THE RELATIVE ABUNDANCE, DIVERSITY AND MICRONUTRITIONAL VALUE OF SMALL FISH SPECIES IN THE KAMUTJONGA FLOODPLAIN, KAVANGO RIVER, NAMIBIA

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ABSTRACT

Floodplains are among the most productive ecosystems on earth, serving as biodiversity hotspots and critical resources for ecological and human communities. They provide essential seasonal habitats for fish migrating from the mainstream to nutrient-rich areas for feeding, spawning, and refuge. These fish not only play a pivotal role in the ecological balance of floodplains but also serve as a primary source of nutrition for riparian communities, where alternative food sources are often limited. Despite their importance, significant gaps remain in understanding fish diversity and abundance in floodplain ecosystems of southern Africa, and the value of their nutritional contribution to local populations.

This study addressed these knowledge gaps by investigating the dynamics of fish abundance and diversity in the Kamutjonga Floodplain and the nutrient composition of small, commonly consumed fish species. The study focused on barbs (*Enteromius* spp.), Zambezi bream (*Pharyngochromis acuticeps*), redbreast tilapia (*Coptodon rendalli*), and threespot tilapia (*Oreochromis andersonii*). It evaluated their contributions to the Recommended Nutrient Intake (RNI) for vulnerable groups, including pregnant and lactating women and young children between one to three years of age. These populations are particularly at risk of nutrient deficiencies, making understanding these fish species' nutritional value crucial for public health.

Fieldwork was conducted during the flood seasons of 2018 and 2019, employing throw trap nets and seine nets at a total of 20 sampling sites across the floodplain. The data collected in

2018 was analysed to assess fish abundance and diversity, while the 2019 samples were subjected to mineral analysis.

A total of 1,389 fish, representing nine families and 35 species, were documented. The Cyprinidae, dominated by hyphen barb (*Enteromius bifrenatus*), accounted for 28.2% of the Index of Relative Importance (IRI), while the Cichlidae, led by southern mouthbrooder (*Pseudocrenilabrus philander*), comprised 12.3%. Seasonal patterns revealed the highest fish diversity during the receding flood phase, whereas fish abundance (measured as Catch per Unit Effort, CPUE) peaked during the rising phase. Juvenile cichlids were particularly abundant during this phase, highlighting the floodplain's critical role as a nursery habitat. This finding reinforces the ecological significance of the floodplain in supporting the early development and growth of fish populations.

Nutritional analyses focused on the mineral content of the four most commonly consumed species. Composite samples were tested for macrominerals (sodium, potassium, phosphorus, calcium, and magnesium) and microminerals (iron, copper, zinc, and manganese). Results showed that small fish, particularly *Enteromius spp*. and *P. acuticeps*, are nutrient-dense, providing significant proportions of essential minerals. For instance, a standard portion (200g for women, 100g for children) of *Enteromius* spp. can meet over 30% of the recommended daily calcium intake and 35% of the recommended zinc intake for both women and young children. *Oreochromis andersonii* stood out for its iron content, with a standard portion capable of fulfilling 70–90% of the daily recommended intake for vulnerable groups. These results highlight the substantial role of small, locally available fish in combating micronutrient deficiencies and enhancing food security.

In conclusion, this study underscores the dual ecological and nutritional value of the fishes of the Kamutjonga Floodplain. By serving as a key nursery habitat, it supports the life cycles of diverse fish species, while the consumption of these fish can significantly address nutritional deficiencies in vulnerable human populations. The findings have direct implications for floodplain fisheries management, emphasizing the need to sustain fish biodiversity while optimizing their role in food security. Future research should focus on understanding the long-term impacts of environmental changes, such as climate variability and land-use shifts, on fish populations and their nutritional contributions to riparian communities.

PREFACE

The data were collected for this thesis from the Kamutjonga Floodplain, Kavango River in the Republic of Namibia between March 2018 and June 2019. These data were obtained from the annual floodplain monitoring surveys conducted by the Namibian Ministry of Fisheries and Marine Resources as part of their mandate. All experimental work was conducted while being registered at the Department of Ichthyology and Fisheries Science, Rhodes University, Makhanda, under Prof. Anthony Booth's supervision, after Prof. Olaf Weyl's tragic passing, and co-supervision by Dr Francois J Jacobs.

The work in the thesis, entitled "*The relative abundance, diversity and micro-nutritional value of small fish species in the Kamutjonga Floodplain, Kavango River, Namibia",* is my original work. It has not previously, in its entirety or partly, been submitted at any university or other higher education institution for the award of a degree.

…….
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September 2025

Certify that the above statement is correct, and as the candidate's supervisor, I have approved this thesis for submission.

……
Professor Anthony J. Booth
Supervisor
September 2025

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CHAPTER 1: GENERAL INTRODUCTION

1.1. Freshwater wetlands

Freshwater wetlands include lakes, lagoons, rivers, streams, and floodplains that sustain diverse terrestrial and aquatic organisms (Mitsch et al. 2015; Kingsford et al. 2016). While only representing approximately 1% of the earth's surface area (Dawson 2012), freshwater ecosystems sustain over 40% of the world's ichthyofauna, comprising approximately 13,000 freshwater fish species (Levêque et al. 2008; Tedesco et al. 2017; Froese 2022). Additional advantages of freshwater ecosystems include the provision of water, the provision of food resources (such as fish and aquatic plants), the stabilization of microclimates, the sequestration of carbon, the provision of raw materials (such as sand and reeds), nutrient recycling, flood mitigation, and the preservation of biodiversity (Mitsch et al. 2015; Grizzetti et al. 2016; Kingsford et al. 2016).

1.2. Floodplains as an important aquatic ecosystem

Floodplains are wetlands at the interface of terrestrial and aquatic ecosystems (Opperman et al. 2017). Floodplains are driven by two major processes, namely hydrology and biogeochemistry. Hydrology involves the water influx and activities in the main river system relating to the magnitude, frequency, duration, timing, and stage. Biogeochemistry encompasses the processes of sedimentation, biological uptake, and the transformation of dissolved organic carbon (DOC) and nutrients into particulate organic carbon (POC) through biogeochemical reactions. These processes influence the water and the soil’s biochemistry and nutrient dynamics (Opperman et al. 2017). As the river inundates the floodplain, water velocity decreases, leading to the deposition of suspended sediments and nutrients. Secondly, the river-

bound and the terrestrially deposited nutrients are broken down and assimilated by the fish and various biota. Finally, due to the favourable environmental conditions in the floodplains, biochemical reactions take place, i.e., the transformation of dissolved organic carbon and nutrients into particulate organic carbon (Opperman et al. 2017). Floodplains are highly productive areas and serve as fish nurseries promoting growth, providing nutrients from the breakdown of built-up allochthonous biomaterial (Winemiller and Jepsen 1998; Agostinho et al. 2018; Barrett et al. 2018). This energy transfer supports the proliferation of small fishes within the temporarily inundated floodplain areas (Junk et al. 1989; Hocutt and Johnson 2001). The flood pulse is considered a principal factor of the existence, productivity, and biota interactions in river-floodplain ecosystems (Junk et al. 1989). The annual flood's timing, duration and extent have driven patterns in species abundance and diversity (Linhoss et al. 2012). Floodplains are dynamic habitats that are neither permanently dry nor permanently inundated with water throughout the season. They provide an ecologically important aquatic-terrestrial transition zone subject to periodic drying and wetting (Junk et al. 1989). During the dry season, floodplains support terrestrial processes such as wildlife and livestock foraging and terrestrial floral growth (Ramberg et al. 2006; Bonyongo 2007). Floodplain ecosystems are a major contributor to the main river's overall productivity rather than the upstream nutrient influx. The main river channel is a refuge during low water and a pathway to foraging and spawning areas in the adjacent floodplains (Junk et al. 1989). Globally, floodplains are among the most species-rich and productive areas rather than the adjacent main river channel (Tockner and Standford 2002). As a result, healthy and connected floodplains are integral for sustainable fisheries and river health on a holistic level. Worldwide, riverine floodplains cover an area of about 2 million km^2 and are estimated to provide services to a value of US$3.9 trillion yr^{-1} (Costanza et al. 1997).

The general annual inundation of floodplains follows a continuum of three general hydrological phases (Hocutt and Johnson 2001; Junk et al. 2004). The encroachment of floodwater characterises the rising phase into the dry savannah grasslands. The peak phase is the maximum water level, while the receding phase is the gradual drying up of the inundated floodplains (Hocutt and Johnson 2001; Siziba et al. 2013). Fish populations have adapted their life cycles to synchronise with annual floods, optimising processes such as spawning and migration (Bayley 1995; Merron 1991). Spawning, for example, can occur during the rising phase, provided that specific biological and physicochemical cues are present within the floodplain, giving the fish communities the opportunity to rapidly colonise vast areas quickly (Merron 1991, Bayley 1995). The floodplain fish community can easily be divided into the two life history strategies of *r* and *K* selection. The *K*-selective strategist has delayed reproduction, low fecundity, parental care and longer lifespan, whereas *r*-selected fishes have the opposite characteristics (Pianka 1970). Furthermore, Parry (1981) explored the reproductive traits along four different meanings or characters and noted that *r*-selection promotes rapid population growth in uncrowded environments, favouring species that occur in ephemeral habitats and allocate a larger proportion of resources to reproduction. Some *K*-selective strategists, i.e., piscivorous largemouth breams *Serranchromis* spp. and tigerfish *Hydrocynus vittatus*, as well as herbivorous redbreast tilapia (*Coptodon rendalli*), initiate spawning well before the flooding in November, whilst the *r*-selected invertivores, mostly dominated by cyprinids, spawn with the rising flood and during the flooding period (Hocutt and Johnson 2001). The *r*-selected strategists, such as the dashtail barb (*Enteromius poechii*), have a high mortality rate, high annual growth rate and are short-lived, a strategy that enables them to dominate quickly and optimally utilise the varying annually inundated habitats of the floodplain ecosystem (Bayley 1995; Reznick et al. 2002). Conversely, the *K*-selected strategists, such as *H. vittatus*, are long-lived, have larger body sizes and exhibit slower growth (Reznick et al. 2002).

The temporal floodplains host different fish species of varying sizes and life stages. Merron et al. (1995) recorded 83 fish species in the Okavango River and its delta, while Van der Waal (1991) only recorded 73 species in the Kavango River system.

1.3. Inland fisheries

1.3.1. Global inland capture fishery

Global inland capture fishery production was 11.5 million metric tonnes of fish in 2020 (FAO 2022). As the two largest contributing regions to inland capture fisheries, production in Asia and Africa was 7.29 million metric tonnes (64%) and 3.21 million metric tonnes (28%), respectively (FAO 2022).

According to FAO (2020) and Loring et al. (2019), fisheries provide livelihoods for 120 million people, of whom nearly 97% live in developing countries, of which 90% are involved in small-scale fisheries. An estimated 2.7 million inland fishers and a further 2.1 million are employed in the post-harvest sector in Africa, representing 16.2% of the world's total inland fishers (Funge-Smith et al. 2019). African fisheries resources are primarily open access and provide a relatively inexpensive animal protein source for subsistence consumption (local communities) and small informal markets (Funge-Smith 2018; Funge-Smith et al. 2019). Together with other anthropogenic impacts, fishing exerts additional pressure on the resource base (Gleick et al. 1995; Stiassny 1996; Kebede et al. 2016). Human activities, such as pollution, habitat loss and degradation, wetland draining, water extraction, and poor land management practices, negatively impact freshwater ecosystems and their related biodiversity (Jackson et al. 2021). Additionally, climate change could, directly and indirectly, impact freshwater ecosystems and

biodiversity. Increasing water temperatures and elevated levels of CO_2 have an impact on the growth and proliferation of wetland plants. Therefore, it inherently affects food chains, nutrient recycling, primary productivity, wetland species composition and relative abundances (Mitsch et al. 2012; Mohammed et al. 2013; Muringai et al. 2022). Rising water temperatures affect the biological, physical, and chemical processes of freshwater fish, significantly influencing their physiology and ecology, including growth, body size, metabolism, maturation, sex determination, mortality, migration, immune response, habitat suitability, reproductive success, interactions with prey species and parasites, and distributional changes (O'Gorman et al. 2016; Harrod et al. 2019). Therefore, managing and preserving freshwater ecosystems and their living aquatic biodiversity is imperative to maintain their biological integrity and sustain rural and riparian livelihoods.

1.3.2. African capture fisheries production

The African rich and diverse inland capture fisheries sector contributes to food security, nutrition, and livelihoods for millions of people. According to the FAO (2022), Africa's inland capture fisheries production was estimated at 3.21 million tonnes in 2020, representing 28% of the global inland capture fisheries production. The region's per capita fish catch of 2.56 kg/year surpasses Asia's 1.99 kg/year, despite Asia's larger population and greater inland water area (Funge-Smith 2018). Inland capture fisheries are important for African communities in rural areas, providing a source of animal protein, essential micronutrients and income. The highest production (about 40%) is from the African Great Lakes region, mainly from small pelagic fish such as the dagaa (*Rastrineobola argentea*), kapenta (*Limnothrissa miodon*), and usipa (*Engraulicypris sardella*) (Kolding et al. 2019). The small pelagic fisheries utilised beach seining and small and medium boats using lights to attract schools of fish. The fish constitute

sales in various formal and informal markets and are consumed together with the traditional dish of maize meal (Kolding et al. 2019).

Subsistence fishing, which constitutes a significant portion of small-scale inland fisheries catches used for local consumption, plays a crucial role in enhancing livelihoods and ensuring food security (Thilsted et al. 1997; Roos 2001; Béné and Heck 2005; Béné et al. 2016a; Funge-Smith 2018). Most of the captured fish are either consumed or directly sold through local informal markets (Béné and Heck 2005; Bennett et al. 2008; Cooke et al. 2015; Béné et al. 2016b; Fluet-Chouinard et al. 2018). According to Abbott et al. (2007), Welcomme et al. (2010), Funge-Smith (2018) and the FAO (2022), inland fisheries production from Africa is highly underestimated, hidden, or under-reported due to scattered, informal markets, landing areas and inadequate reporting of catches, especially that of small subsistence and recreational fisheries. Hence, according to Fluet-Chouinard et al. (2018), individual countries were more prone to underestimate their catches by as much as 68% from household surveys. By extrapolation, the recorded global inland fisheries catch of 2008 could almost double to 16.6 MT, not 10.3 MT as reported. Despite the critical role of fish in enhancing Africa's food security, its production remains underreported, rendering it largely overlooked in food security policies and decisions (Youn et al. 2014; Cooke et al. 2015; Cooke et al. 2016; Funge-Smith et al. 2019). Fish provides essential protein and micronutrients, particularly in low-income countries where other animal-source foods are scarce or costly. However, much of this production is consumed directly by producers or traded informally, leading to its underestimation in official statistics. Consequently, these underreporting limits recognition and support for the small-scale fisheries sector, which sustains livelihoods and nutrition for millions. This lack of data also hinders management interventions aimed at addressing hidden hunger and achieving the second Sustainable Development Goal (SDG) of Zero Hunger by 2030. Improved data collection and reporting systems are, therefore, critical to integrating fish

into food security policies at all levels. Without accurate data, inland fisheries receive less priority, posing significant challenges to managing their resources and ecosystems effectively.

1.3.3. Inland fisheries in Namibia

Mean annual rainfall in northern Namibia ranges from 650 mm in the Zambezi Region to approximately 50 mm in the Kunene Region along the Atlantic coast. This rainfall pattern affects the availability of water resources and agricultural activities in Namibia (Mendelsohn et al. 2013; Awala et al. 2019). Namibia has five major perennial river systems: the Zambezi River, the Kwando-Linyanti-Chobe River, the Kavango River, the Kunene River and the Orange River (Holtzhausen 1991; Tveldten et al. 1996). During years of exceptionally high precipitation, the Cuvelai system, Omadhiya lakes, Lake Liambezi and non-perennial rivers become inundated. Inland capture fisheries are more prevalent in the northern wetland areas of the Kunene-Cuvelai, Kavango, and Zambezi-Chobe-Linyanti River systems (Holtzhausen 1991). Inland capture fisheries in Namibia are estimated to produce approximately 2,800 tonnes per annum, with a per capita production of 1.22 kg. The primary sources of these fisheries are Lake Liambezi during flood years and the Zambezi and Chobe Rivers (Turpie 2008; Funge-Smith 2018). Lake Liambezi experiences periodic cycles of filling and drawdown. Following its inundation in 2010, it became a thriving hub for commercial fisheries, attracting fishers from neighbouring countries (Cooke et al. 2015; Peel et al. 2015). Most of the fish captured in Lake Liambezi were processed and transported to markets in the Democratic Republic of Congo (DRC) (Cooke et al. 2015; Tweddle et al. 2015). Tweddle et al. (2011) estimated that the Zambezi River and its extensive floodplains, excluding Lake Liambezi, yielded approximately 5,000 tonnes annually. This estimate was based on the number of canoes operating within the river system, with a daily average of 950 fishing vessels each collecting a

minimum of 15 kg of fish. Recent reports have suggested that fisheries resources are under pressure in northern Namibia and are a cause for concern (Simasiku et al. 2017). The main factors contributing to this situation are overfishing and the use of destructive fishing gears, while changes in flow-related climate change are forecasted to impact fisheries in the future. These factors threaten local communities' livelihoods and aquatic ecosystems' biodiversity. There is an urgent need for effective management and conservation measures to ensure the sustainability of fisheries resources in northern Namibia (Cooke et al. 2015; Tweddle et al. 2015).

According to the 2011 Census, Namibia's population was 2.1 million, of which 57% live in rural areas. Approximately 223,000 people reside in the Kavango East and West Regions, with 71% living in rural areas and deriving 43% of their income from subsistence agriculture (Namibia Statistics Agency 2011). An estimated 85% of these residents live within 10 km of the Kavango River, highlighting their dependence on its flow for their livelihoods (Sandlund et al. 1992; Mendelsohn et al. 2004). The proximity and reliance on the river resources constitute a noticeable challenge as it places substantial pressure on fishery resources along its perennial rivers. Unsustainable utilisation and impacts such as habitat degradation, pollution, rapid population growth, demand for hydroelectric energy, logging, nutrient enrichment, and climate change strain the ecosystem (Junk et al. 2004). It is a common cause for concern for many African inland fisheries. Due to weak political will and poor resource management (Cooke et al. 2015), enforcement of legislation and resource monitoring remain inadequate. Nonetheless, inland fisheries play a vital role in riparian communities' subsistence, food security, and poverty reduction (Welcomme et al. 2010; Cooke et al. 2015; Tweddle et al. 2015). Fish provide an inexpensive, high-protein and micronutrient supplement to the diet of many rural riparian inhabitants in remote areas and support recreational and commercial fisheries that both contribute to the economy (Hicks et al. 2019; Kolding et al. 2019).

1.3.4. Floodplain fisheries utilisation

Floodplain fisheries resources are explored mostly for subsistence by men, women and children using various traditional and modern fishing gears (pers. obs.). The local names for fishing gear and methods in parentheses are of RuKwangali descent, a commonly spoken language in the Kavango Region (Okeyo et al. 2010). Women and children predominantly use the Kamutjonga Floodplain during the rising and receding flood phases. Utilising maize porridge-baited perforated plastic containers converted into funnel traps, mosquito nets and traditional traps such as fishing corral traps (*Sintunga*), push baskets (*Sididi*), fish fences (*Masasa)* and fish funnels (*Shikuku*) (Van der Waal 1991; Purvis 2002; Okeyo et al. 2010). The names in parentheses for the traditional gear are in a local, widely spoken Kavango people dialect, *Rukwangali.* The gears predominantly captured juvenile cichlids, i.e., threespot tilapia (*Oreochromis andersonii)* and southern mouthbrooder (*Pseudocrenilabrus philander*), and barbs i.e., hyphen barb (*Enteromius bifrenatus*) and straightfin barb (*Enteromius paludinosus*) (Kangausaru 2018; Tiyeho et al. 2019). In shallow areas, a single person can operate plastic containers or traditional traps, whereas fish funnels require up to 40 women and children moving together (Van der Waal 1991). Two or more women use mosquito nets to harvest small-bodied fish and juveniles of larger species, typically yielding less than 1 kg, with the catch shared equally among fishers (Van der Waal 1991). Conversely, young boys and men fish with hook-and-line (*Erowo*) during rising and receding floods in the main river channel, primarily catching *O. andersonii*, *C. rendalli*, *H. vittatus*, and *C. gariepinus* (Muunda 2023, Tiyeho 2023). Men also deploy gillnets (*Ekwe*) year-round in backwaters, across side channels, and along mainstream riverbanks (Van der Waal 1991). These fish provide a valuable source of nutrition for people whose diets may be otherwise lacking sources of macro and micronutrients (Mogobe et al. 2024). Smaller fish species often provide a valuable source of

protein and nutrients for local communities, especially for women and children, during the flood season (Thilsted et al. 1997; Roos et al. 2003; Roos et al. 2007).

1.4. Aims, objectives and thesis outline

Previous research focused on the biology and movement of commercially significant fish stocks in the mainstream Kavango River, such as large and charismatic cichlids and tigerfish (Hocutt et al. 1994; Hay et al. 1996). However, the relative abundance and nutritional benefits of commonly consumed floodplain fish species in the Kavango River for local communities require further investigation to ensure sustainable and optimal use of these fishery resources. Smaller floodplain fish species represent a highly productive and sustainable resource due to their rapid turnover.

The study aimed to assess the relative abundance and diversity of small fish species during the three hydrological flood phases in the Kamutjonga Floodplain, Kavango River, Namibia, and to evaluate the micronutrient content of the commonly consumed species.

The sub-objectives were:

a) To determine the composition of the small fish species community during the seasonal flood cycle using a throw-trap net.
b) To determine the relative abundance and catch per unit effort (CPUE) of the small fish species using a throw trap net.
c) To determine the micronutrient content of selected small fish species that utilise the Kamutjonga Floodplain, Kavango River, Namibia.

d) To compare the mineral composition of small fishes from the Kamutjonga Floodplain, Kavango River, Namibia, with that of other fish species.

e) To assess the contribution of the micronutrient content of selected small fish species from the Kamutjonga Floodplain, Kavango River, Namibia, as estimated in Objective c, to the recommended nutrient intakes (RNI) for pregnant and lactating women and children aged 1–3 years.

The thesis is divided into five chapters. *Chapter 1* provides a general introduction and literature review of the global and Namibian inland floodplain fisheries resources, floodplain ecology and fisheries utilisation. *Chapter 2* highlights the study area and the description of the sampling gear and protocol used in the study. *Chapter 3* investigates the fish community structure across the Kamutjonga Floodplain, Kavango River in Namibia by describing the species composition, species diversity and relative abundance across the three hydrological phases of flooding. *Chapter 4* presents the micronutrient composition of four fish species from the Kamutjonga Floodplains, Kavango River in Namibia, and their potential contribution to the recommended nutrient intake for pregnant and lactating women and young children. To conclude, *Chapter 5* provides a general discussion and conclusion and highlights potential management recommendations.

1.5. Ethical considerations

The research was approved under the Ministry of Fisheries and Marine Resources (MFMR), Directorate of Aquaculture, with the mandate to sustainably manage the living aquatic resources in Namibia. Fish samples were from donations and routine annual floodplain monitoring biological surveys in the Kavango River undertaken by MFMR.

CHAPTER 2: MATERIALS AND METHODS

2.1. Study area

Kavango River

The Kavango River is an unusual river as it flows inland into an inland delta rather than discharging into the sea. It originates in the southern slopes of the Angolan highlands and flows south until it reaches the Namibian border at Katwitwi. It has a catchment area of approximately 115,000 km^2 (McCarthy et al. 1998) (Figure 1). The main tributary into the Kavango River is the Cuito River, which enters from the north. The Cuito River, together with the Cuanavale River, originates in the highlands around 1,400 m asl. They run southward, side by side, until they merge at the well-known town of Cuito Cuanavale, which has an elevation of 1,250 m asl. Near Dirico on the border with Namibia, the Cuito River joins the Kavango River. The whole Cuito basin is covered by sandy, porous, and nutrient-poor soils. The Cuito River contributes about 45% of the total water that reaches the Okavango Delta, while the Kavango provides the other 55%. These ratios, however, change throughout the year. For instance, the Kavango River delivers about twice as much water as the Cuito River from January to June, but the opposite happens from July to December when the Cuito River's flow is about twice that of the Kavango River (Mendelsohn et al. 2019). The tributary contributes to doubling the annual runoff of the mainstream (McCarthy et al. 1998; Hocutt and Johnson 2001). The Cuito River has a higher base flow, forming extensive swamps and floodplains (Conradie et al. 2016). In its upper catchment, floodwaters are stored in the floodplains, being released back into the river during the dry season (Kgathi et al. 2006; OKACOM 2011; Mendelsohn et al. 2019). Together with the flow from the Kavango River, it contributes to various ecosystem services and goods utilised by the riverine communities along the lower Okavango River, the Okavango Delta, and its outflowing rivers (Mendelsohn et al. 2019). However, this is threatened by the upstream developments on the Cuito River, especially the environmental pressures of woodland clearing,

river contamination from urban areas and large farms, and the frequent burning in the lower Cuito catchment (OKACOM 2011; Mendelsohn et al. 2019).

