Rev. Biol. Trop. 46. Supl. 6: 63-79, 1998
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# A trophic flow model of the Golfo de Nicoya, Costa Rica

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(Rec. 17-IV-1998. Rev. 19-V-1998. Acep. 16-VII-1998).

**Abstract:** The Golfo de Nicoya is among the largest tropical estuaries (1530km$^2$) in Central America and the main, and already overexploited, fishing area of Costa Rica. It can be separated into a shallow (< 25m) interior part fringed by mangroves and mud flats and a deeper part that extends to the shelf edge to about 200m. In order to integrate available information on biomass, catches, food spectrum and dynamics of the main species populations of the system, a trophic model of 21 compartments was constructed by the use of the ECOPATH II software. The larger portion of system biomass is confined to the benthic domain (18.4 gm$^{-2}$, mangroves excluded, compared to 13.8 gm$^{-2}$ for the pelagic domain). Mangroves, although only covering 1% of the gulf area, contribute 76% to the system biomass, but only about 1% to the system's primary production. Through their root system, they provide surface area for about 90% of the gulf's biomass of epifauna (12 gm$^{-2}$), the second largest group of the model. It serves as food source for commercially important species and also fuels the system by the production of large amounts of pelagic larvae and faecal material. Based on these findings, it is emphasized that mangroves, even if they cover only small areas of an estuarine system, have a fundamental role in biomass distribution and flow pattern, and must be considered when constructing a trophic model of the system. Most of the system's energy throughput is achieved from the trophic levels I to II (62%) and II to III (34%) as expected for coastal phytoplankton/detritus based systems. Total catch amounts to 3.38 gm$^{-2}$, which is considered intermediate for tropical coastal systems. A high gross efficiency of the fishery (catch/ primary production) of 0.3% confirms the known high level of fisheries exploitation in the Golfo de Nicoya. As shown by the model, shrimps occupy a central role within the gulf as converters of detritus and other food into prey biomass for many predators, that seem to be simultaneously affected by the overexploitation of this resource. The network summary statistics computed for the model suggest an overall picture of the Golfo de Nicoya as a system of a low degree of maturity, which seems to be characteristic for tidally driven, tropical estuarine systems. The results are compared and discussed with other published trophic models of coastal systems. Among these, is Golfo Dulce, a further Costarrican gulf system about 200km south of the Golfo de Nicoya.

**Key words:** Biomass budget, ecosystem structure, estuary, tropical, Costa Rica.

The Golfo de Nicoya (Fig. 1) is located on the Pacific coast of Costa Rica (10°N, 85°W) and represents one of the largest estuaries (1530km$^2$ surface area) of Central America. It extends about 80 km from its narrowest part at the mouth of the Tempisque river to its widest part (about 55km) where it borders with the open ocean (Epifanio *et al.* 1983). For its bathymetry, the gulf can be separated into two distinct zones: the upper gulf, north of Puntarenas, which is shallow (< 25m) and fringed by mangrove stands (about 15176 ha, Jiménez 1994) and mud flats. In this area, the soft sea bottom is made of fine, organically enriched sediments (Maurer & Vargas 1984; Vargas *et al.* 1984). The lower gulf deepens sharply towards the mouth to over 200m, and is surrounded by rocky shores and sandy beaches. The gulf is similar to other tropical estuaries as it is subjected to extreme seasonal variations in riverine flow paralleled by strong variations in salinity and water temperature, but it differs from most temperate counterparts in that much of the nitrogen entering the system comes from offshore deep water, which is upwelled into the gulf

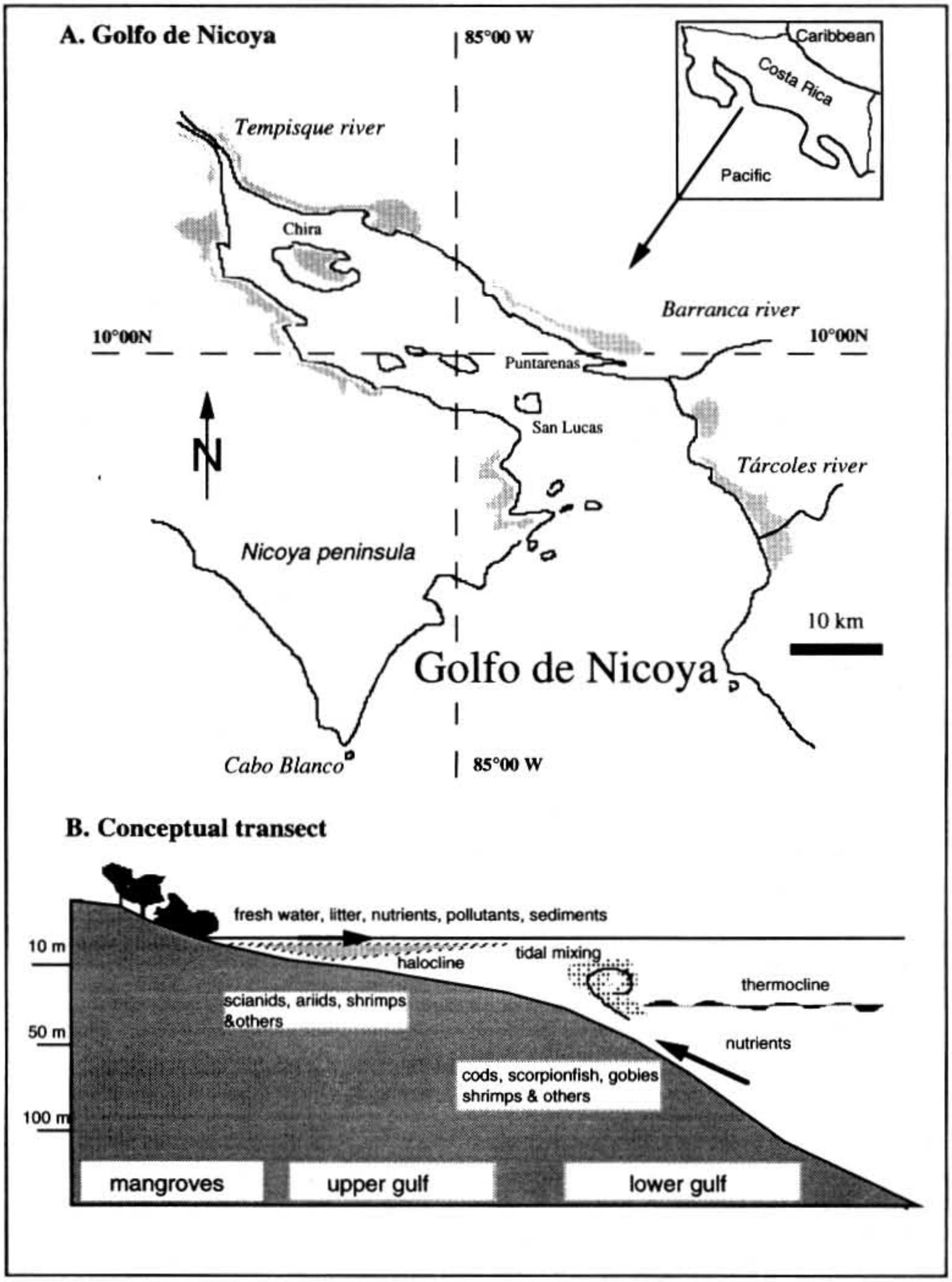

Fig.1 Golfo de Nicoya, Costa Rica (a.) study area; (b.) conceptual transect.

(Voorhis *et al.* 1983).

Due to its high productivity, the gulf is the most important fishing ground of Costa Rica, and contributes 90% of the national fish landings. Species of the families sciaenid, ariid and centropomid 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 3215t in the Golfo de Nicoya 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).

As early as 1979, the University of Costa Rica established a research programme to carry out a long-term multidisciplinary evaluation of the gulf. A milestone for the description and further understanding of the gulf's ecosystem was the oceanographical and biological surveys of the U.S.A. RV Skimmer in 1979-1981, which yielded first quantitative data on the biotic structure as well as on oceanographical conditions of the gulf. Since then, numerous research projects have been conducted and over 100 scientific papers have been written on a great variety of topics (including estuarine flow studies, nutrient dynamics, fish diversity and population dynamics, artificial reefs, zoo- and ichthyoplankton taxonomy and -dynamics, crab larval distribution patterns, mangrove ecology, subtidal and intertidal benthos, contamination, among others), making the Golfo de Nicoya one of the best studied tropical estuaries. In 1993/1994, - fifteen years after the Skimmer survey-, a further expedition to the gulf was conducted by the German RV Victor Hensen, which synoptically sampled data on oceanographical conditions, plankton dynamics, structure of bentho-demersal fish and invertebrate assemblages as well as infauna communities along a depth gradient from shallow waters (20 m) near the mangrove edge to the adjacent and deeper fishing grounds up to the shelf edge (>200 m). This survey, due to its wide coverage of the total gulf area, yielded important additional quantitative data for the entire gulf area (Vargas & Wolff 1996).

