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The Okavango Delta: Fisheries in a fluctuating floodplain system

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Wetlands are among the most productive ecosystems globally characterized by dynamic interactions between terrestrial and aquatic habitats at different scales. These systems support valuable floodplain fisheries that are a major livelihood for riparian communities. Understanding the dynamics of these systems is important for developing adaptive fisheries management paradigms that will facilitate access and sustainability to this cheap but high-quality food and nutrition source. The Okavango Delta in Botswana is a large land-locked complex river-floodplain ecosystem, with a diverse biota, and high environmental heterogeneity due to periodic drying and flooding along a space and time gradient. It is characterized by a multi-species, multi-gear fishery adapted to the seasonal flood pulse. The Delta's fish species assemblage undergoes seasonal changes driven by the flood regime. There is also a dynamic inter-annual variability in the fish species assemblage, particularly between "good" and "bad" flood years. During the wet season, high flows increase connectivity in three dimensions (longitudinal, lateral, and vertical) which facilitates dispersal of aquatic biota, nutrients, and other material among successive locations in the riverscape. However, the dry season results in alteration or reduction in aquatic habitats available for fish reproduction. Similarly, low floods may reduce inputs of nutrient resources from the terrestrial environment that support aquatic food webs and can lead to community disruption, even to the point of local extirpation of stranded fish in fragmented ephemeral pools in the floodplain. Consequently, the periodicity, magnitude and predictability of flows are the major drivers of the systems' capacity to sustain persistent fisheries production and other ecosystem services affecting human welfare. We argue that identification of the processes that sustain production and biodiversity patterns is an essential step towards a better ecological understanding and natural resource management of river-floodplain systems. Based on this review, we debate that floodplain fisheries, like in the Okavango Delta, should be exploited using a diverse exploitation pattern to ensure a harvesting regime in balance with system productivity. Such balanced fishing pattern, based on traditional fishing practices, facilitates the provision of food and nutritional value of the fishery to marginalized communities.

KEYWORDS

Okavango Delta, floodplain fisheries management, fluctuating, balanced fishing, flood pulse

1 Introduction

Tropical inland fisheries, while producing at least 15–20% of the global fish production, are based on the tiny fraction (≈0.04%) that tropical aquatic freshwater systems contribute to the world's freshwater resources (Kolding and van Zwieten, 2006). Most importantly, inland fisheries provide vital proteins, micro-nutrients, jobs and income for some of the most marginalized communities of the world (Allan et al., 2005; Welcomme, 2011; HLPE 2014; Béné et al., 2015), but a growing global population, with a consequent increase in food demand, will place increased pressure on the global water resources (e.g. http://www.waterforfood.org/). According to Molden and de Fraiture (2004), this situation is of particular concern in Africa, where pressure on water resources is expected to increase rapidly within the next two decades. In addition, climate change will likely increase water stress in southern Africa (Boko et al., 2007) because of reduced (Clark, 2006) or increased variability in precipitation across the continent (Tadross et al., 2005), which will affect fish productivity (Magadza, 2011; Gownaris et al., 2018) and increase food insecurity. An increased pressure on resources has raised concerns of overexploitation exacerbated by lack of knowledge on ecosystem response to changes in species, size, and trophic composition of fish assemblages (Allan et al., 2005). However, "where there is water there is fish" (Kolding et al., 2016) and since the hydrological regimes are key drivers of productivity and structure in freshwater ecosystems (Gownaris et al., 2018) there is compelling need to understand and appreciate the dynamics of floodplain fisheries better because of their prevalence, high productivity, and intrinsic value to riparian communities in Africa.

Floodplain fisheries are generally considered among the most productive in the tropics (Junk, et al., 1989; Welcomme, 2009), with an average potential fish production rate of 2.5–4 times that of tropical lakes and reservoirs on a water surface area basis (Bayley, 1991). The Okavango Delta (Figure 1) is one of the largest inland river deltas in the world (Allanson, et al., 1990) with a fishery which is predominantly artisanal and subsistence, combined with a small-scale commercial gillnet fishery (Mosepele, et al., 2003). In common with most African inland fisheries, it is characterized by a multi-species, multi-gear fishery harvesting the fish community across different trophic levels, species, and sizes (Mosepele, 2019). Approximately 65% of the 25,000 people (based on 1995 population estimates) who live within the periphery of the Delta depend on the fishery as a source of livelihood (Mosepele, 2001). Due to competing interests in the Delta's fish resources, particularly between the flourishing tourist and angling industry and the local people, there has been a long history of stakeholder conflicts and repeated allegations of over-exploitation of the fish resource and deterioration of the environment (Mosepele et al., 2014). However, apart from a preliminary analysis (Mosepele and Kolding, 2003) there have been no informed assessment studies on the Okavango Delta fishery. Because of the complex and dynamic nature of the fishery (approximately 71 species and high seasonal variability, Mosepele, 2019), using conventional single-species fish stock assessment, based on steady state assumptions, is considered only partly adequate for a comprehensive and accommodating evaluation of the fishery. The Okavango Delta is subject to seasonal flooding which, like elsewhere, plays a key role in determining the potential and nature of its fishery (Mosepele et al., 2009). However, a comprehensive understanding of the relationship between the hydrological regime and the dynamics of the fishery, the productivity, and the trophic interrelationships remains limited and dispersed.

This study is a systematic review of over two decades of research work in the Okavango Delta. Data used in Figure 3–5 are based on data that were collected over several years as part of a PhD work and are described comprehensively in Mosepele (2019). The aim of this review is to examine the relationship between fish dynamics and environmental variability which allows for assessment of an optimum fishing regime in a flood-pulsed floodplain fishery of the Okavango Delta. Establishing this relationship is important towards identifying the key drivers of change, the potential range of fluctuations, and resilience in floodplain fish communities. Understanding this relationship will aid in floodplain fisheries and water management, as a step beyond prevailing management regimes based on steady state theories and models (Mosepele, 2014).

Tropical and sub-tropical floodplains are dynamic pulsating systems, which are constantly changing at various spatio-temporal scales, but where the seasonal fluctuations are also essential for regeneration and maintenance of the ecosystem. Proper understanding of floodplains is essential towards their conservation aligned with the socio-economic development of riparian communities. The fundamental philosophy underpinning this review is that floodplains are dynamic, interconnected aquatic-terrestrial systems driven by seasonal flooding at variable intra and inter-annual scales and that management needs to be equally dynamic, flexible, and adaptive.

2 Description of the study area

The Okavango River basin (Figure 1) is located in a semi-arid environment with one of most sparsely populated basins in southern Africa. It is a large endorheic (no outlet) system that spans three countries (Angola, Namibia, and Botswana) (Ashton and Neal, 2003; McCarthy et al., 2003).

The catchment of the Okavango River Basin is estimated to be approximately 530 000 km^2 at its largest extent (Andersson et al., 2003). The basin is located in a water scarce region, and future planned water abstractions are projected to amount to

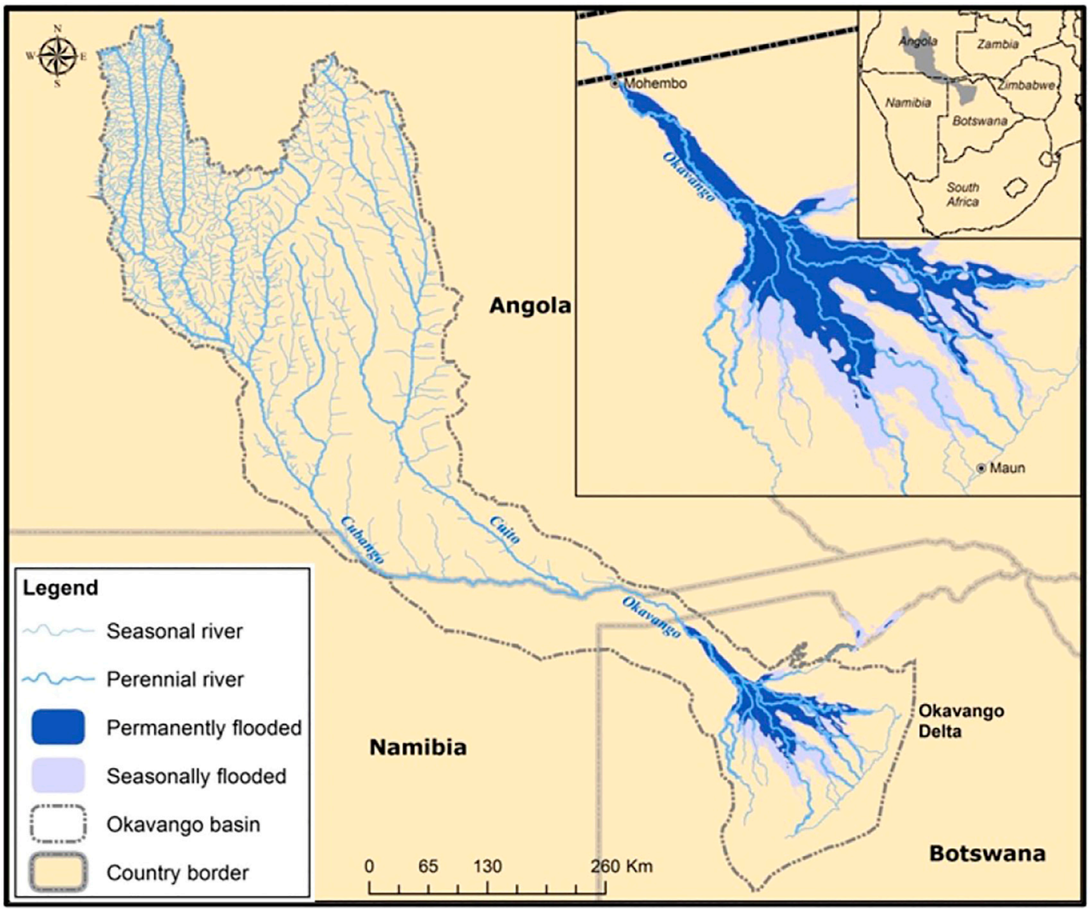

FIGURE 1
Map of the Okavango River basin in southern Africa, with the three countries sharing the drainage basin. The insert shows the Okavango Delta inside Botswana, which is the focus of this study (Source: The ORI GIS Laboratory).

