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Application of loop analysis to benthic systems in northern Chile for the elaboration of sustainable management strategies

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ABSTRACT: The present contribution is an extension of the trophic models that we have previously designed for benthic communities in Tongoy Bay (north-central Chile). It represents the first attempt to use Levins' loop analysis in a complex harvested system along the Chilean coast. Ecological and extended eco-social models were developed for seagrass, sand-gravel and sand habitats in order to propose sustainable management strategies for the harvest of the red algae *Chondrocanthus chamissoi*, the scallop *Argopecten purpuratus*, the snail *Xanthochorus cassidiformis* and the crab *Cancer polyodon*. Based on Levins' loop analysis it was possible to estimate both the local stability (sustainability) for each of these model systems and to simulate the changes in the standing stocks of the main groups as response to external factors. Our results suggest that to increase the standing stocks of adult scallops the following man-made interventions should be implemented: (1) seagrass habitat: partial removal of the 3 sea star species *Luidia magallanica*, *Heliaster helianthus* and *Meyenaster gelatinosus*; and (2) sand-gravel habitat: seeding of scallop recruits and juvenile scallops, and removal of the sea star *H. helianthus* only. According to our results, the sand habitat would not support any harvest. The extended model for the seagrass and sand-gravel habitats were found sustainable only if the fishermen were 'self-damped', that is, when the fishing effort and fish quota were restricted. Even though loop analysis did not allow for explicit quantitative reasoning, 'what if' questions can be answered with sufficient understanding and realism. Therefore, this qualitative modelling appears as a valuable complementary mathematical tool defining and assessing the sustainability of management options within a holistic scope. We also recommend the application of this framework in other benthic management areas along the Chilean coast.

KEY WORDS: Feedback dominance · Loop analysis · Management · Scallop · Starfish · Sustainability · Upwelling

INTRODUCTION

A conceptual model aids in integrating our knowledge and improving our understanding of mechanisms underling a particular complex system of interest. In the past decades, a lot of theoretical and experimental attention has been given to the dominance of direct and indirect interactions and causality effects in determining the structure and functioning of natural communities and ecosystems (Levins 1974, Paine 1980, Patten 1985, Abrams 1991, Wissinger & McGrady 1993, Wootton 1994, Menge 1995, Fath & Patten 1999, Underwood 1999). Loop analysis is a robust theoretical framework used to assess the propagation of the direct and indirect effects in complex systems (Levins 1974, 1998a). Loop analysis has been applied successfully to

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several systems (Briand & McCauley 1978, Lane & Blouin 1985, Lane & Collins 1985, Lane 1986). Therefore, it appears to be an alternative modelling approach to analyse natural complex systems. Loop analysis offers the advantage that quantifiable and non-quantifiable variables, the relationships between ecological and social sciences, and the propagated effects of anthropogenic impacts to systems can be assessed. Additionally, loop analysis requires neither detailed exact equations nor voluminous measurements but instead focuses on the nominal character of the interactions (positive, negative or zero), the structure of the network, and the dominance of negative and positive feedbacks. In short, it sacrifices precision for generality and realism (sensu Levins 1966, 1993).

In previous studies, we have developed quantitative (steady-state and dynamical) mass-balance models for 4 different benthic habitats within southern Tongoy Bay, Chile (Wolff 1994, Ortiz & Wolff 2002a,b,unpubl.; see Fig. 1) using ECOPATH II (Christensen & Pauly 1992), ECOSIM and ECOSPACE software (Walters et al. 1997). Emergent properties of these webs were described and management policies such as to remove 'undesirable' predators that feed on commercially important species were proposed. The conclusions drawn from the models may be biased however as (1) harvest pressures operate selectively only on the adult size groups of the valuable species; (2) other types of ecological relationships were possibly missed (i.e. mutualism, amensalism, commensalism and com-

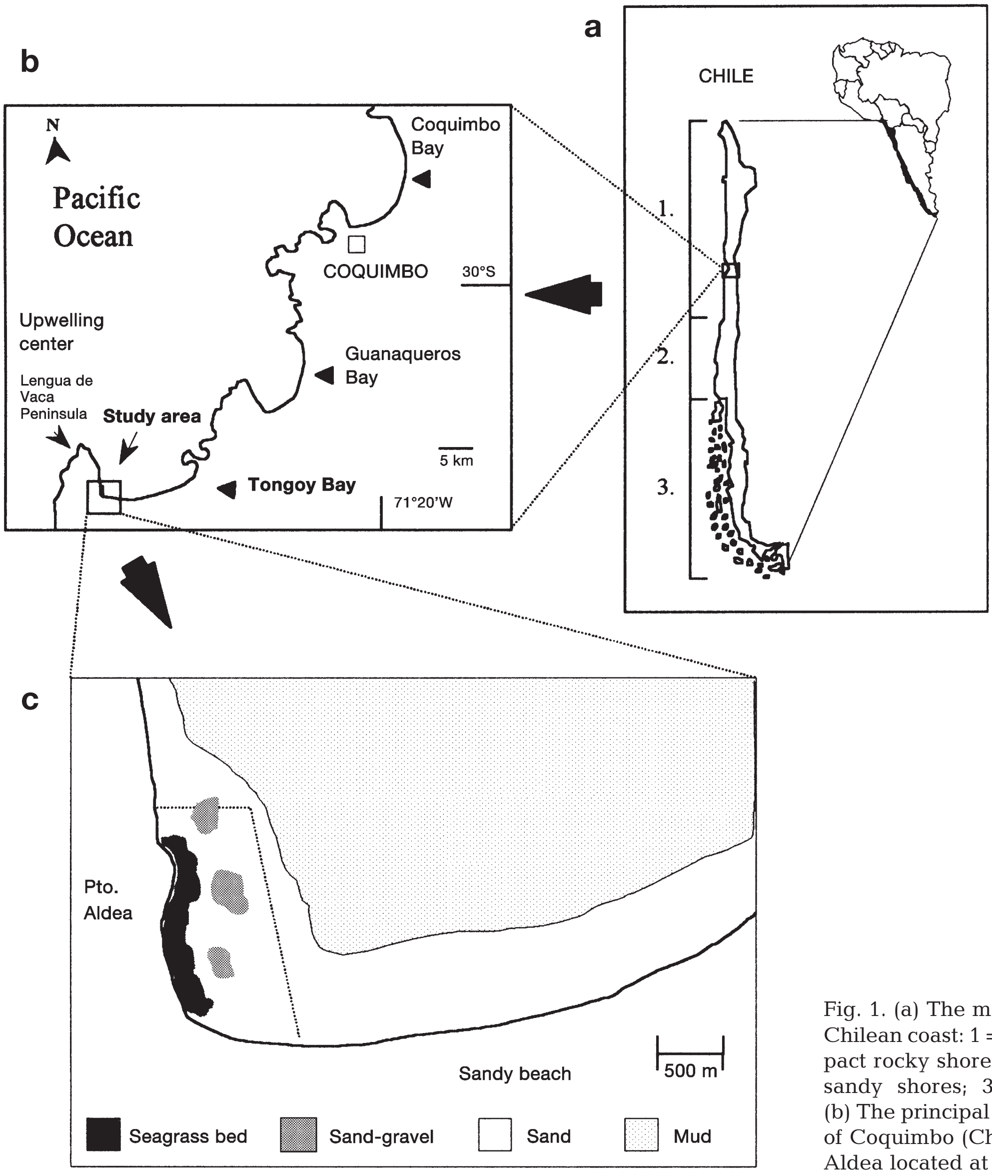

Fig. 1. (a) The main littoral types along of the Chilean coast: 1 = dominated by exposed compact rocky shores; 2 = dominated by exposed sandy shores; 3 = mostly insular systems. (b) The principal bay systems of the IV Region of Coquimbo (Chile). (c) Study area of Puerto Aldea located at southern part of Tongoy Bay

petition); and (3) the action of the fishermen from outside of these quantitative abstractions were considered.

