Fish, Floods, and Ecosystem Engineers: Aquatic Conservation in the Okavango Delta, Botswana

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The Okavango Delta, Botswana, is a major wetland surrounded by the Kalahari Desert. The delta supports a diverse fish fauna that depends on highly seasonal flooding from inflowing rivers, and on the actions of ecosystem engineers (hippopotamuses, elephants, and termites), for creation and maintenance of their habitats. Conflicts in resource use, especially water, are likely to affect fish populations and the Okavango ecosystem in the near future. We present conceptual models of this remarkable aquatic ecosystem in relation to fish and fisheries as the basis for future research and conservation efforts. Developing understanding of the environmental flow requirements of the delta is key to the management of the Okavango Delta as an ecosystem supporting diverse and abundant fish and wildlife. Once developed, this understanding can be used to allocate water within the Okavango watershed.

Keywords: hippopotamus, elephants, termite mounds, flow regime, environmental flows

The Okavango Delta, Botswana, a giant oasis in the Kalahari Desert of southern Africa, is an immense alluvial fan created by the rivers that drain the highlands of Angola (Mendelsohn and el Obeid 2004). It is perhaps most famous for its dense populations of African megafauna, from elephants to lions to crocodiles. However, it is also one of the largest intact wetlands in the world, which is reflected in its designation as a floodplain wetland of global significance under the Convention on Global Wetlands (Ramsar) (*www.wetlands.org/RDB/Ramsar_Dir/Botswana/BW001D02.htm*), the largest such wetland under the convention. It is less recognized for its importance as a regional center of fish diversity and abundance. The fish support subsistence, commercial, and sport fisheries (Merron and Bruton 1995, Mosepele and Kolding 2003). The fish are also crucial components of the Okavango food web, central to the cycling of nutrients and subsidizing populations of predatory birds, mammals, and reptiles. At the same time, the megafauna, especially hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*), have major interactions with the environment that are essential for maintaining fish populations.

Here we examine the Okavango Delta ecosystem from the perspective of fish and fisheries, presenting conceptual models of key interactions within the system. The models consist of descriptions of the system's components and their interactions, centering on fish. We then present some options for more quantitative modeling of hydrology as a major driver of the qualitative model. Finally, we examine conflicts in resource use that may affect fish populations (and the ecosystem of which they are part) in the near future. Our purpose is to present a description of a remarkable aquatic ecosystem as the basis for future research and conservation efforts.

The delta environment

The Okavango Delta (figure 1) is one of the largest inland alluvial fans in the world (McCarthy and Ellery 1994). Typically, the wetted delta ranges seasonally in size from 8000 to 16,000 square kilometers (km^2) (Turton et al. 2003a, Mendelsohn and el Obeid 2004), but during wet periods can reach about 28,000 km^2 (Ramberg et al. 2006). The parts of the delta that flood on a regular basis vary on longer time scales

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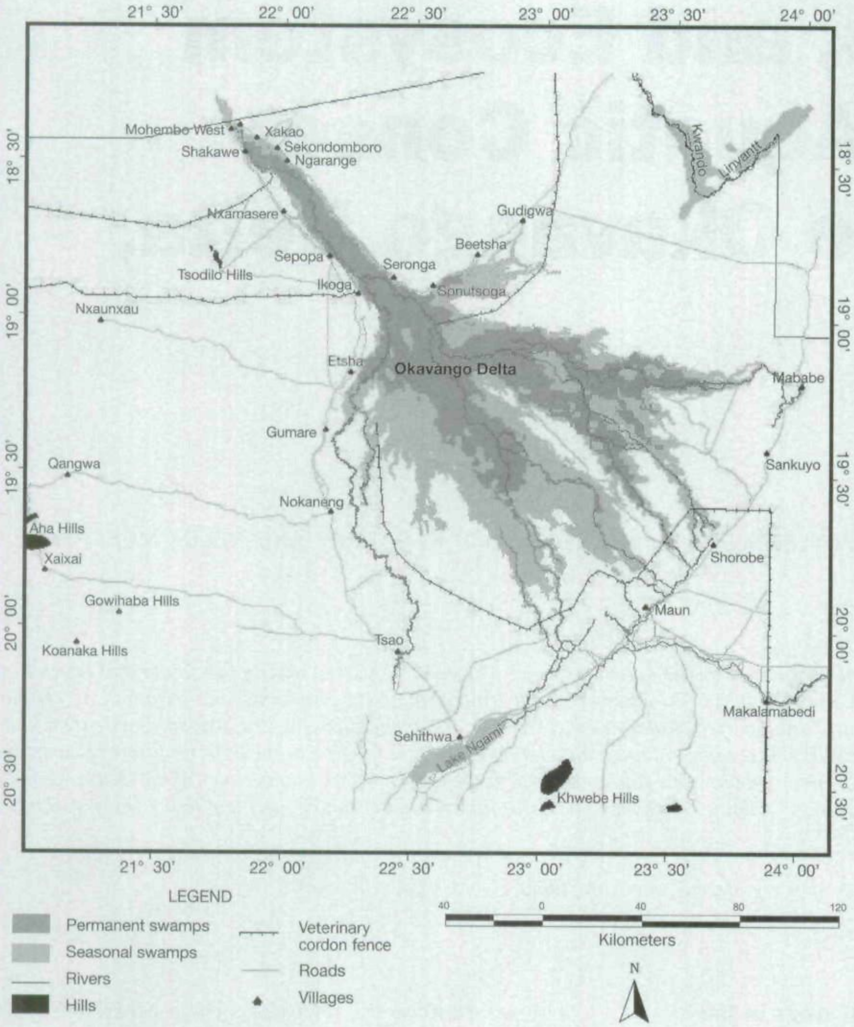


Figure 1. Map of Okavango Delta, Botswana.

as the result of tectonic activity that causes broad, if subtle, changes to land surface elevations (Gumbricht et al. 2004); in the past 50 to 100 years, for example, the general flow through the delta has shifted toward the northeast (Turton et al. 2003b).

The delta depends on annual flooding to maintain its complex and dynamic ecosystem, although summer rainfall (an average 45 centimeters per year) is also an important source of water (McCarthy et al. 2000). Annually, the floods peak in the upper delta between February and April and reach the distal end of the delta five months later, between June and August, during the dry winter season, when they are receding in the upper delta (Gieske 1997).

