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RESEARCH ARTICLE

# Fisheries and water level fluctuations in the world's largest desert lake

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## Abstract

Hydrological regimes are significant drivers of fisheries production in many African Lakes due to their influence on fish habitat and food availability, breeding success, and catchability. Lake Turkana, Kenya, will undergo substantial changes in hydrology due to water regulation and extraction along the Omo River in neighboring Ethiopia, which provides over 90% of its water. The objective of this study was to predict how the lake's fisheries, which provide an important livelihood and protein source in the region, will respond to hydrological change. While variations in fishing effort are poor predictors of fisheries catch in the lake, water levels and their fluctuations strongly influence fisheries production. Seasonal oscillations play a particularly important role, and with complete loss of these oscillations, the lake's predicted fisheries yield will decrease by over two thirds. The fishery is predicted to collapse at a lake level decline of 25 m, regardless of seasonal amplitude magnitude. The lake's total littoral habitat, where fisheries are currently concentrated, will increase in surface area with lake level declines of <25 m. However, the extent of productive, dynamic littoral habitat will decrease with dampening of the lake's seasonal oscillations. The most severe habitat loss will occur in the lake's Turkwel Sector, which hosts the region's highest human population densities, and North Sector, where inter-tribal conflict over resources is common and likely to be exacerbated by lake level decline. The continued ecological functioning of Lake Turkana necessitates immediate efforts to develop and apply a water resource management plan rooted in science.

KEYWORDS
fisheries, flood pulse, habitat, hydropower, Lake Turkana, Omo River, water level fluctuations

## 1 | INTRODUCTION

Lake Turkana, Kenya, is the world's largest permanent desert lake and Africa's fourth largest lake by volume. Fishing has taken place on the lake for at least 10,000 years (Owen, Barthelme, Renaut, & Vincens, 1982), but the first attempts to create a commercial fishery did not occur until the 1940s (Kolding, 1989; KMFRI, 2008). In the 1960s, Mann (1962) deemed this system the "last great lake remaining in Africa with its fish population in a pristine, natural condition." There have been several attempts since this time to expand the Lake Turkana fishery, though few have been met with success (Kolding, 1989). Over the past decade, the lake has contributed only 5% of the freshwater fisheries yield in Kenya, where inland catches are still overwhelmingly dominated by Lake Victoria (KNBS, 2015).

The growth of Lake Turkana's fisheries has been historically limited by socioeconomic factors and by the fisheries' unpredictability, discussed further below. The lake is located in one of the most remote regions in northwest Kenya and mainly accessed over poorly maintained roads, thereby restricting fish export potential. Fish handling, fish preservation, and processing are mainly done via inefficient traditional methods due to limited fresh water and the lack of processing facilities, leading to high post-harvest losses (KMFRI, 2007). Other constraints include the choppiness of the lake's open waters, highly fluctuating water levels, a lack of harbor facilities, and high parasite loads among the lake's fishes (KMFRI, 2007; Moravec, Charo-Karisa, & Jirka, 2009).

In addition to these limitations, fishing is culturally considered a less desirable livelihood by many of the tribes living around the lake. The only exception is the El Molo, the "original fisherfolk" (Neumann, 1898), a predominantly fisheries-dependent tribe numbering only 200 purebred people. The Daasanech, a dominant tribe on the lake's eastern shores, refer to members of their tribe without livestock as "gal dies," a term that translates to "fisherman" but is understood to have a negative connotation (Gifford-Gonzalez, Stewart, & Rybczynski, 1999). The Turkana, who dominate the western shores of the lake, are a traditional pastoral community with strong cultural attachment to cattle as an indicator of wealth and social status (Pavitt, 1997; Anderson & Broch-Due, 1999).

Nonetheless, Lake Turkana's fisheries provide a valuable protein source and alternative livelihood in the region, which is plagued by chronic droughts and food security challenges (e.g., Ojwang et al., in press). Fishes from the lake are one of the main sources of micronutrients, often in highly bioavailable form. Nearly 75% of the population is reliant on food aid for sustenance (Snyder, 2006), and malnutrition rates are lower in fisheries livelihood zones than in pastoralism and agropastoralism livelihood zones (NDMA, 2014; 2015; Figure 1c). Resorting to fishing is a common strategy for pastoralists who lose livestock to drought or cattle rustling (Yongo et al. 2010), and fishery products have historically played an important role in food security around the lake during periods of famine (Kolding, 1989; Watson & van Binsbergen, 2008; Yongo, Abila, & Lwenya, 2010).

The human population surrounding the lake, and hence pressure on the region's environmental resources, is growing (KNBS, 2015). Turkana County, on the lake's western shores (Figure 1a), had 855,399 residents during the 2009 census, with a per capita growth rate of 0.65%. In Marsabit County, on the lake's eastern shores (Figure 1a), the population was considerably smaller (291,166 residents) in 2009 but had a higher per capita growth rate (1.55%; KNBS, 2015). If sustainably exploited, Lake Turkana's fisheries could improve the welfare of locals, particularly at a time of increasing climate instability, and contribute considerably to national gross domestic product. The importance of alternative livelihoods in providing adaptive capacity for local communities has been noted in the case of several African lakes (e.g., Lake Chad; Sarch & Birkett, 2000; Sarch & Allison, 2001).

The productivity of the Lake Turkana fishery is, however, highly variable and climate-sensitive. This trait is not unique to Lake Turkana. Water level variables, including absolute lake level and intra- and inter-annual fluctuations, are widely accepted as central factors structuring lake ecosystems and their fisheries (e.g., Leira & Cantonati, 2008; Wantzen, Junk, & Rothhaupt, 2008; Kolding & van Zwieten, 2012; Kolding, van Zwieten, Marttin, & Puolain, 2016; Gownaris et al., in review). In African lakes, for example, water levels and their fluctuations have been shown to be more important in predicting yield than fishing effort variables (Jul-Larsen, Kolding, Overå, Nielsen, & van Zwieten, 2003a, 2003b).

Water level fluctuations at inter- and intra-annual scales may influence habitat by altering substrate availability (e.g., Gasith & Gafny, 1990) and the abundance, productivity, and diversity of primary producers, from phytoplankton through macrophytes (Hill et al., 1998; Lamberts & Koponen, 2008; Arias et al., 2014; Janssen et al., 2014). In many lakes, seasonal fluctuations are particularly important to ecosystem functioning, as described by the "flood pulse concept," originally developed for riverine systems but later extended to lakes (Junk, Bayley, & Sparks, 1989; Wantzen et al., 2008). Interactions within the aquatic/terrestrial transition zone (ATTZ), the portion of the littoral that fluctuates between wet and dry conditions dependent on seasonal

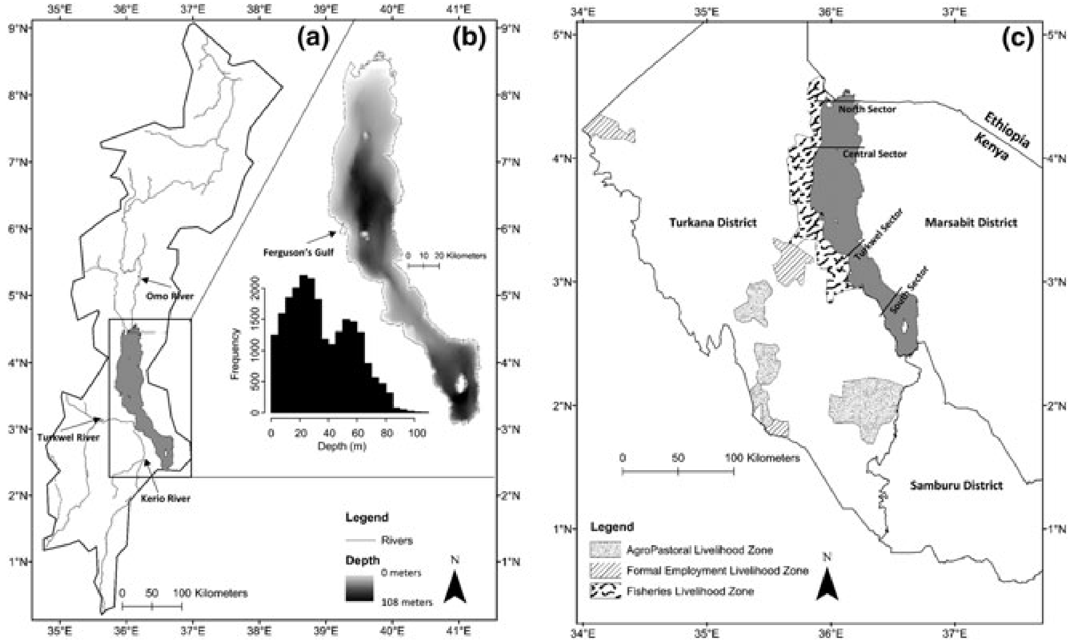

**FIGURE 1** Maps of the Lake Turkana region showing various relevant features: (a) Watershed of Lake Turkana showing permanent (Omo River) and ephemeral (Turkwel and Kerio Rivers) inflows to the lake, (b) bathymetry of Lake Turkana (Davidson & Smith, 2011; Syracuse University, 2011) displayed as a bathymetry raster and as a histogram of pixel depth, measured in meters, and (c) Lake Turkana's sectors and administrative districts and livelihood zones surrounding Lake Turkana as defined by the National Drought Management Authority, 2015.

fluctuations, lead to the accumulation and resuspension of nutrient-rich organic matter, better nutrient recycling, and subsequently enhanced productivity (e.g., Kolding & van Zwieten, 2006; Lamberts & Koponen, 2008; Arias et al., 2014). In shallow lakes, seasonal floods are an important source of nutrients (Jul-Larsen et al., 2003a,b), and in deeper lakes, they may influence internal nutrients mixing (Zohary & Ostrovsky, 2011). Crucially, seasonal changes in water level and associated changes in physiochemical characteristics often signal breeding movements of fishes, particularly in systems close to the equator where there is little seasonal variability in temperature and daylength (Lowe-McConnell, 1987; Gownaris unpublished data).

