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Biomass flow structure and resource potential of two mangrove estuaries: insights from comparative modelling in Costa Rica and Brazil

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Abstract: Trophic models were compared for mangrove fringed estuaries in Costa Rica (Gulf of Nicoya, at the Pacific shore) and Brazil (Caeté estuary, NE of Belem) in order to evaluate biomass and energy flow distributions, productivity and fisheries potential, and to obtain guidelines for conservation and management of these systems. As the same network modelling approach (ECOPATH II) and a similar number of system compartments were used, a comparison based on the network models seemed attractive. Differences in biotic structure, energy flow and resource productivity's between both systems and their causes were assessed. They proved to be substantial and largely due to differences in topography, tidal regime and mangrove cover between both systems. While the Gulf of Nicoya is exposed to semidiurnal tides and an efficient daily water exchange between the mangrove stands and the gulf and thus to a strong mangrove matter export to the gulf water, the mangrove forest of the Caeté estuary is flushed each fortnight only and the largest part of the mangrove production thus remains within the forest. This is reflected in great differences in food web structure and the amount and type of resources produced in both systems. In the Gulf of Nicoya, detritus matter exported from the mangroves to the estuary feeds an aquatic food web with shrimps and other aquatic detritivores in the centre of the web, while in the Caeté estuary, most energy remains in the benthic domain of the mangrove forest where it is transferred to an enormous biomass of leaf consuming mangrove crabs, the principal resource of this system. Findings imply that generalizations among mangrove systems need to be tempered with caution and differences in trophic relationships among systems must be considered. Rev. Biol. Trop. 54 (Suppl. 1): 69-86. Epub 2006 Sept. 30.

Key words: Brazil, Costa Rica, Gulf of Nicoya, Caeté, mangroves, estuaries, resource potential, trophic structure, modelling.

Over the past two decades, fisheries science has expanded beyond the study of the population dynamics of single species (resources) striving to focus on the ecosystem context. Many studies on the trophic interrelations in multispecies fisheries have found that a great proportion of annual resource production (sometimes >50 %) is being consumed within the ecosystem and that fishery-induced or natural changes in prey-predator abundance can profoundly change the relative abundance (and consequently the catch) of target species of the fishery. In recent years "fishing down the food web" has occurred in many, if not most areas of the world. Thus, catch composition has changed from a predominance of older and larger fish, many of them feeding as top predators high in food webs, to a situation in which small fish and invertebrates increased dominance. As has been demonstrated, the biomass flow structure of these ecosystems has significantly changed with consequences for the resilience of the ecosystem and its resources (Pauly *et al*. 1998).

From the structure of the network and the flows of biomass between the compartments, ecosystem descriptors can be derived to characterise a system in terms of its degree of growth and development, its transfer efficiency between trophic levels, its fishery efficiency (catch/total primary production) and others (Ulanowicz and Mann 1981, Ulanowicz 1986, Baird and Ulanowicz 1993). This approach thus allows quantitative comparisons of ecosystems and their categorization according to degree of maturity and capacity to withstand perturbations, fishery efficiency and other characteristics (Christensen and Pauly 1993, Wolff 1994, Wolff *et al*. 1996).

The great advantage of this approach is that a large quantity of data can be integrated to give a holistic description of an entire ecosystem, in which the important biota on one hand, but also the biomass fluxes between them can be presented. As these models are based on average (usually annual) rates of consumption and production for organisms along a large size spectrum, multi-scale problems of ecosystem research are addressed. All values for compartment biomass and flows are given on an area basis (km^2; m^2); exports (ie. fishery catch) from and imports to the system are explicitly considered.

The two ecosystems compared in this study are exploited, tropical, coastal estuaries of quite different ecological and topographical features. The Gulf of Nicoya (Costa Rica), extends from a mangrove fringed shallow estuary to an open oceanic Bay of >100m depth and represents the centre for the Costa Rican shrimp and finfish fishery. The Caeté estuary (Brazil) is a mangrove-dominated shallow estuary, in which a leaf eating crab (*Ucides cordatus*) is the most prominent resource, while finfish and shrimp harvest is comparatively low.

The objective of the present study was to comparatively analyse the biotic structure and biomass flow distribution of these two systems as related to their fishery potential and present use. It was expected that this comparison might allow for a more general understanding of the relationship between the resource potential of a mangrove estuary and its food web structure as well as its topographical and hydrographical features.

MATERIAL AND METHODS

Ecosystems descriptions

Detailed descriptions of the Gulf of Nicoya and Caeté estuaries are given in Wolff *et al.* (1998, 2000, respectively).

The Gulf of Nicoya (Fig. 1) covers an area of about 1 530 km^2. It can be classified into a shallow (<25m) mangrove fringed estuary with mudflats and a deeper lower part that opens to the ocean. Like the Caeté estuary, it is subjected to strong seasonal variations in salinity and water temperature, but differs from the latter in that much of the nitrogen entering the system comes from offshore deep water which is upwelled into the gulf (Voorhis *et al*. 1993). Tides are semidiurnal; with average amplitude of 2.5-3.0 m. Incoming tides inundate the mangrove stands every day. Due to its high productivity, the gulf is the most important fishing ground of Costa Rica, and contributes 90 % of the national landings. Species of the families' sciaenids, ariids and centropomids are most important for the fishery inside the gulf, while white shrimps, sardines and lutjanids dominate the central and lower parts. The landings have declined over the past years, while fishing effort has drastically increased. In 1988, fishery costs exceeded the economic revenues from the fishery for the first time (WRI 1991). In 1995, of a total catch of 3 215 ton in the GN region, 63 % was provided by artisanal fishermen, which mostly catch finfish in the inner highly productive part of the gulf (about 90 %); the remaining 37 % were taken by the industrial fishery. About half of it was white shrimp (*Penaeus vannamei*), which seems to be the resource most heavily overfished in the region. Coastal zone development, particularly agriculture and tourism have also increased and impacted the gulf in recent years (Vargas 1995).

The Caeté estuary (Fig. 2) is located in the northern part of Brazil, approx. 200 km east of Belem. The study area (ca. 220 km^2) com-