The amount of flooding shows a high degree of interannual variability (figure 2; Gumbricht et al. 2004). There are also long-term cycles in rainfall that can have large effects on the amount of flooding (McCarthy et al. 2000). Approximately 98% of the annual inflow is lost through evapotranspiration, while approximately 2% appears as output at the distal end of the delta (Gieske 1997, Mendelsohn and el Obeid 2004). Nonetheless, in wet years, water flowing through the delta fills sump lakes such as Lake Ngami in the southwestern end of the delta (figure 1).

The delta has a complex gradient of aquatic habitats: (a) inflowing river and its floodplain (the panhandle), (b) perennial swamp, (c) seasonal swamp, (d) drainage rivers, (e) rain pools, and (f) sump lakes (Merron and Bruton 1995).

The river enters the panhandle as a channel about 200 meters (m) wide and 2 to 8 m deep and meanders for about 100 km through a 15-km-wide floodplain in the panhandle (Merron and Bruton 1995). The channels of the panhandle are clear, sandy bottomed, and swift moving. They are mostly lined with dense stands of papyrus (*Cyperus papyrus*) that can reach 4 m in height. This papyrus wall creates a permeable barrier that both defines the edges of the channel and leaks large amounts of water into the surrounding floodplain (Ellery et al. 2003). As lateral distance from the channels increases, a complex plant community dominated by sedges and grasses becomes dominant, similar to the plant community that emerges downstream as the channels become smaller (Ellery and McCarthy 1994, Ellery et al. 2003).

From the panhandle region, the water moves through a reach of anastomosing channels, fed by a central, meandering, 26-km channel (Smith et al. 1997). Most of the side channels and lagoons in this area come and go in a dynamic equilibrium between sediment deposition and the action of large animals, especially hippos (figures 3, 4). The channels are lined with giant grasses (*Phragmites mauritanus* and *Miscanthus junceus*) or similar plants, with dominance determined by complex interactions of flow, soils, nutrients, and fire (Ellery et al. 2003). Generally, the walls lining the channels are not as dense with stems as are the papyrus stands of the panhandle.

The river next bifurcates into three channels—the Thaoge, Jao, and the Nqoga—just below Seronga, and the waters spread into a vast area of seasonal swamp (figure 1). The Thaoge is currently inactive (Porter and Muzila 1989), so the Jao and Nqoga remain the main source of water for much of the delta, which is distributed through a series of large, semipermanent branch channels. These drainage channels are perennial where they begin, but at their lower ends, they are typically dry for much of the year. The main channels are connected to lagoons by smaller channels. The lagoons are large,

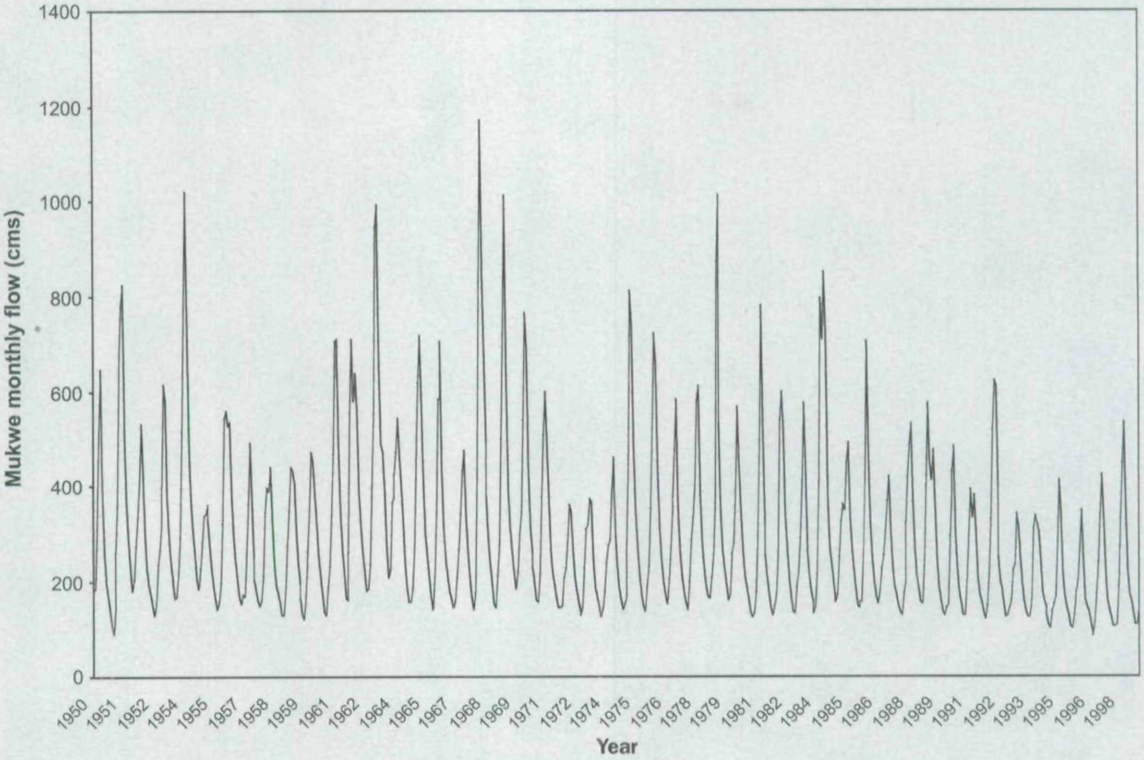


Figure 2. Mean monthly flow of the Okavango River at Mugwe, just upstream of the delta, 1950–1998, showing both the annual fluctuation in inflow to the delta and variation in the annual flood (ca. 350 to 1200 centimeters).

open expanses of water of complex origin that contain dense growths of macrophytes (McCarthy et al. 1993). During wet periods, the more distal small drainage channels deliver water (and fish) to pools that otherwise depend on rainwater to be filled. These pools are important sources of water for wildlife.

