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**Modèles trophiques des
écosystèmes marins
nord-ouest africains**

**Trophic Models
of Northwest African
Marine Ecosystems**

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Guinée-Bissau -- Guinea Bissau**Preliminary Ecopath model of the Guinea-Bissau continental shelf ecosystem (NW-Africa)**

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Abstract

An ecosystem model for the Guinea-Bissau continental shelf is presented with the goal of providing a tool for the understanding of ecosystem dynamics in a multi-species context. The model refers to the period between 1990 and 1992 and covers an area of 40816 km² located between 11° and 12°30'N. A total of 32 ecological groups were included in the model, focusing on the exploited part of the ecosystem. The groups consist of marine mammals, seabirds, turtles, 15 fish groups, 10 invertebrates groups, 2 primary producers, discards and detritus.

A considerable effort went into the process of assembling basic growth parameters and consumption and mortality rates for 166 fish species, accounting for 96% of the demersal fish biomass estimated by trawl surveys.

The preliminary biomass estimates by the model are in agreement with values given in the literature. Future developments of the Guinea-Bissau model should consider improving the estimation of catches and discards, un-reported shark catches, the creation of separate groups for commercially important species, and compilation of more information, mainly on top predators and benthos groups.

Résumé

Un modèle de l'écosystème du plateau continental de Guinée-Bissau fournira un important outil pour la compréhension de la dynamique d'un système multispécifique. Nous présentons ici un modèle pour la période entre 1990 et 1992 dans la zone localisée entre 11° et 12°30'N en Guinée-Bissau. Un total de 32 groupes écologiques a été inclus dans ce modèle, provenant notamment de la partie exploitée de cet écosystème. Les groupes incluent les mammifères et oiseaux marins, les tortues, 15 groupes de poissons, 10 groupes d'invertébrés, 2 producteurs primaires, des rejets et le détritius.

Un effort considérable a été consacré à l'estimation des paramètres de croissance ainsi qu'aux taux de consommation et de mortalité pour 166 espèces de poissons représentant 96% de la biomasse démersale (estimée par chalutages).

Les estimations préliminaires de la biomasse par ce modèle sont similaires aux valeurs données dans la littérature. Les futurs développements du modèle de Guinée-Bissau devraient considérer une amélioration des estimations des prises et des rejets ainsi que les prises de requins non rapportées, la création de groupes distincts pour les espèces commercialement importantes, et la compilation de plus d'information, principalement sur les prédateurs de haut niveau et le benthos.

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Introduction

Human pressure on the marine environment has never been so intense, and the continental shelf of Guinea-Bissau is no exception. The last two decades have progressively indicated fish stock depletion, habitat degradation and an urgent need for management policies that can integrate rational exploitation of fishery resources and nature conservation. There is an emerging consensus among fisheries scientists and managers that, in order to improve on the management of aquatic resources, traditional single-species approaches should be replaced by an ecosystem management perspective which explicitly accounts for ecological interactions, especially those of trophic nature (Walters et al. 1997).

In Guinea-Bissau, numerous studies have been undertaken on different topics ranging from primary production to fisheries, but none have integrated these different elements into an ecosystem perspective. The objective of the present study was to create an ecosystem model for the Guinea-Bissau continental shelf and adjacent areas and thereby to provide a tool for understanding the dynamics of the ecosystem within which the marine fisheries of Guinea Bissau are embedded. This study was developed in a collaborative effort between the Centro de Investigação Pesqueira Aplicada (CIPA, Guinea-Bissau) and the Instituto de Investigação das Pescas e do Mar (IPIMAR, Portugal).

Guinea-Bissau

The marine environment of Guinea-Bissau is characterized by one of the largest continental shelves in the region, approximately 11 900 nm² (40 186 km²) (Strømme 1984), consisting of large shallow areas, large river run-off and extensive mangrove forests lining the mainland coastline and that of the Bijagós Archipelago. These areas are a complex of fishing grounds with highly diverse bottom characteristics and shifting sediments. Furthermore, the coastal areas are characterized by strong currents and occasional strong winds.

The Guinea-Bissau ecosystem, located at the southern limit of the Canary Current System and the western limit of the Gulf of Guinea System, is characterized by strong seasonal variations of oceanographic conditions (Berrit and Rebert 1977). From January to February the continental shelf is marked by upwelling events. Characteristically warm and salty tropical waters dominate from May to June. With the progression of the rainy season (2 500 mm·year⁻¹), the intrusion of warm, low salinity inner waters tend to dominate. As a result of upwelling events and the input of organic matter from river run-off, primary productivity is relatively high in the area, estimated at approximately 240 t·C·km⁻²·year⁻¹ (Berrit and Rebert 1977).

Several studies have demonstrated the seasonal variability of the ecosystem, including the higher productivity during the dry season (Longhurst 1983; Domain 1982). The biota has adopted strategies compatible with this variability, as reflected, e.g., in feeding migrations of fish along the coast (Domain 1979; Boely and Fréon 1979) and the reproductive migration of shrimp into estuaries (Garcia and Lhomme 1979) following the cycle of wet and dry seasons. This area is considered an important nursery ground for several species of fish, turtles, marine mammals and birds (Lafrance 1994a; Fréon 1981; Lopes and Afonso 1993) and is therefore crucial for the maintenance of their populations.

Fisheries in Guinea-Bissau can be divided into three major categories: Industrial, Artisanal and Tuna. The industrial fishery is undertaken exclusively by foreign vessels on a

seasonal basis, operating with trawl nets or, to a lesser extent, with purse seines. In general, the catches of the industrial fisheries are dominated by members of the sciaenid community, i.e., *Arius* sp. *Galeoides decadactylus*, *Polydactylus quadrifilis*, *Argyrosoma regius*, *Pseudotolithus* sp. and *Pomadasys* sp. (Fager and Longhurst 1968; Domain et al. 1999), followed by small pelagics, i.e., *Sardinella* sp., *Ethmalosa fimbriata* and *Decapterus* sp. and to a lesser extent by cephalopods and shrimps, with an estimated total landings of 39 121 t in 1995 (CIPA 1996).

The artisanal fishery operates mainly in coastal areas and the Bissagós Archipelago, with gillnets, longline, handline and beach seine. The catches are dominated by species such as mullets (*Mugil* sp. and *Liza* sp.), sharks and rays (*Carcharhinus* sp., *Sphyrna* sp. and *Rhinobatus* sp.), bonga shad (*Ethmalosa fimbriata*), ilisha (*Ilisha africana*), sardinellas, scads, grunts (*Pomadasys jubelini*), guitarfishes (*Rhinobatus* sp.) and barracudas (*Sphyrna* sp.) (Lafrance 1994c).

The tuna fishery operates differently, involving foreign vessels using longlines, pole and line with live bait, and purse seines (Gregorio Duarte, pers. comm.).

Material and methods

Approach and model definition

The modelling approach used in this study relied on the Ecopath with Ecosim software (Christensen et al. 2000), which is based on an approach originally developed by Polovina (1984b) and subsequently modified by Christensen and Pauly (1992, 1996).

The area covered by the model extends along the Guinea-Bissau shoreline, including the Bissagós Archipelago and the continental shelf until 200 m depth (Figure 1). The inner waters, such as the Geba River, were not considered. The total area of this ecosystem is 40 816 km², located between 11° and 12°30'N. The reference period covered was 1990 to 1992, considering the availability of biomass estimates from trawl and acoustic surveys (INIP and LBM 1992; INIP and CIPA 1993; Saetersdal et al. 1999) and fisheries statistics (CIPA 1996; Lafrance 1994b/c).