The objectives of the present paper were, therefore, to expand the quantitative approaches given by Wolff (1994) and Ortiz & Wolff (2002a,b,unpubl.) using Levins' loop analysis theory and to include the activity of the fishermen. Hence, we assessed the sustainability (local stability) of the benthic habitats within southern Tongoy Bay and their response to alternative management scenarios or adaptive multispecies fisheries (sensu Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999).

MATERIALS AND METHODS

Description of the study area. The study area, Puerto Aldea (Fig. 1), is 1 of 168 fisheries management areas established along the Chilean coast (Castilla 2000). These areas are assigned to local fishermen associations to maximise the sustainable production and exploitation of commercial resources. In this area, several benthic habitats, based on depth, can be recognised: (1) seagrass meadows from 0 to 4 m depth; (2) sand and gravel between 4 and 10 m; (3) sand flats between 10 and 14 m; and (4) mud flats >14 m depth. A complete biotic and abiotic description of these habitats was provided by Jesse (2001). The bay and the benthic system of Puerto Aldea are protected from the prevailing southwest winds by the Lengua de Vaca peninsula. An upwelling centre near this peninsula is among the most important in northern Chile (Daneri et al. 2000), supplying nutrients to the ecosystem and simultaneously preventing stratification within the bay owing to intrusions of upwelled water. Surface water temperatures reach 13 and 17°C in winter and autumn, respectively (Jesse 2001). Four species are harvested: the red algae *Chondrocanthus chamissoi* (ca. 114 t yr^{-1}), the scallop *Argopecten purpuratus* (ca. 16 t yr^{-1}), the snail *Xanthochorus cassidiformis* (ca. 0.6 t yr^{-1}) and the crab *Cancer polyodon* (ca. 0.4 t yr^{-1}).

Loop analysis. Loop analysis expresses relationships between different components of a given system graphically. The relationships are shown as signs (+, – or 0), indicating the type of influence each variable has upon another. For instance, in ecological relationships, (+,–) denotes a predator-prey or parasite-host interaction, (–,–) represents competition between 2 species, while (+,+), (+, 0) and (–, 0) represent mutualism, commensalism and amensalism, respectively. Therefore, a complex system is shown graphically as a network of vertices (circles) and edges (arrows). Each variable is represented by a circle and edges represent the direction and type of interactions. Thus, if at one extreme there is an arrow, it means positive effect, while a circle means negative and zero means null effect.

A dynamical system that can be represented by a set of differential equations as:

$$\frac{dX_i}{dt} = f_i(X_1, X_2, \ldots, X_n; C_1, C_2, \ldots, C_n) \tag{1}$$

where X_n represent the variables and C_n the parameters, can be drawn as a signed digraph (see Figs. 2 to 5) in which the variables are the nodes or large circles, while the directed links or edges are the elements of the interaction coefficient matrix (community matrix coefficients). The link from X_j to X_i is similar to the α_{ij} in Levins' equation (1968):

$$\alpha_{ij} = \frac{\partial f_i(X)^*}{\partial X_j} \tag{2}$$

where * means evaluated at equilibrium.

The element of the graph representing the link from i to j is signum (α_{ij}) where the function signum (X) is 1 when $X > 0$, 0 when $X = 0$, and –1 when $X < 0$.

A path is a series of links from 1 variable through 1 or more remaining variables, without crossing any variable twice. A loop is any closed path, which returns to its starting point, not crossing any intermediate variable twice. The length of a loop is defined by the number of variables the path enters. A self-loop is a loop that starts and ends on the same variable (without passing through any other variable) and hence, it is of length 1. A negative self-loop is called 'self-damping' and a positive self-loop is termed 'self-enhancing'. The value of a path or loop is the product of the signs of the interaction coefficients (α_{ij}). If the values of the coefficients are known, then a number can be obtained. There is usually more than 1 and often many loops in a signed digraph. Loops that have at least 1 variable in common are termed 'conjunct loops', while those that have no variables in common are 'disjunct loops'.

Local stability properties. Feedback at level k, where k is the number of variables, is calculated by:

$$F_k = \sum_{m=1}^{k} (-1)^{m+1} L(m,k) \tag{3}$$

and $L(m,k)$ is the product of m disjunct loops whose combined total length is k. Feedback has the same value as the determinant of order k in the interaction coefficient matrix. In other words, F_k is the coefficient of the $(n - k)^{\text{th}}$ term in the characteristic polynomial equation. The feedback for each level can be calculated by the estimation of the characteristic polynomial related to the interaction matrix, where the polynomial now can be written in terms of the feedback notation as: $F_0\lambda^n + F_1\lambda^{n-1} + F_2\lambda^{n-2} + \ldots + F_{n-1}\lambda + F_n = 0$. For more details see Puccia & Levins (1985: p 162–164). Local stability, as determined by the Routh-Hurwitz criteria, translates into loop terms as Criterion 1: $F_k < 0$, for all k. That is, the negative feedback at every level must exceed the positive feedback; Criterion 2: negative feedback at the higher levels cannot be too much larger than negative feedback at the lower levels in order to conserve the qualitative stability properties of the systems. This condition is a sequence of inequalities which are related to oscillation trajectory. The general expression for this condition is the following: $F_{n-2}\,F_{n-1} + F_{n-3}\,F_n > 0$, where F_n is the feedback of the entire system (n = total number of variables in the system). It is assumed that the system is locally stable when F_n is negative. The stronger the negative feedback F_n, the greater the resistance to external changes (Levins 1998a). Based on this local stability criterion, it is possible to estimate the sustainability of the system and simultaneously explore strategies of stabilisation.

Qualitative predictions. If the parameters (C_n in Eq. 1) of the system are changing slowly enough for the variables to track the movement of the equilibrium, then the equilibrium values of the variables, which are changing in magnitude, and the direction of that change can be evaluated by:

$$\frac{\partial X_i}{\partial C_h} = \frac{\sum \frac{\partial f_j}{\partial C_h} \cdot \sum_k P_{ij}^{(k)} \cdot F_{n-k}^{(\mathrm{comp})}}{F_n} \qquad (4)$$

where C_h is the h^{th} parameter that is changing because of an environmental impact ('impact entering at h'); $\partial f_i / \partial C_h$ is the effect of C_h parameter change on the state of the j^{th} variable; $p_{ij}^{(k)}$ is the path from the j^{th} to the i^{th} variable and includes k variables; $F_{n-k}^{(\mathrm{comp})}$ is the feedback of the complementary subsystem. This subsystem is formed by those variables not on the path of $p_{ij}^{(k)}$; and F_n is the feedback of the whole system, which integrates all variables of the system.

When the complementary subsystem feedback and the feedback of the whole system have the same sign, the effect of a parameter change is the same as the sign of the product of the path. Feedback of opposite sign reverses the effects of the path. In other words, the disjunct and complementary feedback loops are one way to capture simultaneously the propagation of direct and indirect effects into the systems during the estimation of qualitative local stability and predictions.

