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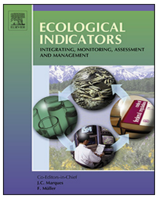

Fish assemblages and size-spectra variation among rivers of Lake Victoria Basin, Kenya

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ABSTRACT

Riverine ecosystems are some of the most biologically diverse on earth, but are also among the most threatened by anthropogenic actions. Lack of local-scale studies monitoring changes in riverine populations makes it difficult to determine how communities respond to region-specific anthropogenic threats. In this study, we compared fish assemblage structure in six rivers in the Lake Victoria Basin (LVB), Kenya. Data collected during different periods between 2004 and 2018 were used to derive abundance size-spectra parameters and community diversity metrics as proxies for ecosystem condition and function. Species dominance in the rivers was high with only five species accounting for $> 72\%$ of cumulative relative abundance while, 33 species contributed $< 10\%$ of all individuals sampled. One-way analysis of similarity test (ANOSIM) indicated significant dissimilarity in fish composition between the rivers (Global $R = 0.405$, $p = 0.0187$) while, similarity percentage analysis (SIMPER) partitioned differences to variations in relative abundance of mainly two species (*Labeobarbus altianalis*, and *Labeo victorianus)*. Eight species were restricted to single river basins suggesting presence of local endemism. Abundance size-spectra parameters (intercepts and slopes) used as proxies for food-web capacity and ecological efficiency fluctuated over time with periods of relative stability, indicating spatial (among rivers) and temporal (yearly) variations in ecological processes in the rivers. The food-web capacity and ecological efficiency indices showed basin-specific relationships with community metrics (dominance, richness, evenness, Shannon-Weiner and Simpson diversity indices) and catch per unit effort (CPUE), suggesting their potential use as indicators of ecosystem structure. The findings of this study show promise in the use of size-spectra parameters as proxies for riverine ecosystem structure and functioning under a gradient of perturbation.

1. Introduction

River basins provide sources of livelihoods and ecosystem services worldwide through the provision of food resources, water and sustenance of biodiversity. However, rivers are among the most threatened ecosystems in the world as a result of human activities, including agricultural runoff and eutrophication (Huntington, 2006, Zhao et al., 2014), damming (Benejam et al., 2016a), climate change (Schindler, 2001; Santos et al., 2014), overfishing (Tockner and Stanford, 2002) and introduction of exotic species (Dudgeon et al., 2006), amongst others. An estimated 65% of global river discharge and aquatic habitats are under moderate to high levels of threats (Vörösmarty et al., 2010), and only a limited number of large rivers of the world are free-flowing (Grill et al., 2019). These threats provide within and between river basin differences in productivity, assemblage structure and ecological processes. These resultant ecological states have mostly been monitored using index-based biomonitoring methods (Karr et al., 1986; Townsend et al., 2009; Mackay et al., 2010). Recent monitoring strategies have employed variation in body size-structure mostly in marine and lake assemblages when exploring changes in fish assemblage structure in response to exploitation levels (Gislason and Rice, 1998; Bianchi et al., 2000), climatic variations (Fabré et al, 2017), and environmental degradation (Emmrich et al., 2011).

Size-structure of aquatic communities often show temporal stability while, the distribution of a community attribute among size-classes (size-spectra) have been linked to environmental perturbations (Kerr and Dickie, 2001). Changes in size-spectra parameters (slope and intercept) in time and space may reflect changes in drivers of community structure (Jennings and Dulvy, 2005; Murry and Farrell, 2014). Thus, the size-spectra parameters are potentially useful for inter- and intra-basin comparisons of fish populations in rivers and monitoring changes caused by human activities. This application is particularly useful in situations where identification of species is problematic, as is the case in tropical systems that are endowed with high biodiversity and endemism

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(Maldonado et al., 2011; Sayer et al., 2018). A limited number of studies applying size-spectra variations as indicators of perturbations exist for temperate rivers and streams (Murry and Farrell, 2014; Broadway et al., 2015; Benejam et al., 2016a,b, 2018), with only one study in the central Amazon Basin (Fabré et al., 2017) representing the tropics. Body size is an important regulator of ecological and physiological functions in many organisms, as it scales with metabolism, affects competitive outcomes, determines predator-prey relationships and organismal productivity (Woodward and Warren, 2007; Blanchard et al., 2009; Brose et al., 2006; Arim et al., 2010, Arranz et al., 2019). Body size also influences population density (Brown et al., 2004) and species diversity. These attributes make size-spectra analysis to be a highly relevant surrogate for ecosystem functioning in tropical aquatic habitats where taxonomic resolutions for species are incomplete and sources of perturbations are varied. Although the parameters of size-spectra analyses have found use in comparing temporal patterns of system productivity and tropho-dynamics (Gislason and Rice, 1996; Jennings and Dulvy, 2005; Benejam et al., 2018), they have hardly been related to community metrics in an effort to determine their utility as proxies for changes in assemblage structure related to human perturbations of ecosystems.

We analyzed size-spectra of the fish communities in six rivers of the Lake Victoria Basin, Kenya, using historical datasets (2014–2018) on fish assemblages from the rivers spanning diverse land-use systems. We tested a hypothesis that abundance-based size-spectra parameters (slopes and intercepts) will scale with fish community structural indices (diversity, evenness, richness, dominance), fish catch per unit effort (CPUE), and vary across river basins. The rivers are impacted by various land-use systems resulting into a gradient in water quality that will likely result into variable fish assemblages. If responsive to perturbations, size-spectra parameters could then serve as indicators of anthropogenic influences and ecosystem productivity and energy transfer efficiency.

2. Materials and methods

2.1. Study sites

The study focused on fish assemblages in six rivers (Awach, Mara, Nyando, Nzoia, Sondu-Miriu and Yala) draining the Kenya side of the Lake Victoria Basin (LVB, Fig. 1). The upper and middle reaches of the LVB Rivers have a favorable climate for agricultural production, and annual rainfall displays a bimodal distribution, with two distinct rainy and dry seasons especially in the upper catchment (Kizza et al., 2009) with the highest precipitation being 2230 mm per year (Table S1). The Mara River is transboundary and originates in the Mau Forest Complex in Kenya and drain into Lake Victoria through Tanzania (Fig. 1), only the Kenyan side was sampled. Three of the rivers (Awach, Nyando and Sondu-Miriu) flow into the lake at Winam Gulf while, Rivers Nzoia and Yala drain into the open water north of the gulf (Fig. 1). The Awach River has the smallest catchment (549.6 km^2), while Mara River is the largest (13, 492.2 km^2), followed by Nzoia River (12,784.9 km^2, Table S1). Streams in the upper reaches of the major river basins such as the Nyando, Nzoia, Sondu-Miriu have moderate to high gradient (Table S1), and have suffered from a combination of expansion of croplands, excessive livestock grazing, human settlement, and discharge of municipal and industrial wastewater (Masese & McClain, 2012; Fouchy et al., 2019). The lower reaches of the rivers are impacted by deforestation and water pollution from diffuse sources. Evaluation of land-use patterns from the 2018 satellite images shows that the catchments are dominated by settlements, agricultural activities and forestland of varying proportions (Table S2). These anthropogenic influences and land-use systems provide a gradient of impacts on the rivers with likely variable responses by the fish communities.

