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Trophic models for investigation of fishing effect on coral reef ecosystems☆

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Abstract

A comparison was made using general trophic models of three coral reef slopes in the Mexican Caribbean. Two reef slopes are in semi-protected areas (Boca Paila, Tampalam) and the third is subject to more intense exploitation (Mahahual). The mass-balanced models of the three reef slopes were derived from fish biomass density data obtained directly from field measurements (fish census). Other trophic groups were derived from published sources. Initial parameters for the three reef slopes were calculated using the Ecopath with Ecosim software. Comparisons of model outputs were done to establish differences between reef slope systems that are semi-protected and unprotected from fishing activities. The most significant results include: partition of production was always lowest for the unprotected reef slope; net primary production was three times higher for the semi-protected slopes than for the unprotected one; total catch in the unprotected reef slope was three and eight times higher than the two semi-protected reef slopes; food chain length increased as total catch increased; the calculated trophic level of the catch was relatively lower in the unprotected reef slope; and catch per net primary production (gross efficiency) was higher in the unprotected reef slope than the semi-protected reef slopes. It is concluded that trophic macrodescriptors can serve as a guide to the hard-to-detect negative effects of coral reef management, aid in decision-making, and emphasize the effects that structural descriptors, (e.g. total fish biomass, diversity indices) do not detect.

Keywords: Food webs; Coral reefs; Fishing effect; Marine protected areas; Reef fish

1. Introduction

Fishing activities have a wide impact spectrum and cause direct and indirect effects on fish populations and ecosystems (Pauly et al., 1998, 2002). These effects have been extensively documented for reef ecosystems (reviewed by Russ, 1991; Jennings and Lock, 1996; Jackson et al., 2001; Russ, 2002). It is also well known that fishing activities directly affect target species' population structure, growth, reproduction, and distribution and have indirect effects on non-target fish species or invertebrate populations and their reef habitats (Jennings and Lock, 1996).

Despite this extensive knowledge, very little is known about the effects of fishing on recorded changes in multispecies communities (see Jennings and Lock review 1996; Russ, 2002), and even less about the responses of different community attributes. Coral reef studies have generally identified changes

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in ecosystem structure in response to fishing based on the structural aspects of fish and coral communities (i.e. biomass and diversity), and have identified the indirect effects of commercial fishing on the trophic structure or key species of a fish community (Jennings et al., 1995; Jennings and Polunin, 1997; Done and Reichel, 1998; Arias-González et al., 1999). Other studies have focused on a global interaction system quantified via matter or energy flow (realized food webs), in addition to biomass state, biodiversity, key species and fish trophic structure (Johnson et al., 1995; McClanahan, 1995; Arias-González et al., 1997; Arias-González, 1998). Despite the increasing number of studies in the area, however, there is still very little information on how the different indicators may vary, or which are most appropriate as indicators of coral reef ecosystem condition.

In recent years, priority has been placed on the identification of indicators and indices that allow detection of changes in ecosystems as structural and functional responses to anthropogenic impact, (e.g. Costanza, 1992). Simultaneously, increasing numbers of environmental managers have become interested in including ecological considerations in management plans and are searching for ecological indicators to assess ecosystem health (Jørgensen, 2000). Impetus is added to these two trends by the increasing knowledge of the enormous impact suffered by aquatic ecosystems from human activities such as overexploitation and pollution, and from climate anomalies (Done and Diop, 2000). All these elements also highlight the urgent need for collection and effective use of ecosystem information to guide management strategies.

Food web analysis (e.g. realized food webs = when the metric of measurement is energy or matter flow, *sensu* Post, 2002) is a potential functional descriptor of coral reef ecosystems. In theory, trophic networks have a series of characteristics that make them excellent possible ecological macrodescriptors (Winemiller, 1990). The study of trophic webs has a number of potential advantages, including the likely prediction of negative effects in cascade caused by anthropogenic impacts in ecosystems, and a greater understanding of ecosystem management (Cohen et al., 1993). Conservation of living resources and biodiversity could be better advanced if the consequences of trophic web modification were predictable. If a trophic network is defined as a model of energy and material flow between organisms via predation processes (Cohen et al., 1993), then the extraction of elements from the intricate food web and the changes produced in the population and community structure by this extraction should produce a disruption in the trophic structure and a direct or indirect change in the trophic web.

The question remains, however, of how extensive and of what magnitude are the changes produced by fishing activities in reef ecosystems? Jackson et al. (2001) showed that the representation of a simplified food web after fishing is necessarily more arbitrary than it is before fishing. For example, the reduction in shark populations through fishing results in a reduction in the sea cow population and a consequent increase in seagrass, plus a simultaneous reduction in predator and grazing fish and corals. One of the most pervasive signs of intensive fishing is "fishing down the food web" in which landings are increasingly dominated by smaller species from lower trophic levels (Pauly et al., 1998; Jennings et al., 2002).

In recent studies conducted on the coral reefs of the Yucatan Peninsula, realized food webs information, using mainly mass-balance models, was used to analyze coral reef structural characteristics (i.e. habitat complexity or reefscapes; González-Gándara et al., 1999), and to compare trophic structure between areas that are semi-protected and unprotected from human impacts (Arias-González, 1998). The reef comparisons used nested model sets as trophic macrodescriptors to develop a measure of anthropogenic impact in coral reef ecosystems (Arias-González, 1998). This analysis suggests that network analysis and associated trophic indicators could reflect coral reef condition or functional response to a specific impact, and allow detection of the negative effects of coral reef management. Use of this kind of analysis is further supported by research done in other ecosystems, which demonstrates the effectiveness of network analysis and mass-balance marine aquatic ecosystem assessment (Baird and Ulanowicz, 1989, 1993; Christensen and Pauly, 1998; Jarre-Teichmann, 1998).

The main objectives of the present study were to show how trophic structure can be used to assess a coral reef system's response to fishing stress, and to test the effectiveness of coastal marine protected areas in sustaining coral reef yield. An analysis was carried out comparing semi-protected and unprotected coral reef systems in the Mexican Caribbean (Arias-

González, 1998; Nuñez-Lara and Arias-González, 1998), taking advantage of a marine protected area that includes coral reef ecosystems. Three of the nine trophic models developed by Arias-González (1998) were employed in the present study. This author developed mass balance models and described general trophic trends in relation to semi-protected and unprotected reefs, but did not use trophic descriptors to investigate the effects of fishing on coral reef ecosystems. In addition to fishing activities, trophic descriptors generated for previous studies using Ecopath (Christensen and Pauly, 1992), but not used in these studies, were used in the present study to broaden the ecological coverage of fishing activities.

