

Trophic dynamics of a mangrove ecosystem in Celestun Lagoon, Yucatan Peninsula, Mexico
[Dinámica trófica la Laguna de Celestun, un ecosistema de manglar en la Península de Yucatán, México]

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ABSTRACT

A trophic model of an estuarine mangrove ecosystem in Celestun Lagoon, Yucatan Peninsula, Mexico, was constructed using the Ecopath approach and software. The objective was to evaluate the importance of vascular plant detritus to the heterotrophic community and to determine holistic ecosystem properties, as required to evaluate mangrove production and its ecological role as a nursery and feeding ground. Based on analysis of stomach contents, 32 fish species were grouped into nine trophic groups, omnivores, phytoplankton and zooplankton feeders, piscivorous and five other groups that include microcrustaceans as an important food source. Overall, the model consisted of 19 functional groups, including primary producers and three levels of carnivores. Detritus was important for the benthic producers, which is a major food for many fish groups. Direct fisheries impact is low, but this ecosystem is a critical habitat for the juveniles of commercial fish species that use the lagoon for food and shelter. Biomass export was considered only for piscivores. The food web consists of short trophic chains with production transferred mainly through microcrustaceans and phytoplankton. It is concluded that this model is a potential tool for use in the management of the Celestun Lagoon.

RESUMEN

Este trabajo es un intento por construir un modelo conceptual de la red alimentaria de una comunidad de manglar estuarino de la laguna de Celestun, un ecosistema tropical localizado en la península de Yucatán, usando el modelo Ecopath. El objetivo es evaluar la importancia del detritus de plantas vasculares en la

comunidad heterotrófica y determinar algunas propiedades del sistema. Este conocimiento es importante para evaluar la producción del manglar y su papel ecológico como un área de crianza y alimentación. Los contenidos estomacales de 32 especies de peces fueron agrupados por sus similitudes tróficas en nueve categorías: Omnívoros y consumidores de fitoplancton y zooplancton, piscívoros y otros cinco grupos que incluyen microcrustáceos como una importante fuente de alimento. El ecosistema está constituido por 19 grupos funcionales con productores primarios y tres niveles de carnívoros. El detritus es importante para los productores bentónicos, los cuales, junto con la comunidad pelágica es el alimento principal para la mayoría de los grupos de peces que usan el manglar para protección y alimento. En el mismo sentido, la exportación sólo fue considerada para piscívoros. La red trófica del ecosistema sugiere cadenas tróficas cortas donde la producción es transferida a través de los microcrustáceos y fitoplancton. Se concluye que este modelo es una herramienta potencial para el manejo de la laguna de Celestun.

INTRODUCTION

Knowledge of trophic fluxes and the efficiency of energy assimilation, transfer and dissipation is basic to understanding ecosystem structure and functioning (Baird and Ulanowicz, 1993). Studies of trophic fluxes and ecosystem functioning exist for Celestun lagoon (Chavez *et al.*, 1993) and the adjacent Campeche Bank (Vega *et al.*, 1993). This study elaborates on these, concentrating on energy transfer within the fish community of the mangrove ecosystem of Celestun Lagoon to enable quantification of its ecological value as a nursery area and feeding ground.

MATERIAL AND METHODS

The Celestun Lagoon ecosystem

Located on the Yucatan Peninsula between 20°45' and 20°58' N and 90°15' and 90°25' W, the area of Celestun Lagoon is approximately 28 km², with a water volume of about 14 x 10⁶ m³ (Fig. 1). It is connected to the open sea in its southern part (Herrera, 1985, 1988). The climate is tropical (mean annual temperature > 26.2°C), with an average annual precipitation of 790 mm in January (García, 1988). The mean salinity is 24 and ranges from 37 at the lagoon mouth to approximately 6 in its innermost parts.

