DYNAMICS OF THE SEASONAL FLOODPLAIN FISHERY OF THE OKAVANGO DELTA, BOTSWANA
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ABSTRACT
Inland fisheries provide vital proteins, jobs and income, for some of the most marginalized communities of the world. Therefore, there is a compelling need to understand the dynamics of floodplain fisheries better because of their intrinsic value to riparian communities. The aim of this study is to examine the relationship between fish dynamics and environmental variability. Establishing this relationship is important towards identifying the key drivers of change, restoration and persistence in floodplain fish communities. This paper reviews literature on floodplain fish communities to highlight their dynamics and contribute to their management. This paper highlights the dynamic interactions between seasonal hydrology and nutrient dynamics in floodplain systems. These dynamic processes, coupled with a heterogeneous system, sustain a diverse fish community that is a key source of livelihoods for the riparian community. Dynamic processes within the fish community, such as distribution, feeding and growth are driven by the seasonal flood pulse. Currently, the fishery is managed through a series of classical management approaches which are incongruent with the nature of the fishery. The best management approach is through balanced harvesting, which has inadvertently been implemented by traditional exploitation practices.

KEY WORDS
Okavango Delta; Fisheries Management; Balanced Exploitation Rates; Balanced Harvesting

1. Introduction

Tropical inland fisheries, while producing at least 15% of the global fish production, are based on the tiny fraction (≈ 0.04 %) that tropical freshwater systems contribute to the world’s freshwater resources [1]. Most importantly, inland fisheries provide vital proteins, jobs and income, for some of the most marginalized communities of the world [2]–[4]. It is internationally recognized that the growing global population, with a consequent increase in food demand, will place pressure on global water resources in the next 20 years (e.g. http://www.waterforfood.org/). According to [5] this situation is of particular concern in Africa, where pressure on water resources is expected to increase within the next two decades. Climate change will increase water stress in southern Africa [6] because of reduced rainfall [7], which will certainly decrease fish yields due to reduced productivity [8]. This will 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 [2]. There is a compelling need to understand the dynamics of floodplain fisheries better because of their intrinsic value to riparian communities.

The Okavango Delta (Fig 1) is one of the largest inland river deltas in the world [9] and floodplain fisheries are in general considered among the most productive in the tropics [10], [11], with an average potential fish production rate 2.5-4x that of tropical lakes and reservoirs on a water surface area basis [12]. The Okavango delta fishery is predominantly artisanal combined with a small-scale commercial gill net fishery [13]. Common with most African inland fisheries, the fishery is characterized by a multi-species, multi-gear fishery harvesting the fish community across different trophic levels [13]. Approximately 65 % of the 25340 people (based on 1995 population estimates) who live within the periphery of the Delta depend on the fishery as a source of livelihood [14]. Due to competing uses of the Delta’s resources, particularly between the tourist industry and the local people, there have been stakeholder conflicts and repeated allegations of over-exploitation of the fish resource and deterioration of the environment. However, apart from a preliminary analysis [15] there have been no rigorous assessment of the Okavango delta fishery. Because of the complex dynamic nature of the fishery (approximately 71 species and high seasonal variability), a conventional fish stock assessment, based on steady state assumptions, is inadequate for a comprehensive evaluation of the fishery. The Okavango Delta is subject to seasonal flooding which is believed to play a key role in determining the nature of its fishery. However, a comprehensive relationship between the role of the hydrological regime and the dynamics of the fishery, the productivity, and the trophic interrelationships has never been established.

The aim of this study is to examine the relationship between fish dynamics and environmental variability. Establishing this relationship is important towards identifying the key drivers of change, restoration and persistence in floodplain fish communities. Better understanding this relationship will aid in floodplain...
fisheries- and water management, where prevailing regimes are based on classical approaches that assume equilibrium conditions [16]. Tropical and sub-tropical floodplains are dynamic pulsating systems which are constantly changing at various spatio-temporal scales, but where the fluctuations are also essential for regeneration and conservation of the ecosystem. Proper management of floodplains is key towards socioeconomic development of riparian communities. The fundamental philosophy underpinning this thesis is that floodplains are dynamic interconnected aquatic-terrestrial systems driven by seasonal flooding and drying that is mediated by a flood pulse at intra- and inter-annual scales.

