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Fisheries catches and the carrying capacity of marine ecosystems in southern Brazil

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Abstract

The carrying capacity of marine shelf ecosystems in southern Brazil for harvestable species is analyzed by (1) quantifying the amount of available primary production appropriated by fisheries catches, (2) evaluating the trend in the mean trophic level of fisheries, and (3) simulating the ecosystem effects of "fishing down the food web" in an intensively exploited shelf region. Fisheries utilize ca. 27 and 53% of total primary production in the southern and south-eastern shelf regions, respectively. Regional variation in the carrying capacity appropriated by fisheries results from differences in the primary production, catch volume and trophic transfer efficiencies. Overall, fisheries landings do not display a trend of decreasing trophic level with time due to the collapse of the sardine fishery and the recent increasing of offshore fishing for higher trophic level species, mainly tunas and sharks. However, the simulations show that fishing down the food web through fisheries that target small pelagic planktivorous fishes, while at first increasing catches in intensively exploited regions, has the potential of decreasing yields, by interrupting major energy pathways to exploited, high-trophic level species. The consequences of these results to the design of precautionary measures for future fishing policies are discussed.

Keywords: Carrying capacity; Shelf ecosystems; Trophic model; Marine fisheries; Brazil

1. Introduction

Recent assessments of the worldwide status of marine capture fisheries reveal alarming signs of human dominance and impact on the oceans. Fisheries alone appropriate ca. 8% of the total marine primary production and up to one-third of temperate continental shelf systems production (Pauly and Christensen, 1995). Over 60% of the most important fish stocks are either overexploited or at the limit of becoming over-exploited by current fishing intensity (Garcia and Newton, 1997), and approximately 27 million t of non-target animals are discarded annually as "trash" fish (Alverson et al., 1994). Also, present exploitation patterns are resulting in a "fishing down marine food webs" phenomenon, from long-lived, high-trophic level piscivorous fish to short-lived, low-trophic level invertebrates and planktivorous pelagic fishes (Pauly et al., 1998).

In line with some of these global trends, marine capture fisheries of Brazil are in a state of crisis caused by the scarcity of resources, over-capitalization of fisheries activities and the lack of sound fisheries management policies. At the same time, there are major efforts to assess the potential production of

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fishery resources in the Exclusive Economic Zone triggered by the country's ratification of the United Nations Convention on the Law of the Sea. Early assessments of the fisheries resources along the coast during the 1970s (Hempel, 1971; Neiva and Moura, 1977) indicated a potential total catch of over 1 million t per year, yet in fact, since the mid-1980s landings have stabilized around 700 000 t per year, and many of the traditional fish stocks have become either fully exploited or overexploited (Dias Neto, 1991a,b; IBAMA, 1994a-c; Reis et al., 1994; Cergole, 1995; Matsuura, 1995; Haimovici et al., 1997). This raises concerns as to whether the level of exploitation can be sustained without impairing the productivity and integrity of the marine ecosystems.

Brazil has an extensive coastline from 5°N to 34°S, including regions of tropical and subtropical climate. Matsuura (1995) divided the Brazilian coast in five regions with distinct environmental characteristics and types of fishing activities (Fig. 1). In the north, biological production is high as a result of the continental runoff from the Amazon river (Teixeira and Tundisi, 1967). The wide continental shelf and the rich benthic community favor the development of trawling activities in this region, mostly for shrimps and large catfishes. The northeast and east regions are oligotrophic due to the influence of tropical waters from the Brazil Current. Rocky bottoms and a mostly narrow continental shelf induced the development of hook-and-line fisheries for rockfishes, sharks and tunas. In

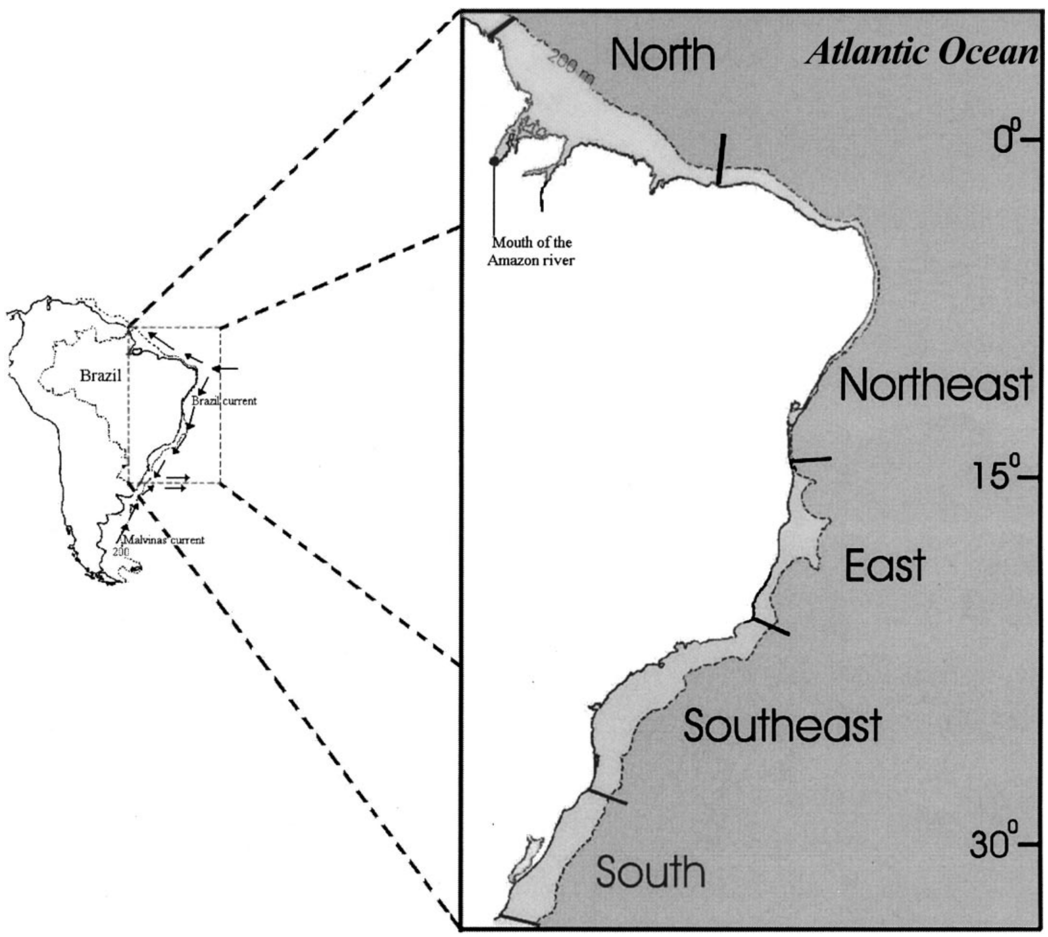

Fig. 1. Shelf regions of Brazil. Regions defined based on environmental characteristics and types of fishing activities, as suggested in Matsuura (1995).

