Assessing the trophic structure and functioning of a large tropical lagoon. Case study: Keta Lagoon, Ghana

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Abstract

A model of trophic interactions in the Keta Lagoon was developed to assess the current state and the energy flow within the food web structure of the system components using an ECOPATH with ECOSIM modelling approach. Seventeen (17) functional groups were identified for the Keta Lagoon model construction. Ecosystem health and maturity parameters were derived using the ecological network analysis. The functional groups identified in the food web were of varied trophic levels ranging from primary producers (trophic level (TL) = 1) to top predators (TL = 3.216). Most fish groups had higher eco-trophic efficiencies (EE > 0.9), indicating their high utilisation within the system. The total system throughput was estimated at 10,287.920 t/km^2/year, with the system depending on the consumption of primary producers. The mean trophic level of the catch (2.762) indicated that the fisheries target fish groups with higher trophic levels. Ecological indices such as the net system production (1,480.452 t/km^2/year), total primary production/total biomass (7.207), total biomass/total system throughput (0.054 t/km^2/year), Finn's cycling index (4.933%), system omnivory index (0.155), ascendency (26.29%) and system overhead (73.71%) indicated that the ecosystem is in its developing stage and prone to environmental disturbance hence, the need for management. The mixed trophic impact routine indicated that the lower trophic level groups positively impacted most of the higher trophic level groups. Also, predatory birds and macro-invertebrates were the most influential functional groups structuring the lagoon. Management strategies that could be implemented include habitat protection, stock enhancement, alternative livelihoods (aquaculture), closed seasons, and enforcement of fisheries regulations.

Keywords: ECOPATH model, ecological indicators, eco-trophic efficiency, fisheries management, food web structure, Keta Lagoon, transfer efficiency, trophic levels

Introduction

Coastal lagoons are shallow brackish water bodies separated from the ocean by a barrier formed by an island, spit, reef, or sandbank and connected to the open sea by one or more narrow channels (Barnes, 1980). Lagoons appear to be generally under marine influences but may be enclosed either partially or wholly depending on the land barrier area that obstructs water exchange between the basin and the ocean (Kjerfve, 1986, 1994; Gonenç and Wolflin, 2005). Due to the shallowness of lagoons, the photic zone receives enough sunlight, which extends to the lagoon floor. These ecosystems usually receive substantial amounts of nutrients from the surrounding catchments, boosting primary and secondary production, which flows to higher trophic levels (Viaroli et al., 1996; Kennish, 2016). According to Anthony et al. (2009), coastal lagoons are favourable habitats for primary producers because of their relatively low flushing rates, with an estimated annual mean primary production rate ranging from around 50 to more than 500 g C/m^2/year. Kennish (2016) stated that increased growth of benthic algae and seagrasses often occurs in lagoons when sunlight penetrates the lagoon floor. Therefore, benthic primary production can exceed phytoplankton production in some lagoons. Coastal lagoons ensure the recycling of nutrients many times before leaving the lagoon system. Nutrient recycling makes lagoonal systems susceptible to nutrient enrichment and sensitive to the accumulation of pollutants, increasing eutrophication rates (Kennish, 1998; Paerl et al., 2006). Nevertheless, the high productivity rates explain why these systems serve as good fisheries nurseries (Kennish and Paerl, 2010).

Coastal lagoons shelter an essential part of global biodiversity, provide a great variety of goods and services for humans, and contribute significantly to coastal fisheries sustenance (Pérez-Ruzafa et al., 2019). They provide essential services such as habitat for aquatic plants and animals, birds, recreational, flood control, salt mining, and traditional or cultural purposes (Ajonina et al., 2014). These habitats of lagoons allow for the practice of traditional and artisanal fisheries that contribute significantly to the economic and dietary needs of the people living within and around lagoonal communities and their countries at large (Addo et al., 2014; Bjork et al., 2008). Lagoons form nursery grounds and adult feeding areas for many commercially important fish species and crustaceans that migrate between this habitat and the sea. Most of these species spawn outside the lagoons and spend at least a portion of their life cycles in lagoonal and adjoining coastal wetland habitats (Barnes, 1980).

Fish and fisheries are essential in most countries and contribute to their economic and general well-being (FAO, 2002; FAO, 2003). However, many fish populations are over-exploited globally with the decline in stocks and the degradation of the ecosystems that sustain them (FAO, 2002; FAO, 2020). Inland capture fisheries contribute significantly to the global annual fish yield and consumption, with an estimated production rate of 12 million tonnes of fish in 2018 (FAO, 2020). Coastal lagoons and wetlands are valuable and sensitive inland systems, and their essential role has been recognised internationally within the framework of the Convention on Wetlands (Ramsar, 1971). Despite the significance of these systems, local communities have always exploited lagoons to harvest fish, crustaceans and molluscs, among others (FAO, 2015). Available landing data rarely reflect the actual yield of lagoon fisheries globally. However, Pérez-Ruzafa and Marcos (2012) provided an estimated total annual catch of coastal lagoon fisheries to be about 694,195.9 tonnes/year globally, with mean productivity of 137.4 (± 21.6 SE) kg/ha/year for about 356 lagoons studied, indicating the high fishery productivity of these systems.

Recently, coastal lagoons have experienced a general decrease in fish yield, mainly due to environmental degradation, overfishing, and the lack of appropriate lagoon management plans (FAO, 2015). To curb the issue of overexploitation and ecosystem degradation, ecosystem-based fisheries management (EBFM) has been proposed as a holistic approach to managing fisheries (Link and Browman, 2017). Its main objective is to sustain marine ecosystems and manage the fisheries they support by limiting their impact on the ecosystem to a minimum extent; a similar approach is considered for inland fisheries management (FAO, 2003; Pikitch et al., 2014). According to Han et al. (2016), understanding the condition of ecosystems and the trophic interactions between each functional group is necessary to analyse the impact of organisms and human activities on the system to develop management schemes. There are different approaches for assessing ecosystem health, and one is ecological modelling. ECOPATH, which uses ecological network analysis, is one of the tools for modelling the ecosystem features and characterises the transfer of energy within different components of an ecosystem (Christensen and Pauly 1993; Christensen et al. 2005).

The Keta Lagoon fisheries are essential both ecologically and economically. Being the largest lagoon in Ghana, it contributes immensely to the indigenous people's nutritional needs and overall livelihood. In addition, the lagoon and its surrounding ecosystems serve as a habitat for different species of fin and shell fishes and invertebrates. It also serves as a roosting, nursery and feeding ground for migratory waterbird species. The diversity in species composition makes this system one of Ghana's most productive brackish water ecosystems. However, the most dominant groups of fish species in the lagoon have been reported to be on the decline with some species rarely found in recent times (Dankwa, 2004; Addo et al., 2014). Although several independent studies have been conducted on the individual components of the lagoon ecosystem, a holistic ecosystem-based assessment including all ecological compartments and trophic interactions has not been carried out for the Keta Lagoon.

According to Abobi, Kluger, and Wolff (2021), the EwE software has already been used to assess fisheries and inform management of African and Asian lakes, lagoons and reservoirs: Reservoir Bagré (Villanueva, Ouedraogo, & Moreau, 2006), Lake Ayamé (Traore et al., 2008) and Lake Koka (Tesfaye & Wolff, 2018) in Africa as well as Parakrama Samudra, Sri Lanka (Moreau, Villanueva, Amarasinghe, & Schiemer, 2000) and Ubolratana reservoir, Thailand (Villanueva, Moreau, Amarasinghe, & Schiemer, 2008), and Wyra reservoir, India (Panikkar & Khan, 2008). In Ghana, the Ecopath modelling approach has been used to assess Tono, Bontanga and Golinga reservoirs (Abobi et al., 2021), Lake Volta (Mensah et al., 2019) and Sakumo Lagoon (Pauly, 2002).