It needs to be emphasized that the estimations of different descriptors used in past studies and the present study are the result of a number of parameters and their interactions within the models. The possibility that structural differences between reefs may be represented in the analysis cannot be discounted. Research is currently in process on other reefs both outside and inside the studied marine protected area. Determining and defining these differences is not easy, especially at sites where no management plans exist to establish control of protected areas and/or where fishery statistics are not reliable. We think it important, however, that fish data collected directly at the study sites was used in trophic model construction and the study of how these models vary under a definition of differential fishing resulting principally from geographic conformation, because no study on this has yet been done for coral reefs.

2. Methods

2.1. Study area

Three reefs on the central and southern Mexican Caribbean coast were included in this study: Boca Paila (20°08′N, 87°28′W), Tampalam 19°08′N, 87°32′W) and Mahahual 18°43′N, 87°41′W) (Fig. 1). Boca Paila and Tampalam reefs are within the semi-protected Sian Ka'an Biosphere Reserve, with Boca Paila located near the northern Reserve border and Tampalam near the southern Reserve border. Mahahual reef is outside the Reserve, approximately 50 km south of Tampalam reef. The 528,000-ha Reserve, created in 1986, includes 120,000 ha of coastal, marine and reef zone areas (Gutiérrez-Carbonell and Bezaury-Creel, 1993), and is divided geographically by the Ascension and Espiritu Santo bays. This section of the reef is 100 km long and has variable development. Another 37,000 ha of marine area, mostly coral reefs, were added in February 1998 (Arias-González, 1998). Since its creation, some restrictions have been implemented on harpoon and net use, though five fishing cooperatives and five independent licence holders continue to operate in the Reserve. They mainly exploit lobster and some have concessions to exploit coral crab, sharks and use coral nets.

Arias-González (1998) provides the following general description of the studied systems: "Mahahual Reef is one of the coastal villages with the greatest amount of local tourism. Due to its easy reef access it is one of the southern Mexican Caribbean coast's most popular attractions. Originally a fishing village, this industry has declined during the last 10 years. The number of remaining so-called independent fishermen operating mainly in this area ranges from 30 to 90. Two cooperatives are also based in the area with an operating range exclusively located on the Chinchorro Bank. The fish caught by the independent fishermen are both for commercial and personal consumption. The principal fish species captured include barracuda, hogfish, groupers, snappers and pluma, and the main fishing methods are harpoon, nets, lines and diving. The three reefs have similar zoning but differ in their reef development. In the Mexican Caribbean, the reef platform gradually widens from north to south, being widest in the southern reefs. Various characteristics distinguish Boca Paila reef from the other two: its submerged crest, its proximity to a coastal lagoon (Boca Paila) and the reef lagoon being open to the sea. These characteristics ensure that the reef lagoon differs substantially from those of the other two systems. The Boca Paila lagoon is deeper, has greater seagrass bed and coral coverage, and larger sediment coverage with algal patches. Tampalam has the least amount of development of the three coral reef ecosystems because the channels in the reef front and slope are lower than those found in Boca Paila and Mahahual. Its reef crest is wide in the north where it joins with the coast. The corals in the Tampalam reef slope are more developed where the slope gradually declines, with abundant, uneven coral reaching heights no greater than 1.5 m. Mahahual has

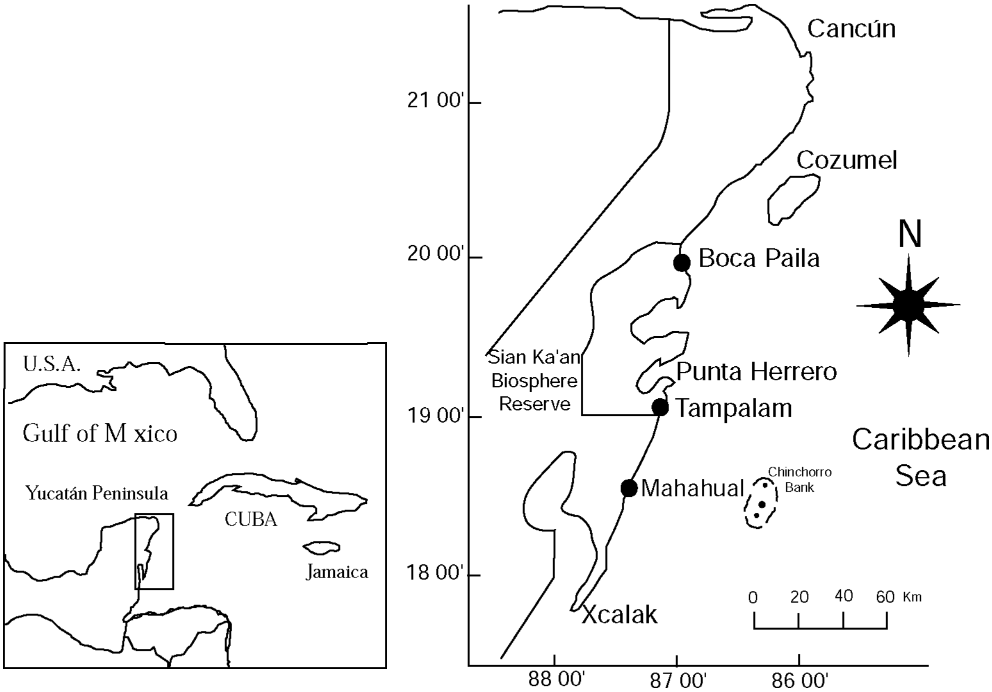

Fig. 1. Location of study site along the Mexican Caribbean coast.

the most developed and complex reef structure with a reef terrace width ranging up to 30 m. Its northern reef crest joins with the coast, producing more extensive seagrass beds within this lagoon than those of the other reefs. The continental shelf's development generates a complex system of large mountain chains".

Boca Paila reef is located north of the bays that divide the Reserve, and Tampalam is to the south, with approximately 80 km between them. The area between the sites is relatively isolated, and serves to diminish the incursion of fishers into distant sites, creating naturally protected areas. This isolation is further enhanced by a lack of terrestrial access: the area can only be entered from Tulum to the north, and from Mahahual to the south. The Reserve also experiences a division in resource use. Its northern portion is primarily used by the tourist industry for sports fishing, diving and lobster trapping, and only very lightly by the commercial fishing fleet. In contrast, the southern portion is primarily used by the commercial fishing fleet for fishing.

