Six decades of ecological research on Lake Kariba: synthesis, knowledge gaps, and future research priorities

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Abstract

Predicting the consequences of global change is a universal challenge in paving the way for a more sustainable and resilient future. Man-made lakes, such as hydropower reservoirs, are grand-scale ecological laboratories which have enormous value for studying the long-term development of freshwater ecosystems. Lake Kariba, in the Middle Zambezi, is the largest man-made lake by volume and represents a rich history as a socio-ecological observatory. We present the past 60 years of aquatic research on the lake, synthesising key changes, and drivers of change, to the limnology, fauna and flora, and fisheries management approaches. Key challenges remain in deriving unequivocal conclusions regarding abiotic interactions and drivers of fisheries potential alongside limited biological studies published in the past 20 years. The opportunities in ecological research, fisheries and socio-economic benefits derived from the lake have the potential to be considerable but are hampered by geopolitics, poor infrastructure and scarce resources. Future priorities include linking biodiversity change and food-web interactions to ecosystem service delivery; using the lake as an observatory for biogeochemical changes in greenhouse gas emissions and nutrient delivery; and as a testbed for interrogating ecological hypotheses. We advocate for the importance of Lake Kariba as an asset for monitoring global change.

Keywords

Socio-ecological systems, ecological succession, Zambezi River, ecosystem services, reservoir, climate change; hydropower lake

Introduction

Ecological change is happening across all realms at alarming rates, yet appropriate assessment of drivers and outcomes are still patchy. Freshwaters are subject to multiple stressors, i.e. pollution and eutrophication, land use change, climate change, over exploitation, biological invasions and habitat degradation (Harrison et al. 2018; Tickner et al. 2020; Bartley et al. 2025), which affect ecosystem functioning and delivery of ecosystem services. The availability of suitable datasets to address how ecological communities change in response to global change is sparse, especially in regions with limited financial capacity. Furthermore, integrating such long-term monitoring datasets through which to predict outcomes of complex interacting processes is challenging, but poses opportunities of huge potential in hypothesis testing and model validation in the context of global change (Lindenmayer et al. 2012; Huge et al. 2017; Cocciardi et al. 2024).

Hydropower dam developments are anticipated to boom in the coming decades as a response towards drought and increased need for energy (Lehner et al. 2011; Zarfl et al. 2015; Abraham et al. 2025). The creation of man-made lakes can be used as grand-scale ecological laboratories where we have a unique chance for observing and monitoring long-term ecological processes such as succession, biotic homogenisation and community impacts of exploitation (Kolding et al. 2003; Poff et al. 2007; Kolding et al. 2015; Rose et al. 2016; Hanson et al. 2016). Beyond the ecological aspects, man-made lakes can be used to understand the role of biogeochemical cycles and fragmentation in riverine ecosystems (Maavara et al. 2020) and the social-ecological feedback loops with respect to indigenous communities, land use change and human social and financial capital (Mhlanga 2009; Cooke et al. 2017; Castro-Diaz et al. 2023). Using current hydropower reservoirs as socio-ecological test systems may help drive better global development policy in the future, especially under future climatic change.

Here, we present Lake Kariba as a key resource in global change science, looking beyond its complex history and enormous role as a resource for ecosystem service delivery, and aim to provide a narrative review of primarily ecological research, alongside biogeochemical and social research focuses. In doing so, we aim to demonstrate the value of Lake Kariba as a natural biological laboratory, provide narrative context to use as a touchpoint for hypothesis

testing research (e.g. Kolding et al. 2015; Xu et al. 2018), and set the scene for the next decade of interdisciplinary, global challenge-focused research in the lake.

Lake Kariba Overview

Lake Kariba (**Fig. 1a**) is by volume the largest man-made lake in the world, located on the Zambezi River in the Middle Zambezi - Luangwa Freshwater Ecoregion (558; Abell et al. 2008). The lake forms part of the international border between Zambia and Zimbabwe, with a catchment area extending over parts of Angola, Zambia, Namibia, Botswana and Zimbabwe. It is divided into five basins: B1 - Mlibizi, B2 - Binga, B3 - Sengwa, B4 - Ume and B5 - Sanyati (Balon and Coche 1974; **Fig. 1a)**. The main purpose for its creation was to provide hydroelectric power for the industrial development of Zambia and Zimbabwe. The dam wall (128 m height × 580 m width) (**Fig. 1b, c**) was completed in 1960, and the filling phase of the lake spanned from December 1958 to September 1963. Primary physical characteristics of the lake are summarised in **Table 1**. Heavy spilling from the sluice gates in the early phases of Lake Kariba caused severe erosion and scouring of the plunge pool, deepening it to 80 m and threatening the integrity of the dam (Tardieux et al. 2025). Thus, between 2017 and 2024/25 there were considerable engineering works underway, as part of the Kariba Dam Rehabilitation Project, to stabilise the dam wall through plunge pool reshaping (Tardieux et al. 2025).

The lake shoreline spans over 1181 km, characterised by towns, tourism and agricultural areas alongside multiple protected areas on the Zimbabwean side, many of which were instituted after the construction of the dam (Mhlanga 2009). Both industrial and artisanal fisheries, as well as recreational activities, play an additional important role for the economy and food security of the two countries (Kolding et al. 2003). However, displacement of the indigenous Tonga people and implementation of exclusionary approaches to conservation caused fragmentation of resource access, widespread poverty and loss of cultural practices (Mhlanga, 2009).

Table 1 Values of physical characteristics of Lake Kariba. All references found in text.

Physical characteristics	Value	Unit
Volume	160	km^3
Length	277	km
Dam Wall dimensions	128 height × 580 width	m
Full capacity; minimum operation level	488; 475.5	metres above mean sea level
Catchment area	663 817	km^2
Shoreline length	1181	km
Maximum; mean depth	97; 29	m
Phosphate	< 25	$\mu g\ L^{-1}$
Nitrate	< 20	$\mu g\ L^{-1}$
Water residence time	2.6	years
Mean temperature	26	°C
Primary production	5	$g\ Cm^{-2}\ day^{-1}$
Conductivity	75	$\mu S\ cm^{-1}$

Hydrology, Limnology and Biological Characteristics

Lake Kariba is undergoing considerable interannual (**Fig. 2a**) and seasonal (**Fig. 2b**) fluctuations in lake levels as a function of drawdowns for hydroelectricity generation and natural changes in river inflow. The lake is at full capacity at 488 meters above mean sea level (m.a.m.s.l) and the minimum operation level for the turbines is 475.5 m.a.m.s.l (**Table 1**). Thus, the maximum operational range in water level is around 12 m, with an average annual draw down of about 3 meters. The minimum level of operation has been reached four times since creation, with the two latest in December 2022 and 2024 at 475.7 m.a.m.s.l. (**Fig. 2a**).