The coast is lined by a 150 m-wide zone of mangrove, i.e., *Rhizophora mangle*. Within the

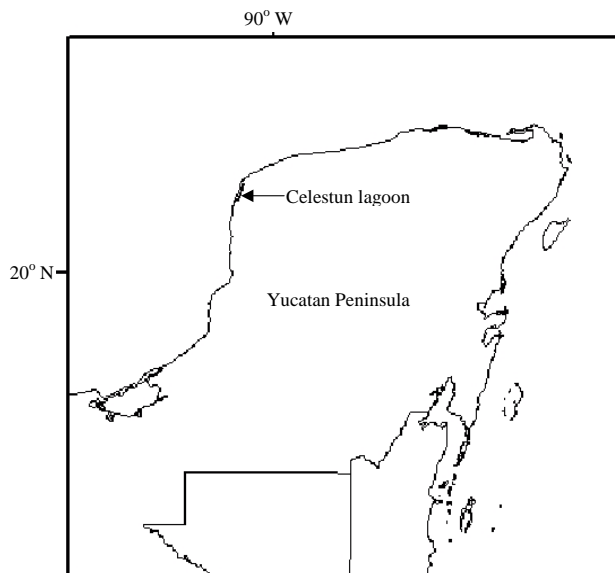


Figure 1: Location of Celestun Lagoon on the Yucatan Peninsula of Mexico. [Localización de la Laguna de Celestún, Península de Yucatán, México].

lagoon the dominant mangrove species are *Laguncularia racemosa* at the head; *Rhizophora mangle* and *Avicennia germinans* in the central area and *Avicennia germinans* near the mouth of the lagoon (Sanchez-Argüelles, 1994). The mangrove fish community, dominated by anchovies (Engraulidae) and morrajás (Gerreidae), is composed of 71 species, mostly juveniles using the lagoon for food and shelter.

The Ecopath approach and software

The Ecopath approach and software were first developed by Polovina (1984) to estimate biomass of various species or groups of an aquatic ecosystem, and later improved by D. Pauly and V. Christensen (Christensen and Pauly, 1992; Pauly *et al.*, 1993, 2000) through the inclusion of various routines implementing ecological theory, notably that developed by Ulanowicz (1986) for the analysis of ecosystem fluxes. Detailed description of Ecopath can be found in Christensen and Pauly (1992) and Pauly *et al.* (2000).

In Ecopath, mass-balance between groups is assumed, and their interactions are described by linear equations (Polovina and Ow, 1983; Christensen and Pauly, 1992; Pauly *et al.*, 2000). The basic equation in the system is defined by equation 1:

$$B_i * P_i * EE_i - \sum_{j=1}^n B_j * Q_{Bj} * DC_{ji} - EX_i = 0 \dots 1)$$

where B_i is biomass for species/group (i), P_i/B_i is production/biomass ratio, EE_i is ecotrophic efficiency, Q_{Bj} is consumption/biomass ratio for predator j , DC_{ji} the fraction of prey (i) in the

average diet of predator (j), and EX_i is export out of the system (including fisheries catches) for species/group i .

Input data and parametrization

For model construction, 32 fish species occurring in Celestun lagoon were aggregated into nine functional groups based on trophic similarity determined from stomach contents analysis. Other groups such as phytoplankton, zooplankton, molluscs, microcrustaceans, polychaetes, macrophytes and detritus were also incorporated, leading to a total of 19 trophic groups (Table 1), and a diet matrix as described in Table 2.

Input data were biomass (B), standardized as wet weight ($t \cdot km^{-2}$), and production/biomass (P/B) and consumption/biomass (Q/B) rates per year. The ecotrophic efficiency (EE), i.e., the fraction of production that is transferred through the trophic web or exported, was left for the model to estimate.

Phytoplankton primary production was determined using the dark and clear oxygen bottle technique (Strickland and Parsons, 1972). Biomasses of benthos and fish were determined from bimonthly samples taken over two years (1992-1994) in the mangrove zone. Benthic productivity was evaluated with the Robertson empirical equation (Rainer, 1982), and P/B ratios were obtained by averaging the values reported by Chávez, *et al.* (1993) and Vega *et al.* (1993). For benthic producers, the indices reported by Yañez-Arancibia and Day (1988) for adjacent regions were used. Zooplanktonic biomass was obtained from Batllori (1988), while the P/B and Q/B ratios were from Chavez *et al.* (1993) for the same area.

For fishes, consumption rates (Q/B) were computed from the empirical model of Palomares and Pauly (1989) described by equation 2 :

$$\ln Q / B = -0.1775 - 0.2018 \ln W_{\infty} + 0.6121 \ln T + 0.5156 \ln A + 1.26 f \dots 2)$$

where W_{∞} is the asymptotic weight in grams, T is the mean habitat temperature in °C, A is the aspect ratio of the caudal fin calculated (as $A = h^2/s$) from the fin height (h) and surface area (s), and f is the food type (0 for carnivores and 1 for herbivores).