2. Materials and Methods

2.1 Description of the Study Area

The Okavango river basin (Fig 1) is one of the driest and sparsely populated basins in southern Africa. It is an endorheic system that drains three countries (Angola, Namibia and Botswana) [17], [18].

The catchment of the Okavango River Basin is approximately 429 000 km² [17] to 530 000km² [19]. Due to the close connection between the Delta and the upstream catchment area, development projects altering the river’s flow are highly likely to impact the delta’s ecological functioning and fisheries productivity. According to Junk [20], large catchment areas are more vulnerable to upstream development which might alter discharge patterns. Since the basin is located in a water scarce area, future water abstractions are projected to increase to an equivalent of about 3% of the mean annual runoff of the Okavango River at Mohembo. However, there is not enough knowledge to accurately predict the scale, significance and resilience of ecosystem responses within the Delta to decreased flows [17] of the scale suggested above.

Currently, the Delta is relatively pristine [21], [22], which however, does not discount threats to its ecological integrity. Threats to the Delta do not only come from within the country driven by local population development pressures [23], but there are also transboundary threats which have heightened with the advent of peace in Angola [19], [21]. [24]. The advent of peace after a prolonged period of civil war has resulted in a repopulation of the headwaters of the Okavango [25], where approximately one million people are expected to settle within the headwaters of the river basin [19]. Concomitant to this, are expected human activities such as agriculture (including irrigation), water abstraction and hydropower development in both Angola and Namibia which are likely to place a demand on the water resources of this river basin [19], [21], [26].

2.2 Flooding Dynamics in the Delta

The Okavango Delta is a 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 [18], [27]. It is located in a dry sub-tropical area with a mean annual rainfall of 475 mm and experiences large annual variations in temperature where October is the hottest month while July is the coldest [21]. Rain normally falls in the period November – March while annual flooding from the Angolan highlands occurs in the period April-September [27]. Annual precipitation, which is out of phase with seasonal flooding [23], [28], contributes approximately between 5% [19] and 42% [27] of the total water input into the Delta, while the rest comes as discharge from the Angolan highlands [27]. Total water storage in the Delta is about 10 000 Mm³ which supports diverse vegetation [23] aquatic and wildlife species [29]. The Delta’s hydrology is unstable (i.e. changes in flow from one part of the Delta to the other), and is driven by various factors such as seismic activity, vegetation dynamics, animal activity and human intervention [21], [23], [30], [31]. This suggests that flow in the web of channels can change at any given time due to variations in these factors. Therefore, the Delta is a highly variable and dynamic system characterized by high inter and intra annual variability in its flow regime [21]. Peak discharge in the Delta’s panhandle occurs in March/April [32] and the flood pulses slowly down the Delta, taking a maximum 6 months [19] to reach the distal ends of the system. This sinusoidal flooding cycle in the Delta results in a period of minimum inundation (November - March) to a period of maximum inundation (May - September) [19][18][32]. There is a time lag between inflow and flood extent in the Delta. According to Ramberg et al [29], water depth variations in the permanently flooded areas are usually very small, while these are normally in the order of 1-2 m in the seasonally inundated parts of the Delta.
Annual average, minimum and maximum flow years in the Delta have a cyclical behavior where a 17.5 year cycle is the most important for annual average and maximum flows [33]. However, there is high inter-annual variability in flooding patterns where good flood years may be followed by poor flood years [21], [25]. The extent of flooding in the previous year and local rainfall also determine the extent of flooding in any one year [21], [25]. While inter-annual variations in rainfall cause variability (lows and highs) in its flooding regime [34], earth movements also cause different parts of the Delta to periodically undergo drying episodes because of shifts in flow [21]. Flooding dynamics in the Delta is critical towards a comprehensive understanding of ecological processes in the Delta, because flood expansion starts several months after the end of the rainy season, making water available throughout the year [32].