The Zambezi River provides about 80% of the inflow, of which is generally divided into two separate events; local floods caused by local rains (November to March), and the much larger Barotse floods from the upper catchment area which reaches the lake in March (Jackson 1961, Allison 1970). Under normal conditions, these events are still recurring each year and observed through a slight increase in lake level from around December/January and a stronger increase from around March to June. From July the lake level decreases until December (**Fig. 2b**). The volume to inflow ratio is low, giving a mean water retention time of only 2.6 years. These lake level changes, both seasonally and interannually, have profound impact on the whole ecosystem in terms of shoreline and littoral vegetation (Skarpe 1997,

149 Machena 1997), productivity (Marshall 1982, 1988; Karenge and Kolding 1995b), and
150 indirectly impacts biodiversity patterns (Kolding et al. in review).
151
152 Limnological and biological characteristics of Lake Kariba are well described elsewhere (see
153 e.g. (Coche 1968, Balon and Coche 1974, Marshall et al. 1982, Machena 1989, Moreau et al.
154 1997; Marshall 2017 for comprehensive reviews) and key variables summarised in **Table 1**.
155 It is a warm (26°C) oligotrophic, monomictic lake with an overturn occurring in June-July.
156 The thermal cycle relates to seasonal heating and cooling of a lake and the mixing and
157 stratification process. Stratification begins around September with a thermocline around 15 m
158 which gradually moves deeper to around 35 m at the time of the turnover. During the
159 stratification period, the oxygen concentration in the hypolimnion declines steadily and often
160 reaches a stage of hypoxia. Calamita et al. (2019) provides a consistent and in-situ
161 measurement database of temperature and oxygen depth profiles within the five basins over
162 60 years, showing a surface temperature increase of 1.5 °C and potential evidence for
163 stratification changes due to lake level alteration (Calamita et al. 2021). There is evidence
164 from other lake systems that nutrient loading from cage aquaculture systems can alter the
165 physical structure of the water column (Fadum and Hall, 2022) but this is yet to be assessed
166 in Lake Kariba.
167
168 The water of the lake is moderately clear (up to 10 m visibility with a decreasing trend from
169 West to East) and low in nutrients with nitrate rarely over 20 µg L^{-1} and phosphate below
170 25µg L^{-1} (Mitchell 1973; Coche 1974). Phytoplankton blooms occur just after turnover, or
171 locally, at the onset of floods from tributaries, but most of the year primary production is very
172 low with a maximum of 5 g Cm^{-2} day^{-1} (Regina et al. 2013). Zooplankton abundance shows
173 variation in response to phytoplankton biomass and undergoes diurnal migrations (Marshall
174 1997). In its initial stages the lake was hyper-eutrophic due to the release of nutrients from
175 the decaying inundated vegetation (van der Lingen, 1973). After 1963, the lake experienced a
176 decrease in phosphate and nitrates and became slightly alkaline (Thornton 1980). The
177 conductivity of the water in the lake has stabilised at about 75 µS cm^{-1} from an original value,
178 before inundation, of less than 30 µS cm^{-1} (Karenge and Kolding 1995b; Magadza et al.
179 2020). A natural gradient in the lake ecosystem exists from west to east, where the western
180 part has more riverine characteristics changing towards a more lacustrine environment near
181 the dam wall (Begg, 1974a). Large river dams, like Kariba, represent one of the most

extensive human alterations of water flow and associated matter from land to sea and act as organic carbon sinks due to sedimentation and mineralization, resulting in decreased transport of organic carbon downstream (Maavara et al. (2017). Most work on nutrient transport around Lake Kariba has been model derived and would benefit from primary data collection to determine accuracy and provide contemporary values.

Fish Fauna

Fish communities also reflect the limnological gradient in the lake. These are dominated by potamodromous species in the west (Cyprinidae and Distichodontidae) and by cichlids in the eastern basins (Begg 1974a; Marshall 1984; Karenge and Kolding 1995a). The fish community, the biology of the fish and the fishery is well described in several reviews and research works (Balon and Coche 1974; Mitchell 1976; Marshall et al. 1982; Kenmuir 1984; Marshall 1984; Karenge 1992; Machena et al. 1993; Karenge and Kolding 1995a; Musando 1996; Kolding et al. 2003; Zengeya and Marshall 2008).

Here we summarise the fish species richness and changes over time (**Table 2**; **Fig. 3a**). Prior to impoundment, 55 fish species were listed as occurring in the Middle and Lower Zambezi (Jubb 1967), Jackson (1961) recorded 28 species in the location of Kariba before inundation and Harding (1966) recorded 33 species in the lake in 1964 after the lake was filled. The species count in the lake gradually increased with Balon (1974c) recording 39 species and Marshall (1984) 43 species. Overall, Bell-Cross and Minshull (1988) list 62 species in the Lake Kariba area (Victoria Falls upriver and south bank tributaries) but many have not been recorded in the lake itself (**Table 2**). Some species appear to have been lost from the lake, these are the rheophilic *Chiloglanis neumanni*, *Opsaridium zambezense* (and possibly also *Zaireichthys rotundiceps*), however they persist in the tributaries of the western basins (Kenmuir 1984; Balon 1974a, c). The construction of the dam walls of both Kariba and Cahorra Bassa was considered to form an insurmountable barrier to anguillid migration (Jubb 1967). However, eels have been recorded on several occasions since (Marshall et al. 1982; Anonymous 1993b) and Balon (1975) showed evidence of recruitment and passage of the dam wall. An updated assessment of the fish biodiversity across the five basins would provide useful information on potential community change, and drivers of such change, as well as fisheries potential at a lake wide scale.

214 **Table 2** List of fish species reported from the Kariba area (modified from Bell-Cross and
215 Minshull 1988). Code numbers refer to the source or sampling programmes where the species have
216 been recorded in the lake: 1 = Jackson (1961); 2 = Harding (1966), 3 = (Balon 1984c); 4 = Marshall
217 (1984); 5 = Karenge and Kolding (1995a), 6 = LKFRI (Anon. 1993,1995), 7 = Zengeya and Marshall
218 (2008); 8= Kolding et al. (in review). Introduced species are marked in bold. - is not recorded

219

Family	Genus	Species	Code
Anguillidae	*Anguilla*	*bengalensis*	12346
		marmorata	-
		mossambica	-
Bagridae	*Zaireichthys*	*rotundiceps*	2
Centrarchidae	*Lepomis*	*macrochirus*	-
	Micropterus	***salmoides / nigricans***	6
Characidae	*Brachyalestes*	*imberi*	12345678
		lateralis	234678
	Hydrocynus	*vittatus*	12345678
	Micralestes	*acutidens*	123467
Cichlidae	*Coptodon*	*rendalli*	12345678
	Oreochromis	*andersonii*	348
		macrochir	245678
		mortimeri	12345678
		niloticus	68
	Pharyngochromis	*darlingi*	1234568
	Pseudocrenilabrus	*philander*	34678
	Sargochromis	*carlottae*	34
		codringtonii	12345678
		giardi	348
	Serranochromis	*angusticeps*	18
		macrocephalus	345678
		robustus	3458

	Tilapia	*sparmanii*	5678
Clariidae	*Clarias*	*gariepinus*	12345678
	Heterobranchus	*longifilis*	1234568
Dorosomatidae	***Limnothrissa***	***miodon***	34568
Hepsetidae	*Hepsetus*	*odoe*	6
Mormyridae	*Hippopotamyrus*	*discorhynchus*	1234568
	Marcusenius	*macrolepidotus*	234568
	Mormyrops	*anguilloides*	1234568
	Mormyrus	*longirostris*	1234568
	Petrocephalus	*catostoma*	8
Cyprinidae	*Carrassius*	*auratus*	-
	Cyprinus	*carpio*	-
	Enteromius	*annectens*	-
		bifrenatus	-
		fasciolatus	123467
		lineomaculatus	34
		mattozi	-
		paludinosus	34
		poechii	348
		radiatus	4
		trimaculatus	-
		unitaeniatus	3467
	Labeo	*altivelis*	12345678
		congoro	1234578
		cylindricus	345678
		lunatus	3
	Labeobarbus	*marequensis*	124568

