LIFE-HISTORY AND STOCK ASSESSMENT OF *CLARIAS GARIEPINUS* IN THE OKAVANGO DELTA, BOTSWANA

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by

THETHELA BOKHUTLO

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This thesis is dedicated to my son, Thapelo for putting up with my extended absence from home, particularly during the lean second year.

Contents

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ABSTRACT

Large catfishes (*Clarias gariepinus* & *Clarias ngamensis*) are not exploited commercially in the Okavango Delta, Botswana. They however constitute a large proportion of the gill net fishery catch (23 %) albeit as by-catch, coming second after cichlids (70 %). Monthly experimetal gill net sampling over 8 years showed that *C. gariepinus* was the most abundant species in the Okavango Delta by mass making up 37 % of the catch composition by fresh weight. Despite the relatively high abundance of *C. gariepinus* in the Okavango Delta, its status has never been fully assessed. For this reason, this study aimed to assess the status of *C. gariepinus* in the Okavango Delta with the particular goal to determine if the species could support a directed commercial gill net fishery.

Investigation of the effects of the flood pulse on abundance of *C. gariepinus* showed that variability in water levels was the major driver of population abundance for this species. Three biological variables: (1) catch per unit effort (CPUE); (2) % catch composition and (3) Shannon's diversity index (H') exhibited a negative and significant relationship with the flood index within a year. The variation in these variables was statistically significant between months. There was a weak positive relationship between water levels and the biological variables between years suggesting increase in productivity of the system at high water levels without a lag period.

Age and growth were determined using sectioned otoliths. Edge analysis showed that growth zone deposition occurred during the drawdown period in summer when water temperature and day length were increasing. The maximum recorded age was 15 years. Growth of this species was best described by the linear models (y = $21.50x + 427.39$ *mm* L_T; $r^2 = 0.35$) for females and ($y = 23.79x + 440.83\ mm\ L_T;\ r^2 = 0.38$) for males. The von Bertalanffy growth model described growth as $L_t = 10000(1 - \exp(-0.002(t + 18.07)))\, mm\, L_T$ for combined sexes $L_t = 10000(1 - \exp(-0.002(t + 18.50)))\, mm\, L_T$, for females and $L_t = 908(1 - \exp(-0.076(t + 7.95)))\, mm\, L_T$ for males. Age at 50 % maturity was attained in the first year of life. Spawning occurred throughout the year with an apparent peak between November and April. The mean total annual mortality rate (*Z*) was 0.25 per year. The mean annual natural mortality rate (*M*) was 0.20 per year and fishing mortality (*F*) was calculated at 0.05 per year.

The life history strategy of *C. gariepinus* was in between the periodic and opportunistic strategies. Therefore management of this species should be aimed at maintaining a healthy adult population and age structure. Since a large portion of the Okavango Delta is already protected and most other parts are also inaccessible to fishers there are enough spatial refugia for the species and the status quo should be maintained. Under this scenario, there is no need for regulation of the current mesh sizes because the species is harvested after maturity and replenishment of exploited populations will always occur from other parts of the system.

Per recruit analyses indicate that the current fishing mortality maintains spawner biomass at levels greater than 90 % of pristine levels. Therefore a commercial fishery may be established using mesh 93 mm to maximize yield with a rotational harvesting strategy. Close monitoring is essential to ensure that re-colonization of overexploited habitats does indeed occur. Recreational angling and commercial gill net fishing need to be separated on a spatial and temporal scale during the feeding run to minimize potential conflicts.

CHAPTER 1

GENERAL INTRODUCTION

Background

The Okavango Delta fishes are an important natural resource for the people of Botswana (Merron & Bruton, 1988). Studies on the biology and ecology (Merron & Bruton, 1988; Merron, 1991; Booth *et al.*, 1995, 1996; Booth & McKinlay, 2001; Mosepele & Nengu, 2003; Mosepele *et al.*, 2005*a*, *b*), stock assessment (Bills, 1996; Mosepele, 2000) and recently genetics (Van der Bank & Smit, 2007) have been conducted on many of the Okavango Delta fishes. Socio-economic aspects of the fishery have been looked at by among others Skjønsberg & Merafe, (1987), Mmopelwa *et al.*, (2005) and Kgathi *et al.*, (2005). The social structure of people in the Okavango region is mainly rurally based (Hay *et al.*, 2000) and the majority of the people derive their livelihood directly from the river (Bokhutlo *et al.*, 2007). Kgathi *et al.* (2005), when assessing the economic importance of the Okavango Delta pointed out that fishing comprises one of the direct use values of the Delta.

The Okavango Delta in northern Botswana (Fig 1.1) is a typical floodplain ecosystem that experiences periodic cycles of inundation and drawdown (Meron, 1991). The flood pulse into the Okavango delta enters Botswana from Namibia at Mohembo around December (summer) and reaches Guma lagoon around March where it often causes massive fish kills before arriving in Maun in winter around June (Bokhutlo *et al.*, 2007). The fishes inhabiting this system therefore have to employ adaptive life-history strategies to cope with fluctuating environmental conditions. According to Welcome (1999), living aquatic resources have to contend with a range of stresses, all of which affect the individual species and their potential to support exploitation and loss of environmental quality.

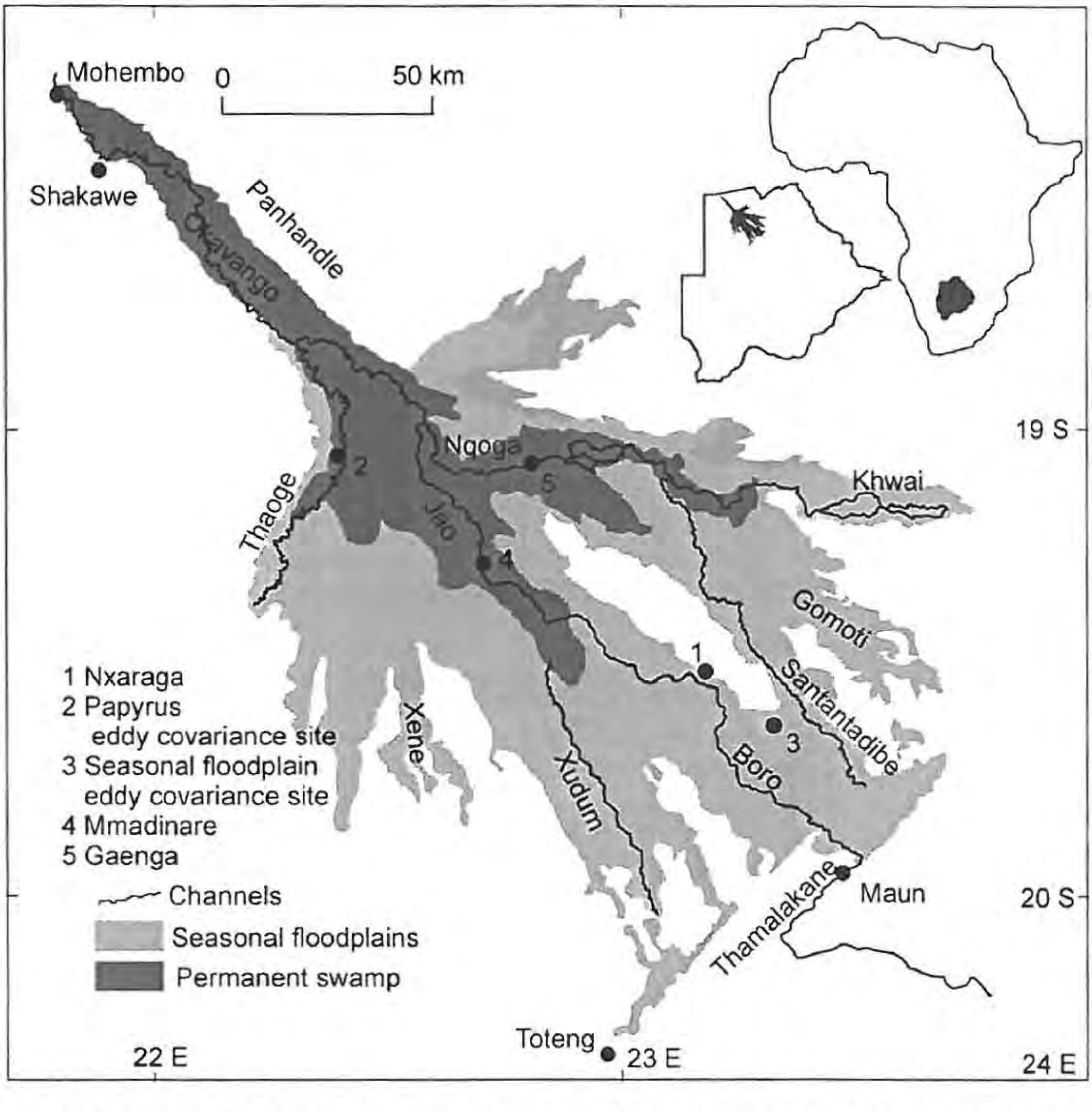

FIG 1.1. A map showing the extent of flooding as well as the major tributaries of the Okavango delta. The position of the Okavango delta in Northern Botswana is illustrated (insert). (Source: Wolski *et al*., 2006).

Apart from the natural environmental fluctuations, particularly the flood regime, Hay *et al.* (1996), postulate that several other factors may also indirectly influence the fish stocks, such as the effects of grazing, soil erosion, deforestation, siltation of the rivers and pollution. Fish, according to Mosepele *et al.* (2009), comprise an important part of the Okavango food web, playing a major role in the nutrient cycle and subsidizing populations of predatory birds, mammals, and reptiles. In the same manner, large herbivores, particularly hippopotamus (*Hippopotamus amphibius*) and elephant (*Loxodonta africana*), interact with the environment in a way that helps to maintain fish populations (Mosepele *et al.,* 2009).

Development of the commercial fishery

Fishery managers have a variety of ways at their disposal through which they can investigate and develop a conceptual frame work for the implementation of fishery development and management plans (Welcomme, 1998). Prior to 2004, when Botswana's fisheries resources were managed under the broad agricultural policy guidelines in the Ministry of Agriculture, the objective was mainly to maximize exploitation of the resource. Therefore, the government made efforts to expand the commercial fishery in the Okavango Delta (Merron, 1991). Initially, this development resulted in increased fish catch from the system (Fig 1.2). Since 1999, however, the catch decreased when government repealed subsidies for the sector and fishing effort decreased.

Characterizing the structure of the Okavango fishery was done first by Mosepele (2001), who detailed the different fishers present in the delta, their gears and fishing practices from the frame survey data of 1997 and later by Bokhutlo *et al.* (2007), who went on to encompass management issues using the 2005 frame survey data. Mosepele (2001) recorded a total of 3289 fishers in the delta of which 44% were female and 56% were male. Of the 3289 fishers, 46 (0.01%) were identified as workers and the vast majority owned and operated their own gear. Some 589 fishing craft were enumerated. Dugout canoes comprised the majority of the fishing craft (63.8%), followed by fiberglass boats (28.5%) and aluminum boats (7.7%). The Bambukushu tribe comprised the majority of the fishers (68%) followed by the Bayei (23.1%), Basarwa (4.9%) and Bakgalagadi (2.6%). Hook and line fishers comprised the majority of participants (45.9%), followed by basket fishers (41.8%), gillnet fishers (13.6%), spear fishers (9.4%) and trap fishers (6.1%).

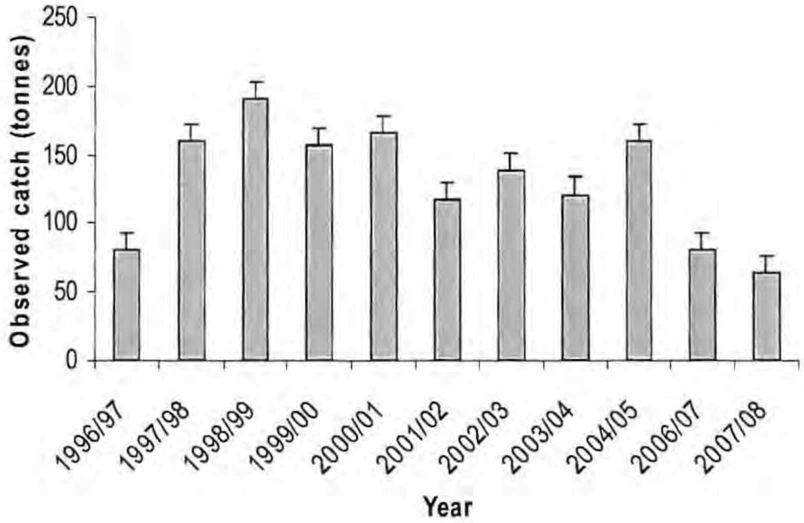

FIG 1.2. Total observed fish catch (+ one standard deviation) from the Okavango Delta between 1996-2008. (unpublished catch data provided by the Department of Wildlife & National Parks-Fisheries Division)

Eight years later, Bokhutlo *et al.* (2007), observed a slight (17.8%) decrease in the total number of fishers. They ascribed this decrease mainly to the cessation of government financial aid, which resulted in fishers abandoning the trade. This could also be explained by the result of the better fishers remaining while those that were not good enough to make a profit after the removal of subsidy exited the fishery. However, contrary to Mosepele (2001), they found that women (Table 1.1) comprised the majority of the fishery (53%) as opposed to men (47%). This was in agreement with what Hay *et al.* (2000) found in the Namibian section of the Okavango River.

The preponderance of women in the fishery therefore elevates the importance of floodplain fisheries as a source of cheap protein for the poor rural communities due to the opportunities proffered by shallow floodplain waters for the use of traditional fishing gear (Bokhutlo *et al.*, 2007). Artisanal fishing is also considered a natural safety net which constitutes an important buffer for households affected by HIV-AIDS related stressors in the Okavango delta (Ngwenya & Mosepele, 2007).

TABLE 1.1. Comparison of sex structure in the Okavango delta fishery between 1997 and 2005. (adapted from Bokhutlo *et al.*, 2007)

Sex	*1997 Frame survey*		*2005 Frame survey*	
	Number	Percentage	Number	Percentage
Male	1812	56	1280	47
Female	1431	44	1423	53

No major demographic changes were observed in the two surveys and generally, the structure of the fishery remained unchanged except for minor inconsistencies. However, it is worth noting that a shift in gill net mesh size preference was observed between the two surveys (Table 1.2). The use of smaller meshed (100 mm stretched mesh size) gill nets was favoured in 2005 as opposed to the larger 115 mm and 125 mm used in 1997. Another observation worth noting was that more people owned gill nets in 2005 than in 1997. Bokhutlo *et al.* (2007) therefore hypothesised that there was probably localized overfishing and the fishery was slowly evolving from the use of traditional gears towards preference of modern factory made gill nets.

TABLE 1.2. Comparison of prevalence of gill nets (25 meters long and 2 meters deep) by mesh size between 1997 and 2005 in the Okavango delta. (Adapted from Bokhutlo *et al.*, 2007)

Mesh size	*1997 Frame survey*		*2005 Frame survey*	
Stretched mesh in (mm)	Total number of gill nets	Percentage	Total number of gill nets	Percentage
50	0	0	62	4.72
63	46	33	0	0
75	116	8.2	77	5.86
100	465	33	716	54.49
115	515	36.5	400	30.49
125	257	18.2	59	4.49
150	11	0.8	0	0

Conflicts between commercial and recreational fishers

Expansion of the commercial fishery had its positive and negative implications on the socio-economic dynamics of the fishery. According to Bokhutlo *et al.* (2007), government financial assistance allowed for the purchase of outboard motors which meant that fishers could now traverse greater distances in the river. These commercial fishers could also afford to fish at night in the safety of an outboard engine powered motor boat. Moreover, they could afford to purchase factory made gillnets which meant improved efficiency of catching fish and the resultant reduction of large fish species in lagoons (Mosepele, 2001; Tweddle, *et al.*, 2003; Bokhutlo *et al.*, 2007). This increased mobility not only increased their catches but also increased the frequency of encounters with tourist operators and recreational anglers. These developments resulted in competition between recreational anglers and commercial fishers and disputes between the two sectors erupted (Bokhutlo *et al.*, 2007). Recreational anglers accused commercial fishers of over fishing, basing their allegations on the decreased catch of trophy-sized cichlids in lagoons (Tweddle, *et al.*, 2003; Bokhutlo *et al.*, 2007).

Ensuing conflicts resulting from the causal connection between the expansion of the commercial fishery and its impact on the recreational fishery have been the focus of recent studies on the Okavango fishery. Setswalo (2007) investigated the conflict between local fishermen and tour operators in the upper panhandle of the Okavango Delta and found that access to fishing grounds was the major source of conflict. The results from his study concurred with what had already been discussed by Mosepele (2001) and Bokhutlo *et al.* (2007).

The Biokavango project was commissioned in 2005 and delved into the issue of fisher conflicts. By working closely with the Department of Wildlife and National Parks-Fisheries

Division (DWNP-FD), the commercial fishers and recreational anglers in a participatory manner, they came up with mitigation measures aimed at abating the conflicts. The project's approach was first to strengthen the Okavango Fishermen Association (OFA) by supporting them in their activities such as preparations for the annual fishers conference and enabling them to get organized by electing a chairman and his assistants. The then defunct Okavango Fisheries Management Committee (OFMC) was also resuscitated. This committee comprises of government departments that have a stake in the fisheries sector in the region and is chaired by Okavango Research Institute (ORI) while DWNP-FD is the secretariat. This endeavor resulted in a platform for dialogue where conflicting parties could discuss their grievances. Through this dialogue and interaction there came a revelation that conflict was not a result of a concern for the decline in fish stocks as the recreational anglers would often purport but rather it stemmed from a social dimension. Conflicting parties had different interests, objectives and expectations with regard to the utilization of the resources. To harmonize the situation, the Code of Conduct for Responsible Fishing in the Okavango Delta was produced and every stakeholder participated in its crafting.

Large Clariid catfishes of the Okavango Delta

Catfishes occupy habitats ranging from upland streams (*Amphilius* spp.) to large river channels (e.g. *Heterobranchus longifilis* Valenciennes, 1840) and seasonal floodplains (*Clarias* species) hence comprising an ecologically diverse component of most major river faunas of Africa (Winemiller & Kelso-Winemiller, 1996). A detailed morphological description of the genus *Clarias* can be found in Gavrioaie & Chisamera (2005) who describe that members of the group generally have a respiratory superbranchial organ and reach a length of about 1 meter.

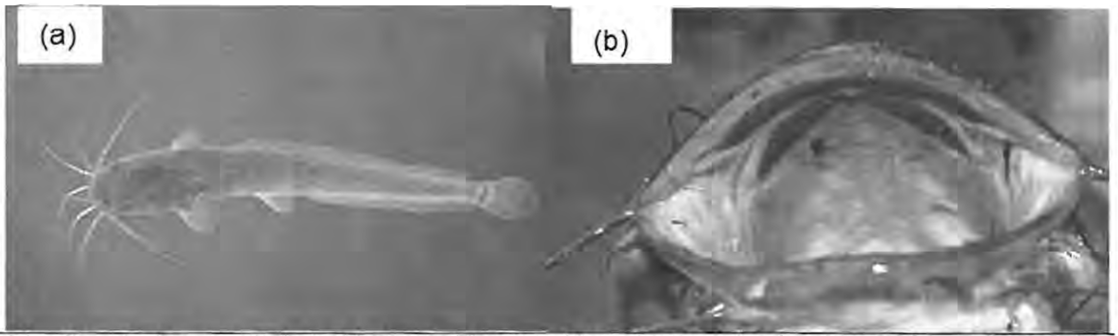

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FIG 1.3. *C. gariepinus* morphological features: (a) external body features showing the prominent large head (b) the distinct sharp teeth with the inner band forming a V shape in the upper jaw. These are the major distinguishing feature between this species and the closely related *C. ngamensis*.

