Trophic Model of a Fringing Coral Reef in the Southern Mexican Caribbean [*Modelo Trófico para un Arrecife de Coral de Tipo Borde-Barrera en el Sur del Caribe Mexicano*]

José Humberto Alvarez-Hernández

Instituto Tecnológico de Chetumal. Apdo.
Postal 267. C.P. 77000
Chetumal, Quintana Roo, México

ABSTRACT

A mass balance trophic (Ecopath) model of a coral fringing reef in the southern Mexican Caribbean was constructed from published data. The trophic analysis of this reef ecosystem resulted in a model with a P/R ratio of 0.87, a high connectance index of 0.35, a relatively low value for the Finn recycling index of 10.1% of the total throughput, and a low relative internal ascendancy of 26%. Comparisons with other coral reef ecosystems for the southern Mexican Caribbean suggest maturity is high for the system modeled in the present study.

RESUMEN

Se construyó un modelo balanceado de flujos trófico de biomasa para el arrecife mixto de tipo borde-barrera en la porción sur del Caribe Mexicano, mediante el programa Ecopath. El análisis trofico de este ecosistema dio una relación P/R de 0.87, un índice de conectancia alto de 0.35, un índice de reciclaje de Finn relativamente bajo de 10.1% de los flujos totales, y un valor bajo de ascendencia interna de 26%. Comparado con otros 6 modelos para ecosistemas arrecifales, el ecosistema arrecifal mixto de tipo borde-barrera en su porción Sur del Caribe Mexicano, aparece como uno de los sistemas mas maduros.

INTRODUCTION

Coral reefs are ecosystems found in warm, well-lit waters of tropical oceans. They show high spatial heterogeneity with a great variety of plants and animals, comparable in biodiversity with tropical forests (Connell, 1978). These systems are found in extensive zoogeographic areas of the Indo-Pacific and the Caribbean (Stoddart, 1969). The latter includes the coral reefs of Bermuda, Bahamas, Florida, the Gulf of Mexico and the Caribbean Sea.

The Atlantic coast of Mexico includes a large reef system, with an area of 1,500 km^2, consisting of fringing and barrier island reefs along the littoral coast of the state of Quintana Roo (Jordán, 1993) in the Yucatan Peninsula (Figure 1).

The system exhibits a clear zonation characterized by a lagoon of variable width and mean depth of 5 to 7 m, covered by seagrasses (*Thalassia testudinum*) and algae (*Halimeda* spp., *Udotea* spp., and *Penicillum* spp.), and inhabited by molluscs and fishes (*Gerres* spp., *Abudefduf* spp., *Acanthurus* spp., and *Sparisoma* spp.). Close to the back-reef, there are isolated colonies of alcyonarian and scleractinian corals reflecting a more consolidated substratum (Muñoz, 1992; Alvarez-Hernández, 1994). The back-reef on the shoreline includes the corals *Acropora palmata*, *A. cervicornis*, *Porites porites*, *Agaricia agaricites*, *A. teniufolia*, *Montastrea annularis*, as well as algae, sponges, molluscs, alcyonarians and an abundance of fishes (Muñoz, 1992; Alvarez-Hernández, 1994).

