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Comparative assessment of food web structure and fisheries productivity of three reservoirs in Ghana

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Abstract

Three Ghanaian reservoirs (Tono, Bontanga and Golinga) were compared through a food web modelling approach (Ecopath with Ecosim) to assess production characteristics and food web structures. The lakes differ in size and morphology, generating specific conditions for fish growth and production. While the two top fishery target species were *Sarotherodon galilaeus* (L.) and *Oreochromis niloticus* (L.) in all reservoirs, the mean trophic level of the catch was lowest in the largest and deepest reservoir (Tono) due to higher trophic level species occupying less accessible deep “refuge” habitats. The smallest lake had the highest fish production under optimal conditions of water supply (17.1 compared with 15.5 and 10.1 t/km^2/year for lakes Bontanga and Tono), but it appears to be most vulnerable under conditions of drought. For the planning and construction of adequately sized reservoirs used for fishery and irrigation purposes, the water budget (ratio of inflow and evaporation) needs to be estimated.

KEYWORDS
fish production, food web, Ghana, irrigation, lakes, morphology

1 | INTRODUCTION

Lake ecosystems, both natural and artificial, are important for people's livelihoods and food sustenance throughout the global South. With increasing anthropogenic and climate change pressures on these ecosystems, effective and sustainable management of their fisheries is therefore essential. Advancing knowledge on the differences and or similarities in trophic relationships and resource productivities among man-made lakes can help scientists manage and plan for the construction of future artificial systems.

Lake ecosystem functioning and structural organisation are controlled by both internal and external factors such as natural predation, nutrient fluxes, abundance and composition of introduced species and fishing. Understanding the dynamics and the impacts of these factors on (top-down and bottom-up) structuring processes is therefore crucial for successful ecosystem-based fisheries management (Jeppesen et al., 1997; Kao et al., 2016).

Conventionally, depth, water chemistry and conductivity have been used to classify lakes and reservoirs (Rai & Hill, 1980; Talling & Talling, 1965) since these parameters appear closely related with productivity (Downing et al., 1990; Henderson & Welcomme, 1974; Ryder et al., 1974). Rawson (1938) was the first to suggest that factors affecting lake productivity could be grouped into climatic, morphometric and edaphic. It has been shown that biological production in lake systems is partly controlled by lake morphology, nutrients and other environmental factors (Kolding & van Zwieten, 2012). Some of these studies suggest that fish productivity per unit area is negatively related to habitat volume, area and mean depth since

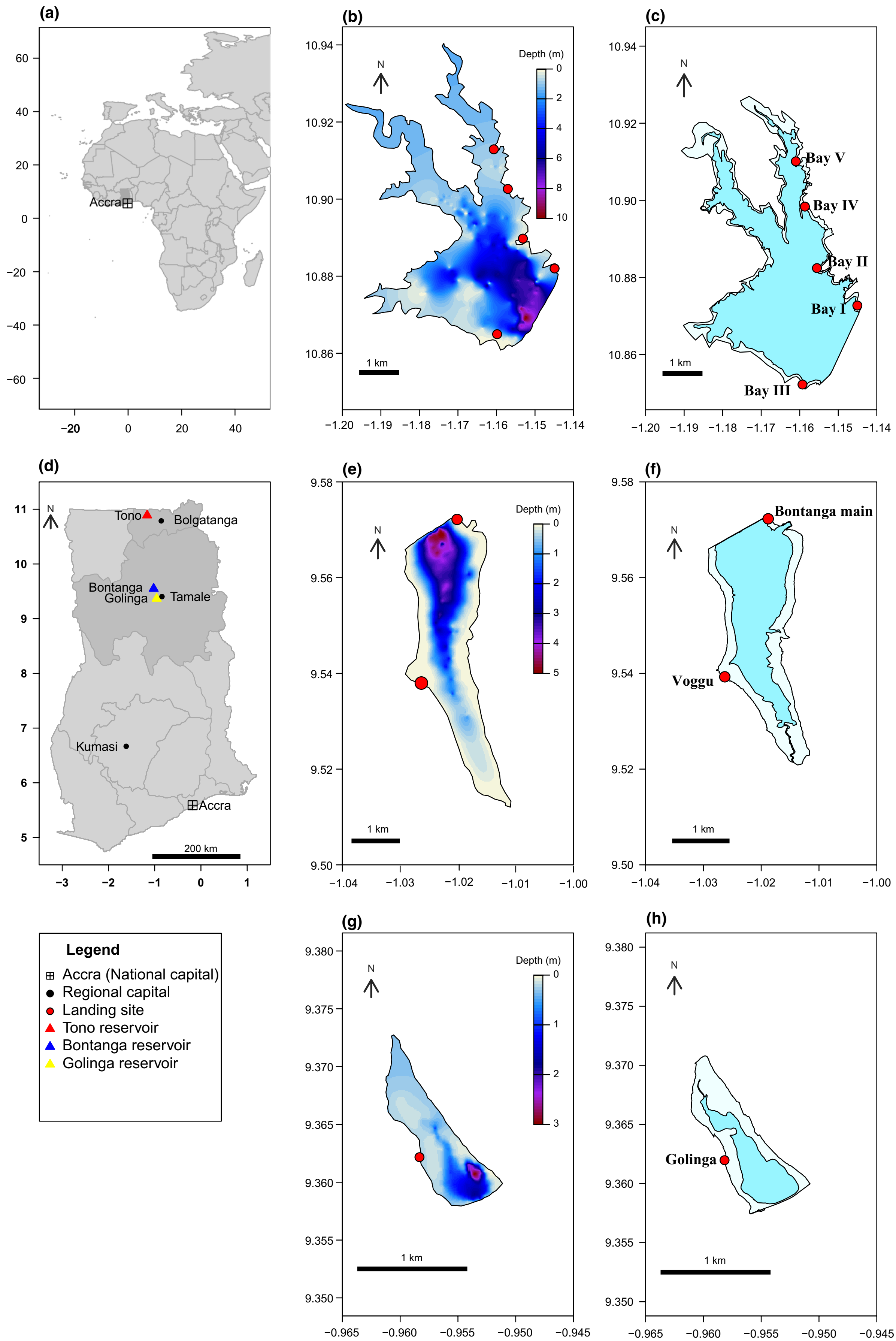
(a)
Accra
(b)
Depth (m)
N
1 km
(c)
Bay V
Bay IV
Bay II
Bay I
Bay III
(d)
Tono
Bolgatanga
Bontanga
Golinga
Tamale
Kumasi
Accra
200 km
(e)
(f)
Bontanga main
Voggu
(g)
(h)
Golinga
Legend
Accra (National capital)
Regional capital
Landing site
Tono reservoir
Bontanga reservoir
Golinga reservoir

FIGURE 1 Overview maps of the African continent (a) and Ghana (d), indicating the location of national and regional capital cities (black dots), as well as the three reservoirs studied in this work (triangles). Bathymetric maps of Tono (b), Bontanga (e) and Golinga (g) reservoirs in Ghana, showing landing sites. The bathymetric data were obtained during the dry season (March–April 2017). Reservoir maps depicting the surface areas of Tono (c), Bontanga (f) and Golinga (h) during dry season (in blue; estimated on 03/04/2017, 25/04/2017 and 26/04/2017, in the three reservoirs, respectively) and wet season (in grey; estimated on 24/08/2016 and 14/08/2016 in Bontanga and Golinga, respectively). The area of the Tono reservoir during the wet season was adapted from Google Earth. For exact values, consider Table 1

many aquatic processes are less intense. Fish are less abundant (per unit area) in larger water bodies because of decreased rates of nutrient recycling into the euphotic layer within these lakes (Downing, 2010). However, the question on how differences in lake morphology and physico-chemical characteristics shape artificial ecosystems productivity, development, maturity and resilience has received limited scientific attention.

Reservoirs are defined as man-made lakes and may either be embedded in a river network or not (Hayes et al., 2017). Reservoirs have been characterised as being rather underdeveloped and unstable ecosystems due to (1) changes in the general status from riverine to lacustrine conditions; (2) eutrophication due to the nutrient input from surrounding rural communities and decomposition of important quantities of submerged plant material; (3) early stage of the succession of the (artificial) fish community; and (4) the development of unregulated fishing activities (Villanueva et al., 2006). Multiple use of reservoirs for irrigational agriculture, animal watering and fisheries also influence food web dynamics and ecosystem maturity.

To evaluate ecosystem effects of fishing, to model the consequences of environmental changes for food web dynamics or to explore different management strategies and respective repercussions on ecosystem dynamics, the Ecopath with Ecosim (EwE) trophic modelling approach was developed (Christensen & Pauly, 1992; Christensen et al., 2000; Polovina & Ow, 1985). The software has been used to assess fisheries and inform management of African lake and reservoirs: Reservoir Bagré (Villanueva, et al., 2006), Lake Victoria (Matsuishi et al., 2001; Natugonza et al., 2019; Natugonza et al., 2016), Lake Ayamé (Traore et al., 2008), Lake Koka (Tesfaye & Wolff, 2018) and Lake Kivu (Villanueva, Isumbisho, et al., 2008; Villanueva, Moreau, et al., 2008). General characteristics of tropical reservoirs often differ remarkably, due to their highly dynamic nature, with water levels and biological productivity largely depending on the inflowing water. Using the EwE software, these differences between lakes can be compared and the level of development and organisation across such artificial ecosystems can be described as resulting from varying physical and environmental characteristics, as well as from potential differences in harvest levels.

The trophic modelling approach of EwE can also be used to study trophic cascades (i.e. indirect effects of predators on plants via predation on herbivores) in lakes and reservoirs. The trophic cascade theory postulates that the disturbance of a trophic level has consequences (cascading effects) over the connected trophic levels above and below (Ribeiro Filho et al., 2014). Lakes with seasonal changes from clear to turbid water conditions have been reported to often go through a fish–zooplankton–phytoplankton cascade, starting with fish mortalities (due to low oxygen conditions), which then leads to shifts in zooplankton size structure and corresponding strong top-down effects on phytoplankton (Jeppesen et al., 1998; Pace et al., 1999).

Nilssen (1984) suggested that all major morphometric features and physical processes are important when tropical man-made lakes are to be compared. Yet, models of tropical lakes, which are more dynamic and perhaps also more complex than temperate ones, rarely have physical processes incorporated in their construction and analysis.

This study focusses on three man-made lakes in northern Ghana (Tono, Bontanga and Golinga; Figure 1) that vary in shape, surface area, mean depth, water level fluctuation, total water volume, the intensity of resource use and agricultural activities in its surroundings. The study compares food web structures and fisheries characteristics of the three systems to provide inputs to ecosystem-based and sustainable management of the fisheries resources.

The specific objectives of this study were:

1. to identify biological groups, their biomass, and their feeding interactions in order to construct food web models for Tono, Bontanga and Golinga reservoirs;
2. to assess differences in the flow structure between the three reservoirs modelled in terms of functional groups characteristics (relative biomass, species composition), primary production, transfer efficiencies between trophic levels, diet matrix and fish catch;
3. to identify those groups that are key ecosystem controllers in the flow networks, and evaluate how differences in the physical features of the reservoirs relate to differences in food web structure and resource productivities.

It is hypothesised that differences in the lakes' physical features (shape, mean depth, overall size, water holding capacity and water throughflow) relate to differences in food web structure and resource productivities, with the smallest and shallow Lake Golinga being the most productive on a per unit area basis.

2 | MATERIALS AND METHODS

2.1 | Description of Tono, Bontanga and Golinga reservoirs

The study was conducted at three reservoirs: Tono (10°52′48″N; 1°9′36″W), Bontanga (9°33′0″N; 1°1′12″W) and Golinga (9°21′36″N; 0°57′14.4″W) (Figure 1). Tono is the largest reservoir in

Parameter	Tono	Bontanga	Golinga
Surface area during wet season (km^2)	18.6	6.7	0.62
Surface area during dry season (km^2)	12.5	3.8	0.3
Seasonal reduction in surface area (%)	32.8	43.3	51.6
Catchment area (km^2)	650	165	124
Mean depth (m)	6.6	5.9	2.7
Maximum depth (m)	13.32	9.70	4.95
Mean Secchi depth transparency (m)	0.73	0.49	0.38
Length of reservoir (m)	3471	1900	690
Water level: wet-dry (m)	10.5–5.04	8.23–2.85	2.8–0.12
Water level variation (m)	5.46	5.38	2.68
Water holding capacity (m^3)	93×10^6	25×10^6	1.23×10^6
Surface area: water volume ratio	0.20	0.27	0.50
*Relative Reservoir Level Fluctuation	82.7	91.2	99.6

TABLE 1 Seasonal fluctuation in surface area and water level of Tono reservoir in the Upper East region of Ghana, and Bontanga and Golinga reservoirs (both in the Northern region of Ghana) from July 2016 to June 2017. The wet season, August 2016; dry season, April 2017. For an overview of seasonal variation of water level, turbidity and Secchi depth see Figure S1. *Adapted from Jul-Larsen et al. (2003): (mean reservoir level amplitude/mean depth)* 100

the Upper East region of Ghana and has a surface area of 18.6 km^2, while Bontanga and Golinga are the largest two reservoirs in the Northern region of Ghana. Bontanga has an intermediate size of 6.7 km^2, while Golinga is a very small reservoir with a surface area of only 0.62 km^2. All reservoirs are within the Guinea Savanna belt where the most prominent rainy season lasts from June to October. Tono, Bontanga and Golinga were constructed in 1985, 1983 and 1974, respectively (Gordon, 2006), primarily to support agriculture irrigation. However, over time, they have become important inland fishing grounds (see Table 1 for further description).

