Trophic structure and flows of energy in the Huizache–Caimanero lagoon complex on the Pacific coast of Mexico

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Abstract

The Huizache–Caimanero coastal lagoon complex on the Pacific coast of Mexico supports an important shrimp fishery and is one of the most productive systems in catch per unit area of this resource. Four other less important fish groups are also exploited. In this study, we integrated the available information of the system into a mass-balance trophic model to describe the ecosystem structure and flows of energy using the ECOPATH approach. The model includes 26 functional groups consisting of 15 fish groups, seven invertebrate groups, macrophytes, phytoplankton, and a detritus group. The resulting model was consistent as indicated by the output parameters. According to the overall pedigree index (0.75), which measures the quality of the input data on a scale from 0 to 1, it is a high quality model. Results indicate that zooplankton, microcrustaceans, and polychaetes are the principal link between trophic level (TL) one (primary producers and detritus) and consumers of higher TLs. Most production from macrophytes flows to detritus, and phytoplankton production is incorporated into the food web by zooplankton. Half of the flow from TL one to the next level come from detritus, which is an important energy source not only for several groups in the ecosystem but also for fisheries, as shown by mixed trophic impacts. The Huizache–Caimanero complex has the typical structure of tropical coastal lagoons and estuaries. The TL of consumers ranges from 2.0 to 3.6 because most groups are composed of juveniles, which use the lagoons as a nursery or protection area. Most energy flows were found in the lower part of the trophic web.
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Keywords: Huizache–Caimanero; ECOPATH; trophic model; ecosystem structure; network analysis; Mexico

1. Introduction

Exploitation of penaeid shrimp is an important economic activity on the Pacific coast of Mexico. The Huizache–Caimanero coastal lagoons support an important shrimp fishery. Nearly 90% of the total shrimp catch consists of one species, *Litopenaeus vannamei* Boone 1931. Three other species of shrimp are also caught in the fishery; *Litopenaeus stylirostris* Stimpson 1874, *Farfantepenaeus californiensis* Holmes 1900, and *Farfantepenaeus brevirostris* Kignsley 1878. The catch is taken in tidal channels using artificial barriers locally known as 'tapos', which prevent the passage of shrimp during emigration. Until the 1980s, this system had important yields, up to 1500 t (de la Lanza & García, 1991) and was the ecosystem with the highest yields per unit area for shrimp fisheries in coastal lagoons of Mexico (Edwards, 1978a). During the last decade, yields notably decreased. Four fin-fish species are also exploited by local fishermen using beach seine and cast nets. During the 1970s, extensive studies were made because of the economical importance of this area. Several were focused on shrimp biology, ecology, and fishery (Edwards, 1978a; Edwards & Bowers, 1974; Menz & Blake, 1980; Menz & Bowers, 1980; Sepúlveda, 1976, 1981). Other biological components of the system were also studied (Amezcua-Linares, 1977; Edwards, 1978b; Gómez-Aguirrre, Licea-Durán, & Flores-Coto, 1974; Paul, 1981; Warburton, 1978, 1979). The need to integrate the available information was recognized by Edwards (1978b), but little progress,

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however, was made in constructing a trophic model because of the lack of an appropriate model approach.

The need to account for both the structure and function of ecosystems with respect to biological sustainability of living aquatic resources has been widely recognized (Botsford, Castilla, & Peterson, 1997; Christensen, 1996; Christensen & Pauly, 1995; Jennings & Kaiser, 1980), and multispecies management has been a challenge. The general objective of our study is to construct a mass-balanced trophic model using the ECOPATH approach (Christensen & Pauly, 1992) to describe the ecosystem structure and quantify flows of energy, with some emphasis on the shrimp stock. Trophic relationships, flows of energy, and transfer efficiencies derived from this model could then be used to evaluate how changes in the biomass of one functional group are propagated through the food web and show its impact on other groups of the ecosystem (Arreguín-Sánchez, 2000; Baird & Ulanowicz, 1989; Christensen & Pauly, 1993; Christian et al., 1996; Ulanowicz, 1986).

2. Materials and methods

2.1. Study area

The Huizache–Caimanero coastal lagoon system is on the Pacific coast of Mexico in southern Sinaloa (Fig. 1). A narrow channel separates the two lagoons, and a barrier island separates the lagoons from the Pacific Ocean. This lagoon system lies between two rivers, which are connected to the lagoons by narrow and winding channels permitting the transport of freshwater into the lagoons in the wet season (June–October) and the entrance of marine water as in a typical estuary. The average area of the system is $175\,km^2$, reduced to $65\,km^2$ during the dry season. Tides are of semidiurnal with a range of $0.85\,m$ (Soto, 1969). Air temperature ranges through the year between 20 and $40\,°C$, and precipitation is between 800 and $1200\,mm$ (de la Lanza & García, 1991). Mangrove swamps surround the lagoon system, with some communities of halophytic plants on the borders of the lagoons.

2.2. Model construction

A mass-balanced model was constructed using the ECOPATH software, which is a useful approach for quantification of trophic interactions and energy flow among biomass groups in ecosystems (Christensen & Pauly, 1992; Polovina, 1984; Polovina & Ow, 1983). Groups may consist of either a single species or multi-species groups representing ecological guilds. The model uses a set of simultaneous linear equations, one for each group in the ecosystem, and assuming mass balance,

the production of the group is equal to the sum of all losses by predation, nonpredatory losses, and export. The generalized mass-balanced equation for each group is

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

where B_i is the biomass of group i; $(P/B)_i$ the production/biomass ratio of i, which is equivalent to the total mortality coefficient (Z) used by fisheries biologists (Allen, 1971; Merz & Myers, 1998); EE_i the ecotrophic efficiency, which is the part of the total production that is consumed by predators or exported out of the system; B_j the biomass of predator j; $(Q/B)_j$ the consumption/biomass ratio of predator j; DC_{ji} the proportion of prey i in the diet of predator j; EX_i the export of group i, which in this study consists of fishery catch when a group is exploited. Based on the equation, the input parameters for each group in the model are B, P/B, Q/B, and EE. Because this equation is balanced, if one parameter is unknown, it can be estimated from the model. In addition, the diet composition of all consumers is required.