the southeast, primary production is mainly driven by seasonal upwelling of nutrient-rich, cold subtropical waters pumped by alongshore winds and by cyclonic vortexes originated from the Brazil Current (Bakun and Parrish, 1990; Matsuura, 1995). The southern part of the Brazilian coast is under the influence of the subtropical convergence between the southward and northward flowing Brazil and Malvinas Currents. The confluence of water masses and the high volume of continental runoff provide physical and chemical conditions for high biological production on the shelf (Seeliger et al., 1997). Trawling is the main type of fishing activity in the south-eastern and southern regions, although the presence of highly abundant pelagic stocks, mainly sardine, in the southeast has also lead to the development of an important purse seine fishery especially since 1950.

The regions also differ in the type of fisheries production. While catches in the north, northeast and east regions are mainly from artisanal activities (Diegues, 1995), in the southern regions it is the industrial fisheries provide most of the landings, accounting for approximately half of the total Brazilian catches (IBAMA/IBGE, 1995). Historically, it was in the south and southeast that industrial fisheries were mostly developed through a series of government incentives, and this is where fisheries data are best documented.

This paper presents a comparative analysis of fisheries in the south-eastern and southern regions of Brazil which aims to assess the carrying capacity of the marine shelf ecosystems for harvestable species. Carrying capacity has been defined as the maximum size of a population or activity that could be indefinitely sustained without degrading the ecosystem's future productivity or suitability for that use (Odum, 1997). In the oceans, carrying capacity is usually referred to as the upper limit of biomass of organisms that can be supported by a set of primary production and food web structure (Christensen and Pauly, 1998). Fisheries yield is directly related to the carrying capacity of marine ecosystems, since there is a maximum sustainable rate of fish production associated with the total fish biomass at the carrying capacity. Fisheries can directly affect the carrying capacity of marine ecosystems by altering the structure of food webs and changing their potential productivity. Ecosystem carrying capacity is analyzed in three ways. First by computing the total flux of energy, originated from primary producers, available to different trophic levels in the food web, and the total primary production required to sustain fisheries catches (Pauly and Christensen, 1995). The ratio of these two quantities provides a measure of the "appropriated carrying capacity" (sensu Rees, 1996) of ecosystems, i.e. the amount of the available energy in an ecosystem already appropriated by fisheries catches. Second, we present a diagnosis of fisheries for the "fishing down the food web" phenomenon using trophic level estimates and national and regional catch statistics. Third, the impact of fisheries on the structure of an exploited ecosystems is evaluated by simulating the effect of a "fishing down the food web" scenario in the southern shelf region, where traditional demersal fish stocks are overexploited and the prospects for increasing yield rely on exploiting abundant small pelagic forage fish.

2. Methods

The method used here to quantify the appropriated carrying capacity follows the approach developed by Pauly and Christensen (1995) for the analysis of primary production required to sustain world fisheries. Primary production required by fisheries (PPR) is estimated based on the trophic level of the species caught, the energy transfer efficiency between trophic levels, and on the primary productivity of the two shelf regions (Table 1). Primary production estimates for the southeast and south were obtained from Brandini (1990) and Odebrecht and Garcia (1997), respectively. Species trophic levels (Table 2) were computed according to Odum and Heald (1975) using available information on diet composition, and from trophic models. In this analysis, primary producers are trophic level 1, and each higher order consumers are trophic level 1 plus the weighted average trophic level of its preys. Rocha et al. (1998) constructed a trophic model of the Ubatuba region in the south-eastern shelf that is here used to calculate the mean trophic transfer efficiency for the region. Mean trophic transfer efficiency for the southern shelf is calculated from the trophic model described below. In these models, transfer efficiencies are calculated as the percentage of throughput entering a trophic level that is subse-

Table 1
Area, primary productivity and total primary production of southern and south-eastern shelf regions of Brazil[a]

Region	Area ($\times 10^{10}$ m^2)	PP (gC m^{-2} per year)			Total PP (10^{12} gC per year)[b]
		Minimum	Likeliest	Maximum	
Southeast	17.14	33	84	158	14.40
South	11.40	72	160	382	18.25

[a] Shelf areas were measured to the 200 m depth line using planimetry.
[b] Based on the likeliest primary productivity.

Table 2
Trophic level of the main species landed in Brazil

Group	Species	Trophic level[a]
Shrimps	*Penaeus brasiliensis*	2.3
	Penaeus spp.	2.3
	Xiphopenaeus kroyeri	2.3
Lobsters	*Panulirus argus*	2.6
	Panulirus spp.	2.6
Small and mid-size pelagics	*Sardinella brasiliensis*[b]	2.8
	Engraulididae	3.0
	Scomber japonicus	3.1
	Scomberomorus spp.	3.3
Common squids	*Loligo* spp.	3.4
Miscellaneous marine fishes[c]	Osteichthyes	3.5
	Micropogonias furnieri[d,e]	3.4–3.5
	Umbrina canosai[f]	3.2
	Cynoscion spp.[g,h]	3.9–4.0
	Macrodon ancylodon[i]	4.3
	Trichiurus lepturus[j]	4.3
	Balistes capriscus[k]	3.4
	Pomatomus saltatrix[l]	4.2
	Pinguipes spp.[k]	3.8
	Ariidae[m]	3.8
	Mugilidae[k]	3.8
Sharks, rays and skates	Elasmobranchs[k,n]	3.4–3.8
Groupers	*Epinephelus* spp.	3.7
	Mycteroperca spp.	3.7
Snappers	Lutjanidae	3.8
	Ocyurus chrysurus	3.8
Common dolphinfish	*Coryphaena hippurus*	3.9
Skipjack tuna	*Katsuwonus pelamis*[o]	3.9
Tuna-like fishes[p,q,r]	*Thunnus alalunga*	3.9
	Thunnus albacares	3.9
	Thunnus atlanticus	3.9
	Thunnus obesus	3.9
	Thunnus thynnus	3.9
	Xiphias gladius	3.9
	Other Scombroidei	3.9

