

Analysis of the ecosystem structure of Laguna Alvarado, western Gulf of Mexico, by means of a mass balance model

V.H. Cruz-Escalona*, F. Arreguín-Sánchez, M. Zetina-Rejón

Av. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Departamento de Pesquerías y Biología Marina, Col. Playa Palo de Santa Rita El Conchalito, A. P. 592, La Paz, Baja California Sur, C. P. 23096, Mexico

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Abstract

Alvarado is one of the most productive estuary-lagoon systems in the Mexican Gulf of Mexico. It has great economic and ecological importance due to high fisheries productivity and because it serves as a nursery, feeding, and reproduction area for numerous populations of fishes and crustaceans. Because of this, extensive studies have focused on biology, ecology, fisheries (e.g. shrimp, oysters) and other biological components of the system during the last few decades. This study presents a mass-balanced trophic model for Laguna Alvarado to determine its structure and functional form, and to compare it with similar coastal systems of the Gulf of Mexico and Mexican Pacific coast. The model, based on the software Ecopath with Ecosim, consists of eighteen fish groups, seven invertebrate groups, and one group each of sharks and rays, marine mammals, phytoplankton, sea grasses and detritus. The acceptability of the model is indicated by the pedigree index (0.5) which range from 0 to 1 based on the quality of input data. The highest trophic level was 3.6 for marine mammals and snappers. Total system throughput reached $2680 \text{ t km}^{-2} \text{ year}^{-1}$, of which total consumption made up 47%, respiratory flows made up 37% and flows to detritus made up 16%. The total system production was higher than consumption, and net primary production higher than respiration. The mean transfer efficiency was 13.8%. The mean trophic level of the catch was 2.3 and the primary production required to sustain the catch was estimated in $31 \text{ t km}^{-2} \text{ yr}^{-1}$. Ecosystem overhead was 2.4 times the ascendancy. Results suggest a balance between primary production and consumption. In contrast with other Mexican coastal lagoons, Laguna Alvarado differs strongly in relation to the primary source of energy; here the primary producers (seagrasses) are more important than detritus pathways. This fact can be interpreted as a response to mangrove deforest, overfishing, etc. Future work might include the compilation of fishing and biomass time trends to develop historical verification and fitting of temporal simulations.

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1. Introduction

Coastal lagoons are recognized as highly productive ecosystems that are used by numerous organisms for feeding, growth, reproduction and refuge (Allen and Horn, 1975; Day and Yáñez-Arancibia, 1982; Day et al., 1989). These ecosystems benefit humans in terms of food production (i.e. fisheries), transportation and recreation (NOAA, 1990). The annual economic value of coastal fisheries in the U.S. Gulf

of Mexico stands around 650 million U.S. dollars (NOAA, 1990). The complexity of the oceanographic conditions that characterize coastal lagoons, as well as their multiple uses and biological diversity, necessitates a holistic approach to assess and manage their living resources.

In highly dynamic ecosystem, the resilience of the food web depends on how energy flows through the system (Hunter and Price, 1992). Many coastal lagoon food webs appear to be highly resilient, as they remain generally intact despite the challenges of an extremely dynamic environment (Day et al., 1989). Understanding how ecosystems react and recover from perturbations is a fundamental goal of ecology (Cottingham and Schindler, 2000). There are two approaches

* Corresponding author.

E-mail address: vescalon@ipn.mx (V.H. Cruz-Escalona).

to predict the dynamics of an ecosystem: experimentation and modeling. Due to their temporal and biological complexity, it is difficult to understand the structure of food webs and trophic interactions by direct observation (Schoenly and Cohen, 1991; Niquil et al., 1999). Ecosystem modeling is an alternative to experimental approaches that can be used to predict ecosystem responses to perturbations and to analyze emergent properties of the ecosystem that are not readily measurable. In this sense, Ecopath models can be used to explore potential impacts on some biotic groups and how they might propagate through the whole ecosystem via the trophic web (Christensen and Pauly, 1993; Pauly et al., 1998; Arreguín-Sánchez, 2000; Pauly et al., 2000; Christensen and Walters, 2004). Such information also permits the evaluation of organizational attributes of an ecosystem such as ascendancy, overhead and development (Ulanowicz, 1986; Arreguín-Sánchez and Chávez, 1995; Vasconcellos et al., 1997; Arreguín-Sánchez and Manickchand-Heileman, 1998; Pérez-España and Arreguín-Sánchez, 2001; Libralato et al., 2002; Coll et al., 2006a).

Laguna Alvarado is an important landing place in the state of Veracruz (Gulf of Mexico). Although at one time Alvarado was a significant oyster fishing ground, today the oyster population has diminished considerably. Also, habitat is being lost along the coast, as new areas for tourism and urban zones are expanded, and intense fishing activities continue. Colmenero-Rolon and Hoz-Zavala (1986) and Colmenero-Rolon (1991) suggested that many species have disappeared from the lagoon as a result of the Miguel Alemán dam construction and because of pollution and boat traffic (Chávez-López and Franco-López, 1992; de la Lanza-Espino and Lozano-Montes, 1999).

Therefore, Laguna Alvarado is one of the most important ecosystems in the Gulf of Mexico, but increased anthropogenic activity in the surrounding terrestrial area coupled with poor waste management planning have contributed to local and regional changes in its hydrological characteristics (Castañeda and Contreras, 2001).

Economic, fishing, and recreational activities in the area, and the high biological diversity that characterizes coastal lagoons, have spurred extensive studies during recent decades. Much of the resulting information is still unpublished. Accordingly, the goal of this study was to integrate on a coherent way the information available from Laguna Alvarado and to construct a mass-balanced model with the aim to describe its trophic structure and study global properties of the ecosystem.