Based on the mass balance of each compartment, consumption equals production plus respiration plus unassimilated food. ECOPATH provided some output parameters that are useful for examining the consistency of the model, such as gross efficiencies (GEs), respiration/assimilation ratio (R/A), and the production/respiration ratio (P/R).

2.3. The input data and the sources

In this study, 26 functional groups were defined; some of them aggregate several species whereas others represent only one genus or species. The selection of fish and some macroinvertebrate groups was based on the most abundant families and on economic importance. Other invertebrate groups were selected because of their importance in the diet of fish groups. Two groups of primary producers (phytoplankton and macrophytes) and a detritus group were also included in the model.

Data used in this work come from published information and were supplemented with that of unpublished reports. All rates and biomasses were expressed as wet weight (ww) and standardized for a year and by the area of the coastal lagoon system. Seasonal variations were not considered in this study. The biomass of fish groups was taken from Warburton (1979). Invertebrate biomasses were taken from Edwards (1978b), and converted into ww from dry weight (dw) using the following conversion factor for different species, or group of species: *Callinectes*: $dw = 29.9\%ww$ (Thayer, Schaff, Angelovic, & LaCroix, 1973), for palaemonids:
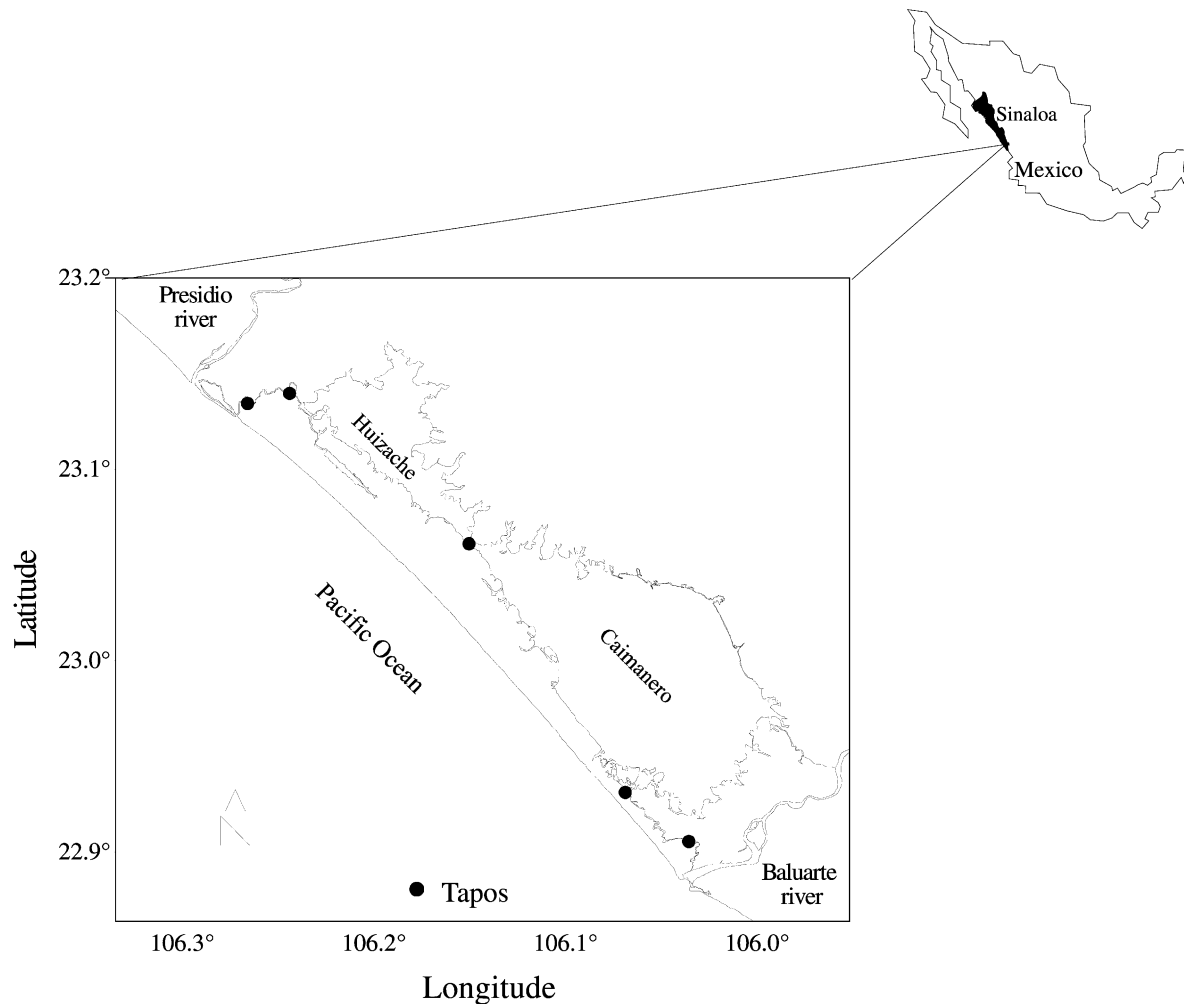
Fig. 1. Study area, Huizache–Caimanero coastal lagoons, Sinaloa, Mexico.

$dw = 24.7\%ww$ (Fonds, Drinkwaard, Resink, Eysink, & Toet, 1987), *Litopenaeus*: $dw = 25.3\%ww$ (Ricciardi & Bourget, 1998), for bivalves: $dw = 8.7\%ww$ (Ricciardi & Bourget, 1998), for microcrustaceans we used the conversion factor of amphipods: $dw = 20.7\%ww$ (Ricciardi & Bourget, 1998) and cumaceans: $dw = 17.4\%ww$ (Ricciardi & Bourget, 1998); and for polychaetes: $dw = 19.9\% ww$ (Ricciardi & Bourget, 1998). Biomass of macrophytes was taken from Flores (1982).

The P/B values for invertebrates were calculated using the relation $P/B = 0.6457W^{-0.37}$ proposed by Banse & Mosher (1980), where W is the individual body mass. For nonexploited fish, P/B was calculated by using the empirical equation by Pauly (1980) and for exploited fish Z was calculated based on data collected from commercial catch.

