

A Trophic Model Of The Cameroon Estuary Mangrove With Simulations Of Mangrove Impacts

Longonje. N. Simon , Dave Raffaelli

ABSTRACT: A network model of trophic interactions in the Cameroon estuary mangrove was developed with the objective to coherently quantify state variables as well as matter and energy flows between system components. A mass balance model was constructed using a dataset collected in the field in 2010 to 2015, supplemented from the literature. A model of 26 compartments (groups) was analysed and parameters pertaining to ecosystem health in terms of productivity, structure and resilience derived. To predict the effects of disturbances (anthropogenic or natural) biomass removal simulations were evaluated using Ecosim routines. The results indicate that Cameroon mangrove estuary is relatively mature system. Ninety eight percent of the total throughput is confined to the 1st and 2nd trophic level with the overall system strongly depending on the consumption of detritus. The distribution of energy and the poor structure of the flows suggest that the network is able to reflect prominent features of the ecosystem. Simulation of mangrove biomass indicates that 40% reduction will reduce crabs biomass (population) considerably within 5 years. Mixed trophic impacts showed that detritus and low trophic levels had a positive influence on most groups.

Keywords: Ecopath model; Mangrove ecosystem; Energy fluxes; Cameroon estuary

1. INTRODUCTION

Anthropogenic activities severely impact almost all natural ecosystems globally. Coastal ecosystems, including mangroves, are particularly at risk because they are subjected to additional threats from terrestrial, freshwater and marine systems. In response to this, conservation efforts are now targeted at the threats to, and sustainability of, the entire ecosystem, as reflected in ecosystem health [1]. Ecosystem health is a concept that sets new goals for environmental management [61]. According to Costanza [15], ecosystem health represents a desired endpoint of environmental management. The advances in this concept are evident from the fact that it is now recognized that a reflexive relationship exists between human systems and natural ecosystems in that the health of one is dependent on the health of the other [1]. According to Rapport et al. [40], healthy ecosystems must not only be ecologically sound, but must also be economically viable and able to sustain healthy human communities. There are different approaches for assessing ecosystem health, and one is ecological modelling, used as a tool to describe complex system-level metrics related to health. Specifically, I use the mass balance model Ecopath [39], this model represents trophic networks that connect species (functional groups) in a system, and the magnitude of flows of materials and higher-level indices within the different functional groups can be calculated from the complex network, which can in turn be related to ecosystem health. I applied the Ecopath with Ecosim model to the Cameroon estuarine mangrove, to evaluate ecosystem structure, its function and organization. Selected ecosystem indicators that could be used to monitor ecosystem status or health were analysed using a set of ecosystem goal functions, representative of Odum's attributes of ecosystem maturity [9].

The attributes represent three different aspects of ecosystem development (1) Complexity in community structure (2) Community energetics and (3) Overall community homeostasis.

- 1) Complexity in community structure includes: the ratio of the number of actual trophic links to the number of possible links (connectance index, CI), and a measure of how feeding interactions are distributed between trophic levels (system omnivory index, OI).
- 2) Community energetics includes: primary production per unit biomass (PP/B), total trophic activity of the system (system throughput, T), biomass per unit production (B/P), Biomass per unit throughput (B/T), and system respiration per unit biomass (R/B).
- 3) Overall community homeostasis includes: Relative ascendancy (RA), system internal flow overhead (O), Finn's cycling index (FCI) and Finn's path length (FP).

The aim of the present study was to obtain a holistic picture of the Cameroon estuarine mangrove ecosystem by (a) constructing of a mangrove ecosystem trophic model in order to quantify its structure and function (b) to determine its flows of energy and (c) tracing and quantifying the biomass flows through the system.

2 STUDY SITE

The coastal and marine environment of Cameroon forms part of the southern section of the Gulf of Guinea Large Marine Ecosystem [29], The coastline stretches from the Equatorial Guinea border at latitude 2° 30' N, to 4° 67' N at the Nigerian border and it is estimated at about 400 km in length [62]; [29]. The coastal area is approximately 9,670 km² [63] and is characterised by estuaries, coral and basalt rocks, sand and rock beaches, swamp and mangrove. About 30% of the coastline is covered with mangrove swamps [21]. The main Cameroon mangrove forests are found east and west of Mount Cameroon with smaller formations dispersed along the estuaries of the other rivers. The main stands of trees are the Rio-del-Rey and the Cameroon Estuary, respectively (Figure 1). The latter covers an estimated surface area of about 75,000 ha (approximately 50 km of coastline), while the former covers an estimated surface area of 175,000 ha (approximately 60 km of coastline from the River Sanaga to the Bimbia

- Department of Environmental Science, University of Buea, P.O. Box 63 Buea, Cameroon Tel +237(0) 74905963. E-Mail: nlongonje@yahoo.com
- Environment Department, University of York, YO 105 DD United Kingdom.

estuary). The floristic composition of Cameroon mangrove is characteristic of the Atlantic mangroves of West Africa. It is dominated by *Rhizophora* and comprises mostly three species, *R. mangle*, *R. harrisonii* and *R. racemosa* [21]. The pioneer species *Rhizophora racemosa* constitute 90-95% of the mangrove area, and may also form tall gallery forests in the Wouri estuary, reaching a height of 40 m, and colonizes recently deposited alluvial soils [30]. *R. mangle* and *R. harrisonii* are found in the drier, more saline landward edge of *Rhizophora* zones and between *Rhizophora* and *Avicennia* stands, but they rarely exceed 6m in height [30]. Other mangrove species include *Avicennia germinans* (black mangrove), which occurs on the higher elevation fibrous clay or sandier soils, *Laguncularia racemosa* and *Conocarpus erectus* (white mangrove), *Acrostichum*

aureum, *Pandanus candelabrum* and the introduced *Nypa fruticans* [21], [30]. Mangroves together with the coastal water (50m in depth) contain major fishery resources of significant economic importance. The annual fish production of both the Rio-del- Ray and Cameroon estuary is approximately 12,800 metric tonnes [47]. Scientific data about the Cameroon mangrove forest are limited. Threats to the system include forest resource exploitation, pollution from offshore oil exploration and large amounts of industrial effluent which drain into the mangrove forest. Assessment of the degree of dependency by the local community on the mangrove ecosystem shows that there is a high degree of interaction between the local residents and the mangrove forests, resulting in a significant level of dependency of the local communities on mangrove resources [46].

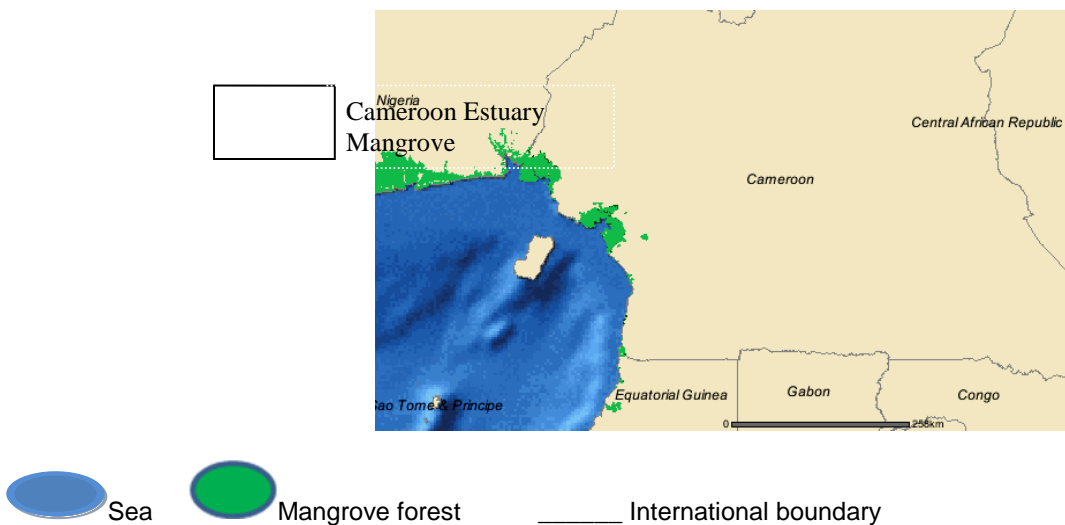


Figure 1: The Cameroon coastline showing study site (Adapted from UNEP–WCMC, 2005)

