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West African reservoirs and their fisheries: An assessment of harvest potential

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ABSTRACT

A major constraint to science-based fish stock management in West Africa is the lack of reliable data on target stocks. This especially holds true for inland fisheries, such as those that operate in reservoirs. Due to the low availability of resources and population data, and the limited number of fisheries experts in the region, state institutions and investigators rely heavily on simple catch statistics and empirical models for their estimations of fish production and potential yields. This paper reviews data from the FAO, and published articles and reports on West African reservoirs, with special reference to their morphometric and environmental features in relation to fish catch. In addition, we analyse primary data on three focus reservoirs. First, to improve and update available models of potential harvests from reservoirs, we regress fish catch data against reservoir surface area data for 30 reservoirs in West Africa, yielding the following equation: Catch (tonnes/year) $= 17.3 \times$ Area $(\text{km}^2)^{0.8626}$. The equation accounts for 95.7% of the variation observed in the fish catches. Analysis of covariance of small (<2 km^2) and large (>2 km^2) reservoirs shows no significant difference ($F = 0.5895$, $p = 0.45$) in the slopes of the two groups. Second, we apply multiple regressions to a sub dataset of 15 reservoirs with surface area and mean depth as predictors; and we also explore reservoir age as a further variable. We find that fisheries productivity is inversely correlated with both mean depth ($r = -0.49$) and surface area ($r = -0.32$), but there is no significant correlation found with reservoir age ($r = 0.03$).

1. Introduction

In developing countries, more than 60 million people rely on freshwater fisheries for their livelihood. Seventy-one low-income countries currently produce nearly seven million tonnes of fish a year, representing 80% of global inland fisheries capture (FAO, 2015). In West Africa, freshwater fish production is highly important to the food security of human populations (Pauly, 2017) with reservoirs, lakes and rivers throughout the region being important sources of protein and micronutrients. This sub-region has an average per capita fish consumption of 12.1 kg/year. Notwithstanding the importance of this industry, limited research has been focused on the reservoir fisheries in Western Africa. The FAO data on fish catch and fish supply in the region suggest that all fish capture from inland waters is being used for consumption within the region (Fig. 1), and

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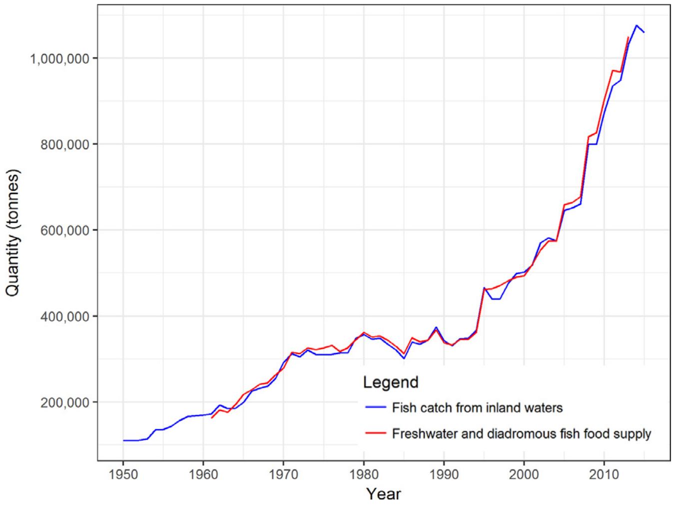

Fig. 1. Fish catch from inland waters and freshwater and diadromous fish food supply in Western Africa. Data Source: (FAO, 2017).

Kolding et al. (2016b) highlight the importance of fisheries and aquaculture to the livelihoods of drylands communities of sub-Saharan Africa. However, despite the fact that it has been widely reported there are several thousand reservoirs (Kolding et al., 2016b; Marshall and Maes, 1994; and Venot et al., 2012) in sub-Saharan Africa, no accurate estimates of the number exist, nor their potential contribution to total inland fisheries capture.

Statistical models (mostly linear regressions) relating morphometric and edaphic factors to fish yields in temperate lakes and reservoirs were developed in the 1950s and 1960s. These showed that fish production in Canadian lakes was related to mean depth (Rawson, 1952), to water chemistry (Moyle, 1956) and to physical and chemical indices (Northcote and Larkin, 1956). Ryder (1965) combined these indices into a “morpho-edaphic index (MEI)” (defined as the total dissolved solids divided by the mean depth), for which he used 23 temperate lakes.

In tropical fresh water fisheries, the first application of Ryder’s MEI was that of Henderson and Welcomme (1974), who applied it to a selected number of African inland waters. The MEI was related to yields from African tropical lakes and reservoirs, and from the Lake Bangweulu System (Toews and Griffith, 1979). In a further development of the model, a review on MEI was made by Schlesinger and Regier (1982) and, subsequently, fish yields from reservoirs were related to MEI by Bernacsek and Lopes (1984), and Marshall (1984). Youngs and Heimbuch (1982) were able to show that the surface area of a lake alone, is a very powerful predictor of catch. Marshall (1984) applied their model: $\log_e$ (Yield, in tonnes per year tyr^{-1})= $7.01 + 0.83 \log_e$ (Area, km^2), for the first time, to 17 African lakes and reservoirs. Later, Crul (1992) used a data set of 25 reservoirs, with catch data spanning from 1954–1984, to update this work and derived the following model: Catch (tyr^{-1}) = 7.09 $Area^{0.94}$ ($r^2 = 0.94$). Ideally, these models should be updated periodically to accommodate new information as it becomes available. For example, studies by Bhukaswan (1980) and Gubiani et al. (2011) showed that the catch obtained from a water body may depend largely on the developmental state of the fishery; a significant finding, such as this, should be reflected in the models. However, due to limited catch data and limited resources, many of the models currently in use are old and in need of updating (Welcomme, 2011). Youngs and Heimbuch (1982); Marshall (1984) and Crul (1992) have all shown that, of all the factors analysed, surface area is the most powerful predictor of total catch in African reservoirs. Other factors such as primary production (Melack, 1976; Oglesby, 1977), water level fluctuations and discharge (FAO, 2016b; Kolding and van Zwieten, 2011) and total phosphorus levels (Hanson and Leggett, 1982), could also be useful predictors of fish yield but, unfortunately, information on these factors is only available for a very limited number of African inland waters. In this paper, we make an inventory of reservoirs in the region and analyse their potential harvest. In developing our model, we consider the following two observations:

(i) The current, observed total catch of reservoirs is not adequately predicted by the Crul (1992) model, since 28 of the West African sub-region reservoirs have catches that exceed the yields predicted by Crul’s model by an average of 50% (See Supplement Table S1).

