Chapter

Review of Aquatic Biodiversity Dynamics in the Okavango Delta: Resilience in a Highly Fluctuating Environment

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Abstract

Wetlands are key ecosystems of high biological diversity that provide valuable ecosystem services. These are particularly important in water stressed semi-arid countries, which enhances their vulnerability to degradation. The Okavango Delta, a key wetland in Botswana, is characterised by dynamic inter and intra specific interactions. There are dynamic biotic and abiotic interactions in the system that enhances its resilience. The flood pulse is the main factor mediating bio-physical dynamics in this system. Despite the various perturbations that have been experienced in the system, the Delta has always been able to absorb them and retain its character at the general ecosystem level. These notwithstanding, there have been some changes at the local scale where the Delta has shifted regimes and entered into altered states as a consequence of either channel or lagoon failure. Management of these systems should ensure that their dynamic characteristics are maintained, and this is enshrined within the panarchy concept. Adopting the resilience framework in natural resources management allows for flexibility in devising management strategies to respond to future unexpected events.

Keywords: ecosystem perturbations, Okavango delta, resilience, panarchy, management

1. Introduction

Ecosystems face a major challenge of consistently providing ecological benefits to humanity balanced with biodiversity conservation [1]. This is even more daunting in freshwater wetlands ecosystems, which are not only biological hotspots [2, 3] but are also sources of key ecosystem services that sustain livelihoods globally [2, 4–7]. Services provided by wetlands are not synergistic [2]. According to Maltby and Acreman [6], wetlands are invariably degraded when management enhances the provision of some services like food, which often happens at the expense of other services like regulating services. This scenario is accentuated in tropical areas where, according to Junk [8], politicians prioritise development over environmental protection. Generally, these development priorities are undertaken without any meaningful assessment of the resultant environmental degradation of the wetland [4]. Subsequently, this approach results in wetlands being undervalued "in decisions relating to their use and conservation" [5]. Therefore, wetlands have been lost, degraded or significantly modified worldwide [9].

Wetlands are among the most important ecosystems in the world [10]. They have high economic importance in dryland Africa [11] and contribute to the livelihoods of many people in Sub-Saharan Africa [12]. Deriving benefits from wetlands puts ecological pressure on them which may affect their integrity and long term functioning [13]. Furthermore, water security is a major concern in most parts of the world [2], which makes wetlands critical sources of water in arid countries. Because of these intrinsic attributes, freshwater wetlands are vulnerable systems. According to Adger [14], the key parameters of concern to assess vulnerability in ecosystem are (i) the stress to which an ecosystem is exposed, (ii) its sensitivity and (iii) adaptive capacity. "Exposure is the nature and degree to which a system experiences environmental or socio-political stress". "Sensitivity is the degree to which a system is modified or affected by perturbations" [14]. According to Walker et al. [15], adaptive capacity refers to processes in ecosystems when they undergo structural reorganisation and reformation driven by internal processes and external influences. Furthermore, Adger [14] argues that ecosystem vulnerability occurs within the wider framework of the political economy of resource utilisation driven by either deliberate or inadvertent human action.

1.1 The human footprint in the Okavango Delta

The Okavango Delta (OD) is one of the main perennial water bodies in northern Botswana [16]. Its rich biodiversity makes it part of some of the world's most important wetlands [16], where the Okavango Delta is not only one of the world's largest Ramsar sites [17], but is also the 1000th World Heritage Site [18]. Historically, this system has sustained human livelihoods [19]. This wetland is vulnerable to degradation due to increased human impacts for livelihoods due to increasing population growth and socio-economic pressures. Increasing economic activity, especially tourism, in the Delta poses a significant threat to the system [20]. Moreover, the OD faces growing threats from increased agricultural activities.

According to Skelton et al. [21, 22], "insecticide spraying, encroachment of cattle onto the seasonal floodplains, pollution from boat engines, disruption of ecosystem function, and alteration of the flood regime," are some of the potential threats facing the OD. This chapter highlights aquatic ecosystem dynamics of the OD. It then discusses management of this dynamic system within the resilience theory within perturbations that occur in the system.

2. Aquatic ecosystem dynamics

Ecosystem processes and dynamics occur at various spatio-temporal scales [23], and the same has been observed for the Okavango Delta (OD). According to Junk et al. [24], the seasonal flood pulse is the key driver of change in freshwater floodplains where key ecosystem processes are mediated along a hydrological gradient. Therefore, this suggests that the deltas hydrological regime is the main factor mediating biodiversity dynamics in the system.

2.1 Okavango delta

The OD (**Figure 1**) is divided into "a confined entry channel called the Panhandle, the permanent swamp, the seasonal swamp and the occasional

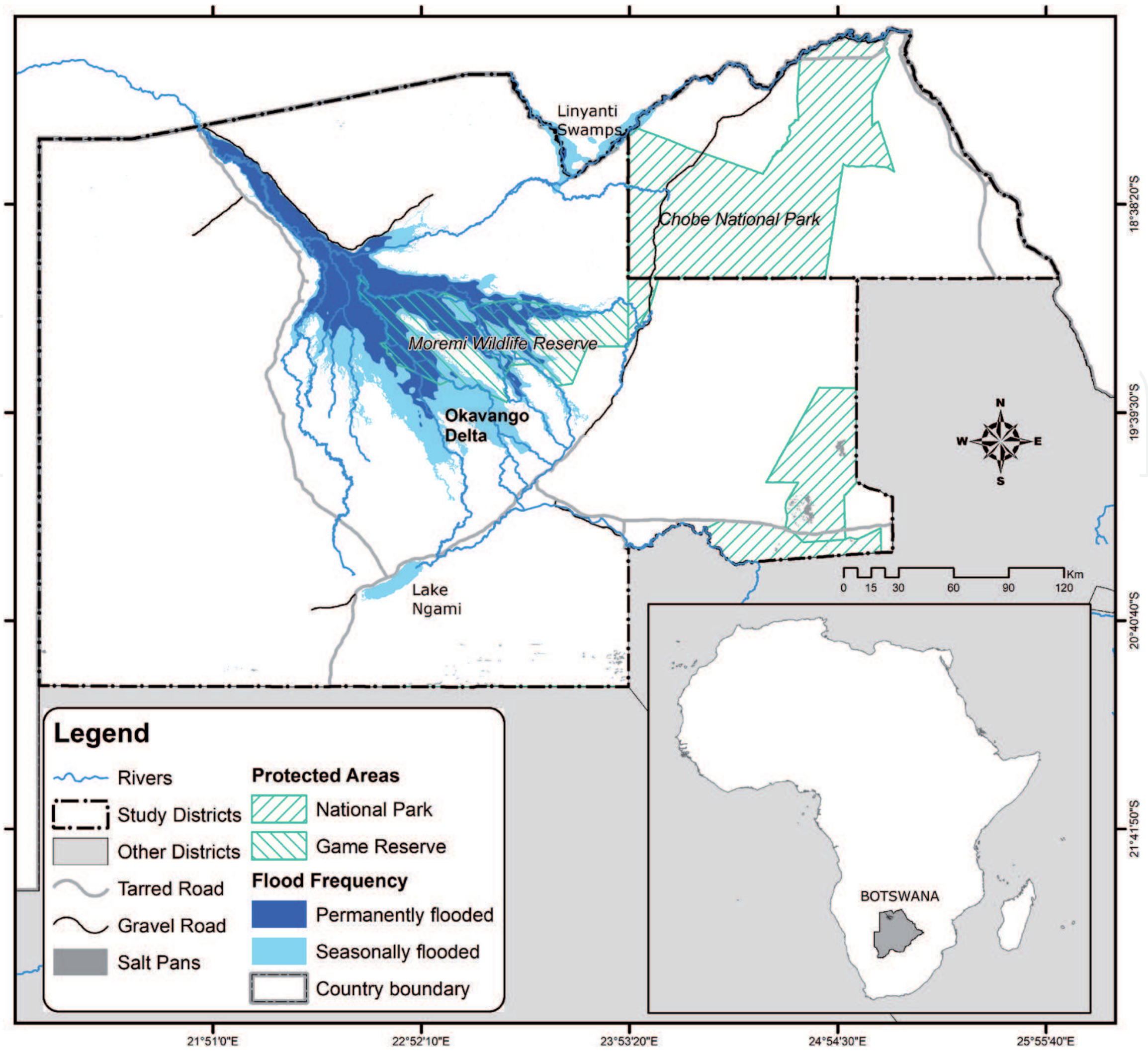

Figure 1.
Map of the Okavango Delta (Map produced by Mr. Masego Dhliwayo of the Okavango Research Institute GIS Laboratory).

swamp" [25, 26] and is one of the largest inland deltas in the world [27]. It is an alluvial fan subjected to annual flooding [28] composed of a mosaic of heterogeneous habitats (**Figure 2A, B, G, H**, [27, 29]) whose total flooded area expands and contracts at seasonal and annual scales. The total flooded area depends primarily on the magnitude of floods from Angola where the Okavango originates. According to Ashton et al. [30], the size of the delta ranges from 6000 to 8000 km^2 during the dry season to approximately 15,000 km^2 during the flood season. It is composed of permanent river channels, semi-permanent river channels, floodplains and lagoons which connect and disconnect due to seasonal flooding [30]. The Delta is also characterised by various isolated pools, ponds and puddles which receive inflow from the rest of the system at intermittent periods [16]. There are approximately 150,000 islands of variable size in the OD [25, 31], out of which approximately 60% of them were developed from termite mounds [25]. Termites are therefore a key ecosystem engineer in the delta [25]. These islands, in combination with the woody vegetation that characterises the islands' fringes, play a key role in removing salts from the OD's waters [31, 32]. Transpiration by woody vegetation creates an osmotic gradient between surface water and groundwater beneath islands and this causes salts to gradually concentrate underneath islands [32, 33] which results in a white salt encrusted centre (**Figure 2B**).