	Opsaridium	*zambezense*	12348
Distichodontidae	*Distichodus*	*mossambicus*	12347 8
		schenga	1234567 8
Kneriidae	*Kneria*	*auriculata*	-
Malapteruridae	*Malapterurus*	*shirensis*	1234568
Mochokidae	*Chiloglanis*	*emarginatus*	-
		neumanni	124
		pretoriae	-
	Synodontis	*leopardinus*	8
		nebulosus	1234567 8
		zambezensis	1234567 8
Poeciliidae	*Aplocheilichthys*	*johnstonii*	12347
		katangae	-
	Gambusia	*affinis*	-
Protopteridae	*Protopterus*	*annectens*	1248
Schilbeidae	*Schilbe*	*intermedius*	1234567 8

224 *Macrophytes*

225 The species, zonation and succession of the native aquatic macrophytes of Lake Kariba are
226 documented by Machena (1988, 1989). During the early stages of the lake after filling, the
227 floating fern *Salvinia molesta* colonised large areas of the lake (Mitchell 1973). From the
228 1970s onwards its biomass gradually decreased and was replaced by increasing amounts of
229 rooted macrophytes down to a depth of around 10 m (Machena 1989; Moreau 1997),
230 whereby *Najas pectinata* and *Ceratophyllum demersum* are found in areas of high water
231 transparency, including in deeper water. On the other hand, *Vallisneria aethiopica* and
232 *Potamogeton octandrus* are found in shallow but turbid water. *Lagarosiphon ilicifolius* was
233 deemed to be a generalist species found across depth and turbidity gradients. There have been
234 minimal studies on the aquatic macrophytes in Lake Kariba since Machena (1988, 1989) but
235 a study on the diet on invasive redclaw crayfish in 2012 (*Cherax quadricarinatus*; see *Species*
236 *introductions*) suggested crayfish consumption may be driving reduction in *V. aethiopica*
237 (Marufu et al. 2018). They further identified *Pontideria crassipes, C. demersum, L. ilicifolius,*
238 *Ludwigia stolonifera, N. pectinata, Panicum repens, P. octandrus, P. pectinatus, Pistia*
239 *stratiotes, Salvinia molesta*, and *V. aethiopica* as the dominant macrophytes in the Sanyati
240 Basin; of these, *P. crassipes, P. stratiotes* and *S. molesta* are invasive (Marufu et al. 2018; see
241 *Species introductions*). As macrophytes provide important fish nursery habitats, are related to
242 invertebrate assemblages (*See Benthic fauna*) and nutrient cycling it would be beneficial to
243 properly map species distributions across the lake's bathymetry. Concerns regarding safety
244 (e.g. dangerous megafauna) during data collection may be a driving factor in the lack of
245 submerged macrophyte research in Lake Kariba. Investment in hydroacoustic technology
246 such as side scan sonar or single bean echo sounders which can be boat mounted can help
247 solve this gap. Albeit species identification and macrophyte biomass estimates are not
248 possible therefore this should be complementary to other sampling activities.

249 *Benthic fauna*

250 Relatively limited research has been carried out on the benthic macroinvertebrate fauna of
251 Lake Kariba compared to the fish fauna. The benthic faunal distribution patterns generally
252 follow that of the submerged macrophytes and do not penetrate deeper than the thermocline,
253 most likely due to recurrent hypoxia (Kautsky and Kiibus, 1997; Machena and Kautsky
254 1988). The assemblage was primarily composed of mussels (*Chambardia wahlbergi*,

Corbicula africana, Mutela dubia and *Coelatura mossambicensis*) (95.8%), snails (*Melanoides tuberculata; Bellamya capillata; Cleopatra sp.; Biomphallaria pfeifferi; Bulinus spp. and Lymnea natalensis*) (4.1%), and insect larvae (0.1%) with the total animal biomass was estimated at 118, 840 tons shell free dry weight, higher than any other comparable lakes (Kautsky and Kiibus, 1997; Machena and Kautsky 1988). Macrophyte and macroinvertebrate relationships were identified by Phiri et al. (2012) who sampled 56 taxa. The structural complexity of *Lagarosiphon ilicifolius* seems to foster higher macroinvertebrate abundance but similar community composition to *Vallisnera aethiopica.* The high mussel biomass (43 kg m^{-1} shoreline) was attributed to the lack of efficient fish predators. Interestingly, Kautsky and Kiibus (1997) note that in Lake Tanganyika, this niche is occupied by the squeaker *Synodontis multipunctatus*, which feeds almost exclusively on mussels (Brichard 1978). More recently, seven snail species were identified on the northern shore of the lake by Muzarabani et al. (2024) as a follow up from a schistosome vector survey (Chimbari and Chirundu, 2003), indicating a shift from biodiversity to disease ecology research on macroinvertebrates (*see Species Introductions section*). These were *Bulinus truncatus, B. forskalii, Gyraulus* sp., *Physella acuta, Bellamya* sp.*, Radix affinis plicatula* and *Pseudosuccinea columella*. Previously detected species, *B. pfeifferi*, *B. globosus* and *R. natalensis* were not sampled nor were any *Schistosoma* spp. The establishment and stability of benthic communities are linked to factors such as water level stabilization and sediment type (Kautsky and Kiibus, 1997; Phiri, 2010). Molecular approaches including barcoding and eDNA would advance understanding of benthic species diversity within the lake. A contemporary assessment of mussel species and their response to drought in Lake Kariba is warranted considering the global loss of freshwater mussels (Modesto et al. 2017; Brian and Aldridge, 2023). More prevalent collaboration between epidemiologists and biologists could provide a unique research line which has the potential to further the aims of both disciplines.

There are no reports of Potamonautid crabs in any pre or post impoundment surveys in Lake Kariba, despite freshwater crabs being present throughout Zimbabwean rivers and the Upper Zambezi Catchment (e.g. Cumberlidge and Daniels, 2008; Dalu et al. 2016; South et al. 2025a). Large benthic decapod crustaceans are now represented by the crayfish, *C. quadricarinatus* (see *Species Introductions section*). It is thus unclear whether there were ever any crabs around the lake or whether they have since disappeared. Determining abundance of crabs in the tributaries would help decipher whether there has been species loss resulting from habitat change or biological invasion.

Zooplankton

Initial colonisation of zooplankton in the newly flooded lake is well described by Harding and Rayner (2001). The zooplankton assemblage changes in accordance with the limnological characteristics of the five basins where the most upstream basin (Basin 1, Mlibizi) has the highest productivity and zooplankton biomass (Kimmel and Groeger, 1984; Masundire, 1997). Although this is also dependent on the nutrient input from the rivers which drain them, as Basin 5 (Sanyati) has higher zooplankton biomass than Sengwa and Bumi due to the Sanyati draining a larger catchment than the Sengwa and Ume rivers (Magadza et al., 1989; Masundire, 1997). Masundire (1997) found 21 pelagic crustacean species during lake wide survey with *Bosmina longirostri* being the most abundant in all basins. The zooplankton assemblage has a seasonal biomass variation in response to nutrient fluxes with two peaks, one associated with the rainy season (January-March) and the other in connection with the lake overturn (June-September) (Masundire, 1994; Masundire, 1997).

Much zooplankton research has been completed with a focus on the interactions with the pelagic kapenta (*Limnothrissa miodon*) fishery. The biomass of zooplankton is very low, having declined dramatically most likely through predation by kapenta (Marshall, 1991). Masundire (1991, 1992) showed a significant relationship between zooplankton biomass and kapenta catch per unit effort (CPUE) when these were delayed by 3-4 months. Additionally, the seasonal peaks of kapenta CPUE in Basin 5 coincides, in a slightly delayed manner, with the seasonal peaks of zooplankton (Anon. 1995). Many of the larger crustaceans, notably the diaptomids, as well as *Chaoborus* became virtually absent by 1972, 10 years after the kapenta introduction. The standing biomass (1985-87) of approximately 157.5 mg wet weight m^{-3} is less than both kapenta and phytoplankton (Marshall, 1997). However, with an estimated P/B ratio of 36.5 (Machena et al. 1993), it would correspond to an annual production of 2,400 kg ha^{-1}, which can easily sustain the estimated kapenta production of around 220 kg ha^{-1} (Machena et al. 1993; Moreau et al. 1977) corresponding to a trophic transfer efficiency of 10%.

