

## A MODEL OF TROPHIC FLOWS IN A PELAGIC AREA OF THE GULF OF GUINEA DURING THE 1990'S

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### SUMMARY

*A mass-balanced trophic flow model is developed in a pelagic area of the Gulf of Guinea. The South Sherbro area (0-5°N, 10-20°W) is subjected to a seasonal and intensive tropical purse seine tuna fishery from October to April. Its size is relatively small compared with the total fishing area. The parameter estimation of the model is based on studies conducted within the framework of the PICOLO programme, conducted by IRD from 1996 to 1999, from observers' trips onboard purse-seiners, and from the literature and expert advice. Twenty functional groups are identified focusing on epi-pelagic species and on top-predators. Different scenarios attempt to test the hypotheses stated for the basic model. Primary production required to sustain fishing activity is estimated at 4%. Results revealed insufficient knowledge (migration and seasonality of the fishing season) for the estimation of tuna biomass and tuna forage biomass. Tuna play a major role within consumption and biomass regulation for their competitors.*

### RÉSUMÉ

*Un modèle de type ECOPATH est développé sur une zone hauturière de l'Atlantique Equatorial Est, soumise à une pression de pêche à la senne importante pendant 7 mois de l'année. Cette zone (0-5°N, 10-20°W), de taille modeste par rapport à la surface occupée par la pêcherie, a fait l'objet d'études approfondies pendant le programme PICOLO conduit par l'IRD entre 1996 et 1999. Les connaissances acquises au cours de ce programme, les résultats d'un programme d'observateurs scientifiques embarqués, les données issues de la littérature ainsi que les renseignements fournis par des experts ont permis de paramétrer ce modèle de flux trophiques. Il comporte 20 groupes fonctionnels et détaille principalement les prédateurs supérieurs. Le modèle de base repose sur des hypothèses fortes qui ont été testées par l'élaboration de différents scénarios. La production primaire requise pour soutenir la pêche est estimée à 4%. Les résultats ont révélé des manques de connaissances pour l'estimation des biomasses de thons et de poissons fourrage, la représentation des migrations et la saisonnalité. Les thons jouent dans ce système un rôle majeur en terme de consommation et de régulation des biomasses des autres prédateurs supérieurs.*

### RESUMEN

*Se ha desarrollado un modelo tipo ECOPATH para una zona de pesca de altura en el Atlántico Ecuatorial Este, sometida a una presión de pesca con cerco importante durante siete meses al año. Esta zona (0-5° N-10-20° W), de tamaño modesto en comparación con la superficie ocupada por la pesquería, ha sido objeto de estudios con detenimiento durante el programa PICOLO, desarrollado por el IRD entre 1996 y 1999. Los conocimientos adquiridos en el transcurso de este programa, los resultados de un programa de observadores científicos embarcados, los datos extraídos de la bibliografía, así como la información proporcionada por los expertos han permitido obtener parámetros para este modelo de flujos tróficos. En él se identificaron veinte grupos funcionales y se detallan sobre todo los depredadores ápice. El modelo de base está fundamentado por hipótesis fuertes que han sido comprobadas mediante la elaboración de diferentes escenarios. La producción primaria necesaria para mantener la pesca se estima en un 4%. Los resultados revelaron una falta de conocimientos en cuanto a las estimaciones de biomasa de túnidos y de peces de forraje, la representación de las*

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migraciones y la estacionalidad. Los t́nidos desempeñan un papel fundamental en este sistema en términos de consumo y regulación de biomásas de otros depredadores ápite.