Ecological Grouping

A total of 32 ecological groups were included in the Guinea-Bissau model, with emphasis on the exploited part of the ecosystem. The groups consist of marine mammals, seabirds, turtles, 15 fish groups, 10 invertebrate groups, 2 primary producers, discards and detritus.

Fish groups

A list of 166 fish species considered in the Guinea-Bissau model was assembled from INIP (Instituto Nacional de Investigaçao das Pescas, Portugal) / LBM (Laboratorio de Biologia Marinha, Guinea-Bissau) trawl surveys (INIP/LBM 1992; INIP/CIPA 1993; CIPA 1996), fisheries statistics (CIPA 1996), reports (Lafrance 1994a,c; Bucal 1994), and other published data. The aggregation of species was based primarily on common habitat, diet composition, and consistent estimates of trophic level. The characteristic species in terms of biomass and importance to the fishery are given by group in Table 1.

The biomass of demersal fish species was estimated using stratified means from the stratified INIP/LBM trawl surveys and the swept-area method (Gallucci et al. 1996; Sparre and Venema 1992). Biomass estimates for 1990 and 1991 were averaged. Small pelagic and pelagic predator (carangids) biomass estimates were obtained from cruise reports of R/V *Dr. Fridtjof Nansen* for the years 1975-1993 (Saetersdal et al. 1999), using 1992 as reference year. Estimates of phytoplanktivorous fish (*Ethmalosa fimbriata* primarily) and mullets were taken from Longhurst (1983), as these species are poorly sampled by trawl surveys.

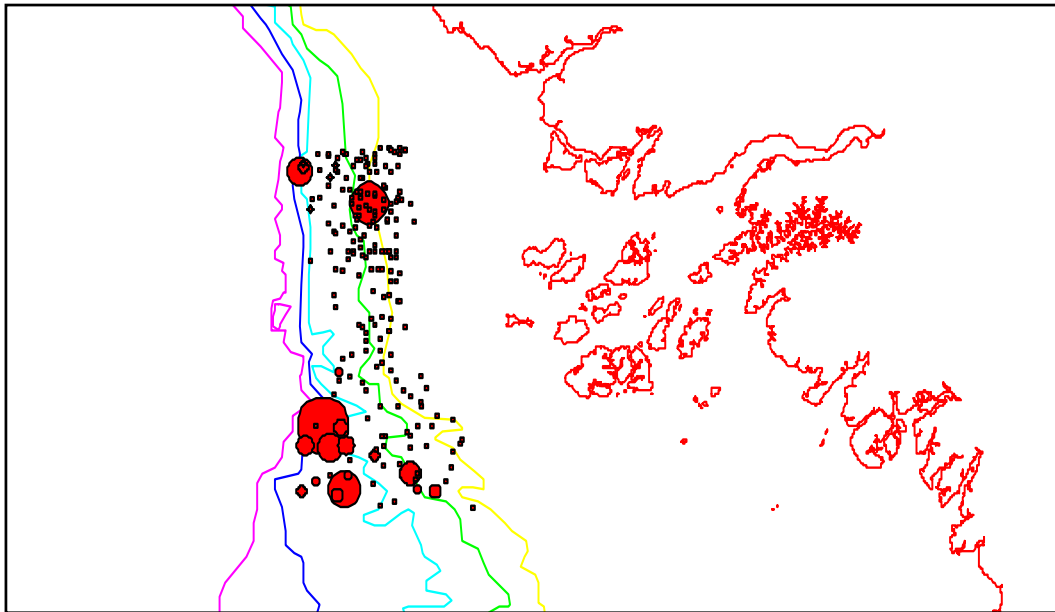


Figure 1. Area covered by the model of the Guinea-Bissau continental shelf ecosystem, including the Bissagós Archipelago and the continental shelf to 200 m depth. Grey circles represent the fish catches obtained and the extent of the surveyed area of the INIP/LBM trawl surveys (1990 and 1991). The bathymetric lines indicate the 50, 100, 200, 500, and 1000 m isobaths, respectively.

There are numerous studies concerning fish species in the region, which have dealt with a number of subjects such as species assemblages, abundance, migration, growth, reproduction, habitat and diet composition (e.g., Caverivière 1989, 1993; Domain 1972, 1979; Domain et al. 1999; Fager and Longhurst 1968; Lima Dias 1994; Longhurst 1957, 1960; Longhurst and Pauly 1987; Marchal and Boëly 1977; Troadec and Garcia 1979). We will therefore not go into detail concerning fish species and the reader should refer to this literature for more detailed information.

Table 1. Representative fish species, in terms of biomass and fisheries catch, by trophic functional group of the Guinea-Bissau model, including the total number of species in each group.

N ^o	Groups	Family	Representative species	No. of spp.
4	Billfish and marlins	Istiophoridae	<i>Istiophorus albicans</i>	4
5	Tuna	Scombridae	<i>Katsuwonus pelamis</i> , <i>Thunnus albacares</i>	4
6	Pelagic sharks	Carcharhinidae	<i>Carcharhinus signatus</i> , <i>C. limbatus</i> , <i>Galeocerdo cuvier</i> , <i>Prionace glauca</i>	10
		Sphyrnidae	<i>Sphyrna mokarran</i>	–
7	Pelagic predators	Trichiuridae	<i>Trichiurus lepturus</i>	11
		Zeidae	<i>Zeus faber</i>	–
		Sphyraenidae	<i>Sphyraena afra</i>	–
		Scombridae	<i>Scomberomorus tritor</i>	–
		Carangidae	<i>Caranx senegallus</i> , <i>Alectis alexandrinus</i>	–
		Elopidae	<i>Elops lacerta</i>	–
8	Benthic predators	Synodontidae	<i>Saurida brasiliensis</i> , <i>Trachinocephalus myops</i>	13
		Ophidiidae	<i>Brotula barbata</i>	–
		Aulopidae	<i>Aulopus cadenati</i>	–
		Sciaenidae	<i>Argyrosomus regius</i>	–
		Muraenidae	<i>Muraena helena</i>	–
9	Demersal sharks	Triakidae	<i>Mustelus mustelus</i>	9
		Squalidae	<i>Squalus blainville</i> , <i>S. megalops</i>	–
		Carcharhinidae	<i>Rhizoprionodon acutus</i>	–
		Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	–
10	Groupers/snappers	Serranidae	<i>Epinephelus aeneus</i> , <i>Mycteroperca rubra</i> , <i>Cephalopholis</i> spp.	5
		Lutjanidae	<i>Lutjanus goreensis</i>	–
11	Rays	Rajidae	<i>Raja</i> spp.	10
		Rhinobatidae	<i>Rhinobatos rhinobatos</i>	–
		Dasyatidae	<i>Dasyatis margarita</i>	–
12	Benthos/fish feeders	Acropomatidae	<i>Synagrops microlepis</i>	29
		Haemulidae	<i>Brachydeuterus auritus</i> , <i>Pomadasy perotaei</i>	–
		Polynemidae	<i>Galeoides decadactylus</i> , <i>Polydactylus quadrifilis</i>	–
		Gerreidae	<i>Eucinostomis melanopterus</i>	–
13	Sparids	Sparidae	<i>Dentex</i> spp., <i>Pagellus bellottii</i> , <i>Pagrus caeruleostictus</i>	8
14	Flatfish	Paralichthyidae	<i>Syacium guineensis</i>	11
		Bothidae	<i>Bothus podas</i>	–
		Soleidae	<i>Dicologlossa cuneata</i> , <i>Microchirus boscanion</i>	–
15	Benthic feeders	Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	17
		Ariommatidae	<i>Ariomma bondi</i> , <i>A. melanum</i>	–
		Triglidae	<i>Lepidotrigla cadmani</i>	–
		Haemulidae	<i>Pomadasy jubelini</i>	–
		Drepaneidae	<i>Drepane africana</i>	–
16	Small pelagics	Clupeidae	<i>Sardinella aurita</i> , <i>S. maderensis</i>	12
		Carangidae	<i>Caranx rhonchus</i> , <i>Trachurus trecae</i>	–
18	Phytoplanktivores	Clupeidae	<i>Ethmalosa fimbriata</i>	2
		Cichlidae	<i>Sarotherodon melanotheron</i>	–

