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Trophic models of São Sebastião Channel and continental shelf systems, SE Brazil

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Abstract. Two trophic models of the São Sebastião ecosystems were built to evaluate differences in their size and organization. The study area is located on the southeastern coast of Brazil. The trophic groups of the systems were based on ecologically or taxonomically related species, considering their relative abundance and similarity of diets and habits. The models, based on the Ecopath software, consist of six fish groups, ten invertebrate groups, Bacterioplankton, Phytoplankton, Zooplankton, and Detritus. Biomass, production, and consumption were estimated for the Inner shelf and the Channel. Primary production was estimated as 2,436 g wet weight m^{-2} $year^{-1}$ on the inner shelf and 1,441 g WW in the channel. Total benthic production was 215.8 and 418.1 g $WW.m^{-2}.yr^{-1}$ on the inner shelf and the channel, respectively. Total fish production plus Cephalopoda was 4.9 g $WW.m^{-2}.year^{-1}$ in the inner shelf and 11.5 g in the channel. Total system throughput was 8161 g $WW.m^{-2}.year^{-1}$ in the inner shelf and 11442 g in the channel. The Channel ecosystem was slightly larger in total biomass, development capacity, cycling, and total throughput. Nevertheless, primary production, and total net primary production showed higher values in the inner shelf ecosystem. In contrast to other shelf systems, detritus pathways are more important than flows originating from phytoplankton, mainly in the Channel ecosystem.

Key words: marine, ecosystem structure, Ecopath, sub-tropical, Brazil.

Resumo. Modelo trófico dos sistemas do Canal de São Sebastião e plataforma continental, SE Brasil. Foram construídos dois modelos de interações tróficas dos ecossistemas de plataforma continental interna e Canal de São Sebastião para avaliar seu tamanho e estrutura. A área de estudo está localizada na costa sudeste do Brasil. Foi utilizado o software Ecopath para construção dos modelos. Com base na similaridade das dietas e hábitos foram estabelecidos seis compartimentos de peixes, dez de invertebrados e um de cada dos seguintes grupos: Bacterioplâncton, Fitoplâncton, Zooplâncton e Detritos. Foram estimados biomassa, produção e consumo. A produção primária foi estimada em 2436 g peso úmido m^{-2} ano^{-1} na plataforma interna e 1441 g no canal. A produção bentônica total foi de 215,8 g m^{-2} ano^{-1} e 418,1 g respectivamente na plataforma e canal. A produção total de peixes mais Cephalopoda foi de 4,9 $g.m^{-2}.ano^{-1}$ na plataforma e 11,5 g no canal. A Transferência total do sistema foi 8161 $g.m^{-2}.ano^{-1}$ na plataforma e 11442 g no canal. O ecossistema do Canal apresentou maiores valores de biomassa total, capacidade de desenvolvimento e transferência total. Apenas a produção primária e a produção primária total líquida atingiram valores mais altos na plataforma interna. Ao contrário de outros sistemas de plataforma, a importância dos fluxos via detrito é maior que a dos fluxos via fitoplâncton, principalmente no ecossistema do Canal.

Palavras-chave: marinho, estrutura do ecossistema, Ecopath, subtropical, Brasil.

Introduction

The yield obtained from any fishing grounds depends ultimately on the amount of solar energy stored by phytoplankton as organic carbon and the efficiency of transfer of this energy through the ecosystem to fish and eventually mankind. Biological productivity varies spatially as well as temporally at all trophic levels of the ecosystem, yet some geographic areas are consistently productive and others are not. Persistent biological and physical characteristics of the ecosystem (i.e. ecosystem structure) determine long-term average productivity.

Fishing activities have altered the marine ecosystem both directly and indirectly, especially in coastal regions where fishing and other anthropogenic perturbations are most intense (Jackson *et al*. 2001). Indirect effects of fishing may have more important impacts on marine ecosystem structure and dynamics than do removals of the fish themselves. Fishing also changes the trophic composition of fish communities, for example, by selectively harvesting predators. Pauly *et al.* (1998) found that the mean trophic level of the species group reported in FAO Global Fisheries Statistics declined from 1950 to 1994, reflecting a gradual transition in landings from long-lived, high-trophic-level, piscivorous demersal fish toward short-lived, low-trophic-level invertebrates and planktivorous pelagic fish. Fishing at lower trophic levels leads at first to increasing catches, then to stagnating or declining catches, indicating that present exploitation patterns are unsustainable.

In the discussion above it is assumed that ecosystem approaches are needed for existing fisheries. However, the changing nature of fisheries is such that many of the traditional single-species fisheries are in the process of changing towards multi-species fisheries, which again emphasises our need to understand the ecosystems before the stocks are over-exploited, as has been the traditional approach in many cases. Fishery scientists have not traditionally taken an ecosystem approach to management, due to the complexity of marine ecosystems and the sampling difficulty. Only recently, concepts of food webs, species richness and diversity have been considered to fisheries management (Botsford *et al.* 1997, Fogarty & Murawski 1998). Network analysis provides tools for bringing these and many other concepts together by depicting ecosystems as a number of compartments interconnected by flows of energy or matter. The compartments may be species or functional groups such as detritivores, young fish, benthos, etc. The analysis depends upon the structure of flows among the system components and their magnitude. The flows are rates per unit of time and may vary greatly at a small scale, but at the ecosystem level are more usually measured on a seasonal or annual time scale. According to Mann *et al*. (1989), network analysis contains a lot of information about the dynamic structure of a whole system and its functions.

