

## Notes on the Community Structure and Biology of Fishes in the Okavango Delta

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### Abstract

The Okavango Delta (Delta) is a dynamic ecosystem constantly in motion. Each year the timing, magnitude, and duration of the annual flood is dependent on rainfall levels in the southern Angolan highlands. The annual floodwaters arrive in the northern Delta in January but do not reach the southern Delta and Thamalakane River until approximately May. With the flood waters the Delta rapidly surges with biological productivity as nutrients are quickly assimilated by aquatic plants, fish, and insects. Many of the 80 fish species undergo annual migrations to spawning and feeding grounds throughout the myriad of waterways.

There are distinct fish communities in the Delta which can be separated from each other by the physical characteristics of the different habitat types with which they co-evolved. An overview of the community structure of the fishes and the environmental factors that limit their distribution is presented in this piece. In the northern riverine floodplain and perennial swamp, a higher species richness was recorded than in the seasonal swamp and drainage rivers.

### Introduction

There are at least 80 fish species inhabiting the myriad of waterways that characterise the Delta's aquatic ecosystem. These species and others from the Chobe River are described in detail in the *Field Guide to Fishes of the Okavango Delta and Chobe River, Botswana* (Bruton *et al.* 2018). The Delta receives an annual pulse of water each year, locally known as the flood. The timing, magnitude, and duration of the flood are not constant from year to year and determined by the periodicity and volume of annual rainfall in the southern Angolan highlands. The annual flood seasonally connects the lagoons and floodplains to the main river channels and facilitates migrations, feeding, and spawning of the various fish species.

The fishes represent a valuable natural resource for the people of Ngamiland. Fish provide a free source of protein and subsistence fishing is common in rural communities using a variety of fishing methods including fish traps, hook and line, and baskets (Merron 1993). The fishery also consists of commercial and sport fishers. The commercial fishery utilizes gill nets set from both traditional *mekoro* (dug-out wooden canoes) or motor boats and harvest fish for sale. Sport fishing is an important activity generating employment through the tourism industry (Merron 1994).

The goals of the research were to identify fish distribution and ecology in the Delta including river channels, perennial swamp, and seasonal swamp habitats and how fish communities respond to the annual flood cycle.

### Study Area

The origins of the Okavango Delta begin in the highlands of southern Angola as the Cubango and Cuito rivers, which merge in Namibia as the Kavango River before entering Botswana as the Okavango River. As the Okavango River enters Botswana it begins to overflow its banks onto a broad riverine floodplain, known as the panhandle, which spans approximately 100 kilometres long and 15 kilometres wide before spreading out into a Deltaic wetland ecosystem (Merron and Bruton 1988). The river then splits into three main branches, the Thoage to the southwest, the Jao and Boro in the centre, and the Nqoga in the Northeast. These rivers spread out into several other river channels, such as the Mborogha and Kwai and perennial lagoons, including Gadikwe, Gobeqca, Xugana, and Xakanika.

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At the southern end of the system the Boro and Santandadibe rivers are main channels flowing out of the Delta. These rivers end against a geological fault line along the Thamalakane River before flowing into the Nghabe and Botleti (Boteti) rivers. The Nghabe and Kunyere rivers flow into Lake Ngami, a terminal lake at the southwestern corner of the Delta (Figure 1). Lake Ngami undergoes dramatic hydrological cycles of extended periods of receiving flood waters and extremely dry periods. During the 1980s and 1990s, the lake was largely dry (Merron 2018).