Non-fish groups

Published data regarding non-fish groups for the region are scarce, particularly in relation to biomass and production. Most studies consider characteristic species and are generally descriptive in nature. However, information on species composition and biomass estimates for demersal cephalopods, shrimps, and crabs were available from trawl surveys. In the following, the non-fish groups are characterized and an indication of available parameter estimates are given (see also Table 2, which gives the source of parameter estimates).

Table 2. Basic input parameters for the Guinea-Bissau model for the period 1990 to 1992, before and after balancing the model. In bold are the values estimated by the model are in parenthesis.

N°	Groups	TL	Biomass (t·km ⁻²)		P/B (year ⁻¹)		Q/B (year ⁻¹)	EE	P/Q
			Before	After	Before	After			
1	Marine mammals	4.0	–	(0.073)	0.100 ^a	0.100	41.070 ^a	0.500	(0.002)
2	Seabirds	3.3	–	(0.002)	5.400 ^b	5.400	80.000 ^b	0.500	(0.068)
3	Turtles	2.9	–	(0.033)	0.200 ^b	0.200	3.500 ^b	0.800	(0.057)
4	Billfish and marlins	4.2	–	(0.024)	–	(0.626)	6.265	0.800	0.100
5	Tuna	3.5	–	(1.059)	–	(0.956)	9.563	0.850	0.100
6	Pelagic sharks	4.6	–	(0.076)	–	(0.210)	2.103	0.500	0.100
7	Pelagic predators	3.5	0.735 ^c	0.735	0.616	0.616	4.440	(0.895)	(0.139)
8	Benthic predators	4.3	0.269	0.269	1.243	1.243	4.959	(0.951)	(0.251)
9	Demersal sharks	4.4	0.238	0.238	0.506	0.506	3.256	(0.716)	(0.155)
10	Groupers/Snappers	3.9	0.039	0.039	0.770	0.770	4.272	(0.909)	(0.180)
11	Rays	3.6	0.095	0.095	0.920	0.920	3.912	(0.663)	(0.235)
12	Benthos/Fish feeders	3.7	1.262	1.262	0.812	0.812	6.282	(0.918)	(0.129)
13	Sparids	3.3	0.731	0.731	0.570	0.570	5.328	(0.950)	(0.107)
14	Flatfish	3.3	0.354	0.354	1.165	1.165	8.004	(0.953)	(0.146)
15	Benthic feeders	3.4	3.190	3.190	0.942	0.942	6.300	(0.893)	(0.150)
16	Small pelagics	2.6	13.230 ^c	13.230	1.149	1.149	9.286	(0.941)	(0.124)
17	Squid	3.0	–	(1.523)	3.100 ^d	3.100	16.640 ^d	0.950	(0.186)
18	Phytoplanktivores	2.1	5.369 ^c	5.369	–	(0.981)	19.103	0.950	(0.051)
19	Mulletts	2.3	0.150 ^c	0.150	–	(1.769)	17.694	(0.914)	0.100
20	Octopus/Sepia	3.4	0.158	(2.984)	1.100 ^f	1.100	3.500 ^f	0.950	(0.314)
21	Gastropods/Bivalves	2.4	–	(5.708)	2.500 ^f	2.500	8.200 ^f	0.950	(0.305)
22	Shrimps	2.9	0.018	(0.875)	5.380 ^f	5.380	19.200 ^f	0.950	(0.280)
23	Crabs	2.8	0.203	(2.682)	2.800 ^f	2.800	8.500 ^f	0.950	(0.329)
24	Small crustaceans	2.3	–	(3.623)	7.010 ^f	7.010	27.140 ^f	0.950	(0.258)
25	Annelids	2.2	–	(6.932)	4.600 ^f	4.600	15.900 ^f	0.950	(0.289)
26	Echinoderms	2.3	–	(4.888)	1.200 ^b	1.200	4.000 ^b	0.950	(0.300)
27	Meiobenthos	2.0	–	(0.387)	100.000 ^b	100.000	215.000 ^b	0.950	(0.465)
28	Zooplankton	2.0	1.857 ^c	1.857	159.356 ^c	(71.547)	165.000 ^b	0.950	(0.434)
29	Phytoplankton	1.0	12.146 ^c	12.146	199.723 ^{eg}	199.723	–	(0.168)	–
30	Benthic algae	1.0	–	(8.446)	13.250 ^b	13.250	–	0.800	–
31	Discards	1.0	–	–	–	–	–	(0.995)	–
32	Detritus	1.0	42.351 ^c	42.351	–	–	–	(0.104)	–

^a Browder (1993);

^b Opitz (1993);

^c Dr. Fridtjof Nansen Programme; Saetersdal et al. (1999);

^d Aliño et al. (1993);

^e Longhurst (1983);

^f Arreguín-Sánchez et al. (1993);

^g Berrit and Rebert (1977);

^h Estimated using empirical equation given in Pauly et al. (1993b).

Marine mammals: Some studies concerning marine mammals in Guinea-Bissau and adjacent areas have been undertaken in recent years. The main focus of these studies was species composition, distribution and conservation status of some of the most important coastal marine mammals (Sequeira and Reiner 1992; Schuhmann 1995; van Waerebeek et al. 2000; Silva and Araújo 2001). However, none of the mentioned studies presented biomass estimates or diet composition for the species occurring in the area. Following Jefferson et al. (1997), the predominant species are bottlenose dolphin (*Tursiops truncatus*), Atlantic spotted dolphin (*Stenella frontalis*), common dolphin (*Delphinus delphis*), short-finned pilot whales (*Globicephala macrorhynchus*), and the Atlantic hump-back dolphin (*Sousa teutzi*). Diet composition was estimated from Pauly et al. (1998) by simple averaging across species. According to Maigret (1994) and van Waerebeek et al. (2000), no regular by-catch or direct catches of marine mammals have been reported in Guinea-Bissau. However, more recently Silva and Araújo (2001) reported the death of several manatees (*Trichechus senegalensis*) entangled in fishing nets or killed by hunters.