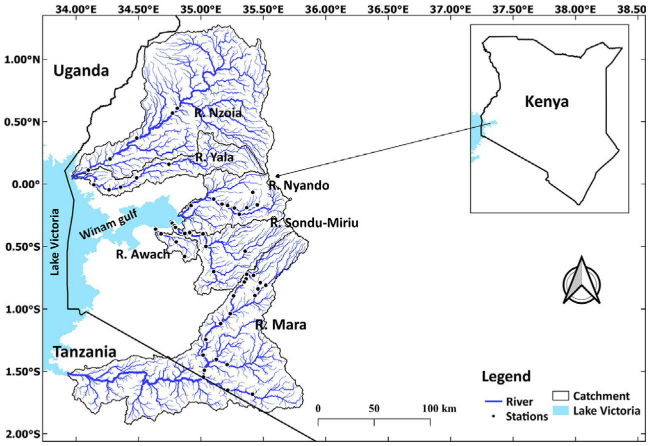

Fig. 1. The rivers (Nzoia, Yala, Awach, Nyando, Sondu-Miriu and Mara) and position of stations sampled for fish assemblages within Lake Victoria Basin, Kenya.

2.2. Field sampling

Fish were sampled from the six rivers using a generator-powered bank electrofisher (Honda GX240 8HP; 400 V 10A, 50 m long cable). Sampling was done during both baseflow and highflow periods, following a single-run depletion methodology, and fish abundance was estimated as catch per unit effort (CPUE, kg/hr). The power of the electrofisher was adjusted depending on the water conductivity at sampling sites (range ~40–350 µS cm^{-1}). Sampling was done during daylight hours whereby one person collected all of the stunned fish using a 17 mm mesh-size hand-net. At each sampling station, a river reach equivalent to roughly 40 times the width of the river was sampled starting from the downstream end and the time taken to sample noted. Whereas this was the standard distance sampled, to ensure a representative sample was collected, fish caught in each stretch were collected until no additional species were encountered. Effort was made to sample all habitats available relative to their prevalence. Captured fish were identified, counted, weighed (0.1 g) and length (cm) measured. Specimens of each fish species were preserved in 75% ethanol for later confirmation of species identifications in the laboratory while, the remaining live fish were returned in the river. Identification was done to species level, except for the haplochromine cichlids and small-bodied cyprinids, which were identified to genus level because of unclear taxonomy in the literature. Species identification followed a combination of taxonomic keys and guides (e.g. Whitehead, 1960; Greenwood, 1962; Eccles, 1992; Skelton, 1993; Eschmeyer and Fricke, 2016). Where more than one name was found, the nomenclature found in Eschmeyer and Fricke (2016) and Froese and Pauly (2018) were adopted. Noting that the generic taxonomy of certain African cyprinids long known as *Barbus* is currently in flux, we instead used the genus *Enteromius* for the small diploid smiliogastrin cyprinids formerly of genus *Barbus,* and for the large hexaploid species, we used *Labeobarbus* (Skelton, 2016; Van Ginneken et al., 2017). Sampling was done during various months between the years 2004 and 2018.

2.3. Data analyses

2.3.1. Assemblage structure

Assemblage structural indices (Shanon-Weinner, Simpson, Evenness and Dominance) were derived following Magurran (2004). Non-metric multidimensional scaling (NMDS) ordination was used to explore any variation in the composition of fish species between the river basins as a result of variable land-use systems and channel differences. Bray–Curtis dissimilarity matrices used for the ordination (Clarke and Warwick, 2001) were derived from the log-transformed abundance data in order to down-weight the influence of the abundant species (Legendre and

Gallagher, 2001). Differences in fish assemblage structure among river basins were further analysed by one-way Analysis of Similarity (ANOSIM) test. ANOSIM tested if the occurrence/distribution of fish species among river basins could account for the variability in the community structure (e.g. NMDS plot). ANOSIM calculates a test statistic (R), which varies between 0 and 1, with higher values indicating greater differences between river basins. One-way Similarity Percentages analysis (SIMPER) was subsequently used to identify which fish species contributed the most to variations in assemblages among rivers as detected by ANOSIM. Statistical Analyses were done in R (Development Core Team, 2017) and Paleontological Statistics (PAST) software package (Version 2.17).

2.3.2. Size-spectra

The size-spectra analysis is based on the theory of tropho-dynamic energy transfer efficiencies, whereby relative abundances of species in a size series of samples is variable, and numbers of individuals (pooled across all species in an assemblage) decreases log-linearly with increase in size (Rice and Gislason, 1996), as a result of decrease in total energy use with increase in size or trophic level (*sensu* Elton, 1927). The general formula for this log–linear relationship between size (x, cm) and numbers (y) within a community is (Rice and Gislason, 1996):

$$\ln(y) = a^{*}\ln(x) + b$$

where, a = slope, and b = intercept of the model or size-spectra.

From theory, differences in productivity between communities should appear as differences in intercepts, whereas differences in transfer efficiencies and mortality rates should appear as temporal or spatial differences in slopes of the above relationship (Rice and Gislason, 1996; Rochet and Trenkel, 2003). Steepening of the slope would indicate a decrease in the number of large fish in the population, an increase in the number of small fish or both as an influence of fishing (Rice and Gislason, 1996; Thiebaux and Dickie, 1993) or other factors (Sprules and Goyke, 1994). We also explored the diversity size-spectra in explaining the community structure of the rivers. The theory behind the diversity size-spectra is that, scarcity of organisms in the larger size groups necessarily reduces the difference in abundance between the rarest and commonest species and decreases the community diversity with increase in size of the individuals (Rice and Gislason, 1996).

In order to determine the relationship between size-spectra intercepts (productivity) and slope (ecological efficiency), we performed a least square regression on the annual pairs (2004–2018) of the parameters for all the rivers in order to test a putative hypothesis that more productive systems will scale positively with system efficiency.

3. Results

3.1. Assemblage structure

A total of 10,234 individuals belonging to 46 species, 12 families and 7 orders were sampled in the six rivers between the years 2004 and 2018. Total species richness ranged from 29 in River Nzoia to a low of 6 in River Awach. Only 5 species had a cosmopolitan distribution in all rivers with 8 species (*Amphilus jacksonii, Clarias liocephalus, Clarias werneri, Coptodon rendalli, Enteromius yongei, Garra dembeensis*, *Labeo cylindricus, and Zaireichthys rotundiceps*) having restricted distribution to only one river basin (Table 1), indicating a likelihood of species endemism in the rivers. Most of the species sampled had a Least Concern (LC) IUCN conservation status while, one species (the Ningu, *Labeo victorianus*) is Critically Endangered (CR), but occurred in all the six rivers at different times (Table 1).