The Kavango River flows eastward for 415 km, forming the border between Angola and Namibia. It then turns southward, flowing 53 km through Bwabwata National Park (formerly the Caprivi Strip) to the Muhembo border point, before entering the Okavango Delta in Botswana (Hocutt et al. 1994; McCarthy et al. 2000; Milzow et al. 2010; Steudel 2013). The river floods annually from December to July, reaching a maximum water level depth of 6 m (Rundu) and a floodplain up to 2km wide (Hocutt and Johnson 2001). The flood phases (rising, peak and receding) were selected according to the historical water discharge data collected by the Okavango Research Institute (ORI) at the Muhembo station (Figure 2).

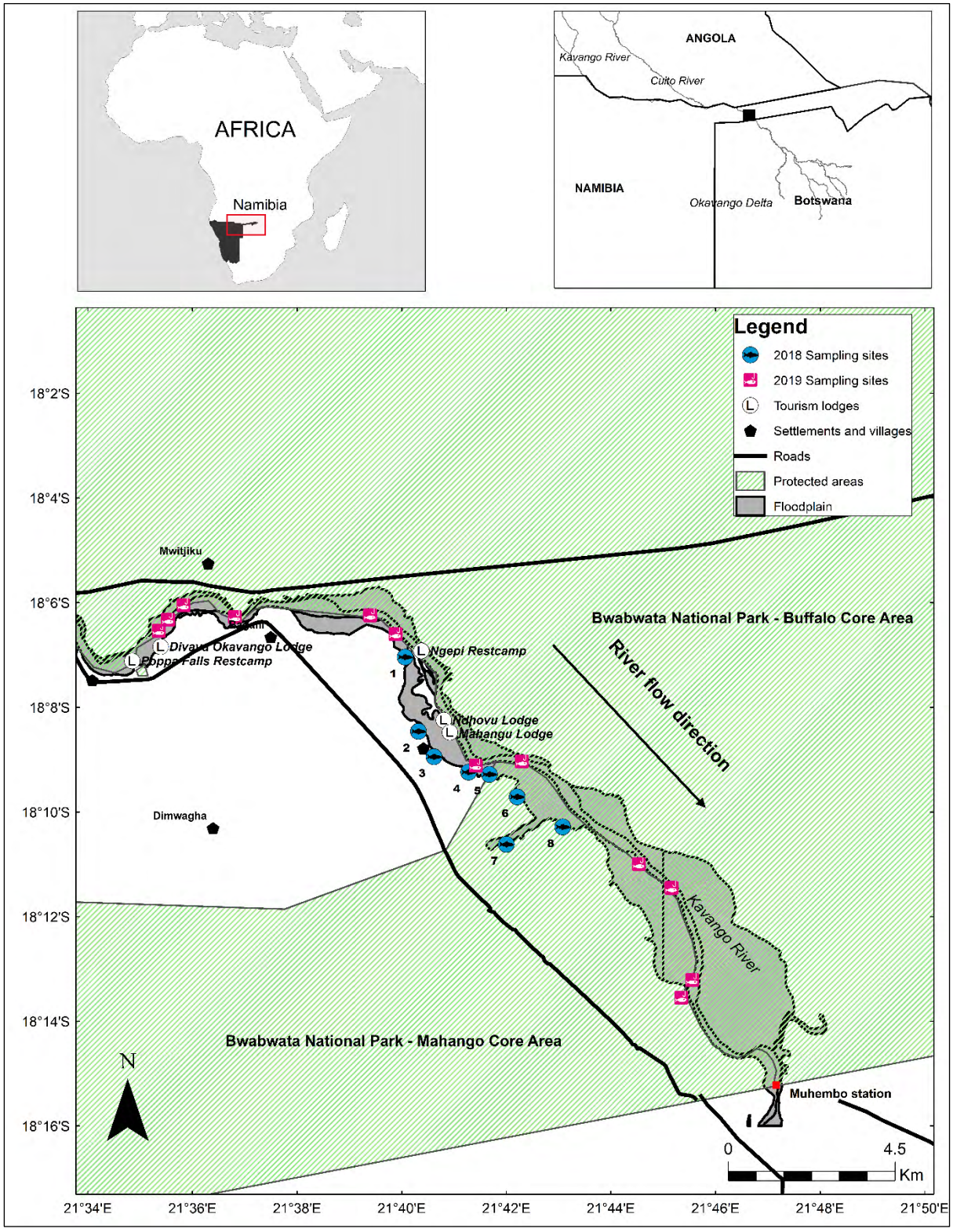

Figure 1. Map of the Kavango River, Namibia, illustrating the location of the study area and numbered fish sampling sites for 2018 (Eight sites for fish abundance) and 2019 (12 sites for micronutrients).

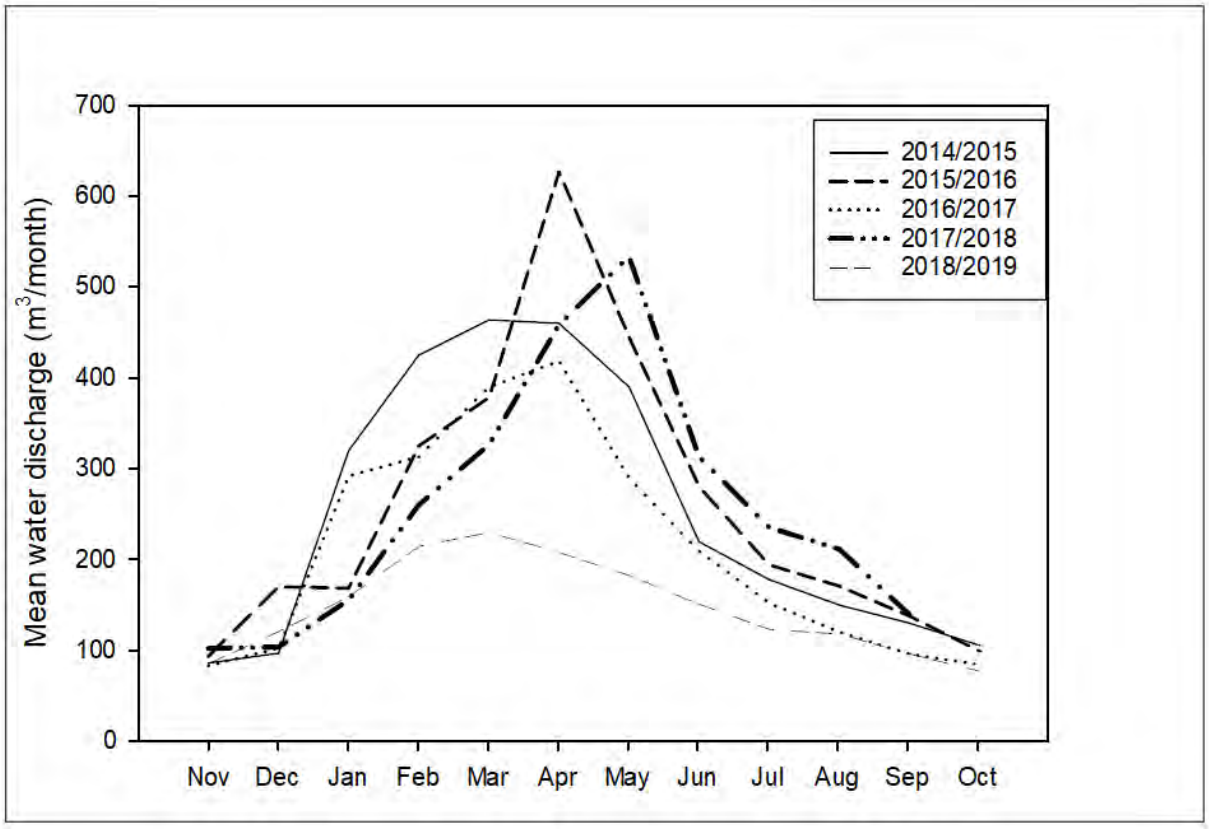

Figure 2. Monthly discharge of the Okavango River at Muhembo gauging station, 2014–2019, sourced from the Okavango Research Institute (2022).

http://168.167.30.198/ori/monitoring/water/

The sampling areas were located adjacent to three villages (Popa, Bagani, and Kamutjonga) and the Mahango Core Area of Bwabwata National Park along the Kavango River. Fish sampling was conducted in 2018 (a typical flood year) for fish abundance studies and in 2019 (a low flood year) for micronutrient composition (Figure 2). In 2018, fish sampling was conducted in the Kamutjonga Floodplains, Kavango River, Namibia; however, in 2019, due to reduced flood levels, fish were collected from shallow littoral zones. The number of sampling sites was 8 and 12, respectively, with sites in the Bwabwata National Park with restricted fishing and boating activities that serve as fish-protected areas (Figure 1).

Kamutjonga Floodplain

The study area, located approximately 20 km southeast of Divundu, Kavango East Region, Namibia, encompasses the Kamutjonga Floodplain, covering 11 km² when fully inundated and extending from Ngepi Camp (18.110°S, 21.664°E), forming the northern boundary, southwards to the Mahango Core Area of Bwabwata National Park (18.172°S, 21.726°E). The Bwabwata–Okavango Ramsar Site, encompassing the Mahango Core Area and the western portion of the Buffalo Core Area (46,964 ha), is a designated Ramsar wetland of international importance, ecologically connected to the Okavango Delta World Heritage Site in Botswana (Atlas of Namibia Team 2022; Ramsar Site Information Services 2024). The study area includes the communal fishing areas covering 5.72 km^2, adjacent to the Kamutjonga village on the southern part, and a 5.87 km^2 area in the Mahango Core Area where fishing and grazing are prohibited. The Kamutjonga Floodplain's vegetation is utilised for grazing by cattle and wildlife, predominantly hippopotamus and other mammalian herbivores, during the dry season (Mosepele et al. 2009; Junk et al. 2012). During seasonal floods, megaherbivore-derived nutrients are transferred into the Kamutjonga Floodplain's aquatic ecosystems, where they enhance floodplain productivity, improve abiotic conditions, strengthen trophic interactions, and support aquatic community diversity (Mosepele et al. 2009; Masese et al. 2018; Stears et al. 2018). Its proximity to the protected area could serve as a source for recruiting various fish species to other areas, as shown by the movement behaviour studies of tigerfish (Jacobs 2017) and large cichlid species (Økland et al. 2010; Thorstad et al. 2015). Ten tourism accommodation establishments (lodges and camps) in the surrounding area employ most members of the local human community. The lodges provide an alternative livelihood strategy for the local inhabitants when not involved in agriculture and part-time fishing. According to Mosepele et al. (2010), only 7% of commercial fishers in the Okavango Delta sold their fish to tourist lodges, while the majority preferred selling to local markets or bartering for grain in

rural communities. Additionally, members of the local community in the study area engage in diverse livelihood strategies, including livestock farming, tourism-related activities (e.g., tour guiding, tracking, and hunting outfitting), collection and use of wild forest products (e.g., thatch grass and reeds), horticulture (e.g., millet, maize, sorghum, melons, groundnuts, beans, spinach, pumpkins, cabbage, and tomatoes), and subsistence fishing (Purvis 2002; Mendelsohn 2006; OKACOM 2011). Similarly, commercial fishermen were found to be involved in farming practices, including livestock and cropping, as shown in their asset profile (Mosepele et al. 2010).

Floodplain habitat and sampling site characteristics

The floodplain habitats were divided into three vegetation areas: open water (1–1.2 m water depth), vegetated areas (0.6–1.0 m), and inundated grasses (<0.4 m). The open water habitat was dominated by emergent, submerged littoral, and floating plants, such as Common weed *Phragmites australis*, Papyrus reed *Cyperus papyrus,* Oxygen weed *Lagarosiphon ilicifolius*, Water chestnut *Trapa natans*, Broad-leaved pondweed *Potamogeton nodosus*, and White-water lily *Nymphaea lotus*. The vegetated areas comprised of *P. nodosus, L. ilicifolius*, Coontail *Ceratophyllum demersum*, Water-snowflake *Nymphoides indica*, Bladderwort *Utricularia gibba*, and Broad-leaved tape grass *Ottelia exserta.* These were found in macrophyte beds during the peak flooding phase. The inundated grasses, Vlei love-grass *Eragrostis rotifer* and Couch grass *Cynodon dactylon*, were most prominent during the receding flood phase. The substrate was primarily clay (Figure 3).

The water quality measurements were taken during the three hydrological phases of flooding, the rising, peak and receding floods. At each sampling site, physicochemical water parameters

including temperature, dissolved oxygen, pH, conductivity and salinity were measured *in situ* using a Hach sension 4QD multi-parameter kit. The water transparency (visibility) was measured using a Secchi disk, and a depth-measuring pole was used to measure the depth at each effort. For depth, an average of four measurements was taken within the cylindrical space of the throw-trap net (Table 1 – 3).

Table 1. Mean values of selected water quality variables measured during the different hydrological phases of flooding in the Kamutjonga Floodplain, Kavango River, Namibia, March to June 2018.

	Flood phase			
Parameter	**Rising**	**Peak**	**Receding**	**Mean**
Water temperature (◦C)	28.79 ± 1.89 ^{c}	23.40 ± 1.14 ^{b}	19.63 ± 3.03 ^{a}	23.94
Conductivity (µScm^{-1})	67.45 ± 15.48 ^{c}	47.42 ± 16.44 ^{a}	53.85 ±23.06 ^{b}	56.24
pH	6.32 ± 1.05 ^{a}	9.01 ± 0.39 ^{c}	7.66 ± 0.43 ^{b}	7.66
Salinity (mgL^{-1})	0.03 ± 0.01 ^{b}	0.01 ± 0.01 ^{a}	0.01 ± 0.01 ^{a}	0.02
Water discharge (m^{3}S^{-1})	337.73 ± 11.45 ^{a}	515.29 ± 44.30 ^{c}	356.68 ± 41.07 ^{b}	403.23
Sample volume (m^{3})	0.57 ± 0.24 ^{b}	1.18 ± 0.30 ^{c}	0.48 ± 0.22 ^{a}	0.74
Depth (m)	0.50 ± 0.21 ^{b}	1.05 ± 0.27 ^{c}	0.43 ± 0.19 ^{a}	0.66
Transparency (%)	83.09 ± 16.62 ^{ab}	78.15 ± 19.81 ^{a}	72.87 ± 21.74 ^{a}	78.04
Vegetation cover (%)	35.28 ± 19.14 ^{b}	29.44 ± 12.14 ^{a}	51.08 ± 21.20 ^{c}	38.60

The results are shown as the average of all taken measures during the different phases with SD.

Values in the same row with different superscripts differ significantly ($p < 0.05$)

* Measured *in situ*

** Sourced from Okavango Research Institute (ORI) data taken at Muhembo station, Botswana

Table 2. Mean values of selected water quality variables per sampling site measured during the hydrological phases of flooding in the Kamutjonga Floodplain, Kavango River, Namibia, March to June 2018.

Site	Location (Coordinates)	Area	Land use	Water temperature (◦C)	Conductivity (µScm^{-1})	pH	Water discharge (m^{3}S^{-1})	Sample volume (m^3)	Depth (m)	Transparency (%)	Vegetation cover (%)
1	-18.11729,21.66769	Communal	Livestock grazing, bridge	22.92	48.61	7.10	434.28	0.58	0.52	89.81	55.51
2	-18.13906,21.67591	Communal	Livestock grazing, bridge	24.69	54.94	7.60	401.91	0.65	0.57	88.36	37.20
3	-18.14906, 21.67689	Communal	Livestock grazing	21.86	65.20	7.12	409.78	0.96	0.85	72.17	41.82
4	-18.1526,21.68905	Communal	Wildlife and Livestock grazing, bridge	24.59	45.70	7.26	439.64	0.79	0.70	84.99	32.82
5	-18.15467,21.69452	Protected	Wildlife grazing	23.88	47.63	7.88	390.32	0.73	0.65	73.26	39.09
6	-18.16179,21.70342	Protected	Wildlife grazing	23.75	44.55	7.89	370.04	0.75	0.66	59.54	41.38
7	-18.17495,21.70052	Protected	Wildlife grazing, waterhole	26.36	93.36	8.58	387.36	0.52	0.46	88.21	23.76
8	-18.17153, 21.71805	Protected	Wildlife grazing	23.47	49.94	7.87	392.54	0.99	0.87	67.98	37.22

Table 3. Mean values of selected water quality variables per sampling site and per hydrological phases of flooding in the Kamutjonga Floodplain, Kavango River, Namibia, March to June 2018.

Site	Flood phase	Location and Area	Water quality parameter							
			Water Temperature (◦C)	Conductivity (μScm^{-1})	pH	Water discharge (m^3S^{-1})	Sample vol (m^3)	Depth (m)	Transparency (%)	Vegetation cover (%)
1	Rising	-18.11729, 21.66769 Communal	27.52	65.13	5.41	326.33	0.30	0.27	94.14	60.27
	Peak		23.98	38.91	8.59	554.87	1.03	0.91	92.76	27.07
	Receding		17.27	41.79	7.29	421.63	0.42	0.37	82.53	79.20
2	Rising	-18.13906, 21.67591 Communal	28.80	79.53	5.99	326.33	0.48	0.42	95.35	37.60
	Peak		23.39	38.99	9.14	549.39	1.17	1.03	91.56	34.60
	Receding		21.88	46.29	7.68	330.00	0.30	0.26	78.16	39.40
3	Rising	-18.14906, 21.67689 Communal	27.24	90.33	5.11	326.33	0.69	0.61	72.31	25.40
	Peak		22.41	44.93	9.01	542.78	1.55	1.37	70.46	45.00
	Receding		15.92	60.35	7.25	360.21	0.65	0.57	73.73	55.07
4	Rising	-18.1526, 21.68905, Communal	30.85	55.67	5.62	326.33	0.57	0.50	84.55	22.80
	Peak		24.81	39.31	8.80	570.96	1.30	1.15	91.31	28.87
	Receding		18.11	42.13	7.37	421.63	0.50	0.44	79.10	46.80
5	Rising	-18.15467 ,21.69452 Protected	27.78	53.80	7.16	349.13	0.60	0.53	78.79	35.67
	Peak		22.02	42.12	8.62	491.83	1.15	1.02	70.78	25.93
	Receding		21.83	46.96	7.85	330.00	0.44	0.39	70.21	55.67
6	Rising	-18.16179, 21.70342 Protected	28.37	50.33	6.78	349.13	0.66	0.59	75.97	33.80
	Peak		24.11	42.21	9.10	431.00	1.00	0.88	52.86	33.53
	Receding		18.76	41.11	7.78	330.00	0.58	0.51	49.79	56.80
7	Rising	-18.17495, 21.70052 Protected	31.67	80.93	7.93	349.13	0.39	0.34	90.72	28.20
	Peak		23.27	87.81	9.57	482.94	0.91	0.80	86.29	15.60
	Receding		24.13	111.35	8.26	330.00	0.25	0.22	87.62	27.47
8	Rising	-18.17153, 21.71805 Protected	28.10	63.90	6.57	349.13	0.88	0.78	72.91	38.53
	Peak		23.19	45.10	9.27	498.51	1.36	1.20	69.20	24.93
	Receding		19.13	40.82	7.77	330.00	0.72	0.64	61.84	48.20

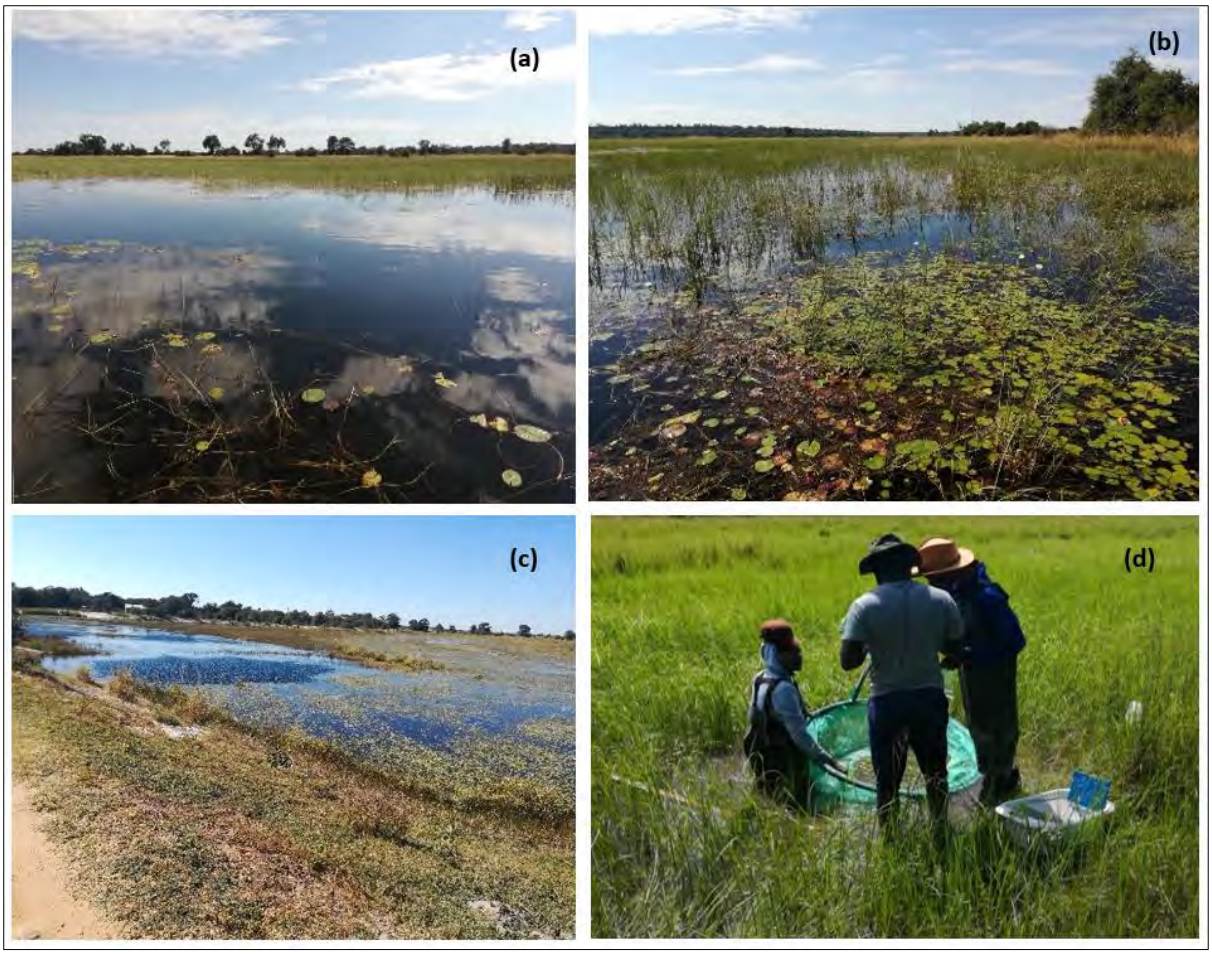

Figure 3. Floodplain habitats: Open areas (a), vegetated areas (b and c), and densely inundated grassland (d).

2.2. Fishing gear and sampling techniques

Throw trap netting

Fish sampling was conducted between March and June 2018 at eight sites during the rising, peak and receding hydrological flood phases. Gear was deployed a total of 15 times at each site (Figure 1). Various methods are utilised for sampling fish from rivers and related wetlands. Traditionally, seine netting in the peripheral areas with shorter nets and gillnets in deeper areas is used (Hay et al. 2000). The sampling gear was unsuitable and posed challenges for fish collection in areas with abundant aquatic vegetation, including floating and anchored

macrophytes. Consequently, 1 m² enclosure trap nets were used to sample fish effectively (Kushlan 1981; Freeman et al. 1984; Chick et al. 1992; Jordan et al. 1997). The Kavango River has low water conductivity, rendering electrofishing inefficient (Booth and McKinlay 2001; Siziba et al. 2011). Chick et al. (1992) conducted studies in Lake Okeechobee and compared four enclosure traps and found that the use of the 1 m^2 is the most effective and preferable method and recommended this method for sampling juvenile and forage fishes in shallow and vegetated habitats. The throw trap net was selected for its proven efficacy in shallow, vegetated floodplains, as validated by Siziba et al. (2011) in the Okavango Delta and Kushlan (1981) in the Everglades marshes. While no site-specific enclosure validation was performed due to logistical challenges, the gear's known capture efficiency of 73% (Freeman et al. 1984) and minimal species bias (Jordan et al. 1997) were deemed sufficient for our objectives, with potential under-sampling of large fishes mitigated through supplementary observations such as extending the sampling effort to 15 times at each site.