Jarre-Teichmann, Palomares, Soriano, Sambilay, and Pauly (1991) developed an empirical formula relating mean annual temperature, body size, and morphometric aspects of the body and the caudal fin to calculate the Q/B of fish. The consumption for invertebrates was calculated from the relation $Q = (R + P)/\text{EA}$ where R is the respiration, P the production, and EA is the efficiency of food assimilation with values of 0.2 for detritus, 0.5 for plants, and 0.8 for animals.

Fishery catch was represented as an average for 3 years; 1984–1986, representing typical years with high, low, and moderate yields. These data were obtained from the catch records of shrimp, centropomids, ariids, gerreids, and mugilids.

Diet composition of consumers was represented in a prey–predator matrix that contains the fraction of the diet of each predator contributed by each prey. Descriptions of the diet composition were taken from the literature for the principal species within each group, or from other similar ecosystems or species groups. The data sources are given in Table 1.

Additionally, the 'pedigree' (Funtowicz & Ravetz, 1990) of each input data was recorded for the calculation of an overall index of model 'quality', based on the origin and quality of input data. Scores for each input data were assigned, from 0 for inputs that did not

Table 1

Diet information sources for the construction of the predator/prey matrix

Group	Species	References
Sciaenids	*Cynoscion xanthulum*	Díaz González and Soto, 1988
Elopids	*Elops affinis*	Díaz González and Soto, 1988
Lutjanids	*Lutjanus novemfasciatus*	Yáñez-Arancibia, 1978
	Lutjanus argentiventris	
Carangids	*Caranx hippos*	Yáñez-Arancibia, 1978
Centropomids	*Centropomus robalito*	Díaz González and Soto, 1988
	Centropomus nigrescens	
Ariids	*Arius guatemalensis*	Díaz González and Soto, 1988
Haemulids	*Anisotremus interreptus*	Bermudez-Alamada and García-Lunas, 1985
	Haemulon sexfasciatum	
Pleuronectoids	*Cynoglossus zanzibarensis*	Meyer and Smale, 1991
Callinectes	*Callinectes arcuatus*	Paul, 1981
Belonoids	*Hemiramphus balao*	Randall, 1967
	Hemiramphus brasilienis	
Clupeoids	*Atherinomuros stipes*	Randall, 1967
	Engraulis mordax	Kucas, 1986
	Dorosoma petense	Davis and Foltz, 1991
Gerreids	*Diapterus peruvians*	Yáñez-Arancibia, 1978
Poeciliids	–	Estimation
Gobioids	*Dormitator latrifons*	Carranza, 1969
Mugilids	*Mugil cephalus*	Yáñez-Arancibia, 1978
Palaemonids	*Macrobranchium* sp.	Palomares et al., 1993
Litopenaeus	*Penaeus* sp.	Chávez et al., 1993
Bivalves	–	Estimation
Microcrustaceans	Microcrustaceans	Arreguín-Sánchez et al., 1993
Zooplankton	–	Estimation
Chanids	*Chanos chanos*	Bagarinao, 1994
Polychaetes	–	Estimation
Gastropods	–	Estimation

Representative species used for the diet of each group are indicated.

originate from local data to 1 for inputs that were obtained in local data. Scores were averaged over all parameters and functional groups of a model to provide an overall pedigree index of quality, and its interpretation can be made analogously to a correlation coefficient because it varies from 0 to 1. A model with a high pedigree index is considered to be of high quality, because it is constructed mainly using accurate estimates based on data from the system that was modeled.

2.4. Summary statistics

A number of statistics describing an ecosystem as a whole have been included into ECOPATH and were used to asses the status of the ecosystem in terms of maturity (Odum, 1969) and for comparison with other similar ecosystems. Summary statistics are totals of consumption, exports, respiration, flows to detritus, primary production. Additionally two global indices were calculated: the system omnivory index, which is the average omnivory index of all consumers weighted by the logarithm of each consumer's food intake; and the connectance index, which is the ratio of the number of existing trophic links with respect to the number of possible links. The mean trophic level (TL) of the catch was calculated as the mean of TLs of groups included weighted by the contribution to total catch.

2.5. Network analysis

Network analysis (Ulanowicz, 1986; Ulanowicz & Kay, 1991) was carried out using ECOPATH software to determine some holistic ecosystem properties and flow indices. Ascendancy, overhead, and development capacity were calculated based on the theoretical and computational methodology suggested by Ulanowicz (1986). The mixed trophic impacts were calculated using the Leontief (1951) matrix routine as developed by Ulanowicz and Puccia (1990). This analysis is useful to determine the expected response of each group to perturbations when an increase in biomass of any group is introduced in the model. Moreover, the trophic structure was aggregated sensu Lindeman (1942) using the approach proposed by Ulanowicz (1995). In this routine the system is aggregated in a linear food chain where the import (on TL I only), consumption by predators, export, flow to the detritus, respiration, and throughput are calculated for each TL. Using this information, the transfer efficiencies between successive discrete TLs can be calculated as the ratio between the sum of the outputs (exports plus the flow that is transferred from one TL to the next) and inputs (throughput on the TL). The following indices were calculated by ECOPATH: total system throughput, which is the sum of the total of all flows occurring in the system; and the Finn cycling index, which is the proportion of the total throughput that is devoted to recycling of material (Finn, 1976).

3. Results

3.1. Balancing the model

The criterion used as a guide for balancing the model was that EEs must be no larger than 1. The first attempt of parameterization gave values of EE greater than 1 for several groups. Because diet composition is the highest uncertain input data (Christensen & Pauly, 1996), small adjustments were made in diet composition to balance

the model, so that the inputs into each compartment are equal to the outputs. Once the model was balanced, an Ecoranger routine was applied to the preliminary model. In this step we considered the uncertainty of the input data, and we assigned 10% for the variation coefficient for all input data. Random input variables were then drawn using a triangular-probability density distribution for all parameters, and the resulting model was then evaluated based on the least sum of squared residuals and physiological and mass-balance constraints. This process was repeated using Monte Carlo simulations. Of the model runs that pass the evaluation criteria, the best fitting is chosen using a least square criterion (Christensen, Walters, & Pauly, 2000). We again used the Ecoranger routine until 3000 'positive' models (outputs with plausible solutions) were achieved from a total of 10,000 runs.