Therefore, the study was undertaken to describe the lagoon's status; to provide information on the trophic interactions among functional groups in the Keta Lagoon and to contribute to the search for sustainable management regimes for the lagoon fisheries.

Material and method

Study area

Keta Lagoon (Fig. 1) is located in the Keta municipality of Ghana and along the delta of the Volta River in south-eastern Ghana. The lagoon is estimated to have a surface area of 300 km^2 which varies with the season. It has an average depth of 0.8 m (maximum 2 m) and coordinates 5°55′ N 0°59′ E (Sorensen et al., 2003; Addo et al., 2014). The lagoon and its surrounding ecotones cover an estimated area of 530 km^2 and stretch for 40 km along the coast. It is detached from the sea by a narrow ridge of 2.5 km in width and 0.92 km at the most limited portion (GCWMP, 1999). The lagoon is connected to the open sea at Anyanui through a tributary of the Volta Lake on the west, to the south and east by the Gulf of Guinea and on the north by the highway linking Accra to Aflao (GCWMP, 1999; Sorensen et al., 2003). Rivers Tordzie and Belikpa are also considered significant streams that flow into the lagoon (Armah et al., 1997). Keta lies within the dry Equatorial region of Ghana, covering the entire south-eastern coastal belt of the country and is one of the driest areas in the country. The wind

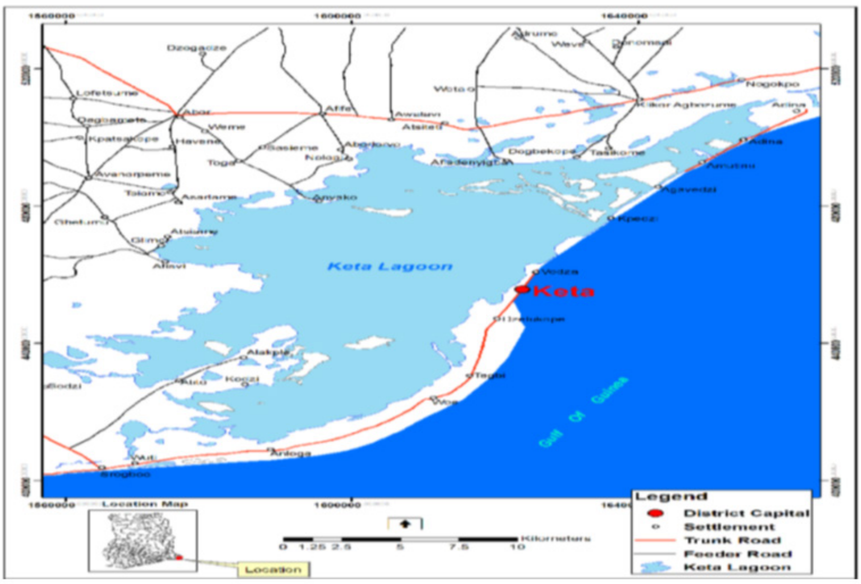

Figure 1 Map of Ghana showing the Keta Lagoon within the Keta Municipality (Lamptey et al., 2014b)

direction of the area is from the southwest (the southwest monsoons) (Tumbulto, 1997; GCWMP, 1999). This region experiences two rainy seasons: March/April to July and September-October, with a mean maximum annual rainfall ranging between 740 mm and 910 mm (Tumbulto, 1997). The mean water surface temperature is 24°C and the maximum temperature of about 31°C (Tumbulto, 1997; Addo et al., 2014).

The population of the area as of 2021 was 182,409. The males were 89,703 representing 49.2% while the females were 92,706 representing 50.8%. (from the Ghana Statistical Service source, Keta Municipal Assembly, 2024). The surrounding floodplain consists of a marsh, scrub, farmlands, and substantial mangrove stands heavily exploited for fuelwood (Ofori-Danson et al., 1999). In 1999, the Keta lagoon was classified as a Ramsar site of ecological importance (Ofori-Danson et al., 1999). The lagoon is essential to its fringing communities, including Anloga Woe, Keta, Kedzi, Anyako, Alakple, Atiavi, and Fiahor (Ababio, 2001). This region is known mainly for its agriculture, fisheries, and aquaculture among other occupations in the area (Ofori-Danson, Entsua-Mensah & Biney, 1999; Finlayson et al., 2000; Lamptey and Ofori-Danson, 2014a).

Modelling approach

For the Keta Lagoon food web construction, the ECOPATH approach of the ECOPATH with ECOSIM (EwE) software Version 6.6.5 (Christensen et al., 2008) was used to evaluate the trophic interaction and food web structure of the Keta Lagoon. For this study, the biological components of the ecosystem were categorised into functional groups based on their typical habitat, the similarity in food composition, and biological characteristics (Yodzis and Winemiller, 1999). The model consists of four input parameters, and these are the mean annual biomasses (*B*), production per biomass ratios (*P/B*), consumption per biomass ratios (*Q/B*), and ecotrophic efficiency (*EE*). For parameterisation, three (3) of the basic parameters are required for each functional group, and the model estimates the fourth (Christensen et al., 2008; Filho et al., 2019). For the model period under consideration, an equilibrium condition where group inputs are balanced to their outputs is typically assumed. The input data are standardised, and the units (wet weights) are expressed as t km^{-2}. The model compartments were connected through a diet matrix of predator-prey linkages. Consequently, each organism's diet was included as input data. Likewise, fish catches from which the biomass was estimated were included in the Keta Lagoon ECOPATH model.

ECOPATH, which is the mass-balance part of EwE, has its master equations as follow:

$$B_i * \left(\frac{P}{B}\right)_i * EE_i = \sum\left(B_j * \left(\frac{Q}{B}\right)_j * DC_{ji}\right) + EX_i + E_i + BA_i \quad (1)$$

Where: B_i is the biomass of functional group i (t/km^2), P/B_i is the annual production to biomass ratio of i and is equivalent to total mortality (Z) in closed systems (Allen 1971; Filho et al., 2019), EE_i is the eco-trophic efficiency which is the amount of the ecological production that flows to a higher trophic level through predation or fishing (Ricker, 1969), B_j is the biomass of a predator group j of the prey group i; Q/B_j is the ration of annual food consumption rate of predator j to the annual biomass of predator j; DC_{ji} is the portion of the group i found in the diet of group j; EX_i is the export or catch of i (gm^{-2} yr^{-1}), E_i is the net migration while BA_i is the biomass accumulation of i (Christensen et al., 2008).

The second equation maintains energy balance for each group as:

$$Q_i = P_i + R_i + GS_iQ_i \quad (2)$$

Where: Qi is the consumption of group i, Pi is the sum of production of group i, Ri is the respiration of group i, and (GSi×Qi) is the unassimilated food of group i.

Input parameters

Functional groups

For the mass balance construction of the Keta lagoon, 17 functional groups were considered ranging from primary producers to top predators (Table 1 and Appendix Table 1).