Selection of boundaries and conceptual models. ***Seagrass habitat:*** Based on the available information given by Wolff (1994), León (2000), Jesse (2001), Ortiz & Wolff (2002a) and Ortiz et al. (unpubl.), 2 conceptual models integrating biological variables as well as the fishers were enunciated. The first represents an ecological approach constituted by 15 variables (see Table 1). Even though depredation was the predominant ecological interaction, other relevant relationships such as mutualism, commensalism, amensalism and competition were also captured by the model. The positive effect (refuge and structure) of seagrass on recruits, juveniles and adults of *Argopecten purpura-*

Table 1. Community matrix for the seagrass habitat. The nominal effect of *j* species on *i* species is shown. This model is constituted by the following 15 variables: 3 age classes for the scallops *Argopecten purpuratus*, adults (*ApA*), juveniles (*ApJ*) and the recruits (*ApR*), and 2 classes for the crab *Cancer polyodon*, adults (*CpA*) and juveniles (*CpJ*), the seagrass *Heterozostera tasmanica* (*Ht*), microbial film (*MF*), primary productivity (*PP*), infauna (*I*), small and large epifauna (*SE* and *LE*), the crab *Paraxanthus barbiger* (*Pb*), the sea starfishes *Meyenaster gelatinosus* (*Mg*), *Heliaster helianthus* (*Hh*) and *Luidia magallanica* (*Lm*), and the fishermen (*F*). Infauna (*I*) includes polychaeta and buried bivalves, *SE* comprises other molluscs such as *Turritella cingulata*, *Nasarius gayi*, *Mitrella unifasciata*, *Nucula pisum* and *Chiton* spp., and *LE* includes other crabs species such as *Hepatus chilense*, *Platymera gaudichaudi* and *Gaudichaudia gaudichaudia*

									j								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
		ApA	*ApJ*	*ApR*	*PP*	*MF*	*I*	*CpJ*	*CpA*	*SE*	*Ht*	*Lm*	*Hh*	*Mg*	*LE*	*Pb*	*F*
	ApA	0	+	+	+	+	0	0	–	0	+	0	–	–	–	–	–
	ApJ	0	0	+	+	+	0	0	–	0	+	0	–	–	–	–	0
	ApR	+	0	–	+	+	0	–	0	–	+	0	0	0	0	0	0
	PP	–	–	–	+	0	–	0	0	0	0	0	0	0	0	0	0
	MF	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	0
	I	0	0	0	+	+	–	–	0	–	+	–	0	0	–	0	0
	CpJ	0	0	+	0	0	+	–	–	+	+	0	0	0	–	–	0
i	*CpA*	+	+	0	0	0	0	+	0	+	0	0	0	0	+	+	–
	SE	0	0	+	0	0	+	–	–	0	+	0	–	–	–	–	0
	Ht	0	0	0	0	+	0	0	0	0	–	0	0	0	0	0	0
	Lm	0	0	0	0	+	+	0	0	0	–	0	–	–	0	0	0
	Hh	+	+	0	0	0	0	0	0	+	–	+	0	–	0	0	0
	Mg	+	+	0	0	0	0	0	0	+	–	+	–	0	0	0	0
	LE	+	+	0	0	0	+	–	–	+	0	0	0	0	0	–	0
	Pb	+	+	0	0	0	0	+	–	+	0	0	0	0	+	0	0
	F	+	0	0	0	0	0	0	+	0	0	0	0	0	0	0	(–)(+)

tus (*ApR*, *ApJ* and *ApA*), infauna (*I*) and small epifauna (*SE*) was considered; this has previously been described for other comparable systems and species (e.g. Pohle et al. 1991, Connolly 1997, Reusch 1998, Bell et al. 1999, Bologna & Heck 1999, Edgar 1999, Rose et al. 1999, Lee et al. 2001). Furthermore, a negative influence or resistance that seagrass (*Ht*) exerts on the mobility of 3 sea star species (*Mg*, *Hh* and *Lm*) was postulated. The microbial film (*MF*) was considered to be positively influenced by faeces of all organisms and to exert a positive effect as food source for filter feeders (*ApR*, *ApJ* and *ApA*) (sensu Prieur et al. 1990), infauna (Kemp 1986, Plante et al. 1989, Grossmann & Reichardt 1991, Plante & Mayer 1994, Plante & Shriver 1998) and equinodermata (Findlay & White 1983). The increase of seagrass productivity due to biodeposition of faecal material of filter feeders (Bertness 1984, Reusch et al. 1994, Peterson & Heck 1999, 2001) can also be depicted by mutualistic relationships between scallops, *MF* and *Ht*. Interrelations within the scallop are conceptualised as follows: *ApR* exerts a positive influence on *ApJ* which in turn exerts a positive influence on *ApA*, whereas *ApR* and *ApA* are connected by a mutualistic interaction. These relationships are similar to those described in population models (Caswell 1989). *ApA* was considered self-enhanced as it supports an intensive harvest. In contrast, both classes of the crab *Cancer polyodon* (adults *CpA* and juveniles *CpJ*) are represented by a prey-predator interaction due to the known cannibalism (Wolff & Cerda 1992). *ApR* and *CpJ* are self-damped due to the environmental constraints on their survival. The seagrass (*Ht*), infauna (*I*) and microbial film (*MF*) are considered self-damped due to substrate limitations. Primary production (*PP*) is self-enhanced because it is assumed that under upwelling regimes there is no nutrient limitation. Two negative interactions (aggressive competition) between *CpJ* and large epifauna (*LE*) (Jesse 2001) and mutual feeding of *Mg* and *Hh* were also considered (M. Ortiz pers. obs.). External (man-made) positive impacts on *ApJ* and *ApR*, and negative ones on *Lm*, *Hh* and *Mg* were assumed (Fig. 2). These external disturbances represent alternative management scenarios to increase the standing stock of *ApA*.

The second model was expanded by integrating the fishermen (*F*) as a variable, which act upon *ApA* and *CpA* through harvest. However, only the *ApA* suffers intensive fishery. It is important to note that *ApA* was not self-enhanced in this model, as fishermen (*F*) were included. The sustainability of the following 5 management scenarios was estimated: [A] increasing the standing stocks of juvenile scallops (*ApJ*); [B] increasing the standing stock of recruits (*ApR*); and [C], [D] and [E] partial removal of the starfish predators *Lm*, *Hh* and *Mg*, respectively. The changes in the variables under an external positive impact on *F* were estimated (Fig. 3).

Sand-gravel habitat: Our ecological model contains 20 variables (Table 2). The same size-classes of scallops and the crab *Cancer polyodon* were considered (*ApR*, *ApJ*, *ApA*, *CpJ* and *CpA*). The self-dynamics for *ApR*, *CpR*, *I*, *PP* and *MF* were as described in the seagrass model. The mollusc *Calyptraea trochiformis* (*Ct*) and the sea squirt *Pyura chilensis* (*Pch*) were considered self-damped due to their sessile life and substrate constraints. Small and large epifauna (*SE* and *LE*) with the same dynamics as described in the seagrass model were also considered. The crab *Paraxanthus barbiger* (*Pb*) was considered self-enhanced because significant seasonal changes in abundance for this species were detected (Ortiz et al. unpubl.). The interactions among the age classes for *Ap* and *Cp* were as described for the seagrass habitat. *ApA* and *CpA* were assumed self-enhanced due to harvest. The red algae *Chondrocanthus chamissoi* (*Chch*), other macroalgae (*OM*: other rhodophytas and *Ulva* sp.) and the herbivorous snail *Tegula* sp. (*T* sp) were also included. *Chch* and *OM* were self-enhanced due to significant seasonal changes in biomass. *Chch* is also intensively harvested. Besides depredation other interactions were also postulated. The substrate (*S*) was assumed to exert a positive effect on *Ct*, *Pch*, *Chch* and *OM* as available substrate. Moreover, a positive effect as available refuge for *CpJ* was considered. *Pch* exerts a negative effect on *Ct* because it overgrows *Ct*. Both *Pch* and *Ct* offer available substrate for *Chch* and *OM*. The changes in equilibrium levels of all variables in this community under external positive impacts on *ApJ*, *ApR*, *S* and negative on *Lm*, *Hh*, *Mg* were estimated. These external disturbances represent alternative management options to increase the standing stock of *ApA* and *Chch*.