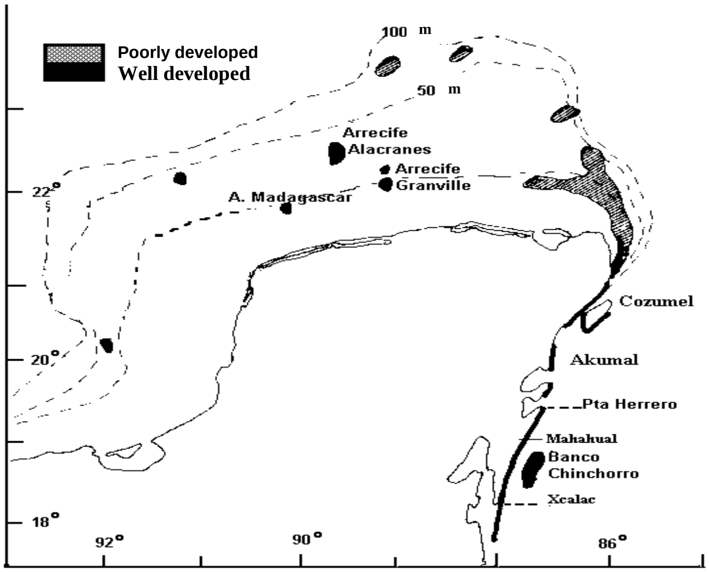

Figure 1: Map of the coral reef systems in the southern Mexican Caribbean (Taken from Chávez, 1994). [*Localización del arrecife de coral de tipo borde-barrera en el sur del Caribe Mexicano (tomado de Chávez, 1994)*].

The exposed fore-reef facing the open sea has a well consolidated substratum, and abundant and diverse coral communities marked by gradients in size, density and diversity. The crest is dominated by alcyonarians (octocorals, particularly plexaurides and gorgonians), together with resistant and fast-growing hermatipic corals such as *Acropora palmata* and *A. cervicornis*. At greater depths, large coral structures of *Montastrea* spp., *Colpophyllia* spp. and *Agaricia* spp., and a great variety of benthic fauna such as sea cucumbers, sponges, molluscs and algae together with larger fishes (*Epinephelus* spp., *Caranx* spp., *Acanthurus* spp., *Chromis* spp. and *Scarus* spp.), are found. Spur and groove systems may be found offshore, at depths of 20 - 25 m (Muñoz, 1992; Alvarez-Hernández, 1994).

The barrier can be divided into northern and southern sectors on the basis of structure, growth and anthropogenic use. The northern sector from Contoy Island to Ascension Bay is characterized by low relief with alcyonarian communities and algae followed by sponges and scleractinian corals (Jordán, 1979). The southern sector, extending from Ascension Bay to Xcalac, is characterized by massive formations of *Montastrea* sp. and *Diploria* sp. in the back-reef while the crest is dominated by hydrocorals and algae, with a well developed fore-reef. Lobster (*Panulirus argus*) and conch (*Strombus gigas*) are fished in both sectors: Tourism was not well-developed at the time of study (early-mid 1990s). Lobster (*Panulirus argus*) and conch (*Strombus gigas*) are fished in both sectors, while tourism is more intense in the north with less development in the south (César-Dáchary and Arnaiz-Burne, 1986).

The objective of this study was to construct a trophic model of a fringing reef typical of the southern sector (Figure 1).

MATERIAL AND METHODS

The southern part of this reef system has a length of about 190 km, with fringing reef, lagoon and barrier island lying on a narrow shelf (Ferre-D'amarre, 1985; Chávez and Hidalgo, 1988). The climate is warm-humid with annual precipitation ranging between 1,100-2,000 mm and mean water temperature of 27.5^{o}C (Ferre-D'amarre, 1985). The oceanic current flows along the coast at speeds often greater than 4 knots. Due to the karstic nature of the Yucatan Peninsula, no rivers exist and fresh-water flows underground (Nolasco-Montero and Carranza-Edwards, 1988).

The Model

The Ecopath program (Christensen and Pauly, 1992; Pauly *et al.*, 2000) was used to construct a mass-balanced trophic model. The basic Ecopath equation is:

$$B_i * PB_i * EE - \sum_{j-1}^{n} B_j * QB_j * DC_{ji} - EX_i = 0$$

where B_i is the biomass of species *i*; PB_i is the production/biomass ratio for species *i*, *EE* is ecotrophic efficiency, QB_j is the consumption/biomass ratio and DC_{ji} the fraction of prey *i* in the average diet of predator *j*.

The required input data were obtained from published literature for the Mexican Caribbean and other regions of the Caribbean. Information was standardized to tons per km^2 of fresh weight for biomass (t·km^{-2}) and year^{-1} for the fluxes (P/B, Q/B). Different conversion factors were used for this purpose (Crisp, 1971). On the basis of the criteria of Opitz (1993), all species were grouped into 11 non-fish groups and 7 fish groups.

