for the models. Our results show that Tongoy Bay exhibited an increase in maturity and development ("health") in 2012 compared to past conditions, which was reflected by (1) an increase in the total system biomass, total system throughput, AMI, and absolute *Ascendency*, (2) higher flow and increased efficiency of transferred energy and its proportion at higher trophic levels, (3) an increase of recycling (FCI), (4) a reduction of NPP/R and NPP/B ratios of the system, and (5) an increase in the number of compartments trophically linked that comprise the *keystone species complex*. We argue that these results are a consequence of reduced fishing pressure on this benthic system in recent years. This study shows that the fishing would not only have a direct impact on exploited species, but would also affect the structure and functioning of the ecosystem. The information obtained could help to improve the management of fisheries resources, evaluating surveillance indicators that can show the putative changes of intervened ecosystems.

© 2016 Elsevier Ltd. All rights reserved.

1. Introduction

The rapid deterioration of ecosystems worldwide has intensified the need to assess the emergent properties (as macroscopic indexes), which allow them to be monitored over time (Mageau et al., 1998; Costanza and Mageau, 1999). Sustainability indexes associated with ecological system theory focus on the ability of ecosystems to withstand natural or anthropogenic disturbances (Rapport et al., 1998; Mayer et al., 2004). It is proposed that "good" healthy ecosystems would be sustainable, if they were capable of maintaining their structure (organisation) and function (activity) over time after suffering external disturbances (Holling, 1973, 1987; Ulanowicz, 1992; Grimm and Wissel, 1997; Costanza and Mageau, 1999). Odum (1969) and Ulanowicz (1986, 1997)

developed two frameworks, which allow us to use several macroscopic indexes related to ecosystem health (Rapport et al., 1998; Costanza and Mageau, 1999; Mayer et al., 2004).

Anthropogenic influences, such as fishing and pollution, have been associated with long-term ecosystem changes in structure, organisation and functioning (Pauly et al., 1998; Gunderson, 2000; Scheffer et al., 2001; Troell et al., 2005; Petersen et al., 2008). These conclusions have focused efforts to apply procedures that allow one to quantify the changes in ecosystems. In this sense, Odum (1969) proposed that maturity of ecosystems occurs when their structural and functional characteristics are maximised, which can be measured as increments of biomass, dominant symbiosis, nutrient conservation, stability, reduced entropy, and increased information. Thereafter, Ulanowicz (1986) developed a framework called *Ascendency*, which is based on network analysis and principles of thermodynamics. *Ascendency* evaluates the degree of growth and flow coherence of an ecosystem. Likewise, *Ascendency* can be used to describe the trend of an ecosystem after natural or anthropogenic disturbances (Costanza and Mageau, 1999; Walters and

Martell, 2004) and used to compare ecosystem trajectories at different times (Wulff and Ulanowicz, 1989; Baird et al., 1991; Monaco and Ulanowicz, 1997; Ortiz and Wolff, 2002a; Heymans, 2003; Christensen et al., 2005).

The flow of matter and/or energy through any network permits one to obtain relevant information about their structure and functioning. Based on this information it is possible to assess the influence of each component upon the entire the food web (Christensen et al., 1996; Pauly et al., 1998; Ulanowicz and Baird, 1999). The *Ecopath with Ecosim* (*EwE*) software was designed for the construction, parameterisation and analysis of trophic mass-balance models for aquatic ecosystems (Christensen et al., 2005). This software can quantify ecosystem macroscopic indexes with regard to its structure and dynamics, and estimate the propagation of direct and indirect effects through the networks as response to different management/harvest scenarios within marine ecosystems (Christensen and Pauly, 1993; Ortiz and Wolff, 2002a; Pikitch et al., 2004; Christensen et al., 2005; Ortiz et al., 2009, 2010). Based on this analysis, we can provide vital information for ecosystem-based management (EBM), which aims to maintain ecosystem services by conserving ecosystem structure and function (Garcia and Cochrane, 2005).

The overall ecosystem productivity of Tongoy Bay, Chile (Fig. 1) is conditioned by the occurrence of periodic upwelling near the centre of the bay (Daneri et al., 2000). The most important components of the system are benthic invertebrates whose food intake exceeds that of pelagic fish and birds (Wolff and Alarcón, 1993; Wolff, 1994). This upwelling has led to the development of important benthic fisheries and consequent human interventions (Ortiz and Wolff, 2002b).

The total landings of the benthic resources from Tongoy Bay have fluctuated substantially since 1985, reaching a peak value in 1992 of ~300 tonne. The main exploited resources are predatory crabs, such as *Romalion polyodon*, the scallop *Argopecten purpuratus*, and clams. Over the last 20 years, the fishery has experienced a downward trend accompanied by changes in the composition of harvested species. These changes would suggest that the benthic system of Tongoy Bay has experienced changes since 1992 that, in turn, could modify the energy/matter flow patterns in this bay. Wolff (1994) and Ortiz and Wolff (2002a) determined several macrodescriptors of the Tongoy Bay benthic ecosystem and evaluated the effects of different fishing management strategies. However, both contributions were independent temporal snapshots of the bay. In the current study we adopt a network analysis – as a general strategy – for examining and comparing the long-term changes of macroscopic indexes as a consequence of fishing activities in the Tongoy Bay benthic ecosystem. To achieve that, three trophic models were constructed in order to represent the "ecosystem state" of the benthic communities for the years 1992, 2002 and 2012. Based on these models, our aim was to better understand the trajectory of the performance measures of this bay.

2. Materials and methods

2.1. Study area

Tongoy Bay (Fig. 1) is located in north-central Chile (30°12′ S–71°34′ W). This bay has high productivity due to the presence of a seasonal (spring and summer) upwelling (Fonseca and Farías, 1987). Seasonal upwelling produces high phytoplankton biomass, which in turn supports fishing and scallop (*A. purpuratus*) aquaculture (Boré et al., 1993). Although scallop aquaculture has increased dramatically over the past 20 years, natural stocks are depleted and benthic landings have experienced a remarkable reduction. In 1998, management areas for benthic resource exploitation were delimited in Tongoy Bay under a territorial user rights for fishing (TURF) as a measure to reduce fishing pressure (Ortiz & Wolff, 2002a)

2.2. Source of data and models assumptions

Three trophic mass-balance models were constructed for the Tongoy Bay benthic ecosystem for the years 1992, 2002 (based on Wolff and Alarcón, 1993; Wolff, 1994; Ortiz and Wolff, 2002a), and 2012 (own sampling data), using *EwE* Software 6.0 (Christensen et al., 2005). The models were fit for the trophically linked biomass pools, concentrating on the major system biomass components (Walters et al., 1997; Pauly et al., 2000; Christensen et al., 2005). Biomass groups were defined as a species or functional group in term of wet weight. Each model represented the annual average condition of the Tongoy Bay benthic ecosystem. For comparisons at the system-level, the three benthic models were constructed with the same number of compartments ($n = 12$), so as to reduce any bias associated with different aggregation strategies (Gaichas et al., 2009). It is important to mention that the fishes, birds and marine mammals were not included in the models due to insufficient scientific information. Wolff (1994) suggests that in Tongoy Bay benthic invertebrate predators are more important in the cycling of biomass than demersal fishes. Although this reduces the realism of the model configuration, the most relevant interdependencies and flows are reflected. This strategy permitted to obtain comparative macrondicators to benthic level over time under similar limitations.