Biomass

Primary producers

Phytoplankton biomass was estimated from the measurement of chlorophyll-a concentration (Brewin et al., 2019; Maslukah et al., 2021) with a mean chlorophyll-a value of 10.98 µgl^{-1} (10.98 mg/m^3) estimated from Finlayson et al. (2000) for the lagoon. The chlorophyll-a concentration was multiplied by the lagoon's euphotic depth (Z_{eu}) to obtain the water column value per area (/m^2); thus, $Z_{eu} = m * Z_{SD}$, where; m is the conversion coefficient, and Z_{SD} is the Secchi depth (Holmes, 1970; Koenings and Edmundson, 1991). Z_{SD} had a mean value of 40cm ≈ 0.4m (Finlayson et al., 2000). A factor of 3 was suggested by Holmes (1970) to be an appropriate standard coefficient in turbid waters. Hence, a conversion coefficient of 3.5 was applied to estimate the value for Z_{eu} = 1.4m, then multiplied by the lagoon's chlorophyll-a concentration of 10.98 µg/l to obtain the water column value of 15.4 mg/m2. The chlorophyll-a value was converted into carbon using the factor of 1:40 –Chlorophyll-a: Carbon (Brush et al., 2002) and then to weight using the conversion factor of 1:14.25-Carbon: wet weight (Brown et al., 1991). The estimated biomass of phytoplankton of the system was 8.788 g WW/m^2.

Biomass for dominant aquatic macrophytes was also estimated from Finlayson et al. (2000). They reported a cumulative macrophytes biomass for Keta and Songhor Lagoons, with a total mean biomass of the dominant species calculated as 776.8 g/m^2. According to their research, macrophyte species at Keta Lagoon were more diverse and abundant than those found at Songhor Lagoon. Hence, 60% of the total mean biomass was assumed to represent the total macrophyte biomass of Keta Lagoon.

Fish species

Fish species for ECOPATH modelling were selected based on their abundance, available data on the catch in the ecosystem and their commercial importance. Nunoo et al. (2014) assumed an estimated value of 11.4 t/ km^2/year as the annual fish yield for the Keta lagoon.

Waterbirds

Predatory waterbird (piscivorous waterbirds) biomass was estimated by multiplying the average wet weight (g) of an adult of a given species by the total bird counts reported by Lamptey and Ofori-Danson (2014b) from the Keta Lagoon. The average wet weights of bird species were taken from a study of the Keta Lagoon and other literature sources (Appendix Table 2). The body mass of the waterbirds was then converted to tonnes. An area of 75km^2, representing 25% of the lagoon's surface area, was estimated to calculate the waterbirds' biomass.

Macroinvertebrates

Macroinvertebrate biomass was obtained from Finlayson et al. (2000). The mean value of the ash-free mass of the most dominant invertebrate species was multiplied by each species' total number in the lagoon to obtain the biomass in mg/m^2, converted to g/m^2.

Detritus

Detritus biomass was estimated following the relationship proposed by Christensen and Pauly (1993),

$$\mathrm{Log}D = 0.954\log PP + 0.863\log E - 2.41 \quad (3)$$

Where; D is the standing stock of detritus, in g.C/m^2, E is the euphotic depth, and PP is the primary production in g.C/m^2/year. A mean value of 0.65 g.C/m^2/d primary production was obtained from a lake in Ivory Coast (Ouattara et al., 2007). The daily PP was estimated to annual PP of 237.2 g.C/m^2/yr and was inserted into the equation with 1.4m euphotic depth estimated by Finlayson et al. (2000) to obtain the value of the standing stock of detritus. The resulting value was converted into wet weight using the assumption of Christensen and Pauly (1993) that one g.C is equal to10 g fresh weight, resulting in the detritus biomass of 9.593 g/m2/year.

Zooplankton

Finlayson et al. (2000) identified Ostracods, Copepods, and Amphipods as the three major zooplankton groups in the Keta Lagoon and provided information on their counts per 50 litres. For the estimation of zooplankton biomass in the system, the mean weights of each species (in mg) (Masundire, 1994; Nalepa et al., 2000; Kaeriyama and Ikeda, 2004) were multiplied by the number of counts of individual species per litre. The value obtained in mg/l was converted to mg/m3, multiplied by the lagoon's mean depth (m), and finally converted to g/m2 for the zooplankton biomass estimation of $3 g/m^2$.

Production/biomass (P/B)

According to Allen (1971), the total mortality (*Z*) of fish groups is equivalent to the production over biomass (*P/B*) ratio of fish groups under the condition assumed for the construction of mass-balance models. Therefore, total mortality rates used in this study as estimates for the *P/B* ratio. The total mortality rates of *Sarotherodon melanotheron*, *Coptodon guineensis*, and *Hemichromis fasciatus* were obtained from a fish stock assessment study on the Keta lagoon by Ababio (2001). In contrast, P/B values for the remaining fish and non-fish groups were taken from fish stock assessment studies or other models with similar ecosystems (Appendix Table 1).

Consumption/Biomass (Q/B)

Consumption is the utilisation of food by a functional group within the system over a certain period (Christensen et al., 2008). It is entered in the EwE model as the consumption per biomass ratio (*Q/B*). The consumption per biomass ratio (*Q/B*) is often estimated using the multiple regression formula (Palomares and Pauly, 1998):

$$Log\left(\frac{Q}{B}\right) = 5.847 + 0.280 Log\left(\frac{P}{B}\right) - 0.152 Log W\infty - 1.360T + 0.062A + 0.510h + 0.390d \quad (4)$$

Where: $W\infty$ = asymptotic weight; T = mean temperature, A = aspect ratio, h and d are about the diet (h = 1, d = 0 for herbivorous fishes; h = 0, d = 1 for detritivorous fishes; h = 0, d = 0 for carnivorous fishes).

Consumption rates of *Pellonula leonensis* and *Coptodon guineensis* were calculated from Fishbase (Froese and Pauly, 2021) with known $W\infty$ and temperature values (Addo et al., 2014; Lamptey and Ofori-Danson, 2014a). Caudal fin shape and feeding habits were also considered to estimate the fish aspect ratio for *Q/B* estimation in Fishbase. *Q/B* for other groups were taken from other models with similar characteristics (Pauly, 2002; Villanueva et al., 2006; Traore et al., 2008; Abobi et al., 2019).

Diet

Diet composition for all fish species was obtained from the information provided in Fishbase (Froese and Pauly, 2021), other models with similar characteristics in Ghana, Nigeria, Senegal and Ivory Coast (Pauly 2002; Villanueva et al., 2006; Traore et al., 2008; Abobi et al., 2019), and other diet composition studies in Ghana, Ivory Coast, and Nigeria. Similarly, diet for non-fish groups was obtained from other models of similar characteristics and general information on the species' diet (Appendix Table 3).

Balancing the model

After entering all the primary input data into the ECOPATH model, it is essential to analyse the outputs to ensure all values are realistic. Firstly, the ecotrophic efficiency (*EE*) was checked to ensure values were ≤ 1.0 for all compartments as values > 1.0 are inconsistent (indicating more of the organism's biomass is consumed than is produced) (Christensen et al., 2005). The production per consumption ratio (*P/Q*) of the model, the compartment was also checked to ensure the values were between the standard range of 0.1 and 0.3 (Christensen and Pauly, 1993; Christensen et al., 2008). The diet composition was analysed, as the diet for each group must sum up to 1 and could introduce inconsistencies if more or less than 1.

The initial input data resulted in an unbalanced model, with some *EE* values >1. Manual adjustments were performed according to the level of uncertainty to achieve mass balance following some principles proposed by Link (2010) and some other ecosystem models (Wolff et al., 2000; Villanueva, 2006; Traore et al., 2008; Abobi et al., 2019).

Pedigree index and categorisation of data sources

According to Christensen et al. (2008), the pedigree of an Ecopath input parameter is a coded statement classifying the source of input data using a pre-defined table for each input parameter and quantifying the uncertainty surrounding the values. This index ranges from 0 to 1 for low-and high-quality models, respectively, providing an index of the model's quality. The maximum values indicate that the model relies mostly on primary data obtained from the study area. Hence, the pedigree routine was used to quantify and assess the quality of input values in the Keta Lagoon model.