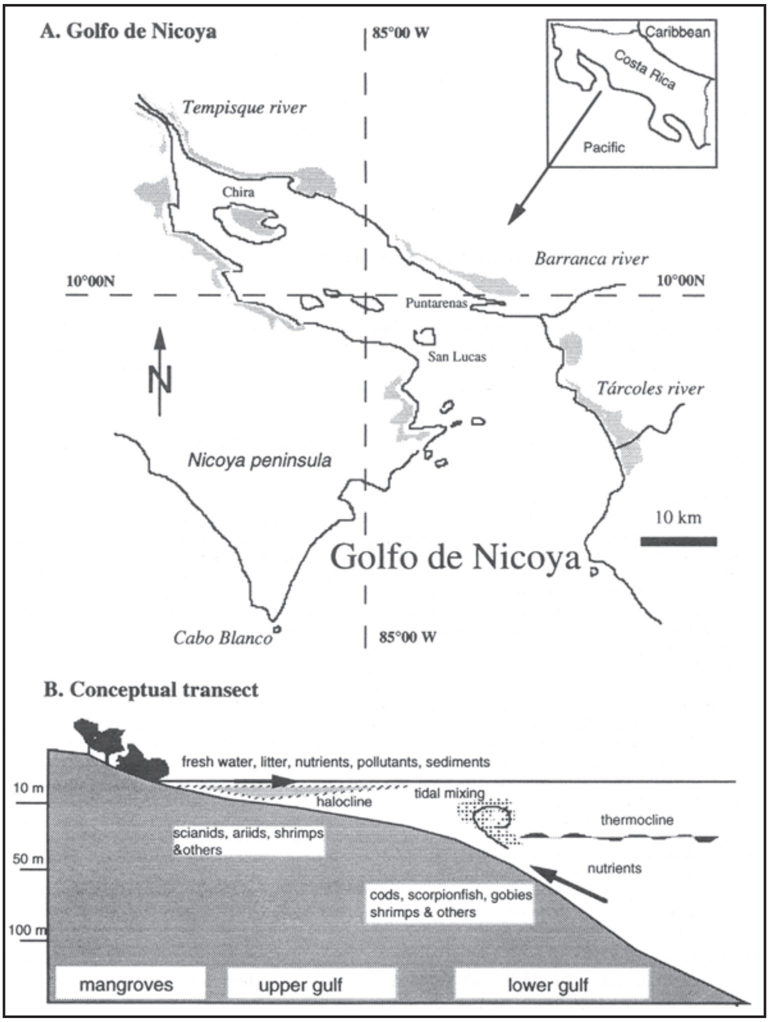

Fig. 1. Gulf of Nicoya, Costa Rica. A. Study area; B. Conceptual transect. Reprinted from Wolff, M., J. Chavarría, V. Koch and J. A. Vargas. 19998. A trophic flow model of the Golfo de Nicoya, Costa Rica. Rev. Biol. Trop. 46 (Supl. 6): 63-79, with permission from RBT.

prises the Caeté estuary as well as the adjacent mangrove-covered peninsula north of the city of Bragança (01°03' S, 46°45' W). The climate is tropical and humid, annual mean daily air temperature ranges from 25.5-26.7 °C, with daily variations from 20.4-32.8 °C (Ribeiro *et al*. 1997). Towards the end of the dry season (June to November), solar radiation and water evaporation (1 450 mm per year) reach their maxima. Average annual rainfall amounts to 2 500 mm and is substantially higher than in the Gulf of Nicoya area (1 500 mm). In the wet season, salinity decreases drastically in the estuary and adjacent channels (from about 37-39 ‰ to <10 ‰ in the central part of the study area) due to rainfall and strong drainage of the wide catchments basin into the Caeté estuary. The tidal regime is semidiurnal, with amplitude of 3-5 m within the estuary. The mangrove forest on the peninsula is inundated entirely only around spring tides, while the mangrove channels and creeks are flooded daily.

A socio-economic evaluation (Glaser *et al*. 1997) revealed that 75 % of the households of the villages in the study area economically depend on the mangrove system. Of a total of 19

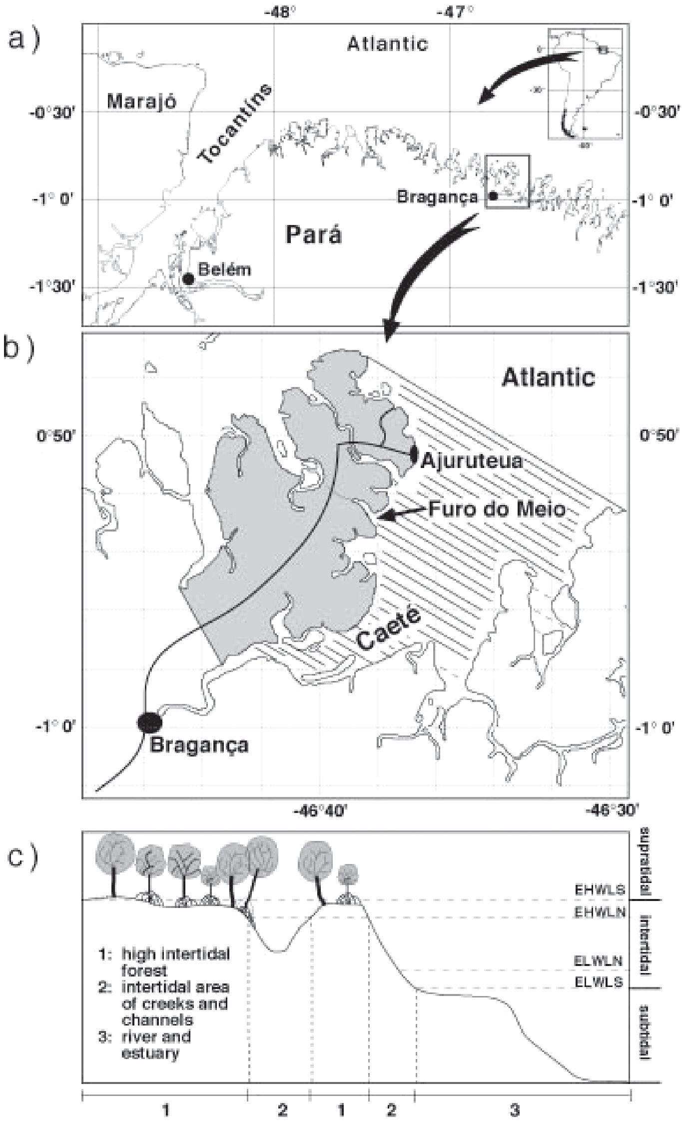

Fig. 2. Caeté estuary, Brazil: A. geographical location; B. study area; C. conceptual transect. 1: high intertidal forest; 2: intertidal area of creeks and channels; 3: river and estuary. Reprinted from Wolff, M., V. Koch, and V. Issac. 2000. A trophic model of the Caeté mangrove estuary (North Brazil), with considerations for the sustainable use of its resources. Est. Coastal Shelf. Sci. 50: 789-803, with permission from Elsevier.

mangrove products, the mangrove crab *Ucides cordatus*, is of highest economic importance. It is collected in most parts of the peninsula and its annual extraction was roughly estimated as 22 million individuals in 1997, corresponding to about 3 300 metric tons (Glaser *et al.* 1997). Further mangrove products of local importance are fish species of the families Sciaenidae, Aridae, shrimps (*Penaeus* spp., *Macrobrachium* sp.), the boreworm (*Neoteredo* spp.), mussels (*Mytella* sp.), and swimming crabs (*Callinectes* sp.). Mangrove wood is used locally for house construction, fishing traps and as firewood for brickworks. The amount extracted annually is estimated as roughly 55 000m^3 (Glaser, pers. comm.).

Information used and brief description of model construction

The basic information used for the present contribution was derived from two trophic models published by the author *et al.* (1998, 2000). Here the model summary statistics of both systems are compared and a further analysis of the original models is done with special emphasis on the Mixed Trophic Impact (MTI) routine (see description below), the matter cycling characteristics and corresponding indices of both systems as well as the biomass distribution of the systems. A short summary of the model groups and data sources follows below. For further details see the above-cited papers.

Gulf of Nicoya

As a first step in defining the model compartments, available information on biomass, catches, P/B ratios, consumption rates (Q/B), as well as growth - and mortality rates for the species/groups of the system was assembled from landing statistics, own survey data of benthic invertebrates and fish (Vargas and Wolff 1996) and literature sources. As the gulf is among the best studied tropical ecosystems (Vargas 1995), the general knowledge about most biota of the gulf is good. For most fish species, Q/B was calculated using the aspect ratio of the caudal fin (Palomares and Pauly 1989). The weight dependent model of Palomares (1987) was applied to the groups "rays and sharks" and "morays and eels". As a next step, species of similar sizes, diets, consumption rates, mortality and production rates were grouped within a compartment, which yielded a total of 21 model groups. As the official landing data were not given for each fish species separately, but for groups of fish such as "primera grande" (first quality fish >2 kg), "primera pequeña" (first quality, <2 kg), and others, which are comprised of different trophic groups, it was difficult to attribute catch values for each of the groups defined in the model. As the total catch was given, we proceeded by allocating a fraction of the total catch to each group proportional to the biomass fraction of the fish surveys (Wolff 1996). The mangroves cover approx. 15 km^2 (Jiménez 1994) representing 1 % of total system area. To convert given production values for phytoplankton carbon into wet weight, we used the following conversion: carbon to dry organic matter, 1:2.5; dry to wet organic matter, 1:5 (Parsons *et al*. 1977). The model groups with the input data as well as the diet matrix are given in Table 1.