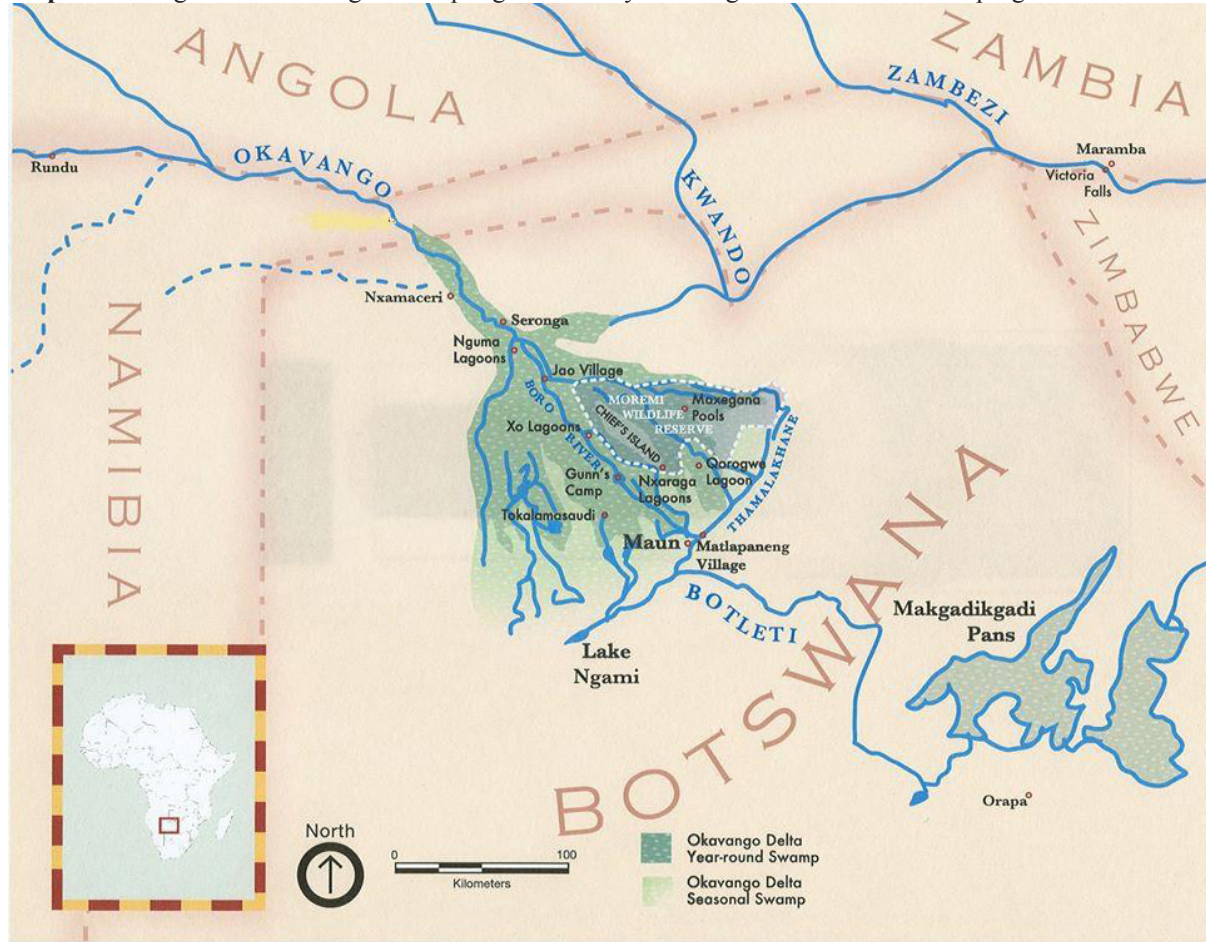
The Delta is a dynamic ecosystem that can vary in size each year depending on the timing, magnitude, and duration of the annual pulse of water that flow from the southern Angolan highlands. These hydrological parameters influence fish distribution throughout the system. The low gradient of the Delta causes the timing of the flood to vary with the greatest fluctuations occurring in the southern end of the system. The floodwaters reach the riverine floodplain in January but do not reach the southernmost portions until May, which can vary each year. The most important feature of the flood is that it restores the Delta by bringing in a new set of environmental conditions.