Results

The food web model and structural analyses

The balanced estimates from each group's input parameters are presented in Table 1. The 17 functional groups included in the Keta Lagoon model were classified by ECOPATH into three (3) trophic levels (TLs) and ranged from 1.0 for primary producers and detritus groups to 3.216 for the top predator (predatory waterbirds). The mean trophic level of the catch (MTLc) was estimated at 2.763. The functional groups with the highest flows to detritus were those within the lower TLs (1.00-2.00). Aquatic macrophytes had the highest flow to detritus, followed by phytoplankton, and the least was *Ethmalosa fimbriata* (Table 1). The Respiration/Assimilation (R/A) and Production/Respiration (P/R) ratios were relatively low and ranged from 0.643 to 0.995 and 0.004 to 0.504. The species with the highest R/A value was the top predator (piscivorous waterbirds). The Omnivory index (OI) showed that most species are diversified in their food consumption and obtain energy from different TLs. These values ranged from 0.010 (zooplankton and *Hemichromis bimaculatus*) to 0.483 (*Callinectes amnicola*). The OI values reflect the system's omnivory index (SOI) of 0.155 and indicate a certain level of specialisation in the consumer's diet and could be due to environmental factors making prey scarce for predators.

The total biomass (excluding detritus)

TABLE 1

Basic input and model estimated output (bold) of the Keta Lagoon

Functional groups	TL	B	P/B	Q/B	EE	P/Q	FD	OI
Piscivorous waterbirds	**3.216**	0.096	0.350	65.000	0.000	0.006	12.430	0.247
Hemichromis fasciatus	**3.176**	1.756	5.040	18.900	0.648	0.267	10.840	0.239
Hemichromis bimaculatus	**3.010**	0.136	4.140	15.456	0.997	0.268	0.505	0.010
Coptodon guineensis	**2.117**	3.100	4.510	35.000	0.953	0.155	24.170	0.105
Sarotherodon melanotheron	**2.071**	3.282	4.000	32.803	0.977	0.129	26.990	0.067
Pellonula leonensis	**3.088**	7.364	4.030	25.900	0.976	0.156	38.850	0.075
Ethmalosa fimbriata	**2.662**	0.136	2.300	16.000	0.969	0.219	0.450	0.231
Strongylura senegalensis	**3.122**	0.124	1.050	20.230	0.534	0.052	0.934	0.061
Hyporhamphus picarti	**2.534**	4.082	3.500	28.377	0.965	0.123	23.670	0.258
Porogobius schlegelii	**3.214**	0.004	3.440	18.600	0.956	0.185	0.016	0.298
Eucinostomus melanopterus	**3.030**	0.934	2.920	26.910	0.711	0.109	5.816	0.345
Callinectes amnicola	**3.096**	2.942	2.000	10.000	0.946	0.250	6.278	0.483
Macro-invertebrates	**2.020**	49.150	5.000	50.000	0.851	0.100	529.300	0.020
Zooplankton	**2.010**	4.500	35.000	140.000	0.995	0.286	127.000	0.010
Aquatic Macrophytes	**1.000**	466.1	5.000		0.492		827.000	
Phytoplankton	**1.000**	8.778	270.000		0.646		838.500	
Detritus	**1.000**	9.593			0.404			0.321

TABLE 2
Distribution of catch and biomass among the various trophic levels of Keta Lagoon

TL	Catch		Biomass	
	t/km^2	%	t/km^2	%
I	0	0	484.5	85.7
II	3.3	28.5	63.2	11.3
III	7.5	65.6	15.1	2.7
IV	0.6	5.6	2.7	0.2
V	0.03	0.3	0.2	0.01

supported by the ecosystem was estimated at 555.188 t/km^2. Primary producers occupying TLI had the largest biomass in the ecosystem, with macrophytes as the main contributor to the biomass (Table 2). Fish biomass and catch of the system were higher at TL III.

The trophic aggregation routine in ECOPATH combined the 17 groups from the Keta Lagoon in a simple food chain (flow diagram) with three trophic levels (Fig. 2). It was observed that most fish groups consumed species of the lower trophic levels TLs I and II (primary producers, detritus, zooplankton, and macroinvertebrates) and were evident in the flows from primary producers to the predators (as well as the combined flows).

Trophic flows

Trophic flows were represented in the Lindeman spine flow diagram, a detritus-based food chain with five discrete TLs (I to V), showing the system's energy transfer rate. The Lindeman spine (Fig. 3) showed the significance of the trophic levels to the entire system's biomass. It was also observed that the TL I had the highest biomass, while the biomass of the functional groups declined as the trophic level increased with fish biomass (12.11 t/km^2) concentrated at TLIII. TLI had the highest flows through the system (63.39%). Hence, their importance in transferring energy to the higher TLs. TL II also contributed immensely (32.67%) to the flow of energy into the system. The most efficient trophic transfer from the flow diagram was from TL II to TL III (TE= 11.2%). The system's mean TE was 9.6% and indicates that each TL contributes about 9.6% of its production to the next TL production.

Mixed trophic impacts (MTI) and keystoneness

In this study, the MTI routine indicated both positive and negative effects on functional groups of the ecosystem. Piscivorous