Caeté estuary

The following assumptions were made prior to the modelling procedure:

1. The exploitation rate (E= fishing mortality/ total mortality) of harvested aquatic groups (land crabs excluded) is considered relatively low (Glaser *et al*. 1997) and is set to the level of E= 0.3;

2. 15 g·m^{-2}·year^{-1} of land crabs are extracted from the area (Glaser *et al*. 1997). This value shall be used to calculate the crab's exploitation rate by the model;

3. A maximum of 10 % of mangrove litter fall is exported from the system (Schories, preliminary estimates);

4. Microphytobenthic algae enter the food web mostly through resuspension into the plankton at low tide (Dummermuth 1997). This group is therefore combined with the phytoplankton in one compartment.

As a first step in defining the model compartments, available information on biomass, catches, P/B ratios, consumption rates (Q/B), as well as growth - and mortality rates for the species/groups of the system was assembled from the MADAM*-Project data bank. Additional information was taken from the literature on other mangrove systems. Species of similar sizes, diets, consumption rates, mortality and production rates were grouped within a compartment. Table 2 shows the input values as well as the diet matrix.

For the biomass/m^2 estimates for phytoplankton and zooplankton an estimate of an average depth of the Caeté estuary of 3 m was used.

*MADAM-Project: 10 years research project on "**Ma**ngrove **D**ynamics **a**nd **M**anagement" of the German Ministry of Science and Education (1994-2005)

Description of the ECOPATH modelling approach

The core routine of ECOPATH II consists in using a set of simultaneous linear equations (one for each group i in the system), ie.:

$$P_i - B_i\, M2_i - P_i\,(1\text{-}EE_i) - EX_i = 0, \qquad \text{(Eq. 1)}$$

where
P_i= the production of (i) (gm^{-2}·y^{-1})
B_i= the biomass of (i) (gm^{-2})
$M2_i$= the predation mortality of (i) (y^{-1})
EE_i= the Ecotrophic Efficiency of (i) (fraction of 1)
1-EE_i= the "other sources of mortality" (y^{-1})
EX_i = the export of (i) (gm^{-2}·y^{-1})

TABLE 1

Gulf of Nicoya estuary, Pacific coast of Costa Rica: input data and diet matrix.

Input table								Diet- Matrix																
No	Group name	TL	B	P/B	Q/B	EE	GE	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	phytoplankton	1	6	180	-	0.658	-	0.75			0.6										0.14	0.6		
2	microphytobenthos	1	0.5	120	-	0.934	-		0.1				0.1								0.1	0.15		
3	mangroves	1	100	0.22	-	0.447	-		0.1												0.05	0.01		
4	zooplankton	2.05	4	40	160	0.5	0.25	0.05	0.25	0.05	0.4	0.12	0.1			0.05		0.07			0.05	0.01		
5	shrimps	2.53	1.5	6	28	0.931	0.214			0.2		0.06	0.12	0.2	0.1	0.1	0.2	0.05	0.05	0.05			0.15	0.06
6	squids	3.54	0.4	8.3	32	0.914	0.259			0.1		0.2	0.03		0.1	0.05		0.05		0.05				0.05
7	small pelagics	2.42	2.6	5.5	28	0.923	0.196			0.65		0.5		0.05	0.2	0.18	0.2	0.1	0.1	0.05				0.45
8	carangids	3.63	0.5	0.8	7.3	0.943	0.11									0.1			0.02					
9	small demersals	3.03	1.3	2.3	12	0.932	0.192					0.02			0.2	0.15	0.2	0.1	0.16	0.14			0.1	
10	flatfish	3.08	0.78	1.8	7.5	0.939	0.24						0.05			0.05	0.05	0.1	0.08	0.08				
11	catfish	3.5	0.5	0.9	4	0.92	0.225											0.05	0.1	0.05				
12	snappers & grunts	3.67	0.4	0.95	4.3	0.962	0.221										0.05	0.05	0.04	0.05				
13	Lizardfish	3.64	0.19	1	7	0.981	0.143									0.02		0.02	0.02	0.04				
14	Scianids & Lutjanids	3.62	0.3	0.6	4	0.963	0.15											0.01	0.05	0.05				
15	Rays & Sharks	3.9	0.09	0.6	2.8	0.954	0.214													0.02				
16	Morays & eels	3.84	0.16	0.75	3.6	0.992	0.208												0.03	0.02				
17	Endobenthos	2.1	0.35	30	150	0.994	0.2		0.15				0.05	0.05		0.05					0.04		0.1	0.1
18	Epibenthos	2.01	12	4	25	0.448	0.16		0.1			0.05	0.5	0.6	0.4	0.2	0.2	0.35	0.2	0.3			0.5	0.3
19	Predatory crabs	3.05	0.5	2	11	0.904	0.182					0.05		0.02		0.05	0.1	0.05	0.15	0.1				0.04
20	Sea/shore birds	3.35	0.05	0.15	65	0	0.002																	
21	Detritus	1	-	-	-	0.336	-	0.2	0.3				0.05	0.08							0.62	0.23	0.15	
								Import																
								Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

TL= trophic level, B= biomass, P/B= production/biomass, Q/B= consumption/biomass, EE= ecotrophic efficiency, and GE= gross efficiency.

TABLE 2

Caeté estuary, Atlantic coast, Brazil, input data and diet matrix (symbols as in Table 1)

		Input data						Diet Matrix															
No	Group name	TL	B	P/B	Q/B	EE	GE	3	4	5	6	7	8	9	10	11	12	13	14	15		17	18
1	mangroves	1	13000	0.15	-	0.679	-						0.9	1							1	0.05	0.05
2	phytoplankton	1	6.4	185	-	0.501	-	0.7	0.25			0.1			0.15	0.2							
3	zooplankton	2.11	1.5	100	300	0.737	0.33	0.1	0.05						0.1	0.7	0.45	0.05					
4	small benthos	2.17	10	12	50	0.898	0.24		0.1	0.5	0.3				0.35		0.15	0.7	0.17	0.05			0.1
5	predatory snail	3.09	2.1	0.5	4	0.646	0.13				0.01								0.01				
6	predatory crabs	3.05	2.5	2	22	0.76	0.09				0.01								0.16	0.15			0.01
7	fiddler crabs	2	14.5	5.5	95	0.654	0.06				0.49							0.15	0.26	0.1		0.56	0.49
8	landcr.(Ucides)	2	80	0.25	14	0.999	0.02															0.22	0.05
9	wood borers	2	2.5	2.2	15	0.945	0.15			0.5													
10	shrimps	2.52	2.2	5.5	25	0.629	0.22				0.03						0.15	0.05	0.1	0.05			0.05
11	pel.feed.<7 cm	2.78	1.9	5.4	20	0.639	0.27				0.01						0.25		0.05	0.15			0.04
12	pel.feed.>7 cm	3.35	1.3	2.3	13	0.856	0.18												0.1	0.15			0.02
13	benth.feed <10 cm	3.1	2	3	8	0.838	0.38				0.05								0.1	0.1			0.04
14	benth.feed >10 cm	3.49	3.2	0.8	4	0.797	0.2													0.25			0.03
15	pred. fish	4	0.7	0.7	4	0.571	0.18																0.01
16	insects	2	0.9	6.2	30	0.886	0.21															0.17	0.1
17	mammals	2.95	0.37	0.5	50	0.973	0.01																0.01
18	birds	3.18	0.3	0.3	60	0	0.01																
19	Detritus	1	-	-	-	0.862	-	0.2	0.6		0.1	0.9	0.1		0.4	0.1		0.05	0.05				
							sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Thus, the total production by group (i) is balanced by predation from other groups ($B_i \cdot M2_i$), by non-predation losses ($P_i(1\text{-}EE_i)$), eg. sedimentation, and losses to other systems (EX), eg. emigration and fishery. Since production is more conveniently estimated from the production/biomass ratio (PB) and the average annual biomass (B), it is expressed as ($P_i = B_i \cdot PB_i$). Predation mortality depends on the activity of the predator and can be expressed as the sum of consumption by all predators (j) preying upon group (i), ie.