In the Okavango Delta, sharptooth catfish, *Clarias gariepinus* (Burchell 1822) and the closely related blunttooth catfish, *Clarias ngamensis* (Castelnau 1861) are frequently caught by fishermen (Van der Bank & Smit, 2007). The two species can be distinguished by a number of morphological features. According to Gavrioaie & Chisamera (2005), among the Clariid species, only two, *C. ngamensis* and *C. lamottei* have an adipose fin. Merron & Bruton (1988) describe *C. gariepinus* as the largest catfish found in the Okavango Delta with a head length that is greater than ¼ SL (Fig 1.3a). *Clarias gariepinus* is generally classified as an omnivorous predator (Merron & Bruton, 1988; Merron, 1991; Winemiller & Kelso-Winemiller, 1996; Cambray, 2003). Winemiller & Kelso-Winemiller (1996) observed that *C. gariepinus* tended to be larger than the co-occuring *C. ngamensis* and tended to feed on larger prey in the upper Zambezi river floodplain. The major morphological feature that distinguishes *C. gariepinus* from *C. ngamensis* is that *C. gariepinus* has sharp teeth that occur in two pads in the upper jaw of which the inner one has a V shape (Fig 1.3b) while *C. ngamensis* has the inner band as a half moon and the teeth are bigger and blunt.

The fishery potential of *C. gariepinus* and the need for management

Large catfishes, *C. gariepinus* and *C. ngamensis* contribute 23% to commercial fishers' catches (DWNP data, chapter 6). Despite the observed high contribution of *C. gariepinus* to the catch composition of the Okavango fishers (see Chapter 3 & Chapter 6), it is not as highly valued in the market as cichlids. Notwithstanding the current economic status of clariids in the Okavango, their economic importance can be enhanced if proper marketing strategies are employed elsewhere, especially in the southern part of the country where it is apparent that they are favoured for their substantive amount of flesh. Therefore, marketing clariids in the southern region market of Botswana could possibly yield substantial economic dividends. Moreover, these species are relatively abundant in the Okavango (see Chapter 3) and therefore could offer an alternative for small-scale commercial fish enterprises in the future.

The corollary of a shift towards intensive exploitation of this species for commercial purposes is that subsistence fishers' livelihoods may be compromised if exploitation is not undertaken on a sustainable basis. It is therefore crucial to undertake a stock assessment of *C. gariepinus* to determine the current status and develop management recommendations for a potential fishery.

Objectives of this thesis

Management of any natural resource should be based on sound scientific knowledge on the biology of the target species. The only stock assessment study conducted by Mosepele (2000) on the Okavango Delta fishes so far was an account from a fish community perspective and was based on a length structured Thompson and Bell yield prediction model. There is a paucity of species specific age based data necessary for the application of predictive fisheries models. The current study therefore aims to determine those biological and population dynamic parameters that are pertinent for the application of the more robust analytical models such as per-recruit analyses (Beverton & Holt, 1957) to obtain better understanding of the dynamics of *C. gariepinus* in the Okavango Delta in order to provide management recommendations.

Specific objectives of the study were as follows:

1. To assess the importance of perennial riverine floodplain connected lagoons as refuges of fish biomass on a temporal scale with particular emphasis on the role of the flood pulse on the relative abundance of *C. gariepinus*.
2. To determine the sex structure and age at maturity for *C. gariepinus* in the upper Okavango Delta, Botswana.
3. To use sectioned otoliths to undertake an assessment of the age and growth of *C. gariepinus* in the Okavango Delta in order to provide estimates of growth rate and mortality rate, two important components of all analytical fisheries models.
4. To assess the status of *C. gariepinus* in the Okavango Delta using Yield Per-Recruit (YPR) and Spawner Biomass Per-Recruit (SBR) analyses (Beverton & Holt, 1957; Ricker, 1975) and provide management recommendations for the potential *C. gariepinus* fishery

To do this, the thesis is organized in seven chapters. After the introduction (Chapter 1) and description of the study area (Chapter 2) the thesis is arranged as follows: Chapter 3 discusses the relative abundance of *C. gariepinus* with relation to changes in the flood magnitude both within and between years. Chapter 4 aims to determine the reproductive biology of the species. In Chapter 5, aspects of age, growth and mortality are investigated. Chapters 4 and 5 provide the input parameters for the application of a yield-per recruit model in Chapter 6. This model is used to recommend a suitable harvest strategy for *C. gariepinus*. Finally, Chapter 7 provides a general discussion and management recommendations.

CHAPTER 2

STUDY AREA AND GENERAL METHODS

The Okavango Delta

The Okavango Delta is a large inland wetland created by the Okavango River (Wolski & Savenije, 2005). The Okavango river originates in Angola and it flows through Namibia ending in the Okavango Delta, which may spill over into the large Makgadikgadi saltpans when the floods are very high (Ramberg *et al.* 2006). The Delta is an alluvial fan covering almost 40 000 Km^2 with a mean surface gradient of approximately 1:3700 in which the inflow of water and sediment from the Okavango River are spread across a meandering convoluted surface through a complex system of channels and floodplains (Gumbricht *et al.*, 2003; Wolski & Murry-Hudson, 2006). The Okavango Delta is one of Africa's most pristine Delta areas and it is rich in biodiversity with a large variety of habitats (Ramberg *et al.*, 2006).

The climate is semi-arid with one distinct rainy season from November to March (Wolski & Savenije, 2005) (Fig 2.1) which is localized (Neuenschwander *et al.*, 2005) and not synchronous with the annual flow (Ringrose *et al.*, 1988). Some of the geographic, limnological and physicochemical characteristics of the Okavango Delta are summarised in Table 2.1. Over a period of 21 years between 1966 and 2000, the mean annual evaporation at Shakawe was estimated at 2367 mmy^{-1} (Alemaw *et al.*, 2003). Other climatic variations such as wind speed, sunshine, humidity and temperature are also illustrated in Fig 2.2.

TABLE 2.1. Some of the Geographic, limnological and physicochemical characteristics of the Okavango Delta, Botswana.

Data	*Value*	*Source*
Permanent swamp area (Km^2)	2 500	Ramberg *et al.* 2006
Seasonal swamp (Km^2)	3 300	Ramberg *et al.* 2006
Total delta surface area (Km^2)	28 000	Ramberg *et al.* 2006
Total dissolved solids (ppm)	48	
Rainfall (m^3/annum)	$\approx 6*10^9$	Gumbricht *et al.* 2003
Total annual sediment load (tons)	500 000	Gumbricht *et al.* 2003

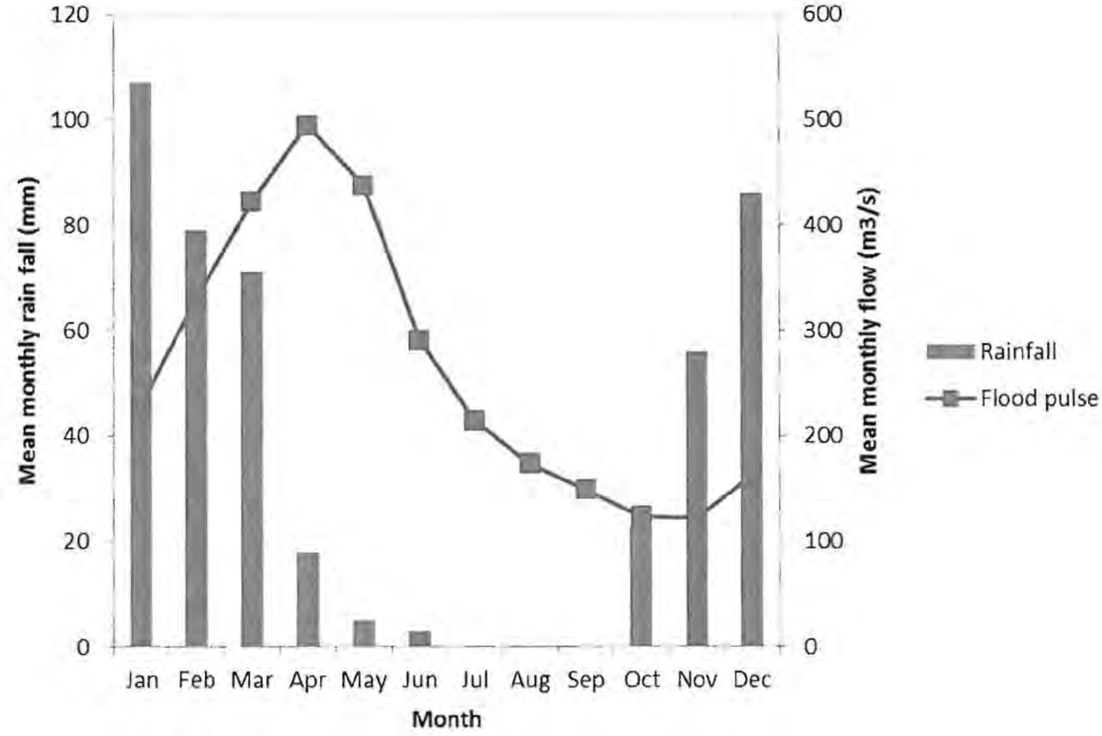

FIG 2.1. The realtionship between monthly average rain fall (mm) and average monthly flow (m^3/s) in the Okavango Delta, Botswana. Rainfall data was sourced from (http://www.uyaphi.com/botswana/weather.htm). Rainfall was gauged in Maun and averaged over 14 years while mean flow was measured at Mohembo. When compared over a 70 year period, Maun and Shakawe rainfall show very similar seasonal trends (Alemaw *et al.*, 2003).The distinct rainy season between November and March is apparent. The rainfall pattern depicts a decline between January and April while the flood magnitude is rising at that time.

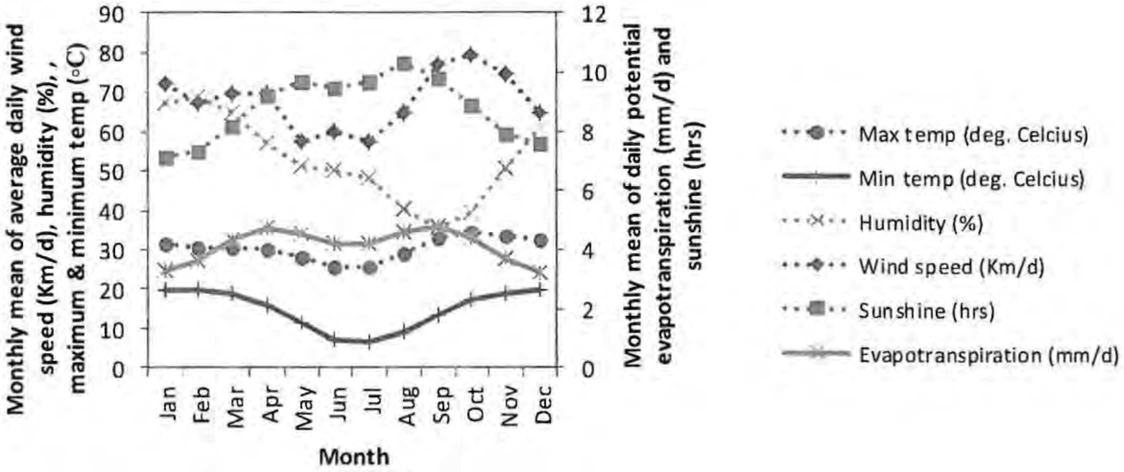

FIG 2.2. Monthly mean climate and evapotranspiration measured at Shakawe (Source: Alemaw *et al.*, 2003)

Origin of data and sampling strategy

For this thesis, data were obtained from various sources as summarised in (Table 2.2). In this chapter, only the general sampling design is described. Detailed specific methods are explained in the relevant subsequent chapters

TABLE 2.2. Data types which were used in this thesis and their sources

Data type	*Data source*
Length frequency data 1999-2009	Department of Wildlife & National Parks – Fisheries Division; This study
Biological Data (age, maturity and sex) (October 2009- October 2010)	This study Okavango Research Institute (ORI)
Hydrology data 1999- 2010	Department of Water Affairs (DWA) through ORI, University of Botswana (UB), Maun campus.
Rainfall data (1999-2010)	(http://www.uyaphi.com/botswana/weather.htm)

Biological data pertaining to sex and gonadal maturity stage were obtained both from the present study and from the long-term monitoring data collected by the Department of Wildlife & National Parks-Fisheries Division as well as by the Okavango Research Institute. For the current study, I participated in the field excursions between October 2009 and

October 2010. I was also responsible for the coordination of the Department of Wildlife and National Parks-Fisheries Division long-term fisheries monitoring programme in the Okavango Delta since 2003.

Long term monitoring by the DWNP (FD)

Length frequency data were obtained through monthly gill net sampling (Fig 2.3) conducted by the Department of Wildlife & National Parks-Fisheries Division. Initially gill nets were set in two major sampling stations; Seronga and Ngarange. In 2004, Guma lagoon was added as a third sampling station for purposes of long term monitoring. Various kinds of gill nets were used in the sampling regime. Between 1999 and 2002, the five panel white research nets with mesh sizes 50 mm, 75 mm, 100 mm, 115 mm and 125 mm stretched mesh were used as well as the Swedish lundgren nets with mesh sizes 12 mm, 16 mm, 20 mm, 25 mm, 33 mm, 44 mm, 50 mm, 60 mm, 66 mm, 76 mm, 86 mm, 100 mm, 120 mm and 150 mm stretched mesh and the Nordic nets with mesh sizes 10 mm, 13 mm, 16 mm, 20 mm, 25 mm, 31 mm, 39 mm, 48 mm, 58 mm, 70 mm, 86 mm and 180 mm stretched mesh. In 2001, the multi mesh nine panel brown nets with mesh sizes 22 mm, 28 mm, 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 118 mm and 150 mm were introduced and maintained to the present while all the other nets were phased out mostly due to lack of funding. At each sampling station, nets were set in three different habitats (lagoons, main channel and floodplains). Usually nets were set for two nights at each habitat except during periods of high floods when lagoons were sampled twice while floodplains and the main channel were sampled once each month. To evaluate trends in catch composition and catch rates between months and between years (Chapter 3) only the brown nets were used since they offered a longer time series of standardized data. Otherwise data from various gill nets were pooled.

FIG 2.3. Department of Wildlife and National Parks-Fisheries Division staff retrieving brown nets during one of their long term monitoring expeditions. This exercise can be challenging in the sometimes fast flowing waters of the Okavango delta.

Otolith sampling

Otoliths were obtained from fish sampled from various localities from October 2009 to October 2010. Otolith data used in this thesis represent samples collected from the entire Delta across a linear gradient from the upper to the lower Delta. The sampling sites are represented in Fig 2.4. Ngarange (Matsaodi lagoon), Seronga (Korao lagoon) and Guma lagoon were sampled between October 2009 and December 2009 with assistance from the Department of Wildlife and National Parks-Fisheries Division. Nxaraga, Thamalakane and Chanoga were sampled between March and October 2010 through assistance from the Okavango Research Institute.

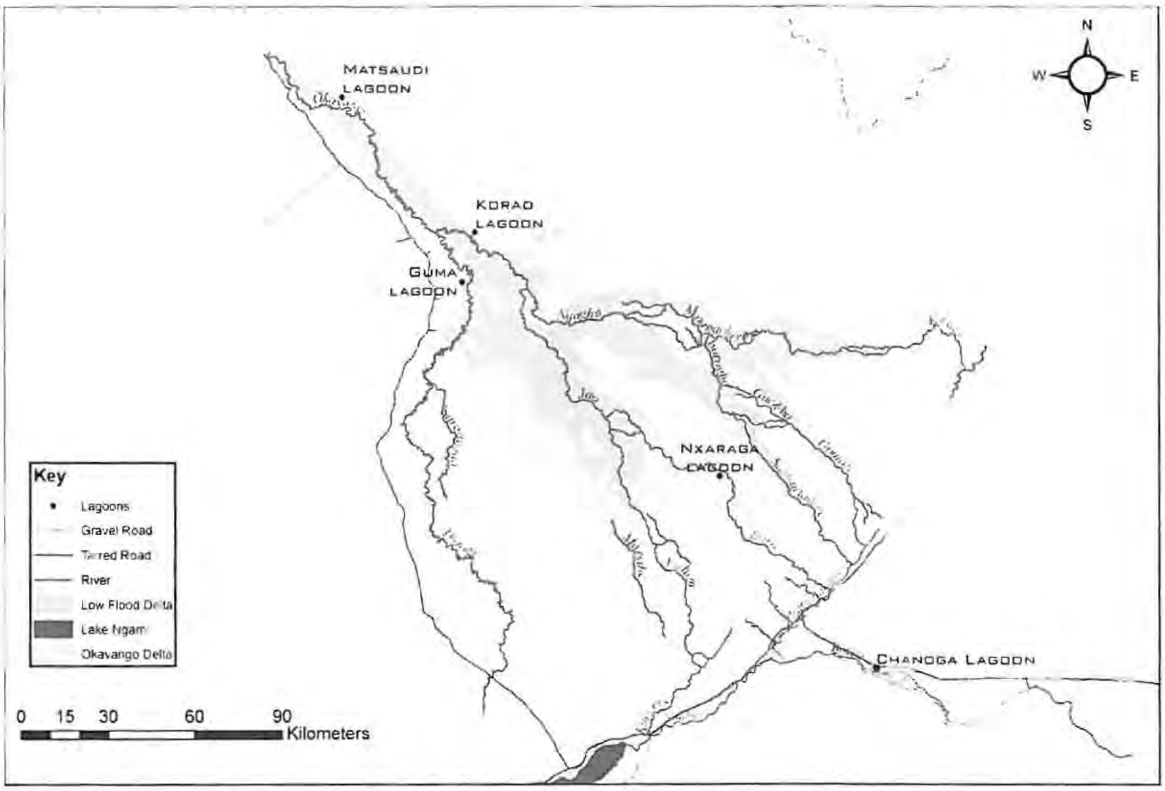

FIG 2.4. Map of the study area showing the major sampling sites from which data used in this thesis were collected. Matsaodi lagoon, Korao lagoon and Guma lagoon were sampled consistently by the DWNP-FD on a monthly basis for their long term monitoring programme. Nxaraga lagoon was sampled by the ORI on a monthly basis, also as a long term monitoring project. Chanoga lagoon was only sampled between March and October 2010 (this study).

The majority of samples were obtained from the commercial gill net fishers between March and October 2010 in the lower Okavango Delta. To supplement gill net samples, a long line of about 100 m was also set over night with 15-20 baited circle hooks between October and December 2009.

Unfortunately field sampling (October 2009-October 2010) yielded insufficient otolith samples to assess for regional differences in growth rate. For this reason otolith samples from the upper and lower Okavango Delta were pooled for analysis under the assumption that the growth of the two populations was similar (Chapter 5). This assumption was tested in Chapter 5 using the randomization test and the test for the difference in growth curves using an Analysis of the Residual Sum of Squares (Chen, 1996; Haddon, 2001). Maturity and reproductive seasonality data (1999-2009) were only collected from the upper Okavango Delta between Ngarange and Guma lagoon. Therefore analyses of these biological variables (Chapter 3 & 4) are valid only for that part of the system.