Although the species richness in the rivers was moderately high (46 species), only five species (*Labeobarbus altianalis, Labeo victorianus, Enteromius neumayeri, Schilbe mystus and Enteromius nyanzae*) numerically dominated the samples. The ribon barbel, *Labeobarbus altianalis,* was most abundant in all the rivers, except in Sondu-Miriu where the Ningu, *Labeo victorianus* dominated (Fig. 2). *Labeo victorianus* was the second most abundant species in rivers Mara (13.7%) and Yala (28.4%) while, the small-bodied barb, *Enteromius neumayeri,* was second most abundant species in Rivers Sondu-Miriu (20.2%) and Nzoia (12.3%) with the African butter catfish, *Schilbe mystus* having nearly the same relative abundance level (~27%) as *L. altianalis* in River Nyando (Fig. 2). The relative abundances of 40 species were very low (< 0.5%) in the rivers.

The NMDS analysis showed not so large differences in fish community structure among river basins (Fig. 3) but sufficiently summarized differences among samples as to explain the assemblage structure with a good fit (stress = 0.0001). Some fish species showed associations with specific river basins. Rivers Mara, Nzoia and Yala had a more homogeneous assemblages compared to Sondu-Miriu and Nyando rivers (Fig. 3). A few species (*Coptodon rendalli, Clarias alluaudi, Rastrineobola argentea, Clarias theodorae, Amphilius jacksonii*) had no distinct association with any of the river basins (Fig. 3). One-Way ANOSIM (with rivers as factors) indicated significant dissimilarity (Global R = 0.41, *p* = 0.019) in fish composition between the river basins. Subsequently, SIMPER analysis partitioned the differences in composition to variations in relative abundance of a few species (Table 2). Differences in assemblage structure between river basins were mostly attributable to variations in relative abundances of *Labeobarbus altianalis* and *Labeo victorianus* and to a small extent to *Clarias liocephalus* and *Enteromius neumayeri* (Table 2 and Fig. 2). For example, differences in relative abundance of *Labeobarbus altianalis* contributed to differences in assemblage structure between Awach and Nyando rivers (contributing 63.8% to the dissimilarity), Awach and Mara rivers (28.1%), Mara and Sondu-Miriu rivers (19.4%), Mara and Nyando rivers (37.0%) and, Nyando and Sondu-Miriu rivers (35.5%) (Table 2). *Labeo victorianus* contributed the most dissimilarity in fish composition between Awach and Sondu-Miriu rivers (31.3%), Mara and Sondu-Miriu rivers (17.8%) and Mara and Nyando rivers (12.5%). The differences in fish composition between Awach and Sondu-Miriu rivers were also contributed to by *E. neumayeri* (21.4%) (Table 2). Overall, assemblage dissimilarity among the six river basins was moderate (59–67% dissimilarity range). Nyando and Sondu-Miriu rivers had the greatest dissimilarity in assemblage structure of 67% with Awach and Nyando rivers having the lowest dissimilarity (59%) (Table 2).

3.2. Community size-spectra analyses

Food-web capacity (or community productivity), as indexed by intercepts (± SE), ranged between 7.72 ± 0.44 for Mara River in 2015 to 14.96 ± 1.08 for River Nzoia in 2004 (Table 3). The food-web capacity showed temporal variability amongst the river basins. The capacity decreased from 11.40 ± 1.32 to 8.99 ± 0.71 in River Awach within six years (2004–2009) while, for Mara the capacity remained fairly stable (CV = 5%) between 2011 and 2012 with a sharp drop to 7.72 ± 0.44 in 2015 that appeared to remain stable at 9.96 ± 0.67 in 2018 (Table 3). For the Nyando River, food-web capacity showed relative stability during 2004–2010 period (CV = 7.8%, Table 3), the same relative stability in food-web capacity was shown for River Sondu-Miriu between 2004 and 2010 (Table 3). The inter-annual trend in food-web capacity for the Mara River (for which time series data were available) was not significant as well ($r^2 = 0.18$, $p > 0.05$).

Ecological efficiency, as indexed by slopes of size-spectra, showed similar patterns to the food-web capacity. The slope ranged from being shallow or efficient (−3.7 to −2.9) for the rivers (Nyando, Nzoia, Sondu-Miriu, Yala and Awach) during 2004 and progressively steepened (−2.84 to 2.023) during 2009 to 2010 indicating temporal decline in ecological efficiency in the river basins (Table 3). Within-river annual trends in ecological efficiency derived for Mara River showed lower efficiency (slope = −2.471) in 2009 that became relatively more efficient (shallower) during 2011–2012 but that showed a general decline in efficiency during 2015–2018 (Table 3). The inter-annual

Table 1

Riverine fish species sampled in Lake Victoria Basin, Kenya, and their conservation status within the IUCN Red List.

Order	Family	Species	Awach	Mara	Nyando	Nzoia	Sondu-Miriu	Yala	IUCN Red list
Cypriniformes	Cyprinidae	*Barbus* sp.		*					–
	Cyprinidae	*Enteromius apleurogramma*			√		√		LC
	Cyprinidae	*Enteromius cercops*	√	√	√	√	√	√	LC
	Cyprinidae	*Enteromius jacksoni*	√		√	√	√		LC
	Cyprinidae	*Enteromius kerstenii*		√	√	√	√	√	LC
	Cyprinidae	*Enteromius neumayeri*		√	√	√	√	√	LC
	Cyprinidae	*Enteromius nyanzae*	√	√	√	√	√	√	LC
	Cyprinidae	*Enteromius paludinosus*		√	√		√	√	LC
	Cyprinidae	*Enteromius yongei*						*	LC
	Cyprinidae	*Garra dembeensis*			*				LC
	Cyprinidae	*Labeo cylindricus*		√					LC
	Cyprinidae	*Labeo victorianus*	√	√	√	√	√	√	CR
	Cyprinidae	*Labeobarbus altianalis*	√	√	√	√	√	√	LC
	Cyprinidae	*Rastrineobola argentea*			√		√	√	LC
	Poeciliidae	*Lacustricola bukobanus*				√		√	LC
Cyprinodontiformes	Protopteridae	*Protopterus aethiopicus*			√			√	LC
Lepidosireniformes	Mormyridae	*Gnathonemus longibarbis*				√		√	LC
Osteoglossiformes	Mormyridae	*Hippopotomyrus grahami*			√			√	LC
	Mormyridae	*Marcusenius victoriae*			√			√	LC
	Mormyridae	*Mormyrus kannume*		√		√		√	LC
	Cichlidae	*Astatoreochromis alluaudi*				√	√		LC
Perciformes	Cichlidae	*Astatotilapia* sp.						*	–
	Cichlidae	*Coptodon rendalli*					*		LC
	Cichlidae	*Coptodon zillii*		√		√	√		LC
	Cichlidae	*Haplochromis* sp.		√	√	√	√		–
	Cichlidae	*Oreochromis leucostictus*			√	√	√	√	CL
	Cichlidae	*Oreochromis niloticus*		√	√	√	√		LC
	Cichlidae	*Oreochromis variabilis*		√	√	√	√	√	LC
	Cichlidae	*Pseudocrenilabrus multicolor*			√	√	√		LC
	Latiidae	*Lates niloticus*			√	√	√	√	LC
	Amphiliidae	*Amphilus jacksonii*				*			LC
Siluriformes	Amphiliidae	*Zaireichthys rotundiceps*		*					DD
	Amphiliidae	*Zaireichthys* sp.		√		√			–
	Bagridae	*Bagrus docmak*		√		√	√	√	LC
	Clariidae	*Clarias alluaudi*			√		√		LC
	Clariidae	*Clarias gariepinus*	√	√	√	√	√	√	LC
	Clariidae	*Clarias liocephalus*		√					LC
	Clariidae	*Clarias theodorae*			√	√	√	√	LC
	Clariidae	*Clarias werneri*		*					LC
	Mochokidae	*Chiloglanis somerini*				√		√	LC
	Mochokidae	*Synodontis afrofischeri*			√	√	√	√	LC
	Mochokidae	*Synodontis victoriae*			√	√	√		LC
	Schilbeidae	*Schilbe intermedius*		√	√	√	√	√	LC
	Schilbeidae	*Schilbe mystus*			√	√			LC
	Mastercembelidae	*Afromastacembelus frenatus*			√	√	√	√	LC
Synbranchiformes									