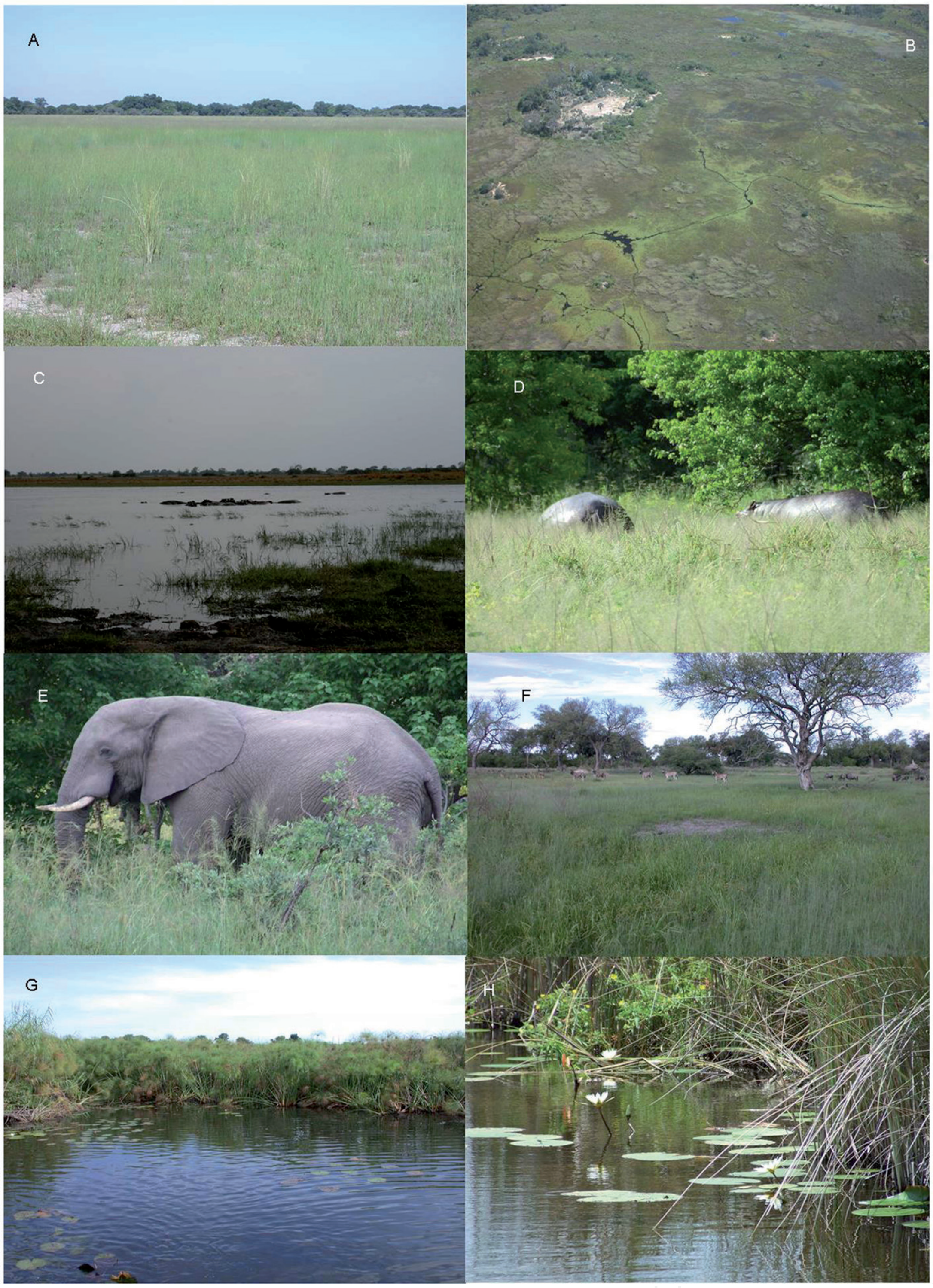

Figure 2.
Heterogeneous habitats of the OD with some of the key animals found in the system where (A) is seasonal grassland habitat with woody vegetation in the background, (B) islands in the OD showing white salt encrusted centres, (C) hippos in a floodplain lagoon, (D) hippos grazing on land, (E) an elephant, (F) herbivores grazing on a seasonal floodplain grassland, (G) river channel with Cyperus papyrus *(papyrus) on the water edge and (H)* Nymphaea nouchali *flowers in the foreground and* Phragmites australis *(reeds) in the background.*

2.2 Flooding dynamics

96% of the total inflow into the OD is lost through evapotranspiration, 2% flows out of the OD through terminal rivers, while the other 2% is lost through infiltration [32, 34]. Peak discharge in the OD occurs around February–March–April (**Figure 3A**, [30, 34, 35]), while maximum flooded extent in the system occurs

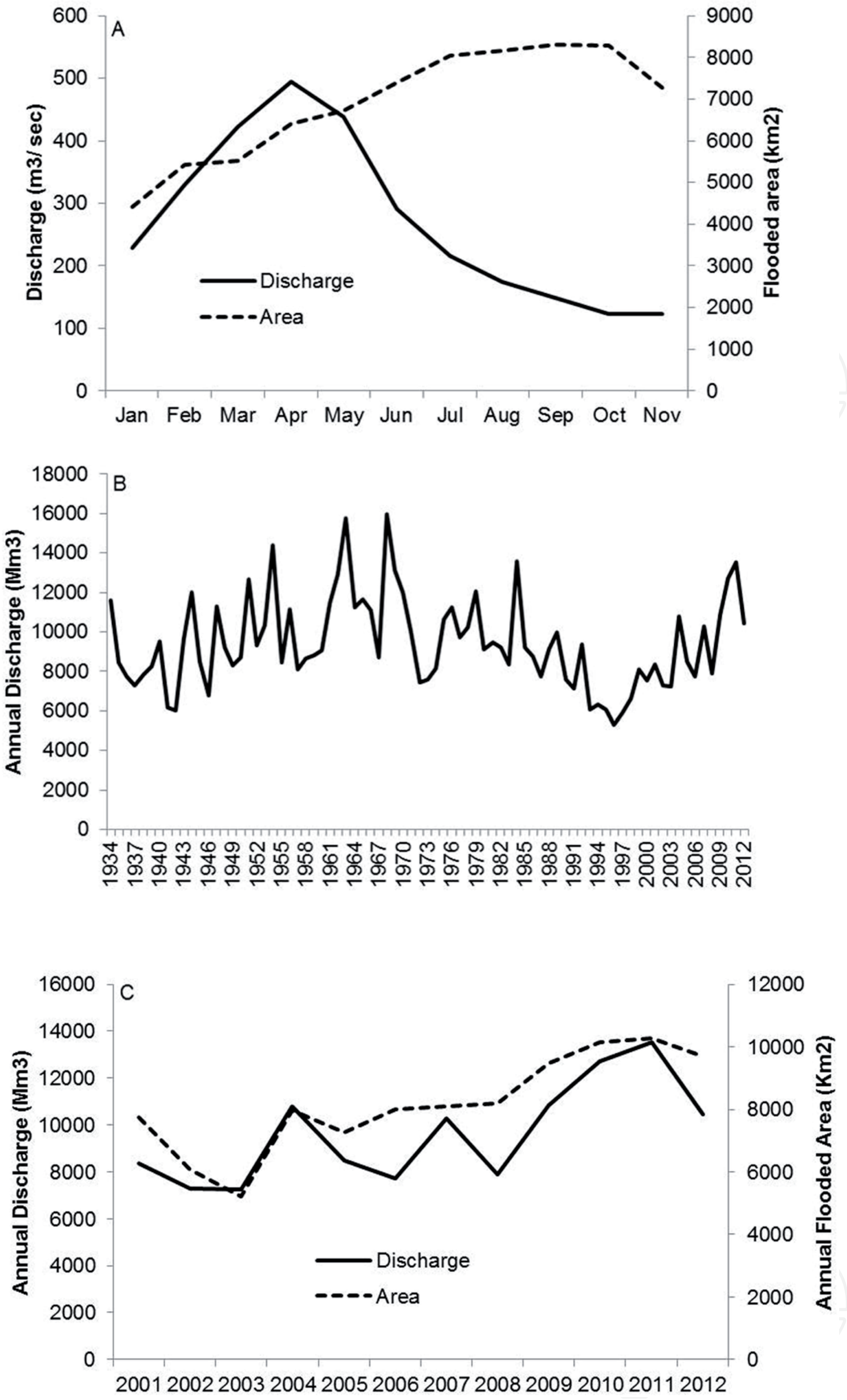

Figure 3.
Map of flooding dynamics in the Okavango Delta showing (A) seasonal discharge and flooded area, (B) annual discharge, (C) annual discharge and flooded area.

around July–August–September (**Figure 3A**, [28, 34, 35]), which is an approximately 5-month time lag between maximum discharge and maximum inundation [35]. The floods percolate slowly across the Delta and reach the mid Delta region around March before reaching the distal ends of the Delta in June–July, during the cold season [26, 30], 6 months after the rain that generated the flow in Angola [28]. On average, the annual food takes 4 months to travel from the inlet at Mohembo, to the outlet at Maun [26, 36, 37]. The amount of flooded area during any flooded season depends on antecedent conditions (**Figure 3C**, [34]), and local rainfall also plays a key role in flooding extent [38]. Inflows into the delta are subject to rainfall patterns in the Angolan catchment area [26]. Prolonged droughts in the 1980s and 1990s caused a decline in the long term average annual inflow into the Delta (**Figure 3B**, [39]). Because of the physiography of the OD, the permanent swamps experience seasonal fluctuations in water levels of approximately 0.2 m while the seasonal swamps undergo fluctuations in excess of 1.5 m [35, 37]. This suggests that the permanent swamps are more hydrologically stable than the seasonal swamps.