2. Materials and methods

2.1. Study area

The Laguna Alvarado system, located in the northwestern central part of the Gulf of Mexico, is comprised of several lagoons: Alvarado, Tlalixcoyan, Buen País and Camaronera (Fig. 1). The lagoon system extends parallel to the coastline in roughly an East-West direction for about 17 km, has a maximum width of 4.5 km and covers 62 km². Water is exchanged

with the Gulf of Mexico via a channel through a 0.4 km wide sand bar.

Laguna Alvarado is a shallow system with an average depth of two meters and is influenced by several rivers (e.g. Papaloapan, Blanco, Acuña) that release masses of fresh water seasonally and induce fluctuations in primary production (de la Lanza-Espino and Lozano-Montes, 1999).

Seasons are well defined, with the rainy season from June to September, the north-winds season from October through February, occasionally extending through March, and the dry season from March through June (Contreras, 1985). Laguna Alvarado is almost entirely surrounded by red mangrove (*Rhizophora mangle*) and is bordered by a landward zone of black mangrove (*Avicennia germinans*) and white mangrove (*Laguncularia racemosa*). *Ruppia maritima* formed very dense stands in the inner zone of the lagoon (Tovilla and García, 1990). Two periods of relative high productivity during the rainy and north-winds seasons (March–August/November–February) are characteristic of Laguna Alvarado. Low productive periods occur during March–April and September–October (Contreras, 1985; de la Lanza-Espino and Lozano-Montes, 1999). The lagoon is characterized by great diversity of interaction with adjacent systems, particularly with an extensive coastal salt marsh, which contributes greatly to its biological productivity. Recently, the Alvarado Lagoon System was recognized as a wetland of international importance and included in the list of RAMSAR Sites (<http://www.wetlands.org>). It is also considered an important conservation site for many threatened species due to its habitat complexity, which includes more than 100 inner lagoons of mangrove forest. At the regional level, Laguna Alvarado system is believed to sustain the biggest population of manatees (*Trichechus manatus*) in Veracruz State.

2.2. Model construction and parameterization

The mass-balanced trophic model was constructed using Ecopath with Ecosim software (Pauly et al., 2000; Christensen and Walters, 2004). The model period is 1991–1994, a time of relatively constant biomass for major commercial species (Chávez-López et al., 2005). Ecopath consists of a set of linear equations representing each of the functional groups in the ecosystem and describes the balance between biomass gains through production and losses involving predation, fishing and other exports. Quantitatively these processes are represented as:

$$B_i \times P/B_i \times EE - \sum_{j=1}^n B_j \times Q_j \times DC_{ji} - EX_i = 0$$

where B_i is the biomass of group (i) in a given period of time, for $j = 1 \dots n$ functional groups; P/B is the production/biomass ratio, which is equal to the instantaneous rate of total mortality Z , under steady state (Allen, 1971); EE is the ecotrophic efficiency of group (i); Q/B = consumption/biomass ratio of group (j); DC_{ji} is the fraction of prey (i) in the average diet of predator (j); EX_i = exports out the system (including

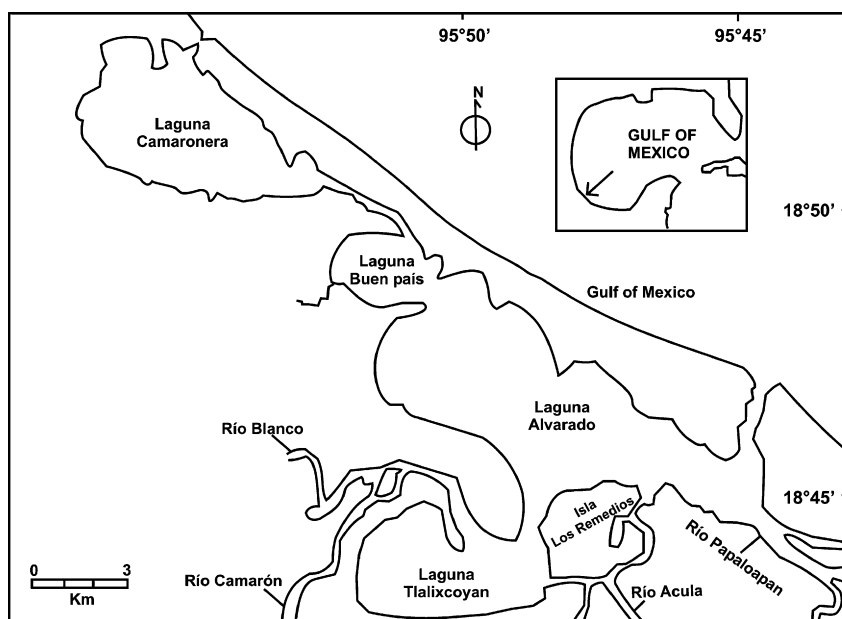


Fig. 1. Study area, in Alvarado coastal lagoon, Veracruz, Mexico.

fisheries catches) of group (*i*); the summation corresponds to total biomass of species (*i*) consumed by predators (*j*).

The model consists of 30 functional groups or compartments. Definition of the groups was based on similarities in their ecological and biological features (e.g., feeding, habitat, mortality) and importance of the species in terms of the fisheries. Given the primacy of Laguna Alvarado as a fishing ground, aggregation of functional groups was guided by species abundance, their relevance as a fish resource and their ecological function in terms of diet and habitat preference.

Most of the inputs used to construct the model were taken from the field or from data collected in the study area. The definition of 18 fish groups was based on the most abundant fish species reported by Chávez-López (1999) in Laguna Alvarado. The biomass (Table 2) and diet of fishes were taken from the field (Franco-López et al., 1992; Franco-López et al., 1996; Chávez-López, 1999) and complemented by FishBase (<http://www.Fishbase.org>) or from the vast published literature about Laguna Alvarado (Table 1).