While multiple hypotheses have been addressed relating to the zooplankton changes within the lake these have been largely correlative and based on data collected pre-2000. There is

much merit in addressing the contemporary drivers of zooplankton assemblages, especially in relation to drought and nutrient enrichment from the aquaculture cages. Kapenta is implicated in the loss of *Chaoborus,* which signifies a major aquatic - aerial nutrient transfer link. The outcomes of this, beyond as a prey source for the fishery, has not been investigated.

Drivers of change

Species introductions

After the creation of the lake a discourse evolved around whether there would be an 'invasion' of Upper Zambezi fish species (Jubb 1974b, 1976a, b, 1977). These species would either a) survive the drop over Victoria Falls, b) were already present in the Middle Zambezi but missed during sampling events or c) pass through the turbines of the Victoria Falls power station (Balon, 1974). Both *L. miodon* and *Serranochromis macrocephalu*s have invaded below the Kariba Dam wall in a similar manner (Marshall, 1998; Zengeya and Marshall, 2008). Zengeya and Marshall (2008) used rotenone surveys and compared the outcomes to historical works to address the 'Upper Zambezi fish invasion' question but found no evidence to support the suggestion that Upper Zambezi species were established within the lake.

Three species can be considered truly non-native invasive fish in the lake; the first is the cichlid *Oreochromis macrochir*, which was stocked into the lake in 1959-62 for fisheries but abundances stayed low (Kolding et al. 2003). Kapenta (*L. miodon*), a small pelagic clupeid, was introduced from Lake Tanganyika in 1967-69 to fill the pelagic fisheries niche in the newly created lake (Bell-Cross and Bell-Cross, 1971). This species, from a few buckets of fish larvae, expanded and populated the whole lake within only four years and now represents the largest and commercially most important stock in the lake (Marshall 1988; Ngalande 1992; Mafuca 2014; Kolding et al. 2019; see *Fishing section;* **Fig. 4a, b, c**). While there is limited evidence of impact on other fish species due to spatial niche differentiation (Marshall 1991; Karenge and Kolding 1995), Marshall (1997, 2012a) related the rapid and almost complete loss of large cladocerans and larval chaoborus by 1972 to the kapenta introduction ten years previously, thus altering the plankton community. The final invasive species is the Nile tilapia (*Oreochromis niloticus*) which has been present in monitoring catches since 1993. Initially introduced around the shoreline for aquaculture, after escapes into the lake were documented, grow-out cages in the lake were allowed which provide constant propagule

pressure. This species now represents a high percentage of catch in the artisanal Zimbabwean gillnet fishery (A.T. Chakandinakira pers. obs). Limited research has been conducted on the ecological impacts of Nile tilapia, but it is implicated in the drastic decline, possibly via competition and hybridisation, of the critically endangered native Kariba bream, *Oreochromis mortimeri* (Chifamba and Videler, 2014, Chifamba 2019; Kolding et al. in review). Some species, e.g. *Micropterus salmoides/nigricans* and *Hepsetus odoe* have been recorded in the lake only once and can be considered failed invasions, whereas *Labeo lunatus* is suggested to be an incorrect identification per Zengeya and Marshall (2008) (**Table 2**).

One decapod, the redclaw crayfish (*C. quadricarinatus*), was introduced into Lake Kariba in 2002 via the aquaculture pathway in Siavonga on the Zambian shoreline (Douthwaite et al. 2018; Madzivanzira et al., 2021a). Crayfish are now widespread throughout all five basins of the lake, as well as below the dam wall, however, no aquaculture processing or crayfish commercial operations have been successful (Marufu et al. 2014; 2018; Madzivanzira et al., 2021a, b). Damage caused by crayfish scavenging on the artisanal gillnet fisheries causes an economic loss of around US$500,000 per year to the Zimbabwean fishery (Chakandinakira et al. 2023). Ecological impacts are somewhat unquantified but certainly they have rewired trophic interactions in the lake (Marufu et al. 2017).

Following the filling of Lake Kariba in 1960, a marked increase in the cover of invasive aquatic macrophytes was observed. The first major invader, *Salvinia molesta* D.S. Mitch. (Salviniaceae), expanded rapidly and covered an estimated 22% of the lake surface by 1962, earning it the local name of Kariba weed, before declining to between 10% and 15% later in the same period (Marshall and Junor 1981). By 1980, *S. molesta* cover had fallen to approximately 1%, a reduction widely attributed to the introduction and subsequent population eruption of *Paulinia acuminata* De Geer (Acrididae), an herbivorous insect in the early 1970s (Mitchell and Rose 1979). The next notable proliferation occurred in 1984, when *Pistia stratiotes* L. (Araceae) experienced a significant bloom in the Sanyati Gorge (du Toit, 1985). This bloom followed a prolonged drought, which was thought to have elevated nutrient concentrations in the system, but the subsequent reduction in Sanyati River flow ultimately inhibited the growth of *P. stratiotes* (du Toit, 1985). A decade later, in 1994, the globally notorious invader *Pontederia crassipes* Mart. ex Solms (Pontederiaceae) was recorded for the first time, expanding to 200 ha by 1996 and peaking at 2,200 ha (Labrada and Fornasari 2002). Following aerial herbicide applications in 1998 and subsequent release of *Neochetina* weevils,

the abundance of *P. crassipes* has remained consistently low (Tumbare 2008). Nonetheless, it continues to proliferate in nutrient-rich sewage treatment ponds along the lakeshore, suggesting low nutrients on the Lake as a factor limiting its bloom on the lake. Most recently, the emerging invader *Hydrocharis laevigata* Humb. & Bonpl. Ex Willd. (Hydrocharitaceae) has been detected at low densities (Howard et al. 2017; Ncube et al. 2025). While low ambient nutrient levels generally constrain the growth of many invasive macrophytes in Lake Kariba, biological control interventions have contributed substantially to the decline of some non-native invasive macrophyte species.

The non-native gastropod *Pseudosuccinea columella,* alongside a non-native Lymnaeid species and a possibly non-native *Radix* sp., was detected in the lake in 2018 (Carolus et al. 2019). These non-native species were associated with invasive *E. crassipes* stands and presented with a high prevalence of *Fasciola* trematode infection. Carolus et al. (2019) linked several species invasions to an invasion meltdown pathway and subsequent parasite spillback with negative implications for human health.