Seabirds: Seabirds of Guinea-Bissau has been studied within the framework of establishing protected areas and their management plans. This is mainly true for inland waters and lagoons, such as Cufada (Araújo 1994), Cacheu or Rio Grande de Buba, but also for the Bissagós Archipelago and coastal mangrove areas (Altenburg and Van Spanje 1989). We can assume that the most common species in the Bissagós Archipelago are Palearctic waders, Curlew sandpiper (*Calidris ferruginea*), Bartailed godwit (*Limosa lapponica*), Whimbrel (*Numenius phaeopus*), Grey plover (*Pluvialis squatarola*), Pink backed pelicans (*Pelecanus rufescens*), and Greater flamingo (*Phoenicopterus ruber*) (Dodman et al. 1999). In coastal mangrove areas, the most common fish, crab and benthos eaters are pied kingfisher (*Ceryle rudis*), blue-breasted kingfisher (*Halcyon malimbica*), and common sandpiper (*Actitis hypoleucos*) (Altenburg and Van Spanje 1989). No estimations of biomass or diet composition were found in the literature for the region.

Turtles: There are at least four species of turtles occurring in Guinea-Bissau waters. The most abundant are considered to be *Chelonia mydas* and *Lepidochelys olivacea*, while *Eretmochelys imbricata* and *Dermochelys coriacea* are rarer (Barbosa et al. 1998; Fortes et al. 1998). The Guinea-Bissau area, the Bissagós Archipelago in particular, is a very important nursery area for the first two species. Juveniles are preyed upon by the monitor lizard, ghost crabs, and plum-nut vulture, while adults are captured by local people for consumption. Also, there are some preliminary estimates of by-catch from the industrial trawl fishery (Broderick and Catry 1998).

Octopus/Sepia: Demersal cephalopods are an important part of the diet of many predators, as can be seen in. This group has been the subject of some studies in Guinea-Bissau as well as in adjacent areas (Lamboeuf 1997; Pereira 1993). During the trawl surveys (INIP and LBM 1992; INIP and CIPA 1993), some of the most important species were identified, such as *Octopus* sp., *Sepia* sp., *Eledone caparti*, and the biomass of the demersal species was estimated.

Shrimps: This group was separated from the other crustacean groups, because it is a target species of the industrial fishery and is of economic importance (Table 4). The more abundant species are *Parapenaeus longirostris*, *Penaeus* sp., *Parapenaeopsis atlantica* (INIP and LBM 1992; INIP and CIPA 1993; CIPA 1996). However, the distributions of these species are not homogeneous. They are found in higher densities in specific areas such as off Cacheu (in the North) and south of Bissagós, which appears to be related to sediment type.

Crabs: This group comprises the crab and other reptant decapod species of Guinea-Bissau, and is subject to a certain level of exploitation (CIPA 1996). They can be considered by-catch of the shrimp- and fish-trawl fisheries. They play an important ecological role in the ecosystem as they are preyed upon by several groups (Table 5). The most abundant species, determined by trawl surveys appear to be *Aristeus* sp., *Calappa rubroguttata*, and *Palinurus mauritanicus*.

Benthic macrofaunal groups in general: These groups included a wide variety of organisms ranging from benthic polychaets to bivalves, gastropods and echinoderms. Some studies have been undertaken such as those of Dexter (1992) and Teixeira and Morato-Gomes (1997) on the macrozoobenthos characteristic of sandy beaches in the Bissagós Archipelago as well as Fernandes (1989), Alva and Vadon (1989), and van Cosel (1993), which described mainly the bivalves and ophiuroids of the coastal areas.

In the Bissagós Archipelago, the bivalves of the family Cardiidae, locally known as 'Combés', are exploited as part of a subsistence fishery and an estimate of catch was included in the model (Table 4). A huge amount of shells of these bivalves can be found around local houses, serving as exterior pavement.

Samples taken during the INIP/LBM trawl surveys for the period 1989 to 1991 indicate that the dominant groups are Annelida, Mollusca, Arthropoda, and Echinodermata, in decreasing order of importance (INIP and LBM 1989, 1990, 1992, 1993; see also Loeuff 1999).

We assumed that the numerical relationship between teleosts and shark/rays in trawl surveys was equal to that observed in the industrial landings, since both gear and area were similar. Thus, the proportion of sharks and rays to total fish catch (trawl surveys) was estimated as 5.2%, giving an estimated elasmobranch catch of 2 251 t. The species composition observed in trawl surveys was used to estimate catch by shark and ray species and gear (Table 6). These groups were incorporated to the model as Annelids, Gastropods/Bivalves, Small (benthic) crustaceans, and Echinoderms, respectively. The reason for differentiating these groups is that one of the co-authors is in the process of determining weights by species or group, which will later make it possible to incorporate biomass estimates in a future iteration of the model.

Zooplankton: A description of the major zooplankton taxa for the Bissagós Archipelago can be found in Esteves and Morato-Gomes' (1997) work. This is a very heterogeneous group, including small herbivorous zooplankton such as copepods and ostracods as well as larger omnivorous and carnivorous species such as chaetognaths, decapod larvae, mysids, euphausiids and salps. In the absence of reliable information on the composition and production of various components of this group, they were aggregated and their biomass was assumed to be similar to that off Sierra Leone (Longhurst 1983).

Phytoplankton: The coastal phytoplankton of Guinea-Bissau has been briefly described by Aníbal and Chícharo (1997) for the Bissagós Archipelago and by Costa (1993) for the mainland coast. The biomass of phytoplankton was assumed to be similar as that estimated by Longhurst (1983) for Sierra Leone. We used a weighted average of $1.215 \text{ gC}\cdot\text{m}^{-2}$ considering the proportion of continental shelf (80%) and estuarine (20%) in the area as well as dry (7 months) and wet (5 months) seasons. The primary productivity (P/B) of phytoplankton was estimated based on biomass from Longhurst (1983) and a primary production of $0.665 \text{ gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Berrit and Rebert 1977), yielding a value of 200 year^{-1} .

Two other groups were included, considering available information on diet composition. These are pelagic squid and benthic algae, the first being an important prey item of large pelagics and the second considering mullets.

Diet Matrix

We were not able to find any relevant information on the diet of fish species in Guinea-Bissau. The most important studies undertaken in neighbouring areas are from Sierra Leone (Longhurst 1957, 1960) or more general descriptions on a regional basis (Caverivière 1989). The problem with this information is that most results are presented in a qualitative form or in terms of abundance and it is problematic to transform this to weight.

Considering the general lack of information given in weight proportions, we attempted to estimate conversion factors from frequency occurrence to weight or numeric frequency to weight; using studies from the Azores where both types of results were given. Using Linear Models, a surprising 50 to 60 % of the variance was explained when considering different predator and prey types including interaction, depending on the conversion attempted (Table 7). Although these are preliminary results and further work is needed, these conversion factors were applied in order to obtain a starting point concerning the diet matrix. In this way, estimates of diet composition, expressed as weight proportions, were obtained for a considerable number of species (Table 3).

When species diet compositions were not available for the region, data from other areas were used, if no diet composition data were found for a given species, we looked for closely related species of the same genus. This search for information on diet data involved bibliographic searches and FishBase 2000 (Froese and Pauly 2000). Unidentified categories in the diet were re-expressed out of 100% to exclude these categories. However, there still remained a considerable amount of subjectivity in estimating diet, for example the re-distribution of diet component 'fish', which is a very common result in diet studies.

The primary sources of information on diet of non-fish groups are the published models of Arreguín-Sánchez et al. (1993) and Opitz (1993), as these adopted a similar division of functional groups.