The geomorphology and ecology of ecosystems are tied together under a framework of complexity through what Stallins (2006) terms "ecological memory." A key concept for understanding the way floodwaters influence the delta's ecosystem is to think of each region as having a memory of the extent and size of past floods. The memory is longest in the seasonal swamp, where extensive flooding in one year may fill clay-bottomed pools and river channels with enough water to keep them watered through one or more drier years, and where swamp vegetation will persist for decades even if the flood regime changes (Gumbricht and McCarthy 2003). In the panhandle, the memory is shorter because most of the region floods annually, but the extent of flooding influences the size of off-channel lagoons and the strength of their connections to the main river channel. Overall, the memory of wet years can sustain species and populations through dry years, while the memory of dry years can reduce the ecosystem effects of wet years, although potentially it can have positive effects on nutrient cycling (see the next section). Overall, the alternation of wet and dry years in an irregular pattern very likely maximizes ecosystem productivity and diversity.

The biophysical processes that occur in the delta also occur in other systems around the world, but the isolated desert location of the Okavango, combined with the strong biotic interactions described here, make it unique. The most similar systems are also in Africa. The Bangweulu Swamps (Zambia) is a system in which seasonal flooding creates dynamic habitats and dispersal pathways for fish (Kolding et al.

Figure 3. Fishing village on an island in a seasonal swamp, along the Boro Channel, Okavango Delta. Photograph: Peter B. Moyle.

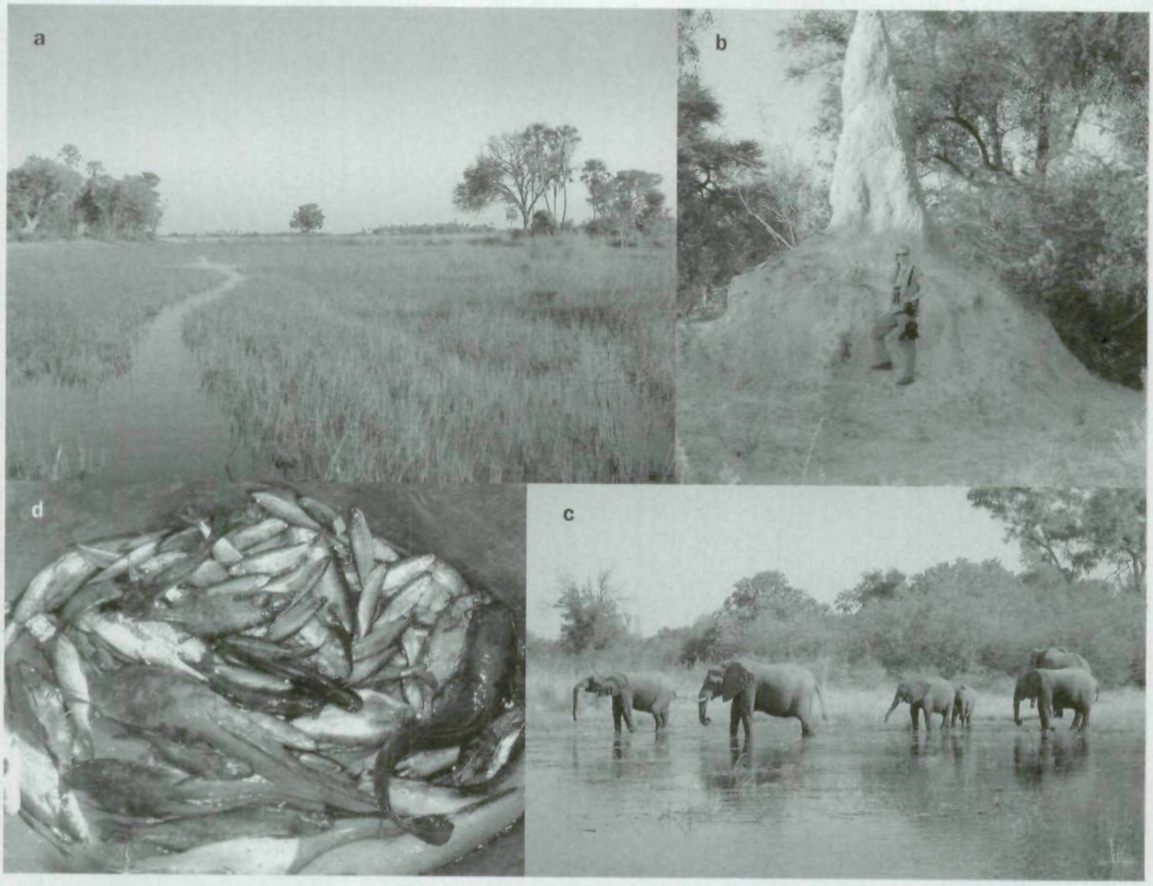


Figure 4. Components of the Okavango ecosystem. (a) Hippo trail through flooded vegetation in seasonal swamp; (b) termite mound; (c) elephants in newly flooded seasonal swamp; and (d) experimental gill net catch of fish, showing the diversity of species. Photographs: Peter B. Moyle.

2003). This seasonal flood pulse, in a lagoon and river channel complex, is also present in the Central Barotse (Zambia) floodplain (Kelly 1968). Likewise, the Shire floodplain (Malawi) is driven by a flood pulse, which maintains an oxbow lake, lagoon, and island complex (Chimatiro 2004). Similar observations of the effect of the flood pulse on fish dynamics have been made in the Solimoes floodplains of the Amazon (Cox Fernandes and de Mérona 1988, Chernoff et al. 2004, Siqueira-Souza and Freitas 2004).

Flooding and key biological processes

The importance of the annual flooding regime to fish and other aquatic organisms is enhanced by a number of large-scale biological processes that link the terrestrial and aquatic ecosystems. Three that have been identified as particularly important are (1) the role of large animals, (2) the role of termites, and (3) the biotic mobilization of nutrients.