So far only few and rather preliminary attempts to carry out ecosystem management have been conducted in Brazil. Contributions to this objective were the studies from Gasalla (2004) and Freire (2005) for South-eastern and North-eastern Brazilian coast, respectively.

Oceanographic and biological studies have been developed in the north area of São Paulo State, mainly on phytoplankton and benthic groups. Fisheries in the area are basically artisanal, in contrast to the central area of the State, where an industrial fishery already gives signal of overexploitation (Dias Neto & Dornelles 1996, Vasconcellos & Gasalla 2001, D'Incao *et al.* 2002). It is therefore of interest to produce a summary of the trophic interactions in the north coast that might be used to further comparison with the central area of the State. This paper is concerned with the structure and size of the São Sebastião Channel and Inner Continental Shelf ecosystems, as a baseline for studying the effects of fishing on the ecosystem structure.

Material and Methods

The study area is located on the continental shelf off São Sebastião (23°30'- 24°30'S and 44°45'- 46°00'W), in south-eastern Brazilian Bight. The area comprises the Channel (CSS) and the Inner shelf of São Sebastião (Fig. 1). The CSS is 24 km long and is 5.8 km and 6.4 wide on its northern and southern entrance, respectively, with an area of 150 km^2. Mean depth is 28 m at the northern entrance and 20 m at the southern entrance (Furtado 1995). An area of 1800 km^2 of the inner shelf was considered and included waters from 10 m to 50 m deep.

Three water masses occur in the area: Coastal Water (CW), characterized by high temperature (> 25°C) and low salinity (< 34); Tropical Water (TW) with high salinity (> 36) and high temperature (> 20°C); and South Atlantic Central Water (SACW) with low temperature (< 20°C) and salinity higher than 35 (Castro & Miranda 1998). During the summer, nutrient-rich SACW moves onshore and is often found in the central and outer portions of the continental shelf (20-100 m), while CW is found in a narrow band inshore. These water movements result in a vertical stratification over the inner shelf, with a

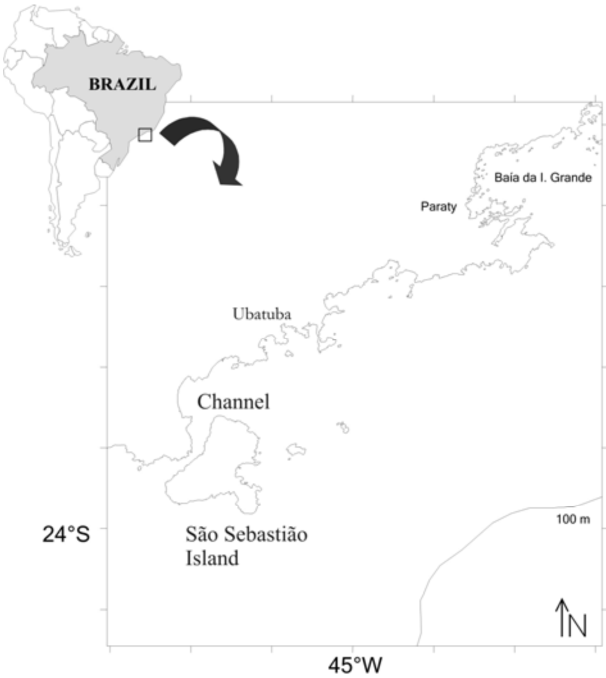

Figure 1. Study area off São Sebastião continental shelf and Channel, SE Brazil.

strong thermocline at middle depths. In the winter, when SACW is restricted to the outer shelf, horizontal and vertical thermal gradients are reduced and almost no stratification is observed on the inner shelf (Castro Filho *et al*. 1987).

The trophic structure of two ecosystems, Channel and Inner shelf of São Sebastião, is analysed by applying the ECOPATH software (Christensen & Pauly 1992). It combines an approach by Polovina (1984) for estimating the biomass and food consumption of various elements of an aquatic ecosystem with Ulanowicz's (1986) analysis of flows among these elements. A trophic flow budget is constructed creating a balance for each component in the model over a given period of time. The compartment balance is based on the Winberg's equation (Winberg 1956):

Consumption (Q) = Production (P) + Respiration (R) + Unassimilated food (U)

The core routine of ECOPATH basically consists of a set of simultaneous linear equations, one for each group "i" in the system:

$$P_i – B_i . M2_i – P_i (1 – EE_i) – EX_i = 0 \quad (1)$$

where: P_i = production of (i) (g m^{-2} yr^{-1}); B_i = biomass of (i) (g m^{-2}); $M2_i$ = predation mortality of (i) (yr^{-1}); EE_i = Ecotrophic Efficiency of (i) (fraction of 1); 1 - EE_i = other sources of mortality (yr^{-1}); EX_i = export of (i) (g m^{-2} yr^{-1}).

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

$$(B_i . M2_i) = \sum_j B_j . Q/B_j . DC_{ji} \quad (2)$$

where: Q/B_i = consumption per biomass ratio of the predator (i) (yr^{-1}) and DC_{ij} = fraction of the prey (i) in the average diet of predator (j).

Thus, equation (1) can be re-expressed as:

$$B_i . P/B_i . EE_i - \sum_j B_j . Q/B_j . DC_{ji} - EX_i = 0 \quad (3)$$

Three of the four parameters B, P/B, Q/B and EE have to be set initially for each group. The remaining parameter is computed by the software.

