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Research Article

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Trophic Modelling of the Cross River Estuary Ecosystem, Nigeria

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Abstract

A trophic modelling of the Cross River estuary ecosystem was undertaken using Ecopath with Ecosim (EwE). Data were obtained from peer reviewed journals, monographs and stock assessment reports and used to construct the Ecopath model used to investigate the structure, function and system throughput of the estuary. These data included biological data such as biomass, production/biomass, consumption/biomass, fish catch and diet composition of each species or functional group included in the model. The network analysis routine was used to estimate trophic levels and trophic interactions of functional groups, health condition and developmental stage, and food web features. Results of Ecopath model revealed three apical predators: Shark, Senegalese tonguesole, and Sea catfish. The ratio of total primary production to total respiration value of 4.182 revealed that the Cross River estuary is an immature ecosystem void of biological and ecosystem pollution and is at its early developmental stage. The mean trophic level of the catch of 2.186 for the system and the high gross food conversion efficiency (GE) of 0.300 for Macrobrachium spp and 0.292 for Penaeid shrimp, revealed high fishing pressure on the herbivores. The estuary ecosystem has a short food chain and low connectance index of 0.1879 which has phytoplankton being grazed upon by zooplankton which in turn are taken up by bonga. Model results and physico-chemical parameters showed that the Cross River estuary is still relatively pristine and immature ecosystem, void of organic pollution and with relatively low primary productivity as evident in relatively low nutrient concentration. The high value of ecotrophic efficiency (EE) of 0.993 for bonga and 0.991 for Macrobrachium spp indicate that the population of these animals are heavily exploited and predated upon in the estuary. Despite that this is a preliminary trophic model, it is clear that fish populations in the estuary are experiencing excessive fishing pressure; thus necessitating management measures to reduce pressure, while relevant data especially on fish diet composition and fish landing should be collected in order to get improved model parameterization in the future.

Keywords: Trophic Modelling, Cross River, Estuary, Ecosystems, Nigeria

Introduction

The trophic modelling of aquatic ecosystems is very important in ecological studies as it is used to investigate the behaviour of whole ecosystems [1]. They are useful tools for describing biomass flow between the different elements of exploited ecosystems and predicting outcomes of alternative fishing policies as well as assessing the ecological importance of observed or predicted effects of toxic chemicals on individual organisms in an ecosystem [2, 3]. Of recent, it has been expanded to investigate the impact of fishing on marine fauna and on their environment. Trophic modelling has also been used to investigate the effect of climate change and pollution on the marine environment [4]. It is believed that both fishing and environmental changes can influence the structure and function of the marine ecosystems [5]. Fishing impact not only affects the target species, but also other organisms and the environment within the wider ecosystem. Because of this, the concept of fishery management has been expanded from the single-species management model (which presents the stock as self-determining through recruitment) to ecosystem-based management, resulting in what is now known as the "Ecosystem Approach to Fisheries" (EAF) or Ecosystem-based fishery management (EBFM) [1, 6, 7]. The Ecosystem Approach to Fisheries (EAF) is an integrated concept encompassing fisheries and ecosystem management.

Fishery management by both fisheries scientists and managers has for long been focused on stock abundance (assessment), with an emphasis on biological sustainability of the fished stock [2]. However, fishery management should take into account, the biological, ecological, economic and social aspects of fisheries and sustainability [5]. While studies on biology can help to understand the life cycle and status of resource species, social and economic studies support understanding of the characteristic situation of resource users, whose activities directly influence the aquatic ecosystem and the resources. Enin advocated for intensive fisheries research from sociological and anthropological perspectives to define effective directions for fisheries management [8]. Therefore, the importance of the status of the ecosystem is increasingly being recognized as in the case of integrated coastal zone management for effective use of coastal resources [9]. Natural systems can change in response to fishing pressure and indirect effects of fishing on non-target species and the marine environment. One important approach to integrating these diverse aspects of fisheries and improving the efficiency of management is to construct ecosystem models. Ecosystem approach is a management strategy that takes into account the wider ecosystem including the human activities which take place in the environment.

Several software tools have been developed and used to increase the understanding of biological interactions among species. Some of these include multispecies virtual population analysis (MSVPA), Nutrient, Phytoplankton, Zooplankton and Detritus (NPZD), Lotka-Volterra, ATLANTIS, Globally applicable Area Disaggregated (GADGET), Ecological Network Analysis (ENA), and Ecopath with Ecosim (EwE) models [5, 7, 10] . EwE software as a popular ecological tool has been variously used to assess trophic interactions in aquatic ecosystems, to describe fishery effects on ecosystem, and to explore policy for fishery management [7, 11, 12]. The mass balance approach has been used to develop models for various aquatic ecosystems and fisheries management including coastal, estuarine, rivers, lakes and ponds ecosystems globally [13]. Examples include: trophic relationship in the fish community of Lake Victoria, Kenya, trophic model of an estuarine ecosystem at the southeast coast of India, and Ecopath theory, modelling, and application to a coastal ecosystem [7, 14, 15]. However, there has been no EwE model developed for the Cross River estuary ecosystem and any Nigeria ecosystems. The only model developed for an ecosystem in Nigeria so far is that of the Lake Chad system using what was called the Ecopath II model [15].

The Cross River estuary is the largest estuary on the Gulf of Guinea [16]. The estuary is located in the tropical rainforest belt of south-eastern Nigeria, covering about 580 km2 with several tributaries such as Calabar River, the Great Kwa River and Akpa Yafe River with creeks and Islands [17]. The estuary is fringed predominantly by mangrove vegetation consisting Rhizophora racemosa and Avicennia africana as the main species. The other vegetation is the nipa palm. The mangrove system serves as both spawning and feeding grounds for fin and shell fishes, thus sustaining important fisheries in Nigeria estuaries, coastal and adjacent waters. Though purely artisanal, the fisheries support a large population of coastal communities in Cross River and Akwa Ibom States, with an estimated 87,990 artisanal fishers [18]. Three main fisheries documented in the estuary include: (1) Pelagic fin-fish fishery targeting a clupeid, Ethmalosa fimbriata (bonga), (2) Demersal fishery targeting majorly catfish, Chrysichthys nigrodigitatus and Croaker, Pseudotolithus species, and (3) Shrimp fishery targeting Nematopalaemon hastatus and Macrobrachium species. Moses estimated that fishery yields from the Cross River accounted for about 34.1% of the total commercial landings in Nigeria [19-22].

This study provides detailed information on the fishery and ecological status of the Cross River estuary. The study describes the trophic status of the fishes of economic importance and other important organisms in the estuary. The study also enhances the establishment of food web and energy pathways of marine organisms. At present, there are only a few box models of trophic interactions among fishes of the estuary which did not consider the ecosystem and other factors [23, 24]. By using Ecopath software, a trophic model of the Cross River estuary was developed to integrate and assemble the existing studies on fisheries and other marine organisms of ecological importance. Ecopath models generate relevant information (trophic level, biomass, production, consumption etc.) at functional group or species levels that is used to explore the position and role of fish species within their food web.

Presently, there is no published work on the modelling of Cross River estuary using EwE. Asuquo (2001) only highlighted the importance of diet composition as a necessary component in the construction of EwE models in a future modelling of the Cross River estuary [23]. The present study hopefully achieved that expectation. According to Asuquo, considering the present shift of emphasis in fisheries science from modelling a single species to multispecies approach, the use of EwE will be necessary in understanding the Cross River estuary fisheries status and its ecosystem dynamism as the knowledge of ecological interactions is very important to an ecosystem approach to fisheries [4, 23]. This study also addressed Ama-Abasi recommendations on food chain study and predation activities on fish species of economic importance in the estuary [25]. Ama-Abasi studied aspects of the biology of E. fimbriata in the estuary and the adjacent coastal waters [25]. He recommended that, future research on bonga should focus on the food chain of the species of major economic importance in the Cross River estuary and its adjacent coastal waters to identify the potential predators of this species. The study also recommended examination of both the pelagic and demersal predators on the survival of the juvenile and larval bonga.

