SCIENTIA MARINA 76(4)
December 2012, 763-779, Barcelona (Spain)
ISSN: 0214-835
doi: 10.3989/scimar.03359.26A

Trophic model of the outer continental shelf and upper slope demersal community of the southeastern Brazilian Bight

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SUMMARY: It is increasingly recognized that demersal communities are important for the functioning of continental shelf and slope ecosystems around the world, including tropical regions. Demersal communities are most prominent in areas of high detritus production and transport, and they link benthic and pelagic biological communities. To understand the structure and role of the demersal community on the southeastern Brazilian Bight, we constructed a trophodynamic model with 37 functional groups to represent the demersal community of the outer continental shelf and upper slope of this area, using the Ecopath with Ecosim 6 (EwE) approach and software. The model indicates high production and biomass of detritus and benthic invertebrates, and strong linkages of these components to demersal and pelagic sub-webs. The level of omnivory indexes in this ecosystem was high, forming a highly connected trophic web reminiscent of tropical land areas. Although high levels of ascendency may indicate resistance and resilience to disturbance, recent and present fisheries trends are probably degrading the biological community and related ecosystem services.

Keywords: modelling, demersal community, Brazil, Brazilian Exclusive Economic Zone, deep sea, ecosystem, southeastern Brazil.

RESUMEN: MODELO TRÓFICO DE LA COMUNIDAD DEMERSAL DE LA PLATAFORMA CONTINENTAL EXTERIOR Y TALUD SUPERIOR DE LA CUENCA DEL SUDESTE DE BRASIL. – La importancia de las comunidades demersales para el funcionamiento de los ecosistemas de plataforma continental y talud son reconocidos alrededor del mundo, incluyendo las regiones tropicales. Esas comunidades son más prominentes en áreas con gran producción y transporte de detrito. Para entender la estructura y funcionamiento de la comunidad demersal en la Ensenada Sureste Brasileña, construimos un modelo trofodinámico con 37 grupos funcionales para representar la comunidad demersal de la plataforma continental externa y el talud superior de esa región, utilizando el paquete Ecopath con Ecosim 6 (EwE). El modelo indica que el detrito y los invertebrados son muy abundantes e importantes en la estructura de este ecosistema. El nivel de omnivoría encontrado en este ecosistema fue alto, conformando una red trófica altamente conectada, a semejanza del de las áreas tropicales terrestres.

Palabras clave: modelización, comunidad demersal, Brasil, ZEE de Brasil, aguas profundas, ecosistema, Sudeste de Brasil.

INTRODUCTION

Demersal communities are often very developed on continental shelves and slopes, especially in temperate zones. This occurs because of the abundance of detritus-based food resources from water-column and nearshore production cycles and coastal watersheds, and the consumption of this detritus by bacteria, invertebrates and vertebrates. Many of the dominant fishes inhabiting such areas are demersal, feeding largely on benthic invertebrates (e.g. Morato *et al.* 1999, Martins *et al*. 2005, Muto 2005, Velasco and Castello 2005, Carvalho and Soares 2006, Bautista-Vega *et al.* 2008). The abundance of these fish communities is reflected in their catches. In Brazil, demersal species (including fishes and invertebrates) represent about 35% of the total fishery landings (IBAMA 2008). Because of the intense exploitation of these resources, many species are overexploited or at risk of collapse (Rossi-Wongtschowski *et al.* 2006, Valentini and Pezzuto 2006, Velasco *et al*. 2007). In Brazil this situation is worsened by the lack of knowledge about these biological communities, particularly in deep sea areas, owing to only minimal investment in research and the lack of specific fisheries statistics.

Aiming to improve information about marine life in Brazil, in 1995 the project "*Avaliação do potencial sustentável de recursos vivos na Zona Econômica Exclusiva do Brasil*" (Assessment of the sustainable potential of living resources in the Brazilian Exclusive Economic Zone – REVIZEE) began to rectify the situation by making an inventory of the living resources along the Brazilian Exclusive Economic Zone (EEZ). This information can be used to estimate the biological composition and diversity of the various marine habitats in this area and, for instance, to estimate the abundance and biomass of various species in each habitat and understand their interdependence and vulnerabilities. This research foundation led to additional studies of diet composition, growth, population biology and ecosystem ecology (e.g. Muto *et al.* 2005, Nascimento 2006, Gasalla *et al*. 2007, Vaz-dos-Santos and Rossi-Wongtschowski 2007, Eleuterio 2008). In the present study, information from these previous studies was used to construct a trophodynamic model of the Brazilian Bight's outer slope and upper continental shelf to refine our understanding of the system as a whole.

The Brazilian EEZ extends beyond the continental slope along most of its length, and the slope fishery is very recent, having begun during the late 1990s (Perez *et al.* 2001, 2002, 2002b). This fishery was highly encouraged by the government, leading to an unregulated fishery. The REVIZEE-Score Sul project consequently detected overexploitation of many species in its 2000-2004 analysis (Valentini and Pezzuto 2006).

The present study is focused on the REVIZEE-Score Sul observations from the southeastern Brazilian Bight area, between Cabo Frio at 22°S and Cabo de Santa Marta Grande at 27°S. This is one of the most productive areas of the Brazilian sea, responsible for approximately 40% of Brazilian fish catches (IBAMA 2008). This area is also a large embayment, and populations restricted to this area in Brazilian waters include the Argentine hake (*Merluccius hubbsi*) stock (Vaz-dos-Santos 2006, Vaz-dos-Santos and Rossi-Wongtschowski 2007) and the Brazilian-sardine (*Sardinella brasiliensis*) stock (Saccardo 1983). This area is naturally-defined by its geography, oceanography and biology, and is thus suitable for modelling as a whole.

The main fishery resources in this area are demersal and benthic organisms such as fishes (teleosts and chondrichthyans) and invertebrates (molluscs and crustaceans). Some of the fish species such as Argentine hake (*Merluccius hubbsi*), Brazilian cod (*Urophycis mystacea*) and blackfin goosefish (*Lophius gastrophysus*) were previously discarded or used as bait, but now feature in the landings. Most of these species are now fully exploited or overexploited (Valentin and Pezzuto 2006). Also, the REVIZEE-Score Sul studies showed some abundant species that were not exploited but were important in the diet composition of targeted species. The stomach contents of some of these species (*Antigonia capros,* a bentho-pelagic invertebrate feeder; Ariomma bondi and *Ventrifossa macropogon,* benthic invertebrates feeders; *Synagrops spinosus* and *Synagrops bellus,* benthic fish and crustacean feeders; and the commercial fishes *Urophycis mystacea* and *Genypterus brasiliensis,* which live and feed near the bottom) were sampled by MCN, GV, and ACZA (unpublished data) and by Nascimento (2006). These diet studies indicate the importance of these species in linking the benthos with upper trophic levels, as many feed on benthos directly and are in some cases prey for top predators.

Although some trophic studies have been performed in this area, we felt that they had underemphasized the benthic community, which has a high biomass and may provide important ecological services. We therefore set out to investigate the ecological importance of the benthic community in this setting by articulating it in the model so that associated flows and dynamics could emerge from the present summaries and later dynamic analyses.

As mentioned above, exploitation of the demersal community of the outer continental shelf and upper slope of the southeastern Brazilian Bight began a decade ago, and it has reached high exploitation levels and is largely unrestricted. A main objective of this research is to understand how fisheries might affect this community, how global scale environmental change (i.e. climate change) may affect it, and how these effects may be combined. The present study is the first step in this research to construct a trophodynamic characterization of this highly developed demersal and bentho-pelagic community.