Eight invertebrate groups were defined, comprising shrimp (Penaeidae), swimming crabs (Portunidae), crayfish (Palaemonidae), infauna (invertebrates such as peracarid amphipods and harpacticoid copepods), polychaetes, bivalves, gastropods and zooplankton. Biomasses of invertebrate groups (Table 2) were calculated based on the work of García-Montes (1988), Reguero and García Cubas (1989), Reguero and García-Cubas (1991), Raz-Guzmán and Sánchez (1992), Raz-Guzmán et al. (1992), Rodríguez-Gamboa (1995) and Winfield-Aguilar (1999). Diets of invertebrates were taken from published literature (Manickchand-Heileman et al., 1998; Winfield-Aguilar, 1999).

Other groups included in the model were sea mammals (bottlenose dolphin), primary producers and detritus. Even

some authors had reported the presence of manatees in Laguna Alvarado, the population size or importance in the lagoon it's unknown, probably because they are not as important as in other Mexican coastal lagoons. We ignore this group because of the insufficient data.

Additional information about input values for B, P/B, Q/B, EE, and diets are shown in Table 1. Values for the various input parameters are shown in Table 2. Predator-prey data is shown in Table 3. Commercial catch data were taken from official records (SEPESCA-INP, 1994). Units were standardized to t km^{-2} wet weight for biomasses, $\text{t km}^{-2} \text{ yr}^{-1}$ for flows, and yr^{-1} for P/B and Q/B. Since this is a mass-balance model, we assumed that parameters represent average conditions throughout the year.

Diets were slightly modified when EEs were higher than one. Several physiological criteria were used to assess the consistency of model: gross efficiency (production/consumption rate) had to be between 0.1 and 0.3 except for very small and fast-growing organisms, a positive flux of mass to detritus had to exist, the respiration/assimilation ratio had to be less than, but close to 1 for top predators, and the respiration/biomass ratio had to be higher for active organisms than for sedentary ones (Zetina-Rejón et al., 2003; Okey et al., 2004).

The “best” possible model, given the available information, was obtained using the Ecoranger routine. This is a semi-Bayesian approach (Christensen and Walters, 2004), which permits variation of input data. Each input is assigned to a predefined probability-density function. Ecoranger provides n-positive solutions based on restricting criteria. In this case, the criteria minimized residuals. Means, standard deviations and residuals for input parameters were estimated after a minimum of 3000 positive solutions, which we considered as acceptable to provide the best possible model.

Table 1
Model inputs and sources for groups in Laguna Alvarado, Mexico

Group	Input	Source
Sea mammals	B	Calculated by model
	P/B	Vidal-Hernández, 2000
	Q/B	Vidal-Hernández, 2000
	Diet	Barros and Odell, 1995
Rays	B	Chávez-López, 1999
	P/B	Wetherbee et al., 1990
	Q/B	Stilwell and Kohler, 1982; Wetherbee et al., 1990
	Diet	Michael, 1993
Scianidae (Croackers)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Chávez-López, 1999; de la Cruz-Agüero, 1993
Lutjanidae (Snappers)	Bi	Chávez-López, 1999
	P/B	González et al., 1994
	Q/B	Manickchand-Dass, 1987
	Diet	Harrigan et al., 1989
Carangidae (Jacks)	B	Chávez-López, 1999
	P/B	de la Cruz-Agüero, 1993
	Q/B	de la Cruz-Agüero, 1993
	Diet	Chávez-López, 1999; de la Cruz-Agüero, 1993
Centropomidae (Snooks)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Chávez-López, 1999; Aliaume et al., 1997
Ariidae (Catfish)	B	Chávez-López, 1999
	P/B	Arreguín-Sánchez et al., 1993 ^a
	Q/B	Vega-Cendejas et al., 1993
	Diet	Vega-Cendejas, 1990; Yañez-Arancibia and Lara-Domínguez, 1988
Pleuronectiformes (Flatfish)	B	Chávez-López, 1999
	P/B	Arreguín-Sánchez et al., 1993a; Terwilliger and Munroe, 1999
	Q/B	Arreguín-Sánchez et al., 1993a; Terwilliger and Munroe, 1999
	Diet	Toeffer and Fleeger, 1995
Hemiramphidae (Halfbeaks)	B	Chávez-López, 1999
	P/B	Warburton, 1979
	Q/B	Zetina-Rejón et al., 2003
	Diet	Sierra et al., 1994; Chávez-López, 1999
Clupeidae (Herrings)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Randall, 1967; Chávez-López, 1999; Abel and Kailola, 1993
Gerreidae (Mojarras)	B	Chávez-López, 1999
	P/B	Abarca-Arenas and Valero-Pacheco, 1993
	Q/B	Abarca-Arenas and Valero-Pacheco, 1993
	Diet	Vega-Cendejas et al., 1993
Poecilidae (Mollies)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Chávez-López, 1999; Zetina-Rejón et al., 2003
Gobiidae (Gobies)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Toeffer and Fleeger, 1995
Cichlidae (Cichlids) Mexican mojarra	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Martínez-Palacios and Ross, 1988
Batrachoididae	B	Chávez-López, 1999

Table 1 (continued)