about 3% of the mean annual daily runoff of the Okavango River when entering Botswana at Mohembo at the distant end of the so-called panhandle (Figure 1). According to Steudel et al. (2013) mean annual daily runoff (1974–1998) at Mohembo is 263$m^{-3}s^{-1}$. However, there is not enough knowledge to accurately predict the scale, significance and resilience of ecosystem responses within the Delta to the anticipated decreased flows (Ashton and Neal, 2003).

Currently, the delta is still relatively pristine (Milzow et al., 2009; Black et al., 2011), which nevertheless, does not discount threats to its ecological integrity. Anthropogenic threats to the delta do not only come from within the country driven by local population development pressures (Porter and Muzila, 1989), but also from transboundary threats which have increased with the advent of peace in Angola (Andersson et al., 2003; Milzow, et al., 2009; Milzow, et al., 2010). After a prolonged civil war, a repopulation of the headwaters of the Okavango has begun (Mendelsohn et al., 2010), where approximately one million people are expected to settle within the river basin (Andersson et al., 2003). Concomitant human activities like agriculture (including irrigation), water abstraction and hydropower development in both Angola and Namibia are expected to place an increased demand on the water resources of the basin (Andersson et al., 2003; Junk et al., 2006; Milzow et al., 2009) and may negatively affect water quantity and quality (Masamba and Mazvimavi, 2008).

2.1 Flooding dynamics in the delta

The Okavango Delta is a vast mosaic of various habitats consisting of swamps, islands and river channels whose aquatic, semi-aquatic and terrestrial phases change constantly at different temporal scales, driven by the flood regime (McCarthy et al., 2003; Ramberg and Wolski, 2008). It is located in a dry sub-tropical area with a mean annual

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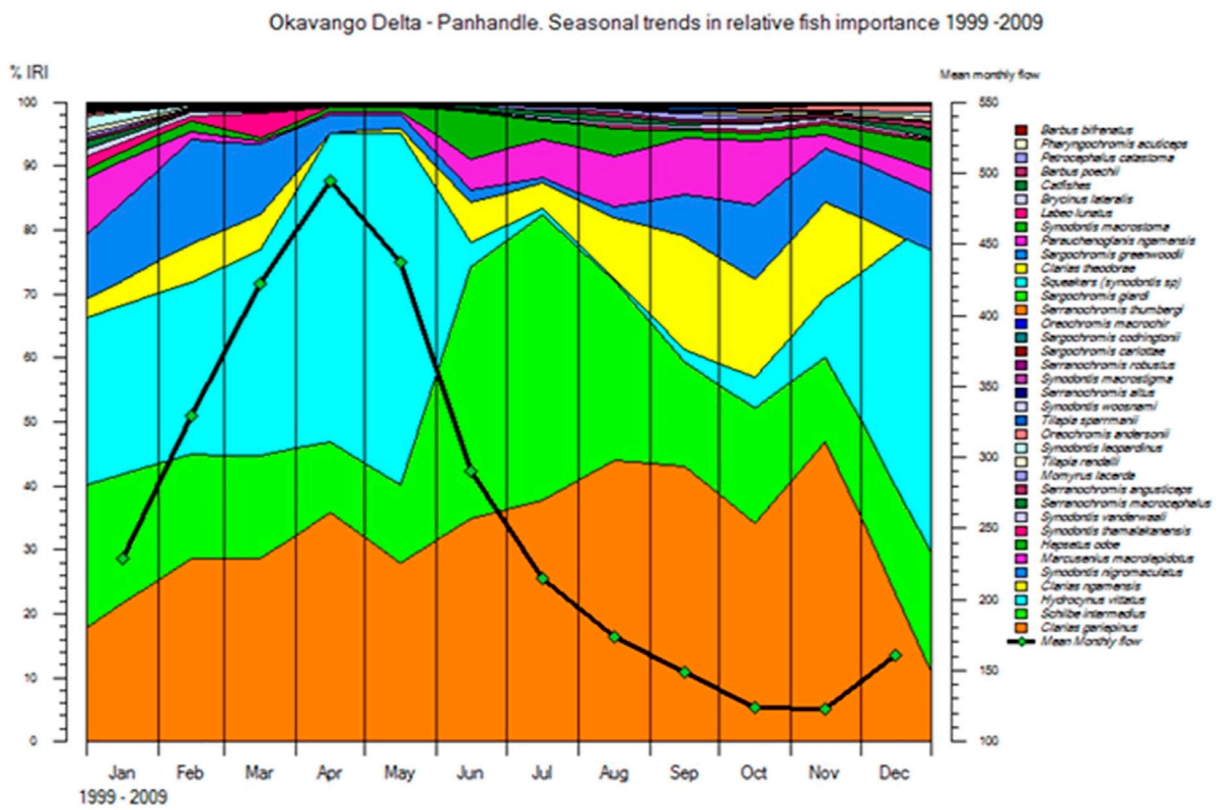

FIGURE 2
Intra annual variations in fish species biodiversity in the Okavango Delta where the black line shows seasonal variability in mean discharge (Source: Mosepele et al., 2017).

rainfall of 475 mm and experiences large annual variations in temperature where October is the hottest month while July is the coldest (Milzow et al., 2009). Rain normally falls in the period November—March while annual flooding from the Angolan highlands occurs in the period April - September (Ramberg and Wolski, 2008). Annual precipitation, which is out of phase with seasonal flooding (Porter and Muzila, 1989; Ramberg et al., 2006a), contributes approximately between 5% (Andersson et al., 2003) and 42% of the total water input into the delta, while the rest comes as discharge from the Angolan highlands (Ramberg and Wolski, 2008). Total water storage in the delta is about 10 Km^3 (about a year's inflow of water) which supports diverse vegetation (Porter and Muzila, 1989) "aquatic" and wildlife species (Ramberg, et al., 2006b). The delta's hydrology is dynamic (i.e. changes in flow patterns from one part of the delta to the other), that varies in response to changes in seismic activity, vegetation dynamics, animal activity (such as hippos) and human intervention (Wilson, 1973; Porter and Muzila, 1989; Wolski and Murray-Hudson, 2006; Milzow et al., 2009), causing the flow in the anastomosis of channels to change at any given time due to variations in these factors.

Peak discharge in the delta's panhandle occurs in March/April (Wolski, et al., 2005) and the flood pulse travels progressively down the delta, taking a maximum of 6 months to reach the distal ends of the system (Andersson et al., 2003). The sinusoidal flooding cycle (Figure 2) in the delta results in a period of minimum inundation (November - March) to a period of maximum inundation (May - September) (Andersson et al., 2003; McCarthy et al., 2003; Wolski et al., 2005). Water depth variations in the permanently flooded areas are usually very small, while normally in the order of 1–2 m in the seasonally inundated parts of the Delta (Ramberg et al. (2006b).

Also inter-annually the flows in the delta have a cyclical behaviour with a 17.5 year periodicity in the annual average and maximum flows (Mazvimavi and Wolski, 2006). However, there is high inter-annual variability in flooding patterns where good flood years may be followed by poor flood years and the extent of flooding in the previous year and local rainfall also affect the extent of flooding in any 1 year (Milzow et al., 2009; Mendelsohn et al., 2010). While inter-annual variations in rainfall cause variability (lows and highs) in its flooding regime (Wolski and Murray-Hudson, 2006), seismic Earth

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movements also cause different parts of the delta to periodically undergo drying episodes (Milzow et al., 2009). Thus, flooding dynamics in the delta are highly dynamic and critical towards a comprehensive understanding of ecological processes in the delta.