These use patterns are reflected in the terrestrial settlement pattern. Boca Paila has only a few scattered houses and there is minimal fishery exploitation. The settlement of Tampalam is a seasonal camp for fishers using only hook-and-line. Finally, the Mahahual area has a number of human settlements with active fishing fleets that use nets, harpoons and lines.

2.2. Trophic models of the Mexican Caribbean coast and Ecopath

Of the energy flow budgets that were developed for the reef front, crest and slope habitats of the Mahahual, Tampalam and Boca Paila coral reef ecosystems (Arias-González, 1998) (Fig. 1), only the reef slope models were employed in the present study. Reef slopes are considered to be relatively stable subsystems in large temporal scale studies (René Galzin, personal communication). Initial parameters (i.e. biomass, production, consumption, ecotrophic efficiency and diet) for the different fish, heterotrophic and autotrophic benthos, and plankton species groups, as well as primary production rates (Tables A.1a and A.1b), were obtained directly from these models (Arias-González, 1998). Original parameters and fluxes for these models were derived by this author, using Ecopath, in the following way:

(a) The fish species, abundances and lengths were based on visual census studies done by Nuñez-Lara (1998). For each of the three reefs studied, the fish counts were done in the morning. The fish lengths recorded by this author were converted to biomass using isometric growth equations, whereby $W = aL^b$. The constants for each fish species were obtained from Munro (1983) and Sierra et al. (1994) for Caribbean fish. For species with no known isometric values, the same constants were used as for fish with similar shapes. Biomass was generated from the average weight values obtained for each species multiplied by the average abundance for each of the species. A diet matrix was developed for most of these species from published data (Randall, 1967; Claro, 1994; Opitz, 1996). Fish were grouped into seven major functional categories (Randall, 1967): (1) fish feeders; (2) ectoparasite feeders; (3) generalized carnivores; (4) "shelled" invertebrate feeders; (5) sessile animal feeders; (6) zooplankton feeders; and (7) plant and detritus feeders. Other (non-fish) organisms were grouped into six functional categories: (8) heterotrophic benthos; (9) zooplankton; (10) microfauna; (11) phytoplankton; (12) autotrophic benthos; and (13) detritus. The unknowns in this study were the non-fish group biomasses. The P/B and Q/B values for the fish groups were estimated using the empirical relationships of Pauly (1980) and Palomares (1991).
(b) P/B and Q/B values and diet for non-fish groups were obtained from Opitz's (1996) information based on analysis of a hypothetical Virgin Island/Puerto Rico reef ecosystem. This author obtained biomass, diet composition of the various consumers, and consumption and production rates for different invertebrate organisms using published data and ecological efficiencies.

The Ecopath with Ecosim software integrates several approaches for global studies of aquatic ecosystems: that originally developed by Polovina and Own (1983) and Polovina (1984, 1985); the network analysis of Ulanowicz (1986); temporal and spatial ecological analysis (Walters et al., 1997, 1999, 2000); as well as policy optimizations (Walters et al., 2002). The conjunction of these approaches is found in the Ecopath with Ecosim (EwE) computer software, which integrates a series of ecological indicators related to ecosystem development attributes (Christensen and Walters, 2003).

The mass-balance modelling approach used here is implemented with a set of simultaneous linear equations represented as follows (Christensen and Pauly, 1992).

$$\frac{B_i P}{B_i \mathrm{EE}_i} = \sum_{j=1}^{n} \frac{B_j Q}{B_j \mathrm{DC}_{ji}} - \mathrm{EX}_i = 0$$

where B_i is the mean biomass of functional group i; P/B_i is its production/biomass ratio; Q/B_i its food consumption per unit biomass; EE_i the ecotrophic efficiency (i.e. the fraction of a prey species' annual production that is consumed by the predator and harvested); DC_{ji} the fraction of prey i consumed by predator j; and EX_i is the export of i.

2.3. Model analysis

The models were developed using a top-down simulation based on visual fish census data collected in the area (Nuñez-Lara, 1998; Nuñez-Lara and Arias-González, 1998). The biomass calculated for each fish species was used as a starting point for the trophic mass-balance model (Table A.1c). It was assumed, by using an EE of 0.95, that natural predation or fishing consumed a large portion of fish production. Fishery catches were estimated from 1998 data obtained directly from fishers who operate in the Mahahual and Tampalam areas and introduced to the model (Tables A.2a and A.2b). Fishing statistics for the zone show catch volume per fishing zone (in this case from Punta Herrero to Xcalak) per species (Fig. 1), and total catch volume for each fishing location (in this case Tampalam and Mahahual). Using this data the percentage of fish catch per location is known, but not the percentage for each species fished per location. To obtain the fishing proportion for each species group it was assumed that the fishing proportions are similar in each of the locations. The species caught in the entire fishing zone were grouped by trophic category. The value of each species per category was then added and the total divided by total catch to obtain a relative catch value per trophic category. This relative value was in turn used to generate a catch value for each trophic category for each of the locations. It was assumed that the fishery catches came directly from the study areas (i.e. between ~1 and 10 km distance from the coast, or 10 km^2), with the exception of Boca Paila, which was assumed to be half of the fishery that operates in Tampalam. The *P*/*B* ratios used to estimate fish production were adjusted to account for the fisheries in the three studied reef systems.

Mass balance was calculated assuming only exports by the fisheries and no imports from contiguous systems. Heterotrophic and autotrophic production was estimated to the level necessary to maintain fish biomass production. To achieve this, the models were assumed to be in an equilibrium state, that is, with a net primary production to respiration ratio close to 1. This was done to avoid production under- or overestimation, because the actual production values for the area are unknown.

Parameters and indices produced by the EwE software were used for the inter-reef comparative analysis.

3. Results

Net primary production, total production and biomass estimates were higher for Boca Paila and Tampalam reefs than for Mahahual (Fig. 2 and Table A.3). This was also true for estimated total system throughput (consumption, respiration, flows to detritus). Overall net primary production was similar for Boca Paila and Tampalam reefs, and three times higher than that at Mahahual reef. Biomass for fish (by trophic class), heterotrophic and autotrophic benthos, zooplankton and microfauna were also higher for Boca Paila and Tampalam reefs than for Mahahual (Table 1).