Introductions of non-native species into Lake Kariba for fisheries and aquaculture are persistent, including suggestions of introducing Nile perch (*Lates niloticus*), which has been strongly urged against by Marshall (2022). Nevertheless, Nile tilapia and kapenta are now relied upon by communities for food and income provisioning in place of native fisheries (Pojana and Jere 2024) and crayfish are now a commodity in Zambia (Rice et al. 2023). Lack of unified policies on non-native species introductions between Zambia and Zimbabwe, minimal appropriate environmental assessments, and disregard for biosecurity and disease management pose serious unregulated threats to the ecology, economy and human wellbeing in the area (Marshall, 2022; Chakandinakira et al. 2023; Ndashe et al. 2024). Without an evidence base, formed from suitable catch assessments and social-ecological household surveys, it is impossible to form a balanced non-native species aquaculture policy nor to promote a shift in investment towards native species aquaculture (Oficaldegui et al. 2025; South et al. 2025b). This is further complicated by the inability of native species to compete with Genetically Improved Farmed Tilapia (GIFT) growth rates and the general lack of financial profitability of the aquaculture sector in Africa without continued donor driven investments (Brummett et al. 2008; FAO 2017; Olapade 2020). For example, Lake Harvest, in Lake Kariba, established over 35 years ago and one of the oldest and biggest commercial fish farms in Sub-Saharan Africa, is apparently still not making a profit. Norfund (a

414 Norwegian Government owned investment fund) invested US$ 21 million in Lake Harvest
415 through African Century Foods in 2011. However, in 2018 Norfund reported that they were
416 losing money but still decided to invest an additional US$ 7 million in 2022 together with
417 AquaSparks (Aquaculture Asia Pacific, 2022 [online]). Norfund sold their shares in 2023
418 with a loss of approximately US$ 15 million (based on a negative IRR of 13.3 %, reported in
419 the 2024 annual report; (Norfund, 2024 [online])) and in 2025 Norfund again admitted that
420 they lost a lot of money, although the company has not shared the exact amount (ABC
421 Nyheter, 2025 [online]). This signifies a crucial issue with aquaculture project sustainability
422 in Lake Kariba. If the crux of the business problem is not transparent then solutions cannot be
423 attained. This directly affects the ability of authorities to fully implement the 2023-2032
424 inshore fishery management plan (ZIMPARKS, 2023)

425

426 Lake Kariba offers an observatory of an enormous man-made habitat within which many
427 species are now introduced and co-occurring. Major knowledge gaps exist with respect to:
428 how these species establish within the current species pool; whether non-native species may
429 facilitate the establishment of more non-natives; the mechanisms and types of ecological and
430 economic impact and how these interact with the socio-economic systems of the communities
431 around the lake. In particular, the impact of aquaculture invasives deserves concerted
432 research effort in the near future as the inland fisheries and aquaculture policies are
433 developed and promulgated across the continent. Addressing novel ways to control and
434 manage biological invasions, while uplifting communities, is imperative to reduce
435 downstream socio-economic and ecological impacts (Madzivanzira et al. 2023).

436 *Climate change*

437 Climate change driven shifts in environmental conditions, such as temperature regimes,
438 dissolved oxygen, precipitation trends (and subsequently water level), are phenomena
439 endured globally. Lake Kariba is subject to increasing temperature (Kling et al. 2014;
440 Calamita et al. 2019; 2021) and historically low water levels resulting from up to a 30%
441 decrease in streamflow within the catchment (Mwangala et al. 2024; **Fig. 2a**). Ndebele-
442 Murisa (2012) suggested that kapenta declines are driven by changes in both lake maximum
443 temperature and lake level. Similarly, Magadza (2011) postulated that temperature increases
444 were responsible for the alleged decline in catch per unit effort (CPUE) of kapenta fisheries.

445 This postulation has been met with rebuttals related to difference in fisheries responses in
446 Zambia and Zimbabwe and a lack of confidence in thermal change data; and the decline in
447 kapenta catches was ultimately attributed to a synergism between the population boom and
448 then decline in introduced kapenta which disrupted the zooplankton assemblage, rather than
449 driven by a single stressor (Marshall 2012a, b). However, both thesis and antithesis relate
450 trends to recorded annual catches and CPUE values, which are highly uncertain due to
451 unreliable statistics, undocumented raising methods, and unrecorded cross-border smuggling
452 of kapenta catches (Kinadjian et al. 2014; Matamzima, 2024). Furthermore, the standing
453 biomass of kapenta from acoustic surveys has not changed between 1995 and 2014, and the
454 suggestion that lake productivity has decreased may be explained by a normal and expected
455 decrease of CPUE with increasing fishing effort (Jul-Larsen et al. 2003; *see Fishing section*).
456 Subsequently, Marshall (2017; 2021) reported a weakening of the thermocline since the
457 1980's, with the deeper portion of the lake experiencing temperature increase but that there
458 has been no shift in the euphotic zone depth. Overall, climate forcing may have facilitated an
459 increase in primary production and algal biomass, with potential synergisms related to
460 population trends in the planktivorous kapenta, though the evidence is weak (Marshall 2017).
461 Magadza et al. (2020) suggested that the warming of Lake Kariba induced the emergence of
462 the blue-green algae *Cylindrospermopsis raciborskii*, resulting in ecosystem disruption and
463 decline of the kapenta catch rates. However, *C. raciborskii* was common, and sometimes
464 even dominant, in the lake during the 1980s (Cronberg, 1997), which didn't seem to affect
465 the kapenta catch rates (Anon. 1992, 1996). In addition, both the demersal and the pelagic
466 stocks fluctuate in relation to lake level changes, which are a proxy for nutrient inputs
467 (Kolding and van Zwieten, 2012), which have as much influence on CPUE as fishing effort
468 (Karenge and Kolding 1995b, Kolding et al, 2003; Kolding et al. in review; **S1B**).
469 Uncertainty still exists related to stratification and thermal cycle within Lake Kariba, which is
470 dynamic and constantly shifting within the lake due to lake level change, riverine input and
471 nutrient loading from aquaculture cages (Begg, 1974b; Calamita et al. 2019; Marshall, 2017,
472 2021; Fadum and Hall, 2022; see *Hydrology, Limnology and Biological Characteristics*).
473 Thus, conclusions on relationships between limnology, temperature and biological aspects are
474 still faced with equivocal interpretations which are limited by primary data.

475 *Fishing*

There are two distinct fisheries in Lake Kariba: the low-cost, multi-species, inshore artisanal gillnet fishery, and the highly mechanized, capital intensive, semi-industrial single-species offshore fishery on the introduced pelagic Tanganyika sardine, kapenta (*L. miodon*). Fishing pressure has steadily increased in both Zambian and Zimbabwean jurisdictional waters, particularly on the offshore kapenta and the inshore Zambian side (Kolding et al. 2003; Kolding et al. 2019, **S1A**). Increases in fishing pressure driven by more licenses granted and cheaper access to fishing vessels are attributed to a decline in the kapenta catch rates, rather than climate-induced effects (Marshall, 2021) (*contra* Magadza, 2011; *see Climate Change section*). Pressure from growth of the fishing fleet was compounded post-2000 with the removal of the closed fishing season (previously May-July) (Matamzima, 2024). While data on the total catches, catch rates and effort of kapenta are difficult to validate (**Fig. 4a, b, c**), because of underreporting and cross-border smuggling between Zimbabwe and Zambia, particularly after 2011 (Kinadjian et al. 2014; African Forum and Network on Debt and Development 2015; Matamzima 2024), there is little evidence that the stock is overfished or that overfishing takes place. The standing biomass was estimated to range between 13 000 and 16 000 tonnes in 1994-95 (Ngalande 1995; Anon 1996) and this had not changed significantly in 2014 when a new acoustic survey estimated a standing stock of 16 277 ± 9 730 tonnes for the whole lake (Mafuca, 2014). With a P/B ratio of around 5.5 per year (Anon. 1992, 1996; Machena et al. 1993; Kolding et al. 2019) the annual production of kapenta will be around 90,000 tons per year. With an estimated maximum total annual catch of between 10,000 - 30,000 tons (**Fig. 4a**), the exploitation ratio would be around 0.1 - 0.3, which is sustainable. The 1992 SADC working group (Anon. 1992) concluded that recruitment overfishing was unlikely, even at high effort levels, since the lake was populated within only two years after the introduction of a small number of juveniles and that the decrease in CPUE by higher effort levels will be relatively small due to the high natural mortality. Thus, limitations to the kapenata fishery would be economic constraints rather than biological.