### **Methods**

The JLB Smith Institute of Ichthyology carried out multiple fisheries surveys between February 1983 and February 1987 at various sites in the Delta (Map 1). Sampling of the fish populations entailed the use of gillnets ranging in size from 24 to 118mm stretch mesh and a 25m x 12mm seine net being the primary sampling methods. Gillnets were set at dusk and retrieved at dawn. Seine net collections were made during daylight hours.

During the course of the research there were no surveys of Lake Ngami as it was dry. However, fish sampling was carried out throughout the Kavango River in Namibia (Skelton and Merron 1987). During the research fish were dissected to determine their feeding preferences and how the food chain of the fish community operates. Reproductive periodicity was established by visual gonad examination.

**Map1:** Okavango Delta showing the sampling sites surveyed during the fisheries research programme.



Source: Map created by Inland Ecosystems, Reno.

## Results

### *Overview of the community structure of fishes in the Delta*

At least 70 fish species were collected during the course of the research programme with other species still under taxonomic study. Merron (1991) synthesized the available information on the fish community collected during the course of the research programme and provided an assessment of the response of various fish species to the annual flood regime. A clear distinction in the composition of the fish communities was recorded between the northern perennially flooded and the southern seasonally flooded habitats. The northern riverine panhandle and perennial swamp are characterized by a greater diversity of fish species, many of which reach a large size, such as the Tigerfish (*Hydrocynus vittatus*) and Sharptooth catfish (*Clarias gariepinus*). In contrast, the southern seasonal swamp and outflowing rivers, such as the Thamalakane that experience a wider fluctuation in annual flood levels, are characterized by a lower diversity of fish species and smaller overall body size.

The top predators also vary between the northern perennial and southern seasonal aquatic habitats. The Tigerfish is the top predator in the northern Delta, whereas the African pike (*Hepsetus cuvieri*) is the top predator in the southern seasonal habitats. The low abundance of Tigerfish in the southern Delta is owing to this species requiring perennial river channels and lagoons to complete its life history, including reproduction. The fish of the Delta depend on the annual flood cycle for their survival. With the rising floodwaters drier areas are inundated and connected to the river and lagoons. All fish species benefit either

directly or indirectly from the rising waters. The annual flood creates an almost immediate availability of nutrients as terrestrial plant and animal matter are integrated into the aquatic system. This increase in nutrients allows aquatic plants to flourish providing a critical food source for juvenile fish. Many fish species migrate and spawn in these newly flooded areas. The annual cycle of flooding and drying reflects the strong mutual interdependence between the terrestrial and aquatic components of the Delta's ecosystem.

The higher the magnitude of the annual flood, the longer the retention time on the floodplain. This leads to a longer spawning period and greater overall fish production. Although there are fluctuating climatic changes controlling the timing, magnitude, and duration of the annual flood from Angola, the Delta does receive a flood cycle each year and a relatively constant pattern in the response of the fish communities is apparent. The fishes have adjusted to the changing water levels by producing large numbers of young to ensure that some will survive the fluctuating wet and dry cycles. Many fishes are trapped in isolated pools during the receding water levels, resulting in a short-lived and plentiful food resource that can be fully harvested by people. Fishes are also consumed by fish-eating birds and crocodiles. The main physical factors influencing the fish communities are a combination of the length of time the water is present and nature of its flow. These factors determine other environmental features, such as the type of aquatic plants present and oxygen levels in the water, both of which influence the type of fish community that occurs.

Merron and Bruton (1988) documented yields for floodplain habitats in excess of 300kg/ha. Highly variable areas of the southern Delta, including Lake Ngami, can produce outstanding fisheries yields after receiving flood waters.

#### *Feeding preferences*

There are seven major fish feeding groups in the Okavango, including predators that feed on other fish, and species that feed on plant material, detritus, molluscs and crustaceans, aquatic insects, and plankton. There are also generalist species that consume all food types. The characin family consists of four species and most noticeable is the Tigerfish that feeds almost exclusively on other fish, with snakes and small mammals also recorded in its stomach contents. Other species of characins analysed, especially the Striped robber (*Brycinus lateralis*) had undigested seeds in their lower intestines consumed from submerged plants. This undigested matter indicates that seeds pass through the digestive tract and out in the faeces. Characins play an important role in spreading seeds and allowing plants to germinate in recently inundated areas with rising flood waters.