Besides the lakes' morphological differences, the number of households (an indicator of pressure on the resources) that depends on the reservoirs for their livelihoods also varies with the reservoir size with 16,250, 4950 and 900 people in the communities around Tono, Bontanga and Golinga, respectively (Ghana Statistical Service, 2012; Namara et al., 2011; Small Grants Programme, 2012).

2.2 | The Ecopath modelling approach

Ecopath with Ecosim (Christensen & Pauly, 1992; Christensen et al., 2000; Polovina & Ow, 1985) was used to construct trophic models of the Tono, Bontanga and Golinga ecosystems. To do so, the various organisms inhabiting each ecosystem were grouped into functional compartments considering as grouping criteria, their common physical habitat, the similarity in food preferences and life history characteristics (Yodzis & Winemiller, 1999). The model input parameters (for each compartment) are annual mean biomasses, rates of production per biomass (P/B), consumption per biomass (Q/B), ecotrophic efficiency (EE), diet matrix, migration rate (if occurring) and fishery data. All model compartments are linked through a diet matrix of prey-predator connections. Fish catches are considered "export" of the system and are further input parameters for the harvested groups.

Usually, an equilibrium condition is assumed for the model period considered, where group inputs are balanced to their outputs. Input data are standardised, and units (wet weights) are expressed as t/km^2. Ecopath expresses each term in a budget equation as a linear function of the mean biomass of each group (i), which results in a system of simultaneous equations for each model group expressed as:

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

where B_i is the biomass of the group i; P/B_i is its production rate; B_j the biomass of any predator j of the prey i; Q/B_j the food consumption rate of j; DC_{ji} is the fraction of i in the diet of j, expressed in percentage of weight; EE_i is ecotrophic efficiency which is the proportion of the ecological production consumed by predators and/or exported (Ricker, 1969) and EX_i is the export (i.e. catch) for any group (Christensen et al., 2008). $E_i + BA_i$ are terms for net migration and biomass accumulation, if occurring.

The second equation ensures energy balance for each group as:

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

where Qi is the consumption of group i, P_i is the sum of production of group i, R_i is the respiration of group i, and ($GS_i \times Q_i$) is the unassimilated food of group i. Ecopath can solve the above-mentioned equation if three of the following parameters are entered for each functional group: B, P/B, Q/B or EE (Christensen et al., 2008).

2.3 | Data collection and grouping of biota into model compartments

The model for Lake Tono has nine fish groups, one predatory bird group and one crocodile group. That of Lake Bontanga has 10 fish groups and one predatory bird group. The Golinga model has 11 fish groups. In addition to these groups, each of the three models has two invertebrate groups (insects plus larvae and zoobenthos), one zooplankton group, two primary producer groups (macrophytes and phytoplankton) and one detritus group (Tables S1, S2 and S3).

2.4 | Input parameters

2.4.1 | Biomass (B)

Primary producers

Chlorophyll *a* was estimated in situ using a multi-parameter water quality probe (OTT Hydrolab DS5X) that was suspended at a depth of 2 m for 24 h each month (July 2016–June 2017), and the data were logged at one-hour interval. The resulting estimates of mean annual chlorophyll *a* concentration (13.9, 17 and 26.1 mg/m^3 for Tono, Bontanga and Golinga, respectively) were then multiplied by the euphotic depth of the respective lake to obtain the water column values per unit area (/m^2). The euphotic depth was estimated from the Secchi depth transparency measurement (73, 49 and 38 cm, for Tono, Bontanga and Golinga, respectively) conducted from July 2016 to June 2017. These values were then converted to euphotic depth of 2.6, 1.7 and 1.3 m at Tono, Bontanga and Golinga, respectively, using Holmes' (1970) equation for turbid waters. Resulting chlorophyll *a* values for the three lakes of 36.1, 28.9 and 33.9 mg/m^2, respectively, were converted into carbon using the factor of 1:40-Chlorophyll *a*:Carbon (Brush et al., 2002) and then to mass with the conversion factor of 1:14.25-Carbon: wet weight (Brown et al., 1991). The resulting estimates for phytoplankton biomass were 20.6, 16.5 and 19.3 g WW/m^2 for Tono, Bontanga and Golinga, respectively (Tables S1, S2 and S3).

The biomass of aquatic macrophytes was estimated following the protocol of Finlayson et al. (2000). The aquatic macrophytes within the reservoirs were collected at four sampling stations: two each on the left and right banks of the reservoirs, respectively, and in five replicates at each sampling point using 0.31 × 0.31 m quadrats, giving an area of 0.1 m^2. The macrophytes were sampled in August 2016 (the peak of the wet season) and April 2017 (the peak of the dry season). All above-ground plant material within the quadrats was removed by cutting, placed into plastic bags and returned to the field base. The plant material was initially sun-dried and then oven-dried to a constant weight at 70°C and weighed. The biomass of aquatic macrophytes was estimated as 51.34, 33.87 and 25.41 t/km^2 for Tono, Bontanga and Golinga, respectively.

Detritus

The detritus biomass (D) was estimated using an empirical relationship that relates detritus biomass to primary productivity and euphotic depth Christensen and Pauly (1993):

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

where *D* is the detritus biomass (g C/m^2), *PP* is the primary production (g C/m^2/year) and *E* is the euphotic depth (m). Since there were no prior estimates of gross primary production in the lakes, mean value of 0.86 g C/m^2/d was obtained from similar reservoir systems in the nearby Ivory Coast (Arfi et al., 2003). This equals a gross primary production of 312.53 g C/m^2/year. Using this value and the respective lake euphotic depth and converting them to wet weight resulted in a detritus biomass of 29.89, 21.19 and 17.01 g/m^2/year for Tono, Bontanga and Golinga, respectively.

Zoobenthos

Biomass of zoobenthos (littoral fauna) mainly consisting of gastropods and bivalves was estimated from samples collected using a hand net with standardised sampling width of 0.25 m that was scooped across a length of 2 m in the littoral zones of the reservoirs at depths not exceeding 0.5 m. The average biomass per swept area was then extrapolated to t/km^2. Since there was insufficient information on insects and larvae, the biomasses of these groups were estimated by the EwE program using an EE of 0.9 in all three lakes assuming these groups to represent important food items of several fish populations (Villanueva, et al., 2006).

Zooplankton

Zooplankton samples were collected from July 2016 to June 2017 using a Hydrobios cylindro-conical net (acc. to Apstein, with a mesh size of 55 μm, opening diameter of 25 cm and length of 100 cm) (Alhassan & Ofori-Danson, 2017). The estimated zooplankton abundances were 1183, 1530 and 2080 individuals/m^3 at Tono, Bontanga and Golinga, respectively. The total number of individuals was converted to wet mass using a conversion factor of 535 μg/C established for zooplankton in tropical reservoirs of West Africa (Aka et al., 2000). To obtain the zooplankton mass per area (m^2), the biomass (m^3) was multiplied by the mean depth of the respective reservoir, resulting in biomass of 4.18, 4.83 and 3.0 t/km^2 for Tono, Bontanga and Golinga, respectively. The zooplankton community in the reservoirs was dominated by copepods (*Thermocyclops*), rotifers (*Keratella*, *Asplanchna* and *Trichocerca*) and cladocerans (mainly *Penilia*).

Fish

Biomasses of the four commercially most important (in terms of landing volumes) species *Oreochromis niloticus* (L.), *Sarotherondon galilaeus* (L.), *Coptodon zillii* (Gervais) and *Auchenoglanis occidentalis* (Val.) were based on estimates from length-based cohort analysis conducted for the species in all three lakes (Abobi, Mildenberger, et al., 2019; Abobi, Oyiadzo, et al., 2019). For all other exploited fish groups, biomass was estimated from total annual yield and fisheries mortality (B = Y/F) assuming F = 0.5 × Z (Rehren et al., 2018). From June 2016 to July 2017, fish landings were recorded for five consecutive days in each month and extrapolated to the monthly catch using an estimate of the average number of fishing days per month. Information was obtained from the fishers at the three reservoirs. The bulk weight of each fisher's catch per day was recorded, and the fish caught were then sorted into species groups, counted and weighed. At Tono, the three landing sites with the largest fisher populations (i.e. bays II, III and IV, Figure 1b,c) were monitored simultaneously for 3 days and bays I and V were monitored for the remaining 2 days. The two landing sites at Bontanga and the single landing site at Golinga were all monitored during the study period.

Predatory birds

Tono and Bontanga reservoirs are important bird habitats. Birds on both reservoirs are dominated by white-faced whistling duck *Dendrocygna viduata* (L.). Between March and May 2017, average populations of 3400 and 1180 birds per day were recorded at Tono and Bontanga, respectively. The adult ducks weigh between 502 and 820 g (Del Hoyo et al., 1992). An average weight of 0.5 kg was used for all species and sizes. The biomass of predatory birds in Tono and Bontanga was then estimated as 0.091 and 0.088 t/km^2, respectively.

Crocodiles

Crocodile biomass was based on a study by Shirley et al. (2009), which surveyed the populations of crocodiles in Ghana and Côte d'Ivoire. *Crocodylus niloticus* Laurenti was the most frequently encountered species and was found almost exclusively in northern, savannah woodland rivers and dams, which include the Tono reservoir and its surrounding environment.

2.4.2 | Production/biomass (P/B)

The P/B ratio under steady-state conditions is equivalent to the total mortality rate (Z) for the fish groups (Allen, 1971). Therefore, the *Z* values estimated through a bootstrapped linearised length-converted catch curve analysis were used for the four commercially important species (Abobi, Mildenberger, et al., 2019; Abobi, Oyiadzo, et al., 2019). For all other fish groups, Z or P/B values were taken from stock assessment studies conducted in the reservoirs or from other similar reservoir ecosystems in the region (i.e. *Clarias gariepinus* Burchell (Khan & Panikkar, 2009; Kwarfo-Apegyah et al., 2008; Tesfaye & Wolff, 2018), *Hemichromis fasciatus* Peters (Kwarfo-Apegyah et al., 2008), *Mormyrus* spp. (Villanueva, et al., 2006), *Synodontis/Schilbe* (Villanueva, et al., 2006), *Pellonula leonensis* (Boulenger) (Niyonkuru et al., 2007), *Brycinus nurse* (Rüppell) (Kwarfo-Apegyah et al., 2008) and *Heterotis niloticus* (Cuvier) (Traore et al., 2008)).

For zooplankton, insects and larvae, gastropods and bivalves (zoobenthos), macrophytes and phytoplankton, P/B values were taken from Lake Ayamé (Côte d'Ivoire; Traore et al., 2008) and the Bagré reservoir in nearby Burkina Faso (Villanueva, et al., 2006) (Tables S1, S2 and S3).

2.4.3 | Consumption rates (Q/B)

Consumption is the intake of food by a group over a defined time period (Christensen et al., 2000), which was entered as the ratio of specific consumption to biomass (Q/B ratio). The empirical equation of Palomares and Pauly (1998) was used to calculate Q/B values:

$$\log\left(\frac{Q}{B}\right) = 7.964 - 1.965T - 0.204\log W_{\infty} + 0.083A + 0.532h + 0.398d \qquad (4)$$

where *T* is the water temperature, $W\infty$ is the asymptotic body weight, h is the food type (0 for herbivores and 1 for predators) and *A* is the aspect ratio defined as $A = h2/s$, with h being the height of the caudal fin and s its surface area. W_{∞} was converted from L_{∞} values using the constant *a* and the slope *b* values from length–weight relationships. $L\infty$, *a* and *b* values for *O. niloticus*, *S. galilaeus*, *C. zillii* and *A. occidentalis* were obtained from Abobi, Mildenberger, et al. (2019) and Abobi, Oyiadzo, et al. (2019) (See Table S4). Data on aspect ratio were obtained from Fishbase (Froese & Pauly, 2019). For species that had unknown aspect ratios, the consumption/biomass (*Q/B*) ratios were taken from other models-Lake Ayamé (Côte d'Ivoire; Traore et al., 2008) and Bagré reservoir (Burkina Faso; Villanueva, et al., 2006). For invertebrate groups, Q/B ratios were mainly obtained from other Ecopath models of similar systems.

