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Modeling an exploited rocky coastal ecosystem: Bahia Tortugas, Mexico

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ABSTRACT

A trophic structure model of the rocky coastal ecosystem in Bahia Tortugas, Mexico was constructed using Ecopath software to represent the main biomass flows in the system. Data for the model came from field observations (biomass estimates, stomach contents, and ecological observations for sea snails, abalones, lobster, some demersal finfishes, and macroalgae) carried out through ten field trips from 2006 to 2008. The results provide a snapshot of how the ecosystem operates. The model considers 23 functional groups. The total system throughput was 553 t/km^2/year, 57% corresponds to internal consumption, 28% to respiration, 14% becomes detritus, and only 1% is removed through commercial fishing. The model suggests that even for exploited populations, predation and competition are heavier stresses than current fishing effort; however, because spiny lobster showed the second highest keystoneness' index value, increasing fishing pressure on this group could strongly impact the entire ecosystem. We believe that this model has the potential to support management by allowing the exploration of the potential impacts of different fishing decisions at ecosystem level.

1. Introduction

Trophic interactions strongly influence the dynamics of ecosystems, and the way they respond to natural and anthropogenic stress. Scientific research in fisheries is currently strongly committed to developing tools to incorporate knowledge on structure and function of the ecosystems, including trophic flow patterns, into an ecosystem approach to fisheries management (García et al., 2003).

Ecosystem indices, multi-species modeling, food web analysis, among others, are expected to become normal components of the fisheries management toolbox. In particular, one area that has called our attention is the development of ecosystem models describing trophic interactions, the most common being the mass-balance model Ecopath with EcoSim (Christensen and Pauly, 1992, 2004).

1.1. Study site

In the western coast of Baja California, Mexico, the region known as Pacifico Norte (Fig. 1), is scarcely populated, and most human settlements are small but permanent fishing towns. In Bahia Tortugas, fisheries remain as the most important productive activity, and virtually all economic agents orbit around them. Fisheries are mostly based on highly valued species like green and pink abalone (*Haliotis fulgens* and *Haliotis corrugata*, respectively) and spiny lobster (*Panulirus interruptus*), and to a lower extent, on sea cucumber, sea snails, and some finfish species. Fishermen are well organized into a cooperative, and together with other cooperatives into a federation (FEDECOOP), which works for common interests, such as negotiations of management decisions with the authority, search and access to markets, and technical analyses. Income for most of the people inhabiting the region is higher than the national average; however, only cooperative members (a relatively small and fixed number) receive direct benefits from the abalone and lobster fisheries (retirement funds, loans, insurance, etc.).

Despite the importance of fisheries in the area, the evaluation of ecosystem scale impacts have been poorly described. An ecosystem approach to fisheries has become the new paradigm in fisheries management; tools to organize the information and explore scenarios are becoming a must-have. We deliver here the first rocky coastal ecosystem model for the region, mostly based on quality field observations.

2. Methods and materials

2.1. The Ecopath model

Trophic interactions and energy flux were evaluated using the Ecopath model (Christensen and Pauly, 1992; Polovina, 1984; Polovina and Ow, 1983). Ecopath models are quantitative descriptions of the average state of biomass organization and flows in a food web. The approach is based on the static description of energy

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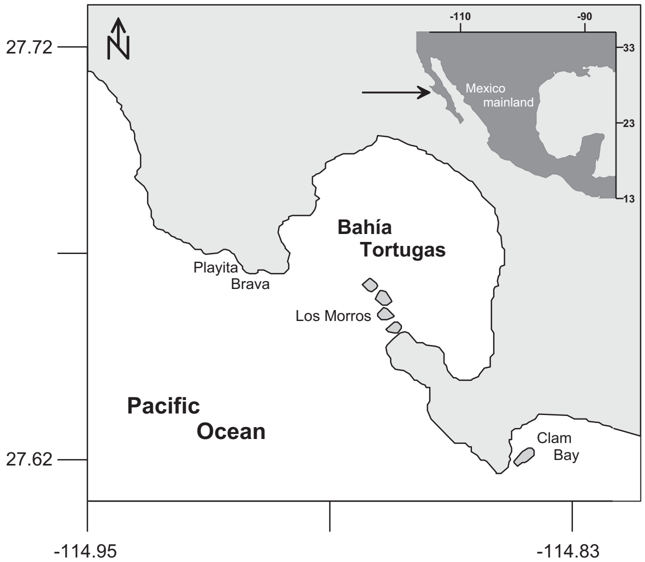