### 2.3 Floodplain Ecology and Primary and secondary Production Dynamics

Seasonal flooding liberates nutrients from the inundated soils as new floodwaters enter the floodplains [35]. The Delta has a heterogeneous mosaic of micro-habitats [28] characterized by oligotrophic [36], [36], [37] waters. Despite the oligotrophic nutrient status, the Delta is a productive system [38] as evidenced by relatively high fish production/biomass in some lower Delta lagoons [39], [40] and high vegetation growth [29]. Several key processes contribute to nutrient dynamics in the Delta; (i) surface waters [36], [37], [41] (ii) soil nutrients [42], (iii) dung from mammals in the seasonal floodplains [43], (iv) mineralization (from senescent plant material and peat) [29], and (v) dust/ atmospheric deposition [42]. Dust deposition is a major nutrient source at receding water levels in the seasonal floodplains [42]. When the new floods arrive, they carry with them allotropic nutrients from upstream runoff which facilitate the initial primary production processes in the Delta. These new floods then dissolve embedded soil nutrients from the terrestrial phase which increase nutrient concentration and availability. This is also coupled with an increase in DOC in the seasonal floodplains [44], due to high organic matter loading [45]. Additionally, dung from the herds of large herbivores (elephants, buffaloes, antelopes) also contributes to the organic matter loading in the seasonal floodplains [46]. Hippos also play a major role in nutrient loading of aquatic ecosystems through transferring terrestrial biomass (grass) into aquatic nutrients (through their dung) into the Delta’s waters [41]. Nutrient loading then switches to atmospheric deposition when the floods have reached their maximum (flooded) extent in the seasonal floodplains [42]. The wetting and drying processes in the Delta facilitate optimum conditions for enhanced primary production in the system [29]. This is consistent with studies from elsewhere [11], [47] which observed that regular flooding and drying in floodplains is an essential nutrient pump for biological production.

Biomass of large mammals in the Delta is approximately 12 t km-2, and is the highest among seven globally important wetlands around the world [26]. The density of mammals in the Okavango Delta is 4-8x higher than expected, primarily because of its high primary productivity, despite the low nutrient status of its soils [29]. These herbivores fertilize the floodplains during the dry season, while seasonal flooding captures these nutrients into the aquatic environment, which then facilitates primary production, and ultimately fish production [26], [38]. This makes the Delta highly efficient in transforming plant carbon into higher food-web levels through terrestrial mammals [26].

Regular flooding and drying episodes in the Delta increase plant diversity [48], which is in accordance with Huston’s [49] “intermediate disturbance hypothesis”. Other drivers of this habitat “disturbance” include erosion and sediment deposition, and actions by biological engineers like elephants, hippopotamus and termites [43]. Frequent disturbances in the Delta create small-scale habitat patches which facilitate the co-existence of different successional stages of plant communities. Flood pulsed systems therefore provide diverse food items to ecosystem food webs, and also act as dry season refuges for migrating mammals. Flooding dynamics in the Delta, coupled with the “out-of-phase” rainfall season, ensure that primary vegetation is available much longer in the Delta for mammals, which increases the land’s carrying capacity [26]. These dynamics enhance ecosystem productivity, and contribute to the high productivity in the Delta, despite its otherwise low water nutrient levels. Biological production processes in subtropical and tropical floodplains systems undergo “boom and bust” conditions driven by seasonal flooding [11], [50], [51]. Accordingly, seasonal flooding in the Delta initiates a “boom” in primary production when the new annual floods inundate the peripheral floodplains [38]. As the floodwaters submerges detritus in the floodplains, microbial decomposition begin to degrade the detritus and other organic matter. There is an initial build-up in N and P concentrations at the start of the flooding season, but these are gradually depleted over time through photolytic degradation and burning. There are spatio-temporal variations in dissolved oxygen (DO) [38], conductivity and P concentrations [52]. DO levels are initially low at the onset of the floods and increase gradually, before reducing again at decreasing flood levels [38]. There is also diurnal variability in DO levels where anoxic conditions are observed at sunrise while peak DO saturation levels occur at sunset [38].