The throw trap net was constructed from a 1.2 m diameter 40 mm diameter black HDPE PVC pipe ring on top for floatation and a 1.2 m diameter heavy metal ring on the bottom for fast sinking. A 1.5 m depth net with a 1 mm mesh size was hung between the two frames, leaving both ends of the frame open (Figure 4). The throw trap net was deployed in the shallow marginal zones of the floodplain (Figure 5). Fish were removed from the trap net using a handheld dip net with 20 cm x 45 cm frame measurements, with a 1 mm mesh size material. The dip net was used ten consecutive times until no fish could be caught in five subsequent scoops (Jordan et al. 1997; Siziba et al. 2011). After three consecutive trials with a random

throw trap net yielded unsatisfactory results, we deployed the net 15 times at each sampling site, with efforts spaced at least 10 m apart.

All captured fish were euthanised using clove oil at 20mg.L^{-1}, kept on ice and transported to the Kamutjonga Inland Fisheries Institute's laboratory for identification. Fish were identified to species level. Individuals that were too small (<10 mm) to accurately classify to species level were classified to family level (Skelton 2001; Bruton et al. 2018). Fish were measured and weighed to the nearest millimetre and gram, respectively (Skelton 2001). All fish were fixed in 10% buffered formalin before being transferred to 70% ethanol concentration for extended storage and further analysis (Huchzermeyer 2013; Booth and McKinlay 2001).

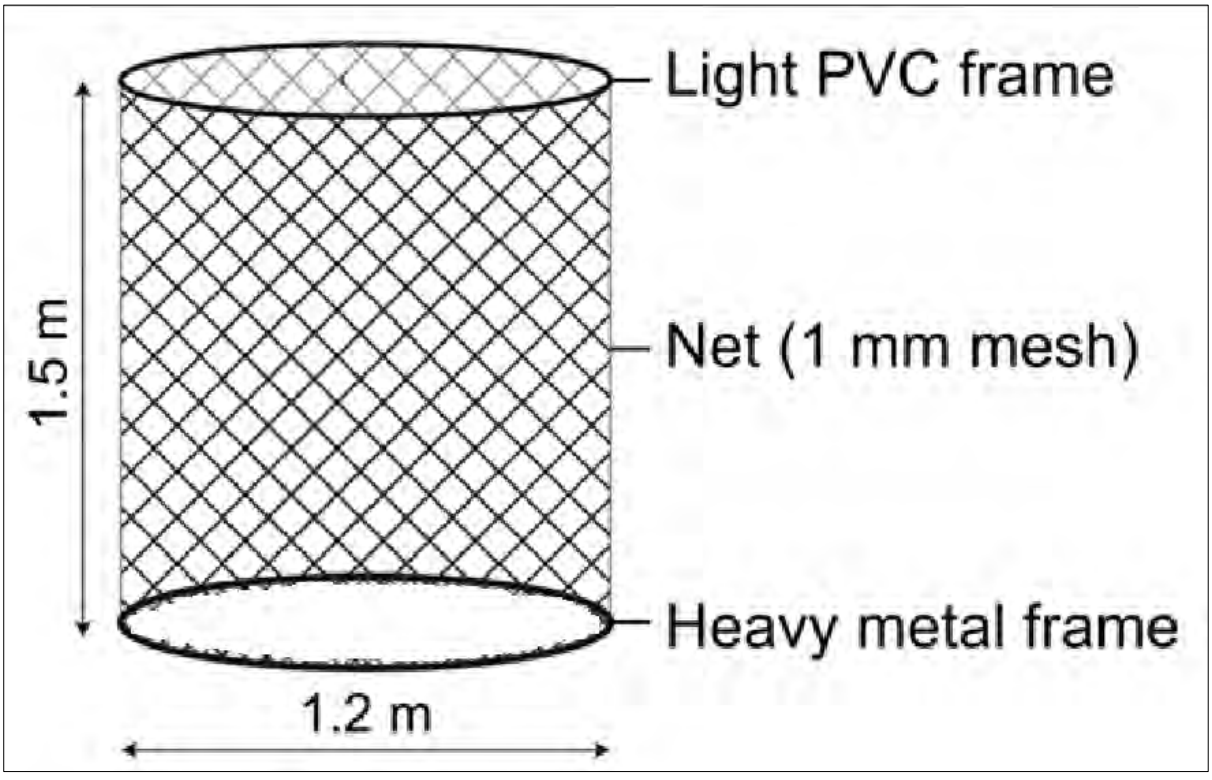

Figure 4. Throw trap net dimensions with both ends of the frame open (Siziba et al. 2011).

Figure 5. (a) and (c) Cylindrical 1m^2 throw trap net deployment and (b) sample collection in vegetated habitat, Kamutjonga Floodplain, Kavango River, between March to June 2018.

Seine netting

From May to June 2019, the littoral zones of the Kavango River fishes were sampled around 12 localities for micronutrient analysis using a seine net. The littoral zones included sand banks, secluded ponds, backwaters and shallow main river channels. The seine net was 10m long x 1.5 m deep, with 1mm mesh material. On average, the sampling effort covered a hauled-swept

area of 100m^2 (Figure 6). The enclosed sampled fish were identified and measured to the nearest gram (g) and length (mm) (Skelton 2001).

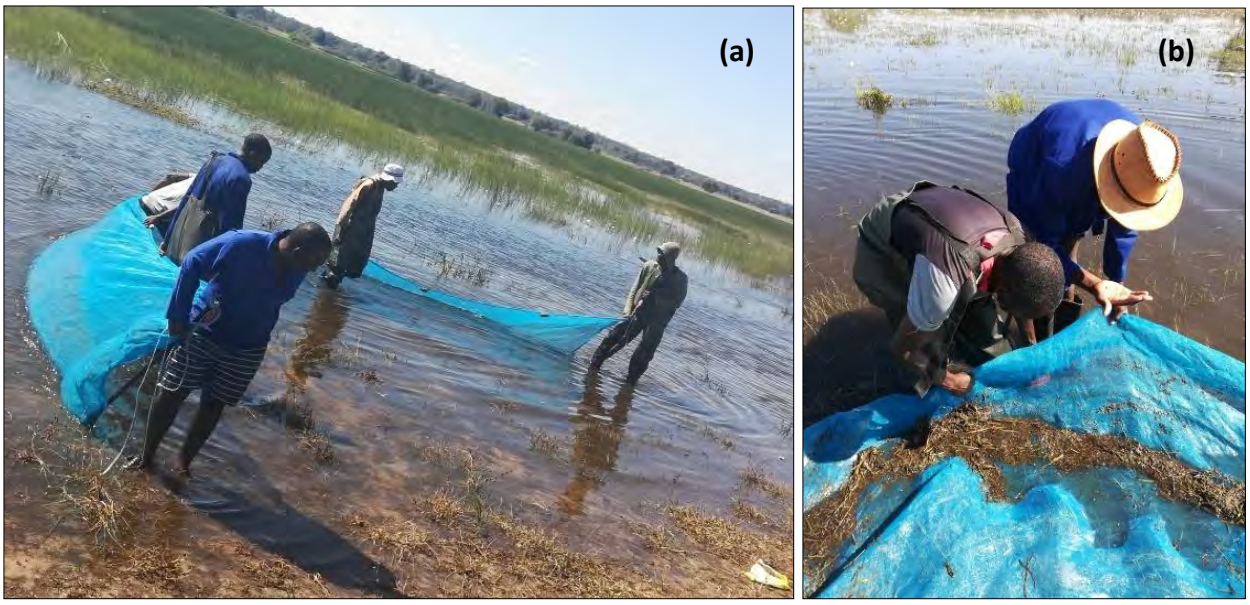

Figure 6. (a) Beach seining and (b) sample collection along the littoral zones of the Kamutjonga Floodplain, Kavango River, Namibia, between May and June 2019.

CHAPTER 3: RELATIVE ABUNDANCE AND DIVERSITY OF SMALL FISH SPECIES IN THE KAMUTJONGA FLOODPLAIN, KAVANGO RIVER, NAMIBIA

3.1. Introduction

The Kavango River basin is a significant transboundary water resource shared between Namibia, Angola, and Botswana. The associated floodplains are situated within the Namibian portion of the basin and are known for their high biodiversity and ecological importance (Mendelsohn and El Obeid 2004). This dynamic ecosystem creates a mosaic of habitats supporting diverse aquatic organisms, including various small fish species (Mendelsohn et al. 2004). Small fish species, such as topminnows, barbs, and small catfish, play a vital role in the floodplain ecosystem. They serve as a critical food source for larger predatory fish, birds, and other wildlife, and they also play a crucial role in nutrient cycling and energy transfer within the food web (Kingsford et al. 2016). Additionally, small fish species are often more sensitive to environmental changes and can serve as valuable indicators of ecosystem health (Hay et al. 1996, Welcomme 2008).

The Kavango River in Namibia hosts 84 species. Namibia's indigenous fish species are distributed across 17 families, with three families comprising over 63% of the known species (Merron and Hocutt 2025). The Cyprinidae, which includes labeos, yellowfishes, barbs, and topminnows, is the most diverse, represented by seven genera and 36 species. The Cichlidae, consisting of river bream, largemouth breams, and tilapia, includes 26 species (one of which is undescribed). The Mormyridae, known as snoutfishes, comprises 15 species, and 27 species of catfish across six families and nine genera. The remaining six families are represented by a

single species: Kneriidae, Hepsetidae, Austroglanididae, Claroteidae, Schilbeidae, and Nothobranchiidae (Merron and Hocutt 2025).

The Kamutjonga Floodplain, located along the Kavango River in northern Namibia, represent a vital freshwater ecosystem supporting diverse fish species. The Kamutjonga Floodplain play a crucial role in supporting local fisheries. These floodplains are highly productive ecosystems that provide essential services such as spawning, nursery, breeding, and feeding grounds for many freshwater fish species (Simasiku and Mafwila 2017). The dynamic interactions between terrestrial and aquatic habitats in these floodplains create a fertile environment that supports a diverse range of fish species (Muunda 2023). A study conducted in the floodplain at Kamutjonga Inland Fisheries Institute (KIFI) found that the Cichlidae, Poeciliidae and Alestidae dominated the fish catches, with species like *Oreochromis macrochir*, *O. andersonii*, *Tilapia sparrmanii*, *Lacustricola johnstoni* and *Brycinus lateralis* being particularly important (Simasiku et al. 2017). These floodplains are not only vital for subsistence fisheries but also serve as critical habitats for the overall health of the Kavango River fish communities (Kangausaru 2018). The seasonal flooding of the Kavango River enhances connectivity and nutrient transport, which in turn supports the growth and reproduction of fish populations (Simasiku et al. 2017). This natural flooding cycle is essential for maintaining the biodiversity and productivity of the river-floodplain system (Muunda 2023). Understanding the relative abundance and diversity of small fish populations within this system is paramount for effective conservation and management efforts. The diversity of small fish species in the Kamutjonga Floodplain underscores the ecological importance of preserving these habitats, which are facing challenges such as overfishing and habitat degradation that threaten fish populations. Therefore, sustainable management is critical to ensure the long-term health of fish communities and the livelihoods they support.

3.2. Materials and methods

3.2.1. Study area and sampling.

The study was conducted on the Kamutjonga Floodplain of the Kavango River using a throw trap net during the three hydrological phases of flooding. The throw trap net was deployed at eight sampling sites, with 15 replicates at each site (Figure 1). The throw trap net was deployed by two individuals starting at 9:00 AM. The trap net was cast approximately 5 meters into either vegetated or open water areas on the floodplain. Upon deployment, the heavy metallic component sank into the substrate, while the PVC float remained buoyant, effectively entrapping fish within the net. In areas with deeper water levels, the net was deployed from a non-motorized boat.

3.2.2. Data analyses

Index of relative importance (IRI)

An Index of Relative Importance (IRI) was used to evaluate catch composition. Pincas (1971) initially used the concept to determine food items by volume, frequency of occurrence, and number of organisms. In recent years, the IRI has been used in fisheries studies to describe the species composition of experimental gillnet catches by Hay et al. (2000), Hay et al. (2002), Næsje et al. (2004), Peel (2012), Hay et al. (2020) and Mosepele et al. (2022) on the Kavango, Kwando, Zambezi Rivers systems and Okavango Delta, Botswana.

An Index of Relative Importance (IRI) was used to determine the most abundant species in the throw trap net catches by number, weight, and frequency of occurrence and calculated as follows:

$$IRI = (\%N + \%W) \times \%FO$$

where $\%N$ and $\%W$ are the percentage contributions of each species by number and mass of each species in the total catch, and $\%FO$ is the percentage frequency of occurrence of each species in the total number of settings. The IRI was computed using *pasgear* (Kolding et al. 2011), which is a database system for analysing fisheries data using methods previously used by Mmopelwa et al. (2009); Peel (2012); Mosepele et al. (2017); Simasiku and Mafwila (2017); Kangausaru (2018); Hay et al. (2020); Muunda (2023) and Tiyeho (2023).

Species diversity, evenness and richness

The Shannon-Wiener diversity index (H') expressed species diversity to estimate the relative abundance of the individuals per species sampled in each effort across the three hydrological phases of flooding by sampling site. The Shannon-Wiener index (H') is a measure of the number of species weighted by their relative abundances and is expressed as:

$$H' = -\sum_{i=1}^{n} p_i \ln p_i$$

where $p_i = \frac{S_i}{N}$ is the proportion of individuals found in the i^{th} species, S_i is the total number of individuals of species *i* and N is the total number of all individuals in the sample.

Shannon's evenness index (J') indicates how evenly these species are distributed amongst the sampled areas throughout the three general hydrological flood phases. The index is an indication of how evenly spread species are in the sample, and is expressed as:

$$J' = \frac{H'}{\ln S}$$

where J' assumes a value between 0 and 1, with a value of 1 indicating that all the species are equally abundant in the area.

Species richness is the number of species found within a particular area.

The species diversity indices calculated from the throw-trap net data were computed using the *R* package *vegan* (Oksanen et al. 2020). Tools for diversity analysis, ordination techniques, and analysis of dissimilarities are all included in the *vegan* package. The *vegan* package's functions of diversity and evenness were used to calculate the Shannon-Wiener index and evenness, respectively (Catano et al. 2020; Oksanen et al. 2020; Yofukuji et al. 2021).

All data were tested for normality using the Shapiro-Wilk test before using a one-way ANOVA to test if mean species richness, Shannon diversity, H' and evenness, J', were different between the three hydrological phases of flooding.

Relative abundance (catch per unit effort)

The relative abundance of fish species i was expressed as catch per unit effort ($CPUE_i$), as follows:

$$CPUE_i = \frac{C_i}{E_i}$$

where C_i is the catch of the species i (in numbers or mass) and E_i is the effort expended to obtain the species i. $CPUE_i$ was standardised as the number of fish caught / area of sampled habitat (m^2) and the mass of fish (g) /area of sample habitat (m^2).

Catch per unit effort (CPUE) data of small fishes were first checked for normality using a Shapiro–Wilk test and for homogeneity of variance using Levene's test. The data were found not to be normally distributed as it had many zero catches. To account for the multitude of zero catches and to derive a more meaningful estimate of relative abundance, the data were transformed using an Δ-*X* distribution model **(**Fletcher et al. 2005**;** Ellender et al. 2010**).** In this

model, Δ is the probability of a non-zero observation occurring and is governed by a Binomial distribution. *X* refers to the statistical distribution of these non-zero observations (Fletcher et al. 2005; Ellender et al. 2010). The non-zero CPUE observations (*CPUEpos*) were assumed to be log-normally distributed, and the expected *CPUE* was calculated by scaling *CPUEpos* by the probability of capture (PC) in any throw-trap net sample. CPUE for any throw-trap net effort i, $CPUE_i$, was calculated using the delta-lognormal model of the form:

$$CPUE_i = PC_i \times \exp\left(\ln(\mathrm{CPUE}_{pos,i}) + \frac{\sigma^2}{2}\right)$$

where PC_i is the probability of capture in any throw-trap net sample *i*, $\ln(\mathrm{CPUE}_{pos,i})$ are the natural logarithm-transformed *CPUEpos* observations, and σ^2 is the variance of $\ln(\mathrm{CPUE}_{pos})$. Differences in CPUE between the three hydrological phases were then compared using a parametric one-way analysis of variance (ANOVA), and post-hoc differences were determined with a Tukey's HSD test at 95% confidence interval (p-value ≤0.05). Tukey's HSD test is a statistical test that can be used to determine whether there were significant differences between the means of CPUE between the three flooding phases.

Table 4. Throw trap net catch composition, Number (No.) of fish per species, percentage number (%N), weight (W), percentage weight (%W), frequency of occurrence (%FO) and the percentage index of relative importance (%IRI) of all species sampled throughout the three phases of flooding (rising, peak and receding) in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

Species	**No**	**% No**	**Weight (kg)**	**% Weight**	**FO**	**% FO**	**IRI**	**% IRI**
Enteromius bifrenatus	219	15.8	0.056	7.2	94	26.1	601	28.2
Enteromius poechii	182	13.1	0.020	2.6	66	18.3	287	13.5
Pseudocrenilabrus philander	125	9.0	0.065	8.5	54	15.0	262	12.3
Coptodon rendalli	114	8.2	0.039	5.1	41	11.4	152	7.1
Enteromius barnardi	97	7.0	0.019	2.4	57	15.8	149	7.0
Enteromius paludinosus	66	4.8	0.045	5.8	44	12.2	129	6.0
Lacustricola johnstoni	108	7.8	0.010	1.3	37	10.3	93	4.4
Pharyngochromis acuticeps	80	5.8	0.016	2.0	33	9.2	71	3.4
Clarias gariepinus	22	1.6	0.088	11.4	16	4.4	58	2.7
Marcusenius altisambesi	25	1.8	0.079	10.2	16	4.4	54	2.5
Schilbe intermedius	30	2.2	0.053	6.9	19	5.3	48	2.3
Enteromius radiatus	40	2.9	0.019	2.4	30	8.3	44	2.1
Enteromius fasciolatus	49	3.5	0.011	1.5	29	8.1	40	1.9
Oreochromis andersonii	23	1.7	0.079	10.3	12	3.3	40	1.9
Enteromius haasianus	51	3.7	0.005	0.7	24	6.7	29	1.4
Clarias ngamensis	14	1.0	0.050	6.5	11	3.1	23	1.1
Hippopotamyrus ansorgii	12	0.9	0.019	2.4	11	3.1	10	0.5
Nannocharax machadoi	21	1.5	0.003	0.4	15	4.2	8	0.4
Petrocephalus catostoma	12	0.9	0.021	2.7	8	2.2	8	0.4
Tilapia ruweti	14	1.0	0.016	2.1	7	1.9	6	0.3
Cichlidae	14	1.0	0.002	0.3	11	3.1	4	0.2
Enteromius sp.	12	0.9	0.002	0.2	7	1.9	2	0.1
Micralestes acutidens	8	0.6	0.004	0.5	7	1.9	2	0.1
Serranochromis angusticeps	5	0.4	0.011	1.4	4	1.1	2	0.1
Pollimyrus castelnaui	6	0.4	0.013	1.7	3	0.8	2	0.1
Tilapia sparrmanii	6	0.4	0.002	0.3	6	1.7	1	0.1
Synodontis spp.	2	0.1	0.010	1.3	2	0.6	1	0.0
Brycinus lateralis	3	0.2	0.004	0.6	3	0.8	1	0.0
Serranochromis macrocephalus	4	0.3	0.002	0.2	4	1.1	1	0.0
Enteromius afrovernayi	5	0.4	0.001	0.1	4	1.1	1	0.0
Sargochromis greenwoodi	5	0.4	0.001	0.1	4	1.1	1	0.0
Lacustricola katangae	4	0.3	0.001	0.1	4	1.1	0	0.0
Enteromius multilineatus	5	0.4	0.002	0.3	2	0.6	0	0.0
Enteromius thamalakanensis	3	0.2	0.001	0.1	2	0.6	0	0.0
Oreochromis macrochir	1	0.1	0.003	0.4	1	0.3	0	0.0
Enteromius unitaeniatus	1	0.1	0.000	0.1	1	0.3	0	0.0
Hydrocynus vittatus	1	0.1	0.000	0.0	1	0.3	0	0.0
Total	1389	100.0	0.771	100.0	-	-	2128	100.0

Multivariate analysis

To investigate relationships between fish families and environmental variables, Canonical Correspondence Analysis (CCA) was conducted using the *vegan* package in R (Oksanen et al. 2020). Fish family abundance data, collected via throw trap nets, were fourth-root transformed to reduce the influence of dominant taxa. Environmental variables were standardised to z-scores for scale comparability. The CCA was implemented as a constrained ordination and assessed associations between fish family abundances and environmental factors. Additionally, hierarchical clustering with complete linkage was applied to a Bray-Curtis resemblance matrix of family abundances and Euclidean distances of environmental variables to evaluate site similarity. A dendrogram visualised these relationships among sampling sites. All analyses used 999 permutations for robust statistical inference.

3.3. Results

3.3.1. Overall catch composition

The throw-trap net was deployed 360 times, equating to 120 times during the three general hydrological phases of rising, peak and receding flooding. A total of 1,389 individuals were collected during the survey, representing nine families and 35 species (Table 4). The five most abundant fish species, accounting for 68.1% of the Index of Relative Importance (IRI) when combined, were the Hyphen barb *E. bifrenatus* (28.2%), Dashtail barb *E. poechii* (13.5%), Southern mouthbrooder *P. philander* (12.3%), Redbreast tilapia *C. rendalli* (7.1%) and Blackback barb, *E. barnardi* (7%) (Table 4, Figure 7 and 8).

Figure 7. The three most abundant barb fish species (a) *Enteromius bifrenatus*, (b) *E. poechii,* and (c) *E. barnardi* caught in the throw-trap net catches in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

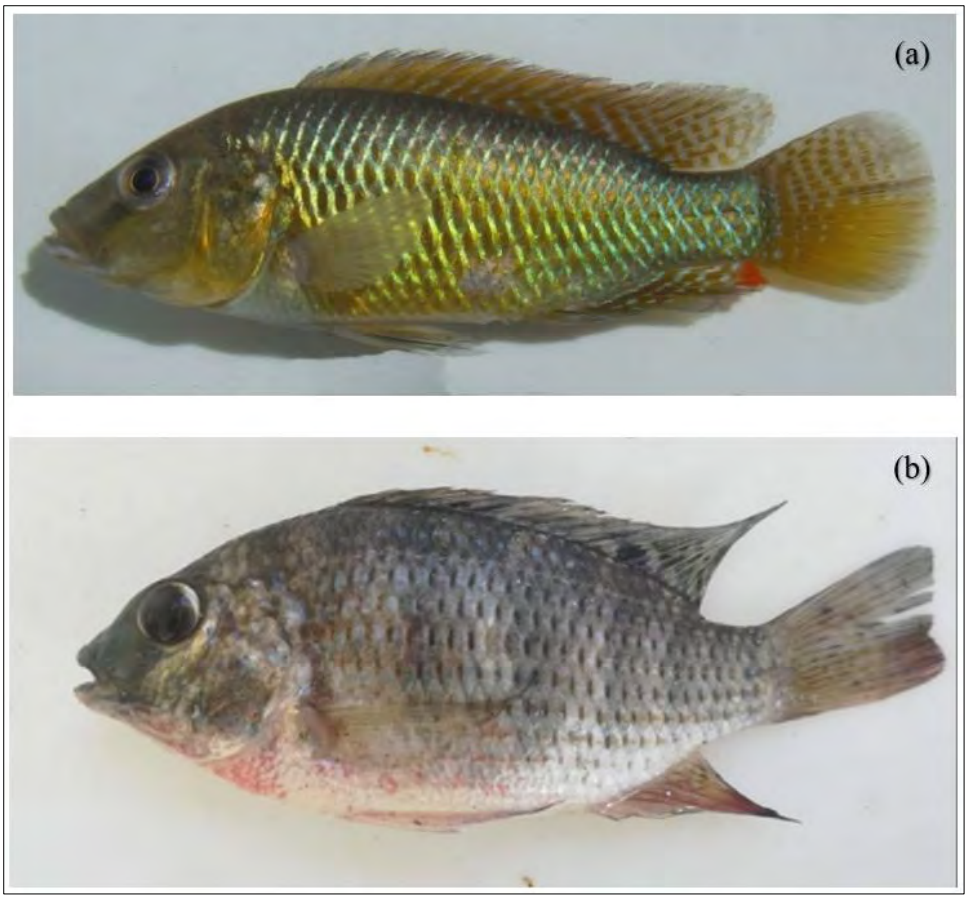

Figure 8. The two most abundant cichlid fish species, (a) *Pseudocrenilabrus philander* and (b) *Coptodon rendalli*, caught in the throw trap net in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

3.3.2. Catch composition by hydrological phases of flooding

From all eight sampling sites, 476 individual fish from eight families and 22 species were sampled during the rising flood phase. Dashtail barb, *E. poechii,* dominated the total catches by number (29.5%) and *O. andersonii* by weight (33.8%). The five most important species accounting for 83.2% of the IRI were *E. poechii* (43.9%), *E. bifrenatus* (15.7%), *O. andersonii* (9.1%), *C. rendalli* (8.1%) and *Clarias gariepinus* (6.4%) (Table 5 and Figure 9). The least common species were *Brycinus lateralis*, *E. fasciolatus*, *Hydrocynus vittatus* and *Hippopotamyrus ansorgii*, each represented by a single individual (Table 4).