While detailed knowledge is now available for most system compartments, no attempts have as yet been made to integrate the available information into a holistic ecological model about the main functional system compartments and trophic flows between them. With the present contribution we attempt to provide this holistic view by the construction of a first trophic model of the gulf. We try to answer the following questions: (1) How is biomass distributed among the various ecosystem components and what are the major pathways of energy flow? (2) How, in particular, is biomass distributed between pelagic and benthic predators, and what are their prey items and consumption rates? (3) What is the productivity potential of - and food availability for - the pelagic and benthic resources of the gulf, considering the need of coastal conservation and fisheries management? (4) What is the role of the small mangrove cover (1% of system area) for the biomass distribution and energy flow within the system? (5) How do the biomass flows in the gulf differ from the open shelf and other gulf systems in the tropics? (6) What are the major ecosystem components on which further study should be concentrated?

For modelling the gulf's ecosystem, we used the ECOPATH II software of Christensen & Pauly (1992), that had also been applied before (Wolff *et al.* 1996) to another Costarrican gulf system, Golfo Dulce, about 200km south of the Golfo de Nicoya . We believed that the comparison of these two neighbouring gulf systems, as modelled by the same approach, would deepen our insight into the specific characteristics of both systems.

ECOPATH II represents a steady state modelling approach, in which biomass production of - and imports to - the system compartments is balanced by consumption and exports. It combines an approach of Polovina (1984) for estimation of biomass and food consumption of the various ecosystem elements (species or species groups) with an approach proposed by Ulanowicz (1986) for analysis of flows between the ecosystem elements and for the calculation of ecosystem indices. Based on these, the size of the system is measured in terms of the sum of flows through all the individual compartments and the degree of a system's realized growth, organization and development is described (Ulanowicz & Mann 1981, Baird & Ulanowicz 1993, see Christensen & Pauly 1993 for a review). These indices are being used to compare a wide variety of ecosystems of different sizes, geographical location and complexity (Baird *et al.* 1991, Ulanowicz & Wulff 1991, Christensen & Pauly 1993), and will be included in our analysis of the Golfo de Nicoya model.

## MATERIALS AND METHODS

**The Golfo de Nicoya environment:** The Golfo de Nicoya is a tectonic estuary, hydrodynamically driven by semidiurnal tides with a mean range of 2.5-3.0 m. A dry season from December to April and a rainy season from May to November exert a significant impact on its water characteristics. During the rainy season most fresh water enters the gulf through the rivers Tempisque, Barranca and Tárcoles with the highest volumes provided by the latter (about 60%), which drains the central valley (Fig.1). The inner part of the gulf is estuarine and stratified, especially during the rainy season, when it receives the run-off from 1500 mm rainfall between May and November (Herrera 1985, Jiménez, 1992). Fresh water stratification becomes less important downstream and thermal stratification prevails in the outer gulf, with the permanent thermocline centered around 30-40m and temperature differences up to 14°C between the surface and bottom waters. Cross-axis horizontal variability is related to the asymmetry of fresh water inflow, namely the discharge of the rivers Barranca and Tárcoles into the eastern part of the bay. Compensating this low salinity outflow along the eastern shore, salt water penetrates along the western edge, thus creating a transversal salinity gradient superimposed on the general estuarine circulation. Position and dynamics of the pycnocline are further complicated by tidal currents and associated internal waves (Voorhis *et al.* 1983). The strong seasonality observed in the gulf is also reflected in the distribution of oxygen and nutrients (Epifanio *et al.* 1983, Chaves & Birkicht 1996). Dissolved inorganic nitrogen varies up to one order of magnitude in the inner gulf, whereas nutrient levels in the outer gulf are low and relatively stable throughout the seasons. Further details on geographical, physical and chemical characteristics of the Golfo de Nicoya are given in Peterson (1960), Epifanio *et al.* (1983), Voorhis *et al.* (1983), Wolff & Vargas (1994), Brenes & León (1995), Lizano (1998).

The physiochemical setting is reflected in the zonation of fish and benthos inhabiting the bay: the inner gulf is dominated by the families Sciaenid and Ariid (Price *et al.* 1980, Bartels *et al.* 1984) as well as stingrays, flatfishes and sea robins, while in the lower gulf cods, scorpionfishes, gobies, cutlassfishes, carangids, serranids and others prevail (Wolff 1996). This latter zone appears to be the nursery ground of at least nine species of penaeid shrimps (Campos *et al.* 1984). Epifanio & Dittel (1984) report differences in dominance of brachyuran larvae in the inner and outer parts of the gulf, probably attributable to changes in bottom communities. Wolff & Jesse (1994) confirm this as they found highest biomass values of stomatopods and crabs in the inner part of the gulf, while shrimp biomass and abundance was highest in the central and outer parts. The shaping of the bottom communities appear to be due to biological factors (e.g. predation, competition) in the inner and by physical factors (e.g. fronts) in the outer gulf (Maurer & Vargas 1984). Numerous benthological studies have been carried out in the Golfo de Nicoya including bottom communities (Vargas 1987, 1988), Meiofauna (De la Cruz & Vargas 1987) and specific groups such as polychaetes (Maurer *et al.* 1988), stomatopods (Dittel 1991), and others (see Vargas 1995 for a review).

Questions about community functions (determination of trophic groups and energy pathways) have not yet been addressed, however, and are the focus of the present study.

**Basic modelling approach:** The core routine of ECOPATH II basically consists in using a set of simultaneous linear equations (one for each group $_i$ in the system), i.e.:

Production by ( i ) less all predation on ( i ) less non predation losses of ( i ) less export of ( i ) = 0, for all i,

or:

$$\Sigma P_i - B_i M2_i - P_i (1-EE_i) - EX_i = 0, \qquad (1)$$

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 mortality" ($y^{-1}$)
$EX_i$ = the export of ( i )($gm^{-2}y^{-1}$)

Thus, the total production by group ( i ) is balanced by predation from other groups ($B_i * M2_i$), by non-predation losses ($P_i(1-EE_i)$) and losses to other systems, e.g. sedimentation and fishery. Since production is more conveniently estimated from the production/biomass ratio (PB) and the average annual biomass (B), it is expressed as ($P_i = B_i * PB_i$). 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 ), i.e.

$$(B_i * M2_i) = \Sigma_j B_j * QB_j * DC_{ji}$$

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.

Two of the three parameters B, PB 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 are treated as initial unknowns. QB of a compartment can also be calculated by the model and treated as an unknown in initial parametrization, if information is available on the amount of prey entering the compartment. For further details of the ECOPATH II model structure see Christensen & Pauly (1992).

### *Selection of model groups (compartments)*

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 research data and the literature. For most fish species, Q/B was calculated using the aspect ratio of the caudal fin (Palomares & 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. As the official landing data are not given for each fish species separately, but for groups of fish such as "primera grande" (first quality fish > 2kg), "primera pequeña" (first quality , < 2kg), 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 is given, we proceeded by allocating a fraction of the total catch to each group that was roughly proportional to the biomass fraction of the fish survey results.

The mangroves cover approx. 15km$^2$ (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 main elements are given in Table 1.The input data as well as the diet matrix used are given in Tables 2 and 3 together with the literature sources used.

## RESULTS AND DISCUSSION

Fig. 2 shows the compartment model of the Golfo de Nicoya ecosystem based on the diet matrix and flows given in Tables 3 and 4. Table 5 contains the summary statistics and network indices computed by the programme. Table 6 gives the transfer efficiencies calculated for each trophic level.

**Balancing the model and evaluation of computed values:** The balancing of the the model was done as described in Wolff *et al.* (1996). Some biomass input values had to be modified as seen by the numbers in brackets in Table 2. Of these, the largest changes were done for the groups phytoplankton (18 to 6) and squids (0.09 to 0.4). Minor changes of input biomass as well as of the P/B and Q/B values were also applied for other groups, of which most remained within narrow bounds around the input value (Table 2). We think that the threefold reduction of the phytoplankton biomass is reasonable, as our input value was derived from measurements in the interior part of the gulf (Córdoba-Muñoz 1993) and from Términos lagoon (Mexico), both representative for shallow estuarine waters in the tropics. The Golfo de Nicoya has this characteristic in its interior part, while towards the outer oceanic part of the gulf, primary productivity can be expected to be far lower. The necessary increase of the biomass values for squids and some of the fish groups and for the predatory crabs also seems reasonable, as our initial values were based on scientific bottom trawl surveys, which are