Input data

Primary production was estimated as the average of the total primary production of phytoplankton, microphytobenthos, zooxanthellae, macroalgae and seagrasses after Lewis (1981a) and De Jesús (1994).

Phytoplankton biomass was taken from Margalef (1973); benthic primary producers from Lewis (1981a) and De Jesús (1994); zooplankton from abundance data (Suárez *et al.*, 1991) converted to weight based on the average weight per group (M. Ornelas, Centro de Investigación y de Estudios Avanzados del IPN, Mexico, pers. comm.); sessile organisms including meiobenthos from Alcolado (1990); macrobenthos from coverage data of Jordán (1990), Muñoz (1992) and Tunnell *et al.* (1993) transformed after Lewis (1981b); molluscs from Aguirre (1988); echinoderms from Lewis (1981a); crustaceans from Glynn (1973); and birds and turtles from Polovina (1984). The biomass of cephalopods was left for estimation by Ecopath.

The fishes were divided into seven groups: a) Sharks and rays of the genera *Carcharinus*, *Ginglymostoma*, *Dasyatis*, and *Urolophus*; b) Sharks, scombrids and jacks of the genera *Rhizoprionodon*, *Sphyrna*, *Scomberomorus*, and *Caranx*; c) Groupers of the genera *Epinephelus* and *Serranus*; d) Schooling reef fish of the genera *Harengula*, *Opisthonema* and *Jenkinsia*; e) Carnivorous fishes of the genera *Lutjanus*, *Ocyurus* and *Priacanthus*; f) Herbivorous fishes of the genera *Abudefduf*, *Scarus* and *Acanthurus*; and g) Omnivorous fishes of the genera *Thalassosoma*, *Alutera* and *Stegastes*. Fish biomasses were determined from visual surveys by Garduño (1981, 1989), Tunnell *et al.* (1993), and Alvarez-Hernández (1994). Diet compositions for fish groups were taken from Randall (1967) and Claro (1990).

Production/biomass estimates were obtained from various sources: phytoplankton (Margalef, 1973); zooplankton, birds and turtles (Polovina, 1984); sessile organisms and echinoderms (Lewis, 1981b); and molluscs, crustacean and cephalopods from the equation relating growth to natural mortality (Pauly, 1980). Growth parameters for molluscs came from Díaz-Avalos (1989) and Solís-Ramírez (1994), crustacean (Arreguín-Sánchez and Chávez, 1985; Cabrera *et al.*, 1990), cephalopods (Solís and Chávez, 1986); fishes (Pauly, 1980), sharks and rays (Alvarez, 1988, Alvarez-Hernández and Arreguín-Sánchez, 1990); sharks (Alvarez-Hernández and Arreguín-Sánchez, 1992), scombrid (Cabrera, 1986), jacks (Claro, 1990), groupers (Arreguín-Sánchez *et al.*, 1987), reef fishes (Leonce, 1990; Claro, 1990), carnivores (Mexicano-Cíntora, 1985; Torres and Chávez, 1987), herbivores and omnivores (Claro, 1990).

Consumption/Biomass ratios for zooplankton, sessile organisms, birds and turtles were determined from Polovina (1984), for echinoderms from Optiz (1993), and for molluscs and cephalopods from the relationship of Pauly (1986) and Pauly *et al.* (1990). Sources of asymptotic weight (W_∞) were similar to those for P/B. For fishes, Q/B were estimated from W_∞, mean habitat temperature (T) and caudal fin aspect ratio (Palomares and Pauly, 1989; Pauly *et al.*, 1993). The annual mean temperature was 27°C (Jordán, 1979) and the fin aspect ratios were taken from photos (Randall, 1968) and video films.