According to Lindholm et al [38] 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. 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 µg 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 [52]. The seasonally inundated floodplains in the Delta have higher concentrations of DOC, K, SiO2, Mg, HCO3, Na and NO3 than permanently flooded areas [37]. 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 surging time lag where new floods arrive at Mohembo (northern Delta), while the previous year’s flood are still receding at Maun (southern Delta) [37].

The sharp increase in zooplankton biomass “boom” at the onset of the floods is inoculated from egg banks in the seasonal floodplains [38], [53]. Regular flooding is important in maintaining micro-crustacean propagules and the diversity of these micro-fauna in the Delta’s floodplains [53]. Cladocerans, copepods and ostracods are the three major groups whose emergence from floodplain sediments is driven by inundation. These micro-crustaceans, which are key fish food [55], then inoculate new flood waters in the seasonal floodplains [53]. Riding on the wave of seasonal flooding are strong fluctuations in zooplankton biomass over the flooding season in the seasonal floodplains [38]. 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. Hoberg et al [38] 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.

2.4 The Flood Pulse and Fish Community Dynamics
2.4.1 Juvenile and small fish species dynamics

Newly inundated floodplains are important habitat for fish recruitment in seasonal floodplains [54]. In Okavango delta this is supported by Hoberg et al [38] who observed that the fish community in the inundated areas was dominated by juvenile cichlids (e.g. Oreochromis andersonii, Tilapia sparrmanii and Coptodon rendalli), 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 abundance starting from the second month of flooding [38]. The boom of primary producers and zooplankton facilitated by seasonal flooding [53], provides abundant food for juvenile fish and small fishes [55] and some adult fish [46]. The subsequent decrease in zooplankton biomass corresponding with an increased abundance of juvenile fish over the flooding season is due to predation [38]. This suggests that failed or poor floods can create a bottle neck in fish production due to failed zooplankton production [53]. Juvenile fish growth on the inundated floodplains is rapid within the first year of life [56]. 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 to permanent channels at drawdown [57]. Foraging of juveniles on the inundated areas is an adaptation that takes advantage of high zooplankton biomass that is triggered by the flood pulse [58]. Less frequently flooded plains show exceptional “booms” in zooplankton biomass and juvenile fish [59], especially after a low flood year [55]. During poor flood years, the zooplankton biomass is less exposed to fish predation, while predation appears to be a strong regulator of zooplankton biomass during good flood years [58]. Large flood years result in extensive flooded areas which facilitate fish breeding, growth and survival and ultimately increased fish production [60], [61]. Therefore, the flood size in the 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 [58].

Wetting and drying processes are necessary in floodplains to increase nutrient turnover, maintain primary production dynamics [11] and hence fish production. However, the pattern of rise and fall of the hydrograph is critical to floodplain fish production. According to King et al [54], 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 [62], which may result in failed fish production. Bigger floods during spawning might also displace eggs and cause increased mortalities [63] which may result in failed recruitment and a poorer year class. However, short lived hardy species in floodplain systems can adjust quickly to extreme hydrological events [20] since most organisms in flood-pulsed systems have developed adaptations to changes in the flood regime [11].

