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A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica

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Abstract: Golfo Dulce is a deep tropical estuary whose ecosystem dynamics are poorly understood. In order to evaluate biomass and energy flow distributions, productivity potential, and to obtain guidelines for conservation management, a steady - state model of 20 compartments (excluding detritus) was constructed using the ECOPATH II software. Total system biomass (10.4 t/km²) and total energy throughput (sum of all flows, T =1405 t/km^2/year) of Golfo Dulce are small compared to other modeled coastal ecosystems. The mayor part of the energy throughput is achieved from primarily pelagic trophic levels I to II (52%) plus II to III (41%). The pelagic fish biomass consumed within the system by top predators (about 1133t) exceeds twice the demersal fish biomass consumed (502t). Artesanal fishery primarily operates on the top trophic levels of the benthic domain and has a very low gross efficiency (catch/ primary production = 0.06%). A nearly balanced production/repiration ratio (P/R= 1.09) and a high mean tranfer efficiency (15%) suggest that the system is near maturity. Contradictory seem the low Ascendency (A= 32.2%) and high Development Capacity (DC = 67.8%) values indicative of a relatively undeveloped system of little internal stability. This contradiction might be explained through the fact that much of the detrital matter produced within the euphotic zone is sedimented away and does not - like in other coastal systems - reenter the food web. Thus, whereas the pelagial represents a tightly coupled rather mature (sub) system, the Golfo Dulce as a whole lacks this degree of maturity due to a very inefficient benthic pelagic coupling, which results from its fjord-like topography. The model reveals that Golfo Dulce acts differently from most tropical coastal ecosystems: it is dominated by biomass and energy flow within the pelagic domain and rather resembles an open ocean system than an estuarine one. Due to its low benthic biomass and low overall productivity, there seems to be no potential for further development of the demersal/semi-demersal fishery inside the gulf. An increase of the pelagic fishing pressure would seriously threaten the populations of resident predators such as dolphins, sharks and large bird species, which have considerable conservation and ecotourism values. Future ecosystem research in Golfo Dulce should focus on the pelagic part of the gulf (microbial loop, plankton, and nekton), on the small benthos, as well as on transfer processes within the pelagic domain, between the pelagial and the benthos, and at the river/gulf and gulf/ocean interfaces.

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

Golfo Dulce is a fjord-like embayment of tectonic origin, located on the southwest coast of Costa Rica (8°30' N, 83°16' W). It is about 50 km long and 10 - 15 km wide, with a surface area of 750 km² and can be divided into 2 parts: a steeply sloped deep inner basin with a flat bottom and maximum depth of about 215 m and a shallow outer basin with a sill depth of 70 m (Fig. 1), marking the borderline for this model. Shorelines are dominated by steep, forested rocky slopes to the north, northeast, and to the south featuring some coral reefs. Gentle, largely deforested slopes with sandy beaches prevail to the west (Puerto Jiménez) and east (Coto-Colorado river basin). Because most rivers entering are small, and basin slopes are steep, mangroves are relatively little developed (about 2000 ha). The small catchment basin (2050 km², excluding Golfo Dulce itself) receives 3000 - 5000 mm of rain per year

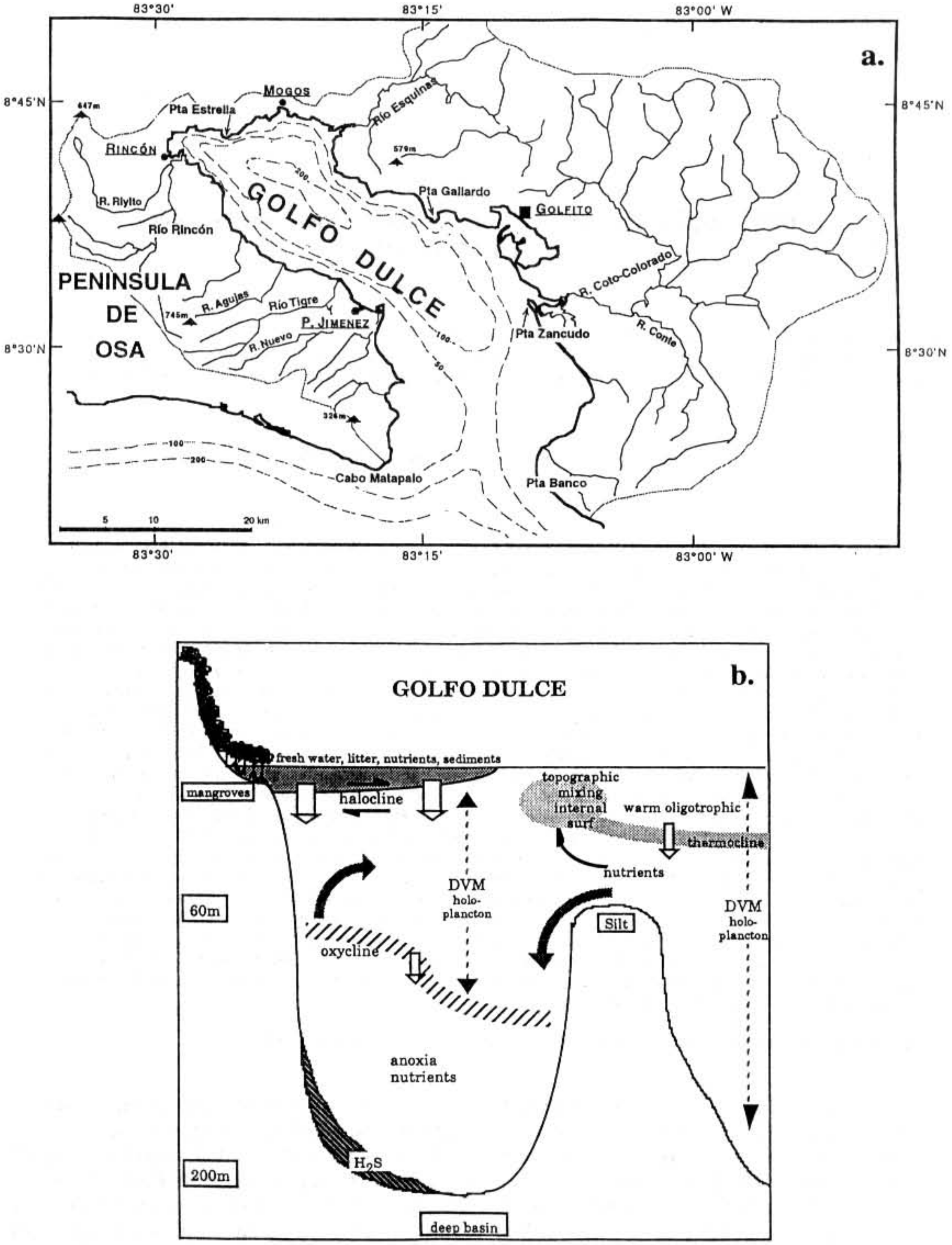

Fig. 1. Golfo Dulce, Costa Rica (a) study area; (b) conceptal transect.