The cichlid family, commonly called tilapia or bream, includes at least 12 species. Several of these species such as the Threespot tilapia (*Oreochromis andersonii*) and Greenhead tilapia (*O. macrochir*) are widespread throughout the Delta and feed on detritus. The Southern mouthbrooder (*Pseudocrenilabrus philander*) feeds on small insects and plant material. Other species of fish in this family, such as the Thin-face largemouth (*Serranochromis angusticeps*) and Nembwe (*S. robustus*) are predatory and feed on live prey. The Redbreast tilapia (*Coptodon rendalli*) is a herbivore feeding almost exclusively on aquatic plant material.

The clariid family includes four catfish species. The most common species is the Sharptooth catfish, which feeds on a wide variety of food items, including fish, insects, frogs, small mammals, bird hatchlings, and plants.

The cyprinid family, commonly called minnows, is the most diverse group of fishes and represented by 14 species. These species are typically generalist feeders that consume a wide variety of prey items feeding on the stalks of aquatic plants. The Upper Zambezi labeo (*Labeo lunatus*) is the largest member of this family inhabiting the Delta and feeds on detritus.

The mormyrid family consists of five species that feed on the aquatic insect fauna. Only a very

small percentage of mormyrids had empty stomachs because they feed constantly. The species name of the Churchill (*Petrocephalus okavanogensis*) is named after the Okavango Delta.

The schilbeid family has only one representative in the Delta, the Silver catfish (*Schilbe intermedius*). This species consumes a wide range of prey items including fish, terrestrial insects, and crustaceans. Silver catfish are equipped with sensory barbells and a large mouth armed with numerous small teeth. The Silver catfish is common throughout the Delta and because it feeds heavily on terrestrial insects it represents a major pathway by which terrestrial resources are assimilated into the aquatic environment.

The mochokid family is represented by at least 5 species, including the Bubblebarb squeaker (*Synodontis thamalakanensis*), named after the Thamalakane River. These fish have a peculiar feeding habitat, often swimming upside down grazing along the stems of aquatic plants. When removed from the water they make a distinctive squeaking noise. A close relative is the Zambezi grunter (*Parauchenoglanis ngamensis*). It was first collected at Lake Ngami, hence the species name.

The afromastacembelid family is represented by one species in the Delta, the Longtail spiny eel (*Mastacembelus frenatus*), which is a unique habitat specialist and lives within the intertwined roots of papyrus lining perennial river channels. This species feeds on aquatic insects and plant material.

#### *Okavango catfish runs*

One of the Okavango's most noticeable fisheries events is the annual catfish runs, which are a predator-prey ecological event most noticeable in the northern riverine panhandle. An annual study of the catfish runs was made over consecutive years including 1984–1987 and 1989–1991 (Merron 1993). Thousands of Sharptooth and Blunttooth (*C. ngamensis*) catfish hunt within the papyrus lining the main river channel in packs recorded up to 0.5km long moving upstream. The catfish slap the papyrus with their caudal fin and suck in fish hiding in the papyrus root balls. The Blunttooth catfish was named after Lake Ngami where it was first collected and described in 1861 by Francis Castelnau.

The start of catfish pack-hunting varies from year to year depending on the magnitude of the annual flood, which affects the timing of the Okavango River's low water phase when the catfish runs occur. The largest shoals of catfish and highest intensity of feeding were observed from mid-September through November.

The papyrus fringe of the main channel turns into a cacophony of sounds from large catfish sucking in prey fish hiding in the papyrus root balls. Tigerfish patrol the main channel during a catfish run, hunting for prey that may have escaped the onslaught of the catfish feeding along the river and papyrus interface. Vast flocks of fish-eating birds also feed on disoriented fish.