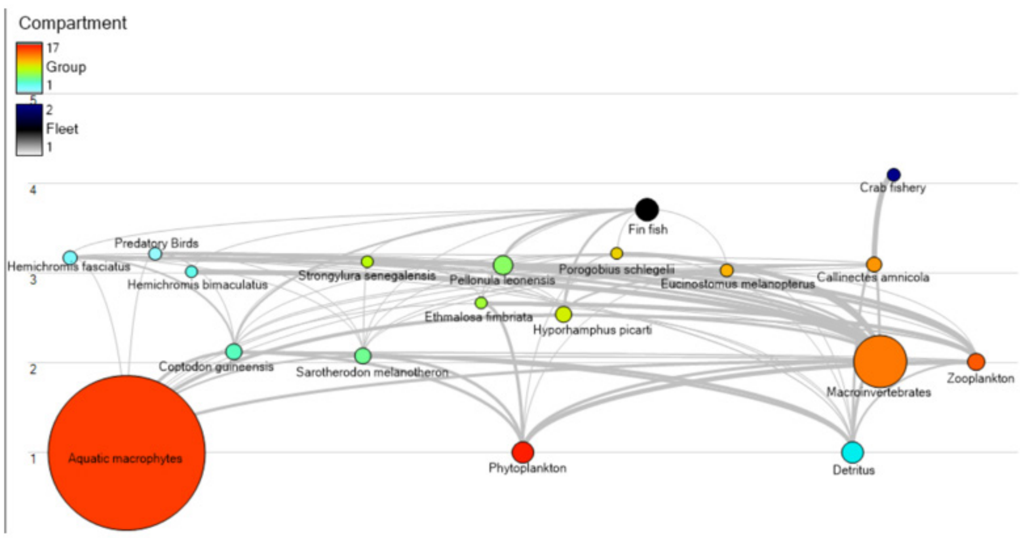

Figure 2 ECOPATH flow diagram and food web of the Keta Lagoon ecosystem model

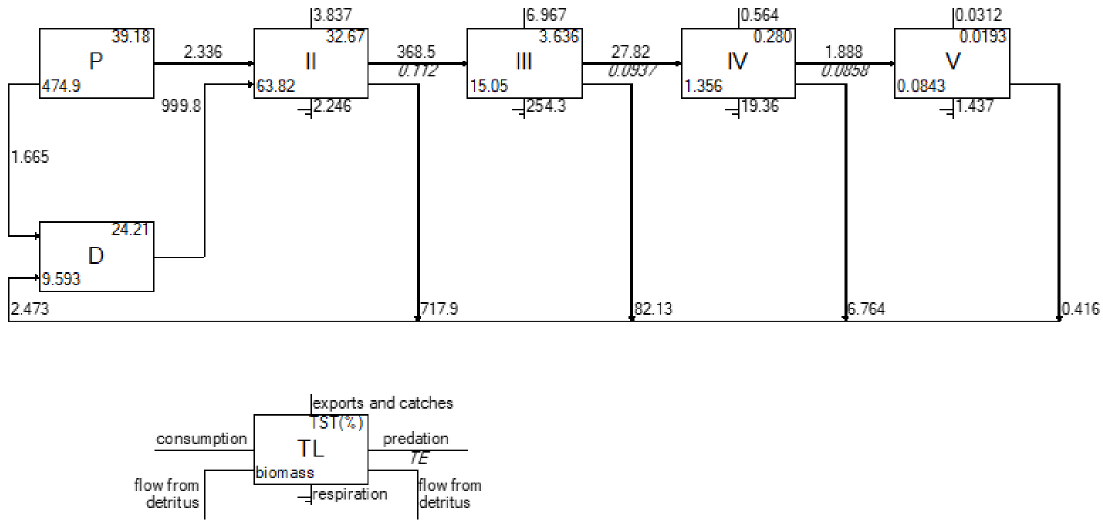

Figure 3 Trophic flows of the Keta Lagoon model are aggregated by integer trophic levels (TL) in the Lindeman spine. TL I is separated into primary producers (P) and detritus (D). Flows are represented in t/km^2/year

waterbirds had the most negative impact on *Hemichromis bimaculatus* and *Callinectes amnicola*. It also affected *Coptodon guineensis* and *Sarotherodon melanotheron* negatively. Macroinvertebrates negatively impacted the lower TLs groups and some fish species (*Coptodon guineensis* and *Sarotherodon melanotheron*) while positively impacting *Hemichromis bimaculatus*, *Porogobius schlegelii* and *Eucinostomus melanopterus*. *Callinectes amnicola* also negatively impacted *Hemichromis fasciatus*, *Eucinostomus melanopterus*, and *Hyporhamphus picarti* while positively impacting *Strongylura senegalensis*. Generally, most functional groups negatively impacted themselves. Also, it is expected that an increase in the main preys' biomass would positively impact their main predators. The MTI analysis (Fig.4) showed the impact of the two fisheries mainly finfish and crab fisheries on the ecosystem. The finfishes had the most significant negative effect on *Strongylura senegalensis* and *Eucinostomus melanopterus*. Conversely, it had a positive impact on *Ethmalosa fimbriata*. While crab fishery had its most substantial adverse impact on *Callinectes amnicola*, being the only crab species included in the model. Piscivorous waterbirds, macroinvertebrates, *Strongylura senegalensis*, phytoplankton,

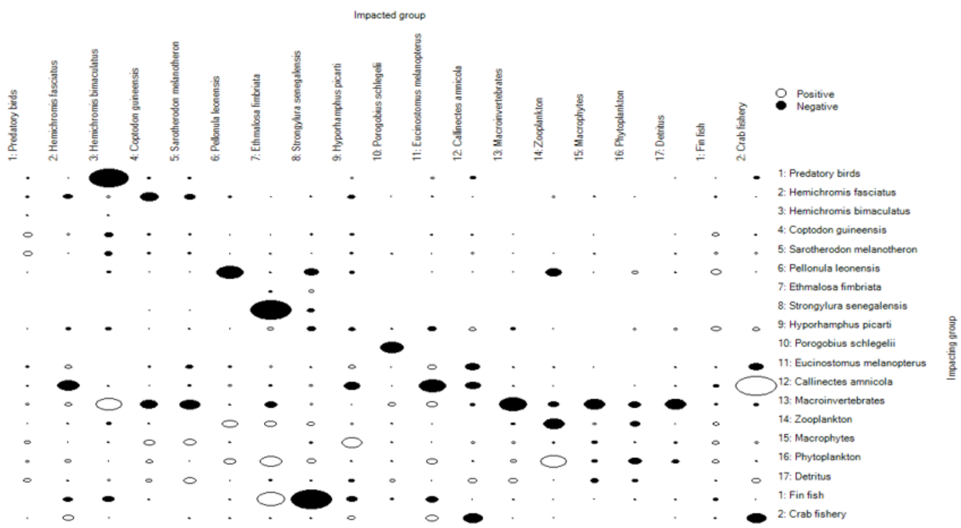

Figure 4 Mixed Trophic Impact (MTI) analysis indicating the impacting and impacted groups of the system. Negative (black) and positive (white) impacts are represented for all functional groups

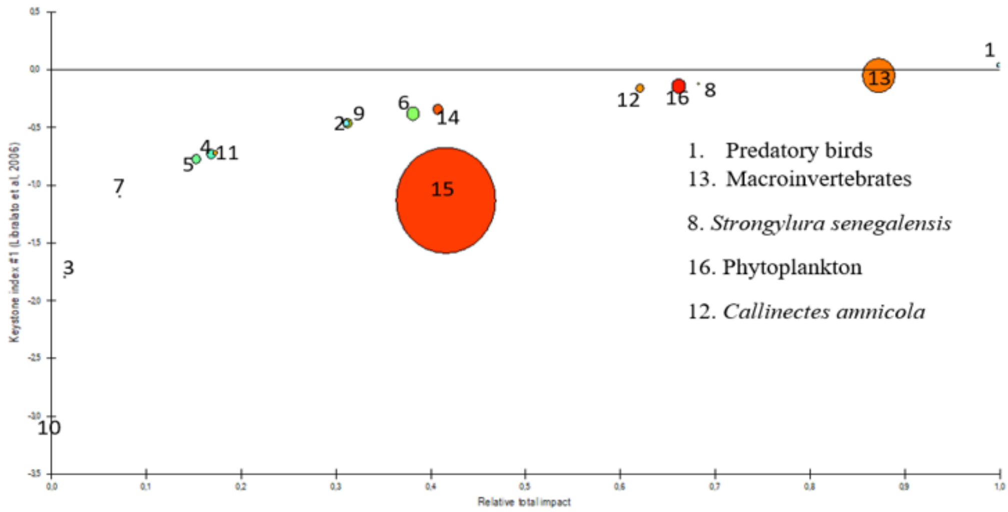

Figure 5 Keystone Index (KSI) analysis of the Keta Lagoon food web (Librarato et al., 2006). The circles are equivalent to their respective biomass

and *Callinectes amnicola* were identified as keystone species of the system (Libralato et al., 2006) (Fig. 5). This heterogeneity in terms of trophic levels indicates a mixed control of biological interactions by top-down approach (piscivorous waterbirds, *Strongylura senegalensis*, and *Callinectes amnicola*) and bottom-up (phytoplankton and macroinvertebrates) mechanisms in the food web (Libralato et al., 2006). The KSI by Libralato et al. (2006) accounts for the relative total impact; hence it was considered for this study.