(Herrera 1985). The wettest months are August through October (>500 mm/month), while the dry season is short (January through March (<100 mm/month). Because of the gulf's topography, water circulation is restricted, resembling that of a high-latitude fjord, and it is one of only three such embayments known in the tropics (e.g. Deuser 1975). The tidal range is 2-4m, yet strong tidal currents are restricted to the outer basin (Quirós 1889).

Environmental conditions favoured growth of coral reefs up to the recent past. But most reefs in the inner basin are now deteriorating as a result of increased sediment loads due to deforestation, nearshore road construction, agriculture in the lowlands, and gold mining in the mountains of the Osa peninsula (Cortés 1993). The mangrove forests are partially threatened by coal production and aquaculture development, and draining of acid mangrove soil for agriculture has caused local fish kills. New economic activities promote local human population growth (tax-free zone in Golfito, ecotourism in Puerto Jiménez), increasing levels of untreated urban runoff. Fishing in Golfo Dulce is artesanal, and total landings make up only about 3% of Costa Ricas catch, yet some large finfish species are already being overfished (Campos 1989). Nevertheless, Golfo Dulce remains a relatively undisturbed estuary with highly unusual geographic, oceanographic and ecological features. Its shores and mangrove forests are nesting grounds for threatened marine turtle species and rare as well as endemic bird species (Hartmann & Acevedo - Gutiérrez 1996), its pelagic waters are home to substantial resident dolphin populations (Acevedo - Gutiérrez 1995), and its watershed includes, on the Osa Peninsula, parts of one of the least disturbed tropical rain forests in Central America.

While the topographical and oceanographic conditions of the gulf are somewhat known through previous studies and data of the recent Victor Hensen - cruise of 1993/94 (Wolff & Vargas 1994), information about the living biota is scarce. The Victor Hensen - cruise yielded the first quantitative data on different macroplankton size compartments of the gulf (Hossfeld *et al.* 1994) as well as on demersal fish and invertebrates (Wolff & Jesse 1994, Koch 1994).

There is now sufficient quantitative information allowing for the construction of a first holistic ecosystem model in order to understand the main energy pathways of the system. The model we are presenting here is an attempt to answer the following questions: (1) How is biomass distributed among the various ecoystem 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 needs of coastal conservation and fisheries management? (4) How do the biomass fluxes in the gulf differ from the open shelf and other gulf systems in the tropics? (5) What are the major ecosystem components on which further study should be concentrated?

To model the gulf's ecosystem, the ECOPATH II software of Christensen & Pauly (1992) was used, which 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. In particular, indices used are "Total System Throughput (T)", which reflects the size of the system in terms of the sum of flows through all the individual compartments. This index is regarded as a measure of the "power"generated within the system. "Ascendency (A)" represents both, size and organization of the flows, while the "Development capacity (C)" is the upper limit to ascendency. The degree of a system's realized growth, organization and development can be given by the A/C ratio (Ulanowicz & Mann 1981), which tends to be low in systems under stress and high in well organized systems. The latter have the tendency to internalize most of their activity, to become relatively independent of external inflows and outflows and are thus tending towards high temporal stability (Baird & Ulanowicz 1993). Other indices used to assess maturity include: (i) trophic transfer efficiencies (supposedly high in mature systems), (ii) the production/respiration ratio (P/R= 1 for mature systems), (iii) the degree of energy cycling which increases with maturity (Odum 1969) as expressed in Finn's cycling index (Finn 1976) and (iv) "Overhead" (O), an indicator of ecosystem stability (Rutledge *et al.* 1976) representing the potential of the system for further development These indices have been used by various authors 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 they will be used in our analysis of the Golfo Dulce model.

In the ECOPATH II model, biomass production of and imports to the compartments is balanced by consumption and exports. Important input parameters for the model are: biomass (B), production per unit of biomass (P/B), consumption per unit of biomass (Q/B), ecotrophic efficiency (EE)- the fraction of the production used within the system (i.e. entering the other compartments) - and export (EX). Respiration (R), respiration per unit of biomass (R/B) and gross efficiency (GE) are output parameters that are crucial for examining the modelling results. The modeller defines the model structure by a prey - predator matrix indicating for each compartment the fractions of the total consumption contributed by each prey source.

MATERIAL AND METHODS

The Golfo Dulce environment: The first - and up to the "Victor Hensen - cruise 1993/94" only - oceanographic account dates back to the early 1970's, through three cruises of RV Thomas G. Thompson (Richards *et al.* 1971; Kuntz *et al.* 1975). During the dryer season (January-March), the latter found a slightly dilute, thermally stratified surface layer, with the major thermocline centred around 40m, and nearly homogeneous deep waters similar to subtropical subsurface water occurring at corresponding depths outside the gulf (Brenes & Leon 1987). CTD measurements during the Victor Hensen cruise (January 1994) confirmed this dry-season picture (Wolff & Vargas 1994). While temperature appears to be the major contributor to the thermocline most of the year, periodic freshwater flushing of the upper 10m in the outer Gulf has been observed after heavy precipitation (Yukihira 1991). Richards *et al.* (1971) found oxygen levels declining rapidly below the surface (< 10% saturation at sill depth), and total anoxia below about 150m, while outside (oceanic) concentrations were > 10% of saturation at that depth. In the deep anoxic water column, H_2S concentrations to about 5 -10 µM developed. The recent Victor Hensen data revealed less oxygen at intermediate depths (dissolved O_2 disappeared at 80 - 100 m depth), yet barely detectable H_2S levels in the deep basin).