2.3 Water quality

The waters of the OD are generally clean and pristine [31, 40], despite the heavy sediment load that they transport annually [30, 36]. However, West [18] has revealed that surface water in some parts of the OD panhandle close to human settlements has high counts of Heterotrophic bacteria, total coliforms and faecal coliforms which makes it harmful to human health. Mogobe [41] found low concentrations of Fe, Mn, Ni, V, Zn, Pb, Cd, Cu, Cr and Co in that order in the OD, which occurred at spatio-temporal scales. Despite the low concentration of these trace metals in the OD, Mogobe et al. [41] highlighted that their concentrations were still a health risk to children in the age range of 6–12 months. Hart [40] also found spatio-temporal variability in several physico-chemical (e.g., conductivity and Si) attributes of surface waters in the delta's panhandle, where TSS values were high near some settlements. Spatio-temporal variations in Beryllium and Aluminium concentrations have also been observed in the panhandle [42]. While concentrations of these heavy metals are generally low in the panhandle, there are times when their limits exceed WHO standards which may cause acute health problems to the panhandle's riparian community [42]. Masamba and Muzila [43] also observed increasing concentrations of major cations (Na, K, Mg and Ca) along the OD which is attributed to evapo-concentration. This observation is consistent with Mosimane [44] who observed a similar trend for the same major cations and also dissolved silica (DSi) and dissolved Boron (B) in the OD. Conversely, concentrations of some trace metals (Co, Cr, Cu, Fe, Mn, Ni, Pb and Zn) generally decreased down the OD which suggests that the Delta acts as a filter for these metals [43]. Mosimane et al. [44] made similar observations for the same trace metals in the Delta. It is noteworthy that while Hart [40] fieldwork was done in 1986 and Mosimane et al. [44] in 2011, 25 years apart, the consistency of the results for conductivity between them suggests that there has been no significant change in the Delta water quality within that period. Generally, the water quality of the OD is good because the values of key parameters falls within international standards for potable water [45]. However, there is concern that some safari establishments might cause localised degradation of water quality as illustrated by depleted DO levels in the periphery of a safari camp in the OD [45].

Water quality in the terminal rivers of the OD is significantly degraded compared to upstream habitats. Tubatsi et al. [46] revealed that turbidity, *E. coli*, and *faecal streptococci* concentrations exceeded those set by the Botswana Bureau of Standards for potable water in the Boro-Thamalakane-Boteti river system, which are outlet rivers of the delta. This is consistent with Tubatsi et al. [47] who observed a spatial variability in water quality from upstream to downstream areas within the same area studied by Tubatsi et al. [46]. Masamba and Mazvimavi [48] also observed spatio-temporal variability in water quality of the Thamalakane-Boteti river system. Water quality was lowest at low flood levels and better at high flood levels [46–48] which reflects a concentration and dilution effect along a hydrological gradient [48]. Coincidentally, diarrheal cases among riparian communities increased significantly during the low flood period compared to the high flood period [46]. The poor water quality of the delta's outlet rivers is caused by various factors like, agricultural activities and pollution from tourism facilities along the river banks [48, 49].

Generally, there is a significant spatial variability in water chemistry in the Delta where the more permanent upstream habitats have lower conductivity and water temperature than downstream areas [20, 21]. Increasing conductivity down the Delta is indicative of evaporative water loss from the system [35]. Downstream habitats are shallower and the higher light penetration facilitates enhanced microbial degradation of organic matter which reduces DO levels in the water column [21]. Generally, there are no significant variations in water chemistry within the seasonal floodplains habitats [16]. However, there is variability in DO percent saturation in the seasonal floodplains which is attributed to higher primary production in some areas [21].

2.4 Nutrient dynamics and primary production

Nutrients into the OD are transported either through incoming water [36, 37, 40], aerosol deposition [36, 50], or herbivore dynamics in the seasonal food-plains [29, 36, 51]. The Delta's riverine habitats are oligotrophic, the swamps and floodplains vary between oligotrophic and mesotrophic while isolated water bodies are generally eutrophic [16]. This observation is consistent with McKay [20] that the OD is generally a nutrient poor system, where Ca is the most abundant cation in the system. Aerosol sediments/nutrients are estimated at 250000 tons year^{-1} in the OD [36] while approximately 450,000 tons year^{-1} are transported through incoming water [30]. Moreover, approximately 300,000 tons year^{-1} of suspended sediments (170,000 tons year^{-1} of aelion sand and 300,000 tons of kaolinite) are transported by incoming water [30]. Hart [40] estimated a total suspended solid load of 1×10^5 tons year^{-1}. Therefore, total nutrient loading in the system is an average of 725,000 tons year^{-1}. According to Garstang et al. [36], most of back-swamp habitats derive their nutrient input from aerosols and peat, and none from water. This makes aerosol nutrient deposition critical for the high productivity observed in the seasonal floodplains.

The shallow, seasonally flooded floodplains are the key engine of nutrient cycling in the OD [21, 44] where most of the primary production occurs [21, 31]. Initial flooding in the seasonal floodplains elicits increased concentrations of P and N which gradually decreases over time with decreasing flooded area [50, 52]. These initial nutrients were trapped in the soil and subsequently dissolved in the oncoming floodwaters. However, more nutrients, especially total N, nitrates and chlorides are added on the water through dust deposition as the flooding progresses [50]. Furthermore, Hoberg et al. [52] observed that both Chlorophyll *a* (μg l^{-1}) and primary production (μC l^{-1}) increase rapidly within the first week of new floods in the floodplains, followed by a gradual decrease towards the end of the first month of flooding.

The seasonal floodplains are also play a key role in DOM and DOC cycles in the Delta [16, 21, 26]. DOM and DOC fluxes are also mediated by the seasonal flood pulse in the Delta where DOM mobilisation is facilitated by annual flooding [26]. The new floods facilitate DOM microbial degradation which then results in an increase of vegetation derived DOC with increasing floods. The flood pulse in the floodplains also facilitates bacterial consumption of DOC [26]. There are higher DOC concentrations along the delta [26] and also between channel and floodplains habitats [53], which has been attributed primarily to evapo-concentration [26, 53]. Therefore, river-wetland interactions and evapo-concentration are the key drivers of carbon cycling in the Delta [26, 53]. The general trend is that the concentration of solutes increases from upstream habitats to the terminal rivers of the Delta [53]. According to Mladenov et al. [54], there are dynamic fluxes in DOC concentrations in the seasonal floodplain where DOM/DOC availability in the water column alternates between vegetation derived and microbial sources mediated by seasonal flooding. However, organic C derived from vegetation is a greater input to DOC in the floodplains than microbial sources within the floodplain. Overall, vascular plants are the main source of DOM in the system and the continuous input of freshly leached DOM from the floodplains is facilitated by inundation [55].

2.5 Micro-invertebrates

Forty-six micro-invertebrate taxa composed of 27 rotifers, 12 Cladocerans, 6 copepods and 6 ostracods have been identified in the temporary floodplains [56], distributed heterogeneously among the different micro-habitats. Conversely, 59 micro- invertebrate taxa were identified in the seasonal floodplains (i.e., seasonal, temporary and rarely flooded floodplains), composed of 35 rotifer species, 20 micro-crustacean species and four other taxa groups [57]. These dynamics are flood pulse driven [56, 57]. Micro-invertebrate diversity was highest within sedges while abundance was highest among floodplain grass [56]. Copepods were the most dominant taxa in the floodplains [56, 57]. Meanwhile Siziba et al. [57] revealed that micro-invertebrate diversity was high in seasonal floodplains while their density was significantly highest in the rarely flooded floodplains. Taxa of micro-invertebrates that emerged from frequently flooded floodplains sediments was higher than those that emerged from sediments of rarely flooded floodplains [58]. Therefore, while rarely flooded floodplains are key habitats for micro-invertebrate production in the OD, Siziba et al. [58] argue that high flooding frequency of seasonal floodplains is necessary to ensure that the integrity of propagules from this habitat is maintained.