3 METHODS

The trophic interactions and energy fluxes of Cameroon estuary mangrove ecosystem were evaluated using Ecopath with Ecosim model for biomass estimations and consumption of different species groups within aquatic ecosystems [39],[38],[57],[35],[23],[11]. The model considers that all inputs are equal to the outputs for each species group through a series of simultaneous linear equations, which for each functional group is expressed as: Biomass by (i) = all predation on (i) + non-predation biomass losses of (i) + export of (i) The terms in the equation may be replaced as follows:

Production by (i) = $B_i \cdot P/B_i$

Predation biomass losses of (i) = $\sum (B_j \cdot Q/B_j \cdot DC_{ji})$

Other losses of (i) = $(1 - E_{Ei}) \cdot B_i \cdot P/B_i$

For each component in the system, this leads to the linear equation

$B_i \cdot P/B_i \cdot E_{Ei} - \sum (B_j \cdot Q/B_j \cdot DC_{ji}) - Ex - BA_i = 0$

Where, B_i and B_j are biomasses of prey (i) and predators (j) respectively. $(P/B)_i$ = Production /Biomass ratio, equivalent to total mortality (Z) of group i, in most circumstances. E_{Ei} = Ecotrophic Efficiency; the fraction of the total production of a group i, utilized in the system. $(Q/B)_j$ = Consumption/Biomass ratio of group j, DC_{ji} = fraction of i in the diet of predator j, EX_i = export of group i, BA_i = biomass accumulation of group i. All the variables are expressed at time t. Data requirements for Ecopath models are a minimum of three of the four following parameters for each group: Biomass (B), Production per unit biomass (P/B), Consumption per unit biomass (Q/B) and Ecotrophic efficiency (EE). Once the three parameters are entered for each group, the diet composition matrix is constructed (a diet matrix is constructed by indicating the percentage of each prey that occurs in each predator diet), and a balanced Ecopath model is obtained, several network parameters are evaluated, and these will determine the ecosystem's structure, maturity, and stability according to Odum [34], and hence reflect the system's ecosystem health [9]. Ecopath was modified several years ago with the inclusion

of the dynamic simulation routines Ecosim [38],[57]. Ecosim is a time-dynamic simulation model capability of Ecopath, for exploring past and future impacts, environmental disturbances, changes in predator-prey interactions and physiological behaviour due to mass changes. Ecosim comprises a series of differential equations [56]. The main equation is

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i) B_i$$

Where dB_i/dt = growth rate during the time interval dt of group (i) in terms of its biomass B_i , g_i is growth efficiency (production/consumption ratio), F_i is fishing (removal) mortality rate of group i, M_i = natural mortality rate (excluding predation) of group i, e_i is emigration rate, I_i = immigration rate, and Q_{ij} (Q_{ji}) is the consumption rate of type i (j) biomass by type j (i) organisms. The consumption rates Q_{ji} are calculated based on the 'foraging arena' concept, where the biomass of each prey i (B_i) is divided into vulnerable and an invulnerable components (Walters et al., 1997), and it is the transfer rate (v_{ij}) between these two parameters that determines if control is top-down (Lotka-Volterra), bottom-up (donor-control) or an intermediate type. This will lead to the rate equation:

$$Q_{ij} = \frac{V_{ij} a_{ij} B_i B_j}{V_{ij} + V^b_{ij} + a_{ij} B_j}$$

Q_{ij} is the trophic flow of biomass per time between prey (i) and predator (j), B_i and B_j are the biomasses of prey and predators, respectively; a_{ij} is the rate of effective search for prey i by predator j, and V_{ij} and V^b_{ij} are prey vulnerability parameters, usually with default setting $V_{ij} = V^b_{ij}$. Parameters V_{ij} and V^b_{ij} represent prey vulnerabilities; it is the rate of exchange of biomass between two prey behavioral states: a state in which all predators have full access to prey and a state in which the prey have complete protection from predators. Thus, not all prey biomass is vulnerable to predation at any given time, and predator-prey relationships are limited by behavioral and physical mechanisms [56]. Ecosim is designed so that the user can specify the type of trophic control (Lotka-Volterra type vs donor control) that mediates any interaction in the food web. Maximum consumption rates are assumed. For low predator biomass or high prey vulnerability (V_{ij}) the functional relationship is Lotka-Volterra type interaction (bottom-up) flows, which imply a strong 'top-down' effect. For high predator biomass or low prey vulnerabilities the functional relationship approaches a donor-controlled (bottom-up) [56]. Prey vulnerabilities can be specified by adjusting the proportion of prey in vulnerable and invulnerable states. This is done by adjustment of the v values, which are scaled such that pure Lotka-Volterra type control = 1 and pure donor-control = 0. In the real world predator-prey interactions are characterised by this mixture of trophic control.

3.1 Describing functional groups

To construct an Ecopath model, the first step is to define the functional groups. These can be based on ecological

similarities or function or a mixture of both. They can also be based on value-driven criteria, such as commercial status or importance to the local community. Functional groups can be individual species, size classes within species or broader taxonomic groupings. Due to extreme difficulties in parameterising some ecosystems to include all species, several food webs might be constructed for the same location depending on the information needed. Thus, for the Cameroon mangrove system, which has several hundred species, different versions of food web, differing in the number and kind of functional groups and complexity, could be constructed. For this study, the selection of functional groups to represent the Cameroon mangrove food web was a product of a collaborative process. A number of stakeholders and experts (including myself) participated in the discussion to produce functional groups based on the following criteria:

- The species must be representative and abundant
- The species must be relevant to the overall aims of the study
- There must be some relevant data for those species (although not necessarily for the Cameroon mangrove forest).

In the final iteration, based on these criteria, 26 functional groups were selected for this model (Table 1): 13 fishes, 3 kinds of birds (11 species), groupings of 3 crabs, mangroves, phytoplankton, zooplankton, detritus, benthos, shrimps and insects. All the species within a functional group have ecological similarities, defined by similarities in diet, production and consumption rates, life history, and habitat associations, but also sometimes on value-driven criteria, such as commercial status or importance for subsistence users. Because of the nature of the Cameroon mangrove forest, where mangrove wood products are used extensively as source of energy to smoke fish, it is important therefore to consider the mangrove forest as a primary producer and make the link with fishing pressure. The functional group benthos was included because of its contribution to the diets of other groups.

Table 1. Descriptions of some functional groups of the mangrove ecosystem in Cameroon.