The role of large animals. The conspicuous mammals, birds, and reptiles that attract so many tourists to the Okavango region are important players in determining the physical and biological structure of the delta's ecosystem, as ecosystem engineers (as defined by Wright and Jones 2006). For physical structure, hippo, elephant, and perhaps Nile crocodile (*Crocodylus niloticus*) are most important because of their size and abundance. Hippos are particularly important because their amphibious life style requires extensive daily movements between water and land (McCarthy et al. 1998a). These movements create incised, vegetation-free pathways through which water can flow during flooding (figure 4). These channels may become major river channels when the old channels fill with sand and avulse. In the panhandle and permanent swamp areas, hippos regularly break through the dense papyrus and reeds that form the stream banks, diverting water and sediment into adjacent areas. Because they favor deep lagoons for resting during the day, the hippo-created channels usually lead to lagoons. When these channels are recaptured by the main river, the lagoons fill with sediment (McCarthy et al. 1998a). These ever-changing channels and lagoons created by the actions of hippos are major habitats for fish.

Elephants, with an expanding population of about 35,000 individuals in the delta (Mendelsohn and el Obeid 2004, Ramberg et al. 2006), also create channels, both by walking through flooded vegetation and through creation of depressed pathways during the dry season, which then serve as conduits for floodwater. Elephants also have major impacts on trees through their feeding activity; they kill and mangle the plants and disperse seeds through their dung. Extensive removal of trees by elephants on the largest island of the delta, Chiefs Island, and elsewhere may result in major rises in the salinity of the channels, through changes in water moved through transpiration. This observation is based on findings from McCarthy and Ellery (1994), who observed that large plants on islands act as "transpirational pumps" by removing water and leaving salts in the groundwater of islands. Subsequently, these islands act as salt sinks and hence assist in keeping the delta's water less saline. Removing large trees from islands can stop this process, resulting in greater salinity of seasonal floodplain waters, with potential catastrophic effects on swamp vegetation and fish (Mendelsohn and el Obeid 2004).

Elephants, hippos, buffalo, and other mammalian herbivores have exceptionally high densities in the Okavango Delta (Ramberg et al. 2006). They not only affect the structure and composition of delta vegetation, but presumably play a major role in converting vegetation biomass into forms that readily fertilize floodwaters, promoting fish production. The full importance of mammalian herbivores as a nutrient source for the aquatic ecosystem, compared with other sources (e.g., decaying vegetation), still needs to be determined (Hoberg et al. 2002). However, there is evidence that small and relatively shallow lagoons in the delta, which are most likely to be heavily fertilized by animal dung, sustain high fish production (Fox 1976). The role of piscivorous birds, mammals (e.g., two otter species), reptiles (e.g., Nile crocodile, water monitor), and fishes in recycling nutrients in the system is also not well understood, but, given their abundance and diversity, it is bound to be considerable. The Nile crocodile in particular is often noted as a keystone predator and scavenger in African systems; its role in the Okavango is poorly understood, although fish (mainly catfishes and cichlids) and macroinvertebrates are major food items (Blomberg 1976).

The impact of large herbivores, especially hippos, is somewhat similar in other African floodplain systems. The activities of hippos and elephants in combination create many of the large pools in floodplain rivers, which provide refuges for fish during the dry season (Naiman and Rogers 1997). These pools and lagoons are subsequently fertilized by hippo dung, which promotes primary production, while the action of hippos in stirring the water prevents formation of anoxic conditions (Kilham 1982, Gereta and Wolanski 1998, Wolanski and Gereta 1999).

The role of termites. Much of the upland topography of the delta is the result of the actions of a termite, *Macrotermes michaelseni* (Dangerfield et al. 1998). During dry periods, or when water shifts away from an area, termites colonize areas with suitable clay soils and vegetation and build subterranean nests, each topped by a large mound full of passages. The function of the mound is to ventilate the nest, into which vegetation is carried to support the gardens of fungi that the termites eat. The mounds can be up to 4 m high and cover 50 m^2. When a termite colony is killed by inundation, the mound erodes, creating a small island, which then becomes a favorable site for recolonization by termites (Dangerfield et al. 1998). As this process repeats, the island grows in size. Because of the combination of elevation above low floods and nutrient-enriched soils, termite islands become colonized by trees and other plants (figures 3, 4). The islands then become favored places for living and feeding by mammals and birds, resulting in positive feedback loops that fertilize the soils and bring in seeds from other areas, contributing to successional processes (McCarthy et al. 1998b). With regard to fish, the 150,000 termite-derived islands not only determine the location of channels but also provide a source of complex cover and habitat along main channels (fallen trees, often the result of elephants' actions), a source of terrestrial insects as fish food (Mosepele et al. 2005), and a place for avian predators to nest and aggregate. It is also likely that the flooding of live termite colonies results in localized influxes of nutrients from the fungi gardens and from the termites themselves. Given that termites in general are among the most important herbivores in the region and feed largely on woody debris (Dangerfield et al. 1998), their actions may be a major mechanism for delivering terrestrial resources to the aquatic system. According to de Oliveira-Filho (1992), termite mounds also have a major effect on the floodplain morphology of the Mato Grosso in central Brazil, with presumably similar beneficial effects for fish.

The mobilization of nutrients. The waters of the delta are oligotrophic (Cronberg et al. 1996), but flooding almost immediately raises nutrients to high levels, especially in lagoons and off-channel areas. The nutrients come from three principal sources: soil, detritus from plants, and mammalian feces (Hoberg et al. 2002). It is likely that grazing and other actions of large mammals, combined with the highly porous sandy soils, make the nutrients from all three sources more readily available. In the panhandle, the sudden availability of nutrients in the early stages of flooding is followed by large blooms of phytoplankton and then zooplankton. The zooplankton, mainly cladocerans, hatch from resting stages in the soil and feed on detritus and phytoplankton (Hoberg et al. 2002). As flooding proceeds, many fish species move into flooded areas to spawn. The flooded areas soon contain large numbers of larval and juvenile fishes, which feed primarily on zooplankton. Presumably, the grazing of these fishes is largely responsible for the major decline in zooplankton populations as the season progresses. These dynamics reflect the strong mutual subsidies between the terrestrial and aquatic components of the ecosystem (Hoberg et al. 2002).