MATERIAL AND METHODS

Study area

The study area was the outer continental shelf and upper slope of the southeastern Brazilian Bight, located between Cabo Frio (22°S) and Cabo de Santa Marta Grande (27°S). A large-scale boundary current, the Brazil Current, flows poleward along and beyond the continental shelf break of the Brazilian Bight. This cur-

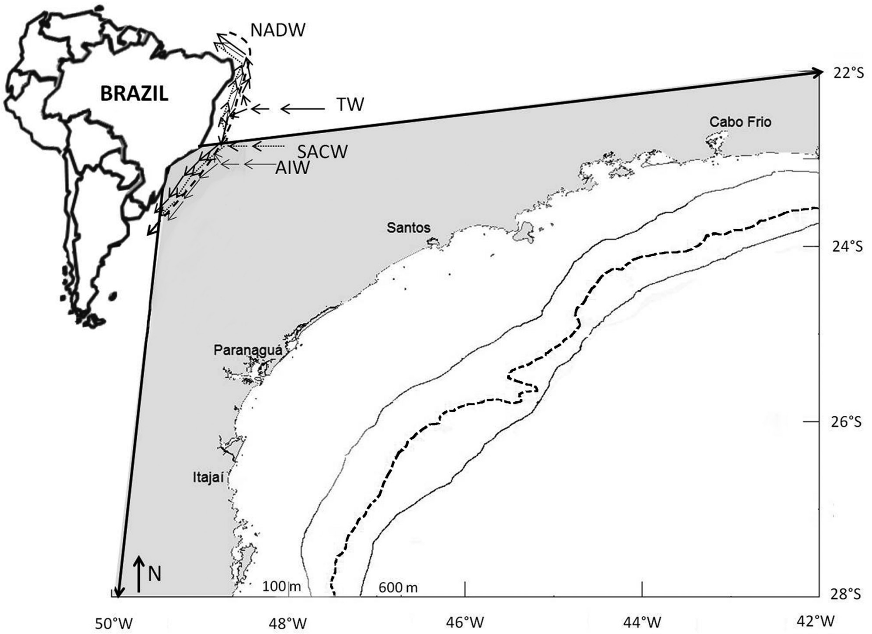

Fig. 1. – Map of the modelled area (between 100 and 600 m). This drawing is based on REVIZEE (MMA 2006). The dashed line represents the continental shelf break (200 m). Arrows represents the main currents: South Atlantic Central Water (SACW); Antarctic Intermediate Water (AIW); Tropical Water (TW); North Atlantic Deep Water (NADW).

rent, along with the alongshore and cyclonic curl of the wind stress over the Bight, forms a doming of the density structure and this all drives closed gyral circulation cells within the Bight. In addition, there is an intense coastward penetration of cool South Atlantic Central Water (SACW) over the continental shelf floor during the summer season. The SACW contrasts with the overlying warm, tropical surface water, resulting in a strong two-layer vertical stratification, a strong thermocline at depths of 10 to 15 m, and corresponding stability of the water column (Bakun 1996, MMA 2006, Rossi-Wongtschowski and Madureira 2006; Fig. 1).

This site was extensively sampled during the REVIZEE-Score Sul project. The fish community was sampled by bottom trawl surveys in the isobaths 100, 150, 200, 300, 400, 500 and 600 m between the winter of 2001 and the autumn of 2002 (Haimovici *et al.* 2008). The invertebrate community was collected by conical traps (for crabs) between autumn 1996 and spring 1998 and by van Veen benthic samplers, box-corers and rectangular dredges between summer 1997 and autumn 1998 (Amaral and Rossi-Wongtschowski 2004).

The modelling area of 81658 km^2, based on Haimovici *et al.* 2008, includes the outer continental shelf and upper slope between 100 and 600 m. The model represents the year 2001 when most fish samples were collected, although a large part of the invertebrate data were collected in the 1990s. The main fish species of this system were defined by Haimovici *et al.* 2008, comprising about 80% of the total fish biomass of this system in 2001, and these made up the fish functional groups in the model. A number of fish species were therefore not included in this iteration of the model because of practical limitations of data and analytical time, but these can be included in future model iterations with additional efforts.

To build the trophic model we used Ecopath with Ecosim version 6, a modelling tool initially developed by Polovina (1984) and further developed since then (Christensen and Pauly 1992, Walters *et al.* 1997, Christensen and Walters 2004, Christensen *et al.* 2008). This program can be used to build a mass balanced model that provides a quantitative representation of the ecosystem in terms of trophic flows and biomasses for a defined time period (Velasco and Castello 2005, Coll *et al.* 2007, Christensen *et al.* 2008). The ecosystem is represented by functional groups, which can be single species, groups of ecologically related species, or ontogenetic stages of a species. The key principle of Ecopath is mass balance i.e. the energy of one group is used by another or is recycled via detritus, a portion of which re-enters the system through detritivores and as nutrient that is consumed by primary producers (Christensen *et al.* 2008). Two linear equations represent the energy balance within a group and the energy balance among groups.

$$P_i = Y_i + B_i \times M2_i + E_i + BA_i + P_i(1 - EE_i) \qquad (1)$$

where P_i is the total production rate of i; Y_i is the total fishery catch rate of i; B_i is the biomass of the group; $M2_i$ is the total predation rate for group i; E_i is the net migration rate (emigration – immigration); BA_i is the biomass accumulation rate for i; while $M0_i = P_i \times (1 - EE)$ is the "other mortality" rate for i. EE_i is the ecotrophic efficiency of i and is the proportion of production used in the system, e.g. by predators, in biomass accumulation, in migration or in export.

Equation 1 can be re-expressed as:

$$B_i \times (P/B)_i - \sum_{j-1}^{n} B_j \times (Q/B)_j \times DC_{ji} - (P/B)_i \times B_i \times (1 - EE_i) - \\ - Y_i - E_i - BA_i = 0 \qquad (2)$$

where $(P/B)_i$ indicates the production of *i* per unit of biomass and is equivalent to total mortality, or Z, under static conditions (Allen 1971); $(Q/B)_i$ is the consumption of *i* per unit of biomass; DC_{ij} indicates the proportion of prey *i* that is in the diet of predator *j* in terms of volume or weight units. Ecopath parameterizes the model by describing a system of linear equations for all the functional groups in the model (Christensen and Walters 2004, Christensen *et al.* 2008).

The second Ecopath equation is:

$$Q_i = P_i + X_i + R_i \qquad (3)$$

where Q_i is the consumption rate of prey *i* per unit of biomass, P_i is the production of prey *i* per unit of biomass, X_i is the combined excretion and egestion rate of prey *i*, and R_i is the respiration rate. To parameterize the model, three out of four basic parameters must be provided: biomass (*B*), production/biomass (*P/B*), consumption/biomass (*Q/B*), and ecotrophic efficiency (*EE*); the algorithm then estimates the fourth parameter so as to ensure mass balance. Diet composition, catch data, food assimilation, migration and biomass accumulation are also required inputs.

Some of the necessary input parameters were calculated from our own field data (from REVIZEE-Score Sul), based on the mean temperature of water at the most frequent depth where each species occur (annual mean temperature of each depth is based on CTD data from trawl surveys). The estimation of *Q/B* was based on Palomares and Pauly (1998) and *P/B* was based on Jorgensen (1979); in cases of unexploited populations we used Pauly's (1980) natural mortality equation to obtain the *P/B* value. Others were obtained from the literature. This information is summarized in Appendix 1.

The biological community of the outer continental shelf and upper slope of the southeastern Brazilian Bight was divided into 37 functional groups to build the model. Of these groups 12 were invertebrates, 21 were fishes, 2 were detritus (detritus and marine snow) and 1 was phytoplankton; this last group was included as an input for marine snow and in this case all excess production of phytoplankton was converted to marine snow. This effectively means that marine snow is made up of detritus in the system, so the phytoplankton source is used as a proxy for the more diverse sources and feedbacks of marine snow, including microbial loop dynamics. These groups were defined on the basis of habitat, body size, type of food, biology, ecology and physiology of the most abundant and economically important species. The main references for building these groups are Haimovici *et al.* (2008), and Amaral and Rossi-Wongtschowski (2004), who describe the fish demersal and benthos community respectively. The other references used are listed in Appendix 1. Gasalla *et al.* (2007) built a model of the area from Cabo Frio (RJ) to southern Brazil (Chuí – RS) between 100 and 1000 m depth. This initial trophodynamic modelling work in this region synthesized a large amount of knowledge about this system, particularly regarding demersal and pelagic species, which were the focus of that model. Although the model described in the present paper includes part of the area modelled by Gasalla *et al.* (2007), we focused more on the demersal and benthic community, providing more detail about this community, recognizing the importance of benthic and demersal invertebrates for the structure, functions and flows of the broader biological community. The functional groups of the present southeastern Brazilian Bight model and the main species comprising them are listed in Table 1.

The main commercial species are *Lophius gastrophysus* (blackfin goosefish); *Urophicis mystacea* (Brazilian cod); *Trichiurus lepturus* (cutlassfish); *Helicolenus lahillei* (blackbelly rosefish); *Lopholatilus villarii* (tile fish); *Merluccius hubbsi* (Argentine hake); *Prionotus punctatus* (searobin) and *Pagrus pagrus* (red porgy), here represented as a single-species functional group; and *Paralichthys* sp. (flounders) and *Illex argentinus* (squid), here represented as a multispecific functional group. The majority of catches were based on trawls and longline fisheries (Valentini and Pezzuto 2006). Many of these species used to be discarded by the fleets fishing for shrimp, flounder and pelagic species, but in the last 20 years they have become commercial species. Currently, some of these species are overexploited (Rossi-Wongtschowski *et al.* 2006, Valentini and Pezzuto 2006). Also crabs, shrimps, and squids support important fisheries in the area, being among the most important resources, and some species of shrimps and crabs are also at risk of overexploitation (Valentini and Pezzuto 2006, IBAMA 2008).