## KEYWORDS

*Steady state, Ecosystems, Tuna fisheries, Food preferences, Predation*

## 1 INTRODUCTION

We developed an ECOPATH model for the food web of a peculiar pelagic area in the Gulf of Guinea, located between 0-5°N and 10-20°W, and termed the South Sherbo area (SSA) hereafter. A lot of information were collected regarding different species groups of this ecosystem. Actually, a large purse-seine fishery occurs in the SSA from October to March/April, representing a quarter of the yearly catches of the Eastern Equatorial Atlantic (ICCAT statistics; Ménard *et al.* 2000a). The presence of these seasonal tuna concentrations was studied within the context of the PICOLO research programme, conducted by the Institut de Recherche pour le Développement (Ménard *et al.* 1998; Lebourges-Dhaussy *et al.* 2000). Towards that end, a series of cruises were carried out in the SSA to study the physical environmental features and the living organisms (acoustics, trawling). The diet of tuna caught by the purse-seiners in the SSA showed that skipjack (*Katsuwonus pelamis*) and juveniles of yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*) of the same size (average fork length 46 cm) feed mainly on small-size mesopelagic fish *Vinciguerria nimbaria* (Ménard *et al.* 2000b). This forage fish aggregates day and night in the top 200 m of the sea (Marchal and Lebourges 1996) becoming available to the surface predators like tuna. By combining available information (data from the PICOLO programme, data collected by scientific observer onboard purse-seiners, and fishery statistics) and expertise on the SSA, we thus attempted to describe the trophic interactions in the SSA for 1991-1996 period, using the ECOPATH with EcoSim approach (Christensen and Pauly 1992; Walters *et al.* 1997, 1999, 2000). The comparison with other models (Shannon and Jarre-Treichmann 1999; Kitchell *et al.* 1999) allowed us to deal with the large uncertainty around many of the parameter estimates used in the model.

## 2 MATERIAL AND METHODS

### 2.1 The ECOPATH model

The ECOPATH model was developed by Polovina (1984) and then modified by Christensen and Pauly (1992). The steady state approach was extended to a temporal dynamic simulation tool called EcoSim (Walters *et al.* 1997, 2000). ECOPATH models have been developed for a large variety of systems. The pertinent software and documentation are free and available at [www.ecopath.org](http://www.ecopath.org). An ECOPATH model is based on a balance of the inputs and of the outputs for each component (“box”) of the ecosystem under study, and on a balance for the flows between the components. For each living group of organisms:

$$\text{Consumption } (Q) = \text{Production } (P) + \text{Respiration } (R) + \text{Unassimilated food } (U).$$

Moreover, a set of simultaneous linear equations describes the interactions between groups within the ecosystem. These interactions are based on the predation relationships: the production of the group *i* is balanced by the sum of predation on the group *i* by the other groups, by the export from the system (fishing or emigration) and by other mortality (i.e., non-predatory biomass losses of *i*). Therefore, for each group *i* within the ecosystem,

$$B_i \cdot (P/B)_i \cdot EE_i - \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} - Ex_i = 0$$

where  $j$  is any of the predators of  $i$ ,  $B_i$  is the biomass of  $i$ ,  $(P/B)_i$  is the production of  $i$  per unit of biomass (= total mortality under steady-state conditions),  $(Q/B)_i$  is the consumption per unit of biomass for the consumer  $j$ ,  $DC_{ji}$  is the average fraction of  $i$  in the diet of  $j$  (in term of mass),  $EE_i$  is the ecotrophic efficiency of  $i$  (= the fraction of the total production of  $i$  consumed by predators or exported from the system), and  $Ex_i$  is the exports of  $i$  from the system (by emigration or fishery catch). The required parameters are: biomass ( $B$ ), production per unit of biomass ( $P/B$ ), ecotrophic efficiency ( $EE$ ), consumption per unit of biomass ( $Q/B$ ), assimilation efficiency, diet composition, exports (mortality and other exports). One of those parameters can be estimated by solving the linear equations. A model is considered to be in mass-balance once acceptable results for the unknown parameter and respiration are obtained.

## 2.2 Parameterisation of the model

The SSA covers an area of 617 400 km<sup>2</sup>. The period modelled is from 1991 to 1996. All state variables were scaled in biomass units per area using wet weight. Flows and rates were expressed on an annual basis. We focused on the epipelagic zone (0-500 m), with a high resolution at the top of the food web, and with aggregations for the low trophic levels. A total of 20 functional groupings was used: 12 of them included fish and the others invertebrates and detritus. We attempted to aggregate prey types with a minimum of vertical trophic overlap. A conversion factor of 14.25 was used when biomass, production or consumption were given in units of carbon (Jarre-Teichmann *et al.* 1998). For most groups, 20% of the food consumed was assumed to be unassimilated, except for zooplankton for which a rate of 30% was applied.