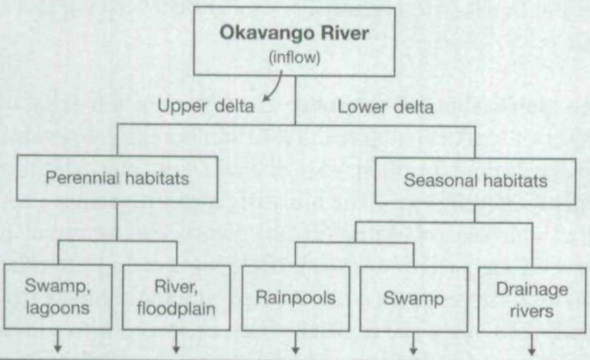
It is likely that similar interactions take place throughout the delta because most aquatic invertebrates are widespread, although the invertebrate fauna of seasonally flooded rain pools tends to be distinct (Appleton et al. 2003). The importance of the mutual subsidies may vary from year to year because there is considerable variability in invertebrate diversity and abundance among years with low and high flood levels in the delta (Appleton et al. 2003).

Fishes of the Okavango Delta

There are approximately 71 fish species in the Okavango Delta (Merron 1991, Masundire et al. 1998, Tweddle et al. 2003) with highly diverse morphologies (Ramberg et al. 2006). Different groups of species inhabit different delta habitats (figure 5; Merron 1991, Mosepele and Mosepele 2005). In the lower delta, there are about 62 fish species (Merron 1993a), with different fish assemblages in permanent and seasonal swamps (Mosepele and Mosepele 2005). The permanent swamp populations are characterized by high abundance of tigerfish (*Hydrocynus vittatus*), sharptooth catfish (*Clarias gariepinus*), and threespot tilapia (*Oreochromis andersonii*), while the seasonal swamp fish populations are dominated by silver catfish (*Schilbe intermedius*) and African pike (*Hepsetus odoe*) (Merron and Bruton 1995). Tigerfish (an important predator and sport fish) do not occur in seasonal swamps except during years of high floods (Mosepele and Mosepele 2005). In addition, similar species have different life-history strategies in permanent and seasonal swamps (Merron 1991). There can also be differences within species. Thus, Mosepele and colleagues (2005) showed that three cichlid species (*Oreochromis andersonii, Oreochromis macrochir,* and *Tilapia rendalli*) had different life-history parameters (i.e., growth, mortality, growth performance, and length at maturity) in different habitats. Individuals from seasonal floodplains generally have faster growth rates than individuals from the upper delta (Mosepele et al. 2005).

The dominant species of predatory fish is an important difference between perennial and seasonal swamps. In fast-flowing riverine habitats in the upper Okavango Delta, the tigerfish is a major piscivore; it is replaced in this role by the African pike in the slower-flowing, well-vegetated seasonal Okavango swamps. The African pike is an ambush predator and relies on dense vegetation for cover while waiting for prey (Merron et al. 1990). The relative absence of tigerfish from seasonal swamp and drainage rivers can be related to their preference for perennial large, open water lagoons and river channels (Fox 1976, Merron and Bruton 1995, Okland et al. 2005), and their absence may allow the more sluggish pike to become a dominant piscivore. In both habitats, large predatory catfishes, especially the sharp-tooth catfish and blunt-tooth catfish (*Clarias ngamensis*), and predatory cichlids (largemouth breams, *Serranochromis* spp.) are also common. During the dry season, large aggregations of the two catfishes move up river channels to feed on smaller fishes that become concentrated in the channels as off-channel habitats diminish (Merron 1993b). These runs of feeding catfish are followed by tigerfish, largemouth bream, aquatic birds, and other predators to take advantage of prey chased from hiding by the catfishes.

The life cycle of most fish in the delta is presumably similar to that of the few well-studied species in the area (Booth et al. 1995, Booth and Merron 1996), especially greenhead tilapia (*Oreochromis macrochir*) and redbreast tilapia (*T. rendalli*). After flooding has occurred and water temperatures start to rise, adult fish move into flooded habitats to spawn. The embryos hatch within a few days and become larvae, which feed on the abundant zooplankton. In most areas, juvenile fish grow rapidly in the protection of vegetative cover and shallow water for roughly four to six months, gradually moving into deeper water (e.g., lagoons) as they grow larger. Tilapia species can reach 10 to 12 cm in this time period, reducing the size range of predators that can consume them (Booth et al. 1995, Booth and Merron 1996). The fastest-growing individuals may actually spawn in their second flooding season, but many continue to devote most of their energy to growth, and spawn in their third flooding



Swamp, lagoons	River, floodplain	Rainpools	Swamp	Drainage rivers	Species
X	X	–	–	–	1. Tigerfish
X	X	–	X	X	2. African pike
X	X	–	–	–	3. Upper Zambezi labeo
X	X	–	X	X	4. Silver catfish
X	X	X	X	X	5. Sharptooth catfish
X	X	X	X	X	6. Blunt-tooth catfish
X	X	X	X	X	7. Leopard squeaker
X	X	–	X	X	8. Spotted squeaker
X	X	–	X	X	9. Threespot tilapia
X	X	–	X	X	10. Greenhead tilapia
X	X	–	X	–	11. Thinface largemouth
X	X	X	X	–	12. Nembwe
X	–	–	X	X	13. Brownspot largemouth
X	X	–	X	X	14. Redbreast tilapia
X	X	X	X	X	15. Banded tilapia

Figure 5. Abundance of 15 fish species important to fisheries in the Okavango Delta, by major habitat type. X = always present; — = usually absent. Scientific names for the fishes are 1,* Hydrocynus vittatus; *2,* Hepsetus odoe; *3,* Labeo lunatus; *4,* Schilbe intermedius; *5,* Clarias gariepinus; *6,* Clarias ngamensis; *7,* Synodontis leopardinus; *8,* Synodontis nigromaculatus; *9,* Oreochromis andersonii; *10,* Oreochromis macrochir; *11,* Serranochromis angusticeps; *12,* Serranochromis robustus; *13,* Serranochromis thumbergi; *14,* Tilapia rendalli; *and 15,* Tilapia sparrmanii. *Common names are from Skelton (2001). Source: Updated from Mosepele (2000).

season. Growth in most species slows considerably once they become reproductively mature, but some individuals may live 10 to 13 years. Not all species follow this pattern, however, especially those living in the more unpredictable seasonal swamp. African pike, for example, have flexible spawning times and their bubble nests allow them to produce young even when levels of dissolved oxygen (DO) are low (Merron et al. 1990).