The purpose of this study therefore was to build a trophic model of Cross River estuary, characterize the ecosystem and assess the fisheries components of the ecosystem using EwE. EwE is a type of graphic ecological models that shows the interrelationships among various components of a system. The model was also used to investigate the ecosystem health. This work described the construction and calibration of the trophic model. It will therefore answer questions on the dynamics and the response of the ecosystem to the impact of fishing, climate change and pollution.

Materials and Methods

Study Area

The study area is the Cross River estuary located in the southeast of Nigeria, with an area of about 193nm2 [26]. It is situated between latitudes 4030' N and 4058'N and Longitudes 80 09' and 8030'E (Figure.1). The Cross River estuary is regarded as an extension of the shallow continental shelf region of Nigeria, classified as a drowned-river-mouth type of estuary [17]. It is the largest estuary on the Gulf of Guinea [19]. The Cross River, Calabar River, Great Kwa River and Akpa Yafe River are the main tributaries that empty into the Cross River estuary [25]. Cross River estuary provides habitat for a large number of economically important fish and invertebrate species that support a large population of coastal communities, predominantly artisanal fishers. Like most estuaries, the Cross River estuary serves many purposes for marine organisms including long-term residence, breeding and nursery.

The estuary is characterized by some islands, broad mud flats, and numerous large and small tidal creeks. The tidal creeks are separated from the main river channel by sand bars. Some of the islands include: Alligator, James, Parrot, and Tobacco Islands while broad mud flats include Johnson, Cleaves, Smith, James, and Kwa flats with minimal depth of about 5 to 6m. Sediment type is basically soft and muddy, in some places the sediment consists of fine and coarse sands which are regularly exposed at low tide. The estuary is about 42km long from the meeting point of Cross and Calabar Rivers (buoy 32, off Tobacco Island) to the mouth of the estuary (buoy 11) and about 20km wide from off James Town at the eastern bank to Ine Ekoi at the western bank. The depth has been described to range from 1 m to 14 m with average ranging between 6 m to 8 m with deepest part found at south eastern mouth of the estuary. The depth profile fluctuates from one location to the other and can best be described as undulating [19, 23]. The vegetation is dominated by salt tolerant trees such as mangroves, nipa palms (Nypa fruticans) and some other plants such as ferns Acrostichium sp. The mangroves consist of three families: Rhizophoraceae (red mangroves), Lambretaceae (white mangroves) and Avicenniaceae (black mangroves) and five species; Rhizophora racemosa, R. harrisoni, R. mangle, Laguncularia racemosa and Avicennia africana [19, 27, 28].

Ecosystem Modelling

Defining the Cross River estuary System

The species included in the model were selected based on the following criteria: (1) their distribution and abundance in the estuary, and (2) economic importance, and grouped according to size and feeding pattern. Basic parameters (biomass, production/biomass ratio, consumption/biomass ratio, diet composition, catch) were taken from published literature, stock assessment studies and monographs. The organisms used in the Cross River estuary model were arranged into 28 functional groups within 6 main groups. The main groups consisted of; sea birds (1 functional group), fishes (18 functional groups), invertebrates (5 functional groups), zooplankton (1 functional group), phytoplankton (1 functional group), discards (1 functional group) and detritus (1 functional group) (Table 1).

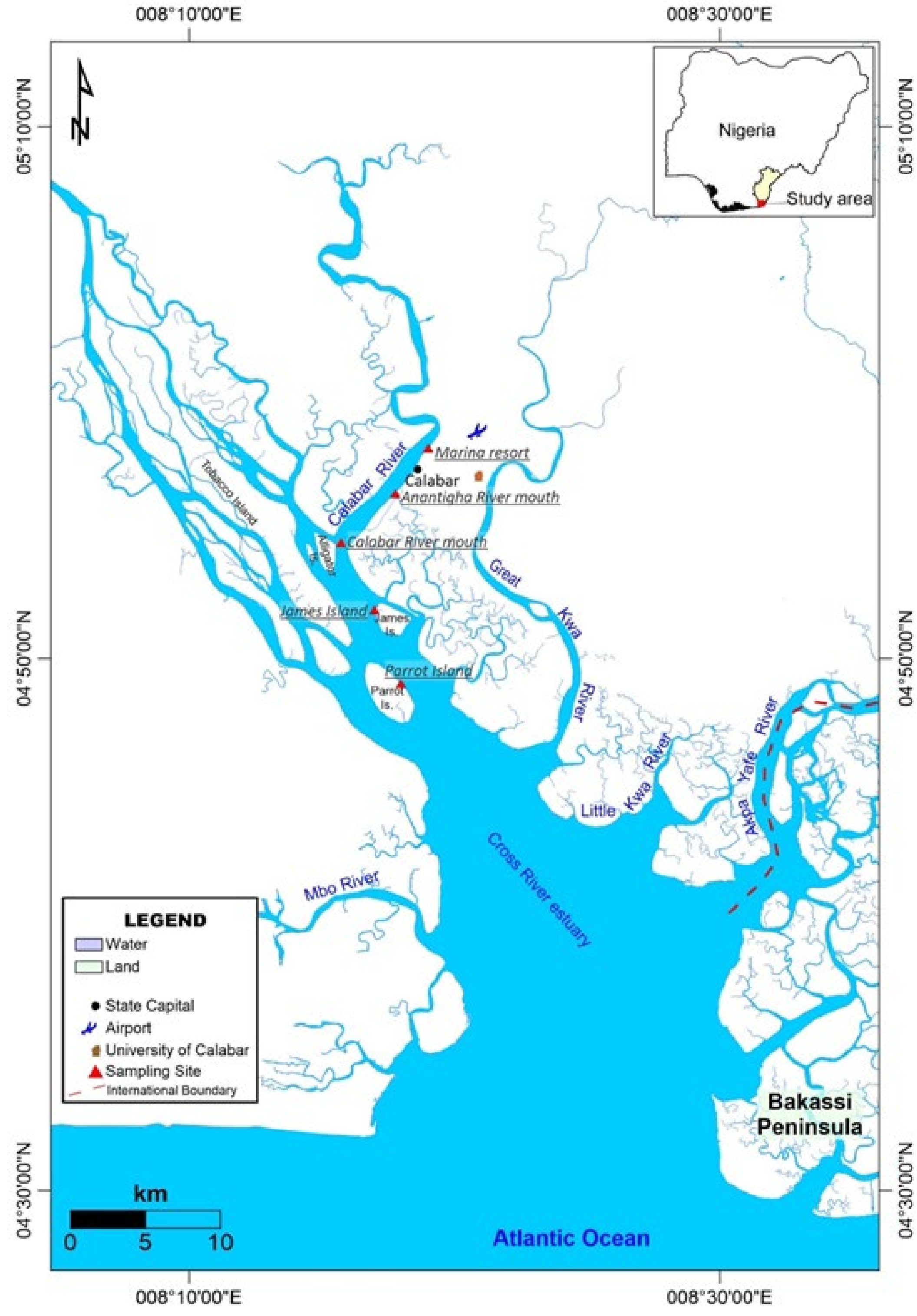

Figure 1: Map of the Cross River estuary and tributaries, showing sampling locations.