### 2.2.1 Phytoplankton

During the PICOLO programme, the primary production in the SSA was estimated at 1 mg.C.m<sup>-3</sup>.h<sup>-1</sup>, giving a production of 7 490 t.C.km<sup>-2</sup>. This value was similar to the new production estimated by an ocean circulation model (André, pers. comm.), and to the CZCS data (Monger *et al.* 1997). Biomass was estimated at 37 t.km<sup>-2</sup> from a biogeochemical model (Aumont, pers. comm.). Therefore, P/B was estimated at 200 year<sup>-1</sup>.

### 2.2.2 Detritus

No information is available on this compartment. The empirical equation of Christensen and Pauly (1993) was used:  $\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E$ , where  $D$  is the detritus standing stock in g.C.m<sup>-2</sup>,  $PP$  is the primary production in g.C.m<sup>-2</sup>.year<sup>-1</sup> and  $E$  is the euphotic depth in m. Assuming that  $E$  equals 60 m, the detritus biomass was estimated at 488 t.km<sup>-2</sup>.

In the Gulf of Guinea, the ZOOPLANKTON compartment was principally studied by Roger (1982a and b), Le Borgne (1982, 1983), Le Borgne and Roger (1983), and Le Borgne *et al.* (1983).

### 2.2.3 Microzooplankton (50-200 µm)

Roger (1982) reported an annual biomass of 2 t.km<sup>-2</sup>. Production and consumption were estimated by Le Borgne (1982) and Le Borgne *et al.* (1993) who gave a range from 124 to 840 year<sup>-1</sup> for P/B, and 37 to 40 % for P/Q (gross efficiency). Diet was based on the study of Shannon and Jarre-Teichmann (1999): 40% phytoplankton, 40% detritus (bacteria) and 20% microzooplankton.

### 2.2.4 Mesozooplankton

Biomass was estimated at 24 t.km<sup>-2</sup>, P/B at 53 year<sup>-1</sup>, and P/Q at 31 % (Le Borgne 1983; Roger 1982). Diet was assumed to be 50% each of phytoplankton and microzooplankton (Shannon and Jarre-Teichmann 1999).

### 2.2.5 Macrozooplankton, Micronekton

Macrozooplankton, gelatinous zooplankton, cephalopods, small epipelagic fish, mesopelagic fish and *Vinciguerria nimbaria* are separate groups in the model. *V. nimbaria* was split from the mesopelagic group because it is a major link in the food web of the apex predators in the SSA. At first, biomass of small epipelagic fish, mesopelagic fish and *V. nimbaria* was estimated by acoustics, taking into account the night and day behaviour (Marchal and Lebourges 1996; Lebourges-Dhaussy *et al.* 2000). The target strength of all the fish was assumed to be the same (-56.7 dB), and instantaneous recorded densities was extrapolated to the whole area. The estimated biomass are reported in **Figure 1**.

The difference between the night and day total values led us to assume a vertical ascension at night of mesopelagic fish inhabiting deeper than 500 m during the day. Macrozooplankton and cephalopods were then estimated using the averaged trawl composition estimated during the PICOLO programme: 27% *Vinciguerria nimbaria*, 60% other fish, 4% Cephalopod, and 9% Crustacean (major component of macrozooplankton). *V. nimbaria* feed on mesozooplankton only, Q/B is estimated at 29 year<sup>-1</sup> (Riandey 2000), and P/B was estimated at 8 year<sup>-1</sup>. The remaining production and consumption parameters were taken from FISHBASE (Froese and Pauly 1998).

Biomass of macrozooplankton was estimated at 4.2 t.km<sup>-2</sup>, and biomass of cephalopods at 1.9 t.km<sup>-2</sup>. Diet of cephalopods is comprised of 38% mesopelagic fish, 12% cephalopods, 24% epipelagic fish and 26% macrozooplankton (Piatkowski *et al.* 2001). Jellyfish and salps are sometimes abundant in the SSA. It was assumed that these organisms consist of 99% liquid. Based on the estimation of Roger (1982), wet biomass of gelatinous zooplankton was estimated at 7.5 t.km<sup>-2</sup> in the SSA. Diet was assumed to be 25% each of phytoplankton, detritus, microzooplankton and mesozooplankton, as assumed by Shannon and Jarre-Teichmann (1999). P/B was fixed at 2.5 year<sup>-1</sup> (Christensen 1995).

