

Description of the East Brazil Large Marine Ecosystem using a trophic model

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SUMMARY: The objective of this study was to describe the marine ecosystem off northeastern Brazil. A trophic model was constructed for the 1970s using Ecopath with Ecosim. The impact of most of the forty-one functional groups was modest, probably due to the highly reticulated diet matrix. However, seagrass and macroalgae exerted a strong positive impact on manatee and herbivorous reef fishes, respectively. A high negative impact of omnivorous reef fishes on spiny lobsters and of sharks on swordfish was observed. Spiny lobsters and swordfish had the largest biomass changes for the simulation period (1978-2000); tunas, other large pelagics and sharks showed intermediate rates of biomass decline; and a slight increase in biomass was observed for toothed cetaceans, large carnivorous reef fishes, and dolphinfish. Recycling was an important feature of this ecosystem with low phytoplankton-originated primary production. The mean transfer efficiency between trophic levels was 11.4%. The gross efficiency of the fisheries was very low (0.00002), probably due to the low exploitation rate of most of the resources in the 1970s. Basic local information was missing for many groups. When information gaps are filled, this model may serve more credibly for the exploration of fishing policies for this area within an ecosystem approach.

Keywords: modelling, ecosystem, fishery, South-western Atlantic, Brazil, northeastern Brazil.

RESUMEN: DESCRIPCIÓN DEL GRAN ECOSISTEMA MARINO DEL NORESTE DE BRASIL USANDO UN MODELO TRÓFICO. – El objetivo de este estudio fue describir el ecosistema marino del noreste de Brasil. Se construyó un modelo trófico para representar la década de los 70 usando el modelo Ecopath con Ecosim. El impacto de la mayor parte de los 41 grupos funcionales fue pequeño, probablemente debido a lo intrincado de la matriz trófica. No obstante, las fanerógamas marinas y las macroalgas tuvieron un fuerte impacto positivo sobre los manatíes y los peces arrecifales herbívoros, respectivamente. Los peces arrecifales omnívoros tuvieron un impacto negativo sobre las langostas espinosas, y los tiburones sobre el pez espada. Las langostas espinosas y el pez espada presentaron los mayores cambios de biomasa durante el período de simulación (1978-2000); las biomasa de atunes, otros grandes pelágicos y tiburones sufrieron disminuciones en ese período; se observó un ligero aumento en la biomasa de los odontocetos, de los grandes peces arrecifales carnívoros y de la lamprea. El reciclaje de materia orgánica por parte del fitoplancton fue importante en este ecosistema con baja productividad primaria. La eficiencia de transferencia media entre los niveles tróficos fue de 11.4%. La eficiencia bruta de la pesca fue muy baja (0.00002), probablemente debido a la baja tasa de explotación de la mayor parte de los recursos pesqueros en la década de los 70. No fue posible obtener las informaciones básicas locales para muchos grupos. Se estima que cuando se generen y estén disponibles más datos específicos locales, el modelo aquí elaborado puede ser mejor usado para el análisis de políticas pesqueras para esta área con una aproximación ecosistémica.

Palabras clave: modelaje, ecosistema, pesquería, Atlántico sudoeste, Brasil, Brasil noreste.

INTRODUCTION

Ecosystem models are representations of complex systems that attempt to depict their main com-

ponents and the interrelations among these components. These representations, which can be physical, verbal, graphical or mathematical, reflect the interest of the modeller, if only because of their partial char-

acter (Haddon, 2001). For this study, the long-term interest is the exploration of the effect of fisheries on the major functional groups of the marine ecosystem off northeastern Brazil.

Modelling requires the proper definition of the ecosystem to be studied. This is a difficult task, particularly in the marine realm, due to the absence of fixed boundaries. Longhurst (1998) proposed a hierarchical classification for the oceans, in which the most general levels are the biomes, subdivided into fifty-seven provinces. One of these provinces is the Guianas Coastal Province. However, this province encompasses two sub-regions that are influenced very differently by the Amazon River. Matsuura (1995), more appropriately, proposed the division of the Brazilian coast into five sub-regions. The northeast sub-region, the object of this study, is characterised by rocky substrates and low primary production due to the influence of the warm North Brazil and Brazil currents. This sub-region corresponds to the East Brazil Large Marine Ecosystem (LME) (Sherman *et al.*, 2007). LMEs have been proposed as a conceptual framework for ocean management (Sherman, 1993) and their use should facilitate the comparison of the results obtained here with the ones obtained in other studies.

Many models have been built to describe marine ecosystems around the world (see e.g. contributions in Christensen and Pauly, 1993). In Brazil, Rocha *et al.* (1998), Vasconcellos (2000), Vasconcellos and Gasalla (2001), Gasalla and Rossi-Wongtschowski (2004), and Velasco and Castello (2005) modelled the southeastern and southern regions. Two other areas were also modelled in terms of trophic interactions: one to the north of the area modelled here (Wolff *et al.*, 2000), and one to the south (Telles, 1998). The present study aims to describe the marine ecosystem off northeastern Brazil, representing the East Brazil LME, and will allow for the comparison with other previously modelled regions. The resulting model may serve for the exploration of policy options for the fishery sector in northeastern Brazil.

MATERIAL AND METHODS

Study area

The total area modelled here encompasses 1075000 km² and corresponds to the Exclusive Economic Zone (EEZ) off northeastern Brazil (Fig. 1;

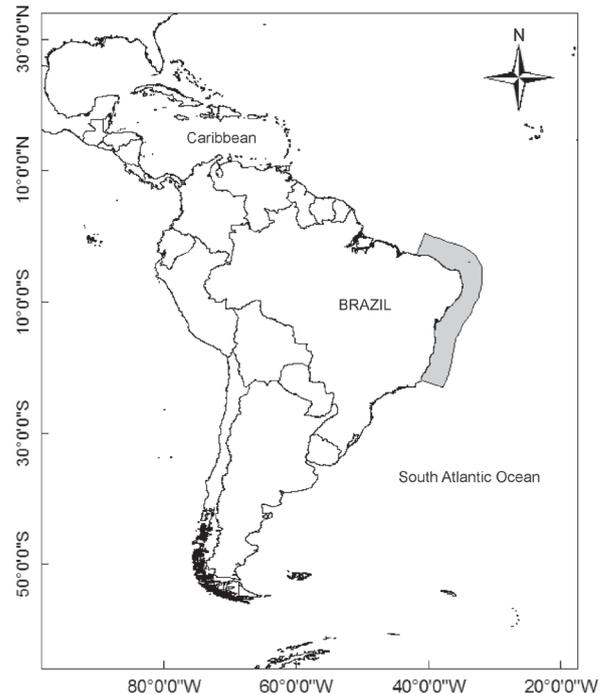


FIG. 1. – Location of the East Brazil Large Marine Ecosystem (gray) along the Brazilian coast.

East Brazil – LME 16). The shelf is mostly narrow (down to 20 km), but reaches up to 220 km at the southernmost part (Ekau and Knoppers, 1999). A total of 1200 km² of coral reefs are found in this region (Spalding *et al.*, 2001). Creed (2003) estimates that Brazil has a seagrass coverage of 200 km², 70–80% of which is located in the northeastern region (Joel Creed, Lab. Benthic Marine Ecology, Rio de Janeiro, pers. comm.).

Mass balance model

A trophic model was constructed for the East Brazil LME for the 1970s using Ecopath with Ecosim (EwE version 5.1; www.ecopath.org; Polovina, 1984; Christensen *et al.*, 2005; Christensen and Walters, 2004). Forty-one functional groups were used to describe the area (Table 1), and these were chosen based on the distribution area, maximum body size, trophic level, and consumption rates of each species. This division was intended to encompass all exploited groups for a posterior analysis of the effect of fisheries on population trends. Groups were kept generic to include all catches that are recorded by common name and each group includes various species. One group (dolphinfish *Coryphaena hippurus*) was split into stanzas (juveniles and adults) to properly represent its complex trophic ontogeny (Christensen

TABLE 1. – Basic input for the 1970s Ecopath with Ecosim model for the marine ecosystem off northeastern Brazil. B = biomass in the habitat area (wet weight); P/B = production/biomass; Q/B = consumption/biomass; and EE = ecotrophic efficiency^a. Only significant digits are presented.