(√) Present in more than one river, (*) present in only one river, Least Concern (LC), Data deficient (DD), Critically Endangered (CR)

(2009–2018) trend in ecological efficiency derived for Mara River was, however, not significant ($r^2 = 0.25$, $P > 0.05$).

Temporal patterns of the abundance size-spectra showed that all the slopes and intercepts were significant ($p < 0.05$, Table 3) with very low numbers at mid-sizes above 55 cm and a floor-effect at size range beyond 55 cm (Fig. 4a). The diversity size-spectra derived for Mara River showed an expected negative linear relationship (Fig. 4b), with a dome effect at size ranges of 0–10 cm, likely due to sampling biases at small sizes, and a floor effect at size ranges above 50 cm (Fig. 4b).

3.3. Relationship between size-spectra parameters, community metrics and CPUE

The relationships between the annual slopes (ecological efficiency) and intercepts (food web capacity) and the community metrics (diversity, evenness and dominance indices) are shown for the Mara River in Fig. 5. The food web capacity showed significant and strong positive relationship with species dominance in the river ($r^2 = 0.811$, $p < 0.05$) (Fig. 5a). The relationship was also significantly strong but negative for both Simpson ($r^2 = 0.811$, $p < 0.05$) and Shannon-Weiner ($r^2 = 0.76$) diversity indices (Fig. 5a). Diversities decline at high community productivity (increasing intercepts) perhaps reflecting the high species dominance. Similarly, a moderately strong relationship was found between the intercept (food web capacity/productivity) and fish species richness in Mara River ($r^2 = 0.51$) that contrasted with a weak one for Evenness ($r^2 = 0.42$, Fig. 5a). For the annual slopes (ecological efficiency), there was also significant ($p < 0.05$) and strong positive relationship with Dominance ($r^2 = 0.78$) reflecting increasing dominance with increasing functional efficiency, and negative relationship with both Simpson index ($r^2 = 0.78$) and Shannon-Weiner index ($r^2 = 0.71$; Fig. 5b), reflecting decreasing diversities with increasing functional efficiency. There was poor negative relationship between slopes and evenness ($r^2 = 0.41$) but a weakly positive one with species richness ($r^2 = 0.39$) (Fig. 5b), which is similar to the intercept patterns, indicating poor predictive power of slope for these metrics in the Mara River. Non-significant relationships were found between the slopes, intercepts and the community metrics when pooled for all the six river basins.

The relationship between food-web capacity (intercepts) and CPUE (kg/hr) for the 14 years (where data on CPUE were available among the six rivers) was not significant; CPUE, kg/hr = 0.1055Intercept + 2.349, $r^2 = 0.201$, $p > 0.05$). However, the