The trophic compartments of the system are based on ecologically and taxonomically related species, considering their relative abundance and similarity of diet and habits. The compartments were: Detritus, Phytoplankton, Bacterioplankton, Zooplankton, Cnidaria, Mollusca (detritivorous Gastropoda and Bivalvia), Carnivorous Benthos, Detritivorous Polychaetes, Other Detritivorous Benthos, Penaeidea-Caridea, Brachyura-Anomura, Echinodermata, Cephalopoda, Benthic-feeding Fishes, Pelagic-feeding Fishes, Piscivorous Rays, Other Rays, Piscivorous Fishes, and Pelagic Fishes for the Channel and Inner Shelf of São Sebastião systems. A Polyplacophora compartment was also considered for the Channel.

Data used to construct the models came from a variety of sources including direct measurements, literature values from other shelf systems, and assumptions considering a total energy balance. Field data were mainly obtained under the project "Oceanography of the Inner Shelf of São Sebastião (OPISS)" in the beginning of the 1990's. Sampling techniques are described in Gianesella-Galvão *et al*. (1997), Pires-Vanin *et al*. (1997) and Rossi-Wongtschowski *et al*. (1997). Biomass and flow rates are in units of g $WW.m^{-2}$ and g $WW.m^{-2}.year^{-1}$, respectively.

Data of Phytoplankton biomass and primary production off São Sebastião (Saldanha-Corrêa & Gianesella IN PRESS) were converted to wet weight considering 0.06 g C = 1 g wet weight (Walsh 1981). As data of biomass and production of bacteria and zooplankton were not available for the area, minimal biomass values were estimated by the

Ecopath program and P/B values were attributed based on data of the Ubatuba ecosystem (Rocha *et al*. 2003).

For benthic invertebrates and demersal fishes, data were obtained primarily from studies carried out in Ubatuba and São Sebastião ecosystems, showed in Pires-Vanin (IN PRESS) and Soares *et al*. (IN PRESS). Unpublished data were also considered, as well as diets from other areas when local information was not available. Production of the benthic compartments was estimated from their P/B values, calculated using the empirical relationship proposed by Brey (1999). Because of the lack of P/B estimates for Cnidaria and Polyplacophora, data cited by Opitz (1991) were used. All the planktonic and benthic consumption estimates were based on gross efficiency ratios (production per consumption). A value of 0.50 was used for bacterioplankton and of 0.25 for zooplankton (Valiela 1995). For the benthic groups, we used gross efficiencies of 0.09 for herbivores and 0.30 for carnivores, following the empirical relationship found by Brey (1999). An intermediate value of 0.15 was assumed for omnivores.

Godinho-Peria (1995) and Santos (1998) estimated production per biomass ratios (P/B) for some key fish species in the area. Mortality rates from literature were also used. Consumption/biomass ratios (Q/B) for teleost fish species were calculated using the empirical formula of Palomares and Pauly (1989). Daily rations for rays were obtained from the literature (Berestovskiy 1989).

In both Channel and shelf models, crustacean biomass could not sustain the high predation pressure from different groups. Considering the small size and the high mobility of these organisms, a loss of biomass probably occurred during handling of samples or due to the kind of the sampler. In order to account for the demand by predators, new values were estimated using ecotrophic efficiency equal to 0.95 for Penaeidea-Caridea and Other Detritivorous Benthos. Production and consumption from the latter were also altered to sustain consumption from other compartments.

After balancing the model, a number of statistics that summarize food webs were obtained. The total system throughput (TST) is defined as the sum of all flows in the system. The ratio of total system biomass by TST is directly proportional to system maturity where estimate value tends to be low during the ecosystem development phase and increases as a function of maturity (Christensen 1995). Ascendency (A) is a measure of the average mutual information, that is, the uncertainty of the path that a particle of biomass or energy will follow in the system, weighed by TST. Ascendency is a measure of system growth and development of network links. The upper limit of ascendancy is developmental capacity (DC) (Ulanowicz 1986). The ratio between DC and TST measures the system diversity of flows (Wulff & Ulanowicz 1989). The system omnivory index, which is the average of all consumers weighed by the logarithm of each consumer's food intake, and the connectance index, which is the number of actual trophic links in relation to the number of possible links, measure the distribution of feeding interactions among trophic levels and characterize the extent to which a system displays web-like features (Gardner & Ashby 1970). Average path length corresponds to the mean number of trophic links in each trophic pathway, while cycling corresponds to the fraction of TST that was actually recycled, as expressed by the Finn cycling index (Finn 1976).

Results

The input values and estimated parameters of the balanced models are given in Table I. Diet composition matrixes used for the model in Channel and Inner shelf are respectively given in Tables II a and b.

Flows originating from detritus were more important than flows originating from phytoplankton, both in the Inner Shelf (0.53) and Channel (0.72). In both systems, the greatest flows were from phytoplankton to zooplankton and from detritus to Detritivorous Polychaetes, Echinodermata, and Other Detritivorous Benthos (Fig. 2a, 2b). The amount of detritus in the São Sebastião inner shelf does not seem to be limiting (EE = 63 %), in contrast to the Channel, where it was necessary to import detritus to supply detritivores consumption.

Zooplankton faecal pellets, dead zooplankton and phytoplankton, and nekton carcasses all contribute to the supply of food to the benthos. Benthic detritus feeders were extremely important in terms of biomass, followed by carnivorous benthos. Benthic compartments were low trophic-level consumers, between 2.0 (detritivores) and 2.6 (omnivores, carnivores) (Fig. 2a, b). Therefore these values indicate that a substantial part of the diet of benthic predators consists of producing-level compartments, i.e., Phytoplankton and Detritus. Brachyura-Anomura occupied a slightly higher level (~3), similar to the Pelagic Fishes. Other Rays and Benthic Feeding Fishes showed intermediate trophic levels (3.5). Groups consuming a high proportion of fish were treated as top predators, with trophic levels near or above 4.0 (Cephalopoda and some demersal fishes). Nonetheless, top predators such as tunas, and sharks were not included due to the lack of local information.