| Group name | B (tonnes·km ⁻²) | P/B (year ⁻¹) | Q/B (year ⁻¹) | EE | Catches (tonnes·km ⁻²) |
|-----------------------------------|---------------------------------|------------------------------|------------------------------|---------|---------------------------------------|
| 1. Manatee | 0.00 | 0.06 | 27.38 | 0.00 | 0 |
| 2. Baleen whales | 0.39 | 0.03 | 4.62 | 0.30 | 0.003130 |
| 3. Toothed cetaceans | 0.14 | 0.08 | 10.85 | 0.50 | 0.000307 |
| 4. Seabirds | 0.02 | 5.40 | 80.00 | (0.38) | 0 |
| 5. Sea turtles | 0.16 | 0.15 | 22.00 | 0.50 | 0.000006 |
| 6. Tunas | 0.04 | 0.82 | 8.00 | 0.99 | 0.003420 |
| 7. Other large pelagics | 0.03 | 0.64 | 9.60 | 0.72 | 0.005786 |
| 8. Dolphinfish | 0.00 | 4.36 | 20.44 | (0.43) | 0.000872 |
| 9. Dolphinfish juveniles | 0.00 | 13.08 | 59.21 | (0.31) | 0 |
| 10. Swordfish | 0.01 | 0.29 | 4.00 | 0.99 | 0.000190 |
| 11. Sharks | (0.03) | 0.27 | 4.00 | 0.60 | 0.004471 |
| 12. Rays | (0.10) | 0.50 | 3.50 | 0.41 | 0.001871 |
| 13. Small pelagics | (0.60) | 4.41 | 12.45 | 0.99 | 0.004061 |
| 14. Needlefishes | (0.12) | 5.42 | 18.95 | 0.99 | 0.000656 |
| 15. Southern red snapper | 0.01 | 0.73 | 5.30 | (0.90) | 0.005490 |
| 16. Large carnivorous reef fishes | (0.24) | 0.37 | 6.34 | 0.81 | 0.015600 |
| 17. Small carnivorous reef fishes | (0.97) | 1.57 | 9.22 | 0.86 | 0.002100 |
| 18. Herbivorous reef fishes | (1.12) | 0.55 | 23.13 | 0.39 | 0.000052 |
| 19. Omnivorous reef fishes | (1.14) | 0.44 | 10.57 | 0.95 | 0.005680 |
| 20. Demersal fishes | (1.35) | 1.93 | 10.27 | 0.95 | 0.041052 |
| 21. Mulletts | (0.76) | 1.03 | 22.60 | 0.86 | 0.008000 |
| 22. Spotted goatfish | 0.05 | 0.82 | 10.80 | (0.24) | 0.000045 |
| 23. Benthopelagic fishes | (0.07) | 0.78 | 3.18 | 0.80 | 0.000768 |
| 24. Bathypelagic fishes | 1.17 | 1.90 | 5.44 | (0.71) | 0 |
| 25. Spiny lobsters | (0.01) | 1.28 | 7.40 | 0.99 | 0.007960 |
| 26. Other lobsters | (0.61) | 0.35 | 7.40 | 0.90 | 0 |
| 27. Shrimps | (3.90) | 2.73 | 13.45 | 0.99 | 0.012430 |
| 28. Crabs | (1.51) | 5.23 | 10.82 | 0.99 | 0.005300 |
| 29. Squids | (0.18) | 6.40 | 36.50 | 0.90 | 0 |
| 30. Octopus | (0.15) | 1.90 | 6.76 | 0.85 | 0.000005 |
| 31. Other molluscs | (2.53) | 3.30 | 18.87 | 0.95 | 0.001580 |
| 32. Other crustaceans | (1.59) | 19.58 | 50.77 | 0.95 | 0.000003 |
| 33. Other invertebrates | (7.00) | 2.34 | 6.74 | 0.91 | 0 |
| 34. Zooplankton | (2.17) | 26.04 | 165.00 | 0.95 | 0 |
| 35. Corals | (0.06) | 1.09 | 4.23 | 0.98 | 0 |
| 36. Microfauna | 5.99 | 308.00 | 560.00 | (0.09) | 0 |
| 37. Phytoplankton | 12.09 | 157.04 | NA | (0.08) | 0 |
| 38. Macroalgae | 98.41 | 13.25 | NA | (0.09) | 0 |
| 39. Mangroves | 77.76 | 66.46 | NA | (0.004) | 0 |
| 40. Seagrasses | 0.05 | 100.00 | NA | (0.09) | 0 |
| 41. Detritus | 201.91 | NA ^b | NA | (0.33) | 0 |

^aValues in parentheses were estimated by Ecopath with Ecosim. ^bNA = not applicable.

et al., 2005). Details of the species included in each group are presented in Freire (2005).

The basic input data of biomass (B_i), production/biomass (P_i/B_i), consumption/biomass (Q_i/B_i), and/or ecotrophic efficiency (EE_i) for each functional group were provided together with diet composition (DC_{ij}) and landings. Data were gathered from scientific papers, reports, theses, unpublished sources, and FishBase (Froese and Pauly, 2007, see also www.fishbase.org). The values of each basic input data for each species were used to calculate an average value of that basic input for each functional group. For each group, only one of the basic input data could be missing and was then estimated by the model, according to the two EwE master equations:

$$P_i = Y_i + E_i + BA_i + M0_i \cdot B_i + M2_i \cdot B_i \quad (1)$$

where: P_i = total production rate for each functional group i ; $P_i = B_i \cdot (P_i/B_i)$; Y_i = catch rate of i ; E_i = net migration rate for group i (emigration minus immigration); BA_i = bioaccumulation rate of i ; $M0_i$ = non-predation mortality rate for $i = P_i \cdot (1 - EE_i) / B_i$; B_i = biomass of group i ; EE_i = ecotrophic efficiency (proportion of the production used in the system); $M2_i$ = total predation rate for

$$i = \sum_{j=1}^n Q_j \cdot DC_{ji};$$

Q_j = consumption by predator $j = B_j \cdot (Q_j/B_j)$; and DC_{ji} = diet composition = fraction of the diet of predator j that is made up of prey i , and:

$$Q_i = P_i + R_i + UF_i \quad (2)$$

where: Q_i = consumption by functional group i ; R_i = respiration by i ; and UF_i = food of i that remains unassimilated.

Estimates of biomass for northeastern Brazil were absent in most cases and were thus mostly estimated by the model or obtained from models of similar regions. Biomass was expressed in wet weight density (tonnes·km⁻²) and all rates were expressed on an annual basis. The biomass of manatees (*Trichechus manatus*) was estimated based on a total population of 400 individuals (Medeiros *et al.*, 2000) and an individual mean weight of 400 kg (Edwards, 2000). For baleen whales and toothed cetaceans, estimates for the East Brazil LME were obtained from K. Kaschner (Fisheries Centre/UBC, Vancouver-Canada, pers. comm.; Kaschner *et al.*, 2001). These estimates were annual means based on a model predicting global distributions of marine mammals and as such were likely to be only gross estimates of local abundance.

Total biomass for tunas and tuna-like fishes were obtained from assessments performed for each specific stock by the International Commission for the Conservation of Atlantic Tuna (ICCAT). The hypothesis of one single stock was considered for yellowfin *Thunnus albacares* and bigeye *Thunnus obesus* tunas and two stocks for albacore *Thunnus alalunga* (northern and southern). Biomass estimates were divided by the total distribution area of the species following the latitude limits defined in Collette and Nauen (1983). For the first two tuna species, total biomass was available in ICCAT documents. For albacore, total biomass was calculated using a conversion factor (CF_1) based on an estimate of spawning biomass (ICCAT, 2004), considering an age-at-maturity of 5 years and 8 years of longevity:

$$CF_1 = \left(\sum_{a=j}^k S_a \cdot W_a / \sum_{a=1}^k S_a \cdot W_a \right) \quad (3)$$

$$TB = SSB / CF_1 \quad (4)$$

where: S = survival, a = age, j = age-at-maturity, k = longevity, TB = total biomass, and SSB = spawning biomass. For all three tuna species, biomass per area was estimated for East Brazil using mean catches for the period between 1995 and 2000 as a correction factor: $CF_2 = (\text{Catch}_{\text{LME}} \cdot \text{Area}_{\text{TOTAL}}) / (\text{Catch}_{\text{TOTAL}} \cdot \text{Area}_{\text{LME}})$. The resulting biomass of this

group in the East Brazil LME (B_{LME}) was calculated from: $B_{\text{LME}} = TB \cdot CF_2$. Mean catches for 1995-2000 were used in CF_2 instead of 1970s values, as tuna fisheries developed in Brazil in the last few years and thus, earlier catches would not be considered an adequate index of local abundance (Walters, 2003). This procedure was also applied to the southern stock of swordfish *Xiphias gladius*, based on the spawning biomass, considering an age-at-maturity and maximum age of 5 and 15 years, respectively (ICCAT, 2004). For other large pelagics, biomass was estimated considering one single Atlantic stock of white and blue marlins, and of sailfish. For some species/groups, biomass estimates had to be adjusted to the local habitat: spotted goatfish *Pseudupeneus maculatus* (Opitz, 1996), squids (Vasconcellos, 2002), and detritus (Pauly *et al.*, 1993). The biomass values for all other functional groups were as in the original sources described in Freire (2005). For groups with no estimate of biomass available, an estimate of ecotrophic efficiency for similar groups from similar areas was used (mainly the Caribbean), and biomass was estimated by EwE.