[a] Trophic level estimates are from the model in Fig. 2, from diet composition studies (references in table footnote), and/or from other published trophic models (Christensen and Pauly, 1993).
[b] Goitein (1983) and Gasalla and Oliveira (1997).
[c] Vazzoler et al. (2000).
[d] Gasalla (1995).
[e] Vazzoler (1975).
[f] Haimovici et al. (1989).
[g] Gasalla (1995).
[h] Vieira (1990).
[i] Juras and Yamaguti (1985).
[j] Martins and Haimovici (1997).
[k] Froese and Pauly (1998).
[l] Haimovici and Krug (1992).
[m] Araujo (1984).
[n] Soares et al. (1992).
[o] Vilela (1990).
[p] Zavala-Camin (1987).
[q] Vaske (1992).
[r] Vyalov and Ovchinnikov (1980).

quently passed on to the next trophic level or harvested. PPR estimates are based on a conversion factor of 0.06 g carbon=1 g wet weight of catches (Walsh, 1981) and on the mean transfer efficiency per trophic level, i.e.

$$\mathrm{PPR} = \mathrm{catches}\,\alpha^{(\mathrm{TL}-1)}$$

where $\alpha=\mathrm{TE}^{-1}$, and TE is the mean trophic transfer efficiency between consecutive trophic levels (TLs). PPR is commonly expressed as a percentage of the total primary production (%PP).

In order to account for uncertainties on parameter estimates, a Monte Carlo sampling procedure was designed to generate confidence intervals around the estimated PPR values. Two sources of uncertainties were considered: uncertainty on primary production, which was represented by triangular distributions defined by the most likely, minimum and maximum values in Table 1, and uncertainty on the species trophic level, which we considered to be within a 10% error around our estimates. Relatively small variations in the trophic level of an organism are expected from shifts in its diet following changes in prey abundance, but large variations will be generally limited by biological constraints imposed, for instance, by morphology (e.g. a piscivore will never succeed in filter-feeding on plankton).

Catch statistics obtained from Haimovici et al. (1997), Haimovici (1998) and from the Instituto de Pesca, São Paulo, and IBAMA/CEPSUL were used in the analysis of PPR between the two shelf regions. FAO catch statistics of reported Brazilian catches were used to compute the mean trophic level of landings in Brazil from 1950 to 1994.

We explored the ecosystem effects of ''fishing down the food web'' for anchovy in the southern shelf with a simplified mass-balance model (ECOPATH; Christensen and Pauly, 1992) of the trophic interactions in the pelagic ecosystem (Tables 3 and 4, Fig. 2). The model was constructed based on the pelagic species association described by Mello et al. (1992) for the winter and spring, and depicts anchovy as the dominant planktivorous fish species, being responsible for most of the transfer of energy from lower trophic levels to higher order consumers (Fig. 2). The system is defined by the coordinates 32–43°30′S and 51–54°W with a total area of 28 661 km^2.

Table 3
Parameters of the trophic model of the pelagic ecosystem off southern Brazil[a]

Species/group	TL	*B* (t km^{-2})	*P/B* (per year)	*Q/B* (per year)	EE	Yield (t km^{-2} per year)
Cutlassfish	4.25	0.240[b]	0.410[d]	2.050[e]	*0.852*	0.015[c]
Hake	4.11	*0.085*	0.355[d]	1.750[e]	0.950	0.004[c]
Sharks	3.94	*0.342*	0.400[f]	4.000[f]	0.950	0.130[c]
Other pelagics	4.02	*0.748*	0.570[f]	5.300[f]	0.950	0.405[g]
Weakfish	3.59	2.000[h]	0.480[d]	2.340[e]	*0.935*	0.306[c]
Mackerel	3.11	*1.329*	0.340[f]	2.710[e]	0.950	0.033[g]
Jack Mackerel	3.11	0.300[i]	0.350[i]	3.000[e]	*0.958*	0.054[g]
Anchovy	3.00	13.710[j]	1.290[k]	5.155[e]	*0.240*	–
Squids	3.32	0.200[l]	1.500[f]	3.230[f]	*0.894*	–
Marine shrimps	2.00	*0.298*	3.930[m]	19.130[f]	0.950	0.040[g]
Zooplankton	2.11	9.000[n]	64.920[n]	324.600	*0.619*	–
Phytoplankton	1.00	16.700[o]	100.000[o]	–	*0.965*	–
Detritus	1.00	150.000[p]	–	–	*1.148*	–

[a] Values in italic and trophic levels (TLs) were estimated by the model.
[b] Martins and Haimovici (1997).
[c] Haimovici (1998).
[d] Based on Peterson and Wroblewski (1984).
[e] Based on Palomares and Pauly (1989).
[f] Based on other trophic models (Christensen and Pauly, 1993).
[g] Haimovici et al. (1997).
[h] IBAMA (1993).
[i] Saccardo (1980).
[j] Lima and Castello (1995).
[k] Freire (unpublished).
[l] Haimovici (1997).
[m] D'Incao (1991).
[n] Resgalla Jr. (unpublished).
[o] Odebrecht and Garcia (1997).
[p] According to Pauly et al. (1993).

Table 4
Diet matrix of the model of the pelagic ecosystem off southern Brazil[a]

Prey/predator	1	2	3	4	5	6	7	8	9	10	11
1. Cutlassfish[b]	0.140	–	–	–	–	–	–	–	–	–	–
2. Hake[c]	0.020	0.100	–	–	–	–	–	–	–	–	–
3. Sharks[d]	–	–	–	–	–	–	–	–	–	–	–
4. Other pelagics[e]	–	–	–	–	–	–	–	–	–	–	–
5. Weakfish[e,f]	0.120	–	0.050	0.050	0.050	–	–	–	0.050	–	–
6. Mackerel[e]	–	–	–	0.100	–	–	–	–	–	–	–
7. Jack Mackerel[e]	0.030	0.030	0.020	–	–	–	–	–	–	–	–
8. Anchovy[g]	0.570	0.800	0.330	0.300	0.450	–	–	–	0.150	–	–
9. Squids[h]	0.050	0.030	0.030	0.050	–	–	–	–	–	–	–
10. Mar. shrimps[i]	0.010	–	0.070		0.200	0.010	–	–	–	–	–
11. Zooplankton	0.010	–	–	0.050	0.200	0.990	1.000	0.900	0.800	–	0.100
12. Phytoplankton	–	–	–	–	–	–	–	0.050	–	0.200	0.550
13. Detritus	–	–	–	–	–	–	–	0.050	–	0.800	0.350
Import	0.050	0.040	0.500	0.450	0.100	–	–	–	–	–	–

[a] Values represent the proportion of the diet of a predator (column) made of a given prey (row). Some of the groups (mainly sharks, weakfish, and other pelagics) have several feeding habitats such as the outer shelf and benthic habitats. For these groups an import was included as a ''prey'' in the diet composition.
[b] Martins (1992).
[c] Haimovici et al. (1993).
[d] Castello et al. (1997).
[e] Castello (1997).
[f] Vieira (1990).
[g] Schwingel and Castello (1995).
[h] Haimovici (1997).
[i] Based on other trophic models (Christensen and Pauly, 1993).