Changes in lake level and their fluctuations have in the past resulted in “booms” and “busts” of some Lake Turkana fish populations (Kolding, 1993a; Kolding, 1995). The catch per unit effort (CPUE) of the lake's fisheries was shown to vary significantly with the previous year's lake level between 1972 and 1988, with higher lake levels leading to increased CPUE (Kolding, 1992). In line with a higher CPUE, fishermen around the lake have reported that incomes from fishing tend to increase during periods of higher lake level (Kaijage & Nyagah, 2010). Over geological time scales, the species composition of Lake Turkana's fisheries has changed in relation to its water level status, with a predominance of large species during high lake stands and small species during low lake stands (Wright, Forman, Kiura, Bloszies, & Beyin, 2015). Furthermore, rates of primary production, which are positively correlated with fish production in lakes (Melack, 1976; Downing, Plante, & Lalonde, 1990), are linked to riverine inputs of nutrients in the system (Tebbs, Avery, & Odermatt, 2015).

In the case of Lake Turkana, links between fisheries and hydrology are driven largely by the dependence of the lake's physiochemical characteristics on inflow from the Omo River, Ethiopia (Figure 1b). The Omo River, the lake's “umbilical cord” (Kolding, 1992), accounts for 80–90% of the water that enters the lake (Yuretich & Cerling, 1983). The remaining water comes from ephemeral rivers that drain the Kenyan highlands (i.e., the Turkwel and Kerio rivers) and local precipitation, which is less than 250 mm/year (Avery, 2012). With no surface outlet, the water budget is a balance between river inflow and evaporation (Butzer, 1971). The lake's closed-basin nature, arid surroundings, and strong dependence on one inflowing river make it a highly pulsed, variable system (e.g., Butzer, 1971; Street-Perrott & Roberts, 1983). Due to its proximity to the equator, the lake's seasonality is largely determined by a flood pulse, which reaches the system approximately 3 months after the heavy rains in the Ethiopian Highlands (Hopson, 1982; Kolding, 1989). Many of the lake's fishes migrate up the Omo River or ephemeral inflowing rivers to breed during the flood pulse, and species breeding within the lake often shows marked breeding peaks during flood seasons (Hopson, 1982, Gownaris, Pikitch, Ojwang, Michener, & Kaufman, 2015).

The Omo River also plays a central role in the Ethiopian government's plans for the country's economic development. A series of five dams (the Gilgel Gibe dams) have been planned along the river. The recently commissioned (January 2015) Gilgel Gibe III dam will lead to a reduction of 2 m in lake level during the period of reservoir filling and subsequent dampening of the lake's seasonal flood cycle (Avery, 2010; Velpuri & Senay, 2012). If the scheduled 10-day artificial floods are released from the dam (in August/September; flows of approximately 1,600 $m^3/s$), Lake Turkana's average seasonal fluctuations would decline from 1.1 to 0.7 m (Avery, 2012). In addition to the dams, land downstream is being cleared for over 200,000 ha of sugarcane and cotton plantations. Extraction of water for these plantations and their associated irrigation will lead to further reductions in lake level. These irrigation operations will require 34% of the Omo River's annual flow, assuming a moderate irrigation efficiency of 70%, and as much as 44% of the river's flow at low irrigation efficiencies of 45% (Avery, 2012). Water demands for these known irrigation projects translate to lake level declines of 13–22 m (Avery, 2012).

Due to Lake Turkana's close connection with the Omo River, development projects altering the river's flow are highly likely to impact the lake's natural functioning and fisheries productivity. Lake Turkana has been described as the “least studied and understood” of the African Great Lakes (Kolding, 1992). Although there have been several recent studies on the lake's fish and fisheries (e.g., KMFRI, 2007; KMFRI, 2008; Muška et al., 2012; Gownaris et al., 2015), considerable research effort is needed before the impacts of upstream development can be comprehensively understood. It has been proposed that research efforts should focus on understanding the effect of hydrological changes and their concomitant ecological impacts (Avery, 2012; Velpuri & Senay, 2012).

In this study, we review the evolution of and changes to the lake's fisheries since the seminal works conducted on the system (i.e., Hopson, 1982; Källqvist, Lien, & Liti, 1988; Kolding, 1989) and revisit the roles that variations in fishing effort (number of fishermen, fishing vessels, nets, or hooks) and water levels and their fluctuations have played in the productivity of these fisheries. To further examine the influence of changing water inflow patterns, we simulated habitat availability in the lake at different water levels using a geographic information system (ArcGIS 10.3) model and determined the relationship between the seasonal flood pulse and extent of the ATTZ.

## 2 | METHODS

### 2.1 | Potential drivers of fisheries

The development of Lake Turkana's fisheries from the beginning of the 20th Century has been extensively described by Hopson (1982); Kolding (1989), and Kolding (1995). This study's description of Lake Turkana's fisheries is based on fisheries catch and effort data collected by the State Department of Fisheries under Kenya's Ministry of Agriculture, Livestock and Fisheries (MoALF). Collection of fisheries data by MoALF focuses primarily on the western side of the lake, where the majority of fishing occurs. Lake Turkana fisheries data used in this study included fisheries yield data from 1993 to 2014 and fishing effort data (number of fishermen, fishing vessels, nets, and hooks) from 1993 to 2007. Yield data on species composition were available for the following time periods: (a) 1963 and most years 1969–1988 (Kolding, 1995), (b) 2004 (MoLFD, 2008), and (c) 2006, 2011, and 2013 (KNBS, 2012; 2013; 2014).

Detailed descriptions of the hydrology of the Omo River and Lake Turkana have recently been provided by Avery (2010; 2012); Velpuri and Senay (2012) and Velpuri, Senay, and Asante (2012). Data on Lake

Turkana's absolute water levels and fluctuations were provided by the USDA/NASA G-REALM program (TOPEX/Poseidon satellite 1992–2003, Jason-1 satellite 2002–2009, OSTM satellite 2008–2015; www.pecad.fas.usda.gov). Throughout this study, water levels are given in meters above sea level (masl), while depths and decline magnitudes are given in meters (m). Water level values published by the United States Department of Agriculture (USDA) are relative to the satellite's reference datum for the system, which was calculated to be 362.87 masl with an accuracy of ±10 cm. To our knowledge, reliable gauge data for Lake Turkana are not available to validate these satellite data. Avery (2012) compiled gauge data for Lake Turkana from local authorities but found that these data were unlikely to accurately portray the system. For example, while satellite data show the expected lake level increase associated with a known large flood pulse in July, 2007, this feature was not evident in the gauge data (Avery, 2012). Where reliable gauge data exist for African lakes, they are in good agreement with satellite data (e.g., Lake Tana, $r^2 = 0.76$: Ayana, 2007; Lake Victoria, $r^2 = 0.99$: Crétaux et al., 2011; Lake Kivu, $r^2 = 0.85$: Munyaneza, Wali, Uhlenbrook, Maskey, & Mlotha, 2009).

Water level for a given year ($WL_Y$) was measured as the average water level of all records for that year, which are taken by satellite approximately every 10 days, and is meant to represent the general status (i.e., high or low stand) of the lake's water level at a given time. The change in water level from one year to the next ($WL_\Delta$) was calculated as $WL_Y – WL_{Y-1}$ and signifies whether the lake is in an increasing or decreasing phase. Intra-annual fluctuation was calculated in two ways, as the standard deviation in water levels ($WL_{stdev}$) and as the water level amplitude ($WL_{amp}$, i.e., $WL_{max} – WL_{min}$) for a given year and provides a measure of the strength of the flood pulse. As explored later, and as expected based on the definition of the ATTZ, there is a high covariance between the extent of the ATTZ and the strength of the flood pulse. However, flood pulse magnitude informs several other important lake characteristics, including the seasonal influx of allochthonous nutrients and the strength of physiochemical breeding cues, and was hence used for regression analyses instead of the ATTZ extent.