Group	Input	Source
(Toadfish)	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Whorff, 1992
Sparidae (Pinfish)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Darcy, 1985
Mugilidae (Mulletts)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Chávez-López, 1999
Belonidae (Needle fishes)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Bowman et al., 2000
Eleotridae (Fat Sleepers)	B	Chávez-López, 1999
	P/B	Pauly, 1980 ^a
	Q/B	Palomares and Pauly, 1989 ^b
	Diet	Teixeira, 1994; Winemiller and Ponwith, 1998
Portunidae (Swimming crabs)	B	García-Montes, 1988
	P/B	Millikin and Williams, 1984; Lorán et al., 1993; Murphy et al., 2001
	Q/B	McClintock et al., 1993; Murphy et al., 2001
	Diet	Laughlin, 1982
Palaemonidae (Crayfish)	B	Rodríguez-Gamboa, 1995
	P/B	Rodríguez-Gamboa, 1995
	Q/B	Zetina-Rejón et al., 2003
	Diet	Rodríguez-Gamboa, 1995
Penaeidae (Shrimp)	B	Sánchez and Soto, 1993
	P/B	Arreguín-Sánchez et al., 1993
	Q/B	Arreguín-Sánchez et al., 1993
	Diet	Hunter and Feller, 1987; Arreguín-Sánchez et al., 1993
Infaua	B	Winfield-Aguilar, 1999
	P/B	Optiz, 1993
	Q/B	Optiz, 1993
	Diet	Zimmerman et al., 1979; Manickchand-Heileman et al., 1998
Bivalves	B	Reguero and García-Cubas, 1989
	P/B	Zetina-Rejón et al., 2003
	Q/B	Zetina-Rejón et al., 2003
	Diet	Zetina-Rejón et al., 2003
Gastropods	B	Reguero and García-Cubas, 1989
	P/B	Zetina-Rejón et al., 2003
	Q/B	Zetina-Rejón et al., 2003
	Diet	Zetina-Rejón et al., 2003
Zooplankton	B	Calculated by model
	P/B	Vega-Cendejas et al., 1993
	Q/B	Arreguín-Sánchez et al., 1993
	Diet	Manickchand-Heileman et al., 1998
Wigeongrass (<i>Ruppia maritima</i>)	B	Tovilla and García, 1990
	P/B	Zieman et al., 1989; Kinney and Roman, 1998
Phytoplankton	B	de la Lanza-Espino and Lozano-Montes, 1999
	P/B	Arreguín-Sánchez et al., 1993
Detritus	B	de la Lanza-Espino and Lozano-Montes, 1999

^a $\log_{10} M = -0.0066 - 0.279 \log_{10} L + 0.6543 \log_{10} K + 0.4634 \log_{10} T$.

^b $\ln(Q/B) = -0.178 - 0.202 \ln W + 0.612 \ln T + 0.516 \ln A + 1.26 F$.

Table 2

Input data for the Alvarado Laguna Ecopath model. Data in parenthesis were estimated by the model (P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency)

Functional Group	Catch (t Km ⁻²)	Biomass (t Km ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	EE
Sea mammals		(0.07)	0.01	39.46	0.01
Rays		0.10	0.92	7.90	(0.04)
Croakers	0.05	1.81	0.61	6.70 ^a	(0.75)
Snappers	0.06	0.80	0.59	4.33 ^a	(0.54)
Jacks		0.29	0.76	8.76	(0.60)
Snooks	0.08	0.79	0.42	6.07 ^a	(0.74)
Catfish		4.98	1.24	8.94	(0.91)
Flatfish		0.58	1.86	9.08	(0.37)
Halfbeaks		0.73	1.09	9.11	(0.70)
Herrings		(1.27)	2.05	12.63 ^a	0.75
Mojarras	0.05	5.52	2.27	14.90 ^a	(0.71)
Mollies		0.03	3.46	13.86 ^a	(0.50)
Gobies		2.51	0.46	2.39	(0.82)
Mexican mojarras		0.87	1.30	8.07 ^a	(0.78)
Toadfishes		0.51	0.60	4.27 ^a	(0.16)
Pinfishes		0.17	0.73	7.99 ^a	(0.55)
Mullets	0.02	0.29	1.22	12.06 ^a	(0.72)
Barracudas		0.46	1.05	6.86 ^a	(0.17)
Fat Sleepers	0.08	0.16	0.46	2.35 ^a	(0.40)
Swimming crabs	0.03	1.55	2.39	8.55	(0.27)
Palaemonidae		1.09	3.50	18.84	(0.03)
Shrimp	0.26	2.69	6.38	24.37	(0.33)
Infauna		5.20	7.88	27.36	(0.81)
Worms (polychaeta)		(3.86)	6.22	26.50	(0.71)
Bivalvia		3.85	2.38	10.63	(0.78)
Gasteropoda		1.92	3.23	15.97	(0.10)
Zooplankton		(7.36)	20.20	87.8	0.90
Wigeongrass		21.05	14.92	—	(0.66)
Phytoplankton		(8.26)	118.19	—	0.85
Detritus		45	—	—	(0.28)

2.3. Model analysis

Additionally, the “pedigree” (Funtowicz and Ravetz, 1990) of each input datum was recorded to calculate 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 originate from local data to 1 for inputs that were obtained from local data. Scores were averaged over all parameters and functional groups to provide an overall pedigree index. A model with a high pedigree index was considered to be of relatively high quality because it was constructed mainly using accurate estimates based on data from the modeled system.

2.4. Structural analysis

Functional groups were aggregated to represent discrete trophic levels (sensu Lindeman, 1942) to estimate biomass distribution and transfer efficiencies among trophic levels. The origins of flows from primary producers to detritus were calculated along with the sum of all flows. Throughputs cycled with and without detritus were calculated in order to evaluate the role of detritus.

Considering that all functional groups are associated and global impact among groups can be estimated, Ecopath with Ecosim improved the inverse matrix of Leontief (1951), as suggested by Ulanowicz and Puccia (1990). The matrix enables to analyze how a hypothetical increase in the biomass of one group affects the biomass of another and shows how changes at one level of the food web affect others (cascade effects).

2.5. Network analysis

A number of statistics that summarize food webs are included in the Ecopath software and were used to examine various indicators based on trophic flow description, thermodynamic concepts, information theory and network analysis (Odum, 1969; Shannon et al., 2003; Christensen and Walters, 2004; Coll et al., 2006a; Villanueva et al., 2006). Trophic level of the catch (TLc) was calculated as the mean of the trophic levels of the included groups weighted by the relative biomass contribution to total catch. The mean path length corresponds to the mean number of trophic links in each trophic pathway. Primary production required, which is estimated on the basis of the average catch, the trophic level of the resources and the ecotrophic efficiency of transfer. The total system throughput (TST) is defined as the sum all flows in the system. It represents the “size of the entire system in terms of flow” (Ulanowicz, 1986). The ratio of total system biomass to the total system throughput (B/TST) is directly proportional to system maturity where estimate value tends to be low during ecosystem development phase and increases as a function of maturity (Christensen, 1995).