2.4.4 | Diet composition

Diet composition of predatory birds and crocodiles was derived from Villanueva, et al. (2006). Stomach content studies provided references for the diet of *A. occidentalis* (Abobi, Oyiadzo, et al., 2019). At Golinga, the diet composition for *S. galilaeus* was based on Alhassan et al. (2011) and that of *C. zillii and Hemichromis* spp. was based on Atindana et al. (2014). For all other fish species, information on diet composition was taken from Fishbase (Froese & Pauly, 2019) and two other similar models in the region (Traore et al., 2008; Villanueva, et al., 2006). The relative contribution of each group as prey for the respective group predating on them is shown in Tables S5, S6 and S7.

2.4.5 | Fisheries yield (Y)

Estimates of total annual catch for the target fish groups were based on field surveys as described in 2.4.1. Four main fishing methods are practised in the reservoirs, and their respective contribution to the total catch (t/km^2/year) is presented.

2.5 | Balancing the models

The model balancing was guided by the values of the ecotrophic efficiency (EE) and gross efficiency (GE). The model parameters were calibrated to obtain EE values for all the groups <1.0 and gross efficiency values (GE = P/Q) within 0.1 and 0.3 (Christensen & Pauly, 1992; Christensen et al., 2000; Christensen et al., 2008). *Hemichromis fasciatus* group had a GE of 0.308, and the predatory birds in Tono and Bontanga reservoirs had a GE of 0.004. Other functional groups of the Cichlidae family (i.e. *O. niloticus*, *S. galilaeus* and *C. zillii*) had low GE values between 0.042 and 0.091. Further groups of GE values below 0.1 included *Auchenoglanis occidentalis* in Tono and Bontanga reservoirs and *Brycinus nurse* and *Labeo* spp. in Golinga. For groups which had initial EEs above 1, values of uncertain parameters were changed within a range of ±15% until the model was balanced as outlined in the Ecopath User Manual (Christensen et al., 2008).

2.6 | Ecological and network indicators used to compare the models

The following ecological network analysis metrics: (1) Average Path Length (APL), (2) Finn Cycling Index (FCI), (3) Mean Trophic level (MTL), (4) Detritivory to Herbivory ratio (D:H) and (5) Keystoneness suggested by Fath et al. (2019) were used to compare the three systems. Additional indices of ecosystem maturity, such as total primary production/total biomass, net primary production/total respiration, total biomass/total system throughput (TB/TST) and net primary production−total respiration (NPPTR), were also used to compare the developmental state between the three lakes. According to Odum (1971), the ratio between total primary production and total system respiration (TPP/TR) would approach unity in a mature system. TPP/TB ratio and NPPTR tend to have low values in mature systems, whereas the ratio of biomass to total system throughput tends to increase as the system matures (Christensen, 1995).

The trophic aggregation routine (Lindeman, 1942) was used to: (1) calculate the efficiency of transfers within discrete trophic levels as the proportion of the flow entering a trophic level that is transferred to the next one (Christensen & Pauly, 1992) and (2) calculate the Detritivory to Herbivory ratio (D:H) (Fath et al., 2019). The trophic structures and ecotrophic efficiencies of the 3 lake ecosystems were then compared and related them to lake morphology and environmental characteristics.

2.7 | Mixed trophic impact (MTI)

The mixed trophic impact routine (Ulanowicz & Puccia, 1990) was used to: (1) evaluate the effect that a short-term increase in the biomass of a group will have on the biomass of the other groups in the ecosystem and (2) assess how a small increase in catch of one fishing gear impacts the catch of the other gears and the biomass of the functional groups.

2.8 | Keystoneness index

Derived from the MTI routine, a keystoneness index (Libralato et al., 2006) was calculated to quantify the impact of each of the model groups on all other groups of the system relative to the group's biomass. A keystone group is a group that would significantly affect other groups even with relatively small biomass. It is defined as:

$$\mathrm{KS_i} = \log\left[\varepsilon_i\left(1 - p_i\right)\right] \tag{5}$$

where KS_i is the keystoneness of group *i*, ε_i is the overall effect of group *i*, and p_i is the proportional biomass of group i. Functional groups that have low biomass and high overall effect are attributed high values of keystoneness (close or higher than zero).

3 | RESULTS

3.1 | Trophic relationships and structural analyses

The relative importance of top predatory group (a group with TL>3) differed between the lakes: in Tono, these are crocodiles (TL = 3.58), predatory birds (TL = 3.37), *H. fasciatus* (TL = 3.19) and *C. gariepinus* (TL = 3.06). In Bontanga, these are predatory birds (TL = 3.40), *H. fasciatus* (TL = 3.25) and *C. gariepinus* (TL = 3.06), while in Golinga, *H. fasciatus* (TL = 3.19) and *C. gariepinus* (TL = 3.08) were the top predators (Tables S1, S2 and S3; Figure 2). The top predators differed in biomass between the reservoirs. This holds particularly for *C. gariepinus* in Bontanga and Golinga where their biomasses were 13 and 9 times higher than in Tono (Tables S1, S2 and S3; and Figure 2). Similarly, the biomass of *H. fasciatus* in Golinga was significantly higher than in Tono and Bontanga. The mean trophic level of the catch was 2.18, 2.3 and 2.31 (see Table S8) at Tono, Bontanga and Golinga, respectively. The estimated fisheries gross efficiencies for all reservoirs were low. They were estimated as 0.0013%, 0.0025% and 0.0024%, for Tono, Bontanga and Golinga, respectively (see Table S8). The proportion of fish biomass at TL I and II in Tono were almost the same, that is 48.08% and 47.72%, respectively, while the fish biomasses in Bontanga and Golinga were concentrated at TL II with 65% and 64% (Table 2), respectively. In terms of fish catch distribution by trophic level, 83.8%, 73.5% and 72.5% of the catch from Tono, Bontanga and Golinga, respectively, were obtained from TL II (Table 2). The lower catch obtained from the higher TLs (≥III) in Tono explains why the catch has a lower mean trophic level than for Bontanga and Golinga.

3.2 | Ecological indicators and network analyses

The Average Path Length (APL), Finn Cycling Index (FCI) and Detritivory to Herbivory ratio (D: H) were all highest and lowest in

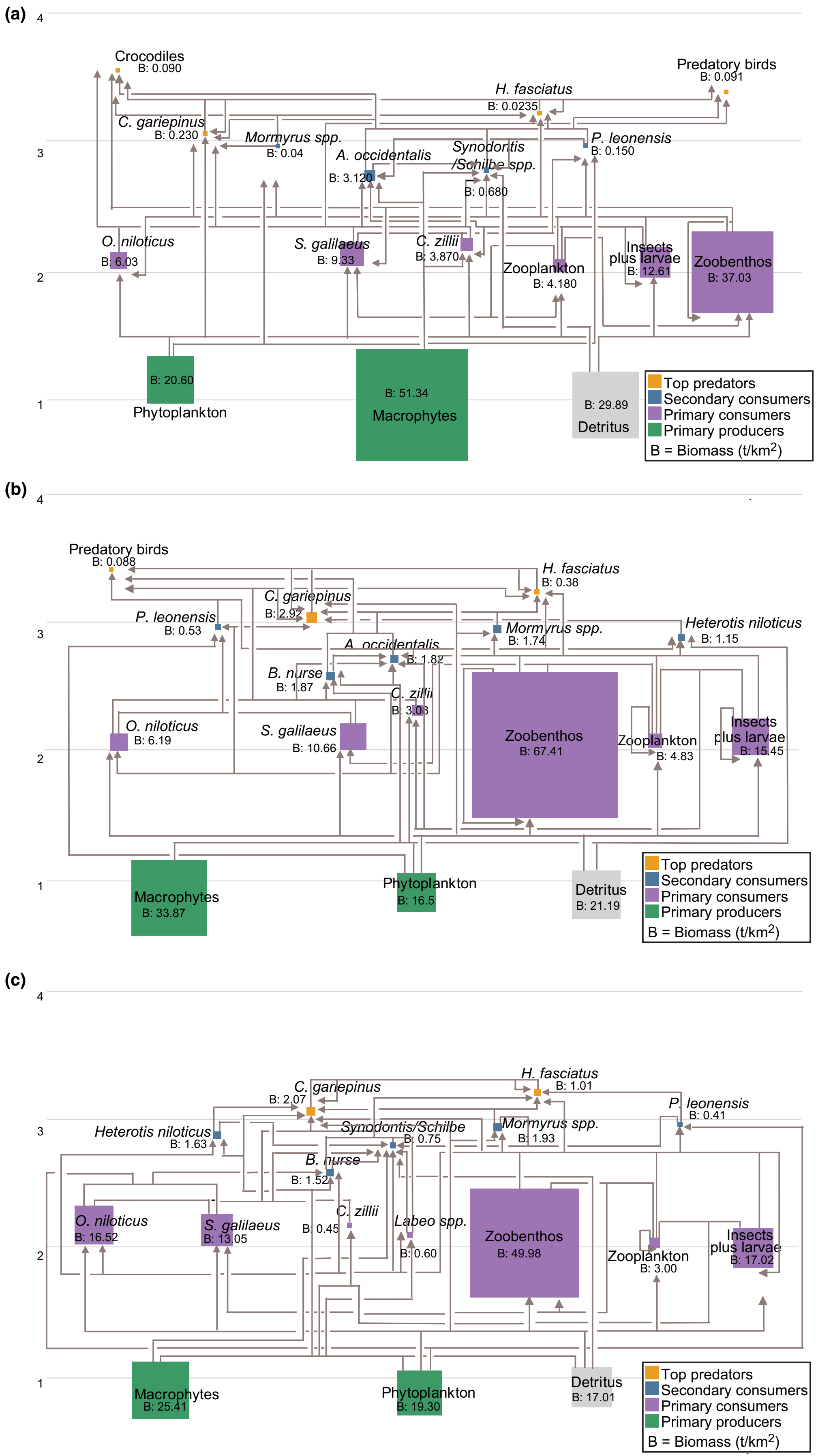
(a)
4
3
2
1
Crocodiles
B: 0.090
Predatory birds
B: 0.091
H. fasciatus
B: 0.0235
C. gariepinus
B: 0.230
Mormyrus spp.
B: 0.04
A. occidentalis
B: 3.120
Synodontis /Schilbe spp.
B: 0.680
P. leonensis
B: 0.150
O. niloticus
B: 6.03
S. galilaeus
B: 9.33
C. zillii
B: 3.870
Zooplankton
B: 4.180
Insects plus larvae
B: 12.61
Zoobenthos
B: 37.03
B: 20.60
Phytoplankton
B: 51.34
Macrophytes
B: 29.89
Detritus
Top predators
Secondary consumers
Primary consumers
Primary producers
B = Biomass (t/km2)
(b)
4
3
2
1
Predatory birds
B: 0.088
H. fasciatus
B: 0.38
C. gariepinus
B: 2.92
P. leonensis
B: 0.53
Mormyrus spp.
B: 1.74
Heterotis niloticus
B: 1.15
A. occidentalis
B: 1.82
B. nurse
B: 1.87
C. zillii
B: 3.03
O. niloticus
B: 6.19
S. galilaeus
B: 10.66
Zoobenthos
B: 67.41
Zooplankton
B: 4.83
Insects plus larvae
B: 15.45
Macrophytes
B: 33.87
Phytoplankton
B: 16.5
Detritus
B: 21.19
Top predators
Secondary consumers
Primary consumers
Primary producers
B = Biomass (t/km2)
(c)
4
3
2
1
H. fasciatus
B: 1.01
C. gariepinus
B: 2.07
P. leonensis
B: 0.41
Heterotis niloticus
B: 1.63
Synodontis/Schilbe
B: 0.75
Mormyrus spp.
B: 1.93
B. nurse
B: 1.52
C. zillii
B: 0.45
Labeo spp.
B: 0.60
O. niloticus
B: 16.52
S. galilaeus
B: 13.05
Zoobenthos
B: 49.98
Zooplankton
B: 3.00
Insects plus larvae
B: 17.02
Macrophytes
B: 25.41
Phytoplankton
B: 19.30
Detritus
B: 17.01
Top predators
Secondary consumers
Primary consumers
Primary producers
B = Biomass (t/km2)

FIGURE 2 Food web diagrams (EwE output) of the reservoirs Tono (a), Bontanga (b) and Golinga (c) in Ghana. Box sizes are scaled proportional to functional group's biomasses (for exact values, compare Table S1, Tables S2 and S3, and the y-axis describes their trophic level (TL). The *colours* describe trophic groups: primary producers (TL = 1.0), primary consumers (TL 2.0–2.5), secondary consumers (TL 2.6–3.0) and top predators (TL > 3). For Ecopath input values, please consider Tables S1-S7

TABLE 2 Distribution of catch (C- t/km^2/yr) and biomass (B- t/km^2) among the various trophic levels of Tono reservoir in the Upper East region of Ghana, and Bontanga and Golinga reservoirs (both in the Northern region of Ghana). Values obtained from *Flows and biomasses* under the Network Analysis routine of Ecopath output