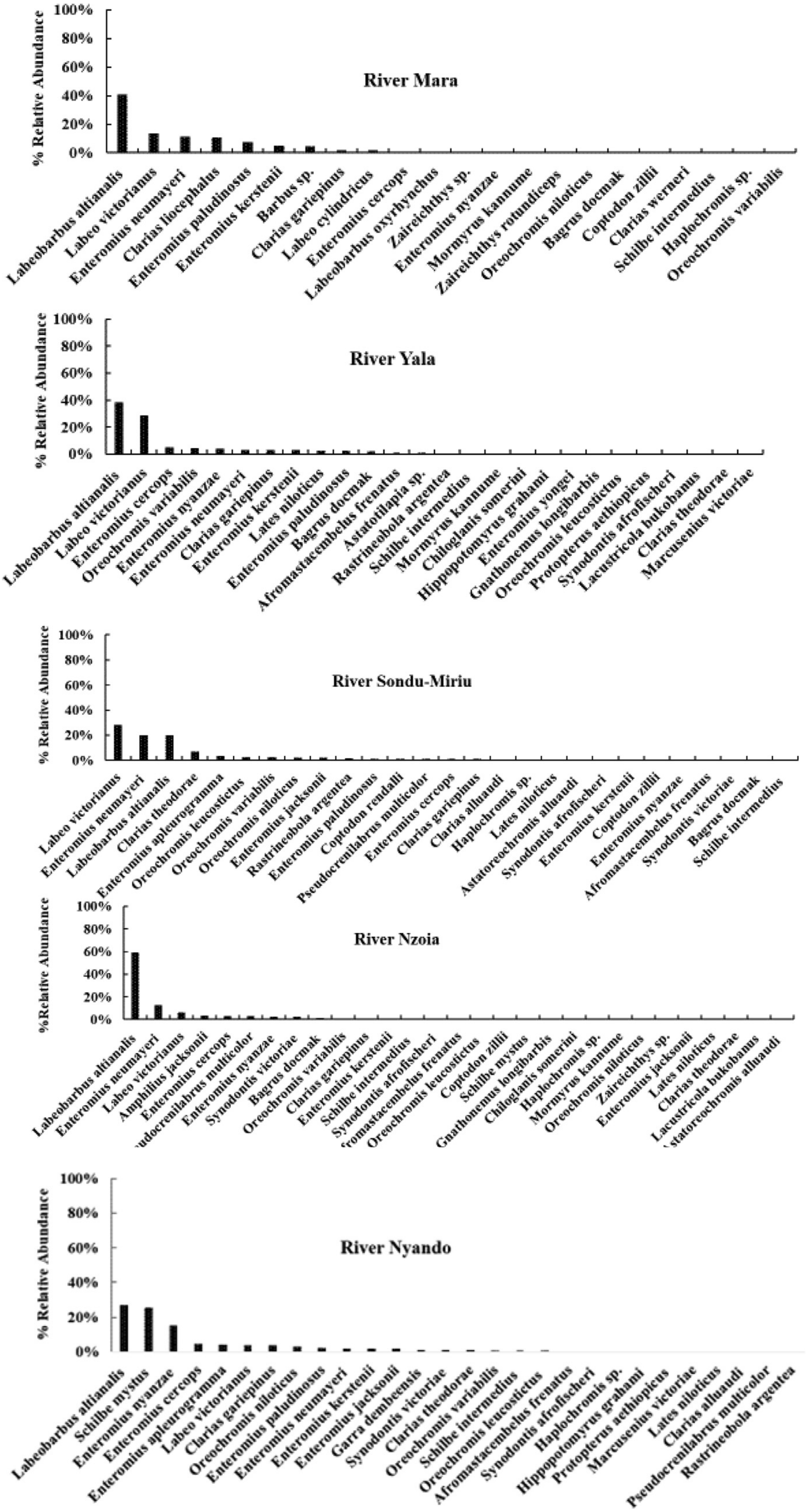

Fig. 2. Relative abundance of fish species in five river catchments of Lake Victoria Basin, Kenya. River Awach not included due to low species numbers.

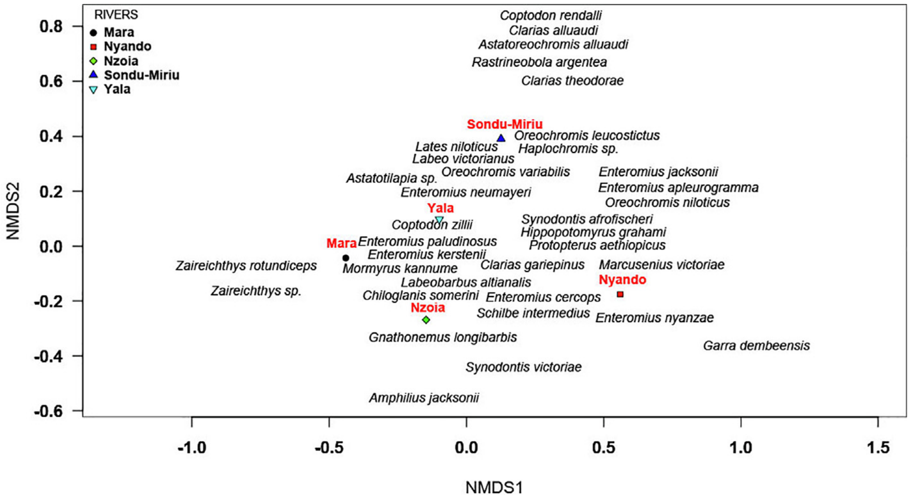

Fig. 3. Non-metric multi-dimensional scaling of fish species associations with the river catchments in Lake Victoria Basin, Kenya. River Awach not included due to low species numbers.

Table 2
One-way SIMPER analysis of fish abundance among five rivers in Lake Victoria Basins, Kenya. Significant contributions to dissimilarities are in bold.

	Awach vs Nyando		Awach vs Mara		Awach vs Sondu-Miriu		Mara vs Sondu-Miriu		Mara vs Nyando		Nyando vs Sondu-Miriu	
Species	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. Dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %	Av. dissim	Contrib. %
Rastrineobola argentea	0.02	0.03	_	_	1.57	2.36	1.16	1.95	0.02	0.02	1.00	1.50
Afromastacembelus frenatus	0.53	0.90	_	_	0.23	0.34	0.17	0.29	0.41	0.65	0.31	0.47
Astatoreochromis alluaudi	_	_	_	_	0.32	0.48	0.24	0.40	_	_	0.21	0.32
Bagrus docmak	_	_	0.10	0.15	0.05	0.07	0.05	0.09	0.06	0.09	0.03	0.05
Barbus sp.	_	_	3.54	5.42	_	_	2.22	3.72	2.14	3.43	_	_
Chiloglanis somerini	_	_	0.21	0.33	_	_	0.10	0.18	0.10	0.16	_	_
Clarias gariepinus	2.06	3.48	2.08	3.19	1.86	2.81	0.80	1.34	2.30	3.69	2.53	3.79
Clarias liocephalus	_	_	7.94	**12.18**	_	_	4.94	8.28	4.77	7.66	_	_
Clarias theodorae	0.68	1.15	_	_	5.64	8.51	4.10	6.87	0.51	0.81	3.08	4.62
Clarias werneri	_	_	0.05	0.07	_	_	0.03	0.05	0.03	0.05	_	_
Coptodon rendalli	_	_	_	_	0.98	1.48	0.73	1.22	_	_	0.63	0.95
Coptodon zillii	_	_	0.16	0.25	0.23	0.35	0.16	0.26	0.08	0.12	0.14	0.21
Enteromius apleurogramma	0.51	0.86	_	_	2.81	4.24	2.08	3.49	0.35	0.56	1.51	2.26
Enteromius cercops	2.06	3.50	2.00	3.07	1.31	1.97	0.77	1.28	1.12	1.80	1.24	1.85
Enteromius jacksonii	0.20	0.33	0.06	0.10	1.47	2.22	1.10	1.85	0.14	0.22	0.97	1.46
Enteromius kerstenii	0.06	0.09	3.57	5.47	0.41	0.62	2.06	3.46	2.15	3.45	0.27	0.41
Enteromius neumayeri	0.09	0.16	6.19	9.48	14.15	**21.35**	8.01	**13.43**	4.18	6.71	8.78	**13.16**
Enteromius nyanzae	5.39	9.14	4.23	6.48	3.42	5.15	0.28	0.48	5.14	8.25	4.67	6.99
Enteromius paludinosus	_	_	5.34	8.18	0.74	1.12	2.84	4.76	3.26	5.24	0.47	0.70
Haplochromis sp.	_	_	0.05	0.08	0.17	0.26	0.12	0.20	0.03	0.04	0.11	0.16
Labeo cylindricus	_	_	1.95	2.99	_	_	0.99	1.65	0.96	1.55	_	_
Labeo victorianus	6.61	**11.19**	7.14	**10.94**	20.75	**31.30**	10.64	**17.84**	7.81	**12.54**	12.51	**18.74**
Labeobarbus altianalis	37.66	**63.82**	18.33	**28.10**	5.67	8.55	11.59	**19.43**	**23.07**	**37.04**	23.72	**35.54**
Labeobarbus oxyrhynchus	_	_	1.03	1.58	_	_	0.52	0.87	0.51	0.82	_	_
Lates niloticus	_	_	_	_	0.73	1.10	0.55	0.92	_	_	0.48	0.73
Mormyrus kannume	_	_	0.30	0.47	_	_	0.16	0.27	0.16	0.25	_	_
Oreochromis niloticus	0.70	1.18	0.18	0.28	0.27	0.41	0.22	0.36	0.64	1.03	0.65	0.97
Oreochromis variabilis	0.73	1.24	0.03	0.05	1.82	2.75	1.29	2.16	0.51	0.81	1.04	1.56
Pseudocrenilabrus multicolor	_	_	_	_	1.10	1.66	0.81	1.36	_	_	0.71	1.06
Schilbe intermedius	0.77	1.31	0.06	0.09	0.05	0.07	0.05	0.09	0.66	1.06	0.62	0.93
Schilbe mystus	0.11	0.19	_	_	_	_	_	_	0.09	0.15	0.09	0.13
Synodontis afrofischeri	0.06	0.09	_	_	0.50	0.76	0.38	0.64	0.05	0.07	0.33	0.50
Synodontis victoriae	0.79	1.34	_	_	0.05	0.07	0.03	0.06	0.65	1.05	0.64	0.95
Zaireichthys rotundiceps	_	_	0.15	0.23	_	_	0.10	0.17	0.10	0.16	_	_
Zaireichthys sp.	_	_	0.54	0.83	_	_	0.34	0.57	0.33	0.53	_	_
Overall average dissimilarity (%)	**59.0**		**65.2**		**66.3**		**59.7**		**62.3**		**66.7**	