CHAPTER 3

THE FLOOD PULSE AND ABUNDANCE OF *C. GARIEPINUS* IN PERENNIAL FLOODPLAIN CONNECTED LAGOONS OF THE OKAVANGO DELTA, BOTSWANA

3.1. INTRODUCTION

The relationship between the flood pulse and fisheries has been a subject of interest in many parts of the world. The flood pulse concept was formulated by Junk, *et al* (1989) who proposed that the pulsing of a river discharge, the flood pulse, is the major force controlling biota in river floodplains. From the aquatic view point, the flood pulse concept identifies the predictable inundation and retraction of water on the floodplain of a pristine system as a principal agent controlling adaptations of most of the biota (Bayley, 1995). Baran *et al* (2001) studied this relationship in the Mekong Basin and concluded that fish production can be related to the flood levels in the same year while Krykhtin (1975) observed that the abundance of the non-anadromous fishes in the Amur River altered periodically as a function of fluctuations in flow of the river. However, Baran *et al* (2001) emphasised that the relationship between flood levels and fish production was particularly true for dominant species with a short life span and might not be the case for species with a longer life span. Moreover, Karenge & Kolding (1995) observed no evidence of adverse effects on the fisheries due to fluctuating lake levels in man-made Lake Kariba.

The diversity of fisheries in tropical floodplain rivers is well documented by Hogarth & Utomo (1994) who discuss the adaptation of gear use by fishers in these systems to particular times in the flood cycle. Merron & Bruton (1988) and Merron (1991) conducted the first comprehensive study on the effects of the flood pulse on the ecology of the Okavango Delta fishes and concluded that the annual flood regime was important in maintaining the fish populations in this system. However, these studies were conducted over a relatively short period of time. Lack of long-term monitoring data on fisheries has been pointed out as the major bottleneck in confirming the flood pulse concept (Baran *et al*, 2001; De Graaaf, 2003). Subsequent biological studies conducted by Mosepele (2000), Mosepele & Nengu (2003) and Mosepele *et al.* (2005b) made no attempt to link the flood pulse with the population dynamics of the fishes except for mention of the possibility of the influence of the flood pulse in the separation of fish stocks between the upper and lower Okavango Delta.

The aim of this chapter was to assess the importance of perennial riverine floodplain connected lagoons as refuges of fish biomass on a temporal scale with particular emphasis on the role of the flood pulse on the relative abundance of *C. gariepinus*.

3.2. MATERIALS AND METHODS

Experimental gill net fishing

This chapter utilizes a time series of gill netting spanning a 9 year period from 2001 to 2009. Data for 2001-2002 were obtained from the long time monitoring by the Department of Wildlife and National Parks-Fisheries Division while data from 2004-2009 were collected by myself or by fish scouts under my supervision.

In all years, experimental fishing was undertaken using multifilament, multi-panel research nets made up of 10-m long panels with stretched mesh sizes of 22, 28, 35, 45, 57, 73, 93, 118 and 150 mm each. These nets were used to sample the fish community from Guma lagoon, Korao lagoon and Matsaodi lagoon (Fig 2.4). Nets were set over night, set in the evening and lifted the following morning after approximately 12 hours. Fish were then removed from each panel and processed separately before being pooled later for further analysis. Each fish was identified to species level, and then total length (L_T) and the wet weight were taken. Each lagoon was sampled on three nights, every month between 2001 and 2009. However, data from Guma lagoon was collected (monthly) between 2004 and 2009. There was no sampling during 2003. Therefore, data, though collected at slightly different intervals, were collected for eight years from the lagoons, monthly.

Hydrology

Hydrological data were obtained from the Department of Water affairs in Maun and collated by the hydrology unit at the University of Botswana, Okavango Research Institute in Maun. Data for 2009 were unfortunately not available and all analyses pertaining to water flows were restricted to 2008. Daily flow rates entering at Mohembo were averaged by month and year to get the mean monthly and annual flows. These data were then superimposed on the biological data to make observations on the relationship between water flows and fish abundance.

Data analysis

Species diversity

All the data collected were stored and analysed using Pasgear II (Kolding & Skaalevik, 2010). Data from the three lagoons and for all species sampled were pooled and used to calculate Shannon's diversity index to determine species diversity between months and between years. The Shannon's diversity index is defined as:

$$H' = -\sum_{i=1}^{S} P_i \,.\, L_n(P_i) \tag{3.1}$$

where P_i is the relative abundance, i.e. the number of individuals for each species divided by the total number of individuals for all species (S) in each sample (Begon *et al.* 1990).

Catch composition

As a measure of relative abundance or commonness of each species (i) in the catch composition an index of relative importance (%IRI, Kolding 1989) was used:

$$\%IRI_i = \frac{(\%W_i + \%N_i)\cdot\%F_i}{\sum_{j=1}^{S}(\%W_j + \%N_j)\cdot\%F_j}\cdot 100, \tag{3.2}$$

where $\%W_i$, $\%N_i$ and $\%F_i$ is the weight, number and frequency of each species (i) expressed as a percentage of all the species in the total catch. $\%W_j$, $\%N_j$ and $\%F_j$ is the weight, number and frequency of occurrence of each species in the total number of settings (j) and S is the total number of species encountered in all settings.

Catch rates

Catch per unit effort was calculated for every month and for each year between 2001 and 2009. CPUE was calculated as: $\text{CPUE} = \frac{1}{y}\sum_{i=1}^{n} W_i \cdot \frac{SU}{U_i}\cdot\frac{ST}{T_i},$ (3.3)

where y = effort, e.g. number of net panels (or fleet) settings and n = number of samples, W_i = catch (in weight or numbers) in set$_i$ or sample$_i$, SU = standard relative effort unit (size) of a net panel, U_i = actual effort (size) of net, ST = standard time unit (hours or minutes) of a setting, Ti = actual time unit of setting$_i$. In this case $y = n$ as each individual net set was considered a sample. CPUE was standardized for 10 m long net panels set over 12 hours.

The confidence intervals were calculated as:

$$\overline{CPUE} \pm t_{(n-1)} \cdot SE(CPUE) \qquad (3.4)$$

where t is students t-value (at the 95% confidence limit) and n = sample size (number of observations). The standard error (SE) is the standard deviation (SD) divided by the square root of n.

Statistics

To test for differences in CPUE and catch (Kg of fresh weight) between months and between years, a one way analysis of variance (ANOVA) was applied. Before the analysis, data were assessed for normality using the distribution fitting criterion in STATISTICA 9 to ensure that the assumptions of ANOVA were met. Where data were found to be skewed, logarithmic transformation (X = Ln (X+1)) was performed to normalise the data. When logarithmic transformation did not work, square root transformation was used instead. The relationship between water flows, (independent variable) and the dependent biological variables was modeled analytically in Pasgear II (Kolding and Skaalevik, 2010) using linear least squares regression. Regressions were performed both annually and monthly to explain inter and intra annual variations.

3.3. RESULTS

Catch composition

A total of 113514 fish weighing 15842 kg and comprising 52 species were captured during the study period. Based on overall IRI, *C. gariepinus* was second in importance to *Schilbe intermedius* (Table 3.1). The percentage composition by number for *C. gariepinus* was lower (4.3%) when compared to species such as *S. intermedius* (26.4%), *Marcusenius* *macrolepidotus* (17.7%) and *Brycinas lateralis* (20.8%). *Clarias gariepinus* contributed the highest percentage by fresh weight to catch composition. The lowest percentage contribution of *C. gariepinus* to catch composition by fresh weight was during April while the highest was during August (Fig 3.1a). The proportion of *C. gariepinus* in gill net catches differed significantly between months (One way ANOVA; $P < 0.05$; *df* = 35) and the relationship between mean monthly flow and CPUE was negative and significant (Linear regression; $r^2 = 0.61$; $P < 0.05$; *df* = 11).

Between years, high catches of *C. gariepinus* were recorded in 2001 and 2007 and low catches in 2002 and 2006 (Fig 3.1b). There was however, no significant difference in catch of *C. gariepinus* from year to year (One way ANOVA; $P = 0.08$; *df* = 23). The relationship between mean annual flow and catch was positive but not significant (Linear regression; $r^2 = 0.24$; $P = 0.27$; *df* = 6)

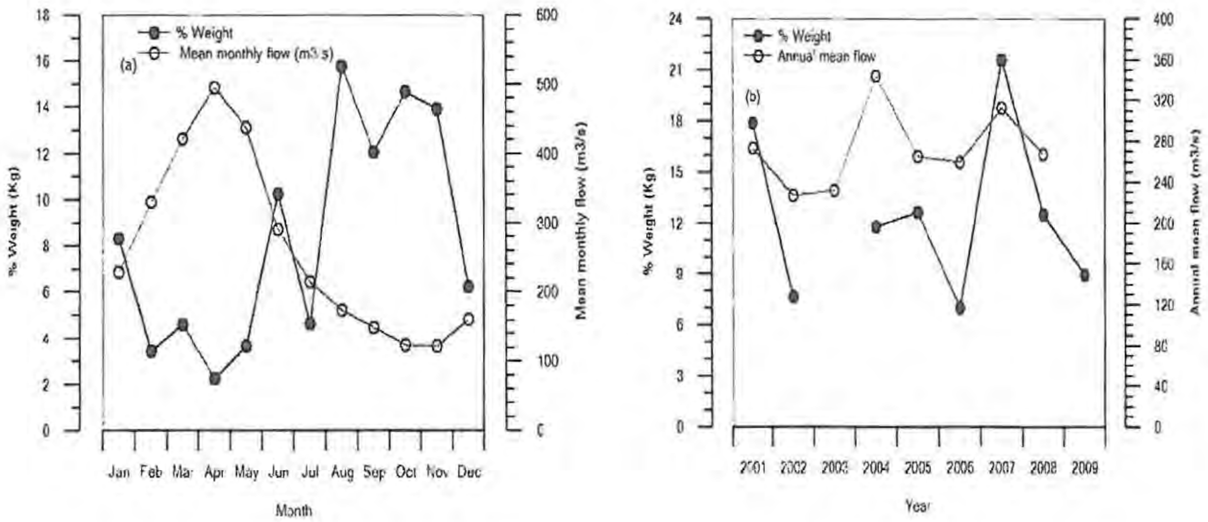

FIG 3.1. Percentage contribution of *C. gariepinus* to the catch composition by weight (kg) within a year (a) and between years (b) with relation to the flood regime shown by mean monthly flow and annual mean flow

Table 3.1. Comparison of catch composition in % weight (kg), % number and % frequency of occurrence as well as the % index of relative importance (IRI) of all species in the perennial floodplain connected lagoons of the upper Okavango delta, Botswana. All the fish that could not be identified to species level were grouped by family and are marked with (*).N=1241 net settings. (Data was provided by the DWNP-FD for the period 2001-2009). Shannon's diversity index, H' is also shown.

Species	*No*	*% No*	*Weight(kg)*	*% Weight*	*FRQ*	*% FRQ*	*IRI*	*% IRI*	*H`*
Schilbe intermedius	30003	26.43	2149.93	13.57	2649	15.42	1166	35.47	0.35
Clarias gariepinus	4833	4.26	5923.54	37.39	1909	11.11	875	26.62	0.13
Marcusenius macrolepidotus	20106	17.71	745.11	4.70	1603	9.33	396	12.05	0.31
Hydrocynus vittatus	4781	4.21	2084.74	13.16	1564	9.10	299	9.10	0.13
Brycinus lateralis	23554	20.75	207.50	1.31	558	3.25	135	4.11	0.33
Clarias ngamensis	2349	2.07	1750.96	11.05	854	4.97	123	3.74	0.08
Synodontis nigromaculatus	6712	5.91	423.48	2.67	1267	7.37	120	3.65	0.17
Hepsetus odoe	2896	2.55	694.86	4.39	973	5.66	74	2.25	0.09
Synodontis thamalakanensis	1892	1.67	104.33	0.66	668	3.89	17	0.52	0.07
Petrocephalus catastoma	4076	3.59	25.60	0.16	374	2.18	15	0.46	0.12
Serranochromis macrocephalus	823	0.73	207.46	1.31	425	2.47	10	0.30	0.04
Momyrus lacerda	800	0.70	264.42	1.67	353	2.05	9	0.27	0.04
Barbus poechii	2653	2.34	22.00	0.14	321	1.87	9	0.27	0.09
Synodontis vanderwaali	1164	1.03	77.18	0.49	445	2.59	7	0.21	0.05
Serranochromis angusticeps	677	0.60	180.27	1.14	345	2.01	7	0.21	0.03
Synodontis leopardinus	1027	0.90	68.98	0.44	419	2.44	6	0.18	0.04
Tilapia sparrmanii	1047	0.92	62.63	0.40	357	2.08	5	0.15	0.04
Oreochromis andersonii	395	0.35	196.76	1.24	217	1.26	4	0.12	0.02
Synodontis macrostigma	669	0.59	24.71	0.16	274	1.59	2	0.06	0.03
Tilapia rendalli	326	0.29	106.61	0.67	161	0.94	2	0.06	0.02
Synodontis woosnami	480	0.42	29.71	0.19	238	1.39	2	0.06	0.02
Serranochromis altus	199	0.18	142.19	0.90	105	0.61	1	0.03	0.01
Sargochromis codringtonii	301	0.27	38.17	0.24	160	0.93	1	0.03	0.02
*Squeakers (synodontis sp)**	388	0.34	18.21	0.11	124	0.72	1	0.03	0.02
Serranochromis robustus	143	0.13	78.87	0.50	90	0.52	1	0.03	0.01
Sargochromis carlottae	193	0.17	30.70	0.19	120	0.70	0	0.00	0.01
Oreochromis macrochir	150	0.13	61.25	0.39	81	0.47	0	0.00	0.01
Serranochromis thumbergi	151	0.13	16.66	0.11	98	0.57	0	0.00	0.01
Sargochromis giardi	86	0.08	37.01	0.23	53	0.31	0	0.00	0.01
Clarias theodorae	78	0.07	30.77	0.19	35	0.20	0	0.00	0.01
Sargochromis greenwoodii	82	0.07	11.30	0.07	49	0.29	0	0.00	0.01
Pharyngochromis acuticeps	93	0.08	2.68	0.02	61	0.36	0	0.00	0.01
Synodontis macrostoma	98	0.09	4.68	0.03	50	0.29	0	0.00	0.01
Parauchenoglanis ngamensis	61	0.05	4.37	0.03	37	0.22	0	0.00	0.00
Labeo lunatus	40	0.04	10.73	0.07	24	0.14	0	0.00	0.00
Pseudocrenilabrus philander	49	0.04	0.53	0.00	28	0.16	0	0.00	0.00
Hippopotamyrus ansorgii	37	0.03	0.19	0.00	21	0.12	0	0.00	0.00
Hippopotamyrus discorhynchus	16	0.01	0.16	0.00	14	0.08	0	0.00	0.00
Pollimyrus castelnaui	16	0.01	0.07	0.00	10	0.06	0	0.00	0.00
Barbus paludinosus	18	0.02	0.11	0.00	7	0.04	0	0.00	0.00
Barbus radiatus	10	0.01	0.03	0.00	8	0.05	0	0.00	0.00
Tilapia ruweti	7	0.01	0.94	0.01	5	0.03	0	0.00	0.00
Serranchromis longimanus	9	0.01	0.24	0.00	6	0.03	0	0.00	0.00
Barbus codringtonii	4	0.00	0.79	0.00	2	0.01	0	0.00	0.00
Ctenopoma multispine	3	0.00	0.03	0.00	3	0.02	0	0.00	0.00
Barbus unitaeniatus	3	0.00	0.00	0.00	3	0.02	0	0.00	0.00
Barbus fasciolatus	4	0.00	0.00	0.00	2	0.01	0	0.00	0.00
Leptoglanis theodorae	2	0.00	0.78	0.00	1	0.01	0	0.00	0.00
Hemichromis elongatus	2	0.00	0.12	0.00	2	0.01	0	0.00	0.00
*All bream (cichlids)**	2	0.00	0.01	0.00	2	0.01	0	0.00	0.00
Barbus bifrenatus	2	0.00	0.00	0.00	2	0.01	0	0.00	0.00
Clarias liocephalus	1	0.00	0.01	0.00	1	0.01	0	0.00	0.00
Barbus afrovernayi	1	0.00	0.01	0.00	1	0.01	0	0.00	0.00
Barbus eutaenia	1	0.00	0.01	0.00	1	0.01	0	0.00	0.00
*Barbus spp**	1	0.00	0.00	0.00	1	0.01	0	0.00	0.00
Total	**113514**	**100**	**15842.36**	**100**	**17181**	**100**	**3287**	**100**	**2.32**

Species Diversity

The diversity index increased markedly from May, reaching a peak in October during low flood levels before sharply decreasing from November and reaching the lowest value in April when the flood was at its peak (Fig 3.2a). This negative relationship between the flood pulse and diversity between months was significant (Linear regression; $r^2 = 0.77$; $P < 0.05$; *df* = 11). Between years, diversity index was high in 2001. The lowest diversity was in 2002. Years of high floods tended to result in high species diversity while years of low floods resulted in low species diversity (Fig 3.2b). This positive relationship was not statistically significant (Linear regression; $r^2 = 0.4$, $P = 0.12$; *df* = 6).

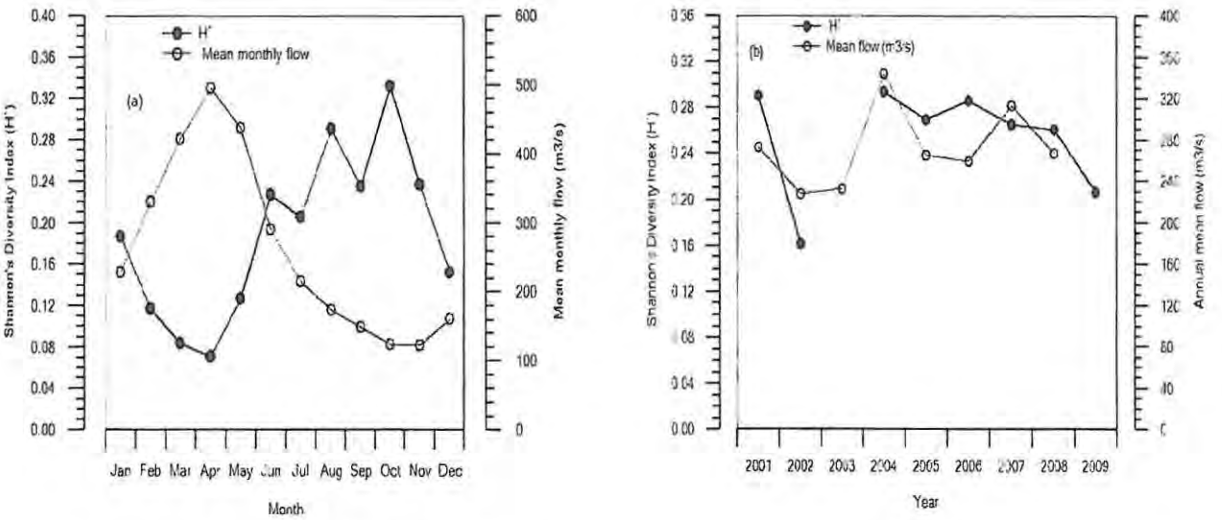

FIG 3.2. Variations in species diversity within a year (a) and between years (b) with relation to the flood regime indicated by the mean river flow rates in Mohembo.

Catch per unit effort (CPUE)

Of all the 52 species sampled between 2001 and 2009 *C. gariepinus* had the highest CPUE (Table 3.2). CPUE generally increased between May and November (the falling flood limb) and there was a general decrease in catch rates between December and April (the rising flood limb) (Fig 3.3a). Lowest CPUE were observed in April (0.17 ± 0.55 kg per net set), when the flood was at its peak and highest catch rates in November (0.66 ± 2.16 kg per net set) at the low water level. There was significant variation in CPUE between months (One way ANOVA; $P < 0.05$; *df* = 35). The relationship between CPUE and the mean monthly flow was negative and significant (Linear regression; $r^2 = 0.54$, $P < 0.05$; *df* = 11).