Limited evidence of over-exploitation of tigerfish (*Hydrocynus vittatus*) or their prey in the artisanal fisheries in Zimbabwe has been presented (Magquina et al. 2020). Although both fishing pressure and catches in the inshore fishery in Zambia is 6-7 times higher than on the Zimbabwean side, there is also no evidence of overfishing there (Kolding et al. 2003, 2015). Thus, inshore catch rates in Zambia are lower than in Zimbabwe due to more fishers, but overall catches are higher. Most of the attempts to calculate sustainable yields (Marshall, Junor and Langerman, 1982; Marshall, 1985; Moyo, 1986, 1990; Kinadjian et al. 2014) are

509 from classic single species stock assessment models based on catch and effort variables, with
510 the underlying basic assumption of ecological stability and constant regenerative capacity.
511 However, most of the results from these analyses have proven of dubious value (Kolding et
512 al. 2003). Anon. (1992, 1996) concluded that the relation between effort and CPUE for the
513 kapenta stock was not better than a relation obtained from random numbers. There is thus
514 limited evidence from standard modelling approaches to indicate a detrimental effect of
515 fishing pressure on the biodiversity and stocks of Lake Kariba and hydrologically driven
516 nutrient inputs, either directly from affluent rivers, or indirectly through the annual
517 fluctuations (**Fig. 2b**) reflecting that the floodpulse concept appears to be the most important
518 driver (Junk et al. 1989; Kolding and van Zwieten 2012).

519 There has been conflicting discourse on the suggested drivers of change in the kapenta
520 fishery. Therefore, we present here the current available data for the kapenta fishery: total
521 catches, effort (annual total number of nights fished) and associated catch rates (kg. night^{-1})
522 of Zambia and Zimbabwe (**Fig. 4a, b, c**, see **S1A** for data and data sources and treatment).
523 Total reported catches decreased from around 30000 tons in 1990 to around 10000 tons in
524 2023. Over this period the total number of fishing rigs increased from around 450 to 1650,
525 predominantly because of a doubling of the number of rigs (from 632 to 1200) in Zambia
526 from 2011 onwards. Nevertheless, over this period catch rates in Zambia, based on reported
527 catches and effort by individual fishing companies decreased only by around 30%, while
528 those in Zimbabwe decreased close to 80%. It is not clear what causes these different
529 trajectories, and certainly discrepancies may be due to underlying reliability issues in data
530 collection, processing and reporting of kapenta catch data.

531 Earlier analyses showed a close relation between kapenta catches and changes in lake levels
532 (Karenge and Kolding, 1995), and Kolding et al. (2003) concluded that lake level changes
533 had a higher effect on stock dynamics than fishing effort on both inshore and offshore stocks.
534 Using the new expanded data set we examined these relations again (**Table 3**; *See S1B for the*
535 *full analysis*). Increased average lake levels have a strong negative effect on lake wide
536 kapenta catches. This is most likely a dispersal effect of shoals of kapenta: Marshall (1988)
537 already described the highly patchy distribution of the kapenta shoals with low biomasses
538 nearshore. Changes in lake levels two years previously had a strong positive effect on
539 kapenta catches though not as strong as absolute lake levels. In the past, this effect has been
540 associated with increased nutrient levels with increased inflow of the lake (Marshall 1982;

Anon. 1992; Karenge and Kolding 1995). However, a lag of two years is long in terms of the life history of kapenta, with an expected average lifespan of one year. An alternative explanation could be that, while the inflowing water of the Zambezi is low in nutrients, nutrient leaching from the aquatic terrestrial transition zone during water level rise which only reaches the pelagic zone during seasonal and annual drawdown is resulting in a delayed effect compared to the direct effect of riverine inflow of water. Zambian catches, on the other hand, are not significantly affected by the lake levels and changes in lake levels but seem mainly driven by effort – though with low explanatory value. However, effort itself, in terms of numbers of nights fished, is positively related to water level (**Table 3**). Thus, total kapenta catches and those of Zimbabwe are primarily driven by (changing) lake levels, and while the relation is not present in Zambia also here the fishery seems driven by lake levels through effort. These results come with an important caveat as they are dependent on a somewhat inconsistently collected and problematic data set, with unclear raising procedures and likely high amounts of unrecorded catches, and further work on an assessment of the quality of the data remains to be done.

Table 3 Parameter estimates of best models in a multiple regression analysis after model selection based on AIC relating total annual Kapenta catches (ton) for the whole lake, Zambia and Zimbabwe as response variable with their respective time series of explanatory variables effort (boat nights fished), effort^2, absolute lake level (WL, m.a.s.l.) and Delta lake levels with lags of 1 (ΔWL1, m) and 2 (ΔWL2, m) years. The significance of the parameter estimates is indicated as ***=p<0.001, **=p<0.01 and ns=not-significant. Pseudo r^2 represents the explained deviance of the model (see S1-B for further explanation).

Model (time series)	Response variable	Explanatory variables					
		Effort	Effort^2	Wl	ΔWL(1)	ΔWL(2)	Pseudo r2
Whole lake (1981-2011)	Catch (ton)	77***	-	-1921***	-	963***	0.82
Zambia (1982-2023)	Catch (ton)	60**	-1 ns	-	161 ns	-	0.29
	Effort (nights)	-	-	2415***	-	-	0.25
Zimbabwe (1981-2011)	Catch (ton)	-	-	-1310***	-	837***	0.69

There are considerable discrepancies in perspectives on subject matter such as the exploitation of the kapenta stocks and management priority settings. From the very beginning of the lake, Zambian policy tended to prioritise food and employment, whereas Zimbabwean policy favoured conservation measures, with about 40% of the Zimbabwean lakeshore designated as sanctuaries (Kolding et al. 2003, **Fig. 1a)**. Thus, the shared owners of the lake's resources are often in direct conflict with one another with limited cross-border cooperation (Malasha 2003; Whande et al. 2006; Nyikahadzoi et al. 2017). It has been suggested that standard biological models are insufficient to determine reliable stock assessments for kapenta and therefore there is a need for more frequent acoustic biomass surveys in combination with development of more complex ecosystem models that in addition can appraise abiotic and biotic interactions (e.g. shifts caused by Nile tilapia and *Salvinia molesta* abundance changes) (Magadza 2006; Nyikahadzoi and Raakjaer 2014). Nonetheless, standard assessment models are not necessary when both biomass and total catches are available, but this depends on reliable reporting and up to date acoustic surveys (Anon. 1992; Kolding et al., 2019). Furthermore, multispecies models are applicable and available for assessment of biotic interactions (e.g. Machena et al. 1993; Moreau et al. 1997) but can be developed with new techniques such as co-occurrence network interaction modelling (Cazelles et al. 2016).

Absence of suitable fisheries sustainability tools is often mentioned as limiting the effectiveness of any management or policy decision and stalling development of harmonized transboundary policy. Beyond the two primary fisheries - rig and gillnet, the rod and line fishery - both recreational and for food - is underrepresented in the literature but may have valuable insights for inland fisheries management and community upliftment around Kariba. For example, the rod and line food fishery is dominated by women and provides a potential opening for increasing gender equity in food systems (Chapata et al. 2024). Overall, understanding the functioning of Kariba's multispecies and multigear fisheries and the rights, goals and aspirations of its resource users is as important as the fisheries ecology in developing future policies (Jul-Larsen et al. 2003: Kolding and van Zwieten, 2011, 2014; Allison et al.2012; Béné et al. 2010). Therefore, programmes must be specifically designed to incorporate both the social and ecological dynamics of the intertwined system.