### 2.2.6 Tuna

Three groups were considered because intraguild cannibalism and overlapping are common feature of diets for tuna: (1) adults of yellowfin and bigeye tuna (Fork Length > 90 cm; mainly unassociated schools); (2) juveniles of yellowfin and bigeye tuna (mainly FAD-associated schools); and (3) skipjack tuna (mainly FAD-associated schools). We bounded artificially the SSA. Then, local biomasses should be estimated taking into account the temporal and spatial dynamics of tuna in the Gulf of Guinea. However, fish movements are not explicitly represented in the assessments of tuna populations, and such data were not available. Based on the steady-state hypothesis of ECOPATH, we assumed that the total mortality  $Z$  is equal to  $P/B$  (Allen 1971). Fishing mortality, natural mortality, exploitation rates and catches were based on the most recent assessments (Stock Assessment Session of the SCRS, see **Table 1**). Biomasses were thus estimated at 0.108 t.km<sup>-2</sup> for skipjack, 0.034 t.km<sup>-2</sup> for yellowfin and bigeye adults, and 0.073 t.km<sup>-2</sup> for juveniles. Tuna diet composition was already studied in the SSA (Ménard *et al.* 2000b). To take into account the seasonal presence of tuna in the SSA, we set a high diet proportion as "Import" in the ECOPATH diet composition matrix, assuming that tuna spent 40% of its feeding time outside the modelled system.

Otherwise, FISHBASE and the ECOPATH model of Kitchell *et al.* (1999) provided the ranges for the remainder parameters:  $P/B = 1.8 \text{ year}^{-1}$  and  $Q/B = 23 \text{ year}^{-1}$  for skipjack, 0.9 year<sup>-1</sup> and 17 year<sup>-1</sup> for yellowfin and bigeye adults, and 2.5 year<sup>-1</sup> and 27 year<sup>-1</sup> for juveniles.

### 2.2.7 Billfishes, Associated Fauna, Chondrichthyans and Marine Mammals

These groups were distinguished in the model, but we estimated their biomasses together from data collected by scientific observers onboard purse-seiners. For each by-catch group  $i$ , biomass is estimated as:

$$B_i = \frac{1}{E_{i,j}} \sum_j \left( \frac{Y_{i,j}^{obs}}{Y_{T,j}^{obs}} Y_{T,j} \right)$$

where  $Y_{i,j}^{obs}$  = total catch of  $i$  with fishing mode  $j$  during observers' trips;  $Y_{T,j}^{obs}$  = total tuna catch with fishing mode  $j$  during observers' trips;  $Y_{T,j}$  = total tuna catch with fishing mode  $j$  (mean of 1991-1996) in the SSA.  $E_{i,j}$ , exploitation rate of  $i$  with fishing mode  $j$ ; with  $i \in$  [sharks ; ray ; billfishes ; marine mammals ; big associated fauna ; small associated fauna], and  $j \in$  [FAD ; unassociated school].

Biomasses were estimated at 19 kg.km<sup>-2</sup> for billfishes, 5 kg.km<sup>-2</sup> for sharks, 50 kg.km<sup>-2</sup> for large-size associated fauna, 54 kg.km<sup>-2</sup> for small-size associated fauna, 0.7 kg.km<sup>-2</sup> for marine mammals and 0.2 kg.km<sup>-2</sup> for ray. Diet of sharks was established from Cortés (1999). For other groups, FISHBASE was used and completed by literature for marine mammals (Santos *et al.* 2001), billfishes (Hernandez-Garcia 1995; Velasco and Quintans 1999; Stilwell and Kolher 1982) and discussed with experts (Séret, pers. comm.). Production parameter P/B was estimated using decomposition equation  $P/B = M + F$  (Christensen and Pauly 1993) where  $M$  is natural mortality provided by FISHBASE and  $F$  is fishing mortality estimated from observers' trips.