Between years, CPUE was low in 2002, 2006 and 2008 (years of low floods) while they were relatively higher during 2001, 2004 and 2007 (years of high floods) (Fig 3.3b). There was, however, no significant difference in CPUE between years (One way ANOVA; $P > 0.05$; *df* = 23) and there was no significant relationship between mean annual flow and CPUE (Linear regression; $r^2 = 0.54$, $P = 0.06$; *df* = 6).

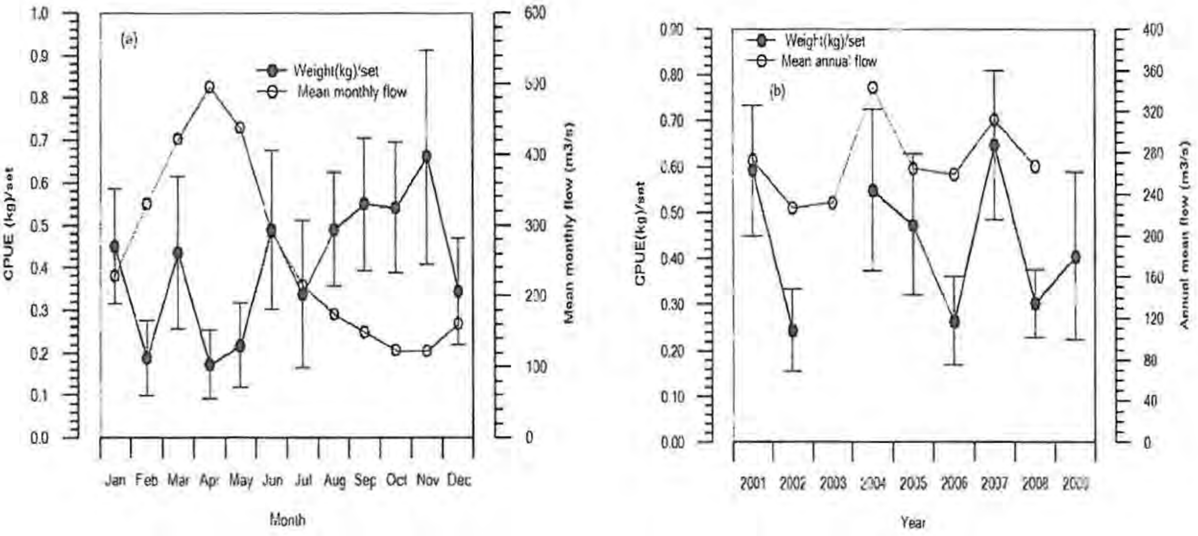

Fig 3.3. Variations in catch rates within a year (a) and between years (b) with relation to the flood regime shown by mean monthly flow and mean annual flow.

Table 3.2. Comparison of Catch per Unit effort expressed as number of fish per net set and kg per net set for the ten most abundant species from perennial floodplain connected lagoons of the upper Okavango delta, Botswana. (Data was provided by the Department of Wildlife and National Parks-Fisheries Division for the period 2001-2009), N=1241 net settings.

Species	*No/set*	*SD No/set*	*Weight(kg)/set*	*SD Weight(kg)/set*
Clarias gariepinus	0.48	1.46	0.57	1.58
Schilbe intermedius	3.49	16.71	0.23	0.72
Hydrocynus vittatus	0.45	2.43	0.2	0.81
Clarias ngamensis	0.27	1.34	0.19	0.89
Marcusenious macrolepidotus	2.03	16.59	0.08	0.44
Hepsetus odoe	0.28	1.28	0.07	0.28
Synodontis nigromaculatus	0.77	4.6	0.05	0.25
Momyrus lacerda	0.09	0.6	0.03	0.2
Oreochromis andersonii	0.04	0.36	0.02	0.2
Serranochromis macrocephalus	0.09	0.61	0.02	0.16
Other	5.14	30.46	0.17	0.51

3.4. DISCUSSION

According to Mosepele *et al.* (2009), in both perennial and seasonal swamps in the upper Okavango, large predatory catfishes, especially the sharp-toothed catfish (*C. gariepinus*) and the blunt-toothed catfish (*C. ngamensis*) and predatory cichlids are common. Merron (1991) observed that in riverine floodplain-connected lagoons of the Okavango Delta, mass composition was dominated by *H. vittatus*, *C. gariepinus* and to a lesser extent *S. intermedius* and *H. odoe*. This concurs with the current study where the fish fauna in the three perennial lagoons sampled in the upper delta was dominated by predators such as *C. gariepinus* (Table 3.1). *Hepsetus odoe and H. vittatus* were found among the top ten most important species in the Catch per Unit Effort of these habitats. Chimatiro (2004) observed that in the lower Shire River floodplain fisheries in Malawi the abundance of fish was determined by habitat type, although there was some overlap between habitats due to seasonal changes in the hydrology and climatic conditions. Furthermore, observations made by Khumalo (2006) in Mnjoli Dam (Swaziland) revealed that the abundance of different species in different areas appeared to correlate with their habitat preferences. This is in agreement with (Welcomme, 1985) who points out that similar sub systems are often separated by considerable distances of inimitable biotope, leading to the formation of distinct species communities adapted to similar conditions along the length of the river.

The floodplain environment varies seasonally, both within the year, and between different years (Hogarth *et al*, 1999). Fish production and yield is closely linked to the extent of these variations (Welcome, 1988). This phenomenon was observed in the present study where the contribution of *C. gariepinus* to the catch increased during months of low flood and decreased during months of high flood within a year. CPUE showed a similar trend which was statistically significant. This observation is supported by Welcome (1975, p.18) who stated that "In general, fish are concentrated in permanent bodies of water in the dry season and spread over the floodplain in the floods". In the upper Zambezi, Winemillar & Jepsen (1998) observed that during the low water period top predators of floodplain habitats such as *H.odoe* and *S. intermedius* inhabited lagoons. Moreover, De Graaf (2003) observed that the fish catch had strong seasonal variation in the flood plain fisheries of Bangladesh with the highest catch observed when the flood water receded towards the river and the lowest catch during the dry season. This therefore shows that the increased catch that occurs during flood recession is temporary, resulting from the concentration of fish in lagoons.

Merron (1991) observed that the 'concentration and dilution' effects of the flood on the fish stocks of the Okavango were occurring only in the riverine floodplain, seasonal swamps and drainage rivers while in the perennial swamp and riverine floodplain-connected lagoons a greater yield was recorded at high water levels within a year. In the present study, only perennial riverine floodplain-connected lagoons were sampled and higher catch rates were realised at low water levels within a year thus contradicting Merron (1991). An explanation for this could be that the Merron (1991) study was conducted during the prolonged drought period of the 80's while this study was conducted during a protracted wet period particularly between 2004 and 2008 and that could have had a bearing on fish behaviour particularly with regard to lateral migrations between the perennial and seasonal swamps. De Graaf (2003) cautions that drawing conclusions from a short time series of monitoring data in floodplain fisheries can be difficult and even misleading. For this reason, differences between the current study and the Merron (1991) study may be a result of the shorter 3-year time series of data available to Merron (1991) and the 8-year data series available for the current study.

Food web dynamics of fishes inhabiting floodplain river systems are intricately woven in the fabric of the system. According to Merron (1991), in the riverine floodplain and perennial swamp, an insectivore-predator food chain appears to be the main food pathway. An example of this observation is the annual catfish pack-hunting event where bulldogs, *M. macrolepidotus*, an insectivorous fish, are fed on by *C. gariepinus*, an omnivorous predator (Merron, 1991). This event occurs annually at low water levels in the main river channels of the Okavango delta as a response to the annual flood regime (Merron, 1993). This may also explain the increase in abundance of *C. gariepinus* during the drawdown period of the flood since pack-hunting makes the species to be more vulnerable to gill nets due to the increased movement and aggregation for communal feeding.

Flood plains of low gradient rivers are inundated slowly. This allows for biological processes to occur in the shallow moving water resulting in a positive relationship between productivity and water flow (Junk *et al.*, 1989). Winemiller (1989) ascribes this relationship in part to increase in primary production and relaxed interspecific competition. This scenario was observed in the Okavango Delta which has a low gradient hence resulting in slow floodplain inundation. Even though the association between the flood pulse and *C. gariepinus* abundance between years was not significant in this study, there was sufficient evidence that the flood pulse enhanced productivity of the system between years without a lag period. This was demonstrated by the observed increase in diversity, catch composition and CPUE during years of bigger floods. Moreover 54 % of the variation in CPUE was explained by fluctuations in flood levels between years (Fig 3.3). This agrees with Meron (1991) who found that in the Okavango Delta, yield fluctuated widely, from low catches in extremely dry years to very large catches shortly after periods of large floods. Similar observations were made by De Graaf (2003) who obtained a significant relation between the flood index and annual yield in the floodplain fisheries of Bangladesh.

In conclusion, this chapter suggests that the flood pulse is the major driver of fish population abundance both within and between years in the Okavango Delta. Moreover, perennial riverine floodplain connected lagoons appear to be an important refuge for the population of *C. gariepinus* especially during the drawdown period of the flood pulse. The dominance of predators in lagoons (Merron, 1991, Winemiller & Jepson, 1998) could imply that there may be intense competition for food in these environments. To further understand the implications of the flood on the population dynamics of *C. gariepinus* requires an investigation into its reproductive biology (Chapter 4) and its growth (Chapter 5).

CHAPTER 4

REPRODUCTION OF *C. GARIEPINUS* IN THE OKAVANGO DELTA, BOTSWANA

4.1. INTRODUCTION

In order to make scientifically sound decisions about management of fish resources, it is important to have the basic knowledge of the biology of the species (Turan *et al.*, 2005). Environmental changes have a direct influence on the life history of a species and life histories, which are based on fundamental demographic trade-offs, determine how the population responds to these changes (Kolding & Zwieten, 2006). Furthermore, Kolding & Zwieten (2006) suggest that the most important characteristics of these trade-offs can be demonstrated by the relationships between three basic demographic parameters: survival, fecundity, and the onset and duration of reproductive life.

Attainment of sexual maturity marks a very important change in the life of an individual because it presents potential conflict between allocation of resources to reproduction or to survival and growth (Wooton, 1990). A species's reproductive success depends on the place and timing of reproduction (Wooton, 1990). Change of allocation of resources from reproductive to competitive activities should only occur in habitats where these will improve the survival of future offspring (Lowe-McConnell, 1987). Furthermore, it is through reproduction that species ascertain perpetuation of their kind and when coupled with genetic change, reproduction may bring about speciation (Lagler *et al.*, 1962). Therefore it is imperative to study reproductive strategies of species for successful management of a fishery. The aim of this Chapter was to determine the sex structure and age at maturity for *C. gariepinus* in the Okavango Delta, Botswana. Age at maturity is important in population dynamics modeling. The null hypothesis that breeding does not depend on time of the year was tested.

4.2. MATERIALS AND METHODS

Clarias gariepinus were collected on a monthly basis from commercial fishers as well as through independent surveys between October 2009 and October 2010. Upon capture, each specimen was weighed to the nearest gram, measured to the nearest mm total length (L_T) and sexed. Fish were then dissected, and each gonad was assigned a stage for reproductive activity according to the criteria in Table 4.1.

Additional data on the length frequencies and maturity were obtained from the Department of Wildlife and National Parks-Fisheries Division fishing surveys conducted between 1999 and 2009 using gill nets (see Chapter 2). These data were only collected from the upper Okavango Delta between Ngarange and Guma lagoon. Therefore analyses in this Chapter are valid only for the upper Delta.

Maturity

Length at 50 % sexual maturity ($L_{50\%}$) was determined as in Booth & Khumalo (2009) by fitting a logistic ogive to the proportion of reproductively active fish, i.e., either mature, ripe or ripe running. Fish were grouped into 10 mm length classes as in Ellender (2008) and the proportion of sexually mature fish (ψ) per length class (L) was fitted with a logistic ogive of the form: $\psi = \frac{A+(B-A)}{\left(1+e^{((L_{m50}-L)/\delta)}\right)}$ (4.1)

where A is the horizontal asymptote on the left side of the curve, B is the horizontal asymptote on the right side, L_{m50} is the mean length at 50% sexual maturity and δ is the width of the logistic ogive. The model fit was implemented in R, version 2.14.0 using the *nls*() self-starter function [*SSfpl*()] and the package nlrwr.

TABLE 4.1. Macroscopic gonad development scale used to determine breeding seasonality of *C. gariepinus* in the Okavango delta. Adapted and modified from (Owiti & Dadzie, 1989; cited by Degraaf & Janssen, 1996)

Maturity stage	Gonad Development	Macroscopic appearance
1	Immature/Resting	The ovary is colourless to translucent brown, lanceolate and lobular in appearance, occupying the posterior quarter of the body cavity. In fish larger than 10cm the ovary can be distinguished from the testis due to its smoothness in contrast to the serrated edges of the testes
2	Developing	The ovary is translucent, brown in colour and occupies about one third of the length of the peritoneal cavity. The testis is translucent/grey and positioned under the vertebral column.
3	Mature (Ripening)	The ovary is opaque, brownish in colour occupying about one half of the ventral cavity. The testis is white and clearly distinguishable with prominent serrated margins.
4	Ripe	The ovary is large, opaque, turgid and brown-green in colour. The eggs are yolk laden and clearly visible to the naked eye. The ovary occupies four fifths of the peritoneal cavity. A highly developed capillary network is visible. The testis is white and turgid
5	Ripe running	The eggs are translucent and flat. They ooze out freely with pressure on the belly. The testis is swollen with whitish serrated edges. When pricked with a sharp object, milt oozes out.
6	Spent	The ovary is flaccid, flabby and bloodshot, with thick whitish tough walls. The genital aperture of the female looks inflamed. Some translucent and opaque (residual) eggs visible to the naked eye. The testis is a deflated white grey sac.

Sex ratio

To test for differences in the sex ratios a chi squared test of independence was used. The test was performed on length classes that were greater than the length-at-50% maturity grouped into length classes 400-499mm L_T, 500-599 mm L_T, 600-699 mm L_T, 700-799 mm L_T, 800-899 mm L_T and 900-999 mm L_T. The Kolmogorov Smirnov test was used to test for the differences in the length frequency distributions of the sexes. These analyses were performed using the software package STATISTICA 10.

Breeding season

Breeding seasonality was determined by using the six–stage macroscopic gonad development scale (Table 4.1). The percentage of ripe (Stage 4) and ripe and running (Stage 5) fish of the population was calculated monthly and a periodic logistic regression model (Flury & Levri, 1999) was fitted to the observed data to determine the period of peak spawning. The Flury & Levri (1999) model was of the form:

$$\log it(\theta) = \beta_0 + \beta_1 C + \beta_2 S \tag{4.2}$$

where $\log it(\theta)$ is the natural log of the odds that the fish are ripe and running in a given month. $\beta_0, \beta_1 \, and \, \beta_2$ are the parameters to be estimated. The model has two regressor variables C and S which were obtained from:

$$C = \cos\left(\frac{2\pi}{P}T\right) \text{ and} \tag{4.3}$$

$$S = \sin\left(\frac{2\pi}{P}T\right) \tag{4.4}$$

where P is the period of the periodic phenomenon and T is the time variable (Flury & Levri, 1999). In this case, time was measured in months and the period was one year: $P = 12$. To estimate parameters of the model, maximum likelihood methods were employed assuming that the proportion of ripe and running fish per month is a binary random variable defined as:

$$y = \begin{cases} 1 \text{ } \mathit{if\ ripe and running} \\ 0 \text{ } \mathit{if\ otherwise} \end{cases} \tag{4.5}$$

with probabilities $\Pr(y=1)=\pi(x)$ and $\Pr(y=0)=1-\pi(x)$ where x is the corresponding explanatory variable (time, in this instance) (Dobson, 2002). If there are n such random variables $y_i,\dots y_n$ which are independent with $\Pr(y_i=1)=\pi(x_i)$, then the contribution to the joint probability from a given data point (x_i,y_i) is described as:

$$\varsigma(x_i)=\pi(x_i)^{y_i}\left[1-\pi(x_i)^{1-y_i}\right] \tag{4.6}$$

Therefore, the joint probability, which is the likelihood function, is defined as

$$l(\beta_0,\beta_1,\beta_2)=\prod_{i=1}^{n}\varsigma(x_i) \tag{4.7}$$

Using the solver routine in Excel, the log likelihood, $\ln(l(\beta_{0,}\beta_1,\beta_2))$ was maximized to obtain optimum model parameter estimates.

Hypothesis testing

To test if the probability of ripe and running fish depends on the time of year, the fit of the full model was compared to the fit of the reduced model ($H_{0;}\log it(\theta)=\beta_0$) using the likelihood ratio χ^2 statistic which is also known as the G statistic (Sokal & Rolf, 1995). The G^2 statistic is defined in Quinn & Keough (2002) as:

$$G^2=-2(\ln L\,reduced-\ln L\,full) \tag{4.8}$$

The model's goodness of fit was assessed using the analogue of R^2 used as a measure of explained variance in ordinary least squares regression. The analogue used was of the form:

$$r_L{}^2 = \frac{[\ln(L_0) - \ln(L_M)]}{\ln(L_0)} = 1 - \frac{\ln(L_M)}{\ln(L_0)} \quad (4.9)$$

where L_0 is the likelihood for the model with only the intercept and L_M is the likelihood for the model with all predictors (Quinn & Keough, 2002).

Length weight relationship

The relationship between length and weight was described by the power relationship as:

$$W = q(L_T)^b \quad (4.8)$$

where W is the weight (g) and L_T is the total length in (mm) and q and b are the parameters estimated using linear regression analysis of natural logarithm-transformed dependent and independent variables (Booth & Khumalo, 2009).

Condition factor

To determine variations in the condition factors (*CF*) of *C. gariepinus* between months and between years the mean monthly and yearly sample weights ($\overline{W}$) were compared with the predicted weight (W_{pred}) from the generalized length-weight relationship (King, 1995) such that:

$$CF_w = \frac{\overline{W}}{W_{pred}} \quad (4.9)$$

This method is considered more robust than the Fulton's Condition Factor (K) because it accommodates assessment of condition for fishes such as *C. gariepinus* that have a wide length range (Bagenal & Tesh, 1978). The method also allows for reference to average condition while taking into account allometric growth (Bruton, 1979*b*) and is considered most appropriate for determining seasonal variation in the condition of fish within a population (King, 1995). The disadvantage of relative condition is that it is population specific and therefore cannot be used to compare the condition of fish from different populations (Wooton, 1990). This is however not a problem in the current study as the objective was to determine within population differences of *CF*.

Condition factor-length relationship was represented by the linear relationship:

$$CF = a + bL \tag{4.10}$$

where L is the length in (mm) and a and b are the estimated parameters using ordinary linear regression analysis.

4.3. RESULTS

Maturity

The length at 50 % maturity was estimated at 294 mm, 95% CI= [293,299] L_T for combined sexes (Fig 4.1a). Females tended to mature earlier $L_{50} = 290$ mm, 95% CI = [280,300] L_T than males $L_{50} = 301$ mm, 95% CI = [291,311] L_T. Length at 100% maturity was 400 mm L_T for both males and females (Fig 4.1b&c).

Sex ratio

Examined *C. gariepinus* samples ranged in size from 117 mm to 1060 mm L_T (Fig 4.3). The overall sex ratio of females to males was 1: 0.94 which did not differ from unity. This was however dependent on length (Chi square test for unity, $\chi^2 = 247.6; df = 5; P < 0.001$) with females being more dominant at smaller lengths and males making up more of the population at lengths larger than 500 mm L_T (Fig 4.2). The larger males were also represented by the larger mean length for males as opposed to females (Fig 4.3).