## 2.2 | Regression analyses

A suite of multivariate linear regression models was developed to relate yield from Lake Turkana's fisheries to fishing effort variables (numbers of fishers, hooks, net, and vessels) and hydrological variables (water level, inter-annual fluctuations, and intra-annual fluctuations). Models pertaining to effort variables were restricted to 1993–2007, as these were the years in which effort data were available. Two sets of models were created for the water level variables, one that coincided with the effort variable model (1993–2007) and one that covered the full time frame of data availability for these variables (1993–2014). The following steps were followed to ensure robust model development:

1. All variables were checked for normality using the Shapiro–Wilk test (Shapiro & Wilk, 1965).
2. A cross-correlation analysis was run for the matrix of all variables to test for significant covariance among independent variables.
3. A cross-correlation function was used to test for potential time lags in the relationship between independent and dependent variables (maximum lag of 5 years). Inclusion of time lags has proved to be important in similar analyses (e.g., Kolding, 1995; Jul-Larsen et al., 2003a, 2003b), as strong year classes resulting from optimal hydrological conditions do not immediately enter the fishery. This step was not taken for effort variables, for which there is no biological rationale for lags.
4. A Box–Cox test (Box & Cox, 1964) was run on regression between each independent variable and the dependent variable to determine whether transformation of the dependent would improve model fit. The resulting lambda value (transformation that maximized the log-likelihood) was used to transform the dependent variable before further analysis.
5. Linear regressions were created to test for the relationship between the dependent variables and effort and water level variables, respectively. Regressions included two-way interaction terms among independent variables. The function “step” in R was used and parameterized to sequentially simplify the model in both directions with a maximum number of 1,000 steps. This function simplifies models based on Akaike information criterion (Akaike, 1998; Aho, Derryberry, & Peterson, 2014). The resulting models were examined to ensure that no superfluous variables (i.e., non-significant variables) were retained due to the conservative nature of this function. If significant relationships persisted after model simplification, models were used to predict future fisheries yield.
6. A variance inflation factor was calculated for the final simplified models to further ensure the lack of cross-correlation among retained variables.

## 2.3 | Bathymetry data

Bathymetry data used in this study were from geophysical surveys of Lake Turkana undertaken by Fugro Survey Africa Ltd. (4°22′N to 2°51′N) and by Syracuse University (2°51′N to 2°25′N) for Tullow Oil from June to October 2011 (Davidson & Smith, 2011; Syracuse University, 2011; Figure 1b). The spheroid and datum used by both studies were World Geodetic System 1984, with a local projection of Universal Transverse Mercator Zone 36 North. The lake vertical datum was confirmed using a Precise Point Positioning GPS system, Fugro's SkyFix-XP, then reduced to an elevation of 364 masl using the 2008 Earth Gravitational Model (EGM2008; Pavlis, Holmes, Kenyon, & Factor, 2008). This datum was later adjusted to 366.5 masl to coincide with the Government of Kenya's control points and historic topographic maps.

Fugro Survey Africa LTD conducted depth measurements using a dual frequency (33 and 210 kHz) single beam echo sounder (SBES) transducer interfaced with a Simrad EA400 topside recording unit and Starfix.Seis software (Davidson & Smith, 2011). These SBES readings were verified by comparing against a depth to the seabed using a pole lowered into the water and a tape measure at a depth of approximately 2 m, resulting in an acceptable error of ±15 cm. These readings were also verified against the stand-alone echo sounder unit on the Fugro Survey Africa LTD vessel. East to west grid lines were initially conducted at 1 km (4°22′N to 4°00′N) but were increased to 2 km (4°00′N to 3°30′N) then 3 km (3°30′N to 2°51′N) due to time constraints. Grid lines in the north to south direction were conducted at intervals of 5 km. Data collection by Syracuse University was conducted using a Knudsen 320 B/P SBES transducer interfaced with Sounder Suite acquisition software along east to west grid lines of approximately 2 km (2°51′N to 2°25′N). Bathymetry data collected by Fugro Survey Africa LTD and Syracuse University were combined and interpolated by employing a parabolic kriging function with a search radius of 3200 m and an output cell size of 0.25 km$^2$ in Starfix.Seis software.

## 2.4 | Habitat modeling

Hopson (1982) used beach seining and trawling to characterize four fish communities in Lake Turkana related to depth: a littoral community (shoreline to 4 m deep), an inshore demersal community, an offshore demersal community, and an offshore pelagic community. In this present study, habitat availability was assessed for two depth zones, littoral (>0 m to ≤4 m) and non-littoral (>4 m), as the demarcation between inshore and offshore communities depends on time of day and turbidity (Hopson, 1982). Habitat in Lake Turkana also varies along a north–south gradient. The lake lies in two grabens and is often broken into four sectors, the North, Central, Turkwel, and South Sectors (Figure 1c, Table 1). Differences in bathymetry, exposure to the lake's strong southeasterly winds, and proximity to inflowing rivers influence the shoreline features, primary productivity, turbidity, and conductivity of the four sectors (Table 1).

To simulate lake level declines from 0 to 50 m (i.e., 366.5 masl to 316.5 masl), a model was created in ArcGIS 10.3 and run for each sector of the lake by sequentially decreasing each pixel by a depth of 1 m. For each lake level decline scenario, the surface area and volume of total, littoral, and non-littoral habitat were assessed by sector. Surface area for a given sector and/or depth zone was calculated by multiplying the number of pixels by the pixel area, 0.25 km$^2$, then summing. The surface area of each pixel was multiplied by the pixel's depth to calculate pixel volume. Pixel volumes were summed to calculate the total volume within a given sector and/or depth zone for each lake level decline scenario.

To further place habitat changes in the context of the lake's fishery, human population densities in the year 2012 were examined within each of the lake's sectors. Due to the uniformly low population density along the lake's eastern shores (KNBS, 2015), this analysis focused on the western shore population. Estimates of population density were made using LandScan (2012), which provides population count data for pixels of approximately 1 km$^2$ (30 arc-second resolution). The maximum distance that dependent communities live from the lake's shores is unknown (Avery, 2012). A lake buffer of 10 km was used for population analyses to approximate (a) the width of the "Fisheries Livelihood Zone" defined by the National Drought Management Authority (NDMA, 2015; Figure 1c) and (b) the maximum distance that communities living around the lake must walk for water (Kaijage & Nyagah, 2010). Within each sector, the LandScan dataset was clipped to include only those pixels within 10 km of the lake at a

**TABLE 1** Characteristics of the four sectors of Lake Turkana. Summarized from Hopson (1982)

| Sector | Shore | Shoreline features | Primary sediment | Wind exposure | Bathymetry | Max depth |
|---|---|---|---|---|---|---|
| North | | | | | | |
| | Western | 7 lagoons; 6 rivers/creeks*; 10 sand bars, spits, and ridges | sand | mostly moderate | gradual slope with few fault lines | 42 m |
| | Eastern | 5 lagoons; 2 rivers/creeks; 5 sand bars, spits, and ridges; 1 offshore rock | mud | mostly moderate | | |
| Central | | | | | | |
| | Western | 7 lagoons; 7 rivers/creeks; 9 sand bars, spits, and ridges | sand | extreme at north, moderate towards south | symmetric slope; drops off at 30 m | 93 m |
| | Eastern | 3 lagoons; 7 rivers/creeks; 11 sand bars, spits, and ridges; 2 offshore rocks | mud/sand | mostly moderate | | |
| Turkwel | | | | | | |
| | Western | 6 lagoons; Kerio and Turkwel Rivers; 3 rivers/creeks; 18 sand bars, spits, and ridges | sand (mud near rivers) | mostly moderate | shallow area with few fault lines and a submerged reef | 53 m |
| | Eastern | 2 lagoons; 3 rivers/creeks; 14 sand bars, spits, and ridges; 2 offshore rocks | sand/mud | moderate | | |
| South | | | | | | |
| | Western | 3 rivers/creeks; 2 offshore rocks | stones/ boulders/ massive rocks | extreme | steep slope with uneven topography | 108 m |
| | Eastern | 1 lagoon; 2 rivers/creeks; 2 sand bars, spits, and ridges; 4 offshore rocks | stones/ boulders/ massive rocks | extreme at north, low towards south | | |

water level of 366.5 masl (Euclidean distance) of the lake's shoreline. The minimum, maximum, mean ± s.d., and mode of the population density and the number of pixels with a population density of >20 persons/km$^2$ within each sector were calculated.