For exploited fish groups, the instantaneous rate of total mortality (Z) was used as an estimate of P/B (Allen, 1971). Groups such as tunas and other large pelagics, for which biomass estimates were available for each species, had a Z value estimated using biomass as a weighting factor. Some estimates were calculated using length-frequency distributions from the REVIZEE-Score NE (Living Resources from the Brazilian Exclusive Economic Zone - Northeastern Score) (see Freire, 2005 for details).

Group-specific studies on the annual consumption of food (Q) were lacking in this region, with the exception of Wiedemeyer (1997) for estuarine areas. Q/B estimates for almost all groups were obtained from similar models for the same or similar species (Palomares and Pauly, 1998). Gross conversion efficiency (production/consumption, P/Q) values resulting from these estimates were expected to be between 0.1 and 0.3, a limit considered physiologically realistic (Christensen *et al.*, 2005). Q/B was changed when necessary to produce P/Q values within this range.

The diet matrix for each functional group was obtained as the percentage of each group in terms of total wet weight (or volume) in the diet of the predator, based on the sources presented in Freire (2005). Imports were not included in the matrix due to the lack of information on net migration rate for most of

the species. The mixed trophic impact – MTI (*sensu* Leontief, 1951) was estimated based on the diet composition:

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \quad (5)$$

where: $DC_{i,j}$ = the diet composition term indicating how much j contributes to the diet of i and $FC_{j,i}$ = the term representing the proportion of the predation on i due to predator j .

Landing data used in the model were mostly obtained from the data compiled by Freire (2005) for 1978. These data were chosen to represent the 1970s, as 1978 was the earliest year for which landing data were separately recorded for industrial and artisanal fisheries. For tuna and tuna-like fishes, landings originating from industrial fisheries were retrieved from the CATDIS-ICCAT database due to its completeness. For marine mammals, total landings compiled by Freire (2005) were split according to the number of minke (baleen) and sperm whales (toothed) caught in 1978 (Singarajah, 1985), considering their mean individual weight (Trites and Pauly, 1998). All values were expressed in tonnes·km², considering the total study area as basis for biomass support. The database compiled by Freire and Pauly (2006) was used to establish the correspondence between common name and functional group. Catches recorded by broad categories such as ‘outros peixes’, ‘mistura’, ‘caíco’, and ‘outras espécies’, all representing unidentified species, were not included.

Time-dynamic simulation

The resulting model was expected to be able to reproduce observed trends in the time series of abundance, natural, fishing or total mortality, or catches available for any of the functional groups. This was done using the Ecosim module of EwE, which allows for time-dynamic simulation of changes in biomass (Pauly *et al.*, 2000; Christensen *et al.*, 2005):

$$\frac{dB_i}{dt} = g_i \sum_j^n Q_{ji} - \sum_j^n Q_{ij} + I_i - (M0_i + F_i + e_i) \cdot B_i \quad (6)$$

where: dB_i/dt = change in biomass of group i ; g_i = net growth efficiency; Q_{ji} = consumption of group j by group i ; n = number of functional groups; Q_{ij} = consumption of group i by group j ; I_i = immigration of group i ; $M0_i$ = non-predation natural mortality rate of group i ; F_i = fishing mortality rate of group

i ; e_i = emigration of group i ; and B_i = biomass of group i .

One of the pillars of Ecosim is the ‘foraging arena theory’, which states that prey are not always available to predators, but interchange from vulnerable to invulnerable pools based on the trade-off between the risks of being eaten or starving (Walters and Juanes, 1993; Christensen *et al.*, 2005). Thus, the amount of a prey i consumed by predator j (Q_{ij}) depends on the vulnerability (v_{ij}) and is defined by:

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j}{2v_{ij} + a_{ij} \cdot B_j} \quad (7)$$

where: a_{ij} = effective search rate of predator j feeding on prey i ; B_i = prey biomass; and B_j = predator biomass. The rate at which prey move from one pool to another is called vulnerability (v_{ij}) and its value is high if the ecosystem is dominated by a top-down control. The converse applies if a bottom-up control is dominant. Vulnerabilities cannot be directly estimated, so they were evaluated by changing the default values ($v_{ij} = 2$) to fit the predicted Ecosim simulations to the observed time series of relative or absolute biomass, using times series of fishing mortality or fishing effort to drive changes in biomass for those groups for which data were available. The sum of the squares between the observed and the predicted time series was used to decide which value produced the best fit. Changes in the vulnerability settings were made in one group at a time, beginning with those better rooted in local data. Times series of catch per unit of effort (CPUE) or B/B_{MSY} were used to adjust the vulnerability values for the following groups: spiny lobsters and southern red snapper (Ivo and Pereira, 1996; Paiva, 1997; Castro e Silva *et al.*, 2003; Antônio Adalto Fonteles Filho, Inst. Marine Sciences LABOMAR, Fortaleza, pers. comm.), albacore, yellowfin and bigeye tunas (ICCAT, 2004; ICCAT, 2005a), swordfish (ICCAT, 2003), sharks (ICCAT, 2005b), blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) (ICCAT, 2004), skipjack (*Katsuwonus pelamis*) (ICCAT, 1999), and sailfish (*Istiophorus albicans*) and longbill spearfish (*Tetrapturus pfluegeri*) (ICCAT, 2004). These time series were translated into biomass trends using the biomass defined in the Ecopath model as the starting point. Trends in F/F_{MSY} were used to drive changes in biomass for blue marlin, white marlin and sailfish/spearfish (ICCAT, 2004), and skipjack (ICCAT, 1999).

TABLE 2. – Diet matrix for the 1970s Ecopath with Ecosim model for the marine ecosystem off northeastern Brazil^a.

| Prey / Predator | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|-----------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1. Manatee | | | | | | | | | | | | | | | | | | |
| 2. Baleen whales | | | | | | | | | | | | | | | | | | |
| 3. Toothed cetaceans | | | | | | | | | 0.0018 | | 0.0250 | | | | 0.0082 | | | |
| 4. Seabirds | 0.0035 | | 0.0177 | | | | | | | | | | | | | | | |
| 5. Sea turtles | | | | | | | | | | | | | | | | | | |
| 6. Tunas | | | | 0.0126 | 0.0251 | | 0.0086 | | | 0.0264 | 0.1702 | | | | | | | |
| 7. Other large pelagics | | | | | | | 0.0264 | 0.0351 | | | | | | | | | | |
| 8. Dolphinfish | | | | | | | | | 0.0019 | | | | | | | | | |
| 9. Dolphinfish juv. | | | 0.0029 | 0.0105 | 0.1783 | | | | | 0.0194 | | | | | | | | |
| 10. Swordfish | | | | | | | | | | | | | | | | | | |
| 11. Sharks | | | | | | | | | | | | | | | | | | |
| 12. Rays | 0.2500 | 0.0834 | 0.0976 | | 0.4568 | 0.1626 | 0.3247 | 0.2273 | 0.0153 | 0.0835 | 0.1239 | 0.0302 | 0.0877 | 0.3944 | 0.0100 | 0.0107 | | |
| 13. Small pelagics | | | | | 0.0334 | 0.0059 | 0.0041 | | | | | | 0.1972 | | 0.0649 | | | |
| 14. Needlefishes | | | | | | | | | | | | 0.0010 | | | | | | |
| 15. Southern red snapper | | | 0.0034 | 0.0001 | | | | | | | | | | | | | | |
| 16. Large carnivorous reef fishes | 0.0310 | 0.0009 | 0.0009 | | 0.0030 | 0.1030 | | | | 0.0295 | 0.0193 | | | | | | | |
| 17. Small carnivorous reef fishes | 0.0247 | 0.1089 | 0.3023 | 0.3023 | 0.1235 | 0.1158 | 0.0158 | | | 0.0986 | 0.1915 | 0.0942 | | | | | | |
| 18. Herbivorous reef fishes | 0.0019 | 0.0012 | 0.0003 | 0.0003 | 0.0003 | 0.0402 | 0.0071 | | | | 0.0404 | 0.0188 | | | | | | |
| 19. Omnivorous reef fishes | 0.0377 | 0.1245 | 0.0535 | 0.0535 | 0.2989 | 0.0553 | 0.0014 | | | 0.0986 | 0.0267 | 0.0188 | | | | | | |
| 20. Demersal fishes | 0.0720 | 0.2890 | 0.1331 | 0.0163 | | 0.0003 | 0.0003 | 0.0003 | | 0.0734 | 0.3537 | | | | 0.0392 | | | |
| 21. Mullet | | | | 0.0000 | | | | | | | | | 0.0295 | 0.0051 | 0.0015 | | | |
| 22. Spotted goatfish | 0.0001 | | | 0.0069 | | | 0.0046 | 0.0605 | | | | | | 0.0002 | | | | |
| 23. Benthopelagic fishes | 0.0300 | 0.0845 | 0.0063 | | 0.2978 | 0.3547 | 0.0659 | 0.0659 | 0.3602 | 0.0376 | | | | | | | | |
| 24. Bathypelagic fishes | | | | | | | | | | | | | | | | | | |
| 25. Spiny lobsters | | | | | | | | | | | | | | | | | | |
| 26. Other lobsters | | | | 0.0034 | | | | | 0.0001 | 0.0002 | | | | | | | | |
| 27. Shrimps | | | 0.0043 | 0.0001 | 0.0014 | | | | | | 0.0092 | 0.0038 | 0.0680 | 0.0103 | 0.1081 | 0.0457 | 0.2012 | 0.1353 |
| 28. Crabs | | | | 0.2209 | 0.0739 | 0.0022 | 0.0003 | 0.0001 | 0.0001 | 0.0001 | 0.0001 | 0.0209 | 0.1443 | 0.0859 | 0.0074 | 0.0457 | 0.2563 | 0.1349 |
| 29. Squids | | | | 0.0192 | | 0.0968 | 0.1552 | 0.0281 | 0.2809 | 0.1272 | 0.0766 | 0.0005 | | | 0.0101 | 0.0032 | 0.0009 | |
| 30. Octopus | | | 0.0043 | | | 0.0126 | 0.0186 | 0.0022 | 0.0022 | 0.0022 | 0.0567 | 0.0018 | | | 0.0101 | 0.0323 | | |
| 31. Other molluscs | 0.0300 | 0.0048 | 0.0328 | | | 0.0003 | 0.0003 | 0.0002 | | 0.1433 | 0.0374 | | | | 0.0406 | 0.0055 | | |
| 32. Other crustaceans | 0.0057 | 0.0229 | 0.0003 | | 0.0118 | 0.0118 | 0.0002 | 0.0016 | 0.0617 | 0.1432 | 0.0143 | | | | 0.0306 | 0.0643 | | |
| 33. Other invertebrates | 0.0135 | 0.0043 | 0.2969 | 0.2200 | | | | | | | | | | | 0.0077 | 0.0350 | 0.0283 | 0.0732 |
| 34. Zooplankton | 0.6420 | 0.1057 | 0.4539 | 0.0060 | 0.0060 | 0.0004 | 0.0002 | 0.0510 | | 0.0001 | 0.0348 | 0.3935 | 0.6100 | | 0.0026 | 0.1373 | | |
| 35. Corals | | | | 0.0118 | | | | | | | | | | | | | | |
| 36. Microfauna | | | | | | | | | | | | | | | | | | |
| 37. Phytoplankton | 0.0436 | | | | 0.1569 | | | | | | 0.2077 | | | 0.0436 | 0.0173 | | | 1.0000 |
| 38. Macroalgae | 0.1465 | | | | | | | | | | | | | | | | | |
| 39. Mangroves | 0.7964 | | | | 0.0302 | | | | | | | | | | | | | |
| 40. Seagrasses | | | | 0.1095 | 0.0028 | | | | | | | 0.0003 | 0.0199 | | | | | |
| 41. Detritus | | | | | | | | | | | | | | | | | | |