Once the model was balanced and the ecosystem parameters estimated, we used the Ecoranger routine (Christensen and Pauly, 1996) to obtain the best fitting model. Ecoranger implements a semi-Bayesian approach in which parameters from the first balanced model are taken as initial values. Triangular distributions and the minimization of residuals as criterion for constraint were selected. It was decided that at least 3000 positives solutions were required to obtain parameter distributions and their modal values, assuming this solution is representative of a stable ecosystem model.

RESULTS AND DISCUSSION

The input parameters for each functional group are given in Table 1 and the diet compositions in Table 2. First attempts with Ecopath resulted in an unbalanced model due to EE values greater than one for some groups. The model was balanced applying small changes in some diets (considering diet composition as the input parameter of highest uncertainty), taking as criterion that values for Ecotrophic Efficiency should be less than unity.

Biomass decreased for echinoderms, sessile organisms, mollusks and crustaceans. This could be due to the sampling technique used (coverage), which overestimates larger organisms and underestimates smaller animals (Anon., 1984). It was necessary to increase the biomass of small and cryptic fishes and reduce the biomass of sharks because the technique used (visual census) tends to overestimate biomass for some groups (Opitz, 1993; Venier and Pauly, 1997).

The estimated fish biomass for the southern reef was 204.6 $t \cdot km^{-2}$, which is higher than the 163 $t \cdot km^{-2}$ and 170 $t \cdot km^{-2}$ reported for reefs in the Virgin Islands (Randall, 1963) and the Gulf of Batabanó, Cuba (Claro, 1990), respectively. However, biomass was similar to the 209 $t \cdot km^{-2}$ reported for the Great Barrier Reef of Australia (Talbot and Goldman, 1972).

In general, excellent descriptive information of the coral reef benthic fauna is available; however, more quantitative information of the trophic ecology of the associated invertebrates is required.

The trophic analysis of this reef ecosystem (Table 1, Figure 2) showed similar results to those found by Polovina (1984), Opitz (1993), Aliño *et al.* (1993), Arias-González (1994) and

Table 1: Parametrization of the model for a coral reef in the southern Mexican Caribbean. Accumulated biomass for detritus was 855.9 t·km^{-2}. Unassimilated food proportion was assumed as 0.2 for all consumers. P/B: production/biomass; Q/B: consumption/biomass; EE: ecotrophic efficiency; TL: trophic level; Omn.: omnivory index; Resp.: respiration; Assim.: assimilation. Values in brackets were estimated by Ecopath. [*Parámetros de entrada usados para la construcción de un arrecife de coral de tipo borde-barrera en el sur del Caribe Mexicano. Biomasa acumulada para detritos fue de 855.9 t·km^{-2}. Se supuso una proporción de 0.2 de alimento no asimilado para todos los consumidores. P/B=Producción/Biomasa, Q/B=Consumo/Biomasa, EE=Eficiencia Ecotrófica*].