3.2. Trophic structure

The input and estimated data by ECOPATH after Ecoranger are given in Table 2, and the predator–prey matrix used is given in Table 3. Most EEs were estimated by the model, whereas the biomass for phytoplankton, zooplankton, and gastropods were estimated assuming values for EE according to specific characteristics of each group. The EE for elopids was estimated as 0 given that no predator consumes this group.

Consumption, production, assimilation, respiration (Odum & Heald, 1975), and TL (Christensen & Pauly, 1992), were calculated for each group included in the model and the values are given in Table 4. The TL of primary producers is set by default equal to 1, and for the other groups it was calculated according to the TL of the prey and its contribution to the predator's diet. Top predators were sciaenids, elopids, lutjanids, carangids, centropomids, and ariids with TL values between 3.4 and 3.6. Minor fish and invertebrates constituted the second TL, mainly clupeoids, mugilids, and Callinectes with TL between 2.6 and 3.0. Generally, food assimilation, as a function of production, exponentially decreases with the increase of the TL. Then highest production can be observed in low TLs, except for the less abundant groups in the system, like poeciliids, gobioids, palaemonids, and chanids. The contribution to detritus was larger by autotrophs, zooplankton, and benthic organisms, such as Callinectes, Litopenaeus, bivalves, microcrustaceans, and polychaetes, possibly suggesting excess primary and secondary production. In general, the omnivory index was larger in the groups occupying the second TL, suggesting that top predators at higher TLs have a narrow diet.

A box model depicting flows of energy representing the major trophic interactions in the study area is shown in Fig. 2. Trophic interactions are 'web-like' where most flows occur in the lower part of the trophic web.

Table 2
Input data for the Huizache–Caimanero ECOPATH model

	Group	Biomass (t km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	Catch (t km^{-2})
1	Sciaenids	0.590	0.399	4.987	(0.106)	
2	Elopids	0.014	0.430	5.154	(0.000)	
3	Lutjanids	0.017	0.220	2.732	(0.733)	
4	Carangids	0.049	0.527	6.196	(0.873)	
5	Centropomids	0.623	0.930	2.513	(0.430)	0.040
6	Ariids	1.058	0.785	2.736	(0.498)	0.340
7	Haemulids	0.227	0.593	2.279	(0.661)	
8	Pleuronectoids	0.203	0.392	1.658	(0.761)	
9	Callinectes	5.520	2.228	6.285	(0.098)	
10	Belonoids	0.330	1.073	8.891	(0.968)	
11	Clupeoids	2.780	0.839	5.669	(0.837)	
12	Gerreids	0.494	1.526	5.108	(0.760)	0.080
13	Poeciliids	0.004	3.432	13.770	(0.905)	
14	Gobioids	0.192	0.455	2.367	(0.894)	
15	Mugilids	3.720	1.095	4.273	(0.522)	1.410
16	Palaemonids	0.529	1.228	4.172	(0.842)	
17	Litopenaeus	2.568	3.163	10.654	(0.843)	5.530
18	Bivalves	7.670	2.241	10.680	(0.606)	
19	Microcrustaceans	11.707	11.443	35.795	(0.804)	
20	Zooplankton	(10.558)	18.624	84.963	0.936	
21	Chanids	0.011	1.518	5.564	(0.520)	
22	Polychaetes	19.202	6.166	26.641	(0.772)	
23	Gastropods	(2.025)	3.222	15.606	0.909	
24	Phytoplankton	(35.421)	19.617	–	0.910	
25	Macrophytes	380.820	8.197	–	(0.068)	
26	Detritus	3,829.787	–	–	(0.231)	

Data within parenthesis were estimated by the model (P/B, production/biomass; Q/B, consumption/biomass; EE, ecotrophic efficiency).

Table 3
Predator–prey matrix for Huizache–Caimanero model. Each value represents the proportion of the prey in the diet of the predator

	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	Sciaenids					0.016																		
2	Elopids																							
3	Lutjanids		0.038																					
4	Carangids	0.005				0.005																		
5	Centropomids	0.060					0.012																	
6	Ariids						0.025																	
7	Haemulids	0.025	0.108	0.041			0.002																	
8	Pleuronectoids	0.010					0.006		0.041															
9	*Callinectes*	0.019		0.028	0.018	0.019	0.074			0.026														
10	Belonoids	0.070	0.019		0.026		0.044																	
11	Clupeoids	0.110		0.162	0.101	0.110	0.089			0.025	0.100													
12	Gerreids	0.051		0.085	0.231	0.055	0.029			0.003														
13	Poeciliids			0.018		0.002		0.005			0.002													
14	Gobioids	0.003	0.063	0.097	0.023	0.007	0.003		0.020		0.004				0.006									
15	Mugilids	0.060	0.262	0.201	0.103	0.097	0.005			0.009														
16	Palaemonids	0.033	0.007			0.022	0.011	0.103		0.009	0.006													
17	*Litopenaeus*	0.035	0.134	0.094	0.103	0.200	0.075	0.095		0.016	0.007		0.007											
18	Bivalves			0.047	0.082		0.047	0.044	0.024	0.284			0.112			0.005								
19	Microcrustaceans	0.461	0.244	0.094	0.263	0.225	0.386	0.454	0.514	0.231	0.120	0.214	0.073	0.291	0.157	0.240	0.008	0.108		0.097	0.025		0.044	
20	Zooplankton					0.042		0.108			0.279	0.485	0.188		0.133	0.027	0.105		0.292	0.012	0.162	0.027		
21	Chanids						0.003																	
22	Polychaetes	0.041	0.068	0.031		0.110	0.042	0.074	0.185	0.079	0.035		0.105	0.282	0.218	0.131	0.283	0.269		0.173		0.042	0.010	
23	Gastropods	0.005	0.043	0.023		0.025	0.041	0.052	0.047	0.090	0.154		0.107		0.047	0.116							0.054	
24	Phytoplankton												0.100						0.531	0.074	0.620	0.603		
25	Macrophytes				0.011	0.010	0.064	0.045		0.031	0.293	0.098	0.227	0.427	0.121	0.072	0.105	0.145		0.206		0.183	0.193	0.562
26	Detritus	0.012	0.014	0.079	0.039	0.055	0.042	0.020	0.169	0.197		0.103	0.175		0.324	0.409	0.499	0.478	0.177	0.438	0.193	0.091	0.753	0.438