In the panhandle region, the off-channel lagoons appear to be crucial for fish production. During periods of flooding, most fishes spawn in flooded areas, where their young rear in the flooded vegetation and shallow lagoons. As the water recedes, many juveniles move out of the drying shallow lagoons into the deeper lagoons and water of the main channel. During lower-flow years, even larger lagoons may become too shallow, warm, and low in DO to support large predatory fish (such as tigerfish, which require flowing water and high DO levels), so they become important rearing refuges for many of the smaller tilapia (e.g., banded tilapia, *Tilapia sparrmanii,* and redbreast tilapia), catfish, and minnow (Cyprinidae) species (Merron 1991). There is clearly a complex and dynamic interaction among the river, flooded swamp, and lagoons, because fish habitat varies among years (related to degree of present and past flooding) and among species.

In contrast, the least diverse habitats of the delta are rain pools, which are maintained by rainfall during most years and fill with floodwaters only in wet years. In July 2005, for example, we observed pools that had been without contact with floodwaters for several years filling with water flowing down elephant trails. Such water carries juvenile fishes with it, including those that survive after contact breaks off; these are mainly species that can breathe air (e.g., *Clarias* catfishes) or otherwise live in stagnant water (Merron and Bruton 1995).

Fisheries

The ultimate predators on fish in the delta are humans, but so far the delta's fish stocks are not overexploited (Mosepele 2000, Mosepele and Kolding 2003). There are three basic fisheries in the delta: recreational, commercial, and subsistence (Merron 1991, Mosepele and Kolding 2003). The recreational fishery is concentrated in the upper delta, while the commercial fishery is more widespread but involves only about 40 full-time fishermen (Kgathi et al. 2005). According to Mosepele and colleagues (2003), the five most important species in the recreational fishery are tigerfish, nembwe, three-spot tilapia, deepcheek bream (*Sargochromis greenwoodii*), and thinface largemouth (*Serranochromis angusticeps*). The principal commercial species are three-spot tilapia, redbreast tilapia, green-head tilapia, nembwe, thinface largemouth, and hump-back largemouth (*Serranochromis altus*); various catfishes are also harvested, although they are rarely target species as are the tilapia (Mosepele 2000, Mosepele and Kolding 2003, Mosepele et al. 2005).

The subsistence fishery involves about 3000 fishermen who use a variety of traditional fishing gear (Mosepele 2000). Although the main fish species targeted are small tilapia and cyprinids, different fishing gears harvest different species and different sizes of fish (Mosepele et al. 2005). Mosquito nets, used as small seines, harvest small species such as Johnston's topminnow (*Aplocheilichthys johnstoni*) and spot-tail barb (*Barbus afrovernayi*) (Mosepele et al. 2003). Other gear, such as fishing baskets, harvest mainly banded tilapia and straightfin barb (*Barbus paludinosus*), although hook-and-line gear and gill nets may be used to harvest larger species. Overall, the dominance of relatively low-intensity, multispecies, multigear fisheries is presumably a major reason that fish biomass and diversity remain high in most areas that are fished (Jul-Larsen et al. 2003, Mosepele et al. 2005). In addition, the life-history patterns (e.g., rapid growth, high reproductive rates) of most of the fishes permit moderately high exploitation rates. Thus, the fishes appear to be able to sustain present levels of exploitation while retaining their importance in ecosystem processes (e.g., recycling nutrients, food for birds and mammals). According to Jul-Larsen and colleagues (2003), this broad exploitation pattern may result in decreased biomass but still maintains species richness in the fish community.

Fish, fisheries and flooding: Conceptual model

The fish and fisheries of the Okavango Delta depend on annual inflow and rainfall cycles to create and sustain floods for their survival (figure 6). The floods periodically connect

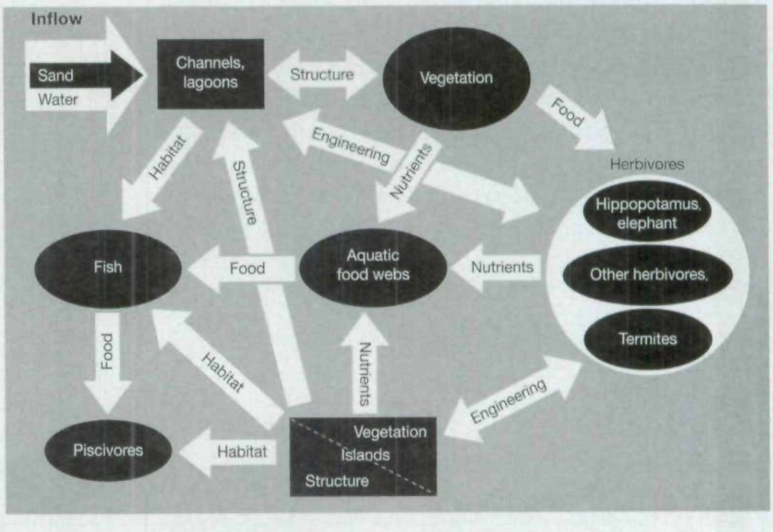


Figure 6. A simplified, fish-oriented conceptual model showing the relationship between major physical (boxes) and biological (ovals) factors in the Okavango Delta. Arrows indicate positive effects (e.g., formation of channels and lagoons is strongly influenced by growth of papyrus and other vegetation, which depend on the water delivered by the channels). The input of water and sand, which is highly variable from year to year, influences the strength of all of the other interactions. Thus, reduced input of water and sand over an extended period of time will ultimately reduce fish populations.

all the lagoons and swamps to the main river channel and facilitate migrations and spawning of the various fish species. The floodwaters also incorporate terrestrial plant and animal matter into the aquatic system, where it forms the basis of the food web. This food input is used by fish for growth and reproduction. The shallow swamps are also important for providing safe nursery sites for fish larvae and juveniles during their early stages of development.

The main factors influencing fish communities in the Okavango appear to be a combination of the length of time the water is present and the nature of its flow. These factors determine other physical features such as aquatic plant communities and DO levels that influence the fish community present. The higher the magnitude of the annual flood, the longer the water is retained on the floodplain, leading to a longer spawning period and greater overall production of fish (Merron 1991). Although there are wide oscillations in the timing, magnitude, duration, and even location of the annual flood (Ellery and McCarthy 1994, Mazvimavi and Wolski 2006), the relatively predictable pattern (figure 2) is apparent in responses of the fishes, such as the annual catfish runs (Merron 1993b). This pattern is illustrated in figure 7, which shows strong peaks in the commercial catch of catfish (*C. gariepinus* and *C. ngamensis* combined) every September.