The ratio of net primary production to total respiration (PP/TR) is another system maturity index (Odum, 1969; Pérez-España and Arreguin-Sánchez, 1999) and should be near zero in a truly balanced ecosystem. The system omnivory index, which is the average 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 to the number of possible links, measure the distribution of feeding interactions among trophic levels and characterizes the extent to which a system displays web-like features. An individual group with a low omnivory index is a specialized feeder. High values indicate the group feeds on organisms at many different trophic levels.

Also, the Ecopath model provided estimates of system ascendancy, overhead, and developmental capacity. Ascendancy (A) is a measure of the average mutual information, that is, the uncertainty of the path that a particle of biomass or energy will follow in the system, weighted by the total system throughput. Ascendancy is a measure of system growth (i.e. age, size) and development (i.e. organization) of network links. The upper limit of ascendancy is developmental capacity, while the difference developmental capacity (C) and ascendancy is referred to as overhead, which is the energy in reserve of an ecosystem especially in case of perturbations (Ulanowicz, 1986; Ulanowicz and Norden, 1990; Monaco and Ulanowicz, 1997). The relative ascendancy (A/C) is the fraction of

Table 3
Predator — Prey matrix for the last run of the model representing diet composition for groups in the Laguna Alvarado ecosystem model

Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Prey																											
1. Sea mammals		0.001																									
2. Rays		0.005																									
3. Croakers	0.129			0.026		0.029								0.029		0.011		0.034									
4. Snappers			0.001			0.003																					
5. Jacks	0.027			0.007		0.005				0.001						0.014											
6. Snooks				0.007	0.029		0.003											0.01									
7. Catfish	0.35	0.2	0.105		0.025	0.358	0.008							0.133	0.108			0.01									
8. Flatfish		0.017	0.011	0.026		0.009	0.001								0.021			0.038									
9. Halfbeaks			0.007				0.004											0.092									
10. Herrings	0.268			0.138	0.045	0.027	0.003		0.009	0.007								0.042		0.027							
11. Mojaras	0.084		0.166	0.129	0.186	0.283	0.034	0.119	0.016			0.019	0.093	0.161	0.08			0.471	0.12	0.003						0.001	
12. Mollies		0.009		0.026		0.002			0.002	0.001		0.002						0.004									
13. Gobies		0.012	0.009	0.344	0.079	0.008	0.003	0.037	0.004							0.098											
14. Mexican mojaras				0.077		0.093												0.128									
15. Toadfish		0.086																0.014									
16. Pinfish						0.011				0.001																	
17. Mulletts		0.006			0.011	0.006										0.022		0.007		0.011							
18. Needlefish			0.007																								
19. Fat Sleepers		0.009						0.001				0.03	0.001														
20. Swimming crabs		0.026	0.011		0.022	0.026	0.001	0.011					0.004	0.019						0.034							
21. Crayfish						0.012								0.006	0.013												
22. Shrimp	0.141	0.26	0.153	0.121	0.108	0.111	0.013								0.022				0.019		0.023						
23. Infauna					0.364	0.015	0.056	0.48	0.125	0.07	0.017	0.223	0.47	0.111	0.459	0.293	0.085	0.027	0.404	0.3	0.124	0.023	0.016	0.03	0.007	0.065	0.004
24. Polychaetes		0.098	0.337				0.216	0.136									0.072							0.024			
25. Bivalves		0.029	0.136		0.082		0.031	0.027					0.065		0.052	0.1										0.104	
26. Gastropods		0.008			0.005								0.009		0.008	0.081	0.014		0.109	0.014						0.006	
27. Zooplankton							0.081	0.038	0.296	0.462	0.367	0.24	0.328	0.008		0.203	0.082		0.171		0.147	0.054	0.357	0.12	0.39	0.004	0.004
28. Wigeongrass		0.236		0.099			0.545	0.151	0.548	0.236	0.316	0.189	0.031	0.216	0.027		0.174	0.122	0.196	0.366	0.494	0.393	0.123	0.405	0.268	0.591	
29. Phytoplankton										0.222	0.289	0.236		0.008	0.21	0.179	0.329					0.196	0.44	0.151	0.335	0.231	0.991
30. Detritus			0.056		0.045						0.011	0.06		0.309			0.243			0.226	0.235	0.311	0.064	0.271			

possible organization that is actually realized (Ulanowicz, 1986) and its negatively correlated with maturity (Christensen, 1995).

3. Results

3.1. Modified input parameters and data quality

More than half of the original input data showed values for $EE > 1$, indicating model imbalance. In these cases, EE values were adjusted by modifying input diet compositions (Pauly et al., 1993). Modified input parameters are shown in the Table 2 and the diet matrix for the final run of the model is shown in the Table 3. The largest changes in diet matrix were realized in the fish and crustacean groups. After balancing, model consistency was explored by comparing outputs with independent estimates such as fishing mortalities or respiration/biomass ratio, which must be higher for active than sedentary organisms (Christensen and Walters, 2004). The pedigree index of the model ($PI = 0.5$), ranked within the intermediate values when compared with other models previously constructed (L. Morissette, unpublished data).

3.2. Structural analysis

The trophic level $TL = 1$ was assigned to producers, most fish and invertebrate groups were located in the third and second trophic levels, respectively. The maximum TL in the system was for marine mammals and snappers ($TL = 3.6$), which together with snooks ($TL = 3.5$), constituted the top predators. The mean TL of catches is 2.3 due to the relative importance of primary consumers (Table 4) with a low gross efficiency (actual catch/primary production) of about <0.001 .

The ecosystem was divided into five discrete trophic levels; in which 91% of the total flows occurred in the first two

trophic levels (Fig. 2). Flows originating from primary producers and detritus were combined to evaluate transfer efficiencies by trophic level (Fig. 2). Transfer efficiency dropped 18.3% from level I to II; and thereafter continued decreasing. The mean transfer efficiency for trophic levels II–V was 13.8%.