### 3 RESULTS AND DISCUSSION

Values of parameters for which the model was balanced are shown in **Table 2**. The criterion used for balancing the model was ecotrophic efficiency ( $EE$ ) = 1. P/B and Q/B were changed when necessary but we avoided to change the structure of the diet composition matrix (Annex). The biomass of the small-size associated fauna was increased in order to take into account the biomass of *Auxis thazard* that is probably underestimated in the by-catch data. Diet of Cephalopods was slightly changed and the number of groups that prey on *Vinciguerria nimbaria* was increased. Main estimated parameters are presented **Table 2**, and summary statistics **Table 3**. The highest trophic level of the food web is occupied by billfish (5.2). Billfish, sharks, marine mammals and yellowfin and bigeye adults have TL greater than 4.5, relatively low P/B values, and modest biomasses, whereas skipjack, juveniles of tuna and associated fauna have TL between 4.1 and 4.5, higher P/B values, and substantial biomasses.

The system omnivory index (a measure of how the feeding interactions are distributed between trophic levels) is estimated at 34%, showing the complexity of the trophic relationships in the SSA. But the food web structure focused on the top predators that have opportunist diets. The primary production required to sustain the catches in the SSA during the 1990s was estimated at 4% (for a total net primary production of 7,400 t.km<sup>-2</sup>.year<sup>-1</sup>). Such a concept of primary production equivalents allows to compare the effects of fishing at different trophic levels or in different ecosystems. Pauly and Christensen (1995) found 1.8% in average for the open ocean ecosystems. Our result seems to confirm the high fishing pressure on tuna in the SSA. The global trophic transfert efficiency was estimated at 9.8% between the discrete trophic levels (*sensu* Lindeman 1942), with a total system throughput of 21,897 t.km<sup>-2</sup>.year<sup>-1</sup>.

There was uncertainty about many of the parameter estimates used in the initial realization of the balanced model. We thus investigated alternative scenarios to explore the influence of some of the parameters and of some of the choices we did. First, we aggregated all the forage fish in one group: meso-pelagic fish, epi-pelagic fish, and *Vinciguerria nimbaria*. The group has then a high biomass (38.7 t.km<sup>-1</sup>), and a low  $EE$ . Most of the statistics and indices were similar, except the PPR that decreased (3.1%) because of the simplification of the links in the food web. However, this simplified structure does not allow us to take into account the function of some peculiar species or functional group of species. The second scenario aimed to estimate the biomasses of the forage fish groups. Indeed, these biomasses were estimated from acoustic data (instantaneous biomass and not on an

annual basis). Because of the very low *EE* values obtained with the basic model, we could suspect an over estimation. We fixed the *EE* at 0.99. Biomasses of meso-pelagic fish, epi-pelagic fish, and *Vinciguerria nimbaria* were then decreased by 21%, 66%, and 83%, respectively. The changes were substantial, and the system appeared more mature than the basic model. Actually, the use of the ECOPATH model to estimate unknown biomasses was pertinent in this case, because forage fish groups are probably well “used” in the system. In the third scenario, we estimated the biomass of the phytoplankton, once the *EE* was fixed at 0.95%. We obtained 16.55 t.km<sup>-2</sup>, i.e. half the value of the basic model. All the statistics changed substantially, and the PPR was then estimated at 9.04%. In this scenario, the oligotrophy of the SSA was confirmed. The last scenario aimed to separate the two groups of the associated fauna in five new groups, in order to take into account the different main species: carangidae (6 species); mahimahi (2 species); balistidae (2 main species); scombridae (*Auxis thazard*, *Euthynnus alleteratus*, *Acanthocybium solandri*); and other epi-pelagic species (including belonidae, lobotidae, barracuda, kyphosidae). Biomasses of these groups were estimated from observers’ trips, and diets were based on the literature and Fishbase. The new estimation of the basic parameters of this model did not lead to substantial changes. However, the observation of how the flows for each group were distributed on discrete trophic levels, showed the heterogeneity of the two groups for the associated fauna in the basic model. In this scenario, the mahimahi group was close to the tuna adult group. However, the parameterisation of the balistidae group appeared to be not suitable.

In this work, we attempted to mix all the information collected in a peculiar and small area of the Gulf of Guinea, in order to develop a trophic model in an open sea system. To have an “image” of the structure of the food web, strong hypotheses have been stated. In this approach, we pointed out the necessity to reach to a compromise between the complexity of such a dynamical system (a huge number of species across many trophic levels, interactions, temporal and spatial scales...), and the motivation to resume it in a steady state approach.

