

A trophic model for exploring possible ecosystem impacts of fishing in the Gulf of Paria, between Venezuela and Trinidad[☆]

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Abstract

The Gulf of Paria is a semi-enclosed estuarine area between Trinidad and Venezuela. Fisheries for demersal and pelagic species are important, and shared by nationals from both countries. In this study, a trophic model is constructed, and several whole system statistics and network flow indices determined for this ecosystem. Possible impacts of trawling on the biomass of model components, through simulation of the effects of varying fishing mortality rate, were also explored. The model components consist of 15 fish groups, 5 invertebrate groups, seabirds, phytoplankton, detritus and discards. Results indicate that the food web is dominated by the detrital pathway, and that the export of detritus out of the system is significant. Mixed trophic impacts show that detritus and lower trophic levels have a significant positive impact on other groups, i.e. they exert bottom-up control of the food web. Mean transfer efficiency is 12.2%, Finn cycling index 7.2%, path length 6.2, omnivory index 0.2, and system ascendancy and overhead 42 and 58%, respectively. Results suggest that, although the Gulf appears to be relatively mature, it may experience some degree of instability due to exploitation and the large seasonal variation in salinity, among other factors. Simulations of different fishing mortality rates show a strong impact on the biomass of system components. Increasing fishing mortality by 50% for 5 years resulted in a marked decrease in biomass of fish groups accompanied by an increase in that of invertebrates, notably penaeids and crabs. Fish biomass recovers after fishing pressure is relaxed, while that of crabs declined further. On the other hand, a reduced fishing mortality rate elicited the opposite response in system components, except for crab of which the biomass again declined significantly when that of fish increased. Biomass of groups at higher trophic levels obtained during trawl surveys conducted in 1945, before trawl fishing was introduced in the Gulf, were significantly higher than current biomass, except for carangids, penaeids, and possibly clupeoids. This may indicate a possible shift towards a system dominated by lower trophic levels.

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1. Introduction

The Gulf of Paria is a shared body of water on the northeastern continental shelf of South America, between eastern Venezuela and the west coast of the island of Trinidad (Fig. 1). The Gulf is very produc-

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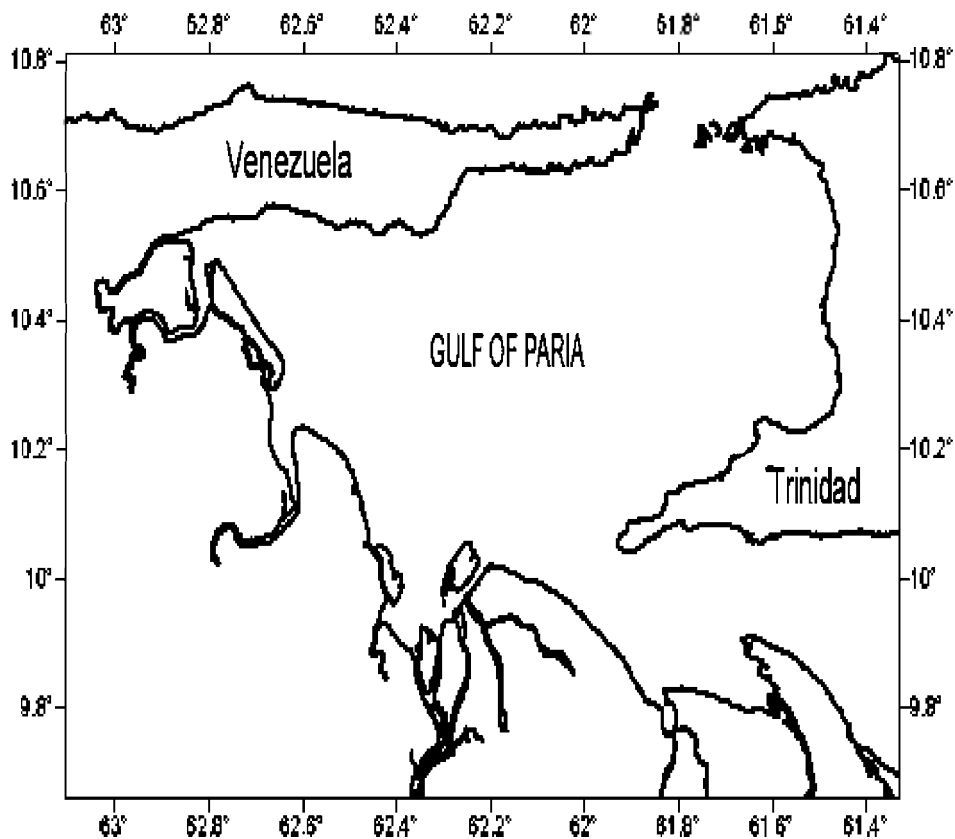


Fig. 1. Study area, the Gulf of Paria.

tive and supports valuable fisheries in both countries for penaeid shrimps and demersal fish, as well as for small and medium-sized pelagic species. Commercial fishing for demersal species became established in the second half of the 20th century, with the major fishery being the trawl fishery for penaeid shrimps. As is characteristic of tropical demersal shrimp fisheries, large quantities of bycatch consisting of juveniles of commercially important finfish such as sciaenids, carangids and gerreids are caught, most of which is discarded at sea (Maharaj and Recksiek, 1991; Jobity et al., 1997; Marcano et al., 1997).

Over the last decade, landings and catch per unit of effort of shrimp and finfish from the Gulf have declined (Marcano et al., 1999; Novoa, 2000) and it is likely that the average size of individual fish landed has decreased. Also, data presented by the Trinidad and Tobago Fisheries Division in 1999 on bycatch of artisanal trawlers, and observations by the first author

suggest a marked increase in the abundance of portunid crabs. These trends suggest that trawling has had an impact on the ecosystem, but there are no studies to date to support this. The ecosystem impact of trawling has been documented for other marine systems, for example, the Gulf of Thailand (Beddington, 1984; Christensen, 1998) and the Java Sea (Buchary, 1999). A decline in landings of targeted species, accompanied by marked alterations in fish abundance and body size, has already been demonstrated on other continental shelves subjected to long-term trawling (Caveriviere, 1982; Longhurst and Pauly, 1987; Anthony, 1993).