	Tono				Bontanga				Golinga			
	Catch		Biomass		Catch		Biomass		Catch		Biomass	
TL	t/km^2/year	%	t km^2/year	%	t/km^2/year	%	t/km^2/year	%	t/km^2/year	%	t/km^2/year	%
1	0	0	71.9	48.1	0	0	46.6	28.3	0	0	44.7	28.9
2	8.4	83.8	71.4	47.7	11.4	73.5	106.7	64.8	12.4	72.5	98.4	63.6
3	1.6	15.4	5.9	4	3.8	24.4	10.6	6.5	4.3	25.1	10.7	6.9
4	0.08	0.8	0.33	0.22	0.31	2	0.79	0.48	0.39	2.3	0.79	0.51
5	0	0	0.01	0.01	0.016	0.1	0.039	0.02	0.02	0.1	0.04	0.03
Total	10.1	100	149.6	100	15.5	100	164.7	100	17.1	100	154.7	100

the intermediate (Bontanga) and largest reservoir (Tono), respectively (Figures 3 and 4; Table S8). The Mean Trophic Level of the Catch (MTLC) of Tono (2.18) was lower than Bontanga (2.30) and Golinga (2.31) (Figures 3l and 4b; Table S8). The smallest reservoir (Golinga) had similar Total System Throughput (TST) as the largest reservoir (Tono, being 30 times larger in surface area than Golinga) (Figures 3a and 4i; Table S8). The medium-sized reservoir (Bontanga) had the lowest proportions of TST export and TST flow to detritus (Figure 3b,e). The consumption flows of the largest reservoir (Tono) are nearly twice that of Bontanga (Figure 3d), which is about 3 times smaller in surface area than Tono. The mean transfer efficiencies calculated were low for all reservoirs: 4.8%, 6.5% and 6.6% for the Tono, Bontanga and Golinga, respectively. The highest catch and the highest biomass per unit area were observed for Golinga (the smallest) and Bontanga (medium-sized) reservoirs, respectively, and the lowest catch and biomass per unit area values were calculated for Tono, the largest reservoir (Figures 3k,o and 4a,e; Table S8).

3.3 | Mixed trophic impacts (MTI) and keystoneness

In Tono, an increase in predatory bird biomass would positively impact *Mormyrus* spp. and *Coptodon zillii* populations since these species' top predators, that is *H. fasciatus* and *C. gariepinus*, are negatively impacted. The cichlids groups have negative impacts on themselves, reflecting a high within-group competition for resources. A slight increase in the biomass of insects will be beneficial to most fish groups in the three reservoirs. The insect and larvae group biomass increase would positively impact *Mormyrus* spp., *H. fasciatus*, *B.* nurse and *H. niloticus* biomasses in both Bontanga and Golinga, while in Tono only *A. occidentalis* and *Mormyrus* spp. of the fish groups would benefit. This highlights the relative importance of insects and larvae in the food web of the three ecosystems.

With regard to the keystoneness index (Libralato et al., 2006), the predatory birds' group ranks first in Tono, while phytoplankton occupies the 1st rank in both Bontanga and Golinga reservoirs. In Tono, the next ranks in keystoneness are occupied by phytoplankton and omnivorous fishes (Figure 5a). In Bontanga, *C. zillii* (benthic herbivorous fish), *C. gariepinus* (carnivorous fish), insects and larvae and predatory birds were the next functional groups in order of decreasing keystoneness (Figure 5b), while in Golinga, the next four functional groups of the keystoneness rank order were *Brycinus nurse* (small pelagic omnivorous fish), *H. niloticus* (omnivorous fish) and carnivorous fishes: *H. fasciatus* and *C. gariepinus* (Figure 5c).

3.4 | Differences in total catch and fisheries productivity among reservoirs

Species catch composition and catch per unit area differed among the reservoirs, with total catch per unit of area being highest for the small (17.11 t/km^2/year in Golinga), lowest in the largest (10.07 t/km^2/year in Tono) and intermediate in the medium-sized lake (15.51 t/km^2/year in Bontanga; Figure 6; and Table S8). The highest contribution to the catches in Tono and Bontanga was from *S. galilaeus* (5.54 and 7.30 t/km^{2,} respectively), while *O. niloticus* catches (6.9 t/km^2) were the highest in the smallest reservoir (Golinga: Tables S1, S2 and S3).

4 | DISCUSSION

Developing fisheries and improving productivity in lakes and reservoirs have been the focus of several West African state ministries

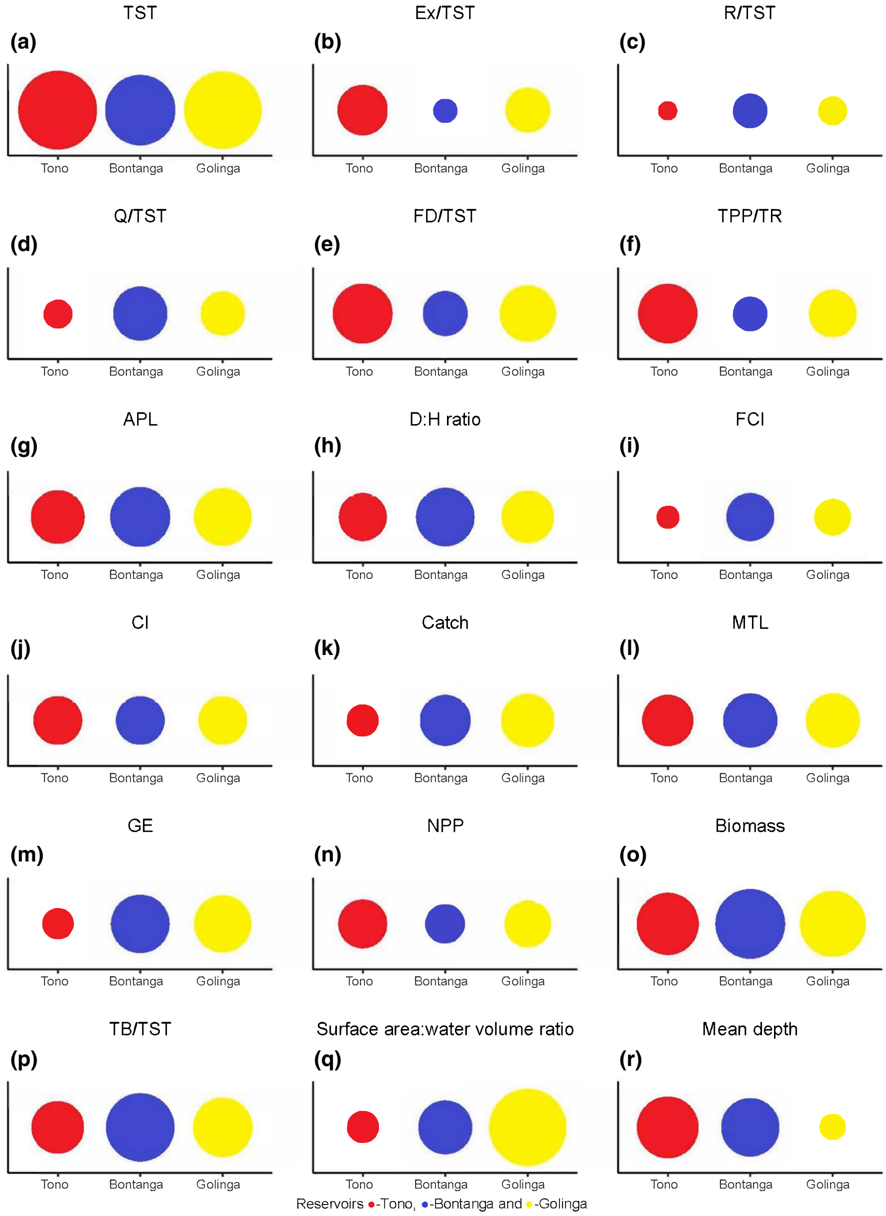

FIGURE 3 Comparison of system indicators of the three reservoirs (Tono in red, Bontanga in blue, Golinga in yellow). The sizes of the bubbles are comparable within each subplot. Ex/TST, export/ total systems throughput (proportion); FD/TST, flow to detritus/total systems throughput (proportion); MTL, mean trophic level of the catch; Q/TST, consumption/total systems throughput (proportion); R/TST, respiration/total systems throughput (proportion); TPP/TR, total primary production/total respiration; TST, total systems throughput. 1) APL, average path length; CI, Connectance index; D:H, detritivory to herbivory ratio; FCI, Finn cycling index; GE, gross efficiency; MTL, mean trophic level of the catch; NPP, net primary production; TB/TST, total biomass/total systems throughput. For exact values, see Table S8

that are responsible for primary industries management. However, reservoirs in the semi-arid regions of Sub-Saharan Africa are threatened by climate change and expanding human populations. Natural river damming has been one of the main human interferences in natural ecosystems in the past 5000 years (Gubiani et al., 2011) and represents the principal way of creating an artificial lake. In Ghana, there are over 1000 dams, with 98% of them being small irrigation dams with individual surface areas not exceeding 5 km^2. Most of these are in northern Ghana, due to the particular aridness of the area. Apart from Akosombo and Bui dams on the Volta system in Ghana, which were constructed for electricity generation, all other dams were constructed mainly for agricultural irrigation purposes. Nevertheless, lakes and reservoirs are the main sources of inland fish production in Ghana. Understanding food web dynamics and ecosystem functioning of these important reservoir ecosystems is crucial for establishing meaningful ecosystem-based management strategies for sustaining local livelihoods.

In this study, three reservoir ecosystems were compared, and standardised methods for field and fisheries data sampling and model construction were used. Judging from the high pedigree values obtained for all models (Tono = 0.72, Bontanga = 0.79 and Golinga = 0.68; Table S8), the input data quality can be considered comparatively high (see Christensen et al., 2008) (Figures S5 and S6). However, some differences in the Pedigree index among the reservoirs were noted and can be related to the number of specific studies on the different reservoirs that supported the models parameterisation. Villanueva, et al. (2006) highlighted the problems associated with using model input parameters from similar models found in the literature and recommended to estimate them whenever possible from in situ sampling of each system. In the present models, biomass, which is one of the most important input parameters in Ecopath, was estimated from in situ sampling and several PB values were derived from in situ fisheries assessments (Abobi, Mildenberger, et al., 2019; Abobi, Oyiadzo, et al., 2019). Furthermore, diet composition of

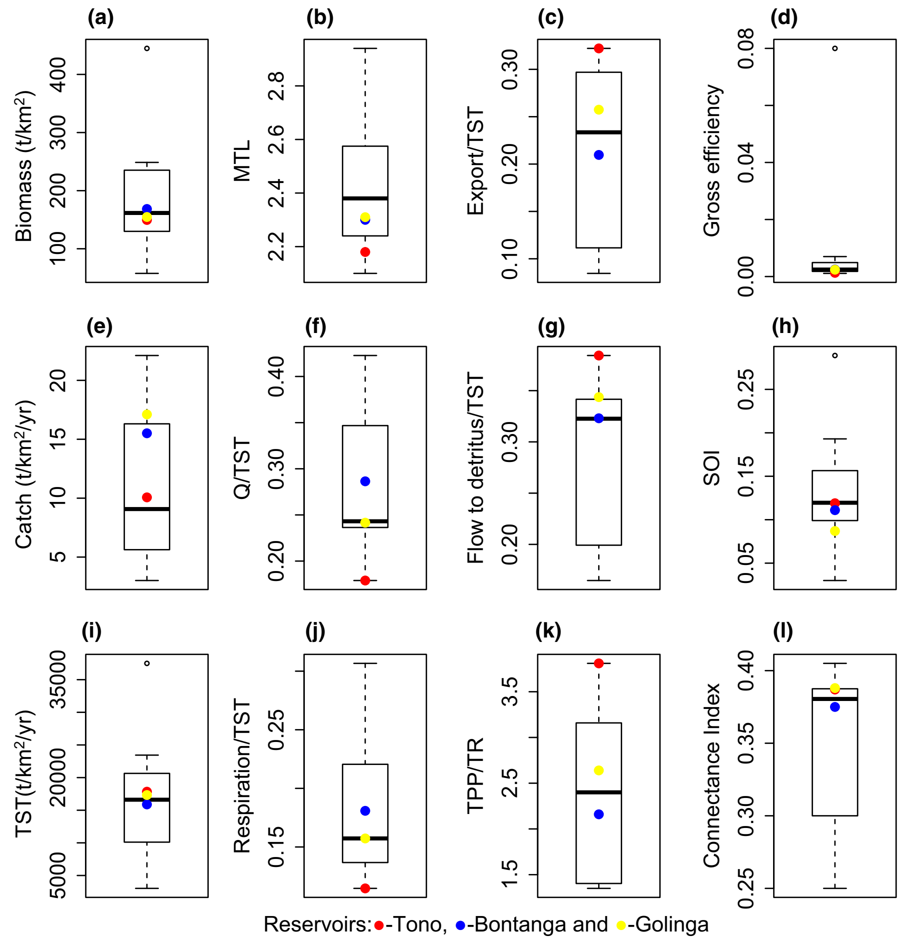

FIGURE 4 Results of ecological indicator calculation for the three studied reservoirs (Tono in red, Bontanga in blue, Golinga in yellow) in comparison with the range of values presented for similar lakes in literature: Ayamé, Côte d'Ivoire (Traore et al., 2008); Bagré, Burkina Faso (Villanueva et al., 2006); Koka, Ethiopia (Tesfaye & Wolff, 2018); Ubolratanad, Thailand, (Villanueva, Isumbisho, et al., 2008; Villanueva, Moreau, et al., 2008); Parakrama Samudrad Sri lanka (Villanueva, Isumbisho, et al., 2008; Villanueva, Moreau, et al., 2008); and Wyrae, India (Panikkar & Khan, 2008). The smallest observation (sample minimum), lower quartile, median, upper quartile, largest observation (sample maximum) and outliers are indicated in the boxplots. MTL, mean trophic level of the catch; Q/TST, consumption/total systems throughput (proportion); SOI, system omnivory index; TPP/TR, total primary production/total respiration; TST, total systems throughput (proportion). For exact values, see Table S8

A. occidentalis in the reservoir systems was analysed from stomach analysis (Abobi, Oyiadzo, et al., 2019) and QB values were calculated for all target fish species based on Abobi, Mildenberger, et al. (2019),

Abobi, Oyiadzo, et al. (2019) and Froese & Pauly (2019) (Table S4). Using these system-specific input data, the models are thus expected to have a high degree of realism.