Basic Parameters, Diet Composition and Catch

Data on the functional groups, basic input parameters (biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), diet composition, and fisheries (catch data), were compiled from existing literature and stock assessment reports from the Cross River estuary ecosystem and its tributaries [18, 26, 29-33]. Additional data were gathered from similar ecosystems such as Qua Iboe River, Lagos Lagoon and Epe Lagoon where such data were unavailable or inadequate from the Cross River estuary. Most of the P/B and Q/B values were obtained from studies on the Guinea – Bissau and Gambian Continental Shelf Ecosystems; while the remaining values were generated by the model (Table 1). Diet data used were both quantitative and qualitative (Table 2). Qualitative data were converted using conversion equation from Frequency of Occurrence (FO) to Relative Weight Composition (RWC) [34]. Fish catch data were obtained from trawl fishery and artisanal fishery [26, 31]. Fish biomass data were obtained from fish landings (Table 3).

Mass balanced ecosystem model with Ecopath

The Cross River estuary ecosystem model was developed using Ecopath with Ecosim (EwE) version 6 [35, 36]. The EwE software tool is a common and flexible framework for quantifying food webs and for analysing ecosystem dynamics [2]. The core routine of Ecopath is derived from the Ecopath programme of Polovina [37]. EwE consists basically of three components which include: Ecopath (a static, mass balanced snap shot of the ecosystem); Ecosim (a time-dynamic simulation module for policy exploration); and Ecospace (a spatial and temporal dynamic module for exploring impact and placement of protected areas) [35]. Ecopath is based on two equations; the first is the master linear equation and requires that for each functional group (i) in a typical ecosystem, mass balance should occur over a given time period, usually one year (except for seasonal modelling). The functional group represents organisms (either as a mixed group of species, individual species or an ontogenic fraction of a species) inhabiting an ecosystem at a particular period of time such that:

Production = catch + predation mortality + biomass accumulation + net migration + other mortality, and formally expressed as:

$$B_i \cdot (P/B)_i = \sum B_j \cdot (Q/B)_j \cdot DC_{ji} + Y_i + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1-EE_i) \quad (1)$$

Table 1: Sources of basic parameters used in the Ecopath model ("EwE" represents value generated by the model)

S/N	Functional Group	Biomass	P/B	Q/B	EE
1	Seabird	[39]	[39]	[39]	EwE
2	Shark	[39]	[39]	[39]	EwE
3	Estuarine catfish	[26, 31]	[33]	EwE	EwE
4	Sea catfish	[26, 31]	[29]	EwE	EwE
5	Bobo croaker	[26, 31]	[66]	[40]	EwE
6	Croaker spp	[26, 31]	[41]	[39]	EwE
7	Senegalese tonguesole	[26, 31]	[39]	[39]	EwE
8	Giant Africa threadfin	[26, 31]	[42]	[40]	EwE
9	Lesser African threadfin	[26, 31]	[40]	[40]	EwE
10	Guinean barracuda	[31]	[43]	[40]	EwE
11	Largehead hairtail	[26, 31]	[40]	[40]	EwE
12	Grunts	[26, 31]	[40]	[40]	EwE
13	Bonga shad	[26, 31]	[18]	[39]	EwE
14	West African Ilisha	[26, 31]	[40]	[40]	EwE
15	Mullets	[31]	[40]	[40]	EwE
16	Guinean sprat	[31]	[40]	[40]	EwE
17	Moon fish	[26, 31]	[40]	[40]	EwE
18	Gobies	[26, 31]	[44]	EwE	EwE
19	Daisy stingray	[26, 31]	[40]	[40]	EwE
20	Swim crab	[26, 31]	[40]	[40]	EwE
21	Macrobrachium spp	[31]	[32]	EwE	
22	Penaeid shrimps	[19]	[30]	[40]	
23	Gastropods/Bivalves	EwE	[40]	[40]	

24	Small crustaceans	EwE	[40]	[40]	EwE
25	Zooplankton	EwE	[39]	[39]	
26	Phytoplankton	EwE	[39]	[39]	
27	Discards				EwE
28	Detritus/sand grains				EwE

Table 2: Sources of Diet Composition data used in the Ecopath model

	Functional Group	Scientific name	Diet Information	Location	References
1	Seabird		Quantitative	Guinea-Bissau, Continental Shelf	[40]
2	Shark		Quantitative	Guinea-Bissau, Continental Shelf	[40]
3	Estuarine catfish	*Chrysichthys nigrodigitatus*	Quantitative	Nigeria, Cross River estuary	[45]
4	Sea catfish	*Arius sp (Arius catisculatus)*	Quantitative	Gambia, Continental Shelf	[39]
5	Bobo croaker	*Pseudotolithus elongatus*	Quantitative	Nigeria, Cross River estuary	[45, 46]
6	Croaker spp	*Pseudotolithus typus, P. senegalensis*	Quantitative	Benin Republic, Nerashore waters	[47, 48]
7	Senegalese tonguesole	*Cynoglossus senegalensis*	Quantitative	Nigeria, Cross River estuary	[49, 50]
8	Gaint Africa threadfin	*Polydactylus quadrifilis*	Qualitative	Nigeria, Warri River	[51]
9	Lesser African threadfin	*Galeoides decadactylus*	Qualitative	Nigeria, Coastal waters	[52, 53, 54, 51]
10	Guinean barracuda	*Sphyraena afra*	Quantitative	Guinea-Bissau, Continental Shelf	[40]
11	Largehead hairtail	*Trichiurus lepturus*	Qualitative	Nigeria, Cross River estuary	[55]
12	Grunt	*Pomadasys jubelini, P. peroteti*	Quantitative	Nigeria, Bonny River	[56]
13	Bonga shad	*Ethmalosa fimbriata*	Qualitative	Nigeria, Cross River estuary	[55]
14	West African Ilisha	*Ilisha Africana*	Qualitative	Nigeria, Cross River estuary	[57]; www.fishbase.org
15	Mullet	*Liza falcipinnis, Mugil cephalus*	Qualitative	Nigeria, Cross River estuary	[24, 58, 59]
16	Guinean sprat	*Pellonula leonensis*	Quantitative	Guinea-Bissau, Continental Shelf	[40]
17	Moon fish	*Psettias (Monodactylus) sebae*	Quantitative	US, Southern Gulf of California	[60]
18	Gobies spp	*Gobioides ansorgei*	Qualitative	Nigeria, Badagry Creek	[61]
19	Daisy stingray	*Dasyatis margarita*	Quantitative	Guinea-Bissau, Continental Shelf	[40]
20	Swim crab	-	Qualitative	Brazil, Fortaleza Bay, Ubatuba (SP)	[62]

21	Macrobrachium spp	*Macrobrachium vollenhoevenii, M. macrobrachium*	Qualitative	Nigeria, Epe Lagoon; Kwa River	[63]
22	Penaeid shrimps	*Parapenaeus longirostris, P. kerathurus, Parapenaeopsis atlantica*	Quantitative	Guinea-Bissau, Continental Shelf	[40]
23	Gastropods/Bivalves	*Tympanotomeus fuscatus,*	Quantitative	Guinea-Bissau, Continental Shelf	[40]
24	Small crustaceans	*Nematopamous hestatus, Palaemonetes africanus, Alpheus pontederiae*	Quantitative	Gambia, Continental Shelf	[39]

Table 3: Cross River estuary landings by gear (Total catch (t/km²/year)