1. Mangrove	Rhizophora spp., Avicennia spp, Laguncularia racemosa
2. Phytoplankton	Diatoms, dinoflagellates and others
3. Zooplankton	Neritic copepods, bivalve larvae, ostracods, mysids, nauplii, fish eggs and others
4. Shrimps	Peneaus spp, Parapenaeopsis atlantica, Penaeus notiali
5. Mangrove crabs	Sesarmid species
6. Fiddler crabs	Uca species,
7. Other crabs	Scylla serrata, Cardisoma carnifex and others
8. Ilisha africana	
9. Pseudotolithus spp	P. senegalensis, P. typus and P. elongates
10. Pentanemus quinquarius	
11. Sardinella maderensis	

12. *Brachydeuterus auritus*
 13. *Dreprane africana*
 14. *Arius* spp *A. heudelotii* and *A. parkii*
 15. *Pomadasys jubelini*
 16. *Galeoides decadactyl*
 17. *Raja miraletus*
 18. *Lutjanus* spp *L. goreensis* and *L. dentatus*
 19. *Mugil curema*
 20. *Caranx* spp *C. senegallus*, *C. hippo* and *C. senegalensis*
 21. Shorebirds *Finfoot (Podica senegalensis)*, *Avocet (Recurvirostra avosetta)*, *White-footed plover (Charadrius marginatus)*, Common
 Green shank (Tringa nebularia), Common
 sandpiper (Actitis hypoleucos).
 22. Birds of prey *Black kite (Milvus migrans)*, *Fish eagle (Haliaeetus vocifer)*, *Palm nut vulture (Gypohierax angolensis)*, *Harrier hawk (Polyboroides typhus)*
 23. Insectivorous birds *Grey flycatcher (Muscicap cassini)*,
 Pied crow (Corvus albus)
 24. Benthos
 25. Insects
 26. Detritus *Organic matters and associated like bacteria*

Table .2. Mangrove biomass estimate

Station	No of plots	No of trees	Biomass (t/ km ²)
1	4	61	1.22
2	3	56	2.02
3	3	68	0.24
4	3	95	7.66
5	4	109	18.87
6	4	116	3.43
7	3	59	1.01
8	4	134	28.74
9	3	71	1.222
Total	31	769	64.40

Fish

Data were obtained from six selected villages (Table 3) considered representative of the study area. These villages were selected because they were principal landing points, easy accessibility and village cooperation. This fishery uses only dug-out canoes (3 to 7m in length), which are manually driven by one or two persons using a wooden paddle. The fishing gear is mainly gill net and line trap, the average mesh size is 60mm and an average area of 10.95 m² (i.e. 7.3 m length and 1.5 m width). Generally, the fishermen leave the village early in the morning between 5am and 7.30am, depending on the weather and tidal amplitude, and return between 1pm and 3.30pm (fishing time approximately 8 hours), hauling is done manually for recovering the net and the entangled fish into the canoe. The sampling procedures were as follows: once the catch was landed on the village beach, I bought it. We then sorted out the fish into species and identified, counted and weighed. The fishes were then sold back to the fishermen. Additional information was gathered through interviews. Data collected were: (1) Fish catch identified to species level (2) Biomass of catch (total weight in kg) (3) Types of fishing gear used (4) Estimated area fished (km²). Fish biomass (Table 3) was estimated by "sweep area" method used to determine the density of fish per square kilometre (Sherman, 1994). If the mean weight of catch is W, and A is the area swept, then: Fish density = W/A (kg/km²). W = the weight catch per month A = average area covered during fishing trip (approximately 6.7km²) Q = is efficiency of the net, or catchability coefficient, which represents the amount of the fish, caught by the fisherman relative to the amount that escaped being caught. In this case, Q was estimated as 60%. A¹ = is the whole area surveyed which is equal to the total water area (approximately 1500km²).

$$\text{Biomass of fish} = (W/A)/Q \times A^1$$

The P/B ratio (Table 4) of fish is equivalent to total mortality (Z) which is estimated as the sum of natural mortality (M) and fishing mortality (F):

$$Z = F+M$$

Natural mortality was calculated using the Von Bertalanfy growth function (VBGF):

3.2 Ecopath input parameters

The input parameters for each group were: the biomass (B), the production/ biomass ratio (P/B), the consumption/ biomass ratio (Q/B) and ecotrophic efficiency (EE). Input parameters were estimated from the field or extracted from the literature, either from studies done within a similar mangrove ecosystem (in Central Atlantic region) or on the West Africa continental shelf. The diet matrix was constructed by designating the proportion of each prey that occurs in each predator's diet. Diets were derived mostly from the scientific literature, except for crabs groups where stomach content analysis had been carried out. The degree of confidence, that the parameters are appropriate for the Cameroon is expressed through the data pedigree coding option.

Mangrove

Mangrove above-ground biomass was estimated from 31 plots (each 10 m x 10m) using a plots method [14]. All trees within the plot were identified and the diameter at breast height (dbh) and height (h) was measured. The approach of Fromard [24] was used to calculate the above-ground biomass from diameter at breast height (dbh, in cm). Biomass (g) = a(dbh)^b Where b and a are slope and intercept respectively. For *Rhizophora* species, b= 2.6, a = 128.2; For *Laguncularia racemosa* b =2.5, a=102.3 and; For *Avicennia germinans* b =2.4, a = 0.14. Total biomass (t/ km²) was then calculated by multiplication of the tree biomass by tree density (n/km²). Mangrove biomass calculated was 64.4 t/km². P/B values for mangrove were obtained from the literature (Table 2)

$$M = K^{0.65} L_{\infty}^{-0.279} T^{0.463}$$

Where, K is the curvature parameter for the VBGF. L is the asymptotic length of the fish. T is the average environmental temperature estimated at 20.5° C Fishing mortality was calculated as the average total catch during the survey period. The total catch was estimated by multiplying the average catch per month by the number of months (12), divided by the average biomass. Length data and the curvature parameters were taken from literature and “fish- base” (Table 4). P/ B ratios for the following species *Lutjanus* spp, *Caranx* spp and Shrimps were extracted directly from literature.

Table 3. Fish biomass estimates from six villages within the Cameroon mangrove system

Sample site /Coordinates	Mukuro N 04° 22' 486" E 009° 22' 979"	Appollo N 04° 04' 072" E 009° 22' '455"	Mabeta N 03° 59' 982" E 009° 18' 808"	Mboko N 03° 58' 344 " E 009° 27' 81'2"	Mboma N 03° 513'40" E 009° 47' 91'2"	Yoyo N 03° 381'71" E 009° 36' '274"	Average Biomass (t/km ²)
Fish species	BIOMASS (t/km ²)						
Ilisha africana	0.552	1.252	1.935	0.125	1.216	0.877	0.993
Pseudolithus spp	2.198	0.405	1.306	0.353	1.179	1.030	1.078
Pentanemus quinquarius	0.646	0.148	0.687	0.123	0.076	0.084	0.294
Sardinella maderensis	0.219	0.019	3.774	0.259	0.300	0.504	0.846
Brachydeuterus auritus	0.683	0.479	0.841	1.226	1.604	4.858	1.615
Arius spp	2.636	-	3.552	1.521		-	2.570
Shrimps	-	-	0.435	0.274	0.334	-	0.348
Pomadasys jubelini	-	0.338	-	0.267	0.263	-	0.289
Lutjanus spp	-	2.974	-	0.610	2.377	2.108	2.017
Galeoides decadactylus	-	0.390	-	-	1.004	1.215	0.869
Raja miraletus	-	-	2.114	-		1.175	1.645
Caranx spp	-	-	0.392	0.187	0.571	0.511	0.415
Deprane africana	-	-	1.858	1.769	0.776	1.179	1.396
Mugil curema	-	-	3.478	-	0.239	-	1.858

Table 4 Natural and fishing mortality

Fish species		Natural mortality	Fishing mortality	Total mortality	Information sources
Ilisha Africana	$L_{\infty} = 22 K = 2.33$	2.962	0.044	3.006	Fish base http://www.fishbase.org
Pseudotolithus spp	* $L_{\infty} = 67.18 K = 0.25$	0.508	0.140	0.648	[19]
Pentanemus quinquarius	$L_{\infty} = 34 K = 1.081$	1.592	0.183	1.775	Fish base http://www.fishbase.org
Sardinella maderensis	* $L_{\infty} = 29.1 K = 0.63$	1.171	0.089	1.26	[19]
Brachydeuterus auritus	$L_{\infty} = 20.6 K = 0.363$	0.901	0.128	1.029	Fish base http://www.fishbase.org
Arius spp	* $L_{\infty} = 61.8 K = 0.22$	0.479	0.661	1.14	[19]
Mugil curema	$L_{\infty} = 39.7 K = 0.68$	1.128	0.240	1.367	Fish base http://www.fishbase.org
Pomadasys jubelini	$L_{\infty} = 45 K = 0.3$	0.640	0.100	0.731	Fish base http://www.fishbase.org
Lutjanus spp				0.770	[3]
Galeoides decadactylus	$L_{\infty} = 54.5 K = 0.41$	0.743	0.080	0.823	Fish base http://www.fishbase.org
Raja miraletus	$L_{\infty} = 87.9 K = 0.193$	0.399	0.161	0.56	Fish base http://www.fishbase.org
Caranx spp				0.655	[49]
Drepane africana	$L_{\infty} = 40.1 K = 0.24$	0.572	0.280	0.82	Fish base http://www.fishbase.org
Shrimps				5.380	[3]