3 The Okavango Delta's floodplain ecology

Seasonal flooding liberates nutrients from the inundated soils as new floodwaters enter the floodplains (Welcomme, 1988; Lindholm et al., 2007). The delta has a heterogeneous mosaic of micro-habitats (Siziba et al., 2011a) characterized by low nutrient concentrations (Krah et al., 2006) and oligotrophic waters (Cronberg et al., 1995; McKay et al., 2011). Despite its oligotrophic state, the delta is a productive system (Høberg et al., 2002) as evidenced by relatively high fish production/biomass in some lower delta lagoons (Fox, 1976; Mosepele et al., 2011) and fast vegetation growth (Ramberg et al., 2006a). Several key processes contribute to nutrient dynamics in the delta; (i) surface waters (Cronberg et al., 1995; Garstang et al., 1998; McKay et al., 2011) (ii) soil nutrients (Krah et al., 2006), (iii) dung from mammals in the seasonal floodplains (Mosepele et al., 2009), (iv) mineralization (from senescent plant material and peat) (Ramberg et al., 2006a), and (v) windblown dust/atmospheric deposition (Krah et al., 2006), the latter is a major nutrient source at receding water levels in the seasonal floodplains.

When the new floods arrive, they carry allotropic nutrients from upstream runoff, which facilitate the primary production processes in the delta (Krah et al., 2006). The new floods also dissolve embedded soil nutrients from the terrestrial dry phase, which increase nutrient concentration and availability (Tsheboeng et al., 2014). This is also coupled with an increase in Dissolved Organic Carbon (DOC) in the seasonal floodplains (Mladenov, et al., 2005), due to high organic matter loading (Mladenov, et al., 2007). Additionally, dung from the herds of large herbivores (elephants, buffaloes, antelopes) also contributes to the organic matter loading in the seasonal floodplains (Mosepele et al., 2012). Hippos also play a major role in nutrient cycling of aquatic ecosystems by converting terrestrial biomass (ingested grass) into aquatic nutrients in the delta's waters where they defecate (Garstang et al., 1998). Ultimately, water borne and internal nutrient loading switches to atmospheric deposition when the floods have reached their maximum extent in the seasonal floodplains (Krah et al., 2006). The alternating wetting and drying processes in the delta facilitate optimum conditions for enhanced primary production in the system (Ramberg et al., 2006b). This is consistent with studies from elsewhere (Junk et al., 1989; Ward and Stanford, 1995) which observed that regular flooding and drying in floodplains is an essential recycling nutrient pump for biological production.

Average biomass of large mammals in the delta is approximately $12\,t\,km^{-2}$, and is among the highest in wetlands around the world (Junk et al., 2006). The density of mammals in the Okavango Delta is 4–8 times higher than expected from its standing nutrient status, primarily because of its high efficiency in primary productivity from recycling nutrients (Ramberg et al., 2006b). This positive feedback loop in fertilization makes the delta highly efficient in transforming plant carbon into higher food-web levels through terrestrial mammals (Junk et al., 2006).

Regular flooding and drying episodes in the delta increase plant diversity (Tsheboeng et al., 2014), in accordance with Huston's (1979) "intermediate disturbance hypothesis". Other "disturbing factors" include erosion and sediment deposition, and actions by biological engineers like elephants, hippos and termites (Mosepele et al., 2009). Frequent disturbances in the Delta create small-scale habitat patches, which facilitate the co-existence of different successional stages of plant communities (Tsheboeng and Murray-Hudson, 2013). Generally, flood pulsed systems provide diverse food items to food webs, and act as dry season refuges for migrating mammals (Junk et al., 1989; Junk et al., 2006; Bartlaam-Brooks et al., 2011). Flooding dynamics in the delta, coupled with the "out-of-phase" rainfall season, ensure that fresh primary vegetation is available much longer in the Delta for herbivore mammals, which increases the land's carrying capacity (Junk et al., 2006). All these interrelated dynamics enhance ecosystem productivity, and contribute to the high productivity in the Delta, despite its oligotrophic clear water.

In addition to a high average biological basis production, the aquatic processes in subtropical and tropical floodplains systems undergo "boom and bust" conditions driven by seasonal flooding (Lowe-McConnell, 1987; Junk et al., 1989; Bunn et al., 2006; Schongart and Junk, 2007; Kolding and van Zwieten 2012). The seasonal flooding in the Okavango Delta initiates a "boom" in the aquatic primary production when the new annual floods inundate the peripheral floodplains (Høberg et al., 2002). As the floodwaters submerge the floodplains, microbial decomposition begins to degrade the accumulated detritus, dung, perennial plants, and other organic matter. There is an initial build-up in nitrogen and phosphorous concentrations at the start of the flooding season, but these are gradually depleted over time through photolytic degradation and burning in the dry floodplains. There are spatio-temporal variations in dissolved oxygen (DO) (Høberg et al., 2002), conductivity and phosphorous concentrations (Siziba et al., 2011b). DO levels are initially low at the onset of the floods and increase gradually, before reducing again at decreasing flood levels (Høberg et al., 2002). There is also diurnal variability in DO levels where anoxic conditions are observed at sunrise while peak DO saturation levels occur at sunset (Høberg et al., 2002).

The initial flooding in the delta results in a "boom" in chlorophyll *a* and primary production processes, followed by a "bust" towards the end of the flooding cycle. During the first week of flooding, chlorophyll *a* concentration increases from 2.6 to 23.5 μg L^{-1} before receding to 10 μg L^{-1} by the end of the flooding season (Høberg et al., 2002). Similarly, primary production increases from 63 μg C L^{-1} day $^{-1}$ at the onset to 264 μg C L^{-1} day $^{-1}$ within a week of flooding, before settling to 82 *μ*g C L^{-1} day $^{-1}$ by the end of the first month of flooding. However, there is spatial variability in chlorophyll *a* concentration across the delta's microhabitats (Siziba et al., 2011a). The seasonally inundated floodplains in the delta have higher concentrations of DOC, K, SiO_2, Mg, HCO_3, Na and NO_3 than permanently flooded areas (Mackay et al., 2011). Like the mosaic pattern of the delta itself, there are spatial and temporal variations in water chemistry. This complex system is further exacerbated by a rolling time lag where new floods arrive at Mohembo (northern delta), while the previous year's flood are still receding at Maun (southern delta) (Mackay et al., 2011).

The zooplankton biomass "boom" at the onset of the floods is inoculated from egg banks in the seasonal floodplains (Høberg et al., 2002; Siziba et al., 2012). Regular flooding is important in maintaining micro-crustacean propagules and the diversity of these micro-fauna in the Delta's floodplains (Siziba et al., 2012). Cladocerans, copepods and ostracods are the three major groups whose emergence from floodplain sediments is initiated by inundation. These micro-crustacea, which are key fish food (Siziba et al., 2013), then inoculate new flood waters in the seasonal floodplains (Siziba et al., 2012). Riding on the wave of seasonal flooding are strong fluctuations in zooplankton biomass over the flooding season in the seasonal floodplains (Høberg et al., 2002). Zooplankton biomass peaks at about 10 mg DW L^{-1} during the first month of flooding, which gradually declines to 1 mg DW L^{-1} towards the end of the flooding season. Høberg et al., (2002) also observed a species succession in zooplankton species during the flooding season. *Moina micrura* is the dominant species during the onset of the flood, whose populations then decrease to the end of the first month of flooding. Zooplankton populations are then dominated by *Daphnia laevis* during the second month of flooding, while *Chydorus* spp. dominates the zooplankton community at the end of the flooding season.

4 An overview of the Okavango Delta fishery

Structure of the fishery: Based on two previous frame surveys in the delta, there are approximately 3000 fishers in the Okavango Delta fishery (Mosepele, 2001; Bokhuto et al., 2007). Generally, the number of fishers has gradually decreased over time (SADC, 2016). Approximately 7% of the fishers constitute a small-scale commercial fishery (Mosepele, 2001; Bokhuto et al., 2007) composed of modern gill nets and aluminium boats outfitted with outboard engines (Mosepele, 2001). Earliest records of fishing in the delta include extensive use of traditional fishing traps, weirs, traps, spear fishing, and traditional hook and line all used in different habitats and across hydroperiods (Kay, 1962; Maar, 1965) and these fishing gears are still the most common gears in the fishery (Mosepele et al., 2003).

TABLE 1 Total annual fish yield/estimates from the Okavango Delta fishery based on various sources where data with an * are estimates from the Fisheries Division while data with[1] are from various sources.

Year	Yield (tons yr–1)	Source
1974[1]	1,200	Gilmore (1976)
1976[1]	400	Gilmore (1976)
1985[1]	500	Norplan (1985)
1987[1]	360	Mmopelwa (1989)
1988[1]	231	Mmopelwa (1989)
1989	98	Merron (1993)
1990[1]	350	Scudder et al. (1993)
1991	157	Merron (1993)
1996	71	FAO (2003)
1998	182	FAO (2003)
2000*	152	Arntzen (2005)
2001*	111	Arntzen (2005)
2001	385	Mosepele (2001)
2002*	114	Arntzen (2005)
2003*	92	Arntzen (2005)
2005	1850	Arntzen (2005)
2006	450	Turpie et al. (2006)
2019	614	Mosepele (2019)

These different fishing gears and methods are used across different habitats and hydroperiods in the delta (Mmopelwa et al., 2009). This suggests that generally, the Okavango Delta has retained its traditional/artisanal character (Cassidy et al., 2011). According to Mosepele et al. (2003), there are five different types of fishers in the Okavango Delta; basket fishers, traditional hook and line fishers, gill net fishers, trap fishers and spear fishers. Recreational tourist fishers are another key group in the delta's fishery (Mosepele, 2000; SADC, 2016). Traditional hook and line and basket fishers are the major groups in the delta (Mosepele, 2001; Mosepele et al., 2003). NORFICO (1986) defined fishers as either occasional, seasonal or professional. Furthermore, Turpie et al. (2006) defined fishers as either "traditional" or "modern" where the latter own at least one gillnet.