Using the Ecopath modelling approach, it was possible to describe similarities and to quantify the differences in functional groups composition and food web structures of the three man-made reservoirs. Several functional groups are similarly represented in the three models (Tables S1, S2 and S3), which is not unexpected since all the reservoirs are located within the Guinea Savannah ecoregion of northern Ghana. However, the species have differing biomasses and productivity levels in each ecosystem and some functional groups occupied different trophic levels in each ecosystem (e.g. *Synodontis/Schilbe* and *H. fasciatus*). While the models were considered to exhibit high realism (see above), the PREBAL diagnostic plots (Figures S7–S9) suggest that the biomasses of *C. zillii*, *O. niloticus* and zooplankton may be underestimated in the model for Tono reservoir, as may be the case for the biomasses of *B. nurse*, *C. zillii*, *O. niloticus*, zooplankton and phytoplankton for the Bontanga reservoir and *B. nurse*, *C. zillii*, *Labeo* spp. and zooplankton in the Golinga reservoir. Biomasses of zoobenthos and macrophytes, to the contrary, may potentially be overestimated in the three models. The model for Golinga, in addition, might have the biomasses of *S. galilaeus* and insect and larvae groups being overestimated. In all the three models, the vital rates of the producers were generally lower than their prey (Figures S7–S9). The unexpected relative low biomass levels estimated for the harvested species mentioned may be explained by a large part of the stock's standing stock being constantly removed by the fishery.

4.1 | System differences

After a reservoir is created, the fish community that establishes thereafter tends to be distinctive for each impoundment. This depends on many factors, such as the geography and climate of the lake basin and its catchment, physical and chemical characteristics of its water mass, the composition of the original fish fauna of the basin and the presence or absence of introduced species (Guiral et al., 1999; Winemiller, 1995). Despite these attributes, which are unique to each case, certain characteristics are common to all (Jackson et al., 1988) due to their geographic setting, such as the principal structure of food webs being based on primary producers (macrophytes and phytoplankton), benthic consumer groups and higher predators.

Using the Ecopath modelling approach, differences in food web structures and resource productivities of the three man-made lakes Tono, Bontanga and Golinga were described and quantified. While

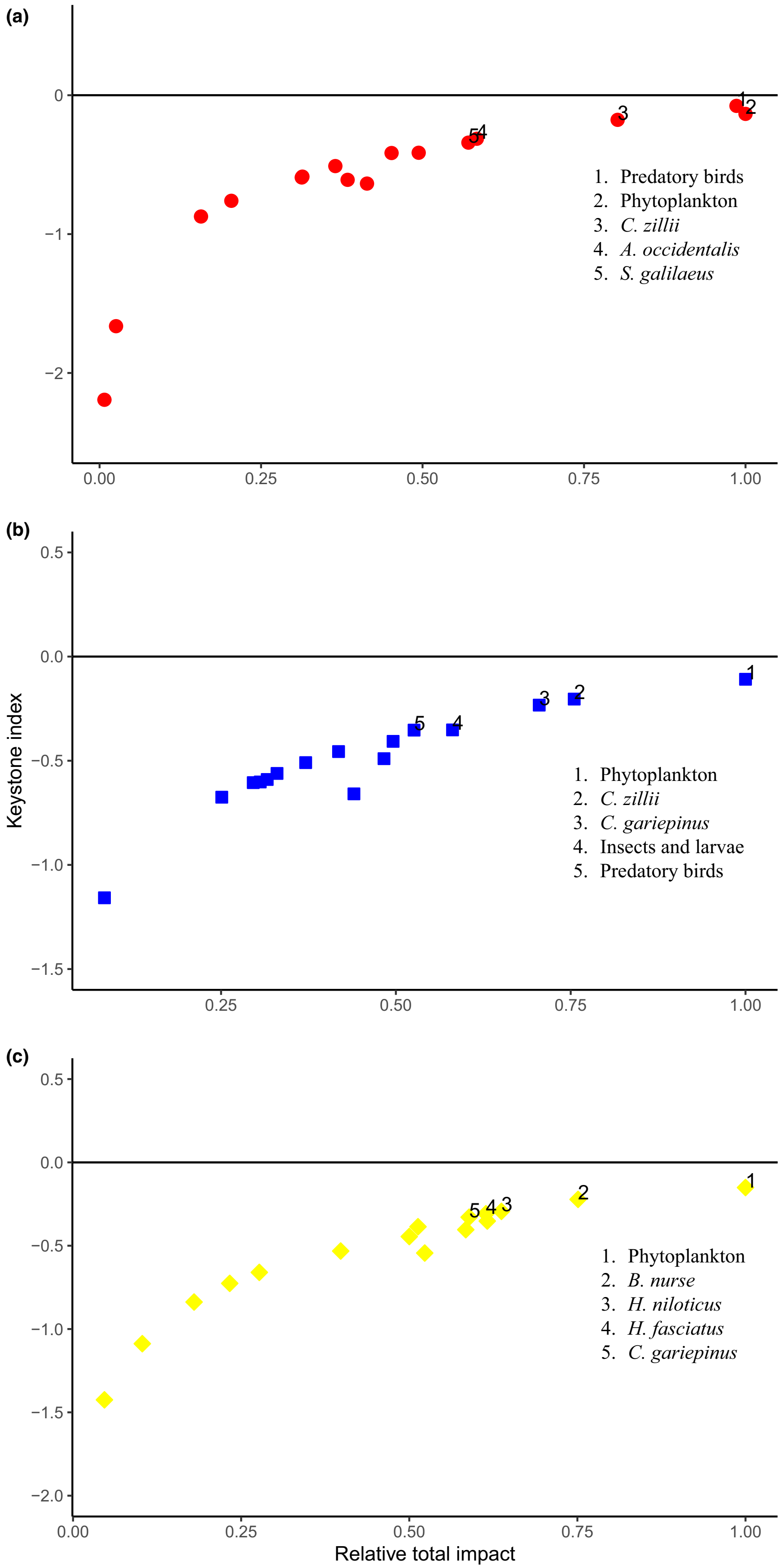

FIGURE 5 Keystoneness as calculated from EwE for the functional groups of the food webs of Tono (a), Bontanga (b) and Golinga (c) reservoir trophic webs. For each functional group, the keystoneness index (*y*-axis) is reported against the overall effect (*x*-axis). Overall effects are relative to the maximum effect measured in each trophic web; thus, for the *x*-axis, the scale is always between 0 and 1. The species are ordered by decreasing keystoneness, and keystone functional groups are those exhibiting indices close to zero

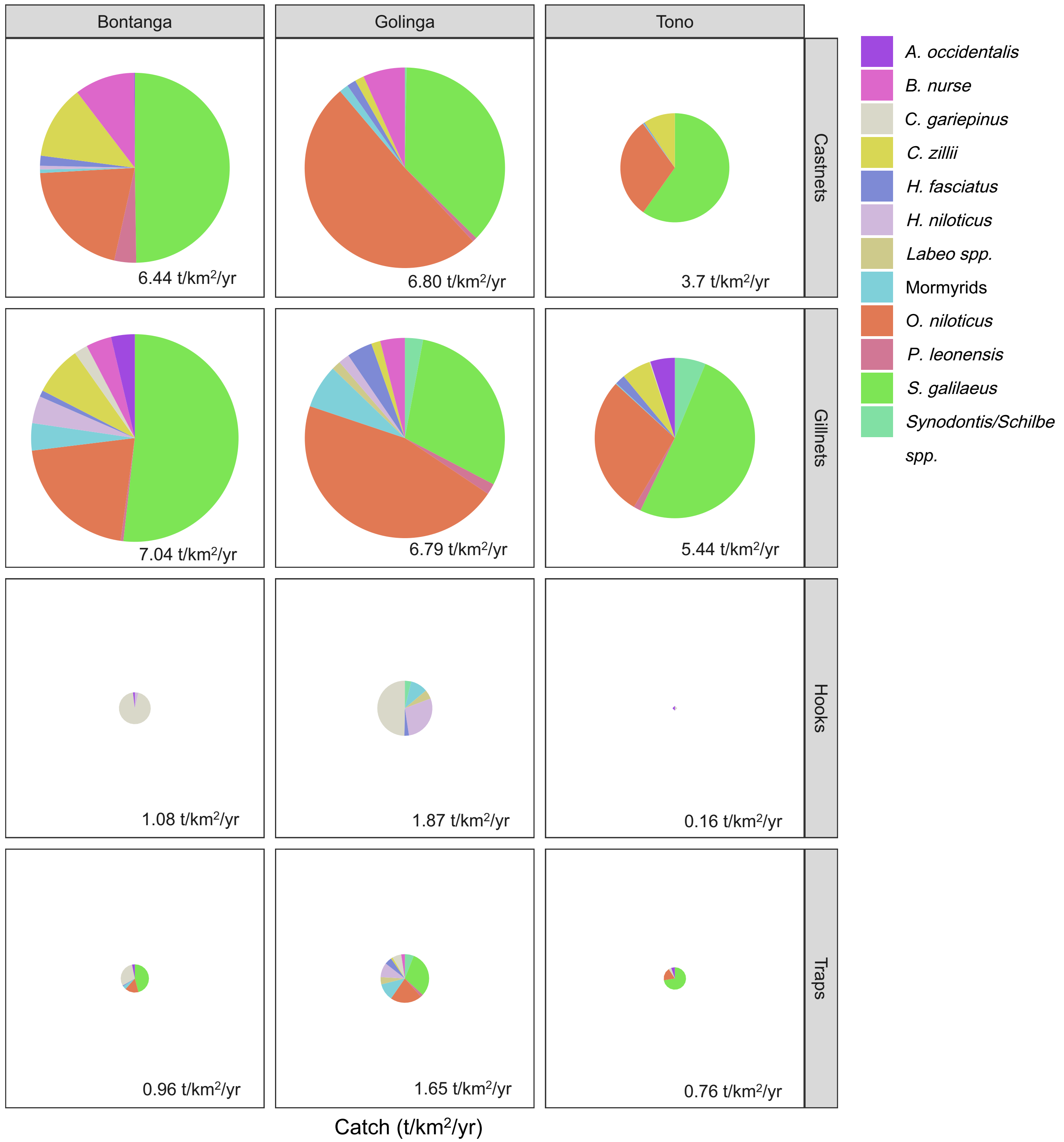

FIGURE 6 Total annual catch (t/km^2/year) per fishing gear (castnets, gillnets, hooks and traps) targeting the fish groups in the three reservoirs (Tono, Bontanga and Golinga). The exploitation of the fisheries resources at the lakes was studied from July 2016 to June 2017. The size of the pie is proportional to the total catch per gear per lake, and total values are also provided. For an overview of catch per trophic level, see Table 2

all the fish species encountered during the study exist in Bontanga, six species (*Brycinus nurse*, *Citharinus citharinus*, *Distichodus engycehpalus*, *Malapterurus electricus*, *Polypterus endlicheri* and *Protopterus annectens*) are lacking in Tono reservoir, whereas in Golinga, four species (*Auchenoglanis occidentalis*, *Citharinus citharinus*, *Distichodus engycehpalus* and *Protopterus annectens*) were not found. The species also differ in productivity levels between the different reservoirs and some functional groups occupy different trophic levels (TL) in each ecosystem, indicative for food web differences between the lakes (e.g. *Synodontis/Schilbe* spp, and *H. fasciatus*). As an example, Nile tilapia (*Oreochromis niloticus*) is twice as productive in Lake Golinga than in Tono and Bontanga, due to the species' preference for shallow waters (FAO, 2009). Tono, the deepest reservoir, had the lowest mean trophic level of the catch due to its deep zones, which seem to serve as refuge habitats for high-trophic-level fish species against fishing, while the medium-size and smallest shallow reservoirs had more high-trophic-level fish species exposed to fishing.