Variability in the amount of flooding is important to sustain fish and fisheries. While low-flood years may result in the loss of some recruitment of fish and reduce fisheries temporarily, they also allow terrestrial processes that may ultimately increase fish production. Thus, dry years allow termites to colonize new areas, elephants and hippos to create new channels, and dung to accumulate that will provide nutrients when flooding returns. High-flow years inundate termite islands, provide more habitat for hippos (and increase their numbers and activity), and mobilize soil nutrients. The extent of these positive feedback loops is poorly understood, but they are very likely considerable. The conceptual model diagram (figure 6) illustrates only a few of most conspicuous interconnections among physical and biological aspects of the delta, but nonetheless suggests both the complexity and potential fragility of the system if key pathways are disturbed by human activity, such as water removal.

Conflicts in resource use

Water demand is increasing in the three developing countries in the Okavango catchment: Angola, Namibia, and Botswana (Mbaiwa 2004, Mendelsohn and el Obeid 2004). So far, the total amount of water diverted from the Okavango River and its tributaries has been small relative to total flow, and no impacts from upstream diversions have been detected. However, future water impoundments and diversions could cause major changes to the Okavango Delta ecosystem. For example, reduced peak inflow associated with upstream storage facilities could change the amount of water flowing into the lagoons along the panhandle, which play an important role in fish production. Likewise, permanently reduced inflow associated with substantial out-of-basin diversions or with the expansion of irrigated agriculture would increase the amount of dry grasslands on the periphery of the delta, reducing habitat for wildlife and fish. Thus, a key to long-term persistence of the Okavango Delta as an ecosystem that supports abundant fish and wildlife is developing an understanding of the environmental flow requirements of the delta, and then using this understanding to allocate water in the rest of the Okavango watershed.

The first part of this linked analysis has culminated in a GIS (geographic information system)-based hydrologic model for the delta (Wolski et al. 2006). This model has been used to assess the impact of various delta inflow scenarios on ecological conditions in the delta (Murray-Hudson et al. 2006). We have extended this work by attempting to link environmental flow requirements for the delta to a planning model that explicitly captures other management objectives. This model is a modified version of an existing Okavango basin application of the Water Evaluation and Planning (WEAP) model developed by the Stockholm Environment Institute. The WEAP model was modified to test hypotheses related

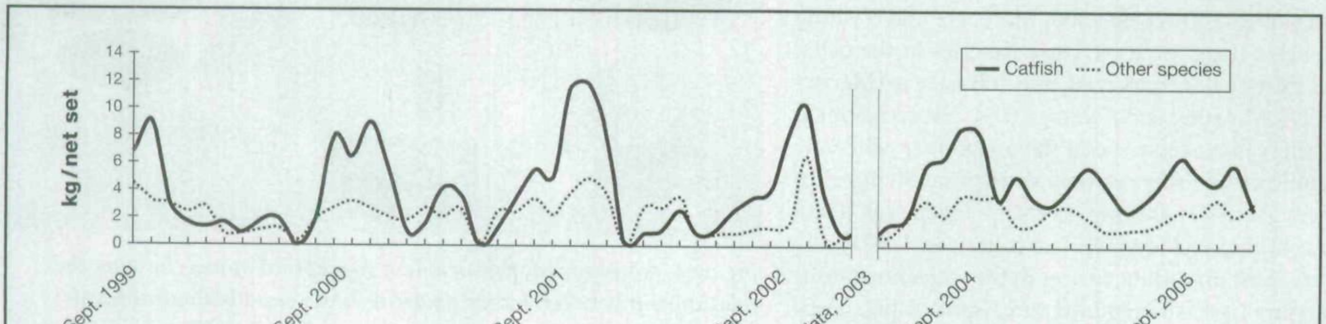


*Figure 7. Seasonal variations in catch rates (cpue [catch per unit effort], in kilograms per net set) of two catfish species (*Clarias gariepinus *and* Clarias ngamensis*) compared with 42 other species sampled from the Okavango Delta in the period 1999–2005.*

specifically to fish and flows. We basically developed a structured conceptual model (figure 8) that assumed that fish abundance and diversity was a function of the total inflow to the delta and of the percentage of the panhandle region covered in natural vegetation (i.e., not grazed by livestock). This conceptual model was shared and further modified by participants in a workshop on environmental flow requirements for the Okavango Delta (held 15–16 June 2005 in Maun, Botswana; Soderstrom et al. 2005).

The existing WEAP planning model of the Okavango Basin explicitly describes both the current state of the upper basin as well as several scenarios for greater use of water. The model is based on the same simulated historic hydrologic conditions (Hughes et al. 2006) that were used to investigate the hydrologic impact of various delta inflow scenarios (Murray-Hudson et al. 2006). In order to capture the ecological memory described above, the fish-based conceptual model of environmental flows was expanded to include an interannual component. Under this model, a sequence of dry years was managed to maximize delta inflows at the expense of water-management objectives for the upper basin. During a series of wet years, the system was operated to extend the period of relatively high delta inflow, also at the expense of upper basin objectives. Otherwise, diversions were permitted under a standard set of conditions.

Using these assigned priorities, we found that simulated environmental flows resulted in an average shortfall of less than 25% to upstream users, even during simulations in which highest water demand coincided with the driest period described in the hydrologic record. This confirmed that minor hydrologic manipulations in the upper basin are likely to have little effect on the delta ecosystem, at least under present and historic conditions. However, more complex mathematical and GIS-based models (Murray-Hudson et al. 2006, Wolski et al. 2006) indicate that climate change may greatly accentuate the impacts of dams and diversions during droughts that are more extreme than any in the historic record.