2.4.2 Adult Fish

Community structure and distribution: Floodplain fish dynamics are tied to the flooding regime [64] and the fish communities are structured along a hydrology-water chemistry gradient [65], [66]. However, due to inter-annual differences in flooding regimes, fish communities among years are stochastically different driven by the seasonal, dilution and expansion dynamics[43], [67]. Studies from other wetlands have shown that poor flood years are dominated by opportunistic fish species [68], [69], 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 [70]. The Delta’s fish
community is dominated by C. gariepinus at maximum flooded area, while H. vittatus dominates the fish community at minimum flooded area [67]. Furthermore, poor flood years are dominated by tolerant, 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) [67]. Therefore, consistently poor flood years in the Delta will be dominated by C. gariepinus while predominantly good flood years will be dominated by S. intermedius [67].

Furthermore, at a large spatial scale, [71] observed spatial differences in fish community structure among several lagoons in the Delta. Generally, upper Delta lagoons have higher fish species diversity than lower Delta lagoons. One key factor contributing to these community differences is hydrological stability in the upper Delta vs. hydrological variability in the lower Delta.

Reproduction: While spawning for some floodplain fish species is cued by rising water levels [56], [72]–[74], others spawn at low water levels [75], [76] based on Humphries et al [75] “low flow recruitment hypothesis”. However, peak spawning for some fish species in the Delta occurs at low flood levels in the main channel at high water temperatures, while other species spawn during maximum flooded area in the floodplains at low water temperatures [67], [77]. Van der Waal [72] observed that spawning for some members of cichlids was not associated with a hydrology. However, other studies[56], [67] found that spawning for the majority of cichlids is associated with a hydrological gradient, while others [67] revealed that spawning for some other cichlids (e.g. Serranochromis macrocephalus and C. rendalli) was significantly associated with water temperature , which agrees with van der Waals [72] observations.

Growth and Feeding: Floodplain fish growth is fastest during increasing water levels [78]–[80] and peaks at maximum flooded area to take advantage of the available food in the floodplains [57], [80]. During the low flood season intra-specific competition for food [46] decreases fish growth rates [56], [81]. Dudley [56] also observed that growth of floodplain fish differed significantly among years driven by flooding and temperature. While some studies have observed no size differences for Clarias gariepinus in the Delta, upper Delta populations follow K life histories while lower Delta populations are more r selected [77], [80].

The feeding ecology of most floodplain fish species is flood-pulse driven [46]. After the feeding and growing of the juveniles on the floodplains during high water, a key feature is increased piscivory at receding water levels by fish predators when young fish are forced back into the main channels [82]. This “concentration effect” at receding water levels facilitates predation by piscivorous fish. Thus, although prolonged inundation during years of good flooding might enhance fish growth and production of prey species [61], [82], it may negatively affect the abundance of large piscivorous fish species in channels [83]. Hence high flood years may have a positive impact on prey species like Oreochromis andersonii in the Delta. These dynamic processes illustrate the variability of floodplain fish dynamics and the need for adaptive approaches in both exploitation and management.

2.4.3 Floodplain Fisheries Management

Nature of the fisheries: The preceding overview has highlighted the dynamic interactions and processes between floodplain fish communities and the unstable environment. Floodplains are dynamic ecosystems characterized by strong intra and inter annual variability, where the flood pulse is a key driver of all processes [11], [51]. Inland fisheries in Africa are small scale and labor intensive [3]. They are characterized by multi-species assemblages, of different sizes exploited by diverse fishing gears and methods [3], [84], [85]. In the Okavango Delta, the hydrological regime is a major driver of change in the biology and ecology of the fish species in these systems [43], [46], [58], [67], [80], [86]. Like other floodplains the fisheries are dynamic due to environmental variability. This makes conventional management approaches based on steady state equilibrium assumptions inconsistent and incompatible [16], [87]–[89].