4.1 Production/yield

Catch statistics are a major challenge in most fisheries around the world (FAO, 2020) particularly in inland fisheries

(Welcomme, 2011) and Botswana is not an exception. Generally, data on fish catches are fragmented (Arntzen, 2005) and irregular. Therefore, there is a lack of accurate catch statistics from the Okavango Delta, and most of the initial records are best estimates (Mosepele, 2003). Subsequently, the period between 1970 and 1987 is characterized as a time of poor/uncertain data, while fish yield data from 1996 are relatively better (Mosepele, 2003). Table 1 summarizes fish production data from the Okavango Delta. Turpie et al. (2006) attributes these discrepancies to the presence of different actors in the delta's fishery. However, inter-annual variability in flooding patterns can also cause discrepancies in fish production estimates. Fishing effort in the delta is driven by the seasonal flood regime (Mosepele et al., 2018), where most traditional/artisanal fishers are only active during good flood years (Mosepele, 2001). Furthermore, Mosepele (2000) and Mosepele (2001) highlights that catch data is only collected from gill net fishers, which would underestimate the total annual production from the fishery. The extent of flooding in the delta also opens up new fishing grounds which would increase the total annual fish production from the system. According to Mosepele (2019), fishery yield is driven by the delta's flood regime at a 2-year time lag. This fishery-flood relationship is an illustration of Junk et al.'s (1989) flood pulse concept.

Turpie et al. (2006) estimated the total annual private use value of the delta's fishery at approximately US$ 490,000 (based on 2005 exchange rates), which was approximately 9% of the total value from the delta's wetland resources. Despite this relatively low use value, the delta's fishery is a source of livelihoods and food security for subsistence fishers (Mosepele et al., 2006) who increase fish catches as the first and second coping strategy during periods of food shortage (Mosepele et al., 2006; Ngwenya and Mosepele, 2008; Mmopelwa et al., 2009). Subsistence fishers either sell their surplus fish for cash or barter them for grain (Ministry of Agriculture, 1997; Mosepele, 2001; Mmopelwa et al., 2009). Therefore, subsistence fishing is a source of income for 40% of subsistence fisher households in the delta, where fishing income is used on food, toiletry, and clothing (Ngwenya and Mosepele, 2008). This is in accordance with Mmopelwa et al. (2009) who observed that subsistence fishing has socio-cultural, socio-economic and food security value to the delta's subsistence fishers.

Furthermore, the presence of a small-scale and yet profitable commercial fishery (Mmopelwa et al., 2005) makes it an integral part of the delta's rural livelihoods strategy (Mosepele and Ngwenya, 2010). The small-scale commercial fishery is not only a source of rural employment (Mosepele, 2001; Mmopelwa et al., 2005; Mosepele and Ngwenya, 2010), but fishery revenue is also invested into either agriculture (Mendelson et al., 2010; Mosepele and Ngwenya, 2010) or other economic activities (Mosepele, 2001). Kgathi et al. (2018) observed that the small-scale commercial fishery also contributes to fish regional trade, which may contribute to a reduction of Botswana's food import bill. Generally, most of the fish catch goes towards livelihood support (Arntzen, 2005) which makes fish not only a valuable safety-net (Mendelson et al., 2010) but also a resource (Mosepele, 2001). Traditional (artisanal) fishing is also identified as a natural safety net against HIV/AIDS comorbidities in the delta (Ngwenya and Mosepele, 2008). Based on income generated, fishing was the second most important economic activity in the region after cattle farming in the 1990s (Mosepele, 2003).

5 Fish community dynamics in the Okavango Delta

5.1 Juvenile and small fish species dynamics

Newly inundated floodplains are an important nursery habitat for fish recruitment (Junk et al., 1989; de Oliveira et al., 2020). In the Okavango Delta the inundated areas are dominated by juvenile cichlids (e.g. *Oreochromis andersonii*, *Tilapia sparrmanii* and *Coptodon rendalli*), catfish (*Clarias gariepinus*), and cyprinids (e.g. *Barbus bifrenatus* and *B. barnardi*) during the first month of flooding. Fish fry and juveniles were observed at increasing frequency starting from the second month of flooding (Høberg et al., 2002). The boom of primary producers and zooplankton initiated by the seasonal flooding, serves as abundant food sources for the juvenile fish and small fishes (Siziba et al., 2013) and also some adult fish (Mosepele et al., 2012). The subsequent decrease in zooplankton biomass corresponding with an increased frequency of juvenile fish over the flooding season is largely due to predation and decreased primary productivity (Høberg et al., 2002; Siziba et al., 2013). This suggests that failed or poor floods cause a bottle neck in fish production due to failed zooplankton production (Siziba et al., 2012).

Juvenile fish growth on the inundated floodplains is rapid within the first year of life (Dudley, 1974). Rapid growth ensures that juvenile fish are large enough to (i) avoid being stranded in the floodplains at receding floods, and (ii) avoid heavy predation when migrating into the permanent channels at draw-down (Booth and Merron, 1996). Foraging by juvenile fish in the inundated areas is an adaptation for taking advantage of high zooplankton biomass (Lindholm et al., 2007), and these shallow areas also act as a predator refuge due to highly fluctuating DO concentrations (Kolding 1993; Mosepele et al., 2017). Less frequently flooded areas (those only flooded occasionally at very high flows) show exceptional "booms" in zooplankton biomass and juvenile fish (Siziba et al., 2011b), especially after a low flood year (Siziba et al., 2013). During poor flood (i.e. low flood) years, the zooplankton biomass is less exposed to fish grazing, while predation appears to be a strong regulator of zooplankton biomass during good flood years (Lindholm et al., 2007). Large flood years result in extensive flooded areas which appear to particularly facilitate fish breeding, growth and survival and ultimately increased fish production (Lowe-McConnell, 1987; de Graff, 2003). Thus, the flood volume in the Okavango Delta is a major driver of fish production, where relative fish biomass during a high flood year can be double that of a low flood year (Lindholm et al., 2007).

Alternating wetting and drying processes are necessary in floodplains to increase nutrient turnover, maintain primary production dynamics (Junk et al., 1989) and hence fish production. However, the pattern of rise and fall of the hydrograph is influencing floodplain fish production. According to King et al. (2003), a "relatively slow rate of rise and fall" of the seasonal hydrograph creates optimum conditions for fish species to utilize the floodplain for recruitment. Conversely, a rapid rise and fall in the hydrograph may offset the balanced time lag between primary production and fish production (Tockner et al., 2000), which may result in less successful fish production. However, short lived hardy species in floodplain systems can adjust quickly to extreme hydrological events (Junk et al., 1989; Junk, 2002).

5.2 Large fish community

5.2.1 Structure and distribution

Floodplain fish communities are structured along a hydrology-water chemistry gradient at both seasonal and annual scales (Zeug et al., 2005; Zeug and Winemiller, 2007; Mosepele et al., 2017). However, due to inter-annual differences in flooding regimes, fish communities among years are stochastically different driven by the seasonal dilution and expansion dynamics of the hydrological cycle (Mosepele et al., 2009; Mosepele et al., 2017).

Studies from other areas have shown that poor flood years are dominated by opportunistic fish species (Laë, 1995; Petry et al., 2003), which have fast growth rates and high fecundities. Other studies show that good flood years are dominated by iliophagous (mud-eaters) species, which are preceded by piscivores in poor flood years (Agostinho et al., 2001). Similar kinds of species dynamics driven by flooding at an annual scale have also been observed in the Okavango delta. Seasonally, the Delta's fish community, as judged by experimental catch rates, is dominated by *C. gariepinus* at maximum flooded area, while tiger fish (*H. vittatus*) dominates the fish community in the channels at minimum flooded area (Mosepele et al., 2017). Furthermore, poor flood years are dominated by hardy, multiple spawning species (i.e. *C gariepinus*) while good/high flood years are dominated by opportunistic, highly fecund, total spawning species (i.e. *Schilbe intermedius*) (Mosepele et al., 2017). There are, however, spatial differences in fish community structure among lagoons across the delta (Mosepele et al., 2011). Generally, upper delta lagoons have higher fish species richness than lower Delta lagoons. One factor that may contribute to these community differences is relative hydrological stability in the upper delta vs increased hydrological variability in the lower delta.