TABLE 2 (cont.). – Diet matrix for the 1970s Ecosim model for the marine ecosystem off northeastern Brazil^a.

| Prey / Predator | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 |
|-----------------------------------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|-----------|----------|--------|--------|---------|
| 1. Manatee | | | | | | | | | | | | | | | | | | |
| 2. Baleen whales | | | | | | | | | | | | | | | | | | |
| 3. Toothed cetaceans | | | | | | | | | | | | | | | | | | |
| 4. Seabirds | | | | | | | | | | | | | | | | | | |
| 5. Sea turtles | | | | | | | | | | | | | | | | | | |
| 6. Tunas | | | | | | | | | | | | | | | | | | |
| 7. Other large pelagics | | | | | | | | | | | | | | | | | | |
| 8. Dolphinfish | | | | | | | | | | | | | | | | | | |
| 9. Dolphinfish juv. | | | | | | | | | | | | | | | | | | |
| 10. Swordfish | | | | | | | | | | | | | | | | | | |
| 11. Sharks | | | | | | | | | | | | | | | | | | |
| 12. Rays | | | | | | | | | | | | | | | | | | |
| 13. Small pelagics | 0.0004 | 0.0016 | | | 0.0929 | 0.0954 | | | | | | | | | | | | |
| 14. Needlefishes | | | 0.0465 | | | | | | | | | | | | | | | |
| 15. Southern red snapper | | | | | | | | | | | | | | | | | | |
| 16. Large carnivorous reef fishes | 0.0001 | | | | | | | | | | | | | | | | | |
| 17. Small carnivorous reef fishes | 0.0071 | | | | 0.0002 | | | | | | | | | | | | | |
| 18. Herbivorous reef fishes | 0.0002 | | | | 0.0003 | | | | | | | | | | | | | |
| 19. Omnivorous reef fishes | 0.0019 | | | 0.0440 | | | | | | | | | | | | | | |
| 20. Demersal fishes | 0.0599 | 0.0500 | | | 0.0443 | 0.0003 | | | | | | 0.0164 | | | | | | |
| 21. Mulllets | 0.0314 | | | | 0.0446 | | | | | | 0.0392 | 0.0228 | | | | | | |
| 22. Spotted goatfish | | | | | | | | | | | | | | | | | | |
| 23. Benthopelagic fishes | 0.0443 | | | | | | 0.0011 | 0.0147 | | | | | | | | | | |
| 24. Bathypelagic fishes | 0.0076 | 0.0564 | | | | | 0.1271 | 0.0106 | | | | | | | | | | |
| 25. Spiny lobsters | 0.0008 | | | | | | | | | | | | | | | | | |
| 26. Other lobsters | | | | | | 0.0001 | | | | | | 0.0141 | | | | | | |
| 27. Shrimps | 0.0405 | 0.2587 | | | 0.2250 | 0.2210 | 0.0255 | | | 0.1934 | 0.1612 | 0.0730 | | | | | | |
| 28. Crabs | 0.2336 | 0.0718 | | | 0.3110 | 0.0036 | | | 0.0422 | | | 0.2049 | | | 0.0008 | | | |
| 29. Squids | 0.0004 | | | | | | 0.0051 | | | | 0.0123 | 0.0110 | | | | | | |
| 30. Octopus | 0.0045 | | | | | | 0.0003 | | | | 0.0003 | 0.1113 | | | | | | |
| 31. Other molluscs | 0.1749 | 0.0084 | 0.0024 | 0.0770 | 0.0412 | 0.0309 | 0.2930 | 0.5000 | 0.0021 | 0.0090 | | 0.1856 | 0.0087 | | 0.0006 | | | |
| 32. Other crustaceans | 0.2791 | 0.1729 | 0.0050 | 0.1530 | 0.3046 | 0.0839 | | | 0.3689 | 0.0726 | 0.0615 | 0.1961 | | | 0.0032 | | | |
| 33. Other invertebrates | 0.0849 | 0.2021 | 0.0024 | 0.1900 | 0.0887 | 0.0371 | 0.1075 | 0.5000 | 0.0398 | 0.0905 | | 0.1144 | 0.0172 | 0.0113 | 0.0159 | | | |
| 34. Zooplankton | 0.0074 | 0.1567 | 0.0050 | | 0.0607 | 0.6429 | | | 0.1682 | 0.0054 | 0.5975 | 0.0251 | 0.0779 | 0.0273 | 0.0438 | 0.0500 | 0.1625 | |
| 35. Corals | | | | | | | 0.0054 | | | | | | | 0.0001 | 0.0003 | | | |
| 36. Microfauna | 0.0001 | | 0.0188 | | | | | | | 0.0018 | | | 0.1985 | 0.1182 | 0.0696 | 0.4000 | 0.5875 | |
| 37. Phytoplankton | 0.0010 | 0.1930 | | | | | | | 0.0009 | | | 0.5020 | | 0.0339 | 0.3300 | | | |
| 38. Macroalgae | 0.0470 | 0.0407 | 0.1050 | | | | 0.1022 | | 0.0710 | 0.1179 | | | 0.0752 | 0.3086 | 0.1429 | | 0.0134 | |
| 39. Mangroves | | | | | | | | | 0.2624 | | | | | | | 0.0045 | | |
| 40. Seagrasses | 0.0114 | | | | | | 0.0134 | | | 0.0013 | | | | 0.0000690 | 0.000001 | | | 0.00004 |
| 41. Detritus | 0.0137 | 0.0361 | 0.6685 | | | | | | 0.3499 | 0.2026 | | | 0.1204 | 0.5344 | 0.6889 | 0.2200 | 0.2500 | 0.9821 |

^aFunctional groups 37–40 and 41 do not require predator column as they refer to primary producers and to the product of the degradation of all groups included in the model, respectively.