(ii) Crulś model was developed using datasets from a broad region (Africa). Considering the potential geographic differences in resource productivities (highlighted by Marten and Polovina (1982); Welcomme and Bartley (1998); and Yamada and Ruttan (1980)), our model, in contrast to Crul’s, is limited to datasets from Western Africa only.

Reservoirs are man-made impoundments created mostly as a result of dam construction on rivers. They are used for community purposes including drinking water supply (e.g. Weija, and Barekese, Ghana), irrigation farming (e.g. Tono, Ghana; Bagré, Burkina Faso), and hydroelectric power generation (e.g. Kainji, Nigeria; Manantali and Sélingué, Mali). These waterbodies vary greatly in their surface areas and in other morphometric features such as their mean depth, water holding capacity and discharge. In most West African countries, fisheries normally develop as an incidental benefit or an intended livelihood as a result of reservoir construction. Considering the stagnating trend in marine capture fisheries production in the region, the potential contribution of reservoirs, and other inland water bodies, to capture fisheries production in the region should be explored to provide essential information for national fisheries management strategies. Additionally, the question of how morphometric characteristics of reservoirs, in the semi-arid region of West Africa, relate to fisheries productivity needs to be understood.

The tilapiine species (*S. galilaeus* and *O. niloticus*) of the family Cichlidae are the main fisheries resources in most African lakes and reservoirs (FAO, 2003). We present here, known data from a selection of the reservoirs. At Asejire reservoir, Nigeria, 19 fish species from 16 genera and 13 families were recorded during experimental gill nets fishing; the family Cichlidae were the most dominant, among which *Tilapia marie* was the most common species (Ipinmoroti et al., 2017). In Ghana, targeted cichlid species represented 89%, 74%, and 71% of the total catch composition (landed weight) at Tono, Bontanga, and Golinga reservoirs, respectively (Abobi et al., 2019). In Côte d'Ivoire, the catch composition of Taboo reservoir showed predominance of *Chrysichthys* spp. (58.4%) and tilapiine fish (35.8%). Other fish species such as *Clarias* spp. (2.5%), Mormyrids (1%), *Heterotis niloticus* (0.8%) and *Schilbe* spp. (0.7%) were represented (Aliko et al., 2014). In the Reservoir Ayamé, Côte d'Ivoire, the most abundant families were Alestidae (36.61%), Cichlidae (34.19%), and Claroteidae (13.43%) (Mamadou et al., 2019) and in Reservoir Buyo, Côte d'Ivoire, the fish biomass was dominated by Cichlidae (32.27%) and Claroteidae (26.35%). In Mali, the top five most frequently encountered species at: i) Reservoir Manantali were *Lates niloticus* (74.6%), *Sarotherodon galilaeus* (65.7%), *Oreochromis aureus* (61.2%), *Synodontis schall* (43.1%), and *Synodontis ocellifer* (40.8%); and ii) Reservoir Selengue were *Chrysichthys nigrodigitatus* (34.6%), *Auchenoglanis occidentalis* (34.1%), *Sarotherodon galilaeus* (32%), *Labeo senegalensis* (29.4%), and *Synodontis membranaceus* (26.4%) (Laë et al., 2004).

The main objective of this contribution is, thus, to review the sparse information on total fish catch of West African reservoirs and derive an updated, predictive model for fisheries production from the reservoirs. Following the reasoning of Oglesby (1977) and Petrere (1996), on the relationship between lake size and fish yields, the paper explores the potential differences in productivity between small and large reservoirs, and considers further potential predictors for the fish catch (such as mean reservoir depth and age).

2. Materials and methods

2.1. Geographic and climatic characteristics of West Africa

West Africa covers an area of approximately 6 million km^2, which is about 20% of Africa's total land area. The region lies between longitudes 18°W and 16°E, and latitudes 3° and 28°N, and it is bounded in the west and south by the Atlantic Ocean, in the north by the Sahara desert, and in the east by the Central African nations of Chad and Cameroon. The topography of the region is mainly flat (with most parts lying less than 300 m above mean sea level), although there exist several isolated high points in the coastal areas (Andam-Akorful et al., 2017).

The climate of Western Africa can be described predominantly as that of a dryland encompassing arid, semi-arid and dry sub-humid regions, corresponding to aridity index values of 0.05–0.20, 0.20–0.50 and 0.50–0.65 respectively. The region is conventionally classified into three sub-climatic zones namely: i) the dry north, known as the Sahel, which lies just below the Sahara desert; ii) the Sudano transitional zone; and iii) the relatively wet Guinean zone located in the south (Meynadier et al., 2010). The geographic distribution of wet and dry regions depends on the latitude and the distance from the Atlantic Ocean while the degree of aridity increases from south to north and to a lesser extent from west to east, as reported by Menz (2010). Temperatures in the lowlands of West Africa are high throughout the year, with annual means usually above 18 °C. In the Sahel, maximum temperatures can reach above 40 °C (for further details on the region's climate see CILSS, 2016).

2.2. Data sources, use and collection

2.2.1. Data sources

For this review, two FAO databases were used: i) FishstatJ provided data for the analysis of West African inland fisheries production and consumption; and ii) Aquastat provided data on the reservoirs' physical features. In addition, published articles and reports containing information on specific reservoir's physical features, fisheries production and catch statistics were used (Table 1). The Aquastat data were checked for consistency by comparing them with published literature.

2.2.2. Data use and collection

First, data from the Aquastat database (FAO, 2016a), and other sources (see Supplement Tables S2 and S3), were used to estimate the number of reservoirs and their total surface area in West Africa.

Second, data on water level fluctuations, surface area fluctuations and fish catches from three reservoirs in Ghana (namely Tono, Bontanga and Golinga) were obtained from July 2016 to June 2017 through field data collection. The water level was recorded monthly from fixed graduated poles at the three reservoirs. Using a Garmin GPS, the area of the three reservoirs was measured in August 2016 (peak of flood season) and in April 2017 (peak of dry season). Total fish landings were recorded for five consecutive days staring from Monday to Friday at Tono, and from Tuesday to Saturday at Bontanga and Golinga in each month and extrapolated to the monthly catch using an estimate of the average number of fishing days per month. Respective information was obtained from the fishers at the three reservoirs.

Table 1
Morphometric and catch data of the 30 reservoirs. MR* indicates the 15 reservoirs used in the multiple regression analysis.