Table 4
Biological parameters of groups as estimated by ECOPATH model for Huizache–Caimanero coastal lagoons ecosystem

	Group	TL	Consumption (t km⁻² year⁻¹)	Production (t km⁻² year⁻¹)	Respiration (t km⁻² year⁻¹)	Assimilation (t km⁻² year⁻¹)	Flow to detritus (t km⁻² year⁻¹)	Omnivory index	GE	*R/A*	*P/R*
1	Sciaenids	3.6	2.942	0.236	2.118	2.354	0.799	0.15	0.08	0.90	0.11
2	Elopids	3.5	0.072	a	0.052	0.058	0.020	0.16	0.08	0.90	a
3	Lutjanids	3.5	0.046	0.004	0.033	0.037	0.010	0.26	0.08	0.89	0.12
4	Carangids	3.5	0.304	0.026	0.217	0.243	0.064	0.16	0.09	0.89	0.12
5	Centropomids	3.4	1.566	0.579	0.673	1.252	0.643	0.22	0.37	0.54	0.86
6	Ariids	3.4	2.895	0.829	1.485	2.316	0.996	0.32	0.29	0.64	0.56
7	Haemulids	3.2	0.517	0.135	0.279	0.414	0.149	0.12	0.26	0.67	0.48
8	Pleuronectoids	3.1	0.337	0.080	0.190	0.269	0.086	0.28	0.24	0.71	0.42
9	*Callinectes*	3.0	34.693	12.337	15.456	27.755	18.029	0.35	0.35	0.56	0.80
10	Belonoids	2.9	2.934	0.354	1.993	2.347	0.598	0.40	0.12	0.85	0.18
11	Clupeoids	2.9	15.76	2.332	10.275	12.608	3.532	0.34	0.15	0.81	0.23
12	Gerreids	2.7	2.523	0.754	1.265	2.019	0.685	0.36	0.3	0.63	0.60
13	Poeciliids	2.7	0.055	0.013	0.030	0.044	0.012	0.36	0.25	0.68	0.43
14	Gobioids	2.7	0.454	0.087	0.276	0.364	0.100	0.35	0.19	0.76	0.32
15	Mugilids	2.6	15.896	4.075	8.643	12.716	5.126	0.36	0.26	0.68	0.47
16	Palaemonids	2.4	2.207	0.650	1.116	1.766	0.544	0.30	0.29	0.63	0.58
17	*Litopenaeus*	2.4	27.359	8.122	13.765	21.888	6.748	0.31	0.3	0.63	0.59
18	Bivalves	2.4	81.916	17.177	48.344	65.532	23.163	0.31	0.21	0.74	0.36
19	Microcrustaceans	2.3	419.052	133.976	201.278	335.242	110.056	0.28	0.32	0.60	0.67
20	Zooplankton	2.2	897.08	196.641	521.023	717.664	192.001	0.24	0.22	0.73	0.38
21	Chanids	2.1	0.061	0.017	0.032	0.049	0.020	0.13	0.27	0.65	0.53
22	Polychaetes	2.1	511.56	118.426	290.849	409.248	129.287	0.08	0.23	0.71	0.41
23	Gastropods	2.0	31.629	6.526	18.762	25.288	6.916	0.00	0.21	0.74	0.35
24	Phytoplankton	1.0		694.845	–	–	62.536	–	–	–	–
25	Macrophytes	1.0		3125.485	–	–	2909.048	–	–	–	–
26	Detritus	1.0		–	–	–	–	–	–	–	–

GE, gross efficiency; *R/A*, respiration/assimilation; *P/R*, production/respiration ratio.

[a] Unable to estimate since this group is not preyed upon.

The main flows occur from phytoplankton to zooplankton and from detritus to invertebrates. Predators like carangids, elopids, and centropomids consume important amounts of *Litopenaeus*. Living primary producers represented different roles in the ecosystem. Most production from macrophytes flows to detritus; little of their production is consumed. Most of phytoplankton production is incorporated into the food web by the zooplankton.

The commercial catch TL was 2.5, and this is because the most important fishery in this coastal lagoon complex is shrimp ($TL = 2.4$) and only few fish are commercially exploited, such as centropomids ($TL = 3.4$), ariids ($TL = 3.4$), and mugilids ($TL = 2.6$) (Table 5).

3.3. Network analysis

The ascendancy (*A*) was 6853 flowbits and development capacity (*C*) of the ecosystem was 23,289 flowbits (Table 5), which represents 0.3 of network efficiency (*A*/*C* ratio). The mixed trophic impact analysis is repre-

sented in Fig. 3, and gives information of how any group in the system impacts another. Here the importance of detritus is noticeable; it has positive impacts on several groups. The two fisheries that occur in this ecosystem, shrimp and some fish species are positively impacted by detritus because this is the main source of food for shrimp and mugilids. Microcrustaceans also have ecological importance because of positive impacts on several predators. Some groups at intermediate TLs, such as the mugilids, gobioids, gerreids, and clupeoids, have positive impacts on top predators. The analysis shows an effect known as 'trophic cascade' where top predators have a negative impact on prey, but this has an indirect positive impact on the food of prey.