Except for a few highly commercialized fisheries in systems like the Amazon and Mekong [90], most floodplain fisheries are a major source of food, nutrition and income for impoverished riparian households [3], [91], [92]. Therefore, their primary value to local communities is their contribution towards household food security [92], though some African inland fisheries are slowly morphing towards commercial or recreational fishing [84]. Riparian communities in floodplain fisheries systems use various traditional techniques [93]–[95] to optimize utilization of the fish assemblages, and the same is observed in the Okavango Delta [96], [97], [85]. This makes floodplain fisheries a major repository of traditional ecological knowledge [88] and cultural heritage [20]. Therefore, any floodplain fisheries management regime should incorporate these facts into its management objectives.

Effort regulation: Gear restrictions and mesh regulations remain some of the easiest regulations to implement in fisheries management regimes, and these have been assiduously implemented in floodplain fisheries. The key argument behind this approach is to maintain the aggregate fishing effort closer to the “maximum economic yield” (MEY) which would in turn maximize the wealth of the sector [4]. Furthermore, this efficient economic exploitation of the fishery is assumed to save fish stocks from over-exploitation/collapse [4], [84]. Arguments such as these are attractive to policy makers and make it easier for them to enact policies aimed at effort reduction. The fundamental argument is that fishers are the main cause of fish stock dynamics, which is otherwise assumed
to be in ‘steady state’. Therefore “effort” needs to be managed. However, this study has shown that the Okavango Delta, like other floodplains, is environmentally driven with the seasonal flood pulse as the key driver. Poor floods result in reduced fish production due to failed recruitment and good floods result in high productivity. Fishing effort is also functionally driven by the seasonal flood pulse, where fishers regulate their effort and fishing methods based on seasonal flooding [85]. The structural heterogeneity of the Delta also has a major regulating impact on fishing effort in the Delta [85].

Mesh or gear regulation: The fundamental questions in fisheries management are how to catch the fish (this is based on gear restrictions) and how much fish to catch (which is based on effort regulation). A key philosophical argument is to “save” the young fish and exploit the big fish, which forms the basis for selectivity [94]. Most fishing gears are selective regarding species, sizes and habitats fished [94]. Therefore, while gear restrictions and mesh regulations are aimed at preventing growth overfishing [94], [98], young fish however, can sustain higher fishing pressure than older fish [94], [85]. In addition, regulating selectivity will invariably unbalance the fishing mortality on the various components in the ecosystem. For example, males of O. andersonii, O. macrochir and C. rendalli (which are key commercial species in the Okavango Delta), grow larger than females [99]. Hence selective harvesting with large mesh sizes would “select out” 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 [100]. Focusing exploitation exclusively on the mature part of the population will also alter the demographic composition and truncate the reproductive fraction. A decreased reproductive potential reduces the resilience of fish populations exposed to size selective fishing mortality to external disturbance. It therefore makes ecological sense to also exploit younger age classes than only old big fish which are the engines of population growth. Big Old Fat Fecund Females (BOFFFs) are more fecund than smaller/younger fish [101]–[103]. Smaller/younger fish are also more productive than bigger/older fish [104]. It makes biological sense to exploit populations in proportion to their natural productivity, as suggested by the concept of ‘Balanced harvest’ [104], [105].

Similar species from different habitats in the Delta have different life history strategies [15], [80], [92] where lower Delta species are generally r selected while upper Delta species are K selected [106]. While O. andersonii from 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 counterparts. Moreover, lower Delta populations of these three cichlids were found to mature earlier than those from the upper Delta [92]. A similar observation was made for C. gariepinus as discussed in section 1.5.2 above. Mosepele et al [39] observed that in general most upper Delta species were significantly bigger than their lower Delta counterparts. These spatial differences in life history strategies were attributed to differences in fishing pressure [39], [92]. Therefore, mesh regulations aimed at exploiting slower growing, bigger sized fish in the upper Delta would exclude the faster growing, early maturing, and smaller sized individuals in the lower Delta. Furthermore, some cichlids adapt to fishing mortality by increasing their growth rates [107], while other cichlids adapt to intense fishing pressure by maturing earlier and increasing their fecundity [108]. From a multispecies point of view, the smallest fish species in the Delta is approximately 32 mm long (TL) while the largest species is over 1 m long, with a graduation of sizes in between them [85]. Implementing mesh (or gear) regulations will certainly skew fishing mortality towards one side of the population size spectrum, resulting in a structural change of the fish community, and possibly also ensuing functional changes. According to 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 [103].