EwE is based on a series of linear equations and assumes a mass balance system between the compartments of the model. The general equation can be expressed as follows:

$$\frac{dB}{dt} = P_i - (B_i * M2_i) - P_i * (1 - \text{EE}_i) - \text{EX}_i \qquad (1)$$

where biomasses are at steady state, P_i is production ($\text{g m}^{-2}\,\text{year}^{-1}$), B_i is biomass (g/m^2), $M2_i$ is predation mortality (year^{-1}), EE_i is ecotrophic efficiency (%) which quantifies the proportion of the production that is utilised in the system, $1 - \text{EE}_i$ is other mortality of i (year^{-1}), and EX_i is export i ($\text{g m}^{-2}\,\text{year}^{-1}$). Production is estimated by the relationship of production/biomass (P/B) and average annual biomass (B) and is expressed as: $P_i = B_i * (P_i/B_i)$. Predation mortality depends on the predator activity, and it is defined as the sum of consumption by all predators (j) preying on a species or group (i) and can be expressed as:

$$B_i * M_i = B_j * \frac{Q_j}{B_j} * \frac{D_{ji}}{C_{ji}} \qquad (2)$$

where Q_j/B_j is the consumption/biomass of predator j (year^{-1}) and D_{ji}/C_{ji} is the i fraction of prey in the diet spectrum of predator j. For each functional group and/or species, the key input parameters are B_i, P/B_i, Q/B_i, and EE_i. At least three of these input parameters must be known for each group; the model estimates the fourth. The functional groups comprised species with similar trophic roles: (1) Predatory snails (PS) (e.g., *Xanthochorus* sp. and *Priene* sp.), (2) Predatory crabs (PC), such as *Cancer* sp. and *Homalaspis plana*, (3) Seastars (SS) (e.g. *Heliaster helianthus*, *Meyenaster gelatinosus*, and *Luidia magallanica*), (4) Small epifauna herbivores (SEH) (e.g., *Tegula* sp. and *Fissurella* sp.), (5) Large epifauna (LE) (e.g., *Pagurus* sp. and *Alpheus* sp.), (6) Small epifauna (SE) (e.g., *Caprella* sp. and *Nereis* sp.), (7) Bivalves (Biv) (e.g., *Mulinia edulis* and *Ensis macha*), (8) Zooplankton (Zoo), (9) Macrophytes (Ma) (e.g., *Chondrochanthus chamissoi*, *Ulva* sp., *Rhodymenia* spp.), and (10) Phytoplankton (Phy). The crab *Romalion polyodon* (RP) and the scallop *A. purpuratus* (AP) were included as individual compartments into the model because of their commercial importance. Information about diet matrices, productivity, and consumption of these functional groups was obtained from Wolff (1994) and Ortiz and Wolff (2002a) and
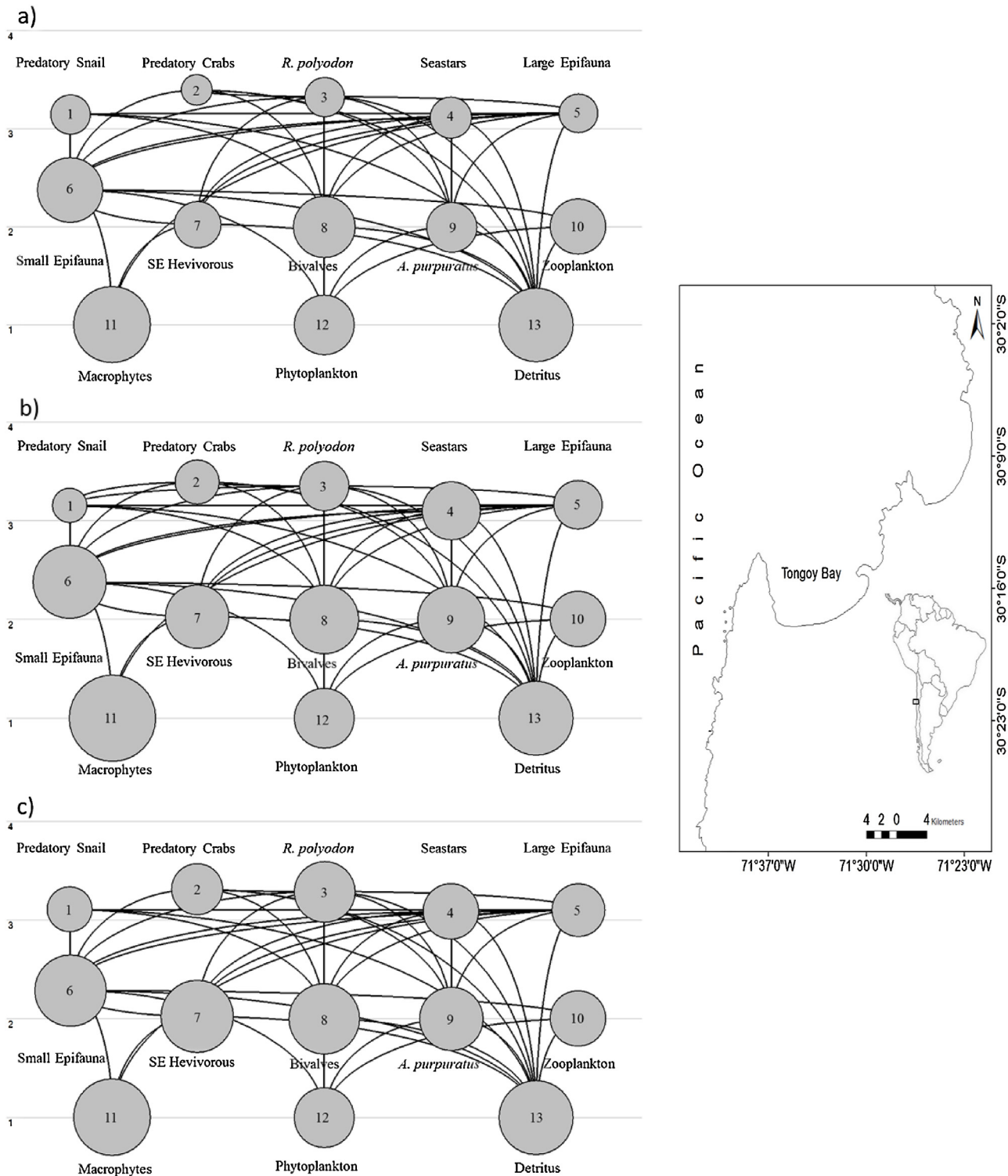
Fig. 1. Study area: Tongoy Bay, northern Chile. Trophic models for the benthic ecosystem during 1992 (a), 2002 (b) and 2012 (c). Vertical position approximates the trophic level. The circle size is proportional to the compartment (population and/or functional groups) biomass (g wet weight mm^{-2}). Numbering in circles correspond to species or functional groups (see Table 1 for details).

was weighted according to the species that formed each group (Table 1). Fish landing statistics were obtained from the National Fisheries Service (Sernapesca, 2013).

The benthic model system of Tongoy Bay for the year 2012 was constructed using the average biomass of the benthic community in the most extreme seasons (summer and winter). To do this, 28 transects were positioned perpendicular to the shoreline in the bay

at a depth between 4 and 20 m. At each transect, benthic organisms were sampled in three quadrats (0.5 m × 0.5 m) at 4, 8, 12 and 20 m depth. A total of 336 samples were taken per season. In each quadrant, the biomass (g wet weight m^{-2}) of benthic macro flora and macro fauna were obtained. The phytoplankton and zooplankton biomass (g mm^{-2}) at 20 m depth was estimated for the year 2012 from information generated by the environmental monitoring

Table 1
Final parameters for ecopath models representing the Tongoy Bay's benthic ecosystem for 1992s, 2002s and 2012s, where TL = trophic level, B = biomass and C = catches are reported in wet weight, P/B = turnover rate, Q/B = consumption rate, EE = ecotrophic efficiency, P/Q = gross efficiency and F = fishing mortality.