Fig. 1. West coast of Baja California Peninsula and location of the Bahia Tortugas area.

flows in an ecosystem developed by Polovina (1984); all species are aggregated and represented in the model as ecologically functional groups connected as predators and prey through a diet composition matrix. In the Ecopath description, 'mass-balance' or conservation of energy is assumed for every identified component of the ecosystem and the ecosystem as a whole. Its basic premise is that, in a given time period, the system will be in balance. In other words, production is equal to consumption and is defined by the following equation:

$$P_i - B_i M2_i - P_i(1 - EE_i) - EX_i = 0 \quad (1)$$

where for an i group, P_i is production, B_i is biomass in tonnes wet weight, $M2_i$ is mortality by predation, EE is ecotrophic efficiency, and EX_i is export. Ecotrophic efficiency is the proportion of organisms that die by predation and export, including fishing extraction. The first term represents production, the second represents losses by predation, the third represents losses that are not assigned to predation or export, and the last term represents losses by export. The equation is equal to 0 because it is at balance. Because material transfers between groups are through trophic relationships, Eq. (1) is re-expressed:

$$B_i\left(\frac{P}{B}\right)_i EE_i - \sum_{j=1}^{n} B_j\left(\frac{Q}{B}\right)_j DC_{ji} - B_i\left(\frac{P}{B}\right)_i (1 - EE) - EX_i = 0 \quad (2)$$

where subscript j represent predators, B_j is their biomass in tonnes wet weight, P/B is production to biomass ratio, which is equal to the instantaneous rate of total mortality (Z) at equilibrium (Allen, 1971).We used an annual base. EE_i and EX_i are the same as in Eq. (1), Q/B_j is consumption to biomass ratio of group j, DC_{ji} is the fraction of prey i in the diet of predator j. Each group was represented by a similar equation; a system of linear equations was established in which at least three of the four parameters (B, P/B, Q/B, and EE) of each group was known and only one was estimated by the model if needed. In summary, Eq. (2) describes the biomass flow balance between inputs and outputs for each group.

2.2. Functional groups

Most species were included in functional groups sharing similar trophic roles, and only those of particular interest were kept as individual groups: commercially important species such as abalone; lobster and some snails; and ecologically interesting species such as the giant kelp *Macrocystis pyrifera*. Our classification resulted in 23 functional groups in total, including five groups of fin fishes; five groups of benthic mollusks; four groups of benthic algae; two groups of crustaceans; sharks, octopus; polychaetes; holoturides; echinoderms; sea lions and detritus (Table 1). Data for the model came from field observations (biomass estimates, stomach contents, and ecological observations for sea snails, abalones, lobster, some demersal finfishes, and macroalgae, carried out through ten field trips from 2006 to 2008). For the rest of the groups except fishes, we used published reports. In most cases, the software computed fish biomass, since Eq. (1) assumes balance between terms, assuming a value of EE based on literature for the same or a similar species when no input data were available (Table 3).

2.3. Parameters estimations

A predator–prey matrix was developed using field observations of stomach contents (unpublished data) or from reports for similar species or groups when no data were available. Fishing fleets and catches (Y_i) of important species were included in the model, impacting on the following groups: pink and green abalone, spiny lobster, some snails, croakers, sharks, groupers, grunts, and crabs. Data were obtained from fisheries regional offices.

P/B and Q/B values for all finfish groups were calculated using FishBase (Froese and Pauly, 2009). Because P/B corresponds to total mortality (Z), we used mortality values reported in the literature for most of the functional groups. The Q/B relation represents the amount of food ingested by a group with respect to its own biomass in a given period. For fish groups, Q/B values were computed with the empirical equation of Jarre et al. (1990) that considers environmental temperature, fish weight and size, and caudal fin morphology; we used the average value for the species into a specific functional group or the value corresponding to the most representative specie (more abundant into the functional group). For the rest of groups, Q/B values were taken from literature.