$$(B_i * M2_i) = \sum_j B_j * QB_j * Dc_{ji}, \qquad \text{(Eq. 2)}$$

where:
QB_j= consumption/biomass ratio of the predator j (y^{-1}) and
DC_{ji}= fraction of the prey (i) in the average diet of predator j.
Equation (1) can be re-expressed as:
$B_i * PB_i * EE_i - \sum_j B_j * QB_j * DC_{ji} - EX_i = 0$, (Eq. 3)

Three of the four parameters B, PB, QB and EE have to be set initially for each group. The remaining parameter is computed by the software. Particularly for some lower-trophic level groups, EE is sometimes changed by the program, even when P or PB is treated as initial unknowns. QB of a compartment can also be calculated by the model and treated as an unknown in initial parameterisation. For further details of the ECOPATH-model structure see Christensen and Pauly (1992).

A set of 16 summery statistics were computed for both systems and comparatively analysed (Table 5). In addition the “Mixed trophic impact” (MTI) routine of the programme was used as a form of an ordinary sensitivity analysis (Majkowski 1982). It is based on an approach of Leontief (1951) to reveal direct and indirect interactions in the economy and was further developed by Ulanowicz and Puccia (1990) and introduced into ECOPATH. The impact routine was used as a tool for indicating the possible impact of direct and indirect interactions (including competition) between model compartments. The table values are relative to each other and proportional to the strength of the impact.

RESULTS

Fig. 3 and 4 show the compartment models of the Gulf of Nicoya (GN) and Caete (CE) estuarine systems. While the number of compartments is similar (21 and 19 respectively), there are important differences in compartment biomasses and energy flows between both systems. Most remarkable is the enormous land crab biomass in the CE system, while this species is almost absent in the GN system and not considered for the model. The mangrove biomass of CE is two orders of magnitude higher than in GN (13 000 gm^{-2} compared to 100 gm^{-2}), and there is no epibenthos compartment, while this compartment is the second largest in the GN system. It is also seen from both figures that the number of fish compartments is higher in the GN system, as is the combined biomass of all fish. Fig. 5 and 6 exhibit the roles of the land crab and the shrimps in the Caeté and Nicoya systems respectively, and also show the biomass pyramids of both systems. The low trophic level of the land crab, its great amount of mangrove litter consumed and the small numbers of predators are in great contrast to the picture of shrimps in the Nicoya system. Here, many predators heavily depend on this compartment of the system. The biomass pyramids reveal that absolute biomass as well as relative biomass of the first trophic level is far greater in the Caeté system. Table 1 and 2 give the input data as well as the diet matrix for the GN and CE systems respectively, Table 3 and 4 show the results of the Mixed Trophic Impact (MTI) analysis for both systems respectively.

Table 5 gives 16 important summary statistics of both systems as derived from the ECOPATH models.

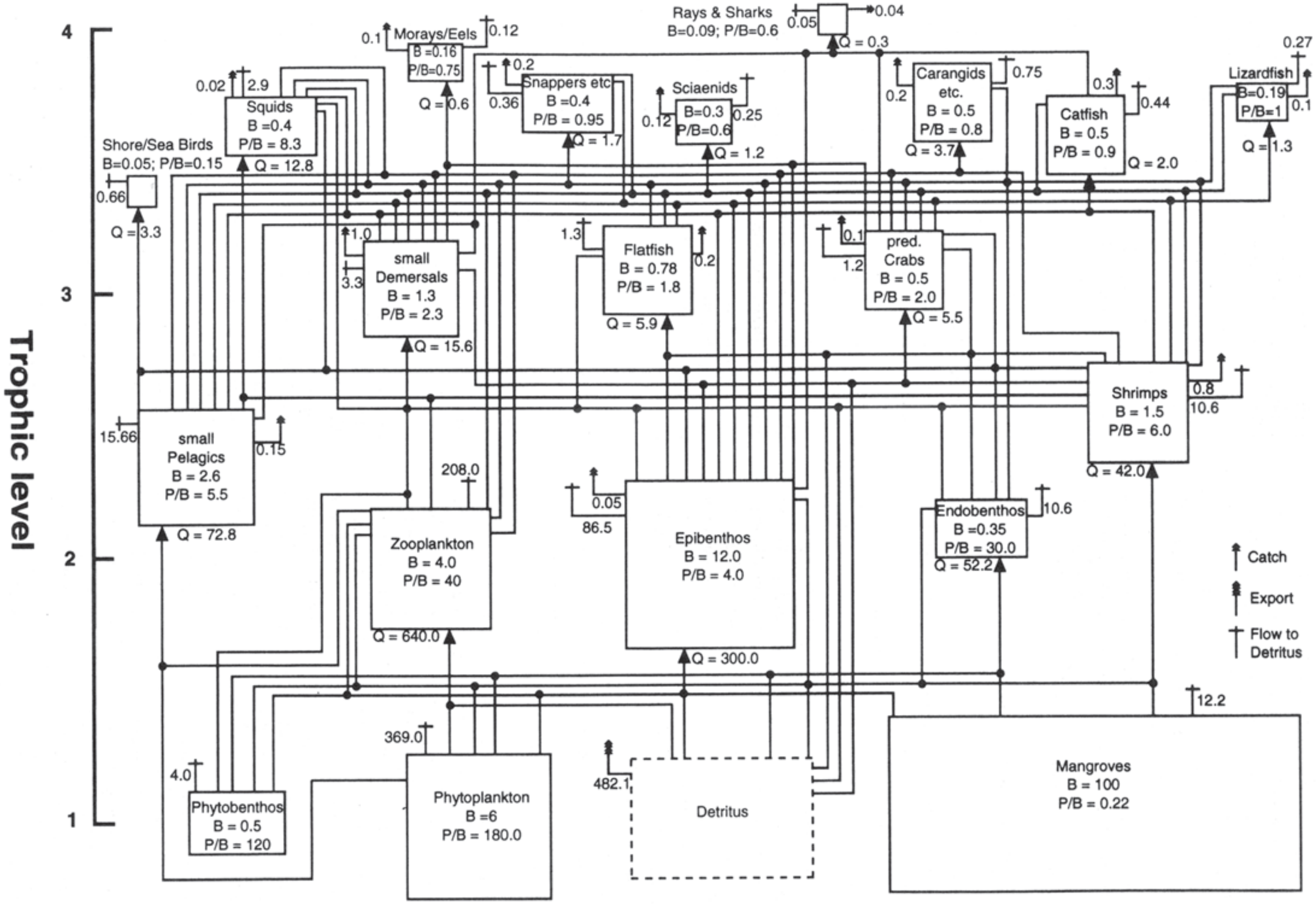

Fig. 3. Gulf of Nicoya trophic model. Box size is proportional to square root of compartment biomass, Q-values represent the total consumption of each box, and flows are given in gm^{-2} (wet mass). Reprinted from Wolff, M., J. Chavarría, V. Koch and J. A. Vargas. 19998. A trophic flow model of the Golfo de Nicoya, Costa Rica. Rev. Biol. Trop. 46 (Supl. 6): 63-79, with permission from RBT.