*Average of different study from Djama [19]

The Q/B ratios (Table 5) were estimated from the empirical relationship proposed by Palomares and Pauly [4].
 $\log Q/B = 7.964 - 0.204 \log W_{\infty} - 1.965T + 0.083A + 0.532h + 0.398d$

Where W_{∞} (or asymptotic weight) is the mean weight that the individuals of a population would reach if they were to grow indefinitely, T' is the mean environmental temperature expressed as $1000 / (^{\circ}\text{C} + 273.15)$; A is the aspect ratio of the caudal fin, indicative of metabolic activity and expressed as the ratio of the square of the height of the caudal fin and its surface area; 'h' and 'd' are dummy variables, indicating herbivores (h=1, d=0), detritivores (h=0, d=1) and carnivores (h=0, d=0).

Table 5 Q/B ratio and sources of information

Fish Species	Total Length (cm)	Weight (g)	Caudal fin aspect ratio (A)	Q/B	Information sources
Ilisha Africana	7.50	3.62	2.88	55	[31],[58], [53]
Pseudotolithus spp	40.5	448.58	0.88	6.4	[7], [18],[20]
Pentanemus quinquarius	34	107.43	1.65	9.9	[22]
Sardinella maderensis	37.3	929	4.01	12.2	[58]
Brachydeuterus auritus	30	487.71	2.19	63	[43], [42]
Drepane Africana	45	750	1.61	8.1	[31]
Arius spp	83	8500	2.76	6.1	[45]
Pomadasys jubelini	60	1918	2.37	7.7	[42], [31]
Galeoides decadactylus	50	1378.86	3.22	9.7	[22], [16]
Raja Miraletus	63	1236.45	1.32	6.9	[32], [22]
Lutjanus spp	80	16119.27	1.7	4.3	[2]
Mugil curema	90	680	1.91	21.8	[41]
Caranx spp	67	32	4.41	24.3	[48]
Shrimps				28	[17]

Birds

Bird biomasses were estimated by multiplying the average wet weight of an adult of a given species by the average bird abundance [29]. Average bird abundance values were obtained from a study carried out in the Cameroon Rio del

Rey mangrove estuary [50], and the average wet weights were taken from Fry et al. [25], [26]. Biomass estimates were 0.0207 t/km^2 , 0.022 t/km^2 and 0.015 t/km^2 for shorebirds, insectivores, and birds of prey, respectively. P/B and Q/B ratios were taken from the literature (Table 8).

Crabs

Crab biomasses were estimated using excavation and surface sample collection methods [28]. The crabs collected were sedated in ice water for a few minutes, washed and stored in 70% alcohol and later identified and weighed (wet

weighted) (Table 6). The P/B and Q/B ratios for these crabs were taken from literature (Table 8).

Table 6. Biomasses of crabs at stations studied

Station	Average weight (g)		
	Sesarmid	Fiddlers (Uca)	Others
1	5.2005	0.707	1.22
2	2.826	2.319	0.55625
3	4.0499	1.13	0.611
4	4.767	1.146	0.864
5	5.13	1.763	0.951
6	7.2215	1.054	0.9625
7	3.441	1.523	3.399
8	4.319	1.7435	0.892
9	3.445	0.992	3.388
Average total weight	4.489	1.3755	1.427

Phytoplankton

Phytoplankton biomass was estimated from Froneman [24]. He reported chlorophyll a concentrations of 0.11 to 2.01 mg/l. This is equivalent to a water column concentration of 0.11 g/chl. To convert this to the standard unit of measurement used in the model (wet weight in $t/km^2 = g/m^2$), conversion factors reported in the literature were used. A factor of 25 was used to convert g chl a to g C, while the factors 2.5 and 5 were used to convert g C to g dry weight, then to g wet weight, respectively [36]. Phytoplankton biomass was thus approximately $34.4 t/km^2$. The P/B ratio of 180 was extracted from Wolff [59].

Zooplankton

Zooplankton biomass was estimated from Froneman [24]. A mean biomass conversion ratio of 0.59 ± 0.08 reported by Gate et al (1982), was used to convert dry weight to wet weight, hence zooplankton biomass was estimated at $27.13 t/km^2$. Also a P/B ratio = 50 and a Q/B ratio = 160 were extracted from Wolff et al. [60].

Insects, Benthos and Detritus

Insect and benthos biomass, P/B and Q/B values were extracted from literature (Table 7 and 8) while the biomass of detritus was estimated as "extremely large" following recommendation in Ecopath.

Table 7. Biomass value for benthos and insects

Groups	Biomass (t/km ⁻²)	Information sources
Benthos	4.593	[33]
Insects	0.61	[54]

Table 8. P/B and Q/B ratios

Group	P/B Values	Q/B Values	Information sources
Mangrove	0.22		[59]
Phytoplankton	180		[59]
Zooplankton	50	160	[60]
Mangrove crabs (Sesamidae)	2	14	[60]
Fiddler crabs (Uca)	5.5	95	[60]
Others crabs	0.25	22	[60]
Shorebirds	5.4	60	[3]
Birds of prey	0.1	65	[33]
Insectivorous birds	0.3	10	[60]
Insects	15.54	51	[54]
Benthos	12	20	[60]

3.3 Diet composition input data

Diet information for crabs was obtained directly from stomach content analysis carried out back at the University of York. Literature data were used for all other functional groups (Table 9).

Table 9. Diet composition

	PREY				PREDATOR							
	3	4	5	6	7	8	9	10	11	12	13	14
1 Mangrove	-	-	0.6	0.5	0.9	-	-	-	-	-	-	-
2 Phytoplankton	0.8	0.1	0.1	-	-	0.3	-	-	0.4	0.2	0.3	0.2
3 Zooplankton	-	0.4	-	0.05	-	0.3	0.4	0.1	0.2	0.4	0.3	0.2
4 Shrimps	-	-	-	0.05	-	-	-	-	-	-	-	-
5 Mangrove crabs (Sesamidae)	-	-	-	-	-	-	-	-	-	-	-	0.1
6 Fiddler crabs (Uca)	-	-	-	-	-	-	-	-	-	-	-	0.1
7 Other crabs	-	-	-	-	-	-	-	-	-	-	-	0.1
8 Ilisha africana	-	-	-	0.05	-	-	0.3	0.05	-	-	-	-
9 Pseudolithus spp	-	-	-	0.05	-	-	-	0.05	-	-	-	-
10 Pentanemus quinquarius	-	-	-	-	-	-	-	-	-	-	-	-
11 Sardinella maderensis	-	-	-	-	-	-	0.2	0.1	-	-	-	-
12 Brachydeuterus auritus	-	-	-	-	-	-	-	-	-	-	-	-
13 Dreprane africana	-	-	-	-	-	-	-	0.05	-	-	-	-
14 Arius spp	-	-	-	-	-	-	-	0.05	-	-	-	-
15 Pomadasys jubelini	-	-	-	-	-	-	-	0.05	-	-	-	-
16 Galeoides decadactylus	-	-	-	-	-	-	-	0.05	-	-	-	-
17 Raja Miraletus	-	-	-	-	-	-	-	0.05	-	-	-	-
18 Lutjanus spp	-	-	-	-	-	-	-	0.05	-	-	-	-
19 Mugil curema	-	-	-	-	-	-	-	-	-	-	-	-
20 Caranx spp	-	-	-	-	-	-	-	-	-	-	-	-
21 Shorebirds	-	-	-	-	-	-	-	-	-	-	-	-
22 Birds of prey	-	-	-	-	-	-	-	-	-	-	-	-
23 Insectivorous birds	-	-	-	-	-	-	-	-	-	-	-	-
24 Benthos	-	0.1	0.1	0.2	-	0.1	0.1	0.4	-	0.1	0.4	0.3
25 Insects	-	-	-	-	-	-	-	-	0.2	-	-	-
26 Detritus	0.2	0.4	0.2	0.1	0.1	0.3	-	-	0.2	0.3	-	-
	1	1	1	1	1	1	1	1	1	1	1	1