The diet matrix was adjusted by modifying initial values and producing small changes (Table 2). We selected this approach because diet is the source of the greatest uncertainty: thus, we avoided large modification of the feeding patterns of functional groups (Morales-Zárate et al., 2004). Consistency of the model was mainly verified by EE < 1 as the primary criterion and comparing trends in the respiration to biomass ratio (R/B), which must be higher for active species than for sedentary groups.

2.4. Ecological indexes

The model was used to evaluate some flow indices, such as total system ascendency (measure of ecosystem flow; Christensen, 1994, 1995; Pérez-España and Arreguín-Sánchez, 2001), total system throughput (sum of flows and measure of ecosystem size; Ulanowicz and Norden, 1990), and path length (average number of groups that an inflow or outflow passes through). Additionally, mixed trophic impacts of each group and other physiological information about species groups and the ecosystem, such as transfer efficiencies and omnivore index (Christensen and Pauly, 1993; Vega-Cendejas and Arreguín-Sánchez, 2001) were estimated. We also used the method for identifying keystone species in the food web proposed by Libralato et al. (2006).

3. Results

Table 3 shows values of the balanced model, including those estimated by the software. The first column shows the trophic level (TL), a dimensionless index (Christensen et al., 2000). In Ecopath, TL can be an integer or a fraction, as suggested by Odum and Heald

Table 1
Functional groups and input parameters sources for the rocky coastal ecosystem model for Bahia Tortugas, Mexico. Empty spaces correspond to parameters that were calculated by the model.

Group name	Species	Information source			
		Biomass	*P*/*B*	*Q*/*B*	Diet
Articulated corallines		1		–	–
Eisenia	*Eisenia arborea*	1		–	–
Macrosystis	*Macrocystis pyrifera*	1		–	–
Other Macroalgaes	*Cystoceira osmundacea*, *gelidiales*	1		–	–
Megastrea undosa	*Megastrea undosa*	1			1
Megathura crenulata	*Megathura crenulata*	1			1
Other gastropodes	*Tegula* spp, *Ocenebra foveolata*	1			1
Pink abalone	*Haliotis corrugata*	1			8
Green abalone	*Haliotis fulgens*	1			8
Polychaetes	*Platynereis dumerilii*		5	5	
Holoturides	*Parastichopus parvimensis*		6	6	
Spiny lobster	*Panulirus interruptus (adultos)*		10		
Echinoderms	*Strongilocentrotus purpuratus*, *S. franciscanus*, *Pisaster ochraceus*		11	11	
Crabs	*Callinectes* ssp				7
Sharks	*Mustelus* sp. and *Hetorodontus* sp.	12		10	2,12
Octopus	*Octopus* ssp		6	6	
Malachantidae fish	*Caulolatilus princeps*, *Caulolatilus hubbsi*		2	2	9
Serranidae fish	*Epinephelus acanthistius*, *Epinephelus niphobles*, *Mycteroperca xenarcha*, *Paralabrax clathratus*, *Paralabrax nebulifer*, *Mycteroperca rosacea*		2	2	9
Sciaenidae fish	*Cynoscion* spp, *Menticirrhus panamensis*		2	2	9
Ballistidae fish	*Ballistes* ssp., *Balistapus undulatus*, *Balistes polylepis*		2	2	9
Haemulidae fish	*Cheilotrema saturnum*, *Microlepidotus inornatus*, *Ophioscion strabo*, *Semicossyphus pulcher*		2	2	9
Sea lions	*Zalophus californiensis*	3	10		
Detritus		4	–	–	

(1) Unpublished field data given by Guzman del Proo (2006); (2) FishBase; (3) Unpublished field data given by Ramade (2009); (4) Supossed; (5) Arreguín et al. (2002); (6) Gorostieta Monjaraz (2001); (7) Paul (1981); (8) FAO (2009); (9) Cruz-Escalona (1998); (10) Del Monte Luna (2004); (11) Salcido-Guevara and Arreguín-Sánchez (2007); (12) Unpublished field data given by Espinoza and Galvan (2010).