Bathymetry data for Lake Turkana were also used to determine the influence of changing $WL_{amp}$ on the availability of ATTZ habitat. A similar analysis has been conducted to further understand the impacts of Mekong River flow alteration on the Tonle Sap Lake in Cambodia (Kummu & Sarkkula, 2008). The extent of the ATTZ was determined by finding the total area that was dry during $WL_{min}$ (pixel depth of less than 0 m) but wet during $WL_{max}$ (pixel depth of greater than 0 m) using the ArcGIS model described above. Changes to the ATTZ were calculated (a) historically for the years with available water level data (1993–2014) and (b) for potential future scenarios. For future scenarios, mean lake levels were based on potential water level declines of up to 50 m (from January, 2015, water level of 365.34 masl) at 5 m intervals; a 2 m decline was included to represent the filling of the Gibe III reservoir. A baseline $WL_{amp}$ of 1.12 m was determined based on the water level data compiled for 1993–2014 and was added to each lake level to simulate a flood pulse. At each lake level, 10 $WL_{amp}$ scenarios were run, which represented between 10 and 100% of the baseline $WL_{amp}$. The area of the ATTZ was then calculated for each combination of lake level and $WL_{amp}$, following the methods described above.

## 3 | RESULTS

### 3.1 | Fisheries drivers

The reported yields of Lake Turkana's fisheries have fluctuated greatly during the study period. Annual yields from 1993 to 2014 ranged from approximately 900 to 11,000 metric tons, averaging close to 5,000 metric tons (Figure 2a). The year of highest yield (1998) was also the year of highest magnitude $WL_{amp}$. Low yields over this period coincided with the drying of Ferguson's Gulf in some years (e.g., 1993–1995 and 2006–2007), but in other years, low yield occurred when Ferguson's Gulf was inundated (e.g., 2000–2003 and 2012–2014). Ferguson's Gulf, a 10 km$^2$ lagoon, has primary production rates that are three orders of magnitude greater than the open lake and is intermittently the lake's most productive fisheries area for tilapia (Kolding, 1993a; Figure 1a). This area dries up at lake levels below 362.3 masl.

Species composition of catches changed considerably over the period of 1960 to 1980, from being dominated by the large potamodromous *Citharinus citharus* and *Distichodus niloticus* to mainly lacustrine *Oreochromis niloticus* and other tilapia species, *Lates niloticus* and *Labeo horie*, but has remained similar since the 1980s (Figure 3). Apart from the number of hooks used, all effort variables increased from 1993 to 2007, with a particularly rapid increase in effort after the year 2000 (Figure 2b). Both the number of fishermen ($r^2$ = 0.92, $p$ < 0.0001) and number of vessels ($r^2$ = 0.79, $p$ < 0.00001) increased linearly over this time period. The average number of fishermen each year from 1993 to 2007 was 4,797, using on average 385 vessels, 6,187 nets, and 13,300 hooks. The reported average annual catch per fisher was 1.09 tons of fish from 1993 to 2007.

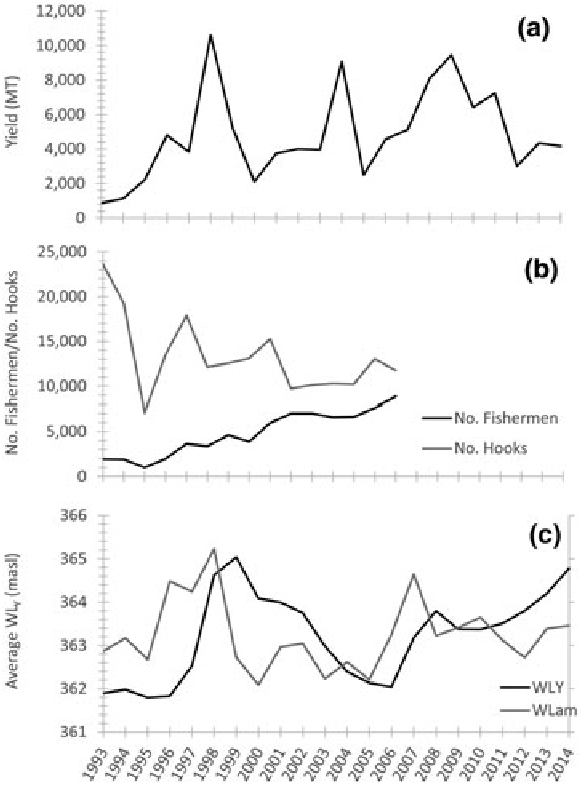

**FIGURE 2** Fisheries (yield and effort) and hydrological characteristics of Lake Turkana: (a) Yield from the Lake Turkana fishery for 1993–2014. Data collected by Kenya's Ministry of Agriculture, Livestock and Fisheries, (b) Effort in terms of number of fishermen and number of hooks in the Lake Turkana Fishery for 1993–2007. Data collected by the Kenyan Ministry of Fisheries and Agriculture, (c) Average annual water level ($WL_Y$; meters above sea level) and seasonal amplitude ($WL_{amp}$; meters) for Lake Turkana from 1993 to 2014. Note that, over this time period, yield peaked in 1998, corresponding with the highest seasonal amplitude. Satellite data collected from the United Stated Department of Agriculture Global Lakes and Reservoirs Database

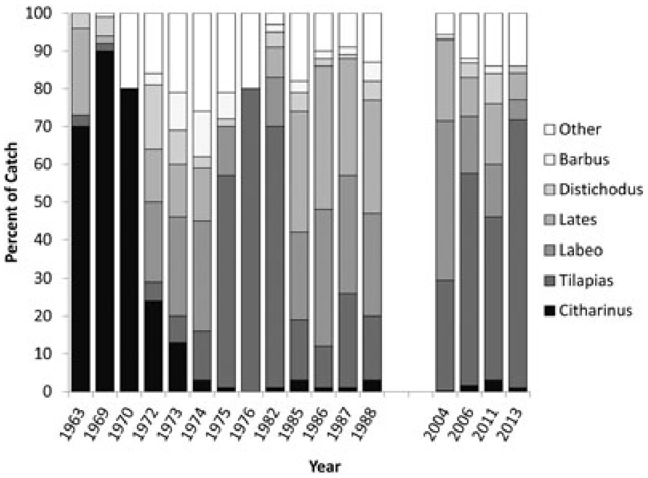

**FIGURE 3** Species catch composition for the Lake Turkana fishery (available years). Data for 1963–1988 are taken from Kolding (1995), with some years excluded due to a high percentage of unspecified catches. Data for 2004 from MoLFD (2008). Data for 2006, 2011, and 2013 are taken from KNBS (KNBS, 2012; 2013; 2014). Data on catch composition are not available for most years after 1989

The $WL_Y$ generally increased from 1993 to 1999, decreased from 2000 to 2006, then increased again from 2006 to 2014, with minimum (~362 masl) and maximum (~365 masl) values in 1995 and 1999, respectively (Figure 2c). Half of the years showed a positive $WL_{\Delta}$, with the greatest being approximately 2 m, and the other half showed a negative $WL_{\Delta}$, with a minimum of approximately −1 m. Lake level seasonality for 1993–2014 indicates that, on average, water level was at its lowest point in June and peaked in November (Figure 4). The flood cycle is fairly regular but does vary from year to year and is confounded by inter-annual water level changes in some years. The highest water level recorded by USDA occurred between April and July in 75% of years (1993–2014). The lowest lake level recorded by USDA was more consistent, occurring between October of the current year and January of the following year in all but 1 year studied. The average $WL_{amp}$ for 1993–2014 was 1.12 m, within the 1 to 1.5 m seasonal variation noted elsewhere for this system (e.g., Avery, 2012, Figure 2). The seasonal flood cycle in 2015 was greatly altered by the commissioning of Gilgel Gibe III during the month of January (Figure 4).

All dependent and independent variables were normally distributed apart from the number of vessels and $WL_{stdev}$, which were not used in the final analyses due to cross-correlation with other variables. The number of fishermen had a positive significant correlation with the number of vessels ($r^2 = 0.85$, $p < 0.001$) and the number of nets ($r^2 = 0.41$, $p < 0.01$), but not with the number of hooks. The number of hooks and number of fishermen were retained for regression analysis, as the number of fishermen was believed to be a more direct measure of effort than the number of boats or nets for this system. Interestingly, none of the effort variables were significantly correlated with water level variables.

When regressed with yield, the number of fishermen and number of hooks had a lambda of 0, so the dependent was log transformed before regression analysis. The most parsimonious model for effort retained only one variable, the number of hooks, which showed a significant negative correlation with yield ($r^2 = 0.31$, $p < 0.05$; Table 2). A variance inflation factor was not calculated, given that only one variable was retained in the model.