Group No.	**Group Name**	**Biomass (t·km^{-2})**		**P/B (year^{-1})**		**Q/B (year^{-1})**		**EE**	**Catch (t·km^{-2})**	**TL**	**Flow to Detritus (t·km^{-2})**	**Net Efficiency**	**Omn.**	**Resp.**	**Assim.**
		initial	**final**	**initial**	**final**	**initial**	**final**								
1	Sharks and rays	0.40	0.40	0.12	0.13	7.30	5.70	*(0.87)*	0.030	*(3.634)*	*(0.1)*	*(0.020)*	*(0.189)*	*(0.2)*	*(0.2)*
2	Sharks/scombr./jacks	3.40	3.40	0.55	0.53	9.42	8.49	*(0.70)*	0.030	*(3.495)*	*(0.6)*	*(0.079)*	*(0.267)*	*(2.1)*	*(2.2)*
3	Groupers	2.80	2.80	0.39	0.48	4.00	3.74	*(0.58)*	0.010	*(3.777)*	*(0.2)*	*(0.115)*	*(0.094)*	*(0.7)*	*(0.8)*
4	Schooling reef fishes	36.00	33.00	1.55	1.24	15.50	14.66	*(0.57)*	-	*(3.057)*	*(15.3)*	*(0.124)*	*(0.365)*	*(43.2)*	*(49.4)*
5	Carniverous fish	47.50	50.00	1.20	1.25	9.80	6.63	*(0.66)*	0.600	*(2.983)*	*(12.4)*	*(0.142)*	*(0.354)*	*(31.0)*	*(36.1)*
46	Herbiverous fish	81.90	99.00	1.44	1.69	31.00	31.65	*(0.32)*	-	*(2.003)*	*(52.8)*	*(0.051)*	*(0.004)*	*(181.4)*	*(191.2)*
7	Omniverous fish	8.00	16.00	1.60	1.97	13.70	13.62	*(0.81)*	-	*(2.508)*	*(2.5)*	*(0.152)*	*(0.359)*	*(7.6)*	*(9.0)*
8	Birds	0.02	0.02	5.40	10.68	80.00	73.30	*(0.27)*	-	*(4.017)*	-	*(0.083)*	*(0.027)*	*(0.1)*	*(0.1)*
9	Sea turtles	0.07	0.07	0.20	1.52	3.50	3.57	*(0.22)*	-	*(2.951)*	-	*(0.073)*	*(0.615)*	-	-
10	Cephalopods	10.00	10.00	3.40	2.63	11.40	9.43	*(0.36)*	0.230	*(3.349)*	*(0.2)*	*(0.355)*	*(0.153)*	*(0.5)*	*(0.7)*
11	Echinoderms	605.00	733.00	1.20	0.87	4.00	2.37	*(0.69)*	-	*(2.081)*	*(57.4)*	*(0.403)*	*(0.075)*	*(103.6)*	*(173.4)*
12	Crustaceans	250.00	224.00	2.75	2.18	10.00	9.94	*(0.62)*	0.220	*(2.693)*	*(79.9)*	*(0.343)*	*(0.319)*	*(126.6)*	*(192.7)*
13	Molluscs and worms	510.00	364.00	3.00	3.90	15.00	13.08	*(0.65)*	0.830	*(2.152)*	*(224.0)*	*(0.254)*	*(0.138)*	*(491.0)*	*(658.0)*
14	Sessile animals	907.00	842.00	1.48	1.54	9.00	7.35	*(0.78)*	-	*(2.000)*	*(183.4)*	*(0.217)*	-	*(520.4)*	*(664.8)*
15	Zooplankton	17.50	41.00	45.00	30.90	165.00	158.62	*(0.99)*	-	*(2.098)*	*(68.1)*	*(0.412)*	*(0.098)*	*(118.5)*	*(201.6)*
16	Benthic producers	1641.00	1641.00	13.25	13.25	-	-	*(0.47)*	-	*(1.000)*	*(961.2)*	-	-	-	-
17	Phytoplankton	47.00	47.00	70.00	70.00	-	-	*(0.95)*	-	*(1.000)*	*(59.3)*	-	-	-	-
18	Detritus	600.00	600.00	-	-	-	-	-	-	*(1.000)*	-	-	*(0.372)*	-	-

Table 2: Diet composition for the functional groups of the coral reef ecosystem in the southern Mexican Caribbean showing proportion of each prey (row) comprising average diets of predator (column). [*Matriz presa / predador mostrando la composición de las dietas para los principales grupos en el ecosistema de coral de tipo borde-barrera en el sur del Caribe Mexicano*].