According to Hoberg et al. [52], *Alona affinis*, *Ceriodaphnime quadrangula*, *Chydorus* sp., *Daphnia laevis*, *Macrothtrix* sp., *Moina micrura* and *Simocephalus vetulus* dominated the zooplankton community in the seasonal floodplains over a 3-month flooding season (June–August). Soil egg banks are the main inoculum of these zooplankton populations. These hatch from nesting eggs in soil egg banks [52, 58–60] where Cladocera, copepods and ostracods are the major groups [58]. The zooplankton biomass also fluctuated in relation to flooding in the seasonal floodplains where biomass peaked towards mid-June before almost becoming extinct in late August, at the end of the flooding season. Species succession characterised zooplankton population dynamics during the course of the flooding season [52, 59]. Initially, the zooplankton community in early June was dominated by *Moina micrura*, whose biomass was then surpassed by that of *Daphnia laevis* in early July [52, 59].

Overall, zooplankton species diversity is lowest in the permanent swamps and highest in the seasonal floodplain [60]. Species abundance and diversity also varies between habitats, where littoral habitats are less diverse and are dominated by *Caridina africana*. Some lagoons are dominated by *Tropodiaptomus kissi* while others by *Bosmina longirostris* [40]. Moreover, species diversity increases with increasing flood inundation in the seasonal floodplains [60]. Juvenile fish start appearing in the seasonal floodplains around July, which coincides with pronounced cyclomorphosis in *D. laevis.* A reduction in the *D. laevis* populations is then followed by an increase in *Chydorus* sp. towards the end of the flooding period in August [52]. This zooplankton production in the seasonal floodplains grazes down phytoplankton biomass whose abundance gradually decreases in concert with zooplankton populations [59]. Generally, the seasonal floodplains have higher abundance of desmids than the permanent swamps [27]. This agrees with Cronberg et al. [16] who also observed that desmid populations were more abundant and diverse in shallower parts of the OD. Ultimately, seasonal floodplains are a source habitat for the cladorecan meta-community where ephippia are dispersed from seasonal floodplains to other habitats in the delta, possibly by wind and mammals [60].

2.6 Seasonal vegetation dynamics and herbivore populations

Seasonal wetting and drying processes are key to enhancing primary production in the Delta. Drying processes release nutrients which are then trapped in the water column during the wetting phases [61]. At low water levels, herbivore herds (**Figure 2F**) enhance nutrient loading in the system through bioturbation and defecation [21, 29, 31, 51]. Flooding dynamics in the seasonal floodplains facilitate soil nutrients transport [62]. This is consistent with Bonyongo and Mubyana's [63] analysis that seasonal flooding is a key source of soil nutrients that sustains vegetation growth in the system. Flooding predictability and an extended feeding period have made the Delta one of the most productive systems globally, which maintains herbivores populations 4–8× more than similar wetlands [51]. Furthermore, hippos graze on nutrient rich soil vegetation like *Cynodon dactylon* and they end up enriching lagoons through defecation (**Figure 2C, D**, [29, 36, 64]). These nutrient enriched lagoons are therefore able to maintain high fish biomass production [64, 65]. Essentially, herbivores in the Delta create a nutrient loop where they feed on floodplain grass, deposit their dung which contributes nutrients to the system, which are trapped by new floods, which are released during the drying phase and are also used in grass production [29, 51].

2.7 Aquatic macro-invertebrates

Ninety-four Odonata species made up of 33 Zygoptera and 61 Anisoptera species have been described in the OD. Moreover, 37 micro-crustacea (16 Copepoda and 21 Cladocera) and 22 mollusca species (16 Gastropoda and 6 Bivalvae) have also been described for the OD [51]. The Delta's macroinvertebrate populations are relatively uniform across the Delta, but are structured along micro-habitats within the delta's macro-habitats [66, 67]. However, one exception to this is *A. caridinum* (freshwater shrimp) whose abundance decreases along a hydrological gradient from the upper to the lower Delta [66]. There are approximately 184 morpho-species taxa in the OD, which cover 63 families [67]. The dominant taxa in the OD are Hemiptera and Mollusca, while Oligochaeta, Lepidoptera and Acarina have only one family each [67]. Dallas and Mosepele [67] observed that marginal vegetation has the highest number of morpho-species per habitat while backwater detritus habitats in the OD have the lowest morpho-species richness. Apart from chironomids, sediments have a paucity of invertebrate taxa which Appleton [66] attribute to anoxic conditions caused by microbial degradation of organic matter.

2.8 Fish

There are 71 fish species in the OD [61] distributed heterogeneously among the different habitats [29]. Generally, fish species diversity is higher in the permanent swamps and lowest in the seasonal floodplains [68, 69]. Based on the Index of Relative Importance (%IRI), the fish community is dominated by *Clarias gariepinus* (**Figure 4J**), *Schilbe intermedius* (**Figure 4H**) and *Hydrocynus vittatus* (**Figure 4G**), respectively. *C. gariepinus* dominates the community during years of poor/low floods while *S. intermedius* dominates the fish community during years of good/high flood years [70]. *Clarias gariepinus* (sharp-tooth) is the biggest fish species in the OD while *Rhabdalestes maunensis* is the smallest species found in the delta [71]. Insectivores are the dominant feeding guild in the fish community [70] which attests

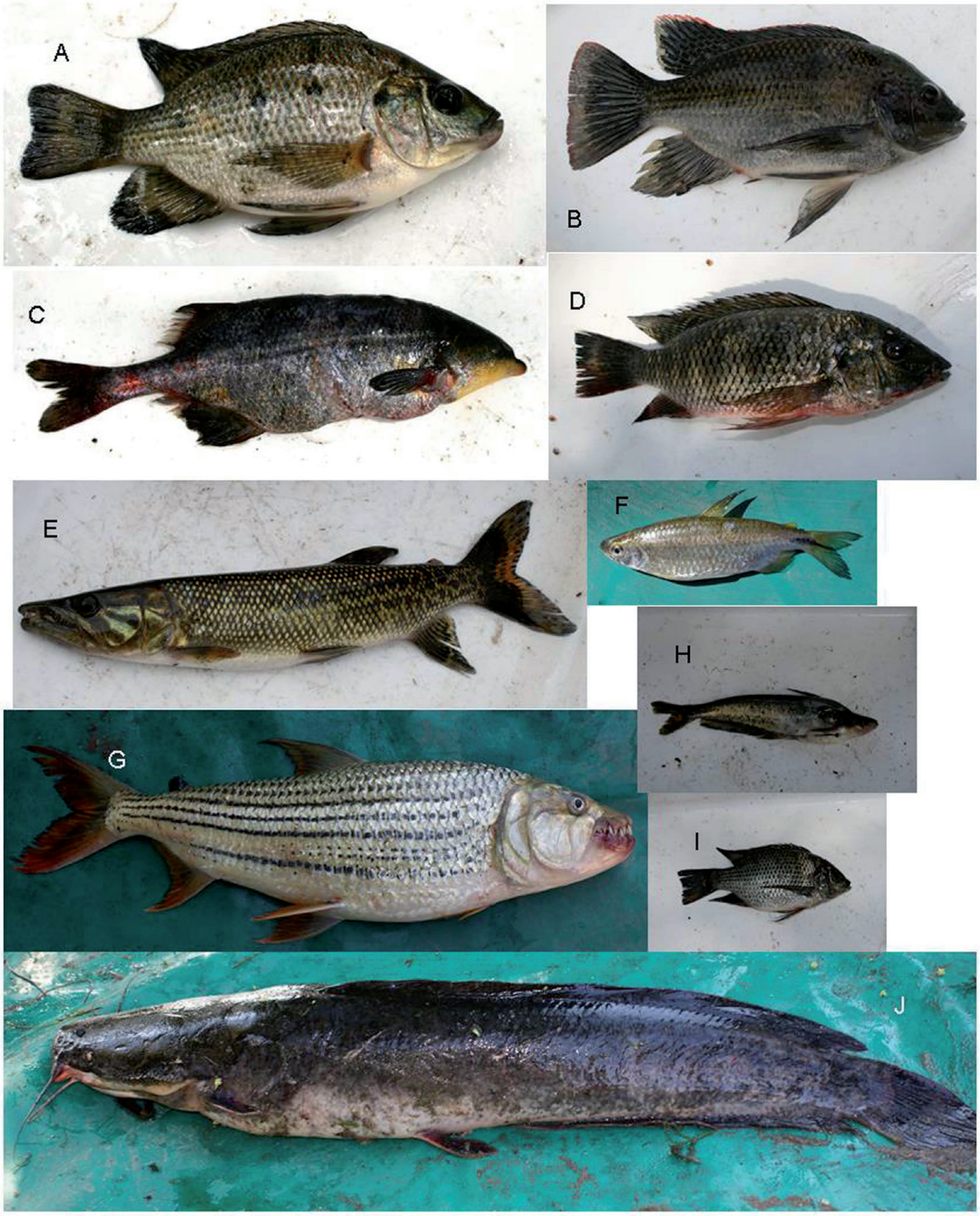

Figure 4.
Some key fish species in the OD showing (A) Oreochromis andersonii, *(B)* O. macrochir, *(C)* Marcusenius altisambesi, *(D)* Coptodon rendalli, *(E)* Hepsetus cuvieri, *(F)* Brycinus lateralis, *(G)* Schilbe intermedius, *(H)* Hydrocynus vittatus, *(I)* Tilapia sparrmanii, *and (J)* Clarias gariepinus.

to the importance of terrestrial food sources in the system. According to Mosepele [71], half of the fish species in the OD do not grow bigger than 17 cm (total length), while only 10% of the fish species growth bigger than 65 cm (Total Length). Therefore, the OD fish community is dominated by smaller sized fish species.