≠ [MR *]	Country	Reservoir name	Location	Surface area [km^2]	Mean depth [m]	Age [in 2018]	Total annual catch [tons/yr]	Year of catch report	Yield [kg/ha/yr]	Source [Area; Catch; Mean depth]
1MR	Burkina Faso	Bagré	11°28′36.78″N 0°32′48.10″W	150	20	24	1040	2004	69.3	(Vanden Bossche and Bernacsek, 1990b; Béné, 2007; Villanueva et al., 2006)
2 MR	Burkina Faso	Kompienga	11° 4′ 55.56″ N 0° 41′ 59.28″ E	150	11.68	30	1243	1997	82.9	(Vanden Bossche and Bernacsek, 1990b; Béné, 2007; Ouédraogo et al., 2015; Cecchi et al., 2008)
3 MR	Côte d'Ivoire	Ayamé	05°35′59.99″N 03°13′22.54″W	180	10	67	1061	1996	58.9	(Traore et al., 2008; Laë, 1997; Duponchelle and Legendre, 2000)
4	Côte d'Ivoire	Buyo	06°14′32″N 07°02′05″W	900		38	4345	1992	48.3	(Van der Knaap, 1994; Lévêque, 1999)
5	Côte d'Ivoire	Gboyo		0.07			4.442	1999	634.6	(Gourdin, 1999); (de Morais, 2001)
6	Côte d'Ivoire	Katiali		0.24			4.082	1999	170.1	(Gourdin, 1999; de Morais, 2001)
7	Côte d'Ivoire	Korokara T		0.07			1.925	1999	275	(Gourdin, 1999; de Morais, 2001)
8 MR	Côte d'Ivoire	Kossou	7°1′52.57″N 5°28′23.16″W	900	10	47	7000	2000	77.8	(Lévêque, 1999)
9	Côte d'Ivoire	Nambingué	8″ to 10″ N, 5″ to 6″ W	0.1			1.825	1999	182.5	(Gourdin, 1999; de Morais, 2001)
10	Côte d'Ivoire	Sambakaha		0.15			7.572	1999	504.8	(Gourdin, 1999; de Morais, 2001)
11	Côte d'Ivoire	Taboo	06°12′38″N 05°05′02″W	34.6		40	70.67	2006	20.4	(Aliko et al., 2014; Aliko et al., 2014)
12	Côte d'Ivoire	Tiaplé		0.07			1.069	1999	152.7	(Gourdin, 1999; de Morais, 2001)
13	Côte d'Ivoire	Tiné	8″ to 10″ N, 5″ to 6″ W	0.45			5.811	1999	129.1	(Gourdin, 1999; de Morais, 2001)
14	Ghana	Afife	6° 04′ N, 0° 55′ E	5.5		56	70	1988	127.3	(Vanden Bossche and Bernacsek, 1990b);GIDA
15 MR	Ghana	Barekese	6°50′22.34″ N 1° 42′ 55.62″W	6.4	6.4	48	80	1988	125	(Vanden Bossche and Bernacsek, 1990b; Amuzu, 1975; Tetteh et al., 2006)
16 MR	Ghana	Bontanga	9° 33′ 2.88″ N 1° 01′ 7.68″ W	6.7	5.9	32	105.82	2017	158	This study; (Quarcoopome et al., 2008)
17 MR	Ghana	Dawhenya	5°46′58.09″ N 0° 03′ 05.62″E	2.2	5.4	43	30	1988	136.4	(Vanden Bossche and Bernacsek, 1990b; Alhassan, 2011; Sam-Amoah and Gowing, 2001)
18 MR	Ghana	Golinga	9° 21′ 48.96″ N 0° 57′ 18″ W	0.62	2.7	44	10.66	2017	172	This study; (Gordon, 2006)
19 MR	Ghana	Kpong	6° 13′ 51″ N 0° 5′ 29″ W	25.2	5	37	186.68	2013	74.1	(FAO, 2016a; Nunoo and Asiedu, 2013; Quarcoopome et al., 2011)
20 MR	Ghana	Tono	10° 53′ 6″ N 1° 09′ 18″ W	18.6	6.8	43	187.20	2017	101	(FAO, 2016a); This study; (Vanden Bossche and Bernacsek, 1990b)
21	Ghana	Vea	10° 52′ 30″ N 0° 50′ 42″ W	4.05		53	33.5	2010	82.7	(Adongo et al., 2014; Okrah, 2010; Vanden Bossche and Bernacsek, 1990b)
22 MR	Ghana	Weija	5°35′10.82″ N 0° 21′ 16.62″W	37	5	41	420	1988	113.5	(Vanden Bossche and Bernacsek, 1990b; Asante et al., 2008)
23 MR	Mail	Manantali	13°11′44″N 10°25′44″W	500	21	31	1500	1999	30	(Lévêque, 1999; Kantoussan et al., 2009)
24 MR	Mail	Selingue	11°38′17.7″N 8°13′47.2″W	400	5	38	4000	1999	100	(Lévêque, 1999; Kantoussan et al., 2009)
25	Nigeria	Asejire	7°21′45″N 4°08′00″E	23.69		29	1029	1985	434.4	(Ita et al., 1985; Ita, 1993; FAO, 2016a)
26	Nigeria	IITA		0.78		49	13.8	1986	176.9	(FAO, 2016a); (Ita, 1993); (Peacock, 2010)
27 MR	Nigeria	Kainji lake	10°22′N 4°33′E	1270	11	50	13,361	2001	105.2	(Vanden Bossche and Bernacsek, 1990b; Fernando and Holčík, 1982; Abiodun, 2002)
28	Nigeria	Kiri	9°44′59″N 12°1′0″E	115		36	2473	1985	215	(Ita et al., 1985; Ita, 1993; FAO, 2016a)
29 MR	Nigeria	Shiroro	9°59′7″N 6°54′58″E	312	36	29	3489	1990	111.8	(FAO, 2016a; Ita, 1993; Ovie and Adeniji, 1994)
30	Senegal	Diama	16°13′0.20″N 16°24′53.63″W	235		32	4500.0	2003	191.5	(FAO, 2016a; Degeorges and Reilly, 2006)