5.2.2 Reproduction

While spawning for some floodplain fish species is cued by rising water levels (Dudley, 1974; van der Waal, 1985; Welcomme, 1985; Godinho et al., 2010; Montcho et al., 2011), others spawn at low water levels (Vasquez et al., 2009). In the Okavango Delta, peak spawning for some fish species occurs at low flood levels in the main channel at high water temperatures, while other species spawn during high water levels in the floodplains at low water temperatures (Merron et al., 1990; Mosepele et al., 2017). Van der Waal (1985) observed that spawning for some cichlids was apparently not associated with hydrology, while other studies (Dudley, 1974; Mosepele et al., 2017), found that spawning for the majority of cichlids is associated with a hydrological gradient, However, for some cichlids (e.g. *Serranochromis macrocephalus* and *C. rendalli*) spawning was mostly associated with water temperature, which agrees with van der Waal's (1985) observations.

5.2.3 Growth and Feeding

Floodplain fish growth is fastest during increasing water levels (Power, 1984; Bayley, 1988; Bokhutlo et al., 2015) and peaks at maximum flooded area to take advantage of the available abundant food in the floodplains (Booth and Merron, 1996; Bokhutlo et al., 2015). During the low flood season, intra-specific competition for food (Mosepele et al., 2012) decreases growth rates (Dudley, 1974; Martin et al., 2011). At inter-annual scale, growth of floodplain fish in Kafue, Zambia, differed significantly among years according to flooding and temperature (Dudley, 1974). In the Okavango, there are significant phenotypic differences in maximum size between upper and lower delta *Clarias gariepinus* populations (Mosepele et al., 2011) and some cichlid species (Mosepele and Mosepele, 2005). The phenotypic differences in size for *C. gariepinus* are attributed to hydrological differences between the upper and lower delta (Bokhutlo et al., 2016). Similarly, Merron and Bruton (1988) observed that differences in hydrology between upper and lower delta habitats account for the phenotypic differences in cichlids between these habitats.

Like most other features, the diet and feeding ecology of floodplain fish species is flood-pulse driven (Lowe-McConnell, 1987; Mosepele et al., 2012). After the feeding and growth of the juveniles on the floodplains during high water, a dominant feature is increased piscivory at receding water levels by fish predators when all the young fish are forced back into the main channels (Bayley, 1988; Mosepele et al., 2012). This "concentration effect" at receding water levels facilitates predation by piscivorous fish, as well as fishers. These dynamic processes illustrate the variability of floodplain fish dynamics and the need for adaptive approaches in both exploitation and conservation.

6 Floodplain fisheries management

6.1 Nature of the Okavango Delta fisheries

The preceding overview has highlighted the dynamic interactions and processes between floodplain fish communities and the highly dynamic environment in the delta. Floodplains are unstable, seasonally fluctuating ecosystems characterized by strong intra and inter annual variability, where the flood pulse is a key driver of practically all processes (Junk et al., 1989; Schongart and Junk, 2007). Inland fisheries in Africa are generally small-scale and labour intensive (Welcomme, 2011). They are characterized by multi-species assemblages, of different sizes exploited by diverse fishing gears and methods (van Zwieten et al., 2003; Welcomme, 2011; Kolding and van Zwieten 2014; Mosepele, 2019). In the Okavango Delta, the hydrological regime is a major driver of change in the biology and ecology of the fish community (Lindholm et al., 2007; Mosepele et al., 2009; Linhoss et al., 2012; Mosepele et al., 2012; Bokhutlo et al., 2015; Mosepele et al., 2017). Like the habitat, the fisheries are dynamic, fluctuating, and constantly changing and are never in stable equilibrium and the environmental drivers are in general much more important in regulating productivity than the fishing effort (Jul-Larsen et al., 2003, Kolding and van Zwieten 2006; Kolding and van Zwieten 2012). This makes conventional management approaches based on steady state assumptions inconsistent and difficult (Staples et al., 2004; Mosepele, 2008; Welcomme et al., 2010; Mosepele, 2014).

Except for a few highly commercialized fisheries in freshwater systems like the Amazon and Mekong (Welcomme et al., 2014), most tropical floodplain fisheries are a major source of localized food and nutrition and mostly serving as subsistence for riparian households (Junk, 2002; Mosepele et al., 2006; Welcomme, 2011). Their primary value to local communities is their contribution towards household income and food security (Mosepele et al., 2006), though some African inland fisheries are slowly morphing towards commercial or recreational fishing as well (Kolding and van Zwieten, 2014). Fishers in floodplain fisheries systems use various traditional techniques (Cerdeira et al., 2000; Kolding et al., 2003; van Zwieten et al., 2003) to adapt and optimize utilization of the ever changing fish assemblages, and the same is observed in the Okavango Delta (Mosepele et al., 2007; Mmopelwa et al., 2009; Mosepele, 2019). Floodplain fisheries are thus also a major source of traditional ecological knowledge (Mosepele, 2008) and cultural heritage (Junk, 2002). Therefore, floodplain fisheries management plans should incorporate these characteristics (i.e. cultural values and traditional knowledge) into their management objectives.

6.2 Effort regulation

Gear restrictions and mesh regulations are fixed constant attributes and remain some of the easiest and cheapest regulations to implement in fisheries management regimes (Misund et al., 2002), and these have been widely implemented in floodplain fisheries. The fundamental question in fisheries management is how to regulate the fishing mortality, which is a combination of how to catch the fish (regulated by gear and mesh restrictions) and how much fish to catch (which is based on effort regulation). The key approach to regulate the 'how' question is to control gear selectivity (see next section), while effort on the other hand is sometimes regulated to maintain the aggregate fishing effort to obtain a "maximum sustainable yield" (MSY). An efficient economic exploitation of the fishery is assumed to save fish stocks from over-exploitation/collapse (Bene et al., 2010; Kolding and van Zwieten, 2014). Arguments such as these are attractive to policy makers and introduce policies aimed at effort reduction. The classical argument is that fishing effort is the main factor influencing fish stock dynamics, which is otherwise assumed in "steady state" and since catch is a function of effort, it needs to be managed. The alternative assumption would be that effort is controlled by the current production (Kolding and van Zwieten 2011; Kolding and van Zwieten 2014), and therefore largely self-regulated as in natural predator-prey relationships. According to Mosepele and Kolawole (2017), law enforcement in fisheries is prioritised over rural people's livelihoods. This is a consequence of implementing classical management approaches in fisheries management. Subsequently, anecdotal evidence indicates that people's livelihoods were curtailed through the implementation of these management approaches in the delta (Daily Maverick, 2017).

6.3 Mesh or gear regulation

A key theoretical argument for regulating the gear selectivity is to protect the young fish and target the big fish in order to prevent so-called growth overfishing (Kolding and van Zwieten, 2011). Most fishing gears are selective regarding species, sizes and habitats fished (Kolding and van Zwieten, 2014, Figure 3 and Table 2) but regulating selectivity on certain sizes or species will invariably change the natural composition of the various components in the ecosystem (Garcia et al., 2012). For example, males of *O. andersonii, O. macrochir* and *C. rendalli* (these are the three most important commercial fish species in the Okavango Delta), grow larger than females (Dudley, 1974). Hence, selective harvesting with large mesh sizes would tend to select the males from the populations of these three species resulting in unbalanced sex ratios. Such scenario can alter the breeding sex ratio of an exploited population and ultimately reduce its reproductive potential (Fenberg and Roy 2008). Focusing