The modal length for males was 500 mm L_T while that for females was 470 mm L_T. Length frequency distributions were significantly different between the sexes (Kolmogorov-Smirnov test, $P < 0.001$).

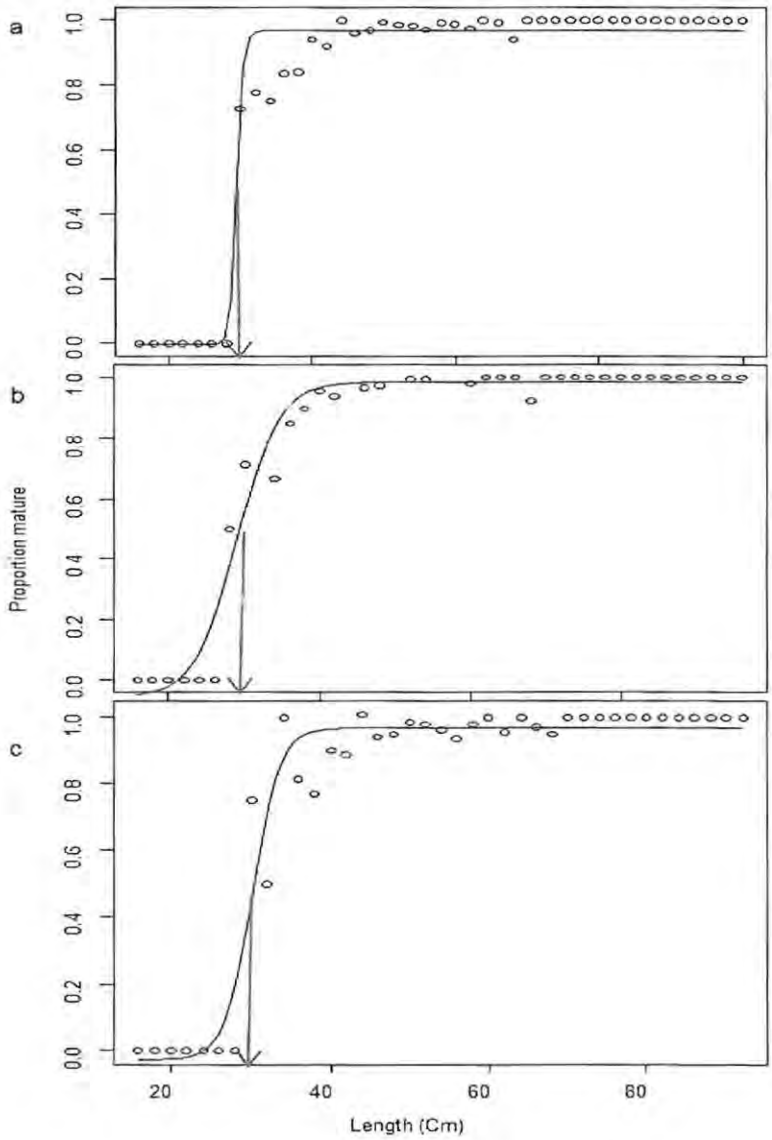

FIG. 4.1. Proportion of sexually mature *C. gariepinus* for combined sexes (N=4222) (a) females (N=2240) (b) and males (N= 1985) (c) sampled from the Okavango delta, Botswana. Length at 50% maturity was estimated at 294 mm L_T, 290 mm L_T and 301 mm L_T for combined sexes, females and males respectively. Data were obtained from the upper Delta. (Data source: Department of Wildlife and National Parks-Fisheries Division, 1999-2009).

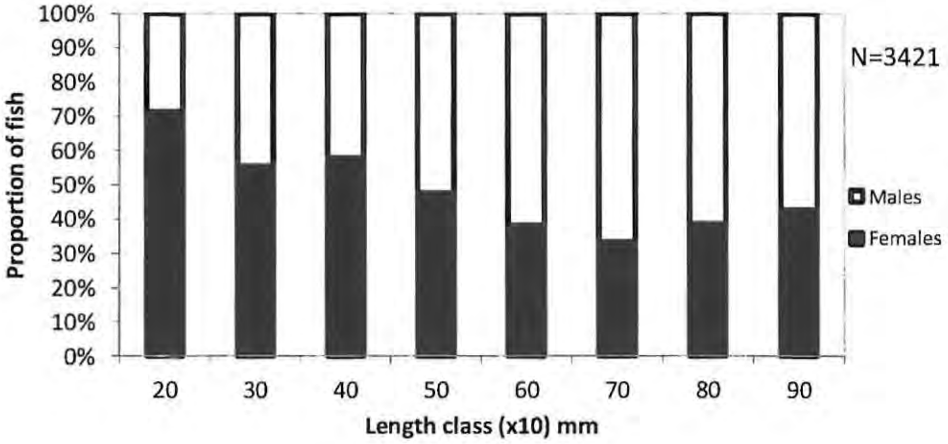

FIG. 4.2. Changes in sex ratio with size of *C. gariepinus* in the Okavango delta, Botswana. (Data source: Department of Wildlife and National Parks-Fisheries Division, 1999-2009)

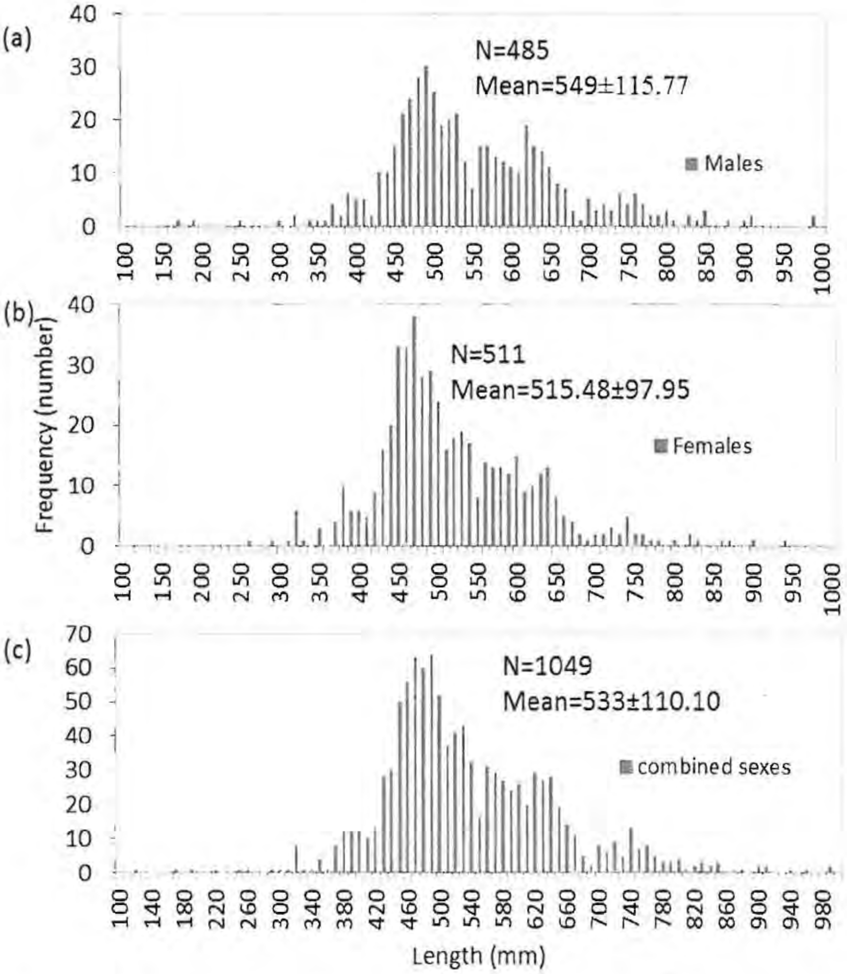

FIG. 4.3. Length frequency distribution of male (a) female (b) and combined sexes (c) of *C. gariepinus* sampled from the upper Okavango Delta, Botswana. (Data obtained from Department of Wildlife and National Parks-Fisheries Division between 2001 and 2009).

Breeding season

Fishes in reproductive stages 3 to 6 were present in the population throughout the year (Fig 4.4a). The percentage of actively spawning fish (ripe and running) was highest between November and April with the highest proportion (63%) observed during January. These months were therefore presumed to represent the spawning period. The periodic logistic regression model fitted to the proportion of ripe and running fish predicted that February was the peak spawning month and that August was the month when spawning was lowest (Fig 4.4b). When compared to river flow (Fig 4.4b), it is apparent that spawning commences with increasing flow rates in November and peaks just before the maximum flood. Parameter estimates of the periodic logistic regression model are presented in Table 4.2. The H_0 that $\log it(\theta) = \beta_0$ could not be rejected (Table 4.3). Only the H_0 that $\beta_2 = 0$ was rejected at P ≤ 0.05 and 1 degree of freedom. Therefore spawning was dependent on the time of the year.

TABLE 4.2. Parameter estimates from the periodic logistic regression model predicting the proportion occurrence of ripe and running *Clarias gariepinus* over a period of 12 months in the Okavango Delta, Botswana.

Parameter	*Estimate*
β_0	-1.547
β_1	0.703
β_2	1.324
d.f	3

TABLE 4.3. Significance test of the periodic logistic regression model predicting the occurrence of ripe and running *Clarias gariepinus* in the Okavango Delta, Botswana. The H_0 that at least one of the regression coefficients equals zero could not be rejected at $P \leq 0.05$ and 2 degrees of freedom. The H_0 that $\beta_2 = 0$ was rejected at $P \leq 0.05$ and 1 degree of freedom. Therefore inclusion of the sine (*S*) regressor variable improved the model fit.

Log-likelihood of full model: -5.453

Reduced model	H_0	Log-likelihood	G^2	*P*	r_L^2	*d.f*
β_0	$\beta_1 + \beta_2 = 0$	-6.453	2	0.184	0.155	2
$\beta_0 + \beta_1$	$\beta_2 = 0$	-8.372	5.84	0.009	0.35	1

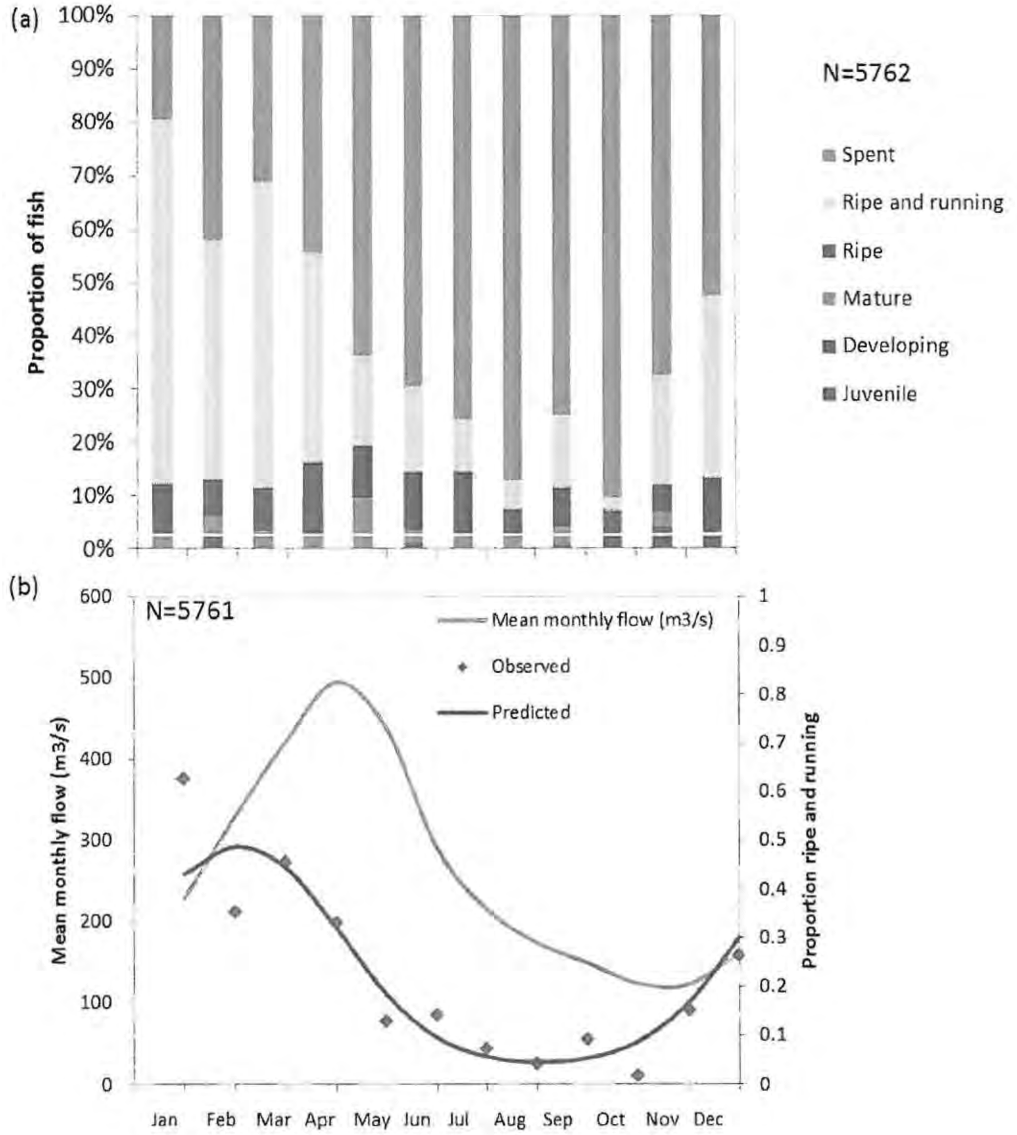

FIG 4.4. Variations in proportion of gonad maturity stages between months (combined sexes) for *C. gariepinus* (a) and the proportion of ripe and running (R&R) fish per month with relation to the mean monthly flow (b). Spawning appears to be influenced by the level of the flood in a positive way. Even though breeding occurs throughout the year, the peak breeding season appears to be between the months of November and April. The model predicts February and August as the peak and lowest breeding months respectively (b). (Data provided by Department of Wildlife and National Parks-Fisheries Division for the period 1999-2009). Samples were obtained from the upper Delta. The monthly mean flow was measured at Mohembo in the upper Delta.

Length -weight relationship.

The length-weight relationship for males was $W(g) = 0.000012 * L_T(mm)^{2.92}$ (95% CI_q = [0.0000091, 0.000017]; 95% CI_b = [2.87, 2.96]; n=486). Females length-weight relatioship was $W(g) = 0.000014 * L_T(mm)^{2.90}$ (95% CI_q = [0.0000096, 0.000019]; 95% CI_b = [2.85, 2.95]; n=511). The relationship between total length (L_T) and weight (W) for combined sexes is illustrated in Fig 4.5 and was best described by $W(g) = 0.000013 * L_T(mm)^{2.91}$ (95% CI_q = [0.000011, 0.000017]; 95% CI_b= [2.87, 2.94]; n = 1046).

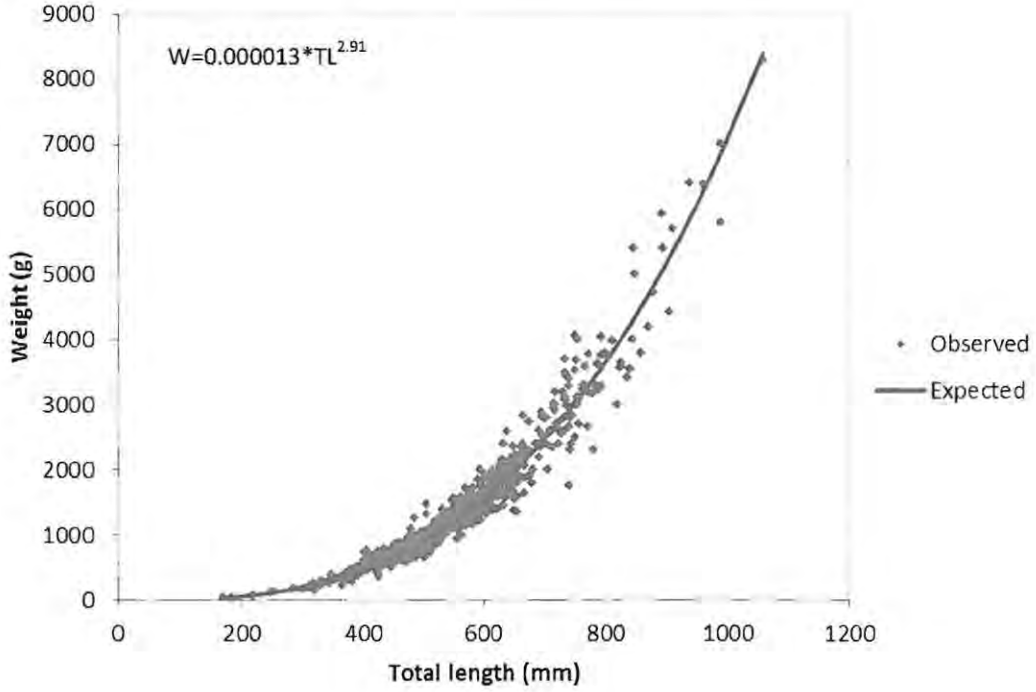

FIG.4.5. Length-weight relationship (combined sexes) for *C. gariepinus* in the Okavango Delta, Botswana (n=1046). Fish were sampled from the upper Delta. (Data source: DWNP-Fisheries Division).

Condition Factor

There was no significant relationship ($r^2 < 0.0001$, df = 1045, p>0.05) between total length (L_T) and relative mean condition factor (CF) as is illustrated in Fig 4.6.

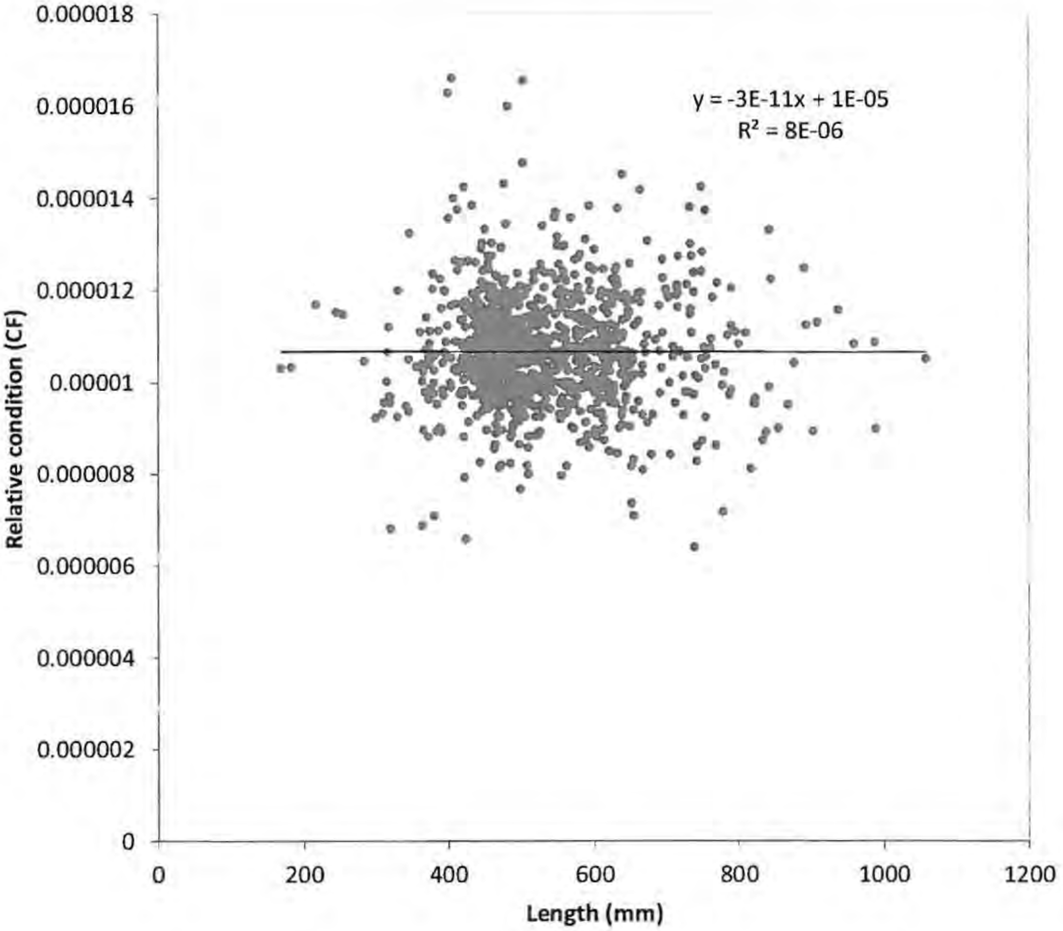

FIG.4.6. The relationship between total length (mm) and relative condition factor (*CF*) for *C. gariepinus* in the Okavango Delta, Botswana (*n*=1046). Fish were sampled from the upper Delta. (Data source: DWNP-Fisheries Division).