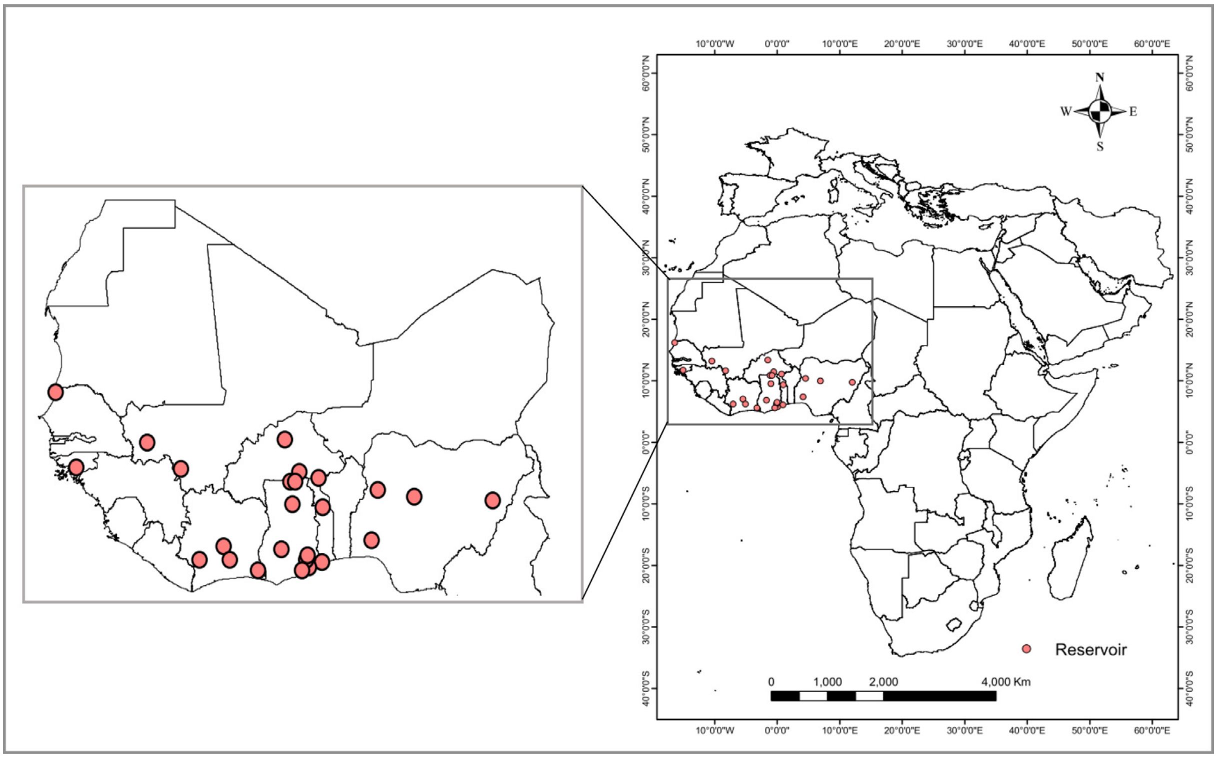

Fig. 2. Map of Africa: the dots show the locations of 30 reservoirs analysed in the model.

2.3. Catch, surface area, age and mean depth data from selected West African reservoirs

From seven West African countries, 30 small to large reservoirs were analysed for correlation between catch and surface area (Fig. 2 and Table 1). All the reservoirs were included in a single-predictor regression. Then, for a subset of 15 reservoirs that had additional information on age and mean depth, a multiple regression analysis was conducted.

2.4. Modelling approaches used

Approach 1: Simple catch-area regression

A simple catch-area regression was first constructed for all 30 reservoirs with double-logarithmic transformation (1):

$$ln(\text{Catch}) = a + b.ln(\text{Area}) \tag{1}$$

Where fish catch is in tonnes per year and reservoir area is in square kilometres. The resulting single regression line was then tested for an inflection point using a technique described by Somerton (1980) to check if small and large reservoirs differed in terms of their catch-area relationship. The data were repeatedly divided into two groups and regressions were calculated for each group. The residual sum of squares of both lines was then summed and the calculation was repeated with another pair of regression lines until the residual sum of squares approached a minimum. An inflection point exists if the pooled residual sum of squares of a pair of the resulting regression lines is significantly lower than the residual sum of squares of a single line. The dataset was then fitted using the dummy variable regression (DVR) method, which is an analysis of covariance (ANCOVA) for comparison of two regression lines (Fox, 1997). Our DVR model consisted of ln (Area) as a quantitative explanatory variable or the covariate, size (i.e. the reservoir group with two levels: A, above 2 km^2; and B, below 2 km^2) as the dummy variable or factor and the interaction between the dummy variable and the covariate. The resulting equation was:

$$ln(\text{Catch}) = ln(\text{Area}) + \text{Size} + \text{Size} : ln(\text{Area}) \tag{2}$$

Approach 2: Multiple linear regressions

Using a subset of the data (15 reservoirs that had information available on both age and mean depth), multiple linear regression relationships were fitted to test for the effect of the two additional variables (i.e. age and mean depth) in explaining the catch variations of the datasets. A three-way combination of the main effects led to an increase of variance due to the small sample size. The multiple regression relationships were preceded by a simple catch-area regression fitted for the 15 reservoirs, followed by multiple regression using both mean depth in meters (3) and reservoir age in years (4).

a) $$ln(\text{Catch}) = \text{a} + \text{b}.ln(\text{Area}) \times ln(\text{mean depth}) \tag{3}$$

b) $$ln(\text{Catch}) = \text{a} + \text{b}.ln(\text{Area}) \times ln(\text{Age}) \tag{4}$$

As it is widely known that using allometric equations to predict unknown values of y produces a logarithmic transformation bias (Smith, 1993), the predicted fish yield