Mixed trophic impacts are given in Fig. 3a and 3b in Channel and Inner shelf respectively. The impact may be direct or indirect. As a prey, a group causes a positive impact on others. As a direct predator, the impact is negative. Phytoplankton, Zooplankton and Detritus had a positive impact on most other groups. The impact was higher for their direct consumers, such as Pelagic Fishes on Zooplankton or Bacterioplankton on Detritus. Negative impacts were due to zooplankton as a consumer of phytoplankton and bacteria) or as a competitor for the same food source. Benthic Feeding Fishes were indirectly impacted by Detritus. Pelagic Fishes had only a small indirect impact, via Detritus, Bacterioplankton, and Zooplankton. The competition between Bacterioplankton and Benthic Detritivores must be regarded as an artefact of the model construction, as only one single detritus group was included in this model. Detritivorous Benthos had a positive impact as prey on Carnivorous Benthos and Benthic Feeding Fishes.

Prey groups had a different degree of importance for different fish consumers. Polychaetes (detritivores and carnivores), Other Detritivorous Benthos, and Echinoderms were very important in the system, both as prey and as predators. Brachyura-Anomura was a key consumer, impacting many compartments. Piscivorous Rays and Other Rays, although important predators, were little consumed in the system. It should be noted, however, that top predators not included in these models could prey on them.

Ecosystem statistics are shown in Table III. The Channel ecosystem was slightly larger than the inner shelf ecosystem in total biomass, development capacity, cycling, and total throughput. The inner shelf ecosystem showed higher values of primary production and total net primary production. It might be considered that both systems are not very large in size, but are relatively well organized.

Table I. Biomass (B, g.m^{-2}), production per biomass (P/B, year^{-1}) and consumption per biomass (Q/B, year^{-1}) for the compartments in the São Sebastião inner shelf and Channel. Values between parentheses were estimated by the program. In case of adjustment, initial values were placed below each new value.

	Inner shelf				Channel			
	B	**P/B**		**Q/B**	**B**	**P/B**		**Q/B**
Phytoplankton	16.170	152.80			9.430	152.80		
Zooplankton	(7.159)	40.00	&	160.0	(7.351)	40.00	&	160.0
Bacterioplankton	(0.386)	250.00	&	500.0	(1.168)	250.00	&	500.0
Cnidaria	0.251	1.00	*	3.3	0.511	1.00	*	3.3
Detritivorous Polychaeta	11.266	6.32		70.2	36.997	4.87		54.1
Mollusca	3.283	5.29		58.8	13.101	2.92		32.4
Carnivorous Benthos	2.093	6.63		22.1	8.064	5.59		18.6
Polyplacophora					0.922	0.42	*	2.8
Penaeidea-Caridea	0.578	4.99		33.3	1.483	3.62		24.1
	0.343				1.241			
Brachyura-Anomura	0.984	4.42		14.7	5.742	3.33		11.1
Other Detritivorous Benthos	7.916	7.86		87.3	15.281	5.59		62.1
	6.842							
Echinodermata	28.390	1.58		17.6	34.870	1.28		14.2
Cephalopoda	(0.852)	3.00		10.0	(1.041)	3.00		10.0
Benthic-feeding fish	1.351	0.96		3.8	2.540	0.96		3.8
Pelagic-feeding fish	0.304	1.30		5.2	0.099	1.50		6.0
Piscivorous fish	0.254	0.94		3.8	0.063	1.09		4.4
Piscivorous rays	0.322	0.54		5.4	0.400	0.54		5.4
Other rays	0.049	0.54		5.4	0.049	0.54		5.4
Pelagic fish	2.035	2.50		12.5	2.206	2.50		12.5

* cited in Opitz (1991) & attributed

Table II a. Diet composition matrix in percentage of volume of prey groups in São Sebastião Channel.

	Prey/Predator	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**
1	Phytoplankton	0.900				0.200						0.050	0.050						0.100
2	Zooplankton	0.010		0.340		0.300	0.100			0.200		0.050	0.120						0.900
3	Bacterioplankton	0.090			0.050							0.070	0.010						
4	Cnidaria							0.001						0.004			0.001		
5	Detritivorous Polychaeta			0.005				0.150		0.100	0.030		0.060	0.190	0.001	0.004	0.009	0.135	
6	Mollusca			0.005				0.050			0.070		0.010	0.001					
7	Cephalopoda						0.070				0.030			0.030	0.110		0.002		
8	Carnivorous Benthos							0.064			0.075								
9	Polyplacophora																		
10	Peneidea+Caridea			0.020			0.050				0.015			0.300	0.003	0.244	0.200	0.326	
11	Brachyura-Anomura						0.180				0.120			0.160		0.001	0.673	0.061	
12	Other Detritivorous Benthos			0.150			0.150	0.100		0.200	0.100	0.030	0.050	0.050	0.006	0.036	0.055	0.376	
13	Echinodermata			0.030				0.085		0.030	0.100			0.110					
14	Benthic-feeding fish										0.010			0.150	0.120		0.060	0.102	
15	Piscivorous fish														0.200				
16	Pelagic-feeding fish													0.005	0.080				
17	Piscivorous rays																		
18	Other rays																		
19	Pelagic fish						0.450								0.480	0.715			
20	Detritus		1.000	0.450	0.950	0.500		0.550	1.000	0.470	0.450	0.800	0.700						

Table II b. Diet composition matrix in percentage of volume of prey groups in São Sebastião Inner Shelf.