		Predator														
Fct. Group	**Prey**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**
1	Phytoplankton	0.597	0.055	0.001	0.157	0.091	-	-	-	0.009	-	0.020	-	0.204	-	-
2	Benthic producers	-	0.426	0.493	0.180	0.695	-	0.377	-	0.983	0.352	-	-	-	-	-
3	Zooplankton	0.089	-	0.002	0.076	0.003	0.197	-	-	0.003	0.105	0.049	-	0.289	0.103	-
4	Sessile Animals	-	-	0.093	0.122	0.074	-	0.111	-	-	0.063	0.042	-	0.044	-	0.023
5	Molluscs worms	-	-	0.045	0.194	0.003	0.542	0.052	-	-	0.141	0.200	-	0.191	0.018	0.258
6	Crustaceans	-	-	-	0.041	-	0.156	0.291	-	-	0.045	0.202	0.421	0.230	-	0.181
7	Echinoderms	-	-	0.005	0.180	-	-	0.030	-	-	0.045	0.170	-	-	0.049	0.008
8	Cephalopods	-	-	-	-	-	0.095	-	-	-	-	-	-	-	0.049	0.018
9	Sea Turtles	-	-	-	-	-	-	0.044	-	-	-	-	-	-	-	-
10	Birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Herbivorous fish	-	-	-	-	-	-	-	0.020	-	0.016	0.077	0.099	-	0.345	0.056
12	Omnivorous fish	-	-	-	-	-	-	0.047	0.019	-	0.015	0.015	-	-	0.099	0.082
13	Carnivorous fish	-	-	-	-	-	0.006	0.049	0.116	-	-	0.014	0.469	-	0.172	0.178
14	Groupers	-	-	-	-	-	0.001	-	-	-	-	0.001	0.012	-	-	0.011
15	Clupeoids	-	-	-	-	-	0.003	-	0.845	-	0.002	-	-	0.042	0.125	0.158
16	Scombridae/Sharks	-	-	-	-	-	-	-	-	-	-	-	-	-	0.040	0.027
17	Sharks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	Detritus	0.314	0.519	0.361	0.050	0.134	-	-	-	0.005	0.216	0.211	-	-	-	-

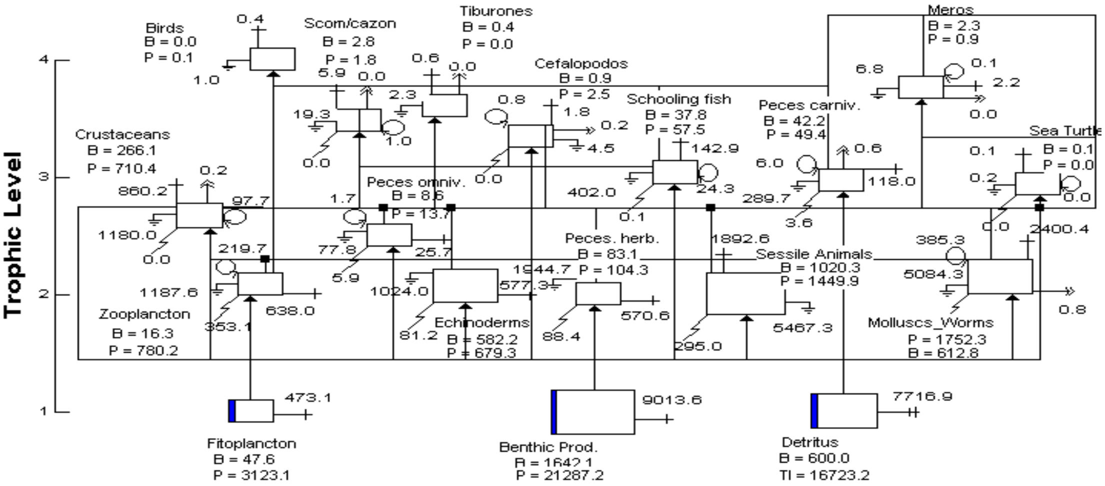

Figure 2: Trophic flow diagram of the ecosystem model for a coral reef in the southern Mexican Caribbean. Flows are in t·km^{-2}·year^{-1}. [*Diagrama de bloques ilustrando los principales flujos de biomasa en un arrecife de coral de tipo borde-barrera en el sur del Caribe Mexicano. Flujos en t·km^{-2}·año^{-1}*].