Comparison with other ecosystems

In order to compare different ecosystems, system statistics provided by EwE were used: total system throughput, sum of all production, calculated total net primary production, phytoplankton biomass and production, zooplankton biomass and production, total primary production/total respiration, total primary production/total biomass, total biomass/total throughput, total biomass (excluding detritus), omnivory index, proportion of total flux originating from detritus, mean transfer efficiency between trophic levels, total catches, mean trophic level of the catch, gross efficiency, and primary production required to sustain the catches (for details of each statistic see Christensen *et al.*, 2005). An analysis of the sensitivity of these statistics obtained with 41 functional groups was performed after aggregating the original groups into 31 and 21 groups.

RESULTS

Mass balance model

The basic input matrix obtained in the balanced trophic model of the 1970s for the marine ecosystem off northeastern Brazil is presented in Table 1. Forty-one functional groups were included to describe the main trophic relationships, with an estimated total biomass (excluding detritus) of 222 tonnes·km⁻². The diet matrix for the 1970s model is presented in Table 2. The mixed trophic impact (MTI) analysis allows for a better understanding of the impact of one group over the others. Most of the impacts are quite modest, probably due to the highly reticulated diet matrix. However, seagrass and macroalgae exerted a strong positive impact on manatees and herbivorous reef fishes, respectively (Fig. 2). Omnivorous reef fishes had a strong negative impact on

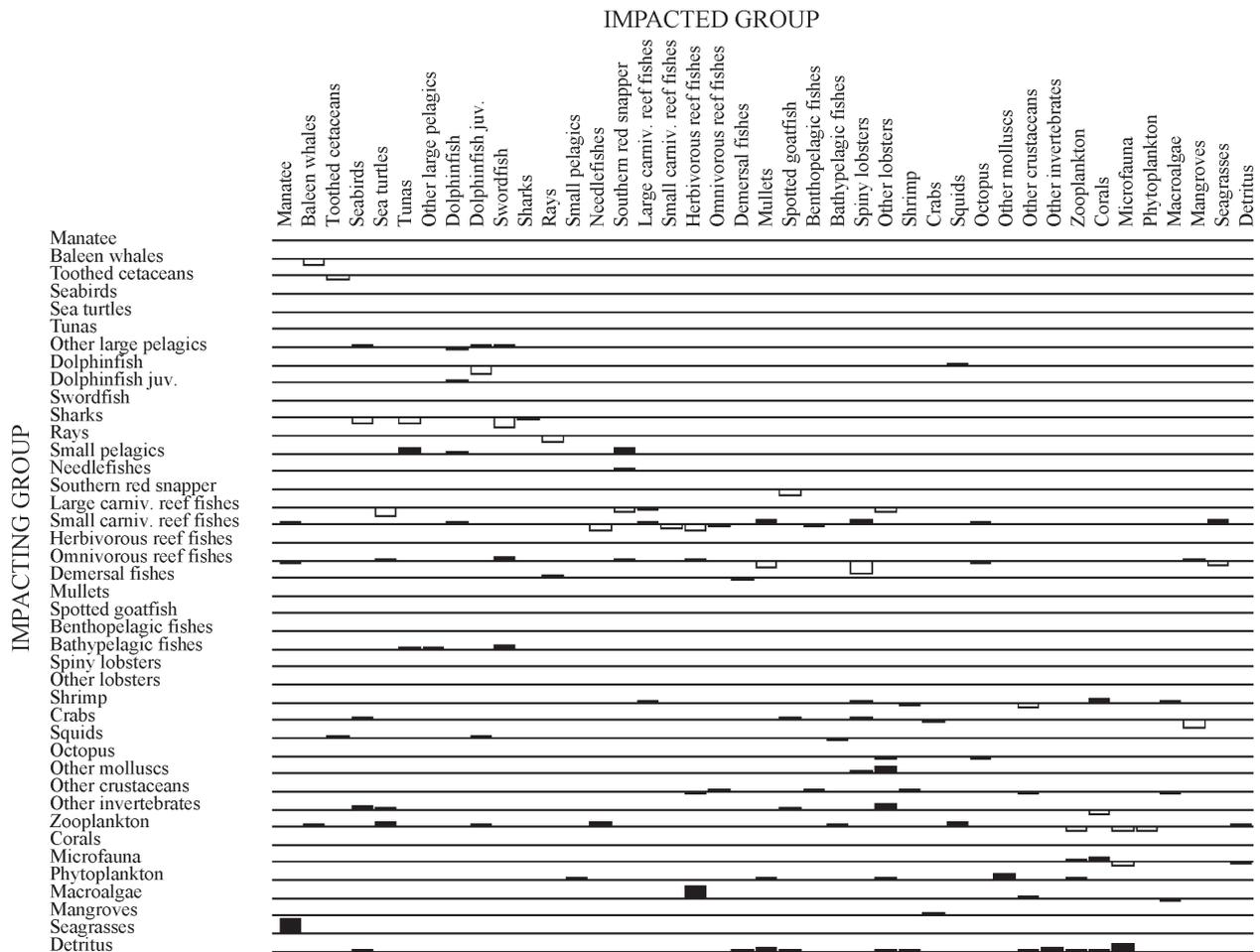


FIG. 2. – Mixed trophic impact in the northeastern Brazil marine ecosystem for the 1970s *sensu* Leontief (1951), calculated as how much a prey *i* contributes to the diet of a predator *j* minus the proportion of the predation on *j* due to predator *i*. The impact in each group is positive when placed above the line and negative when below.

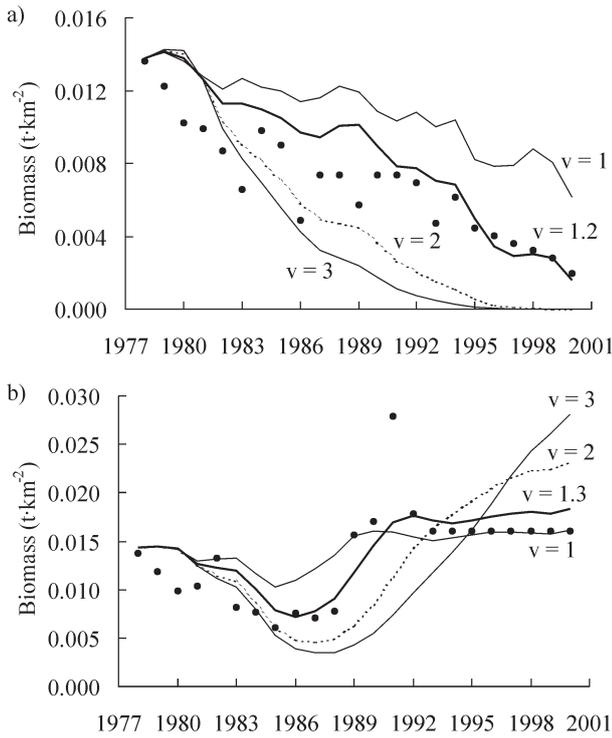


FIG. 3. – Verification of the model: observed time series (dots) of biomass for spiny lobsters (a) and southern red snapper (b) off northeastern Brazil and estimated values from Ecopath with Ecosim under four values of vulnerability ‘v’ (lines) for the period from 1978 to 2000. The thicker line is associated with the vulnerability value used in the final version of the model.

spiny lobsters. Sharks, as predators, had a negative impact on swordfish.

Time-dynamic simulation

The model was able to reproduce the observed changes in biomass available for spiny lobsters, southern red snapper, and tuna and tuna-like fishes after adjustments in the vulnerability were made from the default (2.0). Thus, for spiny lobsters and southern red snapper, the vulnerabilities that resulted in the best fit were 1.2 and 1.3, respectively (Fig. 3), indicating that these groups were close to their carrying capacity (a value of 1) in the 1978-base year. For swordfish and other large pelagics, low values (1.3 and 1, respectively) produced the best fit as well (Fig. 4), with a similar interpretation with regard to carrying capacity. For tunas, a vulnerability of 8 was able to produce a good fit between the ICCAT series of biomass and the value predicted by the model. This high vulnerability indicates that tunas were further from their carrying capacity, i.e. given a higher abundance, tunas would be able to increase the pre-