Group name	Trawler	Purse Seine	Seine net	Gillnet	Pushnet	Trap	Total catch
Estuarine catfish	0.6916	-	-	0.16121	-	-	0.85279
Sea catfish	0.0083	-	-	0.00134	-	-	0.00961
Bobo croaker	0.5321	-	-	1.09064	-	-	1.62274
Croaker spp	0.0032	-	-	0.00025	-	-	0.00347
Senegalese tonguesole	0.2220	-	-	0.01462	-	-	0.23658
Giant Africa threadfin	0.0593	-	-	0.11759	-	-	0.17689
Lesser African threadfin	0.0070	-	-	0.00557	-	-	0.01255
Guinean barracuda	0.0086	-	-	0.01018	-	-	0.01877
Largehead hairtail	0.0295	-	-	0.00152	-	-	0.03098
Grunts	-	-	-	0.00272	-	-	0.00272
Bonga shad	0.0003	319.11	-	0.30792	-	-	319.4182
West African Ilisha	0.0039	-	-	0.00486	-	-	0.00875
Mullets	0.0007	-	-	0.00344	-	-	0.00412
Guinean sprat	-	-	-	0.00407	-	-	0.00407
Moon fish	0.0271	-	-	-	-	-	0.02706
Daisy stingray	0.0212	-	-	-	-	-	0.02121
Swim crab	-	-	-	0.0141	-	-	0.0141
Macrobrachium spp	-	-	1.5474	0.0004	0.3418	0.3057	2.1953
Total catch	1.6145	319.11	1.5474	1.74043	0.3418	0.3057	324.6599

Sources: Trawlers [26]; Purse seine, seine net, gill net, push net & trap (Holzloehner et al., 1998).

Where: Bi is the biomass of species group i, P/Bi is the production/biomass ratio of i, Bj is the biomass of consumers or predators j, Q/Bji is the consumption of i per unit of biomass of j, DCji is the fraction of prey, i in the diet of the predator j (diet composition), Yi is the total fishery catch rate of i, Ei is the net migration rate of i, BAi the biomass accumulation rate of i, and EEi is the ecotrophic efficiency (i.e. proportion of the production that is utilized in the system).

Model Parameterization

The biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) and Ecotrophic Efficiency (EE) are initial parameters that are required to establish the mass – balanced ecopath model. Ecopath requires that at least 3 of the 4 basic parameters are entered with catch rate (Yi) and diet composition (DCji) with the series of linear equations solving for the fourth equation. Trophic interactions among groups are presented by a diet matrix that quantitatively describes the fractions that every group has in each other group's diet.

The basic inputs parameters were obtained as described below:

Biomass

Biomass is the total mass of a species/functional group within a habitat. In Ecopath model, biomass is the biomass in habitat area (i.e. the average biomass per unit area in the habitat area where the group occurs) multiplied by habitat area. Biomass estimates (in t/

km2) were obtained for all functional groups based on equation (2). According to Lees and Mackinson biomass can be estimated using the formula [4]:

Biomass (t/km^2) = abundance * average Body weight (t) / study area (261. 66 km^2) ______________________2)

Biomass was calculated for species of commercial importance by dividing the total weight of catch in kilogramme by the total area of the estuary in square kilometre. Biomass of seabird and shark were taken from Guinea – Bissau model. Other functional groups (zooplankton, phytoplankton, discards and detritus) were left to be estimated by the model.

Production/Biomass ratio (P/B)

Production is the elaboration of tissue by a group over the period of time expressed as year-1. Production (P) is entered as P/B which is equal to instantaneous total mortality (Z); i.e. sum of fishing mortality (F) and natural mortality (M) for commercial species.

According to Allen, total mortality under steady state condition is equal to P/B. P/B for most species was obtained from total mortality (Z) estimates from stock assessment on commercial species from the estuary [64]. P/B for other species were collected from Guinea – Bissau and Gambian models. No species was left for the model to estimate (Table 1).

Consumption/Biomass ratio (Q/B)

Consumption is the intake of food by a group over a time period usually one year. Consumption is entered as Q/B (expressed in t/km2/year) and is calculated from empirical equation derived from Palomares and Pauly [65].

ln Q/B = 1.117 – 0.202lnW_∞ + 0.612lnT + 0.516log10A +1.26f ______________________3)

Where: W∞ = asymptotic weight of the fish of a given population (in g), T = temperature (in 0C), A = an index of the mean activity level of the fish of a given species, derived from the shape ("aspect ratio") of their caudal fin, f = food type (carnivore, f=0, or herbivore f=1).

Q/B values for this model were taken from similar ecosystem models of Guinea-Bissau and Gambia. Only values for estuarine catfish, sea catfish, Macrobrachium spp (shrimps) and gobies species, were left to be estimated by the model (Table 1).

Ecotrophic Efficiency (EE)

Ecotrophic Efficiency is the fraction of the ecosystem production that is used within the system. Values for EE in the model were assumed for five functional groups based on values varying between 0 and 1 as recommended [36]. Values for other groups were estimated by the model. EE values can be expected to be close to 1 for organisms heavily exploited and/or predated and equal to zero for any group not consumed by predators in the system (Table 1).

Production/Consumption ratio (P/Q)

The calculation of Production/Consumption ratio was not necessary as at least three input parameter values only were required for the model to run. P/Q values were however estimated by the model (Table 1).

Diet Composition

Diet composition data were obtained from sundry literature sources with the majority from the Cross River estuary (Table 2). Others were obtained from studies of nearby and similar ecosystems such as Qua Iboe River and Imo River estuaries, and Lagos and Epe Lagoons. A few others were obtained from Guinea – Bissau and Gambian models. Some of these diet compositions were both quantitative and qualitative. Qualitative data were converted from Frequency of Occurrence in percentage/dominance to relative weight data using equations developed by Stobberup et al.[34]. There were prey items in the diet of some functional groups adapted from nearby ecosystems that did not occur in the Cross River estuary. These prey items in the diet were placed in a functional group with similar species. Where there is no similar species the prey items were redistributed by percentage in the diet of other functional groups.

Model Balancing

In order to achieve balancing of the model, these input data (B, B/P, Q/B, EE) for individual functional groups were adjusted within the range of values reported in the literature to obtain output within a given range of values. The expected range of values varied among functional groups [36]. EE and P/Q values are expected to fall between 0 and 1, and 0.1 and 0.3/0.35 respectively.

After the missing parameters are estimated (output) using equation (1) so that mass balance is achieved within each group, energy balance is also ensured within individual groups using the second master equation below [35];

Consumption = production + respiration + unassimilated food and formally expressed as follows:

Bi.(Q/B) i = Bi . (P/B)i + Ri + Ui ____4)

Where: Bi is the biomass of the group i (t/km2), Q/Bi is the consumption/biomass ratio of i (per year), P/Bi is the production/biomass ratio of i (per year), Ri is respiration by i (t/km2 year), and Ui is unassimilated food by i (t/km2 year-1).

Fishes in the model

Data on fishes from the estuary included in this model were collected from sundry sources and were divided into three categories: demersal, pelagic and shell fishes [8, 19, 26, 31]. There were 11, 7 and 4 functional groups for demersal, pelagic and shell fish respectively (Table 4). Each functional group in the demersal and pelagic categories represents a single species in the model, except for croaker spp group that consisted of Pseudotolithus typus and P. senegalensis. In shell fish category, all functional groups constitute more than a single species. These species are all of economic importance in the estuary. Most of the basic parameters were taken from Amorim et al. and Mendy [19, 40]. Biomass was calculated from Lowenburg and Kunzel, Holzloehner et al. while most P/B and Q/B were taken from Amorim et al [26, 31].