Merron (1993) documented an interesting finding pertaining to the catfish runs where the stomach content analyses revealed that the catfish exhibit a unique pack-hunting behaviour selectively feeding on electro-generating mormyrids, particularly the Bulldog (*Marcusenius altisambesi*). Bulldog fish generate an electrical signal from their bodies to detect bottom-living invertebrates on which they prey. The catfish can detect the electrical currents through their sensory barbels enabling them to selectively seek out Bulldogs. The behaviour of catfish preying specifically on Bulldogs is a unique feeding specialisation recorded only from the Okavango Delta in Africa.

#### *Reproductive strategies*

The Delta's 70 fish species exhibit one of three spawning strategies classified as non-guarders, guarders, and bearers. Non-guarders, such as the Tigerfish and Catfish, release their eggs and sperm into the water in large schools of individuals where fertilisation takes place. The eggs then settle on plant roots where they develop unprotected.

Guarders, such as the Redbreast tilapia and Okavango tilapia (*Tilapia ruweti*) protect their developing eggs and young in a nest often hollowed out in the sand. Bearers, such as the Threespot and Greenhead tilapias, protect their eggs and young in the mouth until they are of a sufficient developmental stage to be released.

### Discussion

The fishes of the Okavango Delta are a valuable natural resource for the people of the region and Botswana generally. Fish provide a free source of protein and revenue for many rural communities. The commercial fishery contributes to the local economy. The sport fishery also provides revenue and employment. It is important to note that the Delta is home to at least 7 fish species that bear its name, including Churchill (*P. okavanogensis*); Bubblebarb squeaker (*S. thamalakanensis*) and Thamalakane barb (*Enteromius thamalakanensis*) both named after the Thamalakane River; Blunntooth catfish (*C. ngamensis*) and Zambezi grunter (*P. ngamensis*), named after Lake Ngami; Slender robber (*Rhabdalestes maunensis*), named after the town of Maun; and Okavango tilapia, whose southernmost limit of distribution in Africa is the Delta.

The Okavango ecosystem contains one of Africa's most significant fish faunas with a very high diversity of families (15) and genera (39), particularly when compared to the Southern Rift Valley lakes. For example, Lake Malawi is dominated by only one family, the cichlids. More than 60 fish species reach their southern limit of distribution in Africa within the waters of the Delta. The system serves as an ecological transitional zone between the tropical fish faunas to the North, such as the Zambezi and Congo, and the subtropical fish faunas to the South, including the Limpopo River and beyond.

In the Okavango Delta, the main flow of biological energy is from the northern perennial waterways to the southern seasonal swamp and outflowing rivers. In the perennially flowing waters the fish community is more diverse and ecological processes, such as seasonal spawning migrations and feeding strategies, are more complex (Merron 1991). These ecological processes within the fish community, such as the annual catfish runs, have evolved over time and are finely tuned to the hydrology of the system, including the unique behaviour of catfish preying specifically on Bulldogs as described previously (Merron 1993). The widely fluctuating hydrology of the seasonal swamp and drainage rivers do not permit the time necessary for complex ecological fisheries interactions to develop.

### Conclusion

The Okavango Delta is becoming more developed and its waters may have to be considered in the long-term plans for the future development of countries within its watershed, including Angola, Namibia, and Botswana. The balance between the growing developmental needs of the countries surrounding the watershed and conservation of the natural fauna and flora is a challenge. Conservation of the fishes does not mean preservation, but the wise utilisation of this important natural resource to improve the quality of life of all the people by integrating fisheries conservation and development sustainably.

The Delta is a dynamic ecosystem that varies each year depending on the timing, magnitude, and duration of the annual flood. These factors have a profound influence on fish distribution and abundance in the system. By monitoring the fishes, scientists can provide valuable information for the region's planners regarding the potential effects on fishes from proposed development activities.

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