On Boca Paila reef and Tampalam reef, respectively, fish groups accounted for 1 and 0.6% of total production, 2 and 0.8% of net primary production, 15 and 11% of total biomass, and represented 11 and 8% of total system consumption. Herbivorous fish, sessile animal feeders, fish feeders and generalized carnivores had the highest estimated food intake in both reefs; shelled invertebrate feeders also belonged in this category for Tampalam reef. For Mahahual reef, fish groups represented 0.9% of total production, 1% of net primary production, 15% of total biomass, and 10% of total system consumption. Herbivorous fish, zooplankton feeders, sessile and shelled invertebrate feeders and generalized carnivores had the highest estimated food intake. These values were derived from the values summary table (Table A.3) and the production, consumption and biomass values per trophic group table (Table 1).

Partition of total production varied considerably between reefs, though it was always lowest on the

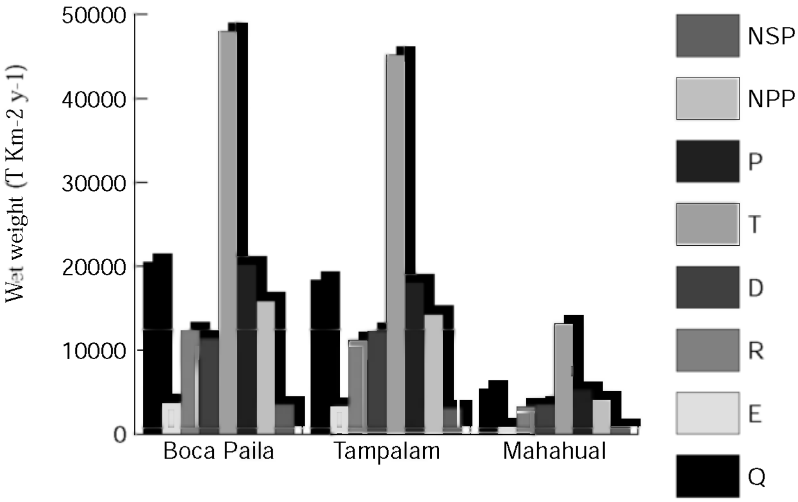

Fig. 2. Sum of all consumption (*Q*), of all exports (*E*), of all respiratory flows (*R*), of all flows into detritus (*D*), total system throughput (*T*), sum of all production (*P*), calculated net primary production (NPP) and net system production (NSP) in t wet weight per km^2 per year.

Table 1
Biomass (t wet weight per km^2), production and consumption (t wet weight per km^2 per year) in the three coral reef slope system models

	Groups								
	Boca Paila			Tampalam			Mahahual		
	B (%)	*P* (%)	*Q* (%)	*B* (%)	*P* (%)	*Q* (%)	*B* (%)	*P* (%)	*Q* (%)
Fish feeders	2.08	0.14	0.93	0.56	0.04	0.22	0.88	0.11	0.60
Ectoparasite feeders	0.44	0.04	0.21	0.05	0.00	0.03	0.10	0.01	0.10
Generalized carnivorous	1.73	0.22	0.72	1.46	0.10	0.68	2.28	0.28	1.18
Shelled invertebrate Feeders	0.88	0.06	0.39	2.86	0.16	1.36	1.35	0.11	0.81
Sessile animal feeders	2.87	0.16	1.41	1.90	0.08	0.82	2.99	0.16	1.54
Zooplankton feeders	1.06	0.21	0.77	0.62	0.06	0.44	0.78	0.12	0.55
Plant and destritus feeders	5.58	0.30	6.21	3.25	0.17	4.58	4.56	0.27	6.72
Heterotrophic benthos	12.30	8.30	24.82	15.22	11.98	33.69	13.62	12.60	29.91
Zooplankton	3.77	8.19	33.26	1.95	4.37	17.76	1.80	4.56	17.96
Microfauna	0.42	5.71	31.27	0.41	6.85	40.43	0.33	6.08	40.63
Phytoplankton	3.47	30.42	–	2.76	24.80	–	2.38	24.37	–
Autotrophic benthos	65.39	46.24	–	68.97	51.38	–	68.92	51.32	–
Total	1018.73	20180.21	20496.66	1014.96	18053.11	18346.19	333.43	5265.74	5432.85

Mahahual reef slope. Division of total production was, however, very similar within trophic groups in the three reefs (Fig. 3). The highest autotrophic and heterotrophic benthos, phytoplankton, zooplankton and total fish production was estimated in Boca Paila reef while microfauna production was the highest in Tampalam reef. Fish production in Boca Paila was nearly twice that at Tampalam, and four times that at Mahahual. Tampalam had the highest estimated shelled invertebrate feeders production (Table 1). This was notably increased by heterotrophic benthos production, which resulted in the high net primary production and total production for this system (Table A.3).

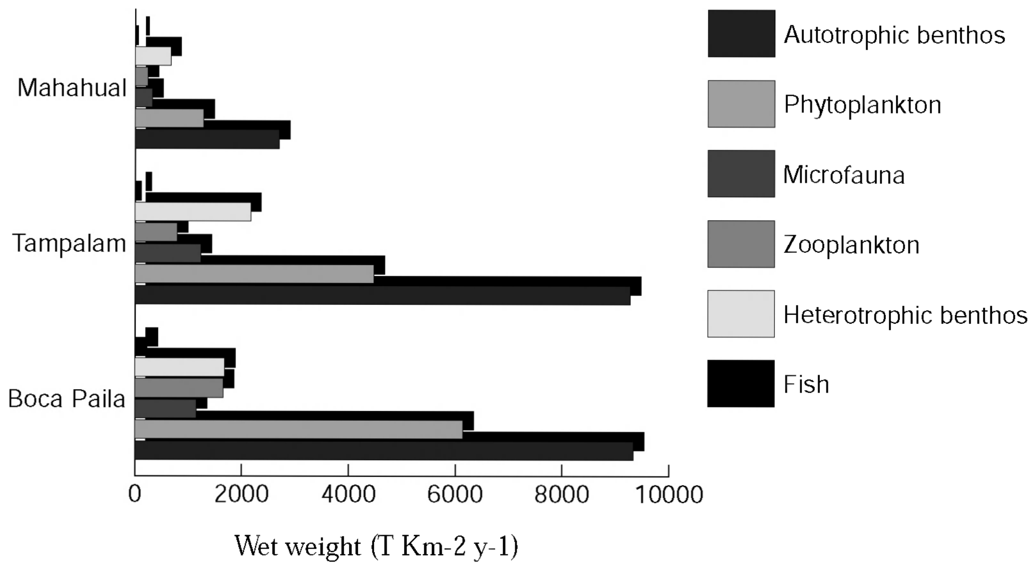

Fig. 3. Partition of total production (t wet weight per km^2 per year) of fish, heterotrophic benthos, zooplankton, microfauna, phytoplankton and autotrophic benthos in the three coral reef slope system models.