Absolute lake level ($WL_Y$) was not significantly correlated with $WL_{amp}$, $WL_{stdev}$, or $WL_{\Delta}$. Intra-annual fluctuations as measured by amplitude ($WL_{amp}$) were significantly correlated with intra-annual fluctuations as measured by standard deviation ($WL_{stdev}$; $r^2 = 0.91$, $p < 0.001$) and with inter-annual fluctuations ($r^2 = 0.62$, $p < 0.001$). Amplitude was chosen to represent intra-annual fluctuations over standard deviation, which was not normally distributed. Teasing apart the influence of inter- versus intra-annual fluctuations is unfeasible due to their high correlation. Because future inter-annual fluctuation scenarios are not available from current hydrological predictions for Lake Turkana, and because intra-annual fluctuations may be a more important driver of productivity in tropical lakes than are inter-annual fluctuations (e.g., Gownaris et al., in review), intra-annual fluctuations were used in the final analysis. The cross-correlation function determined the relationship between $WL_Y$ and yield to be strongest at a lag of 1 year (though the strength of the relationship was similar at lags of 0 to 3 years) and between $WL_{amp}$ and yield at a lag of 0 years. The water level variables used for regression analysis were therefore the water level the preceding year ($WL_{Y-1}$) and $WL_{amp}$.

The Box–Cox test suggested equal validity of either a log (lambda = 0) or square root (lambda = 0.5) transformation of the dependent for $WL_{Y-1}$ and $WL_{amp}$; a log transformation was chosen for ease of comparison with the effort variable model and to ensure that model predictions were properly constrained to be ≥0. The most parsimonious model for water level variables was borderline significant ($r^2 = 0.40$, $p = 0.05$) and retained both $WL_{Y-1}$ and $WL_{amp}$ but not their interaction term (Table 2). The extended water level variable and yield

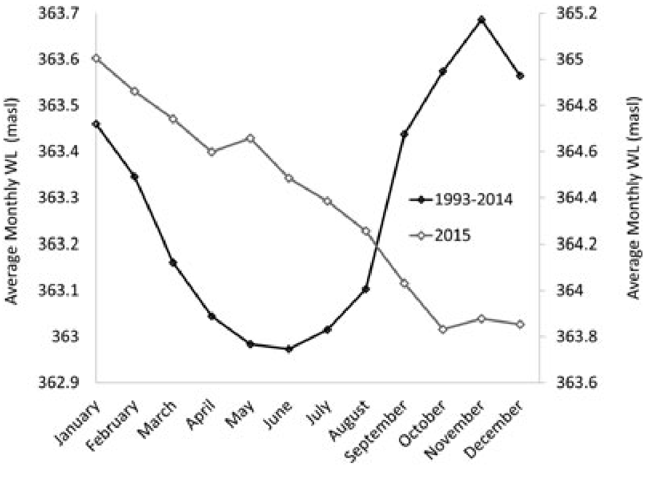

**FIGURE 4** Lake Turkana monthly water levels in meters above sea level averaged by month across years for 1993–2014 (black line; primary axis) and averaged by month for 2015 (grey line; secondary axis). Seasonal fluctuations play a key role in controlling the biology of the lake's fishes and will be considerably dampened by the construction of the Gibe dams along the Omo River. Satellite data are compiled from the United States Department of Agriculture Global Lakes and Reservoirs Database at a 10-day temporal resolution

**TABLE 2** Parameters included in the most parsimonious linear models relating Lake Turkana effort and water level variables to fisheries yield for 1993–2007 and 1993–2014, respectively

| **1993–2007: Effort variables** | |
|---|---|
| Intercept | −9.355 (5.112) |
| Hooks (no.) | −8.972e-05 ($3.673\times10^{-05}$)** |
| 1993–2007: Water level variables | |
| Intercept | −106.74 (56.88) |
| Seasonal amplitude (m) | 0.9846 (0.3645)** |
| Previous year lake level (masl) | 0.3136 (0.1562)* |
| 1993–2014: Water level variables | |
| Intercept | −110.91 (183,000) |
| Seasonal amplitude (m) | 1.0060 (0.3168)*** |
| Previous year lake level (masl) | 0.3252 (0.1271)** |

Fisheries data (yield and effort) collected by Kenya's Ministry of Agriculture, Livestock and Fisheries. Water Level data collected from the United States Department of Agriculture Global Lakes and Reservoirs Database.

masl, meters above sea level.

*$p < 0.10$.

**$p < 0.05$.

***$p < 0.01$.

data (1993–2014) resulted in the same variable lags and a similar parsimonious model to that resulting from the 1993–2007 data (Table 2). The most parsimonious model for this time frame included $WL_{Y-1}$ and $WL_{amp}$ with no interaction term and showed greater significance than that of the limited time frame model ($r^2 = 0.36$, $p < 0.05$). The variance inflation factor for this model was low (1.22), suggesting that the model was not influenced by independent variable covariance. In both the 1993–2007 and 1993–2014 models, $WL_{amp}$ was a stronger driver than was $WL_{Y-1}$ (Table 2).

Several potential future scenarios were tested using the final water variables regression model (Table 3); these scenarios were based on the hydrological analyses of Avery and Eng (2012) and Velpuri and Senay (2012). The lake levels tested were as follows: (a) the 2015 lake level (~365 masl), (b) the predicted lake level upon filling of the Gibe III reservoir (~363 masl), and (c) the lake level under the maximum decline predicted for current hydrodevelopment plans (~340 masl). At each lake level, three potential future $WL_{amp}$ magnitudes were tested: (a) the average $WL_{amp}$ (1.12 m) for 1993–2014, (b) the $WL_{amp}$ predicted if the proposed artificial flooding is adhered to (0.7 m), and (c) the complete loss of a flood pulse (0 m). All model predictions for fisheries yield under the 2015 lake level scenarios (365 masl, varying $WL_{amp}$) and reservoir filling scenarios (363 masl, varying $WL_{amp}$) fell within the range of yields reported for 1993–2014 (Table 1). At 365 masl, which assumes no decline in absolute lake level, the loss of a flood pulse halves the system's fisheries yield as compared to the 1993–2014 average (Table 3). If $WL_{amp}$ is held constant, a decline in lake level of only 2 m leads to a 50% reduction in yield. At more severe water level declines, the fishery collapses, with yields far below those reported in the past (Table 3). In all cases, a loss of $WL_{amp}$ led to an over two-thirds reduction in fisheries yield as compared to the scenario using the average $WL_{amp}$ of 1.12 (Table 3).

## 3.2 | Habitat modeling

Using the bathymetry data described above, the total lake area at the zero datum of 366.5 masl is 6,837 km$^2$, with a volume of 236 km$^3$. The following description gives an overview of the results of lake level simulations produced by the GIS model. These changes are discussed in terms of lake level decline in reference to the zero datum of 366.5 masl. A decline of 25 m is used as a benchmark throughout these descriptions, as this approximates the maximum decline predicted by Avery and Eng (2012) given the current development agenda.

**TABLE 3** Scenarios for future Lake Turkana hydrological regimes and predicted fisheries catch

| Previous year lake level (masl) | Seasonal amplitude (m) | Predicted yield (MT) | 95% Confidence intervals (MT) |
|---|---|---|---|
| 365 | 1.12 | 7,563 | 4,332–13,204 |
| 365 | 0.70 | 4,956 | 2,954–8,319 |
| 365 | 0.00 | 2,451 | 1,175–5,118 |
| 363 | 1.12 | 3,946 | 3,112–5,004 |
| 363 | 0.70 | 2,586 | 1,776–3,767 |
| 363 | 0.00 | 1,279 | 579–2,825 |
| 340 | 1.12 | 2 | 0–1,044 |
| 340 | 0.70 | 1 | 0–775 |
| 340 | 0.00 | 1 | 0–482 |

masl, meters above sea level.

At a decline of 25 m in lake level, the model shows a decrease of 58% in lake surface area and 40% in lake volume (Figure 5). These declines would occur largely in the lake's non-littoral (≤4 m) habitats. Conversely, littoral surface area and volume would nearly double as lake level declines up to 21 m, but then begin to slowly decrease as lake level recedes further. The overall ratio of surface area to volume (SA:V) of the lake would increase with lake level declines, from 29 at a 0 m decline to 43 at a 25 m decline (Figure 6). This increase would steepen at lake level declines >25 m, reaching an SA:V of 75 at a lake level decline of 50 m.

Predicted changes in surface area and volume vary greatly by sector based on differences in bathymetry (Figure 5). The most drastic changes would occur in the North Sector, in which surface area and volume would decline 85% and 97%, respectively, under a 25 m lake level decline scenario. The Turkwel Sector would also decrease considerably, by over 51% in area and 85% in volume at this level of decline. At lake level declines >42 m, the North Sector would disappear completely and the Turkwel Sector would be greatly reduced and consist largely (80% by surface area) of littoral habitat (Figure 5). Drastic declines in the extent of the Turkwel Sector would lead to the separation of the system into two smaller lakes (Figure 1c), which would occupy what are now the Central and South Sectors, respectively.

Due to their greater depth and steeper bathymetry, declines in the Central and South Sectors would be less severe. The Central Sector would decrease by 32% in surface area and by 55% in volume and the South Sector by 13% in surface area and by 47% in volume at lake level declines of 25 m (Figure 5). As seen for the lake overall, the area of littoral habitat would increase within each sector at lake level declines up to 20 m, but begin to decrease beyond declines of 20 m in the North and Central Sectors and 30 m in the Turkwel Sector. The SA:V would increase in all sectors with lake level decline, but most notably in the North Sector, where it would increase from 61 to 335 for the 25 m decline scenario.