Argentine hake is an important resource in terms of biomass and catch in the area. It is known that the diet of this species differs considerably between life stages, and it exhibits a high level of cannibalism (Angelescu and Prenski 1987, Bezzi *et al.* 1994, Brown *et al.* 2004). Therefore, to ensure consistency between ontogenetic groups (juveniles and adults), a multi-stanza representation (Christensen and Walters 2004) was used for modelling this group. Two groups were defined considering the diet composition and behaviour: Juveniles with lengths of less than 28 cm, and adults with lengths of more than 28 cm (Vaz-dos-Santos *et al.* 2009). (P/B) and diet composition were provided for both groups from Bezzi *et al.* (1994), Brown *et al.* (2004) and Sánches (2009).

The fishing statistics we used for the model were based on the official statistic of the Ministry of the Environment (MMA). We specified a rate of fishery

TABLE 1. – Name and main components of each functional group.

- Blackfin goosefish
  - *Lophius gastrophysus*
- Cutlassfish
  - *Trichiurus lepturus*
- Rosefish
  - *Helicolenus lahillei*
- Tile fish
  - *Lopholatilus villarii*
- Argentine hake
  - *Merluccius hubbsi*
- Searobin
  - *Prionotus punctatus*
- Red porgy
  - *Pagrus pagrus*
- Demersal sharks
  - *Mustellus* sp.
  - *Squalus* sp.
  - *Carcharhinus* sp.
  - *Heptranchias perlo*
- Argentine croaker
  - *Umbrina canosai*
- Bentho-pelagic fishes
  - *Caelorinchus marinii*
  - *Xenolepidichthys dalgleishi*
  - *Sphoeroides pachygaster*
  - *Beryx splendens*
- Large bentho-pelagic fishes
  - *Lepidopus altfrons*
  - *Malacocephalus occidentalis*
  - *Thyrsitops lepidopoidees*
  - *Zenopsis conchifera*
- Deepbody boarfish
  - *Antigonia capros*
- Silver-rag driftfish
  - *Ariomma bondi*
- Pink cusk-eel
  - *Genypterus brasiliensis*
- ***Synagrops*** **sp.**
  - *Synagrops bellus*
  - *Synagrops spinosus*
- Brazilian cod
  - *Urophycis mystacea*
- Longbeard grenadier
  - *Ventrifossa macropogon*
- Squid
  - *Illex argentinus*
  - *Loligo plei*
  - *Loligo sanpaulensis*
- Large demersal fishes
  - *Nemadactylus bergi*
  - *Epinephelus nivelatus*
  - *Pseudopercis numida*
  - *Ariosoma opistophthalmus*
  - *Bassanago albescens*
  - *Conger esculentus*
  - *Conger orbignianus*
- Demersal fishes
  - *Mullus argentinae*
  - *Polymixia lowei*
  - *Chilomycterus spinosus*
  - *Dactylopterus volitans*
  - *Bellator brachychir*
  - *Saurida* sp.
- Benthic fishes
  - *Paralichthys isosceles*
  - *Paralichthys patagonicus*
  - *Paralichthys triocellatus*
  - *Bembrops heterurus*
  - *Raneya brasiliensis*
- Skates
  - *Atlantoraja cyclophora*
  - *Atlantoraja platana*
- Predator crustaceans
  - *Hemisquilla brasiliensis*
  - *Squilla* sp.
- Predator molluscs
  - *Conus villepinii*
  - *Chicoreus* sp.
  - *Polinices lacteus*
  - *Nassarius* sp.
  - *Bursa ranelloides tenuisculpta*
  - *Conus mazei*
  - *Calliostoma* sp.
  - *Nanomelon viperinus*
  - *Symplectoscyphus* sp.
  - *Scaeurgus unicirrhus*
  - *Vosseledone charrua*
  - *Eudendrium* sp.
  - *Acryptolaria* sp.
  - *Ancilla* sp.
  - *Nanomelon* sp.
  - *Eledone massyae*
  - *Octopus vulgaris*
- Other predator invertebrates
  - *Nausithoe* sp.
  - *Atorella* sp.
  - *Ctenodiscus* sp.
  - *Astropecten* sp.
  - *Allostichaster hartii*
- Omnivore invertebrates
  - *Acanthochitona* sp.
  - *Echinocyamus grandiporus*
  - *Stylocidaris lineata*
  - Isopoda
  - Amphipoda
  - Chaetognatha
- Crabs
  - *Chaceon* spp.
  - Euprognatha sp.
  - *Stenocionops* spp.
  - *Portunus* spp.
  - *Munida* spp.
  - *Scyllarides deceptor*
- Shrimps
  - *Alpheus* spp.
  - *Heterocarpus* spp.
  - *Rhynchocinetes* spp.
  - *Acanthephyra* spp.
  - Oplophorus sp.
- Bivalves
  - *Corbula* spp.
  - *Limopsis janeiroensis*
- Polychaetes
  - *Exogone* (*Exogone*) sp.
  - *Nereis* spp.
  - *Diopatra* spp.
  - *Kinbergonuphis* spp.
  - *Mooreonuphis* spp.
  - *Nothria* spp.
  - Eunicidae
  - *Pseudovermilia occidentalis*
  - *Sphaerosyllis* (*Prosphaerosyllis*) sp.
  - *Spiophanes berkeleyorum*
  - *Spiophanes* spp.
  - *Micronereides capensis*
  - *Pseudovermilia* sp.
  - Ampharetidae
- Other detritivore invertebrates
  - *Pyura* sp.
  - *Ophiura ljungmani*
  - *Ophiura* sp.
  - *Ophiomisidium pulchellum*
  - *Ophiothrix rathbuni*
  - *Amphiura complanata*
  - *Raspailia* spp.
  - *Cupuladria* sp.
  - *Discoporella umbellata*
  - *Bouchardia rosea*
  - *Democrinus* sp.
- Infauna
  - Nematoda
  - *Nephasoma* sp.
  - *Aspidosiphon mexicanus*
  - *Aspidosiphon laevis*
  - Echiura
  - Priapulida
  - Hemichordata
- Zooplankton
  - Zooplankton
- Marine snow
  - Phytoplankton (not consumed by the pelagic system)
- Detritus
  - Dead organic matter of the system (cycled)

discards for all groups, normalized to represent 25% of the total catch, based on data from Haimovici (2007), who found a range of 24% to 53% depending on gear and species. This applied estimate was thus conservative. The input data for each functional group are shown in Table 2.

The diet matrix was based on diet composition studies. The non-fished species that represented individual functional groups, in addition to Brazilian cod and pink cusk-eel, were analysed by MCN, ACZA and GV (unpublished data). The diet information for other functional groups was based on data from the literature (Soares 1992, Tubino 1999, Muto *et al.* 2005, Martins *et al.* 2006, Rodrigues 2007). The complete reference list is in Appendix 1. The original diet matrix is shown in Table 3.

The model generated with the data was not balanced initially, 11 functional groups needed to be balanced: Argentine hake, searobin, Argentine croaker, S*ynagrops* sp., squid, large demersal fishes, demersal fishes, benthic fishes, other predator invertebrates and omnivore invertebrates. The main problem in balancing this model was to coordinate ways to fix problems in the biomass of some groups, especially Argentine hake. This is a multistanza group that is highly fished, but only the adults are removed; the juveniles are dis-

TABLE 2. – Input data. B_i, initial biomass (t km^{-2}); EE, ecotrophic efficiency; P/B, production/biomass ratio (yr^{-1}); Q/B, consumption/biomass ratio (yr^{-1}). Landings and discards in t km^{-2} yr^{-1}.