(1975). We obtained three discrete *TL*s. Primary producers together with detritus are in the first *TL*, while sharks, sea lion and octopus are included as top predators; the rest of the groups are ranking between 2 and 3.1. In general, *TL*s are lower than in other systems (Table 4), the models considered for comparison include one in the same region (west coast of the Baja California peninsula), three for inside the Gulf of California, and two for the Gulf of Maine, focused on lobster (*Homarus americanus*), and build for two different decades. In our model biomasses calculated by the software are relatively low for fish groups. However, we believe these values are coherent with observations mentioning that large biomass of fishes are distributed out off the bay (Mario Ramade, *personal commun.*). The calculated *P*/*B* values are all in the range of many other systems. The *Q*/*B* value calculated for sea lion is lower than those calculated for other systems; it properly reflects that even when there are relatively large population concentrations near the reef, most of the individuals feed outside the bay, where fishes are more abundant.

Table 2
Adjusted diet matrix for the rocky coastal ecosystem in the in the Bahia Tortugas model.

	Prey	Predator																	
		5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Articulated corallines	0.07	0.08	0.08	0.00	0.00	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.60	0.13	0.00
2	*Eisenia arborea*	0.07	0.03	0.03	0.00	0.00	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.24	0.25	0.00	0.00
3	*Macrosystis pyrifera*	0.13	0.24	0.06	0.80	0.80	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.65	0.00
4	Other macroalgae	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.29	0.00	0.13	0.00
5	*Megastrea undosa*	0.00	0.01	0.28	0.00	0.00	0.00	0.00	0.01	0.13	0.00	0.01	0.00	0.00	0.00	0.00	0.03	0.03	0.05
6	*Megathura crenulata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.05
7	Other gastropodes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01	0.02	0.00	0.21	0.00	0.00	0.00	0.08
8	Pink abalone	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
9	Green abalone	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
10	Polychaetes	0.28	0.39	0.28	0.00	0.00	0.00	0.00	0.38	0.28	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
11	Holoturides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
12	Spiny lobster	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.07
13	Echinoderms	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.09	0.00	0.02	0.49	0.00	0.03	0.00	0.00	0.00	0.08
14	Crabs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.37	0.00	0.00	0.00	0.11	0.00	0.08
15	Sharks	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00	0.13	0.00	0.00	0.01	0.00	0.00	0.00	0.06
16	Octopus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.13	0.00	0.00	0.08	0.00	0.00	0.00	0.08
17	Malachantidae fish	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.08
18	Serranidae fish	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.08
19	Sciaenidae fish	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.08
20	Ballistidae fish	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.08
21	Haemulidae fish	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.13	0.00	0.00	0.26	0.00	0.00	0.00	0.08
22	Sea lions	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
23	Detritus	0.12	0.26	0.28	0.20	0.20	0.19	1.00	0.38	0.12	0.50	0.00	0.10	0.22	0.40	0.47	0.01	0.07	0.00

Table 3
Input and estimated values (in bold) for the rocky coastal ecosystem in the Bahia Tortugas model.

	Group name	*TL*	Biomass	*P/B*	*Q/B*	*EE*
1	Articulated corallines	1	4.71	**5.90**	–	0.90
2	*Eisenia*	1	3.94	**7.18**	–	0.90
3	*Macrosystis*	1	20.00	**4.03**	–	0.90
4	Other Macroalgaes	1	0.87	**27.63**	–	0.99
5	*Megastrea undosa*	2.7	15.96	**0.74**	2.50	0.90
6	*Megathura crenulata*	2.4	2.80	**0.42**	2.34	0.90
7	Other gastropodes	2.8	8.00	**0.56**	2.80	0.99
8	Pink abalone	2	5.50	**0.31**	3.50	0.99
9	Green abalone	2	6.00	**0.19**	3.50	0.99
10	Polychaetes	2	**8.57**	4.00	8.50	0.99
11	Holoturides	2	**3.55**	1.40	3.00	0.99
12	Spiny lobster	2.6	**1.79**	0.99	4.20	0.99
13	Echinoderms	3.1	**6.55**	0.95	3.18	0.99
14	Crabs	2.5	**2.32**	2.02	4.20	0.99
15	Sharks	3.7	1.00	**0.81**	5.00	0.99
16	Octupus	3.7	**1.81**	1.39	3.50	0.99
17	Malachantidaes fish	2	**1.13**	1.00	3.00	0.99
18	Serranidae fish	3	**3.77**	1.13	3.80	0.99
19	Sciaenidae fish	2	**4.94**	0.87	3.20	0.99
20	Ballistidae fish	2.2	**4.27**	1.00	3.40	0.99
21	Haemulidae fish	2.1	**5.67**	1.45	3.10	0.99
22	Sea lions	3.6	6.00	0.10	**0.95**	0.05
23	Detritus	1	50.00	–	–	**0.90**