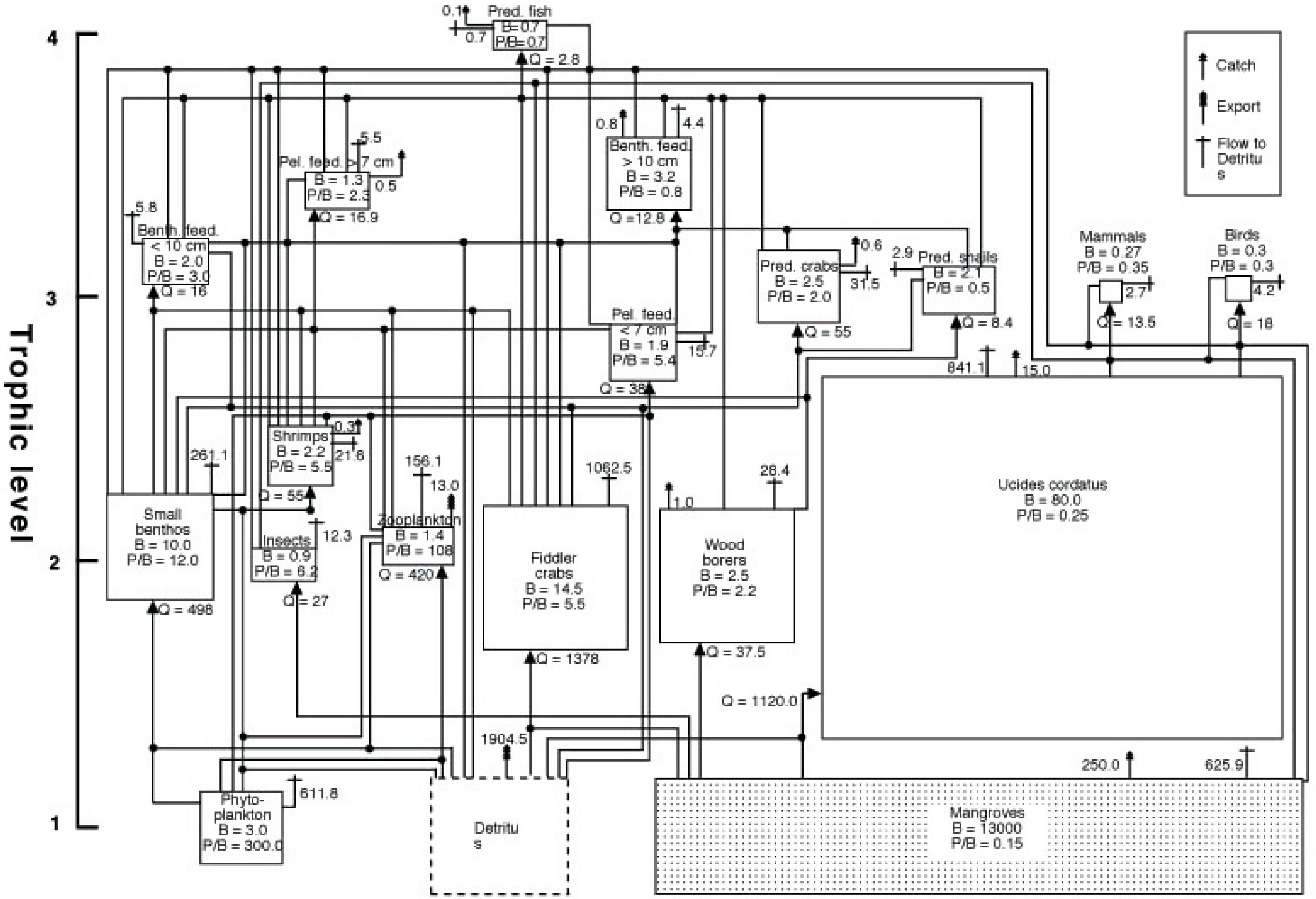

Fig. 4. Caeté estuary trophic model. Box size is proportional to square root of compartment biomass (except for mangrove compartment); Q-values represent total amount of biomass entering the compartment, flows are given in gm^{-2} (wet mass). Reprinted from Wolff, M., V. Koch, and V. Issac. 2000. A trophic model of the Caeté mangrove estuary (North Brazil), with considerations for the sustainable use of its resources. Est. Coastal Shelf. Sci. 50: 789-803, with permission from Elsevier.

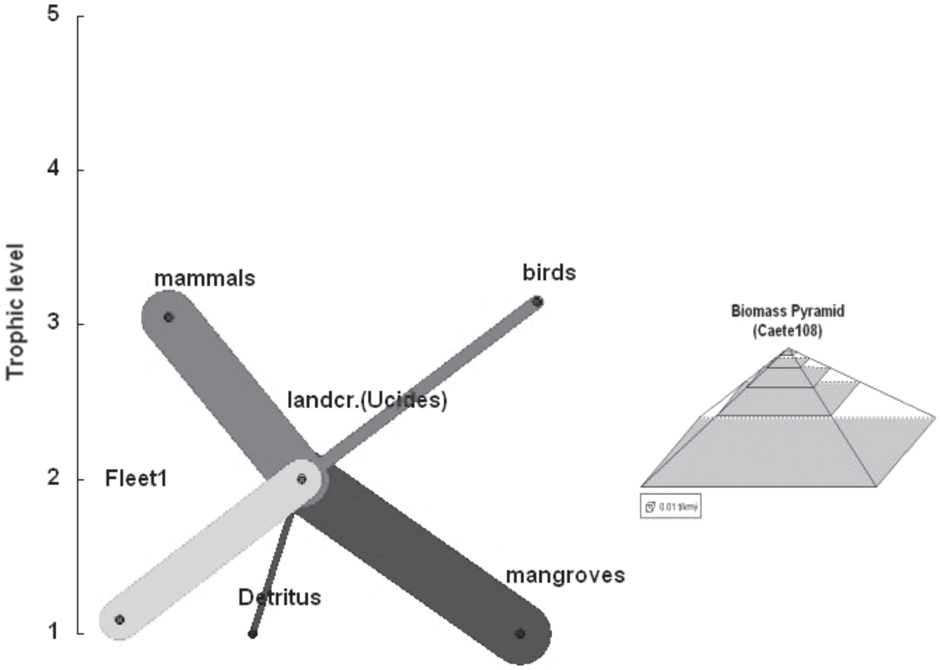

Fig. 5. Caeté estuary. Role of land crabs (*Ucides cordatus*) in the ecosystem and system biomass pyramid; black bar: food biomass coming from mangrove, dark grey bar: food biomass to predators; light grey bar: catch (widths of bars proportional to amounts transferred).