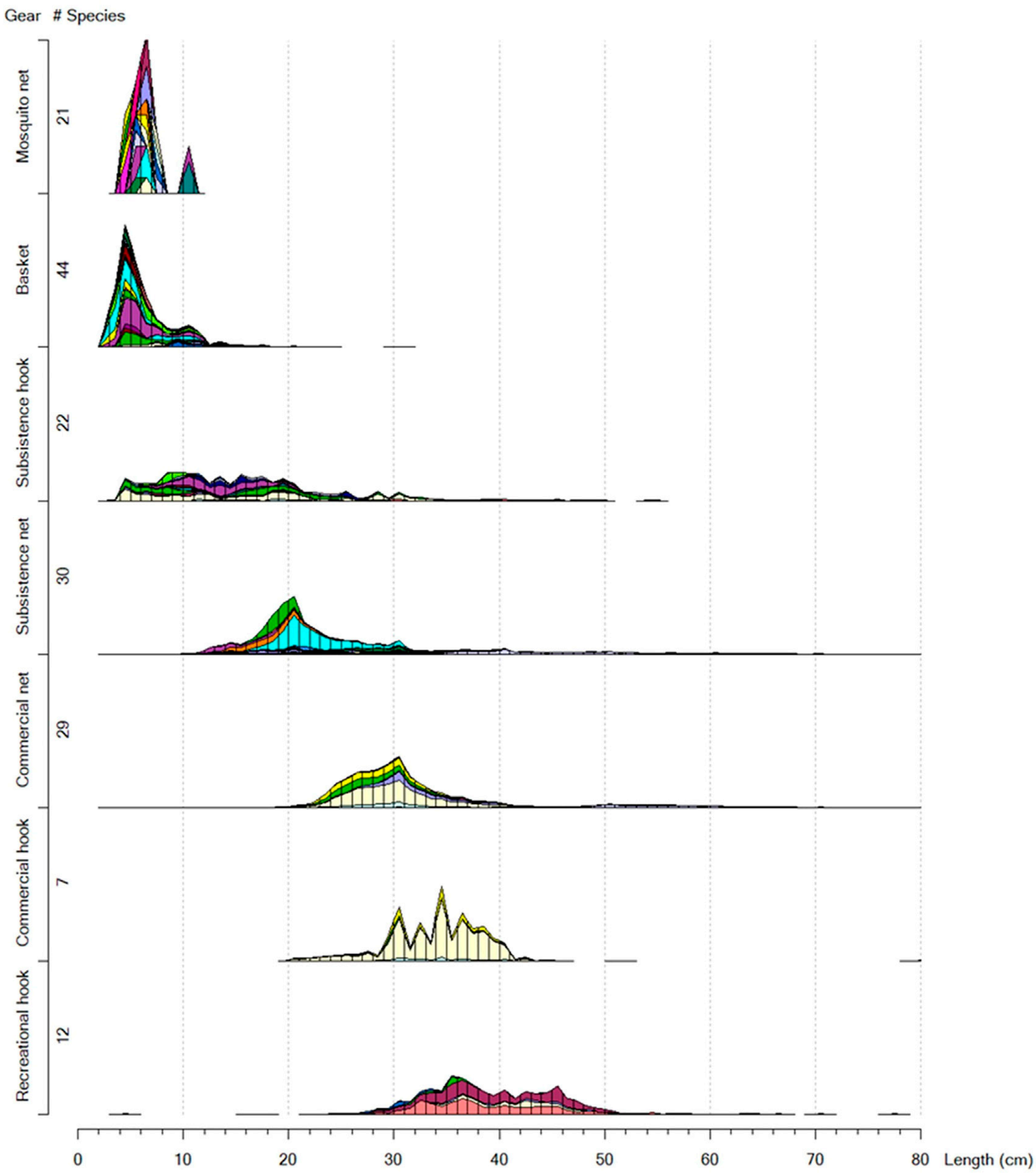

FIGURE 3
Gear signatures in terms of species and size selectivity of the seven most frequently encountered fishing methods in the Okavango Delta. The order of the species is according to the maximum lengths encountered in the catch. Each gear has its own specific signature and there is a clear overall difference in sizes and partly targeted species between the commercial/recreational fishery, targeting larger species and sizes, and the subsistence fishery, targeting smaller species and sizes (Source: Mosepele, 2019)

exploitation exclusively on the mature part of the population will also alter the demographic composition and potential recruitment. It therefore makes ecological sense to also target younger and more productive age classes than only old big fish, the so-called (BOFFFs, Big Old Fat Fecund Females, Hixon et al., 2014), which are the engines of new recruitment by being more fecund and having better egg quality than smaller/younger fish (Trippel, 1995; Walsh et al., 2006; Kolding et al., 2015a). Smaller/younger fish are also relatively more productive than bigger/older fish (Law et al., 2012). Therefore, in order to maintain the natural structure and composition of fish communities it has been suggested to exploit populations in proportion to their natural productivity, the so-called 'Balanced harvest' concept (Garcia et al., 2012; Law et al., 2012; Zhou et al., 2019).

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TABLE 2 List of 63 fish species caught in the Okavango fishery and relative abundance (%) in each of the common gear types. Sorted by ascending maximum size as shown in Figure 3.

Species	Mosquito net	Basket	Subsistence hook	Subsistence net	Commercial net	Commercial hook	Recreational hook	Total	Max length (cm)
Caridina spp	3.3	—	—	—	—	—	—	0	
Barbus haasianus		0	—	—	—	—	—	0	3
Aplocheilichthys hutereaui		0	—	—	—	—	—	0	3
Barbus brevidorsalis	3.3	0.1	—	—	—	—	—	0	4
Barbus multilineatus		0.3	—	—	—	—	—	0	4.5
Aplocheilichthys johnstoni	6.7	0	—	—	—	—	—	0	5
Hemigrammocharax machadoi	3.3	0.9	—	—	—	—	—	0	5
Aplocheilichthys katangae	—	0	—	—	—	—	—	0	5
Mesobola brevianalis	—	0	—	—	—	—	—	0	5
Hemigrammocharax multifasciatus	—	5.4	—	—	—	—	—	0.1	5
Barbus fasciolatus	6.7	0	—	—	—	—	—	0	6
Nannocharax macropterus	6.7	0	—	—	—	—	—	0	6
Synodontis macrostigma	3.3	0	—	—	—	—	—	0	7
Barbus barnardi	3.3		—	—	—	—	—	0	7
Microctenopoma intermedium		3.3	—	—	—	—	—	0	7.3
Synodontis macrostoma	3.3	0	—	—	—	—	—	0	8
Barbus thamalakanensis	3.3	0.2	0.8	—	—	—	—	0	9
Clarias stappersi	—	1.4	—	—	—	—	—	0	9.5
Barbus unitaeniatus	3.3	—	—	—	—	—	—	0	10
Brycinus lateralis	—	2	0.5	—	—	—	0.1	0	10
Barbus paludinosus	—	1.6	—	—	—	—	—	0	10
Barbus radiatus	6.7	0.2	—	—	—	—	—	0	10
Ctenopoma multispine	—	1.2	—	—	—	—	—	0	11
Hippopotamyrus ansorgii	3.3	0	—	—	—	—	—	0	12
Barbus poechii	—	9.7	3.9	—	—	—	—	0.2	13.1
Pharyngochromis acuticeps	—	2.3	—	—	—	—	—	0.1	14
Pseudocrenilabrus philander	6.7	2.2	0.3	—	—	—	—	0	14.5
Synodontis woosnami	—	—	—	—	—	—	—	0	20
Petrocephalus catastoma	—	0.3	—	10.7	0	—	—	1.1	20
Barbus afrovernayi	6.7	1.4	—	0	—	—	—	0	20
Synodontis vanderwaali	—	—	—	0	0	—	—	0	22

(Continued on following page)

TABLE 2 (*Continued*) List of 63 fish species caught in the Okavango fishery and relative abundance (%) in each of the common gear types. Sorted by ascending maximum size as shown in Figure 3.

Species	Mosquito net	Basket	Subsistence hook	Subsistence net	Commercial net	Commercial hook	Recreational hook	Total	Max length (cm)
Pollimyrus castelnaui	—	—	—	0	—	—	—	0	22
Synodontis thamalakanensis	—	—	—	0	0	—	—	0	23
Oreochromis placidus	—	—	—	—	0	—	—	0	24
Synodontis leopardinus	—	—	—	0	—	—	—	0	26
Serranchromis longimanus	3.3	—	—	—	—	—	0.1	0	30
Clarias theodorae	—	—	—	0	—	—	—	0	30
Marcusenius altisambesi	—	1.7		2.3	—	—	—	0.3	30
Sargochromis greenwoodii	3.3	—	1.2	0.1	0	—	3.4	0.1	36
Serranochromis thumbergi	3.3	2.3	4.6	0	0.6	—	—	0.6	38
Serranochromis macrocephalus		0.1	8	0.1	0.6	—	0.5	0.7	39
Tilapia sparrmanii	6.7	25.2	16.4	5.4	0.1	—	—	1.2	39
Tilapia ruweti	—	5.1	0.5	0	0	—	0.1	0.1	40
Sargochromis codringtonii	—	2.8	1.7	0.1	0.2	—	0.2	0.2	40
Sargochromis carlottae	—	—	4.1	1	0.6	—	—	0.7	41
Hemichromis elongatus	—	—	—		0	—	0.1	0	42
Synodontis nigromaculatus	—	0	—	10.5	0.1	—	—	1.1	44
Labeo lunatus	—	—	—	0.2	0	—	—	0	45
Schilbe intermedius	6.7	2.4	1.1	31.1	0.3	—	—	3.4	46
Cyphomyrus discorhynchus	—	—	—	1.8	0	—	—	0.2	47
Oreochromis macrochir	—	0.3	0.8	0.6	15.9	12.5	—	13.5	47
Coptodon rendalli	—	14.9	16.8	1	13.7	2.7	3.6	11.9	49
Momyrus lacerda	—	1.2	—	2	0.3	—	—	0.5	49
Leptoglanis conspicuus	—	—	—	—	—	—	—	0	50
Serranochromis altus	—	—	0.4	0.3	0.3	—	0.1	0.3	52
Hepsetus cuvieri	3.3	2.6	0.3	4.2	0.1	—	0.2	0.5	55
Serranochromis robustus	—	0	3.3	1.2	2.2	1.7	31.8	2.1	62
Serranochromis angusticeps	—	2.9	3	5.5	10.2	0.7	3.7	9	64
Oreochromis andersonii	3.3	4.4	27.6	2.6	41.3	77.8	9.8	38.4	73
Sargochromis giardi	—	0.9	1.3	2	6	4.4	—	5.3	74
Hydrocynus vittatus	—	0.3	2.1	3.2	1.8	0.1	43.8	1.8	82
Clarias ngamensis	—	0.3	0.5	0.3	0.2	—	0.2	0.2	85
Clarias gariepinus	—		0.8	13.7	5.4	—	2.5	6	100
Total	100	100	100	100	100	100	100	100	