Production/Biomass ratios were taken as equivalent to total mortality (Z) (Pauly *et al.*,

2000), assuming steady-state of the ecosystem (Allen, 1971). Fisheries catches were not included, but this was, at least in part, compensated for by a fish biomass export of $0.26 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$, a relatively high value because most species are juveniles and use the mangrove ecosystem as nursery area, then leave. The assigned catch value to all the components was zero.

To balance the model, it was necessary to adjust P/B and Q/B of the fish groups due to their excessively high EE values (>1) in the first run of the model. This might have been caused by the fact that initial input for Q/B and P/B applied to the adults, when in reality the mangrove is used by juveniles with growth and mortality rates higher than those of adults. Discrepancies between zooplankton and microcrustaceans biomass were also found, and the values adjusted correspondingly (Table 1).

Once the model was balanced, we used the Ecoranger routine (Pauly *et al.*, 2000) to obtain the 'best-fitting' model. Ecoranger consists of a semi-Bayesian approach in which parameters from the first balanced model provide 'prior' distributions. Triangular distributions were assumed for all parameters and the minimization of residuals was used as criterion. It was decided that at least 3000 positives solutions were required to obtain parameter distributions and their modal values.

RESULTS

Highest values of P/B and Q/B correspond to the groups at the base of the trophic web, e.g., phytoplankton, zooplankton, insects, and micro- and macrocrustaceans (Table 1). The highest values of EE occurred with the microcrustacean (0.945) and phytoplankton (0.951). The groups with the lowest EE values include fishes (Table 1), most likely an effect of the fisheries catches not having been included.

Trophic flows within the system are presented in a three-dimensional pyramid (Figure 2). The highest proportions of the fluxes come from the herbivore level (50%) and first carnivore level (35%). Similarly, the highest transfer efficiency (17.4%) occurred at the first trophic level (herbivore and detritivore).

Impacts of direct and indirect interactions (including competition) among components of the system were evaluated using the mixed

trophic impact routine (Ulanowicz, 1990; Christensen and Pauly, 1992; Pauly *et al.*, 2000). Figure (3) shows the positive and negative impacts of an increase in the biomass of each group on the others. The groups with the strongest positive impact on others include detritus, macrophytes, phytoplankton and microcrustaceans. It can be seen that apex predators (piscivorous and 'other fishes') have a negative impact on the other fish groups.

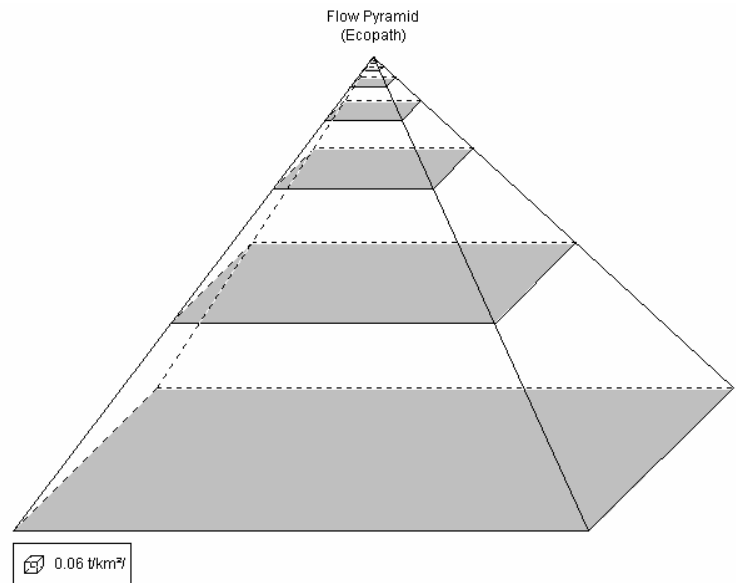


Figure 2: Trophic fluxes represented as a flow pyramid for first order consumers (Trophic Level II) to top predators (Trophic Level V). The volume of each compartment is proportional to the total throughput of that level ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) and the top angle to the geometric mean of the transfer efficiencies between trophic levels. [*Flujos tróficos representados como una pirámide de flujos, desde consumidores de primer orden (Nivel Trófico II) hasta predadores tope (Nivel Trófico V). El volumen de cada compartimento es proporcional al total de flujos de cada nivel ($\text{t}\cdot\text{km}^{-2}\cdot\text{año}^{-1}$) y el ángulo en el extremo distal a la media geométrica de las eficiencias de transferencia entre niveles tróficos*].