2.8.1. Community structure

The Delta fish community undergoes temporal variability along a hydrological gradient [70] and is also characterised by spatial variability [65, 72]. On a temporal scale, this variability is driven by fish longitudinal and lateral migrations [73].

Lagoons, which are a key fish habitat in the Delta, are dominated by the Cichlidae family [65]. According to Mosepele et al. [65], lagoons along a spatial gradient in the OD have different fish community structures, and morphometric attributes of some species are also significantly different among them. *Marcusenius altisambesi* (**Figure 4C**) and *Brycinus lateralis* (**Figure 4F**) contribute to the differences in fish species assemblages among the lagoons [72]. Mosepele et al. [65] also revealed that dry season fish biomass in seasonal floodplain lagoons was significantly higher than those from permanent swamp lagoons. This observation agrees with Mosepele et al. [72] who also showed that there are significant differences in fish abundance among lagoons in the Delta. Moreover, fish dynamics in the lagoons is driven by environmental variability [72]. Insectivores are the dominant fish feeding guild in the lagoons [65]. Notably, *Hydrocynus vittatus* (tiger-fish), which is one of the top piscivores in the system, is found mostly in the upper delta whilst *Hepsetus cuvieri* (African Pike, **Figure 4E**) also a top piscivore, is found mostly in the lower seasonal delta [69, 73, 74]. *H. vittatus* is a visual predator which occupies riverine habitats of the permanent swamps while *H. cuvieri* is an ambush predator which prefers sluggish backwater habitats found in the seasonal floodplains [64, 69].

2.8.2 Life history strategies

The Delta's seasonal flood pulse is a key driver of fish population dynamics in the system [75]. Most fish species undertake longitudinal migrations along the Delta's main channel as a reaction to the onset of the floods [68, 73]. However, some species then migrate into the seasonal floodplains once the new flood waters spill onto the floodplains [70]. Different species have developed plastic life history strategies as an adaptation to this dynamic system [68]. *S. intermedius* in the permanent swamps spawn in February just before peak floods, while the same species reaches peak spawning in October, almost 3 months after the floods' arrival in the seasonal floodplains [76]. *Oreochromis andersonii* (**Figure 4A**), *O. macrochir* (**Figure 4B**) and *Coptodon rendalli* (**Figure 4D**) between permanent and seasonal parts of the OD have different growth rates [74]. However, juvenile cichlids of *Tilapia sparrmanii* (**Figure 4I**) and *C. rendalli* grow faster in the permanent swamps lagoons than those from the seasonal floodplain lagoons [72]. Merron [68] showed that *O. andersonii* from the seasonal floodplains mature at a smaller size, grow faster and are less fecund than those from the permanent swamps. Therefore, fish species from the permanent swamps were *K* strategists while those from the lower delta were *r* strategists. This agrees with Bokhutlo [77] who established that there are two distinct populations of *C. gariepinus* between the permanent swamps and the seasonal floodplains. Their study showed that *C. gariepinus* from the seasonal floodplains grow faster and reach a smaller maximum size compared to those from the permanent swamps. Due to the lower DO levels in the seasonal floodplain habitats, *H. cuvieri* lays its eggs in an oxygen enriched foam nest to enhance the probability of survival for its young [68]. Moreover, several key cichlid species are mouth-brooders, which is also adaptation strategy to enhance the survivability of their young in a low DO environment [31].

2.8.3 Biology and ecology

Fish feeding [68, 73, 76, 78], spawning [70, 73, 76], growth [77, 78] and mortality [78] are all flood pulse driven [71] in the OD. The annual catfish run is perhaps the most visible impact of flooding on fish feeding ecology in the delta [68, 73]. In this phenomenon, *Clarias gariepinus* undertake seasonal feeding migrations at receding water levels when their prey species are back migrating from the drying out floodplains. Mosepele et al. [78] has also showed that the feeding ecology of some selected species is driven by the hydrological regime. They showed that *S. intermedius* diet is driven by discharge while that of *Marcusenius altisambesi* is driven by water depth. Mosepele et al. [78] showed that *S. intermedius* preyed on terrestrial insects. This agrees with Mosepele et al. [78] who revealed that diet for 1-year-old *S. intermedius* includes ants and bees at the onset of floods which were possibly drowned by advancing floods in the seasonal floodplains. Mice were found in the diet of 2-year-old *S. intermedius* at peak floods in the seasonal floodplains. This opportunistic feeding behaviour was also observed by Merron and Mann [76], who observed that terrestrial insects constitute 14% of *S. intermedius* diet. Mosepele et al. [78] showed that seeds were found in the diet of *Brycinus lateralis* and 1-year-old *Marcusenius altisambesi*. Mmusi et al. [79] then showed that *B. lateralis* ingests *Nymphaea nouchali* seeds which remain viable after passage through its gut. They concluded that *B. lateralis* might be one of the dispersal agents for *Nymphaea nouchali*, which makes *B. lateralis* a key ecosystem engineer. Generally, the Delta's fish community is characterised by trophic differentiation, diet flexibility and ontogenetic diets which minimises competition for food and maximises energy uptake [78].

2.8.4 Floodplain dynamics

Fish spawning behaviour is partitioned along a hydrological gradient in the OD [70]. Massive spawning among the delta fish species occurs just before maximum inundated area in the delta. The fingerlings then migrate out onto the seasonally flooded floodplains where they graze on zooplankton. However, seasonal floodplains are used not only by fish juveniles, but also by small sized fish species. Siziba et al. [80] observed that 38 small sized fish species belonging to 11 families used the seasonal floodplains. Species from the Poecilidae family dominate the primary and temporary flooded floodplains, while juveniles from the Cichlidae family dominate the rarely flooded floodplains [52, 80]. This is consistent with Siziba et al. [57] who observed that *temporary* floodplains are key nursery sites for juvenile fish. According to Siziba et al. [81], micro-crustacea dominated the diet of juvenile cichlids from rarely flooded floodplains than for those from frequently flooded floodplains. *M. spinosa*, *C. sphaericus*, and *M. micrura* dominated the diet of juvenile cichlids from rarely flooded floodplains while *Chydorus sphaericus* dominated the juvenile cichlid diet from frequently flooded floodplains.

2.9 Aquatic vegetation

There are approximately nine distinct plant communities in the Delta distributed along a hydrological gradient. Seven of these are wetland communities which range from permanently flooded swamps to the seasonally flooded floodplains. The remaining two communities are riparian woodlands that are not flooded but have species whose roots are in the water table of the both the permanent and seasonal floodplains [82]. *Cyperus papyrus* (papyrus) and *Phragmites australis* (and *P. mauritanius*) (reeds) dominate the permanent swamp habitats of the OD [31]. According to Ellery et al. [35], *C. papyrus* exists as unattached "semi-floating mats of rhizomes and roots". Papyrus enhances water velocity in the river channels through constriction of the channel by inward growth of channel margin vegetation [35]. Furthermore, the permanent swamps are characterised by aquatic grasses like *Vossia cuspidata* and *Echinocloa pyramidalis*, while the lower reaches are dominated by a patchy mosaic of aquatic, semi aquatic and terrestrial vegetation [82]. According to Mendelsohn et al. [31], dense growth of papyrus and reeds dominates the deeper waters of the permanent swamps while swamp grass dominates the shallower portions of the swamps. However, this vegetation does not encroach into the river channels as long as the water current is strong. The main channel river banks of the permanent swamps are "flanked by peat deposits" characterised by species like *Miscanthus junceus* and *Pennisetum glaucocladum* [35].

3. Theoretical framework: resilience in ecosystems

Resilience is a broad concept that incorporates the ecological character of ecosystems and the broader expanse of more complex socio-ecological systems [83, 84]. At the ecosystem level, resilience is the capacity of an ecosystem to maintain its identity amidst disturbance [15, 23, 85], or the rate at which species composition in an ecosystem returns to equilibrium following a major reduction in species [86]. Holling [87] defines resilience as the ability of systems to absorb change and disturbance and still maintain the same relationships between populations. Resilience has also been defined as the ability of an ecosystem to return to its reference state after a perturbation [84] or the capacity to deal with perturbations [88]. According to Angeler et al. [3], resilience is the capacity of ecosystems to absorb change without "moving to another stable state". This capacity lies in the regenerative ability of ecosystems to continue to provide services that are essential for human livelihoods [89]. Therefore, resilience is the capacity of ecosystems to absorb disturbance, or the buffer capacity of ecosystems that allows persistence [87, 90]. However, Peterson et al. [91] define resilience as the measure of the amount of change or disruption that is for a system to undergo regime shifts.

Based on these definitions, the three elements of resilience are (i) the amount of change that an ecosystem can undergo, (ii) the degree to which an ecosystem is capable of self-organisation, and (iii) the degree to which an ecosystem can build the capacity to learn and adapt [92]. Moreover, latitude, resistance, precariousness and panarchy are four crucial aspects of resilience identified by Walker et al. [85]. These various ecological definitions of resilience suggest that there are several ecological stable states of ecosystems which are occupied by resilient systems [3, 87]. Therefore, ecosystems can operate at different levels of what has been termed either "basins of attraction" [3, 85, 87] or "domains of attraction" [93]. However, the ability of an ecosystem to tolerate disturbance is finite [94], and when critical perturbation limits are exceeded, a different pattern of behaviour in the ecosystem may emerge [93, 95]. Therefore, when resilience is breached, system behaviour can in some cases change catastrophically from one basin of attraction to another [96].