At both investigation periods, nutrient levels were low near the surface, typical of non-upwelling shelf waters. Nitrate increased with depth to a peak just below the thermocline. Richards *et al.* (1971) concluded from their observations that deep water renewal was slow and restricted to occasional intrusion of dense subsurface water into the Gulf, which simultaneously advected nutrients into the photic zone. The Victor Hensen observations confirm this hypothesis, yet the flushing periodicity remains uncertain (Wolff & Vargas 1994).

Sediment studies during the Victor Hensen expedition revealed mostly unconsolidated soft olive-black sediments mixed with leaves and wooden sticks, similar to sediments found during one of the Thompson cruises (Nichols-Driscoll, 1976). Total organic carbon (TOC) and carbonate contents were not uniform. Highest TOC levels were found along the western side of the Gulf (>2.3%) which drains the forested and mountainous Osa peninsula and the mangrove forest of Rincon. The levels decreased across the deep basin to the eastern Gulf (1.3 - 1.8%). Nevertheless, these values are higher than TOC in other nearshore subtidal tropical soft sediments (typically < 1%, Alongi 1989).

Up to the Victor Hensen Cruise, there has been only one benthic faunal study, in form of a grab-survey (Nicholls-Driscoll 1976). The recent Victor Hensen collections include cores for analyses of meiobenthos and macrobenthos and trawl tows for demersal fish and macroinvertebrates. Preliminary results confirm the azoic nature of the deep anoxic basin already observed by Nichols-Driscoll, and an overall lower species richness than in Gulf of Nicoya. Coral reefs, however, have been studied in detail (Cortés 1990, 1991, 1992). Reefs in the inner Gulf are either dead or severely degraded by siltation. Reefs closer to the outer Gulf, away from major river inflow, however, appear healthy. Secchi depths in Golfo Dulce observed recently (Victor Hensen Cruise) ranged from was 50-60m deep. The only accounts of plankton are some sporadic observations in the early 1990s, macrozooplankton and ichthyoplankton tows of the Victor Hensen cruise (Wolff & Vargas 1994) as well as punctual community productivity and respiration rate measurements (Kuntz *et. al.* 1975). High numbers of phytoplankton, nanoplankton (flagellates) and bacteria were recently observed in the surface water. They dropped rapidly, to < 10% of the surface value at 40m (Hartmann & Acevedo-Gutiérrez 1996). Phytoplankton was dominated by diatoms and dinoflagellates, and red-tide dinoflagellates occurr. Below 40 m, dead phytoplankton prevailed, along with some bacteria (Víquez and Hartmann, in prep.). Bacteria increased again near the bottom, and were characterized by autotrophic cells containing sulfur granules. Sulfate-reducing bacteria were present in the surface water and also near the bottom, but not in the middle water column (Thamdrup 1994). High rates of oxic respiration were measured above the pycnocline (Thamdrup 1994). Nevertheless, as for phytoplankton abundance, values dropped rapidly from the surface to the pycnocline. Some data reported from the 1970's Thompson cruises indicate equally strong stratifications of nanoplankton primary production and of ATP-carbon biomass. The same cruise data showed that water-column productivity and chlorophyll a were much lower than recently measured in the Gulf of Nicoya, corresponding to average values of mesotrophic tropical shelf waters. Photosynthesis and respiration in the water column were relatively well balanced (P:R 0.9 to 1.2 including net zooplankton), which is unusual for tropical estuaries. Nanoplankton contributed over 85% to respiration in the photic zone, compared to <15% for net zooplankton (Hartmann & Acevedo-Gutiérrez 1996). Ichthyoplankton and macrozooplankton collections from the Victor Hensen cruise show differences in volume and species composition between inner and outer Golfo Dulce. Detritivorous zooplankton (e.g. ostracods) and some offshore species of copepods and chaetognaths were found to be important components of the net zooplankton in inner Golfo Dulce (Hossfeld *et al.* 1994). Overall, the plankton volumes were lower than in the highly productive Golfo de Nicoya.

While diversity of demersal fish and invertebrates is comparably low (Wolff & Vargas 1994), pelagic fish, pelagic birds, and large pelagic predators appear more diverse and abundant than in typical tropical estuaries (Acevedo - Gutiérrez 1995, Hartmann & Acevedo-Gutiérrez 1996).

Based on the above information, a conceptual transect of the oceanographic features of Golfo Dulce has been elaborated (Fig.1b).

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:

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

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)
$1\text{-}EE_i$= 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 ($P_i(1\text{-}EE_i)$) 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.

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

Equation (1a) can be re-expressed as:

$$B_i * PB_i * EE_i - \Sigma_j B_j * QB_j * DC_{ji} - EX_i = 0, \qquad (1b)$$

where

PB_i = production/biomass ratio (y^{-1}) ,
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 the literature, landing statistics and own research data. 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 morays & eels. As a next step, species of similar sizes, diets, consumption rates, mortality and production rates were grouped within a compartment. As a result, a 20 - compartment model was developed (Fig.2) consisting of the following groups:

(1) Dolphins, (2) Birds, (3) Carangids , (4) Rays and sharks , (5) Snappers & Grunts, (6) Morays & Eels, (7) Pufferfish, (8) Catfish, (9) Flatfish, (10) Lizardfish, (11) Serranids & Scorpaeanids, (12) Small Demersals (<20cm), (13) Small Pelagics, (14) Portunid Crabs, (15) Shrimps, (16) Epibenthos >10mm, (17) Benthos <10mm, (18) Zooplankton, (19) Phytoplankton, (20) Bacteria.

Table 1 summarizes the parameter values obtained for these groups and used as initial input for the ECOPATH II program. Information to set the diet matrix was taken from literature sources, unpublished university reports and from own observations (see Table 3).

For the phytoplankton biomass, the following conversions were used: Chl.a to carbon, 25:1; carbon to dry organic matter, 1: 2.5; dry to wet weight organic matter, 1: 5 (Parsons *et al.* 1977). For the biomass/m^2 estimates for phytoplankton, zooplankton and bacteria, the average depth of the euphotic layer of the gulf (50m) was considered.