Table 4: List of Fish species included in the Cross River estuary Ecosystem Model

Fish Group	Common Name	Scientific name
Demersal	Shark	Negaprion brevirostris, Carcharthinus plumbeus
	Estuarine catfish	Chrysichthys nigrodigitatus
	Sea catfish	Arius sp (Arius catisculatus)
	Bobo croaker	Pseudotolithus elongatus
	Croaker sp	Pseudotolithus typus, P. senegalensis
	Senegalese tonguesole	Cynoglossus senegalensis
	Gaint African threadfin	Polydactylus quadrifilis
	Lesser African threadfin	Galeoides decadactylus
	Largehead hairtail	Trichiurus lepturus
	Daisy stingray	Dasyatis margarita
	Goby	Gobioides ansorgei
Pelagic	Guinean barracuda	Sphyraena afra
	Grunt	Pomadasys jubelini, P. peroteti
	Bonga shad	Ethmalosa fimbriata
	West African Ilisha	Ilisha africana
	Mullet	Liza falcipinnis, Mugil cephalus
	Guinean sprat	Pellonula leonensis
	Moon fish	Psettias (Monodactylus) sebae
Shell fish	Macrobrachium sp (Prawns)	Macrobrachium vollenhoevenii, M. macrobrachium
	Penaeid shrimp	Parapenaeus longirostris, P. kerathurus, Parapenaeopsis atlantica
	Gastropods/Bivalves	Tympanotomeus fuscatus,
	Small crustaceans	Nematopamous hestatus, Palaemonetes africanus, Alpheus pontederiae

Mendy with a few obtained directly from literature on the estuary [8, 19, 29, 66].

In this study, total mortality from literature was used to represent P/B. Under steady state condition, the total mortality is equal to the P/B ratio [64].

Ecological Parameters and Indicators

Among the ecological parameters and indicators calculated by Ecopath routine of EwE software include the parameters discussed below:

Trophic Level (TL)

The trophic level (TL) was used to estimate the trophic position of individual species or functional group in the food web. Within EwE, trophic level (TL) of individual functional groups was calculated in the model using the equation below as incorporated into a routine of the software [67]:

$TLj=1+\sum_{i=1}^{n} DCji\ .TLi$ ______________ (5)

Where: TLj is the trophic level of a predator, DCji is the fraction of prey, i in the diet of the predator j, and TLi is the trophic level of its prey i.

Omnivory Index (OI)

Omnivory Index (OI) is a measure of the distribution of feeding interactions among trophic levels by functional groups. OI was calculated according to using the equation below [68]:

$OI_j = \sum_{i=1}^{n} [TLi\text{-}(TLj\text{-}1)]2.DCji$ ______________________(6)

where: OIj is the OI of a predator j, TLi is the trophic level of prey i, TLj is trophic level of predator j and DCji is the fraction of prey i in the diet of predator j. Zero (0) value indicates consumer specializes on a single trophic level, large values indicate consumer feeds on many trophic levels.

Mortality Index

Mortality coefficients were calculated from equations 1,7, 8, 9 as incorporated into a routine of the software.

$M2_i = (\sum Bi.\ Q/Bi\ .DCji)/Bi$ _________________ (7)

$Fi= Yi/Bi$ ____________________________________ (8)

$MO_i= (1 - EE_i).\ P/B_i$ ___________________________ (9)

Where: Q/Bi is the consumption per biomass ratio of predator j, DCji is the proportion of prey i in the diet of predator j, Bi is the average biomass of i, and Yi is the catch of i.

Flow Analysis

Trophic flow diagram of the ecosystem was built using Ecopath routine. Trophic flow diagram shows the movement of energy from one trophic level to the next via the food web. The diagram shows the position of each functional group revealing their relative role, impact, and relative biomass in the ecosystem.

Mixed Trophic Impacts (MTI)

After balancing the model, the network analysis routine incorporated in EwE, was used to estimate system properties and flow indicators [69]. Mixed trophic impacts (MTI) which is a routine in Network Analysis is used as an indicator of relative impact of a change in the biomass of one group on other groups within the ecosystem. Given the mass balance model of a trophic network, the MTI is estimated for each pair of functional groups (i,j) of the trophic web by constructing an n, diet (positive direct impact) x n, consumption (negative direct impact) matrix, based on the concept of Ulanowicz and Puccia using the equation (10) below. MTI represents the sum of direct and indirect impacts [70]. The indirect impact normally results from inter-group competition and trophic cascade.

$$MTI_{i,j} = DC_{i,j} - FC_{j,i} \qquad (10)$$

where: i, jth elements represent the interaction between the impacting group j and the impacted group i, DCi,j is the fraction of prey i in the diet of predator j, and FCj,i is a host composition term giving the proportion of the predation on i that is due to j as a predator. During calculation of host composition, fishing fleets are considered as 'predators'.

Results

Features of the Cross River estuary

The results of a balanced trophic model after meeting the criteria, Ecotrophic Efficiency (EE) values of between 0 and < 1 and gross food conversion efficiency (GE) 0.10 – 0.35, are presented in Table 5. Ecotrophic Efficiency (EE) value for sea birds and shark was 0.00 because they are top predators. The highest value was 0.993 for bonga shad, followed by 0.991 for Macrobrachium spp. Other species with high EE values were croaker species and Senegalese tonguesole with 0.990 and 0.950 respectively. These values suggest high exploitation rates and predation of these species in the ecosystem.

Production per Consumption ratio (P/Q) values in this system ranged from 0.001 to 0.378 for Seabird and Mullet species respectively suggesting that seabird has the lowest gross food conversion efficiency (GE) as top predator. The values of 0.300 and 0.292 for Macrobrachium and Penaeid shrimps show that these species have maximum food conversion efficiency.

Omnivory Index (OI) values estimated ranged between 0.00 (phytoplankton, discards and detritus) and 0.84 (stingray) (Table 5). The zero value shows the species is a specialised consumer and as such feeds on a single trophic level in the ecosystem.

Table 5: Basic Parameters after model balancing (Values in bold estimated by the model)

Group name	TL	B (t/km²)	P/B (/year)	Q/B (/year)	EE	P/Q	OI
Seabird	3.26	0.004	0.10	100	0	0.001	0.169
Shark	4.40	0.0055	0.30	3.00	0	0.100	0.390
Estuarine catfish	3.57	1.29	6.27	27.26	0.416	0.230	0.347
Sea catfish	3.84	0.15	1.85	7.400	0.038	0.250	0.251
Bobo croaker	3.46	2.45	3.71	19.96	0.720	0.186	0.016
Croakers	3.66	1.220	0.93	4.959	0.990	0.188	0.121
Senegalese Tonguesole	3.87	0.357	1.60	7.000	0.950	0.229	0.491
Giant Africa threadfin	3.50	0.267	3.28	16.82	0.321	0.195	0.067
Lesser African threadfin	3.70	0.039	1.81	6.282	0.827	0.288	0.049
Guinean barracuda	3.71	0.029	1.60	5.440	0.502	0.294	0.436
Largehead hairtail	3.11	0.468	0.62	4.440	0.742	0.139	0.008
Grunts	3.68	0.049	0.94	6.300	0.076	0.150	0.032
Bonga shad	2.17	48.30	6.91	19.10	0.993	0.362	0.158
West African Ilisha	3.35	0.232	2.15	9.286	0.854	0.231	0.096
Mullets	3.19	0.622	1.50	3.969	0.502	0.378	0.192
Guinean sprat	2.64	0.615	1.15	9.286	0.869	0.124	0.332
Moon fish	3.38	0.818	3.15	9.286	0.438	0.339	0.171
Gobies	3.39	0.200	9.21	36.84	0.931	0.250	0.109
Daisy stingray	3.40	0.458	0.92	3.912	0.225	0.235	0.841