Table 3. Diet matrix for the balanced Guinea-Bissau ecosystem model, given in weight proportions.

	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Marine mammals	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Seabirds	-	-	-	-	-	0.030	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Turtles	-	-	-	-	-	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Billfish and marlins	-	-	-	-	-	0.050	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Tuna	0.222	-	-	0.36	-	0.150	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Pelagic sharks	-	-	-	-	-	-	-	-	-	0.040	-	-	-	-	-	-	-	-	-	-	-	-
7	Pelagic predators	0.080	0.019	-	0.17	-	0.043	0.01	-	0.232	0.010	-	-	-	-	-	-	-	-	-	-	-	-
8	Benthic predators	-	-	-	-	-	0.010	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Demersal sharks	-	-	-	-	-	0.220	-	-	0.001	0.001	-	-	-	-	-	-	-	-	-	-	-	-
10	Groupers/snappers	-	-	-	-	-	0.010	-	0.005	0.001	-	-	0.001	-	-	-	-	-	-	-	-	-	-
11	Rays	-	-	-	-	-	0.026	-	-	0.289	0.100	0.040	-	-	-	-	-	-	-	-	-	-	-
12	Benthos/fish feeders	-	0.052	-	-	-	0.150	0.02	0.207	0.020	0.011	-	0.011	-	-	-	-	-	-	-	-	-	-
13	Sparids	-	-	-	-	-	0.010	0.01	0.043	0.023	0.010	0.060	0.031	-	0.010	-	-	-	-	-	-	-	-
14	Flatfish	-	0.052	-	-	-	0.010	-	0.020	0.070	0.201	0.220	0.020	-	0.010	-	-	-	-	-	-	-	-
15	Benthic feeders	-	-	-	-	-	0.010	-	0.460	-	0.100	-	0.204	0.050	-	-	-	-	-	-	-	-	-
16	Small pelagics	0.550	0.190	-	0.27	0.733	0.150	0.50	-	-	-	-	-	0.005	-	-	-	-	0.125	-	-	-	-
17	Squid	0.137	0.094	-	0.20	0.080	0.100	0.16	-	-	0.030	-	0.029	-	-	-	0.020	-	-	-	-	-	-
18	Phytoplanktivores	-	0.076	-	-	0.143	-	0.30	0.020	-	0.070	-	0.043	-	0.010	-	-	-	0.083	-	-	-	-
19	Mulletts	-	0.095	-	-	-	-	-	0.040	-	0.002	-	0.002	-	-	-	-	-	-	-	-	-	-
20	Cephalopods	-	-	0.022	-	-	-	-	0.121	0.024	-	0.180	0.012	0.026	-	0.130	-	-	-	-	-	-	-
21	Gastropods/bivalves	-	-	0.400	-	-	-	-	-	-	0.063	0.030	0.126	0.107	0.080	0.250	-	-	-	-	-	0.28	0.05
22	Shrimps	-	-	-	-	-	-	-	-	-	0.218	0.150	0.155	0.050	0.050	0.079	-	-	-	-	-	0.05	-
23	Crabs	-	0.105	0.125	-	-	-	-	0.084	0.199	0.029	-	0.122	0.120	0.116	0.060	0.017	-	-	-	-	0.16	-
24	Small crustaceans	-	0.105	-	-	-	-	-	-	-	-	0.036	-	0.140	0.296	0.084	0.036	-	-	-	0.05	0.05	0.05
25	Annelids	-	-	0.023	-	-	-	-	-	-	0.015	0.120	0.163	0.192	0.194	0.200	-	-	-	0.10	0.15	0.05	0.05
26	Echinoderms	-	-	0.040	-	-	-	-	-	0.100	-	0.044	0.051	0.100	0.057	0.030	-	-	-	-	0.11	-	-
27	Meiobenthos	-	-	-	-	-	-	-	-	-	0.100	-	-	-	0.140	-	-	-	-	-	0.05	-	0.15
28	Zooplankton	0.011	0.210	0.150	-	0.044	-	-	-	-	-	-	0.015	0.070	0.030	0.052	0.501	0.728	0.05	0.10	0.20	0.10	0.03
29	Phytoplankton	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.426	0.064	0.85	0.25	-	0.030	0.10
30	Benthic algae	-	-	0.240	-	-	-	-	-	-	-	-	-	0.120	-	0.001	-	-	0.05	0.25	-	0.15	0.10
31	Discards	-	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	Detritus	-	-	-	-	-	-	-	-	0.041	-	0.120	0.014	0.020	0.007	0.114	-	-	0.05	0.20	-	0.20	0.22
	Sum	1.000	1.000	1.000	1.00	1.000	1.000	1.00	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	1.00	1.00	1.00	1.00

Estimation of Fisheries Catch

Several studies focusing different aspects of the Guinea-Bissau fisheries are available. These include the fisheries economic, political and legislative aspects (e.g., Rackowe and Pinho 1989), fish stock assessment (e.g., dos Santos 1994; CECAF 1992; Cadima and Caramelo 1984) and fisheries technology and its development (e.g., Baage et al. 1989; Kaczynski 1989; Anon. 1988a, b, c, d; Epler 1984). Official landings of the industrial fisheries in Guinea-Bissau were taken from CIPA (1996). At present, we have only some indications on discards and the values were assigned using our best judgment.

Considering the lack of reliable statistics for the artisanal fisheries, these were estimated assuming: (1) an average number (considering both wet and dry seasons) of 7 775 fishers that operates in the region (Luísa Ferreira, pers. comm. to Jardim and Esteves 1997); and (2) an annual estimated catch by fishers in Guinea-Bissau of 2 148 kg·year⁻¹. This value resulted from the average between the Bissagós Archipelago (2 061 kg·year⁻¹) and coastal area of Cacheu (2 234 kg·year⁻¹) (CIPA reports). The total artisanal catches were estimated as 16 697 t. The species composition of artisanal catches was based on Lafrance (1994b and c).

The estimated catches of tuna in 1991 are available from ICCAT (www.iccat.es), given as catch by species by 5° degrees square. As the EEZ of Guinea Bissau extends into two of these 5° squares, a correction factor was calculated based on the proportion of the Guinea Bissau EEZ to the total area of the two 5° squares. The resulting correction factor is 0.244 (24.4 % of the tuna catches), which is used to obtain estimates of tuna and sailfish catches.

The reported landings of sharks and rays were not consistent with observed catches during the trawl surveys. This is probably due to the occurrence of shark finning in the area, which means that dead or dying animals are returned to the sea without reporting. Another possible reason is the unreported export of considerable amounts of dried sharks to neighbouring countries, such as Senegal and Gambia (Abobarin et al. 1999).

We assumed that the proportion between teleosts and shark/rays in trawl surveys was equal to those observed in the industrial landings, since both gear and area were similar. In this way, the proportion of sharks and rays to total fish catch (trawl surveys) was estimated as 5.2%, giving an estimated elasmobranch catch of 2 251 t. The species composition observed in trawl surveys was used to estimate catch by shark and ray species and gear.

In relation to artisanal fisheries, the estimated catches of sharks and rays were based on the study by Bucal (1994). This study provided information on species composition, CPUE, and average weights, which were extrapolated. Extrapolation considered 2 000 boats fishing 60 days per year with one set a day and that 51% operate with gears that catch sharks and rays. This yielded an estimate of 5 170 t·year⁻¹, but this estimate was abandoned because it yielded a biomass of pelagic sharks that was far too high. Instead, the catch was of pelagic sharks was reduced and the total catch of sharks and rays set to 2 539 t.