The flow diagram is presented in Figure (4). The groups are placed on the Y-axis according to their trophic levels as estimated by Ecopath. Here, top predators (piscivores) have a lower trophic level (3.6) than in adjacent systems (Chavez *et al.*, 1993; Vega *et al.*, 1993). Flows to detritus are between $1.4 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for omnivores and $199.0 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ for zooplankton. With regards to cannibalism, flows with a value of $0.3 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ correspond to insects and $17.2 \text{ t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ to fishes.

Table 1: Parameterization of the mass balanced model for a mangrove ecosystem trophic model of Celestun Lagoon, Yucatan Peninsula, Mexico. Values in brackets were estimated by Ecopath. [*Parametrización de un modelo trófico de un ecosistema de la laguna de Celestun, Península de Yucatán, México*].

Group Name	Biomass	P/B	Q/B	EE	Flow to detritus	Net Efficiency	Trophic level	Omnivory index	Respiration	Assimilation
1. Micro-zoo-phyto	0.007	3.12	7.45	(0.125)	(0.030)	(0.523)	(2.883)	(0.183)	(19.908)	(41.780)
2. Phytoplankton-feed	0.001	2.62	5.97	(0.160)	(0.002)	(0.549)	(2.421)	(0.272)	(1.272)	(2.818)
3. Microcrust.-phyto	0.22	2.57	8.51	(0.438)	(0.001)	(0.377)	(2.818)	(0.199)	(0.932)	(1.498)
4. Microcrust.-mollusc	0.006	2.52	8.37	(0.077)	(0.025)	(0.376)	(3.008)	(0.253)	(26.601)	(42.654)
5. Microcrust.-feeding	0.009	3.09	7.09	(0.262)	(0.032)	(0.545)	(3.049)	(0.171)	(22.308)	(49.006)
6. Omnivores	0.47	3.06	8.97	(0.426)	(0.001)	(0.426)	(2.486)	(0.266)	(1.564)	(2.727)
7. Piscivores	0.004	2.77	6.13	(0.453)	(0.011)	(0.565)	(3.553)	(0.413)	(8.621)	(19.812)
8. Other fish	0.012	3.33	8.23	(0.752)	(0.030)	(0.506)	(3.033)	(0.577)	(40.057)	(81.049)
9. Zooplankton	0.010	13.75	69.91	(0.650)	(0.195)	(0.246)	(2.010)	(0.010)	(438.651)	(581.651)
10. Zooplankton-feeding	0.10	3.76	8.47	-	-	(0.555)	(3.085)	(0.068)	(0.762)	(0.610)
11. Microcrust-zoo	0.20	3.58	10.97	(0.707)	-	(0.408)	(2.998)	(0.031)	(1.687)	(1.755)
12. Insects	0.001	15.54	51.93	(0.808)	(0.008)	(0.374)	(2.010)	(0.010)	(15.862)	(25.342)
13. Microcrustaceans	0.009	15.75	50.51	(0.945)	(0.095)	(0.390)	(2.040)	(0.038)	(213.045)	(349.125)
14. Macrocrustaceans	0.004	4.01	14.86	(0.877)	(0.014)	(0.337)	(2.601)	(0.450)	(31.906)	(48.146)
15. Molluscs	0.026	1.84	9.58	(0.845)	(0.058)	(0.240)	(2.222)	(0.175)	(154.336)	(203.096)
16. Polichaeta	0.010	3.84	13.48	(0.664)	(0.039)	(0.356)	(2.000)	-	(67.704)	(105.144)
17. Phytoplankton	0.007	65.55	-	(0.951)	(0.023)	-	(1.000)	-	-	-
18. Benthic producers	0.153	7.45	-	(0.096)	(1.033)	-	(1.000)	-	-	-
19. Detritus	(2.400)	-	-	(0.642)	-	-	(1.000)	(0.444)	-	-

Table 2: Diet matrix showing proportional diet composition for a mangrove ecosystem trophic model of the Celestun Lagoon, Yucatan Peninsula, Mexico. [*Matriz presa / predador mostrando la composición de las dietas para un modelo trófico de un ecosistema de la laguna de Celestun, Península de Yucatán, México*].