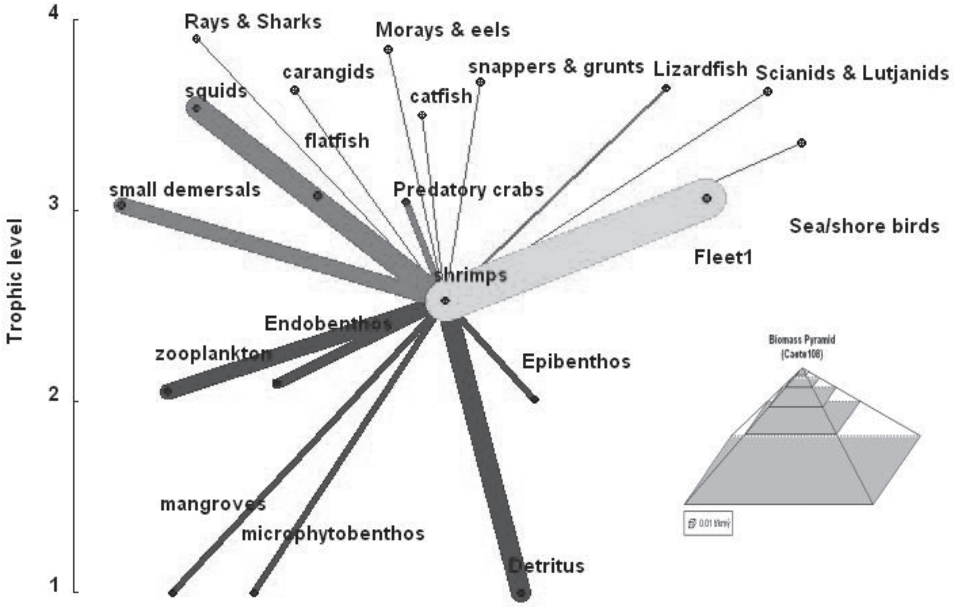

Fig. 6. Gulf of Nicoya. Role of shrimps (*Penaeus* sp.) in the ecosystem and system biomass pyramid; black bars: food biomass from prey compartments; dark grey: food biomass to predators; light grey bar: catches (widths of bars proportional to amounts transferred).

TABLE 3

Caeté estuary: Mixed Trophic Impact-analysis showing direct and indirect impacts between groups (underlined those impacts that exceed +/- 10 %)

		Impacting \ Impacted																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	crab	fish
1	mangroves		0.00	-0.01	-0.01	0.27	-0.09	0.00	0.12	0.40	0.01	0.07	-0.12	0.04	-0.01	-0.08	0.67	0.07	0.11	-0.01	0.71	-0.02
2	phytoplankton	0.00		0.34	0.11	0.03	0.02	0.02	0.00	-0.02	0.08	0.24	0.21	0.07	0.03	0.06	0.01	-0.03	0.04	-0.05	0.00	0.03
3	zooplankton	0.00	-0.29		-0.03	0.00	-0.02	-0.02	0.00	0.00	-0.09	0.16	0.27	0.01	-0.01	0.06	0.01	-0.01	-0.01	-0.01	0.00	0.00
4	small benthos	-0.01	-0.05	-0.13		0.16	0.10	-0.10	0.01	-0.13	0.12	-0.11	-0.02	0.35	0.09	0.03	0.04	-0.09	0.04	-0.04	0.00	0.08
5	predatory snail	0.01	0.00	0.00	-0.02		0.00	0.00	0.00	-0.56	0.00	0.01	0.00	-0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00
6	predatory crabs	-0.02	0.03	0.04	0.04	-0.44		-0.23	0.01	0.34	-0.04	-0.02	0.01	-0.42	0.01	0.12	0.03	-0.01	-0.12	0.15	-0.01	0.02
7	fiddler crabs	0.03	-0.07	-0.05	-0.14	-0.13	0.14		-0.05	0.13	-0.21	-0.04	-0.12	-0.16	0.04	-0.13	-0.09	0.06	0.23	-0.36	0.03	0.03
8	landcr.(Ucides)	-0.53	0.01	0.01	0.00	-0.18	0.04	-0.05		-0.30	-0.02	-0.05	0.08	-0.02	-0.01	0.04	-0.57	0.10	-0.07	-0.02	-0.45	0.00
9	wood borers	-0.01	0.00	0.00	-0.01	0.35	0.00	0.00	0.00		0.00	0.00	0.00	-0.01	0.00	0.00	-0.01	0.00	0.00	0.00	-0.01	0.00
10	shrimps	0.00	0.01	0.00	-0.12	-0.03	-0.03	0.01	0.00	0.02		-0.06	0.08	-0.04	0.04	0.01	0.00	-0.03	0.04	0.00	0.00	0.04
11	pel.feed.<7 cm	0.00	0.06	-0.13	0.01	0.00	0.00	0.01	0.00	-0.01	-0.05		0.12	-0.01	0.00	0.11	0.01	-0.03	0.04	0.00	0.00	0.01
12	pel.feed.>7 cm	0.00	-0.02	0.05	0.02	0.02	-0.02	0.00	0.00	-0.01	-0.27	-0.52		0.01	0.02	0.04	0.00	0.01	-0.01	0.00	0.00	0.02
13	benth.feed <10 cm	-0.01	0.01	0.01	-0.05	-0.02	0.00	-0.02	0.01	0.01	-0.10	0.03	-0.04		0.03	0.07	0.01	-0.03	0.02	0.02	0.00	0.03
14	benth.feed >10 cm	0.00	-0.01	-0.02	0.00	0.08	-0.31	0.07	0.00	-0.06	0.03	0.14	-0.32	-0.01		-0.14	-0.01	-0.01	0.05	-0.05	0.00	0.63
15	pred. fish	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00	-0.01	0.03	-0.02	-0.02	0.00	-0.28		0.00	0.00	0.00	0.00	0.00	-0.14
16	insects	-0.01	0.00	0.00	0.01	0.00	0.00	-0.02	-0.02	-0.01	0.00	0.00	0.00	-0.01	0.00	-0.05		0.06	0.08	0.01	-0.01	-0.01
17	mammals	0.11	0.01	0.01	0.03	0.06	-0.03	-0.09	-0.15	0.04	0.05	0.02	0.01	0.04	-0.01	0.04	-0.45		-0.08	0.07	0.09	0.00
18	birds	-0.08	0.00	0.01	0.00	-0.04	0.04	0.00	0.12	-0.04	-0.09	-0.05	-0.03	-0.12	-0.03	-0.63	0.15	-0.94		-0.01	-0.07	-0.10
19	Detritus	-0.03	-0.14	-0.01	0.21	-0.09	0.23	0.42	0.05	0.05	0.22	0.00	-0.03	0.06	0.15	-0.06	-0.11	-0.01	0.23		-0.03	0.12
	crab fishery	0.27	-0.01	-0.02	0.00	0.09	-0.13	0.07	-0.66	-0.04	0.03	0.13	-0.21	0.08	0.00	-0.04	0.30	-0.09	0.05	-0.01		-0.01
	finfish fishery	0.00	0.00	0.01	0.00	-0.04	0.11	-0.03	0.00	0.03	-0.02	-0.05	0.13	0.00	-0.19	-0.29	0.00	0.01	-0.02	0.02	0.00	-

TABLE 4

Gulf of Nicoya: Mixed Trophic Impact-analysis showing direct and indirect impacts between groups (underlined those impacts that exceed +/- 10 %)