Table 2
Transfer efficiency (%) and biomass (t wet weight per km^2) of each trophic level for each coral reef slope system model

	Trophic category									
Boca Paila[a]										
Source	I	II	III	IV	V	VI	VII	VIII	IX	Geometric mean (%)
Producers	–	19.6	20.3	7.0	2.8	0.2	–	–	–	14.1
Detritus	–	12.6	20.7	7.3	2.9	0.2	–	–	–	12.4
Total	–	16.4	20.4	7.1	2.9	0.2	–	–	–	13.4
Biomass	701.567	142.034	120.227	49.198	5.565	0.141	0.000	–	–	
Tampalam[b]										
Source	I	II	III	IV	V	VI	VII	VIII	IX	Geometric mean (%)
Producers	–	23.2	16.6	8.9	7.8	7.4	7.0	3.7	–	15.1
Detritus	–	10.4	18.9	9.1	7.9	7.4	7.4	3.7	–	12.1
All flows	–	15.7	17.5	9.0	7.9	7.4	7.2	3.7	1.9	13.5
Biomass	727.980	142.725	107.285	32.857	3.783	0.309	0.021	0.001	0.000	
Mahahual[c]										
Source	I	II	III	IV	V	VI	VII	VIII	IX	Geometric mean (%)
Producers	–	24.0	19.4	11.3	10.9	10.8	10.5	7.9	–	17.4
Detritus	–	9.9	21.6	11.5	10.9	10.8	10.8	8.0	–	13.5
All flows	–	15.8	20.2	11.4	10.9	10.8	10.6	7.9	8.4	15.4
Biomass	237.731	46.560	36.564	11.277	1.201	0.085	0.006	0.000	0.000	

[a] Proportion of total flow originating from detritus: 0.43.
[b] Proportion of total flow originating from detritus: 0.51.
[c] Proportion of total flow originating from detritus: 0.50.

Fisheries were more significant on Mahahual reef. Total estimated catches in this reef were three times higher than for Tampalam and eight times higher than for Boca Paila. The fishery gross efficiency estimates were 0.000079 for Boca Paila, 0.000174 for Tampalam and 0.002399 for Mahahual (Table A.3). The fisheries were found to act at the same trophic levels as generalised carnivores on Boca Paila and Tampalam reefs, and as invertebrate feeders on Mahahual reef. Maximum catches in the studied reefs are from piscivorous and carnivorous fish (Table A.2).

Trophic group characteristics exhibited a similar pattern, as illustrated by a Lindeman Spine, which condenses the trophic structure of the systems by aggregating groups into a single linear chain (Kay et al., 1989). Estimated biomass by trophic level was higher for Boca Paila and Tampalam reefs than for Mahahual reef (Table 2). Each group can act as a predator on several different trophic levels. Tampalam reef had higher biomass values in trophic levels I, II, VI, VII and VIII than did Boca Paila reef, while Boca Paila had higher biomass values in trophic levels III, IV and V. These differences may be due to a higher fish biomass level and lower heterotrophic benthos biomass for Boca Paila reef.

Transfer efficiency for Mahahual was generally higher than at Boca Paila and Tampalam reefs (Table 2), which had similar transfer efficiencies. Total geometric mean transfer was 13.4% for Boca Paila, 13.5% for Tampalam and 15.4% for Mahahual. Tampalam and Mahahual had the longest Lindeman chain length (9) and Boca Paila the shortest (6). This may have resulted from their having the lowest activity in the highest trophic level, which is evident in biomass reduction in fish, generalized carnivores and invertebrate fish feeders.

The highest total number of pathways was found for Mahahual reef (193), followed by Boca Paila (181) and Tampalam (154) reefs (Table 3). The maximum number of pathways for Mahahual reef was in the fish feeders and intermediate trophic levels, mainly among generalized carnivores and shelled invertebrate feeders. Boca Paila and Tampalam reefs also had the most pathways in the fish feeders category. Of the three reefs, Mahahual had the highest number of fish feeder pathways. The lowest average trophic level, after weighting for biomass, was found in Tampalam (2.57) followed

Table 3
Number of pathways, trophic level (TL), primary production required (PPR: t wet weight per km^2 per year), consumption (Q: t wet weight per km^2 per year) and PPR to Q ratio

Compartments	Number of paths	TL	PPR	Q	PPR/Q
Boca Paila					
Fish feeders	89	3.76	16015	190.79	83.94
Ectoparasite feeders	6	3.01	457	43.54	10.50
Generalized carnivorous	46	3.43	4057	147.69	27.47
Shelled invertebrate feeders	8	3.01	843	80.71	10.44
Sessile animal feeders	7	2.99	2990	289.29	10.34
Zooplankton feeders	8	3.01	1344	158.19	8.5
Plant and destritus feeders	8	2.72	9849	1272.66	7.74
Heterotrophic benthos	6	2.01	16156	5087.76	3.18
Zooplankton	2	2.00	6817	6817.29	1.00
Microfauna	1	2.00	6408	6408.43	1.00
Total	181	–	–	20496.35	–
Tampalam					
Fish feeders	76	3.84	6775	39.48	171.61
Ectoparasite feeders	5	3.12	33	4.64	7.11
Generalized carnivorous	37	3.37	5261	125.64	41.87
Shelled invertebrate Feeders	10	3.13	1895	250.27	7.57
Sessile animal feeders	7	3.08	1029	150.65	6.83
Zooplankton feeders	5	3.12	565	79.83	7.08
Plant and destritus feeders	7	2.74	4185	840.51	4.98
Heterotrophic benthos	5	2.12	14532	6180.99	2.35
Zooplankton	1	2.00	3258	3257.66	1.00
Microfauna	1	2.00	7417	7417.18	1.00
Total	154	–	–	18346.86	–
Mahahual					
Fish feeders	96	3.52	791	32.45	54.64
Ectoparasite feeders	5	3.12	16	5.54	6.52
Generalized carnivorous	46	3.32	1345	64.19	19.40
Shelled invertebrate feeders	23	3.12	273	43.75	9.18
Sessile animal feeders	7	3.09	413	83.77	6.38
Zooplankton feeders	1	3.00	397	30.04	4.26
Plant and destritus feeders	8	2.59	1344	365.12	3.90
Heterotrophic benthos	5	2.12	3967	1624.80	2.50
Zooplankton	1	2.00	1477	975.87	1.00
Microfauna	1	2.00	2396	2207.25	1.00
Total	193	–	–	5432.77	–

by Mahahual (2.59) and Boca Paila (2.63). Maximum trophic level for Boca Paila was 3.76, for Tampalam it was 3.84, and for Mahahual it was 3.52.