A new paradigm: Classical single-species assessment models are incongruent to multi-species, multi-gear fisheries [3], [88], [89]. A more balanced exploitation pattern harvesting all trophic levels of floodplain fish species communities is likely the best management approach for floodplain fisheries in terms of both yield and maintaining the fish community structure [85], [98]. This “balanced harvesting” (BH) regime [104], [105] was actually applied by fisher communities in the Okavango Delta as an adaptation to the dynamics inherent in floodplain fisheries [97] and is a common attribute of floodplain fisheries [3]. The only fish stock assessment done in the Delta revealed that the fish stocks were under-exploited [109] and that the fish community was being exploited rationally resulting in a relatively balanced exploitation pattern [85]. The current exploitation regime uses several different fishing gears and methods to exploit the Delta’s diverse species assemblage [85]. Such a diversified fishing pattern (Fig 2) should remain as part of the management regime in floodplain fisheries.
Selective fishing can cause evolutionary change in exploited populations [116], [117] which occurs through a three stage process; (a) fishery managers set the parameters of selection, (b) fishers apply the mortality and, (c) the exploited fish stocks are then exposed to the selective mortality [117]. Hence, exploited stocks undergo changes in growth and maturation [118][117], and selective fishing essentially causes ecosystem imbalances [94], [117], [119]. The principle of Balanced Harvest (BH) has been strongly criticized, because it does not conform to ‘basic population dynamics’ as developed by [120]. However, BH is a concrete proposal for implementing the Ecosystem Approach to Fisheries (EAF) [121], which does not only make ecological and biological sense in floodplain fisheries [111], but it is also sensitive to the cultural value of floodplain fisheries [88]. Diversified fishing techniques, as it is practiced in the Okavango Delta, facilitates that most species across various sizes and habitats- in the fish community are exploited, which approximates an “ecological optimal exploitation” [85] that will “maintain species and size structures” of these communities. It also allows impoverished households (especially those headed by women), to have access to high quality protein, which again ensures that young children (under 5 years old) from these fishing households have a relatively good nutritional status [122]. BH was intended to reduce adverse ecological impacts of fishing while also supporting sustainable fisheries [105]. 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” [20].

4. Synthesis and Conclusion

Alternating flooding and desiccation processes in subtropical and tropical floodplains are key for primary production [50], which is critical for the maintenance of secondary production in these systems [11]. Hence, the seasonal flood pulse in the Delta, driving the dry and wet floodplain phases, is a key contributor towards enhanced ecosystem production in an otherwise oligotrophic environment. Seasonal flooding not only changes the physical landscape of the Delta, by re-connecting isolated lagoons and creating diverse micro-habitats, it also enhances nutrient dynamics in the 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 loading in the system. This terrestrial based nutrient loading drives aquatic primary production which is eventually transformed into fish biomass. Coupling high temperature and floodplain inundation provides optimum conditions for tropical fish growth and recruitment [54], [63]. Generally, fish growth...
is fastest during the warm season at increasing floods [99] and slowest during the cold season at receding floods [61]. However, one major “anomaly” about the Okavango Delta is that flooding is thermally decoupled [123], where maximum flooded area occurs in the southern hemisphere winter, when temperature is not optimum for fish growth. To adapt to this anomaly, Humphries et al [63] found that some fish species in the Australian Murray-Darling River system spawn in the main channel during low floods in summer. A similar observation was made in the Okavango Delta where peak spawning season for some fish species occurs during the low flood season [67]. This observation is in support of Humphries et al [63] “low flood recruitment hypothesis” in the Okavango Delta.