	Prey/Predator	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**
1	Phytoplankton	0.900				0.200					0.050	0.060						0.100
2	Zooplankton	0.050		0.340		0.300	0.100		0.200		0.100	0.120						0.900
3	Bacterioplankton	0.050									0.050							
4	Cnidaria							0.005					0.001			0.001		
5	Detritivorous Polychaeta			0.005				0.150	0.100	0.030		0.060	0.500	0.001		0.009	0.135	
6	Mollusca			0.005				0.050		0.070								
7	Cephalopoda						0.100			0.100			0.005	0.100		0.002		
8	Carnivorous Benthos							0.040		0.050		0.010						
9	Peneidea-Caridea			0.020			0.120			0.050			0.090	0.003	0.047	0.200	0.326	
10	Brachyura-Anomura						0.150			0.050			0.060		0.003	0.673	0.061	
11	Other Detritivorous Benthos			0.150			0.150	0.120	0.200	0.100	0.030	0.050	0.150	0.07	0.020	0.055	0.376	
12	Echinodermata			0.030				0.085	0.030	0.100			0.140					
13	Benthic-feeding fish									0.050			0.054	0.140		0.060	0.102	
14	Piscivorous fish													0.230				
15	Pelagic-feeding fish						0.030							0.055				
16	Piscivorous rays																	
17	Other rays																	
18	Pelagic fish						0.350							0.400	0.930			
19	Detritus		1.000	0.450	1.000	0.500		0.550	0.470	0.400	0.770	0.700						

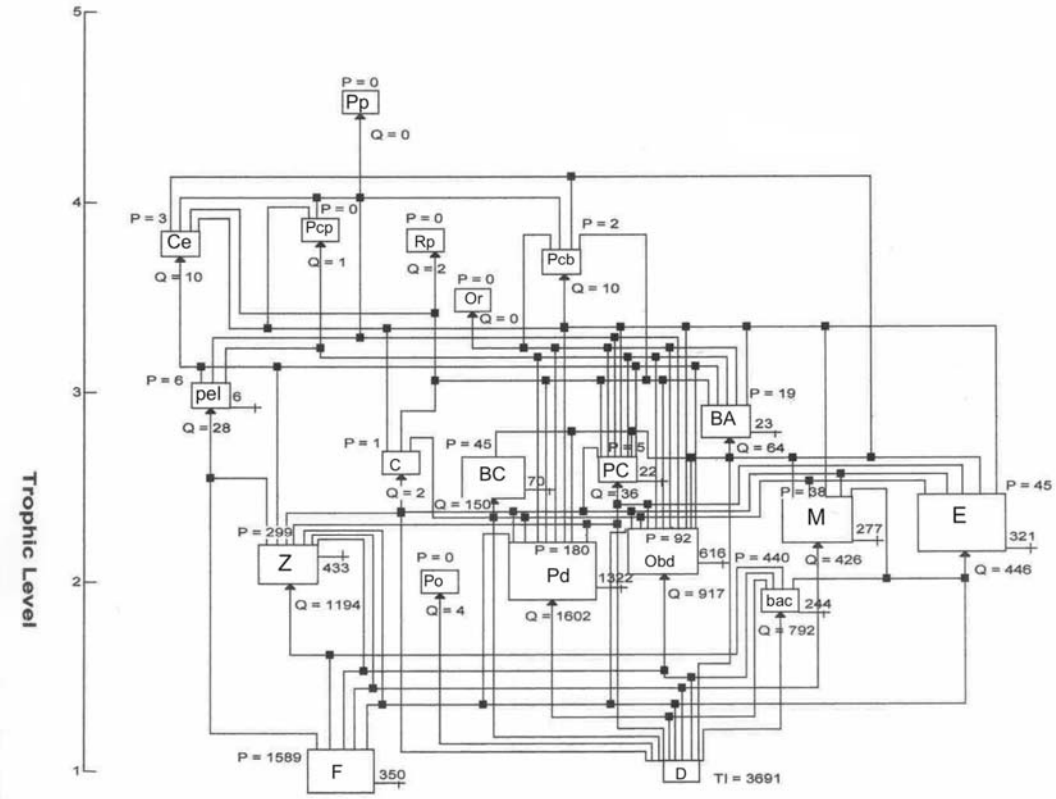

Figure 2a. Flow diagram (g ww. m^{-2}. year^{-1}) in the Channel of São Sebastião. Vertical axis indicates trophic level, which is defined as one for primary producers and detritus, and one plus the average trophic level of preys in case of consumers. The size of the compartment is proportional to the biomass (g ww. m^{-2}) of the group showed. Q = consumption. P = production. Phytoplankton (F), Zooplankton (Z), Bacterioplankton (Bac), Cnidaria (C), Polyplacophora (P), Cephalopoda (Ce), Mollusca (M), Carnivorous Benthos (BC), Detritivorous Polychaeta (Pd), Other Detritivorous Benthos (Obd), Penaeidea-Caridea (PC), Brachyura-Anomura (BA), Echinodermata (E), Benthic-feeding Fish (Pcb), Pelagic-feeding Fish (Pcp), Piscivorous Rays (R), Other Rays (Or), Piscivorous Fish (Pp), Pelagic Fish (Pel) and Detritus (D).