The average human population density on the lake's eastern shores in 2012 was low, with 73% of pixels having a population of zero and an additional 17% of pixels having a population of only one (Table 4). The highest density pixels within 10 km of the lake's western shoreline were found in the Central Sector. The Turkwel Sector, however, had the highest proportion of pixels with a population density of >20 persons/km$^2$ (39%) among the four sectors (Table 4).

The extent of the ATTZ varied from 42.48 km$^2$ in 2000 to 157.50 km$^2$ in 1998, with a mean of 83.53 km$^2$. For the years 1993–2014, there was a strong significant positive correlation between $WL_{amp}$ and the extent of the ATTZ ($r^2 = 0.86$, $p < 1 \times 10^{-9}$; Figure 7a). The future scenarios model shows a linear decrease in the extent of the ATTZ with a decrease in $WL_{amp}$ (for all lake level decline scenarios $r^2 = 0.997$ and $p < 1 \times 10^{-10}$; Figure 7b). At a given $WL_{amp}$, the extent of the ATTZ would be nonlinearly related to lake level decline and peak at intermediate declines, as also seen for total littoral

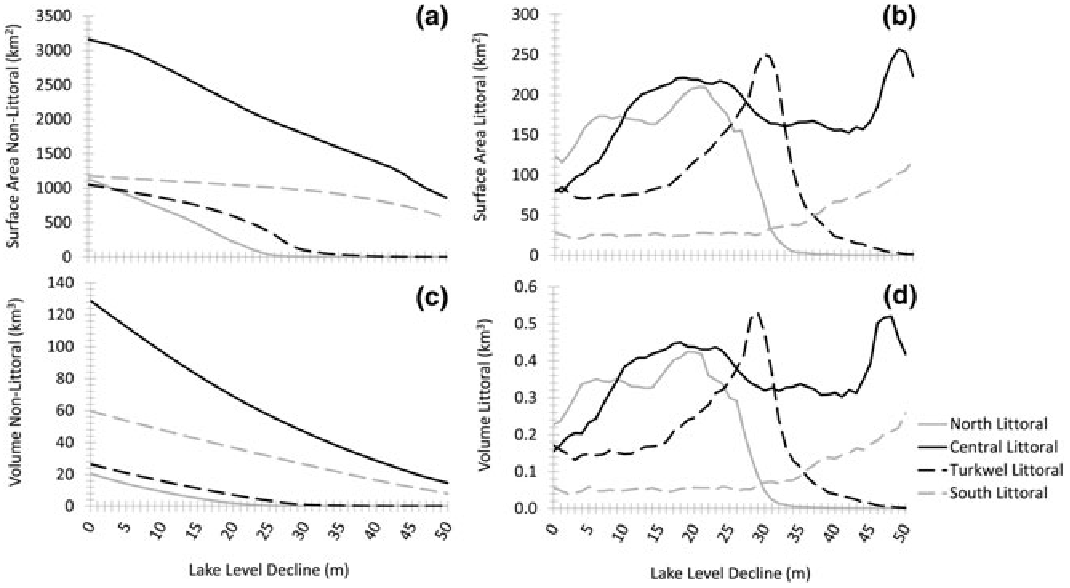

**FIGURE 5** Surface Area [(a) non-littoral habitat; (b) littoral habitat] and volume [(c) non-littoral habitat; (d) littoral habitat] along lake level declines of 0–50 m (366.5–316.5 meters above sea level), shown by habitat type within each of Lake Turkana's four sectors. Littoral habitat is defined as habitat that is ≤4 m in depth

habitat. The influence of the magnitude of $WL_{amp}$ on ATTZ extent would be strongest at intermediate lake level declines (Figure 7b).

## 4 | DISCUSSION

### 4.1 | Fisheries trends and drivers

Lake Turkana is located in a region undergoing rapid development in several sectors. This study highlights the trade-offs associated with three sectors existing in the context of transboundary management in the region: hydropower, large-scale irrigation agriculture, and fisheries. As previously seen by Kolding (1992) for the period 1972 to 1988, this study found significant links between Lake Turkana's hydrology and fisheries catch for the years 1993–2014. The time lags between lake level and catch coincide with the recruitment age of the top fishery species in Lake Turkana, which range from 6–10 months (*O. niloticus*) to 3–4 years (*L. niloticus*), indicating that higher lake levels produce larger year classes.

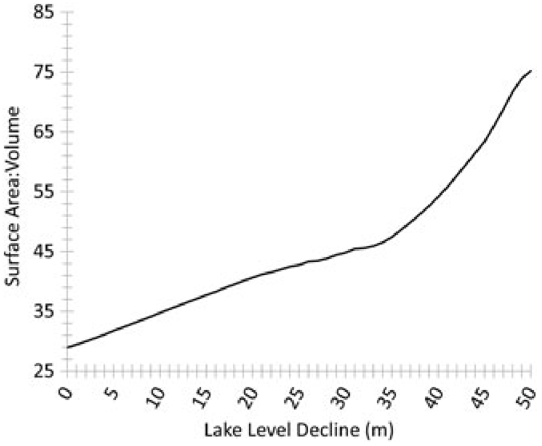

**FIGURE 6** Change in the surface area to volume ratio of Lake Turkana along lake level declines of 0–50 m (366.5–316.5 meters above sea level)

Lake level alone was a strong predictor of fisheries catch in the 1970s and 1980s (Kolding, 1992). The current study builds on this earlier work by highlighting the role of absolute lake levels and their fluctuations in driving fisheries productivity. In fact, water level fluctuations were found to be the strongest drivers among the hydrological parameters studied (Table 2), as also seen in Lake Kariba (Karenge & Kolding, 1995). These fluctuations are already undergoing changes due to the recent commissioning of Gilgel Gibe III (Figure 4). The scenarios tested here suggest that extreme reductions in absolute lake level (i.e., 25 m) will lead to a collapse of the fishery and that, at any lake level, loss of the flood pulse will lead to over a two-thirds reduction in fisheries yields (Table 3).

Research on other African lakes has shown that, in many cases, fisheries catch is more strongly related to hydrological variables than to fishing effort (Jul-Larsen et al., 2003a, 2003b; Kolding & van Zwieten, 2012). Lake Turkana appears to follow this pattern. Fishing effort does not significantly predict yield in logical manner (Figure 2), with an increase in the number of hooks used leading to a decrease in overall fish yield. This unexpected relationship may suggest reporting inaccuracies for this effort variable, which was the only effort variable that was not significantly correlated with the others compiled (i.e., the number of fishermen, number of nets, and number of vessels). Furthermore, there is little anecdotal support that fish productivity is driven by fishing effort in this system. In spite of nearly linear increase in most effort variables, Lake Turkana's fisheries yield showed cyclical fluctuations between 1993 and 2014, with peaks of 9,000–10,000 metric tons occurring approximately every 5 years, in 1999, 2004, and 2009, respectively (Figure 2).

These findings are in agreement with historical declines in Lake Turkana's fish stocks (Figure 3; Kolding, 1995), which appear to have

**TABLE 4** Population parameters of Lake Turkana's four sectors

| Sector | Sector area (km2) | Total population (#) | Max (#/km2) | Mean (#/km2) | SD (#/km2) | Mode[a] (#/km2) | Percent ≥20[b] (#) |
|---|---|---|---|---|---|---|---|
| North | 499 | 5,868 | 160 | 11.76 | 13.88 | 12 | 13.63 |
| Central | 1,329 | 16,386 | 1,442 | 12.33 | 53.97 | 5 | 14.3 |
| Turkwel | 884 | 13,186 | 74 | 14.92 | 15.15 | 21 | 38.8 |
| South | 583 | 712 | 20 | 1.22 | 2.09 | 1 | 0.17 |
| Eastern | 3,202 | 5,890 | 1,793 | 1.84 | 38.14 | 2,340 | 0.35 |

Data are shown for a 10 km buffer around Lake Turkana's shores at a lake level of 366.5 meters above sea level. Population metrics calculated using the 2012 LandScan dataset.

[a] Pixels with a population of 0 are not included in the calculation of mode.

[b] Percent ≥20 refers to the percent of 1 km$^2$ pixels in which there were more than 20 people.