Biological phases and drivers of inshore fish assemblage change in Lake Kariba

There are rich outcomes to be gleaned from utilising two long-term datasets (water levels and fish diversity and abundance over 52 years) in Lake Kariba. Understanding the complex dynamics of the ichthyofauna relies upon the long and varied history of biological research in Lake Kariba and paves the way for a new and reinvigorated ecological research focus.

Several authors (e.g. Evans and Vanderpuye 1973; Balon and Coche 1974) assert that there are three typical stages in the biological development of new freshwater reservoirs. These are: i) the filling phase, ii) the low production phase and iii) the stable phase. The first phase is characterized by high biological productivity of species which used to inhabit the riverine system. This is a common phenomenon that has also been observed in other man-made lakes, such as Lake Volta in Ghana (Lowe-McConnell 1973) and Lake Kainji in Nigeria (Lelek and El-Zarka 1973). The succession of phases in Lake Kariba appears slightly different, whereby four distinct phase clusters are identified in the fish community over time (**Fig 3a**, **b**, **c**; *S2*). This may be related to the highest productivity occurred in a second discernible phase after the filling phase when the abundant submerged terrestrial vegetation decomposed and increased the productivity of the lake including that of fish. The end of the filling phase around 1965 was characterized by declining trends in most of the original potamodromous riverine species (**Fig. 3a**). This could have been the result of loss of breeding grounds and general deoxygenation of the water column due to the colonization of bays and estuaries by the floating fern *S. molesta* (Mitchell 1973; Machena 1989), or the general failure of these species to adjust to the new lacustrine environment. The low production and slow succession during the filling period may also be attributed to the hyper-eutrophic conditions that existed in the water (Mitchell 1973; Machena 1989) which was just a pea-coloured algal soup in sheltered bays. Such an environment would have reduced the amount of dissolved oxygen and hence affected colonization by the former lotic fish species. Diversity has been negatively correlated with productivity in numerous cases of eutrophication problems (Peet et al. 1983; Feng et al. 2023). In Lake Volta, soon after dam closure, there were fish kills that were associated with oxygen depletion (Evans and Vanderpuye 1973). The increasing eutrophication of Lake Victoria (Hecky 1993; Kolding et al. 2008) has also resulted in recurrent fish kills (Ochumba 1990; Schofield and Chapman 2000).

A second phase, characterized by low productivity and low species diversity as the riverine species adjust to the lacustrine environment, is common in new reservoirs (Petr 1978). The stabilization of lake levels during the early succession phase (1967-1974) coupled with the

reduction in nutrient load, provided for the establishment of aquatic macrophytes and a benthic fauna (Marshall 1982; Machena 1989; Kautsky and Kiibus 1997), creating development of a mosaic of new niches.

Increased species diversity and production characterize the third so-called stable phase. Petr (1978) considered the stabilized stage of man-made lakes to be reached when fluctuations in biological parameters of production exceeded only lightly, if at all, those in natural lakes of similar physical characteristics, including latitude and elevation. Here, the dominant species shifted from the predator *H. vittatus* to the cichlid *S. codringtonii* (**Fig. 3a**). Karenge and Kolding (1995b) found that the recruitment of *S. codringtonii* had no relationship with hydrological changes, while the recruitment of the potamodromous *H. vittatus* showed a relatively high dependency on the hydrological regime. The increase of *S. codringtonii* may be attributed to its feeding habits, as it feeds on gastropods and bivalves (Kenmuir 1984, Skelton, 2024) which became very abundant during this period (Kautsky and Kiibus 1997). However, the significant decrease of *H. vittatus* when food sources, such as kapenta, apparently were becoming abundant, came as a surprise and it was even suggested to have the species listed as endangered (Sanyanga 1995). There are several possible explanations for this decrease. For one, during the early part of the lake's history, it may have been purely due to a predator–prey relationship. In response to an increase in prey items during the early part of the early succession phase, the abundance of *H. vittatus* overshot that of its food sources. Fluctuation of *H. vittatus* over time thus seem related to both predator prey relationships and density dependent processes whereby the observed decline in juvenile *H. vittatus*, despite the plentiful amount of food available for the adult population, was a result of density-dependent processes mainly operating on the young and juvenile part of the population (Karenge and Kolding, 1995b). A similar 'reversed' predator-prey situation was postulated for Lake Victoria where the sudden explosion of juvenile Nile perch (*Lates niloticus*) only happened 25 years after its introduction and coincided with the collapse of the zooplanktivorous haplochromines (van Zwieten et al. 2016).

Following a cluster analysis (**S2**) we now see a four-phase development in the Lake Kariba inshore fish community (**Fig. 3a, b, c**) whereby:

Phase one (1960 – 1965; **Fig 3c**), the filling phase, was characterized by constant rising water level until reaching capacity in 1963 (**Fig. 2a**). The fish community was predominantly

characterised by large species, the catfish *Clarias gariepinus* and potamodromous species: the labeos *Labeo congoro* and *L. altivelis* (**Fig 3a**).

Phase Two (1967-1974, with transitional years in 1978 and 1980; **Fig 3b, c**) was a period with high and stable lake levels (**Fig. 2a**). *H. vittatus* was dominating, with increasing numbers of large cichlids such as *O. mortimeri* and *S. codringtonii* (**Fig. 3a**). *Cyphomyrus discorhynchus* also became relatively more abundant in this phase (**Fig. 3a**). With the establishment of macrophytes two cichlid species, the indigenous *O. mortimeri* and *S. codringtoniii* became dominant, but this was also the peak period of tigerfish (*H. vittatus*).

Phase Three (1975-1977, 1979, and 1982 – 1992; **Fig. 3b, c**) is characterised by an upsurge of *S. codringtonii*, *M. longirostris* and C. rendalli, while *H. vittatus*, *S. codringtonii* and *C. discorhynchus* remained abundant (**Fig. 3a).** In the middle of the period (~1980-1999) a significant drop in lake levels took place (**Fig. 2a**). To maintain the water level needed for power generation the floodgates remained closed for nearly the whole period. Phase three was the peak period of the large bottlenose *M. longirostris* but the dominance of tigerfish started to wane.

Phase four (1993 – 2012; **Fig 3c**), was characterised mostly by a strong increase of the squeaker *Synodontis zambezensis*, in addition to the non-native species *O. niloticus*. This is a period of pronounced lake level fluctuations (**Fig. 2a**). *Oreochromis mortimeri* became less dominant in the fish community while *S. macrocephalus* and *S. zambezensis*, which were practically absent in the two first phases, became dominant (**Fig. 3a**). By this time the riverine *L. congoro* and the rare electric catfish *Malapterurus shirensis* were no longer recorded in the monitoring program (LKFRI, unpublished data).

Knowledge gaps & Future frontiers

As shown in this review, the long-term monitored development of man-made Lake Kariba has proven its value as a grand-scale ecological laboratory, which has enabled a deeper understanding of complex biological phenomena and interactions with physical and anthropogenic drivers of change. There is an urgent need for a comprehensive, lake wide, systems survey covering both inshore and pelagic fish, benthic invertebrates, plankton and macrophytes alongside hydrological features such as the thermal cycle, nutrient dynamics,

and physico-chemical parameters. Much of the research on Lake Kariba has tried to link these aspects but have not had the appropriate resources with which to tackle the complexity of the system. Furthermore, there is little primary data available post-2000 with which to probe such questions.