Fig. 2 shows a conceptual biomass flow diagram. The size of the boxes is proportional to the biomass for each group, and lines are the fluxes between groups. Boxes are distributed on the *Y*-axis according to the trophic level. The mixed trophic impact analysis showed that the most affected groups were impacted more by predation and competition than by fishing pressure (Fig. 3); in fact, the positive impact from resources over the specific fleets is very clear, whereas the negative impact from the fleets over the resources is not. Moreover, fishing techniques at the reef are very selective, causing none or very small negative impacts over incidental resources.

Trophic interactions were analyzed by trophic niche overlaps (Table 6). Values close to the unit indicate a large overlap. We found a high overlap between some gastropods (abalones and sea snails); most of demersal finfish; spiny lobster with some finfish like serranidae, sciaenidae and ballistidae families; and lower for haemulide fish with octopus and other gastropos.

Table 4 shows the basic attributes of the system: the total system throughput was 553 t/km^2/year, where internal consumption accounts for 57% of total flows; respiration for 28%; detritus for 14%; and export out of the system (commercial fishing) for 1%. Total primary production to respiration ratio (TPP/*R*) was 1.05 t/km^2/year, indicating TPP is approximately 60% greater than respiration. The total primary production to biomass ratio was 1.34 t/km^2/year, which suggests a nearly mature state, because this rate is lower when the system approaches maturity (Odum, 1969; Christensen, 1995). The connectance index is the proportion of theoretically possible trophic connections with a value of 0.23, very near of the others it was compared.

Table 5 shows an ascendency (*A*) value of 545.8 flowbits, with 15.6% corresponding to internal flows. Ascendency is a measure of the information content in the ecosystem deriving from information theory (Ulanowicz and Norden, 1990); it is symmetrical, and will have the same value whether calculated from input or output. The upper limit for the size of ascendency corresponds to development capacity (*DC*). In this case, *DC* was of 2580 flowbits. With those parameters, we interpreted ascendency in the current state of the ecosystem to be 20% of development capacity (*A*/*DC*). The difference between *DC* and *A* is the system overhead, that is, the maximum energy reserve of the ecosystem for potential use against disturbances (Ulanowicz, 1986). We obtained a high overhead compared with other ecosystems, and it was probably a result of the connections between groups in the system.

To identify keystone functional groups, we followed the method proposed by Libralato et al. (2006), based on the mixed trophic