Sources of information: 3 [59] 4 [33] 5, 6, 7 own estimates, 8 [53]; 9 [44]); 10 [17]; 11 [44]; 12. [6]; 13, 14 [17]) 15[33]

Table 9. Diet composition (continued)

PREY		PREDATOR										
		15	16	17	18	19	20	21	22	23	24	25
1	Mangrove	-	-	-	-	-	-	-	-	-	0.9	0.1
2	Phytoplankton	-	-	-	-	0.8	-	-	-	-	-	0.5
3	Zooplankton	0.6	0.2	0.05	0.1	-	0.6	-	-	0.05	-	-
4	Shrimps	-	0.1	0.05	0.2	-	-	-	-	0.05	-	-
5	Mangrove crabs (Sesamidae)	--	0.1	0.05	0.1	-	-	-	-	-	-	-
6	Fiddler crabs (Uca)	-	0.1	0.05	0.1	-	-	-	-	-	-	-
7	Other crabs	-	0.1	0.05	0.1	-	-	0.1	-	-	-	-
8	Ilisha africana	-	-	0.1	0.05	-	-	-	0.1	-	-	-
9	Pseudotolithus spp	-	-	0.1	-	-	-	-	0.1	-	-	-
10	Pentanemus quinquarius	0.05	-	0.1	-	-	-	-	0.1	-	-	-
11	Sardinella maderensis	-	-	0.1	0.05	-	-	-	0.1	-	-	-
12	Brachydeuterus auritus	-	-	0.1	-	-	-	-	0.1	-	-	-
13	Dreprane africana	-	-	0.1	-	-	-	-	0.1	-	-	-
14	Arius spp	0.05	-	0.1	-	-	-	-	0.1	-	-	-
15	Pomadasys jubelini	-	-	-	-	-	-	-	0.05	-	-	-
16	Galeoides decadactylus	-	-	-	-	-	-	-	0.05	-	-	-
17	Raja Miraletus	-	-	-	-	-	-	-	0.05	-	-	-
18	Lutjanus spp	-	-	-	-	-	-	-	0.05	-	-	-
19	Mugil curema	-	-	-	-	-	-	-	0.05	-	-	-
20	Caranx spp	-	-	-	-	-	-	-	-	-	-	-
21	Shorebirds	-	-	-	-	-	-	-	-	-	-	-
22	Birds of prey	-	-	-	-	-	-	-	-	-	-	-
23	Insectivorous birds	-	-	-	-	-	-	-	-	-	-	-
24	Benthos	0.1	0.4	0.05	0.3	-	0.4	0.9	-	-	-	-
25	Insects	-	-	-	-	-	-	-	0.05	0.9	-	-
26	Detritus	0.2	-	-	-	0.2	-	-	-	-	0.1	0.4
		1	1	1	1	1	1	1	1	1	1	1

Sources of information 16 [17]; 17, 18, 20 [44]; 21, 22, 23 [59],[3], [60] 24, 25 [54].

3.4 Balancing the model

After entering all the basic inputs into the Ecopath model, the first step is to check if the outputs are sensible, in other words, whether the biomasses of all groups can be supported by their consumption rates and the productivities of their prey. The initial model was unbalanced, as is usually the case in constructing any Ecopath model. The following steps were then taken to balance the model.

1. The ecotrophic efficiency for each group was checked for inconsistencies, where the model calculated the EE > 1. The biomass of some groups was adjusted, but not greater than 20% of the original input value. The basic empirical estimates for most parameters in the system remained unaltered. However, for the model to balance, specifying reasonable EE values for Shrimps, Pseudotolithus spp, Ilisha africana, Sardinella

maderensis and Pentanemus quinquarius was necessary because the biomasses of these groups needed to be otherwise adjusted by more than 40%. Ecotrophic efficiency is usually estimated by the program or assumed to be around 0.95 to 0.9 as proposed by Christensen et al. [13] in the Ecopath manual.

2. Diet composition for each group must sum to 1.
3. Data pedigree information was incorporated, which expresses how close to the Cameroon field site the information is. For instance, fish biomass and crab biomass were collected on site and have a high pedigree, whilst zooplankton biomass has a lower pedigree, because these data were collected elsewhere. This information provides Ecopath with

different scopes for adjusting the data when mass-balancing.

4. Sensitivity analysis was done to evaluate the accuracy of parameters estimated. Once the model was balanced, various ecosystem attributes were evaluated, these attributes include those given by Odum [34] and Christensen [10], allowing inferences to be drawn about the health of the ecosystem. A pedigree index of 0.52 was obtained from the model, implying that the model is of reasonable quality [12]. Using Ecosim, I changed the biomass of several groups to evaluate the effect of doing so on other species. The effect of changing mangrove biomass by 10%, 20% and 40% was evaluated on crabs and 10% to 80% for fish groups over a period of 20 years.

4 RESULTS

4.1 Structure and network analysis

The balanced parameter estimates for the model are shown in Table 10. These parameters include trophic estimates, biomass estimates, production / biomass estimates, consumption / biomass estimates, production / consumption ratios, gross efficiency estimates and omnivory index estimates. The mangrove food web consists of 3 trophic levels and 17 sublevels, which range from 1.0 to 3.74 (Figure 2). The trophic level (TL) is an important index because it identifies an organism's food preferences. The highest values correspond to insectivorous birds, followed by the fish *Pentanemus quinquarius* and *Pseudolithus* spp, whilst the lowest values correspond to the primary producer; mangrove, phytoplankton and detritus (Table 11).

Complexity in community structure

The omnivory index (OI) value is 0.143, which is quite low indicating a highly specialised consumer system. The low OI value may be due to some groups being highly specialized and environmental conditions might alter the availability of prey. An OI value of zero was estimated for zooplankton, which feed almost entirely on phytoplankton (80%), other crabs that feed almost on mangrove (90%), *Mugil curema* that feed virtually entirely on phytoplankton (80%), shorebirds that feed practically entirely on benthos (90%), insects that feed on mangrove (90%) and benthos that feeds mostly on detritus and phytoplankton (90%). The highest OI value of 0.450 was estimated for fiddler crabs, which take prey from many trophic levels (Table 12).