	Groups/specie name	TL	B (g/m^2)	P/B (year)	Q/B (year)	EE	P/Q (year)	Ca (g/m^2)	F (year)
Periods (years) 1992									
(1)	Predatory snails (PS)	3.2	3.8	1.6	5.6	0.29	0.29	0.7	0.18
(2)	Predatory crabs (PC)	3.4	1.7	1.8	8.2	0.69	0.22	–	–
(3)	*R. polyodon* (RP)	3.3	3.8	1.1	9.5	0.90	0.12	0.8	0.21
(4)	Seastars (SS)	3.1	4.6	1.0	4.3	0.13	0.24	–	–
(5)	Large epifauna (LE)	3.2	3.6	1.4	9.5	0.95	0.15	–	–
(6)	Small epifauna (SE)	2.4	43.7	3.5	9.8	0.76	0.36	–	–
(7)	SE herbivorous (SEH)	2.0	7.9	2.2	10.0	0.99	0.22	–	–
(8)	Bivalves (Biv)	2.0	32.3	2.0	9.9	0.48	0.20	10.9	0.37
(9)	*A. purpuratus* (AP)	2.0	10.6	2.1	9.9	1.00	0.21	6.1	0.58
(10)	Zooplankton (Zoo)	2.0	18.0	40.0	160.0	0.11	0.25	–	–
(11)	Macrophytes (Ma)	1.0	128.5	4.8	0.0	0.14	–	–	–
(12)	Phytoplankton (Phy)	1.0	28.0	250.0	0.0	0.45	–	–	–
(13)	Detritus (Det)	1.0	100.0	–	–	0.07	–	–	–
Periods (years) 2002									
(1)	Predatory snails (PS)	3.2	2.4	1.5	5.5	0.98	0.27	0.6	0.25
(2)	Predatory crabs (PC)	3.4	6.0	1.0	6.6	0.98	0.15	–	–
(3)	*R. polyodon* (RP)	3.4	10.0	1.1	9.5	0.90	0.12	0.4	0.04
(4)	Seastars (SS)	3.1	24.0	1.1	4.8	0.13	0.23	–	–
(5)	Large epifauna (LE)	3.2	9.5	1.5	9.7	0.88	0.15	–	–
(6)	Small epifauna (SE)	2.4	98.0	4.0	13.5	0.83	0.30	–	–
(7)	SE herbivorous (SEH)	2.0	38.7	2.2	9.9	0.65	0.22	–	–
(8)	Bivalves (Biv)	2.0	61.0	1.0	9.9	0.71	0.10	–	–
(9)	*A. purpuratus* (AP)	2.0	55.0	2.1	9.9	0.77	0.21	16.0	0.29
(10)	Zooplankton (Zoo)	2.0	18.0	40.0	160.0	0.34	0.25	–	–
(11)	Macrophytes (Ma)	1.0	348.6	4.4	0.0	0.34	–	114.0	0.33
(12)	Phytoplankton (Phy)	1.0	28.0	250.0	0.0	0.57	–	–	–
(13)	Detritus (Det)	1.0	100.0	–	–	0.16	–	–	–
Periods (years) 2012									
(1)	Predatory snails (PS)	3.1	6.7	1.5	5.5	0.39	0.28	0.2	0.03
(2)	Predatory crabs (PC)	3.3	12.2	1.7	9.2	0.86	0.19	–	–
(3)	*R. polyodon* (RP)	3.3	30.1	1.1	9.5	0.85	0.12	2.6	0.09
(4)	Seastars (SS)	3.1	18.4	1.0	4.2	0.13	0.24	–	–
(5)	Large epifauna (LE)	3.1	13.9	2.0	9.2	0.94	0.22	–	–
(6)	Small epifauna (SE)	2.3	81.8	4.4	12.2	0.97	0.36	–	–
(7)	SE herbivorous (SEH)	2.0	86.0	2.3	10.5	0.59	0.22	–	–
(8)	Bivalves (Biv)	2.0	72.9	1.7	9.8	0.61	0.17	0.2	0.00
(9)	*A. purpuratus* (AP)	2.0	37.6	2.2	9.9	0.98	0.22	0.1	0.00
(10)	Zooplankton (Zoo)	2.0	18.0	40.0	160.0	0.28	0.25	–	–
(11)	Macrophytes (Ma)	1.0	133.5	12.0	0.0	0.56	–	0.8	0.01
(12)	Phytoplankton (Phy)	1.0	28.0	250.0	0.0	0.55	–	–	–
(13)	Detritus (Det)	1.0	100.0	–	–	0.14	–	–	–

programme in Tongoy Bay (www.ceaza.cl). Despite high inter-week variability in phytoplankton and zooplankton biomass, the overall average annual estimates (all groups) had low variability, and thus, the three models were constructed using each the annual magnitudes.

2.3. Balancing and calibration of models

The balance of each model was achieved according to procedures described by Christensen et al. (2005). Balancing was achieved by verifying that the ecotrophic efficiency (EE) was <1.0 and the P/Q ratio was between 0.1 and 0.3 for all compartments (Christensen et al., 2005). During model balancing, average biomass was slightly adjusted to within 1 standard deviation of its original (average) value. Some P/B values were also adjusted up to 15% of their initial magnitudes. Diet composition (DC_{ji}) was adjusted slightly in the three models, differing from the initial values utilised by Ortiz and Wolff (2002a). Details on diet composition are given in Appendix A.

2.4. Ecosystem metrics and maturity

Several macroscopic indexes were calculated to compare the ecosystem structure and function for each model. Total system throughput (TST) is the sum of all of the biomass flows within an ecosystem and quantifies the "size of the entire system in terms of flow" (Ulanowicz, 1986). TST can be partitioned into total system consumption ($\sum Q$), total export ($\sum EXP$), total respiration ($\sum R$), and total flow to detritus ($\sum FD$). System respiration provides an activity measure of the upper levels of the trophic web and represents the proportion of consumption not directed to production. Other indexes included the sum of all system production ($\sum P$), and net primary production (NPP), which provide an index of activity in the ecosystem associated to the first trophic level. Likewise, the total biomass without detritus (B), mean trophic level of catch (TLC), total catch (Ca), and gross efficiency (GE) were also calculated. The indexes given by Odum (1969) – related to ecosystem maturity and development – were also used in the current study: (1) the total primary production/total respiration (NPP/R), (2) the total primary production/total biomass (NPP/B), (3) the biomass supported per unit of energy flow (B/TST), (4) net system production (P), (5) connectivity (CI), (6) omnivory index (OI), (7) average path length (APL) and (8) Finn's cycling index (FCI) (Finn, 1976). In the case of the transfer efficiency (TE) of each TL is calculated as the ratio of the summed exports from a given TL plus the flow transferred from one TL to the next TL, which indicates how efficient a transfer is from one TL to the next (Lindeman, 1942). Regarding Ulanowicz's (1986, 1997) indexes, we have *Ascendency* (A), overhead (O$_v$),

developmental capacity (C), internal redundancy (internal flows Ov_i/C_i), systems entropy (H), and AMI (average mutual information). *Ascendency*, it is the product of AMI and total activity of the system, is defined in terms of flow as:

$$A = \sum_{i,j} T_{i,j} \log \left(\frac{T_{i,j}T_{0,0}}{T_{i,0}T_{0,j}} \right), \tag{3}$$

and the developmental capacity is expressed as:

$$C = \sum_{i,j} T_{i,j} \log \left(\frac{T_{i,j}}{T_{0,0}} \right) \tag{4}$$

where T is the flow, i, j represent the prey and predator, respectively, and 0 is the sum of flows of preys or predators, with $T_{i,0}$ being the flows from one prey to all their predators, $T_{0,j}$ the consumption of a predator over all its prey, and $T_{0,0}$ represents total sum of flows over preys and predators. Overhead (O_v), is derived from the difference between Ascendency (A), and the developmental capacity (C).