Variations in *CF* within a year and between years are shown in Fig. 4.7. Generally condition factor was high when the flood magnitude was high and low during low floods within a year. The lowest *CF* value was observed in September while the highest was in December. Between years, condition factor was highest in 2004 and lowest in 2006. The positive relationship between *CF* and mean flow was more pronounced during the protracted wet period (2004-2007).

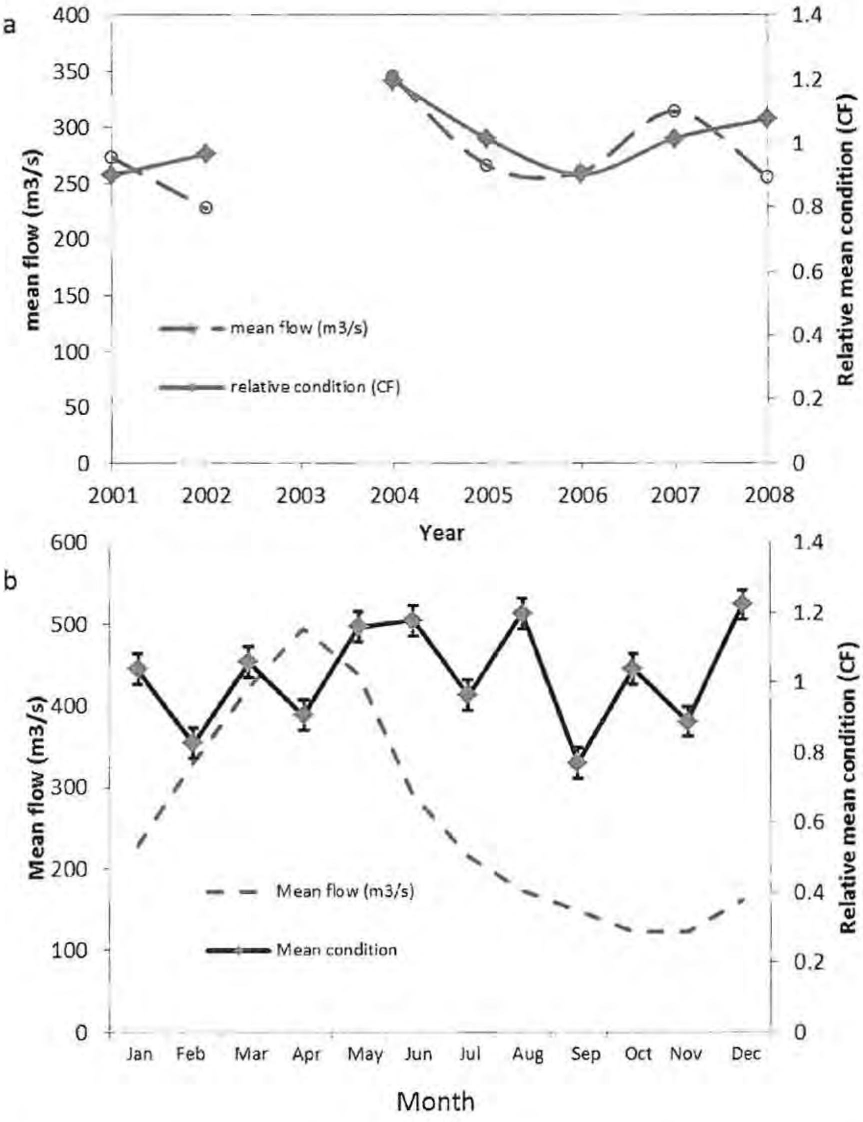

FIG.4.7. Temporal variation in relative condition of *C. gariepinus* between years (a) and between months (b). Samples were obtained from the upper Delta. The annual and monthly mean flows were measured at Mohembo in the upper Delta.

4.4. DISCUSSION

Maturity and sex structure

Results of the current study show that *C. gariepinus* in the Okavango Delta reproduce early in life, with L_{mat} being approximately 30% of the maximum length and that females appear to mature at smaller sizes than males. This corresponded to an age of 1 year (Chapter 5). These observations were consistent with findings reported by Mosepele & Nengu (2003) for this species in the Okavango Delta. Mosepele & Nengu (2003) estimated that females matured at 273 mm L_T and males at 362 mm L_T. Similar results were also obtained elsewhere for this species. Willoughby & Tweddle (1978) found that females matured earlier (290 mm L_T) than males (320 mm L_T) in the Shire River in Malawi. Abdulkarim (2009) estimated that *C. gariepinus* reached first maturity at 290 mm L_T in the Gubi Dam, Nigeria. In the River Asi in Turkey, Yalçin *et al.* (2001) report that for both sexes of *C. gariepinus*, the majority of fish attained first maturity in the first year and by the end of the second year all of them were sexually mature and the smallest mature female was 233 mm L_T while the male was 247 mm L_T.

The consistently smaller size at sexual maturity for females when compared to males in the different populations of *C. gariepinus* may be ascribed to allocating more resources to reproductive activities by females when they reach maturity while sexual selection could be favouring the larger size for males. However, in other populations of *C. gariepinus*, both sexes reached sexual maturity at the same size (Bruton, 1977; Chimatiro, 2004) but males continued to grow to larger sizes after maturity. Attainment of sexual maturity in the first year of life was consistent with the life history traits of non-guarders.

Empirical data with a large sample size collected over 10 years (Fig.4.5) indicated that *C. gariepinus* in the Okavango Delta were sexually dimorphic with males attaining a larger size than females. Sexual dimorphism has been observed in the Okavango Delta for another catfish species (*Schilbe intermedius*) where females were larger than males (Merron & Mann, 1995). Moreover, Van der Waal & Schoonbee (1975) observed for *C. gariepinus* in the Elands River that males were consistently larger than females for the same year group and the growth rate between the sexes was different. In the River Asi in Turkey, Yalçin *et al.* (2002) showed that for the age groups 0-3, absolute length increments were larger for males than females. There is a complex interplay between the factors determining the evolution of sexual dimorphism (Shine, 1989). In males, sexual selection may favour large body size while in females increase in size may be favoured by fecundity selection with ecological competition between the sexes accentuating the differences (Shine, 1989). The mating behaviour of *C. gariepinus* as described by van der Waal (1974) implies male dominance whereby the male had to actively chase after the female before spawning could occur. This may explain in part why males tend to grow to larger sizes. Moreover, Bruton (1977) observed that males had to fight to earn courtship with a female and therefore a larger size would increase the probability of winning a fight resulting in subsequent courtship.

Another explanation could be that upon reaching maturity, females start to invest more resources on gonad development as opposed to somatic growth. This is supported by Yalçin *et al.* (2002) who report that after maturity, females grew faster than males in terms of weight. They attributed this observation to gonadal development. Males tend to have smaller gonads (approximately 2% of body weight) (Willoughby & Tweddle, 1978) than females (about 35% of body weight) (Hastings, 1973; *In* Willoughby & Tweddle, 1978). Therefore the energy allocated to reproduction in males is negligible. During the feeding run and floodplain inundation that both provide good feeding conditions (Merron, 1991; Merron, 1993), males, by virtue of having small gonads may end up with excess energy that may be switched from reproduction to somatic growth. The cumulative result of this may be a bigger size for males compared to females. However, the study of optimal reproductive strategies in males is not easy because one would have to develop a male fecundity function that describes for instance in the case of *C. gariepinus*, how energy invested in such activities as competition for mates and courtship contributes to male reproductive success (Lester *et al.*, 2004).

Breeding season

Fishes living in flood plain habitats show a diversity of reproductive strategies which enable them to cope with the difficulties associated with breeding in such habitats (Welcomme, 1979). They usually breed seasonally, coinciding spawning with the rising flood and maturation takes place at a relatively young age (Welcomme, 1979). These strategies were observed for *C. gariepinus* in this study. Spawning was synchronised with the rising flood and the beginning of the rainy season, supporting observations made by Merron (1991). This was similar to observations on *C. gariepinus* made by Bruton (1979a) in Lake Sibaya (South Africa) and by Willoughby & Tweddle (1978) in the Shire River (Malawi).

From the foregoing therefore, it is apparent that spawning in the Okavango Delta for this species is mainly cued by the arrival of the flood pulse (Fig. 4.4). This agrees with Merron (1991) who found that spawning occurred at different times in the Okavango delta depending on the arrival of the flood. Merron (1991) observed that in the seasonal swamp and drainage rivers spawning occurred between July and December which was during the flood peak while in the riverine floodplain and perennial swamp spawning occurred between January and April also coinciding with the rising flood. This is supported by Welcomme (1979) who discusses that for flood plain fishes, the synchronization of the reproductive cycle with the flood is so good that in systems where the flood pulse takes time to progress downstream (such as the Okavango delta which has a low gradient), the breeding of downstream populations is delayed relative to the fish upstream.

The synchronization of spawning with the rising flood may be a strategy to optimize growth of juveniles by spawning during a period when flooding provides abundant allochtonous food and the floodplain vegetation provides a refuge from predators. This agrees with Lowe-McConnell (1987) who suggests that selection should favour production of the young at the time of year when conditions are most suitable for their survival.

Clarias gariepinus in the Okavango Delta appears to have a protracted peak spawning period between November and April. However mature, ripe and spawning fish were observed throughout the year. The protracted spawning period was also observed for this species in Lake Sibaya (Bruton, 1977), Shire River (Willoughby & Tweddle, 1978, Chimatiro, 2004) and the Okavango Delta (Merron, 1991). Bruton (1977) noted that the species spawns under a narrow range of environmental conditions and therefore, even though the fish may be mature, they will not breed until conditions are favourable which may result in different spawning times from one year to the next (Bruton, 1977). This may also explain the presence of mature fish throughout the year. However the presence of ripe and running fish even during the lowest flood level could not be explained adequately and warrants further investigation.

In the River Asi in Turkey, spawning was observed to be more dependent on temperature than on other factors (Yalçin *et al.*, 2001). Moreover, temperature was found to be more important than day length in controlling the ovarian cycle of *C. gariepinus* under hatchery conditions (Richter *et al.*, 1987). In the Okavango Delta, the proportion of ripe and running fish increased with increase in both day length and water temperature (Fig.4.8). Therefore water temperature and day length could be acting as major intermittent spawning cues for *C. gariepinus* during low floods in the Okavango Delta and it is not clear where spawning occurs during this time.

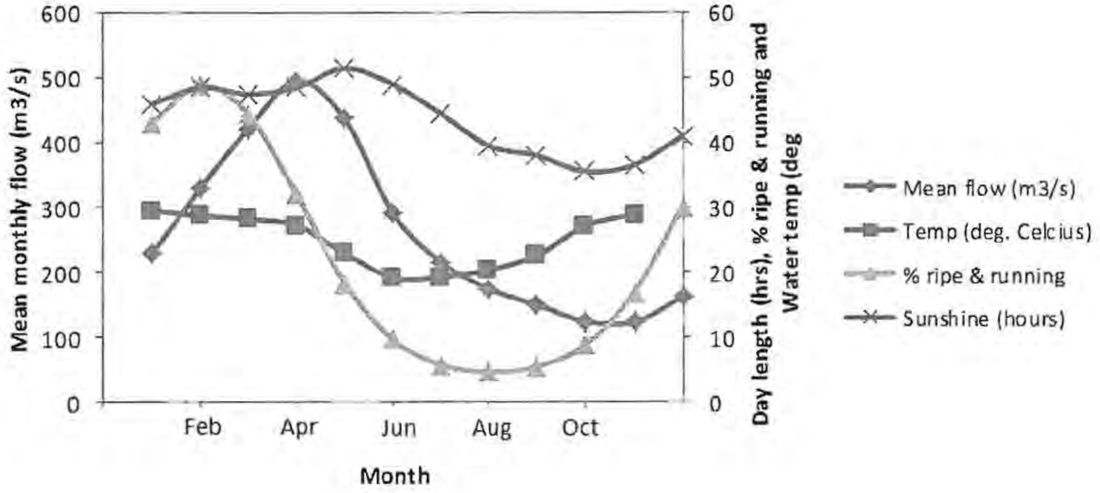

FIG 4.8. The relationship between spawning periodicity, the flood pulse, water temperature and day length for *C. gariepinus* in the upper Okavango Delta, Botswana. The proportion of ripe and running fish increases with increase in the three factors. Day length was scaled up with a factor of 5.

Variation in the mean condition of *C. gariepinus* was observed between months. Seasonal variations in mean condition of floodplain fishes have been reported elsewhere. Yalçin *et al.* (2002) observed that the monthly fluctuation in the condition of catfish was more related to changes in temperature and feeding. In the Okavango Delta, even though condition fluctuated between months without a particular distinct pattern, the lowest *CF* was observed in September at low water levels. During periods of low water level, the fish concentrate in the permanent water bodies and environmental stress, due to the deteriorating water quality and high temperatures may result in poor body condition. Fish condition varies with changes in water quality. Benejam *et al.* (2008) observed that roach and bleak lost about five to six percent of their condition within ten days when the water quality deteriorated and they regained almost their initial condition within six days when water quality improved in a eutrophic reservoir. However lowest *CF* values during the more developed gonadal stages might mean resource transfer to the gonads during the reproductive period (Abowei *et al.*, 2009). Therefore due to its hardy nature, the lowest *CF* observed for *C. gariepinus* in September could be a result of resource transfer to the gonads in preparation for the peak breeding season as opposed to the effects of poor water quality.

Abowei *et al.* (2009) report that fish condition gives information when following up the degree of feeding activity of a species to verify whether it is making good use of its feeding source. The highest *CF* was observed in December when water levels were rising. During the filling phase of the flood pulse, inundation of floodplains offers more habitat opportunities as well as more food and the fish migrate out of the perennial water bodies into the seasonal swamps. This is followed by an intensive feeding frenzy during the high water phase which results in improved body condition (Merron, 1991; Chimatiro, 2004). This agrees with Winemiller and Jepsen (1998) who associate newly inundated floodplains with conducive conditions for successful feeding, growth and reproduction.

Conclusions and management implications

Data presented in this chapter has shown that male *C. gariepinus* attain larger L_T than females. Females tend to reach maturity earlier than males and breeding occurs throughout the year with peak breeding occurring between November and April which coincided with the flood regime. As a result, it is most likely that increased water flow and initiation of flooding was the major spawning cue for *C. gariepinus* in the Okavango Delta. Gonadal development on the other hand appears to have been triggered by increasing day length and temperature. It must also be noted that the current peak spawning period in the upper delta falls within the legislated closed season in Botswana (January-February) and from this perspective the current management strategy is appropriate for this species in this section of the river. However, in the lower Delta, spawning occurs between July and December (Merron, 1991) which coincides with the fishing season. This may affect the population negatively in this part of the system. Further, any fishery targeting this species should take into consideration the length at maturity and ultimately gill net mesh sizes need to be selected that capture these fish at lengths larger than maturity.

CHAPTER 5

AGE, GROWTH AND MORTALITY OF *C. GARIEPINUS* IN THE OKAVANGO DELTA, BOTSWANA.

5.1. INTRODUCTION

In fisheries science, age determination is one of the most important aspects as it forms the basis for calculations of growth rate, mortality rate and productivity, ranking it among the most influential of biological variables (Campana 2001). The age and growth of *C. gariepinus* have been investigated using length frequency analysis methods (Vander Waal & Schoonbee, 1975; Willoughby & Tweddle, 1978; Bruton & Allanson, 1980; Quick & Bruton, 1984; Wudneh, 1998; Mosepele & Nengu, 2003), vertebrae (Pivnička, 1974; Willoughby and Tweddle, 1978, Yalçin *et al*, 2002), sectioned spines (Vander Waal & Schoonbee, 1975; Bruton & Allanson, 1980; Quick & Bruton, 1984) and sectioned otoliths (Bruton & Allanson, 1980; Quick & Bruton, 1984; Chimatiro, 2004; Richardson *et al.*, 2009; Wartenberg, 2009) with varying degrees of success.

In the Shire River in Malawi, Willoughby & Tweddle (1978) used moving modes from length frequencies as well as vertebrae and mark-recapture methods to age *C. gariepinus*. They cautioned that due to high variability in the growth of individual fish, results from length frequency analysis should be assumed tentative. Similarly, Van der Waal & Schoonbee (1975) contended that establishment of age on the basis of moving length frequency modes for *C. gariepinus* was of limited applicability and the considerable overlap between the lengths of consecutive age groups precluded the use of length frequency methods for the estimation of *C. gariepinus* growth in Van der Kloof Dam (formerly P.K. le Roux Dam), South Africa (Quick & Bruton, 1984). In Lake Sibaya, Bruton & Allanson (1980) successfully applied length frequency methods to describe growth rates of juvenile *C. gariepinus*. The use of length frequency analysis therefore appears limited to juvenile fish that tend to grow rapidly and are likely to exhibit distinct modes indicating separation of size classes on a temporal scale. For the larger, long lived fishes, however, most authors recommend the use of hard parts.

Quick & Bruton (1984) used sectioned spines in the Van der Kloof Dam. In that study 86% of the total spines examined had clear rings but the majority of spines (73%) from fish larger than 700 mm L_T were rejected due to possible resorption of one or more rings. As a result Quick & Bruton (1984) recommended sectioned otoliths as an appropriate ageing method. Kaunda & Hecht (2003) compared the aging accuracy of spines and otoliths in a closely related species, *Bathyclarias nyasensis*, from Lake Malawi and also encountered the problem of resorption in spines which resulted in higher rejection rates for these structures compared to otoliths. However, very high aging success with minimum rejection rates (3.3%) for spines was achieved in the Elands and Olifants Rivers by Van der Waal & Schoonbee (1975). In this case, it is particularly instructive to note however that their age estimates were only up to a maximum of 10 years. This shows that spines can only be reliably used for younger fish while for older fish, aging using spines becomes uncertain and the likelihood of underestimating age increases. This is supported by Weyl & Booth (2008) who discuss that earlier studies using spines and vertebrae consistently underestimated the longevity of *C. gariepinus* possibly due to the effect of bone resorption which was more pronounced in spines than in vertebrae. As a result, Weyl & Booth (2008), recommended otoliths as the most appropriate structure for ageing adult *C. gariepinus* as these metabolically inert structures are not prone to resorption.