An expanded model integrating the fishers (*F*) who harvest on *ApA*, *Chch* and *CpA* was enunciated and the sustainability of the following management scenarios was assessed: [A] increasing the standing stock of juvenile scallops (*ApJ*); [B] increasing the standing stock of recruits (*ApR*); [C], [D] and [E] partial removal of the predatory starfish species *Lm*, *Hh* and *Mg*, respectively; and [F] increase the available substrate (artificial) for increasing algae settlement. The changes in the variables under an external positive impact on *F* were estimated (Fig. 4).

Sand habitat: The ecological model was constructed with 13 variables (Table 3). Juvenile- and adult-size classes for the crab *Cancer coronatus* (*CcJ* and *CcA*) and for the sand mussel *Mulinia* sp. (*MJ* and *MA*) were considered. Both classes of *C. coronatus* were connected as prey-predator pair due to cannibalism (Jesse 2001) and the classes of *Mulinia* sp. were connected by a mutualistic relationship. The crab *C. polyodon* (*Cp*), the snail *Xanthochorus cassidiformis* (*Xc*) and the starfishes *Meyenaster gelatinosus* (*Mg*) and *Luidia magallanica* (*Lm*), the small and large epifauna, infauna, primary productivity and microbial film (*SE*, *LE*, *I*, *PP* and *MF*) were also included. *MF*, *I* and *PP* were assumed under a similar self-dynamic to the other habitats based on the same explanation. A self-enhanced dynamic

Table 2. Community matrix for the sand-gravel habitat. The nominal effect of *j* species on *i* species is shown. This model includes the following 21 variables: 3 size classes for the scallops and the crab *Cancer polyodon* (*ApA*, *ApJ*, *ApR*, *CpA* and *CpJ*), the mollusc *Calyptraea trochiformis* (*Ct*), the sea squirt *Pyura chilensis* (*Pch*), small and large epifauna (*SE* and *LE*), infauna (*I*), primary productivity (*PP*), microbial film (*MF*), the crab *Paraxanthus barbiger* (*Pb*), the sea starfishes *Meyenaster gelatinosus* (*Mg*), *Luidia magallanica* (*Lm*) and *Heliaster helianthus* (*Hh*), the red algae *Chondrocanthus chamissoi* (*Chch*), other macroalgae (*OM*) (other rodophytas and *Ulva* sp.), the herbivorous snail *Tegula* sp. (*T* sp), artificial substrate (*S*) and the fishermen (*F*)

											j										
		1 *ApA*	2 *ApJ*	3 *ApR*	4 *PP*	5 *S*	6 *Ct*	7 *CpJ*	8 *CpA*	9 *Pch*	10 *OM*	11 *Chch*	12 *I*	13 *SE*	14 *LE*	15 *MF*	16 *Tsp*	17 *Pb*	18 *Lm*	19 *Hh*	20 *Mg*	21 *F*
	ApA	0	+	+	+	0	0	0	–	0	0	0	0	0	–	+	0	–	0	–	–	–
	ApJ	0	0	+	+	0	0	0	–	0	0	0	0	0	–	+	0	–	0	–	–	0
	ApR	+	0	–	+	0	0	–	0	0	0	0	0	–	0	+	0	–	0	0	0	0
	PP	–	–	–	+	0	–	0	0	–	0	0	–	0	0	0	0	0	0	0	0	0
	S	0	0	0	0	–	–	0	0	–	–	–	0	0	0	0	0	0	0	0	0	0
	Ct	0	0	0	+	+	–	0	–	–	0	0	0	0	–	+	0	–	0	–	–	0
	CpJ	0	0	+	0	+	0	–	–	0	+	+	+	+	–	0	+	–	0	0	0	0
	CpA	+	+	0	0	0	+	+	0	+	0	0	0	+	+	0	+	+	0	0	0	–
	Pch	0	0	0	+	+	+	0	0	–	0	0	0	0	–	+	0	–	0	–	–	0
	OM	0	0	0	0	+	+	0	0	+	+	–	0	–	–	0	–	–	0	0	0	0
i	*Chch*	0	0	0	0	+	+	0	0	+	0	0	0	–	–	0	–	–	0	0	0	–
	I	0	0	0	+	0	0	–	0	0	0	0	–	–	–	+	0	–	–	0	0	0
	SE	0	0	+	0	0	0	–	–	0	+	+	+	0	–	0	0	–	0	–	–	0
	LE	0	+	0	0	0	+	+	–	+	+	+	+	+	0	0	+	–	0	0	0	0
	MF	+	+	+	+	0	+	+	+	+	0	0	+	+	+	–	+	+	+	+	+	0
	Tsp	0	0	0	0	0	0	0	–	0	+	+	+	0	–	0	0	–	0	–	–	0
	Pb	+	+	+	0	+	+	0	–	+	+	+	+	+	+	0	+	+	0	0	0	0
	Lm	0	0	0	0	0	0	0	0	0	0	0	+	0	0	+	0	0	0	–	–	0
	Hh	+	+	0	0	0	+	0	0	+	0	0	0	+	0	0	+	0	+	0	–	0
	Mg	+	+	0	0	0	+	0	0	+	0	0	0	+	0	0	+	0	+	+	0	0
	F	+	0	0	0	0	0	0	+	0	0	+	0	0	0	0	0	0	0	0	0	(–)(+)

Table 3. Community matrix for the sand habitat. The nominal effect of *j* species on *i* species is shown. This model comprises the following 14 variables: 2 age classes for the crab *Cancer coronatus*, adults (*CcA*) and juveniles (*CcJ*), and also 2 classes for the sand mussel *Mulinia* spp., adults (*MA*) and juveniles (*MJ*), the crab *C. polyodon* (*Cp*), the predator snail *Xantochorus cassidiformis* (*Xc*), the sea starfishes *Meyenaster gelatinosus* (*Mg*) and *Luidia magallanica* (*Lm*), small and large epifauna (SE, LE), infauna (*I*), primary productivity (PP), microbial film (MF) and the fishermen (*F*)

								j							
		1 *CcA*	2 *CcJ*	3 *Cp*	4 *Mg*	5 *Lm*	6 *MF*	7 *SE*	8 *LE*	9 *PP*	10 *I*	11 *MJ*	12 *MA*	13 *Xc*	14 *F*
	CcA	+	+	–	0	0	+	+	+	0	+	+	+	+	0
	CcJ	–	–	–	0	0	+	+	–	0	+	+	0	0	0
	Cp	+	+	0	0	0	0	+	+	0	0	0	+	+	–
	Mg	0	0	0	0	+	+	+	0	0	0	0	0	+	0
	Lm	0	0	0	0	0	+	0	0	0	+	+	+	0	0
	MF	+	+	+	+	+	–	+	+	+	+	+	+	+	0
i	SE	–	–	–	–	0	0	0	–	0	+	0	0	–	0
	LE	–	+	–	0	0	0	+	0	0	+	+	+	+	0
	PP	0	0	0	0	0	0	0	0	+	–	–	–	0	0
	I	–	–	0	0	–	+	–	–	+	–	0	0	–	0
	MJ	0	–	0	0	0	+	–	–	+	0	–	+	–	0
	MA	–	0	–	0	–	+	–	–	+	0	+	–	–	0
	Xc	–	0	–	–	0	+	+	–	0	+	+	+	0	–
	F	0	0	+	0	0	0	0	0	0	0	0	0	+	(–)(+)

was consisdered for *Cp* and *Xc* due to harvest pressure, and for *CcA* because this group presents relevant seasonal migration between sand habitat and deeper systems (Jesse 2001). *CcJ* were considered self-damped due to the environmental constraints on their survival, and *MJ* and *MA* due to their semi-sessile behaviour and substrate limitations. Depredation predominated in this ecological model. The changes in the equilibrium standing stocks of the variables as response to negative external perturbations on *Lm*, *Mg* and *MA* were assessed. Both represent alternative management strategies.