The aggregation analysis shows the presence of six discrete TLs, but the flow to the last level was negligible and is not represented in Fig. 4. Transfer efficiency at each integer TL is given within TLs. The geometric-mean transfer efficiency was 8.3% to the whole system with higher transfer efficiencies at low TLs. Conventionally, detritus and primary producers are assigned to
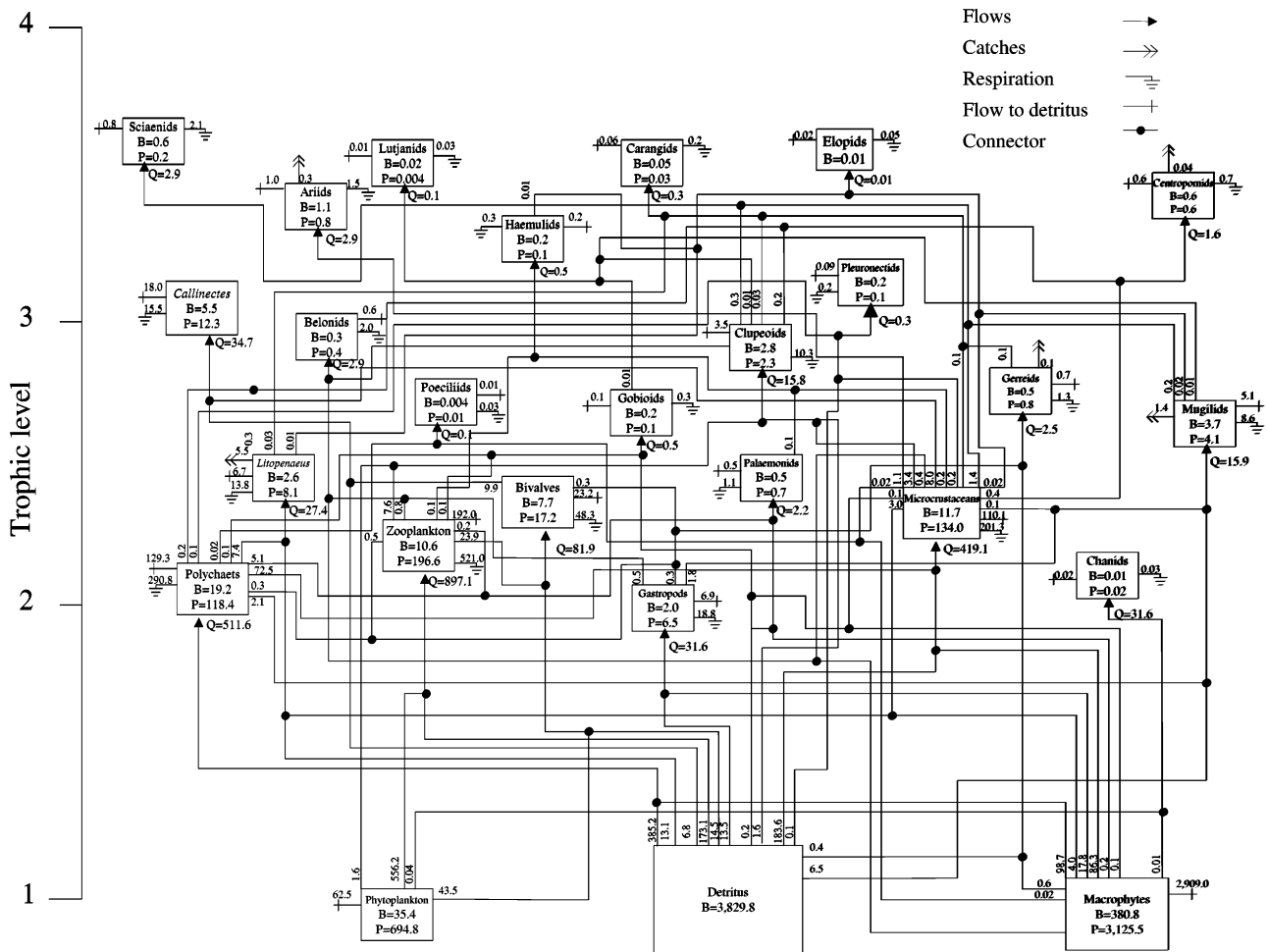

Fig. 2. Flows of energy in a mass-balance trophic model for Huizache–Caimanero, Sinaloa, Mexico. For simplicity, only flows >10% of the total are represented. *B*, biomass ($g\,m^{-2}$); *P*, production ($g\,m^{-2}\,year^{-1}$); *Q*, consumption ($g\,m^{-2}\,year^{-1}$).

Table 5
Summary statistics and network flow indices of Huizache–Caimanero coastal lagoon ecosystem

Attribute	Value	Units
Sum of consumption	2051.84	$t\,km^{-2}\,year^{-1}$
Sum of exports (fishery catch)	7.39	$t\,km^{-2}\,year^{-1}$
Sum of respiration	1138.16	$t\,km^{-2}\,year^{-1}$
Sum of flows to detritus	3471.17	$t\,km^{-2}\,year^{-1}$
Total system throughput	6668.56	$t\,km^{-2}\,year^{-1}$
Sum of all production	4320	$t\,km^{-2}\,year^{-1}$
Total net primary production (PP)	3816.43	$t\,km^{-2}\,year^{-1}$
Total PP/total respiration (R)	3.35	
Total PP/total biomass (B)	7.85	$year^{-1}$
Total biomass (excluding detritus)	486.33	$t\,km^{-2}$
Mean TL of fishery catch	2.5	–
Ascendancy	6853	Flowbits
Overhead	16,463	Flowbits
Development capacity	23,289	Flowbits
Finn's cycling index	9.90	%

the first TL. In Fig. 4, the detritus box is separated from primary producers to show the amount of energy that is flowing through it. The proportion of flow originating from detritus with respect to total flows from TL one is 0.5, indicating that half of the flow supporting the food web structure comes from that source. Only about 22% of primary production flows to the second TL and the rest returns to detritus. The fishery was found acting mainly in the second and third levels.

4. Discussion

The input data used in the model were taken from studies made on the coastal lagoon complex during the 1970s. This is important when we consider the biomass balancing situation because of the natural variability of ecosystems (Christensen & Pauly, 1993). The reliability of the model appears to be acceptable, because the three parameters used to check its consistency have values within the expected ranges (Table 4). The GE values fall within the reported range. The R/A ratio for all groups was less than 1, and was higher for top predators whose production is relatively low. Also, the P/R ratio was less than 1 in all groups. In addition, the pedigree index, which is an overall index of model quality with respect to the inputs (Christensen et al., 2000), was 0.73 for the Huizache–Caimanero model, indicating an acceptable quality of the model, given that most input data came from local estimations using local data and only minor parameters were taken from other ECOPATH models for similar areas.