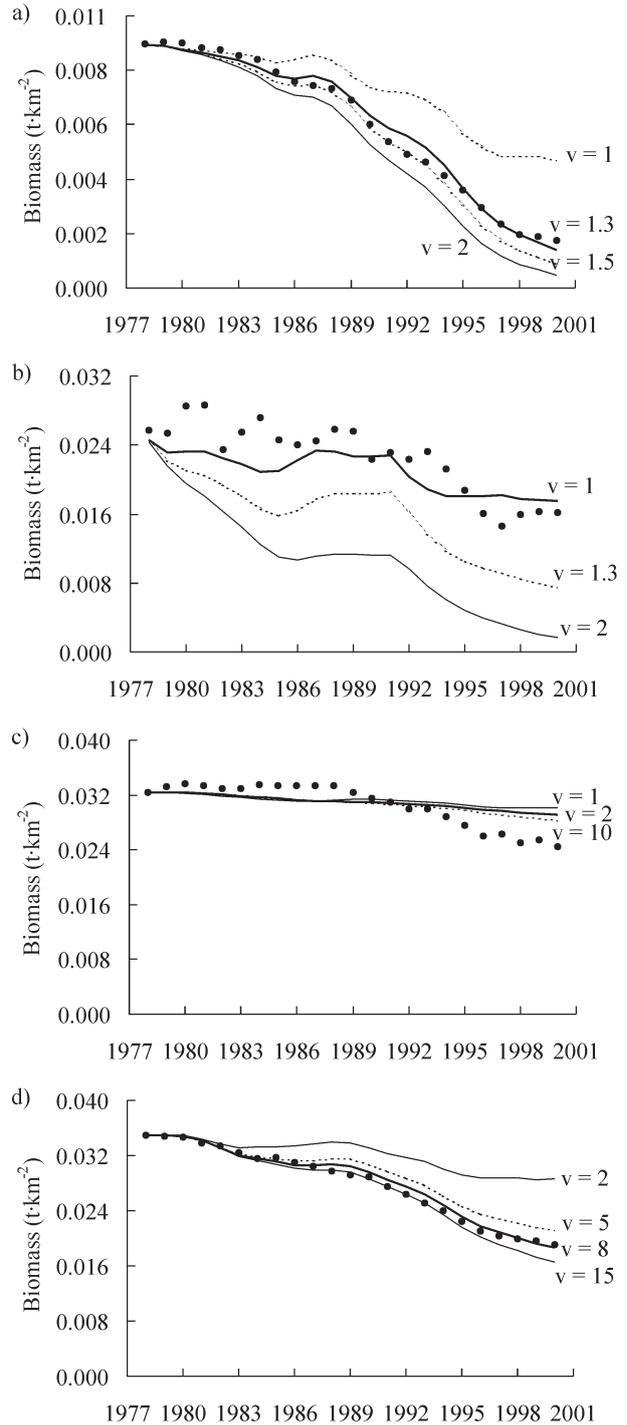


FIG. 4. – Verification of the model: observed time series of biomass (dots) and estimated values (lines) from Ecopath with Ecosim under different settings of vulnerability (v) for swordfish (a), other large pelagics (b), sharks (c), and tunas (d) off northeastern Brazil in 1978-2000.

dation mortality they cause on their prey eight-fold. For sharks, changes in vulnerability did not result in much difference in the predicted values. The model was still able to capture some of the decline of

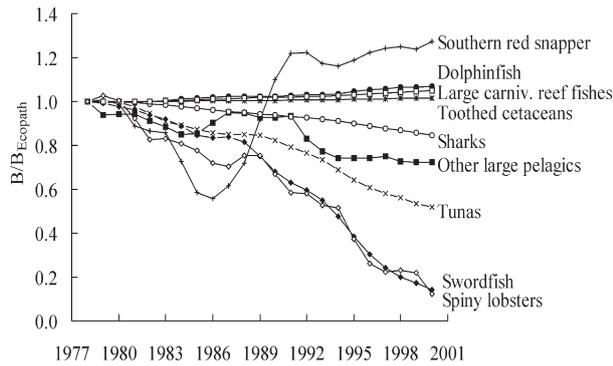


FIG. 5. – Changes in biomass in relation to the Ecopath level (1.0) for some groups included in the 1970s model of the marine ecosystem off northeastern Brazil (1978–2000). The remaining groups did not show any changes.

sharks observed in the Atlantic, but not at the level indicated by ICCAT (2005b).

After the vulnerabilities adjustments were made, the final changes in biomass could be assessed. The largest changes were observed for spiny lobsters and swordfish (Fig. 5), which respectively declined to 12 and 14% of the biomass at the beginning of the period (1978). Tunas, other large pelagics, and sharks presented intermediate decline rates of biomass, reaching 52, 72, and 85% of the original biomass, respectively. A slight increase in biomass was observed for toothed cetaceans, large carnivorous reef fishes, and dolphinfish (1.7 to 6.9%). Southern red snapper (*Lutjanus purpureus*) showed a decline in biomass until 1996 and seemed to recover to levels above that observed in the Ecopath base-level. For

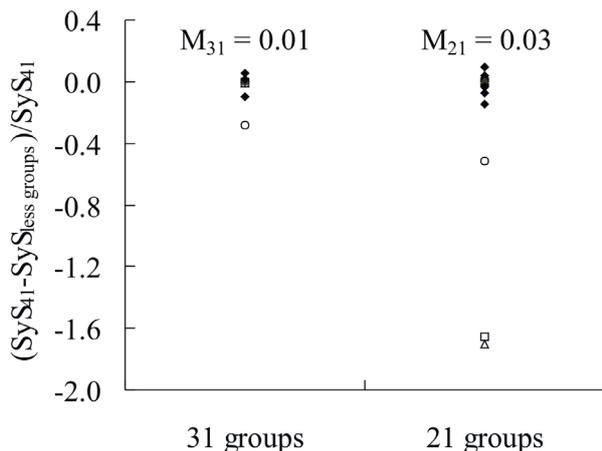


FIG. 6. – Variation of the system statistics (SyS) for the East Brazil Large Marine Ecosystem obtained with Ecopath with Ecosim models using 31 and 21 groups ($SyS_{less\ groups}$) in relation to the original 41 groups model (SyS_{41}). Open circles correspond to the connectance index, open squares to the throughput cycled (excluding detritus), and open triangles to the predatory cycling index. M_{31} and M_{21} indicate the mean absolute variation of the system statistics using 31 and 21 groups in relation to the baseline (41 groups).

the remaining species, changes in biomass (positive or negative) were very low and are not shown.

Comparison with other ecosystems

After aggregating the original model with 41 functional groups into models with 31 and 21 groups, all system statistics provided by EwE remained within the range between +20 and –20% of the original value, with the exception of the connectance index, the throughput cycled (excluding detritus), and the predatory cycling index (Fig. 6). Thus, these statistics were not used in the comparison of ecosystems. The East Brazil LME presented a total system throughput of 23042 t·km²·year⁻¹ (Table 3). Of this total, 18% represented consumption by predators, 30% was exported, 6% was lost via respiration, and a very high proportion flowed into the detritus group (46%). Total primary production was 8375 t·km²·year⁻¹, with 22% originating from phytoplankton and the remaining from mangroves, macroalgae, and seagrass. Only 3.4% of this production was consumed and the rest went into the detritus. The primary production of this system exceeded the respiration (P/R=1.5) and the total biomass (P/B=15.4) of all functional groups included in the model.

Catches added up to 0.13 t·km²·year⁻¹ (Table 3): demersal fishes (33%), reef fishes (17%), shrimps (10%), spiny lobsters (6%), tuna and tuna-like fishes (5%) and others (29%). The mean trophic level of the catch was 3.4, and the primary production required to sustain these catches was 1.3%. The gross efficiency of catches in this area, defined as the ratio of catch to primary productivity (Christensen *et al.*, 2005) was 0.00002.

The trophic aggregation analysis indicated the existence of ten discrete trophic levels (*sensu* Lindeman, 1942). The ninth trophic level encompassed only dolphinfish, swordfish, and sharks (Table 4). Microfauna and herbivorous reef fishes were the only functional groups besides primary producers that operated at one single trophic level. The mean transfer efficiency between trophic levels (geometric mean weighted by flows for trophic levels II–IV) was estimated at 11.4%. Transfer from level I to II was low (6.4%), increasing to a maximum from level III to IV (16.6%) and decreasing thereafter to 4.3% at level IX. The estimated omnivory index (Christensen *et al.*, 2005) was 0.21.

TABLE 3. – System statistics obtained from Ecopath with Ecosim for the 1970s model of East Brazil Large Marine Ecosystem (off northeastern Brazil), for other models of marine ecosystems off Brazil, and for models representing shelf ecosystems in tropical areas.