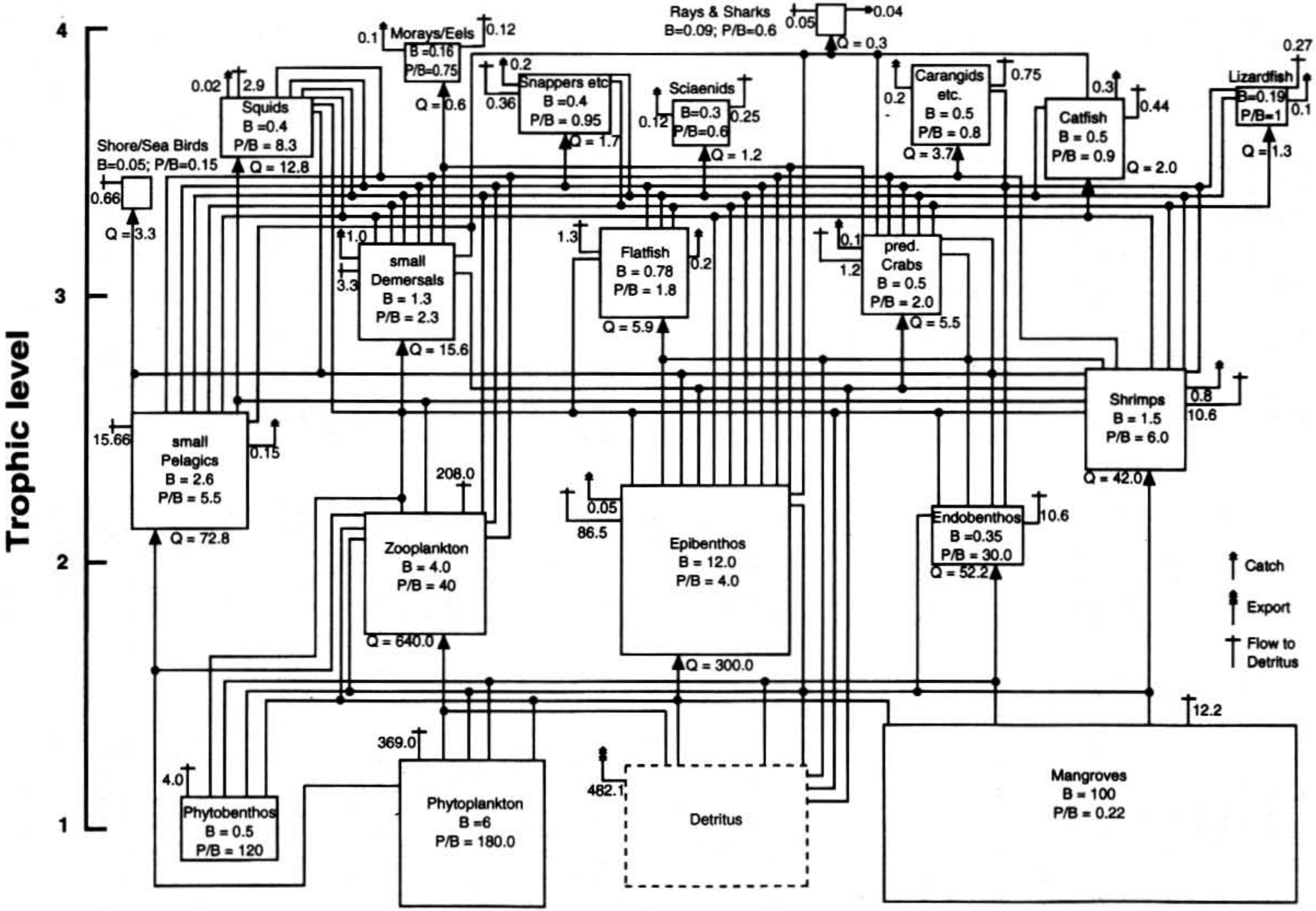

Fig. 2. Golfo de Nicoya trophic model. Box size is proportional to the square root of the compartment biomass, Q represents the total consumption of each box, the flows are given in gm$^{-2}$ (wet weight).

TABLE 1

*System compartments as used for the Golfo de Nicoya Model*

| Groups | Main Elements |
|---|---|
| 1. Phytoplankton | Diatoms, dinoflagellates and others |
| 2. Microphytes | Benthic diatoms |
| 3. Mangroves | Rhizophora sp., Avicennia sp., Pelliciera sp. |
| 4. Zooplankton (>300u) | Neritic and ocean copepods, bivalve larvae, foraminifers, ostracods, mysids, nauplii, fish eggs, chaetognathes & others |
| 5. Shrimps | Penaeus spp.; Trachypenaeus spp., other penaeids; Solenocera app. Sicyonya spp. Pandalidae |
| 6. Squids | Loliolopsis diomedeae, Lolliguncula panamensis |
| 7. Small pelagics | Neopisthopterus tropicus; Anchoa lucida; A. spp. Opisthopterus spp. |
| 8. Carangids & others | Caranx caninus; C. otrynter; C. speciosus; C. vinctus; Peprilus medius; P. snyderi; Selene brevortii; S. oerstedii; S. peruviana; Trachinotus paitensis |
| 9. Small demersal fish | small & juv. Sciaenids, Haemulids, Triglids, Gerreids, Serranids, Scorpionids, Gobies & others |
| 10. Flatfish | Achirus kluzingeri; Syacium ovale; S. latifrons; Symphurus chabanaudi; S. callopterus; S. elongatus; Cyclopsetta querna; Etropus crossotus; Citharichthys platophrys & others |
| 11. Catfish | Arius dasycephalus; A. dovi; A. platypogon; A. osculus & others |
| 12. Snappers & Grunts | Lutjanus guttatus; L. spp.; Haemulon scuderi; Anisotremus dovii; Calamus brachisomis & others |
| 13. Lizardfish | Synodus scituliceps; S. evermanni; S. sechurae |
| 14. large Scianids | Cynoscion albus; C. phoxocephalus; C. spp. |
| 15. Rays & sharks | Dasyatis longus; Urotrygon chilensis; Raya velezi; Rhinobates leucorhynchus; Narcine brasiliensis & other rays; sharks: Mustelus lunulatus |
| 16. Moravs & eels | Cynoponticus coniceps & others |
| 17. Endobenthos | Capitellid and spionid polychates & others |
| 18. Epibenthos | Gastropoda; Bivalvia; Majidae; Parthenopidae; Leucosidae; Paguridae; Diogenidae; Sea urchins, sea stars; |
| 19. Predatory crabs | Callinectes toxotes; C. sapidus; C. arcuatus; Portunus asper; P. iridescens; P. acuminatus; Euphylax robustus; Squilla spp; Callapidae; Xanthidae |
| 20. Sea/shore birds | Pelicanus spp.; Podiceps dominicus; Sula spp.; Phalacrocorax olivaceus; Oceanodroma microsoma; Fregata magnificens; Anhinga anhinga; & others |
| 21. Detritus | |

known to operate with a low catch efficiency, thus yielding underestimates. We did not modify our initial catch values, which were assembled from landings statistics (INCOPESCA 1995) but also from estimates derived from the proportion of different fish and invertebrate groups within the shrimp by-catch as reported by Campos (1986). The model - value for total catch (3.38g $m^{-2}$) translates to 5070 t for the total area (1500 $km^{-2}$), a value that we consider realistic, as official landing statistics do not include the by catch.

The gross efficiencies (GE = production / consumption) calculated for the fish and invertebrate groups are between 0.11 (Carangids) and 0.26 (Squids), well within the range reported by Mann (1982), Caddy & Sharp (1986) and Conover (1974) (for zooplankton). The respiration to assimilation ratios (R/A) are as expected from literature data given in Humphreys (1979) and Huebner & Edwards (1981).

**Trophic structure, transfer efficiencies:** The larger portion of system biomass is confined to the benthic domain (18,4 $gm^{-2}$, mangroves excluded, versus 13.8 $gm^{-2}$ for the pelagic domain). According to the model results, epibenthos,

TABLE 2

*Golfo de Nicoya- input data and literature sources*

| Group | Biomass $^1$ | Catch $^2$ | P/B $^3$ | Q/B $^4$ | Literature source |
|---|---|---|---|---|---|
| 1.Phyoplankton | 18 (6) | - | 180 | - | 1,3- Robertson & Blaber (1992) : estimates for Terminos Lagoon, Mexico, Córdoba-Muñoz (1993) |
| 2.Microphytobenthos | 0,8 (0.5) | - | 110 (120) | - | 1,3- estimates baesd on Dummermuth (1997) assuming microphytobenthos to cover 4% of area |
| 3.Mangroves | 100 | - | 0,22 | - | 1- after Jimenez (1995) and considering 1% mangrove cover; 3 - after Diaz (1993) and after Day et al. (1987) |
| 4.Zooplankton (>300 m) | 3,7 (4.0) | - | 50 (40) | 160 | 1 -Wangelin & Wolff (1996), Hossfeld et al. (1994) 3+4: Huntley & Lopez (1992) |
| 5.Shrimps | | 0,8 | 4,4 (6.0) | 21 (28) | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3- Palacios et al .(1993); 4- own estimate |
| 6..Squids | 0,09 (0.4) | 0,02 | 8,3 | 32 | 1-Koch (1994); 2-estimate based on Campos (1986);3-based on Majid & Khaliluddin (1994) Laptikhovskij (1995); 4- Palomares (1987) |
| 7.Small pelagics | | 0,15 | 4,8 (5.5) | 20 (28) | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 8. Carangids & others | 0,15 (0.5) | 0,2 | 0,8 | 7,3 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 9.Small demersal fish | 1,3 | 1 | 2,3 | 8 (12 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 10. Flatfish | 0,3 (0.78) | 0,2 | 1,9 (1.8) | 6,5 (7.5) | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 11. Catfish | 0,35 (0.5) | 0,3 | 0,8 (0.9) | 4 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 12. Snappers & Grunts | 0,13 (0.4) | 0,2 | 0,75 (0.95) | 4,3 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 13. Lizardfish | 0,12 (0.19) | 0,1 | 1 | 5,5 (7.0) | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 14. large Sciaenids | 0,3 | 0,12 | 0,6 | 4 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3: analysis of catch data; 4: aspect ratio |
| 15. Rays & sharks | | 0,04 | 0,6 | 2,8 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3- Pauly & Christensen (1993); 4- Palomares (1987) |
| 16. Morays & eels | 0,1 (0.16) | 0,1 | 0,75 | 3,6 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995); 3- own estimate; 4- Palomares (1987) |
| 17. Endobenthos | 0,2 (0.35) | - | 15 (30) | 30 (150) | 1- Maurer & Vargas (1984); 3- Tumbiolo & Downing (1994); 4- own estimate |
| 18. Epibenthos | 12 | 0,05 | 3,9 (4.0) | 15 (25) | 1- Jesse (1996); Maurer et. al (1978); 2- Incopesca (1995) 3- Tumbiolo & Downing (1994); 4- Griffiths (1980) |
| 19. Predatory crabs | 0,2 (0.5) | 0,1 | 2. 0 | 11 | 1- Wolff (1996); Bartels et al. (1984); 2- INCOPESCA (1995) 3- Dittel et al. (1985); 4- own estimate |
| 20. Sea/shore birds | 0,02 (0.05) | - | 0,15 | 65 | 1-Dunlop et al .(1988); 3,4 - Muck & Pauly (1987) |
| 21.Detritus & bacteria | | - | | | |