A total of 361 individuals representing 28 species and nine families were sampled during the peak flooding phase. Hyphen barb, *E. bifrenatus,* dominated the catches in terms of number (22.7%) and weight (13.6%). The five most important species accounting for 79.9% of the IRI were *E. bifrenatus* (47.3%), *E. barnardi* (14.8%), *P. acuticeps* (7%), *Lacustricola johnstoni* (6.8%) and *E. paludinosus* (4%) (Table 5 and Figure 9). The least common species were *Serranochromis macrocephalus*, *Lacustricola katangae*, *E. unitaeniatus*, and *Sargochromis greenwoodi*, represented by at least two individuals (Table 2).

During the receding flood phase, we sampled 552 individuals, accounting for 27 species representing eight families. Southern mouthbrooder, *P. philander*, dominated the catches in number (16.7%) and weight (12.3%). The five most important species accounting for 69.3% of the IRI, were *P. philander* (30.7%), *C. rendalli* (12.6%), *E. bifrenatus* (12.4%), *E. fasciolatus* (7.4%) and *L. johnstoni* (6.2%) (Table 5 and Figure 9). The least common species were *O. macrochir*, *L. katangae*, *E. afrovernayi*, and *Micralestes acutidens*, each represented by at least two individuals (Table 4).

Table 5. Throw-trap net catch composition in percentage Number (%N), percentage Weight (%W), percentage Frequency of Occurrence (%FO) and percentage Index of Relative Importance (%IRI) of all fish species sampled through the three hydrological phases (rising, peak and receding) from Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

	Flood rising (n = 476) (February to March)				**Peak flood** (n = 361) (April to May)				**Receding flood** (n = 552) (June to July)			
Species	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI	%N	%W	%FO	%IRI
Alestidae	**0.4**	**0.3**	**0.6**	**0**	**2.5**	**2.8**	**2.2**	**0.6**	**0.2**	**0.1**	**0.3**	**0**
Brycinus lateralis	0.2	0.2	0.3	0	0.6	1.5	0.6	0.1				
Hydrocynus vittatus	0.2	0.1	0.3	0								
Micralestes acutidens					1.9	1.3	1.7	0.7	0.2	0.1	0.3	0
Cichlidae	**21.8**	**54**	**14.4**	**35.1**	**15**	**8.9**	**10.3**	**11.9**	**42.2**	**34.8**	**15.6**	**48.7**
Cichlidae	2.3	1	2.2	0.6	0.8	0.1	0.8	0.1				
Coptodon rendalli	9	7.2	5.8	8.1	0.8	0.4	0.6	0.1	12.3	7.5	5	12.6
Oreochromis andersonii	4.4	33.8	2.8	9.1					0.4	5.5	0.6	0.4
Oreochromis macrochir									0.2	1	0.3	0
Pharyngochromis acuticeps					7.2	2.7	5.6	7	9.8	2.6	3.6	5.7
Pseudocrenilabrus philander	3.6	6.7	3.3	2.9	4.4	4.7	3.3	3.9	16.7	12.3	8.3	30.6
Sargochromis greenwoodi	0.8	0.2	0.8	0.1	0.3	0.1	0.3	0				
Serranochromis angusticeps	0.6	4	0.8	0.3					0.4	1.1	0.3	0.1
Serranochromis macrocephalus	0.4	0.4	0.6	0	0.6	0.3	0.6	0.1				
Tilapia ruweti									2.5	4.8	1.9	1.8
Tilapia sparrmanii	0.6	0.6	0.8	0.1	0.8	0.4	0.8	0.1				
Clariidae	**6.3**	**23.7**	**6.1**	**5.9**	**0.8**	**16.5**	**0.6**	**0.5**	**0.5**	**15.9**	**0.8**	**0.6**
Clarias gariepinus	4	15.3	3.9	6.4	0.6	12	0.3	0.4	0.2	9	0.3	0.3
Clarias ngamensis	2.3	8.4	2.2	2	0.3	4.5	0.3	0.2	0.4	6.9	0.6	0.5
Cyprinidae	**64.9**	**15.6**	**22.5**	**58.1**	**55.7**	**30.2**	**18.9**	**78.9**	**39.9**	**22.1**	**18.1**	**45.5**
Enteromius afrovernayi					0.8	0.2	0.6	0.1	0.4	0.1	0.6	0
Enteromius barnardi	7.4	1.4	5.3	3.9	11.6	4.5	7.2	14.8	3.6	1.4	3.3	2.1
Enteromius bifrenatus	19.5	3.3	8.1	15.7	22.7	13.6	10.3	47.3	8	4.5	7.8	12.3
Enteromius fasciolatus	0.2	0.2	0.3	0	2.2	0.8	1.9	0.7	7.2	2.7	5.8	7.3
Enteromius haasianus					7.5	1.1	3.6	3.9	4.3	0.7	3.1	2
Enteromius multilineatus									0.9	0.7	0.6	0.1
Enteromius paludinosus	5.5	2.2	5.3	3.5	4.2	6.1	3.1	4	4.5	7.4	3.9	5.9
Enteromius poechii	29.4	6.9	14.2	43.9	1.4	0.3	1.1	0.2	6.7	2	3.1	3.4
Enteromius radiatus	2.3	1.5	2.8	0.9	4.2	3.2	2.5	2.3	2.5	2.3	3.1	1.9
Enteromius sp.	0.6	0.1	0.6	0	0.8	0.3	0.8	0.1	1.1	0.2	0.6	0.1
Enteromius thamalakanensis									0.5	0.2	0.6	0.1
Enteromius unitaeniatus					0.3	0.2	0.3	0				
Distichodontidae	**0.4**	**0.1**	**0.6**	**0**	**1.9**	**0.4**	**1.7**	**0.2**	**2.2**	**0.7**	**1.9**	**0.2**
Nannocharax machadoi	0.4	0.1	0.6	0	1.9	0.4	1.7	0.5	2.2	0.7	1.9	0.7
Mochokidae					**0.6**	**3.8**	**0.6**	**0.1**				
Synodontis spp.					0.6	3.8	0.6	0.3				
Mormyridae	**3.2**	**4.9**	**2.5**	**0.6**	**5.8**	**24.9**	**2.5**	**3.7**	**3.4**	**17.6**	**2.2**	**1.9**
Hippopotamyrus ansorgii	0.2	0.1	0.3	0	1.4	3.5	1.4	0.9	1.1	2.9	1.4	0.7
Marcusenius altisambesi	2.9	4.9	2.5	1.7	1.1	12.6	0.6	1	1.3	11.3	1.4	2.2
Petrocephalus catostoma					1.7	3.7	1.4	1	1.1	3.4	0.8	0.5
Pollimyrus castelnaui					1.7	5.1	0.8	0.7				
Poeciliidae	**1.5**	**0.8**	**1.9**	**0.1**	**13.9**	**1.6**	**4.2**	**3.1**	**10**	**1.6**	**5**	**2.3**
Lacustricola johnstoni	1.5	0.8	1.9	0.4	13.3	1.5	3.6	6.8	9.6	1.4	4.7	6.6
Lacustricola katangae					0.6	0.1	0.6	0	0.4	0.2	0.6	0
Schilbeidae	**1.5**	**0.6**	**1.9**	**0.1**	**3.9**	**11**	**1.4**	**1**	**1.6**	**7.2**	**1.9**	**0.7**
Schilbe intermedius	1.5	0.6	1.9	0.3	3.9	11	1.4	2.6	1.6	7.2	1.9	2.2
Species richness	22				28				27			
Evenness	0.79				0.78				0.79			
Diversity	1.76				1.79				1.81			

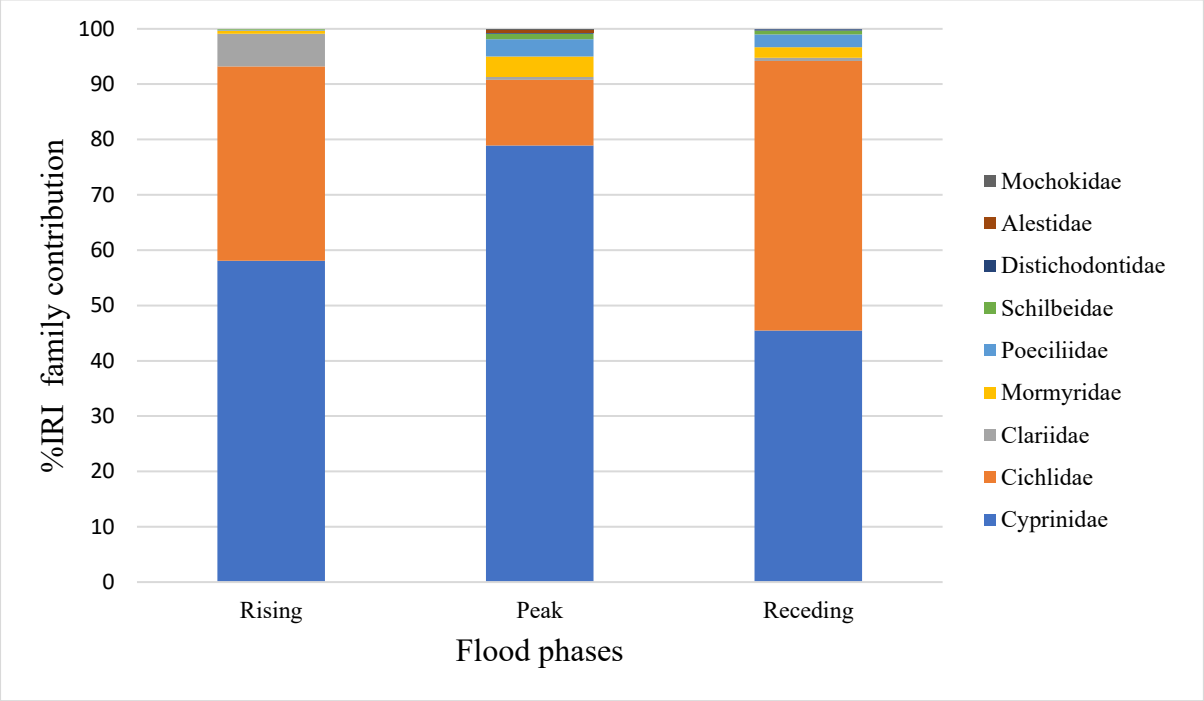

Figure 9. Percentage Index of Relative Importance (%IRI) family contribution by flood phases of all fish caught in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

3.3.3. Catch composition by sampling sites 1 - 8

The abundance and catch composition of fish varied among the eight sampling sites. Sites 1 - 4, 6, and 8 were primarily dominated by the Cyprinidae, whereas sites 5 and 7 exhibited a higher prevalence of the Cichlidae. Notably, at site 7, cichlids accounted for a remarkable 92.7% of the total catch (Figure 10).

During the rising phase, it was observed that sites 2, 3, and 4 were dominated by cyprinids, with a dominance exceeding 90% IRI. On the other hand, site 7 exhibited a clear dominance of cichlids. Interestingly, sites 6 and 8 displayed a more even distribution of fish families,

indicating a balanced presence of different species. These findings highlight the varying dominance patterns of cyprinids and cichlids across the different sampling sites during the rising period (Figure 11).

During the peak period, there was a clear domination of cyprinids from site 1 to site 4 exceeding 80% IRI. It is noteworthy that site 4 showcased complete dominance by cyprinids. On the other hand, the remaining sites exhibited an equivalent representation of various fish families, indicating a more balanced species distribution. These findings emphasize the significant influence of cyprinids during the peak period, particularly at site 4, while highlighting the more diverse composition observed at the other sites (Figure 11).

During the receding phase, it was observed that, apart from sites 2 and 7, where the cichlids predominated, the cyprinids exhibited greater prevalence compared to other fish families. It is interesting to note that, similar to the rising phase, site 7 was entirely dominated by cichlids. However, the most diverse and evenly distributed variety of fish families was found at site 8 (Figure 11). These findings highlight the dynamic changes in fish composition during the receding phase, with cyprinids showing overall prevalence and site 8 showcasing maximum diversity among the sampled sites.

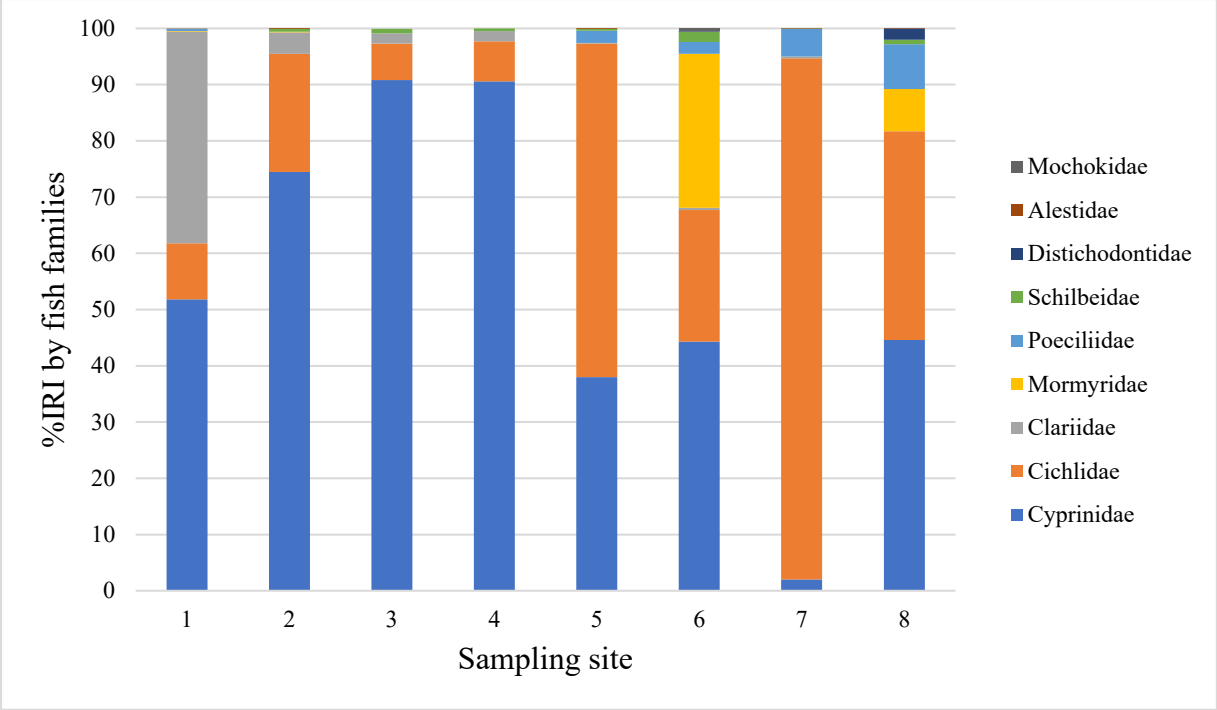

Figure 10. The overall percentage Index of Relative Importance (%IRI) by fish families at sampling sites (1-8), all fish caught in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

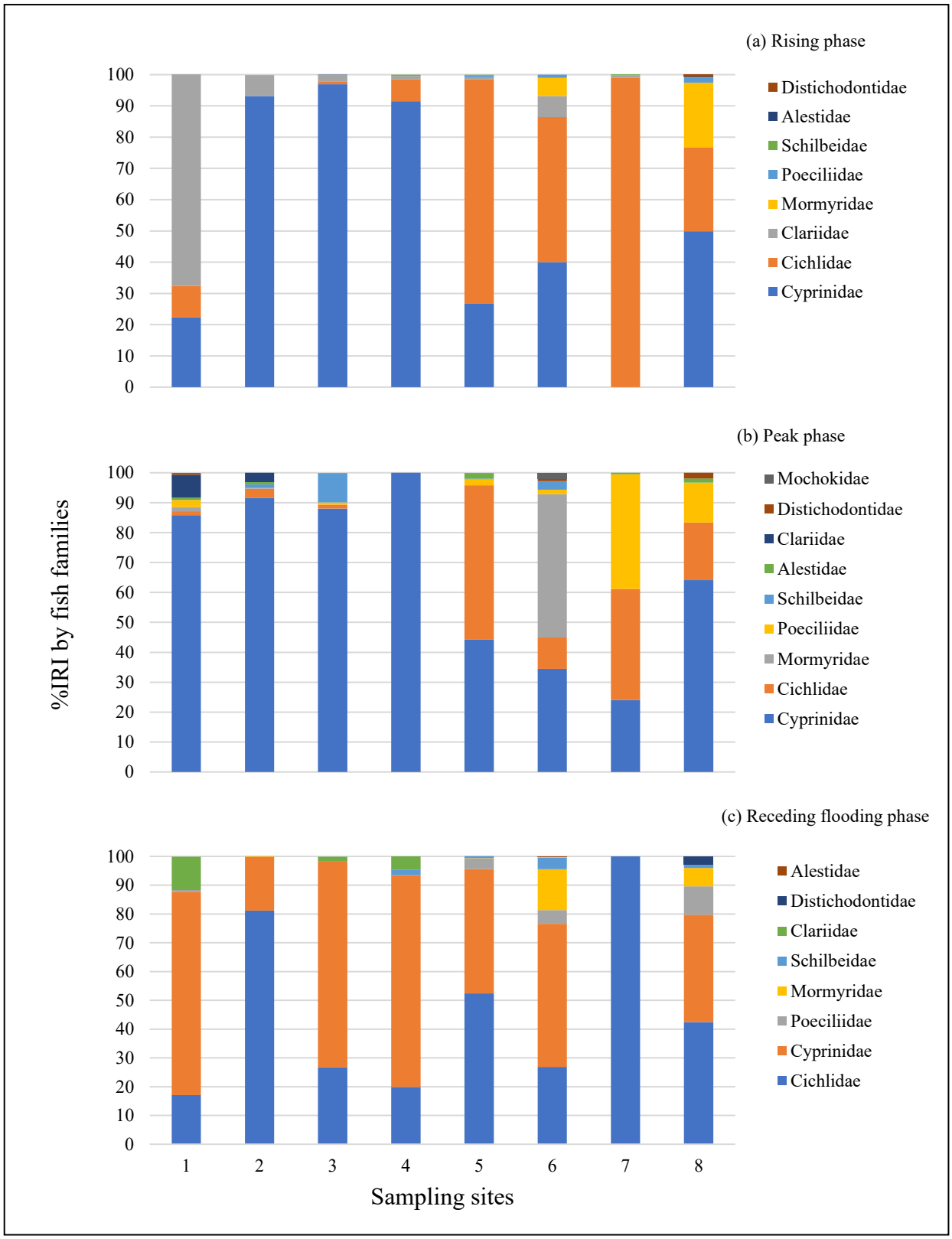

Figure 11. Percentage Index of Relative Importance (%IRI) by the fish family for sampling sites 1 - 8 of all fish caught according to flood phases in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

3.3.4. Species richness and diversity by hydrological phases of flooding

Species richness (number of species)

The total species richness throughout the different flood phases and sites was 35. Species richness was similar between the peak (n = 28) and receding phases (n = 27), with the lowest species richness recorded in the rising phase (n = 22). The Cyprinidae was the most species-rich family, representing 7, 10 and 11 species at the rising, peak, and receding phases. No statistically significant differences in species richness existed between the three phases ($F_{2,21}$= 0.12, P = 0.89) (Figure 12).

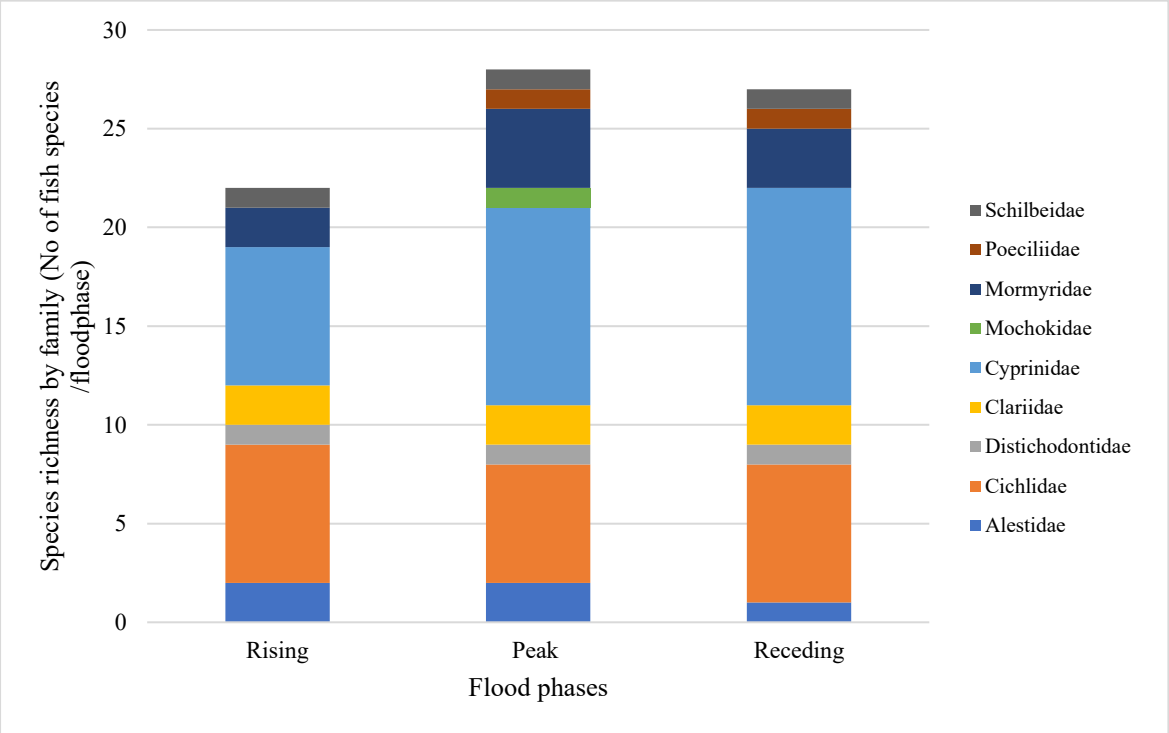

Figure 12. Species richness by family in the throw-trap net catches according to flood phases in the Kamutjonga Floodplain, Kavango River, Namibia, sampled between March and June 2018.

Species diversity

Species diversity (*H'*) was the highest at the receding phase (1.81 ± 0.23), with comparable values at the peak phase (1.79 ± 0.19) and lowest at the rising phase (1.76 ± 0.15). There were no statistically significant differences in species diversity between the three phases ($F_{2,21}$ = 0.01, P = 0.97) (Table 6).

Species evenness

Species evenness (*J'*) was the highest at receding (0.79 ± 0.05), followed by rising (0.79 ± 0.04) and peak (0.78 ± 0.04). As with diversity, there were no significant differences ($F_{2,21}$ = 0.02, P = 0.98) in the evenness between the three phases (Table 6).

Table 6. Species diversity by Shannon-Wiener diversity (*H'*) and evenness (*J'*) diversity indices for throw-trap net sampling in the Kamutjonga Floodplain, Kavango River, Namibia, between March and June 2018.

Indices	Rising	Peak	Receding
H’	2.27	2.65	2.70
J’	0.79	0.78	0.79

3.3.5. Species Richness and diversity by sampling site and flood phases

Species richness (number of species)

Sites 5 and 8 were equally the most species-rich sites during the rising (n=14) and receding (n=17) flood phases. However, site 6 was the species-rich area at the peak period (n=20). Moreover, Site 7 at receding had the least species (n=3). There were statistically significant

differences in species richness between the eight sites and the three hydrological phases of flooding ($F_{8,23}$ = 5.713, P = 0.002) (Table 7).

Species diversity

Site 7 displayed the lowest species diversity throughout the three flooding phases. The most diverse areas at different flood phases were as follows: Site 5 (H' = 2.38) at rising, site 6 (H' = 2.42) at peak and Site 8 (H' = 2.19) at receding. There were statistically significant differences in species richness between the eight sites and the three hydrological phases of flooding ($F_{8,23}$ = 5.7, P = 0.002) (Table 7).

Species evenness

The greatest unevenness in the fish distribution was observed at site 7 throughout the phases. During the rising and receding phases, site 7 showed dominance of over 95% by the Cichlidae. Whereas site 1, had the most evenly distributed species. There were statistically significant differences in species richness between the eight sites and the three hydrological phases of flooding ($F_{8,23}$ = 10.55, P < 0.001) (Table 7).

Table 7. Species richness (number of species), diversity and evenness at sites 1 – 8, throughout the three hydrological phases of flooding of all fish caught from the Kamutjonga Floodplain, Kavango River, Namibia.