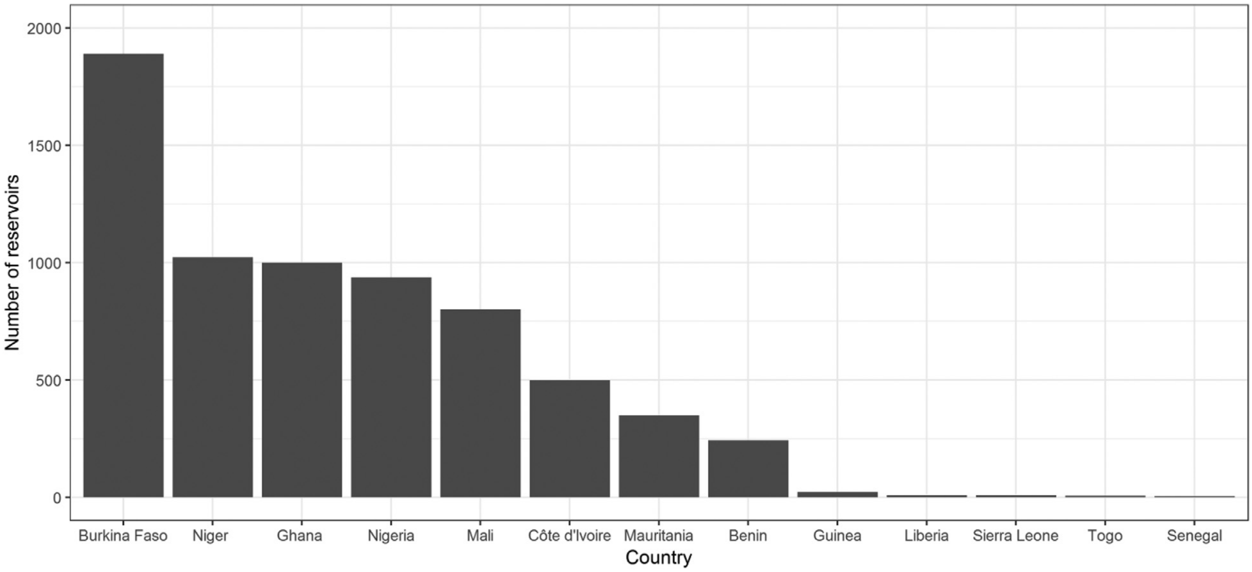

Fig. 3. Number of reservoirs by country in West Africa. For exact values and sources of data consider Supplement Table S2.

values in log scale were back-transformed with a correction factor (5) for natural logarithms provided by (Sprugel, 1983) as:

$$CF = \exp\left(\left(SEE^2\right)/2\right) \quad (5)$$

The term SEE is the (residual) standard error estimate of the regression equation.

The models were checked to see if the errors were independent, normally distributed in each group, and had a constant variance in each group (homoscedastic). These assumptions were assessed by interpreting the residual plot and the histogram of residuals. Then, residuals of the models were tested to see if they were normally distributed using both the Anderson-Darling and Cramer-von Mises normality tests. Both tests revealed no evidence against normality ($p = 0.08$ and $p = 0.08$ for Model 1, and $p = 0.60$ and $p = 0.58$ for Model 2, for the Anderson-Darling and Cramer-von Mises normality tests, respectively). The assumptions of linear models were adequately met for the data (Supplementary material A and B). All data analyses were conducted using R 3.5.0 software (R Core, 2018).

3. Results

Assessment of the number of reservoirs in western Africa and their overall surface

We estimate that there are about 6894 reservoirs in West Africa with combined surface area of 27,504 km^2 (See Supplement Table S3). Most of them have been reported as small reservoirs with surface areas within the range of 1–1000 ha ($\leq$10km^2). Burkina Faso appears to be the country with the highest number of small reservoirs (Fig. 3, Supplement Table S1). The two largest reservoirs in the sub-region with surface areas above 1000 km^2 at upper storage level, are the Volta (8482 km^2) and Kainji lakes (1270 km^2). However, the FAO Aquastat database is not exhaustive. It has only 420 reservoirs registered in the sub-region and it has no records of small reservoirs with surface area below 10 ha (<0.1 km^2).

The three focus reservoirs of Northern Ghana used in this study (namely Tono, Bontanga and Golinga) were seen to have significant intra annual change in their surface area and water levels (Table 2); the smallest reservoir (Golinga) lost more than 50% of its surface area during the dry season. Monthly water levels of the reservoirs were inversely correlated with total catches, with correlation coefficient (r) giving values of −0.70, −0.93 and −0.56 for Tono, Bontanga and Golinga reservoirs, respectively (Appendix A).

3.1. Catch-area relationship of West African reservoirs

Using segmented regression, as applied by Somerton (1980), we found an inflection in reservoir size at 2 km^2. However, analysis of covariance showed that the resulting two groups (A and B for reservoirs with surface areas above and below 2 km^2, respectively; see Appendix B) had no significant difference in their slopes, with $F = 0.5895$, d.f. =26, 3, and $p = 0.45$, (for more detail see Supplementary Material C). Thus, the catch-area relationship was modelled with a single equation for all the reservoirs. The resulting model was:

Model 1: Catch (tonnes/year), Area (km^2)

$$\text{Catch} = 17.3(95\%\text{CI}: \ 13-23) \times \text{Area}^{0.8626\ (95\%\text{CI}:\ 0.7915-0.9336)}$$

$$n = 30, r^2 = 0.957, p = 1.3e-20, \quad \text{Mean Squared Error} = 0.3402$$

The correction factor for adjusting the back-transformation of the predicted yields to the original scale (fish catch in tonnes per year) is 1.1999. The fit to the catch-area dataset explains 95.7% of the variation of observed catches. The expected fish catch of a reservoir with a known area can be observed from Fig. 4.

Table 2
Seasonal fluctuation in surface area and water level of Tono, Bontanga and Golinga reservoirs of Ghana from July 2016 to June 2017; measurements taken in the flood season (August 2016) and the dry season (April 2017). For monthly variation in fish catch and water level in the reservoirs, see Appendix A.

Parameter	Tono	Bontanga	Golinga
Surface area during flood 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
Mean depth (m)	6.6	5.9	2.7
Maximum depth (m)	13.32	9.7	4.95
Water level variation (m)Water level: Flood-Dry (m)	5.4610.5–5.04	5.388.23–2.85	2.682.8–0.12
*Relative Reservoir Level Fluctuation	82.7	91.2	99.6

* Adapted from (Jul-Larsen et al., 2003): mean reservoir level amplitude/mean depth* 100.

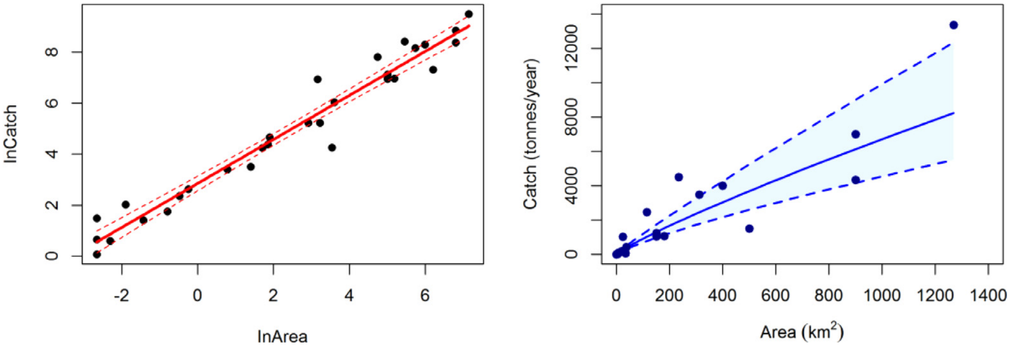

Fig. 4. The ln- transformed (left) and back-transformed (right) catch-area data with the best-fit line (solid) superimposed and 95% confidence zone shown (within dotted lines).