shrimps and small demersal fish are the most prominent benthic groups in terms of biomass, while plankton, small pelagic fish, carangids and squids dominate the pelagic biomass. In terms of food intake, zooplankton and epibenthos are the most important pelagic and benthic groups with an intake of 640 gm$^{-2}$ and 300 gm$^{-2}$ respectively (see Table 4). Demersal fish (groups 8,11,12, 13,14,15,16,) consume twice the amount (10.8 gm$^{-2}$) than predatory crabs (5.5 gm$^{-2}$). Of the pelagic predators, squids and birds consume 12.8 gm$^{-2}$ and 3.25 gm$^{-2}$ respectively. The groups phytoplankton, zooplankton, mangroves and epibenthos have the lowest ecotrophic efficiencies (the fraction of the total production consumed within the system), and thus represent the main providers of detritus.

Mangroves, although covering only 1% of the total area, contribute 75.7% to the system biomass but only about 1% (22g m$^{-2}$) to the primary production. Nevertheless, through litter fall, mangrove production can be assumed to be of great importance in fuelling the detrital food chain in the inshore areas of the gulf. More importantly, however, seems the role of the mangrove root system as a hard substrate for epifauna. As shown by Büttner (1997), the surface area of the roots is about twice the ground area covered by mangroves and average epifaunal biomass can reach values of 1400g dw m$^{-2}$. This represents about 90% of the epifaunal biomass of the entire gulf and explains, why epibenthos is the second largest box in our model. It serves as an important food source for invertebrate predators and many commercially important fish species of the inshore gulf area. Through the release of enormous quantities of pelagic larvae and of faecal material, epibenthos also provides food to many of the, zooplankton filter and suspension feeders of the entire system. It is thus evident, that even small areas of mangrove vegetation (like in the Golfo de Nicoya), have an enormous importance for the biomass distribution and energy flow pattern within the estuary. Trophic models of estuaries that do not include mangrove vegetation and associated fauna will grossly underestimate system biomass and energy flow.

The computed mean transfer efficiency between trophic levels of 14.9% (Table 6), is very close to the 15% value given by Ryther (1969) for coastal zones and within the range of 10 to 20% commonly reported in the literature (Odum 1971; Barnes & Hughes 1988). It is almost identical to the value (15%) calculated for the Golfo Dulce system in southern Costa Rica by Wolff *et al.* (1996). As seen by the flow pyramid (Fig. 3), most of the system's energy throughput is achieved from the trophic levels I to II (62%) and II to III (34%) as expected for coastal phytoplankton/ detritus based systems with strong benthopelagic coupling. The situation differs from the one in the Golfo Dulce, where phytoplankton and benthic production is low and where the pelagic community seems to be more tightly structured (Wangelin & Wolff 1996) leading to a larger fractional throughput in the higher trophic levels (Wolff *et al.* 1996). In the Golfo de Nicoya most energy is transferred from the primary producers and the detritus pool to the next trophic level. The ingestion by detritus and phytoplankton feeders alone represents 82% of total system consumption (Tables 3 and 4).

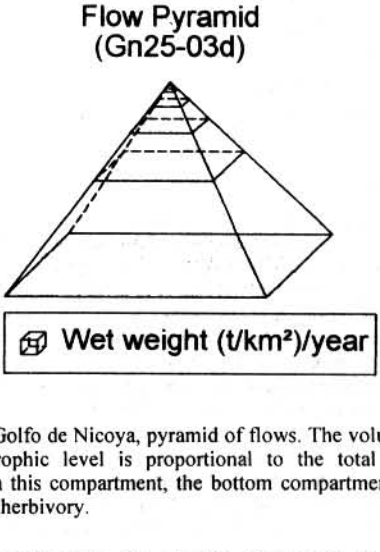

Fig.3. Golfo de Nicoya, pyramid of flows. The volume of each trophic level is proportional to the total flows through this compartment, the bottom compartment represents herbivory.

According to the model estimates, a large quantity of detrital matter (482 gm$^{-2}$) is exported by the system. Of this, a part will be sedimented away, another serves as food for deep water detritus feeders, such as squat lobsters, that were found in dense shoals and comparatively high biomasses in the deep water of the outer gulf area (Jesse, 1994).

**Summary statistics:** The model estimate of total system throughput (T) of 3049.3 gm$^{-2}$ exceeds twice the value of the Golfo Dulce model (1404.6) and even more the value reported for

TABLE 3

*Golfo de Nicoya. Prey-predator matrix used for the model. Numbers represent weight fractions of food ingested*

| Groups | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. Phyoplankton | 0,75 | | 0,6 | 0,6 | | | | | | | | | | 0,14 | 0,6 | | |
| 2. Microphytobenthos | | 0,1 | | | | 0,1 | | | | | | | | 0,1 | 0,15 | | |
| 3. Mangroves | | 0,1 | | | | | | | | | | | | 0,05 | 0,01 | | |
| 4. Zooplankton (>300) | 0,05 | 0,25 | 0,05 | 0,4 | 0,12 | 0,1 | | | 0,05 | | 0,07 | | | 0,05 | 0,01 | | |
| 5. Shrimps | | | 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 | | | 0,1 | | 0,2 | 0,03 | | 0,1 | 0,05 | | 0,05 | | 0,05 | | | | 0,05 |
| 7. Small pelagics | | | 0,65 | | 0,5 | | 0,05 | 0,2 | 0,18 | 0,2 | 0,1 | 0,1 | 0,05 | | | | 0,45 |
| 8. Carangids & other | | | | | | | | | 0,1 | | | 0,02 | | | | | |
| 9. Small demersal | | | | | 0,02 | | | 0,2 | 0,15 | 0,2 | 0,1 | 0,16 | 0,14 | | | 0,1 | |
| 10. Flatfish | | | | | | 0,05 | | | 0,05 | 0,05 | 0,1 | 0,08 | 0,08 | | | | |
| 11. Catfish | | | | | | | | | | | 0,05 | 0,1 | 0,05 | | | | |
| 12. Snappers & Grun | | | | | | | | | | 0,05 | 0,05 | 0,04 | 0,05 | | | | |
| 13. Lizardfish | | | | | | | | | 0,02 | | 0,02 | 0,02 | 0,04 | | | | |
| 14. large Scianids | | | | | | | | | | | 0,01 | 0,05 | 0,05 | | | | |
| 15. Rays & sharks | | | | | | | | | | | | | 0,02 | | | | |
| 16. Morays & eels | | | | | | | | | | | | 0,03 | 0,02 | | | | |
| 17. Endobenthos | | 0,15 | | | | 0,05 | 0,05 | | 0,05 | | | | | 0,04 | | 0,1 | 0,1 |
| 18. Epibenthos | | 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 | | | | | 0,05 | | 0,02 | | 0,05 | 0,1 | 0,05 | 0,15 | 0,1 | | | | 0,04 |
| 20. Sea/shore birds | | | | | | | | | | | | | | | | | |
| 21. Detritus & bacteria | 0,2 | 0,3 | | | | 0,05 | 0,08 | | | | | | | 0,62 | 0,23 | 0,15 | |
| Sum | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

Literature sources:

Groups 1), 2) and 3) are producers, not consumers. 4) Petipa *et al.* (1977); 5) Moriarty & Barclay (1981), Froglio & Gramitto (1988), Stoner & Zimmerman (1988); 6) Sauer & Lipinski (1991), Hernandez-García (1992); 7) Okera (1973), Vasconcelos Filho *et al.* (1984), Campos & Corrales (1986), Szelitowski (1990), Bussing & Lopez (1994); 8) own data, Randall (1967), Vasconcelos Filho et al. (1984), Popova & Sérra (1983), Brewer *et al.* (1989), Sudekum *et al.* 1991, Smith *et al.* (1992) Bussing & Lopez (1994)); 9) own data, Salini *et al.* (1990), Bussing & Lopez (1994), Campos & Corrales (1986), de Souza Braga & de Souza Braga (1987), Szelitowski (1990), Bussing & Lopez (1994); 10) own data, Mac Pherson (1978), Szelitowski (1990), Garcia- Abad *et al.* (1992), Bussing & Lopez (1994); 11) Sheridan *et al.* (1984), Reis (1986), Yañez- Arancibia & Lara- Dominguez (1988), Rojas- Beltran (1989), Salini *et al.* (1990), Tilney & Hecht (1990), Szelitowski (1990), Bussing & Lopez (1994); 12) own data, Popova & Sérra (1983), Campos & Corrales (1986), Parrish (1987), Salini *et al.* (1990), Szelitowski (1990), Bussing & Lopez (1994); 13) Sweatman (1984), Vasconcelos Filho *et al.* (1984), Bussing & Lopez (1994); 14) own data, Campos & Corrales (1986), Bussing & Lopez (1994), Sheridan *et al.* (1984) 15) own data, Randall, (1967), Salini *et al.* (1990), van Dykhuizen & Mollet (1992), Ishihara *et al.* (1993), Stilwell & Kohler (1993), Gilliam & Sullivan (1993), Bussing & Lopez (1994); 16) own data, Bussing & Lopez (1994); Yukihira *et al.* (1994) 17) own data; 18) Perez & Bellwood (1988), Nojiima (1989), Tokeshi *et al.* (1989) Manjulatha & Babu (1991), Frid (1992), Woods (1993); 19) Laughlin (1982), Williams (1982); Giovanardi & Manfrin (1984), Dittel *et al.*(1985); 20) Muck & Pauly (1987).