Community energetics

The energetic attributes of the ecosystem (Table 12) shows that the system mature and stability. These attributes include connectivity index (CI), total system throughput (T), system total primary production / total respiration ratio (PP/R), primary production / biomass ratio (PP/B), and biomass over throughput (B/T). The connective index (CI) is the number of actual links to the number of possible links for a given food web [11]. According to Odum [34] food web structure changes from linear to web like as the system mature. Hence, CI is correlated with maturity [11]. The Cameroon mangrove CI is 0.174 which is close to the value 0.191 reported by Villanueva [55] for Ebere lagoon in Ivory

Coast and lower than 0.3 reported by Vega-Cendejas and Arreguín-Sánchez [54] for Yucantan Peninsula in Mexico. The total system throughput (T) is the size of the entire system in terms of flow [51],[52], [12]. A high T value means the system is capable of growth, suggesting the system is full of energy and resilience. The total system throughput (T) value is 18, 615 t/km².yr, relatively high compared to 3,049 reported by Wolf et al. [59] for Golfo de Nicoya (Costa Rica), 6,240 reported by Villanueva [55] for Ebere lagoon (Ivory Coast) and 10, 558 reported by Wolf [60] for Craeté mangrove estuary (Brazil). Total system primary production and total respiration ratio (PP/R) shows the balance between production and consumption. When the PP/R ratio is close to 1, this indicates a mature ecosystem [34], [55]. When the PP/R ratio is greater than 1, production exceeds respiration and indicates the system is in an earlier development stages. When PP/R is less than 1, this indicates the system is accumulating a lot of organic matter. The PP/R value for this study is 1.865, it is consider low when compared to 15.9 reported by Vega-cendajas [54] for Yucantan Peninsula mangrove (Mexico) and 3.305 reported by Wolf et al, [60] for Craeté mangrove estuary (Brazil). The transfer efficiency for the Cameroon mangrove system is 6.4%, which is low compared to 9.8% reported by Vega-Cendejas and Arreguín-Sánchez [54] for Yacatan Peninsula (Mexico) and 14.9 % reported by Wolf et al. [59] for Golfo de Nicoya (Costa Rica) meaning that the system is relative inefficient to recover after disturbance. The model estimate of primary production/ biomass of 38.6 compared to 23.9 reported by Wolf ([60] for Craeté mangrove estuary (Brazil), the system was reported to be relatively mature, hence this indicates that the Cameroon system is mature and may therefore be relatively stable. Flow indicators related to "overall community homeostasis", which describes the size and the degree of organization with which the material is being processed within the system, is within the range of most mangrove or estuary ecosystems. These are closely linked to ecosystem efficiency, maturity and development [52]. These indicators include ascendancy (9929.25) and relative ascendancy (0.250). Energy use and matter recycling in the system are important processes in ecosystem functioning [34] and are measured as Finn's cycling index (FCI) and Finn's mean pathway. The model estimated value for FCI is 2 which are relatively low compared to 5.5 for Golfo de Nicoya (Costa Rica) and Finn's mean pathway of 1.717 estimated by the model is also relatively low compared to 3.4 and 4.4 reported for Craeté mangrove estuary (Brazil) and Yacatan Peninsula (Mexico).

Table 10. Basic input and model estimated output (**bold**) of the Cameroon mangrove estuary

	TL	Habitat Area (km ²)	Biomass (t/km ²)	P/B	Q/B	EE	P/Q	OI
1 Mangrove	1.00	1.000	60.870	15.000	-	0.564	-	-
2 Phytoplankton	1.00	1.000	34.400	180.000	-	0.712	0.313	-
3 Zooplankton	2.00	1.000	27.130	15.000	160.000	0.129	0.280	-
4 Shrimps	2.50	1.000	0.417	5.380	19.200	0.950	0.161	0.250
5 Mangrove crabs (Sesamidae)	2.10	1.000	2.400	2.250	14.000	0.422	0.058	0.090
6 Fiddler crabs (Uca)	2.41	1.000	1.300	5.500	95.000	0.319	0.091	0.452
7 Other crabs	2.00	1.000	2.500	2.000	22.000	0.456	0.550	-
8 <i>Ilisha africana</i>	2.50	1.000	1.993	3.006	55.000	0.950	0.101	0.250
9 <i>Pseudolithus</i> spp	3.22	1.000	1.780	0.648	6.400	0.950	0.179	0.159
10 <i>Pentanemus quinquarius</i>	3.29	1.000	0.294	1.775	9.900	0.950	0.030	0.151
11 <i>Sardinella maderensis</i>	2.40	1.000	1.015	1.260	42.200	0.950	0.016	0.290
12 <i>Brachydeuterus auritus</i>	2.50	1.000	1.615	1.026	63.000	0.780	0.101	0.250
13 <i>Dreprane africana</i>	2.70	1.000	1.396	0.820	8.100	0.134	0.187	0.210
14 <i>Arius</i> spp	2.65	1.000	2.570	1.140	6.100	0.440	0.187	0.303
15 <i>Pomadasy jubelini</i>	2.80	1.000	0.289	0.731	7.700	0.760	0.095	0.160
16 <i>Galeoides decadactylus</i>	2.99	1.000	0.869	0.828	9.700	0.223	0.085	0.284
17 <i>Raja Miraletus</i>	3.33	1.000	1.645	0.560	6.900	0.008	0.081	0.146
18 <i>Lutjanus</i> spp	3.14	1.000	2.017	0.770	4.300	0.010	0.179	0.102
19 <i>Mugil curema</i>	2.00	1.000	1.858	1.367	21.800	0.350	0.063	-
20 <i>Caranx</i> spp	2.80	1.000	0.415	0.655	24.300	0.083	0.027	0.160
21 Shorebirds	3.00	1.000	0.021	0.160	65.000	0.000	0.002	-
22 Insectivorous birds	3.74	1.000	0.150	0.100	10.000	0.000	0.010	0.167
23 Birds of prey	3.03	1.000	0.022	12.000	60.000	0.000	0.200	0.012
24 Benthos	2.00	1.000	12.000	15.000	80.000	0.571	0.188	-
25 Insects	2.00	1.000	20.600	12.000	30.000	0.054	0.400	-
26 Detritus	1.00	1.000	10000000	-	-	0.308	-	0.274

TL: trophic level; **B:** biomass (t/km²); **P/B:** annual production/biomass ratio; **Q/B:** annual consumption/biomass ratio; **EE:** ecotrophic efficiency; **P/Q:** annual production/ consumption ratio; **OI:** omnivory index

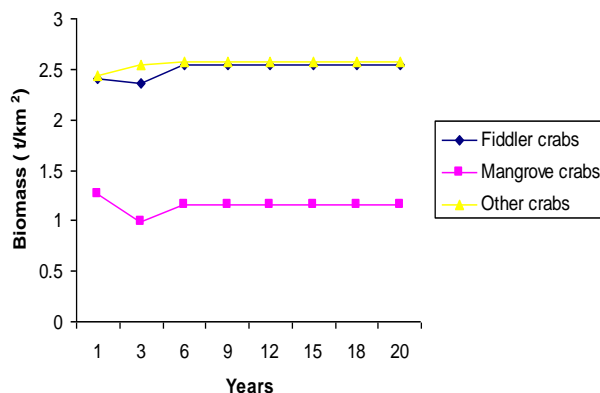
Table 11 Summary statistics and basic flows and indices

Parameter	Value	Unit
Sum of all consumption	6723.632	t/km ² .yr
Sum of all exports	3305.708	t/km ² .yr
Sum of all respiratory flows	3810.424	t/km ² .yr
Sum of all flows to detritus	4775.025	t/km ² .yr
Total system throughput	18615	t/km ² .yr
Sum of all production	893	t/km ² .yr
Total net primary production	7105.1	t/km ² .yr
Total primary production/total respiration	1.865	t/km ² .yr
Net system production	3294.4	t/km ² .yr
Total primary production/total biomass	38.6	t/km ² .yr
Total biomass/throughput	0.01	t/km ² .yr
Total biomass (excluding detritus)	184.2	t/km ² .yr
Connectance index	0.3	t/km ² .yr
System omnivory index	0.143	t/km ² .yr
Ascendancy (flow bits)	9929.2	
Relative ascendancy	0.25	
Overhead (flow bits)	19117.1	
Overhead (%)	48	
Capacity (flow bits)	39661.3	
Transfer efficiencies	6.3	
Finn's cycling index (FCI %)	2	
Finn's mean path length	1.717	
Flow to detritus		
Zooplankton	2050.348	t/km ² .yr
Phytoplankton	1785.893	t/km ² .yr
Mangrove	397.640	t/km ² .yr
Insect	357.515	t/km ² .yr

4.2 Simulated effects of mangrove biomass changes

Simulations were done on 10%, 20%, 30% and 40% mangrove biomass changes. Figure 2a shows the crab biomass position within 20 years after simulation. The simulated effect of mangrove biomass changes on crabs was marked at 40% decline. The biomass of the entire crab declined within 5 years and then started to recover. The simulation is characterised by oscillations, with a maximum biomass reached at 18 years for most of the species (Figure 2b).