Indices / Site	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Species Richness								
Rising	10	7	10	9	14	12	8	14
Peak	10	10	8	6	13	20	9	14
Receding	11	9	10	11	17	13	3	17
Species diversity (*H'*)								
Rising	2.09	1.48	1.82	1.79	2.38	1.58	1.08	1.78
Peak	2.14	2.10	1.51	1.23	1.96	2.42	1.11	1.65
Receding	2.09	1.83	1.76	1.73	2.16	1.81	0.31	2.19
Evenness (*J'*)								
Rising	0.91	0.76	0.79	0.67	0.68	0.63	0.52	0.67
Peak	0.93	0.91	0.72	0.68	0.76	0.81	0.51	0.63
Receding	0.87	0.84	0.76	0.72	0.76	0.70	0.28	0.77

3.3.6. Relative abundance - Catch per unit effort (CPUE)

CPUE by number

The CPUE by number was not significantly different between the three hydrological flood phases ($F_{2,268}$ = 1.48, P = 0.23) at all the sites (1 – 8). CPUE was highest during the rising phase (3.8 fish/m^2) compared to the receding phase (3.3 fish/m^2) and peak phases (3.1 fish/m^2). The corrected CPUE was calculated using the Δ-X model (Figure 13 and 14). There was a great number of zero catches, equating to about 25% of catches within the three phases of flooding as depicted in figure 13 (a).

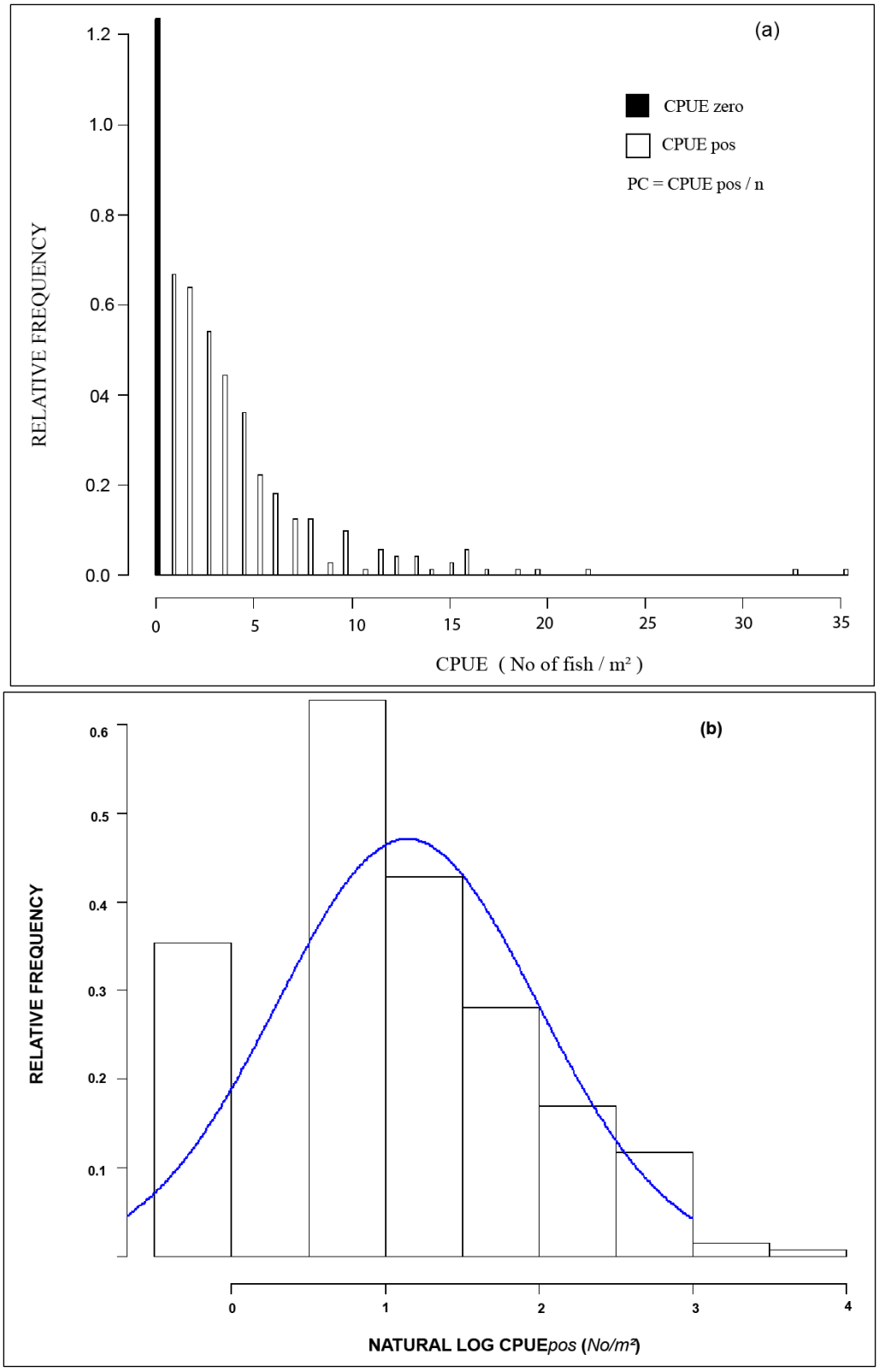

Figure 13. (a) Observed frequency distribution of CPUE by number and (b) log-normal distribution of $CPUE_{pos}$ (CPUE excluding zero catches) in the Kamutjonga Floodplain, Kavango River, Namibia, sampled between March and June 2018.

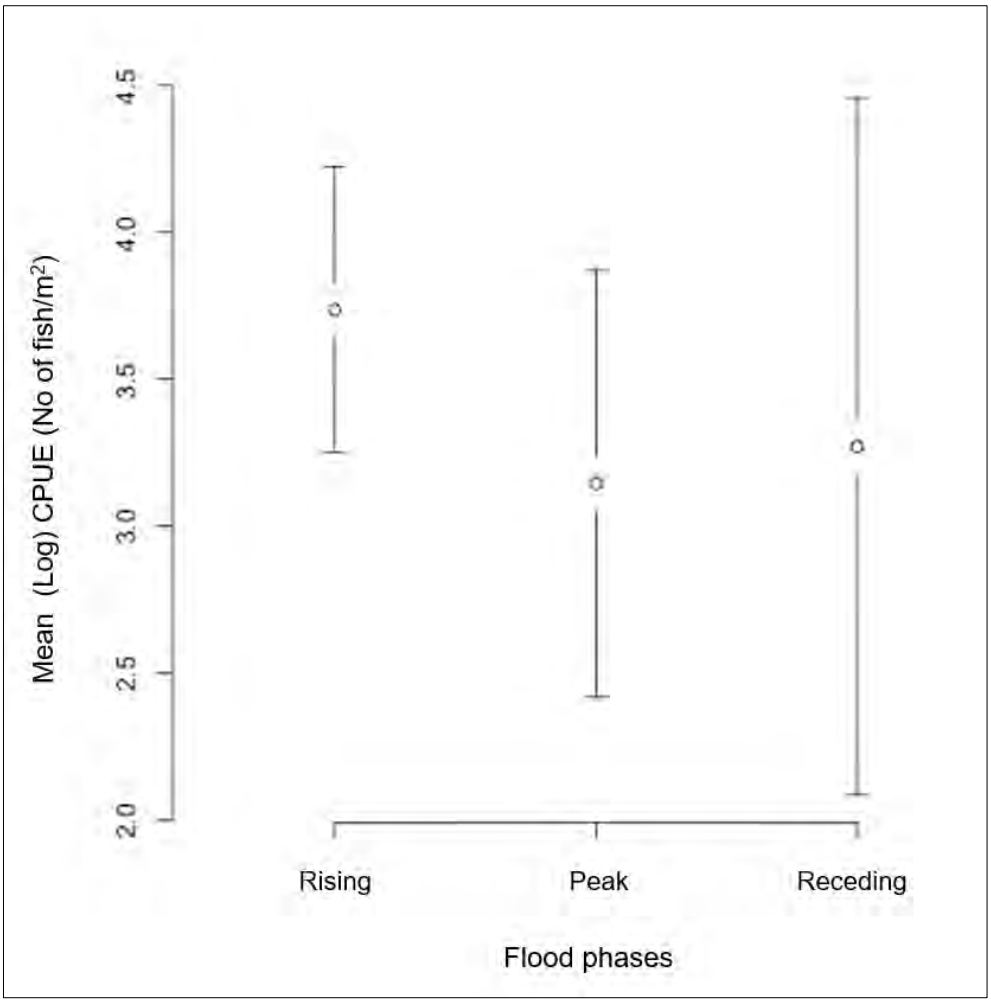

Figure 14. Mean (Log) CPUE at 95% confidence intervals for the number of fish caught per m^2 during the three flood phases from Kamutjonga Floodplain, Kavango River, Namibia, sampled between March and June 2018.

CPUE by mass (weight)

CPUE by weight was the highest during the receding phases (2.9 g/m^2), followed by the rising phase (2.6 g/m^2), and the peak (2.5 g/m^2). CPUE by weight was not significantly different ($F_{2,21} = 0.02$, $P < 0.01$) between the flood phases at all sites (1 – 8). The corrected CPUE was calculated using the Δ-X model (Figure 15 and 16).

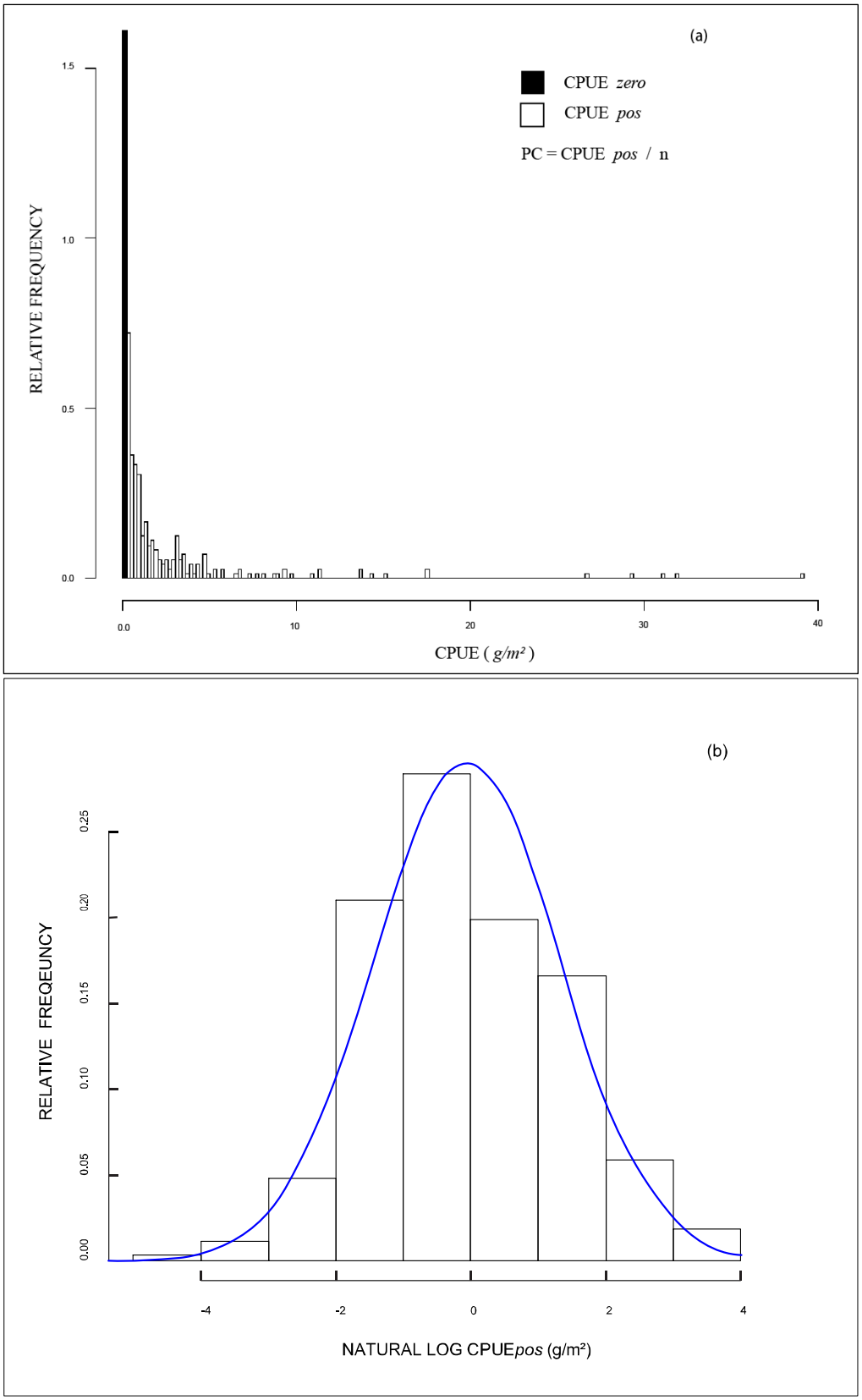

Figure 15. (a) Observed frequency distribution of CPUE by weight in grams and (b) log-normal distribution of $CPUE_{pos}$ (CPUE excluding zero catches) in the Kamutjonga Floodplain, Kavango River, Namibia, sampled between March and June 2018.

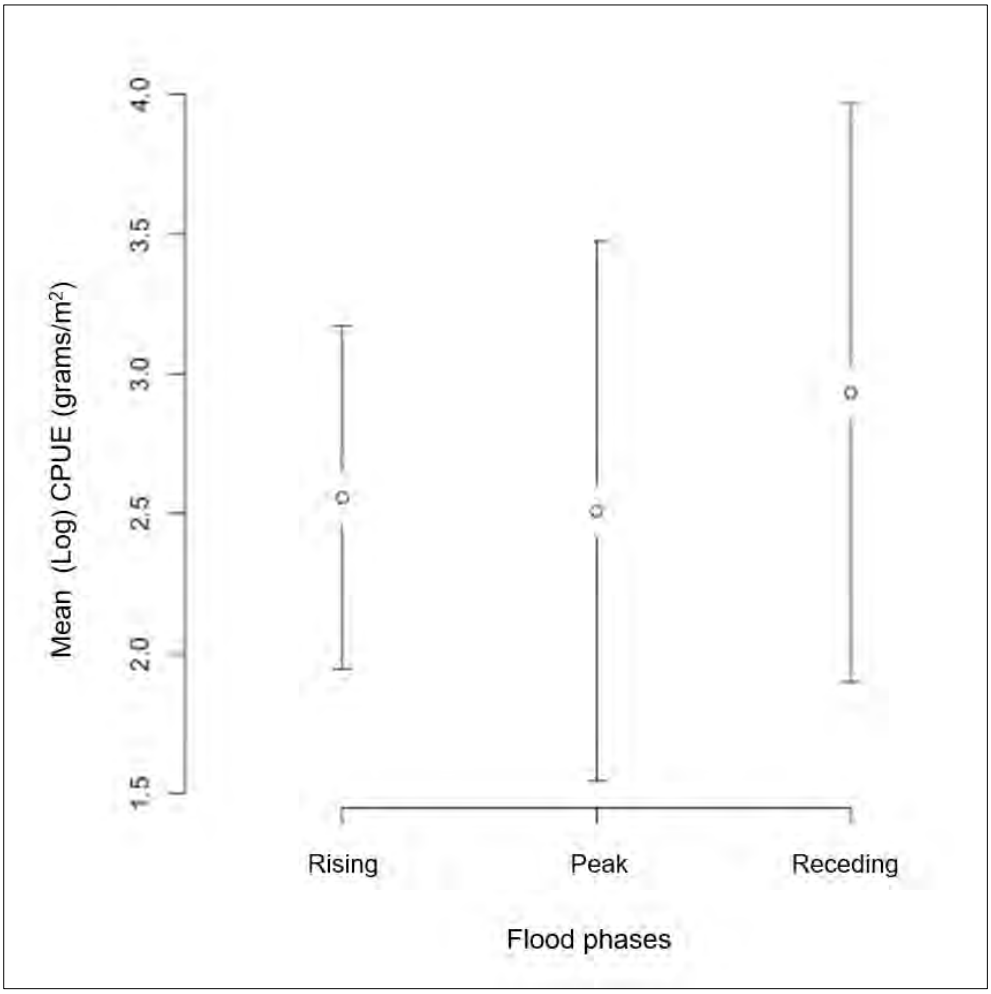

Figure 16. Mean (Log) CPUE at 95% confidence intervals for the weight of fish caught per m^2 during the three flood phases from Kamutjonga Floodplain, Kavango River, Namibia, sampled between March and June 2018.

Multivariate analysis results / Community and environmental patterns

The Canonical Correspondence Analysis (CCA) biplot (Figure 17) visualises the relationships between fish family abundances (e.g., Cyprinidae, Cichlidae) and environmental variables (e.g.,vegetation cover, conductivity) across eight sites (S1–S8) on the Kamutjonga Floodplain. The first axis (CCA1) explains the primary gradient, likely reflecting a connectivity-vegetation continuum, with positive values associated with high vegetation cover and negative values with

water discharge and sample volume (indicating deeper, more connected areas). The second axis (CCA2) captures a temperature-clarity gradient, with positive values linked to warmer, clearer water and negative values to vegetation cover.

Significant results from the permutation test ($p < 0.05$ for all axes) confirm that environmental variables explain variation in fish communities beyond random chance. Sites like S6 and S5, positioned toward positive CCA1, align with high vegetation cover, correlating with elevated species richness (e.g., 20 species at S6 during peak phase, Table 7) and abundance of vegetation-associated families like Cichlidae (e.g., *C. rendalli*). Conversely, S7, near high conductivity and positive CCA2, shows low diversity ($H' = 0.31$, $J' = 0.28$ during receding phase), suggesting stress from isolation and drying, consistent with reduced horizontal connectivity (Figure 17).

Environmental arrows (e.g., Vegetation cover, longest arrow) indicate strong influences, with angles suggesting co-variation (e.g., vegetation with transparency) or opposition (e.g., conductivity with discharge). Fish families like the Mochokidae and Mormyridae cluster near vegetation, reflecting habitat preference, while the Cyprinidae align with discharge, indicating riverine affinity. This supports findings by Siziba et al. (2011) on habitat structure driving cichlid abundance in the Okavango Delta, adaptable to this floodplain context.

The dendrogram based on fish family abundances reveals distinct clustering between sites in the communal area (S1–S4) and the protected area (S5–S8). Similarly, species diversity and evenness varied between these areas, with greater diversity observed in the protected area. In contrast, the environmental dendrogram, constructed using Euclidean distances, paired most

sampling sites at a distance of 6, with the exception of site 7, which was characterised by highly variable environmental conditions (Figure 18).

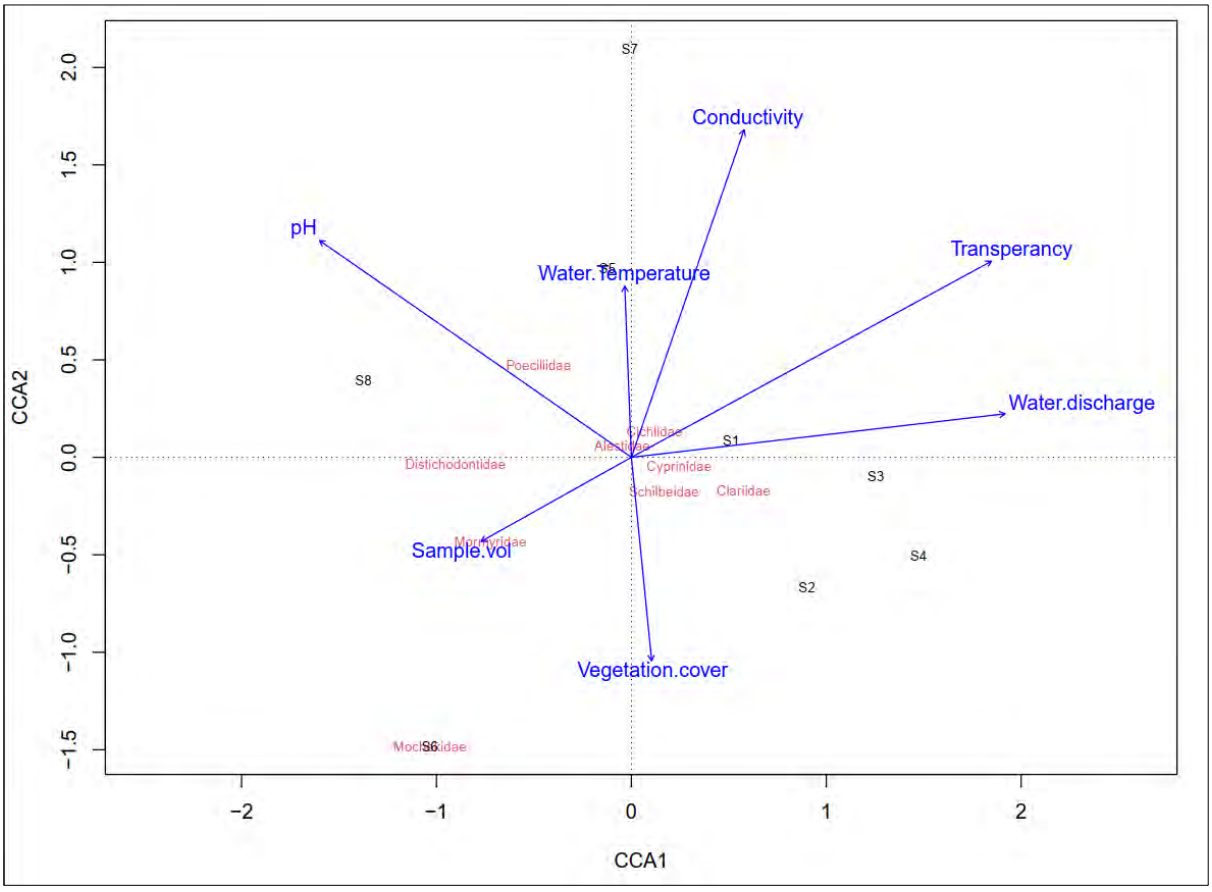

Figure 17. Canonical Correspondence Analysis ordination of fish family abundances constrained by environmental variables.

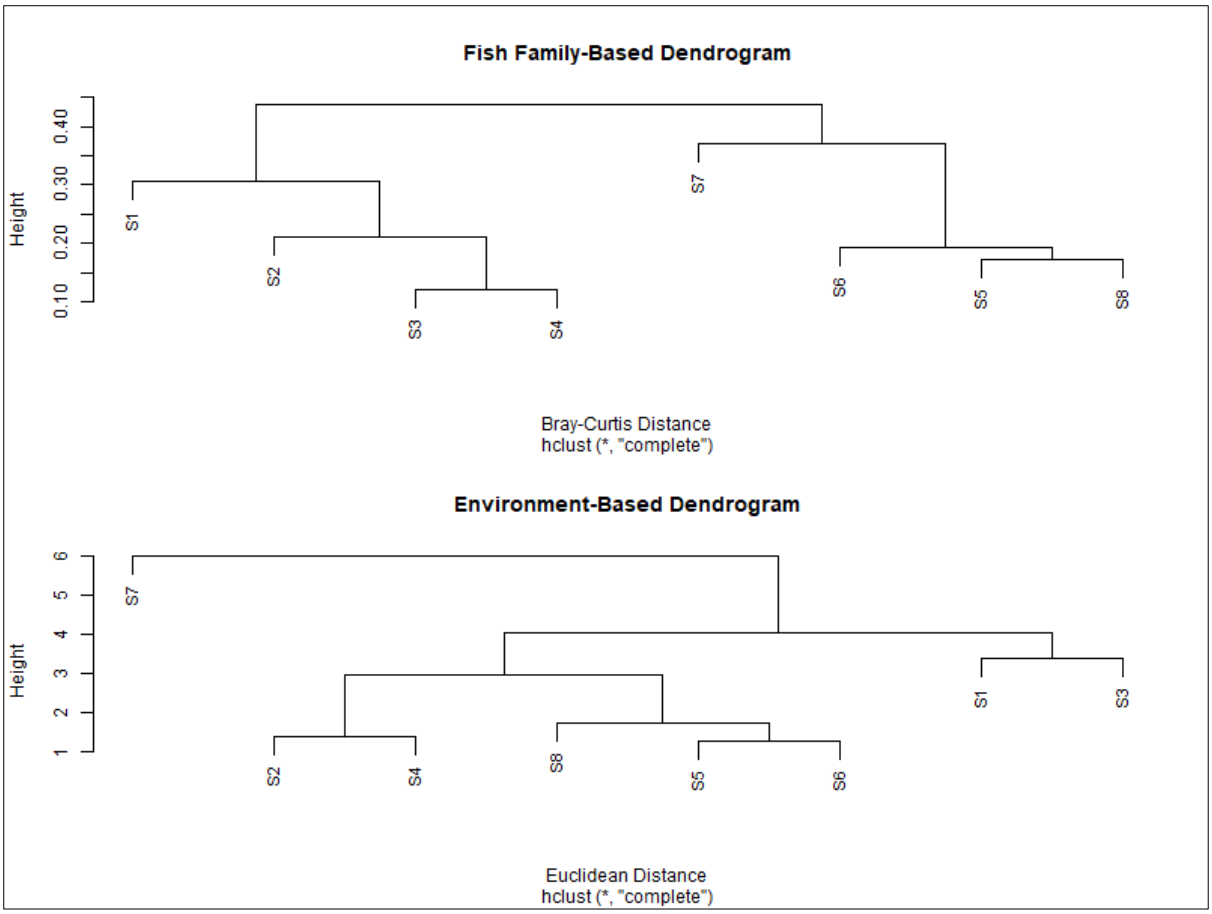

Figure 18. Dendrogram of site similarity based on family abundances and environmental variables.