Some dominant processes in ecosystems create "discontinuities" in the structural features of the system which are expected to persist despite the normal dynamics of the system [95, 97]. Changes in the structure of the system will only be observed if the system is pushed beyond the "limits of its resilience" [95, 98, 99]. It is therefore important to highlight the adaptive responses of socio-ecological systems to a transforming biosphere in order to understand ecosystem resilience and hence prevent collapse [97]. Generally, freshwater ecosystems are exposed to various pollutants from human impact which can alter the structure and functioning of these systems [94]. A concomitant exposure of aquatic wetlands to multiple stressors like physical hydrological alterations, climate change, species changes and pollution may enhance the vulnerability of these systems [3]. The combined effects of these stressors make ecosystems more vulnerable to changes that could previously be absorbed [90]. On the other hand, diversity in systems (i.e., genetic, species and landscape levels of biodiversity) enhances their ability to cope with shock and stress, which reduces their vulnerability [84, 98]. Vulnerable ecosystems have lost resilience, which implies loss of adaptability [90] which may result in an ecosystem collapse.

Resilience in ecosystems is enhanced by a suite of interactions between biotic and abiotic components of systems which create loosely structured hierarchical systems [98]. Resilience varies across scales, and this cross-scale structure, which is also described as a panarchy, is manifest as a nested set of adaptive cycles with clearly differentiated structures across scales [100, 101]. According to the panarchy approach, during reorganisation at a given scale within ecosystems, conservative structures at larger scales provide a system memory that allows for reorganisation around the same structures and processes instead of shifting to a different regime [84, 101]. Panarchy allows for adaptive management that enhances the resilience of ecosystems. According to Allen et al. [102], the three elements for managing systems for resilience are, taking action to prevent unwanted regime shifts from occurring, ensuring that the diversity of elements and feedback loops that keeps a system in the desired state is maintained, and reducing the likelihood of system crashes or flips to different states. These regime shifts result in shifts in ecosystems services, with consequent impacts on human societies [103]. That notwithstanding, Angeler et al. [104] has shown that these different stages are also as equally resilient as the original state. However, the new resilient state might not provide the ecosystem goods and services that were provided by the original ecosystem in its unaltered state. Therefore, systems may be ecological resilient but not socially acceptable [83], because of this loss in ecosystem services. Ultimately, the loss of resilience in ecosystems reduces their capacity to adapt to change [83].

The SES approach is central to the resilience framework theory [105]. According to Cummings [106], SES theory encapsulates ideas from resilience and vulnerability, among other disciplines. Subsequently, Carpenter [105], argue that important aspects of resilience in socio-ecological systems (SES) cannot be observed directly, but must be inferred. A key aspect of resilience theory in SES is its emphasis on adaptive capacity in analysing human/ecological relations [107]. Therefore adaptive dynamics are inherent to SES's. This argument agrees with Folke et al. [108] discussion that resilience within socio-ecological systems means the ability of an SES to continually change and adapt but remain within certain critical thresholds. Therefore continuous transformation and adaptation are key tenets of resilience theory in SES. Transformation and adaptation in ecosystems are encapsulated in the adaptive cycle theory which suggests that SES tend towards the four characteristic phases of (i) rapid growth and exploitation (*r*),

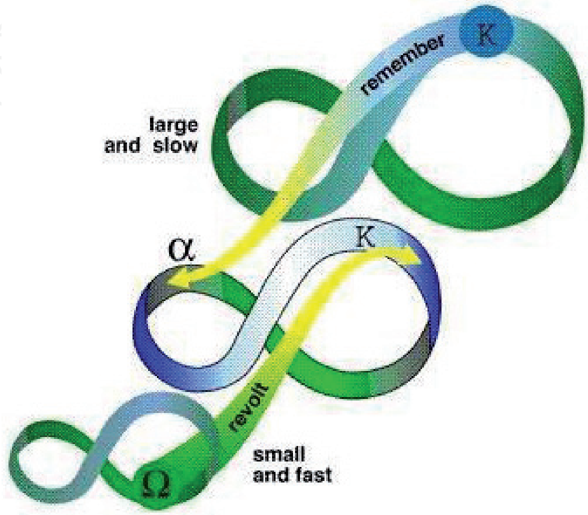

Figure 5.
A representation of a Panarchy (This figure was originally published in Panarchy: Understanding transformations in human and natural systems, edited by Lance H. Gunderson and C.S. Holling 2002. https://www.resalliance.org/panarchy) [Accessed: 15 May 2020].

(ii) conservation (*K*), (iii) collapse (Ω), and (iv) reorganisation (α) (**Figure 5**) [23, 85, 92, 100, 105, 109]. The period between the K and Ω phases is characterised by increased connectivity which results in decreased resilience in the ecosystem [93]. Resilience in the SES is high during the exploitative or the *r* phase [23]. This adaptive cycle shows two different loops where the first loop (*r* to *k*) is the slow gradual phase of growth and accumulation, while the second loop (Ω to α) is a rapid reorganisation phase [100, 109]. These define what Holling [98] defines as panarchy, “a concept that explains the evolving nature of complex systems” (**Figure 5**). It is the hierarchical structure in which SES undergo the adaptive cycle described above, which is represented in **Figure 5**.

4. Perturbations in the system: the past, present and future

Various bio-physical perturbations have been experienced in the OD, in the past, currently and also possibly in the future. These perturbations will invariably affect the resilience of the system, and may also result in regime shifts in the system from one basin of attraction to another. While these regime shifts may not result in ecosystem collapse, they may nonetheless result in some losses of ecosystem services. This might result in a system that is not socially acceptable. Nonetheless, most potential major impacts on the OD are external to the system [28] and can occur upstream in either Angola or Namibia. Most of these potential impacts are agricultural activities, water abstraction schemes or dams [30, 51]. However, any upstream developments that might affect the integrity of the OD will be confined within the framework of treaties and conventions at regional and global scales [39]. While OKACOM is the key regional entity mandated with management of shared water resources, it is currently “ill equipped” to deal with economic and socio-political pressures that underpin water use and allocation strategies in the region [110].

Climate change is another potentially major perturbation that can affect the overall ecosystem function and resilience of the OD. Some models predict increased temperatures over the region which may increase evapotranspiration rates from the delta [111], while other models indicate that there is still uncertainty on the overall impact of climate change on the delta [38]. Furthermore, tsetse spraying and channelling are some of the past major perturbations in the OD [51]. In fact, Moses [111] argues that climate change may cause ecosystem collapse which will result in loss of ecosystem services in the OD.

4.1 Tsetse fly spraying

Some key biological perturbations include what has been termed nuisance insects. “Nuisance insects” is one of the wetlands attributes that has created an “antagonistic relationship” between wetlands and humans [7]. These insects created a biological barrier that prevented cattle from accessing wetlands grass for cattle during the dry season [112]. According to Junk et al. [7], river-flooded grasslands associated with flood-pulsed wetlands are characterised by high productivity. Therefore, Tsetse fly could be classified as nuisance insects because they reduced/impeded socio-economic activity within the OD. This agrees with Ramberg et al. [61] who observed that the Tsetse fly (*Glossina morsitans*) protected the OD against farming, especially livestock production, until it was eradicated from the system.

Various control measures have been undertaken to eradicate the Tsetse fly from the delta. This included game destruction and bush clearing, fences to restrict wildlife movement [112, 113], large scale ground applications and aerial spraying of Dieldrin and Endosulfan, and ultimately spraying with Deltamethrin [112].

Insecticide applications have had some negative impacts on some of the OD's biodiversity like fish [114, 115], piscivorous birds [115] and aquatic invertebrates [116]. Direct fish mortalities were observed from Endosulfan spraying for Tsetse fly in the OD, even though no significant differences in diet were observed for *S. intermedius* and *M. lacerda* [114]. Kingfishers feeding rates decreased after fish populations within their vicinity died from aerial spraying with Endosulfan [115]. Moreover, The Deltamethrin spraying resulted in significant reductions in the abundance of some common aquatic invertebrate taxa, while other habitat specific taxa disappeared after the spraying [116].

However, aerial spraying with Deltamethrin had minimal impact on fish [117] while aquatic intevebrates at the community level recovered after 1 year [116]. According to Merron [117], some surface feeding fish species like *Aplocheilichthys johnstoni* and *Barbus haasianus* only showed some disorientation after Deltamethrin spraying. Moreover, the Atyidae and Pleidae families were negatively affected and their abundances were still low a year after Deltamethrin spraying. Furthermore, a morpho-species, Notonectidae, were also negatively affected by the Deltamethrin spraying 1 year later [116].

4.2 Channelling and other human impacts

One of the outlet rivers from the OD was dredged in the 1970s ostensibly to increase water flow to Maun [118, 119] and further downstream to the diamond mines in central Botswana [119, 120]. This involved "straightening, bunding and dredging the original river channel". However, this process resulted in a loss of the fringing wetland areas around the channel [119, 121]. Creating channels in the OD has been used extensively in the past to facilitate water flow in the system [122]. Most of these channels were created to bypass river blockages in the system that were created by river rafts made form papyrus that were used traditionally as water transport. These were discarded on and along river channels and they subsequently facilitated river channel failures because they provided initiation material for growth of emergent vegetation which ultimately blocked channels [122].