Primary production required (PPR) for sustaining fish yield, total consumption (Q) and PPR/Q ratio by trophic level is shown in Table 3. The maximum difference in PPR was mainly in the fish feeder group, which had approximately twice the PPR at Boca Paila reef than at Tampalam reef, and 20 times more than that at Mahahual reef. Although the PPR for sustaining yield of piscivorous fish at Boca Paila was considerably higher than at Tampalam, the PPR/Q ratio was higher in the latter. For Mahahual reef, energy conversion in this group was less than in the other two reefs.

4. Discussion

Trophic level has been proposed as a potential indicator of fishery effect in aquatic ecosystems (Pauly et al., 1998, 2002). This kind of analysis can be based on identification of the trophic level of captured fish or on in situ analysis of fish populations in a studied system. Unfortunately, we were unable to directly define trophic levels for the fishery captures from Mahahual and Tampalam because the captures at each are aggregated to a fishery zone. Nonetheless, significant observations were made that recorded fishing captures are concentrated in the fish feeders, generalized carnivorous and sessile animal feeders trophic groups.

The results of these simulations are apparently adequate for determining relative condition of the three reefs, as they show the effect of fishery activity and how the unprotected Mahahual reef is more affected by exploitation than the two semi-protected reefs. The top-down approximation used in the analysis reveals the effects of fishing-related exploitation in the three reefs. Information on the area's fisheries shows a direct relationship between the resources exploited by the fishery and the result obtained in this study: a lower trophic level in the Mahahual reef catch. This is relevant because it clearly suggests fishery activity effects on reef trophic structure, mainly on Mahahual reef, and a contrasting effect from the semi-protected status of the Boca Paila and Tampalam reefs.

The principal data suggesting these effects are the large differences in PPR (by a factor of 3) to sustain fish biomass consumption, total production and throughput between the exploited reef and semi-protected reefs. If the estimated net primary production for Boca Paila and Tampalam is taken as being close to current levels, then that for Mahahual indicates production of autotrophic and heterotrophic biomass that will not be consumed by certain fish groups. Theoretically, this would result in structural differences between Mahahual and the semi-protected reefs.

Some support for this is provided by recent analyses done with data from the same region which showed greater algae coverage in the semi-protected reefs than in the unprotected reef. This suggests high algae consumption by a high herbivorous fish biomass in unprotected reefs, probably due to reductions in predation by piscivorous and generalized carnivores (Arias-González et al., 2000a,b; Ruiz-Zárate et al., 2003; Nuñez-Lara et al., 2003). A recent study (Nuñez-Lara et al., 2003) of 8 coral reefs (4 within the Reserve and 4 outside it) showed a generally greater number of species and higher organism density in the semi-protected reefs than in the unprotected reefs, and larger-sized herbivores in the unprotected reefs. This effect is not clear in the original data used in the models (Table A.1), as can be seen in the herbivore biomass values for Boca Paila and Mahahual being very similar, and quite high for Tampalam. It should also be taken into account that the Mahahual reef structure is in generally good condition compared to other unprotected reefs where the effects of past anthropogenic activities are quite obvious (Ruiz-Zárate et al., 2003).

Further support for structural differences is found in data showing that the number of juvenile lobsters recorded at the protected Tampalam Reef is three times greater than that recorded at the unprotected Mahahual Reef (Arias-González et al., 1999).

The most obvious quantitative differences in the trophic structure of the three model reefs were the higher production of fish belonging to the fish feeder, generalized carnivore, sessile animal, zooplankton, and plant and detritus feeder groups on Boca Paila reef; and the higher production of shelled invertebrate feeders on Tampalam reef. These high flows produce a strong effect, resulting in higher production of benthic heterotrophs and autotrophs for Boca Paila and Tampalam reefs than for Mahahual reef.

Overall, differences between the semi-protected reefs and Mahahual were strong and clear. Analysis of the three reefs suggests a descending condition gradient extending from Boca Paila south to Mahahual, with Tampalam being in an intermediate state. This is likely linked to fish biomass production estimated for the three reefs, which also exhibits a decreasing gradient, with the exception of shelled invertebrate feeders on Tampalam reef. Fish biomass production was highest for Boca Paila, intermediate for Tampalam and lowest for Mahahual. This suggests that the protected status of the Reserve does effect Tampalam and Boca Paila reefs, and that the differences between them are linked mainly to the effect of a probable selective fishery on Boca Paila.

The recent study of Nuñez-Lara et al. (2003) using a grouping analysis of fish species abundance at 8 reefs in the Mexican Caribbean showed one grouping of the semi-protected reefs and another of the unprotected reefs. The only exceptions were Tampalam, which did not fit with either of the two reef groups (and is thus considered an atypical reef), and the Punta Allen reef within the Reserve, which was grouped with the unprotected reefs. According to these authors the gradient not only coincides with latitudinal variation but with variation in protection level against human exploitation (e.g. fishing activities). However, the possibility that structural differences between reefs may be represented in the analysis cannot be discounted.

Levels of human development and fishery exploitation are strongly coincident with the fish biomass gradient. If the number of fishers is used as a fishery index, Boca Paila would have an index of 5 (in reality this would be 0 since no fishery statistics exist for this reef), Tampalam one of 10, and Mahahual one of 120 (these reefs do have fishing activity data, as shown in Table A.3). The distance of the Boca Paila and Tampalam reefs from fishing settlements also likely serves as an additional protective element within the overall protective mantle of the Reserve.

An interesting result of the comparative analysis of the three reef models was the short Lindeman chain length of the Boca Paila reef model, associated with this reef's maximum fish biomass production, especially fish feeders and generalized carnivores, which also decreased relative system efficiency. This shows the sensitivity of the reef models to small changes in fish biomass production and exploitation. The Tampalam and Mahahual models, with more exploitation and less control over the highest trophic levels, especially fish feeders, had longer Lindeman chain lengths and much higher efficiency. This suggests that even minimal fish extraction may cause a detectable change in the trophic structure of a system. It also suggests that even slight increases or decreases in the biomass production of fish feeders and generalized carnivores may produce a significant effect in the food web structure.