The total fish biomass per unit area and the total annual catch per unit area were highest in the smallest (Golinga) and lowest in the largest (Tono) reservoir. The latter also had the lowest mean trophic level of the catch (Figure 4b) reflecting the high contribution of low-trophic-level fish species (e.g. *O. niloticus*, *S. galilaeus* and *C. zillii*) and the absence of predatory species in the catches. The total fish biomass differs between Tono, Bontanga and Golinga (23.69, 30.34 and 39.94 t/km^2), but all values were within the reported range for other tropical African and Asian inland waters such as lakes Koka (Tesfaye & Wolff, 2018), Bagré (Villanueva, et al., 2006) and Parakrama Samudra (Panikkar & Khan, 2008), with 19.24, 22.63 and 54.7 t/km^2, respectively.

According to Gubiani et al. (2011), Kolding & van Zwieten (2012), Tundisi (1993a), Tundisi (1993b), Tundisi (1988), Tundisi et al. (1993) and Tundisi (1990), the main drivers of lake ecosystem structure and function are as follows: (1) morphometry/shape – the more dendritic a reservoir, the more complex is its morphometry, which introduces several components and increases spatial heterogeneity and variability, creating high biological diversity and gradients in physical and chemical state variables; (2) hydrological cycle and flow characteristics (Baijot et al., 1997) with changes in water level leading to variations in volume, thus modifying niche availability and enhancing nutrient input during floods; and (3) evolution or ageing – the characteristic of succession within a reservoir – with eutrophication having been considered as a major feature of ageing.

According to Post et al. (2000), ecosystem size, rather than resource availability, determines a food-chain length in natural lake ecosystems. This ecosystem-size hypothesis is based on the observed relationship between ecosystem size and species diversity, habitat availability and habitat heterogeneity (Cohen & Newman, 1991; Holt, 1993; Post et al., 2000). Gubiani et al. (2011), on the other hand, tested the relationship between age and maturity in 30 Neotropical reservoirs and concluded that maturity is an inherent characteristic of reservoir ageing, regardless of human interference, reservoir area or the number of species. This alludes to Odum's central theory of ecosystem development (Odum, 1969).

Among the system development indicators proposed by Fath et al. (2019), the Average Path Length (APL, Figure 3g), Detritivory to Herbivory ratio (D: H, Figure 3h) and Finn Cycling Index (FCI, Figure 3i) were highest in Bontanga, the lake with intermediate age and the highest fish species diversity. Moreover, Bontanga was the lake with the lowest P/R ratio, the highest gross efficiency of the fishery and the lowest total primary production /total biomass ratio. All these descriptors suggest that Bontanga is the furthest developed of the three systems studied.

Comparing the P/R results of this study with a meta-analysis by Christensen and Pauly (1993), the intermediate-sized Bontanga appears to be close to a mature state, while Golinga (the smallest) in a developing and Tono (the largest) in an immature state (see also Table S8). The TST of the three systems were higher than those estimated for lakes Bagré in Burkina Faso (Villanueva et al., 2006), Koka in Ethiopia (Tesfaye & Wolff, 2018) and Ubolratana in Thailand (Villanueva, Isumbisho, et al., 2008; Villanueva, Moreau, et al., 2008), but were below the TST values of 23,442.0 and 37,497 reported from Parakrama in Sri lanka (Villanueva, Isumbisho, et al., 2008; Villanueva, Moreau, et al., 2008) and Wyra in India (Panikkar & Khan, 2008), respectively (Figures 3a and 4i; and Table S8).

The largest reservoir (Tono) had the highest primary production (and highest biomass of both phytoplankton and macrophytes) among the three studied reservoirs, which could be related to nutrient loading from terrestrial sources. However, its fish biomass and catch per unit area (Figures 4e and 6) were lowest, and the flow from primary producers to the detritus pool highest, which suggests that its primary production does not directly drive fish production at the higher trophic levels of this lake. A further explanation for the low catches may be that the fishery is unable to access the high-trophic-level species in the deeper more central part of the lake, which would confirm the general low exploitation rates in this lake (Abobi, Mildenberger, et al., 2019). The smallest shallow reservoir (Golinga) had the highest concentrations of dissolved organic carbon and total dissolved nitrogen (See Figure S2) due to high inputs of organic material from agricultural fields and the reservoir's shallow depth. This also supports the high total net primary production calculated for the reservoir.

Due to intense farming in the catchment area of the Tono reservoir, higher nutrient concentrations in Tono than Bontanga were expected, but the nutrient concentrations at the depth of 2 m were similar in both reservoirs (See Figures S2 and S3). This could be due to: (1) immediate and efficient uptake of nutrients transported to the Tono reservoir by primary producers in the water column as suggested by the high transparency of the lake (See Figure S1); and (2) storage of remaining nutrients in the sediments of the comparatively deep Tono reservoir resulting in minimal concentration in the upper water layers (i.e. at the sampling depth of 2 m).

Detritus has an important role in all three reservoir ecosystems studied, but its relative export in Bontanga is approximately 6% lower than the export in Tono and Golinga, (Figures 3e and 4g). As a consequence, less detritus is accumulated and eutrophication is less severe. Although the Tono ecosystem had the highest biomass of macrophytic primary producers, the low transfer efficiency value (4.8%) observed is another reflection of the low coupling/energy transfer between the primary producers and the upper trophic levels. This is further supported by the low EE values estimated for the primary producer groups of this system (Table S1). Moreau, et al., (2001) reported a similar low transfer efficiency of 4.65% in Parakrama Samudra reservoir in Sri Lanka attributing it to the inefficient use of primary production. The low transfer efficiency is also reflected in Tono, where predatory birds exert roles as high TL keystone species with an important top-down control of the food web.

Bontanga appears as the most mature and developed reservoir system based on the system indices calculated, and the overall high fish species diversity found here.

4.2 | Implications for resource management

4.2.1 | Effects of water level fluctuations on fisheries productivity

The findings on total fish catch per area support the stated hypothesis that the smallest reservoir (Golinga) is the most productive system (17.1 t/km^2 fisheries landing; Figure 4e), while it also has the highest intra-annual fluctuation in surface area (52% reduction; Figure 1h, Table 1). This confirms the findings of Kolding et al. (2016) that the more the water level in the system fluctuates on a regular basis, the higher the average productivity. Similarly, shallow and small Africa lakes were described as the most productive by Fernando and Holčík (1982), with fisheries productivity generally declining with increasing lake size Downing (2010). Further studies have shown that seasonal fluctuations in water level are associated with enhanced productivity (Junk et al., 1989; Kolding, 1993; Wantzen et al., 2008) and that small reservoirs can be richer in mineral concentrations than large artificial lakes, but less stable (in Burkina Faso; Baijot and Moreau (1997)). Kolding et al. (2016)) reported increased phosphorous mobilisation following wet–dry cycles owing to the alteration of physical, microbial and chemical processes in the aquatic terrestrial transition zone. However, there should be a sufficient amount of rainfall with associated run-offs to drive the nutrient enrichment of the reservoirs.

It is important to note that in years of high evaporation and little rainfall, too small reservoirs, while highly productive under "normal conditions," may lose a large part (if not all) of their fish productivity. This also means that trends in rainfall, evaporation and siltation can be crucial to the resilience and productivity of over 6000 small and shallow reservoirs in the region (Kolding et al., 2016). There are four main seasons that affect fishing in the lakes and reservoirs of northern Ghana: dry season (January to March; lowest water level), pre-wet season (April to June; water level rising), wet season (July to September; highest water level) and post-wet season (October to December; water level drawdown) (Abban et al., 2000).

Temperature and precipitation data from the Climate Change Knowledge Portal (CCKP, 2019) show differences of 0.44, 0.42 and 0.41°C in average monthly temperature in Tono, Bontanga and Golinga, respectively, when comparing the two periods 1961–1990 and 1991–2016. For the same period, monthly average rainfall decreased by 0.7 mm in Golinga and rose by 1.94 and 0.22 mm in Tono and Bontanga, respectively. However, according to predictions by the Environmental Protection Agency of Ghana (EPA, 2007), rainfall in the entire northern Ghana shall decline between 2.8% and 10.9% by 2050. Considering that Tono, Bontanga and Golinga have surface area: water volume ratios of 0.20, 0.27, and 0.50, respectively, expected water shortage will thus be most severe in the smallest reservoir (Golinga). The larger, rounder and deeper lakes will thus be less affected.

These thoughts are aggravated by the apparent trend of surface area reduction of the studied reservoirs. For the smallest lake (Golinga), a surface area of 1.92 km^2 reported in 1998 (Obodai & Kwofie, 2001; Obodai et al., 2009) was reduced by 68% to 0.62 km^2 in 2016 (present work). Similarly, the intermediate-sized reservoir's (Bontanga) surface area was reduced by 13% from 7.70 km^2 in 2001 (Kwarfo-Apegyah & Ofori-Danson, 2010; Obodai & Kwofie, 2001; Obodai et al., 2009) to 6.70 km^2 in 2017 (present work). Although no baseline value for the surface area of the largest reservoir (Tono) could be found, the 33% surface area reduction from wet to dry season (in 2017) seasonal variations observed during this study period indicates the potential magnitude of change and overall size reduction.

Siltation (sediment loading) is perhaps the single most important factor that affects reservoir ecosystem size, causing a continuous reduction in overall surface area of the reservoir and mean depth. When combined with climatic drivers (i.e. unpredictable rainfall pattern and high evaporation), seasonal changes may become more drastic in the reservoirs affecting system resilience and stability. These dynamics should be carefully monitored and potential mitigation strategies developed, especially when reservoirs reflect important socio-economic contributions to livelihoods of surrounding human communities.

4.2.2 | Impacts of human activities on reservoir ecosystems

In addition to climatic-environmental dynamics, human activities within the catchment area of a reservoir affect the ecosystem functioning and, together with fishing, cause changes in fish species composition and size structure. Adongo (2015) indicated that Tono and Golinga are the reservoirs with the highest number of farmers engaged in irrigated farming at the upstream area of the reservoirs (139 farmers and a farmed area of 42 ha at Tono; 24 farmers and an area of 2.5 ha at Golinga and 11 farmers and an area of 1.2 ha at Bontanga). The number of people (/km^2) depending on the reservoirs is highest for the smallest lake (Golinga) and lowest for the intermediate-sized lake (Bontanga). Unregulated agriculture within catchment areas is a challenge that both Tono and Golinga are already facing. Around the smallest reservoir (Golinga), land preparation for crop cultivation and lack of erosion control likely contribute to the observed high turbidity and associated low water transparency during the dry and the pre-wet seasons (Figure S1). Because there are no legal requirements for protection of buffer zones around rivers, waterbodies and wetlands, the desired minimum buffer width of 60–90 m recommended under the Riparian Buffer Zone Policy for Managing Freshwater Bodies in Ghana (Water Resources Commission, 2013) for protecting reservoir shoreline against degradation and potential future threats (like climate change) is not implemented.

Farming activities including ploughing of land, slash and burn, and animal grazing within the immediate width of the flood zone reduce lake-side vegetation, render the reservoir flood area bare and accelerate erosion and sediment transport. Consequently, the conversion of the reservoirs' buffer zones into croplands and grazing grounds contribute to the reduction in the overall surface area and the mean depth of the reservoir. In the area of the largest reservoir (Tono), the excessive use of fertiliser for crop production has been widely reported (Adazabra et al., 2013; Anim-Gyampo et al., 2013; Pelig-Ba, 2011). As a consequence, aquatic macrophytes develop excessively and affect water quality and fishing activity. This is supported by Adongo (2015) who described distinctive conditions of the three reservoirs. Accordingly, Tono contains considerable amounts of sediments due to irrigated farming at the upstream of the reservoir and floods, Bontanga (the intermediate-sized reservoir) is in good condition, although it contains some sediment. Golinga (the smallest reservoir) is highly loaded with sediments and weeds and has an average siltation rate of 7.7 cm/year. This lake is projected to be filled with 50% sediments in the year 2041, while this percentage is likely to be reached for the lakes Bontanga and Tono in the years 2123 and 2179, respectively (Adongo et al., 2019). This implies a potential loss in fisheries production due to aquatic habitats modification and/or removal and hence urgently requires intervention if fisheries productivity was sought to be maintained.