The unit for H, AMI, A, and A_i/C_i is the "flow.bit", that is, the product of flow and bits. A bit is a unit of information that corresponds to the amount of uncertainty associated with a single binary decision (Christensen et al., 2005). A detailed description of *Ascendency* is given in Ulanowicz (1986, 1997, 2009) and Ulanowicz and Norden (1990).

2.5. Species/functional groups impacts and keystoneness

To assess the impact of different species/function groups in the ecosystems, the mixed trophic impacts routine (Ulanowicz and Puccia, 1990) was used, in which the trophic impact of stock (i) on (j) (MTI_{ij}) is estimated as the product of all predator–prey interactions across all potential trophic pathways connecting two groups or species, indicating how a small increase in the group biomass of any variable can impact the biomass of the other compartments. The impacts are relative and comparable between groups. Additionally, we estimated two indexes of "keystoneness" in the three model systems. The first index is defined by Libralato et al. (2006), as follows:

$$\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2} \tag{5}$$

where m_{ij} is obtained from MTI analysis and is the product of all the net impacts of all related functional groups i, j in the food web system. The overall relative effect (ε_i) is expressed in terms of the maximum effect measured in the food web. The "keystoneness" (KS_i) of each group is expressed as:

$$KS_i = \log[\varepsilon_i * (1 - p_i)] \tag{6}$$

where p_i is the contribution of the functional group i to the total biomass of the food web.

The second index used was "keystone species complex" (given by Ortiz et al., 2013). This concept assumes that there is a core of interacting species or functional groups with keystoneness properties. Estimation of the keystone species complex is based on the following quantitative and semi-quantitative analysis: (1) functional indexes based on steady-state and dynamic trophic models (using top-down, bottom-up and mixed flow controls), (2) structural indexes based on bottom-up, mixed and top-down control mechanisms, and (3) qualitative (or semi-quantitative) keystone species indexes generated using loop models based on mixed control.

3. Results

Table 1 summarises the input parameters and the results of the three balanced benthic trophic models of Tongoy Bay (Fig. 1). The biomass of most groups increased notably between 1992 and 2012. The principal compartments with an increment of biomass were the small epifauna herbivores (SEH) (from 7.9 to $86\,g$ wet weight m^{-2}), and the crab *R. polyodon* (from 3.8 to $30.1\,g\,w\,w\,m^{-2}$). It is relevant to note that the lowest biomass of the scallop *A. purpuratus* ($10.6\,g\,w\,w\,m^{-2}$) corresponded to the year 1992, coinciding with the year with the greatest fishing pressure. The greatest biomass of macrophytes was reached at 2002, during this year, the commercial red alga *C. chamissoi* dominated macrophyte group and was heavily exploited.

All benthic trophic models showed substantial changes over time (Table 2). The TST was 18% higher in 2002 than in 1992, reaching its greatest value in 2012. In addition, ΣQ and ΣR increased both in absolute terms and relative to TST. However, ΣEXP had the opposite trends in 2012. Total production and primary production (ΣP and NPP) increased until the last period of the study (2012), whereas total biomass (B), catch (Ca) and gross efficiency (GE) presented a non-monotonous response. Macroscopic indexes such as the *Ascendency* showed an increase in the benthic system over the last 20 years (Table 2). Contrary, the NPP/R and NPP/B ratios decreased. The FCI (as the percentage of total flow in the food web) increased from 1992 to 2012 (Table 2). Despite the increased value of AMI in 2012, the relative *Ascendency* (A/C) was lower than that observed in 1992. In contrast, the *Overhead* increased from 1992 to 2012 (Fig. 2a).

The distribution of the total biomass and catch in different trophic levels in the benthic system of Tongoy Bay is summarised in Table 3. The proportion of biomass decreased from 54.6% in 1992 to 30.0% in 2002 in trophic level I, but increased in trophic level II. Likewise, from 1992 to 2012, the proportion of biomass in the upper trophic levels (III) increased. In the benthic model corresponding to 2012, the catches were mainly obtained from trophic level III, in contrast to what was observed for 1992, when catches were mainly obtained from trophic level II. All types of flows into the system showed an increase from 1992 to 2002. Most of these flows (65%) were concentrated in trophic levels I and II for the three models, which resulted in an increase of the average transfer efficiency of 6.4% and 9.4% for 1992 and 2012, respectively (Table 2).

The propagation of direct and indirect effects estimated using mixed trophic impact (MTI) for the three models shows differences regards to the compartments having the main effects (Fig. 3). The functional groups that generated the greatest propagation effects were the phytoplankton and the small epifauna herbivorous (SEH). It is important to mention that – in general terms – the compartments that propagated the highest impacts in remaining variables came from three different trophic levels (primary, secondary and tertiary producers) and they were linked trophically. Those compartments that appeared in two or three models presented a similar qualitative patter of impacts, with the exception of *R. polyodon*, which propagated its highest impacts in 2012. The keystone index (KS_i) (Libralato et al., 2006) from the three models indicated phytoplankton as the compartment with most keystoneness properties (Fig. 4). However, the *keystone species complex* (Fig. 5) indicated two cores of keystone species/functional groups. The first core was comprised of the crab *R. polyodon*, the bivalves and the phytoplankton for the model corresponding to 1992. The second core consisted of the seastars (SS) and the scallop *A. purpuratus*, corresponding to the models for 2002 and 2012 (Table 4). All species and/or functional groups belonging to the *keystone species complex* were trophically related, comprising between 22.4 and 34.7% of the total system biomass.

Table 2
Summary statistics after mass-balance process by *EwE*, network flow indices and information flow Indices for benthic ecosystem model of Tongoy Bay for 1992, 2002 and 2012. Trend indicates direction towards a mature system (± indicating increase/decrease respectively). N/a is associated with fisheries and would not be applicable.