Tamiahua lagoon in Mexico (822.4) by Abarca-Arenas & Valero Pacheco (1994). The very low value of the latter system can be explained as the authors report a strong oil impact on the system that has led to a 90% reduction of benthic producers.

Throughput values of many other systems are much higher, however. Mendoza (1993) reports for the Northeastern Venezuelan Shelf a value of 7621, Chavez *et al.* (1994) for the Celestun Lagoon in Mexico of 8969 and Wolff (1994) for the Tongoy bay (upwelling) ecosystem in Northern Chile an even higher value of 20 835.

The mean trophic level of the Golfo de Nicoya fishery (4.06, about the level represented by rays and sharks) reflects the fact that the fishery operates as a top predator of the system. Several harvested groups are predatory fish that themselves feed upon higher trophic levels. While this value is much higher than for upwelling fisheries, where the fishery concentrates primarily on planktivorous fish (Jarre *et al.* 1991), it is lower

TABLE 4

*Golfo de Nicoya. Parameter values entered (in bold) and calculated by the ECOPATH II - software. (Explanation of symbols: P/B,Q/B, EE and GE see material and method section; FI: food intake; R: respiration; A: assimilation)*

| | group | catch | biomass | P / B | Q / B | EE | GE | FI | R / A | P / R | R / B |
|---|---|---|---|---|---|---|---|---|---|---|---|
| (1) | 1.Phyoplankton | - | ***6,000*** | ***180,00*** | - | 0,660 | - | - | - | - | - |
| (2) | 2.Microphytobenthos | - | ***0,500*** | ***120,00*** | - | 0.930 | - | - | - | - | - |
| (3) | 3.Mangroves | - | ***100,000*** | **0.22** | - | 0,450 | - | - | - | - | - |
| (4) | 4.Zooplankton (>300u) | - | ***4,000*** | ***40,00*** | ***160,00*** | 0,500 | 0,250 | 640,00 | 0.690 | 0,460 | 88,00 |
| (5) | 5..Shrimps | ***0,800*** | ***1,500*** | ***6,00*** | ***28,00*** | 0,930 | 0,210 | 42.00 | 0,730 | 0,370 | 16,40 |
| (6) | 6..Squids | ***0,020*** | ***0,400*** | ***8,30*** | ***32,00*** | 0.910 | 0,260 | 12,80 | 0.680 | 0,480 | 17,30 |
| (7) | 7.Small pelagics | ***0,150*** | ***2,600*** | ***5,50*** | ***28,00*** | 0,920 | 0,200 | 72,80 | 0.750 | 0,330 | 16,90 |
| (8) | 8. Carangids & others | ***0,200*** | ***0,500*** | ***0,80*** | ***7,30*** | 0,940 | 0,110 | 3,70 | 0,860 | 0.160 | 5,04 |
| (9) | 9.Small demersal fish | ***1,000*** | ***1,300*** | ***2,30*** | ***12,00*** | 0,930 | 0,190 | 15,60 | 0,760 | 0,320 | 7,30 |
| (10) | 10. Flatfish | ***0,200*** | ***0,780*** | ***1,80*** | ***7,50*** | 0,940 | 0,240 | 5,90 | 0.700 | 0,430 | 4,20 |
| (11) | 11. Catfish | ***0,300*** | ***0,500*** | ***0,90*** | ***4,00*** | 0,920 | 0,230 | 2,00 | 0,720 | 0,390 | 2,30 |
| (12) | 12. Snappers & Grunts | ***0,200*** | ***0,400*** | ***0,95*** | ***4,30*** | 0,960 | 0,220 | [illegible] | 0,720 | 0.380 | 2,49 |
| (13) | 13. Lizardfish | ***0,100*** | ***0,190*** | ***1,00*** | ***7,00*** | 0,980 | 0,140 | 1,33 | 0,820 | 0,220 | 4,60 |
| (14) | 14.Scianids<br>& Lutjanids (>20cm) | ***0,120*** | ***0,300*** | ***0,60*** | ***4,00*** | 0,960 | 0,150 | 1,20 | 0,810 | 0,230 | 2.60 |
| (15) | 15. Rays & sharks | ***0,040*** | 0,090 | ***0,60*** | ***2,80*** | 0,950 | 0,210 | 0,30 | 0,730 | 0,370 | 1,64 |
| (16) | 16. Morays & eels | ***0.100*** | ***0,160*** | ***0,75*** | ***3,60*** | 0,990 | 0,210 | 0,60 | 0.740 | 0.350 | 2.13 |
| (17) | 17. Endobenthos | - | ***0,350*** | ***30,00*** | ***150,00*** | 0,990 | 0,200 | 52,50 | 0,750 | 0,330 | 90,00 |
| (18) | 18. Epibenthos | ***0,050*** | ***12,000*** | ***4,00*** | ***25,00*** | 0,450 | 0,160 | 300,00 | 0,800 | 0,250 | 16,00 |
| (19) | 19. Predatory crabs | ***0,100*** | ***0,500*** | ***2,00*** | ***11,00*** | 0.900 | 0,180 | 5,50 | 0.770 | 0,290 | 6,80 |
| (20) | 20. Sea/shore birds | - | ***0,050*** | ***0,15*** | ***65,00*** | 0,000 | 0,002 | 3,25 | 0,990 | 0,003 | 51,85 |
| (21) | 21.Detritus & bacteria | 482.090 | | | | 0,340 | - | - | | | |

than the one for the Golfo Dulce model (5.3). This is due to the fact that within the Nicoya gulf an important fraction of the total catch is made up by shrimps and small pelagic fish, that feed on the lower trophic levels.

The annual catch of 3.38 gm$^{-2}$ is about 15 times higher than that reported for Golfo Dulce, showing the low resource productivity of the latter. While this value seems reasonable as an average for the entire gulf, it must be stressed, that large parts of the resource biomass is confined to the inner and central part of the gulf, as revealed by the research surveys mentioned.

The amount harvested is similar to that given by Arreguin-Sanchez *et al.* (1993) for the Southwestern Gulf of Mexico (about 3.32 gm$^{-2}$). It is, however, higher than that reported for the continental shelf of Mexico (2.8) by Browder (1993) and for the South China Sea ecosystem (0.83) (Silvestre *et al.* 1993). Higher values are reported for the Northeastern Venezuelan Shelf (5.2 gm$^{-2}$) (Mendoza 1993), for Campeche bank, Mexico (4.82) (Vega-Cendejas *et al.* 1993), or for Maputo Bay, Mozambique (7.05) (DePaula *et al.* 1993). It thus seems that the catch/area obtained in the Golfo de Nicoya can be considered intermediate for tropical coastal systems.

The gross efficiency of the fishery (catch/primary production) computed by the model (0.3%) appears high when compared to the Golfo Dulce model (0.06%) or the Northeastern Venezuelan Shelf (0.15%) (Mendoza 1993), indicating the high overall exploitation rate. This result is consistent with the fact that many populations of shrimp and commercial fish have drastically declined over the past years due to overexploitation (INCOPESCA, 1990-1995). The most affected resources seem to be the shrimp stocks (especially white shrimp). Catch volumes have decreased from about 1326 t in 1983/84

TABLE 5

*Golfo de Nicoya. (a) Summary statistics; (b) Network flow indices. For further explanations see text and Christensen & Pauly (1992)*

**(a) Summary statistics**

| | | |
|---|---|---|
| sum of all consumption | 1161 | |
| sum of all exports | 485,5 | *sedimentation, fishery |
| sum of all respiratory flows | 676,5 | |
| sum of all flows into detritus | 726,3 | |
| total system throughput (T) | 3049,3 | |
| sum of all production | 1414,3 | |
| fishery´s mean trophic level | 4,06 | |
| it´s gross efficiency (catch/ prim. prod.) | 0,003 | |
| total net primary production (PP) | 1162 | |
| total PP / total respiration (R) | 1,718 | |
| total biomass / total throughput | 0,04 | |
| total biomass (excl. detritus) | 132,12 | |
| pelagic biomass | 13,5 | |
| benthic biomass (exc. mangroves) | 19,2 | |
| total catches | 3,38 | values in g / $m^2$ |

**(b) Network flow indices**

| **Source** | Ascendency | | Overhead | | Capacity | |
|---|---|---|---|---|---|---|
| | Flowbits | % | Flowbits | % | Flowbits | % |
| Import | 0 | 0 | 0 | 0 | 0 | 0 |
| Internal flow | 1306 | 10,5 | 6936,3 | 56 | 8242,3 | 66,5 |
| Export | 986,3 | 8 | 340,2 | 2,7 | 1326,5 | 10,7 |
| Respiration | 944,9 | 7,6 | 1873,7 | 15,1 | 2818,5 | 22,8 |
| Totals | **3237,1** | **26,1** | **9150,2** | **73,9** | **12387,3** | **100** |

| | | |
|---|---|---|
| Throughput cycled | 35,4 | t/ $km^2$/ year |
| Finn´s cycling index | 5,5 | (% of total throughput) |

(Campos 1986) to 759 t in 1995 (INCOPESCA 1996) and present shrimp sizes are reported to be much reduced.