3.4. Discussion

During the annual inundation of the Kamutjonga Floodplain, a temporary subsistence fishery emerges and plays a vital role in riparian community income, employment, food security, and poverty alleviation efforts (Kolding et al. 2016; Barrett et al. 2018). Various species inhabit and utilise the inundated floodplain areas. Amongst them are the juvenile cichlids and barbs of the genus *Enteromius,* which are widely harvested by the local communities using various gears. The number of fish families sampled underlines the importance of floodplain connectivity for juvenile fishes, who can use it for recruitment and nursery purposes.

3.4.1. Catch composition

The overall catch composition observed across the annual flood season highlights a consistent dominance of cyprinids and cichlids. This pattern raises important questions about their ecological roles and influence on fish community dynamics throughout the flood cycle. Notably, cyprinids appeared to dominate during the rising and peak phases of the flood, with *E. poechii* and *E. bifrenatus* being the most represented species, respectively. This dominance during these phases suggests that cyprinids are particularly well-adapted to the conditions and resources available during these periods. In contrast, the receding phase saw a shift, with cichlids becoming more prominent in the catches, driven largely by the dominance of *P. philander*. This temporal shift in species composition suggests differing ecological strategies and adaptations between these families, which may be linked to changes in water levels, habitat availability, and food resources during the flood cycle. The cichlids breed early in the flood cycle, move as very small fish onto the filling floodplain and then dominate the community with the drawdown phase.

The findings align with previous studies conducted by Siziba et al. (2011), Simasiku (2014), Kangausaru (2018), Mosepele et al. (2022), Muunda (2023) and Tiyeho (2023), all of whom reported similar dominance of the Cyprinidae, Cichlidae, and, in some cases, Poeciliidae. These consistent patterns across various studies reinforce the importance of these families within floodplain systems and their potential as indicators of ecological conditions. Future research could explore how environmental factors, such as hydrology and habitat structure, interact with these families' life histories to influence their dominance during different flood phases.

The dominance of cichlids in catches can be attributed to their representation of both *r*-selected and *K*-selected life history strategies (Hocutt and Johnson 2001). In addition, cichlids use a diversity of habitats and environmental conditions and primarily feed on detritus (Merron 1991**;** Winemiller and Kelso-Winemiller 2003). These differences can be ascribed to seasonal fluctuations in the abundance and diversity of floodplain fish communities, which may be influenced by intensified fishing activities (Miethe et al. 2010).

3.4.2. Catch composition according to sampling sites

Fish abundance and catch composition exhibited variations among the eight sampling sites. Four of the eight sampling sites were located within a designated conservation area where fishing activities were strictly prohibited. On the other hand, the remaining four sites were situated closer to inhabited areas with higher fishing pressures. These sites experienced higher levels of fishing activity due to their proximity to human settlements, potentially impacting the fish population and catch composition in those areas. The overall observation indicates that cyprinids dominated in the four sites outside the protected area, whereas cichlids dominated in the protected sites. This difference in dominance could be attributed to variations in the sampling sites, particularly the habitats. The areas outside the park are exposed to fishing

pressure, while the fish within the park are undisturbed by anthropogenic activities. The areas outside the park were located near human settlements and infrastructure, including bridges used for fishing and various other activities. However, despite being located within a protected area during the rising and peak periods, site 7 was predominantly dominated by cichlids, with no significant differences in species diversity observed in the flooding phases. This could be attributed to the shallow water levels with high pH and turbidity and the area frequently utilised by wildlife and aquatic birds. These factors contribute to disturbances in the area, making it a less favourable environment for maintaining species diversity among fish populations.

3.4.3. Species richness and diversity

In this study, 35 species were observed across the three general flooding phases. Tiyeho (2023) conducted a study on the Kamutjonga Floodplain, analysing the catches of local fishers using various fishing gear. The research identified 23 fish species in 2020 (Tiyeho 2023). This finding is consistent with other research conducted in similar areas and on the Kavango River. For instance, Kangausaru (2018) reported a similar species distribution trend, recording 34 fish species in the Kamutjonga Floodplain through fisher catches and seine netting during the 2017 annual flood. Similarly, a study by Simasiku (2014) in the Kavango River floodplains, specifically in the Kamutjonga area, employed seine nets and multigear sampling techniques and sampled 24 species.

3.4.4. Species richness and diversity during the flooding phases

During the rising phase (February to March)

We observed 22 species during the rising phase, dominant at sites 5 and 8. There was lower horizontal connectivity between the river and the adjacent floodplain area. Hence, lower diversity and evenness were observed. There was an increased abundance of the herbivorous

C. rendalli in the littoral zones during the rising and receding phases, and this could be attributed to the higher percentage of vegetation cover observed. Siziba et al. 2011, observed that the abundance of woody debris and high chlorophyll might have attracted an abundance of cichlids in the rarely flooded floodplain areas in the Okavango Delta. According to Lowe-McConnell (1958), tilapiines have a diverse diet that includes algae, macrophytes, zooplankton, and detritus. Winemiller and Kelso-Winemiller (2003) found that algae and detritus were present throughout the entire sampling period during the long drawdown period, and they would not be a limiting factor on fish abundances. However, the nutritional value of the various algae and detritus is different. In contrast, the *r*-selected small cyprinids (i.e., *E. poechii and E. bifrenatus)*, which use the floodplain for reproduction and as a nursery area, tend to synchronise their breeding relatively with the onset of flood and growth of littoral zones plants **(**Hocutt and Johnson 2001). Hocutt and Johnson (2001) found that the number of cyprinids, primarily represented by *E. poechii*, *E. paludinosus*, and *E. radiatus*, increased with the onset of flooding in February, reaching peak abundance around May, June, and September. With the onset and progression of floods, there is a breakdown of allochthonous material, which increases primary production and can support the growth and abundance of fish. Similarly, the *K*-selected species, such as the herbivores (i.e. *C. rendalli*) and piscivores (*Serranochromis* spp. and tigerfish), tend to breed in the advent of the flood during the low flow month of November, reaching juvenile size by February **(**Hocutt and Johnson 2001). Hence, they tend to be more abundant during the rising phase, declining as the flood advances. Similar to our results, juvenile cichlids were most dominant in the catches in February and May, using the area for nursing and spawning **(**Bell-Cross et al. 1988**).**

Peak phase (April to May)

At the peak phase, the inundated floodplain is at its widest, encompassing varying habitats and nutrients from the breakdown of macrophytes. We observed 28 species, which were most dominant at sites 6 and 8. However, we observed a lower probability of capture at the peak flooding phase and deeper water levels due to the increased sampling area for the throw trap net. During this study, higher diversity and richness were observed at the peak flooding phase, which concurs with observations by Hocutt and Johnson (2001**)** during the peak flow months (February to May) when seine net sampling in the Kavango River floodplains. However, the omnivores (i.e., *B. lateralis, C. gariepinus and S. intermedius*) and piscivores (i.e., *H. vittatus* and *S. macrocephalus*) had a declining representation throughout the phases. These fish feed on a wide range of available prey.

Receding / drawdown phase (June to July)

Higher diversity and evenness were observed during the drawdown compared to the preceding phases. This could be attributed to the lower water levels and concentration of fish as the flood recedes. Notably, site 7 had the least evenness and diversity, dominated mainly by the cichlid family. The sites within the protected area showed the highest species richness and diversity, especially at sites 5 and 8 (Figure 12).

Overall, the species diversity differed among the three hydrological phases of flooding and sites due to the differences in the habitat and the water levels. This could be attributed to the different life-history strategies of the resident species, varying residency times and use of the floodplain littoral zone.

3.4.5. Relative abundance (Catch per unit effort)

Catch per unit effort by number was similar amongst the three hydrological phases. Mean CPUE by number was slightly higher at the rising and receding phases than at the peak. The lower abundance at the peak could be attributed to the higher water level and area for fish refuge amongst the macrophytes and increased habitat complexity provided by the extended floodplain area. Catch per unit effort by weight was different amongst the three hydrological phases. The fish exhibited a higher overall body weight during the receding phase. This observation indicates that they utilise the floodplain for their growth, likely breeding or entering the system as juveniles and benefiting from the enriched nutrients derived from macrophytes, detritus, and other fish (Purvis 2002).

3.4.6. Multivariate analysis

The Canonical Correspondence Analysis (CCA) biplot revealed significant environmental drivers shaping fish community structure across the Kamutjonga Floodplain, Kavango River, Namibia, with the first axis (CCA1) delineating a connectivity-vegetation gradient and the second axis (CCA2) reflecting a temperature-clarity gradient. The statistical significance of all CCA axes ($p < 0.05$ from permutation tests) underscores that environmental variables explain substantial variation in fish family abundances, validating the hypothesis that habitat heterogeneity influences community composition in this floodplain system. This finding aligns with the dynamic nature of floodplain ecosystems, where seasonal flooding and drying phases create distinct ecological niches (Junk et al. 1989).

The positive association of CCA1 with vegetation cover, evident in sites S5 and S6, highlights the critical role of littoral habitat structure in supporting diverse fish communities. These sites, characterised by elevated species richness (e.g., 20 species at S6 during the peak phase, Table

7), host families such as Cichlidae (e.g., *C. rendalli*), Mochokidae, and Mormyridae, which cluster near vegetation in the biplot. This pattern suggests that dense vegetation provides refuge, spawning grounds, and foraging opportunities, particularly for herbivorous and bottom-feeding species, consistent with observations of increased *C. rendalli* abundance in vegetated zones during rising and receding phases (Siziba et al. 2011). The co-variation of vegetation cover with transparency further supports this, as clearer water in vegetated areas may enhance visibility for visual predators like Mormyridae, reinforcing habitat quality as a diversity driver.

In contrast, the negative end of CCA1, associated with water discharge and sample volume, indicates a preference for deeper, more connected habitats, as exemplified by the Cyprinidae's alignment with these variables. This riverine affinity suggests that cyprinids thrive in areas with higher water flow, likely during the rising phase when floodplain connectivity peaks, facilitating dispersal and resource access. The opposition between vegetation cover and discharge in the biplot reflects a trade-off between isolated, vegetated pools and open, flowing channels, a pattern common in floodplain systems where hydrological connectivity mediates species distribution (Tockner et al. 2000).

The CCA2 gradient, driven by warmer, clearer water (positive values) versus vegetation cover (negative values), further elucidates community responses to environmental stress. Site S7, positioned toward high conductivity and positive CCA2, exhibits low diversity (H' = 0.31, J' = 0.28 during the receding phase), indicative of ecological stress from isolation and drying. Elevated conductivity, a proxy for ionic concentration in shrinking water bodies, likely exceeds tolerance thresholds for many species, reducing evenness and richness. This aligns with the reduced horizontal connectivity observed during the receding phase, where isolated pools become inhospitable, supporting fewer taxa (e.g., only three species at S7, Table 7). The

negative impact of temperature on diversity, as suggested by CCA2, may reflect thermal stress in shallow, drying sites, further compounding these effects.

The environmental arrows in the biplot, with vegetation cover as the longest, emphasise its dominant influence, corroborated by Spearman correlations and linear regression models. This dominance is ecologically significant, as habitat structure is a well-established driver of biodiversity in wetlands (Junk et al. 1989). The clustering of Mochokidae and Mormyridae near vegetation, versus Cyprinidae near discharge, mirrors habitat specialisation observed in the Okavango Delta, where cichlids and bottom-dwellers exploit vegetated refugia (Siziba et al. 2011). This adaptability to floodplain conditions suggests evolutionary strategies tailored to seasonal flooding, a finding that enhances the generalizability of this study to similar systems.

However, the small sample size (n = 8 sites) poses a limitation, potentially inflating the significance of CCA axes due to overfitting (Legendre and Legendre 2012). The near-perfect canonical correlations (e.g., ~0.99) may reflect this, cautioning against overinterpretation of minor axes. Additionally, the study's reliance on throw trap net sampling may under sample rare or mobile species, particularly in deeper channels, skewing abundance estimates. Future research should expand spatial coverage and incorporate seasonal replicates to validate these gradients across hydrological cycles.

In conclusion, vegetation cover emerges as a primary driver of abundance and diversity on the Kamutjonga Floodplain, fostering rich communities in vegetated littoral zones, while conductivity and temperature constrain diversity in isolated, drying sites. These findings support the importance of habitat management in floodplain conservation, suggesting that maintaining vegetation during receding phases could mitigate biodiversity loss. Comparative studies with other southern African floodplains, using longitudinal data, could further elucidate

these dynamics, informing adaptive management strategies in the face of climate-induced hydrological shifts.

3.5. Conclusion

This study investigated the small fish community inhabiting the Kamutjonga Floodplain of the Kavango River during the annual flooding. A total of 35 fish species were caught across the three phases at eight sampling sites. The catches were dominated by different species depending on the phase; *Enteromius* spp., notably *E. poechii* and *E. bifrenatus*, dominated at the rising and peak phases. In contrast, *P. philander* was more prevalent during the receding phase. Species richness peaked during the peak phase as the fully inundated floodplains provided diverse habitats. However, fewer species were present as the waters receded. Relative abundance (CPUE) was highest by number at the peak phase but peaked by mass during the drawdown. These patterns indicate that the floodplains serve as important nursery areas where small fish utilise enriched resources for growth before retreating to the river. In addition, the large numbers of small fish moving into inundated floodplains act as both consumers and prey, and serve as vital links in nutrient cycling and energy flow. The greater numbers and diversity of small fish in the rising and peak phases exploit available resources. This foraging behaviour transfers nutrients from the aquatic system into higher trophic levels, supporting predators such as birds, larger fish, and mammals. The findings highlight the critical ecological role played by the Kamutjonga Floodplain in supporting small fish diversity, which acts as a base of the food web and sustains the ecosystem biodiversity.

CHAPTER 4: MICRONUTRITIONAL VALUE OF SMALL FISH SPECIES IN THE KAMUTJONGA FLOODPLAIN, KAVANGO RIVER, NAMIBIA

4.1. Introduction

Globally, over two billion people are estimated to be deficient in essential vitamins and micronutrients (Kawarazuka and Béné 2011; Mohanty et al. 2016). Deficiencies of these important nutrients at specific life stages, such as during pregnancy, breastfeeding and early childhood, can result in serious health problems that are often only detected later in life (Black et al. 2013). As a result, nutrient deficiencies can severely affect communities' physical, social, and economic development. This is particularly evident in developing countries (Béné and Heck 2005; Kawarazuka and Béné 2011; FAO 2019). Undernourishment and severe food insecurity in sub-Saharan Africa are increasing exponentially, and an estimated 23.2% of the population suffered from chronic food deprivation in 2017 (Béné and Heck 2005; FAO 2019; Keeley et al. 2019).

In Namibia, recent studies showed that about 30% of the population is malnourished with one out of every three children under five suffering from micronutrient deficiencies of iron, folic acid, iodine, and vitamin A (Keeley et al. 2019). These deficiencies are attributed primarily to heavily refined starch-based diets (e.g., rice, wheat, cassava, and maize) that do not contain essential vitamins and micronutrients but are consumed regularly (FAO 2020; Akter et al. 2022). A cheap and accessible source of essential vitamins and micronutrients is therefore required to supplement these diets. The importance and use of fish in this regard is widely recognised. Africa’s developing countries have an estimated per capita fish consumption of 9.9 $kg.yr^{-1}$, constituting up to 21% of animal protein intake (FAO 2021). Most of Namibia's northern population is close to permanent or temporary freshwater resources that sustain small-

scale fisheries (Tveldten et al. 1996). Fish obtained from these small-scale fisheries are the only freely accessible or affordable food source available to a vast majority of the riparian communities and are utilised fresh, frozen or dried (Kawarazuka and Béné 2011; Funge-Smith et al. 2019; Akter et al. 2022; Islam et al. 2023). Namibia's per capita fish consumption is 12.5kg.yr^{-1}, equating to 34.25g.day^{-1} (FAO 2021). A standard portion was assumed to be 200g.day^{-1} for pregnant and lactating women (PLW) and 100g.day^{-1} for young children aged between one and three years (Van der Waal 1991). According to Van der Waal (1991), women in the Kavango River floodplains harvested approximately 600 grams of small freshwater fish daily, sufficient to meet the protein requirements of three individuals. Traditionally, small-sized fish are consumed whole, while the medium and larger fish are eviscerated and descaled before food preparation. Fish are rich in protein, fatty acids and contain essential vitamins and micronutrients (Roos et al. 2003; Mohanty et al. 2016). While essential vitamins and micronutrients are only required in small quantities, they play a vital role in improving the overall health, development, and prevention of non-communicable and lifestyle diseases (Mohanty et al. 2016). For this study, we focused on selected micronutrients (macro and microminerals) and their potential contribution to PLW and young children, from four commonly captured fish species from the Kamutjonga Floodplain in the Kavango River, Namibia. The macronutrients such as protein, amino acids and fats do not form part of this study as they are well-documented in many other studies. Additionally, due to limited funding, we focussed on the selected minerals, excluding vitamins (water and lipid soluble) and selenium.

The four most commonly harvested species for subsistence by women and children using traditional traps and hook and line in Kamutjonga floodplains, according to Tiyeho (2023),

were juveniles of threespot tilapia (*Oreochromis andersonii)*, redbreast tilapia (*Coptodon rendalli)*, and small-bodied species such as Zambezi River bream (*Pharyngochromis acuticeps)* and barbs of the genus *Enteromius* (*Enteromius barnardi, E.bifrenatus, E.eutaenia, E.fasciolatus, E.paludinosus, E.poechii, E.radiatus and E.unitaeaniatus)*. The selected fish species from the Kavango River floodplains were analysed to assess their dietary contributions of macrominerals (sodium [Na], potassium [K], phosphorus [P], calcium [Ca], and magnesium [Mg]) and microminerals (iron [Fe], copper [Cu], zinc [Zn], and manganese [Mn]). These nutrient profiles were used to evaluate the extent to which these fish meet the Recommended Nutrient Intakes (RNIs) for pregnant and lactating women (PLW) and children aged one to three years. Additionally, the nutritional value of these species was compared with that of other commercially important fish species to determine their relative dietary significance.

4.2. Materials and methods

4.2.1. Study area and fish sampling

Fish specimens were collected during routine monitoring surveys of the Namibian Ministry of Fisheries and Marine Resources on the floodplain. from 12 different localities along the Kavango River close to the villages of Bagani, Mwitjiku and Kamutjonga from May to June 2019 (Chapter 2 and Figure 1). Fish were identified to species level, and their length (in mm) and weight (in g) of individual fish were measured (Table 5). Fish samples were prepared for nutritional analysis and stored at -20°C. Fish were prepared following local preferences for consumption. Small-bodied species *Enteromius* spp. and *P. acuticeps* and juveniles of the larger cichlids *C. rendalli* and *O. andersonii* were prepared whole. The samples were prepared in triplicate and were transported frozen to the laboratory for mineral analysis.

4.2.2. Mineral analysis

The mineral analysis was conducted at the Analytical Laboratory Services Laboratory, Windhoek, Namibia. The macrominerals (Ca, Mg, Na, P and K) and microminerals (Fe, Cu, Zn and Mn) were analysed using methods described in Shahidi et al. (1999). Approximately two grams from each sample were dried at 550ºC until they turned into ash. The ash was dissolved with 6N hydrochloric acid (HCI) and 6N nitric acid (HNO_3). The mineralised sample was prepared by diluting it to a total volume of 50 mL with 2 N hydrochloric acid and Milli-Q water, then stored under refrigeration. The mineral content of the sample was analysed by inductively coupled plasma (ICP) analysis using standardised techniques from the Association of Official Analytical Chemists (AOAC) (Watson, 1994). A one-way analysis of variance (ANOVA) and Tukey's multiple comparison test (MCT) were used to compare micronutrient content between the different fish species (Shahidi et al. 1999, Sarma et al. 2018).

4.2.3. Potential contribution to Recommended Nutrient Intakes (RNI)

For each nutrient, a calculation was computed to represent how the nutrient content of a standard serving portion of a fish could potentially meet the daily Recommended Nutrient Intake (RNI) for pregnant and lactating women and young children. The RNI is defined as the daily nutrient intake set at the Estimated Average Requirement (EAR) plus two standard deviations, meeting the needs of nearly all healthy individuals in an age- and sex-specific group (WHO 2004). The EAR is the average daily nutrient intake level that meets the needs of 50% of healthy individuals in an age- and sex-specific group (WHO 2004). Adequate Intake (AI) is the recommended average daily nutrient intake level based on observed or experimentally determined approximations of nutrient intake by a group of healthy individuals, assumed to be

adequate for maintaining health (Institute of Medicine [IOM], 2000). It is used when data are insufficient to determine an EAR.

According to van der Waal (1991), a standard serving portion of fresh fish was assumed to be 200g.day^{-1} for PLW and 100g.day^{-1} for children aged 1 to 3. The basic assumption is that women in the floodplain harvest a total of 600g.day^{-1} of freshwater fish, which could potentially meet the protein needs of three individuals. The average moisture content in raw tilapia (78.08%) and carp (76.31%) was used, U.S.EPA (2011) (Table A1 in the Appendix). The dry-weight mineral residue levels for use with wet-weight (as consumed) intake rates were converted, as follows (U.S.EPA 2011):

$$C_{ww} = C_{dw}\left[\frac{100 - W}{100}\right]$$

Where:

C_{ww} = wet-weight concentration

C_{dw} = dry-weight concentration, and

W = percent water content

The mineral contribution of fish to the Recommended Nutrient Intake (RNI) was expressed as the percentage Daily Value (DV%), which represents the percentage of the RNI provided by a specific mineral from a fish species, as shown in Table 7 (Sarma et al. 2018). The potential contribution to RNI for pregnant and lactating women (PLW) and young children (aged 1 – 3) was calculated using the formula below as described by Egun and Oboh (2022).

$$N_{sp} = \frac{N_A \times S_p}{100}$$

$$\%RNI_i = \frac{N_{s_P}}{RNI_i} \times 100$$

where, N_A is the amount of nutrient (mg.100g^{-1}), S_p is the assumed standard portion of sourced food (fish) per day, N_{sp} is the nutrient amount in a standard portion, RNI_i is the daily recommended nutrient intake for nutrient *i,* and *% RNI_i* is the percentage contribution to daily RNI from an assumed standard portion.

For PLW, an average of the mineral requirements during all trimesters of pregnancy and breastfeeding up to 12 months was used to calculate the RNI value (WHO 2004) (Table 7). The Adequate Intake value (AI) was used for Na, K and Mn as the RNI value was unavailable (Meyers et al. 2006). The potential contribution was calculated as a percentage of average RNI using a standard portion of each species, 200g.day^{-1} for PLW and 100g.day^{-1} for children. The bioavailability of iron (10%) and zinc (moderate, ~30%) was considered, as absorption depends on factors such as animal-derived foods, phytates, and food preparation methods (WHO 2004; Bogard et al. 2015). The Recommended Nutrient Intake (RNI) values used in this study, equivalent to the Recommended Dietary Allowance (RDA) established by the Institute of Medicine (IOM, 2000), served as the reference for calculating nutrient contributions. According to guidelines from the Food and Drug Administration (FDA, 2016) and Nölle et al. (2020), fish samples providing a percentage Daily Value (%DV) of 20% or more per 100 g of edible portion (EP) are considered a good source of a specific nutrient, while those with a %DV below 5% are considered low (Table 7).

4.3. Results

4.3.1. Characteristics of collected fish.

Four commonly harvested small fish species were collected from the Kamutjonga Floodplain, all were in the size range of 20-40 mm (Table 8).

Table 8. Average length and weight of various fishes used for nutrient analysis.

Scientific name	Number of fish in the sample	Average body length (mm)	Average body weight (g)	Anatomical parts excluded prior to analysis
Enteromius spp.	169	31.95 ± 6.72	0.47 ± 0.41	Raw, whole
Pharyngochromis acuticeps	291	32.03 ± 4.66	0.45 ± 0.17	Raw, whole
Coptodon rendalli	272	35.26 ± 7.52	0.86 ± 0.52	Raw, whole
Oreochromis andersonii	79	27.54 ± 5.39	0.42 ± 0.25	Raw, whole

4.3.2. Mineral composition

Macrominerals

Amongst all the fish species analysed, calcium (Ca) exhibited the highest macromineral content, ranging from 544.87 ± 12.76 mg.100g^{-1} in *C. rendalli* to 1,340.43 ± 18.85 mg.100g^{-1} in *P. acuticeps* (Table 9). In contrast, magnesium (Mg) was the lowest, with values ranging from 29.83 ± 0.45 mg/100g in *O. andersonii* to 42.47 ± 0.98 mg/100g in *P. acuticeps*. Analysis of variance revealed significant differences in macromineral content between the selected species (ANOVA, $P < 0.05$). These variations suggest species-specific physiological adaptations, potentially linked to habitat conditions such as water hardness or dietary availability on the Kamutjonga Floodplain. The elevated Ca levels, particularly in *P. acuticeps*, may reflect a reliance on calcium-rich environments or diets, while the lower Mg content across species could indicate limited magnesium uptake, warranting further investigation into environmental or trophic influences.