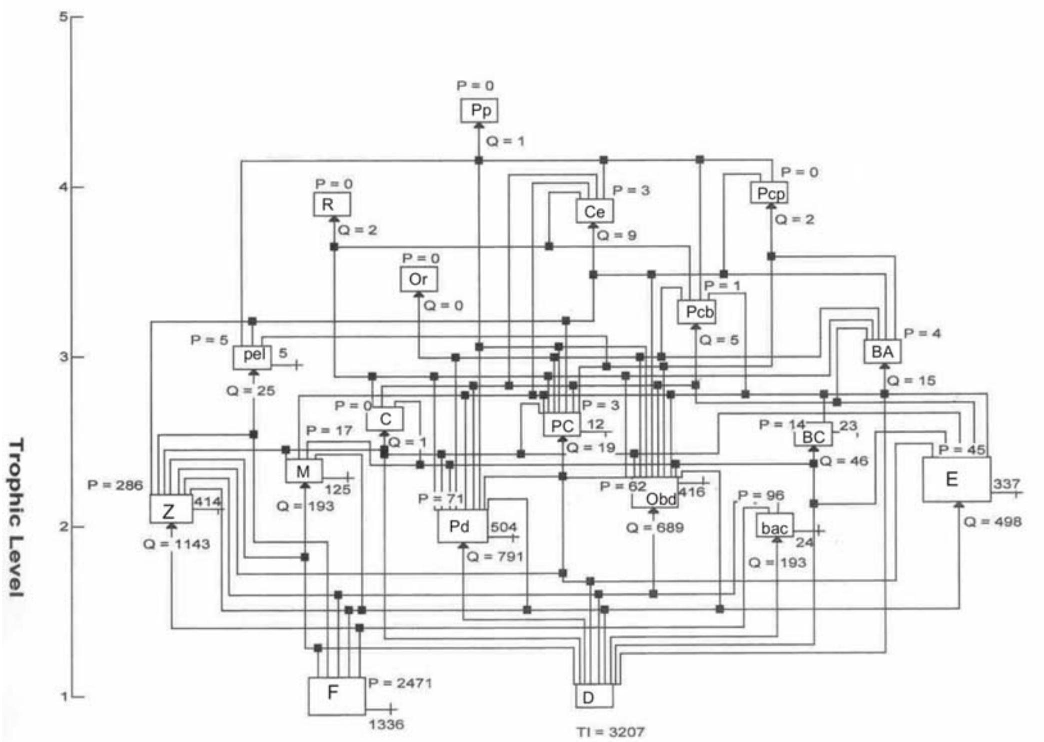

Figure 2b. Flow diagram (g ww. m^{-2}. year^{-1}) in the São Sebastião inner shelf. Vertical axis indicates trophic level, which is defined as one for primary producers and detritus, and one plus the average trophic level of preys in case of consumers. The size of the compartment is proportional to the biomass (g ww. m^{-2}) of the group showed. Q = consumption. P = production. Phytoplankton (F), Zooplankton (Z), Bacterioplankton (Bac), Cnidaria (C), Cephalopoda (Ce), Mollusca (M), Carnivorous Benthos (BC), Detritivorous Polychaeta (Pd), Other Detritivorous Benthos (Obd), Penaeidea-Caridea (PC), Brachyura-Anomura (BA), Echinodermata (E), Benthic-feeding Fish (Pcb), Pelagic-feeding Fish (Pcp), Piscivorous Rays (R), Other Rays (Or), Piscivorous Fish (Pp), Pelagic Fish (Pel) and Detritus (D).

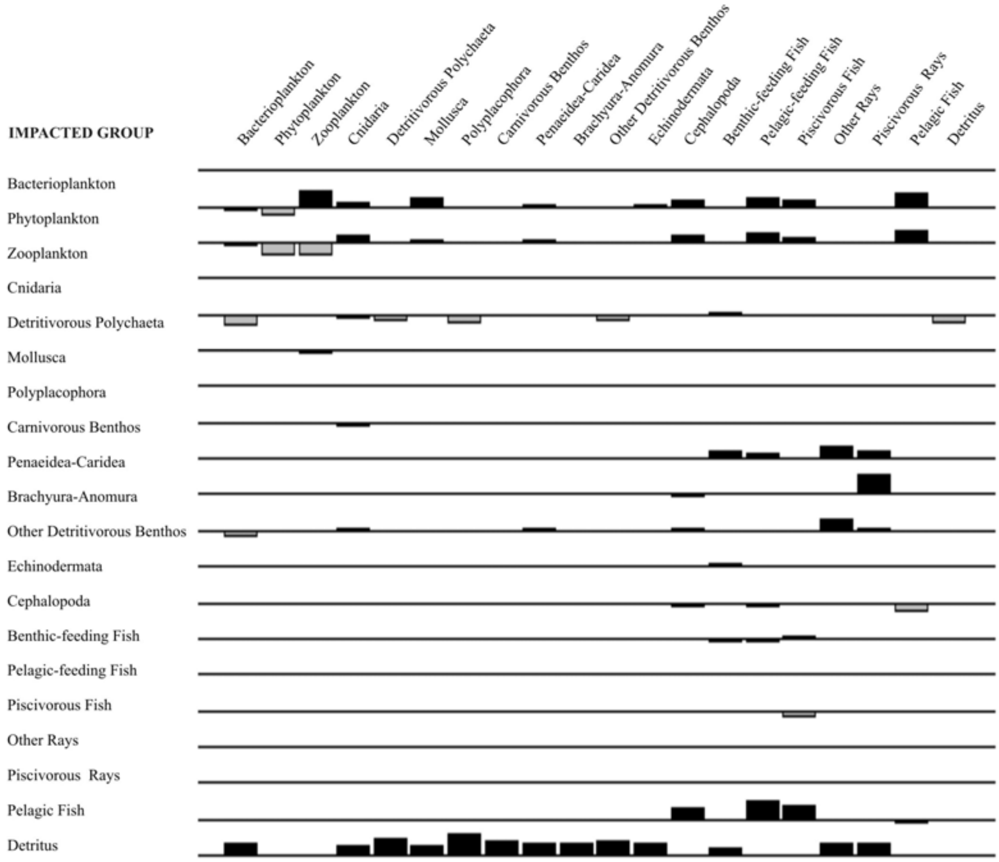

Figure 3a. Direct and indirect impacts that an increase in the biomass of groups on the left of the histograms would have on groups positioned above them in São Sebastião Channel. Bars pointing upwards show positive impacts while those pointing downwards show negative impacts. Impacts are relative, but comparable between histograms.