Trophic mass-balance models in ECOPATH rely on a system of linear equations which for any given group i can be represented for any time interval by

$$B_i\left(\frac{P}{B}\right)_i \mathrm{EE}_i - \sum_{j=1}^{n} B_j\left(\frac{Q}{B}\right)_j \mathrm{DC}_{ji} - (Y+\mathrm{EX})_i = \Delta B_i \quad (1)$$

where B_i is the biomass of i during the period in question, $(P/B)_i$ the production/biomass ratio, EE_i the ecotrophic efficiency, i.e. the fraction of the production of i that is consumed within the system or harvested, Y_i the yield (with $Y_i=F_iB_i$, and F as the fishing mortality), B_j the biomass of consumers or predators, $(Q/B)_i$ the food consumption per unit of biomass of j, and DC_{ji} the fraction of i in the diet of j. ΔB_i is the biomass accumulation rate per time in cases where the analysis does not use data from an initial equilibrium situation. ''Fishing down the food web'' was simulated by increasing fishing mortality F for anchovy from 0 to 1 per year, while maintaining F constant for other exploited groups. We used ECOSIM (Walters et al., 1997) to calculate the predicted changes in equilibrium biomasses of species/group and the total catch from the system over the range of F values for anchovy. The model provides biomass predictions of each group in the system as affected directly by fishing and predation, changes in food availability, and indirectly by fishing or predation on other groups in the system (Walters et al., 1997). Different hypotheses about ''top-down'' versus ''bottom-up'' control of trophic interactions were tested by setting the maximum instantaneous mortality rate that consumer j could ever exert on food resource i (see Walters et al., 1997). Setting low values (in our case four times the baseline mortality rate) lead to bottom-up control where prey availability governs the productivity of predators, while high values (20 times the baseline mortality rate) lead to top-down control where changes in the biomass of predators lead to cascade effects in the food web.

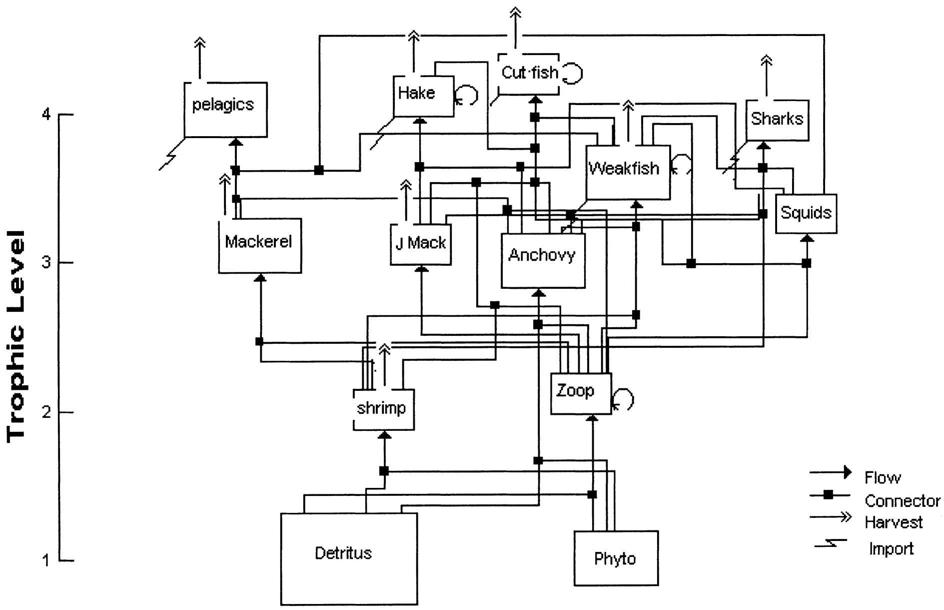

Fig. 2. Flowchart of trophic relationships in the pelagic association off southern Brazil. It describes the flows between groups (boxes), the biomass of each group (area of boxes proportional to the log of biomass), and the respective trophic levels. Only the consumption flows are shown. For full parameter descriptions, see Tables 3 and 4.

3. Results

3.1. PPR and trophic levels

PPR estimates by shelf region and species landed are shown in Tables 5–7. Fig. 3 shows the expected PPR when uncertainties on primary production and species trophic level are taken into account. Fisheries in southern Brazil already use a large proportion of the productive capacity of the shelf ecosystems. In the south, primary production required to sustain catches has changed little from the 1970s to the 1990s, being

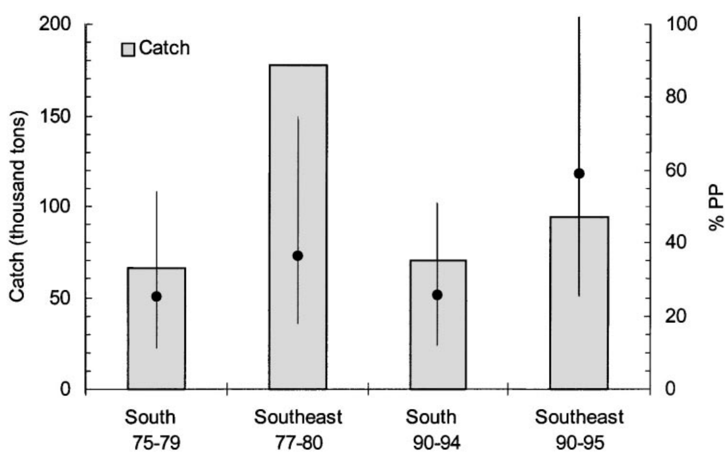

Fig. 3. Fisheries landings and PPR estimates for the south and southeast during two time periods. PPR is expressed as percentage of total primary production. The mean (dot) and 95% interval (line) of PPR estimates were obtained by resampling from the primary production and trophic level estimates.