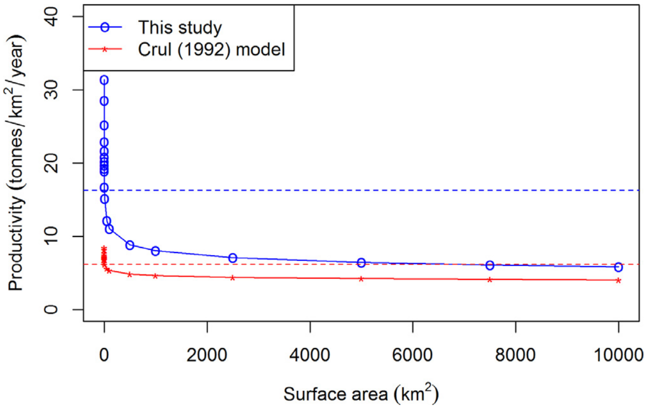

Fig. 5. Comparison of productivity estimate from this study and from Crul's model (1992). The dotted lines represent the means of the estimates.

3.2. Fish productivity and yield predictions

Using a range of reservoir surface area values, we compared the fish productivity predicted (tonnes/km^2/year) by the model of this study to that of Crul's model. The model of this study predicted, on average, more than twice what Crul's model predicts (Fig. 5, Supplement Table S4). A *t*-test on the data showed that the mean of the productivity estimates (of Crul's 6.2 tonnes/km^2/year and this study's 16.3 tonnes/km^2/year: see Supplement Table S4) are significantly different ($t = -5.7252$, df = 38, p-value=0.00000136; see Supplement Material D). Analysis of the sub-dataset (i.e. the 15 reservoirs where additional information was available) showed that the fish productivity per unit area of the reservoirs was inversely correlated both with mean depth ($r = -0.49$) and area ($r = -0.32$), but not with age ($r = 0.03$) (Fig. 6).

3.3. Multiple regression with area, age and mean depth data of 15 reservoirs

While a multiple linear regression of catch against area (km^2), age (year) and mean depth (m) of the 15 reservoirs did not produce a reliable model, catch regressed against area and mean depth produced a predictive model (hereafter referred to as Model 2) that explained 87% of the variation in fish catch.

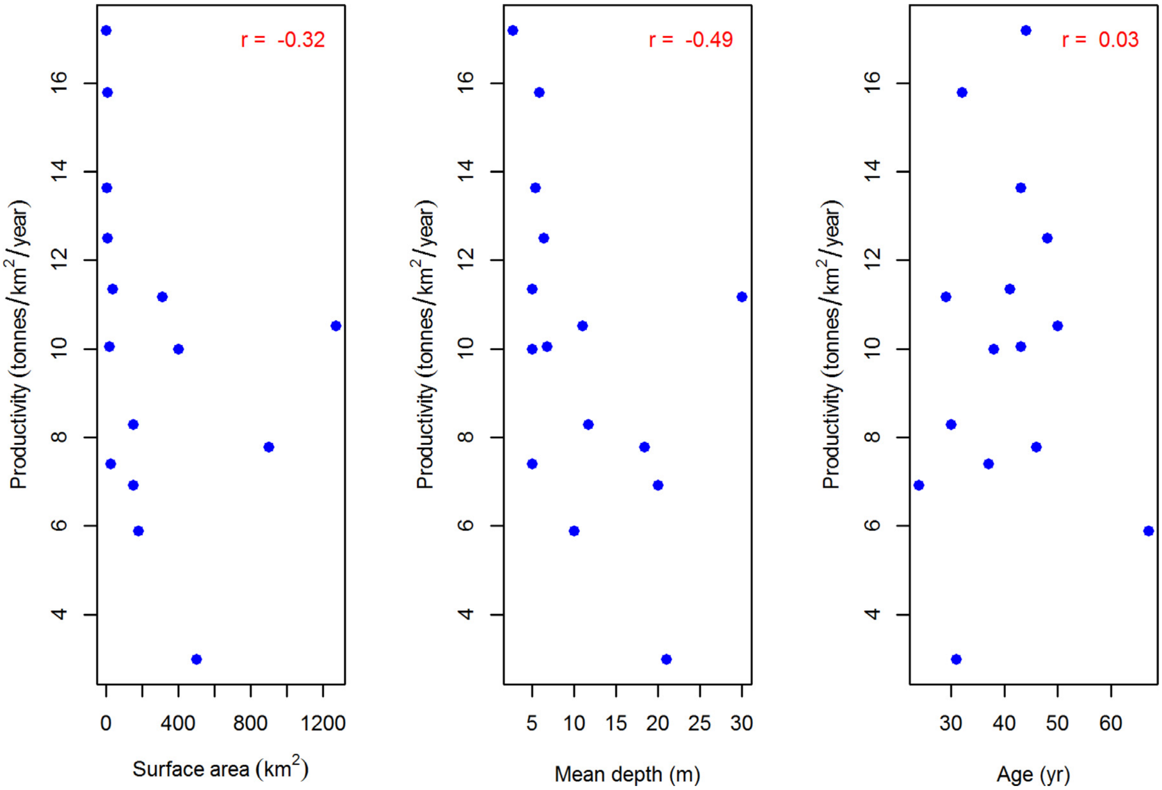

Fig. 6. Correlation between productivity and surface area (km^2), mean depth (m) and age (yr) of 15 reservoirs.

Table 3
Confidence limits of the parameters of Model 2 (i.e. multiple linear regression).

Parameter	Coefficient	Lower limit	Upper limit
(Intercept)	3.5005850	2.3507990	4.6503710
Area	0.0148636	0.0073007	0.0224264
Depth	0.1490164	0.0168920	0.2811408
I(Area^2)	−0.0000051	−0.0000099	−0.0000003
Area: depth	−0.0004363	−0.0008053	−0.0000673

Details on residuals and summary statistics of the model are available in Supplementary B.