Table 3

Statistics of fit of linear models to annual number size-spectra for fish species caught in Rivers; Awach, Nyando, Nzoia, Sondu-Miriu,Yala and Mara between the years 2004 and 2018 in Lake Victoria Basin, Kenya. n = sampling points per river.

			Model Fit			Slope			Intercept		
Year	River	n	F	*p*	r^2	Est.	s.e	t	Est.	s.e	t
2004	Awach	4	54.1	0.001	0.88	−2.99	0.41	−7.35	11.40	1.32	8.61
	Nyando	5	152.2	0.001	0.95	−3.18	0.26	−12.34	13.87	0.86	16.20
	Nzoia	5	132.0	0.001	0.9429	−3.735	0.325	−11.49	14.96	1.08	13.84
	Sondu-Miriu	5	125.1	0.001	0.9542	−3.798	0.34	−11.18	14.52	1.07	13.54
	Yala	5	101.5	0.001	0.9269	−3.509	0.348	−10.07	14.39	1.16	12.43
2009	Awach	4	91.1	0.001	0.9193	−2.023	0.212	−9.54	8.99	0.705	12.76
	Mara	5	28.2	0.001	0.8011	−2.471	0.465	−5.31	10.22	1.15	6.77
	Nyando	5	110.4	0.001	0.9404	−2.84	0.27	−10.51	11.874	0.885	13.42
2010	Nyando	5	80.5	0.001	0.9096	−3.027	0.337	−8.97	12.81	1.12	11.42
	Sondu-Miriu	6	30.3	0.012	0.9109	−3.147	0.568	−5.54	12.78	1.61	7.93
2011	Mara	10	79.9	0.001	0.909	−3.748	0.419	−8.94	14.94	1.39	10.72
2012	Mara	12	63.1	0.001	0.8875	−3.355	0.422	−7.95	13.91	1.4	9.91
2015	Mara	12	127.2	0.001	0.9408	−1.597	0.142	−11.28	7.719	0.44	17.52
2018	Mara	19	99.3	0.001	0.9255	−2.028	0.204	−9.97	9.964	0.677	14.73

relationship was significant and strong when derived for Mara River, although this was for only 4 years when data on CPUE were available; CPUE, kg/hr = 0.198 Intercept + 0.2061, $r^2 = 0.643$, $P < 0.05$.

The intercepts and slopes of the annual (2004–2014) size-spectra of fish communities from all the six rivers showed a strong positive relationship (productivity increases as ecological efficiency increases, (Fig. 6) described by the equation:

$$\text{Intercept} = -3.2904\text{Slope} + 2.5702,\ r^2 = 0.96,\ P < 0.05$$

Overall, high annual productivity (elevated intercepts) in the rivers supported communities with high ecological efficiency (shallower slopes) while, within-basin productivity supported higher ecological efficiency in years when productivity was high and vice versa (Fig. 6).

3.4. Discussion

The study found a moderately high diversity of fish species (n = 46) in the six river basins. However, there was high species dominance with only five species having a cumulative relative abundance of > 72%, while, 33 species had very low (≤1%) specific relative abundances and a cumulative relative abundance of < 10%. In addition, 8 species were only found in particular river basins supporting the notion of high endemism associated with East African freshwater bodies (Kocher, 2004; Darwall et al., 2005). The influent rivers of Lake Victoria were historically populated by a diverse assemblage of fish species (Mugo and Tweddle, 1999; Ochumba and Manyala, 1992), but some of these species (e.g., *M. kannume* and *Oreochromis variabilis*) have since been depleted and their conservation status is currently unclear with likely local extinctions. Extinction of riverine fishes has been evaluated to be higher than natural extinction rates (Dias et al., 2017; Tedesco et al., 2012) or that of terrestrial animals (Ricciardi and Rasmussen, 1999). Therefore, the low relative abundance of many fish species in the LVB and the restricted distributions of some species, reported in this study and other recent studies (Sayer et al., 2018), can easily tip the species abundance to local extinctions in the face of increasing anthropogenic threats and lack of long-term monitoring initiatives.

The East African river basins are continuously affected by a number of threats caused by agricultural runoff, discharges of municipal and industrial wastewaters, deforestation of catchments and riparian vegetation, introduction of exotic species, and fishing (Verschuren et al., 2002; Masese and McClain, 2012; Kishe-Machumu et al., 2018). It is difficult to determine the long-term effects of these stressors on the LVB ichthyo-diversity in the absence of continuous ecological monitoring; however, these threats are known to affect freshwater biodiversity at a global scale (Dudgeon et al., 2006; Jenkins, 2003; Dias et al., 2017; Carpenter et al., 2011). ANOSIM test indicated differences in fish assemblages between the rivers while, SIMPER analysis attributed the differences mostly to variations in relative abundance of only four species (mostly *Labeobarbus altianalis*, *Labeo victorianus* and to a lesser extent to *Clarias liocephalus* and *Enteromius neumayeri*). The fish assemblages are likely affected by different drivers that are basin-specific indicating that management of riverine fish populations will likely be more effective at basin or sub-catchment scales rather than at the larger LVB-scale. The anthropogenic influences on the rivers are likely to vary in space and time following variation in land-use systems in the river catchments.

The temporal changes in abundance size-spectra showed variable patterns with a progressive temporal decline in food web capacity in Awach River reflecting declining productivity perhaps because of changes in water quality or anthropogenic influences in this river, with likely effects on ecological processes (Benejam et al., 2018). For rivers Mara, Nyando and Sondu-Miriu the food web capacity largely showed temporal stability likely to reflect within-basin compensatory mechanisms to exploitation or perturbations that modulate temporal variability in system productivity and efficiency. The ecological efficiency showed progressive decline in the rivers from 2004 to 2010 except for Mara River that showed alternating low–high efficiency with time. The variations of these parameters in time and space has been used to infer changes in riverine fish assemblage structure and function (Benejam et al., 2016b) or levels of environmental stress on fish assemblages (Fabré et al., 2017).