Ecological indicators and network analyses

Summary statistics and ecological network indices of the Keta lagoon

Fishing impact

The total fish catch of the system was 11.40 t/km^2 (Table 3), with a mean trophic level of the catch at 2.76. The MTLc was within the range

TABLE 3

Ecosystem Indicators of Keta Lagoon ECOPATH model

Network indices	Value	Unit
Sum of all consumption	3,810.038	t/km^2/year
Sum of all exports	1,484.262	t/km^2/year
Sum of all respiratory flows	2,520.958	t/km^2/year
Sum of all flows into detritus	2,472.659	t/km^2/year
Total system throughput	10,287.92	t/km^2/year
Sum of all production	4,528.482	t/km^2/year
Mean trophic level of the catch	2.762	
Gross efficiency (catch/net p.p.)	0.003	
Calculated total net primary production	4,001.410	t/km^2/year
Total primary production/total respiration	1.587	
Net system production	1,480.452	t/km^2/year
Total primary production/total biomass	7.207	
Total biomass/total throughput	0.054	t/km^2/year
Total biomass (excluding detritus)	555.188	t/km^2
Total catch	11.400	t/km^2/year
Connectance Index	0.329	
System Omnivory Index	0.155	
ECOPATH pedigree	0.521	

TABLE 3 *cont.*
Ecosystem Indicators of Keta Lagoon ECOPATH model

Network indices	Value	Unit
Total transfer efficiency	9.646	%
Finn's cycling index (FCI, of total throughput)	4.93	%
Ascendency (A)	26.29	%
Overhead (O)	73.71	%
Capacity (C)	41301	Flowbits
Average Path Length	2.57	
D:H	0.723	

of *Ethmalosa fimbriata* and *Hyporhamphus picarti*. *Pellonula leonensis* was the highest caught fish species from the catch data, while *Porogobius schlegelii* was the least caught species. From the model, *Strongylura senegalensis* showed a high rate of exploitation (F/Z) (0.476), while other species showed low exploitation rates ranging between 0.089 to 0.200. Most fish groups had high EE values (> 0.9) except for a few species (*Hemichromis fasciatus*, *Strongylura senegalensis* and *Eucinostomus melanopterus*) that had lower EE values indicating a high predation or fishing rate of those species.

The primary production required to sustain the Keta lagoon fisheries (PPR%) considering all TLI groups (detritus and primary producers) was 8.366%. A significant percentage of the PPR was to support the production of *Strongylura senegalensis*, *Callinectes amnicola*, *Pellonula leonensis* and *Eucinostomus melanopterus*.

Discussion

Lagoonal food webs are more complex than fresh and marine water ecosystems, mainly due to the fluctuation of marine and freshwater emigrants and the accompanying changes in the entire ecosystem (Amara et al., 2000; Sreekanth et al., 2016). Mass-balance modelling using ECOPATH provides an in-depth understanding of the overall development, stability, and energy transfer in an ecosystem (Lal et al., 2021). The total estimated biomass of the Keta lagoon fishery (22.4 t/km^2) is similar to and within the ranges reported in other tropical inland waters (Villanueva et al., 2005; 2006; Traore et al., 2008; Abobi, 2019; Abobi et al., 2021).

From the ECOPATH model, groups with higher *EE* values indicate a high predation or fishing pressure on these groups (Table 1). All cichlid species except *Hemichromis fasciatus* had high *EE* values (> 0.9), which conform to what was reported for adult tilapia species (0.986) in the Sakumo II Lagoon in 2002 (Pauly, 2002). The high *EE* value for *Sarotherodon melanotheron* is due to the abundance of this species in the Keta lagoon fish catch making it one of the most dominant fish species of the lagoon (Dankwa et al., 2014; Lamptey and Ofori-Danson, 2014). This species has also been identified to be very productive in most West African lagoons and estuaries (Pauly, 2002; Villanueva et al., 2006; Adité and Winemiller, 1997; Panfili et al., 2004).

Among the fish groups, *Strongylura senegalensis* had the most negligible *EE* value, which implies their low biomass within the lagoon ecosystem or might also indicate the non-availability of their predators in the ecosystem or the model. The higher *EE* values observed in this study for the other fish groups could be due to the availability of their predators in the lagoon (Christensen et al., 2008).

The ecosystem's invertebrates (*Callinectes amnicola* and other macroinvertebrates) had high *EE* values. These indicate that these species are highly preyed on or are mostly captured. The most commercially and economically important crustacean species of the Keta Lagoon is the blue swimming crab *Callinectes amnicola* (Gyampoh et al., 2020), and its abundance and utilisation are evident in its high *EE* value. The high *EE* value of macroinvertebrates of the Keta lagoon is indicative of their importance in the diet of species in the higher TLs. A high degree of feeding pressure on zooplankton by the higher TL species is reflected in their high *EE* value of 0.995. This observation is consistent with other tropical inland ecosystems (Wolff et al., 2000; Abobi, 2019; Abobi et al., 2021; Lal et al., 2021). These trends regarding the ecotrophic efficiencies indicate a non-selective fishery operating in the lagoon, capturing all trophic components irrespective of their size, particularly seine nets of smaller mesh sizes as proposed by Lamptey and Ofori-Danson (2014a).

Primary producers (phytoplankton and aquatic macrophytes) and detritus had low *EE* values and implied that these groups are minimally utilised in the system. Furthermore, the study showed that phytoplankton is an essential food source in the Keta Lagoon that sustains mostly the zooplanktonic groups and forms the base of the food web structure. The remaining biomass flows towards detritus and is indicated by the high values of their flows into detritus (Table 1). Although most functional groups in the system do not utilise macrophytes, they are harvested by the people living around the lagoon for weaving mats, baskets, and thatch for roofing (Finlayson et al., 2000).

Piscivorous waterbirds had a low *P/Q* value, although their diet mainly comprised fish species and macroinvertebrates and. This low value could be attributed to waterbirds channeling more energy into feeding than other activities such as movement, reproduction, roosting, amongst others. The functional group with the highest *P/Q* value was the zooplankton species due to their small sizes and ability to produce faster than other species under favourable conditions. Species such as *Hemichromis fasciatus*, *Hemichromis bimaculatus*, *Ethmalosa fimbriata*, and *Callinectes amnicola* had high *P/Q* values due to their carnivorous feeding habits and the quality of their diets (Traore et al., 2008). The remaining species had low *P/Q* values due to using a small portion of their energies towards reproduction.

Ecosystem flow indices

The model estimate of total system throughput (TST, the sum of all flows) of 10,287.92 t/km^2/year is lower when compared to most tropical coastal and inland systems (Wolff, 2000; Villanueva et al., 2006; Traore et al., 2008; Abdul and Adekoya, 2016; Longonje and Raffaelli, 2016; Abobi, 2019; Abobi et al., 2021; Lal et al., 2021). The lower TST value of this model than most tropical models is probably due to the low biomass and *P/B* of phytoplankton, as systems with higher TST showed high biomass and *P/B* values for the phytoplankton group. The sum of all consumptions contributed significantly (3,810.038 t/km^2/year) to the sum of all flows through the system (Table 3).

The estimated TLs ranged between 1 and 3.216, with fish species occupying levels between 2.071 to 3.214 (Table 1). The estimated mean trophic level of the catch was at 2.763, indicating the fishery exploits groups between the middle and higher TLs and can be said to be targeting one of the commercially important species of the lagoon *Ethmalosa fimbriata* (TL 2.662). The high MTLc is also evident in the high catch rates of TL III species (7.5 t/km^2), constituting 65.6% of the catch across all the TLs (Table 2).

The contribution of each trophic level to the entire energy flow through the system is presented in the Lindeman Spine diagram (Fig 3). From the diagram, flows decreased with increased TL, justifying the importance of the primary producers and detritus in supporting the energy flows, indicating a bottom-up control in the Keta lagoon. Similarly, the trophic efficiency (TE) between TLs decreases as TL increase (TL II = 11.16%, TL III = 9.371%, TL IV = 8.580%, TL V = 6.136%). The decline might be attributed to the change in energy use, as it is converted from one state to another as it moves up the

TL (Lal et al., 2021). This trend of decreasing transfer efficiency has been observed in many coastal lagoons and inland systems from the tropics and subtropics (Wolff et al., 2000; Lira et al., 2018). The mean TE of the Keta lagoon ecosystem was 9.646% and is at the lower end of the ranges proposed by Christensen and Pauly (1993) for the 41 trophic models and below the standard estimate of 10% presented by Lindeman (1942). Villanueva et al. (2006) suggested the low transfer efficiency estimated for Lake Nokoué than Ebrié lagoon to be due to the use of "acadjas" in the system, limiting predation, which could also be a reason at Keta lagoon. The low TE recorded for this system also provides information on the development of the Keta lagoon.