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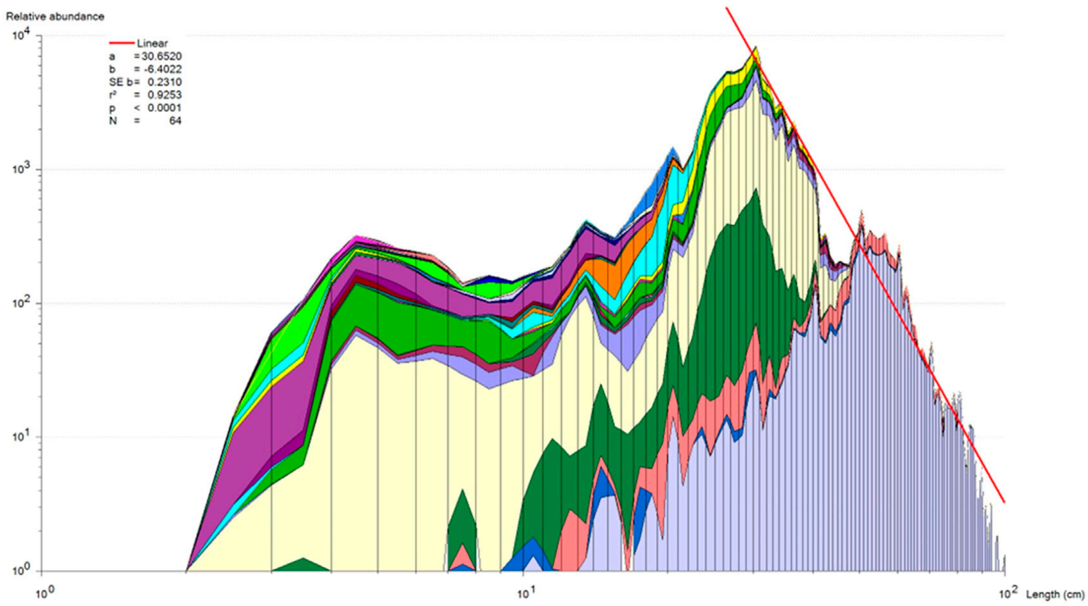

FIGURE 4
Relative biomass-size distribution of the Okavango Delta fishery represented by cumulated standardized (number caught per gear sample) log-log converted catch-curve in the seven most frequently encountered fishing methods (see Figure 3). The slope of the catch curve from 28 cm TL to 100 cm TL is almost identical (p = 0.073) to the theoretical undisturbed Sheldon spectrum slope of −6, which indicate that the fishery is pretty balanced in this size range, consisting of mainly catfishes, tigerfish and larger cichlids. Species and sizes below 28 cm TL are relatively underutilized in terms of a fully balanced fishery (Source: Mosepele, 2019)

Similar species from different habitats in the delta display different phenotypic life history strategies (Merron and Bruton, 1988; Mosepele, 2000; Mosepele and Mosepele 2005; Bokhutlo et al., 2015) where lower delta species are generally smaller, upper delta species are generally larger (Merron and Bruton, 1988; Mosepele et al., 2011). While *O. andersonii* from the lower delta has slower growth than those from upper Delta, *O. macrochir* and *C. rendalli* from the lower Delta grow faster than their upper delta conspecifics (Mosepele, 2000). Moreover, lower delta populations of these three cichlids were found to mature earlier than those from the upper delta (Mosepele and Mosepele 2005). A similar observation was made for *C. gariepinus* (Bokhutlo et al., 2015). Wild tilapias are frequently observed to mature early and breed prolifically in small shallow water bodies, but not in larger, deeper environments (Lowe-McConnell 1982; Kolding 1993), and this 'stunting' is apparently driven by the fluctuating oxygen conditions found in shallow environments (Kolding et al., 2008).

From a multispecies point of view, the smallest fish species (Total Length) in the delta is approximately 3 cm while the largest species is over 1 m with a graduation of sizes in between them (Mosepele, 2019, Figures 3, 4). Implementing conventional mesh (or gear) regulations will skew fishing mortality towards larger sizes of the community size spectrum (Figure 4), causing a structural and demographic change of the fish community, and possibly also effecting functional changes. Selective fishing, can in the long run also cause evolutionary change in exploited populations (Rochet, 1998; Law, 2000). As a consequence, exploited stocks undergo changes in growth and maturation (Rochet, 1998; Law, 2000), and selective fishing essentially causes ecosystem imbalances (Schindler et al., 1998; Law, 2000; Kolding and van Zwieten, 2011). According to the Convention on Biological Diversity (CBD), a major component of the Ecosystem Approach to Fisheries (EAF) is to maintain the structure and function of the natural communities as close as possible to the natural stages.

6.4 A new paradigm—balanced fishing

Classical single-species assessment models are incompatible with multi-species, multi-gear fisheries (Mosepele, 2008; Welcomme, et al., 2010; Welcomme, 2011). A more balanced exploitation pattern, harvesting species of all sizes and all trophic levels in proportion to their individual productivity, is likely the best management approach for floodplain fisheries in terms of both yield and maintaining the fish community structure (Kolding et al., 2003; Mosepele 2014; Kolding et al., 2015b; Mosepele 2019). There are at least nine different fishing gears/methods observed in the Okavango Delta, with specific catch signatures (Figure 3), but which collectively

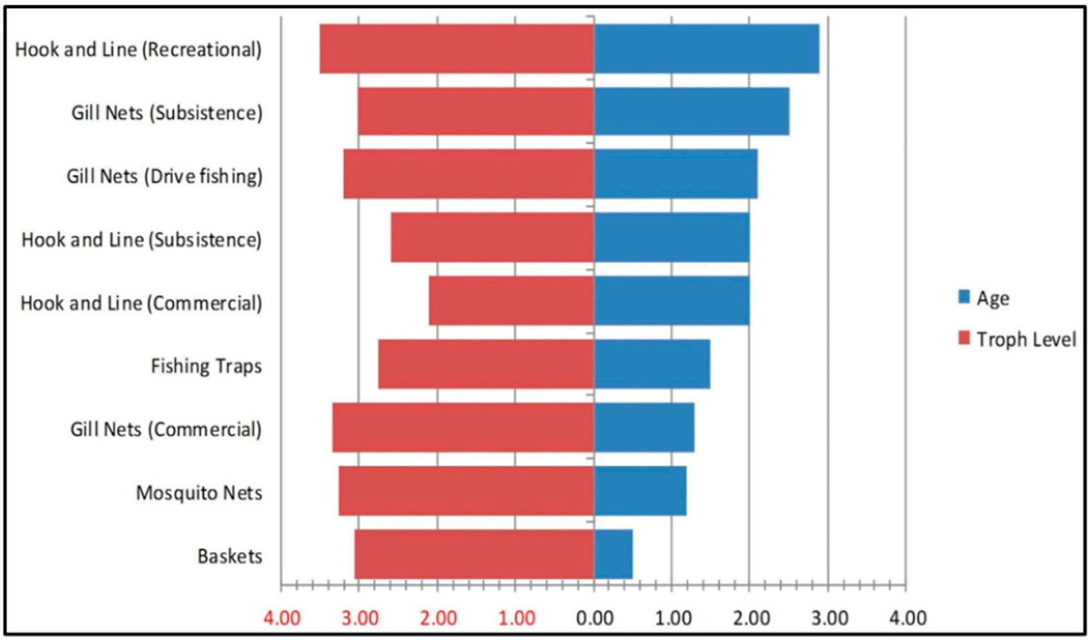

FIGURE 5
Effect of various fishing gears and methods on the Okavango Delta's fish community where the red scale on the *x*-axis represents the mean trophic level of each species calculated from Mosepele et al., 2012, while the black scale represents the mean age of each fish species calculated from Froese and Binohlan (2000) (Source: Mosepele, 2019)

harvest the fish community across different age classes, species and trophic levels (Figures 4, 5) (Mosepele et al., 2003; Mmopelwa et al., 2009). A cumulated log-converted multispecies and multi-gear catch curve (Figure 4; Table 3) shows that the fishery is approximately "balanced" on all sizes above 28 cm TL (being not significantly different from a theoretical slope of −6), but smaller sizes and species are still under exploited compared to larger sizes. Such multi-species harvesting pattern, by the diversified gear assemblage (Figure 3) is a common attribute of floodplain fisheries (Kolding et al., 2003; Kolding and van Zwieten, 2014). The only fish stock assessment of the delta so far (Mosepele and Kolding, 2003), showed that i) the fish stocks were generally under-exploited and ii) that the fish community was being rationally exploited by using several different fishing gears and methods to harvest the delta's diverse species assemblage (Mosepele, 2019, Figure 5).