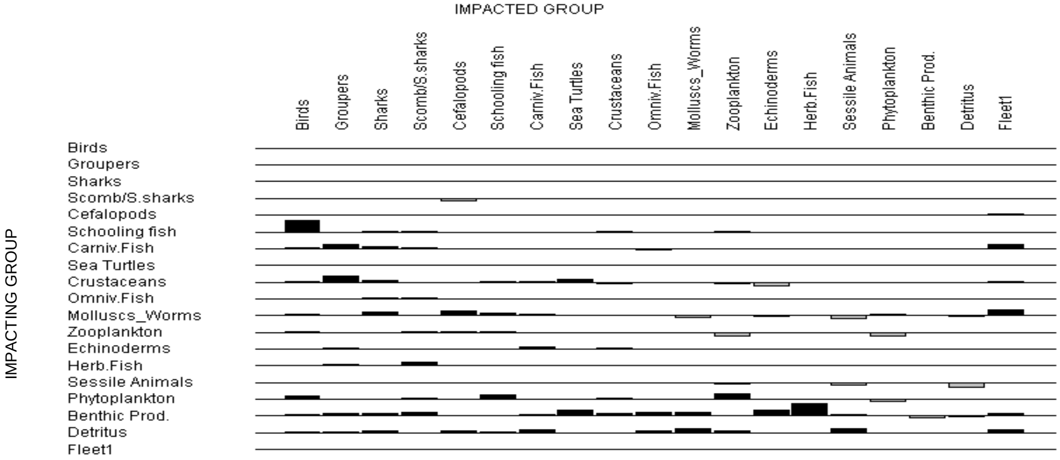

Figure 3: Mixed trophic impacts in the coral reef model of the southern Mexican Caribbean. [*Impactos tróficos relativos entre los principales componentes del ecosistema del arrecife de coral de tipo borde-barrera en el sur del Caribe Mexicano*]

Venier and Pauly (1997), particularly in form of high values of EE, indicating that predation is an important mechanism for biomass regulation. Production is based mainly on detritus and benthic autotrophic organisms. The trophic web is characterized by a number of trophic links with short cycles to obtain an effective recycling of matter and energy.

Figure 3 illustrates mixed impacts (black = positive; gray = negative) of increase in biomass of each group on the others. The results indicate that benthic producers play an important role, interacting with many other groups. The greatest trophic impacts are by groups of the lower trophic levels.

From the overall energetic point of view, the production to respiration ratio (P/R) of the present study compared well with others (Lewis, 1981a; Kinsey, 1985). The ecosystem presented here and that of the Virgin Islands presented values less than one, suggesting a heterotrophic system, with a strong tendency for storage of organic matter. Other ecosystems had values above one, behaving autrotrophically (Odum, 1969). Moreover, the overall P/B ratio of the reef studied here had a low value (P/B= 4.7 year^{-1}), indicating a low biomass accumulation rate.

The connectance index (number of actual trophic links in relation to the number of potential links) was high (0.35), suggesting a diversity of functional groups (Pimm, 1982). The Finn cycling index (FCI), which expresses the proportion of flows that are recycled (Finn, 1976), was 10.1%, suggesting a relatively low internal stability (Odum, 1969). This may reflect a degree of stress in the system (Ulanowicz, 1986; Baird *et al.*, 1991; Christensen and Pauly, 1996).

From the various global indices for comparison of ecosystem development, the Relative Ascendancy (A/C %) (Ulanowicz, 1986; Kay *et al.*, 1989) excludes the influence of total flows (T) over the Ascendancy (A) and development capacity (C) within the ecosystem (Mann *et al.*, 1989), which is considered a suitable index to evaluate ecosystem stability (Rutledge *et al.*, 1976). Ascendancy presents the same behavior as those reported by other authors (Baird *et al.*, 1991; Christensen, 1994), i.e., it decreases as maturity increases, (Christensen, 1995). The model here shows a low A/C, suggesting a high level of system maturity. The general literature suggests greater maturity for the Caribbean (e.g., Stheli and Wells, 1971), in that this system has a relative age of 50 to 60 million years compared to 25 million for the Pacific.

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