In terms of basic biological knowledge, there is limited up to date information relating to the current species assemblages and their drivers. While the inshore fish community is well monitored and characterised in the Sanyati Basin, there has been limited work covering the other basins and their inflow tributaries. A multi-taxa survey approach would provide key insights into the complexities of Lake Kariba's food web and set a modern baseline to compare against the work completed between 1970-2000. Undertaking such an endeavour would provide a resource in which to address persistent questions and discrepancies relating to the fundamental ecology of the lake. A granular understanding of the interspecific interactions playing out within the lake would help resolve knowledge gaps regarding certain species population dynamics over time, this could be approached through stable isotope analysis, gut content meta-barcoding or co-occurrence interaction network simulations. There is sparse data on macrophyte diversity and distribution. Mapping macrophytes could better inform risk areas for disease vectors and may indicate ecological impact of invasive crayfish. Loss of macrophyte coverage in certain areas may also be affecting fish recruitment or abundances or low-trophic level feeding fish. Using molecular methods to survey and characterise the understudied invertebrate community of the lake and comparing it to those of the surrounding tributaries would be valuable to identify patterns in assemblage structure and possibly undetected invasive species. In combination these aspects would form the basis of a recent and accurate fisheries assessment from which to build future equitable fisheries policy on. Furthermore, primary data would elucidate trends which can be used for broadscale ecological hypothesis testing relating to species interactions, ecological succession, biological invasions and fishery dynamics.

The discrepancies between fishing statistics reported between Zambia and Zimbabwe are impossible to resolve without fisheries independent data to compare against. This is a leading source of confusion during synthesis as many authors have tried to link these data to

temperature or lake level trends. Without a multi-national, cohesive and transparent fisheries monitoring fleet, the next best option would be the development of a fisher catch reporting system which could work for multiple fisheries (Ticheler et al. 1998; Calderwood, 2022). There is a clear gap in the use of data from the recreational rod and line fishery, for example the Kariba International Tiger Fishing Tournament could be exploited, thus building on Magquina et al. (2020), to provide real-time, usable fisheries data (Signarolu et al. 2026). Albeit this should be caveated, as self-reporting fisheries must be validated by fisheries independent data and fisheries observers.

In an era of limited budget for biodiversity work, research focus has started to shift to integrate interactions between biodiversity trends and human wellbeing (e.g. Carolus et al. 2019; Hasimuna et al. 2023; Simukoko et al. 2023; South et al. 2025b). Explicitly designing programmes which apply a systems perspective in Lake Kariba is needed. The cultural and social dynamics of each shoreline of the lake are highly variable and deeply connected to the landscape (Whande et al. 2006; Nyikahadzoi et al. 2017; Matamzima, 2024). Future research needs to integrate the connections between people and nature directly, doing so will provide much needed evidence through which to guide policy developments. Embedding classical ecological research into human wellbeing studies can strengthen objectives aligning with the Sustainable Development Goals, such as Life Below Water, No Poverty, Zero Hunger, Good Health and Wellbeing, while advancing interdisciplinary, fundamental science. Lake Kariba, and associated institutions, e.g. Lake Kariba Fisheries Research Institute, University of Zimbabwe Lake Kariba Research Station, Zambian Ministry of Fisheries and Livestock, Zambezi River Management Authority, present a unique platform to address ecological outcomes caused by global change in an ecologically and economically significant waterbody in an understudied biogeographic region.

With this in mind, we identify (in no order) 10 cross-cutting research themes, based on the synthesis within this review, to set the scene for future internationally relevant research on Lake Kariba and signal key resources and publications.

1. Ecological networks under change – using long term datasets to interrogate the more subtle drivers and outcomes of multiple stressors for both conservation and fisheries purposes using functional and taxonomic indicators. Datasets which can be leveraged:

lake levels from satellite altimetry (USDA G-REALM); temperature and dissolved oxygen (Calamita et al. 2019); inshore fish diversity and abundance.

2. The long-term experimental gillnet dataset from Lake Kariba has proven suitable for hypothesis testing aspects of classical succession theory (Balon, 1974; Kolding et al. in review). This can be furthered using a functional trait-based approach rather than a taxonomic approach which would allow results to be generalised and then tested in other locations (Martini et al. 2021; Brown et al. 2023). If a similar dataset becomes available, the same approach holds value across genera.

3. Valuation assessment of inland fisheries ecosystem services and drivers of change from molecular to landscape level to guide future development policy. Fatty acid synthesis and trophic transfer data are available per Taipale et al. (2025). However, integration of household surveys and demographic data on fisheries and aquaculture species reliance is needed to fully achieve this but is currently not readily available (frameworks for assessment can follow Heilpern et al. 2021 and South et al. 2025b).

4. Lake Kariba can provide a forum for a long-term climate change and greenhouse gas emissions monitoring station, which can support decision making to achieve key targets of the Sustainable Development Goals. Current literature shows the potentially enormous impact of the dam on organic carbon mineralisation, greenhouse gas emission, and downstream transport of nutrients (Maavara et al. 2017). Integration of biogeochemical processes and lake metabolism into fisheries science and ecology poses an opportunity for transdisciplinary research (Mariani et al. 2025) but needs considerable infrastructure and co-development to achieve.

5. De-colonialisation of natural resource management practices and how to unify ecological research with social equity, supporting the move from centralised single species approaches to decentralised ecosystem-based approaches (Nyikahadzoi and Raakjaer 2014; Reid et al. 2021; Kolding and van Zwieten, 2011; Kolding et al. 2015)

6. Tests of hypotheses in invasion science, such as biotic resistance and empty niche hypothesis (Enders et al. 2020), using the phenotypically novel redclaw crayfish and Nile tilapia which are phylogenetically similar to native tilapiines as key case studies.

7. Other ecological phenomena can be tested such as the facilitation hypothesis or invasional meltdown (Carolus et al. 2019; Ricciardi and Simberloff, 2025). Whereby, it is assumed that successional or invasive species with traits can alter the environment to make it more habitable for further newcomers. This can be expanded into cross-cutting themes relating to disease vector ecology and interaction changes stimulated by biological invasions.

8. Impacts of anthropogenic change in the lake as well as in the upstream Zambezi basin, with respects to pollutants, plastics, runoff, and development of floating solar voltaics; and the changes to ecological interactions that may result from this and their implications for human wellbeing. Hasimuna et al. (2023) present trace metal accumulation in kapenta and Simukoko et al (2023) addressed the health risk of persistent organic pollutants and perfluoroalkyl substances (PFAS) in Nile tilapia.

9. Potential development of technological advancements, such as trialling and validating the use of fisher targeted mobile phone applications for fisheries monitoring, app-based fish trading to improve access to resources, or solar powered fish drying tools could improve communication around sustainability (Calderwood, 2022; Chiuseu et al. 2025). The inclusion of fishers in scientific data collection (see Ticheler et al 1998), could be a viable alternative if it can be made statistically verifiable and robust.

10. As Lake Kariba is now invaded by multiple floating macrophytes, it is a prime location for development and testing of novel biocontrol agents. Creating a natural experimental arena for treatment can improve both ecology, invasion science and human health.

To delve into any of these themes requires strong and equitable collaboration between researchers and organisations. Lake Kariba has a long history of international research networks, some of which have dissipated over the course of its history. Nonetheless, with infrastructure investment and time taken to strengthen relationships both within southern Africa and beyond, this can be achieved and provide beneficial outcomes to the people of Zimbabwe and Zambia, alongside contributing to internationally relevant science.

Data availability

All data used are available within Supplementary Material or within the references of this paper.

Author contributions

Conceptualisation: JS, LAJN, PAMVZ, JK. Analysis: PAMVZ, JK. Data curation: PAMVZ, ATC, IHT, MM, JK. Writing - Original draft, final draft and editing: JS, LAJN, PAMVZ, TCM, ATC, IHT, GC, MM, JK

Conflict of interest statement

ATC and IHT declare that they are employed by ZimParks and MM declares employment at the Zambian Department of Fisheries. The rest of the authors have no conflicts to declare. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results

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