Table 5
Trophic level, mean catch and PPR estimates for the southern shelf

Species	1975–1979			1990–1994	
	Trophic level	Catches (t)	PPR ($\times 10^{10}$ gC)	Catches (t)	PPR ($\times 10^{10}$ gC)
Micropogonias furnieri	3.5	14308	42.8	14709	44.1
Umbrina canosai	3.2	16900	26.2	9629	14.9
Cynoscion guatacupa	3.9	6439	66.5	8785	90.7
Macrodon ancylodon	4.3	7941	184.0	3966	91.9
Miscellaneous teleosteans[a]	3.5	4052	16.2	4143	14.2
Netuma spp.	3.8	3983	31.1	615	4.8
Trichiurus lepturus	4.3	75	1.8	441	11.0
Demersal sharks[b]	3.8	2584	17.4	5931	39.8
Rhinobatus horkelli	3.4	1010	2.95	460	1.3
Rays and skates	3.6	116	0.5	746	3.2
Marine shrimps	2.3	–	–	1148	0.2
Small and mid-size pelagics[c]	3.2	1549	1.4	3848	5.2
Pomatomus saltatrix	4.2	4290	89.8	3521	73.7
Mugil spp.	3.8	2081	14.7	1524	10.8
Katsuwonus pelamis	3.9	–	–	8088	71.8
Pelagic sharks	3.7	182	1.0	547	3.0
Tuna-like fishes	3.9	915	8.5	2402	22.4

[a] *Pogonias cromis*; *Merluccius hubbsi*; *Paralichthys* spp., *Pagrus pagrus*; *Prionotus punctatus*; *Urophycis brasiliensis* and *Poliprion americanus*.
[b] Mostly *Galeorhinus galeus*; *Mustelus schmitti* and *Squatina* spp.
[c] *Brevoortia pectinata*; *Scomber japonicus* and *Trachurus lathami*.

in the order of 27% of the total primary production. Little change is also observed in the mean trophic level of fisheries in the south which have been targeting mostly high-trophic level species (Tables 5 and 7). An increase in catches of tunas and sharks was observed in the southern shelf in the early 1990s accompanying the depletion of important demersal fish stocks, such as *Umbrina canosai*, *Macrodon ancylodon* and catfish species, *Netuma* spp. (Table 5). This alternation of species in the catches did not result in major changes in the PPR or in the mean trophic level of landings between the two periods.

Landings in the southeast are on the other hand dominated by low-trophic level species, sardine and marine shrimps being the most important stocks in terms of catch volume (Table 6). With the collapse of

Table 6
Trophic level, mean catch and PPR estimates for the south-eastern shelf

Species	Trophic level	1977–1980		1990–1995	
		Catches (t)	PPR ($\times 10^{10}$ gC)	PPR ($\times 10^{10}$ gC)	
Micropogonias furnieri	3.4	7126	63.9	4541	40.7
Macrodon ancylodon	3.7	2053	36.7	1870	33.4
Cynoscion jamaiscencis	4.0	1921	92.2	2245	107.7
Balistes capriscus	3.4	–	–	2144	19.8
Sardinella brasiliensis	2.8	146520	193.2	54414	71.7
Rays and skates	3.4			504	4.7
Marine shrimps	2.3	17371	5.1	13997	4.1
Sharks	3.8	517	12.8	2144	53.2
Katswonus pelamis	3.9	1380	47.6	7197	248.5
Tuna-like fishes	3.9	694	25.4	4771	174.9

Table 7
Summary statistics of the mean catch, mean trophic level (TL), mean transfer efficiency (TE), the primary production required by fisheries catches (PPR), and the percentage of the total primary production appropriated by fisheries (%PP) in the southern and south-eastern shelves

Region	Catch (t per year)	TL	TE (%)[a]	PPR ($\times 10^{10}$ gC per year)	%PP
Southern					
1975–1979	66425	3.6	8	505	27.7
1990–1994	70503	3.6		503	27.6
South-eastern					
1977–1980	177582	2.8	5	477	33.1
1990–1995	93826	3.1		758	52.7

[a] Transfer efficiencies are estimated from trophic models in Rocha et al. (1998) and from this paper.

the Brazilian sardine during the late 1980s and early 1990s, and the increase in tuna and sharks catches, there was an increase in the mean trophic level of fisheries from 2.8 to 3.1 (Table 7). Although catches were considerably lower in the latter period, the change in relative importance of the species landed resulted in an increase in PPR from 33.1 to 52.7% of the total shelf primary production. Note that PPR values as high as 100% are obtained for the south-eastern shelf depending on the input values for primary production and trophic level (Fig. 3). Higher PPR values in the southeast result from the combined effect of higher catches, lower primary productivity and lower trophic transfer efficiencies compared to the southern shelf (Table 7).

The increasing trend in the mean trophic level of catches is also observed in the FAO fisheries statistics for Brazil (Fig. 4). Fisheries in Brazil had a relatively constant mean trophic level of the species landed from 1950 to the early 1980s, but show a recent increase in mean trophic level caused by the combined effect of the collapse of small and mid-size pelagics (mostly sardine) and the increasing landings of large pelagic fishes (tunas and sharks) with the development of offshore fisheries.

3.2. Fishing down the food web

A strategy very often proposed to increase catches in exploited ecosystem is to fish down the food web for highly abundant, small pelagic planktivorous fishes, after larger species are depleted. Simulation results of fishing down food web scenario for anchovy in the southern shelf are shown in Figs. 5 and 6. Fig. 5 represents the predicted equilibrium yield and biomass of anchovy, and the percentage change in biomass of all other groups in the system under ''top-down'' and ''bottom-up'' control of trophic interactions. The model predicts considerably smaller yields and optimal fishing mortality rates for anchovy under top-down control (F_{msy} top-down $\sim$0.1 per year; F_{msy} bottom-up $\sim$0.3 per year). Both hypotheses generate a similar pattern of decrease in biomass of higher trophic level species, increase in biomass of mid-trophic level groups and increase in zooplankton biomass with increasing F for anchovy. Predictions of biomass changes at the mid-trophic level are more pronounced under top-down control, where the release in predation mortality due to the depressed biomass of top predators leads to a sharp increase of jack mackerel abundance.