The inverse relationship between over-exploitation of top predators and Lindeman chain length and trophic efficiency implies that over-exploitation of top predators can significantly effect system food chain length. When assembling the Lindeman chain, the compartments are separated into parts according to the different feeding pathways, instead of calculating mean trophic position (Niquil et al., 1999). According to this, over-exploitation should result in a greater range of feeding pathways. The results of the present study suggest that fish extraction from fishery activities disrupts the food chain, lowering trophic level, and increasing Lindeman chain length and system feeding pathways. This implies that species elimination, or the possible dominance of a single species, from fishing activity allows other species to emerge and exploit different feeding pathways. This kind of information has already been integrated into ecological theory, and the implications of increased food chain length are thoroughly discussed in Post's (2002) review.

Sensitivity to normal or high fish extraction can be analyzed by calculating the values for the ratio between PPR and consumption (Q) for each of the reef models, for each trophic level. As can be seen in Table 3, this ratio tends to increase from the lower trophic levels to the highest, for all three reefs. The possible exception is the Mahahual reef model, where the ratio for fish feeders is almost half to one third that for Boca Paila and Tampalam. This may indicate that beyond a certain amount of fish extraction trophic structure can be considerably affected.

Detection of changes through relatively rapid analysis of the actual reef sites allows detection and substantiation of the ecosystem changes suggested by the models. In the present study, the models were used not only as macrodescriptors of change but also for defining future lines of research in areas that may not have been evident with only a structural analysis, such as variation of fish community trophic structure, size-related fish trophic structure, trophic levels and food chain length. Another interest point that can emerge of this study is the potential resaturation of food webs using as control the marine protected areas' food webs.

The analyses in the present study suggest that important differences can be detected between protected and unprotected reefs and that protection, in this case by the reserve, can be highly beneficial to fishery production. Determining and defining these differences is not easy, especially at sites where no management plans exist to establish control of protected areas, and/or where fishery statistics are not reliable.

Given the small number of reefs (replicates) included in this study, it is not clear whether the differences detected reflect system conditions or are a functional response of the system to physical change, or to change in anthropogenic impact. This is difficult to differentiate in ecological studies. However, the sensitivity to established interactions seen in the models strongly suggests that the differences noted in the estimations are closely related to a protective effect from the reserve. In fact, the sensitivity was strong enough to detect changes in the trophic structure of the modelled systems.

A key element in increasing the accuracy and effectiveness of these analyses is to continue applying them in as wide an array of samples as possible. This will allow more exact quantification of coral reef functional patterns in relation to environmental impact. To pursue this, trophic standards need to be determined in a greater number of reefs, both within and outside protected areas. This will allow establishment of standards with which to measure change within and between reefs, as well as standards for exploitation systems.

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Appendix A

See Tables A.1a, A.1b, A.2a, A.2b and A.3.

Table A.1a
Input parameters of trophic groups: inputs

Group name	Trophic level	*B*	PB per year	QB per year	EE
Boca Paila					
Fish feeders	3.8	21217	1303	8993	0.635
Ectoparasite feeders	3.0	4492	1886	9693	0.665
Generalized carnivorous	3.4	17634	2520	8376	0.854
Shelled invertebrate feeders	3.0	8949	1320	9018	0.587
Sessile animal feeders	3.0	29228	1120	9898	0.940
Zooplankton feeders	3.0	10826	3960	14612	0.996
Plant and destritus feeders	2.7	56805	1064	22404	0.946
Heterotrophic benthos	2.0	125281	13371	40611	0.918
Zooplankton	2.0	38438	43008	177356	0.721
Microfauna	2.0	4296	268443	1491799	0.556
Phytoplankton	1.0	35392	173443	–	0.866
Autotrophic benthos	1.0	666176	14008	–	0.428
Detritus	1.0	2000	–	–	0.740
Tampalam					
Fish feeders	3.8	5640	1.30	7.00	0.979
Ectoparasite feeders	3.1	0.480	1.73	9.66	0.950
Generalized carnivorous	3.4	14851	1.21	8.46	0.950
Shelled invertebrate feeders	3.1	29000	1.02	8.63	0.067
Sessile animal feeders	3.1	19290	0.76	7.81	0.950
Zooplankton feeders	3.1	6276	1.66	12.72	0.950
Plant and destritus feeders	2.7	33000	0.95	25.47	0.408
Heterotrophic benthos	2.1	154525	14.00	40.00	0.950
Zooplankton	2.0	19743	40.00	165.00	0.950
Microfauna	2.0	4176	296.00	1776.00	0.500
Phytoplankton	1.0	27980	160.00	–	0.990
Autotrophic benthos	1.0	700000	13.25	–	0.167
Detritus	1.0	2000	–	–	0.725
Mahahual					
Fish feeders	3.5	2950	1880	11000	0.955

Table A.1a (*Continued*)

Group name	Trophic level	*B*	PB per year	QB per year	EE
Ectoparasite feeders	3.1	0.346	1800	16000	0.985
Generalized carnivorous	3.3	7606	1910	8440	0.714
Shelled invertebrate feeders	3.1	4498	1300	9724	0.837
Sessile animal feeders	3.1	9970	0.868	8402	0.949
Zooplankton feeders	3.0	2613	2500	11500	0.950
Plant and destritus feeders	2.6	15213	0.932	24001	0.766
Heterotrophic benthos	2.1	45397	14620	35791	0.938
Zooplankton	2.0	6003	39993	162557	0.953
Microfauna	2.0	1099	291378	2008	0.491
Phytoplankton	1.0	7944	161571	–	0.994
Autotrophic benthos	1.0	229788	11760	–	0.192
Detritus	1.0	2000	–	–	0.740