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**Table 1.** Biomass estimates for tuna groups. Ages 0 to 2 were considered as juveniles for yellowfin (\*) with  $M_0 = M_1 = 0.8$  and  $M_2 = 0.6$ . For yellowfin adults (\*\*) of ages 3 to 5,  $M = 0.6$ . Ages 0 to 2 were considered as juveniles for bigeye (\*\*\*) with  $M_0 = M_1 = 0.8$  and  $M_2 = 0.4$ . For bigeye adults (age 3+),  $M = 0.4$ .

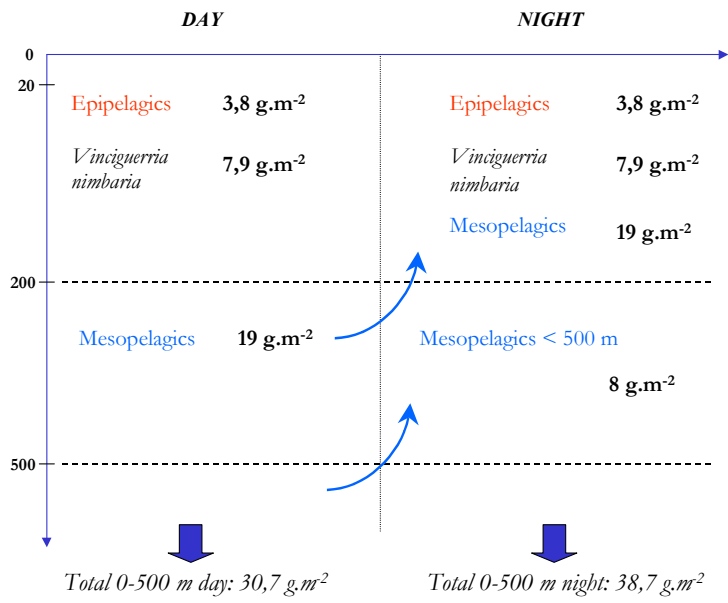
	<i>Skipjack</i>	<i>Yellowfin juvenile*</i>	<i>Yellowfin adult**</i>	<i>Bigeye juvenile***</i>	<i>Bigeye adult****</i>
Catch	25 254	3 794	9 079	4 775	1 238
Fishing mortality	0.3	0.23	1.2	0.14	0.2
Natural Mortality (M)	0.6	0.73	0.6	0.6	0.4
Exploitation rate	0.4	0.3	0.6	0.3	0.33
Biomass	66 923	13 407	15 131	31 830	4 126
Biomass in $t.km^{-2}$	0.108	0.024	0.021	0.052	0.01

**Table 2.** Parameters used and estimated for the ECOPATH model of the SSA. ‘( )’ indicates values estimated by the model assuming mass-balance. All values were normalised to unit surface area using wet weight for biomass and fishery catch. Flows and rate were expressed on an annual basis.

<i>Group</i>	<i>B(t.km<sup>-2</sup>)</i>	<i>Y(t.km<sup>-2</sup>)</i>	<i>P/B(year<sup>-1</sup>)</i>	<i>P/Q(%)</i>	<i>EE</i>	<i>Trophic Level</i>
Adult sharks	0.001	-	0.17	(7.1)	(0.294)	(4.9)
Juvenile Sharks	0.002	0.001	0.5	(5)	(0.568)	(4.7)
Ray manta	0.0002	-	0.17	(15.5)	(0.039)	(3.2)
Billfishes	0.019	0.0001	0.47	(17.2)	(0.177)	(5.2)
Skipjack	0.108	0.04	1.8	(7.8)	(0.548)	(4.3)
Yellowfin and Bigeye adults	0.034	0.016	0.9	(5.3)	(0.549)	(4.8)
Yellowfin and Bigeye juveniles	0.073	0.013	2.5	(9.3)	(0.524)	(4.3)
Associated fauna (big)	0.05	0.001	0.3	(7.5)	(0.050)	(4.5)
Associated fauna (small)	0.095	0.005	1.4	(23.3)	(0.671)	(4.1)
Marine mammals	0.0007	-	0.8	(6.3)	(0.857)	(4.9)
Small mesopelagics	27	-	1.03	(9.4)	(0.342)	(3.1)
Cephalopods	1.9	-	2.5	(14.7)	(0.947)	(4)
<i>Vinciguerrria nimbaria</i>	7.86	-	8.03	(27.5)	(0.182)	(3.1)
Small epipelagics	3.8	-	1.25	(11.4)	(0.775)	(3.5)
Gelatinous	7.5	-	2.5	(12.5)	(0.740)	(2.6)
Macrozooplankton	4.2	-	10	(31.5)	(0.586)	(2.4)
Mesozooplankton	24	-	(53)	31	(0.493)	(2.1)
Microzooplankton	2	-	(450)	38	(0.971)	(2.2)
Phytoplankton	37	-	200	-	(0.428)	1
Detritus	488	-	-	-	(0.368)	1