Obviously, to fully understand the interactions between upper basin management and ecosystem status in the delta, factors other than fish and fish habitat need to be considered. It now appears that holistic methodologies for determining flows seem to be most appropriate for large, complex systems such as the Okavango River and Delta (Tharme 2003), especially where ecological integrity is an important goal (Richter et al. 2003). Holistic approaches rely largely on multidisciplinary panels of experts to develop flow regimes that take into account conflicting interests and values. However, even holistic approaches require a basic understanding of the hydrology of the system, as reflected in the modeling approaches of Murray-Hudson and colleagues (2006) and Wolski and colleagues (2006), as well as close integration with tools to simulate water management, such as the WEAP model.

Other conflicts

Although international attention has focused on potential conflicts over environmental flows, there are other potential conflicts as well (Turton et al. 2003a, 2003b). Conflicts facing the delta that particularly affect fish and fisheries include groundwater extraction, livestock grazing, tsetse fly control, and invasions of nonnative aquatic plants (Ramberg et al. 2006). Grazing, in particular, is a growing problem because creating pasture for cattle, usually by burning seasonal swamp during the dry season (Heinl et al. 2007), directly conflicts with the needs of wildlife and, ultimately, fish (figure 8). These are only a few of the problems that are dealt with in more detail by Merron (1992), Ellery and McCarthy (1994), Alonso and Nordin (2003), Mendelsohn and el Obeid (2004), and Kgathi and colleagues (2005).

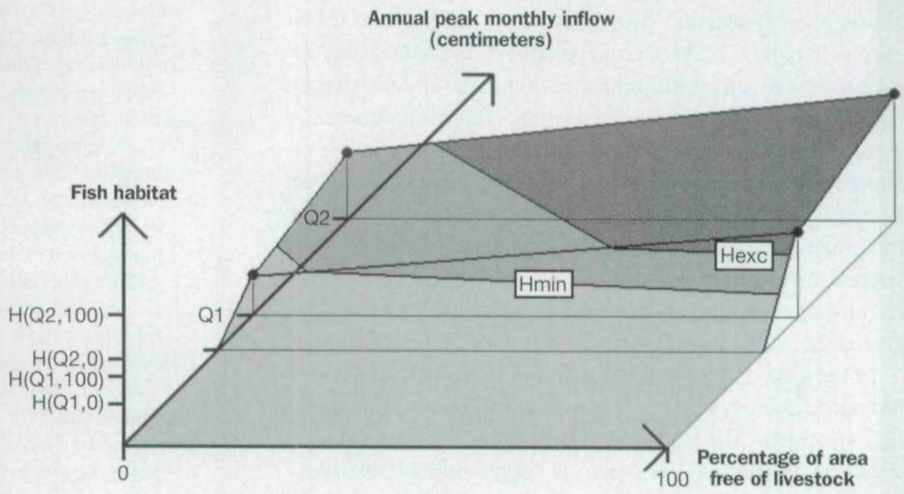


Figure 8. A conceptual model relating the quality of the fish habitat (H) to the peak monthly average inflow in a year (Q) and the percentage of flooded area that is free of livestock. Generally, low levels of flooding result in the conversion of lands to pasture for livestock. The dark gray area of the surface represents regions where conditions are optimal (excellent). Higher peak monthly inflows are needed to achieve optimal conditions as natural vegetation on the floodplain is converted to other uses (e.g, pasture). The medium gray area is where a minimum level of floodplain connection is available to support fisheries. The light gray area represents conditions where the level of connection results in significant declines in fish abundance and diversity because of large-scale loss of habitat. Minimum (Hmin) and excellent (Hexc) levels of fish habitat are created through different combinations of peak monthly average inflow and percentage of flooded areas free of livestock. For a given level of fish habitat, targets can be set for the management variables.

Conclusions

The aquatic ecosystem of the Okavango Delta depends on annual flooding, which shows considerable variability from year to year, yet is fairly predictable in timing and minimum extent. The fishes in the system are adapted to this predictable annual flood regime because (a) flooding increases the total habitat available to fish; (b) flooding mobilizes nutrients stored on the floodplain, which are the basis for the high productivity of the aquatic system; (c) flooded vegetation provides places to spawn and places for young to rear; and (d) flooding maintains the populations of large mammals and termites that create habitat structure. Thus, the more and longer an area is flooded, the higher its production of fish, although year-to-year variability in the extent of flooding is also important. The diversity of life-history strategies and of interactions among the fishes is responsible for high species richness and contributes to the complexity of the ecosystem. Ecosystem complexity is also increased by the strong interactions among terrestrial and aquatic components of the system, such as the geomorphic and nutrient-producing activities of hippos, elephants, and other large animals, and the dependence on fish of many bird and mammal predators.

While the Okavango ecosystem clearly depends on annual high-flow events, most of the fishes have characteristics that make them resilient to periods of drought, when flooding is reduced. For example, many can live 10 or more years and persist in the larger, deeper channels, where their larger size allows some protection from predation. Many of the fishes engage in parental care of embryos and young, increasing the probability of successful reproduction even under extreme conditions. Resiliency under natural conditions does not mean these same fish can persist under conditions highly altered by human activity, such as upstream diversions or decreased habitat and nutrients from management of lands for grazing livestock. However, hydrologic modeling does suggest that sustainable use of the water and related delta resources is possible, if the needs of the delta ecosystem are given highest priority.

In the Okavango Delta, there is apparently a net flow of biological energy (nutrients) from the panhandle and perennial swamp to the seasonal swamps and drainage rivers, which is carried by the seasonal high flows of relatively nutrient-free water from the Angolan highlands. Aquatic habitats in the southern Okavango Delta and drainage rivers that are subject to wide natural fluctuations in flow seem to be able to sustain a greater degree of human exploitation and change than those in the Okavango panhandle and perennial swamp. In the perennially flowing waters of the upper Okavango Delta, the fish community is more diverse, and ecological processes such as seasonal migrations and feeding relationships appear to be more complex (Merron and Bruton 1995). The ecological relationships within the fish community, such as annual catfish runs, in particular are finely tuned to the hydrological, chemical, and biological components of the Okavango ecosystem (Merron 1993b). Understanding and protecting these components and processes is key to maintaining the Okavango Delta as one of the world's most remarkable wild places while also supporting indigenous fisheries and other human uses of the ecosystem. Ongoing international efforts (such as the Okavango River Basin Water Commission) provide the basis for holistic management of the Okavango Delta, but the success of such efforts depends on improved understanding of the ecosystem and of human interactions with it, on an international scale.

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