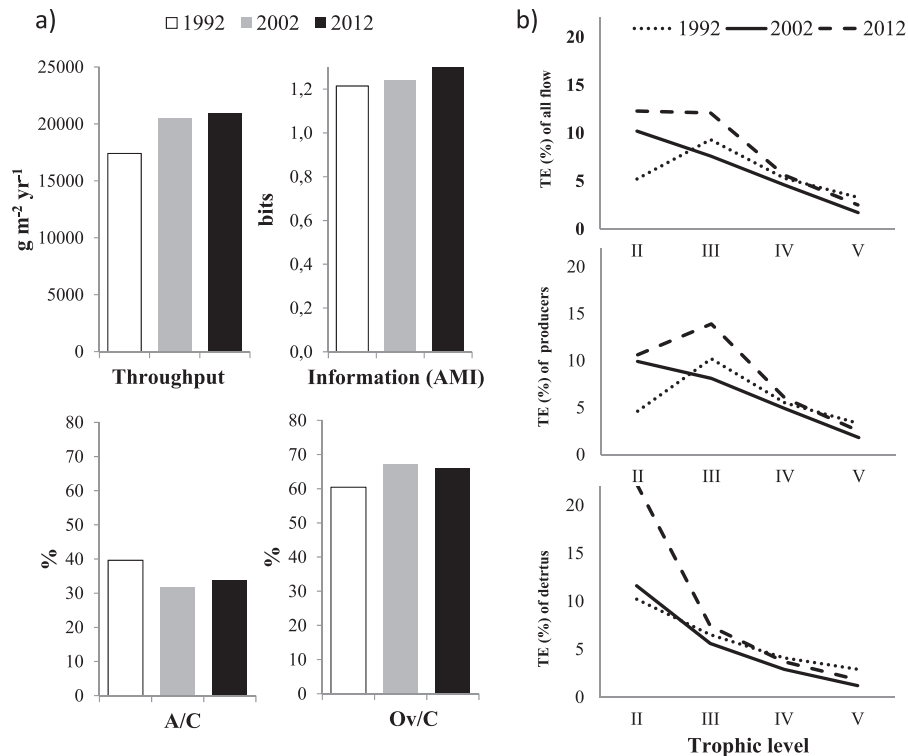| Parameters (unit)/periods		Trend	1992	2002	2012	%Change 1992–2002	%Change 2002–2012
Sum of all consumption (g m^{-2} year^{-1})	$\sum Q$	+	3936.8	6089.2	6506.2	54.7	6.8
Sum of all exports (g m^{-2} year^{-1})	$\sum$EXP	N/a	5461.7	5097.3	4989.6	−6.7	−2.1
Sum of all respiratory flows (g m^{-2} year^{-1})	$\sum R$	+	2148.6	3436.6	3612.4	59.9	5.1
Sum of all flows into detritus (g m^{-2} year^{-1})	$\sum$FD	+	5848.8	5897.4	5821.3	0.8	−1.3
Total system throughput (g m^{-2} year^{-1})	TST	+	17,396.0	20,520.4	20,929.5	18.0	2.0
Sum of all production (g m^{-2} year^{-1})	$\sum P$	+	8611.2	9968.6	10,194.6	15.8	2.3
Mean trophic level of the catch	TLC	+	2.10	1.14	2.7	−45.8	137.9
Gross efficiency of fisheries (catch/net pp)	GE	N/a	0.0024	0.0154	0.0005	531.5	−97.1
Total net primary production (g m^{-2} year^{-1})	NPP	+	7610.4	8533.8	8602.0	12.1	0.8
Total net primary production/total respiration	NPP/R	− (=1)	3.5	2.5	2.4	−29.9	−4.1
Net system production (g m^{-2} year^{-1})	P	−	5461.7	5097.3	4989.6	−6.7	−2.1
Total net primary production/total biomass	NPP/B	−	26.6	12.2	16.0	−54.0	30.7
Total biomass/total throughput	B/TST	+	0.016	0.034	0.026	106.9	−24.4
Total biomass (exc. detritus) (g m^{-2} year^{-1})	B	+	286.5	699.1	539.1	144.0	−22.9
Total catches (g m^{-2} year^{-1})	Ca	N/a	18.5	131.0	3.9	608.1	−97.0
Network flow indices							
Throughput cycled (exc. detritus) (g m^{-2} year^{-1})	TCI	+	67.9	210.06	118.9	209.5	−43.41
Throughput cycled (inc. detritus) (g m^{-2} year^{-1})	TCId	+	261.7	586.22	451.2	124.0	−23.04
Finn's cycling index (% of total)	FCI	+	1.5	2.9	2.2	90.7	−24.48
Total number of pathways (no.)	#P	+	67.0	79.0	67.0	17.9	−15.19
Average path length (APL) (dimensionless)	APL	+	3.34	3.49	3.34	4.5	−4.30
Food web connectance (dimensionless)	CI	+	0.32	0.32	0.31	0.0	−3.68
Omnivory index (dimensionless)	OI	+	0.09	0.11	0.09	16.8	−14.8
Mean transfer efficiency (%)	TE	+	6.42	7.13	9.41	11.1	32.0
Information flow indices							
Ascendency (total) flowbits	A	+	21,127.2	25,492.2	28,301.2	20.7	11.0
Overhead (total) flowbits	O_v	+	32,222.4	53,931.9	55,113.6	67.4	2.2
Capacity (total) flowbits	C	+	53,349.6	80,278.0	83,426.6	50.5	3.9
O_v/C (%)	O_v/C	+	60.4	67.2	66.1	11.2	−1.6
A/C (%)	*A/C*	−	39.6	31.8	33.9	−19.8	6.8
Redundancy	Ov_i/C_i		23.4	20.6	23.7	−12.0	15.1
System entropy	H	+	3.067	3.912	3.986	27.6	1.9
Average mutual information (bits)	AMI	+	1.2140	1.242	1.352	2.3	8.9

Fig. 2. Indices associated to *Ascendency*. *Throughput*, average mutual information (AMI), relative *Ascendency* (*A/C*) and relative overhead (O_v/C) (a), and transfer efficiency values (TE) by trophic levels for all flows, producer and detritus (*b*).

Table 3
Proportional total system biomass (g wet weight mm^{-2}) and catch (g wet weight mm^{-2}) for discrete trophic levels (TL) from benthic ecosystem models of Tongoy Bay for 1992, 2002 and 2012.

TL	Biomass (g/m^2)	B (%)	Catch (g/m^2/año)	Ca (%)
Periods (years) 1992				
I	156.5	54.6	0.0	0.0
II	103.9	36.3	17.0	92.1
III	24.0	8.4	1.3	6.9
IV	2.1	0.7	0.2	1.0
V	0.1	0.0	0.0	0.1
Total	286.5	100.0	18.5	100.0
Periods (years) 2002				
I	376.6	53.9	114.0	87.0
II	251.2	35.9	16.1	12.3
III	65.7	9.4	0.8	0.6
IV	5.4	0.8	0.0	0.0
V	0.2	0.0	0.0	0.0
Total	699.1	100.0	131.0	100.0
Periods (years) 2012				
I	161.5	30.0	0.8	20.6
II	280.6	52.1	0.3	8.6
III	86.2	16.0	2.4	62.1
IV	10.2	1.9	0.3	7.7
V	0.0	0.0	0.0	0.9
Total	538.5	100.0	3.9	100.0

Fig. 3. Mixed trophic impact (direct and indirect effects) for 1992, 2002 and 2012 in response to impacting small epifauna, phytoplankton, zooplankton, *R. polyodon*, macrophytes, seastars and large epifauna. (Number of impacted species/group corresponds to the list in Table 1.)

Fig. 4. Relative overall effect (ε_i) and keystoneness (KS$_i$) of each species/functional group from the benthic ecosystem model of Tongoy Bay for 1992 (a), 2002 (b) and 2012 (c). The number corresponds to keystoneness rankings from 1992 species/functional groups: 1 – phytoplankton; 2 – zooplankton; 3 – small epifauna; 4 – macrophytes; 5 – SE herbivorous; 6 – large epifauna; 7 – *R. polyodon*; 8 – predatory snails; 9 – bivalves; 10 – *A. purpuratus*; 11 – seastars and 12 – predatory crabs.