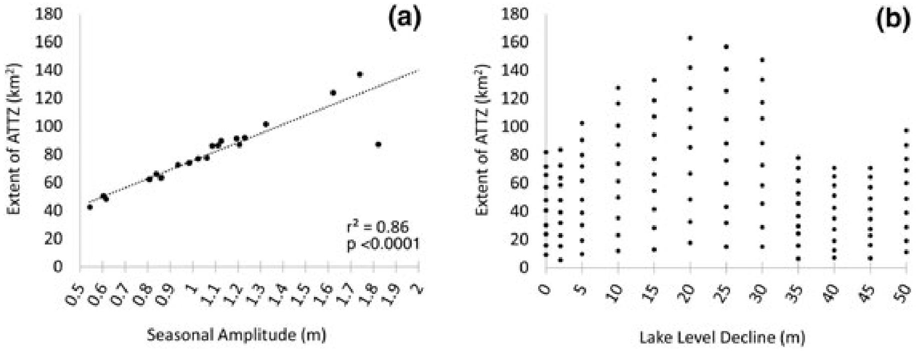

**FIGURE 7** Relationships among seasonal amplitude, lake level, and the extent of the aquatic terrestrial transition zone (ATTZ), defined as the area covered by water only during the seasonal flood pulse: (a) Relationship between the extent of the ATTZ and the seasonal water amplitude for the time period studies (1993–2014), (b) relationships between lake level decline in meters and the area of the ATTZ across different magnitude seasonal amplitudes. Water level decline scenarios include declines in increments of 5 m, with the addition of a 2 m scenario to simulate declines due to dam construction alone (365–315 meters above sea level). Seasonal amplitude scenarios were determined by sequentially decreasing seasonal amplitude by 10% for each water level scenario. For each decline scenario, the highest point represents a natural seasonal amplitude of 1.12 m, while the lowest point represents a seasonal amplitude 10% of the natural amplitude, or 0.112. For all lake level decline scenarios, the area of the ATTZ and seasonal amplitude showed a strong positive correlation (all $r^2 > 0.99$ and $p < 1 \times 10^{-6}$)

been linked to changes in hydrology rather than to fishing pressure. The lake's water levels declined rapidly from the end of the 1970s to the end of the 1980s, leading to changes in the structure of the lake's food web (Kolding, 1993b) and contributing to the population declines of several fish species (Kolding, 1995; Muška et al., 2012). Populations of two of the lake's initial commercially important potamodromous species, *C. citharinus* and *D. niloticus*, collapsed early, possibly due to a combination of overfishing and falling water levels (Kolding, 1995; Figure 3). The open water fishes *H. forskalli*, *A. baremoze* and *Brycinus* spp. also showed heavy declines during this period (Kolding, 1993b; Kolding, 1995; Muška et al., 2012). These declines could not be linked to fishing, however, as there was no pelagic fishery in the lake during that time. Pelagic fishes, particularly small zooplanktivorous species and their predators, have been noted as highly climate sensitive in several other African lakes (e.g., Sarch & Allison, 2001; Jul-Larsen et al., 2003b; Kolding & van Zwieten, 2016).

Given the intimate connection between the Omo River and Lake Turkana, the observed relationship between fisheries productivity and hydrology is perhaps not surprising. Despite its relatively deep nature in the Central and South Sectors, variations in Lake Turkana's biological productivity have been shown to be strongly affected by inflow from the river, as have variations in salinity and turbidity (Hopson, 1982; Källqvist et al., 1988; Tebbs et al., 2015). Links between seasonal floods and breeding peaks are common in tropical and neotropical freshwater systems (e.g., Lowe-McConnell, 1987; Bøgh, Clarke, Jawara, Thomas, & Lindsay, 2003; Agostinho, Gomes, Veríssimo, & Okada, 2004) and have been documented for Lake Turkana (Hopson, 1982), which lies only three degrees north of the equator and hence shows little seasonality in temperature and day length. Lastly, the magnitude of Omo River flow entering the lake alters the distribution and availability of lake habitats and the extent of the ATTZ (see discussion below), which further influence fish spatial dispersion (e.g., tilapia catchability is highest during falling water level; Kolding, 1993a). Inflow from the Omo River therefore affects the fisheries productivity of Lake Turkana through mechanisms related to fish population size (food availability, habitat availability, and breeding cues) and catchability.

### 4.2 | Habitat availability and distribution

Habitat availability, distribution, and quality are key considerations in maintaining the fisheries productivity of Lake Turkana due to their influence on (a) the size of fishable habitat, (b) the location of fishable habitat in relation to human populations, (c) the amount of fish breeding habitat and predatory refuge for juveniles, and (d) nutrient and food availability. The availability and distribution of habitat in Lake Turkana is dependent on lake level and will consequently be impacted by lake level decline (Figure 5). Declines in lake level would also increase Lake Turkana's SA:V and therefore evaporative volume (Figure 6). Due to the extremely arid climate in which the lake is situated, evaporation rates are high (2.3–2.8 m/year; Kolding, 1992) and account for the majority of water lost from the system (Avery, 2012). An increase in the SA:V of Lake Turkana would create a positive feedback loop in which water level declines due to upstream development lead to increased evaporative loss and further declines in water level.

Littoral habitat area is of particular importance in the case of Lake Turkana, as nearly all fishing takes place here. The most common types of fishing gear are gillnets and beach seine nets, both generally limited to shallow inshore habitats (Hopson, 1982; Kolding, 1989; Yongo et al., 2010). The habitat model created here shows that, at lake level declines up to 25 m, Lake Turkana's littoral habitat would increase (Figure 5). Without seasonal fluctuations, however, this increase in habitat coverage would come at the expense of habitat productivity. An increase in static littoral habitat as water levels decline would be coupled with a decrease in dynamic littoral habitat, the ATTZ, due to a dampened flood pulse (Figure 7a). Absolute lake level will also influence the extent of the ATTZ, which peaks at intermediate levels of decline, and modulate the degree to which seasonal amplitude influences this extent (Figure 7b).

Systems with a fluctuating ATTZ are more productive than stable ones (Welcomme & Halls, 2001; Wantzen et al., 2008; Kolding & van Zwieten, 2012), and species that breed and feed within the ATTZ have higher growth rates and lower mortality rates than those that stay in the main water body, known as the "flood-pulse advantage" (Bayley, 1991). Removal of the flood pulse would reduce nutrient influx to the littoral and cause littoral habitats to stagnate and exhibit conditions harmful to fish populations (e.g., low oxygen levels), forcing them into deeper waters, increasing predation pressure, and reducing catchability (Kolding, 1993a). Although macrophytes are not common in Lake Turkana, shoreline grasses are an important component of the lake's littoral habitats. The lake's natural average inter-annual ($WL_{\Delta}$; 0.46 ± 0.48) and intra-annual water level fluctuations ($WL_{amp}$; 1.12 ± 0.40) fall within the range of those most conducive to supporting healthy shoreline vegetation communities (Hill, Keddy, & Wisheu, 1998). Thus, altering the magnitude of these fluctuations would lead to changes in vegetative cover. The lake's native vegetation is already threatened by the invasive woody plant *Prosopis juliflora*, which would gain a competitive advantage at reduced seasonal variability in water level (Mwangi & Swallow, 2005).

Lake level decline would also lead to a widespread loss of the open water habitat. Although less critical than the case of littoral habitat loss due to its greater volume, decreases in the pelagic habitat would limit the carrying capacity of species that live or breed there. Some of the lake's top and most valuable fishery species, including *L. niloticus*, either breed or have life history stages that depend on the lake's deeper waters (Hopson, 1982; KMFRI, 2008). The greatest potential for increased yield from the system is the inclusion of open water fish stocks, which may become possible with increased fisheries investments. As such, the highest estimates of maximum sustainable yield for the system are those that include the lake's small pelagic fishes, which require open water habitat and are sensitive to changes in nutrient inflow (i.e., *Brycinus* and *Alestes* spp.; Kolding, 1995; Table 5). Fisheries focused on small fishes, many of which are for pelagic species (e.g., "Kapenta" fishery in Lakes Tanganyika, Kariba, and Kivu; the "Dagaa" fishery in Lake Victoria; and the "Ragoogi" fishery in Lake Albert) are the most productive among African inland fisheries and make up a large proportion of the catch where they are present (e.g., Mubamba, 1993; Legros & Luomba, 2011; Kirema Mukasa, 2012; Kolding & van Zwieten, 2016). It is also important to note that the majority of the lake's endemic species are found below the 10-m contour, so declines in inshore and offshore habitats would have ecological consequences for these species (Hopson, 1982).

**TABLE 5** Various estimates of maximum sustainable yield (MSY) for Lake Turkana

| Reference | MSY estimate (tons/year) |
|---|---|
| Rhodes, 1966 | 50,000–160,000 |
| Coche & Balarin, 1982 | 20,000–30,000 |
| Hopson, 1982 | 37,000 |
| Hopson, 1982[a] | 560,000 |
| Källqvist et al., 1988 | 15,000–30,000 |
| Källqvist et al., 1988[b] | 22,000 |
| KMFRI, 2008 | 88,404 |

[a] Considerably higher than the first Hopson (1982) estimate due to the inclusion of small pelagic fishes, which may not be sustainable to exploit due to their high climate sensitivity (Kolding, 1995).

[b] The two estimates by Källqvist et al. (1988) differ in methodology, with the second based on the relationship between primary production and fish production described by Melack (1976).