(a)



(b)

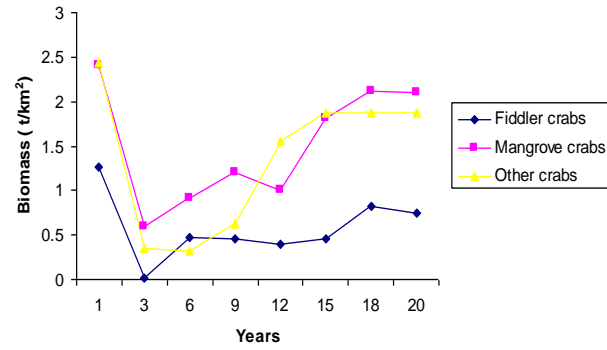


Figure 2 (a). Original crab biomass over 20 years with unchanged mangrove biomass (b) Change in crab biomass with 40% change of mangrove biomass

The effect of changing mangrove biomass on fishes was explored. Figure 3 shows that fish biomass remained unchanged with mangrove biomass changes from 10% to 60%, but at 80% biomass change the effect was marked. The most affected species were *Dreprane africana*, *Lutjanus spp*, *Pomadasys jubelini* and *Arius spp* (Figure 4). It should be noted that there is no direct relationship between mangrove and fish, many intermediate trophic steps are involved.

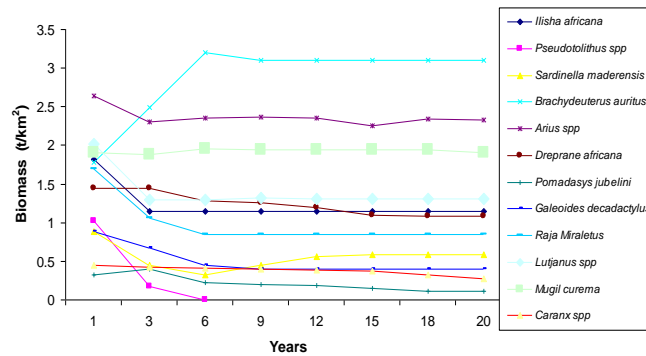


Figure 3 Original fish biomass over 20 years with unchanged mangrove biomass

4.3 Mixed trophic impact analysis

The mixed trophic impact analysis (Figure 5) assesses the direct and indirect impact of biomass change of one group on others. Bars above the line indicate a positive impact, whilst those below the line indicate a negative impact. Generally it can be seen that the pelagic groups will have the most impact on other pelagic groups. Mangrove, phytoplankton and zooplankton have positive impacts on most groups with *Pseudotolithus spp* have a large positive impact on *Dreprane africana*, *Pomadasys jubelini* and *Galeoides decadactylus*. While insectivorous birds positively impact the crabs and some

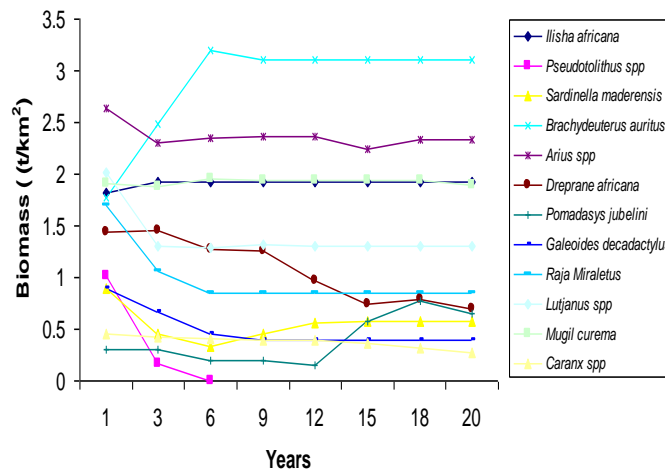


Figure 4. Change in fish biomass over 20 years with 80% change of mangrove biomass

little or no negative impact. An increase in mangrove biomass has large positive impacts on the biomass of crab species, while they have little and no impact on other species. Fiddler crabs have positive impacts on *Pentanemus quinquarius*, *Sardinella maderensis* and *Brachydeuterus auritus* while they large negative impact on shrimps, *Ilisha africana*, *Pseudolithus spp*, *Dreprane africana*, *Pomadasys jubelini* and *Galeoides decadactyl*. fish, they have largely negative impacts on *Raja Miraletus*, *Lutjanus spp* and *Caranx spp*.

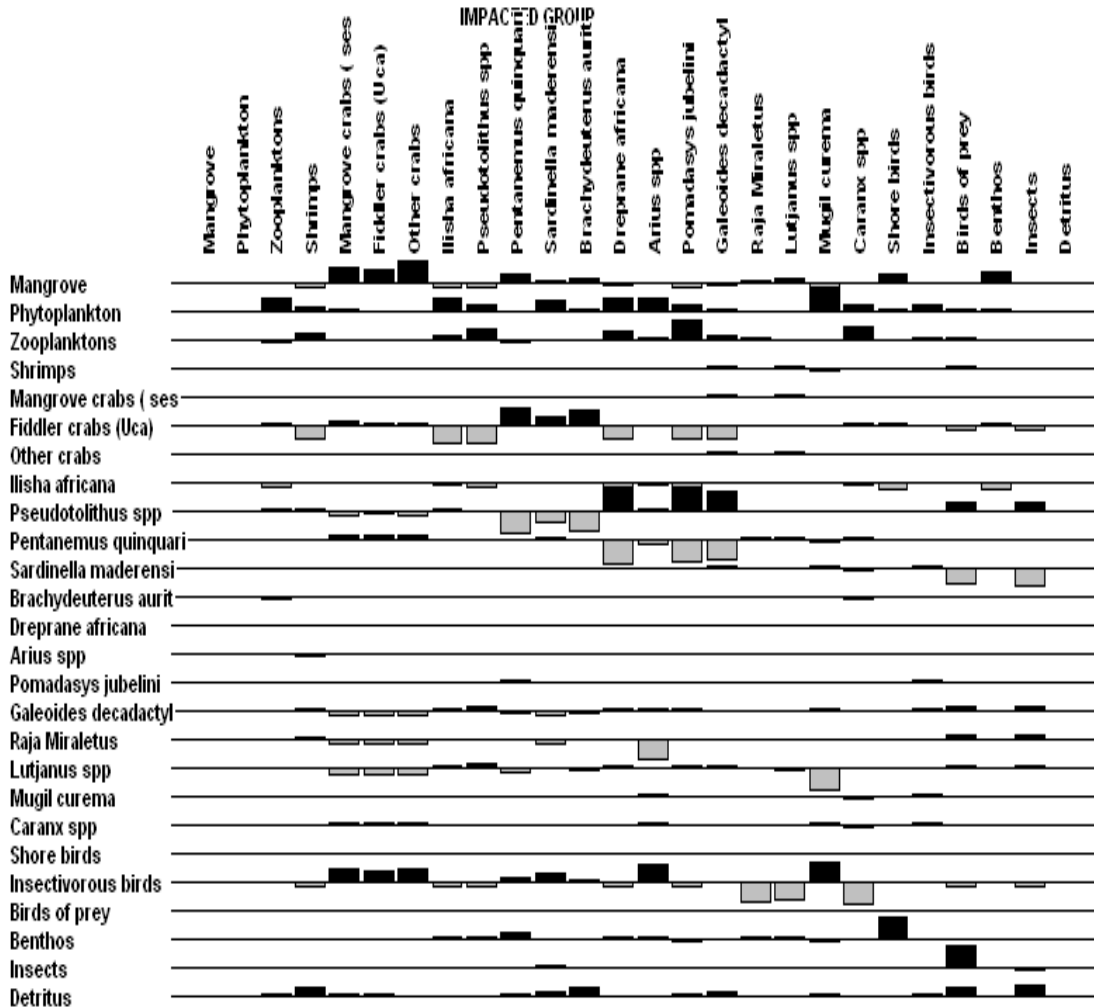


Figure 5. Mixed trophic impact analyses for the Cameroon mangrove ecosystem. The bars show positive (above line) and negative (below line) impacts of each compartment. Impacted groups are shown along the horizontal axis and impacting groups along the vertical axis.