Prey	Predator															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1. Micro-zoo-phyto.	-	-	-	-	-	-	0.11	-	-	-	-	-	-	-	-	-
2. Phytoplankton-feeding	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
3. Microcrust.-phyto.	-	-	-	-	-	-	0.01	-	-	-	-	-	-	-	-	-
4. Microcrust.-mollusc	-	-	-	-	-	-	0.05	-	-	-	-	-	-	-	-	-
5. Microcrust.-feeding	-	-	-	-	-	-	0.16	0.03	-	-	-	-	-	-	-	-
6. Omnivores	-	-	-	-	-	-	0.02	-	-	-	-	-	-	-	-	-
7. Piscivores	-	-	-	-	-	-	0.07	0.03	-	-	-	-	-	-	-	-
8. Other fish	0.02	-	0.01	0.03	0.07	-	0.12	0.17	-	0.07	-	-	-	0.06	-	-
9. Zooplankton	0.24	0.07	0.07	0.01	0.05	0.10	0.02	0.11	0.01	0.82	0.31	-	-	-	0.22	-
10. Zooplankton-feeding	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. Microcrust.-zoo	-	-	-	-	-	-	-	0.005	-	-	-	-	-	-	-	-
12. Insects	0.01	-	0.02	-	0.02	-	0.02	0.05	-	-	-	0.01	-	-	-	-
13. Microcrustaceans	0.54	0.20	0.68	0.33	0.65	0.37	0.25	0.24	-	0.11	0.63	-	-	0.12	-	-
14. Macrocrustaceans	0.01	0.02	-	0.09	0.05	-	0.07	0.04	-	-	-	-	-	-	-	-
15. Molluscs	0.01	-	-	0.36	-	-	-	0.04	-	-	-	-	-	0.29	-	-
16. Polychaetes	-	0.11	-	0.01	0.08	-	0.02	0.01	-	-	0.03	-	0.04	-	-	-
17. Phytoplankton	0.16	0.56	0.19	-	0.05	0.08	-	0.13	0.28	-	-	0.15	0.28	0.11	0.32	0.05
18. Benthic producers	0.01	0.04	0.03	0.04	0.03	0.45	0.07	0.08	-	-	0.03	0.34	-	-	0.23	0.19
19. Detritus	-	-	-	0.13	-	-	-	0.06	0.71	-	-	0.50	0.68	0.42	0.23	0.76