Considering the competing use of the reservoir's water for both irrigational farming and fisheries production, collaborative efforts are needed to form joint working committees to promote sustainable use of the reservoirs for both agriculture and fisheries production. At present, two government ministries are responsible for Food and Agriculture (MoFA) and Fisheries and Aquaculture Development (MoFAD). Moreover, there is the Ghana Irrigation Development Authority (GIDA) and the Irrigation Company of Upper Regions (ICOUR), which manage the Tono irrigation scheme on behalf of MoFA, and the respective District or the Municipal assemblies (Tono-Kassena Nankana Municipal Assembly, the Bontanga-Kumbungu District Assembly and Golinga-Tolon District Assembly). Collaborative efforts of the above government institutions and authorities are accordingly needed.

5 | CONCLUSIONS

The study presents a comparative analysis of the food web structures and fisheries productivity of three reservoir systems in northern Ghana (Tono, Bontanga and Golinga), which are essential for food security and livelihoods of the rural communities in the region. The fisheries are dominated by tilapiine species (*Sarotherodon galilaeus and Oreochromis niloticus*). The study found differences in lakes' morphometric features that generate differences in ecosystem functioning and fishing activity. Bontanga, which has intermediate characteristics (age, overall surface area, water volume, mean depth, water level fluctuation) and less farming activities in the reservoir's catchment area depicted the highest level of system maturity-showing the narrowest ratio of total primary production to total respiration. While fisheries productivity (per unit surface area) is inversely related to lake size, it was concluded that the use of small reservoirs in populated semi-arid environments for both irrigational farming and fisheries production is unsustainable due to problems associated with seasonal water loss, siltation and aquatic habitat degradation.

It is recommended that the states in semi-arid regions of Sub-Saharan Africa include an ecosystem-based fisheries perspective in the planning and construction of dams to augment the agricultural benefits derived from reservoirs. Such addition is urgently needed in the face of predicted climate change impacts and potential food insecurity in the region. It should be noted that, without prior consideration of fisheries in the larger frame of the reservoir investment, any introduction or fisheries creation thereafter may not fit the ecosystem demands and the fisheries potential of the reservoir.

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REFERENCES

Abban, E.K., Kwarfo-Apegyah, K. & Amedorme, K. (2000) *Annual report on fish monitoring in relation to Orchocerciasis Control Programme in Ghana*. CSIR-Water Research Institute, pp. 80.

Abobi, S.M., Mildenberger, T.K., Kolding, J. & Wolff, M. (2019) Assessing the exploitation status of main fisheries resources in Ghana's reservoirs based on reconstructed catches and a length-based bootstrapping stock assessment method. *Lake and Reservoir Management*, *35*(4), 415–434. https://doi.org/10.1080/10402381.2019.1616340

Abobi, S.M., Oyiadzo, J.W. & Wolff, M. (2019) Comparing feeding niche, growth characteristics and exploitation level of the Giraffe catfish Auchenoglanis occidentalis (Valenciennes, 1775) in the two largest man-made lakes of Northern Ghana. *African Journal of Aquatic Science*, *44*(3), 261–272. https://doi.org/10.2989/16085914.2019.1628704

Adazabra, A.N., Gyasi-Antwi, D. & Nyaaba, R.A. (2013) Biomonitoring of non–essential heavy metals concentrations in the Tono irrigation dam using mussel tissues. *American Journal of Environmental Protection*, *2*(6), 121–127. https://doi.org/10.11648/j.ajep.20130206.11

Adongo, T.A. (2015) *Performance assessment of irrigation schemes in northern Ghana using comparative performance indicators*. (MPhil). University for Development Studies, Tamale. Available from: http://www.udsspace.uds.edu.gh

Adongo, T.A., Kyei-Baffour, N., Abagale, F.K. & Agyare, W.A. (2019) Assessment of reservoir sedimentation of irrigation dams in northern Ghana. *Lake and Reservoir Management*, *36*(1), 87–105. https://doi.org/10.1080/10402381.2019.1659461

Aka, M., Pagano, M., Saint-Jean, L., Arfi, R., Bouvy, M., Cecchi, P. et al. (2000) Zooplankton variability in 49 shallow tropical reservoirs of Ivory Coast (West Africa). *International Review of Hydrobiology*, *85*(4), 491–504.

Alhassan, E., Commey, A. & Bayorbor, T. (2011) An investigation into the food and feeding habits of Sarotherodon galilaeus (Pisces:

Cichlidae) in a shallow tropical reservoir. *Research Journal of Fisheries and Hydrobiology*, *6*(2), 74–77.

Alhassan, E.H. & Ofori-Danson, P.K. (2017) Plankton abundance in relation to physicochemical factors in the Bui reservoir of Ghana's Black Volta River. *African Journal of Ecology*, *55*(1), 12–20. https://doi.org/10.1111/aje.12303

Allen, K.R. (1971) Relation between production and biomass. *Journal of the Fisheries Board of Canada*, *28*(10), 1573–1581. https://doi.org/10.1139/f71-236

Anim-Gyampo, M., Kumi, M. & Zango, M.S. (2013) Heavy metals concentrations in some selected fish species in Tono Irrigation reservoir in Navrongo, Ghana. *Journal of Environment and Earth Science*, *3*(1), 109–119.

Arfi, R., Bouvy, M., Cecchi, P., Corbin, D. & Pagano, M. (2003) Environmental conditions and phytoplankton assemblages in two shallow reservoirs of Ivory Coast (West Africa). *Archiv für Hydrobiologie*, *156*(4), 511–534. https://doi.org/10.1127/0003-9136/2003/0156-0511

Atindana, S., Bulley, R., Alhassan, E. & Abarike, E. (2014) *Stomach content Analyses of Tilapia zillii and Hemichromis fasciatus in the Golinga reservoir in the Tolon district of the northern region of Ghana*. Proceedings of the 32ndbiennial conference of the Ghana Animal Science Association. Available from: http://www.udsspace.uds.edu.gh/handle/123456789/222 [Accessed 20th September 2019].

Baijot, E. & Moreau, J. (1997) *Biology and demographic status of the main fish species in the reservoirs of Burkina Faso. Hydrobiological aspects of fisheries in small reservoirs in the Sahel region*. Technical Center for Agricultural and Rural Cooperation ACP-EU, Wageningen, Netherlands, 79–110.

Baijot, E., Moreau, J. & Bouda, S. (1997) *Hydrobiological aspects of fisheries in small reservoirs in the Sahel region: CTA*. The Netherlands: Wageningen.

Brown, P., Painting, S. & Cochrane, K. (1991) Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *South African Journal of Marine Science*, *11*(1), 537–564. https://doi.org/10.2989/025776191784287673

Brush, M.J., Brawley, J.W., Nixon, S.W. & Kremer, J.N. (2002) Modeling phytoplankton production: problems with the Eppley curve and an empirical alternative. *Marine Ecology Progress Series*, *238*, 31–45. https://doi.org/10.3354/meps238031

CCKP. (2019) *Climate change knowledge portal for development practitioners and policy makers*. World Bank Group. Available from: https://climateknowledgeportal.worldbank.org/

Christensen, V. (1995) Ecosystem maturity—towards quantification. *Ecological modelling*, *77*(1), 3–32.

Christensen, V. & Pauly, D. (1992) ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological modelling*, *61*(3–4), 169–185. https://doi.org/10.1016/0304-3800(92)90016-8

Christensen, V. & Pauly, D. (1993) Trophic models of aquatic ecosystems. *Conference Proceedings*, *26*, 390.

Christensen, V., Walters, C.J. & Pauly, D. (2000) *Ecopath with Ecosim: a user's guide*. Penang, Malaysia: Fisheries Centre, Vancouver, Canada and ICLARM, pp. 131.

Christensen, V., Walters, C.J., Pauly, D. & Forrest, R. (2008) *Ecopath with Ecosim version 6 user guide*. Lenfest Ocean Futures Project, 235.

Cohen, J.E. & Newman, C.M. (1991) Community area and food-chain length: theoretical predictions. *The American Naturalist*, *138*(6), 1542–1554 https://doi.org/10.1086/285299

Del Hoyo, J., Elliott, A. & Sargatal, J. (1992) *Handbook of the birds of the world* (Vol. *1*). Barcelona: Lynx Edicions.

Downing, J.A. (2010) Emerging global role of small lakes and ponds. *Limnetica*, *29*(1), 0009–0024.

Downing, J.A., Plante, C. & Lalonde, S. (1990) Fish production correlated with primary productivity, not the morphoedaphic index. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(10), 1929–1936. https://doi.org/10.1139/f90-217

EPA. (2007) *Climate change and the Ghanaian economy*. EPA Accra: Policy Advice Series.

FAO. (2009) Oreochromis niloticus. In *Cultured aquatic species fact sheets*. Text by Rakocy, J. E. Edited and compiled by Valerio Crespi and Michael New. CD-ROM (multilingual). Available from http://www.fao.org/fishery/docs/CDrom/aquaculture/I1129m/file/en/en_niletilapia.htm [Accessed 10th October 2019].

Fath, B.D., Asmus, H., Asmus, R., Baird, D., Borrett, S.R., de Jonge, V.N. et al. (2019) Ecological network analysis metrics: the need for an entire ecosystem approach in management and policy. *Ocean & Coastal Management*, *174*, 1–14. https://doi.org/10.1016/j.ocecoaman.2019.03.007

Fernando, C. & Holčík, J. (1982) The nature of fish communities: a factor influencing the fishery potential and yields of tropical lakes and reservoirs. *Hydrobiologia*, *97*(2), 127–140 https://doi.org/10.1007/BF00011966

Finlayson, C., Gordon, C., Ntiamoa-Baidu, Y., Tumbulto, J. & Storrs, M. (2000) *Hydrobiology of the Songor and Keta lagoons: implications for wetland management in Ghana*. Supervising Scientist Report 152. Supervising Scientist, Darwin, pp. 167.

Froese, R. & Pauly, D. (2019). Editors. 2019. *FishBase*. World Wide Web Electronic Publication. Available from: http://ww.fishbase.org, version (02/2019).

Ghana Statistical Service. (2012) *2010 population and housing census report*. Accra, Ghana: Ghana Statistical Service.

Gordon, C. (2006) *Background Paper for The Multi-stakeholder consultation process for dams development in Ghana*. Volta Basin Research Project, University of Ghana, Ghana, pp. 12–36.

Gubiani, É.A., Angelini, R., Vieira, L.C., Gomes, L.C. & Agostinho, A.A. (2011) Trophic models in Neotropical reservoirs: testing hypotheses on the relationship between aging and maturity. *Ecological modelling*, *222*(23–24), 3838–3848. https://doi.org/10.1016/j.ecolmodel.2011.10.007

Guiral, D., Albaret, J., Baran, E., Bertrand, F., Debenay, J., Diouf, P. et al. (1999) *Les écosystèmes à mangrove*. Rivières du Sud. Sociétés et mangroves ouest-africaines. Cormier-Salem MC, IRD Éditions, Paris, pp. 65–130.

Hayes, N.M., Deemer, B.R., Corman, J.R., Razavi, N.R. & Strock, K.E. (2017) Key differences between lakes and reservoirs modify climate signals: a case for a new conceptual model. *Limnology and Oceanography Letters*, *2*(2), 47–62 https://doi.org/10.1002/lol2.10036

Henderson, H. & Welcomme, R. (1974). *The relationship of yield to morphoedaphic index and numbers of fishermen in African inland fisheries*. CIFA Occasional Paper, 1, FAO Food and Agriculture Organization of the United Nations, CIFA/OP1.

Holmes, R.W. (1970) The Secchi disk in turbid coastal waters 1. *Limnology and Oceanography*, *15*(5), 688–694. https://doi.org/10.4319/lo.1970.15.5.0688

Holt, R.D. (1993) Ecology at the mesoscale: The influence of regional processes on local communities. In Ricklefs, R.E. & Dchluter, D. (Eds.) *Species diversity in ecological communities*. Chicago: Univ. Chicago Press, pp. 77–88.

Jackson, P., Marshall, B. & Paugy, D. (1988) Fish communities in manmade lakes. In: Lévêque, C., Bruton, M.N. & Ssentongo, G.W. (Eds.) *Biology and ecology of African freshwater fishes*. Paris: Editions de l'ORSTOM, pp. 325–350.

Jeppesen, E., Jensen, J.P., Søndergaard, M., Lauridsen, T., Pedersen, L.J. & Jensen, L. (1997). Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. In Kufel, L., Prejs, A. & Rybak, J.I. (Eds.), *Shallow Lakes' 95*. Dordrecht: Springer, pp. 151–164. https://doi.org/10.1007/978-94-011-5648-6_17

Jeppesen, E., Søndergaard, M., Jensen, J.P., Mortensen, E., Hansen, A.-M. & Jørgensen, T. (1998) Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: an 18-year study of a shallow hypertrophic lake. *Ecosystems*, *1*(3), 250–267. https://doi.org/10.1007/s100219900020

Jul-Larsen, E., Kolding, J., Overa, R., Nielsen, J.R. & van Zwieten, P. (2003) *Management, co-management or no management? Major Dilemmas in Southern African freshwater fisheries*. 1. Synthesis report. Food and Agriculture Organisation, UN. FAO Fisheries Technical Paper. No. 426/1.