The fisheries of the Gulf are not managed; although regulations exist (both in Trinidad and Venezuela), they are not properly implemented or enforced. Previous studies in this area have consisted of fisheries surveys (e.g. Whiteleather and Brown, 1945; Ginés, 1972; Manickchand-Heileman and Julien-Flus, 1990;

Cervigón, 1991, 1993) or focused on individual species (Altuve et al., 1995, for the western Gulf; Sturm, 1974; Shim, 1981; Manickchand-Dass, 1987; Manickchand-Heileman and Kenny, 1990, for the eastern Gulf), as well as recent joint assessments of the shrimp resources (Alió et al., 1999a, 1999b). To date, no studies have been conducted on species interactions or on the ecosystem effects of trawling in the Gulf.

In this study, a mass-balance trophic model for the Gulf is constructed and the possible impact of trawling on its ecosystem explored, using the Ecopath with Ecosim software (Walters et al., 1997).

2. Methods

2.1. Study area

The Gulf of Paria (Fig. 1) covers an area of 7600 km². Average depth of the Gulf and the southern channel is approximately 30 m, while depths in the northern channel reach over 150 m. In general, bottom topography is smooth and soft sediments predominate, except in the north where hard substrates occur. The Gulf is a large estuarine area with high water stratification, and has substantial seasonal variations due to river runoff and mixing by tides, currents and wind. The dry season lasts from November to May and the rainy season peaks in July–September.

The main riverine inputs are from the Orinoco and San Juan rivers of South America, and the Caroni River of Trinidad. Surface water temperature in the dry season varies between 25.5 and 28 °C and surface salinity varies between 27 and 35. In the rainy season, surface water temperature is less variable ranging from 28 to 29 °C and surface salinity ranges from close to zero to a maximum of 25 (Giné, 1972; Novoa, 1998).

The Gulf is also subjected to land-based sources of pollutants from industrial and agricultural activities on the eastern side (Trinidad), one of the more industrialized areas in the region (Boodoosingh, 1992). In addition, petroleum exploration and extraction in the waters of the Gulf and in the Atlantic Ocean to the south, may also lead to impacts on the Gulf ecosystem. However, there is no concrete indication of actual or potential effects of these activities on the Gulf ecosystem.

2.2. The fisheries

The muddy substrate with its high detrital content supports a rich and diverse fauna of benthic invertebrates including penaeid shrimps, demersal teleost fishes and elasmobranchs. The major fisheries in the Gulf include industrial and semi-industrial trawl fisheries for penaeid shrimps and a multispecies mix of demersal fish, as well as artisanal fisheries for small and medium-sized coastal pelagic fish.

In the western Gulf fishing has been practised by indigenous peoples since pre-hispanic times. During the second half of the 20th century, particularly during the last 30 years, fishing intensity increased considerably. By the mid-1970s, there were more than 100 trawlers, declining to around 70 boats in the late 1990s. Annual landings of the commercial fleet peaked in the early 1990s at around 9000 t. The main species captured by this fleet are penaeid shrimp (especially *Penaeus notialis*) and sciaenids (*Micropogonias furnieri*, *Macrodon ancyclodon* and *Cynoscion* sp.).

The earliest statistical data available for the small-scale fishery in the western Gulf are for 1969 (Marcano, 1977). By the mid-1990s the total number of boats in this fleet had increased to around 450 and landings exceeded 10,000 t. Both the number of registered boats and landings have declined in recent years. Fishing gears used by the small-scale fleet includes handlines, longlines, bottom and surface gillnets, and more recently small shrimp trawls. The main species captured are catfish (*Arius* sp.), sciaenids (*M. furnieri*, *M. ancyclodon* and *Cynoscion* sp.), carangids (*Caranx* sp.), scombrids (*Scomberomorus brasiliensis* and *S. cavalla*), sharks (*Rhizoprionodon porosus* and *Carcharhinus* sp.) and snappers (*Lutjanus* sp.).

On the eastern side of the Gulf, fishing was also taking place at a subsistence level up until the second half of the 20th century, when commercial trawling was introduced. Up until that time, fishing was conducted with handlines and beach seines mainly for pelagic species such as *S. brasiliensis*, *Caranx* sp., and demersal species such as *M. furnieri* and *Cynoscion* sp. In 1945, an experimental fishery survey revealed good potential for a demersal trawl fishery (Whiteleather and Brown, 1945), following which rapid development of trawling took place. Historical information on the development of trawling in the eastern Gulf is not

available, but as early as 1969 a total of 166 locally registered trawlers had been identified (Jordan, 1969). The main species exploited by this fleet are the penaeid shrimps *P. notialis*, *P. schmitti*, *P. subtilis* and *Xiphopenaeus kroyeri*. The demersal trawl fishery consists of an inshore artisanal fleet, an offshore semi-industrial fleet, both of which operate in the Gulf, and an offshore industrial fleet (Fisheries Division, Ministry of Agriculture, Lands and Marine Resources, Trinidad and Tobago, 1999). Available statistics show that landings of penaeid shrimps ranged from 162 t in 1962 to 321 t in 1997, with a peak of 630 t in 1970 (Annual Fisheries Landing Statistics, Fisheries Division, Ministry of Agriculture, Lands and Marine Resources, Trinidad and Tobago, unpublished).

2.3. Analyses

A mass-balanced trophic model was constructed using the Ecopath with Ecosim software, version 4 (Walters et al., 1997; Christensen et al., 2000; Christensen and Walters, 2003). The model was first constructed using the Ecopath routine which uses a series of simultaneous linear equations, one for each species or group i , to quantify trophic flows among trophic groups (Christensen and Pauly, 1992a, 1992b). The basic equation is expressed as follows:

Production by (i)-all predation on (i)-non-predatory losses of (i)-export of (i): 0, for all i . This can be expressed as

$$B_i \cdot \left(\frac{P_i}{B_i} \right) \cdot EE_i - \sum_{j=1}^n B_j \left(\frac{Q_j}{B_j} \right) \cdot DC_{ji} - EX_i = 0,$$

where B_i is the biomass of group (i); P_i/B_i is the production/biomass ratio of (i), which is equal to the coefficient of total mortality Z under steady-state conditions (Allen, 1971); EE_i is the ecotrophic efficiency, which is that part of production that goes to predation, catches or exports out of the system; B_j is the biomass of predator (j); Q_j/B_j : consumption/biomass ratio of predator (j); DC_{ji} : fraction of prey (i) in the diet of predator (j); EX_i is export of group (i), which, in this study, consisted of fisheries catches. At least three of the parameters B , P/B , EE , and Q/B must be known for each group, while the model estimates the fourth. In addition, diet compositions are required for each living group in the model.