**Table 3.** Summary statistics that may be use for assessing the status of the SSA ecosystem.

<i>Attribute</i>	<i>Value</i>	<i>Dimension</i>
Total system throughput	21897	$t.km^{-2}.year^{-1}$
Total biomass (excluding detritus)	115.65	$t.km^{-2}$
Total catches	0.083	$t.km^{-2}$
Sum of all consumption	7361	$t.km^{-2}.year^{-1}$
Sum of all exports	4507	$t.km^{-2}.year^{-1}$
Sum of all respiratory flows	2894	$t.km^{-2}.year^{-1}$
Sum of all flows into detritus	7133	$t.km^{-2}.year^{-1}$
Sum of all production	9734	$t.km^{-2}.year^{-1}$
Mean trophic level of the catch	4.43	
Calculated total net primary production	7400	$t.km^{-2}.year^{-1}$
Gross efficiency (catches / p.p.)	0.000011	
Net system production	4505	$t.km^{-2}.year^{-1}$



**Figure 1.** Migrations and biomass of micronekton groups.

ANNEX: Diet composition matrix for the model of trophic flows in South Sherbo area from 1991 to 1999

N°	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	Adult sharks	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Juvenile sharks	0.028	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Ray	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Billfish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Skipjack	-	-	-	0.325	-	0.080	-	-	-	-	-	-	-	-	-	-	-	-
6	Yellowfin and Bigeye adults	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Yellowfin and Bigeye juveniles	0.144	0.171	-	0.375	-	0.100	-	-	-	-	-	-	-	-	-	-	-	-
8	Associated fauna (big)	0.107	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Associated faune (small)	0.257	0.306	-	0.125	-	0.050	-	0.206	-	0.400	-	-	-	-	-	-	-	-
10	Marine mammals	0.025	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Small mesopelagics	0.077	0.092	-	-	-	-	0.020	0.190	0.395	0.200	-	0.285	-	-	-	-	-	-
12	Cephalopods	0.072	0.086	-	0.075	0.130	0.035	0.130	0.102	0.102	0.400	-	0.118	-	-	-	-	-	-
13	<i>Vinciguerria nimbaria</i>	-	-	-	-	0.411	0.035	0.420	0.10	0.20	-	-	0.100	-	0.150	-	-	-	-
14	Small epipelagics	0.127	0.151	-	0.100	0.049	0.300	0.010	0.343	0.105	-	-	0.100	-	-	-	-	-	-
15	Gelatinous	-	-	-	-	-	-	-	-	0.082	-	-	0.040	-	0.300	-	-	-	-
16	Macrozooplankton	0.023	0.027	0.200	-	0.008	-	0.020	0.059	0.117	-	-	0.357	-	0.310	-	-	-	-
17	Mesozooplankton	0.014	0.017	0.600	-	-	-	-	-	-	-	1	-	1	0.240	0.250	0.400	-	-
18	Microzooplankton	-	-	0.200	-	-	-	-	-	-	-	-	-	-	-	0.250	-	0.100	0.180
19	Phytoplankton	0.029	0.034	-	-	-	-	-	-	-	-	-	-	-	-	0.250	0.600	0.500	0.420
20	Detritus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.250	-	0.400	0.400
21	Imports	0.098	0.116	-	-	0.400	0.400	0.400	-	-	-	-	-	-	-	-	-	-	-
	Total	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1