3.3. Mixed trophic impacts

Impacts shown in the Fig. 3 are relative but comparable among groups. Benthic primary producers (*Ruppia maritima*) were found to have a positive impact on most functional groups in the system. Detritus also had a positive impact on some since it is a common food source for many species. Groups having a positive impact on top predators included zooplankton, herrings and infauna. The strongest negative impact was that of croakers on halfbeaks. Fig. 3 shows the complete set of mixed impacts among functional groups in the ecosystem. The mixed trophic impact graph indicates that a change in biomass of top predators (e.g. sharks, marine mammals, barracudas) had little or no effect on the biomass of other groups.

3.4. Network analysis

Total system throughput was as much as $2680 \text{ t km}^{-2} \text{ yr}^{-1}$, of which total consumption comprised 47%, flows to respiration 37%, and flows to detritus 12%. Trophic flows from primary producers to consumers were about 7 times higher than flows originating from detritus. Total flows from primary producers amounted to $2342 \text{ t km}^{-2} \text{ yr}^{-1}$, whereas total flows originating from detritus were $328 \text{ t km}^{-2} \text{ yr}^{-1}$ (12% TST). Functional groups with a significant contribution to detritus included phytoplankton ($194 \text{ t km}^{-2} \text{ yr}^{-1}$), zooplankton ($14 \text{ t km}^{-2} \text{ yr}^{-1}$), shrimp ($11 \text{ t km}^{-2} \text{ yr}^{-1}$), and meiofauna ($7 \text{ t km}^{-2} \text{ yr}^{-1}$). The most prominent group in terms of biomass and energy flow in the lagoon was zooplankton. It comprised 10.4% of the system's total biomass excluding detritus and consumed 51% of the available primary production and detritus. About 77% of the consumption of zooplankton was respired.

Recycled throughput amounted to $60 \text{ t km}^{-2} \text{ yr}^{-1}$, of which only $11.7 \text{ t km}^{-2} \text{ yr}^{-1}$ was not detritus. The fraction of total system throughput that was actually recycled, as expressed by the Finn Cycling Index (Finn, 1976) was 0.72%. The predatory cycling index was 0.54% of the non-detritus system throughput. The mean path length was 2.3. Finn's straight-through path length with detritus was 2.2 and without detritus 2.3. The omnivory index was 0.25.

Another measure derived by Ecopath was the connectance index, which compares the actual number of links in a food web to the total number of possible links within the system. The primary production required to sustain the Laguna Alvarado catches was estimated in $31 \text{ t km}^{-2} \text{ yr}^{-1}$. The connectance index in the Laguna Alvarado model was 0.3. The system overhead of Laguna Alvarado was equal to $8613 \text{ t km}^{-2} \text{ yr}^{-1}$, while ascendancy was estimated at $3469 \text{ bits km}^{-2} \text{ yr}^{-1}$.

Table 4
Summary statistics for Laguna Alvarado ecosystem model

Parameter	Value	Units
Sum of all consumption	1265.4	$\text{t km}^2 \text{ yr}^{-1}$
Sum of all exports	179.7	$\text{t km}^2 \text{ yr}^{-1}$
Sum of all respiratory flows	987.5	$\text{t km}^2 \text{ yr}^{-1}$
Sum of all flows into detritus	249.6	$\text{t km}^2 \text{ yr}^{-1}$
Total system throughput	2683	$\text{t km}^2 \text{ yr}^{-1}$
Sum of all production	1574	$\text{t km}^2 \text{ yr}^{-1}$
Mean trophic level of the catch	2.3	
Gross efficiency (catch/net p.p.)	>0.001	
Calculated total net primary production	1291	
Total primary production/total respiration	1.3	
Net system production	303.5	$\text{t km}^2 \text{ yr}^{-1}$
Total system production/total system biomass	3.8	yr^{-1}
Total primary production/total biomass	16.5	
Total biomass/total throughput	0.03	
Total biomass (excluding detritus)	78.1	t km^2
Total catches	0.03	$\text{t km}^2 \text{ yr}^{-1}$
Primary production required	31	$\text{t km}^2 \text{ yr}^{-1}$
Connectance Index	0.3	
System Omnivory Index	0.3	

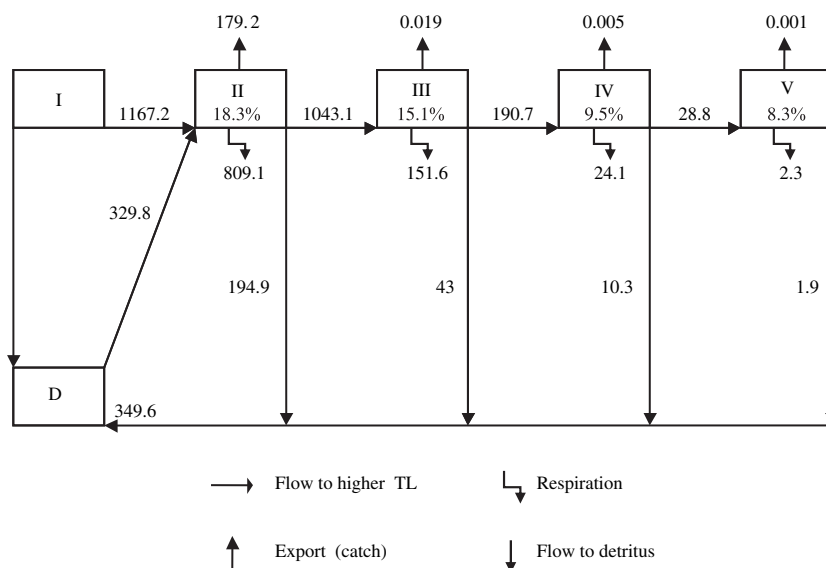


Fig. 2. Simplified trophic model of Alvarado coastal lagoon showing discrete trophic levels I to V. Detritus, as part of TL = I, is separated to illustrate its role. Percentage (%) values indicate trophic efficiencies per trophic level. Numbers on arrows indicate flow of energy expressed in $\text{t km}^{-2} \text{ year}^{-1}$.