2.4. Model groups

Twenty-four ecological groups were defined based on the most abundant families captured during research cruises in the Gulf, on economic importance, and abundance in the fish diets. The fish groups were clupeoids (Clupeidae and Engraulidae), carangids, scombrids, flatfish, ariids, gerreids, trichiurids, lutjanids, serranids, haemulids, sharks, rays, other fish, *M. furnieri* and *Cynoscion* sp., which are the most abundant demersal finfish species caught. Five invertebrate groups are included: penaeid shrimps, crabs (mainly *Callinectes sapidus*), molluscs, heterotrophic benthos and zooplankton. The other groups are seabirds, phytoplankton, trawling discards and sediment detritus.

2.5. Parametrization

Biomass estimates of demersal fish, penaeids and crabs were obtained from trawl surveys conducted on the Trinidad side of the Gulf (Maharaj, 1989; Amos, 1990) as well as from research cruises conducted by the Norwegian research vessel "Dr. Fridtjof Nansen" in the area adjacent to the Gulf off the south coast of Trinidad (Institute of Marine Research, Bergen, 1989). Biomass of detritus was calculated using the empirical formula of Pauly et al. (1993), relating detrital biomass to primary production and euphotic layer depth, which were obtained from Moigis and Bonilla (1985). Biomass of seabirds, pelagic fish groups, molluscs and benthos were calculated by the model. Biomass was expressed as t per km² wet weight.

Production/biomass rates (Z) for fish groups for which biomass (B), catch (C) and natural mortality (M) were available were determined from $Z = C/B + M$. For some fish groups estimates of Z were available from analysis of length-frequency distributions (Institute of Marine Affairs, Trinidad and Tobago, unpublished) while for others Z were obtained from analysis of numbers-at-age (Sturm, 1974; Shim, 1981; Manickchand-Dass, 1987; Manickchand-Heileman and Kenny, 1990). P/B ratios of invertebrates were obtained from the literature for similar ecosystems (Arreguín-Sánchez et al., 1993; Manickchand-Heileman et al., 1998). Mean fish landings and discards by group were provided by both Venezuela (Instituto Nacional de Investigaciones Agrícolas,

Table 1
Input parameters for the Gulf of Paria model

Group	Catch (t per km ²)	Discards (t per km ² per year)	Biomass (t per km ²)	P/B (per year)	Q/B (per year)	EE
Seabirds	–	–	(0.01)	6.00	80.00	0.00
Clupeoids	–	0.060	(2.75)	2.50	9.90	0.95
Carangids	–	0.005	(1.40)	0.98	8.70	0.90
Scombrids	–	–	(0.08)	1.20	10.00	0.80
Flatfish	–	0.024	0.18	1.38	8.00	(0.95)
Ariids	0.012	0.009	0.10	0.62	7.20	(0.92)
Gerreids	0.009	0.021	0.29	0.91	7.50	(0.94)
Trichiurids	0.001	0.010	0.03	0.52	3.40	(0.62)
<i>M. furnieri</i>	0.085	0.019	0.38	1.20	6.10	(0.78)
<i>Cynoscion sp.</i>	0.070	0.030	0.79	1.41	6.80	(0.88)
Lutjanids	0.021	0.012	0.17	0.77	7.80	(0.74)
Serranids	0.004	0.003	0.04	0.73	5.20	(0.66)
Haemulids	0.002	0.006	0.01	0.88	9.80	(0.92)
Sharks	0.091	–	0.06	0.40	4.80	(0.80)
Other fish	0.137	0.081	0.89	0.65	8.22	(0.90)
Rays	0.003	0.003	0.03	0.50	4.90	(0.41)
Penaeids	0.313	–	0.38	2.04	8.21	(0.95)
Crabs	–	0.097	1.40	2.12	8.48	(0.89)
Molluscs	–	–	(1.24)	1.80	8.30	0.95
Benthos	–	–	(9.27)	5.10	33.42	0.80
Zooplankton	–	–	(1.49)	18.70	120.00	0.90
Phytoplankton	–	–	19.84	70.00	–	(0.13)
Detritus	–	–	106.33	–	–	(0.24)
Discards	–	–	0.33	–	–	(0.98)

P/B: production/biomass; Q/B: consumption/biomass, EE: ecotrophic efficiency. All weights are wet weight.

Note. Values in parentheses were estimated by Ecopath.

Ministerio de Ciencia y Tecnología, Venezuela, unpublished) and Trinidad (Annual Fisheries Landing Statistics, Fisheries Division, Ministry of Agriculture, Lands and Marine Resources, Trinidad and Tobago, unpublished). Input parameters and those calculated by the model are given in Table 1.

Consumption rates of fish groups were obtained mainly from Fishbase (Froese and Pauly, 2002), while for invertebrates they were taken from the literature (Arreguín-Sánchez et al., 1993; Manickchand-Heileman et al., 1998). Diet compositions were based on studies conducted on several species in northeastern Venezuela (Arias de Díaz and Bashirulah, 1984; Bashirullah and Acuña, 1988; Rodríguez, 1987; Barreto, 1990; Cervigón, 1991, 1993), in the eastern Gulf (Sturm, 1974; Stonley, 1975; Manickchand-Dass, 1983; Shim, 1981) and on information in Fishbase. However, the original diet composition was modified in the balancing of the model and resulted in the proportions shown in Table 2. This was done

by adjusting the diets of individual groups and re-running the parametrization procedure until all values of ecotrophic efficiency were less than 1.

Once the model was balanced, it was used to determine the trophic level of each group, mixed trophic impacts, trophic transfer efficiencies by trophic levels, and other important biological statistics (Christensen and Pauly, 1992a, 1992b). It was also used to obtain system summary statistics and network flow indices based on theoretical concepts of Odum (1969) and Ulanowicz (1986), among others.