The extended model includes the fishermen (*F*) who harvest on *Cp* and *Xc*. The sustainability of the following 3 management scenarios was evaluated: [A] and [B] represent the partial removal of the sea starfish species *Mg* and *Lm*, respectively; and [C] represents the eventual harvest on *MA*. Therefore, Strategies [A] and [B] represent attempts to increase the standing stocks of *Xantochorus cassidiformis* and *Mulinia* sp., respectively (Fig. 5). The qualitative change in the variables under an external negative impact on *F* was estimated.

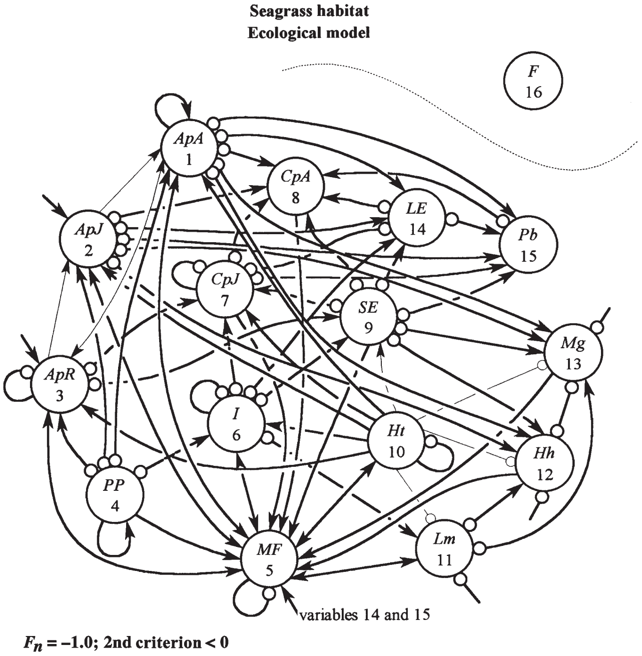

Fig. 2. Ecological model of seagrass community. Holistic sustainability measures (F_n and 2nd criterion). See 'Materials and methods' for more details. Note that only ecological variables are connected. Thin lines indicate postulated relationships based on limited data

RESULTS

Seagrass habitat

Fig. 2 shows the conceptual ecological model for the seagrass habitat. Loop analysis performed on this system indicated that it is not entirely stable because just the first criterion of stability was reached (F_n = –1.0; 2nd criterion < 0). This means that although the system is locally stable, it will oscillate around an equilibrium after disturbance. In regard to the qualitative predictions, positive impacts on the juvenile (*ApJ*) and recruit (*ApR*) scallops, which would correspond to an eventual seeding programme, would produce an unexpected negative effect on the standing stocks of the scallop adults *ApA* (Table 4a). Likewise, a positive impact on *ApJ* would promote the increase of equilibrium values of the 3 sea starfish species. On the other hand, a removal of the 3 sea starfish species would increase the standing stocks of the adult scallops, the crab *Cancer polyodon* (*CpA*) and the *SE* (Table 4a).

Table 4. (a) Qualitative predictions in the equilibrium values (standing stocks) of all variables in the ecological model of seagrass habitat as response to positive external impact on the recruits (*ApR*) and juveniles (*ApJ*) of the scallop *Argopecten purpuratus*, and negative impact on the sea starfish species *Luidia magallanica* (*Lm*), *Heliaster helianthus* (*Hh*) and *Meyenaster gelatinosus* (*Mg*). (b) Qualitative predictions in the ecosocial model of seagrass habitat as response to positive impact on fishermen (*F*)

(a)	Responses														
Input to	*ApA*	*ApJ*	*ApR*	*PP*	*MF*	*I*	*CpJ*	*CpA*	*SE*	*Ht*	*Lm*	*Hh*	*Mg*	*LE*	*Pb*
(+) *ApJ*	–	+	–	–	+	+	+	–	–	+	+	+	+	–	+
(+) *ApR*	–	+	0	0	+	0	0	0	0	0	0	0	0	0	0
(–) *Lm*	+	–	+	+	–	–	+	+	+	–	–	–	–	–	–
(–) *Hh*	+	–	+	+	–	–	0	+	+	–	–	0	–	0	–
(–) *Mg*	+	–	+	+	–	–	0	+	+	–	–	–	0	0	–

(b)	Responses															
Input to	*ApA*	*ApJ*	*ApR*	*PP*	*MF*	*I*	*CpJ*	*CpA*	*SE*	*Ht*	*Lm*	*Hh*	*Mg*	*LE*	*Pb*	*F*
(+) *F*(–)	+	–	–	+	–	+	+	–	–	–	–	+	+	–	+	–
(+) *F*(+)	–	+	+	–	+	–	–	+	+	+	+	–	–	+	–	+

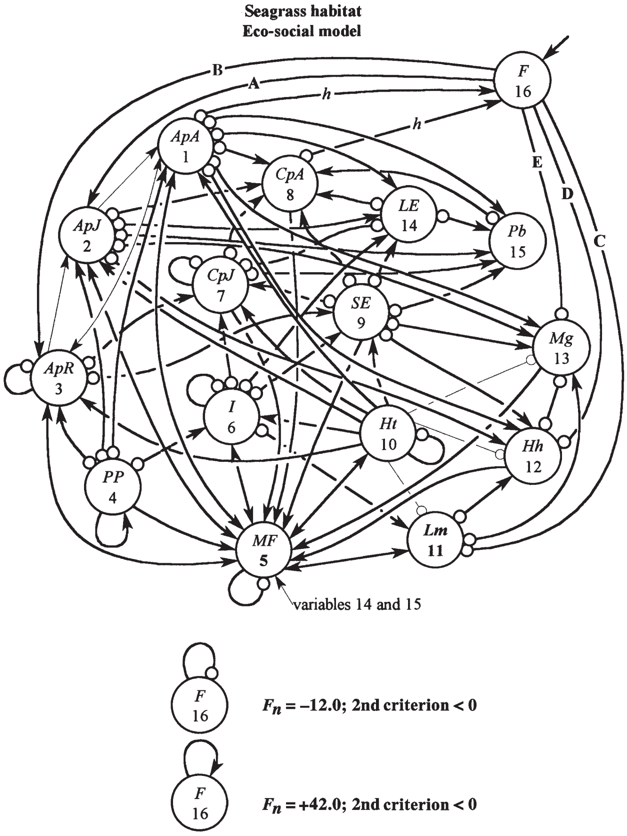

Fig. 3. Ecosocial expanded model of seagrass habitat. Holistic sustainability measures (F_n and 2nd criterion) under 2 fishermen self-dynamics. [A], [B], [C], [D] and [E] management scenarios and *h* is harvest. Thin connections indicate postulated relationships based on limited data

The expanded model is illustrated in Fig. 3. The sustainability of the system strongly depends on the dynamical behaviour of *F*. The sustainability of the system (both criteria) under just fishery activity on *ApA* and *CpA* is reached only if the fishers are self-damped (Fig. 3). Likewise, all other management scenarios explored are only sustainable when *F* is self-damped. The highest sustainability (F_n = –118.0; 2nd criterion > 0) is obtained when all scenarios are simultaneously applied. On the contrary, Scenario [B] presented the smallest local stability (Table 5). An expected decrease in the standing stock of *ApA* is only avoided if *F* is self-damped (Table 4b).