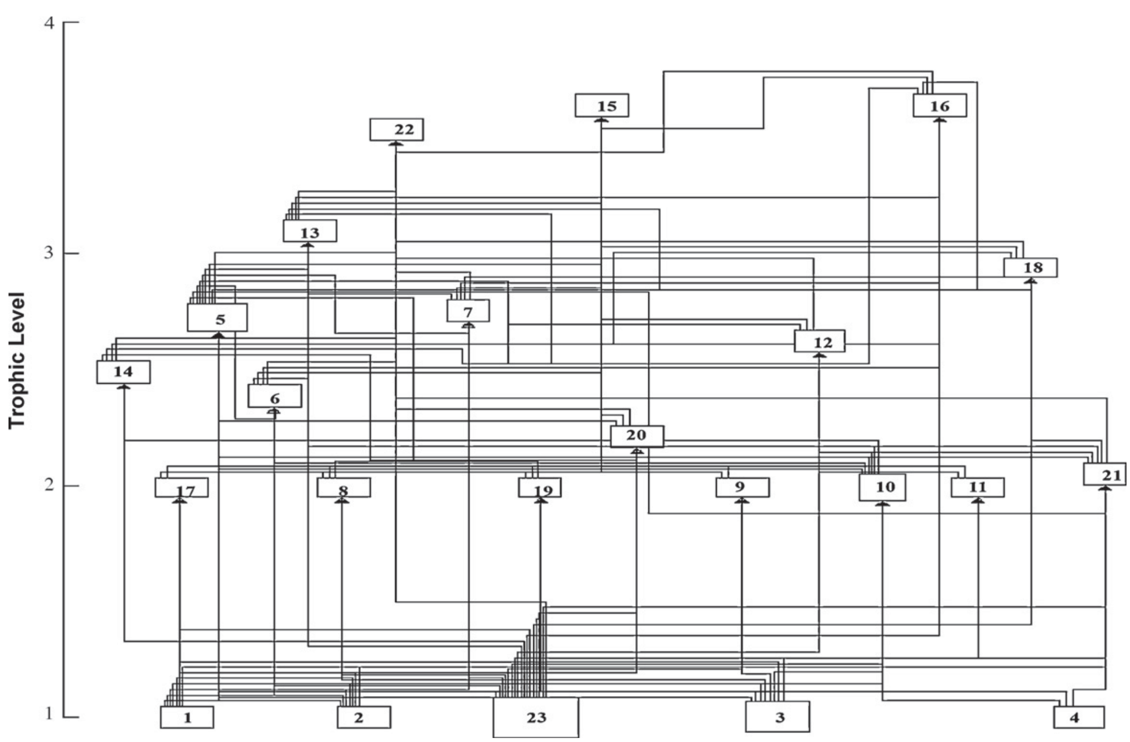

Fig. 2. Flow diagram of biomass showing trophic interactions in the rocky coastal ecosystem in Bahia Tortugas Mexico. All flows are expressed in tonnes/km 2 per year. The number within each box corresponds to the functional group as listed in table 3. Y-axis indicates trophic level and box sizes are proportional to the biomass for each group.

Table 4
Ecosystem properties (system statistics) for the rocky coastal ecosystem in the Bahia Tortugas model as computed by Ecopath, and comparison with other models.

Parameter	Values							Units
	This model	Ulloa model[a]	La Paz model[b]	GOC benthic model[c]	Sinaloa benthic model[d]	American lobster Gulf of Maine model[e] 1980s–1990s		
Functional groups included	23	26	48	27	24	24	24	
Total system throughput	553	129	7545	424.24	8905	18,425	21,408	t/km^2/year
Mean trophic level of the catch	2.07	2.2	3.32	2.87	2.54	3.11	3.05	–
Total primary production/total respiration	1.05	65	3.2	1.038	1.96	2.09	1.76	t/km^2/year
Total primary production/total biomass	1.34	46	58	27.39	10.17	42.56	18.94	t/km^2/year
Total biomass (excluding detritus)	119.13		53.69	63.09	344	207.35	487.39	t/km^2
Total catches	0.46		0.99	4.58	10.2	1.28	2.67	t/km^2/year
Connectance index	0.23	0.2	0.18	0.25	0.24	0.26	0.26	–
System omnivory index	0.23	0.15	0.18	0.33	0.18	0.30	0.29	–
Total market value	3976		0.05					USD

[a] Del Monte Luna (2004).
[b] Arreguín-Sánchez et al. (2007).
[c] Arreguín-Sánchez et al. (2002a,b).
[d] Salcido-Guevara and Arreguín-Sánchez (2007).
[e] Zhang and Chen (2007).

impact analysis. The method allows expressing the relative change of biomasses in the food web that would result from an infinitesimal biomass increase of the observed group, thus identifying its total impact. In our analysis we excluded all the fleets in order to specifically observe keystoneness between biological groups. Fig. 4 shows the keystoneness index for each functional group, against overall effect. The highest keystonenicity corresponds to the *Megastrea undosa* and spiny lobster, then Polychates, *Macrocystis*, and except for the sea snail *Megathura crenulata* and abalones, all gastropodes ranked also relatively high.