As shown by our model, shrimps occupy a central role within the Golfo de Nicoya as converter of much of the system detritus and other bentho -pelagic food into food biomass for several groups (Table 3). Their overexploitation means a significant reduction of the food stock for these predators. For their wide-scale distribution and specific trophic niche within the system, it is improbable that other species can compensate for this lack, and the decline of many commercially important populations of shrimp feeding fish seems the logical consequence of this overexploitation.

The primary production to respiration ratio (P/R) computed by the model (1.72) indicates that more biomass is produced than respired, indicative for a relatively immature system (Odum, 1971). The value is significantly higher than that of Golfo Dulce (1.07) showing the different nature of both gulf systems. The character of an immature system is also confirmed by the low index of recycling (FCI= 5,5%) (Finn 1976) and the Ascendency/capacity (A/C) ratio

(Ulanowicz, 1986) a further descriptor for system maturity. The value computed for the model (26. 1%) (Table 5) is very low, suggesting a low degree of system's maturity. This seems to generally hold for tidally driven, tropical estuarine systems, in which hydrographic and climatic variability is very pronounced. These systems of high system P/R and low A/C ratio are used to environmental stress, and may eventually be considered relatively robust against perturbations (Ulanowicz & Mann 1981, Rutledge *et al.* 1976).

TABLE 6

*Golfo de Nicoya. Transfer efficiencies (TE) for each trophic level; TE=proportion of energy transferred from one trophic level to the next*

| Source | I | II | III | IV | V | VI | VII | VIII |
|---|---|---|---|---|---|---|---|---|
| Producers | - | 8,6 | 17,2 | 14,9 | 14,8 | 16,4 | 15,4 | 17 |
| Detritus | - | 9,6 | 17,9 | 15,4 | 14,8 | 16,4 | 15,1 | 17,1 |
| All flows | - | 8,8 | 17,4 | 15 | 14,8 | 16,4 | 15,1 | 17 |

Proportion of total flow originating from detritus 0,33 X=14.9

We think that the modelling exercise allowed for a coherent picture of the Golfo de Nicoya system and permitted to answer the questions addressed in the study. Moreover, a quantitative basis was obtained through the model construction, for a comparison of the gulf with other tropical coastal systems.

Some shortcomings should be mentioned, however. Although the data basis for the model was comparatively good due to the intensive research in the study area over the past 20 years, for some of the model compartments only crude estimates were available. This especially holds for the biomass and production values for phytoplankton and phytobenthos compartments,which need intensive research in the future. Imports and exports (apart from catches and detritus produced within the system) were not considered in the model. The riverine import has not been quantified and migrating populations of birds, dolphins, sharks or turtles, known to alter the biomass budget by their migratory activities, were not considered as well. Very little quantitative infomation existed for the higher predators such as birds or aquatic mammals. While we included birds, by using rough estimates from the literature, we did not include marine mammals due to the lack of information.

As in most trophic models, the "microbial loop" was not considered and detritus was used as a black box, without partitioning into benthic and pelagic compartments or particulate and dissolved organic matter. We think that a microbial loop study (or model) should be done in addition to the trophic model presented here once the respective data basis is available.

Further limitations are associated with the staedy-state assumption of the model:

It is known that high seasonal variations occur, which can produce intra-annual changes in the trophic structure and productivities of the system compartments. These are not considered in the model, which reports "average conditions". The construction of two seasonal models (rainy, and dry season) would be a worthwhile next step to account for the seasonal dynamics of the system. This, however, requires a data basis as yet not available. Strong modifications of the fishing activities (new targets, increasing effort) can also introduce changes in the ecosystem structure and flow pattern, which are difficult (if not impossible) to predict. It is important to keep this in mind when steady state models are being used as management tools.

## RESUMEN

El Golfo de Nicoya es uno de los estuarios más grandes y sobreexplotados de América Central. Con el propósito de integrar la información disponible sobre el estuario, se construyó un modelo trófico de 21 compartimentos usando el programa ECOPATH II. La mayor porción de la biomasa ( 18.4 g / m$^2$) proviene de los ambientes bénticos, sin incluir manglares, comparado con 13.8 g /m$^2$ de los ambientes pelágicos. Los manglares, que solo cubren el 1 % del área del Golfo y proporcionan el 1 % de la productividad primaria, aportan sin embargo, el 76 % de la biomasa del sistema. Las raíces del manglar aportan 90 % de la biomasa ( 12 g/m$^2$) proveniente de la epifauna, el segundo grupo más grande del modelo, enfatizando el papel fundamental de los manglares en el Golfo de Nicoya. La mayoría del flujo energético ocurre entre los niveles tróficos I y II ( 62 %) y II-III (34 %) según se espera para un ecosistema costero basado en fitoplancton-detritus. Una alta eficiencia bruta de la pesquería ( captura / productividad primaria) de 0.3 % confirma la alta explotación actual. Los camarones son importantes en convertir detritus en otras formas de biomasa. El modelo sugiere que el Golfo de Nicoya es un sistema de poca madurez, característico de estuarios tropicales dominados por las mareas. Se discute las limitaciones del modelo y se orienta la investigación futura. El modelo es comparado con el ya propuesto para el Golfo Dulce, una fosa anóxica también en la costa Pacifica de Costa Rica.

## REFERENCES

Anonymous. 1995. Costa Rican authority for fisheries statistics. Instituto Costarricense de Pesca y Acuacultura (INCOPESCA). San José, Costa Rica.

Arreguin-Sánchez, F., J. C. Seijo & E. Valero- Pacheco. 1993. An application of ECOPATH II to the north continental shelf of Yuacatan, Mexico. p: 269-278. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conference proceedings No. 26.

Baird, D., J.M. McGlade & R.E. Ulanowicz. 1991. The comparative ecology of six marine ecosystems. Phil. Trans.R.Soc. Lond . B. 333: 15-29.

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

Barnes, R.S.F & R.N. Hughes. 1988. An introduction to Marine Ecology. Blackwell Scientific, Oxford.

Bartels, C., K.S. Price, M. López & Bussing, W. 1984. Ecological assessment of finfish as indicators of habitats in the Gulf of Nicoya, Costa Rica. Hydrobiologia 112: 197-207.

Brenes, C.L., & S. León. 1987. Algunos aspectos fisicoquímicos del Golfo Dulce. Ing. Cienc. Quim. 12: 12-16.

Brewer, D. T., S. J. M. Blaber & J. P. Salini. 1989. Feeding biology of *Caranx bucculentus* (Teleostei: Carangidae) in Albatross bay, Gulf of Carpentaria, with special reference to predation on penaeid prawns. Aust. J. Mar. Freshw: Res. 40: 657-668.

Browder, J.A. 1993. A pilot model of the Gulf of Mexico continental shelf, p. 279-284. *In* V. Chrsitensen & D, Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26.

Büttner, H. 1997. Zur Ökologie der Wurzelgemeinschaft der Roten Mangrove (*Rhizophora mangle L.*) an der Pazifikküste Costa Ricas. P.h. D. Dissertation, Bremen University (Germany), 116 p.

Bussing W. A. & M. I. López S. 1994. Demersal and pelagic inshore fishes of the pacific coast of lower Central America, an illustrated guide. Special publication of the Revista de Biología Tropical. Universidad de Costa Rica, 164 p.

Caddy, J. F. & G. D. Sharp. 1986. An ecological framework for marine fishery investigation. FAO Fish. Tech. Paper no. 283. 152 p.

Campos, J.A. 1986. Fauna de acompañamiento del camarón en el Pacífico de Costa Rica. Rev. Biol. Trop. 43: 185-197.

Campos, J. & A. Corrales, 1986. Preliminary results on the trophic dynamics of the Gulf of Nicoya, Costa Rica. An. Inst. Cienc. del mar y Limnol. Univ. Auton. México 13: 329-334.

Campos, J.A. 1989. Evaluación de la pesca artesanal del Golfo Dulce. Primera parte: Golfo interno. Informe Final del Proyecto. Univ. de Costa Rica, Vicerrectoria de Investigación, Centro de Investigación en Ciencias del Mar y Limnología (CIMAR), Proyecto 808 88 561. San José, Costa Rica. 146 p.

Chaves, J. & M. Birkicht. 1996. Equatorial Subsurface Water and the nutrient seasonality distribution of the Gulf of Nicoya, Costa. Rev. Biol. Trop. 44: 41-47.

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

Christensen, V. & D. Pauly (eds.). 1993. Trophic models of aquatic ecosystems. ICLARM Con. Proc. no. 26, 390 p.

Conover, R.J. 1974. Production in marine plankton communities. Proceedings of the First International Congress of Ecology. Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands. p. 159-63.

Córdoba, M. 1993. Productividad primaria en la columna de agua. Golfo de Nicoya, Costa Rica. M.Sc. thesis, Universidad de Costa Rica, San José, Costa Rica.

Day, J.W., W.H. Connor, F. Ley-Lou, R.H. Day & A.M. Navarro. 1987. The productivity and composition of mangrove forests, Laguna de Términos, Mexico. Aquatic Botany 27: 267-284.