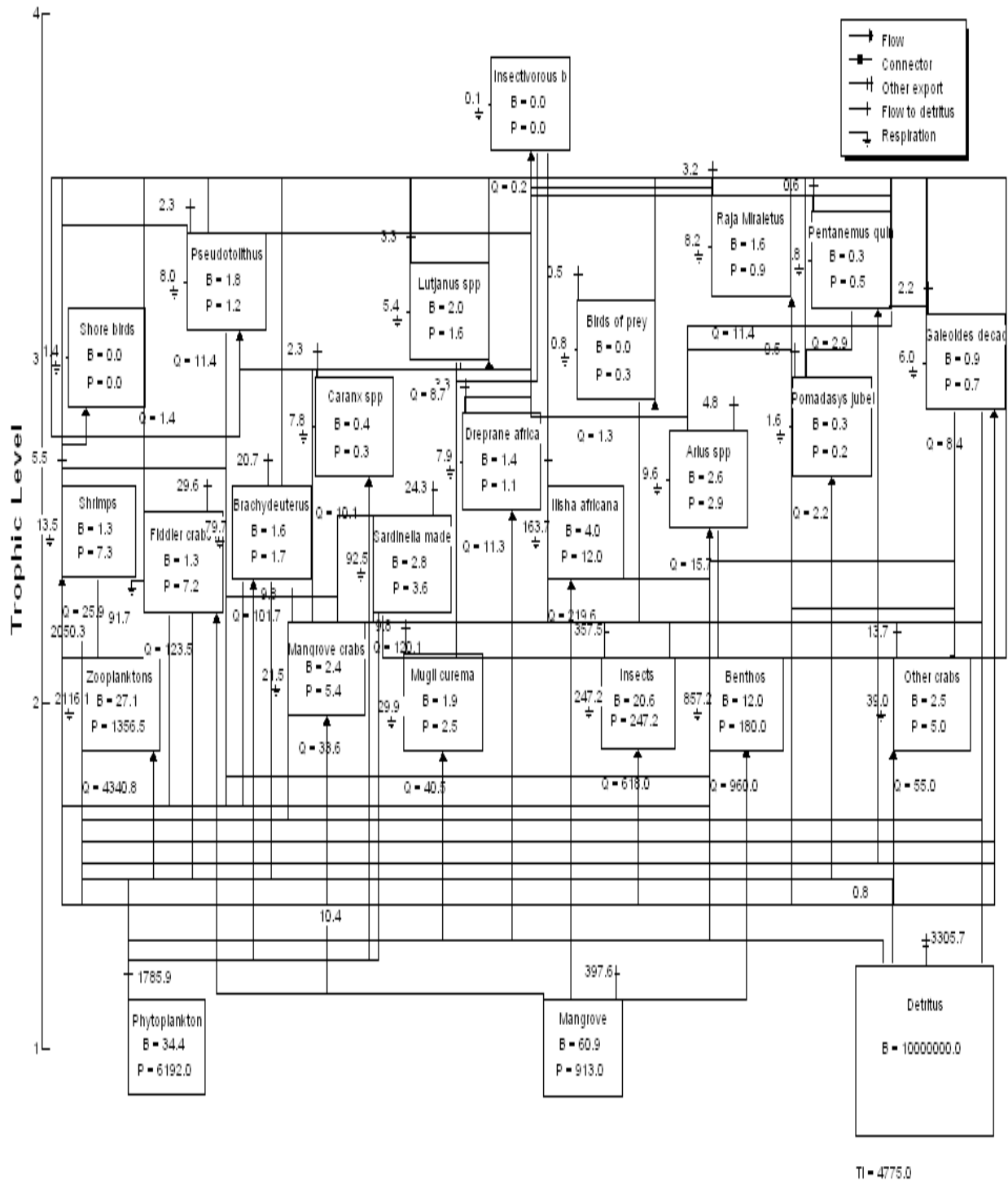


Figure 6. Trophic interactions in the Cameroon mangrove. All the flows expressed in $t/km^2.yr$. Each of the groups is placed on the Y-axis according to their trophic level. Biomass (B), Production (P), consumption (Q), the losses by respiration, the flows to detritus and cannibalism are specified. This is quantitative representation of trophic interactions within the food web of Cameroon mangrove system. The area of each box is a proportion to the logarithm of the biomass of each group.

5 DISCUSSION

The parameter estimates of the programme appear reasonable. Model viability was determined by using the sensitive analysis function i.e. pedigree index [11]. Sensitivity analysis was done to evaluate the accuracy of parameters estimated, it suggests that parameterisation of groups within the model is most sensitive to decreases in biomass estimates and that the impact of changes in the parameters of one group on another is influenced by the trophic dependency of the impacting group on the impacted group. The impacts of an increase in biomass in one group on other groups within the systems can be shown using a mixed trophic impact plot (Figure 5). This can be used to get an overall indication of the sensitivities and responses to reduced biomass in one group on another and dependent upon them. The viability value of 0.52 estimated by the model is an indication that the model was tightly fitted, as the simulation values have remarkably little difference from the original input. The balanced model parameter estimates shown in Table 11 indicate a mixture of a mature and immature system. The mature indices include: total system throughput (T) that is the sum of all flows (consumption, respiration, export and flow into detritus) is 18,615 t/km².yr, appears to be high when compared to other values from tropical coastal system. The system primary production/ respiration (PP/R) ratio estimated by the model is 1.87 (Table 11) indicating that the system is relatively developed [13]; the value is low when compared with other tropical ecosystems. The high ascendancy value of 9,929.2 and relative ascendancy of 0.250 indicate that the system is mature. However, the relative ascendancy of 0.250 reported by Vega-Cendejas and Arreguin-Sánchez, [54] for Yucatan Peninsula (Mexico) was considered high by the author. The total system biomass value is 184.193 t/km².yr which appears high fits well within the range of other tropical systems [12]. The model results show that more than 98.6% of the flows to detritus is from TL 1 and 2, these levels playing a significant role in supporting the energy utilised by higher TL groups, and indicate a detritus-based food web and bottom-top control system, which is typical of a mature system. System energy and matter recycling is an important process in ecosystem functioning [34], and the model low estimate of Finn's cycling index (FCI) and Finn's mean pathway of 1.983 and 1.717, respectively, is indicative of an immature system. The impact of mangrove change for the other functional groups was explored using the Ecosim routine and mixed trophic impact analysis (Figure 5). Mangroves have a positive impact on crab species and some other groups, with little negative or no impact on most species. A 40% change in mangrove biomass resulted to a drastic reduction in crab biomass (Figure 2b). The effect on fishes was obvious on four groups only, and at a high-level of mangrove biomass change (80%) (Figure 3). But modest changes in fish biomass were obvious for most fish groups, which suggest that mangrove is an important functional group for the system, though no direct trophic relationship exists with fishes. Mangroves play indirect role by producing detritus from the assimilation of fallen leaves within the sediment and detritus is utilised by many other groups in the food web or exported by tidal flush. The flows to detritus, from primary and second trophic levels, represent the main flow of energy in the food web.

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