Balancing the model: The first step in verifying whether the model output was realistic, was to check if the ecotrophic efficiency (EE) was < 1.0 for all compartments, as values > 1.0 are inconsistent (it is impossible that more biomass is used than produced by a compartment); if inconsistency was detected, the B or PB values were adjusted; as a second step, the GE (gross efficiency) and R/B values were checked for their consistency by comparing them with literature data as were the missing Q/B, P/B values calculated by the program. The biomass of the group Small Benthos had to be estimated by the programme. Some modifications of the Q/B and P/B of other compartments had to be done, but all these remained within narrow limits (max. ± 20% of the original input values used). Some larger biomass changes had to be done for the following groups: (3) from 0.07 to 0.15; (4) from 0.2 to 0.1; (5) from 0.02 to 0.1; (13) 0.04 to 0.38; (14) 0.01 to 0.195; (15) from 0.05 to 0.131; (16) from 0.12 to 0.555. The changes for the pelagic groups (3),(13), (14) and (15) seem to be justified as our sampling of these groups was very inefficient, due to the demersal sampling gear. Group (4) might have been overestimated due to the fact that a single sample hit a dense shoal (32 specimens) of *Mustelus lunulatus* Group (5) was probably undersampled as these fish are known to occurr primarily in rocky habitats not quantitatively covered by our sampling.

RESULTS AND DISCUSSION

Evaluation of the compartment parameters: Fig. 2 shows the compartment model for the "balanced" Golfo Dulce ecosystem. The boxes are aligned along the y-axis as a function of the estimated trophic level and the area is proportional of the double square root of the biomass. Table 2 summarizes the input values for the final run and those that were computed by the programme. The diet matrix is shown in Table 3.

The parameter estimates of the programme seem reasonable. The gross efficiencies (GE) for the fish and invertebrate compartments are between 0.089 and 0.289, in the range reported by Mann (1982) and Caddy & Sharp (1986). Our Zooplankton value (0.187) is within the range reported by Conover (1974). The GE for

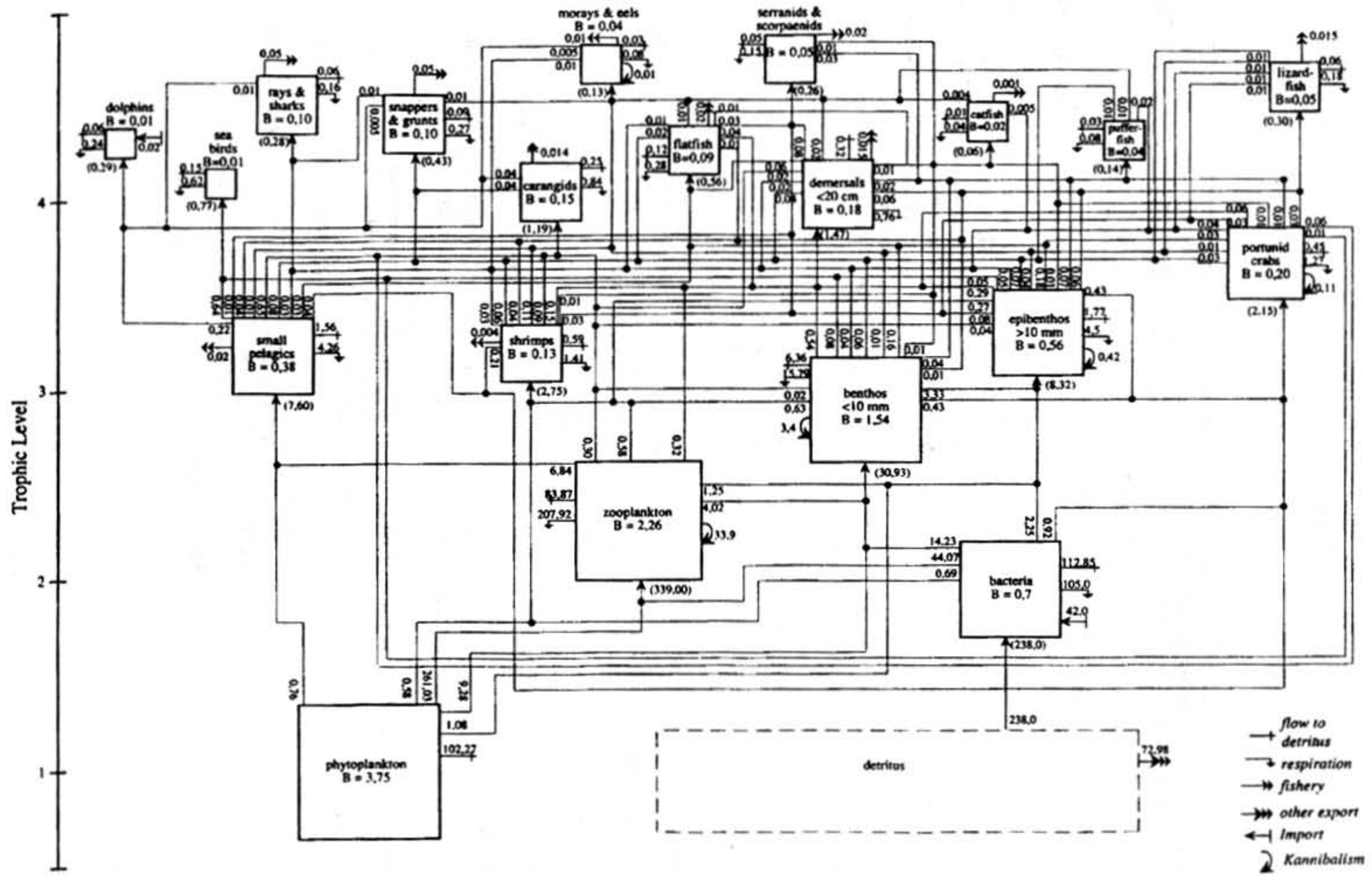

Fig. 2. Golfo Dulce. Trophic model. The box size is proportional to the square root of the compartment biomass; numbers in parenthesis represent the total amount of biomass entering the compartment; all flows are in g m^{-2} (wet weight); for further explanation see text.