Model 2: Catch (tonnes/year), Area (km^2), mean depth (m)

$$\ln\text{Catch} = 3.5 + 0.015\ \text{Area} + 0.15\text{Depth} - (0.00005 \times \text{Area}^2\ ) - (0.00044\ \text{Area}\ \times\ \text{Depth})$$

$$n = 15, r^2 = 0.8738, p = 0.000172, \quad \text{Mean Squared Error} = 0.4994$$

See Table 3 for the confidence limits of the parameters.

4. Discussion

4.1. Assessment of reservoirs in West Africa

It has been widely reported that there are several thousand reservoirs in sub-Saharan Africa (Kolding et al., 2016b; Marshall and Maes, 1994; Venot et al., 2012). Our study estimated a total of 6894 reservoirs covering approximately 27,504 km^2 of area in the West African sub region. We estimated that the reservoirs of the region combined contribute 11,6806.3 tonnes (95% CI: 42,435.1–320,883.8 tonnes) per annum to the inland capture fisheries of the region, which represented 12.4% of the region's total inland fish catch (940,767 tonnes/annum on average) as reported by the FAO (2008–2015). Our results were comparable to estimates by Petr (1994) who reported that, in Africa, reservoir fisheries contribute about 15,000 tonnes (10%) to the overall inland fishery of the continent. Our model, and that of Crul (1992), were both developed with datasets of man-made lakes only and, are thus, comparable.

4.2. Models and harvest potential estimate

In our study we followed the modelling approach of Youngs and Heimbuch (1982), which regresses the logarithm of fish catch against the logarithm of reservoir surface area. Our model accounts for 95.7% of the observed variation in catches of the reservoirs. However, our potential yield estimates greatly exceed those of the model by Crul (1992). This difference may be explained by multiple factors. We believe that the higher current catches of the reservoirs in the region are in part, due to restocking activities that were accelerated mainly in the 1990s (Ouedraogo, 2010). Population growth has contributed to an increase in fishing pressure and, together with gear diversification and the optimization of fishing techniques, may have driven total harvest levels to increase. Petr (1994) observed that fish production in Africa kept pace with the rise in human population and reported that, over a period of 17 years, the human population increase of 79% corresponded to a 74% increase in fish production. So, it is reasonable to assume that the difference in the estimates between the model of this study, in 2018, and the previous model of Crul (1992) can be attributed to the above factors. Furthermore, increases in the productivity of reservoirs are also related to eutrophication. Nixon (1995) defined eutrophication as 'an increase in the rate of supply of organic matter to an ecosystem'. Eutrophication tends to affect shallow lake systems more than deeper tropical lakes (Kemka et al., 2006). Population growth, intensified agriculture (including the use of agrochemicals) and deforestation are the main drivers of nutrient-rich inflows into shallow tropical reservoirs (Ndebele-Murisa et al., 2010; Ntiba et al., 2001).

Our study shows that productivity per unit area greatly decreases as the size of the reservoir increases; a reservoir with surface area of 1 km^2 is twice more productive (per unit area) than a 100 km^2 reservoir. These results corroborate findings by Fernando and Holčík (1982) that small and shallow African lakes are more productive than larger ones. Most small reservoirs are constructed mainly for community water storage and livestock watering. Animal wastes and dung deposition at the edges of the reservoirs are sources of both nitrogen and phosphorus (Ansari et al., 2010; Kolding et al., 2016b). Consequently, small reservoirs are highly productive. Baijot et al. (1997) found that small reservoirs in Burkina Faso are richer in mineral concentrations than large artificial lakes, but are less stable. Our findings that there is a decline of fish productivity per unit area as both reservoir surface area and mean depth increase agrees with a study by Downing (2010), according to which, fish productivity generally declines with increasing lake size. Depth, water chemistry and conductivity have all been used to classify lakes and reservoirs (Rai and Hill, 1980; Talling and Talling, 1965), since these parameters appear to be closely related with productivity (Downing et al., 1990; Henderson and 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 factors. It has been shown that biological production in lake systems is partly controlled by lake morphology, nutrients and other environmental factors (Kolding and Van Zwieten, 2006; Kolding and van Zwieten, 2012; Fig. 7a). Some of these studies suggest that fish productivity per unit area is negatively related with habitat volume, area, and mean depth since many aquatic processes are less intense, and fish is less abundant (per unit area) in larger water bodies. This is attributed to decreased rates of nutrient recycling to the euphotic layer within these lakes (Downing, 2010; Fig. 7b and c). The tilapiine species, *O. niloticus* and *S. galilaeus*, which are the mainstays of most reservoir fisheries, are more productive in the relatively small Golinga than in the large Tono and Bontanga (Abobi et al., 2019), due to the species' preferences for shallow waters (FAO, 2009).

Reservoirs serve multiple community needs and, in this light, their resources are often subjected to severe competition between irrigation farming and fisheries. Therefore, in estimating reservoir fisheries production, the effects of water drawdown caused by irrigation should be considered; as intensive use of reservoir waters for farming reduces the size of the aquatic habitat available to fish production. According to Jul-Larsen et al. (2003); Kolding and van Zwieten (2011); Kolding and van Zwieten (2012); Kolding et al. (2016b) and Gownaris et al. (2017), however, there is increasing evidence that inland fish production in Africa is more dependent on external climatic drivers, such as seasonal variability of water levels, than on human exploitation rates or management interventions. The relation between seasonal variability of surface water bodies and fish production is consistent with our observations on the three reservoirs in northern Ghana, where the drawdown of water for irrigation during the dry seasons, rather than external climatic drivers, significantly reduces reservoir surface area and depth. Golinga reservoir, a small water body with a surface area at full storage of 0.62 km^2 experienced 52% and 2.68 m reduction in surface area and water level, respectively, mainly as a result of intensive withdrawal of water for irrigation during the dry season. Similar observations on small reservoirs in Burkina Faso have been made by Kolding et al. (2016b). This phenomenon means that in years of high evaporation and little rainfall, these small reservoirs, while highly productive under "normal conditions", may lose a large part (if not all) of their fish productivity if abstraction for irrigation continues. Kolding et al. (2016b) asserts that the impact of water level fluctuations in African lakes and reservoirs is inversely proportional to the size and depth of the system, implying that trends in rainfall, evaporation and siltation will be crucial to the resilience and productivity of the over 6000 small and shallow reservoirs in the region.