Fig. 6a shows the changes in the total production (catches from all groups) at trophic level with increasing equilibrium fishing mortality for anchovy. Fishing down the food web has the effect of increasing yield up to a threshold fishing mortality rate for anchovy F_{msy} beyond which fisheries production become gradually impaired by overfishing and by divergence or complete interruption of major energy pathways to the higher trophic levels. With the overfishing of anchovy, total catches decrease and the mean trophic level of catches increases (lesser low-trophic level species in the catches). The backward bending curve between the mean trophic level of catches and total catch suggests that production at trophic level becomes considerably smaller when anchovy is overfished, i.e. the system is unable to capitalize the energy previously available for fisheries and other organisms at the higher trophic

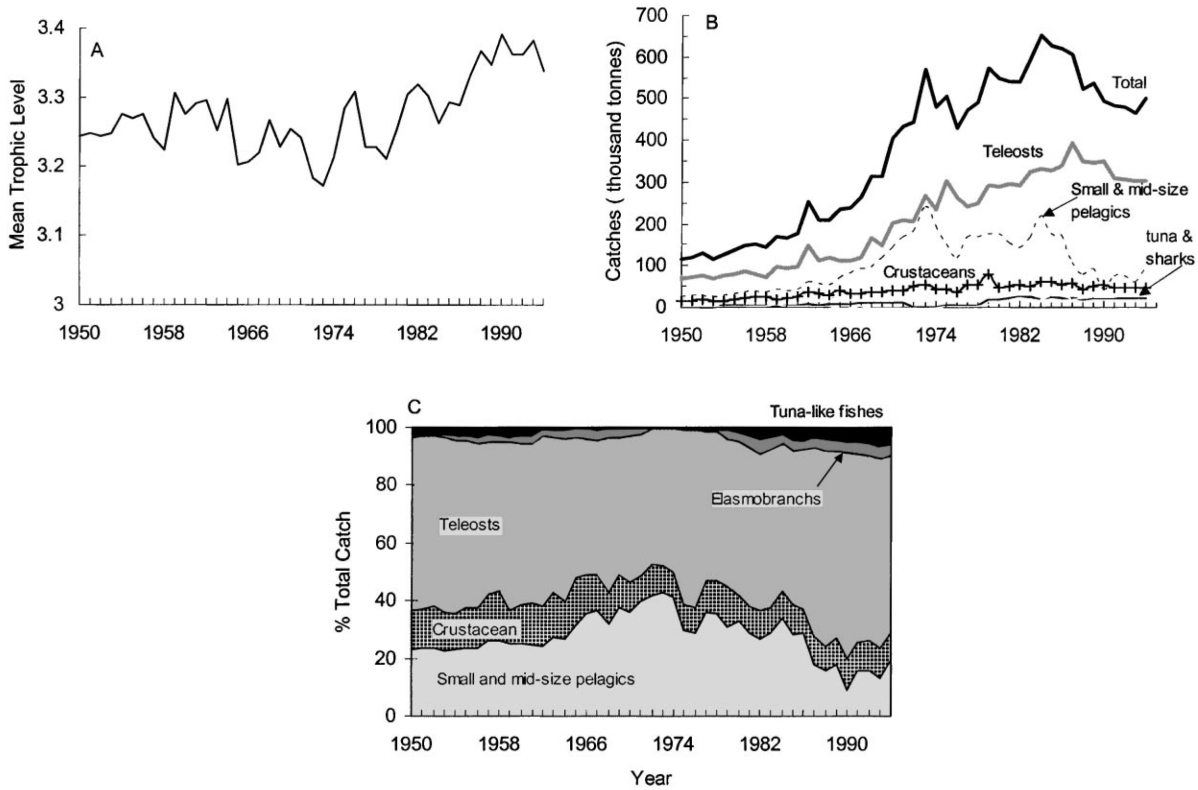

Fig. 4. Mean trophic level (A), and species composition (B and C) of total Brazilian landings (source: FAO).

levels. The depressed abundance and productivity of top predators in turn impede the complete recovery of the mean trophic level of catches, which become composed mainly by mid-trophic level groups also targeted by fisheries. Parallel changes occur in the mean trophic level of the system (Fig. 6b). The mean trophic level of the system is smaller than that of fisheries catches (due to the contribution of zooplankton and phytoplankton), and shows a progressive decrease with the increase in anchovy exploitation. With "bottom-up" control, total system production at the end of the simulation is smaller than that originally obtained before fishing down the food web. These generic effects are attenuated under "top-down" control when the model predicts that total catch may remain high after anchovy depletion as a result of the sharp increase in abundance of other mid-trophic level species (e.g. Jack Mackerel, Fig. 5) also targeted by fisheries.

4. Discussion

The primary production required to sustain marine capture fisheries in southern Brazil is estimated to vary between 27 and 53% of the total shelf primary production. Results indicate a level of fisheries impact in this portion of the Brazilian coast comparable to the most intensively exploited temperate shelf ecosystems of the world (Pauly and Christensen, 1995), where fisheries utilize up to one-third of the primary production. Fisheries in the upwelling ecosystem of the south-eastern shelf appropriate a larger proportion of the primary production than in the southern shelf due to the combined effect of higher catches, lower primary productivity and lower trophic transfer efficiencies. Upwelling ecosystems are considered relatively inefficient in transferring energy up the food web. Trophic transfer efficiencies of ca. 5% were estimated by Jarre-Teichman and Christensen