TABLE 1

Golfo Dulce. Model - input data and literature sources

	group	biomass ^{1}	catch ^{2}	P/B ^{3}	Q/B ^{4}	Literature
(1)	**Dolphins**	0,010		0,05	28,00	1: estimate based on Acevedo (1992); 3+4: own estimates
(2)	**Birds**	0,011		0,07	70,00	1: own estimate; 3+4: Muck & Pauly (1987)
(3)	**Carangids**	0,070	0,014	0,70	7,90	1: Wolff & Jesse (1994); 2: landing statistics; 3: own estimate, 4: aspect ratio
(4)	**Rays / Sharks**	0,200	0,050	0,60	2,80	1: Wolff & Jesse (1994); 2: landing stat.; 3: Pauly & Christensen (1993); 4:W∞ model of Palomares (1987)
(5)	**Snappers / Grunts**	0,020	0,050	0,75	4,30	1: Wolff & Jesse (1994); 2: landing statistics; 3: Pauly & Christensen (1993), 4: aspect ratio
(6)	**Morays / eels**	0,027	0,010	0,75	3,60	1: Wolff & Jesse (1994); 2: landing statistics; 3: own estimate; 4:W∞ model of Palomares (1987)
(7)	**Pufferfish**	0,050		1,00	4,00	1: Wolff & Jesse (1994); 3: own estimate; 4: aspect ratio
(8)	**Catfish**	0,003	0,001	0,80	4,00	1: Wolff & Jesse (1994); 2: landing statistics; 3: own estimate; 4: aspect ratio
(9)	**Flatfish**	0,070	0,020	1,90	6,50	1: Wolff & Jesse (1994); 2: landing statistics; 3: length frequency analysis of catch data; 4: aspect ratio
(10)	**Lizardfish**	0,050	0,015	1,00	5,50	1: Wolff & Jesse (1994); 2: landing statistics; 3: length frequency analysis of catch data; 4: aspect ratio
(11)	**Serranids / Scorpaenids**	0,040	0,020	1,10	5,20	1: Wolff & Jesse (1994); 2: landing statistics; 3: length frequency analysis of catch data; 4: aspect ratio
(12)	**Demersals < 20 cm**	0,070	0,015	2,30	8,00	1: Wolff & Jesse (1994); 2: landing statistics; 3: own estimate; 4: aspect ratio
(13)	**Small Pelagics**	0,020	0,020	4,80	20,00	1: Wolff & Jesse (1994); Palacios & Phillips (1984);2: landing statistics;3: analysis of catch data; 4: aspect ratio
(14)	**Portunid Crabs**	0,007		2,30	11,00	1: Wolff & Jesse (1994); Dittel et al. (1985); Paul (1982);3:own estimate; 4: own estimate
(15)	**Shrimps**	0,051	0,004	6,00	21,00	1: Wolff & Jesse (1994); 2: landing statistics; 3: Pauly & Christensen (1993); 4: own estimate
(16)	**Epibenthos > 1 cm**	0,120		3,90	15,00	1: Wolff & Jesse (1994); 3: production model of Tumbiolo & Downing (1994); 4: own estimate
(17)	**Benthos < 1 cm**			5,50	19,00	3: production model of Tumbiolo & Downing (1994); 4: own estimate
(18)	**Zooplankton**	2,260		28,00	150,00	1: v. Wangelin & Wolff (1996) ; 4: Huntley & Lopez (1992)
(19)	**Phytoplankton**	3,750		100,00		1: Kuntz et .al. (1975); Blackburn et al. (1970); Conover (1974) 3: own estimate
(20)	**Bacteria**	0,700		170,00	400,00	3: Vinogradov et al. (1977); 4: own estimate

TABLE 2

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

group	catch	biomass	P / B	Q / B	EE	GE	FI	NE	R	A	R / A	P / R	R / B
(1) Dolphins	-	**0,010**	**0,05**	**28,00**	0,000	0,002	0,29	0,002	0,235	0,235	0.998	0.002	22.35
(2) Birds	-	**0,011**	**0,07**	**70,00**	0.000	0,001	0,77	0,001	0,615	0.616	0.999	0.001	55.93
(3) Carangids	**0,014**	0.150	**0,70**	**7,90**	0.907	0,089	1.19	0.111	0,843	0.948	0.889	0.125	5.62
(4) Rays / Sharks	**0,050**	0.100	**0,60**	**2,80**	0,931	0,214	0,28	0,268	0.164	0,224	0.732	0.366	1.64
(5) Snappers / Grunts	**0,050**	0.100	**0,75**	**4,30**	0,942	0.174	0,43	0.218	0.269	0.344	0.782	0,279	2.69
(6) Morays / eels	**0,010**	**0,036**	**0,75**	**3,60**	0,982	0,208	0,13	0,260	0,077	0,104	0.740	0,352	2.13
(7) Pufferfish	-	**0,036**	**1,00**	**4,00**	0,922	0,250	0,14	0,313	0,079	0.115	0.688	0,455	2.20
(8) Catfish	**0,001**	0,016	**0,80**	**4,00**	**0,950**	0.200	0,06	0,250	0,038	0.050	0.750	0.333	2,40
(9) Flatfish	**0,020**	**0,086**	**1,90**	**6,50**	0,943	0,292	0,56	0,365	0,284	0.447	0.635	0,576	3,30
(10) Lizardfish	**0,015**	**0,054**	**1,00**	**5,50**	0,960	0,182	0,30	0,227	0,184	0.238	0.773	0,294	3,40
(11) Serranids / Scorpaenids	**0,020**	**0,049**	**1,10**	**5,20**	0,957	0,212	0,25	0,264	0,150	0.204	7.360	0,359	3.06
(12) Demersals < 20 cm	**0,015**	0.184	**2,30**	**8,00**	**0,950**	0,287	1,47	0,359	0,755	1.178	0.641	0.561	4.10
(13) Small Pelagics	**0,020**	0.380	**4,80**	**20,00**	0,976	0,240	7,60	0,300	4,256	6.080	0.700	0.429	11.20
(14) Portunid Crabs	-	0.195	**2,30**	**11,00**	0,958	0.209	2,14	0,261	1,267	1.716	0.739	0,354	6.50
(15) Shrimps	**0,004**	0.131	**6,00**	**21,00**	**0,950**	0,286	2,75	0,357	1,413	2.198	0.643	0,556	10.80
(16) Epibenthos > 1 cm	-	0,555	**3,90**	**15,00**	**0,950**	0,260	8,32	0,325	4,495	6.659	0.675	0.481	8.10
(17) Benthos < 1 cm	-	1,628	**5,50**	**19,00**	**0,980**	0,289	30,92	0,362	15,788	24,740	0.638	0,567	9,70
(18) Zooplankton	-	**2,260**	**28,00**	**150,00**	0.746	0.187	339,00	0,233	207,920	271.200	0.767	0.304	92.00
(19) Phytoplankton	-	3,750	**100,00**	-	0,727	-	-	-	-	-	-	-	-
(21) Bacteria	-	0,700	**170,00**	**400,00**	**0,522**	**0,425**	280,00	0,532	105,000	224,000	0.469	1.133	150,00
(22) Detritus	-	-	-	-	0,765	-	-	-	-	-	-	-	-