	Group	Impacting\Impacted																					
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Fishery
1	phytoplankton		-0.24	0.05	0.26	-0.09	0.13	0.39	0.18	0.07	0.09	0.14	0.10	0.06	0.12	0.07	0.08	0.01	0.30	0.02	0.27	-0.22	0.07
2	microphytobenthos	-0.01	-0.01		0.06	-0.02	0.06	-0.01	0.01	0.02	0.10	0.01	0.02	0.00	0.02	0.01	0.00	0.01	0.03	0.07	0.05	0.03	-0.02
3	mangroves	0.01	0.00		0.00	0.09	0.01	-0.01	0.01	0.00	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.00	0.01	0.01	0.00	0.00	0.02
4	zooplankton	-0.31	0.16	0.06		0.07	0.03	0.01	0.06	0.00	0.11	0.05	0.00	0.03	0.02	0.05	0.07	0.14	0.18	0.11	0.06	-0.21	0.00
5	shrimps	0.05	0.07	0.22	0.02		0.12	-0.05	0.03	0.02	0.08	0.07	0.05	0.08	0.09	0.11	0.13	0.42	0.12	0.03	0.04	0.06	0.19
6	squids	-0.03	0.00	0.05	0.08	-0.15		-0.33	0.02	0.02	0.05	0.01	0.01	0.07	0.02	0.01	0.04	0.06	0.00	0.02	0.12	-0.04	-0.04
7	small pelagics	0.05	-0.04	0.01	0.15	-0.10	0.26		0.31	0.03	0.04	0.13	0.11	0.07	0.05	0.05	0.02	0.08	0.05	0.13	0.35	0.06	0.04
8	carangids	0.00	-0.01	0.01	0.00	0.04	0.17	-0.02		0.00	0.00	0.04	0.06	0.04	0.03	0.04	0.06	0.01	0.01	0.17	0.02	0.00	0.05
9	small demersals	0.03	0.10	0.07	0.00	-0.09	0.06	0.08	0.06		0.60	0.00	0.01	0.05	0.12	0.05	0.12	0.04	0.15	0.09	0.01	0.04	0.18
10	flatfish	0.01	0.08	0.06	0.02	-0.10	-.01	0.01	0.03	0.03		0.06	0.00	0.02	0.03	0.00	0.00	0.05	0.09	0.16	0.03	0.01	0.03
11	catfish	0.00	0.00	0.00	0.00	0.01	0.03	-0.01	0.02	0.14	0.08		0.04	0.04	0.00	0.04	0.01	0.00	0.00	0.01	0.00	0.00	0.04
12	snappers & grunts	0.00	-0.01	0.00	0.00	-0.01	0.06	0.00	0.43	0.06	0.02	0.02		0.15	0.03	0.01	0.03	0.00	0.01	0.01	0.01	0.00	0.01
13	Lizardfish	-0.01	-0.02	0.01	0.00	0.00	0.01	-0.02	0.06	0.05	0.01	0.01	0.17		0.00	0.02	0.01	0.01	0.02	0.14	0.01	-0.01	0.00
14	Scianids & Lutj.	0.00	0.00	0.00	0.01	0.00	0.02	-0.01	0.00	0.05	0.00	0.07	0.14	0.14	0.11		0.01	0.01	0.00	0.00	0.03	0.00	0.00
15	Rays & Sharks	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.01	0.05	0.01	0.01	0.07		0.05	0.00	0.00	0.03	0.00	0.00	0.00
16	Morays & eels	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.01	0.04	0.03	0.09	0.14	0.20		0.00	0.00	0.02	0.00	0.00	0.01
17	Endobenthos	0.02	-0.05	0.22	0.02	0.05	0.00	-0.01	0.02	0.00	0.02	0.02	0.03	0.00	0.01	0.01	0.01		0.04	0.04	0.07	-0.08	0.01
18	Epibenthos	-0.12	-0.55	0.12	0.07	-0.15	0.09	-0.07	0.08	0.15	0.24	0.18	0.04	0.07	0.18	0.14	0.20	0.10		0.22	0.16	-0.14	0.07
19	Predatory crabs	0.00	0.04	0.04	0.01	-0.05	0.00	-0.01	0.05	0.19	0.09	0.05	0.01	0.04	0.02	0.11	0.07	0.00	0.04		0.02	0.01	-0.03
20	Sea/shore birds	0.00	0.02	0.01	0.02	0.01	0.06	-0.06	0.03	0.02	0.03	0.01	0.02	0.01	0.02	0.02	0.02	0.02	0.03	0.13		0.00	-0.01
21	Detritus	-0.06	-0.08	0.20	0.07	0.25	0.02	-0.03	0.03	0.05	0.12	0.01	0.02	0.04	0.00	0.00	0.01	0.31	0.04	0.19	0.06		0.08
22	Fishery	-0.01	-0.04	0.00	0.00	-0.06	0.09	-0.01	0.28	0.13	0.08	0.46	0.30	0.27	0.42	0.60	0.67	0.02	0.05	0.12	0.02	-0.02	

TABLE 5

Selected summary statistics of the Gulf of Nicoya (Costa Rica) and Caeté estuary (Brazil) trophic models

Summary statistics	Gulf of Nicoya	Caeté	Units
Extension of study area	1530	220	km^2
Total net primary production	1162	3134	gm^{-2} $year^{-1}$
Pelagic biomass	13.5 (41 %)	12 (9 %)	gm^{-2} $year^{-1}$
Benthic biomass	19.2 (59 %)	120.4 (91 %)	gm^{-2} $year^{-1}$
Production/respiration (P/R)	1.72	3.31	-
Mean transfer efficiency	14.9	9.8	%
Total catches	3.38	18.3	gm^{-2} $year^{-1}$
Total throughput	3049	10559	gm^{-2} $year^{-1}$
Throughput cycled	35.4	95.6	gm^{-2} $year^{-1}$
Fisheries trophic level (FTL)	4.06	3.1 (2.1 mangroves.incl.)	-
Primary production required/ total catch (PPR/C)	117	3.53	-
Fisheries gross efficiency (FE)	0.3	0.58 (8.6, mangroves.incl.)	%
Ascendancy	26.1	27.4	Flowbits(%)
Finn's cycling index	5.46	17.9	% of Throughput
Finn's mean path length	2.64	3.4	
Connectance index	0.30	0.23	
Proportion of flows from Detritus	0.33	0.53	

For a further description of these statistics and indices see Christensen and Pauly (1992)

DISCUSSION

The comparative analysis of the biotic structure and biomass flow distribution of the systems considered in this study was led by the question of how the biotic structure of a mangrove dominated estuary determines the resource potential and how sustainable resource management could be improved by knowing the biotic structure and biomass flow distribution of the system.

The Caeté estuary (CE) revealed a significantly higher primary production (exceeding Gulf of Nicoya (GN) by 2.7 times) due to the large mangrove cover. Catches in the CE exceed those of GN even more (5.4 times on a per area basis). Thus, the total catch of both systems is similar although the area extension of GN is about seven times that of CE.

The enormous harvest of 18.3 gm^{-2} (mangroves excluded) in the CE goes along with a high fisheries efficiency (FE= 0.58 %) although mean transfer efficiency between trophic levels was lower than for the GN model (9.8 % compared to 14.9 %). The reason for this high FE is the mangrove crab *Ucides cordatus*, which is the principal resource of the system besides the mangrove tree itself. As this crab is a primary consumer, the trophic level of the fishery (FTL) is low (3.1) compared to the GN system (4.1). If the substantial mangrove harvest of CE was included in the calculations the values differ even more (FE= 8.6 %) and (FTL= 2.1) respectively.

The most important resources of GN are, to the contrary, predatory fish like carangids, catfish, snappers and grunts, morays, flatfish as well as an important amount of shrimps. Only small quantities of these groups are produced and harvested in the CE, where shrimps are of minor importance, and pelagic top predators are also insignificant. This difference is also revealed in the ratio of primary production required/catch (Table 5), which is 33 times higher in the Nicoya system, in which fish predators of high trophic levels dominate the catches.