De la Cruz, E. & J.A. Vargas. 1987. Abundancia y distribución vertical de meiofauna en la playa fangosa de Punta Morales, Golfo de Nicoya, Cos ta Rica. Rev. Biol. Trop. 35: 363-367.

DePaula e Silva, R., M.I.Sousa, & A.M Caramelo. 1993. The Maputo Bay ecosystem (Mozambique). p 214-223. *In* V. Vhristensen and D. Pauly (eds.). Trophic models of aquatic ecosystem. ICLARM. Conf. Proc. 26, 390 p.

de Souza Braga, F.M. & M.A.A. de Souza Braga, 1987. Study on the diet of Prionotus punctatus (Bloch 1797) (Teleostei, Triglidae) in the region of Anchieta Island, Sao Paulo state, Brazil. Rev. Bras. Biol. 47: 31-36.

Díaz, L. 1993. Producción y Descomposición de Hojarasca de *Rhizophora* spp. (Rhozophoraceae) en el Estero Morales, Golfo de Nicoya. Tesis de Maestría. Universidad de Costa Rica. 90p.

Dittel, A. 1991. Distribution, abundance and sexual composition of stımatopod crustacea in the Gulf of Nicoya, Costa Rica J. Crust. Biol. 11: 269-276.

Dittel A. 1993. Cambios en los hábitos alimentarios de *Callinectes arcuatus* (Crustacea: Decapoda) en el Golfo de Nicoya, Costa Rica. Rev. Biol. Trop. 41: 639-646.

Dittel A., C. E. Epifanio, J. B.Chavarría. 1985. Population biology of the portunid crab *Callinectes arcuatus* Ordway in the Gulf of Nicoya, Costa Rica, Central America. Est. Coast. Shelf Sci. 20: 593-602.

Dummermuth, A. 1997. Primärproduktion des Phytoplanktons und des Mikrophytobenthos in einer nordbrasilianischen Mangrove (Bragança, Pará). Thesis, Bremen University (Germany). 136 p.

Dunlop, J.N., R.D. Wooler, N.G. Cheshire. 1988. Distribution and abundance of marine birds in the eastern Indian Ocean. Aust. J. Mar. Freshwat. Res. 39: 661-669.

Epifanio, C.E. & A.I. Dittel. 1984. Seasonal abundance of Brachyuran crab larvae in a tropical estuary: Gulf of Nicoya, Costa Rica, Central America. Estuaries 7: 501-505.

Finn, J.T. 1976. Measures of ecosystem structure and function derived from analysis of flows. J. Theoret. Biol. 56: 363-380.

Frid C. L. J., 1992. Foraging behaviour of the spiny starfish *Marthasterias glacialis* in Lough Ine, Co. Cork. Mar. Behav. Physiol. 19: 227-239.

Froglia C. & M. E. Gramitto, 1987. Notes on growth and biology of *Solenocera membranacea* (Risso 1816) in the central Adriatic sea (Decapoda: Solenoceridae). Inv. Pesq. 51: 189-199.

García- Abad M., H. Yañez- Arancibia, P. Sánchez-Gil, M. Tapia. 1992. Distribución, reprodución y alimentación de *Syacium gunteri* Ginsburg (Pisces, Bothidae), en el Golfo de México. Rev. Biol. Trop. 39: 27-34.

Gilliam D. & K. M. Sullivan, 1993. Diet and feeding habits of the southern stingray *Dasyatis americana* in the central Bahamas. Bull. Mar. Sci. 52: 1007-1013.

Giovanardi O. & G. P. Manfrin, 1984. Summary of biological parameters of *Squilla mantis* L. in the adriatic sea. FAO Fish. Rep. no. 290. p.131-134.

Herrera, W. 1985. Clima de Costa Rica. Universidad Estatal a Distancia, San José, Costa Rica.

Hernández- García V., 1992. Preliminary notes about feeding of three species of flying squids (Cephalopoda, Ommastrephidae) in the Northwest Africa area. ICES Council meeting Papers, Copenhagen, Denmark, 13 p.

Huebner, J. D. and D.C. Edwards.1981. Energy Budget of the Predatory Gastropod *Polinices duplicatus*. Mar. Biol. 61: 221-226.

Humphreys, W. F. 1979. Production and respiration in animal populations. J. Anim. Ecol. 48: 427-453.

Huntley, M. E. & M. D. G. López. 1992. Temperature dependent production of marine copepods: a global synthesis. The American Naturalist 140: 201-242.

Ishihara, H., K.Homma, Y.Takeda & J.E. Randall. 1993. Redescription, distribution and food habits of the Indo-pacific dasyatid stingray *Himantura granulata*. Jap. J. Ichthyol. 40: 23-28.

Jarre, A., P. Muck & D. Pauly. 1991. Two approaches for modelling fish stock interactions in the Peruvian upwelling ecosystem. ICES Mar. Sci. Symp. 193: 178-184.

Jiménez, J.A. 1994. Los Manglares del Pacífico Centroamericano. Fundación UNA, Heredia, Costa Rica. p. 352.

Koch, V., 1994. Report on non- crustacean invertebrate collections: Quantitative notes. pp. 22-24. *In* Wolff M. & J. A. Vargas (eds.), 1994. RV Victor Hensen Expedition 1993/1994 - Cruise Report. ZMT Contribution 2, 109 p.

Laptikhovskij, V.V. 1995. Mortality and production of the squid *Sthenoteuthis pteropus* (Steenstrup) (Ommastrephidae) in the eastern Tropical Atlantic. Biology and Population dynamics of fishes in the Atlantic Ocean. SB. Nauchn. Tr. Atlant.: 142-154.

Laughlin R. A., 1982. Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the apalachiola Estuary, Florida. Bull. Mar. Sci. 32: 807-822.

Lizano, O. 1998. Dinámica de las aguas en la parte interna del Golfo de Nicoya ante altas descargas del Río Tempisque. Rev. Biol. Trop. 46. Supl. 6: 11-20.

MacPherson E., 1978. Régimen alimentario de *Symphurus nigrescens* (Pisces, Cynoglossidae) en el mediteraneo occidental. Inv. Pesq. 42: 325-333.

Majid, A. & M. Khaliluddin.1994. Estimates of growth and mortality in the squid *Lologo duvaucili* found in Pakistan waters. Mar. Res.: 47-56.

Manjulatha, C. & D. E. Babu, 1991. Functional organisation of mouth parts and filter feeding in *Clibanarius longitarsus* (Crustacea, Anomura). Mar. Biol. 109: 121-127.

Mann, K.H. 1982. Ecology of coastal waters. Studies in ecology ( 8). 322 p.

Maurer, D. & J. A. Vargas, 1984. Diversity of soft bottom benthos in a tropical estuary: Gulf of Nicoya, Costa Rica. Mar. Biol. 8: 97-106.

Mendoza, J.J. 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem, p. 285-297. *In* V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Muck, P. & D. Pauly. 1987. Monthly anchoveta consumption of guano birds, 1953- 1982. pp. 219-233. *In* The peruvian anchveta and its upwelling ecosystem; three decades of change, edited by D. Pauly & I. Tsukayama, ICLARM studies and reviews 15.

Nelson, G.A. & M.R. Ross. 1992. Estimates of gastric evacuation and consumpon rates in little skate (*Raja eri-*

*nacea*). ICES Council Meeting papers, Copenhagen, Denmark, 15 p.

Nojima, S. 1989. Ecological studies on the sea star *Astropecten latespinosus* Meissner. VI. Seasonal changes in stomach contents, preference of food items, size preference and the kinds of switching in feeding habits. Publ. Amakusa. Mar. Biol. Lab.10: 17-40.

Odum, E.P. 1971. Fundamentals of ecology. W.B. Saunders Co, Philadelphia. 574 p.

Okera W., 1973. The food of two species of sardines - *Sardinella gibbosa* and *S. albella* - in East African waters. J. Mar. Biol. Ass. India 15: 632-651.

Palacios, J.A., Rodriguez, J.A. & R. Angulo. 1993. Estructura poblacional de *Peneaus stylirostris* (Decapoda: penaeidae) en el Golfo de Nicoya, Costa Rica. Rev. Biol. Trop.: 233-237.

Palomares, M. 1987. Comparative studies on the food consumption of marine fishes with emphasis on species occurring in the Philippines. Masters thesis, University of the Philippines, 107 p.

Palomares, M. L. & D. Pauly. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freshw. Res. 40: 259-273.

Parrish, J.D. 1987. The trophic biology of snappers and groupers. pp. 405-463. Polovin J.J. & S. Ralston (eds.). *In* Tropical snappers and groupers. Biology and fisheries management. Ocean Res. Mar. Policy. Ser.

Parsons, T.R., M. Takahashi & B. Hargrave. 1977. Biological Oceanographic Processes. Pergamon, New York, 332 p.

Pauly, D. & Christensen, V. 1993. Graphical representation of steady - state trophic ecosystem models. pp. 20-28. *In* V. Christensen & D. Pauly (eds.). Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Perez. O. S. & D. R. Bellwood, 1988. Ontogenetic changes in the natural diet of the sandy shore crab, *Matuta lunaris*. Aust. J. Mar. Fresh. Res. 39: 193-199.

Peterson, C.L. 1960. The physical oceanography of the Gulf of Nicoya, Costa Rica, a tropical estuary. Bull. Inter-am. Trop. Tuna Commn. 3: 139-216.