Bacteria calculated (0,43) is near the value of 0.5, reported by Calow (1977). The respiration to assimilation ratios (R/A) are as expected form compiled literature data given in Humphreys (1979) and Huebner & Edwards (1981).

Trophic structure, transfer efficiencies: The pelagic domain contains about twice the biomass of the demersal compartments (7.25 compared to 3.28gm^2) (Fig.2, Table 5), with the highest food intake achieved by Zooplankton (339g/m^2), followed by Small Pelagics (7.60g/m^2), Carangids (1.19g/m^2), Sea Birds (0.77g/m^2) and Dolphins (0.29g/m^2). In our model, bacteria ingest about 280 g/m^2 of detritus› of which 15% is derived from mangrove litter exported into the system (estimates based on Hartmann & Acevedo-Gutiérrez 1996).

Within the demersal domain, the benthos compartments (16,17) contain about two thirds of the biomass (2.10g/m^2) and account for a food intake of about about 38g/m^2). Demersal fish (compartments 4 -12) represent only 0.7g of the total benthic biomass and account for about 3.60g food intake/m^2. Of the fish groups, Small Demersals account for most of the biomass consumption (1.47g/m^2), followed by flatfish (0.56g/m^2), Snappers & Grunts (0.43g/m^2) and others (0.3 g/m^2).

According to the model results, a significant part of the production of the Plankton compartments (18,19,20) is not directly used in the system (seen by their rather low EE-values) and enters the detritus pool, of which Bacteria use about 80 % (238g/m^2).

Although pelagically driven, the system has relatively low biomass of pelagic predators and our respective model estimates could be ques-

TABLE 3

Golfo Dulce. Prey-predator matrix used for the ECOPATH II - model. Numbers represent weight fractions of food ingested

group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20
(1) Dolphins																			
(2) Birds																			
(3) Carangids	0,13				0,10														
(4) Rays / Sharks	0,02																		
(5) Snappers / Grunts	0,01			0,04		0,05													
(6) Morays / eels	0,01			0,03		0,04													
(7) Pufferfish				0,06	0,02	0,06													
(8) Catfish				0,03		0,02													
(9) Flatfish				0,05	0,05	0,07		0,08		0,05	0,10	0,03							
(10) Lizardfish				0,03	0,02	0,04		0,03			0,05								
(11) Serranids/ Scorp.								0,03		0,10									
(12) Demersals < 20 cm	0,01		0,02	0,07	0,10	0,14	0,15	0,12	0,10	0,20	0,30	0,04							
(13) Small Pelagics	0,76	0,83	0,55	0,11	0,18	0,07			0,05	0,15	0,05			0,02					
(14) Portunid Crabs		0,01	0,05	0,15	0,08	0,10	0,10	0,15	0,05	0,10	0,10	0,04		0,05					
(15) Shrimps			0,08	0,11	0,13	0,05		0,16	0,20	0,15	0,10	0,10		0,10					
(16) Epibenthos > 1 cm		0,06	0,03	0,18	0,17	0,28	0,50	0,21	0,32	0,20	0,30	0,20		0,20	0,10	0,05			
(17) Benthos < 1 cm		0,10	0,02	0,14	0,15	0,08	0,25	0,22	0,28	0,05		0,37		0,20	0,23	0,40	0,11		
(18) Zooplankton			0,25									0,22	0,90		0,21	0,15	0,13	0,10	
(19) Phytoplankton													0,10		0,21	0,13	0,30	0,77	
(20) Bacteria														0,43	0,25	0,27	0,46	0,13	
(21) Detritus																			0,85
Import	0,06																		0,15

Literature sources:

1) Wuertz & Marraele (1993), Kastelein (1993), McKinnon (1994); **2)** Muck & Pauly (1987); **3)** own data, Randall (1967), Vasconcelos Filho et al. (1984), Popova & Sérra (1983), Brewer et al. (1989), Sudekum et al. (1991, Bussing & Lopez (1994)); **4)** own data, Randall, (1967), Salini et al. (1990), Gilliam & Sullivan (1993), Bussing & Lopez (1994); **5)** own data, Popova & Sérra (1983), Campos & Corrales (1986), Salini et al. (1990), Szelitowski (1990), Bussing & Lopez (1994); **6)** own data, Bussing & Lopez (1994); **7)** own data, Bussing & Lopez (1994); **8)** 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); **9)** own data, Mac Pherson (1978), Szelitowski (1990), Garcia- Abad et al. (1992), Bussing & Lopez (1994); **10)** Sweatman (1984), Vasconcelos Filho et al. (1984), Bussing & Lopez (1994); **11)** own data, Salini et al. (1990), Bussing & Lopez (1994); **12)** Campos & Corrales (1986), Szelitowski (1990), Bussing & Lopez (1994); **13)** Okera (1973), Vasconcelos Filho et al. (1984), Campos & Corrales (1986), Szelitowski (1990), Bussing & Lopez (1994); **14)** Laughlin (1982), Williams (1982); **15)** Moriarty & Barclay (1981), Froglio & Gramitto (1988), Stoner & Zimmerman (1988); **16)** Giovanardi & Manfrin (1984)Perez & Bellwood (1988), Nojiima (1989), Tokeshi et al. (1989) Manjulatha & Babu (1991), Frid (1992), Woods (1993), **17)** own data, **18)** Petipa et al. (1977); Phytoplankton (19) is producer not consumer; bacteria (20) are assumed to degrade detritus; other potential detritivores are considered to mainly feed on bacteria growing on detritus.

tioned, especially as there was a great lack of data for the pelagic compartments. The pelagic fish, however, consumed annually by the top predators Carangids (0.65g/m²), Birds (0.64g/m²) and Dolphins (0.22g/m²) amount to about 1133t for the whole gulf area (750km²), which is more than twice the consumption of demersal fish (0.67g/m^2 or 502t for the whole gulf area taken by Serranids & Scorpaeanids, Rays & Sharks, Small demersals and others). Fisheries annualy harvest an additional 164t of primarily demersal species. These comparisons underline the fact that most biomass is cycled within the pelagic part of the system.