2.6. Simulation of the impacts of varying fishing mortality

The balanced model was used to explore the possible impact of varying fishing mortality on the biomass of the major groups by simulating different fishing scenarios in the system using the Ecosim routine (Walters et al., 1997), and evaluating the resulting biomass

Table 2
Diet composition matrix for the Gulf of Paria obtained following balancing of the model

Prey	Predators																				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Seabirds																					
Clupeoids	0.590		0.328	0.720				0.400	0.015	0.190	0.020	0.059	0.060	0.154	0.030						
Carangids	0.280			0.120				0.220	0.018	0.120	0.010	0.010	0.030	0.095	0.020						
Scombrids	0.100							0.010													
Flatfish								0.020		0.020	0.030	0.100		0.120							
Ariids												0.050		0.085							
Gerreids	0.010		0.010					0.010		0.005	0.100	0.100		0.100							
Trichiurids																					
<i>M. furnieri</i>										0.060		0.006		0.016							
<i>Cynoscion sp.</i>			0.020					0.010	0.007	0.100	0.010	0.109		0.028	0.015						
Lutjanids										0.010		0.080		0.030							
Serranids										0.002		0.010		0.010							
Haemulids												0.005		0.002							
Sharks																					
Other fish			0.010	0.020		0.020				0.010		0.006	0.020	0.060	0.010						
Rays																					
Penaeids			0.002	0.010	0.010	0.020	0.010	0.020	0.010	0.001	0.020	0.001	0.020		0.005	0.080		0.020			
Crabs			0.040		0.050	0.110	0.080	0.120	0.150	0.050	0.150	0.030	0.130	0.050	0.100	0.250		0.010			
Molluscs					0.050		0.020		0.200	0.020	0.090	0.060	0.040		0.080	0.110		0.060			
Benthos		0.220	0.250	0.130	0.740	0.630	0.450	0.150	0.450	0.412	0.610	0.314	0.590	0.190	0.440	0.410	0.750	0.720	0.750		
Zooplankton		0.750	0.250				0.340	0.020					0.080		0.120						
Phytoplankton		0.010													0.010						1.000
Detritus		0.020	0.090		0.150	0.210	0.100		0.150		0.050	0.060	0.030	0.050	0.160	0.150	0.250	0.180	0.240	1.000	
Discards	0.020					0.010		0.020						0.010	0.010			0.010	0.010		

changes in the different groups. Ecosim is a time-dynamic simulation model that uses the linear equations of steady-state Ecopath models, isolating the biomass accumulation term and setting up a series of differential equations of the form:

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i$$

where, dB_i/dt represents the biomass growth rate, g_i is the net growth efficiency (production/consumption ratio), C_{ji} is the total consumption rate of group (j), C_{ij} is the predation of all predators on group (i), M_i the non-predation natural mortality rate, F_i is the fishing mortality rate, e_i is emigration rate and I_i is immigration rate.

This leads to predictions of how biomass develops over time as a consequence of changes in fishing patterns or in other ecosystem forcing functions. Ecosim requires a vulnerability setting for all predator-prey interactions controlling the rates with which prey groups are moving between a vulnerable state and one where they are not susceptible to predation by a given predator. The default vulnerability setting corresponds to mixed top-down and bottom-up control (a setting of 0.0 for bottom-up control, to 1 for top-down control). For the present simulations the default was used for all prey groups, apart from penaeids, crabs and benthos, for which the vulnerability setting was 0.9 for top-down control.

Under each scenario, fishing mortality on the trawler fleet, rather than on individual groups, was changed. This was because trawling is relatively non-selective and it was not practical to adjust fishing effort on individual groups. Each simulation was run for 60 years. The three scenarios were exploratory and arbitrarily chosen, and did not reflect any intended fisheries management plans or proposals:

Scenario 1: Relative fishing mortality rate was increased by 50% for 5 years (year 5 to year 10), then reduced to the original level for the remaining time period.

Scenario 2: Fishing mortality was gradually decreased in the first 5 years to no fishing for the next 55 years, until year 60.

Scenario 3: Fishing mortality was doubled for 10 years, then returned to the original level for the remaining time period.

Biomass used in the model (current biomass) were compared with those obtained during trawl surveys conducted in 1945 (Whiteleather and Brown, 1945), before the trawl fishery was introduced and became established in the Gulf. The latter were calculated using the swept area method.

3. Results

3.1. Trophic structure and flows

A balanced model was successfully constructed for the Gulf of Paria ecosystem. In general, EE values are high for the fish groups, while they are low for phytoplankton and detritus (Table 1). The low EE of phytoplankton indicates that only a small proportion of phytoplankton production is grazed in the water column, with the rest going toward detritus. Similarly, the low EE of detritus also indicates that a small fraction of detritus biomass is consumed, with the rest being buried in the sediment or exported out of the system.

Ecopath also calculates the fractional trophic level (TL) for each group; this is a measure of the average trophic level at which a group is receiving energy (Levine, 1980). The routine assigns a TL of 1 to primary producers and detritus, and a TL of 1+ (weighted average of the preys' TL) to consumers, resulting in TLs which are not necessarily integers. The highest fractional trophic levels in the Gulf are occupied by seabirds, trichiurids, scombrids, *Cynoscion* sp., sharks and serranids, while flatfish and ariids occupy the lowest trophic levels among the fish groups (Table 3).

The entire system was aggregated into discrete trophic levels *sensu* Lindeman (1942). This trophic aggregation routine also gives a breakdown of relative flows by TL, and the transfer efficiency (TE) between successive TLs and for the system as a whole. TE is the fraction of the total food intake by a trophic level which is transferred to the next higher level. Results show the presence of 10 integer (discrete) TLs in the Gulf ecosystem. Since the magnitude of flows at trophic levels higher than the fourth is very low, representing only a small fraction of the flows associated with the top predators, these higher levels were omitted from further analyses.

The results of trophic aggregation were used to construct a Lindeman spine, which is a linear chain

Table 3
Fractional trophic level for groups in the Gulf of Paria model

Group	Trophic level
Seabirds	4.1
Clupeoids	3.0
Carangids	3.3
Scombrids	3.9
Flatfish	2.9
Ariids	2.9
Gerreids	3.0
Trichiurids	3.8
<i>M. furnieri</i>	3.2
<i>Cynoscion</i> sp.	3.7
Lutjanids	3.3
Serranids	3.6
Haemulids	3.2
Sharks	3.7
Other fish	3.1
Rays	3.2
Penaeids	2.8
Crabs	2.9
Molluscs	2.8
Benthos	2.0
Zooplankton	2.0
Phytoplankton	1.0
Discards	1.0
Detritus	1.0

showing transfers through each discrete trophic level (Fig. 2). As already noted, trophic flow originating from detritus to consumers is almost twice that originating from primary producers, resulting in a detritivory:herbivory ratio of 1.7. Flows originating from primary producers and detritus were combined to ob-

tain TE by trophic levels. For the Gulf, highest TE is in level III, then declines in level IV (Fig. 2). The geometric mean transfer efficiency for the system as a whole is 12.2%.