In addition to habitat availability, two important factors controlling the productivity of fish species in Lake Turkana are the nutrient-rich, turbid waters entering the North Sector from the Omo River and the strong southeasterly winds blowing from the South Sector (Table 2). Due to the elongated nature of the lake, the influence of these factors differs by sector, and it is therefore important to consider habitat changes in this context. The productive and relatively sheltered North Sector, where lagoonal habitats are common, would be the most affected by lake level decline and will essentially dry up at declines of ≥25 m (Figure 5). The Turkwel Sector would begin to disappear at declines of ≥40 m, which would result in two smaller lakes, existing in the current Central and South sectors (Figure 1c). The lake's South Sector would be the least and last affected by a strong lake level decline, due to its greater depth. However, it is also the least productive habitat due to its distance from the Omo River's nutrient-rich inflow and may experience drastic increase in salinity if it becomes disconnected from the rest of the lake. This sector's rocky coastline, exposure to high winds, and lack of lagoonal habitats will further limit its potential as a productive fishing area (Table 2).

The impact of habitat changes and their distribution on the fisheries of Lake Turkana is also dependent on where human populations have settled around the lake. While population densities along the lake's eastern shores are uniformly low, densities along the lake's western shores vary among the four sectors described above. The South Sector, which will be least influenced by water level declines, is also the least populated (Table 4, Figure 5). In contrast, population density is highest along the Turkwel Sector, which will be heavily impacted by water level declines due to its shallow nature (Table 4; Figure 5).

Widespread movements of human populations surrounding the lake following hydrological changes are possible. Such movements are particularly likely if water level declines are extreme enough to lead to the loss of the North and Turkwel sectors of the lake (Figure 5). The North Sector lies close to the conflict-stricken Illemi triangle (Oba, 1992) and, at high water levels, crosses into Ethiopia. Conflict over fishing rights in the Omo delta has worsened over the past decade and is exacerbated by low lake levels (Kine & Achalei, 2011; Johannes, Zulu, & Kalipeni, 2015; Wright et al., 2015). Some locals warn that resource scarcity will turn Lake Turkana into an “endless battlefield” (Vidal, 2015).

### 4.3 | The future of Lake Turkana's fisheries

The future of the Lake Turkana ecosystem and its fisheries looks bleak given the current development agenda on the Omo River and the associated development impacts on water levels and their fluctuations. The degree to which changing hydrological regimes would influence the abundance of commercially important species or those with potential for fisheries growth depends on their ecological requirements and flexibility (Gownaris et al., 2015). Concerns regarding the impacts of upstream development on Lake Turkana's fisheries have been raised elsewhere (e.g., Avery, 2012; Muška et al., 2012), yet little effort has been made to seriously address these impacts. Monitoring of the ecological status of Lake Turkana and management of its fishery must be strengthened during this period of change. For example, the average recorded catch of around 1 ton per fisherman annually from 1993 to 2007 (Figure 2) is very low when compared to other African lakes (average of catch of 3 tons/fisherman/year; Kolding & van Zwieten, 2012) and suggests that the lake's reported catches may be an underestimate. The lake's fisheries are therefore likely to be undervalued, which downplays their importance when considering development trade-offs. Another example is the grouping of several ecologically distinct species in fishery statistics (e.g., Gownaris et al., 2015), which may generate misleading conclusions regarding the health of various fish stocks in the system.

This study supports and expands previous studies in suggesting that of utmost importance to Lake Turkana's fisheries is maintaining the system's natural flood cycle via the release of an artificial flood of ecologically appropriate timing, volume, and duration from the Gilgel Gibe dams (Table 3, Figure 7). To do so, artificial floods should lead to seasonal increases in water level of approximately 1–1.5 m during July–November (Figure 4). Maintaining natural levels of flood disturbance is a recommendation for any hydro-engineering project (IFC, 2015), but the presence of irrigation infrastructure downstream of the Gilgel Gibe dams make the likelihood of adherence to natural flooding regimes along the Omo River questionable. Recent efforts to develop trade-off-based decision-making frameworks for hydropower development, though most effective when implanted early in the planning process, provide excellent guidance (Poff et al., 2015). Climate change will further complicate water resources management in the region. However, the impacts of hydrological development along the Omo River are likely to be more extreme and immediate than those of climate change, as also found for Tonle Sap Lake, a well-studied system in Cambodia facing similar challenges (Arias et al., 2014).

Although lake level declines of some magnitude are highly likely due to irrigation needs upstream, these declines must be minimized. In particular, declines of >25 m will represent a tipping point in the system due to the shallow bathymetry of the North and Turkwel sectors (Figure 5). Irrigation developments beyond those already planned, which on its own could lead to declines of this magnitude, will therefore irrevocably harm the lake, its fisheries, and the humans that depend on it.

Changes to Lake Turkana's hydrological regime will occur alongside other changes to the system brought on by upstream development. Full consideration of these factors is beyond the scope of this study, but some are listed here. The volume and grain size of sediment entering Lake Turkana from the Omo River will be altered by upstream development in several, sometimes conflicting, ways: (a) a reduced total influx of water may lead to a reduction in sediment influx, (b) the Gibe III reservoir will trap bed load sediment that would have otherwise enter the lake, and sedimentation in the reservoir may ultimately lead to reduced effectiveness of hydropower production (Avery, 2012), and (c) land use change due to plantation development may lead to increased sediment loads (Avery, 2012). Altered sediment inputs will lead to changes in the lake's sediment composition, in turbidity patterns and hence fish breeding cues, and in the extent of the Omo Delta, an important breeding area for many of the lake's fishes (Hopson, 1982). Unfortunately, none of these impacts have yet been quantified (Avery, 2012). If sediment load reductions due to hydropower development are comparable to those measured along the Mekong River, they will exceed 50% (e.g., Kummu, Lu, Wang, & Varis, 2010; Kondolf, Rubin, & Minear, 2014).

The fertilization of crops downstream of the Gibe III dam may lead to increased nutrient influx to Lake Turkana and changes in the lake's nutrient ratios and subsequently in phytoplankton community composition and productivity. Reductions in the volume of freshwater inflow from the Omo River will lead to increased salinity in this borderline saline lake, influencing the lake's phytoplankton, invertebrate, and fish communities (Verschuren, Cocquyt, Tibby, Roberts, & Leavitt, 1999; Wood & Talling, 1988). Apart from Nile Tilapia, for which there is an extensive body of literature regarding salinity tolerance and various proposed upper limits (e.g., Basiao, Eguia, & Doyle, 2005; Lawson & Anetekhai, 2011; Schofield, Peterson, Lowe, Brown-Peterson, & Slack, 2011), the salinity tolerance of the lake's fishes is unknown. Upstream development will also alter the Omo River's morphology, flooding regimes and flow patterns, sediment composition, and vegetation, with implications for fishes that migrate upriver from the lake to breed (e.g., Ligon, Dietrich, & Trush, 1995). It is unknown whether Gibe III could block breeding migration routes of some of the lake's fishes. Although the dam is over 250 km from the Omo Delta, and therefore likely too far to act as a barrier for most species, *Alestes* and *Brycinus* spp. are known to sometimes migrate long distances (Lucas, Baras, Thom, Duncan, & Slavík, 2001).

If Ethiopia's future construction of two additional dams downstream of Gibe III, the Gibe IV and V dams, comes to fruition, all impacts discussed will be exacerbated. In addition to upstream development, several other development opportunities in Turkana have recently sparked the interest of a range of local, national, and international actors (Schilling, Weinzierl, Lokwang, & Opiyo, 2016). The most significant developments include the discovery of oil in the region in 2012 (Enns & Bersaglio, 2015), the large-scale infrastructural project "Lamu Port Southern Sudan-Ethiopia Transport", the discovery of two significant water aquifers in 2013 (Radar Technologies International, 2013), and the construction of a large wind farm on the lake's northeastern shores (LTWP, 2015). The one thing certain about the future of Lake Turkana is that it is highly uncertain, but that large-scale changes will occur. All potential impacts listed warrant considerable future research.

## 5 | CONCLUSIONS

The results of this study are consistent with previous work showing that the productivity of Lake Turkana's fisheries is profoundly linked to the volume and annual patterns of water inflow from the Omo River, Ethiopia. These linkages are driven by the influence of hydrology on fish habitat and food availability, breeding cues, and catchability. Though water level decline will initially lead to an increase in the availability of littoral habitats, productivity will be degraded due to the loss of seasonal inundation cycles (the ATTZ). Water level decline will also lead to a reduction in open water habitat and productivity, as the river is the major source of nutrients to the nitrogen-limited lake. If water level declines are extreme, the system will eventually separate into two smaller lakes, each with drastically altered physiochemical characteristics. These changes will limit the capacity of the lake's fisheries, which serve as an important alternative livelihood in the region. If the impacts on the lake and its fishery are to be minimized, efforts must be made to manage upstream development so as to maintain natural inflows to Lake Turkana, particularly during the lake's flood season.

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