Table A.1b
Composition diet of the trophic groups: diet

	Prey/predator									
	1	2	3	4	5	6	7	8	9	10
Boca Paila										
Fish feeders	0.022	0.089								
Ectoparasite feeders	0.021	0.011								
Generalized carnivorous	0.155	0.051								
Shelled invertebrate feeders	0.018	0.023								
Sessile animal feeders	0.126	0.046								
Zooplankton feeders	0.154	0.090								
Plant and destritus feeders	0.254	0.059								
Heterotrophic benthos	0.250	1	0.599	0.988	0.983	0.581	0.709			
Zooplankton	0.01	0.012	0.419	0.221						
Microfauna	0.126									
Phytoplankton	0.017	0.182	0.643							
Autotrophic benthos	0.022	0.196	0.257	0.357						
Detritus	0.094	0.214	1							
Import sum	1	1	1	1	1	1	1	1	1	1
Tampalam										
Fish feeders	0.007	0.050								
Ectoparasite feeders	0.020									
Generalized carnivorous	0.330	0.020								
Shelled invertebrate feeders	0.010	0.010								
Sessile animal feeders	0.130	0.070								
Zooplankton feeders	0.060	0.040	0.01							
Plant and destritus feeders	0.133	0.060								
Heterotrophic benthos	0.310	1	0.737	0.99	0.96	1	0.65	0.15		
Zooplankton	0.001	0.01	0.12							
Microfauna	0.10									
Phytoplankton	0.19	1								
Autotrophic benthos	0.002	0.03	0.25							
Detritus	0.01	0.01	0.34	0.19	1					
Import sum	1	1	1	1	1	1	1	1	1	1
Mahahual										
Fish feeders	0.008	0.039	0.001							
Ectoparasite feeders	0.019									

Table A.1b (*Continued*)

	Prey/predator									
	1	2	3	4	5	6	7	8	9	10
Generalized carnivorous	0.094	0.018	0.001							
Shelled invertebrate feeders	0.087	0.010	0.002							
Sessile animal feeders	0.131	0.056	0.007							
Zooplankton feeders	0.082	0.054	0.001							
Plant and destritus feeders	0.174	0.069	0.019							
Heterotrophic benthos	0.309	1	0.723	0.945	0.973	0.520	0.153			
Zooplankton	0.008	0.008	1	0.009	0.120					
Microfauna	0.097									
Phytoplankton	0.185	1								
Autotrophic benthos	0.023	0.016	0.017	0.307	0.248					
Detritus	0.096	0.009	0.163	0.199	1					
Import sum	1	1	1	1	1	1	1	1	1	1

Table A.2a
List of species catches in Tampalam and Mahahual reefs: catches of fish species in Mahahual and Tampalam reefs

Fish species name	Commun name	Catch	Functional trophic category	Total catch/ proportion total catch
Mycteroperca phenax, M tigris, M. bonaci, E. guttatus	Abadejo	11635	7	
Mycteroperca interstitialis, M. venenosa	Barrasa	2490	7	
Charcharinus spp., *Nepriopon* spp.	Tiburon	2056	7	
Scomberomorus maculatus, S. regalis, S. cavalla	Carito	80	7	
Rizoprionodon terranove	Cazon	5748	7	80899
Caranx ruber, C. bartholomaei, C. crysos	Cojinuda	619	7	24.87
Seriola dumerilii, S. rivoliana	Coronado	1397	7	
Epinephelus itajara	Cherna	1249	7	
Lutjanus campechanus	Guachinango	5476	7	
Caranx hippos, C. latus	Jurel	3950	7	
Sphyraena barracuda	Picuda	46199	7	
Mycteroperca microlepis, Epinephelus adsensionis, E. cruentatus	Cabrilla	1931	6	
Epinephalus striatus, E. bonaci, E. morio, E. fulvus	Mero	16088	6	
Gerres cinereus, Eucinostomus gula	Mojarra	105330	6	200813
Trachinotus godeii, T. falcatus, T. carolineus	Palometa	2179	6	61.73
Lutjanus griseus, L. apodus, L. jocu, L. analis	Pargo	73647	6	
Aetobatus narinari, Dasyatis americana	Raya	418	6	
Centropomus undecimalis	Robalo	1220	6	
Lachnolaimus maximus	Boquinete	4900	5	
Ocyurus chrysurus	Canane	151	5	
Haemulon plumieri, H. sciurus, H. parra, H. carbonarium, H. macrostomum	Chacchi	16742	5	
Hemiramphidae, Engraulidae	Chencay	8935	5	43557
Eucinostomus argenteus	Chihua	4981	5	13.39
Balistes vetula	Escochin	150	5	
Mugil curema	Liseta	5549	5	
Cynocion nebulosus	Pinta	759	5	
Lutjanus synagris	Rubio	1390	5	
Total catch		325269		
Mahahual catch		102697		
Tampalam catch		25628		

Table A.2b
Catches introduced to the models: catches (t per km^2 per year) introduced to the models

Group/value	Fleet
Boca Paila	
Fish feeders	0.31
Generalized carnivorous	0.77
Shelled invertebrate feeders	0.17
Total	1.25
Tampalam	
Group/value	Fleet
Fish feeders	0.62
Generalized carnivorous	1.53
Shelled invertebrate feeders	0.33
Total	2.48
Mahahual	
Group/value	Fleet
Fish feeders	2.48
Generalized carnivorous	6.15
Shelled invertebrate feeders	1.33
Total	9.96

Table A.3
Summary of results for the three coral reef slope system models

Statistics	Boca Paila	Tampalam	Mahahual	Units
Sum of all consumption	20496.34	18346.86	5432.77	Wet weight (t per km^2 per year)
Sum of all exports	3782.97	3375.75	919.51	Wet weight (t per km^2 per year)
Sum of all respiratory flows	12360.34	11225.95	3313.47	Wet weight (t per km^2 per year)
Sum of all flows into detritus	11396.86	12253.38	3503.05	Wet weight (t per km^2 per year)
Total system throughput	48037.00	45202.00	13169.00	Wet weight (t per km^2 per year)
Sum of all production	20180.21	18053.00	5267.00	Wet weight (t per km^2 per year)
Calculated trophic level of the catch	3.45	3.46	3.34	
Gross efficiency (catch/net primary production)	0.000079	0.000174	0.002399	
Calculated net primary production	15888.93	14292.65	4151.74	Wet weight (t per km^2 per year)
Total primary production/total respiration	1285	1.27	1.25	
Net system production	3528.59	3066.70	838.27	Wet weight (t per km^2 per year)
Total primary production/total biomass	15.60	14.08	12.45	Year
Total biomass	1018.73	1014.96	333.43	Wet weight (t per km^2)
Total catches	1.25	2.48	9.96	Wet weight (t per km^2 per year)

Biomass in t wet weight per km^2, and all other production, consumption and flow values in t wet weight per km^2 per year.

Annex (c) biomass and number of the main species surveyed and trophic groups of the three reef slope studied.

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