4.3 Plants

Biotic components of wetlands play a major role in regulating the hydrology of the OD [123]. Channel encroachment, especially by papyrus growth, contributes to channel failure in the OD [118, 123]. *Ficus verruculosa* is another key plant that has been associated with the failure of some prominent river channels in the OD [118] especially outlet channels [122]. Organic sudds form during summer in the OD's channels and lagoon surfaces. Some of these sudds then form a base for the growth of *Pycreus nitidus*. Other plant species that are associated with sudd formation are *T. capensis* and *Nympahea caerulea* [124]. Eventually, these facilitate dense growth of emergent vegetation [123] which results in channel width narrowing [124], that sometimes results in channel or lagoon failure.

4.4 Animals

Hippopotamus play a major role in river channel development in the OD [31, 123]. They open up channels leading into floodplain lagoons which enhances system connectivity. Hippos normally use the same track to move from lagoons for grazing which enhances water flow in the system [29]. Ultimately these hippo paths develop into river channels which can have a significant impact on the geomorphology of the OD. These new hippo channels can either facilitate flooding and linkages among water bodies on the delta's landscape or they can also contribute to lake failure [125]. Hippo channels also contribute to water loss through channel margins to peripheral floodplains. Therefore, hippos are key drivers of channel and lagoon dynamics in the OD [29, 125].

Elephants, which occur at high populations in the Delta [61], contribute to channel development thereby enhancing water flow [29]. Their heavy weight when they move over floodplains during the dry season creates path depressions which become flood pathways during flooding [29]. At the ecosystem level, these processes affect ecosystem resilience.

5. Discussion

In arid countries, there is a pronounced dry and wet season which acts as a key driver of change in wetlands [126, 127]. The Okavango Delta is flood pulse driven, which is a key driver of seasonal change [38, 61]. Other perturbations that have been identified in this study are exotic species [31], channelization [118], and pollution [30], whose impacts on the wetlands vary in space and time. The seasonal flood-pulse causes ecosystem wide perturbations in these systems, and causes constant ecosystem reorganisation. The flood-mediated change in the systems, where change occurs at various spatio-temporal scales, is a good illustration of the panarchy concept. In this case, at the primary production level, the seasonal flood pulse in the Delta creates boom and bust conditions at the onset of flooding in the seasonally flooded portions of the Delta. These production cycles scale up the ecosystem and ultimately provide goods and services that are characteristic of wetlands ecosystems.

According to Gunderson [23], regime shifts in ecosystems caused by disturbance can result in a resource crisis because the system could normally have a reduced ability to provide ecosystem services. Gunderson [23] discusses that the three management approaches within this scenario are, (i) to do nothing and wait for the system to return to its reference state, (ii) to actively manage the system in an attempt to return it to some desirable state, and (iii) to adapt to the new altered state.

5.1 The do-nothing approach

One example in the OD occurred in the 1980s when Lake Ngami dried up [128]. The lake supported a small scale commercial fishery when it had water [73]. However, a loss of water in the system meant that it stopped providing this ecosystem service. It was also a source of water for livestock in the region [118], and its desiccation meant a loss of this ecosystem service. The lower part of the OD also remained dry for several years [128], with a consequent loss of its ecosystem services. Several studies have shown that the OD is subject to an "80-year climatic oscillation" (**Figure 3B**, [34]) which affects water availability and distribution in the system. Tectonic shifts in the system also sometimes result in water flowing more to the eastern part of the delta, with none (or little) to the western portion [34, 129], which results in Lake Ngami not receiving water. Gumbricht et al. [34] further highlights that dense aquatic vegetation growth also had a compensatory effect of diverting more water to the eastern part of the delta, especially during years of low floods. Essentially, the system is constantly self-organising in concert with these flooding dynamics. In this respect, the desiccation of certain portions of the delta does not necessarily suggest that the system has irrevocably changed into a terrestrial environment. It has retained its flooding memory, and will certainly reflow. This happened to Lake Ngami which received floods in 2004 after being dry for over 20 years [128]. In this case, the "do-nothing" is the best management strategy because the system invariably springs back to its former character. This suggests that the system is still resilient because it was able to revert to its former shape after a perturbation.

5.2 Active management approach

Historically, many attempts have been made to manage the flow regime in the Okavango Delta through physical processes [118, 120, 122]. These attempts were aimed at either unblocking river channels to allow for unimpeded flows [122], or to simply direct water flow elsewhere for human use through dredging [119]. According to Bernard and Moetapele [130], the exclusion of local communities perhaps contributed to the desiccation of the Gomoti River channel, which is one of the outlet Rivers from the OD. They highlight that local people were historically involved in active burning in the Delta during low water levels to allow for free water movements when the floods arrived. Bernard and Moetapele [130] also highlighted that local people actively removed any vegetation build ups they encountered on the river channel during their forays in the Delta. Subsequently, the desiccation of this river channel resulted in a loss of ecosystem services that the peripheral riparian communities used to derive from this river. As highlighted earlier, channelization was common in the OD in the past [118, 122] and also active removal of blockages [122]. In some cases, Ellery and McCarthy [119] noticed significant encroachment of terrestrial vegetation onto the dredged channels. Overall, these active management strategies never served their intended purpose [131] but rather facilitated a shift in regimes of the ecosystem at a local scale.

Tsetse fly eradication is one major activity in the OD which illustrates active management of the system to facilitate access to its ecosystem services. The Tsetse fly is the vector for Trypanosoma which causes sleeping sickness in people and nagana in cattle. This disease is idiosyncratic to Sub-Saharan Africa which affects approximately 50 million people, 48 million cattle with estimated annual losses in cattle production ranging between USD 1–2 million [132]. The ecological impact of eradicating this species has not yet been evaluated in the OD at the ecosystem level. However, it is undoubtable that the presence of this fly restrained or regulated human encroachment to access most ecosystem services provided by the OD. The extensive use of pyrethroids as insecticides has increased their likelihood as aquatic pollutants [133], with unforeseen impacts on aquatic biodiversity. However, spaying for Tsetse fly generally resulted in localised ecological impacts of untargeted aquatic organisms. Eradicating the Tsetse fly using Deltamethrin had two major unforeseen consequences in the Delta, (i) short term impacts which resulted in aquatic macroinvertebrate mortalities in the Delta (ii) Long term impacts where the absence of the Tsetse fly opened up the Delta to a greater human footprint impact. This has resulted in some unsustainable tourism developments that have had negative environmental impacts. These will invariably affect the dynamicity of the system, will increase its vulnerability and imperil its resilience.

5.3 The new altered state approach

The western part of the OD has now transformed into a terrestrial environment from the aquatic ecosystem that used to exist. This was driven by changes in river flow either due to channel blockages by vegetation [118], or to plate tectonic shifts where most water in the system started to flow east of the OD [34]. In this scenario, the best management approach is to accept the new altered state of the system and manage it in the best possible way. Generally, the western portion of the OD has shifted from a floodplain system to a terrestrial habitat which occurred due to the failure for the main channel system in that part of the OD. This regime shift resulted in a grassland ecosystem which has been able to maintain large herbivore herds [134]. It has shifted from a stable aquatic state to a stable terrestrial state.

Ecosystems have been generally shaped and managed to derive services for human livelihoods. Therefore, natural ecosystems are changing rapidly, driven by socio-environmental conditions. Moreover, the speed of global changes through factors such as climate change, and the increasing human footprint are creating a "dynamic, uncertain" and unpredictable future which makes long term planning difficult [135]. Currently climate change is the main driver of ecosystem change that will might the resilience of the OD.

5.4 Ecosystem dynamics in the OD using the panarchy model

The OD is dynamic characterised by inter and intraspecific interactions as highlighted. (i) Rapid colonisation of seasonally flooded floodplains by zooplankton and aquatic macro-invertebrates characterises the *r* phase of ecosystem reorganisation (**Figure 5**). These *r* strategists trap terrestrial energy sources into the aquatic environment (ii) the species in the *K* phase are fish species, which have taken advantage of the *r* strategists to build up biomass in the system. (iii) The omega phase is characterised by floods recession in the delta. These floods recession are characterised by high fish mortalities when fish are stranded in drying out floodplain pools; it is also characterised by intense predation where top fish predators prey on smaller sized fish species back-migrating into the main channel from drying out floodplains; it is also characterised by increased competition for fish prey between piscivores in the system; it is characterised by intense grazing of newly grasses in the seasonal floodplain which are exposed by receding floods. (iv) The alpha phase of the reorganisation phase is characterised by plant regrowth in the seasonal floodplains. This is the time of innovation and creativity in the system where seeds dispersed take root, where the system can be restricted and new stable states created. Seeds dispersed by various agents in the aquatic system start to sprout in new areas in the Delta.