Sand-gravel habitat

The ecological model for this habitat was also found to be only partially sustainable, because only the first criterion of stability was reached (F_n = –96.0; 2nd criterion < 0). An eventual positive external impact on both *ApR* and *ApJ* increases the standing stock of adult scallops *ApA* (Table 6a), while an increase of the available substrate (*S*) does not produce the expected positive effect on the abundance of the commercial red algae *Chondrocanthus chamissoi* (*Chch*). Removal of the sea starfishes *Lm* and *Hh* has a positive direct effect on the *ApA* and a positive indirect effect on the *Chch*. On the other hand, removal of *Meyenaster gelatinosus* (*Mg*) decreases the standing stock of *ApA*. Only a depletion of *Hh* increases the standing stock of the exploited crab *CpA* (Table 6a).

Fig. 4 illustrates the expanded model for the sand-gravel habitat. The harvest on *Chch*, *ApA* and *CpA* met the local stability criteria only when the fishers were self-damped. However, the sustainability for all management scenarios was not obtained. In decreasing order Scenarios [E], [D]+[E], [B]+[E] and [A]+[E] would be the most sustainable patterns of exploitation. Contrary, the Fishing Scenarios [A]+[B]+[C]+[D]+[F] would transform the system into a highly unsustainable one (Table 7). The self-damped dynamic of *F* in this model is not a sufficient condition to buffer the external positive perturbation on itself (Table 6b).

Table 5. Holistic sustainability measures (F_n and 2nd criterion) in the ecosocial model of seagrass habitat under 2 fishermen self-dynamics. Management scenarios: [A] increasing the standing stock of juveniles scallops (*ApJ*); [B] increasing the standing stock of recruit scallops (*ApR*); [C], [D] and [E] partial removal of the sea starfish *Luidia magallanica* (*Lm*), *Heliaster helianthus* (*Hh*) and *Meyenaster gelatinosus* (*Mg*), respectively

Sustainability assessment in the seagrass habitat

Management	Fishermen dynamic	
	Self-damped F_n; 2nd criterion	Self-enhanced F_n; 2nd criterion
[A]	(–) 94.0; > 0	(–) 40.0; > 0
[B]	(–) 8.0; > 0	(+) 46.0; < 0
[C]	(–) 30.0; > 0	(+) 24.0; < 0
[D]	(–) 17.0; > 0	(+) 37.0; < 0
[E]	(–) 17.0; > 0	(+) 37.0; < 0
[A]+[B]	(–) 90.0; > 0	(–) 36.0; > 0
[A]+[C]	(–) 112.0; > 0	(–) 58.0; < 0
[A]+[D]	(–) 99.0; > 0	(–) 45.0; > 0
[A]+[E]	(–) 99.0; > 0	(–) 45.0; > 0
[B]+[C]	(–) 26.0; > 0	(+) 28.0; < 0
[B]+[D]	(–) 13.0; > 0	(+) 41.0; < 0
[B]+[E]	(–) 13.0; > 0	(+) 41.0; < 0
[C]+[D]	(–) 35.0; > 0	(+) 19.0; > 0
[C]+[E]	(–) 35.0; > 0	(+) 19.0; > 0
[D]+[E]	(–) 22.0; > 0	(+) 32.0; < 0
[A]+[B]+[C]	(–) 108.0; > 0	(–) 54.0; < 0
[A]+[B]+[D]	(–) 95.0; > 0	(–) 41.0; > 0
[A]+[B]+[E]	(–) 95.0; > 0	(–) 41.0; > 0
[A]+[B]+[C]+[D]	(–) 113.0; > 0	(–) 59.0; < 0
[A]+[B]+[C]+[E]	(–) 113.0; > 0	(–) 59.0; < 0
[A]+[B]+[C]+[D]+[E]	(–) 118.0; > 0	(–) 64.0; < 0

Table 6. (a) Qualitative predictions in the equilibrium values (standing stocks) of all variables in the ecological model of sand-gravel habitat as response to positive external on the recruits (*ApR*) and juveniles (*ApJ*) scallops and substrate (*S*), and negative on the sea starfish species *Lm*, *Hh* and *Mg*. (b) Qualitative predictions in the ecosocial model of sand-gravel model as response to positive impact on fisherman (*F*)

(a)	Responses																			
Input to	*ApA*	*ApJ*	*ApR*	*PP*	*S*	*Ct*	*CpJ*	*CpA*	*Pch*	*OM*	*Chch*	*I*	*SE*	*LE*	*MF*	*Tsp*	*Pb*	*Lm*	*Hh*	*Mg*
(+) *ApJ*	+	–	+	+	+	+	+	–	+	–	–	+	+	+	–	–	–	–	+	–
(+) *ApR*	+	–	0	0	0	0	0	0	0	0	0	0	0	+	0	0	–	0	0	0
(+) *S*	+	–	–	+	+	–	–	+	+	–	–	+	+	+	–	–	–	–	+	–
(–) *Lm*	+	–	+	+	+	+	+	–	–	+	+	–	+	+	–	–	+	–	+	–
(–) *Hh*	+	–	+	+	+	–	+	+	–	+	+	+	+	+	–	–	–	–	+	–
(–) *Mg*	–	+	–	–	–	+	–	–	+	–	–	–	–	–	+	+	+	+	–	+

(b)	Responses																				
Input to	*ApA*	*ApJ*	*ApR*	*PP*	*S*	*Ct*	*CpJ*	*CpA*	*Pch*	*OM*	*Chch*	*I*	*SE*	*LE*	*MF*	*Tsp*	*Pb*	*Lm*	*Hh*	*Mg*	*F*
(+) *F*(–)	+	+	–	+	–	–	–	+	+	–	+	+	+	–	–	–	+	–	–	+	+
(+) *F*(+)	–	–	+	–	+	+	+	–	–	+	–	–	–	+	+	+	–	+	+	–	–

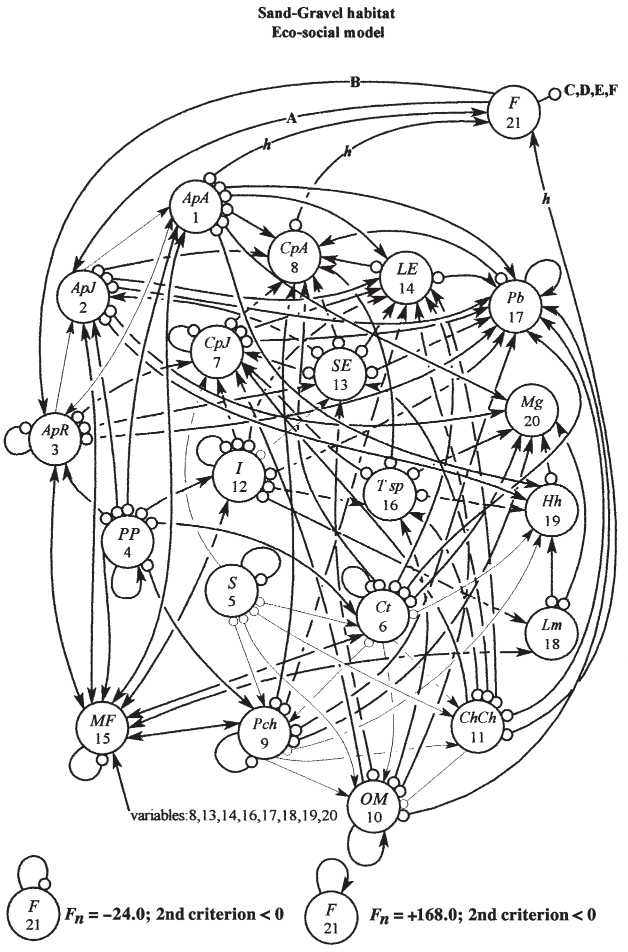

Fig. 4. Ecosocial model of sand-gravel habitat. Holistic sustainability measures (F_n and 2nd criterion) under 2 fishermen self-dynamics. [A] to [F] are management scenarios and *h* is harvest. Thin connections indicate postulated relationships based on limited data

Sand habitat

The ecological model of this habitat is not locally stable ($F_n = 56.0$; 2nd criterion < 0). In regard to the qualitative changes in the variables as response to external impacts on the sea starfish species, a negative perturbation on *Mg* produces a negative direct effect on the snail *Xc* and negative indirect impact on the crab *Cp*, whereas both classes of sand mussel increase. On the other hand, a negative impact on *Luidia magallanica* (*Lm*) produces opposite effects on the same species (Table 8a), whereas a negative impact on *MA* would decrease its standing stock (Table 8a).