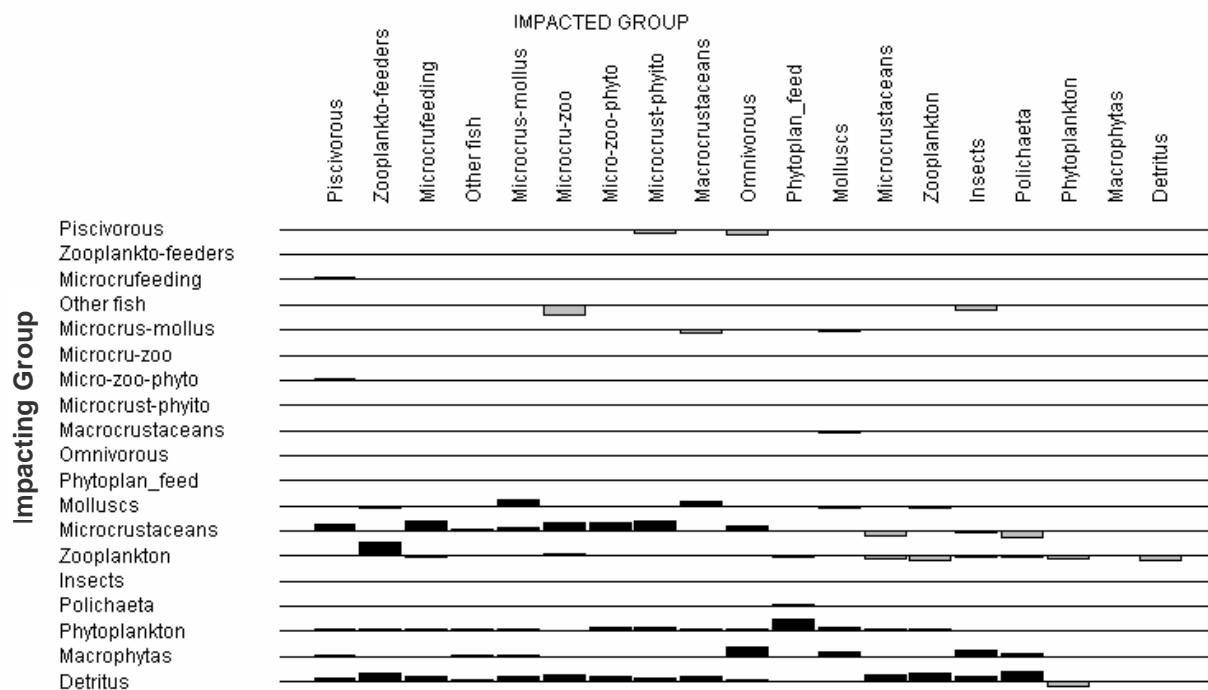


Figure 3: Trophic mixed impacts estimated through the Leontief matrix for the ecosystem of Celestun lagoon, Yucatan Peninsula. Positive impacts are above the line, negative impacts below the line. [*Impactos tróficos estimados a través de la matriz de Leontief para el ecosistema de la laguna de Celestun, Península de Yucatán. Impactos positivos sobre la línea; impactos negativos bajo la línea.*]

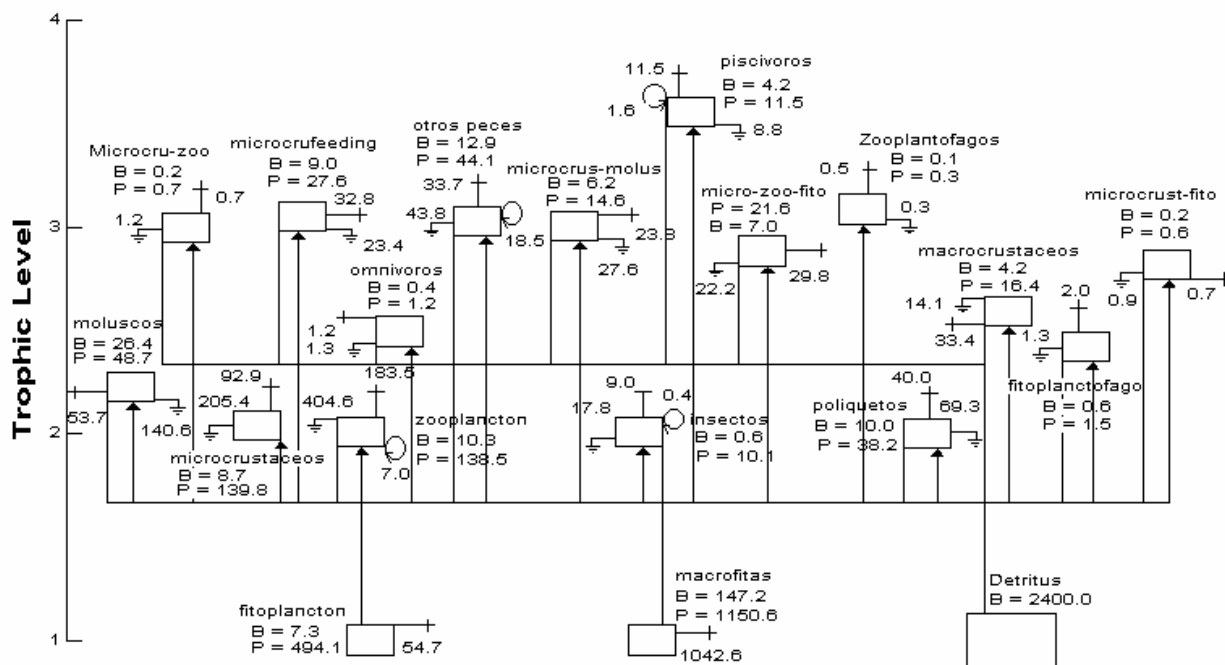


Figure 4: Trophic box model illustrates the main flows of biomass for the ecosystem of Celestún Lagoon, Yucatan Peninsula, Mexico. [*Modelo trófico de bloques ilustrando los principales flujos de biomasa para el ecosistema de la Laguna de Celestun, Peninsula de Yucatán, México.*]

DISCUSSION

This study complements an earlier attempt at understanding, in energetic terms, the fundamentals of structure and function of Celestun Lagoon as a fish nursery. Again, Ecopath appears to be a useful tool for understanding trophic interactions, especially because it enables comparisons between different ecosystems using a common currency (Christensen, 1995).