| Statistic/Ecosystem | This study | | Brazil | | Other shelves | | | Units | | | |
|---|------------|--------------------------------|--------------------------------------|---------------------------------|-----------------------------|--------------------|----------------------|-------|------------------------|---------------------|---------------------------------------|
| | Northeast | Mangrove ^a North | Coral reef ^b Northeast | Shelf ^c Southeast | Shelf ^d South | SE US ^e | Yucatan ^f | | Venezuela ^g | SW GOM ^h | Grenada ⁱ |
| Total system throughput | 23042 | 10559 | 43394 | 9098 | 5584 | 14518 | 2049 | 7621 | 7713 | 14332 | t-km ² -year ⁻¹ |
| Sum of all production | 10364 | 3555 | 13119 | 4178 | 2274 | 5420 | 692 | 3699 | 5029 | 3755 | t-km ² -year ⁻¹ |
| Calculated total net primary production | 8375 | 3134 | 9150 | 2988 | 1670 | 4336 | 454 | 3290 | 4668 | 3115 | t-km ² -year ⁻¹ |
| Phytoplankton biomass | 12.1 | 6 | 16 | 18 | 16.7 | 5.6 | 7.9 | 45 | 45.5 | 36.2 | t-km ² |
| Phytoplankton production | 1900 | 1080 | 1920 | 2988 | 1670 | 1865 | 356 | 3150 | 4687 | 2534 | t-km ² -year ⁻¹ |
| Zooplankton biomass | 2.2 | 1.5 | 28.9 | 10.5 | 9 | 36.5 | 1.7 | 8.2 | 5.7 | 2.5 | t-km ² |
| Zooplankton production | 57 | 150 | 1156 | 945 | 584 | 475 | 30 | 328 | 124 | 100 | year ⁻¹ |
| Total primary production/total respiration | 6.6 | 3.3 | 0.6 | 1.2 | 0.9 | 1.7 | 0.8 | 1.8 | 4.1 | 1.0 | dimensionless |
| Total primary production/total biomass | 37.6 | 0.2 | 5.6 | 20.5 | 37.2 | 9.2 | 7.0 | 27.0 | 44.4 | 24.3 | dimensionless |
| Total biomass/total throughput | 0.01 | 1.24 | 0.04 | 0.02 | 0.01 | 0.03 | 0.03 | 0.02 | 0.01 | 0.01 | dimensionless |
| Total biomass (excluding detritus) | 222.5 | 13132 | 1640 | 146 | 45 | 470 | 65 | 122 | 105 | 128 | t-km ² |
| Omnivory index | 0.21 | 0.11 | 0.16 | 0.28 | 0.26 | 0.22 | 0.28 | 0.32 | 0.36 | 0.26 | dimensionless |
| Prop. total flux originating from detritus | 0.62 | 0.45 | 0.68 | 0.31 | 0.37 | NP | NP | 0.27 | 0.53 | NP | dimensionless |
| Mean transfer efficiency between TL | 11.4 | 9.3 | 10.4 | 12.6 | 6 | NP | 17.6 | 6.6 | 9.2 | NP | % |
| Total catches | 0.13 | 268.30 | NA | 1.67 | 0.99 | 0.79 | 0.09 | 5.20 | 0.31 | 0.08 | t-km ² -year ⁻¹ |
| Mean trophic level of the catch | 3.4 | 2.1 | NA | 2.6 | 3.7 | 3.0 | 4.1 | 3.5 | 4.3 | 4.0 | dimensionless |
| Gross efficiency (catch-10 ⁴ /net pp.) | 0.2 | 86000 | NA | 5.6 | 5.9 | 1.8 | 1.8 | 16.0 | 0.7 | 0.3 | dimensionless |
| Primary production required (catches) | 1.3 | 30.7 | NA | 2.5 | 22.0 | NP | 53.6 | 7.9 | 6.7 | NP | % |
| Study area | 1074984 | 220 | 7 | 97000 | 28661 | 174300 | 100000 | 30000 | 65000 | 25957 | km ² |
| Number of groups | 41 | 19 | 22 | 25 | 13 | 42 | 21 | 16 | 19 | 51 | groups |

^aWolff *et al.* (2000); ^bTelles (1998); ^cGasalla and Rossi-Wongtschowski (2004); ^dVasconcellos and Gasalla (2001); ^eSoutheastern United States, Okey and Pugliese (2001); ^fArreguín-Sánchez *et al.* (1993); ^gMendoza (1993); ^hSouthwestern Gulf of Mexico, Manickchand-Heileman *et al.* (1998); ⁱGrenada and the Grenadines, Mohammed (2003). Note that some statistics were not provided in the original source and were obtained after re-entering the data, wherever the completeness of the basic input allowed. NA = not applicable and NP = not provided.

DISCUSSION

This study represents the first attempt to model the trophic components of the whole marine ecosystem off northeastern Brazil. As a first attempt, this required a considerable effort to gather information for an area that is much less studied than the southeastern and southern regions. The characteristics of the ecosystem modelled in this study will be discussed here and at the same time compared with other models constructed for Brazilian marine ecosystems and for tropical continental shelves along the western Atlantic (Table 3). The models presented for comparison were chosen due to the use of similar methodology. Telles (1998) found much higher biomass for most of the functional groups in the Abrolhos region (southernmost part of the study area). However, Telles modelled a very small (7 km²) reef area, which has been protected since 1983, and which is therefore expected to harbour a higher biomass per unit of area. Wiedemeyer (1997) restricted his analysis to a small mangrove subsystem embedded in an estuarine system (35 km²) and dealt only with the benthic food web. Wolff *et al.* (2000) also analysed a small mangrove area (220 km²) to the north of the area studied and found extremely high total system biomass per unit of area, mainly of mangrove vegetation. Thus, most of the comparisons below will be restricted to shelf areas both in Brazil and other countries.

The total system throughput (23042 t-km²-year⁻¹) indicated that the East Brasil LME was similar to the U.S. Coast and Grenada and the Grenadines in terms of flows. The total primary production off the northeastern coast of Brazil was the highest amongst the mentioned shelves. However, we must consider that some of these models were built to analyse specific subsystems such as the one for south Brazil, which aimed to assess the pelagic subsystem, and did not include coastal systems and all primary production generated by benthic producers. The biomass originating from phytoplankton off northeastern Brazil (12.1 t-km²) was lower than in Venezuela, the southwestern Gulf of Mexico, and Grenada and the Grenadines

TABLE 4. – Relative flows by discrete trophic level for the marine ecosystem off northeastern Brazil in the 1970s model. Flows through the trophic level X are too low to be shown. TL represents the fractional trophic level *sensu* Odum and Heald (1975).

| Group\Trophic level | TL | I | II | III | IV | V | VI | VII | VIII | IX |
|-------------------------------|------|---|--------|--------|--------|--------|--------|--------|--------|--------|
| Manatee | 2.02 | 0 | 0.9865 | 0.0119 | 0.0013 | 0.0003 | 0 | 0 | 0 | 0 |
| Baleen whales | 3.72 | 0 | 0 | 0.4475 | 0.4517 | 0.0906 | 0.0090 | 0.0011 | 0.0001 | 0 |
| Toothed cetaceans | 4.45 | 0 | 0 | 0.0759 | 0.5299 | 0.3330 | 0.0561 | 0.0048 | 0.0003 | 0 |
| Seabirds | 3.45 | 0 | 0.1095 | 0.5045 | 0.2694 | 0.0990 | 0.0164 | 0.0012 | 0 | 0 |
| Sea turtles | 3.15 | 0 | 0.1899 | 0.5298 | 0.2579 | 0.0192 | 0.0030 | 0.0002 | 0 | 0 |
| Tunas | 4.31 | 0 | 0 | 0.1564 | 0.5007 | 0.2991 | 0.0381 | 0.0052 | 0.0005 | 0 |
| Other large pelagics | 4.50 | 0 | 0 | 0.0588 | 0.5434 | 0.3358 | 0.0548 | 0.0066 | 0.0006 | 0 |
| Dolphinfish | 4.58 | 0 | 0 | 0.1057 | 0.4383 | 0.3326 | 0.1048 | 0.0169 | 0.0016 | 0.0001 |
| Dolphinfish juv. | 4.42 | 0 | 0 | 0.1078 | 0.5206 | 0.3065 | 0.0583 | 0.0063 | 0.0005 | 0 |
| Swordfish | 4.56 | 0 | 0 | 0.0304 | 0.5524 | 0.3348 | 0.0719 | 0.0096 | 0.0009 | 0.0001 |
| Sharks | 4.65 | 0 | 0 | 0.0990 | 0.4055 | 0.3445 | 0.1301 | 0.0188 | 0.0020 | 0.0002 |
| Rays | 3.88 | 0 | 0.0003 | 0.3950 | 0.4164 | 0.1596 | 0.0265 | 0.0021 | 0.0001 | 0 |
| Small pelagics | 3.05 | 0 | 0.2796 | 0.4710 | 0.2313 | 0.0153 | 0.0027 | 0.0001 | 0 | 0 |
| Needlefishes | 3.43 | 0 | 0.0515 | 0.5465 | 0.3620 | 0.0376 | 0.0022 | 0.0003 | 0 | 0 |
| Southern red snapper | 4.21 | 0 | 0 | 0.2073 | 0.4979 | 0.2528 | 0.0369 | 0.0047 | 0.0003 | 0 |
| Large carnivorous reef fishes | 4.01 | 0 | 0 | 0.3323 | 0.4466 | 0.1781 | 0.0390 | 0.0037 | 0.0002 | 0 |
| Small carnivorous reef fishes | 3.68 | 0 | 0 | 0.5683 | 0.3267 | 0.0937 | 0.0104 | 0.0008 | 0 | 0 |
| Herbivorous reef fishes | 2.00 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Omnivorous reef fishes | 3.33 | 0 | 0.0722 | 0.6346 | 0.2180 | 0.0631 | 0.0113 | 0.0006 | 0 | 0 |
| Demersal fishes | 3.36 | 0 | 0.0819 | 0.6040 | 0.2594 | 0.0508 | 0.0038 | 0.0001 | 0 | 0 |
| Mulletts | 2.04 | 0 | 0.9664 | 0.0297 | 0.0037 | 0.0002 | 0 | 0 | 0 | 0 |
| Spotted goatfish | 3.50 | 0 | 0 | 0.6389 | 0.2644 | 0.0826 | 0.0132 | 0.0009 | 0 | 0 |
| Benthopelagic fishes | 3.58 | 0 | 0 | 0.5958 | 0.3032 | 0.0929 | 0.0075 | 0.0006 | 0 | 0 |
| Bathypelagic fishes | 3.58 | 0 | 0 | 0.5693 | 0.3895 | 0.0370 | 0.0036 | 0.0006 | 0 | 0 |
| Spiny lobsters | 3.30 | 0 | 0.1156 | 0.5953 | 0.2068 | 0.0677 | 0.0140 | 0.0006 | 0 | 0 |
| Other lobsters | 3.25 | 0 | 0 | 0.7924 | 0.1801 | 0.0272 | 0.0002 | 0 | 0 | 0 |
| Shrimps | 2.73 | 0 | 0.4209 | 0.4450 | 0.1285 | 0.0055 | 0.0001 | 0 | 0 | 0 |
| Crabs | 2.61 | 0 | 0.6124 | 0.2423 | 0.1150 | 0.0291 | 0.0012 | 0 | 0 | 0 |
| Squids | 3.64 | 0 | 0 | 0.5097 | 0.4115 | 0.0724 | 0.0058 | 0.0005 | 0.0001 | 0 |
| Octopus | 3.58 | 0 | 0 | 0.6663 | 0.2503 | 0.0714 | 0.0114 | 0.0006 | 0 | 0 |
| Other molluscs | 2.35 | 0 | 0.7038 | 0.2610 | 0.0348 | 0.0003 | 0 | 0 | 0 | 0 |
| Other crustaceans | 2.17 | 0 | 0.8431 | 0.1440 | 0.0127 | 0.0002 | 0 | 0 | 0 | 0 |
| Other invertebrates | 2.16 | 0 | 0.8810 | 0.0992 | 0.0196 | 0.0002 | 0 | 0 | 0 | 0 |
| Zooplankton | 2.47 | 0 | 0.5789 | 0.4211 | 0 | 0 | 0 | 0 | 0 | 0 |
| Corals | 2.83 | 0 | 0.2500 | 0.6816 | 0.0684 | 0 | 0 | 0 | 0 | 0 |
| Microfauna | 2.00 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Phytoplankton | 1.00 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Macroalgae | 1.00 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mangroves | 1.00 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Seagrasses | 1.00 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Detritus | 1.00 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