Swim crab	2.82	2.130	2.80	9.500	0.912	0.295	0.821
Macrobrachium spp	2.64	3.320	6.85	22.83	0.991	0.300	0.426
Penaeid shrimps	2.46	6.201	5.61	19.20	0.900	0.292	0.422
Gastropads/Bivalves	2.42	10.99	2.50	8.200	0.700	0.305	0.329
Small crustaceans	2.42	8.726	7.01	27.14	0.900	0.258	0.284
Zooplankton	2.10	17.82	30.0	120.0	0.900	0.250	0.099
Phytoplankton	1.00	10000	150	0.000	0.500	-	0.000
Discards	1.00	0.050	25.0	50.00	0.913	0.500	0.000
Detritus/sand grains	1.00	42.35	-	-	0.046	-	0.000

Trophic Levels

Functional groups in the Cross River estuary ecosystem had trophic level range of 1.0 - 4.4 with producers, detritus and discards having a definitional value of 1. The lower values generally belonged to functional groups of small organisms with gradual increase that culminated at top predators. Top predators revealed included shark, Senegalese tongue sole, estuarine catfish and sea catfish. The groups with TL ≥ 3.75 are called apical predators and included Shark (4.40), Senegalese tongue sole (3.87) and Sea catfish (3.84). The trophic level of the functional groups in the food web with TL ≥ 3.0 are sorted in hierarchy in Table 5 and include the following: Guinean barracuda (3.71), Lesser African threadfin (3.70), Grunts (3.68), Croakers (3.66), estuarine catfish (3.57). Others are Giant African threadfin (3.50), Bobo croaker (3.46), Daisy stingray (3.40), Gobies (3.39), Moon fish (3.38), West African Ilisha (3.35), Sea bird (3.26), Mullets (3.19), and Largehead hairtail (3.11). The groups with TL (≥ 3.75) are described as apical predators and include shark (4.40), Senegalese tonguesole (3.87), and Sea catfish (3.84).

Food Web Analysis

The synthesis of energy links between trophic levels in the ecosystem is presented in Figure. 2. A total of 4 trophic levels existed in the ecosystem. Trophic level 4 was occupied by only shark. Trophic level 3 has the highest number of functional groups of 16. They include: Sea catfish, estuarine catfish, croakers, bobo croaker, grunts, Lesser African threadfins, Giant African threadfins, Guinean barracuda, and seabird. Others in this group are Senegalese tonguesole, mullets, largehead hairtail, daisy stingray, gobies, West Africa Ilisha, and Moon fish. For trophic level 2, members included: swim crab, Guinean sprat, Macrobrachium spp, penaeid shrimps, gastropods/bivalves, small crustaceans, bonga, and zooplankton. Phytoplankton, discards and detritus/sand grains occupy the first trophic level.

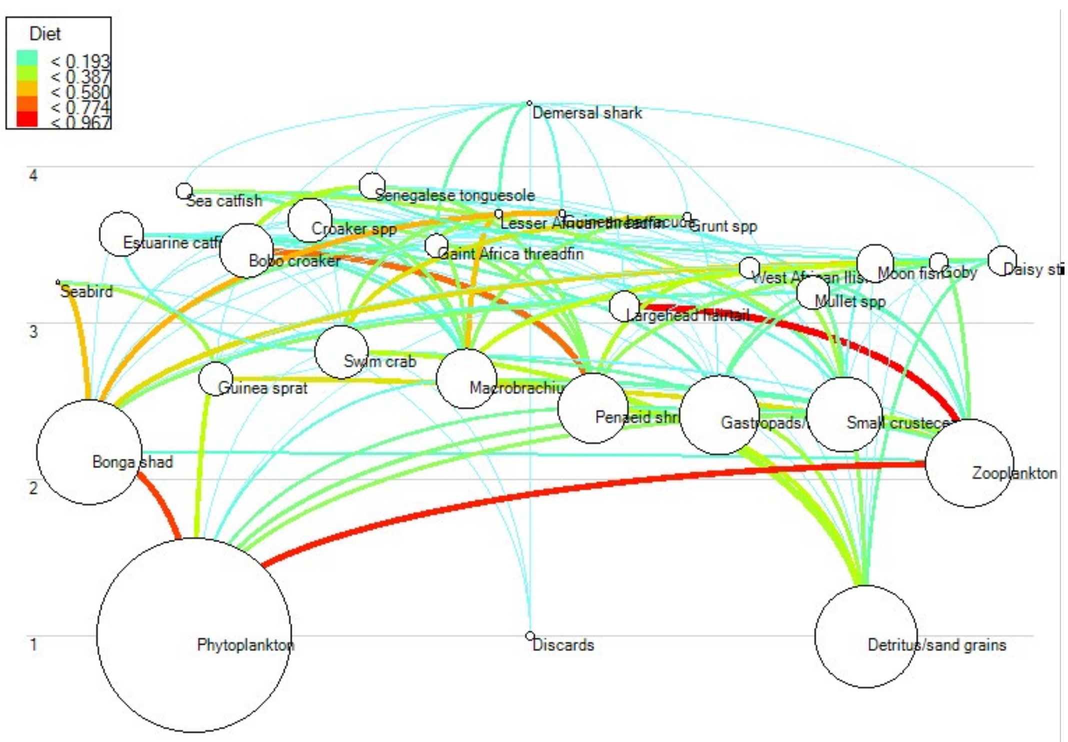

Figure 2: A food web diagram of the Ecopath for Cross River estuary showing trophic interactions among groups. 1-5 represent trophic levels.

The Ecosystem Indicators

The Ecopath model can be used to assess the whole ecosystem state. Table 6 shows relevant system indices for the Cross River estuary. The total biomass excluding detritus in the system was 145.034 t/km2/year signifying the level of the ecosystem maturity. Total biomass is an aspect of community structure and is assumed to increase as the system matures. Biomass is the most important indicator in the study of population and ecosystem science because it is used in deriving other indices such as consumption, production, respiration, assimilation and ecotrophic efficiency. Consumption, production and respiration are indicators of organic matter decomposition. Total respiration was 1, 371.225 t/km2/year and serves as an index of the activity of the system. Total respiration is always high in immature and perturbed systems.

Sum of total flows to detritus was 4, 266 t/km2/year. It is an index of cycling and maturity and is high in immature and perturbed system. Cycling is the proportion of total system throughput that is recycled in the system. Total system throughput (sum of all flows in the system and a measure of ecosystem size) was 13, 764.22 t/km2/year. Throughput and biomass are expected to increase as the ecosystem matures and grows. System Omnivory Index (OI) was 0.2564.37 (Table 6). The zero value for Omnivory Index (Table 6) indicates consumer specializes on single trophic level and large value indicates consumer feeds on many trophic levels. Connectance index was 0.1879. Connectance index (CI) is the measure of the percentage of realised links over possible links in a system. Both OI and CI are used to measure food complexity.

Mortality Rate

Table 7 shows total mortality, fishing mortality, predation mortality, and other mortality rates in the ecosystem. Among the fished groups, bonga shad had the highest fishing mortality rate of 6.613 followed by Senegalese tonguesole and giant African Threadfin with 0.663 value each as well as Macrobrachium spp, Guinean baracuda and estuarine catfish with 0.661 value each. The highest rate of predation mortality was found in phytoplankton (75.0) followed by zooplankton (27.0) and penaeid shrimp (9.572). Total mortality (Z) among fish species of economic importance was higher in gobies (9.21) followed by bonga shad (6.91), Macrobrachium spp (6.85), and estuarine catfish (6.27).