Currently, some of these gears (e.g. mosquito nets) and fishing methods (e.g. drive fishing) are prohibited in the delta (Botswana Government, 2008; Mosepele, 2008; Mosepele, 2014). However, there is no empirical evidence to justify these regulations. About 70% of the species exploited by mosquito nets are generally very small species (e.g. *Barbus radiatus*, *Aplocheilichthys johnstoni*, etc.), which are not caught by other methods (Mosepele et al., 2003; Mosepele, 2019, Figure 3). Restricting this gear will result in decreased catches of these small sized underutilized species, which are primarily harvested by women for subsistence household consumption. Moreover, small fish are usually eaten whole, with heads, bones, skin and viscera, and represent a concentrated source of multiple essential nutrients compared to only eating the flesh of larger species (Longley et al., 2014). Drive fishing is a traditional and efficient method for exploiting *O. andersonii*, *O. macrochir* and *C. rendalli* (Mosepele et al., 2007; Mosepele, 2019). However, prohibiting drive fishing (which would only legalise stationary gill net setting) will skew gill net fishing mortality towards *O. andersonii* (Mosepele, 2000; Mosepele, 2019), while *Coptodon rendalli*, well known for escaping stationary gillnets (Mosepele, 2000; Kolding et al., 2003; Mosepele et al., 2007), will remain relatively unexploited. In addition, prohibiting drive fishing will result in reduced revenue for the delta's commercial fishers which are primarily targeting cichlids. A blanket prohibition of some fishing methods and gears, without informed justification may not only cause ecosystem imbalances, but may also reduce the food security aspect and socio-economic value of the fishery to riparian communities. The principle of Balanced Harvest (BH) has been strongly criticized by Froese et al. (2015), because they argue it does not conform to 'basic population dynamics' as developed by Beverton and Holt (1957). However, the basic population dynamics were single-species, steady state models where fish grow without eating (Tilley et al., 2020), whereas BH is a multi-species concept with a concrete proposal for

TABLE 3 List of 63 fish species caught in the Okavango fishery with mean size, maximum size, and relative abundance in the catch (%). Sorted by ascending maximum size as shown in Figure 4.

Species	Mean size (cm)	Max size (cm)	Relative abundance (No/set)
Caridina spp	—	—	0.001
Barbus haasianus	3.0	3	0.000
Aplocheilichthys hutereaui	3.0	3	0.000
Barbus brevidorsalis	3.4	4	0.001
Barbus multilineatus	3.2	4.5	0.003
Hemigrammocharax multifasciatus	4.1	5	0.056
Hemigrammocharax machadoi	4.0	5	0.010
Aplocheilichthys katangae	5.0	5	0.000
Mesobola brevianalis	4.8	5	0.000
Aplocheilichthys johnstoni	5.0	5	0.002
Nannocharax macropterus	6.0	6	0.002
Barbus fasciolatus	5.5	6	0.002
Synodontis macrostigma	6.2	7	0.001
Barbus barnardi	7.0	7	0.001
Microctenopoma intermedium	6.3	7.3	0.034
Synodontis macrostoma	7.2	8	0.001
Barbus thamalakanensis	6.2	9	0.021
Clarias stappersi	8.9	9.5	0.015
Brycinus lateralis	2.8	10	0.033
Barbus unitaeniatus	10.0	10	0.001
Barbus radiatus	7.0	10	0.003
Barbus paludinosus	5.2	10	0.017
Ctenopoma multispine	7.8	11	0.027
Hippopotamyrus ansorgii	7.0	12	0.001
Barbus poechii	6.0	13.1	0.216
Pharyngochromis acuticeps	8.8	14	0.050
Pseudocrenilabrus philander	6.1	14.5	0.031
Petrocephalus catastoma	18.2	20	1.097
Synodontis woosnami	17.7	20	0.004
Barbus afrovernayi	4.7	20	0.017
Synodontis vanderwaali	13.8	22	0.003
Pollimyrus castelnaui	22.0	22	0.000
Synodontis thamalakanensis	17.7	23	0.005
Oreochromis placidus	23.5	24	0.003
Synodontis leopardinus	19.3	26	0.003
Marcusenius altisambesi	17.8	30	0.260
Serranchromis longimanus	6.0	30	0.001
Clarias theodorae	30.0	30	0.001
Sargochromis greenwoodii	20.7	36	0.072
Serranochromis thumbergi	25.7	38	0.621
Serranochromis macrocephalus	26.0	39	0.698
Tilapia sparrmanii	12.5	39	1.226
Tilapia ruweti	9.2	40	0.101
Sargochromis codringtonii	21.9	40	0.208
Sargochromis carlottae	24.5	41	0.688
Hemichromis elongatus	42.0	42	0.001
Synodontis nigromaculatus	17.8	44	1.148

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TABLE 3 (*Continued*) List of 63 fish species caught in the Okavango fishery with mean size, maximum size, and relative abundance in the catch (%). Sorted by ascending maximum size as shown in Figure 4.

Labeo lunatus	25.8	45	0.046
Schilbe intermedius	21.7	46	3.444
Oreochromis macrochir	28.0	47	13.543
Cyphomyrus discorhynchus	24.2	47	0.199
Momyrus lacerda	32.8	49	0.484
Coptodon rendalli	26.5	49	11.940
Leptoglanis conspicuus	29.8	50	0.036
Serranochromis altus	30.2	52	0.323
Hepsetus cuvieri	27.3	55	0.525
Serranochromis robustus	33.6	62	2.113
Serranochromis angusticeps	30.8	64	8.955
Oreochromis andersonii	30.0	73	38.414
Sargochromis giardi	28.8	74	5.278
Hydrocynus vittatus	48.3	82	1.806
Clarias ngamensis	45.4	85	0.249
Clarias gariepinus	52.8	100	5.958
Total	30.0	—	100

implementing the Ecosystem Approach to Fisheries (EAF) (Kolding et al., 2015b), which does not only make ecological and biological sense in floodplain fisheries (Kolding et al., 2003; Mosepele, 2014), but it is also sensitive to the traditional fishing patterns and cultural value of floodplain fisheries (Mosepele, 2008).

Diversified fishing techniques, as traditionally practiced in the Okavango Delta and many other African inland fisheries (Kolding and van Zwieten, 2014), ensure that most species across various sizes and habitats-in the fish community are exploited. It also allows impoverished households (especially those headed by women), to have access to high quality protein and nutrients, which again ensures that young children from these fishing households have a relatively good nutritional status (Nnyepi et al., 2007; Longley et al., 2014; Kolding et al., 2019). BH was intended to reduce adverse ecological impacts of fishing while also supporting sustainable fisheries (Garcia et al., 2012). Fisheries management should also preserve cultural and heritage practices of fishing communities when these are not proven destructive, because, "culture is a fundamental human right" (Junk, 2002). Therefore, we advocate for balanced fishing that allows the utilisation of diverse fishing gears and methods to exploit the delta's fish community.

7 Conclusion

The seasonal flood pulse in the Okavango Delta, driving the dry and wet floodplain phases, is the main contributor towards enhanced ecosystem production in an otherwise oligotrophic and semi-arid environment. Seasonal flooding not only changes the physical landscape of the delta, by re-connecting isolated lagoons and creating a multitude of diverse micro-habitats, it also enhances nutrient dynamics in both the terrestrial and aquatic system. These alternating micro-habitats ensure continuous succession in plant communities and enhanced plant biomass production (much of which is grazed by large herbivores), thereby contributing to nutrient recycling in the system. Much of this shifting terrestrial and aquatic based food web is eventually transformed into fish biomass.

Fish production is dynamic and fluctuating both seasonally and interannually and comprises many species of various sizes, trophic levels, and life histories, which can only be exploited by deploying a wide range of seasonally adapted fishing methods. Single-species management, based primarily on regulating selectivity towards larger species will distort the fish community structure, will lower the overall yields, and does not comply with an ecosystem approach towards maintaining the structure and function of the natural community composition. It also prevents marginalised groups from using traditional fishing methods for essential and nutritious subsistence household consumption. For these communities, the fish resource is a key source of household food and nutrition security. Leveraging these resources for local communities will contribute significantly to socio-economic development of these communities. Management interventions in floodplain fisheries should be adaptive, practical, realistic, and implementable, which in practice means acceptable to the stakeholders. Most developing countries have limited resources (particularly financial and human resources), and these should be spent on achievable, agreeable, and practical activities. Informed management also necessitates continuous long-term monitoring of exploited fisheries to follow changes and to gradually improve our understanding of fishing patterns and their impact on the fish communities. This involves the collection of fisheries related data across a broad spectrum of activities (e.g. fish consumption, employment creation, various kinds of biological data on species exploited, gear use and efficiencies, etc.) and associated factors/variables (e.g. environmental factors, various land-use activities, etc.). Once these have been documented and understood, they can be integrated into a flexible management system, which will allow for more adaptive management of these resources. Such integration is currently lacking in the Okavango Delta in line with many other floodplain fisheries.

This review has shown that periodic drying and flooding episodes in the delta are necessary for primary production. Therefore, any management efforts implemented in this system should ensure that these natural cycles are maintained. This is consistent with Junk et al.'s (1989) flood pulse concept which highlights the importance of the seasonal flood pulse in maintaining ecosystem productivity in floodplain systems. Mosepele (2009), Mosepele (2019) also highlighted the key role of seasonality in maintaining productivity of the delta's fish resources.

Author contributions

KM: Conceptualization of the paper and did all the major work on the paper. JK: Assisted with the conceptualization and drafting of the paper TB: Assisted with the drafting of the paper. BM and MM: Assisted with the discussion section of the paper, particularly on fisheries management in the Okavango Delta. All the authors also reviewed the final iterations of this paper.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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