(36–46 t·km⁻²), but higher than on the U.S. coast and Yucatan.

Vasconcellos and Gasalla (2001) and Gasalla and Rossi-Wongtschowski (2004) described the large shelf ecosystems in southern and southeastern Brazil. The phytoplankton biomass in those areas was higher than in the marine ecosystem off northeastern Brazil (Table 3). However, the P/B ratio for phytoplankton may be slightly overestimated in the northeastern region (157 year⁻¹), as it resulted in a production level that surpassed the value for southern Brazil. That value was also very close to the P/B for southeastern Brazil (166 year⁻¹), an area associated with upwelling processes and abundant small pelagic fish, notably the Brazilian sardine (*Sardinella brasiliensis*).

One important system statistic of an ecosystem is the omnivory index, which measures the degree

to which a system exhibits weblike characteristics, i.e. how the interactions are spread amongst trophic levels. Pauly *et al.* (1993) suggested the use of this index as an alternative to the connectance index, which is highly affected by the number of functional groups included in the model. The omnivory index was 0.21, very similar to all other shelf systems considered (Table 3), and indicated that the functional groups were specialised, consuming food items of similar trophic levels. If we consider that the omnivory index is correlated with maturity in the same fashion as the connectance index (Odum, 1969), then one would say that northeastern Brazil would be on the immature side of the maturity spectrum. This hypothesis was supported by the high ratio of system primary production to respiration (6.6), but not by the high ratio between system primary production and biomass (37.6).

Detritus seemed to have an important role in the marine ecosystem off northeastern Brazil, considering that only about 3% of the total primary production was consumed and the remaining flowed to the detritus, and 62% of the total flow in this system originated from detritus. Pace *et al.* (1984) point out that failure to properly consider different components of the zooplankton may lead to an overestimation of the detritus originating from phytoplankton. However, this is not expected to produce a large effect for this model as most of the primary production originated from benthic producers. Of all inflow to detritus, about 29% was derived from recycling and may be closely related to the ability of the system to recover from perturbations (Vasconcellos *et al.*, 1997).

Total extractions (catches) from the marine ecosystem off northeastern Brazil were 0.13 t·km⁻², a level similar to southeastern U.S., Yucatan, and Grenada and the Grenadines. The mean trophic level (TL) of the landings was 3.4. In southeastern Brazil, where sardine is the main fish resource (Paiva, 1997), Gasalla and Rossi-Wongtschowski (2004) found a mean trophic level of catches of 2.6. In southern Brazil, the mean trophic level of catches was higher (3.7) than in northeastern Brazil. Even though sardines dominate fisheries in southern Brazil, demersal fishes such as drums, croakers, and hakes (TL = 3.5 to 4.1) are also heavily targeted (Paiva, 1997), leading to an increase in the mean trophic level. The mean trophic level of landings in the Caribbean was higher than that in northeastern Brazil due to the greater importance of tuna fisheries and the deficient coverage of inshore fisheries for lobsters and reef species (Mohammed, 2003).

The gross efficiency of the fisheries (catch divided by net primary production) in northeastern Brazil (0.00002) was the lowest. Indeed, it was one order of magnitude lower than the weighted global average of 0.0002 (Christensen *et al.*, 2005); it is reasonable to assume that the low gross efficiency was related to the under-exploited state of the resources in the 1970s. Correspondingly, the value of primary production required (PPR) for catches originating from northeastern Brazil was very low (1.3%) compared to the values estimated by Pauly and Christensen (1995) for global catches (8%), for tropical shelves (16.1-48.8%), and for other shelf models. PPR is seen as an indication of the ecological footprint of human activities and would imply that catches in northeastern Brazil in the 1970s were having a very low impact on the marine ecosystem.

However, one has to consider that only landings were included in the model. Additionally, landings recorded in very broad categories such as 'outros peixes', 'outras espécies', 'caíco', and 'mistura' (all representing other species) were not incorporated. If all these components had been incorporated, PPR would be higher.

The mean transfer efficiency between trophic levels of 11.4% was very close to the mean calculated by Pauly and Christensen (1995) over 48 trophic models (10%). Pace *et al.* (1984) consider that trophic efficiency is highly variable and the use of a standard value of 10% may be misleading. Note that the values of transfer efficiency for the models presented in Table 3 oscillate between 6.6 and 17.6%, within the range indicated by Pauly and Christensen (1995).

All the comparisons of system statistics may be seriously affected by the definition of the system and its functional groups, as pointed out by Baird *et al.* (1991), and by the origin of the input data. More insight would be gained if a model for the current time were built for the same system and the system statistics for both periods were compared. However, because of the scarcity of basic data for northeastern Brazil, both models (the early and current period) may be based on the same data and system statistics would not differ much (see e.g. Araújo *et al.*, 2005). Besides the absence of basic data for many groups, there is the persistent problem of combining several species into one single functional group, a procedure that can mask important linkages in terms of predation or competition (Paine, 1988).

The model presented here was able to closely reproduce the biomass trends for all groups for which times series were available. However, there were several other groups that did not show any changes in biomass levels. These trends have to be looked at with reservation as some reef species have shown signs of overexploitation (Lessa *et al.*, 2004). Most biomass values were missing in this region and may seriously affect these results. Clearly, this is an area that demands more research.

Another important issue to be addressed in future developments of the model is the effect of changes in the basis of this trophic web on fisheries production, even though no estimate of such changes was available (Creed, 2003). Finally, the effect of the vulnerability settings used in the simulations has to be further assessed.

This study described some of the general features of the flows amongst trophic components in the ma-

rine ecosystem off northeastern Brazil. Indices generally used as indicators of ecosystem maturity did not allow for conclusive answers about the maturity of the East Brazil Large Marine Ecosystem. On the other hand, results indicated that recycling was an important feature of this ecosystem, which was characterised by low phytoplankton-originated primary production supplemented by high production from coastal vegetation. There was some indication that omnivory in shelves (at least tropical shelves) may be lower than in other ecosystems. Some inconsistencies in isolated estimates of biomass were found, as well as gaps in basic information required to better understand this system, even for commercial species. Catch rates were low in comparison with other shelf systems in Brazil and along other tropical shelves in the western Atlantic, which has often served as the driving force for initiatives by the federal government aimed at increasing catches from Brazilian waters. The results presented here may serve as the basis for developing future fishing policies for the marine ecosystem off northeastern Brazil within a multi-species and ecosystem approach.

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