The highest P/B and Q/B values were for zooplankton, microcrustaceans, and polychaetes. These groups are the principal link between primary producers and consumers of higher TLs. The EEs were higher for the groups in the lower TLs. Zooplankton and epifauna

(e.g. microcrustaceans, *Litopenaeus*, palaemonids) are the groups with the highest contribution to the food web, and for this reason their EEs are near 1. The P/B value of *Litopenaeus* was $3.16\,year^{-1}$, which is near to the estimation of Sepúlveda (1976), who estimated $2.39\,year^{-1}$. The Q/B value used for *Litopenaeus* indicates an average consumption of $27.4\,t\,km^{-2}\,year^{-1}$, whereas Edwards (1978b) estimated a value of $13.6\,mg\,C\,m^{-2}\,day^{-1}$, equivalent to $29.8\,t\,km^{-2}\,year^{-1}$.

The EE of detritus is low indicating that it is poorly consumed and consequently biomass accumulation occurs, which can be deposited or exported from the system. This process leads to an accumulation of detritus biomass, which is characteristic of coastal systems (Day, Hall, Kemp, & Yañez-Arancibia, 1989). The main source of detritus in coastal lagoons has been recognized as coming from macrophytes (Odum & Heald, 1975). This occurs in Huizache–Caimanero where most of the production of macrophytes is decomposed to detritus. Vegetation around the lagoon, as mangroves and halophytes, contributes importantly to detritus, which is reflected in the high input value of biomass for this group (Table 2).

The trophic structure of Huizache–Caimanero is typical of tropical coastal lagoons and estuaries in general. The TL of consumer groups ranges from 2.0 to 3.6, which indicates that most populations are composed of juveniles that use this coastal system as nursery or protection area because of abundant food resources in low TLs, which is reflected in the highest biomass and flows in the second TL. Edwards (1978b) found that most fish species in this lagoon were juveniles, and they were the groups with higher TLs, so fish can play an important role in exporting energy out of the system because of the natural emigration of several species after the juveniles matured.

The mixed trophic-impact analysis again shows the important role of detritus in the lagoon as a source of food, impacting positively all groups, including the fishery, suggesting a bottom-up control (Carpenter et al., 1985). In this lagoon, as in many other coastal ecosystems, detritus plays an important role in the trophic web as food source for some groups.

The mean transfer efficiency for this ecosystem was lower than the assumed 10% average (Lindeman, 1942), however, it is within the range 5.8–10.6, which falls within 1 SD of the modal value for aquatic ecosystems (mean 10.13, SD 5.81) computed by Pauly and Christensen (1995). As expected, transfer efficiency declines at higher TLs. Vega-Cendejas (1998) suggests that systems with mangrove vegetation, as tropical coastal lagoons, offer protection and diminish vulnerability to predation. Baird and Ulanowicz (1993) have reported similar patterns of transfer efficiency in four ecosystems in temperate latitudes. The omnivory index was higher in the lower TLs suggesting more complexity in this
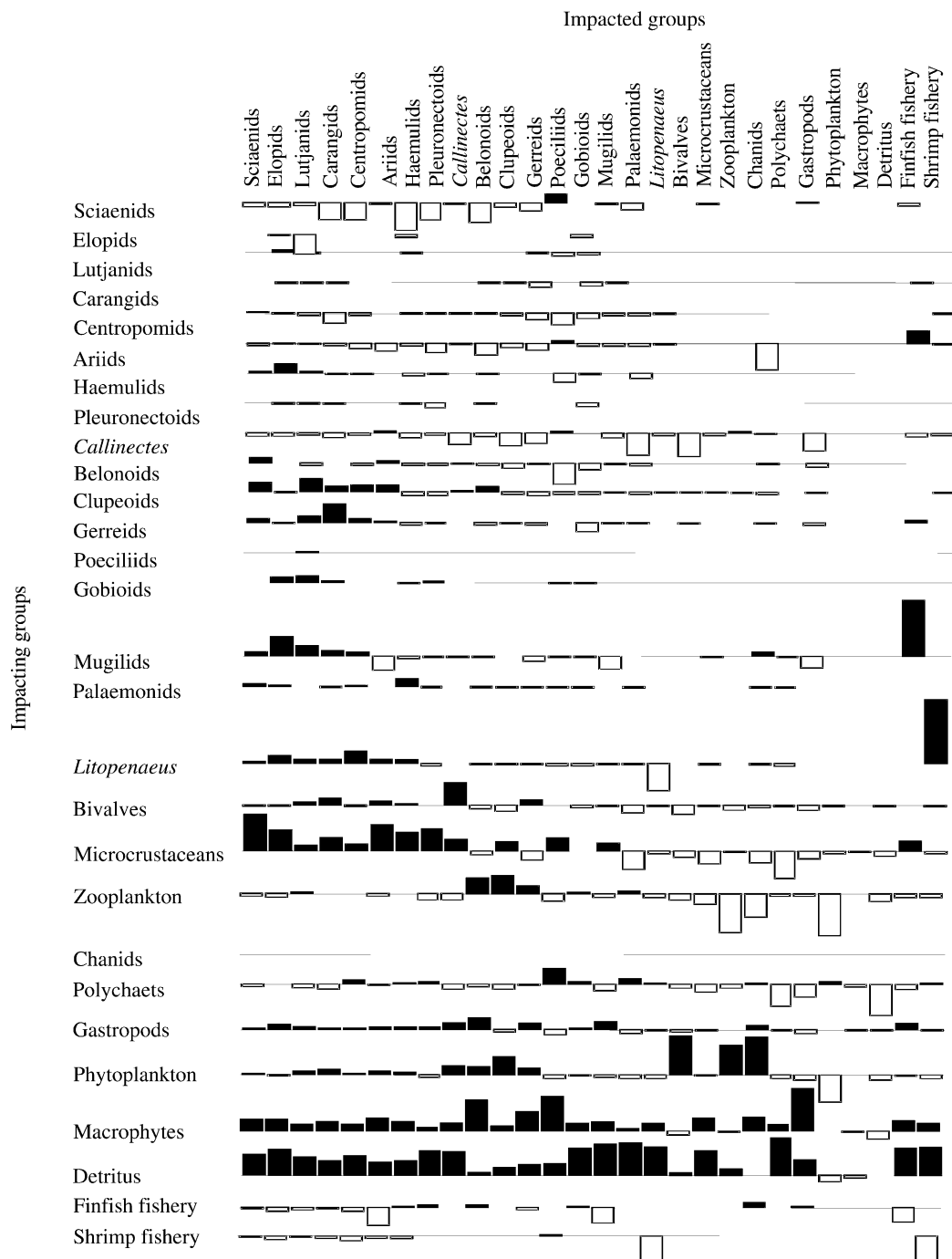
Fig. 3. Mixed trophic impacts showing the effect of each group on others. Magnitudes of impacts are relative and comparable. Black bars = positive impact; white bars = negative impact.

part of the food web. However, the system omnivory index was relatively low indicating most groups have some degree of specialization in their diets.