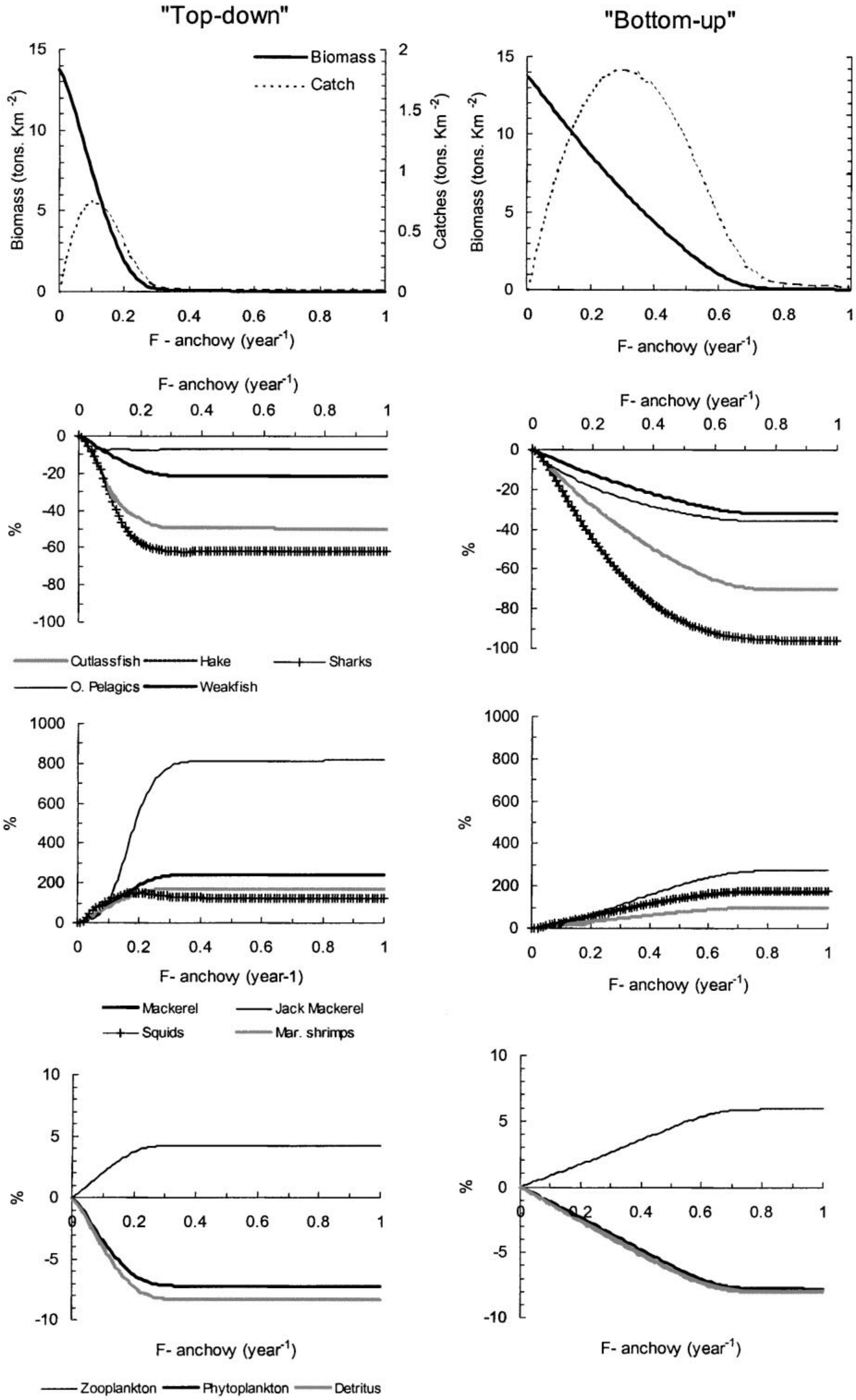

Fig. 5. Equilibrium simulation of increasing fishing mortality for anchovy. Upper panel represents the predicted equilibrium yield and absolute biomass of anchovy. Lower panels show the predicted relative change in biomass of all other groups in the system.

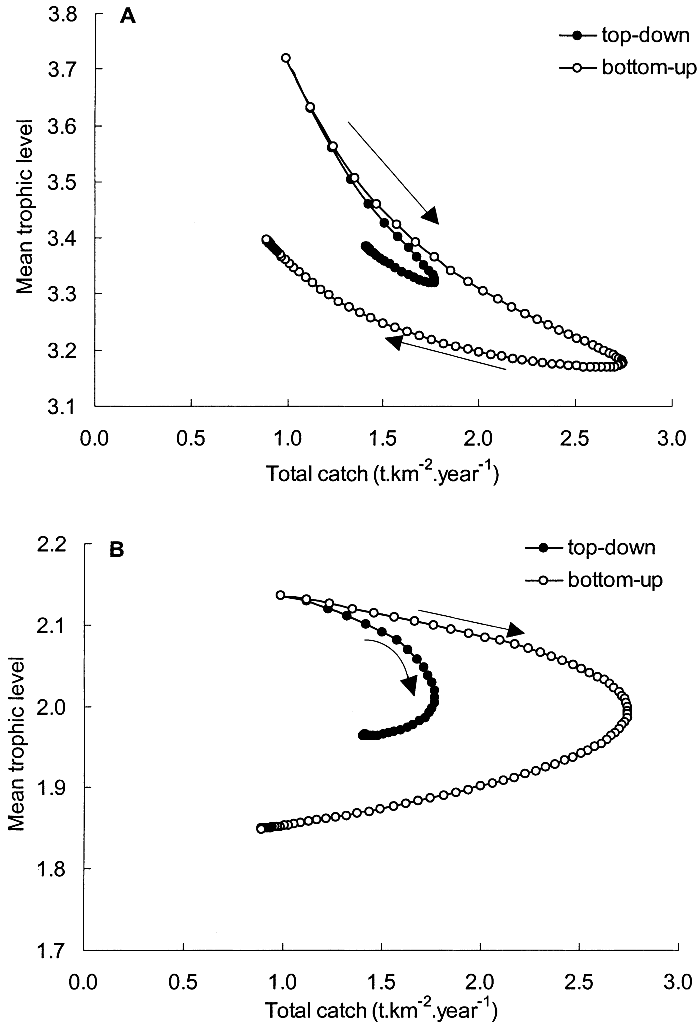

Fig. 6. Relationship between (A) total catch from the system and the mean trophic level of catches, and (B) total catch and the mean trophic level of the system (detritus excluded) with increasing fishing mortality for anchovy. The arrows indicate the direction of increase in *F*, and the dots correspond to 0.01 increments in fishing mortality (from 0 to 1 per year).

(1998) for four major upwelling ecosystems, which are lower than the mean of ca. 10% computed across different types of aquatic ecosystems (Pauly and Christensen, 1995). Their energetic inefficiency seems to be related to the characteristics of primary productivity and food web organization. The high and variable new primary production characteristic of upwelling systems yields a higher export of carbon compared to more stable and less productive systems, where most of the primary production is regenerated (Berger et al., 1989).