4. Discussion

Estuaries and coastal waters are highly productive, valuable ecosystems that are under increasing stress from both anthropogenic factors such as nutrient and other pollutant enrichment and sedimentation, and natural disturbance frequency and intensity arising from global climate change (de la Lanza-Espino and Lozano-Montes, 1999). The greatest asset to successful management of these important marine ecosystems is an understanding both of how external forcing mechanisms reverberate through the complex trophic, physical

setting, and of the biogeochemical interactions characterizing these systems.

To this end, we built a trophic model of Laguna Alvarado, which provides basic information about the structure of the ecosystem, and the energy fluxes within it. This information also allows comparison with other ecosystems based on features of ecological theory suggested by Odum (1969, 1971).

Eighty percent of functional groups were located in intermediate trophic levels (2–3.5). This discovery is not rare, since most groups fed directly or indirectly on primary producers and detritus. It has been reported that several of these

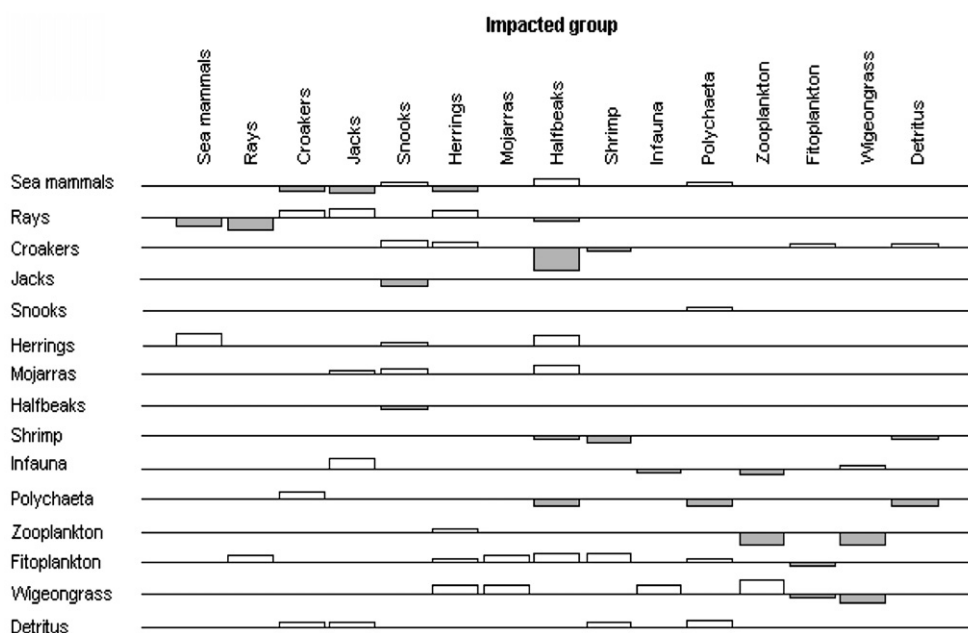


Fig. 3. The Mixed Trophic Impacts from Laguna Alvarado model. Magnitudes are relative. Black bars = positive impact and white bars = negative impact. Only groups with significant impacts are shown.

groups are juvenile organisms of other adjacent systems that penetrate the lagoon for food, protection and reproduction. Additionally, many of functional groups have been identified as closely related to marine grasses (Livingston, 1980, 1982, 1984; Chávez-López, 1999; Luczkovich et al., 2002). Seagrasses in particular perform a variety of functions within ecosystems, and have both economic and ecological value. As habitat, seagrasses offer essential food, shelter and nursery areas (Larkum et al., 1989) to commercial and recreational fishery species and to the countless invertebrates that are produced or migrate there.

The total biomass/total system throughput ratio estimated for Laguna Alvarado appears relatively low when compared with other coastal systems (Table 5). However, the sum of all production (SAP) over total system throughput (TST) is higher in Laguna Alvarado than in other Mexican coastal lagoons in the Gulf of Mexico and close to that of Laguna Huizache-Caimanero in the Pacific Ocean (Table 5).

Odum (1969) indicated that the ratio between total primary production and total respiration (PP/R) is a functional index of the relative maturity of an ecosystem. This ratio would approach 1 as systems mature. In their comparative study of 41 aquatic ecosystems, Christensen and Pauly (1993) found that the bulk of PP/R ratios were in the range between 0.8 and 3.2, although the extreme values were <0.8 and >6.4.

The energy cost by respiration of the Laguna Alvarado ecosystem is one of the highest among the modeled coastal lagoons of Mexico (Table 5), but the proportion of flows to detritus is the lowest. This reflects a high flow of energy through the biotic components of the ecosystem (this is supported by the ratio total consumption/total throughput and to the sum of all production) which are among the highest of these ecosystems. According to our estimates, 80% of production is consumed.

The mean transfer efficiency (13.8%) was consistent with the average 10% suggested by Lindeman (1942), and

comparable to the 15% proposed by Ryther (1969) for coastal areas. Transfer efficiencies in the range 10–20% are commonly reported in the literature (Odum, 1971; Barnes and Hughes, 1988). Other indices reveal that production, energy costs and complexity are close to the averages reported in the literature for similar ecosystems (Abarca-Arenas and Valero-Pacheco, 1993; Arreguín-Sánchez et al., 1993; de la Cruz-Agüero, 1993; Rosado-Solórzano and Guzmán del Proo, 1998; Vega-Cendejas and Arreguín-Sánchez, 2001).