The detritivory to herbivory (D:H) index of the Keta lagoon was lower (0.428) than those reported by Abobi et al. (2021) and Villanueva et al. (2006). The low D:H ratio indicates primary producers' availability as a food source in the system and shows that the energy transferred from TL1 is mainly from the primary producers (phytoplankton and macrophytes). This consumption of primary producers is primarily due to the high biomass of macroinvertebrates and other TLII groups (zooplankton, *Sarotherodon melanotheron*, and *Coptodon guineensis*), which feed on primary producers (mainly phytoplankton). However, it should be noted that this does not indicate high utilization of primary producers across all the trophic levels.

Indicators of ecosystem development and stability

According to Odum (1969), the linear food chain changes to a web-like structure as the system matures. The System Omnivory Index (SOI) and Connectance Index (CI) are some indicators of system complexity, with higher values of these indices indicating the complexity of the food web and the ecosystem's maturity (Duan et al., 2009). The values for CI and SOI in this study were 0.328 and 0.155, respectively. Seven (7) functional groups had OI greater than 0.2 (Table 1), with *Callinectes amnicola* having the highest OI value and indicating that they are opportunistic feeders. The functional groups of the Keta lagoon are less generalised and considered opportunistic feeders due to the intermediate value of SOI (Pereira et al., 2012). Christensen (1995) and Pauly et al. (1998) also stated that low values of SOI close to zero indicate a linear tendency in the food web structure.

According to Christensen (1995), ascendency and overhead index are associated with ecosystem maturity and stability (the ability of a system to withstand unexpected perturbations). In this study, the system ascendency was estimated at 26.3% and is indicative of an immature system. The value obtained from this study is similar to that of Wolff et al. (2000) on the Caeté estuary, Abdul and Adekoya (2016) on Ogun estuary and Lal et al. (2021) on the Uhla river estuary and were considered immature systems. On the other hand, the system overhead was estimated at 73.7% and was within the ranges reported in most tropical coastal systems (Wolff et al., 2000; Abdul and Adekoya; 2016; Lal et al., 2021). Thus, the high SO value indicates that the Keta lagoon system has a certain resistance level to perturbations and can revert to its original state should any disturbance occur.

The total primary production to total respiration (TPP/TR) ratio is also one of the indicators of ecosystem maturity (Odum, 1971). According to Odum (1971), production is expected to surpass respiration in the early stages of ecosystem development, leading to a TPP/TR ratio greater than 1. The TPP/TR ratio of the Keta lagoon model was 1.587, which is greater than one (> 1) and is indicative of a developing system. However, the TPP/TR ratio for this study was relatively low and considered mature when compared with those reported by Wolff et al. (2000), Villanueva et al. (2006), Abdul and Adekoya (2016) and Abobi et al. (2021). The net system production (NSP) estimated for the Keta lagoon ecosystem was 1,480.452 t/km2/year. According to Christensen et al. (2005), developed systems have NSP values close to zero; hence, this system is considered immature. Nevertheless, the NSP value obtained for the Keta lagoon is less when compared to other tropical models (Abdul and Adekoya, 2016; Abobi, 2019; Abobi et al., 2021; Villanueva et al., 2006), indicating its maturity over the other systems. Similarly, the total primary production to the total biomass (TPP/TB) ratio was 7.207 and is low compared to those reported for other tropical models (Villanueva et al., 2006; Abdul and Adekoya, 2016; Abobi et al., 2021; Lal et al., 2021), but higher than that reported by Wolff et al. (2000). The low TPP/TB ratio implies that this ecosystem is approaching a developed stage. The total biomass to the total throughput (TB/TST) ratio was low (0.054). According to Odum (1971), TB/TST is expected to increase to the maximum in developed systems; hence the low value obtained from this study indicates an immature system. Lower values of TB/TST ratio were obtained for most tropical systems (Villanueva et al., 2006; Abdul and Adekoya, 2016; Abobi et al., 2021; Lal et al., 2021), with Caeté estuary having relatively high TB/TST ratios (Wolff et al., 2000).

Another ecosystem maturity and stability indicator is Finn's cycling index (FCI) (Finn 1976). According to Odum (1971), FCI increases with system maturity and stability. The FCI computed for this model was 4.933%. FCI has been reported to vary between 0.19% to 24.8% in estuarine and other coastal ecosystems (Lira et al., 2018). Also, the low FCI computed for this model is below the 10% proposed by Odum (1971) and is indicative of an immature system susceptible to perturbations.

Similarly, Finn's average path length (APL) from this model was 2.569. APL provides information on the ecosystem's health and increases with ecosystem maturity and stability (Christensen, 1995). Therefore, the APL obtained for this model indicate that the system is stressed and susceptible to perturbation. According to Villanueva et al. (2006), a stressed ecosystem is characterised by low APL value and a short food chain controlled by bottom-up forces, justifiable from the MTI plot. Thus, most of the lower TLs positively impacted the higher TL groups. However, all the indicators of the lagoon point out to a developing system that is prone to perturbation.

Conclusion

The Ecopath model developed for the Keta lagoon showed trophic interactions, trophic transfers, and energy flows among 17 functional groups considered for the study. The model also showed the roles each functional group plays in the ecosystem. It was evident from the results of the model that some food resources, mainly primary producers, though contributed significantly to the flows through the Keta Lagoon, were minimally utilised by organisms in higher trophic levels (TL III and IV). All the indicators of ecosystem functioning (TST, NSP, CI, SOI, MPL, the TPP/TR, TPP/TB, and TB/TST ratios) pointed to a developing ecosystem prone to disturbances but with the ability to withstand natural or anthropogenic perturbation based on the high SO and low AS values. Also, predatory birds and macroinvertebrates had the most significant impact on some of the biological groups of the system and were identified as keystone species, important for structuring the lagoon. Species with high *EE* values (*Hemichromis bimaculatus*, *Coptodon guineensis*, *Sarotherodon melanotheron*, *Pellonula leonensis*, *Ethmalosa fimbriata*, *Hyporhamphus picarti*, *Porogobius schlegelii*, and *Callinectes amnicola*) indicated their high utilisation in the system and conform to reports on the Keta lagoon fishery.

The EwE model developed for the Keta lagoon in this study is the first ecosystem modelling work carried out on the system; hence, it can act as a base for future ecosystemic simulations of the lagoon. Reports on the lagoon indicate overexploitation of the fishery, with the fishery impacting *Strongylura senegalensis* (as depicted by the results of the MTI analysis). Based on the results from the model, the Keta lagoon is moving towards maturity compared to other tropical ecosystems. Nevertheless, an ecosystem management approach is suggested as the best way to boost productivity while sustaining the ecosystem structure and functioning. The recommended management strategies for the Keta lagoon include stock enhancement, alternative livelihoods (aquaculture), closed seasons, habitat protection, enforcement of fisheries regulations such as enforcing the existing mesh size regulations and ban of certain fishing gears and methods in the Keta lagoon and other inland waters. This will help prevent the catching of juveniles and reduce by-catches.

Lastly, traditional leaders and other stakeholders should also regulate fishing activities (non-fishing days) and create alternative livelihoods for the fishers to reduce the pressure on the lagoon fisheries.