Growth zone deposition rate in otoliths has been validated by a number of authors (see Weyl & Booth 2008 for review) and have been successfully utilised for ageing *C. gariepinus* in a number of African populations (Chimatiro, 2004; Richardson *et al.*, 2009; Wartenberg, 2009). For this reason, otoliths were chosen as the most appropriate structures for age determination of *C. gariepinus* in the current study.

The aim of this chapter was therefore to use sectioned otoliths to undertake an assessment of the age and growth of *C. gariepinus* in the Okavango Delta in order to provide estimates of growth rate and mortality rate, two important components of all analytical fisheries models.

5.2. MATERIALS AND METHODS

Clarias gariepinus were collected on a monthly basis between October 2009 and October 2010 as described in Chapter 2. Procedures for otolith removal and preparation followed those used during previous studies on *C. gariepinus* (Chimatiro, 2004; Richardson *et al.*, 2009; Wartenberg, 2009). Upon capture, each specimen was weighed to the nearest gram, measured to the nearest mm total length (L_T), sexed and the sagittal otoliths were removed and stored in dry 1.5 ml Eppendorf tubes for later processing and age determination.

From each pair, one otolith was selected randomly and mounted in clear polyester casting resin and sectioned transversely through the nucleus using a double bladed diamond edged saw. Otoliths were sectioned at a thickness of 0.3-0.4 mm and mounted on microscope slides using DPX mountant. Growth zones were visible as alternating opaque and translucent bands (Fig 5.1). Age was estimated by counting the number of opaque rings from the nucleus to the edge of the otolith under transmitted light at varying magnification.

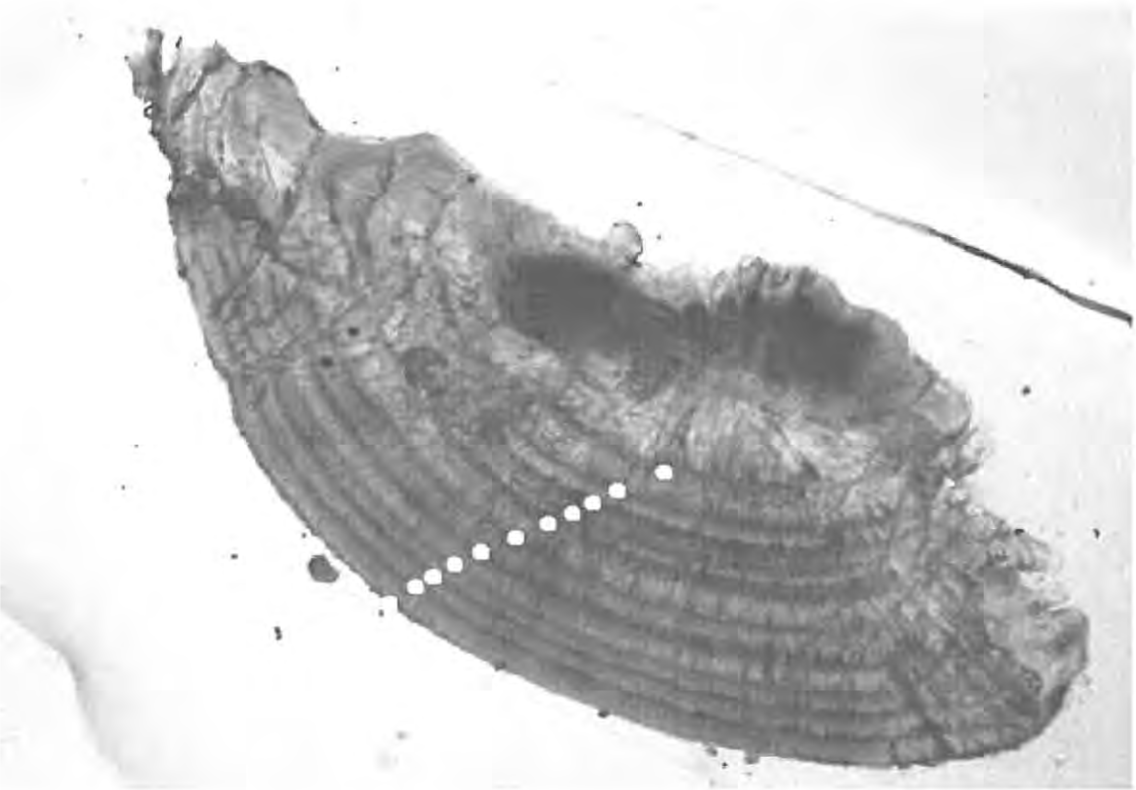

FIG 5.1. Photograph of a sectioned sagittal otolith of a 736 mm L_T male *Clarias gariepinus* with 11 opaque zones. The otolith was viewed under transmitted light and annuli are indicated by white dots.

Otoliths were read twice at an interval of at least two weeks apart without prior knowledge of the length and sex of the fish. If the two readings matched, the age estimate was accepted. If the readings failed to match, a third reading was taken. A match between two of the three readings meant acceptance of the age estimate from the two matching readings. If the three readings differed by not more than two years they were averaged, otherwise the otolith was rejected as unreadable.

Precision and accuracy

To be valid, age estimates from hard parts need to be both accurate and precise. Every ageing study is associated with error that pertains to either accuracy or precision and the two errors are not necessarily linked (Campana, 2001). Accuracy is the closeness of the estimate to the true value and has to do with the relevance of the method and the structure while precision is the reproducibility of the individual measurements on a given structure (Campana & Moksness, 1991; Welch, 1993; Svedäng *et al.*, 1998)

Precision

When bias cannot be readily shown, measuring precision is an important way of assessing the relative ease of using a particular structure for age determination and for assessing the reproducibility of an individual's age determinations (Campana *et al.*, 1995). To assess the precision and amount of variation between the two sets of readings, three common statistical measures were used: the average percent error (APE), the coefficient of variation (CV) and the index of precision (D). An average percent error (APE) in aging the *jth* fish is shown in (Beamish & Fournier, 1981) as:

$$APE_j = \frac{1}{R}\sum_{i=1}^{R}\frac{|X_{ij} - X_j|}{X_j}\cdot 100 \qquad (5.1)$$

Therefore from equation (5.1):

$$\text{APE} = \frac{\sum_{j=1}^{n} APE_j}{n} \qquad (5.2)$$

where X_{ij} is the *i*th age determination of the *j*th fish, Xj is the mean age of the readings and R is the number of readings.

Coefficient of variation (CV) was calculated as in Kimura & Lyons (1991):

$$\mathrm{CV}_j = \frac{\sqrt{\sum_{i=1}^{R} \frac{(X_{ij} - X_j)^2}{R-1}}}{X_j} \cdot 100 \qquad (5.3)$$

From equation (5.3):

$$\mathrm{CV} = \frac{\sum_{j=1}^{n} CV_j}{n} \qquad (5.4)$$

where the definitions for X*ij*, X*j* and R are as previously described for APE

The percent error contributed by each observation to the average age class was estimated by an index of precision (D) (Chang, 1982). The index is defined as:

$$\mathrm{D}_j = \frac{CV_j}{\sqrt{R}} \qquad (5.5)$$

From equation (5.5):

$$\mathrm{D} = \frac{\sum_{j=1}^{n} D_j}{n} \qquad (5.6)$$

If multiplied by the average age for the *j*th fish, the index of precision (D*j*) gives the error in age determination made for each observation.

Accuracy

Validation is defined as a way of establishing the relationship between ring number and age (Geffen, 1992).Validation of growth zone deposition rate is therefore considered a prerequisite for any ageing study (Campana, 2001). Weyl and Booth (2008) reviewed the current knowledge of growth zone deposition rates in *C. gariepinus* otoliths and showed that growth zone deposition rate was annual in otoliths of all assessed populations of *C. gariepinus*. Despite this, validation was deemed necessary for this population. The size of the Okavango Delta made mark recapture methods impractical and, therefore, the periodicity of growth zone formation was estimated indirectly by edge analysis. In edge analysis, the monthly percentage occurrence of opaque zones on the edge of the otolith is recorded and plotted. The distribution is then tested as either unimodal or bimodal using a periodic logistic regression model (Winker *et al.*, 2010*a*, *b*). The hypothesis and goodness of fit tests were conducted as described in Chapter 4.

Modelling growth

Mosepele *et al.* (2005), hypothesized that the fishes in the lower Okavango Delta may be an independent group from those found in the upper Okavango Delta. Their conclusions were based on comparing the length structure of samples drawn from the two regions. Therefore, prior to the process of fitting growth curves a Randomization test[1] was carried out on two samples of fish lengths from the upper and lower Okavango Delta to test the null hypothesis that the observed pattern of fish lengths was independent of capture location. This procedure showed that the two samples did not differ significantly (P=0.76). Furthermore, length at age

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[1] Randomization tests are generally assumed to be superior to ordinary parametric statistical tests because they do not have to adhere to specific predetermined assumptions with regard to the probability distribution (Manly, 1997; Haddon, 2001).

data were separated by capture location, i.e. upper and lower Okavango Delta and growth curves were fitted to the separate populations. The null hypothesis that growth of the two populations is the same was tested using the F-test described in Equation 5.9. For the two populations, there was no significant difference between the growth curves (F=1.03; df=228; P = 0.38). Therefore data from the two regions were pooled for analysis.

Growth was modeled by fitting the three parameter Von Bertalanffy Growth model (VBGF) to the observed length at age data for males, females and for a combination of both males and females. The model was defined as:

$$L_t = L_\infty\left(1-e^{-K(t-t_0)}\right) \tag{5.7}$$

where L_t is the length at age t; L_∞ the asymptotic length; K the Brody growth coefficient and defines the growth rate towards L_∞; t the age of the fish; t_0 the hypothetical age at which fish would have zero length if it had always grown in a manner described by the model (Newman *et al.*, 2000).

To estimate growth parameters, the sum of squared residuals were minimized using the solver routine in Microsoft Excel. Other estimates were obtained using normal likelihoods for comparison. The negative log likelihood minimized was of the form:

$$-veLL = \frac{n}{2}\left[Ln(2\pi) + 2Ln(\hat{\sigma}) + 1\right] \tag{5.8}$$

where $\hat{\sigma}$ is the variance estimated from the data.

Parametric bootstrap resampling (Efron & Tibshirani, 1986) with 1000 bootstrap replicates was used to estimate the model parameter variance, standard error and 95% confidence intervals.

To compare the growth of males and females, an overall test of coincident curves was used (Haddon, 2001). This method compares several curves at the same time and is called the Analysis of the Residual Sum of Squares (ARSS) (Chen *et al.,* 1992). The steps outlined by Chen *et al.* (1992) and Haddon (2001) were followed to execute the analysis and an F-statistic was calculated as:

$$F = \frac{\dfrac{RSS_p - \sum RSS_i}{DF_p - \sum DF_i}}{\dfrac{\sum RSS_i}{\sum DF_i}} = \frac{\dfrac{RSS_p - \sum RSS_i}{3 \cdot (K-1)}}{\dfrac{\sum RSS_i}{N - 3 \cdot K}} \tag{5.9}$$

where F is the F-statistic with 3*(*K*-1) and (*N*-3**K*) degrees of freedom, *K* is the number of curves being compared, *N* is the total or pooled sample size, RSS_p = *RSS* of each curve fitted by pooled growth data, RSS_i = sum of RSS of each curve fitted to growth data for each individual sample and *DF* = degree of freedom (Chen *et al.*, 1992; Haddon, 2001).

Mortality

Instantaneous total mortality (*Z*) was estimated using catch curve analysis (Ricker, 1975). Catch curve analysis was applied to length frequency distributions obtained from both the experimental sampling gear and the commercial fisheries. A normalised age-length key was used to convert length frequency distributions to age frequency distributions (Butterworth *et* *al.*, 1989). The calculated Z is the slope of a regression line fitted to the log-transformed frequency at age according to the equation:

$$\ln(N_t) = \ln(N_0) - Z_t \tag{5.11}$$

where N_t is the numbers at age t (Al-Hussaini *et al.*, 2002). An additional estimate of total mortality was calculated using the method of Butterworth *et al.* (1989) as:

$$Z = \ln\left[1 + \frac{1}{a_m - a_f}\right] \tag{5.12}$$

where a_f is the age at full recruitment and a_m is the age of fully recruited fish.

Natural mortality (M) is described as one of the most difficult parameters to ascertain (Pauly, 1980; Chimatiro, 2004, Bishop *et al.*, 2006) and yet it is one of the most crucial input parameter in the extant fish population dynamics models (Pauly, 1980). Therefore two methods were used to estimate M for comparison. In this study estimates of M were derived using the relationship between growth parameters and water temperature as defined by Pauly (1980):

$$\ln(M) = -0.0152 - 0.279\ln L_\infty + 0.6543\ln K + 0.463\ln T \tag{5.13}$$

where L_∞ and K are the von Bertalanffy growth parameters and T is the mean water temperature. Another estimate of M was obtained using a method based on the maximum age according to Hoening (1983).

$$\ln(M) = 1.46 - 1.01\ln(t_{\max}) \qquad (5.14)$$

where t_{max} is the maximum age in the population.

Survival rate (S) was estimated as: $S = \exp(-Z)$ (5.15)

Fishing mortality (F) was then obtained by subtraction: $F = Z - M$ (5.16)

5.3. RESULTS

Precision

Otoliths from 280 fish were examined. Of the 280 otoliths examined, 25 (9%) could not be aged reliably and therefore were excluded from the analysis. The majority of the unreadable otoliths were for smaller fish <400 mm L_T. For the readable otoliths, APE was 6%, CV was 8.5% and D was estimated at 6%.

Validation

The distribution of opaque zones on the edge of the otolith was unimodal with a maximum from July to December (Fig. 5.2). Therefore, it was assumed that one opaque and one hyaline zone was deposited each year and counts of growth zones corresponded to the age of the fish. Parameter estimates for the periodic logistic regression model predicting the proportion of occurrence of opaque margins on the otolith edges of *C. gariepinus* are presented in Table 5.1. Opaque zone deposition was dependent on time of the year (Table 5.2)

TABLE 5.1. Parameter estimates from the periodic logistic regression model predicting the proportion occurrence of opaque margins on the otoliths of *Clarias gariepinus* over a period of 1 year in the Okavango Delta, Botswana.

Parameter	*Estimate*
β_0	-0.045
β_1	0.122
β_2	-1.632
d.f	3

TABLE 5.2. Significance test of the periodic logistic regression model predicting the occurrence of opaque margins on the otoliths of *Clarias gariepinus* in the Okavango Delta, Botswana. The H_0 that at least one of the regression coefficients equals zero could not be rejected at P $\leq$ 0.05 and 2 degrees of freedom. The H_0 that $\beta_2 = 0$ was rejected at P $\leq$ 0.05 and 1 degree of freedom. Therefore inclusion of the Sin (*S*) regressor variable makes the full model a better fit to the data than the reduced model.

Log-likelihood of full model: -6.713						
Reduced model	H_0	Log-likelihood	G^2	P	r^2	d.f
β_0	$\beta_1 + \beta_2 = 0$	-8.316	3.207	0.20	0.19	2
$\beta_0 + \beta_1$	$\beta_2 = 0$	-10.435	7.444	0.006	0.32	1

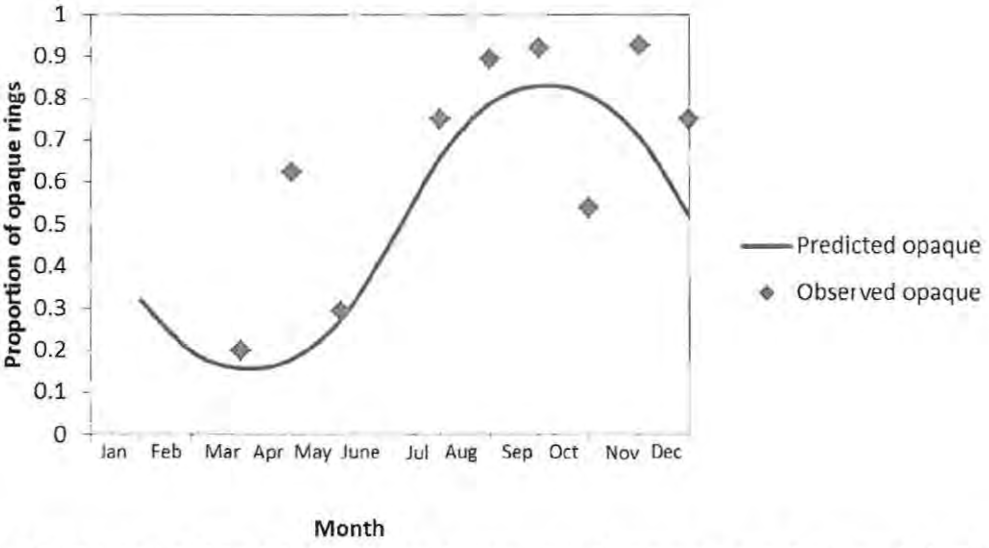

FIG. 5.2. Observed and predicted frequency of occurrence of opaque rings on the edge of otoliths by month of capture. One ring is deposited in a year between July and December. Data labels represent the proportion of opaque rings per month i.e. opaque/total.

Growth

Length at age is summarized in the length at age key presented in Table 5.3. Longevity was estimated at 15 years. The oldest fish was a 960 mm L_T, 6396 g female that was sampled from Guma Lagoon. The Von Bertalanffy growth model parameter estimates are presented in Table 5.4 and fitted growth models are shown for combined sexes (Fig 5.3) and males and females in Fig 5.4. Least squares regression and normal likelihoods produced similar results. Growth between age 0 and 1 was very rapid with fish attaining lengths of about 400 mm L_T. Statistically, from the ARSS, there was no significant difference between the male and female growth curves (F=1.25; df=225; P = 0.29) and for both sexes there was no noticeable decline in growth until the fish reached 15 years. Models, therefore, approximated linear growth. The unreasonably large asymptotic lengths predicted by the model for the combined sexes and the females datasets indicate that, for the data available, the model failed to determine asymptotic length for females or combined sexes. As a result, a linear regression fitted the data equally well and in these cases the linear regression model is also given. The growth of females was best described by ($y = 21.50x + 427.39; r^2 = 0.35$) and males by the relationship ($y = 23.79x + 440.83; r^2 = 0.38$).

TABLE 5.3. Length at age key for *Clarias gariepinus* in the Okavango delta, Botswana.

	Age (Years)															
Length (mm)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**Total**
300																**0**
350																**0**
400	6	5														**11**
450	6	2	7	1	2	1	1			1						**21**
500	13	8	6	12	9	12	2	2		1	1					**66**
550	2	7	12	12	13	5	4	3	1	1	2					**62**
600	1	2	4	2	4	4		1	1		2					**21**
650	1			1	1	2	1		1	1	1	1	3			**13**
700			1		1					1	1	1	1			**6**
750			1	1	1	2			1	1	1	3	1	1		**13**
800							1						2			**3**
850													3			**3**
900							2				1	2	1			**7**
950																**0**
1000					1					1				1	1	**4**
1050																**0**
Total	**29**	**24**	**31**	**30**	**32**	**26**	**11**	**6**	**4**	**7**	**9**	**7**	**11**	**2**	**1**	**230**

TABLE 5.4. Von Bertalanfy growth model parameter estimates, standard deviation (SD) and coefficient of variation (CV) for combined sexes (n=231), females (n=124) and males (n=104) of *C. gariepinus* from the Okavango delta, Botswana.