The system's primary P/R ratio (3.4) estimated by the model indicates an undeveloped stage in Odum's (1969) maturity attributes, which is also suggested by ascendancy (Table 5). However, Christensen and Pauly (1993) found that most ECOPATH models overestimate this when decomposer organisms, like bacteria and fungi,

are omitted in model construction. The primary production/total biomass ratio was 7.85 year^{-1}, similar to that found by Wolff et al. (2000) in a mangrove estuary in north Brazil. This could be because in both systems the biomass in the first TL is huge, but in Huizache–Caimanero this was mainly detritus and in the Brazilian estuary it was mangrove vegetation.

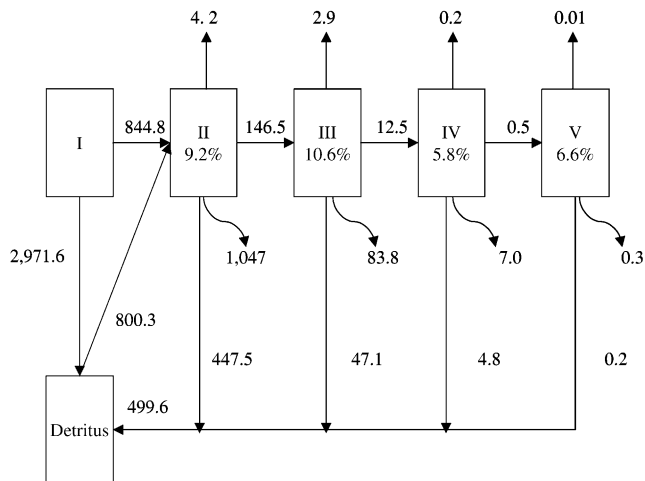The percentage of connectance, 30%, is similar to values reported in other coastal areas. Vega-Cendejas

Fig. 4. Simplified trophic model of Huizache–Caimanero coastal lagoons showing discrete TLs I–V. Detritus, as part of TL=I, is separated to illustrate its role. Horizontal arrows = flows from one level to the following; up arrows=exports (catch); down arrows=flow to detritus; curved arrows=respiration. All flows are in t km^{-2} year^{-1}. Percentage in each box represents transfer efficiencies. Numbers on arrows indicate flow of energy.

values are lower than those obtained by Wulff and Ulanowicz (1989) for Chesapeake Bay and Baird, McGlade, and Ulanowicz (1991) for the Baltic Sea with values of 29.7 and 22.8%. These differing values suggest some latitudinal variation in the way that coastal lagoons systems recycle energy with lower values for the Finn index in tropical systems, probably associated with the large amount of available biomass from the detritus. This aspect should be explored in further work.

Table 6 shows some statistics for several Mexican coastal lagoons. The ratios representing the total of biomass (TB) over total system throughput (TST) and sum of all production (SAP) over TST is higher in the Huizache–Caimanero lagoons than in other coastal lagoons. This means the ecosystem studied here, proportionally, probably accumulates more biomass (energy) than that flowing into the ecosystem since its higher production rates. This gives support to the public concept that this ecosystem contributes a large amount of biomass to fishing activity. Additionally, the ratio representing sum of all flows to detritus over TST is higher in Huizache–Caimanero which strengthens the idea that the system accumulates energy in form of detritus. Other indices suggest that production, energetic costs, and complexity are close to the average values reported in literature for other coastal lagoon ecosystems.

Acknowledgements

and Arreguín-Sánchez (2001) found a value of 30% in Celestun lagoon on the Yucatan peninsula, and Manickhand-Heileman, Arreguín-Sánchez, Lara-Domínguez, and Soto (1998) obtained a value of 40% in Terminos lagoon in the southern Gulf of Mexico. Martens (1987) has suggested that low connectance causes stability, and if we follow this concept, the ecosystem of Huizache–Caimanero coastal lagoons could be considered as relatively stable. The Finn cycling index of 10% was similar to that obtained in other similar areas. Vega-Cendejas and Arreguín-Sánchez (2001) reported a value of 13.4% for Celestun lagoon, and Manickhand-Heileman et al. (1998) 7.0% for Terminos lagoon, both systems being in the southern Gulf of Mexico. These

Table 6
Comparison between some Mexican coastal lagoon ecosystem statistics

	HUICAM[a]	CELESTUN[b]	MANDINGA[c]	TAMIAHUA[d]	TERMINOS[e]
SC/TST	0.308	0.376	0.510	0.463	*0.096*
SR/TST	0.171	0.202	0.255	**0.298**	*0.057*
SFD/TST	**0.521**	0.311	0.235	*0.226*	0.458
SAP/TST	**0.648**	0.411	*0.289*	0.383	0.465
TPP/TR	3.353	1.549	*0.847*	1.047	**7.771**
TPP/TB	7.850	*6.213*	**25.295**	12.156	10.884
TB/TST	**0.073**	0.050	*0.009*	0.026	0.041
CI	0.300	0.296	*0.202*	**0.389**	0.343
SO	0.250	0.189	**0.263**	*0.137*	0.187

Bold values are maximum values; small italicized numbers are minimum values. SC, sum of all consumptions; SR, sum of all respiration; SAP, sum of all production; TPP, total primary production; CI, connectance index; TST, total system throughput; SFD, sum of all flows to detritus; TR, total respiration; TB, total biomass; SO, system omnivory.

[a] Huizache–Caimanero Lagoons; this contribution.
[b] Celestún lagoon (Vega-Cendejas & Arreguín-Sánchez, 2001).
[c] Mandinga lagoon (De la Cruz, 1993).
[d] Tamiahua lagoon (Abarca-Arenas & Valero-Pacheco, 1993).
[e] Terminos lagoon (Manickhand-Heileman et al., 1998).

editing the English-language text. We also thanks the comments made by two anonymous referees.

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