3.2. Mixed trophic impacts

Ecopath uses the Leontief matrix routine (Leontief, 1951) to assess the direct and indirect impacts of a change in the biomass of each group on the other groups (Christensen and Pauly, 1992a, 1992b). Results of this routine illustrate the importance of detritus and lower trophic levels, particularly benthos, in the Gulf ecosystem. These groups have the most pronounced positive impacts on other groups in the system, providing an important food source for the latter groups. Detritus has a positive impact on almost all groups, emphasizing the importance of detritus as the base of the food web in the Gulf. Some fish groups (scombrids, ariids, gerreids, trichiurids, serranids and haemulids), as well as rays, have minimal or no impact on the other groups, due to their relatively low biomass and/or low Q/B ratios. On the other hand, among the fish groups *Cynoscion* sp., carangids and clupeoids show both positive and negative impacts on the highest number of groups in the system through predation or competition.

Mixed trophic impacts of the impact of the trawler fleet indicate that increased fishing mortality will have a negative impact on trichiurids, serranids, haemulids, other fish, rays and shrimps. Discards appear to have

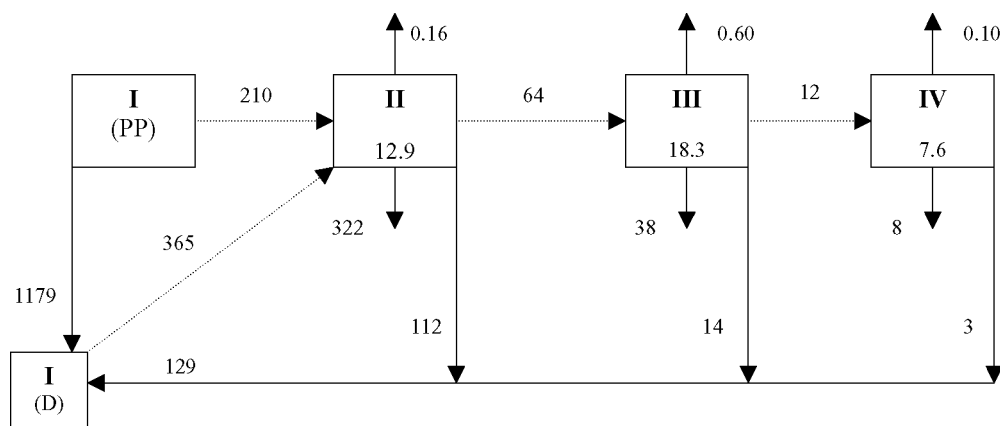


Fig. 2. Lindeman spine showing flows from each discrete trophic level, and transfer efficiency for each level.

no positive impacts on the other groups, and therefore may not be an important food source for consumers, despite the large quantities discarded.

3.3. Primary production required

The trawl fishery in the Gulf is equivalent to a predator with a mean trophic level of 2.97, with almost 80% of the catch coming from trophic levels II and III. Primary production required (PPR) for current total catch from the area is 28.3 t per km², which is equivalent to about 2% of net primary production. For the economically important penaeid shrimp fishery, PPR for present harvest range is 8 t per km² which is equivalent to 0.56% of net primary production.

3.4. Summary statistics and network flow indices

Ecopath computes a number of summary statistics which can be used to assess the maturity of the ecosystem (*sensu* Odum, 1969) and for comparisons among ecosystems. It also gives a number of network flow indices based on concepts developed by theoretical ecologists, notably Ulanowicz (1986). Some of these summary statistics and network flow indices for the Gulf are given in Table 4.

Total system throughput, which describes the size of the system in terms of flow (Ulanowicz, 1986) is an

important parameter for comparison of flow networks. For the Gulf, total system throughput is 2285 t per km² per year, while net system production is 1020 t per km² per year. The ratio between total primary production (PP) and total respiration (*R*), considered to be another important descriptor of system maturity (Odum, 1971), is 3.77 for the Gulf (Table 4).

The connectance index, which is the number of actual links in relation to the number of possible links in the food web (Gardner and Ashby, 1970), is also correlated with system maturity since the food chain is expected to change from linear to weblike as the system matures (Odum, 1971). For the Gulf ecosystem, the connectance index is 0.31. However, since the interpretation of connectance is ambiguous, the system omnivory index, which characterizes the extent to which the system displays weblike features, is suggested as an alternative (Christensen and Pauly, 1993), and is 0.20 for the Gulf (Table 4).

The fraction of an ecosystem's throughput that is recycled, as quantified by the Finn's cycling index, FCI (Finn, 1976), is also thought to be related to system maturity (Odum, 1969; Christensen and Pauly, 1993). Another system descriptor is path length, which is the average number of groups that a flow passes through (Finn, 1980), and which is also expected to increase with system maturity. The FCI and mean path length for the Gulf are 7.2% and 6.2, respectively (Table 4).

A measure of the average mutual information in the system is the ascendancy, which is derived from information theory (Ulanowicz, 1986; Ulanowicz and Norden, 1990). It is a measure of the network's potential for competitive advantage over other network configurations (Ulanowicz, 1986). The upper limit for the ascendancy is the development capacity and the difference between them is the system overhead, which reflects the system's strength in reserve to meet unexpected perturbations (Ulanowicz, 1986). For the Gulf, ascendancy is 2471 (42%), capacity is 5924 and overhead 3452 (58%) (Table 4).

3.5. Simulated impacts of fishing

Scenario 1: Fig. 3 shows variation in the biomass of six model groups (crabs, penaeids, *M. furnieri*, *Cynoscion* sp., Lutjanids and sharks) when fishing mortality is increased by 50% for five years.