Intercepts and slopes of the size-spectra showed positive functional correlation in this study. Although the relationship between system productivity and efficiency are varied (reviewed in Waide et al., 1999), the observed positive correlation indicates that highly productivity rivers will support more efficient and complex food webs of high diversity, with low mortality rates (see also, Bianchi et al., 2000). The Mara River that is prone to water quality changes as a result of organic matter overload from livestock and hippopotami leading to hypoxia and occasional fish kills (Masese et al., 2015; Dutton et al., 2018) and persistent drought stress (Masese and McClain, 2012), was found to be lower down in the intercept-slope function indicating a stressed ecosystem. The within-basin temporal variation in intercept-slope function derived for the rivers further supports the notion that the size-spectra parameters may be proxies of ecosystem function. More data are, however, required to provide basin-specific and scale dependent slope-intercept relationships.

According to theoretical models, the slope of the abundance size-spectrum represents the efficiency of trophic transfer in the food web (Rice and Gislason, 1996; Kerr and Dickie, 2001). Bioenergetic and ecological transfer efficiency models predict size-spectrum slopes of about −0.75 in systems in which food resources of same trophic levels

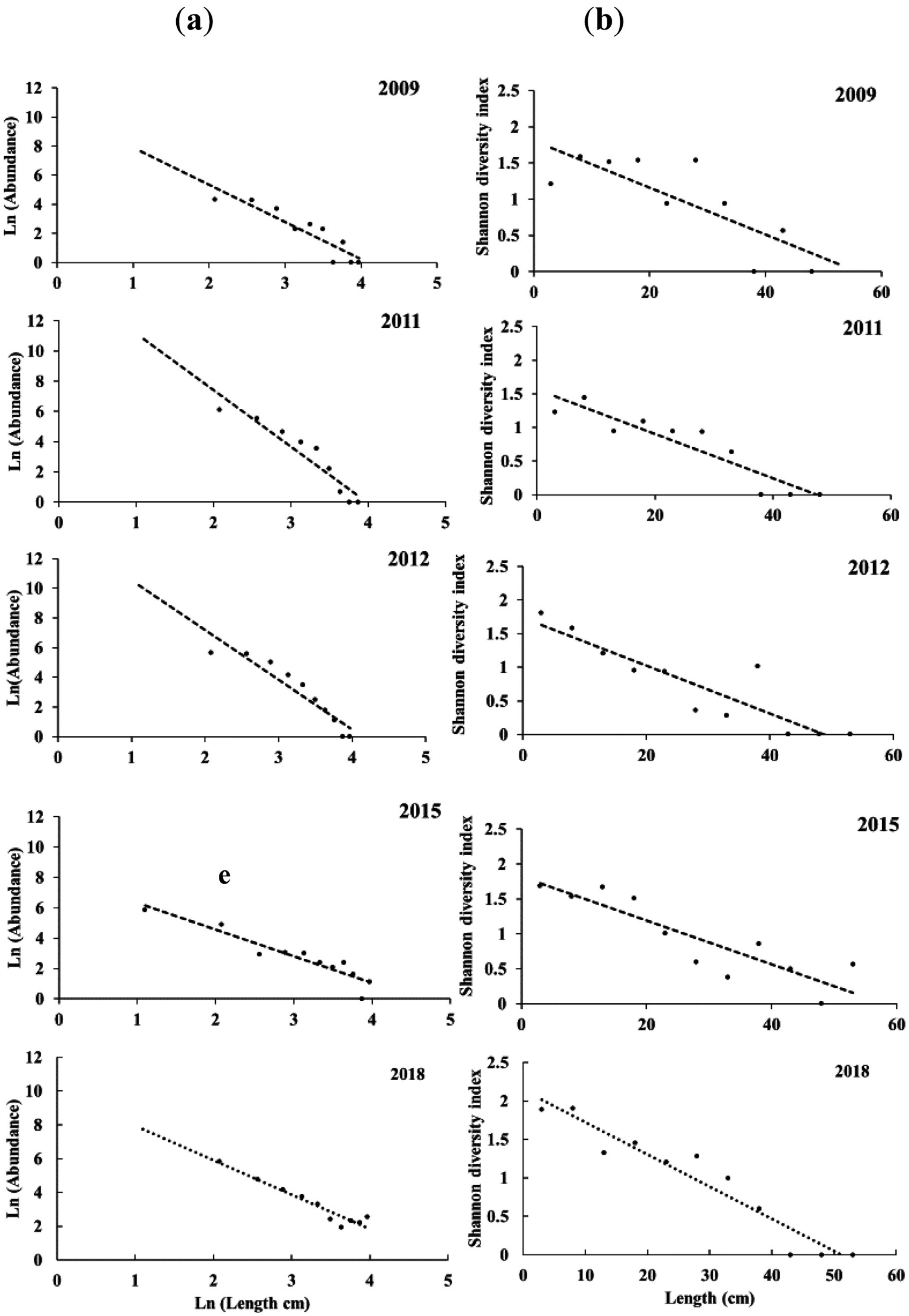

Fig. 4. Annual regression analysis of (a) Ln numbers per 10 cm size-class Vs. Ln Length class and (b) Shannon diversity index in 10 cm size class Vs size-class in the Mara River basin, Kenya. Line is linear model fit to number and diversity size-spectra.