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989). *The flood pulse concept in river-floodplain systems*. Proceedings of the International Large River Symposium. Dodge, DP (Ed). Can. Spec. Publ. Fish. Aquat. Sci, pp. 110–127.

Kao, Y.-C., Adlerstein, S.A. & Rutherford, E.S. (2016) Assessment of top-down and bottom-up controls on the collapse of alewives (Alosa pseudoharengus) in Lake Huron. *Ecosystems*, *19*(5), 803–831. https://doi.org/10.1007/s10021-016-9969-y

Khan, M.F. & Panikkar, P. (2009) Assessment of impacts of invasive fishes on the food web structure and ecosystem properties of a tropical reservoir in India. *Ecological modelling*, *220*(18), 2281–2290.

Kolding, J. (1993) *Trophic interrelationships and community structure at two different periods of Lake Turkana, Kenya: a comparison using the ECOPATH II box model*. Paper presented at the Trophic models of aquatic ecosystems. ICLARM Conference Proceedings, pp. 116–123.

Kolding, J. & van Zwieten, P.A. (2012) Relative lake level fluctuations and their influence on productivity and resilience in tropical lakes and reservoirs. *Fisheries Research*, *115*, 99–109. https://doi.org/10.1016/j.fishres.2011.11.008

Kolding, J., van Zwieten, P., Marttin, F. & Poulain, F. (2016) *Fisheries in the drylands of Sub-Saharan Africa "Fish come with the Rains"*. Building resilience for fisheries-dependent livelihoods to enhance food security and nutrition in the drylands (FAO Fisheries and Aquaculture Circular No 1118). Rome.

Kwarfo-Apegyah, K. & Ofori-Danson, P.K. (2010) Spawning and recruitment patterns of major fish species in Bontanga Reservoir, Ghana, West Africa. *Lakes & Reservoirs: Research & Management*, *15*(1), 3–14. https://doi.org/10.1111/j.1440-1770.2010.00418.x

Kwarfo-Apegyah, K., Ofori-Danson, P. & Nunoo, F. (2008) Exploitation rates and management implications for the fisheries of Bontanga Reservoir in the Northern region of Ghana. *West African Journal of Applied Ecology*, *14*(1), 1–24.

Libralato, S., Christensen, V. & Pauly, D. (2006) A method for identifying keystone species in food web models. *Ecological modelling*, *195*(3–4), 153–171. https://doi.org/10.1016/j.ecolmodel.2005.11.029

Lindeman, R.L. (1942) The trophic-dynamic aspect of ecology. *Ecology*, *23*(4), 399–417. https://doi.org/10.2307/1930126

Matsuishi, T., Muhoozi, L., Mkumbo, O., Budeba, Y., Njiru, M., Asila, A. et al. (2001) A synoptic Ecopath model of biomass flows during two different static ecological situations in Lake Nakuru (Kenya). *Hydrobiologia*, *458*(1–3), 63–74. https://doi.org/10.1023/A:1013171810026

Moreau, J., Villanueva, M., Amarasinghe, U. & Schiemer, F. (2021) Trophic relationships and possible evolution of the production under various fisheries management strategies in a Sri Lankan reservoir. In: De Silva, S.S (Ed.) *Reservoir and culture-based fisheries: biology and management*. Proceedings of an International Workshop held in Bangkok, Thailand from 15-18 February2000. ACIAR Proceedings No. 98, pp. 201–214.

Namara, R.E., Horowitz, L., Nyamadi, B. & Barry, B. (2011) *Irrigation development in Ghana: past experiences, emerging opportunities, and future directions*. Ghana Strategy Support Program (GSSP) Working Paper No. 0027. Ghana: International Food Policy Research Institute-Accra, pp. 50.

Natugonza, V., Ainsworth, C., Sturludóttir, E., Musinguzi, L., Ogutu-Ohwayo, R., Tomasson, T. et al. (2019) Ecosystem models of Lake Victoria (East Africa): can Ecopath with Ecosim and Atlantis predict similar policy outcomes? *Journal of Great Lakes Research*, *45*(6), 1260–1273.

Natugonza, V., Ogutu-Ohwayo, R., Musinguzi, L., Kashindye, B., Jónsson, S. & Valtysson, H.T. (2016) Exploring the structural and functional properties of the Lake Victoria food web, and the role of fisheries, using a mass balance model. *Ecological modelling*, *342*, 161–174.

Nilssen, J.P. (1984) Tropical lakes—functional ecology and future development: The need for a process-orientated approach. *Hydrobiologia*, *113*(1), 231–242. https://doi.org/10.1007/BF00026611

Niyonkuru, C., Lalèyè, A., Villanueva, M. & Moreau, J. (2007) *Population parameters of main fish species of Lake Nokoué, Bénin, West Africa*. Paper presented at the Journal of Afrotropical Zoology, Proceedings of the Third International Conference on Africa Fish and Fisheries, Cotonou, Benin, 10–14 November 2003, Special issue.

Obodai, E. & Kwofie, J. (2001) Fish species composition and efficiency of selected gill nets used in Bontanga Reservoir. *Development Spectrum, An Inter-faculty Journal of the University for Development Studies*, *1*(1), 4–10.

Obodai, E., Muhammad, B., Obodai, G. & Opoku, E. (2009) Effect of fuel wood on the quality of smoked freshwater fish species sold in Tamale Central Market, Northern Region. *Ghana. Ethiopian journal of environmental studies and management*, *2*(2), 27–35. https://doi.org/10.4314/ejesm.v2i2.45917

Odum, E.P. (1969) The strategy of ecosystem development. In Ndubisi, F.O. (eds) *The ecological design and planning reader*. Washington, DC: Island Press. https://doi.org/10.5822/978-1-61091-491-8_20.

Odum, E.P. (1971). *Fundamentals of ecology*. Phyladelphia: WB Saunders Company. Pusat Kajian Sumberdaya Pesisir dan Lautan. Institut Pertanian Bogor, pp. 574.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in ecology & evolution*, *14*(12), 483–488. https://doi.org/10.1016/S0169-5347(99)01723-1

Palomares, M.L.D. & Pauly, D. (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research*, *49*(5), 447–453. https://doi.org/10.1071/MF98015

Panikkar, P. & Khan, M.F. (2008) Comparative mass-balanced trophic models to assess the impact of environmental management measures in a tropical reservoir ecosystem. *Ecological Modelling*, *212*(3–4), 280–291. https://doi.org/10.1016/j.ecolmodel.2007.10.029

Pelig-Ba, K.B. (2011) Levels of agricultural pesticides in sediments and irrigation water from Tono and Vea in the Upper East of Ghana. *Journal of Environmental Protection*, *2*(06), 761–768.

Polovina, J. & Ow, M. (1985) An approach to estimating an ecosystem box model. *Fishery Bulletin*, *83*(3), 457–460.

Post, D.M., Pace, M.L. & Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes. *Nature*, *405*(6790), 1047–1049. https://doi.org/10.1038/35016565

Rai, H. & Hill, G. (1980) Classification of central Amazon lakes on the basis of their microbiological and physico-chemical characteristics. *Hydrobiologia*, *72*(1–2), 85–99. https://doi.org/10.1007/BF0001623

Rawson, D. (1938). Some physical and chemical factors in the metabolism of lakes. In Moulton, F.R. (Ed.), *Problems of lake biology*. USA: Publ. No. 10, American Association for the Advancement of Science, Science Press, pp. 9–26.

Rehren, J., Wolff, M. & Jiddawi, N. (2018) Holistic assessment of Chwaka Bay's multi-gear fishery–using a trophic modeling approach. *Journal of Marine Systems*, *180*, 265–278. https://doi.org/10.1016/j.jmarsys.2018.01.002

Ricker, W.E. (1969). Food from the sea. In Treeman, W.H. (Ed.), *Resources and man, a study and recommendations by the committee on resources and man*. San Francisco, pp. 87–108.

Ribeiro Filho, R.A., de Almeida Pereira, J.M. & Benassi, S.F. (2014). Estimating fish production in the Itaipu reservoir (Brazil): the relationship between fish trophic guilds, limnology, and application of morphoedaphic index. In Ansari, A.A. & Gill, S.S. (Eds.), *Eutrophication: causes, consequences and control*. Springer, pp. 165–190. https://doi.org/10.1007/978-94-007-7814-6_13

Ryder, R.A., Kerr, S.R., Loftus, K.H. & Regier, H.A. (1974) The morphoedaphic index, a fish yield estimator — review and evaluation. *Journal of the Fisheries Research Board of Canada*, *31*(5), 663–688. https://doi.org/10.1139/f74-097

Shirley, M.H., Oduro, W. & Beibro, H.Y. (2009) Conservation status of crocodiles in Ghana and Côte-d'Ivoire, West Africa. *Oryx*, *43*(1), 136–145. https://doi.org/10.1017/S0030605309001586

Small Grants Programme. (2012) *Integrated pest management for promoting sustainable integrated rice-fish farming under irrigation in Golinga*. Available from: https://sgp.undp.org/index.php?option=com_sgpprojects&view=projectdetail&id=13516&Itemid=205.

Talling, J. & Talling, I.B. (1965) The chemical composition of African lake waters. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, *50*(3), 421–463. https://doi.org/10.1002/iroh.19650500307

Tesfaye, G. & Wolff, M. (2018) Modeling trophic interactions and the impact of an introduced exotic carp species in the Rift Valley Lake Koka, Ethiopia. *Ecological modelling*, *378*, 26–36. https://doi.org/10.1016/j.ecolmodel.2018.04.003

Traore, A., Ouattara, A., Doumbia, L., Tah, L., Moreau, J. & Gourène, G. (2008) Trophic structure and interactions in Lake Ayamé (Côte d'Ivoire). *Knowledge and Management of Aquatic Ecosystems* (388), 02. https://doi.org/10.1051/kmae:2008002

Tundisi, J.G. (1988). *Limnologia e Manejo de Represas*. Serie: Monografias em Limnologia, *2* vol 1, Tom0 1,2. ACIESP, Siio Paulo, Brazil.

Tundisi, J.G. (1990) Perspectives for ecological modelling of tropical and subtropical reservoirs in South America. *Ecological Modelling*, *52*(1–2), 7–20. https://doi.org/10.1016/0304-3800(90)90003-Y

Tundisi, J.G. (1993a) Man-made lakes. Theoretical basis for reservoir management. *Vehandlunger International Verein Limnologie*, *25*(2), 1153–1156. https://doi.org/10.1080/03680770.1992.11900344

Tundisi, J.G. (1993b) *Represas do Paraná superior: limnologia e bases científicas para o gerenciamento*. Conferencias de Limnología. Instituto de Limnología Dr. RA Ringuelet, 993.

Tundisi, J.G., Matsumura-Tundisi, T. & Calijuri, M.D.C. (1993) Limnology and management of reservoirs in Brazil. *Comparative reservoir limnology and water quality management*. Springer, pp. 25–55.

Ulanowicz, R. & Puccia, C. (1990) Mixed trophic impacts in ecosystems. *Coenoses*, *5*(1), 7–16.

Villanueva, M.C.S., Isumbisho, M., Kaningini, B., Moreau, J. & Micha, J.-C. (2008) Modeling trophic interactions in Lake Kivu: What roles do exotics play? *Ecological modelling*, *212*(3–4), 422–438.

Villanueva, M., Moreau, J., Amarasinghe, U. & Schiemer, F. (2008) A comparison of the foodweb and the trophic structure between two Asian reservoirs by using ECOPATH with ECOSIM and ECOSPACE. In: Schiemer, F., Simon, D., Amarasinghe, U.S. & Moreau, J. (Eds.), *Aquatic ecosystem and development: comparative asian perspectives*. Leiden, The Netherlands: Biology of Inland Waters, Backhuys Publishers, pp. 413–434.

Villanueva, M.C., Ouedraogo, M. & Moreau, J. (2006) Trophic relationships in the recently impounded Bagré reservoir in Burkina Faso. *Ecological modelling*, *191*(2), 243–259. https://doi.org/10.1016/j.ecolmodel.2005.04.031

Wantzen, K.M., Junk, W.J. & Rothhaupt, K.-O. (2008) An extension of the floodpulse concept (FPC) for lakes. *Hydrobiologia*, *613*(1), 151–170 https://doi.org/10.1007/978-1-4020-9192-6_15

Water Resource Commission. (2013) *Riparian buffer zone policy for managing freshwater bodies in Ghana*. Government of Ghana, Ministry of Water Resources, Works and Housing, p. 35. Available from: http://www.wrc-gh.org/documents/acts-and-regulations/.

Winemiller, K. (1995) Aspects structurels et fonctionnels de la biodiversité des peuplements de poissons. *Bulletin Français de la Pêche et de la Pisciculture* (337–338-339), 23–45. https://doi.org/10.1051/kmae:1995007

Yodzis, P. & Winemiller, K.O. (1999) In search of operational trophospecies in a tropical aquatic food web. *Oikos*, 327–340.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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