Finally, the model indicates that more shrimps are consumed within the gulf than demersal fish (0.74g/m^2) and even Portunid crabs are a very important food source for many compartments (0.42g/m^2).

The Transfer efficiencies calculated (Table 4) are close to the 15% value proposed by Ryther (1969) for coastal zones and in the range (10-20%) commonly reported in the literature (Odum 1971;Barnes & Hughes 1988). They are, however, at the upper end of average values found by Christensen & Pauly (1993) (8%-14%). Fig. 3 shows a modified Lindeman pyramid, in which the volume of each trophic level compartment is proportional to the total throughput at this level.

Ecosystem flow indices, summary statistics: The model estimates a Total system throughput (T), i.e. the sum of all flows (consumption, exports, respiratory flows and flows into detritus) of 1405 t/km^2/year (Table 5), which is low compared to other coastal systems presented by Christensen & Pauly (1993). It is about 66% of what is reported for the North Continental Shelf Ecosystem of Yucatan, Mexico by Arreguin-Sánchez *et. al.* (1994) and only about 7% of what Wolff (1994) reports for a bay system in Northern Chile. Fig. 3 shows that about 93% of the throughput is achieved from the trophic levels I to II (52%) plus II to III (41%). About 48% of the total is due to consumption, 5.2% is exported (sedimentation and fishery), 22% flows into the detritus and 25% are respired.

The total primary production/respiration (P/R) ratio calculated by the model (1.091) (Table 5) is similar to estimates obtained from in-situ primary production and plankton respiration data (P/R = 0.9 -1.2, Hartmann & Acevedo-Gutiérrez 1996). The system thus resembles open ocean conditons, where productivity and respiration tend to be balanced (P/R=1, Christensen & Pauly 1993) and where primary productivity is comparatively low. The system biomass of about 10g/m^2 is very low, lower than for any one of the 41 trophic models presented by Christensen & Pauly (1993). Even in the above-mentioned model of the North Continental Shelf Ecosystem of Yucatan, total system biomass was six times that Golfo Dulce value (65g/m^2). A system picture emerges in which the biomass and energy fluxes are concentrated in the pelagic environment, but where a certain degree of benthic pelagic coupling still takes place. The fisheries mean trophic level (5.3) is very high and reflects the fact that most fishery targets are demersal predatory fish which themselves feed on high trophic levels. The low gross efficiency of the fishery (catch/primary production) (0.06%) underlines the above statement and clearly shows that most of the system's production (which occurs in the

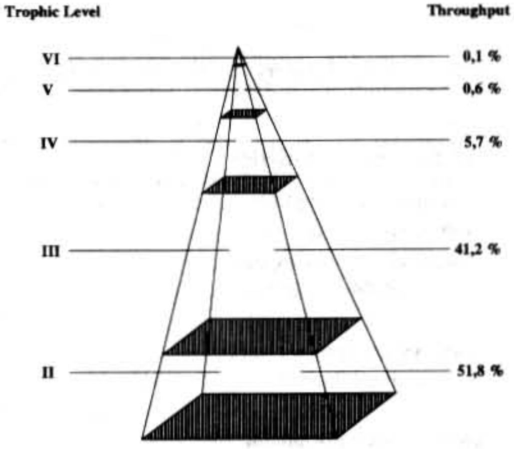

Fig. 3. Golfo Dulce. Modified Lindeman pyramid of flows; the volume of each discrete trophic level is proportional to the throughput (total flow) at that level; the bottom compartment represents herbivory (trophic level II).

TABLE 4

Golfo Dulce. 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	-	5	21,3	12.6	16,2	15,9	15,1	14,4
Detritus	-	22,2	8,8	20.8	15,5	16,2	17,9	14,9
All flows	-	13,7	11,1	17,9	15,7	16,1	15,5	14,8

Proportion of total flow originating from detritus 0,5 X= 15,0

TABLE 5

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

(a) Summary statistics		
sum of all consumption	676,6	
sum of all exports	73,2*	*sedimentation and fishery
sum of all respiratory flows	343,8	
sum of all flows into detritus	311	
total system throughput (T)	1404,6	
sum of all production	572,5	
fishery´s mean trophic level	5,3	
it´s gross efficiency (catch/ prim. prod.)	0,0006	
total net primary production (PP)	375	
total PP / total respiration (R)	1,091	
total biomass / total throughput	0,007	
total biomass (excl. detritus)	10,431	
pelagic biomass	7,25	
total catches	0,219	values in g / m^2

(b) Network flow indices

Source	Ascendency		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Import	97,7	1,9	115,2	2,2	213	4,2
Internal flow	1019,9	19,9	2370,7	46,2	3390,6	66,1
Export	158,4	3,1	156,4	3	314,8	6,1
Respiration	375,3	7,3	835,7	16,3	1211	23,6
Totals	**1651,3**	**32,2**	**3478**	**67,8**	**5129,4**	**100**

Throughput cycled	37,9	t/ km^2/ year
Finn´s cycling index	18,9	(% of total throughput)
Mean length of pathways	3,37	

pelagic part of the system) is not harvested. Harvesting these pelagic fish, however, would seriously reduce the food supply for dolphins,birds, and other large migrating predators, which are direct competitors for a pelagic fishery of the gulf.