Microminerals

Oreochromis andersonii had significantly higher amounts of Fe (21.46 ± 0.10 mg.100g^{-1}) than other species, while the lowest Fe concentration in *C. rendalli* was at 0.76 ± 0.16 mg.100g^{-1}. Zinc content was the second highest in abundance, ranging from 1.26 ± 0.06 mg/100g (*C. rendalli*) to 5.59 ± 0.05 mg.100g^{-1} (*Enteromius* spp.). There were significant differences in micromineral content (ANOVA, $P < 0.05$) between the selected species, with the exception of Cu (Table 9).

Table 9. The micronutrient content of *Oreochromis andersonii*, *Coptodon rendalli*, and small-bodied species, including *Pharyngochromis acuticeps* and *Enteromius* spp., which are the most commonly harvested fish species on the Kamutjonga Floodplain, Kavango River, Namibia (mg/100 g dry weight basis).

Minerals	*Enteromius* spp.*	*Pharyngochromis acuticeps**	*Oreochromis andersonii***	*Coptodon rendalli***
Macromineral				
Na	51.00 ± 0.10 ^{a}	68.83 ± 0.61 ^{b}	72.53 ± 0.45 ^{c}	72.67 ± 0.93 ^{c}
K	212.77 ± 1.82 ^{a}	221.27 ± 1.10 ^{b}	206.13 ± 2.25 ^{a}	267.50 ± 4.90 ^{c}
Ca	1294.00 ± 18.00 ^{c}	1340.43 ± 18.85 ^{d}	850.80 ± 10.20 ^{b}	544.87 ± 12.76 ^{a}
Mg	41.73 ± 0.50 ^{b}	42.47 ± 0.98 ^{b}	29.83 ± 0.45 ^{a}	30.93 ± 0.46 ^{a}
P	782.60 ± 8.46 ^{c}	765.20 ± 10.97 ^{c}	514.53 ± 4.25 ^{b}	434.40 ± 8.11 ^{a}
Micromineral				
Fe	5.52 ± 0.10 ^{b}	6.00 ± 0.06 ^{c}	21.46 ± 0.10 ^{d}	0.76 ± 0.16 ^{a}
Cu	0.17 ± 0.01 ^{b}	0.15 ± 0.01 ^{ab}	0.12 ± 0.01 ^{a}	0.12 ± 0.01 ^{a}
Zn	5.59 ± 0.05 ^{d}	3.34 ± 0.08 ^{c}	1.97 ± 0.01 ^{b}	1.26 ± 0.06 ^{a}
Mn	0.77 ± 0.02 ^{c}	0.48 ± 0.02 ^{b}	0.77 ± 0.03 ^{c}	0.28 ± 0.02 ^{a}

Results are expressed as mean ± SD (n = 3). Values in the same row with different superscripts differ significantly ($p < 0.05$)
* Small-bodied fish species
** Juveniles of larger fish species

Comparison of mineral composition to other fish species

Small-bodied fishes

Enteromius spp. exhibited slightly higher Fe (5.52 mg.100g^{-1}), Zn (5.59 mg.100g^{-1}), and Ca (1,294.00 mg.100g^{-1}) content than *E. radiatus* and *Limnothrissa miodon* as reported by Nölle et al. (2020). However, the Fe content was substantially lower than in *Gudusia chapra* (43.30 mg.100g^{-1}) and *Pethia ticto* (32.80 mg.100g^{-1}) from the study by Bhowmik et al. (2022). The majority of the mineral composition values fell within the ranges specified by FAO (2004) standards and Mogobe et al. (2015), as shown in Tables 9, 11, and 12.

Juveniles of large fishes

The average mineral content in juveniles of *O. andersonii* and *C. rendalli* was comparable to that of *Sargochromis mellandi* and *Tilapia sparrmanii* for most minerals, with the exception of Fe. The Fe content in *C. rendalli* was extremely low (0.76 mg.100g^{-1}) and fell well below all standards. Similarly, *C. rendalli* had the lowest Ca levels. In *O. andersonii*, Fe content (21.46 mg.100g^{-1}) was slightly higher but remained within a close range of *T. sparrmanii* (16.10 mg.100g^{-1}). Overall, all measured minerals were within the ranges established by FAO (2004) and Mogobe et al. (2015) (Tables 9, 11, and 12).

4.3.3. Potential mineral contribution from selected fish to the RNI of the two groups

Pregnant and lactating women

The calculated contributions to Recommended Nutrient Intake (RNI) are not based solely on individual dietary needs or health conditions but indicate potential mineral intake from a standard 200 g/day serving, influenced by preparation methods and dietary diversity (Egun & Oboh, 2022). *Enteromius* spp. and *P. acuticeps* provided the highest Ca contributions (56.2%

and 58.2%, respectively), followed by *O. andersonii* (37%), based on their Ca content (1,294.00 mg.100g^{-1}and 1,340.43 mg.100g^{-1}) (Table 10, Figure 19). Phosphorus (P) contributions exceeded 20%, ranging from 20.3% in *C. rendalli* (based on 250 mg.100g^{-1}) to 36.6% in *Enteromius* spp. (300 mg.100g^{-1}). *C. rendalli* offered the lowest micromineral contribution, failing to meet ≥10% Daily Value (DV) for Fe (0.76 mg.100g^{-1}1.9% DV), while *O. andersonii* led with 65.3% DV for Fe (21.46 mg.100g^{-1}), followed by *P. acuticeps* (18.2%) and *Enteromius* spp. (16.8%) (Table 10, Figure 19). Except for Fe, *Enteromius* spp. and *P. acuticeps* provided higher overall DV% for Ca, P, and Zn.

Young Children between one and three years of age

A standard 100 g serving of fish contributed more than 20% DV for Ca and P across all species (Table 10, Figure 20). *P. acuticeps* offered the highest Ca contribution (61.1%, from 1,340.43 mg.100g^{-1}), while *Enteromius* spp. provided the highest P contribution (38.8%, from 300 mg.100g^{-1}). Similar to PLW, *O. andersonii* contributed the highest Fe DV% (84.4%, from 21.46 mg.100g^{-1}), exceeding RNI needs for this age group.

Table 10. Potential mineral contribution – DV% [a] (daily value percentage) of fish in standard portions[b] to average daily RNI[c] for PLW[d] and children (1-3 years).

	Macrominerals										**Microminerals**							
	Na (mg)		**K (mg)**		**Ca (mg)**		**Mg (mg)**		**P (mg)**		**Fe (mg)[e]**		**Cu (mg)**		**Zn (mg)[f]**		**Mn (mg)**	
	PLW	Child	PLW	Child	PLW	Child	PLW	Child	PLW	Child	PLW	Child	PLW	Child	PLW	Child	PLW	Child
Average daily RNI	1500	1000	4900	3000	1050	500	245	60	975	460	15	5.8	1.15	0.34	8	4.1	2.3	1.2
Fish species																		
Enteromius spp.	1.6	1.2	2.0	1.6	**56.2**	**59.0**	7.8	15.9	**36.6**	**38.8**	16.8	**21.7**	6.7	11.4	**31.9**	**31.1**	15.3	14.6
Oreochromis andersonii	2.2	1.7	1.9	1.6	**37.0**	**38.8**	5.6	11.3	**24.1**	**25.5**	**65.3**	**84.4**	4.9	8.3	11.2	11.0	15.3	14.6
Pharyngochromis acuticeps	2.1	1.6	2.1	1.7	**58.2**	**61.1**	7.9	16.1	**35.8**	**37.9**	18.2	**23.6**	5.8	9.7	19.0	18.6	9.5	9.1
Coptodon rendalli	2.2	1.7	2.5	2.0	**23.7**	**24.9**	5.8	11.8	**20.3**	**21.5**	2.3	3.0	4.9	8.3	7.2	7.0	5.6	5.3

[a] DV % - Daily value percentage, the extent to which a particular mineral from an individual fish contributes to the RNI.

[b] Standard portions – serving 100g for children aged 1 – 3 and 200g for PLW.

[c] RNI – Required nutrient intake is the daily intake that meets the nutrient requirements of almost all (97.5%) apparently healthy individuals in an age – and sex-specific population.

[d] PLW – Pregnant and lactating women, the average values during pregnancy and breastfeeding were used.

[e] Fe – for RNI, 10% bioavailability is considered.

[f] Zn – for RNI, moderate bioavailability is considered.

Bold entries – DV% values of minerals could meet more than 20% of daily RNI for either PLW and children aged 1 to 3.

Table 11. Comparison of the macromineral content and RNI contribution of the most commonly harvested fish species on the Kamutjonga Floodplain, Kavango River, Namibia and other commercially important fish species (mg.100g^{-1}dry weight basis).

Scientific name (Common name)	Na	PLW	Child	K	PLW	Child	Ca	PLW	Child	Mg	PLW	Child	P	PLW	Child	Notes (per 100g)	Source
	mg	*RNI*	*RNI*	*mg*	*RNI*	*RNI*	*mg*	*RNI*	*RNI*	*Mg*	*RNI*	*RNI*	*mg*	*RNI*	*RNI*		
Small-bodied fish																	
Gudusia chapra (Chapila)	208.00	6.9%	5.2%	269.00	2.7%	2%	5191.00	247.2%	259.6%	188.00	38.4%	78.3%	2604.00	133.5%	141.5%	Raw, dried, whole, Bangladesh	Bhowmik et al. (2022)
Pethia ticto (Ticto barb)	206.00	6.9%	5.2%	622.00	6.3%	5%	3892.00	185.3%	194.6%	150.00	30.6%	62.5%	2092.00	107.3%	113.7%	Raw, dried, whole, Bangladesh	Bhowmik et al. (2022)
Enteromius spp. (Barbs)	51.00	1.6%	1.2%	212.77	2.0%	1.6%	1294.00	56.2%	59.0%	41.70	7.8%	15.9%	782.60	36.6%	38.8%	Raw, whole, Namibia	This study
Enteromius radiatus (Beira barb)				246.00	2.5%	2%	1095.00	52.1%	54.8%	45.00	9.2%	18.8%				Washed and left whole, Zambia	Nölle et al. (2020)
*Limnothrissa miodon (*Kapenta)				340.00	3.5%	3%	824.00	39.2%	41.2%	42.00	8.6%	17.5%				Washed and left whole, Zambia	Nölle et al. (2020)
*Limnothrissa miodon (*Kapenta)							2467.00	117.5%	123.4%							Raw, dried, whole, Rift Valley	Longley et al. (2014)
Pharyngochromis acuticeps (Zambezi River bream)	68.83	2.1%	1.6%	221.27	2.1%	1.7%	1340.43	58.2%	58.2%	42.47	7.9%	16.1%	765.20	35.8%	37.8%	Raw, whole, Namibia	This study
Juveniles of larger fish																	
Oreochromis. andersonii (Threespot tilapia)	72.53	2.2%	1.7%	206.13	1.9%	1.6%	850.80	37.0%	38.8%	29.83	5.6%	11.3%	514.53	24.1%	25.5%	Raw, whole, Namibia	This study
Coptodon rendalli (Redbreast tilapia)	72.67	2.2%	1.7%	267.50	2.5%	2%	544.87	23.7%	24.9%	30.93	5.8%	11.8%	434.40	20.3%	21.5%	Raw, whole, Namibia	This study
Tilapia sparrmanii (Banded tilapia)				233.00	2.4%	2%	1055.00	50.2%	52.8%	38.00	7.8%	15.8%				Washed and left whole, Zambia	Nölle et al. (2020)
Sargochromis mellandi (Snaileater)				260.00	2.7%	2%	1028.00	49.0%	51.4%	43.00	8.8%	17.9%				Washed and left whole, Zambia	Nölle et al. (2020)
FAO concentration in fish muscle (ranges)	30-134			19-502			19-881			4.5-452			68-550				FAO (2004)
Fish species, Chanogo, Okavango delta (ranges)	86-145			245-443			413-1290			34-48			435-1375			Edible portion / left whole, Botswana	Mogobe et al. (2015)
This study (ranges)	51-72.67			206.13-267.50			544.87-1340.43			29.83-42.47			434.4-782.6				

Table 12. Comparison of the micromineral content and RNI contribution of the most commonly harvested fish species on the Kamutjonga Floodplain, Kavango River, Namibia and other commercially important fish species (mg.100g^{-1} dry weight basis).

Scientific name (Common name)	Fe	PLW	Child	Cu	PLW	Child	Zn	PLW	Child	Mn	PLW	Child	Notes (per 100g)	Source
	mg	*RNI*	*RNI*	*Mg*	*RNI*	*RNI*	*Mg*	*RNI*	*RNI*	*mg*	*RNI*	*RNI*		
Small-bodied fish														
Gudusia chapra (Chapila)	43.30	144.3%	186.6%	0.50	21.7%	36.8%	11.90	74.4%	72.6%	0.40	8.7%	8.3%	Raw, dried, whole, Bangladesh	Bhowmik et al. (2022)
Pethia ticto (Ticto barb)	32.80	109.3%	141.4%	0.50	21.7%	36.8%	12.70	79.4%	77.4%	0.30	6.5%	6.3%	Raw, dried, whole, Bangladesh	Bhowmik et al. (2022)
Enteromius spp. (Barbs)	5.50	16.8%	21.7%	0.17	6.7%	11.4%	5.59	31.9%	31.1%	0.77	15.3%	14.6%	Raw, whole, Namibia	This study
Enteromius radiatus (Beira barb)	3.93	13.1%	16.9%				4.40	27.5%	26.8%				Washed and left whole, Zambia	Nölle et al. (2020)
*Limnothrissa miodon (*Kapenta)	2.90	9.7%	12.5%				3.70	23.1%	22.6%				Washed and left whole, Zambia	Nölle et al. (2020)
*Limnothrissa miodon (*Kapenta)	11.50	38.3%	49.6%				12.0	75.0%	73.2%				Raw, dried, whole, Rift Valley	Longley et al. (2014)
Pharyngochromis acuticeps (Zambezi River bream)	6.00	18.2%	23.6%	0.15	5.8%	9.7%	3.34	19.0%	18.6%	0.48	9.5%	9.1%	Raw, whole, Namibia	This study
Juveniles of larger fish														
Oreochromis. andersonii (Threespot tilapia)	21.46	65.3%	84.4%	0.12	4.9%	8.3%	1.97	11.2%	11.0%	0.77	15.3%	14.6%	Raw, whole, Namibia	This study
Coptodon rendalli (Redbreast tilapia)	0.76	2.3%	3.0%	0.12	4.9%	8.3%	1.26	7.2%	7.0%	0.28	5.6%	5.3%	Raw, whole, Namibia	This study
Tilapia sparrmanii (Banded tilapia)	16.10	53.7%	69.4%				2.40	15.0%	14.6%				Washed and left whole, Zambia	Nölle et al. (2020)
Sargochromis mellandi (Snaileater)	2.98	9.9%	12.8%				2.20	13.8%	13.4%				Washed and left whole, Zambia	Nölle et al. (2020)
FAO concentration in fish muscle (ranges)	1-5.6			0.001-3.7			0.23-2.1			0.0003-25.2				FAO (2004)
Fish species, Chanogo, Okavango delta (ranges)	1.65-6.39			0.02 -0.21			1.63-8.47			0.06-1.08			Edible portion / left whole, Botswana	Mogobe et al. (2015)
This study (ranges)	0.76-21.46			0.12-0.17			1.26-5.59			0.28-0.77				

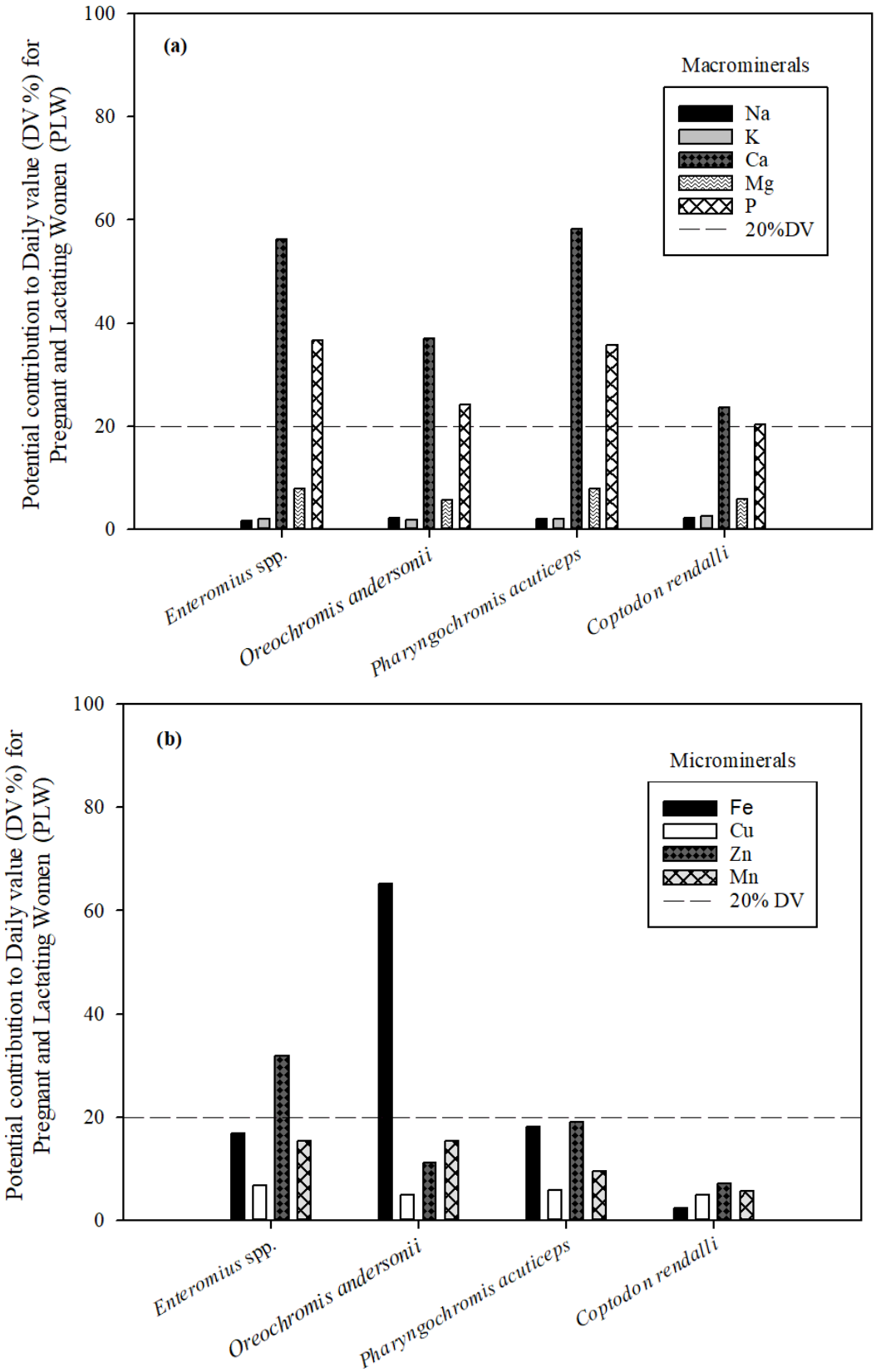

Figure 19. Potential mineral contribution (DV%) to Recommended Nutrient Intakes (RNI) for PLW of (a) macrominerals and (b) microminerals by fish species.

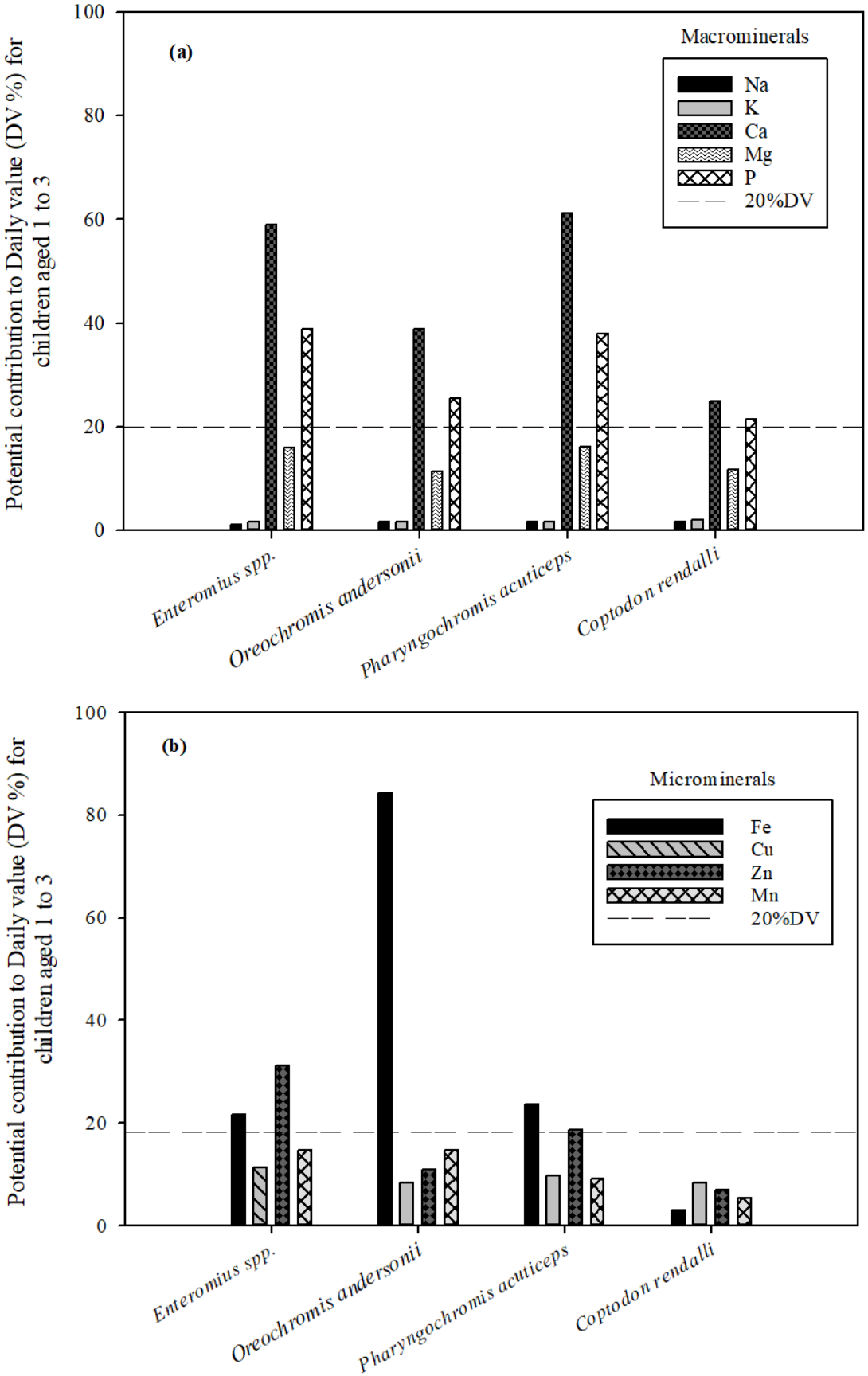

Figure 20. Potential mineral contribution (DV%) to Recommended Nutrient Intakes (RNI), children aged 1 - 3) of (a) macrominerals and (b) microminerals by fish species.

4.4. Discussion

Similar to most developing nations, Namibia is concerned about inadequate micronutrient supply in rural human communities. According to Nölle et al. (2020), "hidden hunger describes a phenomenon where a person is deficient in vitamins, minerals, and in some cases essential amino or fatty acids. The condition is called hidden because many micronutrient deficiencies remain hidden until clinical symptoms of the deficiency are detected." This study demonstrates that small fish harvested from floodplain areas could potentially supplement this nutritional requirement for PLW and young children (Bogard et al. 2015; Mohanty et al. 2016).

In Asia, for example, small-bodied fish accounted for between 50 and 80% of all fish consumed in rural areas in Asia (Roos et al. 2007; Kawarazuka and Béné 2011). The nutrient-dense small fishes like *Amblypharyngodon mola* from India and Bangladesh, *Limnothrissa miodon* from Lake Kariba and Tanganyika and *Engraulicypris sardella* and *Rastrineobola sardella* from Lake Malawi in Africa are a popular and cheaper alternative to larger economically highly valued species such as the cyprinids and tilapias (Genschick et al. 2018). Small fishes have an economy of scale for the rural poor as they can be bought in smaller quantities (Kolding et al. 2019) and are easier to preserve by simply sun drying (Kolding et al. 2019). They require minimal processing and are mostly wholly consumed with heads, viscera, and scales. They are a good source of protein, fatty acids, and micronutrients (Roos et al. 2003; Mohanty et al. 2016). They are a critical component incorporated in food strategies to reduce micronutrient deficiencies in low-income food-deficient countries (Kawarazuka and Béné 2011; Mohanty et al. 2016).