	Functional groups	B_i	EE	P/B	Q/B	Landings	Discards
1	Blackfin goosefish	0.115	-	0.3	2.3	0.0061	0.0003
2	Cutlassfish	0.031	-	2.49	3.1	0.0011	0.0003
3	Rosefish	0.016	-	0.07	4.76	-	-
4	Tile fish	0.021	-	0.74	1.38	0.0006	0.0003
5	Argentine hake	0.283	-	0.95	2.96	0.0022	0.0003
6	Searobin	0.011	-	0.382	9.19	0.0032	0.0028
7	Red porgy	-	0.95	0.89	3.4	0.0011	0.0003
8	Demersal sharks	0.019	-	0.355	2.3215	-	0.0003
9	Argentine croaker	0.075	-	0.6	4.3	0.0053	0.0003
10	Bentho-pelagic fishes	0.085	-	0.404	4.125	0.000008	-
11	Large bentho-pelagic fishes	0.472	-	0.3	3.183	-	-
12	Deepbody boarfish	0.203	-	0.61	5.9	-	-
13	Silver-rag driftfish	0.252	-	1.05	4.6	-	-
14	Pink cusk-eel	0.042	-	0.5	2.8	0.0005	-
15	*Synagrops* sp.	0.168	-	1.08	5.9	-	-
16	Brazilian cod	0.069	-	0.7	2.5	0.0024	0.0014
17	Longbeard grenadier	0.003	-	0.32	2.9	-	-
18	Squid	0.256	-	4.6	36.5	0.0011	-
19	Large demersal fishes	0.028	-	1	4.2	0.0005	-
20	Demersal fishes	0.397	-	0.48	6.507	0.0008	-
21	Benthic fishes	0.077	-	0.07	4.175	0.0017	0.007
22	Skates	0.051	-	0.14	4.432	0.0019	-
23	Predator crustaceans	0.150	-	4.6	14.45	-	-
24	Predator molluscs	0.287	-	4.5	20	0.001	-
25	Other predator invertebrates	0.899	-	0.5	20	-	-
26	Omnivore invertebrates	0.356	-	5.71	20	-	-
27	Crabs	1.580	-	3.17	19	0.0019	-
28	Shrimps	2.673	-	22.01		0.0107	-
29	Bivalves	15.493	-	0.6	20.83	0.000003	-
30	Polychaetes	7.709	-	3.5	20.83	-	-
31	Other detritivore invertebrates	4.215	-	4.5	12.2	0.00007	-
32	Infauna	4.215	-	14.6	40	-	-
33	Zooplankton	3.600	-	104	248	-	-
34	Marine snow	-	-	-	-	-	-
35	Detritus	-	-	-	-	-	-

carded, and there is also cannibalism in the population. The rest of the groups were balanced but the P/Q values very high, requiring some adjustments, mainly to the P/B and P/Q values.

Argentine hake, bentho-pelagic fishes, *Synagrops* sp. large demersal fishes, demersal fishes and benthic fishes were the most difficult groups to balance. This difficulty was probably related to the number of connections that these species have, although the majority are not fished (excluding Argentine hake and the benthic fish groups). The input data of these groups was modified with the aim of balancing the model. The modifications were based on ecological and physiological criteria. Table 4 shows the adjusted input values and several outputs and Table 5 shows the modified diet matrix.The Ecopath algorithm also calculates some key Odum's attributes used to indicate system maturity (Christensen 1995), and we present omnivory index, system omnivory index, connectance, and relative ascendency.

The omnivory index (OI) is calculated as the variance of the trophic level of a consumer's prey groups. A value of the OI close to zero means a specialized predator. A high value means that the consumer feeds on many trophic levels. The system OI is the average omnivory index of all consumers, weighted by the logarithm of the food intakes (Christensen 1995).

The connectance of the system measures the structure of the food web; it is the ratio of the number of actual links to the number of possible links. Ascendency is a measure of the average mutual information in a system, scaled by system throughput, and is derived from information theory. The relative ascendency is the system ascendency over the system capacity.

Also, Ecopath calculates a ranking of a continuum of functional group keystoneness developed by Libralato *et al.* (2006). Keystone species, in this case keystone functional groups, are those with high interaction strengths but low biomasses (Power *et al.* 1996, Okey 2004) Libralato's (2006) keystoneness index calculated by Ecopath is:

$$KS_i = \log [\varepsilon_i(1-p_i)]$$

where KS_i is the keystoneness index; ε_i is the root of the sum of mixed trophic impact matrix value^2 (the mixed trophic impact matrix is the positive or negative impact by one group on another); and p_i is the biomass of impacted group/total biomass (excluding detritus).

RESULTS

This food web is essentially based on detritus (Fig. 2) because it is a deep sea ecosystem, so primary pro-

Table 3. – Original diet matrix based on diet composition studies listed in Appendix 1.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1	Blackfin goosefish																																	
2	Cutlassfish				0.05	0.07				0.01																								
3	Rosefish																																	
4	Tile fish					0.00																												
5	Argentine hake	0.36			0.05				0.05	0.04							0.20		0.22															
6	Searobin																																	
7	Red porgy																																	
8	Demersal sharks																																	
9	Argentine croaker							0.02											0.01															
10	Bentho-pelagic fishes			0.38	0.05												0.01				0.04													
11	Large bentho-pelagic fishes	0.03	0.39	0.07	0.05												0.01																	
12	Deepbody boarfish																							0.01										
13	Silver-rag driftfish																					0.01		0.01										
14	Pink cusk-eel																																	
15	*Synagrops* sp.	0.36							0.00	0.02							0.04		0.05		0.04	0.02	0.05	0.01										
16	Brazilian cod	0.01			0.02																													
17	Longbeard grenadier					0.20																												
18	Squid	0.08	0.02	0.15	0.10			0.05	0.20	0.01	0.04				0.10	0.15	0.51	0.00	0.05		0.03													
19	Large demersal fishes														0.69					0.02		0.05	0.01											
20	Demersal fishes	0.14		0.01											0.01	0.45	0.03				0.05	0.04		0.10	0.10		0.02							
21	Benthic fishes														0.01						0.05			0.01	0.10									
22	Skates																																	
23	Predator crustaceans					0.02	0.04			0.05			0.00	0.01	0.04	0.01	0.02				0.00		0.08	0.10			0.05							
24	Predator molluscs	0.00	0.21					0.12		0.0 11	0.00		0.00	0.26			0.00						0.02	0.10			0.01							
25	Other predator invertebrates											0.10								0.00	0.00		0.00	0.10	0.10	0.10	0.01							
26	Omnivore invertebrates					0.01	0.01			0.17	0.14	0.40	0.10	0.00	0.00	0.00		0.07	0.05	0.01	0.02	0.09	0.08	0.15	0.05	0.15	0.05				0.30			
27	Crabs			0.29	0.03	0.01	0.40	0.04	0.18	0.18	0.18	0.00			0.13	0.38	0.02	0.06	0.02	0.30	0.50	0.22	0.28	0.01	0.08	0.08	0.10							
28	Shrimps				0.03	0.16	0.50	0.30	0.19	0.14		0.00	0.78	0.70			0.01	0.71	0.02	0.07	0.04	0.21	0.30	0.11	0.08	0.08	0.11							
29	Bivalves					0.02														0.05			0.10	0.19	0.15	0.25	0.01							
30	Polychaetes			0.01			0.05	0.10		0.19	0.08	0.40						0.00	0.02	0.50	0.04	0.24	0.08	0.10	0.15	0.15	0.25							
31	Other detritivore invertebrates			0.04				0.15			0.02		0.01	0.00		0.00				0.05			0.00		0.10	0.10	0.01							
32	Infauna			0.02				0.20		0.19		0.07								0.00			0.00		0.10	0.10	0.01				0.20			
33	Zooplankton					0.15							0.03	0.03		0.00		0.06				0.14					0.20	0.05	0.05		0.05			
34	Marine snow																										0.17	0.25	0.25	0.90	0.20	0.50	0.05	1
35	Detritus																											0.70	0.70	0.10	0.25	0.50	0.95	
36	Import	0.02	0.39	0.04	0.62	0.36		0.01	0.38		0.54	0.03	0.08		0.01		0.15	0.10	0.58		0.20													
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4. – Input data modified to balance the model and the main output data. TL, Trophic level; Bf, final biomass (t km^{-2}); P/B, production/biomass ratio (yr^{-1}); Q/B, consumption/biomass ratio (yr^{-1}); EE, ecotrophic efficiency; P/Q, production/consumption ratio or gross efficiency; F, fishing mortality (yr^{-1}); M2, predation mortality (yr^{-1}); Mo, other natural mortality (yr^{-1}); F/Z, exploitation rate; OI, omnivory index; NE, net efficiency; R/A, respiration/assimilation ratio; FD, flow to detritus (t km^{-2} yr^{-1}). The "input" EwE estimated parameters are in bold.