Our PPR estimates may be conservative considering that discards were not included in the calculations, and that part of the catches may remain unreported in official fisheries statistics (Gasalla and Tomás, 1998). Both unreported catches and discards can cause the underestimation of the footprint of fisheries, and bias the estimated mean trophic level of landings. Haimovici et al. (1997) suggested that discards might represent ca. 25% of total annual catches in the southern shelf. Including discards in our estimates for this region, with the same mean trophic level of the species landed, raises the expected PPR for the early 1990s from 503×10^{10} to 611×10^{10} gC per year and from 27.6 to 33.5% of the total primary production. The high PPR values in the southern shelf corroborate the fact that most commercially important estuarine, coastal, and shelf stocks are either fully or over-exploited in the region, and landings are expect to decrease with current fishing pressure (Haimovici et al., 1997). The prospect of increasing catches in the region has to come from two non-exclusive strategies: (i) by better utilizing or recovering stocks which are currently overfished, such as most demersal stocks (Table 5), and/or (ii) by ''fishing down the food web'' for alternative resources not yet utilized, mostly anchovy and jack mackerel (Haimovici et al., 1997).

Fishing down the food web has been shown to increase catches up to threshold fishing intensity beyond which fisheries production may become impaired by shifts in major energy pathways in the system (Fig. 6). Can this type of fisheries-induced change in the ecosystem happen? Fishing down the food web is not an observed phenomenon in Brazil. Instead, fisheries have been targeting high-trophic level species, with the exception of sardine in the southeast, and show a recent increasing trend due to the development of offshore fisheries for high-trophic level species such as tunas and pelagic sharks. This increasing trend of mean trophic level of fish landings was also obtained by Pauly et al. (1998) for the Southwest Atlantic, and attributed to the development of new fisheries, which, according to the authors, tend to mask the fishing down the food web phenomenon. In Brazil, both national and regional data indicate that although fisheries expanded into areas/stocks not previously exploited there is no underlying downward trend in the mean trophic level of catches.

Regional experience with intensive fishing for a forage species in south-eastern Brazil has shifted a system that once supported a large fishery for sardine to one occupied by an abundant population of anchovy, *Engraulis anchoita*, that is not commercially harvested (Castello et al., 1991). Nonetheless, the extent to which the collapse of the sardine fishery and the switch to an anchovy-dominated system was due to human or natural factors is still inconclusive (Rossi-Wongtschowski et al., 1996). Many marine ecosystems underwent major ''regime shifts'' or changes in species composition and production rates apparently triggered by environmental factors but intensified by the effect of fisheries (Steele, 1996). Among the most documented examples are the sardine/anchovy switches in coastal upwelling systems (Lluch-Belda et al., 1989), the gadoid outbursts in the North Sea (Cushing, 1980; Daan, 1980), and the decline of marine mammals and outburst of pollock in the Bering Sea (Trites et al., 1999). On the other hand, recent global assessments of the trophic level of marine fisheries (Pauly et al., 1998) provide evidence of the fishing down food web phenomenon and of associated fisheries-induced changes in the food webs similar to that predicted in Fig. 6.

Much scientific debate on the causes of shifts in species compositions in many marine ecosystems has been focusing on a ''bottom-up'' perspective in which the effect of physical forcing, mediated through climatic–oceanographic processes, leads to changes in primary production and reproductive success of fish populations which in turn will trigger changes up in the food web (Beamish, 1995; Bakun, 1996). An alternative ''top-down'' perspective, mostly applied in the study of lakes, asserts that predation affects directly and indirectly the structure of populations and communities, and production processes at all trophic levels in the food web (Kitchell et al., 1994). Model simulations allowed us to explore the effects of both assumptions in predicting the changes in the food web accompanying the exploitation of anchovy. Under top-down control, the system responded with a marked increase in the biomass of a competitor species due to cascade effects in the food web. This pattern was not observed under bottom-up control, when competitions for food resources were limiting interactions. These results, also obtained by Mackinson et al. (1997) for other ecosystems, differ from the early emphasis placed on food competition as the driving force of species replacement (Cushing, 1980; Daan, 1980), but reinforce the potential role of predation mechanisms and trophic cascades effects in shaping the dynamics of mid-trophic level, forage species. The predicted F_{msy} values for anchovy were also very sensitive to the type of control of trophic interactions. Bottom-up control generally produces a catch curve that achieves an asymptote at higher F_s, predicting that the stock can sustain much higher fishing pressure before it begins to decline. This occurs because under bottom-up control, predation mortality rate ($M_{ij}=Q_{ij}/B_i$) tends to remain more stable, while the consumption rate (Q_i/B_i) of anchovy increases more, due to donor control of total food eaten, making it more productive per biomass. Strong predation control prevents higher yields under top-down control. These results, so far impossible to predict with single-species approaches, offer warning to novice users of multi-species approaches regarding model sensitivity to trophic control assumptions (Mackinson et al., 1997; Walters et al., 1997). The model offers the possibility to test other complementary hypothesis to the classic top-down and bottom-up controls, such as the ''wasp waist'' control suggested by Rice (1995) to represent ecosystems regulated up and down from the middle usually occupied by small pelagic fish. For the hypotheses tested in this paper, the model predicted optimal fishing mortality rates for anchovy close to the range of sustainable F_s for small pelagic stocks observed by Patterson (1992).

This paper confirms that fisheries in southern Brazil already utilize a large proportion of the marine shelf ecosystem carrying capacity. In line with recent stock assessment reports, this indicates that the prospect of increasing catches and recovering the status of fisheries activities must rely on better management of the stocks currently overfished, and those offshore resources currently moderately exploited (as reported in IBAMA, 1994b; Matsuura, 1995), and/or fishing down the food web for abundant short-lived, planktivorous fishes. It is showed, however, that in an intensively exploited ecosystem the proposal for increasing fisheries production by harvesting at lower levels in the food web has the potential risk of aggravating the depletion of high-trophic level species besides altering the structure of the ecosystem, and thus must be approached with caution. The adoption of precautionary measures and ecosystem principles in fisheries policy decisions has been, at least theoretically, common in fisheries literature and government agendas worldwide (see FAO Code of Conduct for Responsible Fisheries, Oceans Act Canada; GESPE, 1997). One such principle states that ''regulation of the use of living resources must be based on understanding the structure and dynamics of the ecosystem of which the resource is a part and must take into account the ecological (...) influences that directly and indirectly affect resource use'' (Mangel et al., 1996). If ecosystem principles and precautionary measures are to be effectively implemented, managers and decision makers have to take the possibility of such ecosystem impacts of fishing down the food web into account when designing policies for the exploitation of marine resources.

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