Table 4. Average landings (t-km-2-year-1) for the different fisheries considered in the Guinea-Bissau region for the period 1990 to 1992 (groups 24-32 in the previous table have zero catches).

N°	Groups	Artisanal	Shrimp net	Cephalopod net	Fish net	Purse seine	Tuna	Total
1	Marine mammals	0.001	–	–	–	–	0.001	0.002
2	Seabirds	0.000	–	–	–	–	0.000	0.000
3	Turtles	0.001	–	–	–	–	–	0.001
4	Billfish and marlins	–	–	–	–	–	0.004	0.004
5	Tuna	–	–	–	–	–	0.115	0.115
6	Pelagic sharks	0.002	0.003	–	0.001	–	–	0.006
7	Pelagic predators	0.073	0.008	–	0.008	0.001	–	0.090
8	Benthic predators	0.001	0.078	0.003	0.052	0.001	–	0.135
9	Demersal sharks	0.023	0.025	0.001	–	–	–	0.049
10	Groupers/snappers	0.006	0.003	0.001	–	–	–	0.010
11	Rays	0.037	0.011	0.001	–	–	–	0.049
12	Benthos/fish feeders	0.049	0.101	0.001	0.073	–	–	0.224
13	Sparids	0.007	0.005	0.003	0.001	–	–	0.016
14	Flatfish	0.000	0.086	0.010	0.023	–	–	0.119
15	Benthic feeders	0.007	0.054	0.003	0.020	0.001	–	0.085
16	Small pelagics	0.009	0.019	0.003	0.028	0.246	–	0.305
17	Squid	–	0.001	–	–	0.000	–	0.001
18	Phytoplanktivores	0.054	–	–	–	–	–	0.054
19	Mulletts	0.148	–	–	–	–	–	0.148
20	Octopus/ <i>Sepia</i>	–	0.087	0.035	0.001	–	–	0.123
21	Gastropods/bivalves	0.001	–	–	–	–	–	0.001
22	Shrimps	–	0.090	–	0.001	–	–	0.091
23	Crabs	–	0.009	–	0.002	–	–	0.011
	Sum	0.419	0.580	0.061	0.210	0.249	0.120	1.639

Parameter Estimation

Production/Biomass ratios (P/B)

For fish groups it was assumed that under steady state conditions: $P/B = Z$ and that $Z = M + F$ (Allen, 1971). Natural mortality (M) was estimated using Pauly (1980) empirical equation:

$$M = K0.65 \cdot L_{\infty}^{-0.279} \cdot T0.463 \quad \dots 1)$$

where L_{∞} is in cm, K in years and T in °C and are values from published data for each species or from FishBase (Froese and Pauly 2000). Temperature values were determined from data obtained from INIP and CIPA (1993) cruises stratified by depth range (0-25 m = 27° C; 26-75 m = 21° C; 76-10 m = 19° C; 101-200 m = 15° C; and 201-300 m = 12° C). Fishing mortality (F) of demersal fish species was estimated from catch and biomass via $B = \text{catch} / F$.

Table 5. Average discards (t-km-2-year-1) estimated for the different fisheries considered in Guinea-Bissau region for the period 1990 to 1992 (groups 5, 27-32 and purse seines are omitted as they are not known to contribute to discards).

N°	Groups	Artisanal	Shrimp net	Ceph net	Fish net	Total
1	Marine mammals	–	–	–	–	–
2	Seabirds	–	–	–	–	–
3	Turtles	–	0.001	–	–	0.001
4	Billfish and marlins	–	–	–	–	–
5	Tuna	–	–	–	–	–
6	Pelagic sharks	–	0.001	–	0.001	0.002
7	Pelagic predators	–	–	–	–	–
8	Benthic predators	–	–	–	–	–
9	Demersal sharks	0.001	–	0.001	–	0.002
10	Groupers/snappers	–	–	–	–	–
11	Rays	0.001	0.001	0.001	0.001	0.004
12	Benthos/fish feeders	–	–	–	–	–
13	Sparids	–	–	–	–	–
14	Flatfish	–	0.001	0.001	0.001	0.003
15	Benthic feeders	–	0.001	0.001	0.001	0.003
16	Small pelagics	–	–	–	–	–
17	Squid	–	–	–	–	–
18	Phytoplanktivores	–	–	–	–	–
19	Mulletts	–	–	–	–	–
20	Octopus/ <i>Sepia</i>	–	–	–	–	–
21	Gastropods/bivalves	–	0.001	0.001	0.001	0.003
22	Shrimps	–	–	–	–	–
23	Crabs	–	0.001	–	0.001	0.002
24	Small crustaceans	–	–	–	–	–
25	Annelids	–	–	–	–	–
26	Echinoderms	–	0.001	0.001	0.001	0.003
	Sum	0.002	0.008	0.006	0.007	0.023

Consumption/Biomass Ratios (Q/B)

The consumption ratios for fish groups were estimated using the empirical equation of Palomares and Pauly (1998):

$$\log Q/B = 7.964 - 0.204 \log W_{\infty} - 1.967 T' + 0.083 \cdot AR + 0.532h + 0.398d \quad \dots 2)$$

where W_{∞} is in g, where the aspect ratio AR for each species was adapted from estimates available in FishBase 2000 (Froese and Pauly 2000) and the dummy variables expressing food type h and d were empirically assigned to each species. T' is an expression of water temperature using $T' = 1000/\text{Kelvin}$.

Assimilation Efficiency

Following Shannon and Jarre-Teichmann (1999), the proportion of unassimilated food consumed was set at 0.20 except for small pelagics, mulletts, and benthos groups, for which a value of 0.30 was used. For zooplankton, a value of 0.35 was used.

Results and Discussion

The final estimated parameters of the model are presented in Figure 3, which show consistent results for the well-studied fish groups. The use of empirical relationships to determine basic parameters such as L_{∞} and W_{∞} of the von Bertalanffy equation as well as Q/B is based on the fact that they are considered conservative properties, which also justifies the use of Q/B estimates from other species or areas with similar ecosystem characteristics.

Considering the lack of information for benthos groups, top predators, cephalopods, and zooplankton, we adopted Q/B and P/B estimates from other areas, based on the fact that these groups are not directly exploited. However, in the case of exploited groups such as tunas and billfish, the model was allowed to estimate biomass and P/B. In such cases, we assume fixed values for ecotrophic efficiency (EE) and gross conversion efficiency (P/Q). The resulting parameters for these groups need to be validated through independent sources of information on abundance or biomass and catches and discards.

In order to achieve mass-balance, the diet matrix was modified considerably. However, it is important to point out that this involved minor adjustments concerning the demersal fish species. Most of the larger adjustments are in relation to the contributions of benthos groups and in some cases the important pelagic prey groups such as small pelagics and squid.

One problem encountered was that the dominant species in terms of biomass estimated by trawl surveys did not coincide with the dominant species in the fisheries statistics. This is also why the number of fish species considered grew from approximately 80 to 166. A first comparison of fish species composition with the results from other surveys (Domain 1972; Diop 1996) indicates a most likely misidentification of the fish species in the fisheries statistics. The functional groups defined appeared to solve this problem by aggregating biomass and catches. However, a simple averaging of Q/B and P/B values was used as input values instead of a weighted average based on biomass, which would have been the preferred method. This simple averaging may have introduced a bias in the estimates of Q/B and P/B.