	Functional groups	TL	Bf	P/B	Q/B	EE	P/Q	F	M2	M0	F/Z	OI	NE	R/A	FD
1	Blackfin goosefish	4.708	0.115	0.4	2.3	**0.572**	0.174	0.059	0.170	0.171	0.149	0.276	0.217	0.783	0.072
2	Cutlassfish	4.652	0.063	0.91	3.1	**0.972**	0.294	0.029	0.836	0.026	0.033	1.721	0.367	0.633	0.041
3	Rosefish	4.179	0.016	0.8	4.8	**0.362**	0.167	-	0.290	0.510	-	0.752	0.208	0.792	0.023
4	Tile fish	4.640	0.021	0.74	2.5	**0.329**	0.296	0.062	0.182	0.497	0.083	2.172	0.370	0.630	0.021
5	Juvenile Argentine hake	3.335	0.797	**2.3**	7.199	**0.981**	0.319	0.008	2.241	0.044	0.003	0.435	0.399	0.601	1.183
6	Adult Argentine hake	4.310	0.360	**0.95**	2.7	**0.926**	0.352	0.004	0.876	0.070	0.004	1.470	0.440	0.560	0.220
7	Searobin	3.161	0.016	0.38	2.5	**0.527**	0.152	0.197	0.003	0.180	0.518	0.135	0.190	0.810	0.011
8	Red porgy	3.400	**0.009**	0.89	3.5	0.950	0.254	0.637	0.208	0.045	0.716	0.377	0.318	0.682	0.007
9	Demersal sharks	3.978	0.019	0.36	2.300	**0.053**	0.157	0.019	0.000	0.341	0.053	1.049	0.196	0.804	0.015
10	Argentine croaker	3.514	0.090	0.6	4.3	**0.886**	0.140	0.004	0.528	0.068	0.007	0.422	0.174	0.826	0.083
11	Bentho-pelagic fishes	3.640	0.160	0.73	4.1	**0.719**	0.178	-	0.505	0.205	-	1.102	0.223	0.777	0.164
12	Large bentho-pelagic fishes	3.847	0.477	0.3	2	**0.991**	0.150	-	0.278	0.003	-	0.128	0.188	0.813	0.192
13	Deepbody boarfish	3.159	0.203	0.61	5	**0.312**	0.122	0.003	0.158	0.420	0.005	0.116	0.153	0.848	0.289
14	Silver-rag driftfish	3.395	0.252	1.05	4.6	**0.988**	0.228	-	1.037	0.013	-	0.338	0.285	0.715	0.235
15	Pink cusk-eel	4.691	0.052	0.5	2.8	**0.919**	0.179	0.072	0.387	0.040	0.145	0.698	0.223	0.777	0.031
16	*Synagrops* sp.	3.855	0.204	1.11	5.6	**0.985**	0.198	-	1.090	0.000	-	0.636	0.248	0.752	0.226
17	Brazilian cod	4.797	0.075	0.7	2.5	**0.994**	0.280	0.033	0.654	0.004	0.047	0.466	0.350	0.650	0.038
18	Longbeard grenadier	3.121	0.003	0.62	2.9	**0.900**	0.214	0.138	0.419	0.062	0.223	0.102	0.267	0.733	0.002
19	Squid	3.967	0.256	6.7	36.50	**0.981**	0.184	0.003	6.523	0.124	-	1.725	0.229	0.771	1.902
20	Large demersal fishes	3.497	0.038	1.08	4.20	**0.855**	0.257	0.227	0.697	0.156	0.210	0.223	0.321	0.679	0.038
21	Demersal fishes	3.478	0.447	1.14	3.90	**0.981**	0.292	0.004	1.114	0.022	0.004	0.571	0.365	0.635	0.358
22	Benthic fishes	3.484	0.280	1.3	5.175	**0.736**	0.251	0.025	0.932	0.343	0.019	0.310	0.314	0.686	0.386
23	Skates	3.438	0.051	0.14	4.4	**0.115**	0.032	0.016	-	0.124	0.115	0.379	0.040	0.960	0.052
24	Predator crustaceans	3.715	0.150	5	14.5	**0.523**	0.345	-	2.615	2.385	-	0.408	0.431	0.569	0.793
25	Predator molluscs	3.334	0.288	4.5	20	**0.873**	0.225	-	3.927	0.573	-	0.263	0.281	0.719	1.317
26	Other predator invertebrates	3.353	0.899	3.5	20	**0.744**	0.175	0.002	2.603	0.895	0.001	0.226	0.219	0.781	4.401
27	Omnivore invertebrates	3.000	4.495	**12**	12	**0.990**	1.000	0.002	11.878	0.120	-	0.477	1.250	-0.250	11.328
28	Crabs	2.050	1.580	3.17	19	**0.808**	0.167	-	2.560	0.610	-	0.048	0.209	0.791	6.967
29	Shrimps	2.050	2.673	6	20	**0.348**	0.300	-	2.088	3.912	-	0.048	0.375	0.625	21.149
30	Bivalves	2.000	15.493	0.6	20.83	**0.751**	0.029	-	0.451	0.149	-	-	0.036	0.964	66.855
31	Polychaetes	2.850	7.709	3.5	20.83	**0.688**	0.168	-	2.408	1.092	-	0.727	0.210	0.790	40.538
32	Other detritivore invertebrates	2.000	4.215	4.5	12.2	**0.429**	0.369	-	1.930	2.570	-	-	0.461	0.539	21.117
33	Infauna	2.000	4.215	14.6	40	**0.598**	0.365	-	8.730	5.870	-	-	0.456	0.544	58.463
34	Zooplankton	2.000	3.6	104	248	**0.092**	0.419	-	9.530	94.470	-	-	0.524	0.476	518.652
35	Phytoplankton	1.000	15	182.96	-	-	-	-	-	182.960	-	-	-	-	2744.4
36	Marine snow	1.000	15	-	-	**0.468**	-	-	-	-	-	-	-	-	-
37	Detritus	1.000	30	-	-	**0.418**	-	-	-	-	-	0.086	-	-	-

duction is indirectly important as a source of marine snow production. The biomass of benthic invertebrates is quite high and this resource is consumed by every functional group.

Demersal fishes, in general, provide the most prominent connection between the recycling of detritus and the top predator groups. In the present model, these top predators are the large demersal species, including some commercial fishes, and the demersal sharks, although the top predators are also eaten by some pelagic species. These demersal fishes are centrally important in transferring energy from the bottom to the water column, but pelagic species in the overlying system are important couplers as well. In the present model the trophic relationship between demersal and pelagic species was specified as exported and imported biomass, and this was a key pathway for constructing the trophic web. Although these species are important for the transfer of energy from the bottom to the water column, benthic invertebrates are also consumed by all trophic levels, showing a high level of omnivory (Table 3).

As benthic invertebrates occupy the lower levels of the food web, fish species are positioned higher in the web, and this is why the mean trophic level of catches is 3.5.

High scores for the OI are exhibited by tilefish (2.172), squid (1.725), cutlassfish (1.721), Argentine hake adult (1.470), bentho-pelagic fishes (1.102) and demersal sharks (1.049). Silver-rag driftfish, Brazilian cod, pink cusk-eel and *Synagrops* sp. also exhibited high OI values, but these were lower than 1. The total connectance of the system is 0.224 and the system OI is 0.422. This food web is comprised of organisms with highly diverse diet compositions.

The predation mortality of a group is the sum of the consumption of this group by the other groups, divided by their own biomass; the value ranges from 0 to 1. In the present model the value of predation mortality is high on omnivore invertebrates (11.88), zooplankton (9.53), infauna (8.73), squid (6.53), predator molluscs (3.93), other predatory invertebrates (3.6), predatory crustaceans (2.62), crab (2.57), polychaetes (2.41), shrimp (2.09), hake juveniles (2.24), other detritivory invertebrates (1.93), demersal fish (1.12), *Synagrops* sp. (1.07), silver-rag driftfish (1.04) and benthic fishes (0.93).

High EE values were found for many groups: cutlassfish, Argentine hake, large bentho-pelagic fishes, silver-rag driftfish, pink cusk-eel, *Synagrops* sp., Bra-