Bogard et al. (2015) reported that small-bodied freshwater fish exhibited higher levels of calcium (Ca), iron (Fe), and zinc (Zn) compared to various large freshwater and marine fish

species. Similarly, Nölle et al. (2020) found that *T. sparrmanii* contained only 1,055.00 mg.100g^{-1} of Ca and 2.40 mg.100g^{-1} of Zn. In contrast, Bhowmik et al. (2022) reported that dried *Pethia ticto*, consumed whole, had substantially higher levels of 3,892 mg.100g^{-1} Ca and 12.70 mg.100g^{-1} Zn, reflecting a more than three-fold increase in Ca content compared to *T. sparrmanii.* This difference likely stems from the inclusion of bones and tissues in whole dried fish, enhancing mineral density.

This study showed that small-bodied fish exhibited higher calcium (Ca) and phosphorus (P) levels compared to the juveniles of larger fish species, such as *O. andersonii* and *C. rendalli*. These findings concurred with those of Bogard et al. (2015), who reported that *Enteromius spp.* and *P.acuticeps* displayed relatively higher Ca and zinc (Zn) levels, contributing to greater Daily Value (DV) percentages toward Recommended Nutrient Intake (RNI). A 200 g meal of *Enteromius spp.* could provide for approximately 5.59 mg of Zn, meeting 31.9% and 31.1% of the RNI for pregnant and lactating women (PLW) and children, respectively, whereas an equivalent portion of *C. rendalli* provided 1.26 mg of Zn, accounting for 7.2% and 7.0% of the RNI for PLW and children, respectively (Tables 9 and 10).

Furthermore, among the investigated fish species, *O. andersonii* offered the greatest nutrient value for iron (Fe) to RNI, with contributions of 65.3% and 84.4% for PLW and children, respectively, while *C. rendalli* showed the least Fe contribution, with 2.3% DV for PLW. The World Health Organization (WHO, 2004) identifies Ca, Fe, and Zn as nutrients of greatest health concern, particularly for PLW and children, underscoring the significance of these findings.

Sodium

Sodium (Na), along with phosphorus (P) and chloride (Cl), which are typical components of extracellular fluid, contributed to osmolarity and regulated fluid balance between intracellular and extracellular compartments (Huskisson et al. 2007). The Na concentration in sampled fish ranged from 51 $mg.100g^{-1}$ to 72.67 $mg.100g^{-1}$, with a mean of 66.26 $mg.100g^{-1}$, falling within the range reported by FAO (2004) (30–134 $mg.100g^{-1}$) and slightly below the range documented by Mogobe et al. (2015) (86–145 $mg.100g^{-1}$) (Table 8). Additionally, the Kavango River catchment, part of the sandy Kalahari Basin, exhibited lower salinity (0.01–0.03 mgL^{-1}), which may influence mineral uptake. The Na concentration varied significantly among species ($P < 0.05$), with the highest level observed in *C. rendalli* (Table 9).

Potassium

Potassium (K) played a critical role in cellular energy metabolism throughout the body, with its regulated intracellular fluctuations and involvement in membrane depolarization being fundamental to neuronal signalling, muscle contraction, and endocrine hormone secretion. Notably, maintaining optimal K levels was essential for the propagation of electrical impulses within myocardial tissue, ensuring efficient cardiac function (Zimmermann, 2001). The concentration of K in the sampled fish from the study area ranged from 206.13 $mg.100g^{-1}$ to 267.50 $mg.100g^{-1}$, with an average of 226.92 $mg.100g^{-1}$, falling within the range reported by FAO (2004) (19–502 $mg.100g^{-1}$) and slightly below that documented by Mogobe et al. (2015) (245–443 $mg.100g^{-1}$) (Table 8). Additionally, a significant difference ($P < 0.05$) was observed among the sampled species, with the highest K level recorded in *C. rendalli* (Table 9).

Calcium

Calcium (Ca) was primarily responsible for bone development, blood clotting, and skeletal and heart muscle contractions (Zimmermann, 2001). An increased risk of bone fractures, osteoporosis, and osteopenia resulted from Ca deficiency (Zimmermann, 2001; Meyers et al., 2006). The concentration of Ca in the sampled fish ranged from 544.87 mg.100g^{-1} to 1,340.43 mg.100g^{-1}, with a mean level of 1,007.53 mg.100g^{-1} (Table 9). These results fell within the ranges reported by FAO (2004) (19–881 mg.100g^{-1}), Kawarazuka and Béné (2011) (198–1,061 mg.100g^{-1}), and Mogobe et al. (2015) (545–1,340 mg.100g^{-1}) (Table 8). The Ca concentration among the sampled fish species was significantly different ($P < 0.05$), with the highest level observed in *P. acuticeps* (1,340 mg.100g^{-1}).

Additionally, all four sampled species met or exceeded 20% of the Ca RNI for pregnant and lactating women (PLW) and children. Small-bodied fish contributed over 50% to the RNI for both groups, slightly surpassing the Ca contribution to RNI of *L. miodon* reported by Longley et al. (2014), but falling well below the levels in small fish documented by Nölle et al. (2020) (Table 11).

Magnesium

Magnesium (Mg) was a critical cation in the body, with various functions, among which it was essential for protein synthesis, energy metabolism, and muscle contraction, and it supported bone structure and DNA/RNA synthesis (Tacon et al. 2020). The Mg concentration in the sampled fish ranged from 29.83 mg.100g^{-1} to 42.47 mg.100g^{-1}, with a mean value of 36.24 mg.100g^{-1} (Table 11). This range fell within the values reported by FAO (2004) (4.5–452 mg.100g^{-1}) and Mogobe et al. (2015) (34–48 mg.100g^{-1}). Additionally, consistent with Mogobe

et al. (2015), the Mg levels in this study were toward the lower end of the FAO (2004) range. *P. acuticeps*, a small fish consumed whole, exhibited the highest Mg concentration at 42.47 mg.100g^{-1}.

Phosphorous

Phosphorus (P) is an electrolyte in the body that maintained electrical gradients and was crucial for the structural components of nucleotide coenzymes. Phosphate, on the other hand, was a fundamental component required for the formation of teeth and bones, as well as energy production (Huskisson et al. 2007). The phosphorus concentration in the sampled fish ranged from 434.4 mg.100g^{-1} to 782.6 mg.100g^{-1}, with a mean value of 624.18 mg.100g^{-1} (Table 11). Higher concentrations were observed in small fish consumed whole, including bones and edible parts, enhancing mineral intake. These levels were consistent with the range reported by FAO (2004) (68–550 mg.100g^{-1}) and fell toward the lower end of the range documented by Mogobe et al. (2015) (435–1,375 mg.100g^{-1}g) (Table 11).

Iron

Iron (Fe) deficiency affected the health of 2 billion people globally, making it the world's most prevalent and widespread nutritional problem. The major health consequences included poor pregnancy outcomes, impaired physical and cognitive development, and increased morbidity risk in children, as well as reduced work productivity in adults (Allen et al. 2006). The concentration of Fe in the sampled fish ranged from 0.76 mg.100g^{-1}to 21.46 mg.100g^{-1}, with a mean level of 8.44 mg.100g^{-1}. These results aligned with the ranges reported by Charrondière et al. (2013) and Kawarazuka and Béné (2011) for fish and seafood. Additionally, only one species, *O. andersonii*, met or exceeded 20% of the Recommended Nutrient Intake (RNI) for pregnant and lactating women (PLW) (72%) and children (93%) (Table 9). By contrast, the

small-bodied fish *Enteromius* spp. and *P. acuticeps* contributed 18% and 20% of the RNI for PLW, respectively (Figure 12).

Copper

Copper (Cu) was crucial as it assisted in iron metabolism and red blood cell formation, contributed to immune system functionality, aided in energy generation, activated neuropeptides, supported the synthesis of connective tissue and neurotransmitters, regulated gene expression, promoted brain growth, influenced pigmentation, and mitigated oxidative stress (Huskisson et al. 2007; Tacon et al. 2020). The copper concentrations in the sampled fish ranged from 0.12 mg.100g^{-1}to 0.17 mg.100g^{-1}, with an average value of 0.14 mg.100g^{-1}. No significant differences ($P > 0.05$) were observed among the fish species (Table 12). These Cu levels fell within the range reported by FAO (2004) (0.001–3.7 mg.100g^{-1}) and Mogobe et al. (2015) (0.02–0.21 mg.100g^{-1}) (Table 9).

Zinc

Zinc (Zn) was essential for growth, immune and nervous system function, and reproduction (Mohanty et al. 2016). It was present in numerous enzymes, including RNA polymerases, which facilitated new protein synthesis (Zimmermann, 2001). Zinc contributed to growth, red blood cell formation, and blood clotting, particularly in young children and pregnant and lactating women (PLW) (Zimmermann, 2001). The mineral was sufficiently available from all sampled fish species, exceeding the minimum bioavailability level of 5%. The concentration of Zn ranged from 1.26 mg.100g^{-1}to 5.59 mg.100g^{-1}of dry weight, with a mean content of 3.04 mg.100g^{-1}. These findings aligned with the values reported for fish and seafood by

Charrondière et al. (2013) and Kawarazuka and Béné (2011) (Table 9). Additionally, only the species *Enteromius* spp. met or exceeded 20% of the Recommended Nutrient Intake (RNI) for PLW (31.9%) and children (31.1%) (Table 10).

Manganese

Manganese (Mn) was essential for protein and carbohydrate metabolism, insulin production, antioxidant protein function, bone and cartilage synthesis, and enzyme activation, playing critical roles in the body (Zimmermann, 2001; Huskisson et al. 2007). In this study, the concentration of manganese ranged from 0.28 $mg.100g^{-1}$to 0.77 $mg.100g^{-1}$, with an average value of 0.58 $mg.100g^{-1}$ (Table 8). Additionally, these levels fell within the range reported by Mogobe et al. (2015) (0.06–1.08 $mg.100g^{-1}$) and exceeded the minimum threshold set by FAO (2004) (0.0003–25.2 $mg.100g^{-1}$) (Table 9).

4.5. Conclusion

This study underscores the potential of small fish harvested from floodplain areas, particularly in Namibia, to address the prevalent issue of "hidden hunger", a condition marked by micronutrient deficiencies affecting rural communities, as highlighted by Nölle et al. (2020). Similar to patterns observed in Asia, where small-bodied fish constitute 50–80% of rural fish consumption (Roos et al. 2007; Kawarazuka and Béné 2011), these nutrient-dense species, such as *Enteromius spp.* and *P. acuticeps*, offer an affordable and accessible solution for pregnant and lactating women (PLW) and young children. Their whole consumption, including bones and viscera, significantly enhances the intake of essential micronutrients like calcium

(Ca), phosphorus (P), iron (Fe), zinc (Zn), and others, aligning with findings from Bogard et al. (2015) and Mohanty et al. (2016).

The data reveal that small-bodied fish consistently exhibited higher Ca and P levels compared to juveniles of larger species like *O. andersonii* and *C. rendalli*, with *P. acuticeps* reaching 1,340.43 mg/100 g Ca and dried *Pethia ticto* showing a threefold higher Ca content (3,892 mg/100 g) than *T. sparrmanii* (Nölle et al. 2020; Bhowmik et al. 2022). This mineral density, driven by whole consumption, supports over 50% of the Ca RNI for PLW and children, surpassing *L. miodon* (Longley et al. 2014) but falling short of some small fish reported by Nölle et al. (2020). For Fe, only *O. andersonii* met or exceeded 20% RNI (72% for PLW, 93% for children), while small-bodied species like *Enteromius spp.* provided 31.9% and 31.1% of Zn RNI from a 200 g meal, outpacing *C. rendalli* (7.2% and 7.0%). Other minerals, sodium (Na), potassium (K), magnesium (Mg), copper (Cu), and manganese (Mn), also fell within reported ranges (FAO 2004; Mogobe et al. 2015), with *C. rendalli* showing the highest Na and K levels, and *P. acuticeps* leading in Mg.

These findings align with global evidence that small fish are a cost-effective, nutrient-rich resource, requiring minimal processing and supporting food security strategies in low-income regions (Kolding et al. 2019; Kawarazuka and Béné 2011). The World Health Organization (WHO 2004) identifies Ca, Fe, and Zn as critical nutrients for PLW and children, and this study demonstrates that floodplain small fish can mitigate these deficiencies, offering a sustainable approach to combat hidden hunger in Namibia and similar developing nations.

CHAPTER 5: GENERAL DISCUSSION

Floodplain fisheries serve as a cornerstone for both ecological integrity and human well-being, underpinning diverse food webs while supplying crucial protein and micronutrients to riparian populations. However, increasing variability in flood regimes poses significant challenges to these systems, necessitating a deeper understanding of their ecological role and nutritional contributions to riparian communities. Fisheries provide income, employment, food and other materials to riparian communities, underscoring their socio-economic and ecological importance (Welcomme 2008, FAO 2021). The riverine ecosystem delivers various ecosystem services that sustain biodiversity and human livelihoods. Many tropical fish communities rely on floodplains as feeding, nursery, and breeding grounds (Junk et al. 1989). The timing and intensity of floodwater inflows have become increasingly unpredictable due to the impacts of climate change. This variability disrupts ecological processes, negatively impacting biodiversity and fish yields. For example, Agostinho et al. (1995) demonstrated in the Paraná River that reduced floodplain inundation leads to a decline in prey species, subsequently lowering yields of commercially important fish. Fish serve as a critical source of protein and micronutrients, providing a lifeline for food-insecure riparian and remote human communities worldwide (Beveridge et al. 2013). Small-bodied fishes, in particular, have been shown to supply essential nutrients for pregnant and lactating women and children under the age of three (Bogard et al. 2015). As they may be the only readily available and substantial micronutrient source in this region, they are of particular importance. Declining floodplain inundation, driven by climate-induced flood variability, threatens fishery resources and nutritional security in regions like Namibia. Urgent research into fish populations, their ecological roles, and nutritional contributions is essential. These insights will inform adaptive management and conservation strategies, ensuring sustainable fisheries and supporting food security for communities dependent on nutrient-rich fish (Allison et al. 2009).

This study focuses on the Kamutjonga Floodplain, highlighting its importance in sustaining biodiversity and addressing nutritional deficiencies in the Kavango East region. The Ministry of Fisheries and Marine Resources of Namibia has mainly focused on using gillnets to access the fisheries; however, some fisheries might not be well-represented using this method, especially those targeting small fish. Hence, introducing throw trap netting and seine netting in a floodplain has provided insights into less documented members of the fish community. Given the demonstrated success of these methods, standardising their application could facilitate comparative analyses across different aquatic systems, enhancing the robustness and consistency of future research.

5.1. Relative abundance and diversity of small fishes

During the 2018 sampling period, Cyprinidae dominated catches in both the rising and receding flood phases, whereas cichlids were most abundant at the peak of the flood. Invertivores consistently accounted for about 60% IRI (based on both the weight and numbers) of the ichthyofaunal community across the three flood phases. Their abundance, alongside omnivores, increased during flooding, while herbivores declined. Species richness peaked at the flood's height, while diversity (H') and evenness (J') were highest during the receding phase. Cichlids contributed significantly to biomass, representing 54% and 35% during the rising and receding phases, respectively.

While the relative abundance of fish (based on CPUE) did not vary significantly across flood phases, catches were higher during the rising phase. This can be attributed to the lower water levels and opportunistic behaviours of *r*-selected species such as cyprinids, which dominate

during such periods. The significant difference in CPUE by mass indicates that fish actively utilise the floodplain system for breeding and feeding. These dynamic highlights the ecological importance of maintaining floodplain connectivity, as fluctuating water levels can create diverse ecological niches, promoting species richness. However, when flood regimes are highly irregular, as seen in recent years, these disturbances may exceed the threshold for resilience, negatively impacting fish communities and their ecological roles (Tockner and Standford 2002).

5.2. Micronutritional content and mineral contribution to RNI

Four species from the Kamutjonga Floodplain were selected to analyse micronutritional content and their contribution to recommended nutrient intake (RNI) in terms of daily value percentage (DV%) for pregnant and lactating women (PLW) and young children between one and three years of age. Small fishes harvested from marginal floodplains could potentially provide micronutrients vital for health, growth, and development, particularly among children under three years of age and pregnant and lactating women (Bogard et al. 2015).

Small fish are consumed whole, with scales, bones, and viscera as important micronutrient sources (Roos 2001; Roos et al. 2003). Micronutrient concentrations in fish differ markedly depending on species, body size, sex, and maturity (Bogard et al. 2015). However, the studied fish compositions are highly comparable and within the range of many fresh and dried fish consumed elsewhere. According to WHO (2004), the minerals Ca, Fe and Zn are considered nutrients of the greatest health concern, particularly to PLW and children. These micronutrients were readily available from the small fishes analysed during the study. Given the high prevalence of micronutrient deficiencies in the Kavango Region, regularly incorporating small floodplain fish like *Enteromius* spp. and *P. acuticeps* into local diets could meaningfully

contribute to reducing malnutrition. It is evident that the micronutrients are not equally available from the various fish species. Small fish species sampled from the Kamutjonga Floodplains generally contributed less than 20% of the Recommended Nutrient Intake (RNI) for key minerals in children under three and pregnant or lactating women. However, wholly consumed small-bodied fish provided higher mineral contributions, particularly iron, with juvenile *O. andersonii* yielding 70–90% of the Daily Value (DV), surpassing other species from the study. As affordable, culturally acceptable nutrient sources, these fish enhance food security for rural communities. Despite limitations in sample size and collection timing, this research highlights the nutritional potential of indigenous fish.

Overall, the results indicate that promoting the consumption of nutrient-dense small fish could help combat micronutrient deficiencies impacting maternal and child health in Namibia. Further research, expanding study locations and seasons, would help validate these findings.

5.3. Conclusion

More than 75% of the residents of the Kavango Region (East and West) resided within 10 km of the river, emphasising the riverine ecosystem's significance as a source of nutrient-dense small fish. This study demonstrated that these small fish, consumed widely across household members, could address and mitigate nutrient deficiencies affecting children under three and pregnant and lactating women (PLW). However, low floods had a negative impact on the most vulnerable, as other animal-source proteins were expensive and inaccessible in remote areas. During low-flow years, women and children experienced increased vulnerability to micronutrient shortfalls and associated lifestyle illnesses due to limited nutrient sources. Additionally, the harvest of larger fish stocks continued unabated, often using illegal or

unsustainable methods. Therefore, this study underscores the importance of the floodplain ecosystem and its habitat for sustaining rural livelihoods along the Kavango River.

5.4. Management recommendations and future research

Freshwater fisheries are being depleted at alarming rates throughout Africa, and there is an urgent need for sustainable utilisation and management strategies (Stiassny 1996, Dudgeon et al. 2006). Commercially important fish, such as cichlids and tigerfish, are declining due to overfishing with illegal gear and unsustainable practices, exacerbated by climate-induced flood variability (Simasiku 2014; Agostinho et al. 1995). In contrast, small fish species are critical to food web dynamics and provide micronutrients like iron and calcium for vulnerable populations (Bogard et al. 2015). Protecting these species is essential for sustainable fishery management and nutritional security in Namibia's riparian communities.

Management recommendations

Drastic management measures must be implemented to ensure sustained beneficiation from this resource. Establishing fish-protected areas such as Sikunga and Impalila fisheries reserves is essential to help preserve natural habitat and associated fisheries (Simasiku et al. 2017). The findings of this study suggest the establishment of a fisheries reserve in the immediate area of Kamutjonga Floodplain and at selected sites along the Kavango River in conjunction with the local communities for input and co-management. Due to constraints in state-level law enforcement capacity, community-based fisheries management, supported by local bylaws and regulatory conditions, offers an alternative governance model. This participatory approach allows residents to derive socioeconomic benefits while maintaining sustainable resource management practices. A comprehensive management strategy should include implementing closed seasons during critical breeding periods, particularly during rising flood phases when

cyprinids are predominant, to protect spawning populations in floodplain breeding grounds (Junk et al. 1989). Additionally, no-fishing zones should be established in areas characterised by dense emergent vegetation, such as *Phragmites australis* and *Cyperus papyrus*, which provide essential habitat for small fish species and facilitate nutrient cycling. These protective measures can be enhanced through the establishment of community-led monitoring programs that leverage local ecological knowledge to supplement official patrol efforts in detecting illegal fishing activities and habitat degradation. To capitalise on the value of the fishery, there is a need to promote the consumption of small-bodied fish to address nutrient deficiencies while ensuring sustainable harvesting practices (Kawarazuka and Béné 2011).

Future research

This study identified the importance of vegetation and its influence on fish abundance. However, the methods employed relied solely on assessing vegetation cover. Future studies should incorporate quantitative approaches, such as the rake method or other suitable techniques, to determine the biomass of emergent, floating, and submerged plants in the study area. This would enable a direct correlation between vegetation composition and fish abundance, aligning with findings from Agostinho et al. (2007) and Pelicice et al. (2005). Furthermore, to understand broader ecological implications, a continuous sampling regime should be implemented both within and outside protected areas, focusing on small fish species to assess the "park effect" (the influence of protected areas on fish communities). Ensuring that sampling sites are located a sufficient distance from protected areas would minimise potential bias from overflow.

Moreover, expanding the research to include other floodplains within the Kavango River system and adjacent rivers, such as the Kwando, Zambezi, and Chobe, would provide a regional

perspective. Seasonal sampling of fish is also essential, as nutritional composition varies significantly between wet and dry seasons (Bogard et al. 2015). Incorporating dried fish products, such as Kapenta (a popular dried fish), would yield additional data on preservation methods and their impact on nutritional value. Finally, socioeconomic surveys documenting fish consumption patterns, preparation techniques, and cultural practices would enhance understanding of fish's nutritional importance in the region. Addressing these gaps would provide reliable data to inform evidence-based resource management and policy decisions.

CHAPTER 6: REFERENCES

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APPENDIX

Table A1. Mean percentage moisture and total fat content for selected fish species.

Table 10-125. Mean Percent Moisture and Total Fat Content for Selected Species (continued)

Species	Moisture Content (%)	Total Fat Content (%)	Comments
	71.50	4.30	Cooked, dry heat
	65.39	7.50	Cooked, moist heat
Salmon, Pink	76.35	3.45	Raw
	69.68	4.42	Cooked, dry heat
	68.81	6.05	Canned, solids with bone and liquid
Salmon, Sockeye	70.24	8.56	Raw
	61.84	10.97	Cooked, dry heat
	67.51	7.31	Canned, drained solids with bone
Sardine, Atlantic	59.61	11.45	Canned in oil, drained solids with bone
Sardine, Pacific	66.65	10.46	Canned in tomato sauce, drained solids with bone
Scup	75.37	2.73	Raw
	68.42	3.50	Cooked, dry heat
Sea Bass	78.27	2.00	Raw
	72.14	2.56	Cooked, dry heat
Seatrout	78.09	3.61	Raw
	71.91	4.63	Cooked, dry heat
Shad, American	68.19	13.77	Raw
	59.22	17.65	Cooked, dry heat
Shark, mixed species	73.58	4.51	Raw
	60.09	13.82	Cooked, batter-dipped and fried
Sheepshead	77.97	2.41	Raw
	69.04	1.63	Cooked, dry heat
Smelt, Rainbow	78.77	2.42	Raw
	72.79	3.10	Cooked, dry heat
Snapper	76.87	1.34	Raw
	70.35	1.72	Cooked, dry heat
Spot	75.95	4.90	Raw
	69.17	6.28	Cooked, dry heat
Sturgeon	76.55	4.04	Raw
	69.94	5.18	Cooked, dry heat
	62.50	4.40	Smoked
Sucker, white	79.71	2.32	Raw
	73.99	2.97	Cooked, dry heat
Sunfish, Pumpkinseed	79.50	0.70	Raw
	73.72	0.90	Cooked, dry heat
Surimi	76.34	0.90	-
Swordfish	75.62	4.01	Raw
	68.75	5.14	Cooked, dry heat
Tilapia	78.08	1.70	Raw
	71.59	2.65	Cooked, dry heat
Tilefish	78.90	2.31	Raw
	70.24	4.69	Cooked, dry heat
Trout, Mixed Species	71.42	6.61	Raw
	63.36	8.47	Cooked, dry heat
Trout, Rainbow, Farmed	72.73	5.40	Raw
	67.53	7.20	Cooked, dry heat
Trout, Rainbow, Wild	71.87	3.46	Raw
	70.50	5.82	Cooked, dry heat
Tuna, Fresh, Bluefin	68.09	4.90	Raw
	59.09	6.28	Cooked, dry heat
Tuna, Fresh, Skipjack	70.58	1.01	Raw
	62.28	1.29	Cooked, dry heat
Tuna, Fresh, Yellowfin	70.99	0.95	Raw
	62.81	1.22	Cooked, dry heat
Tuna, Light	59.83	8.21	Canned in oil, drained solids
	74.51	0.82	Canned in water, drained solids
Tuna, White	64.02	8.08	Canned in oil, drained solids
	73.19	2.97	Canned in water, drained solids
Turbot, European	76.95	2.95	Raw
	70.45	3.78	Cooked, dry heat
Whitefish, mixed species	72.77	5.86	Raw
	65.09	7.51	Cooked, dry heat
	70.83	0.93	Smoked
Whiting, mixed species	80.27	1.31	Raw
	74.71	1.69	Cooked, dry heat