Destabilising forces in ecosystems are important in maintaining diversity [136], and this role is played by the seasonal flood-pulse in the OD. According to Baldwin and Mitchel [126], periodic wetting and drying processes in floodplains are essential for trapping nutrients in floodplain soils which enhances system productivity. This scenario creates a dynamic stable state in the OD, which could be a regime shift from a previous state. Essentially, the OD is constantly changing as a consequence of seasonal flooding. These changes are much more dramatic in seasonal flooding where changes in flood levels are more significant. The system even changes from completely dry ecosystems at temporary or rarely flooded floodplains, to aquatic systems during the flood season, or during years of exceptionally high floods. These extreme flooding events (terrestrial vs. aquatic ecotones) contribute to high ecosystem productivity and diversity. This resilience in the ecosystem also enhances high biodiversity because of the diverse micro-habitats in the system.

5.5 Adaptive management vs. "command and control"

"Command and control" top down management strategies in SES erode the resilience of these systems [23]. Top-down management approaches assume equilibrium conditions in ecosystem which is not a reflection of reality. Most fisheries management approaches in flood pulse systems is based on classical approaches which assume steady state conditions in the ecosystem [137]. Some of these management approaches are based on restrictions on fishing gear, fishing methods and mesh regulations [138]. However, these classical management approaches focus on short-term high yield scenarios [91], which is usually the case in most floodplain fisheries. Peterson et al. [91] argue that this management approach creates ecosystems that are less variable in time and space, which significantly reduces their resilience. Mosepele [71] has argued that classical fisheries management approaches in dynamic flood-pulsed fisheries makes them vulnerable to collapse. It can be argued therefore, that classical fisheries management approaches in floodplain fisheries erodes the resilience of floodplain fish populations.

However, one key approach based on adaptive management approaches is the balanced approach which advocates for a rational exploitation of the fish community across its various trophic levels using various fishing gears and methods [139]. This exploitation regime has been proposed for the OD [71] because it improves the resilience of ecosystems to perturbation [139]. Moreover, co-management regimes in fisheries management have been adopted in the OD [72], and their efficacy has been established in other systems [140]. The co-management approach adopted in the OD is based on an adaptive management framework which allows for management to be tailored to the dynamicity of the system [72]. These adaptive co-management strategies increase resilience in complex SES [141]. According to Olsson et al. [141], local ecological is an essential ingredient of co-management. This is relevant in the case of the OD because Mosepele [141] showed that local fishers have innate ecological knowledge that they use to exploit their preferred fish species in the system.

Wetlands management in most tropical countries have been placed under protected areas [8] which is also the case in Botswana, where the Okavango Delta is a Ramsar Site and parts of it is a game reserve. Despite these management interventions, Junk [8] highlights that protected wetlands in most countries are affected by multiple developmental pressures at “species, community and ecosystem levels”. Junk [8] also argues that cattle in some wetlands outcompetes game animals and “significantly changes vegetation cover”. Similarly, Verhoeven and Setter [142] highlight that wetlands are still in danger of degradation despite being Ramsar protected in 159 countries. It is possible that the eradication of the Tsetse fly from the Delta will result with increased cattle populations which may have a detrimental impact on the Delta’s ecosystem.

Furthermore, development pressures in the developing world sees wetlands as an opportunity for primarily for agricultural development [6]. Conservation takes second place and it is this prioritisation that has resulted in the degradation of wetlands in most developing countries. This is the same philosophy that has resulted in the decimation of wetlands in the developed world. According to Maltby and Acreman [6], technological development and changing economic circumstances has resulted in the hydrological transformation of wetlands which has invariably reduced their resilience. The concepts of wise use and IWRM have now been incorporated into policy regarding wetlands utilisation globally. However, due to limited resources to implement and enforce these principles, these concepts remain aspirations only instead of realistic approaches to wetlands resources management [6].

5.6 Synthesis: resilience theory and panarchy in wetlands management

The biogeochemical, hydrological and ecological processes of wetland ecosystems will always be impacted by humanity at both local and scales [103]. What is important is for managers to work towards minimising these impacts [108]. Minimising the impacts should also be aimed at ensuring that the resilience of these wetlands is maintained. The key variable in wetlands management should be to maintain resilience and decrease the ability of the systems to shift their regimes from one state to another. Resilience theory acknowledges that ecosystems are constantly changing and reorganising, and does not necessarily focus on the stability of systems [84, 109]. Regime shifts are common in ecosystems due to human impacts which reduce resilience of ecosystems [103, 105]. These regime shifts are caused by various perturbations like pollution, climate change, hydrological changes, human exploitation and land use patterns [108]. These are difficult challenges because human population increase is inevitable, and population increases will bring these other factors into play in wetlands management. One of the best approaches towards management of these systems that has been identified in this study is to use the panarchy approach.

The panarchy model essentially acknowledges that systems are composed of sub-sets of self-organising systems at various scales which all contribute to the resilience of the system [100, 105]. Nested hierarchies underpin the theoretical framework of the panarchy and have a stabilising effect on ecosystems because they harbour system memories which the ecosystem uses to revert to its original state after a disturbance [136]. Panarchy argues that adaptive capacity of these systems should be maintained. At the social scale, this calls for adaptive management strategies, which should be progressive and proactive to respond to emergent threats. Therefore, governance of SES should mirror their dynamicity, instead of using steady state philosophical orientations in the utilisation of ecosystem services. Based on the panarchy, SES are constantly morphing in space and time, characterised by varying degrees of resilience. Management should account for these idiosyncrasies, instead of developing utilisation regimes focused on biomass build up only in systems. If utilisation of SES is asynchronous to the adaptive cycle that is modelled by the panarchy, then utilisation pressures may add untenable pressure to these systems, which would make them vulnerable to collapse. This will push them to different stables states, with a potential decrease or loss of services. One key attribute of the resilience theory within the anarchy model is that (i) change is inevitable and (ii) the adaptive cycles within the panarchy occur across scales [136]. This suggests that management should accept that change in wetland ecosystems is indeed inevitable, and this should be incorporated into management paradigms.

Disturbance in ecosystems is part of development where periods of rapid change and transition co-exist and complete each other [90]. Resource managers in SES have focused more on the *r* and *K* phases of the panarchy heuristic model of SES [90], which may invariably drive these systems towards new undesirable regimes. That notwithstanding, exploiting SES during the *r* phase makes sense because Gunderson [23] highlights that ecosystems can usually absorb a wide range of disturbances during this period. However Folke [90] advises that resource management should also focus on the release and reorganisation phases too because new opportunities (or services) may be opened up due to a system reorganisation. Gunderson [23] counters Folke [90] by arguing that while SES are stable at the release/reorganisation phase, this stability is very narrow and the system is generally vulnerable to small disturbances which may push it to a different trajectory. Resilience Alliance [105] also caution that management interventions aimed at reducing system variability and protecting it from disturbance may erode its resilience. Minimum disturbance in systems like the OD can shift them towards new or different stable states. Viewed holistically, Folke [90] highlights that resilience avails the opportunities opened up by disturbance in ecosystems during the system renewal and reorganisation phases. This agrees with Redman and Kinzig [136] who observed that disturbance helps to maintain "diversity, flexibility and opportunities" in ecosystems.

Therefore, wetlands resources management should be flexible, and adopt panarchy as its philosophical orientation. Panarchy provides a framework for natural resource managers on how to manage socio-ecological systems to ensure that they retain their resilience [99]. A mechanistic and deterministic management approach will only accelerate regime shift in wetlands [93, 109], to states that are socially undesirable. Panarchy allows for adaptive management of SES. According to Garmestani and Benson [99], adaptive management and governance of natural resources is the best vehicle for the operationalization of resilience theory.

6. Conclusion

It is commonly assumed that invasive species are transformative drivers that may reduce the resilience of systems and possibly shift them to an undesired regime [101]. According to Angeler et al. [143], ecosystems are hierarchically organised where lower level processes affect processes at higher levels. This process was observed in this study which is illustrated by “boom and bust” conditions at the primary production levels at the onset of the floods in the Okavango Delta. Furthermore, this agrees with Holling [144] who observed that spatio-temporal variability of ecological systems within ecosystems is mirrored in the structure of animal communities. Moreover, despite the disturbances in the system, the OD has largely retained its form and functioning, which suggests that it is still resilient.

Resilience science, which encapsulates adaptive management, adaptive governance and panarchy, should be integrated into environmental law [99] used in natural resources management. Adopting this approach will ensure that the resilient nature of the OD, which accounts for its dynamics in space and time, is maintained. Maintenance of the resilient nature of SES is critical because that will ensure that they continue to provide socially acceptable services. It will ensure that system vulnerability is kept to a minimum, which will also reduce the possibility of the system to shift regimes. Regime shifts, while ecologically stable, might not be desirable as already highlighted. According to Holling [87], adopting the resilience framework in resource management is an affirmation of our insufficient knowledge of natural ecosystems. The resilience framework places emphasis on regional processes and not local impacts, and emphasises heterogeneity in ecosystems.

Adopting the resilience framework in natural resources management allows for flexibility in devising management strategies to respond to future unexpected events. This is adaptive management, devised within the panarchy heuristic model. According to Resilience Alliance [105], adaptive management can enhance the resilience of ecosystems by “encouraging flexibility, inclusiveness, diversity and innovation”. This agrees with Olsson et al. [141] who observed that adaptive management facilitates a philosophical communication between resilience and change which then has potential to create sustainable SES. Ultimately resilience is seen as a key paradigm for policy development and natural resource governance to preserve natural capital in this rapidly changing world [145]. Therefore, the Okavango Delta should be managed to maintain its dynamicity, which will ensure its resilience.

Conflict of interest

“The authors declare no conflict of interest.”

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