Great inter-annual variability was observed in terms of estimated biomass, both in terms of total demersal fish biomass and by species. For example, the total biomass varied from 63 000 t in 1990 to 37 000 t in 1991. However, the total catch rates observed during the INIP/LBM (1989, 1990, 1992 and 1993) surveys suggest a downward trend (Figure 2).

Two species, the bathydemersal *Chlorophthalmus agassizi* and the bathypelagic *Synagrops microlepis*, were responsible for much of the observed variability between 1990 and 1991, accounting for approximately 35 to 40 % of the total biomass. An averaging of biomass estimates of the two years significantly reduces the importance of these two species. However, future developments of the model should differentiate these two new groups, which are concentrated along the continental slope.

Table 6. Abundance of macrozoobenthos (A = g·0.1 m⁻² and in %) determined from samples taken with a Smith-McIntyre grab during the INIP/LBM trawl surveys.

Groups	1989		1990		1991		1989-1991	
	A	%	A	%	A	%	A	%
Cnidaria	3	0.17	3	0.08	15	0.22	21	0.17
Plathelminthes	–	–	–	–	1	0.01	1	0.01
Nemertinea	5	0.28	10	0.25	13	0.19	28	0.22
Annelida								
Polychaeta	803	45.63	1076	27.17	1959	29.07	3838	30.81
Sipuncula	4	0.23	–	–	14	0.21	18	0.14
Mollusca		–		–		–		–
Gastropoda	31	1.76	110	2.78	1257	18.66	1398	11.22
Polyplacophora	1	0.06	1	0.03	–	–	2	0.02
Bivalvia	414	23.52	1413	35.68	803	11.92	2630	21.11
Scaphopoda	1	0.06	6	0.15	1	0.01	8	0.06
Arthropoda		–		–		–		–
Ostracoda	–	–	6	0.15	34	0.50	40	0.32
Copepoda	8	0.45	5	0.13	9	0.13	22	0.18
Cirripedia	5	0.28	–	–	1	0.01	6	0.05
Nebaliacea	–	–	1	0.03	3	0.04	4	0.03
Stomatopoda	3	0.17	–	–	1	0.01	4	0.03
Mysidacea	–	–	16	0.40	–	–	16	0.13
Cumacea	44	2.5	50	1.26	80	1.19	174	1.4
Tanaidacea	26	1.48	57	1.44	48	0.71	131	1.05
Isopoda	34	1.93	30	0.76	32	0.47	96	0.77
Amphipoda	318	18.07	1008	25.45	2216	32.89	3542	28.43
Natantia	14	0.80	38	0.96	51	0.76	103	0.83
Macrura	4	0.23	24	0.61	33	0.49	61	0.49
Brachyura	12	0.68	73	1.84	117	1.74	202	1.62
Pycnogonida	–	–	–	–	1	0.01	1	0.01
Echinodermata								
Asteroidea	–	–	1	0.03	–	–	1	0.01
Ophiuroidea	24	1.36	25	0.63	34	0.50	83	0.67
Holothuroidea	5	0.28	5	0.13	11	0.16	21	0.17
Echinoidea	1	0.06	2	0.05	4	0.06	7	0.06
Total	1760	100	3960	100	6738	100	12458	100

Table 7. Two-factor analysis of variance considering the effects of predator groups and prey groups as well as interaction between these two factors. The resulting model, which is significant, was used to convert diet composition given in frequency of occurrence to weight proportions. Linear model: log % weight ~ log % occurrence + prey group + predator group + prey group * predator group.

	df	Sum Sq	Mean Sq	F value	Pr(>F)
Log-occurrence	1	69.706	69.706	279.4457	< 2.2e-16 ***
Prey group	3	2.420	0.807	3.2342	0.02248 *
Predator group	5	13.878	2.776	11.1273	6.038e-10 ***
Prey group : Predator group	15	14.631	0.975	3.9102	1.695e-06 ***
Residuals	341	85.061	0.249	–	–

Significance codes: * = 0.05, ** = 0.01, *** = 0.001.

Residual standard error: 0.4994 on 341 degrees of freedom.

Multiple R-Squared: 0.5419, adjusted R-squared: 0.5097.

F-statistic: 16.81 on 24 and 341 degrees of freedom, p-value: 0.

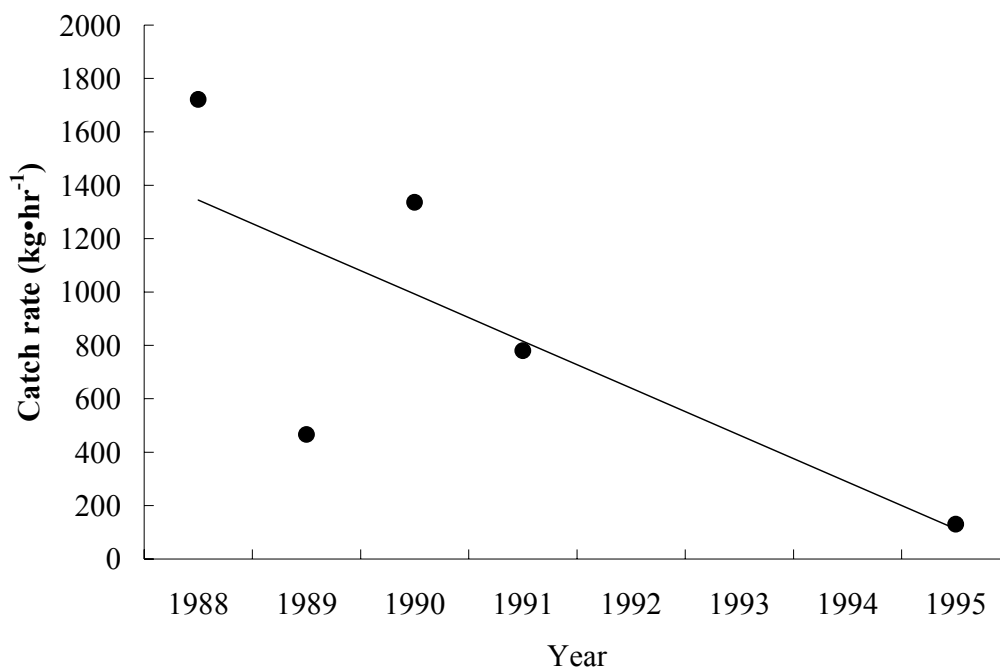


Figure 2. Decreasing trend in total catch (CPUE) rates observed during the INIP/LBM surveys from 1988-1995.

If we consider only demersal fish species of the continental shelf, the estimate of total biomass ranged between 24 000 to 37 000 t, which is comparable to the result of the CNROP/CIPA trawl survey in 1995 (30 000 t; Diop 1996) and the Guinean Trawl Survey in 1964 (40 000 t; Williams 1968).

A comparison of global biomass estimates based on the model, including pelagic and demersal species, with values given in literature is difficult, because it is not clear which species are considered. An estimate of 1.4 million t at the 3rd trophic level is given by Berrit and Rebert (1977), which may be comparable to 1 million t in the present study. But it is not clear what is being compared and this should be considered preliminary.