4. Discussion

Over the past 20 years, the benthic system of Tongoy Bay has experienced an increase in biomass, especially at higher trophic levels. This pattern has caused a relatively greater uniformity in biomass distribution among different trophic groups, which could be the first sign of recovery of this benthic ecosystem. It has been suggested that biomass loss has a negative impact on the production and efficiency of ecosystems, and therefore, intensive fishing can produce changes in ecosystem structure and functioning (Pauly et al., 1998; Pitcher and Pauly, 1998). Based on these results, our model for 1992 indicates an overexploited ecosystem. It is relevant to mention that since 1990 two important benthic resources have collapsed – the scallop *A. purpuratus* (Wolff, 1994; Stotz, 2000) and the bivalve *Mesodesma donacium* (Aburto and Stotz, 2013).
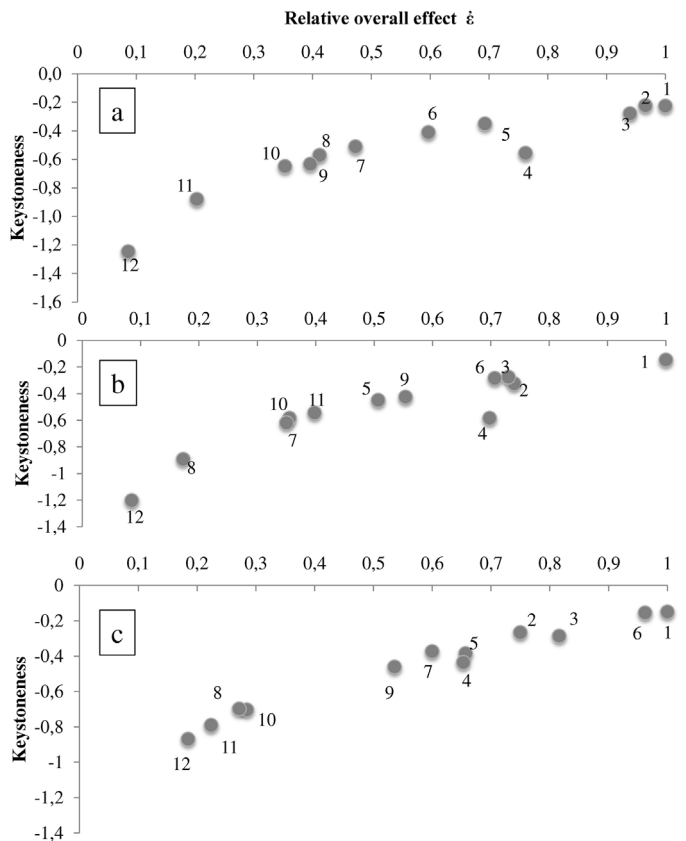
The increases in the aggregate flows and average transfer efficiencies (TE) from 1992 to 2012 indicates that the Tongoy Bay benthic ecosystem is becoming more efficient and less susceptible to perturbations (sensu Ulanowicz and Norden, 1990), which is consistent with Strayer (1991), who suggested that mature
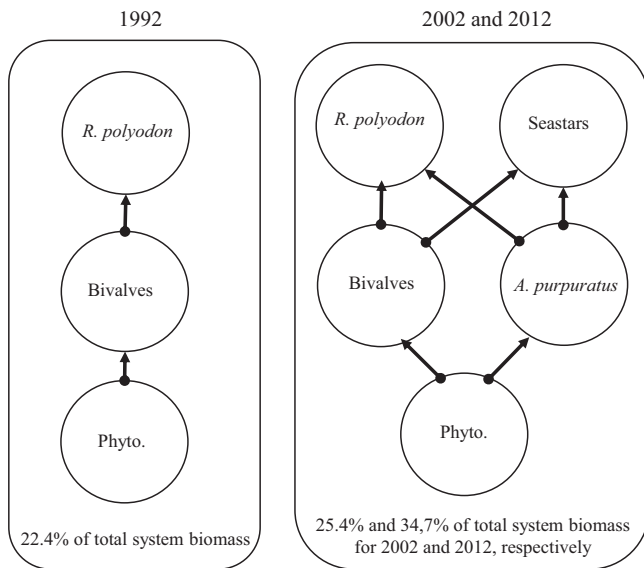
Fig. 5. Core set of functional groups/or species with keystone properties (keystone species complex) from the benthic ecosystem model of Tongoy Bay for 1992 (a) and 2002 & 2012 (b). The small circles and arrows represent negative and positive effects, respectively.

systems have higher rates of TE. The increase of TE is accompanied by increased cycling rates, which also is interpreted as indicating a more mature and less stressed system (Odum, 1969; Baird and Ulanowicz, 1993). Based on the macroscopic indexes calculated using Odum and Ulanowicz's theoretical frameworks, we suggest that the benthic system of Tongoy Bay has grown more "healthy" between 1992 and 2012. Overall, an increase of TST, AMI, and consequently *Ascendency*, were detected, improving the resistance against disturbances (O_v). Even though the FCI has increased in the last 20 years, due to higher abundance of filter feeders and predators, the system is inefficient compared to other exploited benthic ecosystems associated with upwelling (Ortiz et al., 2015).

Even though the NPP/R and NPP/B ratios have decreased during the last 20 years in Tongoy Bay, this system appears less mature than other coastal benthic systems of northern Chile (Ortiz et al., 2010, 2015) and Independencia Bay (Peru) (Taylor et al., 2008).

It is important to mention that all these coastal systems are influenced by a permanent upwelling regime, which has been described – in general terms – as a condition of immature ecosystems (Wolff, 1994; Christensen, 1995; Taylor et al., 2008). The increase of average trophic level supporting the fishery during 2012 suggests a lower rate of exploitation (cf., Pauly et al., 1998), which can be – in part – explained by the implementation of management areas

as a measure to regulate the fishing of benthic resources (Ortiz and Wolff, 2002a).

The reduced harvest in the last years would also explain the increase of the absolute *Ascendency* (Wulff and Ulanowicz, 1989; Arreguín-Sánchez et al., 2002). The magnitudes of relative *Ascendency* (A/C) were close to that recorded for similar benthic systems (Cruz-Escalona et al., 2007; Taylor et al., 2008; Ortiz et al., 2013, 2015). It should be noted that the A/C ratio decreased over time in the current study, showing discrepancies with NPP/R, NPP/B and cycling indexes. However, the A/C values should be interpreted carefully because they were negatively correlated with other maturity indexes (Christensen, 1995). What is notable is that the AMI increased uniformly over the study period, i.e., it became progressively more well-organised. Also, the highest relative overhead ratio (O_v/C), which reflected the energy of system to contend a disturbance, was observed for the model corresponding to 2012, which could be interpreted as the greater resistance of the benthic system against external perturbations (Ulanowicz, 1997).

Our results suggest that the benthic system of Tongoy Bay has become healthier over the years between 1992 and 2012, which confirms that fisheries management has maintained the system within sustainable boundaries under an ecosystem based-management (EBM) strategy (Garcia and Cochrane, 2005; Arkema et al., 2006; Levin et al., 2009). EBM indicators are conservative because they only changes in the cases of an ecosystem are strongly perturbed (Cury and Christensen, 2005). Likewise, surveillance macroscopic indicators can show when an ecosystem has changed and consequently provide operational indicators within a management context (Shephard et al., 2015). Our results show clearly that the benthic system achieved at least two extreme levels of maturity and development over the past 20 years. This situation would preclude the use of time series analysis to estimate flow control mechanisms (vulnerabilities) using dynamical predictions from ECOSIM, because this procedure assumes implicitly that the fishing would only lower the biomass of exploited species, while maintaining the overall properties of the ecosystem constant, which this study indicates is a questionable assumption.