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APPENDIX TABLE 1

Input data and their sources used for the construction of the Keta Lagoon Ecopath model

Functional Groups	B (t/km²)	P/B (yr⁻¹)	Q/B (yr⁻¹)	EE	Catch (t/km²/yr)	Location	Data Sources
Predatory birds	0.096[a]	0.25[b]	63.000[b]		-	[a,b] Ghana	
Hemichromis fasciatus	0.136[a]	4.140[b]	13.440[c]		0.068	[a,b,c] Ghana	[a] Dankwa et al. (2004); [b]Ababio (2001); [c] Villanueva et al. (2006)
Hemichromis bimaculatus						[a,b] Ghana [c]Côte d'Iviore	[a] Dankwa et al. (2004); [b]Abobi et al. (2019); [c] Traore et al. (2008)
Coptodon guineensis	2.672 [a]	4.510 [b]	29.100[c]		1.550	[a,b,c] Ghana	[a] Dankwa et al. (2004); [b]Ababio (2001) [c] Fishbase
Sarotherodon melanotheron	2.026[a]	3.790 [b]	32.803 [c]		1.094	[a,b] Ghana [c]Côte d'Ivoire	[a] Dankwa et al. (2004); [b]Ababio (2001); [c]Villanueva et al. (2006)
Pellonula leonensis	7.364 [a]	4.030 [b]	25.900 [c]		3.682	[a,c] Ghana [b]Nigeria	[a] Dankwa et al. (2004) and Nunoo et al (2014); [b]Uneke et al. (2010) [c] Fishbase
Ethmalosa fimbriata	0.068 [a]	2.300[b]	16.000[c]		0.034	[a,c] Ghana [b] Côte d'Iviore	[a] Dankwa et al. (2004); [b]Niyonkuru et al (2003); [c]Pauly (2002)
Strongylura senegalensis	0.206 [a]	1.050 [b]	20.232 [b]		0.103	[a]Ghana [b] Côte d'Iviore	[a] Dankwa et al. (2004); [b]Villanueva et al. (2006)
Hyporhamphus picarti	4.082 [a]	3.500[b]	28.377[b]		2.041	[a]Ghana [b] Côte d'Iviore	[a] Dankwa et al. (2004); [b]Villanueva et al. (2006)
Porogobius schlegelii	0.004 [a]	3.440 [b]	18.600[c]		0.002	[a] Ghana [b]Benin [c]Côte d'Iviore	[a] Dankwa et al. (2004); [b]Lederoun et al. (2016); [c]Fishbase
Eucinostomus melanopterus	0.934 [a]	2.920 [b]	26.909 [c]		0.467	[a] Ghana [b] Nigeria [c]Côte d'Iviore	[a] Dankwa et al. (2004); [b]Arimoro et al. (2007); [c]Villanueva et al. (2006)
Callinectes amnicola	2.942 [a]	2.000 [b]	10.000[b]		1.471	[a,b,c] Ghana	[a] Dankwa et al. (2004); [b]Pauly (2002)
Macroinvertebrates	49.26 [a]	5.000 [b]	50.000 [b]		-	[a,b] Ghana	[a]Finlayson et al. (2000); [b]Pauly (2002)
Zooplankton	3.000[a]	35.000 [b]	140.000 [b]		-	[b] Ghana	[a] Self-estimate [b] Abobi et al. (2019)
Aquatic Macrophytes	466.1 [a]	5.000[b]	-		-	[a,b] Ghana	[a] Finlayson et al. (2000); [b]Abobi et al. (2019)
Phytoplankton	8.788 [a]	270 [b]	-		-	[a],Ghana [b] Côte d'Iviore and Ghana	[a] Finlayson et al. (2000); [b]Villanueva et al. (2006)
Detritus	9.593[a]				-	[a] Côte d'Iviore and Ghana	[a]Self estimate

APPENDIX TABLE 2

Bird species of Keta lagoon, their abundance, and average body mass

Bird species	Counts	Average body mass (g)	Data sources of body mass
Black-winged Stilt	1931	200	Ntiamoa-Baidu et al. (1998)
Sanderling	534	55	Ntiamoa-Baidu et al. (1998)
Common Sandpiper	1011	55	Ntiamoa-Baidu et al. (1998)
Little Stint	42	25	Ntiamoa-Baidu et al. (1998)
Whimbrel	791	300	Ntiamoa-Baidu et al. (1998)
Greenshank	296	180.5	Robinson (2005)
Spur-winged plover	86	420	Moffat (1981)
Kittlitz's Sand Plover	45	30	Ntiamoa-Baidu et al. (1998)
Black-tailed godwit	12	210	Ntiamoa-Baidu et al. (1998)
Collared pratincole	48	98	Ntiamoa-Baidu et al. (1998)
Common knot	1	120	Ntiamoa-Baidu et al. (1998)
Common tern	1535	175	Wendeln and Becker (1996)
Black tern	72	61.8	van der Winden (2002)
Little tern	831	63.6	Cherubini et al. (1996)
Greater black-backed gull	82	277.4	Ushine et al. (2017)
Long-tailed cormorant	7634	505	Bowmaker (1963)
Western reef heron	1229	500	Ntiamoa-Baidu et al. (1998)
Grey heron	34	1350	Ntiamoa-Baidu et al. (1998)
Little egret	1873	500	Ntiamoa-Baidu et al. (1998)
Green-backed heron	15	250	Ntiamoa-Baidu et al. (1998)
Great white egret	350	1000	Dunning Jr. (1993)
Goliath heron	7	5000	Mock and Mock (1980)
Squacco heron	5	300	Robinson (2005)
Pied kingfisher	1215	74.7	Tjomlid (1973)
White-faced tree ducks	120	706.5	Petrie (2005)
Total	**19,762**		

APPENDIX TABLE 3

Diet matrix of functional groups considered in the Ecopath model of the Keta Lagoon

Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. Predatory birds														
2. *H. fasciatus*	0.03	0.020										0.100		
3. *H. bimaculatus*	0.03													
4. *C. guineensis*	0.185	0.150						0.067		0.035	0.035	0.100		
5. *S. melanotheron*	0.190	0.100						0.100		0.100	0.100	0.150		
6. *P. leonensis*	0.05	0.140				0.080		0.020		0.048	0.105	0.035		
7. *E. fimbriata*								0.100		0.009				
8. *S. senegalensis*								0.003						
9. *H. picarti*		0.050						0.010				0.150		
10. *P. schlegelii*										0.173				
11. *E. melanopterus*												0.050		
12. *C. amnicola*	0.070										0.050			
13. Macroinvertebrates	0.382	0.380	0.990	0.065	0.020	0.22	0.020	0.30	0.374	0.578	0.450	0.200		
14. Zooplankton		0.100		0.050	0.050	0.700	0.635	0.400	0.151		0.100			0.010
15. Aquatic Macrophytes		0.010		0.300	0.150		0.010		0.472		0.050	0.015	0.150	
16. Phytoplankton				0.300	0.150		0.325			0.017	0.100		0.500	0.850
17. Detritus		0.050	0.010	0.285	0.630		0.010		0.003	0.040	0.010	0.200	0.350	0.140
Imports	0.063													

Sources: (1) Ntiamoa-Baidu et al. (1998); Colléter et al. (2012); Abobi et al. (2019). (2) Villanueva et al. (2006); Traore et al. (2008); Kouadio et al. (2019); Abobi et al. (2019). (3) Adite and Winemiller (1997). (4) Villanueva (2006) (5) Villanueva et al. (2006). (6) Adite and Winemiller (1997); Abobi et al. (2019); Ahoutou (2020). (7) Pauly (2002); Villanueva et al. (2006). (8) Villanueva et al. (2006). (9) Earl et al. (2011). (10) Udo (2009). (11) Adite and Winemiller (1997); Villanueva et al. (2006). (12) Pauly (2002); Aderonke (2009). (13) Colléter et al. (2012); Abobi et al. (2019). (14) Traore et al. (2008); Abobi et al. (2019)