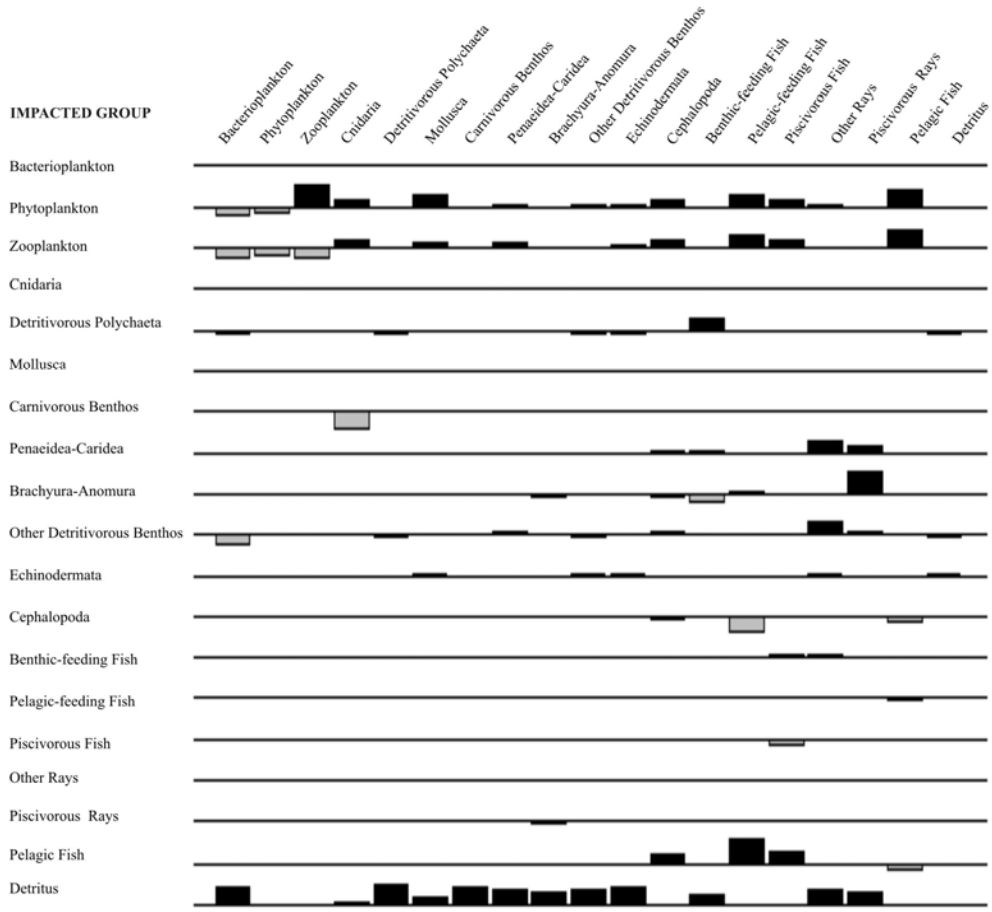

Figure 3b. Direct and indirect impacts that an increase in the biomass of groups on the left of the histograms would have on groups positioned above them in São Sebastião inner shelf. Bars pointing upwards show positive impacts while those pointing downwards show negative impacts. Impacts are relative, but comparable between histograms.

Table III. Ecosystem Statistics from São Sebastião ecosystems. Flows are in g Wet Weight.m^{-2}.year (= ton WW.km^{-2}.year).

	Channel	Inner shelf
Number of compartments	20	19
Sum of all consumption	5910	3632
Sum of all exports		
Sum of all respiratory flows	2203	1322
Sum of all flows into detritus	3329	3207
Total System Throughput	11442	8161
Sum of all production	2445	3080
Calculated total net primary production	1582	2519
Total primary production / Total biomass	11.2	30.1
Primary production / Total respiration	0.7	1.9
Net system production	-621	1197
Total Biomass	141	84
Respiration/Biomass	16	16
Connectance index	0.26	0.28
Omnivory index	0.21	0.21
Diversity of flows	4.68	4.32
Development Capacity	53500	35239
Ascendency %	25.4	23.2
Finn cycling index %	30.1	25.8

Discussion

Solar radiation and detritus are the main production sources of São Sebastião systems. Flows from detritus to consumers were a little more important than flows originating from phytoplankton, mainly in the Channel, but not as important as in the SW Gulf of Mexico, where trophic flows originating from detritus were 2.5 times higher than flows from primary producers (Manickchand-Heileman *et al*. 1998). In the Ubatuba Shelf ecosystem, in the SE Brazilian Bight, flows originating from phytoplankton were higher in summer (0.59), due to the presence of salps, great phytoplankton consumers, while flows from detritus were higher in winter (0.58) (Rocha 1998).