The expanded model is shown in Fig. 5. No sustainability was found for any of the management scenarios explored (Table 9). However, a positive external perturbation impact on *F* does not show a qualitative change on itself and the exploited species would be positively affected (Table 8b).

DISCUSSION

Models for 3 exploited complex benthic systems of Tongoy Bay (northern Chile) were analysed by Levins' (1974, 1998a) loop analysis. Despite the fact that some relationships are based on limited data or comparisons of similar species in other areas, the conceptual models presented here can be considered as realistic descriptions of the processes and relationships underlying each community.

The relative constancy in abundance of the seagrass *Heterozostera tasmanica* (seagrass habitat; M. Ortiz pers. obs.) and the structural function that it provides to most of the invertebrates species (Connolly 1997,

Table 7. Holistic sustainability measures (F_n and 2nd criterion) in the eco-social model of sand-gravel habitat under 2 fishermen self-dynamics. Management scenarios: [A] increasing the standing stock of ApJ, [B] increasing the standing stock of ApR, [C], [D] and [E] partial removal of the predatory sea star Lm, Hh and Mg respectively, and [F] increase of the available substrate (S)

Sustainability assessment in the sand-gravel habitat Management	Fishermen dynamic Self-damped F_n; 2nd criterion	 Self-enhanced F_n; 2nd criterion
[A]	(+) 48.0; > 0	(+) 240.0; > 0
[B]	(+) 12.0; > 0	(+) 204.0; > 0
[C]	(+) 96.0; > 0	(+) 288.0; > 0
[D]	0.0; > 0	(+) 192.0; > 0
[E]	(–) 252.0; > 0	(–) 60.0; > 0
[F]	(+) 204.0; > 0	(+) 396.0; > 0
[A]+[B]	(+) 84.0; > 0	(+) 276.0; < 0
[A]+[C]	(+) 168.0; > 0	(+) 360.0; > 0
[A]+[D]	(+) 72.0; > 0	(+) 264.0; < 0
[A]+[E]	(–) 180.0; > 0	(+) 12.0; > 0
[A]+[F]	(+) 276.0; > 0	(+) 468.0; < 0
[B]+[C]	(+) 132.0; > 0	(+) 324.0; > 0
[B]+[D]	(+) 36.0; > 0	(+) 228.0; < 0
[B]+[E]	(–) 216.0; > 0	(–) 24.0; > 0
[B]+[F]	(+) 240.0; > 0	(+) 432.0; < 0
[C]+[D]	(+) 120.0; < 0	(+) 312.0; > 0
[C]+[E]	(–) 132.0; > 0	(+) 60.0; > 0
[C]+[F]	(+) 324.0; > 0	(+) 516.0; > 0
[D]+[E]	(–) 228.0; > 0	(–) 36.0; > 0
[D]+[F]	(+) 228.0; > 0	(+) 420.0; > 0
[E]+[F]	(–) 24.0; > 0	(+) 168.0; > 0
[A]+[B]+[C]	(+) 204.0; > 0	(+) 396.0; > 0
[A]+[B]+[D]	(+) 108.0; > 0	(+) 300.0; < 0
[A]+[B]+[E]	(–) 144.0; > 0	(+) 48.0; > 0
[A]+[B]+[F]	(+) 312.0; > 0	(+) 504.0; < 0
[A]+[B]+[C]+[D]	(+) 228.0; > 0	(+) 420.0; > 0
[A]+[B]+[C]+[E]	(–) 24.0; > 0	(+) 168.0; > 0
[A]+[B]+[C]+[F]	(+) 432.0; > 0	(+) 624.0; > 0
[A]+[B]+[C]+[D]+[E]	0.0; > 0	(+) 192.0; > 0
[A]+[B]+[C]+[D]+[F]	(+) 456.0; > 0	(+) 648.0; < 0
[A]+[B]+[C]+[D]+[E]+[F]	(+) 228.0; > 0	(+) 420.0; < 0

Reusch 1998, Rose et al. 1999, Lee et al. 2001) seem to be insufficient to produce a stable system. A similar result was obtained for the sand-gravel ecological model. These findings may be a consequence of the significant seasonal changes (biomass) of the scallops in both habitats and of the macroalgae species in the sand-gravel (by harvest) (Ortiz et al. unpubl.). The sand model was estimated to be unstable, which implies that it would not support sustainable harvest activities or management polices. One explanation for this finding may be the seasonal migration between sand and deep systems of the predatory crab *Cancer coronatus* which feeds intensively in the sand habitat (Jesse 2001). Likewise, the intensive fishery on the snail *Xantochorus cassidiformis* and on the predatory crab *C. polyodon* may also have some influence on this instability. These processes (perturbations) suggest that the sand system is constantly being driven between alternative or transitional assemblages, thus preventing the development of a stable community. However, we would propose that more studies be conducted to corroborate our conclusion.

Although the analysis of the ecological models would support some adaptive management strategies (sensu Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999) to increase the standing stocks of the commercial species, these models do not include the dynamics of fishery activities. Our extended models revealed that exploitation in the seagrass and sand-gravel systems can only be sustainable if the fishers are self-damped, implying that fishing effort and catch quota must be constrained. Therefore, both management practices would be recommended. Non-linear theoretical studies that have analysed the fishery effects on multispecies systems came to similar conclusions to the ones presented here (May et al. 1979, Beddington & May 1980, Beddington & Cooke 1982, Azar et al. 1995).

Table 8. (a) Qualitative changes in the equilibrium values (standing stocks) of all variables in the ecological model of sand habitat as response to negative external impact on the 3 sea starfish species *Meyenaster gelatinosus* (*Mg*), *Luidia magallanica* (*Lm*) and the adults of sand mussel *Mulinia* sp. (*MA*). (b) Qualitative predictions in the ecosocial model of sand habitat as response to positive impact on the fishermen

(a) Input to	Responses *CcA*	 *CcJ*	 *Cp*	 *Mg*	 *Lm*	 *MF*	 *SE*	 *LE*	 *PP*	 *I*	 *MJ*	 *MA*	 *Xc*
(–) *Mg*	+	+	–	–	+	+	+	–	–	–	+	+	–
(–) *Lm*	–	–	+	–	–	+	–	+	+	+	–	–	+
(–) *MA*	+	+	+	+	+	+	+	–	–	–	+	–	–

(b) Input to	Responses *CcA*	 *CcJ*	 *Cp*	 *Mg*	 *Lm*	 *MF*	 *SE*	 *LE*	 *PP*	 *I*	 *MJ*	 *MA*	 *Xc*	 *F*
(+) *F*(–)	+	–	+	–	–	–	–	–	+	+	+	–	+	0
(+) *F*(+)	+	–	+	–	–	–	–	–	+	+	+	–	+	0