If we rank the Golfo Dulce system on a ecosystem maturity scale, a mixed picture emerges. According to the P/R ratio calculated (P/R=1.09), the system appears near maturity. A further indication thereof is its high mean transfer efficiency (15%, Table 4), which exceeds that of most of the systems reported by Christensen & Pauly (1993). According to the P/B ratio for the whole system (35.9), on the other hand, Golfo Dulce seems to occupy an intermediate position on the maturity ranking scale (Christensen & Pauly 1993). This seems confirmed by the degree of energy cycling - assumed to increase as systems mature (Odum

1969) - which is also intermediate (Finn's cycling index FCI= 18.9%, Table 5) compared to the 41 systems reported by Christensen & Pauly (1993). The low Ascendency/Capacity ratio (AC = 32.2%, Table 5), also rather suggest a relatively inmature system dependent on external flows (Baird & Ulanowicz 1993). This low A/C value can partly be explained by the low total system throughput (and biomass), which forms part of its calculation. The following reasoning might explain the contradiction regarding the degree of the gulf´s maturity: contrary to most tropical coastal systems, Golfo Dulce has a depauperated benthic domain with very little energy cycling. Much of the detrital matter produced within the euphotic zone enters this domain were most of it is sedimented away and does not - like in other coasal systems - reenter the food web. Thus, whereas the pelagial might be considered as a tightly coupled rather mature (sub) system, the Golfo Dulce as a whole lacks this degree of maturity due to a very inefficient benthic pelagic coupling, which results from its fjord-like topography.

At this stage, the results of the modelling exercise should be viewed as a preliminary approximation of the structure and interactions of of the system. It should be stressed that some of the input values are rough estimates only and others are still lacking. First, the structure and roles of the microbial compartments (including phytoplankton) and of detritus lack detail. The model would gain considerable reality if the entire "microbial loop"- components" as well as detritus (separated into particulate and dissolved organic matter), were included and partioned into benthic and pelagic compartments (e.g. Pace *et al.* 1984), and detritus consumed by detrivores other than bacteria. Second, pelagic compartments lack complexity (there are only 6 pelagic compartments, compared to 13 demersal compartments), due to incomplete pelagic fish sampling, and lack of data on dolphin species other than *Tursiops truncatus* (Acevedo-Gutiérrez 1995), on bird biomass, and on crucial lower- level consumers such as microzooplankton (<200um). Information is also lacking on some benthic compartments (e.g. meiobenthos and microbenthos) and on abundance and productivity of benthic algae. Third, the diet matrix was assembled from a wide range of literature sources, some of which contained only qualitative data.

Finally, imports and exports (apart from catches) are not sufficiently considered in the model. Thus, the imports from mangrove production remain highly speculative. The carbon balance resulting from river and ocean transport is unknown. The discovery of turbidites in the sediments indicates that much of the organic matter from rivers may be directly entering the deep inner basin, foregoing interaction with the pelagic system (Hebbeln, 1994). Birds, in particlular pelicans (often seen migrating by flocks of 10 to 100 individuals) and fregate birds and herds of large whales, sharks, as well as turtles are known to migrate daily or seasonallly through the gulf and may thus also alter the biomass budget of the gulf.

Despite these shortcomings, we feel that the model gives a coherent picture of the Golfo Dulce ecosystem and quantifies conclusions derived from more general observations (e.g. Hartmann & Acevedo - Gutiérrez 1996). It shows that Golfo Dulce acts different from most tropical coastal ecosystems, as it is dominated by biomass and energy flow within the pelagic domain and resembles rather an open ocean system than an estuarine one. Due to its low benthic biomass and productivity there seems no potential for a further development of the demersal and semi-demersal fishery of the gulf. An increase of the fishing pressure on pelagic fish would seriously threaten the large resident predators, such as dolphins and sharks. The model's shortcomings indicate that future ecosystem research in Golfo Dulce should focus on the pelagic part of the gulf (microbial loop, plankton, and nekton), on the small benthos, as well as on transfer processes within the pelagic domain and between the pelagial and the benthos.

RESUMEN

Golfo Dulce es un estuario tropical profundo y su ecosistema es poco conocido. Para evaluar la distribución de biomasa, flujo de energía, potencial reproductivo, así como obtener guías para su administración y conservación, se elaboró un modelo "de estado estable" de 20 compartimentos (excluyendo detritus) con el programa ECOPATH II. La biomasa total del sistema (10.4 t/m^2) y el flujo total de energía (suma de todos los flujos, T = 1405 t/km^2/año) son pequeños en comparación con otros ecosistemas costeros para

los que existen modelos equivalentes. El mayor paso energético es de los niveles tróficos primariamente pelágicos I a II (52%) más II a III (41%). La biomasa de peces pelágicos consumida por los depredadores mayores (aproximadamente 1133t) sobrepasa el doble de la biomasa de peces demersales consumidos (502t). La pesquería artesanal afecta principalmente los niveles tróficos superiores del grupo bentónico y tiene una baja eficiencia bruta (captura/producción primaria = 0.06%). Una proporción casi balanceada de producción/respiración (P/R= 1.09) y una alta tasa media de eficiencia de transferencia (15%) sugieren que el sistema se acerca a su madurez, pero no coinciden con ello la baja "Ascendencia" (A=32.2%) y la alta Capacidad de desarrollo (DC=67.8) calculados por análisis de la red, que por su parte sugieren un sistema relativamente subdesarrollado, con poca estabilidad interna (Baird & Ulanowicz 1993). Este modelo revela que el Golfo Dulce funciona de una manera diferente a la de la mayoría de los ecosistemas costeros tropicales: está dominada por el flujo de biomasa y energía dentro del grupo pelágico y se asemeja más a un sistema oceánico abierto que a uno estuarino. Debido a su baja biomasa béntica y baja productividad general, no parece haber potencial para un desarrollo ulterior de la pesquería demersal y semidemersal dentro del golfo. Un aumento de la presión de pesca pelágica amenazaría gravemente las poblaciones de depredadores residentes como delfines, tiburones y aves grandes, que tienen considerable importancia en conservación y ecoturismo. La investigación futura del ecosistema de este golfo debería concentrarse en la parte pelágica ("lazo" microbinano, plancton y necton), el bentos pequeño, los procesos de transferencia dentro de la sección pelágica, entre la pelágica y el bentos y en las interfases río-golfo y golfo-océano.

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