The present study should enable us to focus future research activities on this important area, and improve our understanding of how this system works. The principal advantage of this model presented here, compared to earlier analyses, is that it was derived using trophic information based on stomach content analysis of the fish species actually occurring in Celestun lagoon. The problem in obtaining a balanced model lay in obtaining growth parameters for the juveniles of various fish species, for which fisheries catches were lacking, and whose energy requirements are different from those of the adults. We hope that the next version of this model will have overcome these deficiencies.

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REFERENCES

Allen, R.R. 1971. Relation between production and biomass. *J. Fish. Res. Board Can.* 28: 1573-1581.

Baird, D. and Ulanowicz, R.E. 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. *Mar. Ecol. Prog. Ser.* 99: 221-237.

Batllori, S.E.A. 1988. Producción secundaria en el Estero de Celestún. MSc Thesis, CINVESTAV-IPN, Unidad Mérida, 140 pp.

Chavez E.A., Garduño, M. and Arreguin-Sanchez, F. 1993. Trophic dynamic structure of Celestun Lagoon, Southern Gulf of Mexico, pp. 186-192. *In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems ICLARM Conf Proc.* 26.

Christensen, V. 1995. Ecosystem maturity - towards quantification. *Ecological Modelling* 77: 3-32.

Christensen, V. and Pauly, D. 1992. ECOPATH II- a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Modelling* 61: 169-185.

García, E. 1988. Modificación al sistema de clasificación climática de Köppen. Instituto de Geografía, Univ. Nal. Autón. de México.

Herrera S.J.A. 1985. Productividad primaria fitoplanctónica del estero de Celestún, Yucatán, durante el periodo de octubre de 1983-abril de 1984. Univ. Autón. de Guadalajara, 56 pp.

Herrera S.J.A. 1988. Productividad primaria fitoplanctónica de la laguna de Celestún, Yucatán. MSc Thesis, CINVESTAV-Mérida, México, 126 pp.

Palomares, M.L.D. and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. *Aust. J. Mar. Freshwat. Res.* 40: 259-284.

Pauly, D., Soriano-Bartz, M.L. and Palomares, M.L.D. 1993. Improved construction, parametrization and interpretation of steady-state ecosystem models, pp. 1-13. *In: V. Christensen and D. Pauly (eds.) Trophic Models of Aquatic Ecosystems. ICLARM Conf. Proc.* 26.

Pauly, D., Christensen, V. and Walters, C.J. 2000. Ecopath, Ecosim and Ecospace as tools for evaluating ecosystem impacts of fisheries. *ICES Journal of Marine Science* 57: 697-709

Polovina, J.J., 1984. Model of a coral reef ecosystem. Part I: Ecopath model and its application to French Frigate Shoals. *Coral Reefs* 3: 1-11

Polovina, J.J. and Ow, M.D. 1983. ECOPATH: A user's manual and program listing. National Marine Fisheries Service, NOAA, Honolulu Adm. Rep. H-83-23.

Rainer, F.S. 1982. Trophic structure and production in the macrobenthos of a temperate Australian estuary. *Estuar. Coast. Shelf Sci.* 5: 423-441.

Sánchez-Argüelles R.D., 1994. Comparación estructural de la comunidad de manglar en dos sistemas lagunares costeros del Estado de Yucatán, México. Univ. Autónoma de Yucatán, 67 pp.

Strickland, J.D.H. and Parsons, T.R. 1972. A practical Handbook of Seawater Analysis. Bulletin, 167, Fisheries Research Board of Canada, 310 p.

Ulanowicz, R.E. 1986. Growth and development of ecosystems phenomenology. Springer-Verlag. New York, 203 pp.

Ulanowicz, R.E. 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5: 7-16.

Vega, C.M.E., Arreguin Sanchez, F. and Hernandez, M. 1993. Trophic fluxes on the Campeche Bank, Mexico, pp. 206-213. *In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM. Conference Proceedings.* 26.

Yáñez-Arancibia, A. and Day, J.W. 1988. Ecología de los ecosistemas costeros en el sur del Golfo de México. La región de la Laguna de Términos. Univ. Nac. Autón. de México, 525 pp.