Even though the compartments that propagated the most impacts to the other variables belonged mostly to the first and second trophic levels, both cores also include predator species, which agree – in general terms – with the keystone species complex derived for each model. In particular, the exploited crab *R. polyodon* in the 2012 model provoked higher quantitative impacts as compared to previous years, which could be explained at least by: (1) an increase of its abundance as response to a reduced harvest, and (2) this crab invokes a strong impact on other components and is also abetted by its cannibalism. Based on the KS_i index (sensu Libralato et al., 2006), phytoplankton appears to play an important role in the benthic system of Tongoy Bay, as can be expected for upwelling systems (Taylor et al., 2008). However, the keystone species complex

Table 4
Key species or group identified by different indices for the benthic ecosystem model of Tongoy Bay for 1992, 2002 and 2012.

Model keystone indexes	Species and/or functional groups Models		
	1992	2002	2012
K_i	*R. polyodon*	*R. polyodon*	*R. polyodon*
KS_i	Phytoplankton	Phytoplankton	Phytoplankton
$KS_{iEcosim\ 1}$ (bottom-up)	Bivalves	Seastars	*R. polyodon*
$KS_{iEcosim\ 1}$ (mixed)	Bivalves	Seastars	Bivalves
$KS_{iEcosim\ 1}$ (top-down)	Bivalves	*A. purpuratus*	Bivalves
$KS_{iEcosim\ 2}$ (bottom-up)	Phytoplankton	*A. purpuratus*	Seastars
$KS_{iEcosim\ 2}$ (mixed)	Phytoplankton	*A. purpuratus*	Seastars
$KS_{iEcosim\ 2}$ (top-down)	Bivalves	*A. purpuratus*	Seastars
KQ_{iLA1} (mixed)	*R. polyodon*	Bivalves	*A. purpuratus*
KQ_{iLA2} (mixed)	*R. polyodon*	Bivalves	*R. polyodon*

index (sensu Ortiz et al., 2013) simultaneously included phytoplankton, two filter feeders species (bivalve), and two top predators (the crab *R. polyodon* and seastar species), coinciding – in part – with Power et al. (1996), who described organisms belonging to different trophic levels as keystone species. Likewise, our results coincides in that the core is constituted by three linked trophic levels, as was described for other benthic system of northern Chile (Ortiz et al., 2013), suggesting a mixed control mechanism, that is, bottom-up and top-down forces acting simultaneously. Moreover, the mixed-flow control mechanism is considered to be more realistic, than bottom-up or top-down (Hunter and Price, 1992; Krebs et al., 1995; Masterson et al., 2008; Muhly et al., 2013). These findings suggest that the distinction between bottom-up and top-down control mechanisms constitutes a false dichotomy in the ecological sciences (Levins, 1998; Ulanowicz, 2009).

The macroscopic indexes estimated for the three trophic models (constructed with a similar number of compartments) improved our understanding about of the structure and dynamics of the benthic system of Tongoy Bay and identified changes in ecosystem health in response to disturbances (Rapport et al., 1998). The intensive fishing in Tongoy Bay before 1992 negatively impacted the ecosystem properties. Most of macroscopic indexes illustrate that this benthic system is now healthier than it was in 1992, which is consistent with the reduction of fishing pressure over the last 20 years. It is important to note that there were no ecosystem-level studies previous to 1992 that could have established how far the benthic system of Tongoy Bay is from a pristine condition. Although this study provides a synthetic analysis of the system-level trajectory of the Tongoy Bay benthic ecosystem, dynamical simulations should be performed to evaluate how the harvest scenarios and/or environmental conditions co-varies with changes in compartments (Levin et al., 2009; Akoglu et al., 2014). This is particularly relevant when the success of management options would depend on the magnitude of the disturbances and the thresholds that might return the ecosystem to historical conditions (Hobbs et al., 2009).

The models presented here were subject to the following simplifications: (1) our trophic analysis represents only the benthic communities. We believe, however, that the most relevant stocks and flows of energy and matter are reflected therein, and the models were built with a similar number of variables; (2) the benthic system of Tongoy Bay as analysed already was in an impacted state; (3) regardless of the well-known limitations of the ECOPATH software, the models constructed here adequately represent those processes driving the system over the short-term.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.04.019.

References

Aburto, J., Stotz, W., 2013. Learning about TURFs and natural variability: failure of surf clam management in Chile, Ocean. Coast. Manag. 71, 88–98.

Akoglu, E., Salihoglu, B., Libralato, S., Oguz, T., Solidoro, C., 2014. An indicator-based evaluation of Black Sea food web dynamics during 1960–2000. J. Mar. Syst. 134, 113–125.

Arkema, K.K., Abramson, S.C., Dewsbury, B.M., 2006. Marine ecosystem-based management: from characterization to implementation. Front. Ecol. Environ. 4 (10), 525–532.

Arreguín-Sánchez, F., Arcos, E., Chávez, E.A., 2002. Flows of biomass and structure in an exploited benthic ecosystem in the Gulf of California, Mexico. Ecol. Model. 156, 167–183.

Baird, D., McGlade, J.M., Ulanowicz, R.E., 1991. The comparative ecology of six marine ecosystems. Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 333 (1266), 15–29.

Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Mar. Ecol. Prog. Ser. 99, 221–237.

Boré, D., Blanco, J.L., Acuña, E., Moraga, J., Olivares, J., Mujica, A., Uribe, E., 1993. Evaluación de la distribución de recursos pelágicos de la IV Región y condiciones oceanográficas asociadas. Informe Técnico IFOP, Chile, Proyecto F.I.P, 57 pp.

Christensen, V., Pauly, D., 1993. Trophic models of aquatic ecosystems. In: ICLARM Conference Proceedings. No. 26, 390 pp.

Christensen, V., 1995. Ecosystem maturity – towards quantification. Ecol. Model. 77, 3–32.

Christensen, N., Bartuska, M., Brown, J., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J., MacMahon, J., Noss, R., Parsons, D., Peterson, C., Turner, M., Woodmansee, R., 1996. Report of the Ecological Society of American Committee on the scientific basis for ecosystem management. Ecol. Appl. 61 (3), 665–691.

Christensen, V., Walters, C.J., Pauly, D., 2005. Ecopath With Ecosim: A User's Guide. Fisheries Centre, University of British Columbia, Vancouver, 154 pp.

Costanza, R., Mageau, M., 1999. What is a healthy ecosystem? Aquat. Ecol. 33, 105–115.

Cruz-Escalona, V.H., Arreguín-Sánchez, F., Zetina-Rejon, M., 2007. Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model. Estuar. Coast. Shelf Sci. 72 (1), 155–167.

Cury, P.M., Christensen, V., 2005. Quantitative ecosystem indicators for fisheries management. ICES J. Mar. Sci. 62 (3), 307–310.

Daneri, G., Dellarossa, V., Quinones, 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.

Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theor. Biol. 56 (2), 363–380.

Fonseca, T., Farías, M., 1987. Estudio del proceso de surgencia en la costa chilena utilizando percepción remota. Invest. Pesq. 34, 33–46.

Gaichas, S., Skaret, G., Falk-Petersen, J., Link, J.S., Overholtz, W., Megrey, B.A., Gjøsæter, H., Stockhausen, W.T., Dommasnes, A., Friedland, K.D., Aydin, K., 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. Prog. Oceanogr. 81, 47–62.

Garcia, S.M., Cochrane, K.L., 2005. Ecosystem approach to fisheries: a review of implementation guidelines. ICES J. Mar. Sci. 62 (3), 311–318.

Grimm, V., Wissel, C., 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109, 323–334.