Table 4
Summary statistics and network flow indices for the Gulf of Paria
(flows in t per km² per year)

Parameter	Value
Sum of all consumption	576.6
Sum of all respiratory flows	368.8
Sum of all flows into detritus	1338.9
Total system throughput	2285.0
Sum of all production	1480.0
Net primary production (PP)	1388.8
Total PP/total respiration	3.8
Net system production	1019.9
Total primary production/total biomass	34.0
Finn's cycling index (%)	7.2
Mean path length	6.2
System transfer efficiency (%)	12.2
Detritivory:herbivory	1.7
Connectance index	0.3
Omnivory index	0.2
Ascendancy (%)	41.7
Overhead (%)	58.3

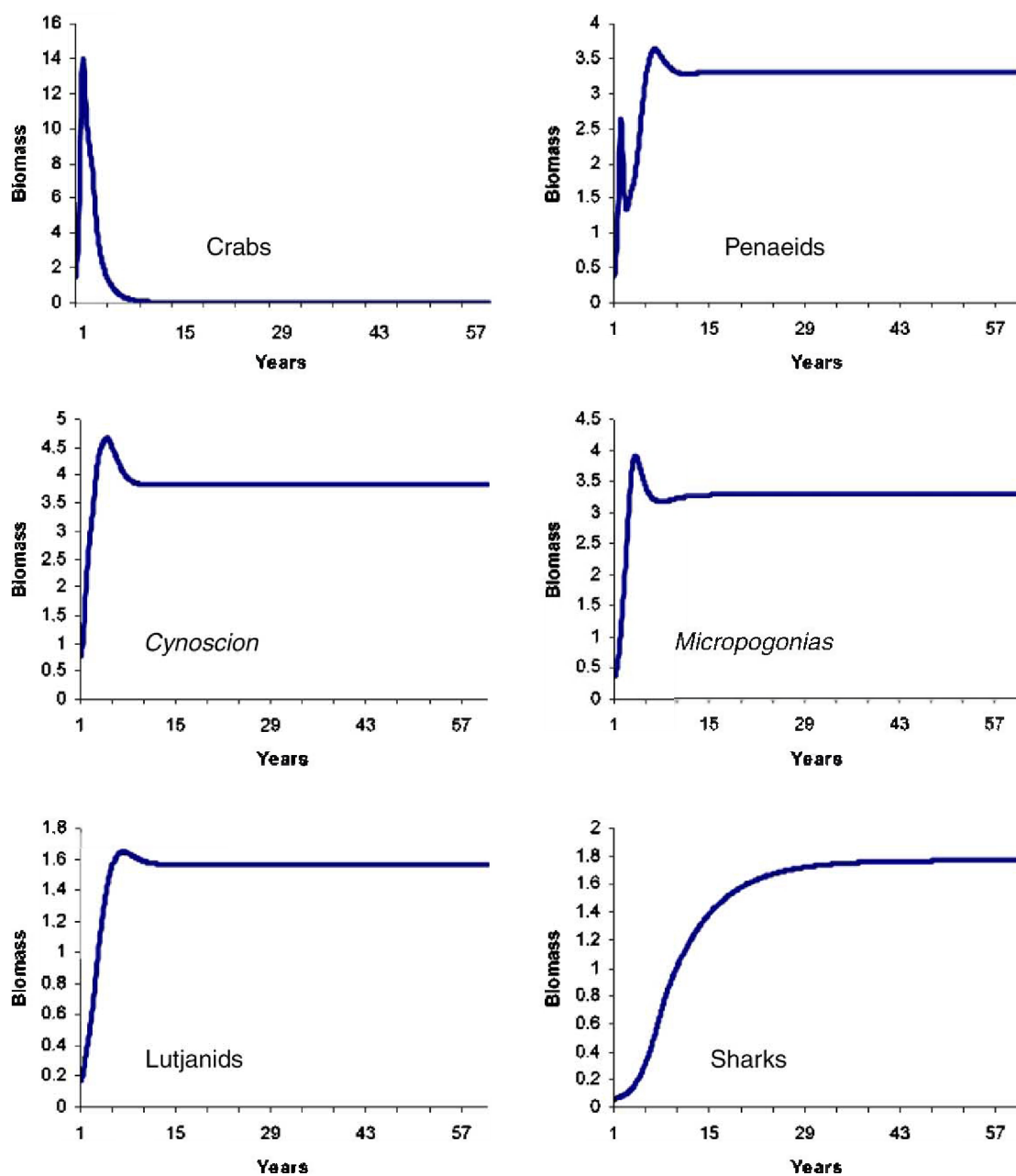


Fig. 3. Simulated changes in biomass of selected groups after an increase in fishing mortality by 50% for 5 years and return to original fishing mortality for remainder of the simulation period.

Following the perturbation, a significant reduction in biomass occurs for most fish groups, while biomass increases for crabs and penaeids. Biomass of *M. furnieri* first decreases, then shows a small increase, followed by a greater increase after the perturbation ends. The biomasses of all the fish groups and penaeids rapidly recover and stabilize at higher levels, following the perturbation, but that of crabs decreases to values about 65% lower than the initial biomass. Notable is that the recovery of sharks is slower than that of the other fish groups. Reducing vulnerability of penaeids and crabs to intermediate levels causes a reduction of shrimp biomass during perturbation, while crab biomass increases.

Scenario 2: The biomasses of fish groups increase when fishing is reduced to zero for 5 years, then decline and stabilize at higher levels than previously existed (Fig. 4). Biomass of sharks shows a slower rate of increase, compared to that of the other fish groups. In contrast to the fish groups, biomass of crabs shows a rapid decline to zero by year 10 when fishing is relaxed. The biomass of shrimps also decreases but recovers to a higher level after fishing mortality is reduced. When vulnerabilities of these two groups are set at intermediate levels, changes in biomass are also negative but declines are not as significant.

Scenario 3: A doubling of fishing effort resulted in chaotic fluctuations and reduction in the biomasses of all demersal groups, except crabs and molluscs (figure not shown). The biomass of all demersal groups is significantly reduced in the first 5 years, while that of crabs increases significantly. Increases in biomass are observed for seabirds, clupeoids and scombrids. Biomass recoveries after the perturbation ends are slower in this case, and may take more than two decades for certain species such as sharks.