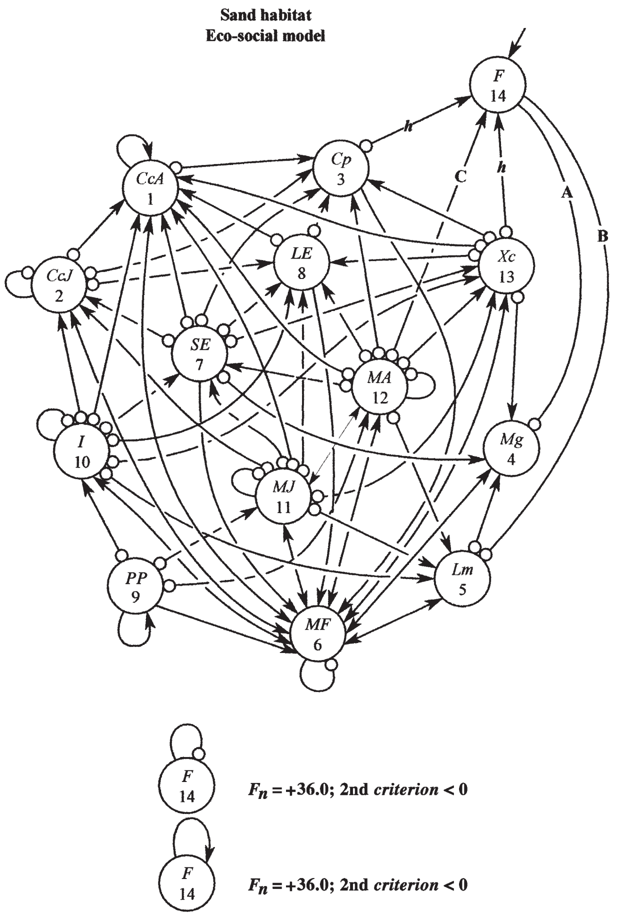

Fig. 5. Ecosocial model of sand habitat. Holistic sustainability measures (F_n and 2nd criterion) under 2 fishermen self-dynamics. [A], [B] and [C] are management scenarios, and *h* is harvest. The soft connections indicate postulated relationships based on limited data

Based on the direct and indirect effects propagated in the seagrass habitat, any action to increase the biomass of recruits and juveniles of the scallop *Argopecten purpuratus* (larvae collectors, introductions) cannot be recommended as they do not have a positive impact on the adult exploited scallops. On the other hand, the partial removal of the 3 sea starfishes *Luidia magallanica*, *Heliaster helianthus* and *Meyenaster gelatinosus* would increase abundance of adult scallop. However, at the same time, an unexpected positive effect would be propagated on standing stock of the crab *Cancer polyodon*. This positive effect on the competitor species can be interpreted as the dominance of a positive feedback at a lower level which may have a negative impact on the holistic stability. These ecosystems are open to several types of natural perturbations which may maximise the influence of this positive feedback on the stability of the entire community, which might be driven to some other moving equilibrium (sensu Levins 1998b). Hence, if our objective is not only to increase the standing stocks of the commercial species, but also to conserve the natural system which they inhabit, this positive feedback must be avoided. One way to depress it may be by fishing the crab *C. polyodon* as well.

In the sand-gravel habitat, a more complex propagation of effects was observed. In this habitat, we recommend implementation of management strategies that favour the abundance of recruits and juveniles of *Argopecten purpuratus*. The artificial introduction (surplus) of available substrate would not increase the abundance of the commercial red algae *Chondrocanthus chamissoi*. Some experimental field studies (J. Macchiavello pers. comm.) confirm our finding. This response might be explained by the parallel increase of the mollusc *Calyptraea trochiformis* and the sea squirt *Pyura chilensis* (both sessile species) which would eventually compete with the macroalgae for the substrate. However, the above 3 interventions would have a positive indirect effect on the sea starfishes *Luidia magallanica* and *Heliaster helianthus*. In this particular situation, we would suggest the removal of *L. magallanica* only to historical levels of ca. 2.0 g wet weight m^{-2} (sensu Ortiz et al. unpubl.) because its further removal would be highly unsustainable for the system. However, based on our analysis, the removal of just the sea starfish *H. helianthus* should be implemented as positive effects would be expected on the standing stocks of the 3 commercial species, the red algae *Chondrocanthus chamissoi*, adult *Argopecten purpuratus* and adult *C. polyodon*.

Finally, we have shown that the loop analysis is a useful theoretical framework and an alternative to the reductionistic abstractions if the holistic sustainability of different anthropogenic interventions is assessed; thus, it represents a way to integrate more quantifiable and non-quantifiable variables as well as relationships

Table 9. Holistic sustainability measures (F_n and 2nd criterion) in the ecosocial model of sand habitat under 2 fishermen self-dynamics. Management scenarios: [A] and [B] partial removal of the sea starfishes *Mg* and *Lm*, respectively, [C] represents an eventual harvest on the mussel adults *MA*

Sustainability assessment in the sand habitat

Management	Fishermen dynamic	
	Self-damped F_n; 2nd criterion	Self-enhanced F_n; 2nd criterion
[A]	(+) 72.0; > 0	(+) 72.0; > 0
[B]	(+) 36.0; > 0	(+) 36.0; > 0
[C]	(+) 64.0; > 0	(+) 64.0; > 0
[A]+[B]	(+) 72.0; > 0	(+) 72.0; > 0
[A]+[C]	(+) 96.0; > 0	(+) 96.0; > 0
[B]+[C]	(+) 64.0; > 0	(+) 64.0; > 0
[A]+[B]+[C]	(+) 96.0; > 0	(+) 96.0; > 0

in the models. This seems particularly important as the widespread crash of exploited populations, reported as the global fishery crisis, appears to be at least in part rooted in reductionistic models and methods (Larkin 1977, Hilborn et al. 1995, Patten 1997, Roberts 1997, Walters et al. 1999). Similar conclusions have been drawn for pest management in agricultural systems (Levins & Wilson 1980, Andow & Rosset 1990, Levins & Vandermeer 1990, Levins 1998c).

CONCLUSIONS

The present work is the first attempt to use Levins' theory to assess the sustainability of different management options in 1 of the 168 territorial management areas established along the Chilean coast. Despite the fact that the models represent 3 different systems and some of the ecological relationships were only based on limited data, similar tendencies were found. For instance, when fishermen are considered self-damped, the sustainability (local stability) strongly increases in seagrass and sand-gravel systems. In other words, fishing effort and catch quota should be restricted. Based on our results, the following management options in seagrass and sand-gravel habitats would be recommended: (1) any activity focused towards the increase of juveniles and recruits of the scallop *Argopecten purpuratus* (collector of larvae, man-assisted introductions) must be exclusively carried out in the sand-gravel habitat; and (2) the 3 starfish species should be partially removed in the seagrass habitat, and only *Heliaster helianthus* in the sand-gravel one. Further studies would have to be focused towards the assessment of the structural function of the seagrass *Heterozostera tasmanica* and the macroalgae species, and of the contribution of bacteria or organic matter as food sources for filter feeders, starfish and crab species. Even though Levins' loop analysis does not allow for explicit quantitative reasoning, 'what if' questions can be answered with sufficient understanding and realism. Based on its mathematics and the dominance of negative and positive feedbacks, we conclude that this theoretical framework should be used in other benthic management areas along the Chilean coast, especially if the aim is to assess the sustainability of different adaptive management options for multispecies fisheries (Walters & Hilborn 1978, Hilborn et al. 1995, Walters & Korman 1999, Walters et al. 1999, Castilla 2000). This theory arises as an alternative to the pure reductionistic measures of sustainability (see Bell & Morse 1999).

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