TABLE 5. – Diet matrix adjusted to balance the model.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1	Blackfin goosefish						0.02																												
2	Cutlassfish				0.03		0.05				0.006																								
3	Rosefish				0.00					0.1																									
4	Tile fish					0.00	0.00			0.04																									
5	Argentine hake juvenile	0.21			0.05		0.05			0.03	0.022							0.14		0.18															
6	Argentine hake adult	0.05			0.01					0.03	0.02							0.06		0.03															
7	Searobin				0.00																														
8	Red porgy		0.01																																
9	Demersal sharks																																		
10	Argentine croaker								0.02											0.01															
11	Bentho-pelagic fishes			0.2	0.05													0.01				0.04													
12	Large bentho-pelagic fishes	0.28	0.2	0.2	0.05													0.01																	
13	Deepbody boarfish	0.02	0.04	0.01												0.05						0.01		0.01											
14	Silver-rag driftfish	0.03	0.00	0.01			0.01									0.04	0.1			0.01		0.01	0.01	0.01											
15	Pink cusk-eel	0.00	0.02	0.01			0.01											0.02			0.01														
16	*Synagrops* sp.	0.11		0.01			0.01			0.00	0.017					0.1		0.02		0.01		0.02	0.02	0.03											
17	Brazilian cod	0.01	0.02	0.01	0.02		0.01									0.2																			
18	Longbeard grenadier															0.01																			
19	Squid	0.08	0.02	0.15	0.1	0.1	0.22		0.05	0.2	0.014	0.04				0.1	0.15	0.51	0.00	0.05		0.03													
20	Large demersal fishes															0.16					0.01			0.01											
21	Demersal fishes	0.09		0.01												0.1	0.25	0.03				0.03	0.04		0.01	0.01									
22	Benthic fishes															0.01						0.08	0.01		0.01	0.02									
23	Skates																																		
24	Predator crustaceans						0.04	0.04			0.050			0.00	0.01	0.04	0.01	0.02				0.00	0.04	0.08	0.1										
25	Predator molluscs	0.00	0.21						0.12			0.00		0.00	0.26									0.02	0.11			0.01							
26	Other predator invertebrates												0.1								0.00			0.00	0.1	0.1	0.05	0.01							
27	Omnivore invertebrates					0.1	0.02	0.01			0.100	0.14	0.35	0.1	0.00		0.00		0.07	0.03	0.01	0.02	0.09	0.08	0.11	0.02	0.15	0.01				0.3			
28	Crabs			0.29	0.03		0.04	0.4	0.04	0.18	0.180	0.18	0.00			0.13	0.38	0.02	0.06	0.02	0.3	0.5	0.22	0.28	0.04	0.08	0.08								
29	Shrimps				0.03	0.1	0.16	0.5	0.30	0.29	0.140		0.00	0.78	0.6		0.1	0.01	0.71	0.02	0.07	0.04	0.21	0.3	0.1	0.08	0.08	0.01							
30	Bivalves						0.02														0.05			0.1	0.08	0.3	0.25	0.01							
31	Polychaetes			0.01				0.05	0.1		0.190	0.08	0.4						0.00	0.02	0.5	0.04	0.24	0.08	0.15	0.15	0.15	0.25							
32	Other detritivore invertebrates			0.04					0.15			0.02		0.01	0.00						0.05				0.15	0.1	0.1	0.1							
33	Infauna			0.02					0.2		0.190		0.07								0.00					0.1	0.1	0.04				0.2			
34	Zooplankton					0.6		0.01			0.07		0.05	0.03	0.13		0.00		0.06	0.02			0.14		0.05	0.05	0.05	0.31	0.05	0.05		0.05			
35	Marine snow																											0.25	0.25	0.25	0.9	0.2	0.5	0.05	1
36	Detritus																												0.7	0.7	0.1	0.25	0.5	0.95	
37	Import	0.13	0.49	0.04	0.62	0.1	0.34		0.01	0.133		0.54	0.03	0.08		0.01		0.15	0.10	0.62		0.2													
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

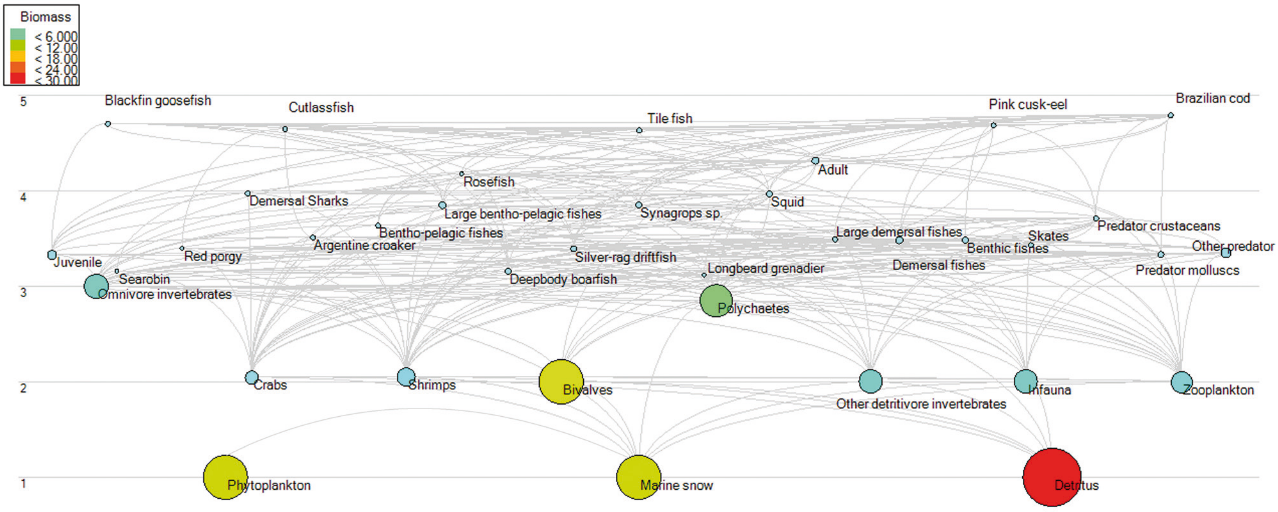

Fig. 2. – Trophic flow of demersal community of the outer continental shelf and upper slope of Southeastern Brazilian Bight the, size of the circles are proportional of its biomasses.

zilian cod, long beard grenadier, squid, large demersal fishes, demersal fishes and crab. This means that the biomasses produced by these species are highly utilized by other organisms in the system, calling for caution in management (conservative levels of exploitation) for these species in an ecosystem-based context.

The total biomass in the system, excluding detritus, is 64.332 t km^{-2}. The relative ascendency (A/C) (49.1%) indicates a high capacity of the system to withstand changes and to recover from disturbance. This high level of ascendency (and implied resilience) is probably related to the high level of omnivory of all compartments of this ecosystem.

Within EwE, network analysis uses two indices that are used to identify keystoneness of species or functional groups. In this model, both indices identified squid (1; 0.205) as the highest scoring species in the system followed by polychaetes (0.88; 0.1), Argentine hake adult (0.836; 0.127), pink cusk-eel (0.787; 0.103), omnivore invertebrates (0.702; 0.0218), shrimp (0.642; –0.0039), demersal sharks (0.548; –0.0544), demersal fishes (0.492; –0,104), *Synagrops* sp. (0.461; –0.131), crab (0.4; –0.213) and cutlassfish (0,388; –0.205).

The mixed trophic impact analysis (Ulanowicz and Puccia 1990) shows that groups that are more negatively impacted by fisheries are skates, demersal sharks, red porgy and searobin. In addition, Argentine hake adult, pink cusk-eel, squid, predator molluscs and polychaetes have a strong negative effect on some other groups. Skates and sharks are probably strongly affected because they have a low biomass, slow growth and reproduction, and high level of discards. Red porgy and searobin support important fisheries, and according to Rossi-Wongtschowski *et al.* (2006) and Cergole *et al.* (2005), respectively, they are overexploited, although there are no direct assessments of the status of these stocks.

DISCUSSION

The southeastern Brazilian Bight outer continental shelf and upper slope biota is supported by detritus, which is consumed by benthic species, which in turn support benthivorous species. Squids, polychaetes, molluscs, demersal fishes and crustaceans in general are fundamental in this ecosystem, as they exhibit high interaction strengths in the food web, as indicated by the keystoneness indexes that are included in EwE. According to Paine (1966) and Mills *et al.* (1993), keystone species are important because they structure the ecosystem, and despite their low biomass, their loss would precipitate many further extinctions through their many connections with another species in the food web. The keystoneness indexes examined here emphasize the dominant interacting species for this ecosystem, but many of them are invertebrates that have high biomass. It is not surprising that these groups are dominant and fundamental to the structure and functioning of this detritus-based system, but they should not be considered keystone species (or keystone functional groups) because their biomasses, abundances, or both, are somewhat high rather than low relative to their interaction strength. It is thus more useful to simply call them "strong interactors" or "dominant species" rather than "keystone species" as the Libralato *et al.* (2006) index rates them. Based on this distinction, we can consider squids, Argentine hake adult, pink cusk-eel, demersal sharks, demersal fishes and *Synagrops* sp. to be keystones if it is indeed true that these groups have a relatively low biomass in this system, as estimated (Fig. 3)

Gasalla *et al.* (2007) also demonstrated the importance of the benthic community in the Southern Brazil Shelf Large Marine Ecosystem (continental shelf and slope), in which our study area is included, reinforcing the importance of detritus and organisms that