Gunderson, L.H., 2000. Ecological resilience – in theory and application. Annu. Rev. Ecol. Syst. 31, 425–439.

Heymans, J., 2003. Revised models for Newfoundland for the time periods 1985–87 and 1995–97. In: Johanna, J.H. (Ed.), Ecosystem Models of Newfoundland and Southeastern Labrador: Additional Information and Analyses for 'Back to the Future'. Fisheries Centre Research Reports, vol. 11, no. 1, 79 pp.

Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. Trends Ecol. Evol. 24 (11), 599–605.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.

Holling, C.S., 1987. Simplifying the complex: the paradigms of ecological function and structure. Eur. J. Oper. Res. 30, 139–146.

Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: bottom-up and top-down forces in natural communities. Ecology 73, 724–732.

Krebs, C.J., Boutin, S., Boonstra, R., Sinclair, A., Smith, J., Dale, M., Martin, K., Turkington, R., 1995. Impact of food and predation on the snow shore hare cycle. Science 269, 1112–1115.

Levin, P.S., Fogarty, M.J., Murawski, S.A., Fluharty, D., 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. PLoS Biol. 7 (1), 23.

Levins, R., 1998. Dialectics and systems theory. Sci. Soc., 375–399.

Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. Ecol. Model. 195, 153–171.

Lindeman, R.L., 1942. The trophodynamic aspect of ecology. Ecology 23, 399–418.

Mageau, M.T., Costanza, R., Ulanowicz, R.E., 1998. Quantifying the trends expected in developing ecosystems. Ecol. Model. 112 (1), 1–22.

Masterson, P., Arenas, F., Thompson, R.C., Jenkins, S.R., 2008. Interaction of top-down and bottom-up factors in intertidal rockpools: effects on early successional macroalgal community composition, abundance and productivity. J. Exp. Mar. Biol. Ecol. 363 (1–2), 12–20.

Mayer, L., Thurston, H.W., Pawlowski, C.W., 2004. The multidisciplinary influence of common sustainability indexes. Front Ecol. Environ. 2 (8), 419–426.

Monaco, M.E., Ulanowicz, R.E., 1997. Comparative ecosystem trophic structure of three US mid-Atlantic estuaries. Mar. Ecol. Prog. Ser. 161, 239–254.

Muhly, T., Hebblewhite, M., Paton, D., Pitt, J., Boyce, M., Musiani, M., 2013. Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. PLOS ONE, e64311.

Odum, E.P., 1969. The strategy of ecosystem development. Science 164, 262–270.

Ortiz, M., Wolff, M., 2002a. Trophic models of four benthic communities in Tongoy Bay (Chile): comparative analysis and assessment of management strategies. J. Exp. Mar. Biol. Ecol. 268 (2), 205–235.

Ortiz, M., Wolff, M., 2002b. Dynamical simulation of mass-balance trophic models for benthic communities of north-central Chile: assessment of resilience time under alternative management scenarios. Ecol. Model. 148 (3), 277–291.

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 ecosistema: 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 multispecies harvest scenario assessments. Aquat. Conserv. 20, 58–73.

Ortiz, M., Levins, R., Campos, L., Berrios, F., Campos, F., Jordán, F., Hermosillo, B., González, J., Rodriguez, F., 2013. Identifying keystone trophic groups in benthic ecosystems: implications for fisheries management. Ecol. Indic. 25, 133–140.

Ortiz, M., Berrios, F., Campos, L., Uribe, R., Ramirez, A., Hermosillo-Núñez, B., González, J., Rodriguez-Zaragoza, F., 2015. 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. Ecol. Model. 309, 153–162.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F., 1998. Fishing down marine food webs. Science 279 (5352), 860–863.

Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, ecosim, and ecospace as tools for evaluating ecosystem impact of fisheries. ICES J. Mar. Sci. 57, 697–706.

Petersen, J.K., Hansen, J.W., Laursen, M.B., Clausen, P., Carstensen, J., Conley, D.J., 2008. Regime shift in a coastal marine ecosystem. Ecol. Appl. 18 (2), 497–510.

Pikitch, E., Santora, C., Babcock, E., Bakuma, A., Bonfil, R., Cconover, 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.

Pitcher, T.J., Pauly, D., 1998. Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. In: Reinventing Fisheries Management. Springer, Netherlands, pp. 311–329.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. Bioscience, 609–620.

Rapport, D.J., Costanza, R., McMichael, A.J., 1998. Assessing ecosystem health. Trends Ecol. Evol. 13 (10), 397–402.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature 413 (6856), 591–596.

Sernapesca, 2013. Anuario Estadístico de Pesca. Ministerio de Economía Fomento y Reconstrucción, República de Chile, 115 pp.

Shephard, S., Greenstreet, S.P., Piet, G.J., Rindorf, A., Dickey-Collas, M., 2015. Surveillance indicators and their use in implementation of the Marine Strategy Framework Directive. ICES J. Mar. Sci., pfsv131.

Stotz, W., 2000. When aquaculture restores and replaces an overfished stock: is the conservation of the species assured? The case of the scallop Argopecten purpuratus in northern Chile. Aquacult. Int. 8 (2–3), 237–247.

Strayer, D., 1991. Notes on Lindeman's progressive efficiency. Ecology, 348–350.

Taylor, H., Wolff, M., Mendo, J., Yamashiro, C., 2008. Changes in trophic flow structure of Independence Bay (Peru) over an ENSO cycle. Prog. Oceanogr. 79, 336–351.

Troell, M., Pihl, L., Rönnbäck, P., Wennhage, H., Söderqvist, T., Kautsky, N., 2005. Regime Shifts and Ecosystem Services in Swedish Coastal Soft Bottom Habitats: When Resilience is Undesirable. Beijer International Institute of Ecological Economics.

Ulanowicz, R.E., 1986. Growth and Development: Ecosystems Phenomenology. Springer, New York, 203 pp.

Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5 (1), 7–16.

Ulanowicz, R.E., Norden, J.S., 1990. Symmetrical overhead in flow networks. Int. J. Syst. Sci. 21 (2), 429–437.

Ulanowicz, R.E., 1992. Ecosystem health and trophic flow networks. In: Ecosystem Health: New Goals for Environmental Management. Island Press, Washington, DC, pp. 190–206.

Ulanowicz, R.E., 1997. Ecology, the ascendent perspective. In: Complexity in Ecological Systems Series. Columbia University Press, New York, 201 pp.

Ulanowicz, R.E., Baird, D., 1999. Nutrient controls on ecosystem dynamics: the Chesapeake mesohaline community. J. Mar. Syst. 19, 159–172.

Ulanowicz, R.E., 2009. A Third Window: Natural Life Beyond Newton and Darwin. Templeton Foundation Press, West Conshohocken, PA.

Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessment. Rev. Fish Biol. Fish. 7, 139–172.

Walters, C.J., Martell, S.J., 2004. Fisheries Ecology and Management. Princeton University Press, U.S, 399 pp.

Wolff, M., Alarcón, E., 1993. Structure of a scallop Argopecten purpuratus (Lamarck, 1819) dominated subtidal macro-invertebrate assemblage in northern Chile. J. Shellfish Res. 12 (2), 295–304.

Wolff, M., 1994. A trophic model for Tongoy Bay – a system exposed to suspended scallop culture (Northern Chile). J. Exp. Mar. Biol. Ecol. 182, 149–168.

Wulff, F., Ulanowicz, R.E., 1989. A comparative anatomy of the Baltic Sea and Chesapeake Bay ecosystems. In: Network Analysis in Marine Ecology. Springer, Berlin Heidelberg, pp. 232–256.