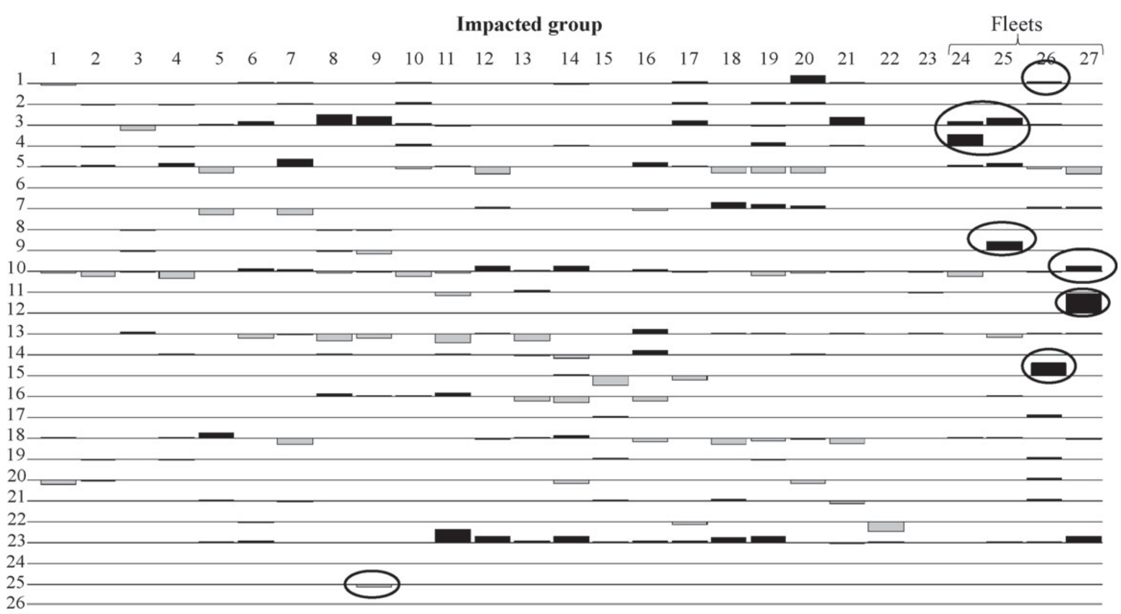

Fig. 3. Plot of mixed trophic impacts for the rocky coastal ecosystem in Bahia Tortugas Mexico. Black bars are positive impacts and grey ones are negative impacts.

Table 5
Totals of flux indices for the rocky coastal ecosystem in the Bahia Tortugas model.

Source	Ascendency		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Internal flow	545.8	15.6	2034	58.2	2580	73.8
Export	20.2	0.6	32.1	0.9	53	1.5
Respiration	134.1	3.8	729.5	20.9	863.6	24.7
Total	700	20	2795	80	3496.9	100

4. Discussion

Models cannot properly capture the landscape of complex processes and interactions of marine ecosystems; however, with them we can at least explore pieces of the puzzle. In our contribution we explored the trophic interactions of one rocky reef in Bahia Tortugas, Baja California Sur, Mexico based on a trophic model that incorporates years of field observations. The model was structured to represent an immature ecosystem, with low total consumption values and respiration fluxes reflecting that internal energy in the system is relatively low, as compared to other coastal ecosystems. Connectancy and omnivory indices also show relatively low values, indicating weak interactions between components of the ecosystem. In fact, the connectance index (0.23) corresponds to a situation where only less than one third of the theoretical interactions are occurring. We believe it might be because most of the functional groups are in trophic levels 2 and 3, where most of the fishing effort is concentrated. An interesting observation was that based on the impact matrix and the niche overlapping analysis, the model suggests that fish resources exploited in the reef are not significantly impacted by the current level of fishing effort (Table 6). In fact, except for the blue abalone no other resource shows negative impacts from the fishery, while the positive impact of the resources on the fishery (i.e. the fisher biomass) is reflected in the impact matrix. Detritus is the functional group with more positive impacts than other groups, however, gastropodes and macroalgae, particularly *Macrosystis*, also show several positive impacts. Also from this matrix, it is relevant to note that there are no negative impacts of fisheries on other groups as incidental catch because fishing practices in the reef (traps, scuba) are highly selective. This result is coherent with the keystonicity analysis, where gastropodes and macroalgae show the highest values after lobster. Zhang and Chen (2007) suggested for the Gulf of Maine that a change occurred between the 1980s and the 1990s, from a system dominated by high trophic level groundfish to a low trophic crustacean species