GN is the centre for the fishery of Costa Rica but catches have dropped to levels that are not profitable any longer. As shown by the model, shrimps occupy a central position in the food web as food source for many fish groups. Overexploitation of the white shrimp *Penaeus vannamei* (catches have dropped by about 50 % in the last years) seems to have severely affected the food web of the whole system. For their wide-scale distribution and specific trophic niche (converter of the system's rich detritus source), it is improbable that other species can compensate for this lack, and the decline of many commercially important populations of shrimp feeding species seems a logical consequence of this overexploitation. The MTI analysis (Table 4) confirms these conclusions, since a biomass increase in shrimps would positively impact several predator groups (squids and fish groups) in the GN system, while in the CE system the predicted impact is negligible.

Mangroves were included as system compartments in the CE and GN models. In both they are the most prominent group (99 and 76 % of system biomass in CE and GN respectively). As the part of the total area covered by mangroves was about 45 % in the CE compared to only 1 % of GN, the relative importance of mangroves for the primary production of the total system (and as habitat for the land crabs) was far greater in the CE area. The MTI analysis (Table 3) reveals the positive effect of an increased mangrove cover on the land crab and crab fishery as well as on wood borers and (indirectly) on predatory snails, while in the GN system just shrimps are positively affected. Conversely the impact of crabs on the mangroves is strongly negative, since at present densities crabs consume >80 % of total litter fall including the seed (propagules) of the mangroves (Rademaker 1998, Nordhaus 2003) The present strong crab fishery might thus be beneficial to the mangroves by reducing crab population density and enhancing the recruitment success of mangroves.

The MTI analysis also suggests that an increase of detritus would positively impact shrimps and endobenthos in GN while in the CE system fiddler crabs would mostly be favoured. Another remarkable difference between both systems is that filter feeders (bivalves, encrusting epifauna) are almost absent in CE while this group represents the second largest one in GN, most of the organisms attached to the roots of the mangroves trees. The MTI analysis suggests, accordingly, that an increase in aquatic primary production (phytoplankton) would favour epibenthos (filter feeders), small pelagic fish, and zooplankton in the GN, while only zooplankton would significantly be favoured in the CE system.

These differences can be explained to a large extent by the topography and tidal regimes of both systems: while the mangrove forest of CE is inundated only each fortnight (at spring- and neap-tide), tides flush the mangroves of GN twice a day, a situation encrusting fauna can very well cope with, while falling dry for 14 days is lethal for most species. These differences in topography and tidal regime likely explain the enormous abundance of land crabs in CE, and the (formerly) large stocks of shrimps in GN: most of the primary energy fixed by the mangroves of CE fuels the "forest ground" benthos through litter fall, of which the land crab and the fiddler crabs are the most abundant organisms. When the forest is inundated each fortnight relatively little of the primary energy is left for entering the estuary. In GN, on the contrary, mangrove litter is daily exported to the estuary providing the material for a rich detritus-based aquatic food chain, within which shrimps play a central role.

To explore the general degree of maturity and possibly indirectly the degree of resilience of the systems (Rutlege *et al*. 1976), we could examine the summary statistics of both systems contained in Table 5.

P/R is higher in CE (3.31) than the GN (1.72). This is indicative for a little developed (growing) system in which total production is much higher than respiration. Energy flow seems very much bottom-up controlled and CE's trophic structure relatively loose. This seems also reflected in the low average transfer efficiency between trophic levels (9.8 %). In addition, Finn's cycling index (FCI) is very high in CE (17.9 %), as is the proportion of flows originating from detritus (0.53 compared to 0.33 in GN). According to Wulff and Ulanowicz (1989) this could also be indicative for a low degree of system maturity. Somewhat unexpected seems the slightly higher level of relative Ascendency (A) in CE (27.4 %) compared to GN (26.1 %). A is a measure of system maturity comprising system size in terms of flows (T) and system complexity in terms of information content (I) (Ulanowicz 1986). An explanation for the higher level of A in CE is the high relative importance of the mangroves (22 %) and crabs (24 %) in the CE system, which is not only the most important in terms of flows (T) but also regarding their information content (I).

In GN, production does not exceed respiration to the same extent and transfer efficiency between trophic levels is significantly higher (around 15 %). This suggests a system of a higher degree of development and tighter trophic structure with more top-down control. It is probable that this system is less resilient to man-induced changes and that the drastic decline in the fishery catches observed over the last decades does not only reflect growth overfishing of some resources but rather a general destabilisation of the entire ecosystem.

For management measures to be successful, the system characteristics described above must be considered. In the case of CE, the land crab biomass should be sustained at the present levels by avoiding recruitment and growth overfishing through a strong control of total fishing effort and a minimum landing size. Further mangrove logging must be impeded as mangroves represent the crab's principal habitat and food source. A potential for a catch increase of finfish and shrimps inside the estuary should not be expected, as overall aquatic resource biomass and production is, for natural reasons, comparatively low.

GN appears as a system already very much altered from its original state through the overexploitation of shrimps and finfish during past decades. Sustainable levels of higher than present catches seem attainable only after a several year's period of strong reduction in fishing effort to allow shrimps and fish resources to reattain the large stock sizes of the late 1970s.

The two mangrove fringed systems compared are extremely different, not only regarding the type of resources available to the fishery but also the biomass and production per area of exploitable populations. This suggests that generalisations regarding fishery resources of mangrove systems and the relationship between coastal mangrove cover and potential catches of aquatic resources should be taken with much care, with adequate attention being given to different geographical ecosystems relationships.

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RESUMEN

Se compararon modelos tróficos para estuarios bordeados por manglares en Costa Rica (Golfo de Nicoya, costa del Pacífico) y Brasil (estuario de Caete, NE de Belem) con el propósito de evaluar la biomasa, flujo de energía, productividad y potencial pesquero, así como obtener guías para la conservación y manejo de estos sistemas. Como en ambos estuarios se utilizó el mismo programa de modelaje (ECOPATH II) y el mismo número de compartimentos, se hizo una comparación entre ambos modelos. Se analizaron las diferencias entre la estructura biótica, flujo de energía y productividad de los recursos entre ambos sistemas y sus causas. Fueron grandes las diferencias entre los sistemas y las mismas están relacionadas con diferencias en las topografías, regímenes de mareas y cobertura de manglares. Si bien el Golfo de Nicoya está expuesto a mareas semidiurnas, a un intercambio eficiente de aguas entre los manglares y el golfo, y a una exportación de materia orgánica hacia el golfo, los manglares del estuario de Caeté son lavados por mareas de tipo diurno y una gran parte de la producción del manglar se queda dentro de este bosque. Esto se refleja en las grandes diferencias en la estructura de las redes tróficas y en la cantidad y tipo de recursos producidos en ambos sistemas. En el Golfo de Nicoya la materia en forma de detrito es exportada desde los manglares hacia el estuario y sirve de alimento a una red trófica con camarones y otros detrívoros en el centro de la red. En el estuario de Caeté la mayor parte de la energía permanece en ambiente béntico del bosque de manglar en donde es transferida a una biomasa enorme de cangrejos consumidores de hojarasca, el recurso principal de este sistema. La comparación de ambos estuarios implica que las generalizaciones entre ecosistemas de manglar deben ser vistas con precaución y deben ser consideradas las diferencias en las relaciones tróficas entre ecosistemas.

Palabras clave: Brasil, Costa Rica, Golfo de Nicoya, Caeté, manglares, estuarios, recursos potenciales, estructura trófica, modelaje trófico, modelos.

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