Petipa, T. S., A. V. Monakov, Y. I. Sorokin, G. V. Voloshina & I. V. Kukina. 1977. Balance of matter and energy in copepods in tropical upwellings of Pacific ocean. Pol. Arch. Hydrobiol. 24: 413-430.

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

Popova, O. A. & L. Sierra, 1983. Feeding of Black Jack, *Caranx ruber* (Carangidae), on the cuban shelf in the Gulf of Batabano. 1. Seasonal and age - dependent dynamics of feeding. J. Ichtyol. 23: 97-105.

Price, K., M. Bussing, W. Bussing, D. Maurer & C. Bartels. 1980. Finfish Survey. *In* Maurer, D., Epifanio & Price, K. (eds.). Ecological assessment of finfish and megabenthic invertebrates as indicators of natural and impacted habitats in the Gulf of Nicoya, Costa Rica. Progress Report of the 1979 International Sea Grant Program, University of Deleware, College of marine Studies, Newark: 83-144.

Randall, J. E., 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Ocean. Miami, vol. 5, p. 665-847.

Reis, E. G., 1986. Reproduction and feeding habits of the marine catfish *Netuma barba* (Siluriformes, Ariidae) in the estuary of Lagoa dos Patos, Brazil. Atlantica, Rio Grande 8: 35-55.

Robertson, A.I. & Blaber, S.J.M. 1992. Plankton, Epibenthos and Fish Communities. *In* Robertson, A.I & D.M. Alongi (Eds.) Tropical Mangrove Ecosystems. Coast. Est. Stud. 41: 173-224.

Rojas–Beltrán, R. 1989. Quelques aspects de l´écologie alimentaire de trois Machoiros (Teleostei, Siluriformes, Ariidae) de la guyane. Cybium 13 :181-187.

Rutledge, R.W., B.L. Bacore & R.J. Mulholland 1976. Ecological stability: an information theory viewpoint. J. Theor. Biol. 57: 355-371.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. The production of organic matter and it conversion to higher forms of life throughout the world ocean. Science 166: 72-76.

Salini J. P., Blaber S. J. M., Brewer D. T. 1990. Diets of piscivourous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. Mar. Biol., 105: 363-374.

Sauer W. H. H. & M. R. Lipinski. 1991. Food of *Loligo vulgaris* on their spawning grounds off the eastern Cape, South Africa. S. Afr. J. Mar. Sci. 10: 193-201.

Sheridan P. F., D. L. Trimm & B. M. Baker. 1984. Reproduction and food habits of seven species of Northern Gulf of Mexico fishes. Contr. Mar. Sci. 27: 175-204.

Silvestre, G., Selvanathan, S & A. H. M. Salleh. 1993. Preliminary trophic model of the coastal fisheries resources of Brunei Darussalam, South China Sea,p. 300-306. *In* V. Christensen & D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Smith, R.L., J.P. Salini & S.J.M. Blaber. 1992. Food intake and growth in the blue spotted trevally, *Caranx bucculentus*, with reference to predation on penaeid prawns. J.Fish.Biol. 40 (3): 315-324.

Stilwell, C.E. & N.E. Kohler. 1993. Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration. Fish. Bull. 91 : 138-150.

Stoner, A. W. & R. J. Zimmerman. 1988. Food pathways associated with penaeid shrimps in a mangrove fringed estuary. Fish. Bull. 86 : 543-551.

Sudekum, A. E., Parrish J. D., Radtke R. L., Ralston S. 1991. Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. Fish. Bull. 89: 493-513.

Sweatman, H. P. A. 1984. A field study of the predatory behavior and feeding rate of a piscivorous coral reef fish, the lizardfish. Copeia 1: 187-194.

Szelitowski, W. A. 1990. Importance of mangrove plant litter in fish food webs and as temporary, floating habitat in the Gulf of Nicoya, Costa Rica. Ph.D. thesis, University of southern California, 228 p.

Tilney, R. L. & T. Hecht. 1990. The food and feeding habits of two co- occurring marine catfish *Galeichthys feliceps* and *G. ater* (Osteichthyes, Ariidae) along the south east coast of South Africa. J. Zool., London, 221: 171-193.

Tokeshi, M., Estrella C., Paredes C. 1989. Feeding ecology of a size structured predator population, the South American sun- star *Heliasther helianthus*. Mar. Biol. 100: 495-505.

Tumbiolo, M. L. & J. A. Downing. 1994. An empirical model for the prediction of secondary production in marine benthic invertebrate populations. Mar. Ecol. Prog. Ser. 114: 165-174.

Ulanowicz, R.E. 1986. Growth and Development: Ecosystems Phenomenology. Springer Verlag, New York.

Ulanowicz, R.E. & K.H. Mann. 1981. Ecosystems under stress. p. 133-137. *In* Platt T., K.H. Mann & R.E. Ulanowicz (eds.) Mathematical models in biological oceanography. UNESCO, Paris.

Ulanowicz, R.E. & F. Wulff. 1991. Comparing ecosystem structures: the Chesapeake Bay and the Baltic Sea. p. 140-166. *In* Cole J., G. Lovett & S. Findlay (eds.) Comparative analysis of ecosystems: patterns, mechanisms and theories. Springer-Verlag, Heidelberg.

van Dykhuizen, G & H.F. Mollet. 1992. Growth, age estimation and feeding of captive sevengill sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium. Aust. J. Mar. Freshw. Res. 43: 297-318.

Vargas, J. A. 1987. The benthic community of an intertidal mud flat in the Gulf of Nicoya, Costa Rica. Description of the community. Rev. Biol. Trop. 35: 229-316.

Vargas, J. A. 1988. A survey of the meiofauna of the Eastern Tropical Pacific intertidal mud flat. Rev. Biol. Trop. 36: 541-544.

Vargas, J. A. 1995. The Gulf of Nicoya estuary, Costa Rica. Past, present and future cooperative research. Helgoländer Meeresunters. 49: 821-828.

Vargas, J. A. & M. Wolff (eds.). 1996. Pacific Coastal Ecosystems of Costa Rica with emphasis on the Golfo Dulce and adjacent areas: a synoptic view based on the RV Victor Hensen expedition 1993/1994 and previous studies. Rev. Biol. Trop. Suppl. 3. 238 p.

Vasconcelos, F. D., Guedes, E. M. Braga Azevedo- Araujo. 1984. Estudo ecológico da regiao de Izamaracá - Pernambuco- Brasil. XXVII. Hábitos alimentares de alguns Peixes estuarinos. Trab. Oceanogr. Fed. PE. Recife 18: 231-260.

Vega-Cendejas, M.E., F. Arreguin-Sanchez & M. Hernandez. 1993. Trophic fluxes on the Campeche Bank, Mexico, p. 206-213. *In* V. Christensen & D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM. Conf. Proc. 26, 390 p.

Voorhis, A., Epifanio, C.E., Maurer, D., Dittel, A. I. & Vargas, J.A. 1993. The estuarine character of the Gulf of Nicoya, an embayment on the Pacific coast of Central America. Hydrobiologia 99: 225-237.

Wangelin von, M. & M. Wolff. 1996. Comparative biomass spectra and species compositin of the zooplankton community of the Golfo Dulce and Golfo de Nicoya ecosystems. Rev. Biol. Trop. 44, Suppl. 3: 135-155.

Williams, M. J. 1982. Natural food and feeding in the commercial sand crab *Portunus pelagicus* L. (Crustacea: Decapoda: Portunidae) in Moreton Bay, Queensland. J. Exp. Mar. Biol. Ecol. 59: 165-176.

Wolff, M. 1994. A trophic model for Tongoy bay - a system exposed to suspended scallop culture (Northern Chile). J. Exp. Mar. Ecol. Biol. 182: 149-168

Wolff, M. 1996. Demersal fish assemblages along the Pacific coast of Costa Rica: a quantitative and multivariate assessment based on the Victor Hensen Costa Rica Expedition (1993/1994). Rev. Biol. Trop. 44, Suppl. 3: 187-214.

Wolff, M & S. Jesse, 1994. Crustaceans. *In* Wolff M. & J. A. Vargas (eds.), 1994. RV Victor Hensen Expedition 1993/1994- Cruise Report. ZMT Contribution no. 2 Bremen, 109 p.

Wolff, M. & J. A. Vargas (eds.), 1994. RV Victor Hensen Expedition 1993/1994- Cruise Report. ZMT Contribution no. 2, Bremen. 109 p.

Wolff, M., Hartmann, H.J. & V. Koch. 1996. A trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. Rev. Biol. Trop. 44, Suppl. 3: 215-231.

Woods, C. M. C. 1993. Natural diet of the crab *Notomithrax ursus* (Brachyura, Majidae) at Oaro, South Island, New Zealand. N.Z. J. Mar. Freshw. Res. 27: 309-315.

Yañez- Arancibia, A. & A. L. Lara - Dominguez, 1988. Ecology of three catfishes (Ariidae) in a tropical coastal ecosystem- Southern Gulf of Mexico. Mar. Ecol. Prog. Ser. 49: 215-230.

Yukihira, H., Shibuno T., Hashimoto H. & K. Gushima. 1994. Feeding habits of moray eels (Pisces: Muraenidae) at Kutchierabu-Jima. Appl. Biol. Sci. Seibutsu-Seisangaku-Kenkyu 33: 159-166.