In summer (rainy season), the productivity of the Ubatuba continental shelf is mainly associated with the presence of the South Atlantic Central Water (SACW) which transports cold, nutrient-rich water onto the shelf (Aidar *et al*. 1993). Higher inputs of suspended matter, sediment, and organic matter of continental origin, are some of the other factors that contribute to increasing the productivity off Ubatuba during this season (Mahiques 1995). Even with this large input of nutrients, the primary production is not high.

The primary production in the São Sebastião inner shelf value (148 gC.m^{-2}.yr^{-1}) was lower than the values estimated for the adjacent Ubatuba shelf (266 gC.m^{-2}.yr^{-1}), and the Brazilian province (302 gC.m^{-2}.yr^{-1}), and was much lower than the "coastal domain" and upwelling provinces (~400 gC.m^{-2}.yr^{-1}), systems with the highest primary productions estimated by Longhurst *et al*. (1995).

Although the study area is dominated by "new" production in summer, flows originating from detritus were very important (> 50 %). The Finn cycling index was relatively high (> 25 %) in both São Sebastião ecosystems, and similar to the values of 11 to 37 % for reef (Opitz 1991, Telles 1998), and other shelf systems, such as Chesapeake Bay (Baird & Ulanowicz 1989), Weddell Sea (Jarre-Teichmann *et al*. 1997), and Gulf of Mexico (Manickchand-Heileman *et al*. 1998).

Detritus utilisation and cycling increase as systems mature (Odum 1969) so the ecosystems studied here may be well-established. Cycling is mainly a function of the degree of detritivory and zero-order cycles (cannibalism) in a system, and both are difficult to quantify (Christensen & Pauly 1993). Although the consumption of detritus was not directly quantified in São Sebastião systems, a great biomass of detritivores observed both in the inner shelf and channel is indicative of its importance. In some coastal areas, factors such as high sedimentation rates, re-suspension, terrestrial input, and input from macroalgal or kelp beds have been reported as relevant for the benthic food supply. The detritus imported to balance the Channel model could have come from seagrasses not considered as a compartment in the model or from the run-off. C/N stable isotope ratios suggested that Ophiuroidea feed on detritus of seagrasses in the Ubatuba coastal area (Matsuura & Wada 1994). A C/N ratio study on the origin of the sedimentary organic matter in some bays off Ubatuba showed areas with a predominance of terrestrial contribution and other areas with the main input from pelagic sources (Mahiques 1995).

System structure might be characterised by many aspects, including size, estimated by total biomass, total throughput, and development capacity. In São Sebastião, all these parameters showed higher values than those observed in temperate shelf systems, such as Weddell Sea (Jarre-Teichmann *et al*. 1997), and in tropical shelves, such as the Venezuelan shelf (Mendoza 1993). On the other hand, the values were lower than those observed in estuaries, such as Chesapeake Bay (Baird & Ulanowicz 1989), and coral reefs (Opitz 1991, Telles 1998).

Ascendency values observed in São Sebastião (23 and 25 %) might be considered low. Ascendencies of 55.6 and 49.5 % were reported to Baltic Sea and Chesapeake Bay, respectively (Wulff & Ulanowicz 1989) and of 34 and 45 % to coral reefs (Polovina & Ow 1983, Opitz 1991, Telles 1998), and Gulf of Paria continental shelf (Manickchand-Heileman *et al*., 2004).

The average path lengths (APL) observed in São Sebastião were high (> 4). Values between 3.3 and 3.6 are reported for Weddell Sea, Baltic Sea, and Chesapeake Bay (Wulff & Ulanowicz 1989, Jarre-Teichmann *et al*. 1997). Of the 41 models compared by Christensen & Pauly (1993), average path lengths rarely were longer than 4. On the other hand, values higher than 6.0 have been observed in continental shelves, such as Gulf of Mexico, and Gulf of Paria (Manickchand-Heileman *et al*. 1998, Manickchand-Heileman *et al*. 2004). According to Christensen & Pauly (1993), oceanic, upwelling, and coral reef systems show shorter APL than estuaries and shelves.

A reference framework for fisheries management based on an index for the percentage of primary production required to sustain fisheries (%PPR) and the average trophic level of the catch (TLc) was developed by Tudela *et al*. 2005. According to them, sustained fished ecosystems involved a TLc > 3.0 and a low to moderate % PPR. For the Ubatuba shelf ecosystem, catches with a TLc of 4.0 requiring a PPR of only 0.1 % were reported by Rocha (1998), based on data obtained in the 1980's. The author herself considered the data might have been underestimated. Even so, it could indicate a sustained fishing condition, in contrast to TLc between 2.8 and 3.6 and % PPR higher than 27.6 reported for south-eastern and southern shelf of Brazil (Vasconcellos & Gasalla 2001). For tropical shelves with a primary production of 310 $gC.m^{-2}.yr^{-1}$ (similar to São Sebastião shelf), Tudela *et al*. (2005) suggest a value of 1.46 $t.km^{-2}.yr^{-1}$ as ecosystem-based maximum sustainable catches.

Sustainability is further identified as the primary objective of ecosystem management. Specification of exploitation levels might consider natural ecosystem variations in establishing management strategies designed to conserve biomass, avoid disruption of fundamental food web structure, and protect critical habitat. The present model gives only one preliminary representation of the trophic interactions in the São Sebastião systems. The limited availability of parameter estimates of the main invertebrate and fish groups reflects a need for process-oriented studies aimed at producing such estimates. Valuable ecological work is conducted, but more studies focused on production aspects and energy flows between the important invertebrate groups and to their predators are called for. Such a development should address the increasing need for management of marine ecosystems so that not just the fishing industry interests, but also environmental concern, are taken into account. It is hoped that studies such as presented here may help to support this development.

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