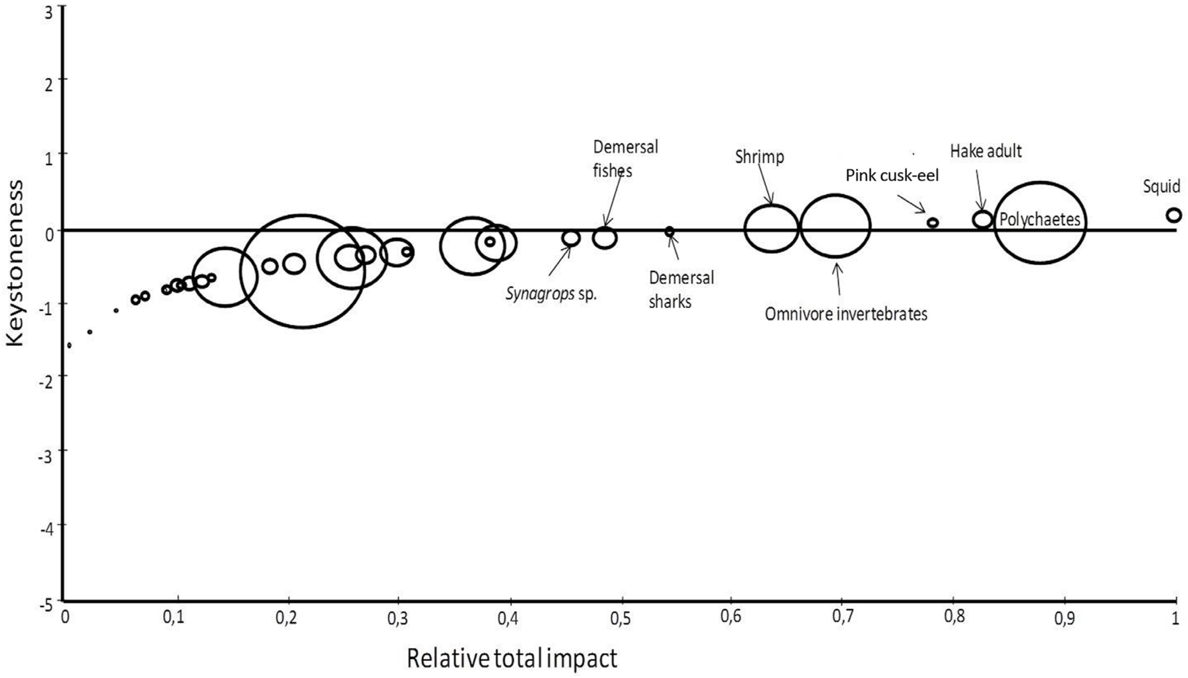

Fig. 3. – Graph of keystone species indices. Circles represent the functional groups; the sizes of each circle are proportional to the relative biomass of each functional group.

help recycle energy and matter in this system. These authors discuss the existence of a large amount of nektonic organisms that feed mainly benthic invertebrates. Velasco (2004) and Velasco and Castello (2005) also described the demersal community of the southern Brazil continental shelf ecosystem as highly important. In that case, however, he highlighted a pelagic species, the anchovy *Engraulis anchoita*, which was prominent in coupling demersal and pelagic sub-systems, eating benthic invertebrates and being prey of large fish predators, both demersal and pelagic.

Gasalla *et al.* (2007) and Freire *et al.* (2008) showed that the Brazilian shelf ecosystems have low primary production. Freire *et al.* (2008) say "The northeast sub-region, the object of this study, is characterized by rocky substrates and low primary production due to the influence of the warm North Brazil and Brazil currents." Gasalla *et al.* (2007; page 31) reported that the estimated phytoplankton biomass is 0.5gC/m^2/day and that this value decreases as the depth increases. Gasalla *et al.* (2007) also state that mean primary production is high because of the existence of a front vortex that causes high productivity events. In the area modelled here, however, detritus was clearly of primary importance to the benthic community. Gasalla *et al.* (2007) first highlighted the low primary production in South Brazil Shelf large marine ecosystem. Freire *et al.* (2008) analysed the East Brazil Shelf large marine ecosystem and pointed out that primary production in this area is lower than in the South Brazil Shelf large marine ecosystem and that almost 95% of this production goes directly to detritus. Gasalla *et al.* (2007) reported that most of the primary production goes to the substrate and is recycled via the invertebrate benthic community. When our present results are added to these previous studies on Brazilian shelf and slope ecosystems, the principal importance of detritus in these settings seems unequivocal.

The mean trophic level of catches is high (3.5) and similar to the mean trophic level of catches found by Velasco (2004) (3.37), Gasalla *et al.* (2007) (3.56) and Freire *et al.* (2008) (3.4). These very high values are probably a characteristic of the Brazilian ecosystems and fisheries. The value of 3.5 corresponds to organisms of mid-trophic levels such as benthopelagic fishes and demersal fish in general. It occurs because catches in this ecosystem are still directed at top predators, almost in the same magnitude as crabs and shrimps, both of which are lower trophic level organisms.

The mixed trophic impact diagram shows prey competition for food, as was also observed by Antony *et al.* (2010). This competition can also be observed in the high mortality of invertebrates in general, all of which are important prey, and of Argentine hake juveniles in particular. Also, the keystone species index shows that squid, polychaetes and different kinds of demersal fishes are very important prey in this system. Therefore, by integrating the strong relationships of the lower trophic level organisms with the information about the high amount of detritus and the low primary production, we can infer that this community is shaped strongly from the bottom up.

This system has a high level of connections between its components, as is shown in the high values of connectance and omnivory. The organisms are strongly connected and have a high diversity of food (they are not specialists). Gasalla *et al.* (2007) also showed a high value for this index (0.23 and 0.337). Freire *et al.* (2008) found medium omnivory (0.21) for the East Brazil Shelf large marine ecosystem, and Rocha *et al.* (2007) also found intermediate values for the channel of São Sebastião (0.26 and 0.21) and São Sebastião inner shelf (0.21 and 0.25), both in part of the area of the present study. Although the values of Rocha *et al.* (2007) and Freire *at al.* (2008) are not as high as those of the present paper and those of Gasalla *et al.* (2007), they are still high. Perhaps the high connectance among organisms in a system and high levels of omnivory are characteristic of tropical and subtropical waters, as can be observed in land ecosystems such as forests (Greenberg 1981, Boedmer 1989) where the biodiversity is high. The high level of ascendency indicated for this system indicates a high capacity of the system to withstand changes and to recover from disturbance (Odum 1969, Christensen 1995) and is probably related to the high level of omnivory of all compartments of this ecosystem

High EE values indicated for some species reflects the consumption of large proportions of the production of these groups within the system (Christensen *et al.* 2008). It can occur sometimes because the species are highly exploited in the system or because they experience a high level of predation. In this study the cutlassfish, with the highest EE, is heavily fished (also often discarded) and pursued by the sport fishery. Moreover, this species has undergone an increase in its catch in the last 15 years that is not well reported (Cergole *et al.* 2005). Argentine hake, pink cusk-eel, Brazilian cod, squid and crab are highly consumed and fished in the system, being some of the most important resources in the demersal trawls (Cergole *et al.* 2005, Rossi-Wongtschowski *et al.* 2006, Valentini and Pezzuto 2006). Demersal fishes, large demersal fishes, large bentho-pelagic fishes, silver-rag driftfish, *Synagrops* sp. and longbeard grenadier are heavily consumed and are also important components in this system. These high EE values can indicate that these species are at risk and reinforce the calls by Cergole *et al.* (2005), Rossi-Wongtschowki *et al.* (2006) and Valentini and Pezzuto (2006) for a suitable management plan for the fishery in this area.

The main difficulty in balancing this model was related to the low biomass of a few functional groups that were subject to high levels of consumption and exploitation. Several factors were involved. First, the biomass estimates were calculated from trawl surveys and this kind of sampling is suitable only for some groups and sizes, but not for all organisms in an ecosystem. Second, the trawl gear did not completely touch the bottom, so benthic fishes and invertebrates were able to escape during sampling. Benthic invertebrates can also escape from benthic samplers such as dredges and sleds. Third, various studies indicate that several of these species were overexploited prior to 2001, the year in which the data were collected (Valentini and Pezuto 2006), thus indicating less biomass than is naturally supported by the system. This situation is very clear for benthic fishes, of which the most important are species of the genus *Paralichthys,* which support an important fishery and are also discarded. This group is clearly overexploited according to Cergole *et al.* (2005). The benthic fish functional group was the most difficult to balance; it was necessary to considerably increase its biomass estimate, probably indicating that the population was not supporting the catches, *i.e.* implying biomass depletion in the model year.

Fisheries policy measures in Brazil are not very appropriate, and sometimes non-existent, allowing a "gold-rush" pattern for some resources after economic discovery (Velasco and Castello 2005), as happened recently with the blackfin goosefish, which went from a discard to an overexploited species in less than 10 years (Valentini and Pezzuto 2006). Despite the current policy shortcomings, this system is recovering from some disturbances because it has a high level of ascendency and overhead. These measures indicate the reserve and the capacity of the system to recover after a disturbance (Ulanowicz 1986)—resistance and resilience. Despite the diversity, high indicated connectance, and high recovery capacity, this system is being highly impacted by fisheries due to their scale and efficiency, and because of the lack of strong catch controls. The lack of knowledge of the impacts on a system that is out of sight is allowing a loss of structure, function, and biodiversity. We strongly recommended that the policy and management of the fishery be improved, as suggested by Cergole *et al.* (2005), Rossi-Wongtschowski *et al.* (2006) and Valentini and Pezzuto (2006), and that increased investments be made in basic research.