Table 6: Summary statistics of the Cross River estuary ecosystem (Indicators)

Parameter	Value	Units
1. Sum of all consumption	3734	(t/km^2/year)
2. Sum of all exports	4394	(t/km^2/year)
3. Sum of all respiratory flows	1371	(t/km^2/year)
4. Sum of all flows into detritus	4266	(t/km^2/year)
5. Total system throughput	13764	(t/km^2/year)
6. Sum of all production	6783	(t/km^2/year)
7. Mean trophic level of the catch	2.186	-
8. Gross efficiency (catch/net p.p.)	0.0566	-
9. Calculated total net primary production	5734	(t/km^2/year)
10. Total primary production/total respiration	4.182	-
11. Net system production	4363	(t/km^2/year)
12. Total primary production/total biomass	39.54	-
13. Total biomass/total throughput	0.0105	-
14. Total biomass (excluding detritus)	145.0	(t/km^2)
15. Total catch	324.7	(t/km^2/year)
16. Connectance Index	0.1879	-
17. System Omnivory Index	0.2564	-

Table 7: Mortality rate for Functional Groups in the Cross River estuary, Nigeria

Functional Group (FGs)	Total mortality (Z)	Fishing mortality	Predation mortality	Other mortality
Seabird	0.10	0.000	0.000	0.100
Shark	0.30	0.000	0.000	0.300
Estuarine catfish	6.27	0.661	1.945	3.664
Sea catfish	1.85	0.064	0.006	1.780
Bobo croaker	3.71	0.662	2.008	1.040
Croakers	0.93	0.003	0.918	0.009
Senegalese tonguesole	1.60	0.663	0.857	0.081
Giant Africa threadfin	3.28	0.663	0.389	2.229
Lesser African threadfin	1.81	0.323	1.175	0.314
Guinean barracuda	1.60	0.661	0.142	0.797
Largehead hairtail	0.62	0.066	0.391	0.159
Grunts	0.94	0.055	0.017	0.870
Bonga shad	6.91	6.613	0.247	0.050
West African Ilisha	2.15	0.038	1.798	0.313
Mullets	1.50	0.007	0.746	0.747
Guinean sprat	1.15	0.007	0.992	0.151
Moon fish	3.15	0.033	1.348	1.768
Gobies	9.21	0.000	8.574	0.636
Daisy stingray	0.92	0.046	0.161	0.713
Swim crab	2.80	0.007	2.546	0.247
Macrobrachium spp	6.85	0.661	6.128	0.061
Penaeid shrimps	5.61	-	9.572	0.561
Gastropads/Bivalves	2.50	-	1.750	0.750
Small crusteceans	7.01	-	6.309	0.701
Zooplankton	30.0	-	27.00	3.000
Phytoplankton	150	-	75.00	75.00
Discards	25.0	-	22.82	2.181

Omnivory Index (IO)

Omnivory Index values ranged from 0.00 to 0.841 trophic level 1 functional groups to Daisy stingray. Daisy stingray had the highest OI of 0.841, followed by swim crab with 0.821. Other functional groups that followed from a distant include Guinean barracuda (0.436), Macrobrachium spp (0.426), Penaeid shrimp (0.422), shark (0.390) and estuarine catfish (0.347) (Table 5). System Omnivory Index estimated by the model was 0.2564 (Table 6).

Mixed Trophic Impact (MTI)

Mixed trophic impact (MTI) of the estuary can be seen in Figure. 3. Here, the fishing gears were considered as predators since they can and do also impact on the ecosystem. The MTI matrix shows the positive direct and indirect impact of a group (in rows) on other groups (in columns) in the ecosystem. Phytoplankton, Macrobrachium spp, crab, and estuarine catfish had a higher positive impact on most groups in the ecosystem. Considering the impact of fishery predators, fishing gears such as trawlers, purse seine and gillnet had high negative effects on their target species such as bonga, Sea catfish, Guinean barracuda and largehead hairtail. Swim crab had very high negative effects on discards, as it fed most importantly on discards. Estuarine catfish had more negative impact on moon fish, mullet spp, gastropods/bivalves and croakers, among others.

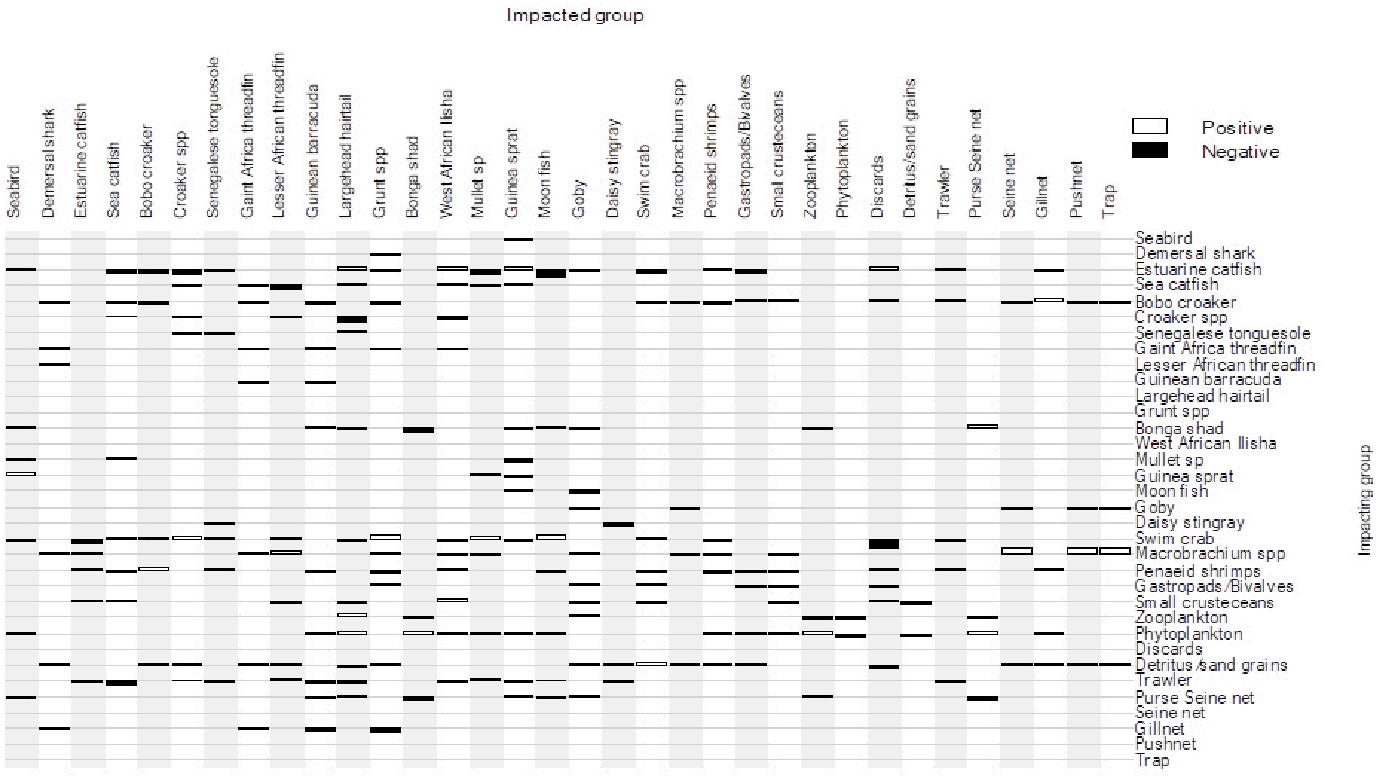

Figure 3: Mixed Trophic Impact within the Cross River estuary. The size of the bar represents the relative response; colour of bars shows the impact of each functional group on other groups in the model; black represents negative impact and grey a positive impact.