The group biomasses used in the model were compared with those of similar groups obtained by trawl surveys in 1945 by Whiteleather and Brown (1945). As expected, biomasses obtained in 1945, before trawl fishing was introduced in the Gulf, are higher than current biomass, except for carangids and penaeids (Table 5). Although no catch data are available for clupeoids from these surveys, they were not reported

Table 5

Biomass used in the model (B_{model}) compared with biomass from 1945 (B_{1945}), before the trawl fishery was established

Group	B_{model}	B_{1945}
Clupeoid	2.75	–
Carangid	1.39	0.08
Flatfish	0.18	–
Ariids	0.10	0.21
Gerreids	0.29	0.61
Trichiurids	0.03	–
<i>M. furnieri</i>	0.38	0.85
<i>Cynoscion</i> sp.	0.79	2.16
Lutjanids	0.17	0.24
Serranids	0.04	–
Haemulids	0.01	0.02
Sharks	0.06	0.52
Other fish	0.89	3.86
Rays	0.03	0.07
Penaeids	0.38	0.25
Crabs	1.40	–

Biomass in t per km².

to be very abundant (Whiteleather and Brown, 1945), and might have had a lower biomass than obtained in the present study.

4. Discussion

This study provides some useful insights into the trophic structure and functioning of the Gulf of Paria. Results indicate that the ecosystem of the Gulf is in many aspects similar to other continental shelf and estuarine ecosystems. Notable is the dominance of the detrital pathway over the grazing pathway. Grazing may not have a major effect in the Gulf, considering the relatively shallow depth and high seasonal nutrient input into this ecosystem. In other estuarine environments grazing has been found to be highly variable and consumes from 2 to 45% of phytoplankton standing crop (Day et al., 1989). The inefficient grazing by herbivores has previously been shown for several other marine ecosystems, for example, the Gulf of Panama (Smayda, 1966), the northern Gulf of Mexico (Flint and Rabelais, 1981), the Sierra Leone continental shelf (Longhurst, 1983), the Texas shelf (Walsh, 1983), the shelf off northeastern Venezuela (Mendoza, 1993), and the southwestern Gulf of Mexico (Manickchand-Heileman et al., 1998). These studies show that pelagic herbivory accounts for no more

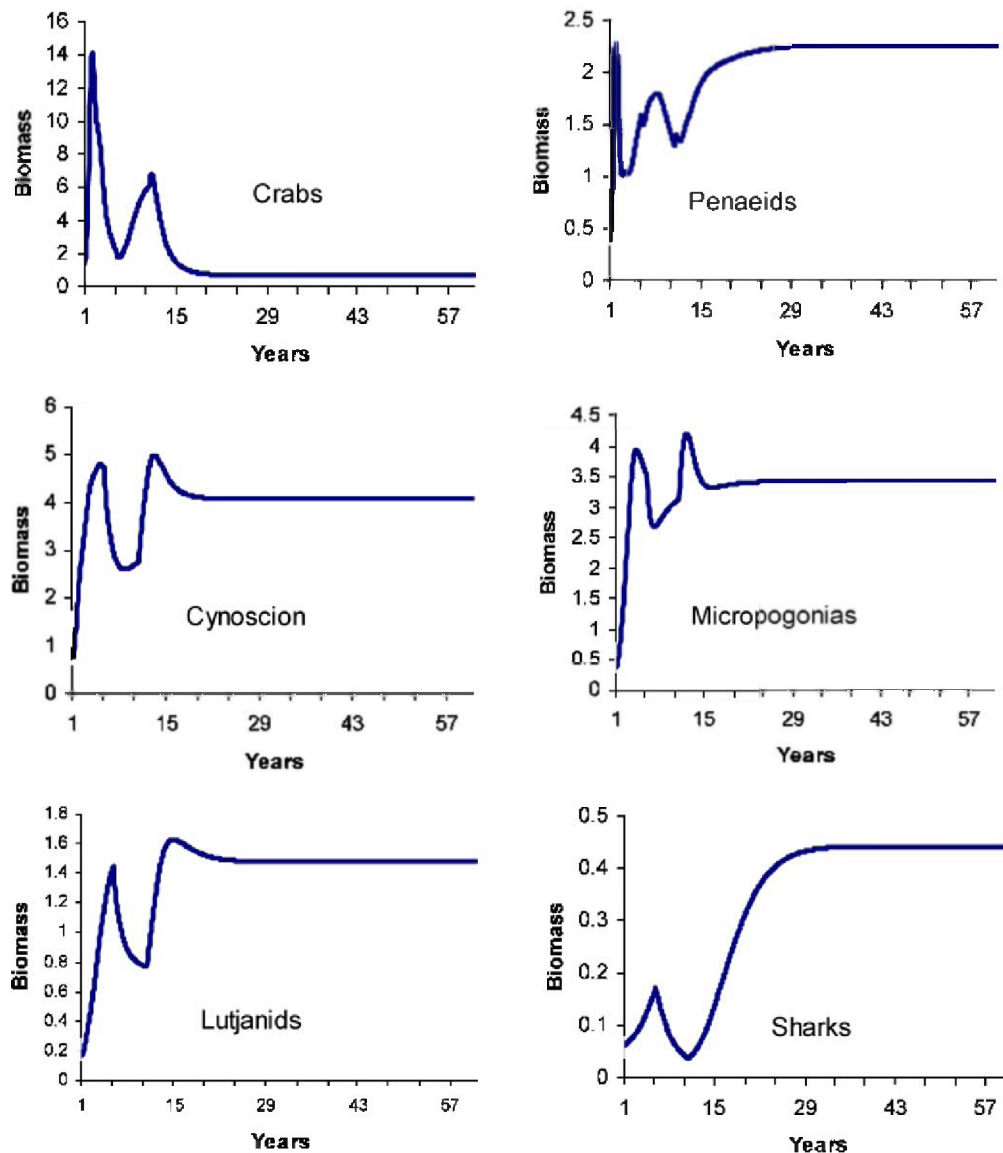


Fig. 4. Simulated changes in biomass of selected groups after a gradual decrease in fishing rate during the first 5 years and return to original fishing mortality for remainder of the simulation period.

than 10–20% of primary production, which is consistent with the findings in the present study.

The export of detritus out of the system, as observed in the Gulf, concurs with the finding of Walsh (1981) and Longhurst (1983) that export of organic carbon to the deep ocean is a general feature of continental shelves. Export of detritus from the Gulf to the Caribbean Sea may be significant, considering the low

consumption of phytoplankton and detritus in the system, the large input from rivers and the flow of water out of the Gulf in a northwesterly direction (Muller-Karger and Aparicio-Castro, 1994).