The geographic area surveyed (Figure 1) was restricted to depths greater than 50 m because of difficulties in operating at lower depths. Thus, the surveys were not a good source of estimates on typical coastal species/groups included in the model. Moreover, the extrapolation method used, which did not consider specific habitat characteristics, can bias the estimates.

There is a large amount of uncertainty concerning the benthos groups, the biomass estimates in particular. We decided to include differentiated groups instead of one 'benthos box', because biomass estimates are expected to become available in the near future. It will then be possible to compare and adjust the model parameters directly. The total biomass of the benthos groups estimated by the model, $\cong 25 \text{ g}\cdot\text{m}^{-2}$, is comparable to estimates given by Domain (1982), ranging from $19.9 \text{ g}\cdot\text{m}^{-2}$ to $49.4 \text{ g}\cdot\text{m}^{-2}$ for the rainy and dry season, respectively. This is reassuring, but it can still be expected that the estimates for these groups will change as better data becomes available.

Mixed trophic impacts

Direct and indirect trophic impacts from one ecosystem component on another were assessed by the Ecopath routine called “mixed trophic impact” (Ulanowicz and Puccia 1990).

The overall analyses of the mixed impact factors (Figure 3) shows that prey species have the highest positive impact on their predators, e.g., the positive impact phytoplankton has on its major predators: small pelagics, phytoplanktivores, gastropods/bivalves and zooplankton. Small pelagics also have a positive impact on their main predators: marine mammals, tunas and pelagic predators. Phytoplankton and benthic algae, the primary producers of the ecosystem, have a positive impact on nearly all compartments, except themselves. All compartments have negative impacts on themselves, which indicates within group competition for resources (Christensen et al. 2000).

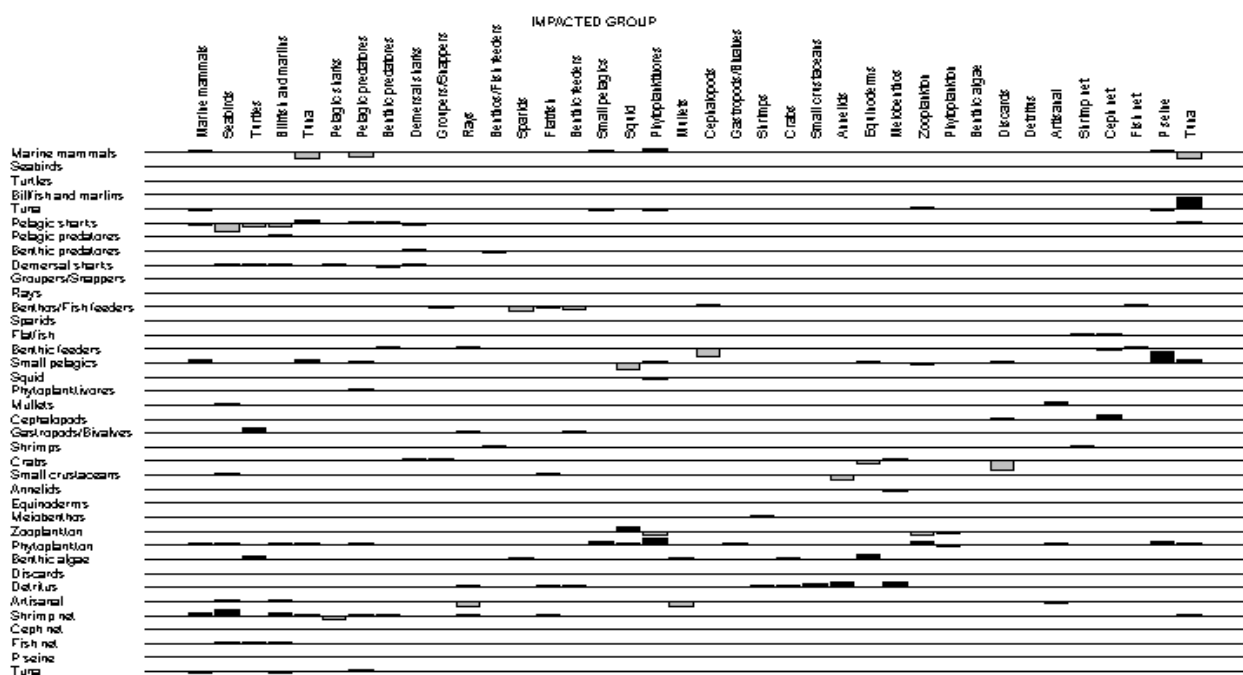


Figure 3. Mixed trophic impacts of model groups in the Guinea-Bissau shelf ecosystem for 1990/1992. Impacted groups are arranged along the horizontal axis and impacting groups down the vertical axis. Positive impacts are show above the zero line for each impacting group and negative impacts below.

The major predators, such as pelagic sharks, marine mammals, demersal sharks and benthos/fish feeders have negative impact on almost all of their prey groups. However, some cases of beneficial predation were observed, indicating that the direct negative impact a predator has on a prey can be outweighed by indirect positive impacts. Marine mammals prey upon small pelagics (55%), but have a positive impact on this group. This is a result of the impact (by predation) of tunas by marine mammals, which also feed on small pelagics (73%). Other example of beneficial predation is the case of pelagic sharks that have a positive impact on some of their preys, such as tuna and pelagic predators.

Some groups have negative impacts on other groups without preying on them. These indirect negative impacts are mainly a result of direct competition for prey species, as in the case of the zooplankton on phytoplanktivorous fish, or a result of an indirect increase of

predation, such as when tunas have a positive impact on pelagic sharks that prey upon marine mammals. The result will be an indirect negative impact of tunas on marine mammals.

Some curious cases of low or null impact, as a result of counteracting positive and negative impacts, are also observed. This is, for instance, the case of the null impact that pelagic predators has on their main prey, the small pelagics.

Several groups have negative impacts on fisheries. Tuna and pelagic sharks have a negative impact on the purse-seine fishery, resulting from the competition for small pelagics, which is the major component of that fishery and important prey for those predators. Other examples are the negative impact of marine mammals on tuna fishery and benthic feeders on cephalopod nets fishery.

The fishery has a positive impact in the high trophic level groups, except for those groups targeted by some of the fisheries. The pelagic sharks suffer a negative impact by all fisheries, while tuna and marine mammals suffer a negative impact by shrimp nets and artisanal fishery, respectively. In general, it appears that the top predators benefit from the removal of their competitors by some of the fisheries.

Several groups have negligible impacts on any other group in the system, probably resulting from their low biomasses. This is the case of seabirds, turtles, billfishes and marlins, groupers/snappers and rays.

Future developments of the Guinea-Bissau model should consider improving the estimation of catches and discards, un-reported shark catches, the creation of separate groups for commercially important species (e.g., *Galeoides*, *Arius*, etc.), and compilation of more information, mainly on top predators and benthos groups. It became apparent during the creation of the model that fisheries catch statistics in Guinea-Bissau are of poor quality, especially in the case of the coastal artisanal fisheries, where no systematic recording is being implemented. Another problem considered important is the underestimation of catches by the international fleet in the EEZ, due to under-reporting or illegal fishing activity.

Considering the lack of information on a considerable number of subjects, collaboration with neighbouring countries will also bring benefits in terms of access to information, longer time series of abundance and catches. A comparison with the results of other Ecopath models in the context of the SIAP project will certainly give indications on ways of improving the preliminary model presented in this study.

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