Intra annual variation in total fish catch of reservoirs is also influenced by seasonal changes in livelihood activities. For example, the lean farming season (dry season) may lead to a sudden boom in fishing activities at reservoirs where there is open access to the fishery. We observed a clear case of a livelihood-induced, seasonal fishing boom between March and April at Golinga reservoir in the Northern region of Ghana. The number of fishers on the reservoir tripled during these two months of lowest water levels. The open access allowed the occasional fishers without wooden canoes to practice "step in and cast" fishing. Therefore, the recorded monthly catches were highest in March and April. Bontanga and Tono, on the contrary, had the highest catches in May. We believe that fish are abundant in the reservoirs during the flood and post flood seasons (July-December), but are mostly harvested when the water level draws down and fish are concentrated in the reservoir increasing their catchability.

Some studies have shown that seasonal fluctuations in water level are associated with enhanced productivity (Junk et al., 1989; Kolding, 1993; Wantzen et al., 2008). Moreover, fluctuations of the aquatic terrestrial transition zone (ATTZ) depend on seasonal water level fluctuations. Kolding et al. (2016b) report on increased phosphorous mobilization following wet–dry cycles owing to the alteration of physical, microbial and chemical processes in the ATTZ. Among the three reservoirs of this

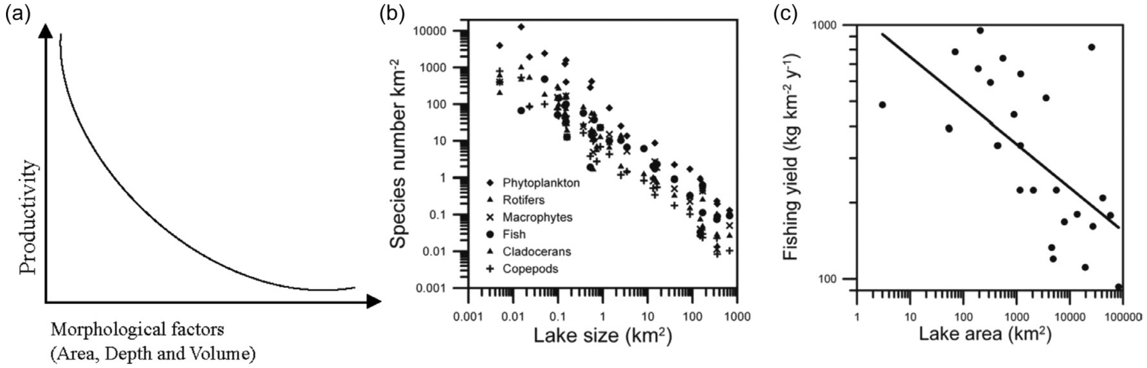

Fig. 7. (a) Generalised morphological effects on the productivity of lakes and reservoirs, adapted from Kolding and Van Zwieten (2006); (b) Species-richness per unit area of various aquatic taxa in lakes of different sizes (after Downing, 2010); and (c) Fish yield and lake-size data summarised by Youngs and Heimbuch (1982) from other sources (Matuszek, 1978; Oglesby, 1977, and Ryder, 1965) and adapted from Downing (2010).

study, Golinga, which is the smallest, had the highest intra annual fluctuation in surface area (52% reduction) but was the most productive with total catch of 17.2 tonnes/km^2/year. Golinga was followed by Bontanga, which had a 43% reduction in its surface area and fish productivity of 15.8 tonnes/km^2/year and, then, by Tono with a 33% reduction in its surface area and fish productivity of 10.1 tonnes/km^2/year. These results confirm a finding by Kolding et al. (2016b), which states that the more the water level in the system fluctuates on a regular basis, the higher is the average productivity.

Youngs and Heimbuch (1982) demonstrated that 97% of the variation in a regression equation was explained by three factors: area, mean depth and total dissolved solids. While a multiple factor model should be applied whenever possible, in Western Africa, data to do this, presently, is unavailable.

In our second modelling approach (Model 2), we showed that depth was a significant predictor but that reservoir age was not. However, we think that this may be due to the low sample size (15) and narrow age difference (most are within 10 years in age) of the reservoirs used for the study. Following the observations by MRAG (1995) on the effect of sample size on multiple linear regression relationships for reservoirs and lakes fish yield, we think that a larger number of reservoirs, with a wider age range, would show a positive relation. This needs to be proven in a follow-up study.

Model 2 may be applied whenever the mean depth of the reservoir is known. However, considering the high coefficient of determination and the low prediction error, we recommend that Model 1 should be preferred until a larger sample size allows for revisiting (and possibly improving) Model 2. The difference of potential yield estimates between these two models largely depends on the interaction effect of area × depth of the individual reservoir being predicted by Model 2. The average difference was 57% for the sub data set analysed.

4.3. Model application, limitations and proxies

The models of this study are suitable for estimating fish catch from reservoirs of West Africa. As the fisheries of these reservoirs are mostly unrecorded and undocumented, their yield contribution to the total fisheries production of the region can be approximated by our models.

We can also think of applying our model equations during the reservoir planning process since the expected fish yield, as well as the potential water supply for other uses can be calculated for a reservoir of a specific area (and depth). This could be compared to expected reservoir construction costs, providing a sound base for cost benefit analysis. This reasoning has been successfully applied in the utilisation of small and medium-sized reservoirs in China, where fishery aspects were taken into account at the planning stage of reservoir construction (De Silva, 2000).

Annual changes in fish catches from lakes and reservoirs are common and the factors behind these changes can vary. Therefore, it would be desirable to constantly update the information and data from the water bodies to be considered for the model. We recommend either continuous biannual surveys, preferably during the peaks of the wet and dry seasons or a full year study every five years. Future data could comprise changes in the: number of fishers/boats, number of active fishing days, introduction/withdrawal of fishing gears/crafts and water volume. Similarly, the average annual water levels of large reservoirs, whose surface areas are monitored by satellites, can be obtained (for example, from the United States Department of Agriculture) and used as proxies for assessing annual variations in the reservoirs' sizes and fish catches.

Our two models, just like those of Youngs and Heimbuch (1982) and Crul (1992), are based on data of catch and surface area (and reservoir depth) and do not include fishing effort or other potentially influencing factors. Following the reasoning of FAO (2016b); Kolding and van Zwieten (2011, 2012); and MRAG (1995), we suggest that further development of catch-area relationships into multiple regression models should be done with one or several of the following additional variables: Chlorophyll "a" (µg/l), number of fishers/number of boats, water level fluctuation (m), volume (m^3) and discharge (m^3/s). It would be useful to obtain depth data on more reservoirs for further progress on empirical models to predict fish yields of West African reservoirs.

Conflict of Interest

There is no competing interest to declare.

Ethical Statement

Authors state that the research was conducted according to ethical standards.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecohyd.2019.11.004. Appendixes are available in the online version.

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