The food web of the Gulf is dominated by the detrital pathway as in many other estuarine systems (Day et al., 1989), with benthic invertebrates playing a significant role in transferring energy from detritus to

higher trophic levels. Detritus and lower trophic levels have significant positive impacts on other groups in the system, suggesting “bottom-up” control of the food web. Odum (1969) suggested that as systems mature they become more dependent on detritivory than herbivory.

Analysis of mixed trophic impacts also shows the importance of detritus and lower trophic levels as a food source in the system, and again illustrates their role in bottom-up control of the Gulf food web. In contrast, fish groups showing negative trophic impacts on other groups through predation have potential for significant top-down control of the food web in this system. Increasing fishing mortality is expected to have a negative impact on penaeids, as well as on some of the fish groups, particularly sharks and rays. In the Gulf, these two latter groups form a relatively large proportion of trawl bycatch, and because of their life history strategy, are highly susceptible to exploitation (Stevens et al., 2000).

The relatively high ecotrophic efficiencies suggest that the system's secondary production is efficiently utilized by predators. The mean transfer efficiency for this ecosystem is close to the value of 10% that is often assumed to exist in ecosystems (Lindeman, 1942), and which was shown to be a good estimate of the average transfer efficiency in aquatic ecosystems (Pauly and Christensen, 1995). The transfer efficiency obtained in this study shows that the Gulf system is very efficient at transferring energy up the food chain, and may indicate a fair degree of stability in the ecosystem.

The primary production required (PPR) for total harvest from the Gulf is lower than the average reported by Pauly and Christensen (1995) for global aquatic systems, and may reflect the dominance of the catch for the Gulf by penaeid shrimps. The PPR for harvest of penaeid shrimps is lower than that for fish groups, despite their higher landings, due to the lower ecological cost of harvesting at lower trophic levels (Jarre-Teichmann, 1998).

As previously mentioned, several ecosystem properties that allow the determination of ecosystem maturity and stability are determined from the model. According to Odum (1971) a PP/R ratio greater than 1 is expected in the early developmental stages of an ecosystem, while in mature systems, it should approach 1. The PP/R ratio obtained in this study is slightly higher than 1, suggesting a system that may

still be maturing. However, the omission of bacteria from this model, and therefore lower total respiration, could account for the high value of PP/R obtained for the Gulf.

Christensen and Pauly (1993) suggested that the Finn's cycling index (FCI) should be related to system overhead by a parabolic relationship, which is related to maturity (*sensu* Rutledge et al., 1976). Intermediate values in this relationship were suggested as being optimal in terms of stability (Christensen and Pauly, 1993). A value of 7.2% for the FCI and system overhead of 58.3% place the Gulf in the lower intermediate range of this relationship, suggesting that it may possess some degree of instability.

The connectance index and system omnivory index are also correlated with system maturity since the food chain is expected to change from linear to web-like as the system matures (Odum, 1971). For the Gulf, the values of these indices are intermediate, suggesting a simplification of the food web, and consequently a system that is not fully mature and stable.

Some degree of instability of the Gulf ecosystem may be caused by its dependence on the seasonal input of nutrients from terrigenous sources, significant fluctuations in salinity and also by the effects of fishing. Furthermore, the Gulf is subjected to pollution from land-based activities which may also result in disturbance of its ecosystem, although this has yet to be substantiated by scientific studies.

Nevertheless, the relatively high system ascendancy and overhead for the Gulf would suggest that this system has a fairly high level of development, is resilient and has strength in reserve (Ulanowicz, 1986). Mendoza (1993) obtained values of 39.6 and 60.4% for ascendancy and overhead, respectively, for the upwelling area off northeastern Venezuela, showing that this system may have a higher resilience than the Gulf.

Attempts to rate the maturity of the Gulf ecosystem in comparison to other similar systems, according to Christensen (1995), shows that the Gulf is similar to the Campeche Bank, Gulf of Mexico (Vega-Cendejas et al., 1993), the continental shelf off Yucatan in the Gulf of Mexico (Arreguín-Sánchez et al., 1993), and the South China Sea (Silvestre et al., 1993). These were ranked in maturity between 29 and 36 out of the 41 ecosystems (with ecosystem 41 showing highest maturity), of Christensen (1995). On the other hand, the Gulf is not as stable and mature as the southwestern

Gulf of Mexico continental shelf which shows higher FCI, path length, connectance, and system overhead, and which was reported to be relatively mature and stable (Manickchand-Heileman et al., 1998).

Responses to the simulated increase in fishing effort were as expected. During increased fishing in scenario 1, the biomass of all fish groups initially declined, then recovered. On the other hand, penaeids and crabs increased in abundance when predatory pressure was reduced due to a reduction in the biomass of their predators. These results could indicate that apparent recent increases in abundance of portunid crabs may be trophically mediated by the effects of increased fishing on their predators.

In scenario 2, under reduced fishing, the biomass of finfish increases initially, then decreases but to higher levels than previously existed. Although the biomass of sharks recovered, the new level represented a significant reduction from the period of reduced fishing, possibly due to their lower P/B ratio, and life history strategy. Again the biomass of crabs declined significantly. Crabs are a significant proportion of the diets of demersal fish groups, and as demonstrated in the different scenarios, increase in biomass of the latter has significant impact on the biomass of crabs as a consequence of increased predation. Although the magnitude of this impact is related to the vulnerability setting used, the same trends are always present.

Following the period of perturbation in both the above scenarios, the biomass of penaeids recovered as did the fish groups. It has been shown that penaeids are able to withstand relatively high fishing pressure, as long as their predators (in this case the fish groups) are also harvested (Pauly, 1982).

Under less intense fishing increments, such as in scenario 1, the relatively fast recovery of the different groups indicates a certain degree of system resilience, as borne out by the network flow indices. However, under heavy fishing in scenario 3, the rapid decline in biomass of most demersal groups to very low levels, except for crabs and molluscs, indicates that system recovery may be relatively slow following large, rapid perturbations, and may take more than two decades for some components to recover.

Current biomass used in the model are lower than those from 1945 for groups for which data is available, except carangids and penaeids which show higher abundances in 1945. This is consistent with

observations in ecosystems subjected to extended periods of trawling, in which the community shifts to one dominated by lower trophic levels (Power and Newlands, 1999; Bianchi et al., 2000). Thus, a decrease in the abundance of species at higher trophic levels through trawling could have resulted in this shift to a dominance of species of lower trophic levels in the Gulf. However, these results are only preliminary and further studies are required to verify the impacts of fishing in the Gulf ecosystem.

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