We found higher transfer efficiencies for primary producers than for detritus. This finding is opposed with that found for other estuarine systems. Manickchand-Heileman et al. (1998) and Zetina-Rejón et al. (2003) indicates the detritus is the main pathway to support the biological communities in the Terminos Lagoon ecosystem. In Alvarado lagoon the combination of numerous freshwater runoff and multiple connected lagoon complexes forms a rich coastal ecosystem (Chávez-López et al., 2005). The water flowing through the system is relatively large ($\sim 50 \times 10^9 \text{ m}^3 \text{ year}^{-1}$), and the estimated water exchange time is less than 0.5 days. With such rapid water exchange, the time of residence of detritus and nutrients in the lagoon is very low and consequently much is exported to adjacent systems (Smith et al., 1997). Laë (1997) observed that re-structurization of food web occurs in case of environmental stress. Ecological and environmental changes due to anthropogenic factors such as resource overexploitation, industrial pollution and mangrove deforest and constructions of dams have contributed to the progressive decrease in the quality and ecological value of estuaries (Whitfield and Elliott, 2002). This appears to occur in Laguna Alvarado where a significant stress has been imposed during the last two decades due to the opening of artificial connections to the sea (Chávez-López and Franco-López, 1992; de la Lanza-Espino and Lozano-Montes, 1999).

Moreover, an important characteristic of the Alvarado Lagoon is the presence of extensive seagrass patches (associated

Table 5
Comparison of ecosystem statistics among coastal lagoon models of Mexico. Maximum values in bold type and minimum values are underlining

Attribute	Huizache	Celestún	Mandinga	Tamiahua	Terminos	Tampamachoco	Alvarado
Pedigree Index	0.30	0.73	0.46	0.62	0.59	—	0.48
Sum of consumptions/total system throughput	0.30	0.37	0.51	0.46	0.09	0.15	0.47
Sum of flows to respiration/total system throughput	0.17	0.20	0.25	0.29	<u>0.05</u>	0.09	0.36
Sum of flows to detritus/total system throughput	0.52	0.31	0.23	0.22	0.45	0.41	<u>0.09</u>
Sum of all production/total system throughput	0.64	0.41	<u>0.28</u>	0.38	0.46	0.46	0.58
Total primary production/total respiration	3.35	1.54	<u>0.84</u>	1.04	7.77	4.57	1.30
Total primary production/total biomass	7.85	<u>6.21</u>	25.2	12.1	10.8	20.5	16.5
Total biomass/total system throughput	0.07	0.05	<u>0.01</u>	0.02	0.04	0.02	0.02
Connectance index	0.30	0.29	<u>0.20</u>	0.38	0.34	—	0.27
System omnivory	0.25	0.18	0.26	<u>0.13</u>	0.18	—	0.25
Mean TL of catch	2.50	—	—	—	2.48	3.08	<u>2.31</u>
Total respiration/total biomass	0.42	0.24	<u>0.03</u>	0.08	0.71	0.22	<u>0.07</u>

with inorganic and organic nutrients often attributed to freshwater runoff). Despite, very few attempts have been made to quantify the transfer of seagrass production into coastal food webs (Livingston, 1982, 1984; Luczkovich et al., 2002), or to determine the importance of seagrass production to primary production generated by other major plant groups (phytoplankton, macroalgae, benthic microalgae, mangroves).

The mixed trophic impact matrix indicated that groups in Laguna Alvarado are closely interconnected. In general, an increase in the biomass of a given group had a direct negative impact on its prey groups and an indirect negative impact on groups competing for the same food resource. Furthermore, a biomass increase in a group had a direct positive impact on the predators of that group, and an indirect positive impact on groups feeding, in turn, on those predators. Therefore, we hypothesize that any significant impact on wigeongrass abundance and distribution has the potential for cascade effect, particularly on wigeongrass-associated functional groups (crabs, shrimp, halfbreaks, pinfish, needlefish, infauna), and could create a situation that is difficult, if not impossible, to reverse.

On other hand, the omnivory index (0.25) of Laguna Alvarado was close with to those calculated for other coastal ecosystems (Table 5) such as the Huizache-Caimanero and Mandinga (0.25–0.24), and was higher than for Celestún, Tamiahua, Términos, and Tampamachoco (0.13–0.18) ecosystems. The larger index in our model than others models appears to be due to a difference in the species and diet compositions of benthic epifauna, whose diet in our model comprises a lower proportion of detritus than in other models. Moreover, the structure of the model can influence results and therefore comparison, so further work would imply to perform comparison with standardized models (Moloney et al., 2005; Coll et al., 2006b).

Laguna Alvarado has a relatively low ascendancy when compared with other systems (Abarca-Arenas and Valero-Pacheco, 1993; de la Cruz-Agüero, 1993; Rosado-Solórzano and Guzmán del Proo, 1998; Manickchand-Heileman et al., 2000; Vega-Cendejas and Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003). The system overhead is approximately 60–65% and ascendancy is approximately 30–35%. This suggests that Laguna Alvarado ecosystem has significant ‘strength in reserve’. Unfortunately, it is unclear whether strength in reserve means resilience or resistance. That is, the system may either be resistant to perturbations, or it may be resilient and ‘bounce back’ quickly. It might even have a combination of both qualities.

The system omnivory index is also one of the highest, but the connectance index is close to average. This suggests that while the complexity of the ecosystem is close to that of other lagoons in Mexico, there is a greater variety in food links. The mean trophic level of catches in Laguna Alvarado (2.3) is the lowest of all the ecosystems shown in Table 5, reflecting the trophic level of shrimp which constitutes 60% of the system total catch. The low TLc in addition to relatively low PPR would probably be related with a high risk of ecosystem overfishing. *Sensu* Tudela et al. (2005) overfished ecosystems have a wider TLc range of 2.2–3.9 and %PPR of 2.8–89.5.

From the present study, it is clear that Ecopath is a useful tool for illuminating fundamental processes involved in trophic interactions and energy fluxes in coastal ecosystems. Future work could include the compilation of fishing and biomass time trends to develop historical simulations and future projections using Ecosim and Ecospace software.

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