The aquatic-terrestrial interface in floodplain systems is a critical component of fish production [11]. Seasonal flooding mediates fish migrations between habitats and is also a major cue for spawning [60], [67]. Moreover, seasonal flooding facilitates the pathway for nutrients that have been accumulated and locked in the terrestrial environment to enter the aquatic system to the benefit of fish production. The key sources of some of these nutrients are large mammals (e.g. elephants, buffalo, hippos, etc.) whose dung in the seasonal floodplains releases nutrients into the aquatic system during the flood season [43], [58]. This resonates with Garstang et al [41] who observed that hippos are a major source of aquatic nutrients in the Delta because they forage on *Cynodon dactylon*, which is a high forage quality grass, and largely defecates in water. Large mammals also play a key role in structural transformation of the Delta through the creation of micro-habitats that also facilitate fish production [43]. Termites are also important by not only serving as a key source of fish food in the Delta [46], [92], [124], but also play a key role in structuring the Delta by habitat modification and releasing nutrients into the aquatic system during seasonal flooding [46]. Basically, the seasonal floods facilitate terrestrial plant and animal organic matter into the aquatic system, where they form the basis of the food web. Variability in the amount of flooding is important towards ecosystem processes in the Delta. While low flood years might result in short-term failed recruitment in the fish community, they also allow terrestrial processes (e.g. proliferation of termite mounds, creation of new channels and habitats by hippos and elephants, mobilization of soil nutrients, etc.) that may later be beneficial to increased fish production. These intertwined dynamics need to be understood and incorporated into floodplain fisheries management techniques.

The core question at the debate on floodplain fisheries management is to determine the driver of change in floodplain fish communities [113]. Is it the flood pulse/ environmental variability, or fishing effort or a combination of both? Various studies have shown that the flood pulse is the key driver of fish community dynamics [11], [85] and fishing effort/ behavior [85]. However, the classical approach to fisheries management has been to “assume” that fishing effort is the only driver and that reduction in fishing mortality through mesh regulations or gear restrictions should be implemented to prevent over-exploitation [84], [94]. It is possible however, that over-exploitation can occur in areas where fishers have limited alternative livelihood opportunities [113]. But different countries have various macro-economic conditions; hence the drivers of fish exploitation, and whether the aim is subsistence food or export revenue, would differ by country. Often fish, as the last remaining open access resource, is a “safety net” during times of economic hardship [94], [125], which is also observed in the Okavango Delta [15]. Hence, the Okavango Delta fishers will generally resort to fishing as a last option, but will otherwise be engaged in several economic activities, including animal husbandry. The propensity to fish until the last fish is removed from the water, or to fish out a system beyond a level when there are no more economic returns, is unlikely to occur in the Delta. Much of the ongoing allegations of overfishing are therefore based more on competitive use of ecosystem services, such as recreational fishing vs. commercial fishing, than on the actual state of the fishery.

Hydrology is the main environmental factor in floodplains, and the seasonal flood pulse is a key driver of change in floodplain fish communities [43], [46], where even fishing effort is regulated by the flood regime [85]. Wetland species, including fish, have developed diverse life history adaptations to environmental variability, where populations exhibit large natural variations in abundance [91]. Given this bottom up driven scenario, it does not make much ecological sense to regulate effort in a fishery whose productivity is flood pulse driven. In most African fisheries, it appears that effort is driven by productivity rather than the opposite as assumed in conventional management [94]. Management interventions in floodplain fisheries should be practical, realistic, implementable, and acceptable to the stakeholders. Most developing countries have limited resources, and these should be spent on achievable and practical activities. What is also necessary is to initiate long term monitoring of exploited fisheries to better understand fishing patterns and their impact on the fish communities. This involves the collection 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, then they can be integrated into a management system which will allow for more holistic management of these resources. Such integration is currently lacking in floodplain fisheries.

References


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