CONCLUSIONS

Our modelling exercise indicated that the outer continental shelf and upper slope biological communities of the southeastern Brazilian Bight are shaped from bottom-up and are supported prominently by detritus, with a high diversity of detritus-supported species and high omnivory throughout the biological community. The demersal fishes are a key, highly connected link between the detritus-supported lower trophic levels and the biological communities of the upper water column, indicating that considerable caution is needed regarding the exploitation of demersal fish stocks from a broader ecosystem and social-ecological perspective. High levels of ascendency indicated by the constructed model, probably related to the high level of omnivory, may indicate that this system has a relatively high capacity to recover from disturbances, but it assumes that disturbances are non-catastrophic and subside. In contrast, unmanaged and uncontrolled fishing for demersal species has increased in this area over the last 20 years, and the scale of depletion and degradation will likely overwhelm the theoretical resistance or resilience of this biological community and quickly lead to a considerably degraded ecosystem and diminished services. Immediate improvements are needed in the policy and management of the uncontrolled fisheries in this region, including explicit investments in the capacities for monitoring the status and integrity of stocks and whole biological communities, identifying and monitoring the social-ecological services they provide, fishing community commitment and enforcement, and management strategy development, evaluation, and adaptation. We strongly recommend the development of an appropriate management plan for the fisheries, in agreement with other researchers working in this area.

ACKNOWLEDGEMENTS

We wish to thank to CAPES and CNPq for the scholarship. The REVIZEE-Score Sul programme, and particularly Dr. Carmen L.D.B. Rossi-Wongtschowski, provided scientific support and data. The *Programa de Pós Graduação em Ecologia* – UNICAMP and UBC Fisheries Centre provided support and facilities. Special thanks are due to Dr. Marta Coll for very valuable suggestions that improved the manuscript. We also thank the Pew Fellows Programme in Marine Conservation through the Pew Environment Group for supporting the participation and contribution of TAO.

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Received February 8, 2011. Accepted April 3, 2012.

Appendix 1. – List of references used to build the trophic model of the demersal community of the southeastern Brazilian Bight.

Functional Group	References				
	Biomass	Diet	P/B	Q/B	
Blackfin goosefish	Haimovici *et al.* 2008	Muto *et al.* 2005	Calculated	Calculated	Schwingel and Andrade 2002 Perez *et al.* 2005 Haimovici and Velasco 2000
Cutlassfish	Haimovici *et al.* 2008	Muto *et al.* 2005	Calculated	Calculated	Magro 2005 Cergole *et al.* 2005 Haimovici and Velasco 2000
Rosefish	Haimovici *et al.* 2008	Muto *et al.* 2005	Calculated	Calculated	Cergole *et al.* 2005 Froese and Pauly 2010
Tile fish	Haimovici *et al.* 2008	Pires-Vanin 2008	Calculated	Calculated	Cergole *et al.* 2005 Cergole *et al.* 2005
Argentine hake	Haimovici *et al.* 2008	Sánches 2009 Brown *et al.* 2004 Bezzi *et al.* 1994	Calculated	Calculated	Vaz-dos-Santos and Rossi-Wongtschowski 2005 Vaz-dos-Santos *et al.* 2009 Cergole *et al.* 2005 Brown *et al.* 2004
Searobin	Haimovici *et al.* 2008	Soares 1992	Calculated	Calculated	Andrade *et al.* 2005
Red porgy	Haimovici *et al.* 2008	Velasco and Castelo 2005	Calculated	Calculated	Rossi-Wongtschowski *et al.* 2006
Demersal sharks	Haimovici *et al.* 2008	Velasco and Castelo 2005 Gasalla *et al.* 2007	Calculated	Calculated	Bonham *et al.* 1949 Velasco and Castelo 2005 Gasalla *et al.* 2007
Argentine croaker	Haimovici *et al.* 2008	Ribeiro 1982 Haimovici *et al.* 1989	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005 Haimovici and Reis 1984 Haimovici and Cousini 1989 Haimovici *et al.* 2006 Froese and Pauly 2010
Bentho-pelagic fishes	Haimovici *et al.* 2008	Muto *et al.* 2005	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005 Froese and Pauly 2010
	Haimovici *et al.* 2008	Muto *et al.* 2005	Calculated	Calculated	Kotlyar 1987 Froese and Pauly 2010 Haimovici and Velasco 2000 Madureira and Rossi-Wongtschowski 2005
Deepbody boarfish	Haimovici *et al.* 2008	Nascimento 2006	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005
Silver-rag driftfish	Haimovici *et al.* 2008	*Analysed*	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005
Pink cusk-eel	Haimovici *et al.* 2008	*Analysed*	Calculated	Calculated	Haimovici and Velasco 2000
Synagrops **sp.**	Haimovici *et al.* 2008	Nascimento 2006	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005
		Analysed	Calculated	Calculated	Haimovici and Velasco 2000
Brazilian cod	Haimovici *et al.* 2008	Nascimento 2006	Calculated	Calculated	Haimovici *et al.* 2008 Madureira and Rossi-Wongtschowski 2005 Martins and Haimovici 2000
Longbeard grenadier	Haimovici *et al.* 2008	*Analysed*	Calculated	Calculated	Cohen *et al.* 1990 Froese and Pauly 2010
Squid	Haimovici *et al.* 2008	Martins 2002 Santos and Haimovici 1997 Rodrigues 2007 Gasalla *et al.* 2010 Santos and Haimovici 2000	Calculated	Calculated	Rodrigues 2007 Gasalla *et al.* 2010 Santos and Haimovici 2000
Large demersal fishes	Haimovici *et al.* 2008	Vaz-dos-santos and Rossi-Wongtschowski 2005 Gasalla *et al.* 2007	Calculated	Calculated	Vaz-dos-santos and Rossi-Wongtschowski 2005 Gasalla *et al.* 2007 Froese and Pauly 2010
Demersal fishes	Haimovici *et al.* 2008	Muto *et al.* 2005 Tubino 1999	Calculated	Calculated	Madureira and Rossi-Wongtschowski 2005 Froese and Pauly 2010

Benthic fishes	Haimovici *et al.* 2008	Sanches 1994 Carneiro 1995 Nobre-leal and Benvenuti 2006	Calculated	Calculated	Haimovici and Velasco 2000 Haimovici and Velasco 2000 Gasalla *et al.* 2007
Skates	Haimovici *et al.* 2008	Schwingel and Assunção 2009 Muto *et al.* 2005	Calculated	Calculated	Casarini 2006 Froese and Pauly 2010 Madureira and Rossi-Wongtschowski 2005
Predator crustaceans	Amaral and Rossi-*Wongtschowski* 2004	Ruppert *et al.* 2005	Antony *et al.* 2010	Antony *et al.* 2010	
Predator molluscs	Amaral and Rossi-*Wongtschowski* 2004	Ruppert *et al.* 2005	Cergole *et al.* 2005		
Other predator invertebrates	Amaral and Rossi-*Wongtschowski* 2004	Ruppert *et al.* 2005	Brey 1991		Brey 1991
Omnivore invertebrates	Amaral and Rossi-*Wongtschowski* 2004	Ruppert *et al.* 2005			Ikeda and Shiga 1999
Crabs	Amaral and Rossi-*Wongtschowski* 2004 Gasalla *et al.* 2007	Ruppert *et al.* 2005	Vetter 1996	Gasalla *et al.* 2005	Vetter 1996 Antony *et al.* 2010
Shrimps	Amaral and Rossi-Wongtschowski 2004 Gasalla *et al.* 2007	Ruppert *et al.* 2005	Calculated	Calculated	Metri 2007 Vetter 1996
Bivalves	Amaral and Rossi-Wongtschowski 2004	Ruppert *et al.* 2005			
Polychaetes	Amaral and Rossi-Wongtschowski 2004	Ruppert *et al.* 2005	Calculated	Calculated	Santos 1994 Souza and Borzone 2000 Ménard *et al.* 1989 Omenta and Amaral 2000
Other detritivore invertebrates	Amaral and Rossi-Wongtschowski 2004	Ruppert *et al.* 2005	Antony *et al.* 2010	Antony *et al.* 2010	
Infauna	Amaral and Rossi-Wongtschowski 2004	Ruppert *et al.* 2005	Antony *et al.* 2010	Antony *et al.* 2010	
Zooplankton	Gasalla *et al.* 2007	Ruppert *et al.* 2005	Gasalla *et al.* 2007	Gasalla *et al.* 2007	
Marine snow		Ruppert *et al.* 2005			
Detritus					