Discussion

Ecological indicators of the Cross River estuary

The Ecopath with Ecosim software has been used in various ways to show trophic flow in many ecosystems e.g. the North Sea model, the Irish Sea model and the Moray Firth, UK model [4, 71, 72]. Ecological matrix have been used as indicators of changes in ecosystem state and maturity in temporal comparison within systems. The mean trophic level of catch was 2.186 suggesting that the Cross River estuary ecosystem fishery depend predominantly on herbivores. According to Pauly et al., mean trophic level of fisheries changes with time [2]. A decline in mean trophic levels means "fishing down marine food webs" where large slow-growing predators are extirpated and replaced with small, fast-growing forage fish and invertebrates. Gross efficiency (GE) (catch/net p.p.) of 0.0566 in this study was higher than the weighted global average of 0.0002 [73]. Generally, high GE value is found in systems with fishery harvesting fish low in the food web and low values with unexploited systems or fishery being concentrated on top predators. This implies that in this estuary, shell fishes and clupeids were mostly harvested as compared to long life span fishes which are piscivorous fishes. The high value recorded also suggests a fishing down scenario on the marine food web, a shift from harvesting high trophic level fishes to harvesting lower trophic level fishes. Ecosystem biomass and system throughput are indicators of ecosystem size and development which are expected to increase as the system matures and grows.

In the early stage of ecosystem development, total primary production (Pp) is expected to exceed total respiration (R) i.e. the ratio between (Pp) and total respiration (R) is > 1. As the system matures the ratio is expected to approach unity (1) and less than one (<1) for mature ecosystems experiencing organic pollution and can be used as a maturity index of an ecosystem. The value of 4.182 revealed that the Cross River estuary system is an immature ecosystem and is at its early developmental stage [74]. The estuary ecosystem has a short food chain and low connectance index of 0.1879 which has phytoplankton that are grazed upon by zooplankton which in turn are taken up by fish. A few herbivorous fishes like bonga and West African Ilisha also graze directly on phytoplankton. Energy in the ecosystem is transferred predominantly by the classic food web. System Omnivory Index (OI) was 0.2564.37. The zero value for Omnivory Index indicates consumer specializes on single trophic level and large value indicates consumer feeds on many trophic levels. Connectance index was 0.1879. Connectance index (CI) is the measure of the percentage of realised links over possible links in a system. Both OI and CI are used to measure food complexity.

Features of the Cross River estuary

The high value of ecotrophic efficiency (EE) of 0.993 and 0.991 indicate that bonga and Macrobrachium spp are heavily exploited and predated upon in the estuary. Others are croaker spp and tonguesole with 0.990 and 0.950 EE values respectively. These values agree with the report of high exploitation of bonga by

Ama-Abasi and Macrobrachium spp by Nwosu in the Cross River system [21, 25]. According to Ama-Abasi, when comparing his work with that Moses, there was a severe decline in total catch after a 25-year period, as evidenced by declining catch rates as well as increasing mortality rates indicating that bonga fishery is under high pressure with the attendant socio-economic implications [16, 25]. Also Nwosu reported that Macrobrachium macrobrachion had high fishing mortality of 7.09/year and exploitation rate (E) of 0.74 for males with fishing mortality of 6.05/year and exploitation rate (E) of 0.66 for females [21]. The study Macrobrachium spp annual production of 99.43 tonnes of Macrobrachium spp with annual yield of 62.32 tonnes, and annual biomass of 13.6 tonnes. Others are pelagic fin-fish fishery targeting juveniles of bonga and demersal fishery targeting croaker particularly P. elongatus. The high EE values in this study agree with these assertions of high fishing pressures with the socio-economic implications and management issues.

Trophic levels and food web analysis

The study revealed three apical predators in the estuary. They included sharks (4.40), Senegalese tonguesole (3.87) and Sea catfish (3.84), with estuarine catfish of 3.57 close to it. This study agrees with the report of Asuquo who identified S. tonguesole and C. nigrodigitatus as apical predators in the Cross River estuary ecosystem [23]. Additionally, the study revealed sharks as apical predator. However, sea birds was not identified as apical predator like in most models of the marine environment. This is likely due to poor data collected on sea birds of the estuary as most of the basic data were lifted from nearby estuaries to construct the model. This further underlines the fact that there exist a wide gap on basic data on species in the estuary. This implies that heavy fishing on these top predators could lead to changes in species composition with small, fast-growing species dominating the system [75].

Mixed Trophic Impact (MTI)

It is obvious that fishing should impact on the ecosystem through removing of biomass from the ecosystem and the cascade of biomass of species feeding on each other through the food web [76]. The approach of Mixed Trophic Impact (MTI) can be used to assess whether changes in biomass of one group can affect the biomass of other groups in the ecosystem [70]. Fishing gears were considered as predators as they can also impact on the ecosystem. The MTI matrix shows the positive direct and indirect impact of a group (in rows) on other groups (in column) in the ecosystem. Phytoplankton, Macrobrachium spp, crabs, and estuarine catfish had a higher positive impact on most groups in the ecosystem. Considering the impact of fishery predators, fishing gears such as trawlers, purse seine and gillnet had a high negative effects on their target species such as bonga, Sea catfish, Guinean barracuda and largehead hairtail. Swim crabs had a very high negative effects on discards, as it fed most importantly on discards. Estuarine catfish had more negative impact on moon fish, mullet spp, and croaker spp. This assertion agrees with two majors concerns raised by trophic interactions for fisheries management. The first concern is the direct effect through the decline in the food resource of important fish stocks causing their damage. Second, the indirect effect of decreasing fish biomass on ecosystem functioning such as trophic cascading [4].

Conclusion

This study is the first trophic model using Ecopath with Ecosim (EwE) for the Cross River estuary ecosystem and forms a basis for further ecological studies on the estuary. The study showed a wide gap in fish biology and ecosystem properties in the Cross River estuary such as catch rates, landings, growth and population parameters of important fish species as well as times series data and split functional groups (due to ontogeneric variation) for model simulation and validation using Ecosim component of the model. Results of ecopath model study showed that the Cross River estuary is still relatively pristine and immature ecosystem void of organic pollution and with relatively low primary productivity as evident in low nutrient concentration throughout the period of study [77-79].

Recommendations

Though data on the diet for most functional groups can be taken from nearby ecosystems and previous models or from the Fish base website (www.fishbase.org), it is apparent that the diet composition can vary according to geographical area or habitat type, thereby differing from one ecosystem to another. In order to build better models in the future and improve on the present one, there is need to vigorously pursue the study of fish diet in the Cross River estuary ecosystem, by examining thousands of fish stomach of different species to attain comprehensive data on their diet. There should be shift from quality study on diet to quantitative study as most of the present studies on diet composition are qualitative studies not relevant to ecological studies. Apart from inadequate data on diet composition for fish species in the estuary, the present study has identified wide gaps in other scientific information. These include catch rates, landings, growth and population parameters of economically important fish species in the estuary among others. Times series of data and split functional groups (due to ontogeneric variation) are required for model simulation and validation using Ecosim component of the model. It is therefore recommended that the government and fishery scientists collect and properly document fish landings. Further studies on diet composition should be split into juveniles and adult groups as a requirement for Ecosim validation.

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