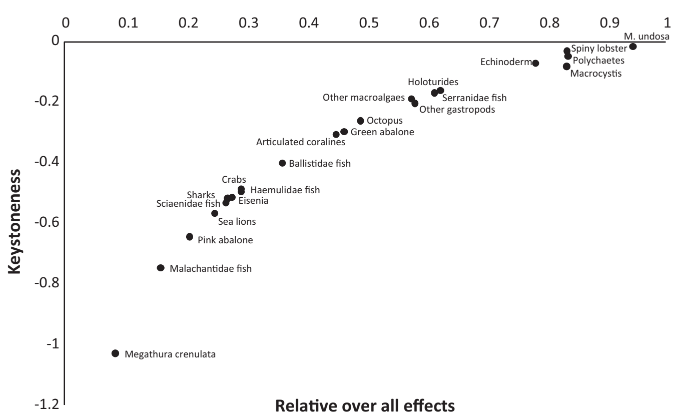

Fig. 4. Keystoneness for the functional groups of the rocky coastal ecosystem in Bahia Tortugas, Mexico. For each functional group, the keystone index is reported against overall effect. Overall effects are relative to the maximum effect measured in the trophic web. The species are ordered by decreasing keystoneness.

Table 6
Trophic niche overlaps between functional groups. Highest values are in bold.

	Group name	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
5	*Megastrea undosa*	1																	
6	*Megathura crenulata*	0.35	1																
7	Other gastropods	0.1	0.26	1															
8	Pink abalone	0.37	0.8	0.23	1														
9	Green abalone	0.38	**0.9**	0.25	**0.99**	1													
10	Polychaetes	0.5	0.3	0.08	0.297	0.31	1												
11	Holoturides	0.36	**0.7**	0.21	**0.99**	0.97	0.29	1											
12	Spiny lobster	0.03	0.21	0.06	0.038	0.08	0.61	0	1										
13	Echinoderms	0.2	**0.7**	0.28	0.474	0.49	0.19	0.45	0.05	1									
14	Crabs	0.04	0.27	0.05	0.017	0.03	0.01	0.0	0.06	0.7	1								
15	Sharks	0.01	0.1	0.02	0	0	0	0.0	0.18	0.02	0	1							
16	Octopus	0.03	0.21	0.84	0.031	0.06	0.02	0.0	0.2	0.17	0.06	0.39	1						
17	Malachantidae fish	0.03	0.38	0.1	0.061	0.12	0	0.0	0.38	0.1	0.1	0.65	0.54	1					
18	Serranidae fish	0.02	0.09	0.03	0.015	0.03	0.62	0.0	**0.8**	0.02	0.02	0.19	0.13	0.25	1				
19	Sciaenidae fish	0.02	0.09	0.03	0.015	0.03	0.62	0.0	**0.8**	0.02	0.02	0.19	0.13	0.25	**0.9**	1			
20	Ballistidae fish	0.02	0.09	0.03	0.015	0.03	0.62	0.0	**0.8**	0.02	0.02	0.19	0.13	0.25	**0.9**	**0.9**	1		
21	Haemulidae fish	0.02	0.06	**0.7**	0.009	0.02	0.45	0.0	0.63	0.12	0.02	0.12	**0.7**	0.16	0.64	0.64	0.64	1	
22	Sea lions	0.04	0.45	0.14	0.106	0.21	0	0.0	0.35	0.11	0.15	0	0.28	0.56	0.14	0.14	0.14	0.08	1

dominated system. The reduction of groundfish biomass tends to have positive effects on the lobster and herring stock biomass as a result of reduced predation (natural mortality). This study also indicates that herring baits discarded back to the sea in the lobster fishery tend to have positive impacts on the lobster stock biomass. We do not think this is also happening in our study system because most of the fishing effort in this region is applied only to abalone and lobster, which raises concerns, particularly after detecting that lobster is the most important component of the ecosystem (highest keystonicity). According to the model, a relatively small change in lobster biomass could strongly affect the ecosystem structure and the fishery. We believe fishing effort for lobster should be carefully observed to maintain fishing mortality close to the current values. Further exploration of alternative resources might prove worthy, especially for fishes. This model can be considered a tool to aid in such exploration.

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