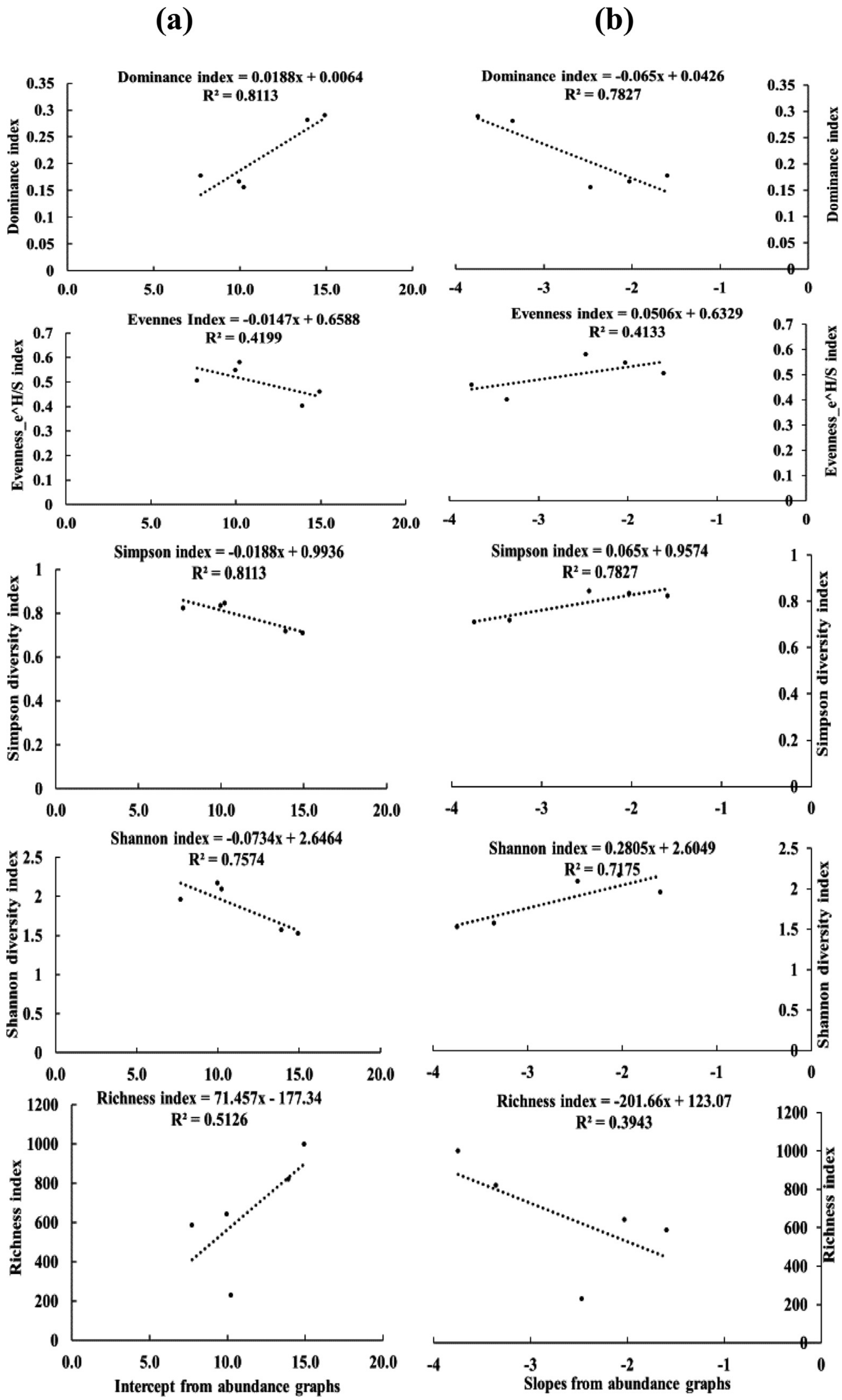

Fig. 5. Regression analysis of community metrics with (a) intercepts and (b) slopes of annual abundance size-spectra for fish species in River Mara, Kenya during 2009, 2011, 2012, 2015 and 2018.

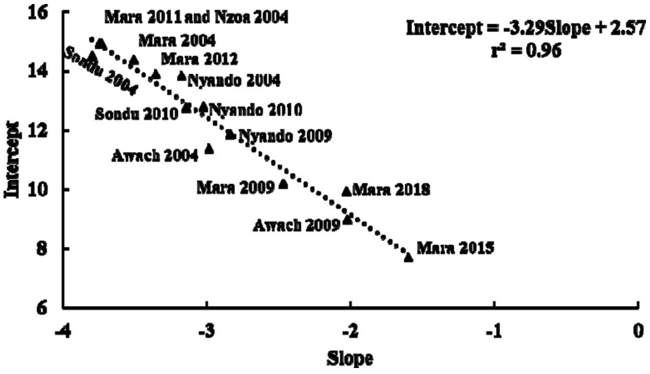

Fig. 6. Relationship between intercepts and slopes of annual size-spectra of fish communities from six rivers in Lake Victoria Basin, Kenya, during 2004 to 2018.

are shared while, slopes < -0.75 are indicative of systems that support many trophic levels and, systems that are supported by allochthonous subsidies having slopes that are > -0.75 (Brown et al., 2000; Trebilco et al., 2013; Benejam et al., 2018). Our results show that all of the studied rivers had annual size-spectrum slopes that were much less than -0.75 supporting the multi-trophic nature of the fish species sampled in the rivers, which is indicative of niche diversification over a long time-scale (Fryer and Iles, 1972; Wiens, 2004). However, the rivers are also supported by allochthonous subsidies from the riparian and floodplain zones that are often grazed by livestock and other large mammalian herbivores (Masese et al., 2015, 2018). There is therefore likely bias when the rule-of-thumb model predictions of ecosystem function (*sensu* Trebilco et al., 2013) are applied to the agrarian tropical systems.

We found strong relationships between the intercepts of size-spectrum and community metrics (dominance and diversity indices) as modeled for the Mara River. However, it is intuitively not certain why intercepts as measures of community productivity should scale negatively with diversity indices. Nonetheless, the rivers show dominance by only a few species and it is likely that productivity would be a reflection of the performance of only these few species thus producing the observed positive intercept-dominance relationships for the river. Fish diversity showed a negative relationship with ecological efficiency in the Mara River unlike the positive relationship of ecological efficiency with dominance. Rivers that are ecologically efficient are likely to be more productive and will support high biomass of only a few species in systems where competition is less due to high species dominance as in these rivers (dominated by only a few species). However, the relationship between ecosystem efficiency and species diversity is variable in the literature and may be system and scale-dependent (reviewed in Waide et al., 1999). No relationship was found between productivity and the community metrics when analyzed for all the rivers indicating variability in basin-specific patterns. The lack of longer and consistent annual data on fish catches from the rivers because of discontinuous sampling precluded robust analysis of basin-specific annual trends in the size-spectra parameters. The resultant low sample sizes is a weakness of the historical datasets used in the study. Additionally, lack of river specific water quality data precluded relating the size-spectra with environmental quality of the rivers. Future sampling design that takes care of seasonal influence on size-spectra, spatial coverage, temporal continuity and water quality parameters will build on these shortcomings.

In conclusion, our results indicate that size-spectra parameters show relationship with community metrics at within-basin scales. It is instructive that slopes and intercepts scaled significantly with the diversity and dominance indices for Mara River indicative of their likely usefulness as proxies for community structure. Positions of the rivers on the slope-intercept function show time-dependent changes in river functioning. We found only a few studies that have examined size-spectra in riverine ecosystems (Benejam et al., 2018; Murry and Farrell, 2014; Broadway et al., 2015; Benejam et al., 2016b; Fabré et al., 2017) and none of these attempted correlations of community metrics with size-spectra parameters as done in this study, making regional comparisons to be difficult. However, the significant relationship between the intercepts and CPUE for Mara River, as would be expected if intercepts are a measure of productivity, has been reported elsewhere (Gislason and Rice, 1996; Benejam et al., 2018) indicating that size-spectra intercepts can be used as proxies of fisheries productivity. We suggest that these relationships should be interpreted as being preliminary because of the limited datasets. With a more frequent and focused sampling approach, these relations can be improved on as they hold promise as indicators of ecosystem functioning in these and other rivers in the Afro-tropics. They are a useful first step in evaluating anthropogenic stressors in data-scarce countries as data analysis are less rigorous, results are intuitively easy to interpret and sampling is less costly.

CRediT authorship contribution statement

Alfred O. Achieng: Conceptualization. **Frank O. Masese:** . **Boaz Kaunda-Arara:** Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106745.

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