Parameter	*Estimate*	*SD*	*CV*
Combined sexes			
L_∞	10000 mm L_T	0.88	0.10
K	0.002	0.000	
t_0	-18.07	1.13	
Females			
L_∞	10000 mm L_T	0.53	0.10
K	0.002	1.48	
t_0	-18.50	6.78	
Males			
L_∞	907 mm L_T	162	0.10
K	0.076	0.32	
t_0	-7.95	17.70	

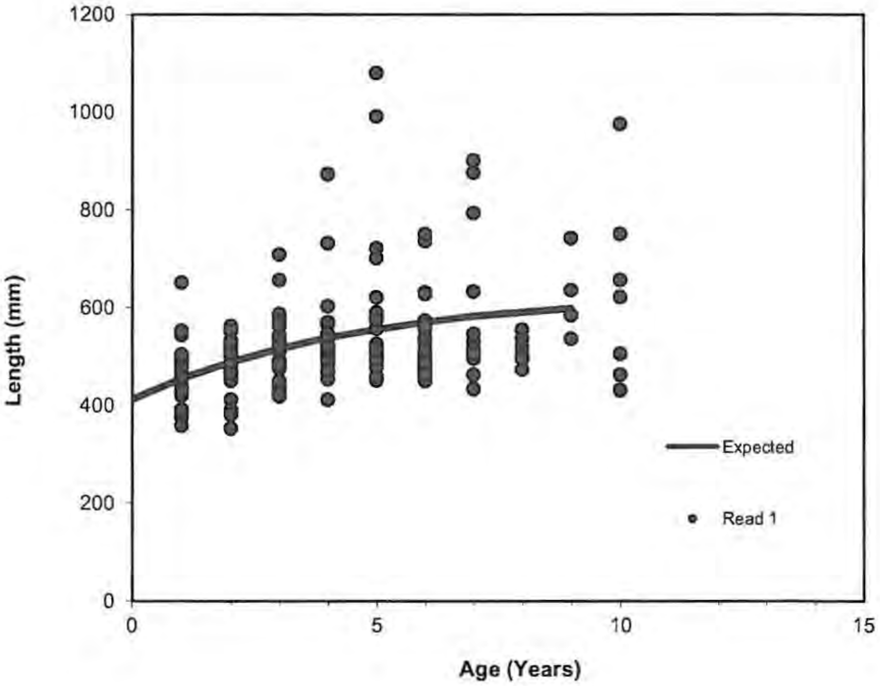

FIG 5.3. Von Bertalanffy growth curve for combined sexes of *C. gariepinus* from the Okavango Delta, Botswana. The model was fitted up to 10 years.

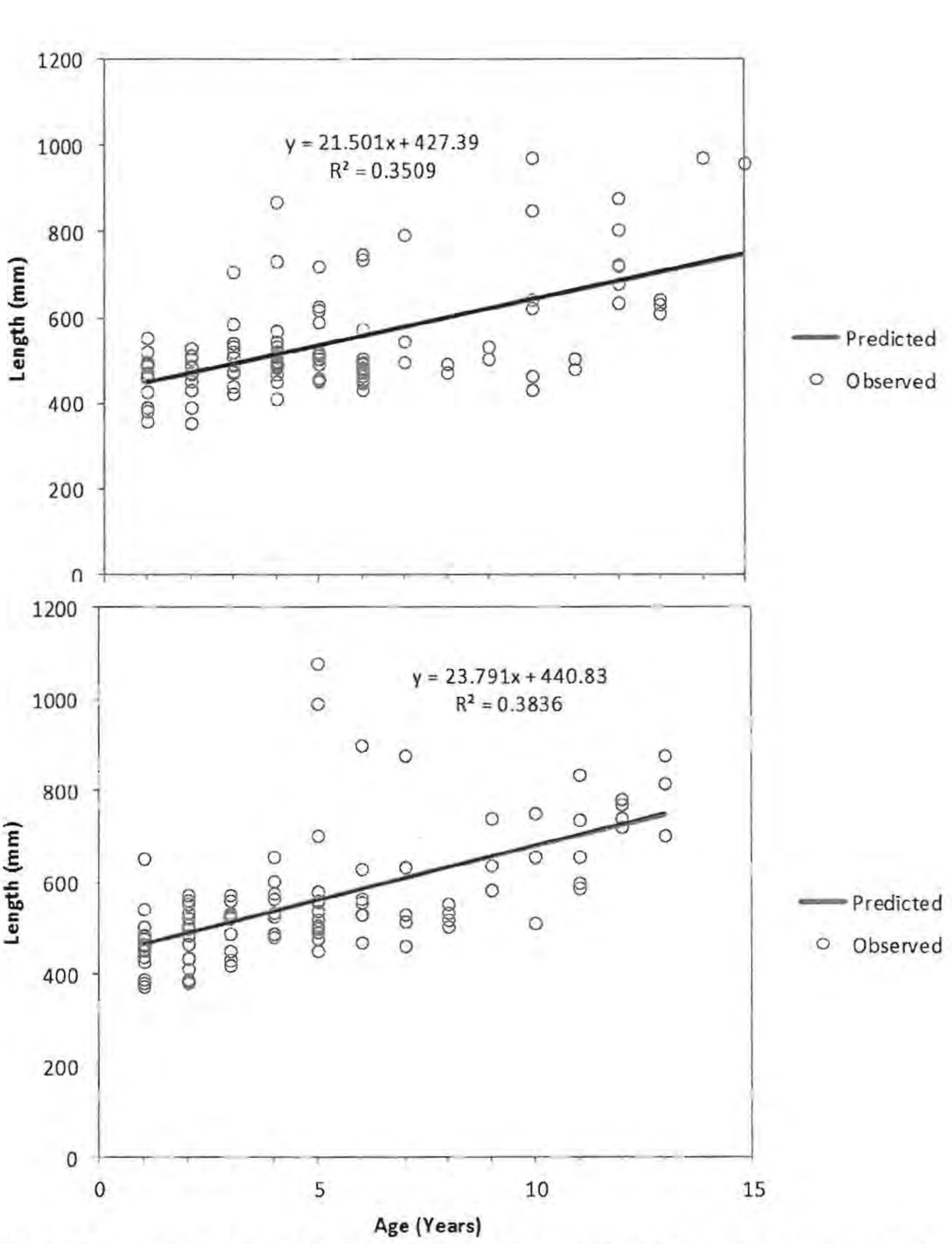

FIG 5.4. A comparison of growth curves for females (a) and males (b) of *C. gariepinus* from the Okavango Delta, Botswana.

Mortality

Instantaneous total mortality (*Z*) was estimated from catch curve analysis as 0.28 yr^{-1} (Fig 5.5). Estimates of natural mortality derived from the equations described by Pauly (1980) and Hoening (1983) are presented in Table 5.5. The estimate of natural mortality obtained from Pauly (1980) was considerably lower than the *Z* estimates from both the catch curve and Butterworth *et al.* (1989). Natural mortality estimated from Hoening (1983) was equal to *Z* from the catch curve and it was reasonable to assume that *Z* may be close to *M*. Due to this variability in the parameter estimates, the two estimates of *Z* were averaged and the two estimates of *M* were also averaged and the resultant estimate of fishing mortality was estimated at 0.05 yr^{-1} while the survivorship (*S*) estimate was 76%.

TABLE 5.5. Estimates of annual total mortality (*Z*) survivorship (*S*) Natural mortality (*M*) and Fishing mortality (*F*) of *C. gariepinus* in the Okavango delta, Botswana.

Parameter	*Estimate*	*Mean*
Z		
Catch curve	0.28	0.25
Butterworth *et al.* (1989)	0.21	
M		
Pauly (1980)	0.12	0.20
Hoening (1983)	0.28	
F	0.05	
S (survivorship)	76%	

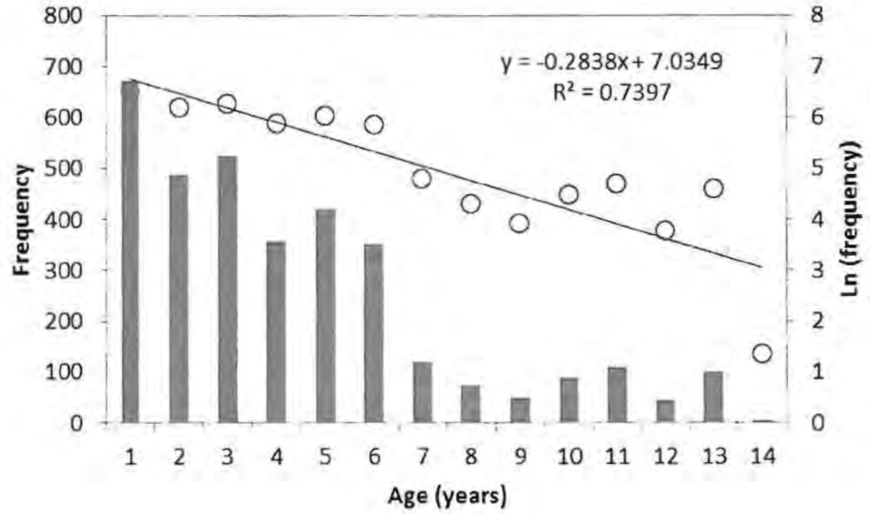

FIG.5.5. Catch curve (open circles) with the corresponding age frequency histogram (solid bars) for *C. gariepinus* in the Okavango delta, Botswana. The estimate of total mortality (*Z*) is derived from the slope of the descending limb of the curve.

5.4. DISCUSSION

Ageing accuracy and precision

In any growth study, precision and accuracy are important prerequisites. In the present study, 91% of the otoliths examined had clearly defined growth zones and precision estimates (APE=6%, CV=8.5%), D=6%) were comparable to those obtained for sectioned otoliths of *C. gariepinus* in Xonxa Dam South Africa (APE = 8.5%; Richardson *et al.*, 2009) and the closely related *B. nyasensis* from Lake Malawi (APE = 14.2%; CV = 10%; D = 7.1%; Kaunda & Hecht, 2003).

Even though edge analysis has problems associated with its usage for age validation, it has proved to be important in determining the timing of growth zone deposition within a year (Campana, 2001). Fitting the logistic regression model to edge analysis data (as in this study) makes it possible to determine the assumed sinusoidal periodicity of growth zone formation (Winker *et al.*, 2010*b*). Moreover, by using the likelihood method (Flury & Levri, 1999;

Dobson, 2002) the frequency of growth deposition within a year can objectively be tested (Winker *et al.*, 2010*b*). *Clarias gariepinus* otoliths from the Okavango Delta revealed a discernable pattern whereby opaque zones tended to be deposited more between July and December while the majority of hyaline zones were observed between January and June. It was therefore concluded that one opaque and one hyaline ring was deposited each year. This was consistent with the case studies reviewed by Weyl & Booth (2008) and indicates that in the Okavango population of *C. gariepinus*, a single growth zone was deposited each year.

Factors influencing the periodicity of growth zone formation

In many river systems, reduction in growth is generally associated with a drop in temperature, reproduction and the drawdown effects (Welcome, 1979). In otoliths viewed under transmitted light, opaque zones signify periods of slow growth while wide hyaline zones are indicative of fast growth (Bagenal & Tesh, 1978). In the Okavango delta the deposition of opaque rings between July and December for *C. gariepinus* coincided with the drawdown period, an increase in temperature, the feeding run and an increase in day length (see Fig 4.8, Chapter 4). A similar pattern has been documented for other Okavango fishes. Booth *et al.* (1995, 1996) showed that in *Oreochromis andersonii* and *Oreochromis macrochir* annulus deposition occurred during the drawdown period in summer when temperatures were high and attributed annulus deposition to reproductive activity.

As energy investment into reproduction must occur before the actual event (Lester *et al.*, 2004) growth retardation for *C. gariepinus* in the Okavango Delta may also be associated with reproductive costs. However, for most species, low water results in either complete cessation or marked reduction in feeding (Welcome, 1979). Therefore, drawdown effects may also impact negatively on the growth of *C. gariepinus* because the amount of food decreases and both intra and interspecific competition increases due to the considerable reduction in exploitable habitat. This causes this omnivorous species to become more of a specialist, feeding more on fish (Merron, 1991) which might require it to expend more energy on foraging instead of growth. The cumulative effects of the drawdown period were evinced by the sharp drop in condition in September which was just prior to the feeding run and the subsequent arrival of floods (See Fig 4.7, Chapter 4).

The feeding run may partly be a strategy for quick recovery from the adverse effects of the drawdown period. It follows therefore that energy obtained from this activity may be channeled towards maintenance activities and gonadal recrudescence prior to spawning instead of somatic growth. Merron (1991) observed that the feeding run resulted in improved reproductive condition and postulated that this was in preparation for the arrival of the flood pulse so that the species could take immediate advantage of conducive environmental conditions for spawning. Moreover, Willoughby and Tweddle (1977) observed that peak feeding for *C. gariepinus* in the Shire River occurred just before the flood peak. The fact that the feeding run in the Okavango Delta does not result in increased growth may support in part the assumption that energy can be allocated to somatic growth or gonadal development but not to both simultaneously (Lester *et al.*, 2004). Moreover, this implies that the less permanent buildup of fat that may accrue from the feeding run is not akin to growth. True growth pertains to the accretion of flesh and bone (Lagler *et al.*, 1962).

The fast growth, indicated by a hyaline margin on the otoliths, was observed between January and June and corresponded to the period when the flood was at its peak. Flood plain inundation is generally associated with increased food resources (Merron & Bruton, 1988; Merron, 1991; Winemiller & Jepson, 1998) which may explain the fast growth observed during this time due to the varied and abundant amount of prey available for consumption. However, the fast growth coincided with spawning which agrees with Willoughby and Tweddle (1978) who also noted that the period of faster growth coincided with the breeding season. This is a paradox since breeding is expected to affect growth negatively (Charnov, 2008, Alos *et al.*, 2010). However, it must be noted that the energetic investment in gonads occurs prior to the actual spawning event and thus it is possible that increased feeding opportunities during flooding outweigh the energetic costs of reproduction over this period (Lowe-McConnell, 1987; Wooton, 1990).

The results on ring deposition should be treated with caution because otolith samples from the upper and lower Okavango Delta were pooled. However, the majority of the samples (March-October) were obtained from the lower Okavango Delta. Therefore since breeding occurs between July and December in the lower Okavango Delta (Merron, 1991) the results indicate that growth arrest for this species in the lower Okavango Delta is mainly a result of reproductive activity.

Growth

Age at length data could not be adequately fitted using the VBGF and modeled growth approximated linear increases in length with age for females and the combined sex data. Several studies have failed to adequately fit the VBGF to length at age data for *C. gariepinus* (Van der Waal & Schoonbee, 1975; Quick & Bruton, 1984; Yalçin *et al.*, 2002) and the closely related *Bathyclarias nyasensis* (Kaunda & Hecht, 2003).

In their attempt to fit the VBGF to length at age data for *C. gariepinus* from the Elands River Van der Waal & Schoonbee (1975) found that there was no noticeable decline in length as age increased. Even the Ford-Walford plot could not converge to L_∞. However, they cautioned that their results were based on a relatively small number of fish older than 6 years. Similar observations were made by Quick & Bruton (1984) in Van der Kloof Dam where a VBGF could not be fitted to the length at age data. Quick & Bruton (1984) observed that there were two phases of growth whereby length increments decreased from the first to the third year and then increased on the fourth and fifth year.

Quick and Bruton (1984) reasoned that this bi-phasic growth pattern was either a result of lumen enlargement in the spines used for ageing the animal or as a result of a dietary shift. In the van der Kloof study, there was an observed enlargement of the spine lumen after four years of growth which resulted in high rejection rates (50%) of spines for fish older than 4 years. This may have resulted in a small sample size to work with for ages > 4 years. Quick & Bruton (1984) postulated that their back calculated growth may have been biased towards faster growing individuals because these fish had spines that were clearer to read. Another hypothesis used to explain the increased growth on the fourth and fifth year was that of a diet switch from invertebrates to fish and a fish diet is believed to enhance growth (Bruton, 1979b). Therefore Quick & Bruton (1984) postulated that the bi-phasic growth may have contributed and important lack of fit for the VBGF in that population. However, the small sample size for fish older than 4 years may have also contributed to the lack of fit. Similarly, Yalçin *et al.* (2002) failed to fit the VBGF to the River Asi population of *C. gariepinus*. They also attributed the lack of fit to the small sample size for fish older than 4 years.

Despite the availability of old and large fish in the present study, fitting a VGBF to length at age data resulted in a large L_∞. The parameter L_∞ is often confused with the maximum length of the fish, which in this case is 1080 mm L_T. However, in a VGBF, K, L_∞ and t_0 are optimized to create a best fit of the VGBF model to the available data. As a result, the fitted VGBF described the growth of this fish to be linear, converging to a very large asymptotic length. A similar observation was made when the model was fitted to the females dataset only. However, when the model was fitted to the males dataset it converged to a biologically sensible asymptotic length (908 mm L_T; Table 5.4) which was closer to the observed *Lmax* (1080 mm L_T). This estimate was comparable to that obtained by Mosepele & Nengu (2003). They estimated an asymptotic length of 905 mm L_T for a combined dataset of males and females using length frequency analysis. Generally *C. gariepinus* from different localities tend to grow to very large sizes. The relatively smaller asymptotic lengths reached by this species in Gubi Dam in Nigeria and Shire River in Malawi were attributed to heavy exploitation (Abdulkarim *et al.*, 2009; Chimatiro, 2004).

TABLE 5.6. A summary of growth parameters and the size at first maturity for *Clarias gariepinus* in different localities. The species generally reaches asymptotic lengths close to a meter and reaches maturity at lengths > 200 mm L_T. N/A stands for not available.

Locality	*Sex*	*L50% (mm L_T)*	*Lmax (mmL_T)*	*t0*	*L_∞ (mm L_T)*	*K*	*Source*
Okavango delta	**M**	**298**	**1080**	**-7.95**	**907**	**0.08**	**This study**
	F	**258**	**975**	**N/A**	**N/A**	**N/A**	
	M	273	N/A	N/A	905 (M+F)	0.26	Mosepele & Nengu (2003)
	F	362	N/A	N/A	N/A	N/A	
Gubi dam	M+F	290	N/A	-1.37	430	0.65	Abdulkarim *et al.* (2009)
Shire River	M	320	N/A	N/A	1394	0.085	Willoughby & Tweddle (1975)
	F	290	N/A	N/A	789	0.167	
	M	249 L_S	N/A	-1.92	503	0.31	Chimatiro (2004)
	F	249 L_S	N/A	N/A	N/A	N/A	
Elands River	M		1005	N/A	N/A	N/A	Van der Waal & Schoonbee (1975)
	F	N/A	1105	N/A	N/A	N/A	
Lake Sibaya	M	N/A	N/A	N/A	760	N/A	Bruton & Allanson (1980)
	F		N/A	N/A	674	N/A	
Van der Kloof dam	M	N/A	N/A	N/A	1150	N/A	Quick and Bruton (1984)
	F			N/A	1020	N/A	
Lake Tana	M	360	N/A	N/A	900 (M+F)	0.2	Wudneh (1998)
	F	305	N/A	N/A	N/A	N/A	
River Asi	M	250	N/A	-0.69	853	0.144	Yalçin *et al.* (2002)
	F	247	N/A	-1.72	829	0.15	
Xonxa dam	M+F		N/A	-0.24	1121	0.2	Richardson *et al.* (2009)
Darlington dam	M+F	528	1460	-2.2	921	0.16	Weyl *et al.* (2010)

In both male and female fish, lengths at age were highly variable resulting in large error around the fitted growth function and a lack of statistical difference between growth rates. Booth *et al.* (1995) also observed large variation in length at age data for *O. andersonii* from the Okavango delta. They attributed this variability mainly to the variable environmental conditions experienced by individual fish in different parts of the floodplain as well as intrinsic genetic variation between the individuals themselves. This is most likely also the case with *C. gariepinus*.

Clarias gariepinus is also highly tolerant of different environmental conditions and is able to utilize the full range of habitats available in the Okavango Delta. The availability and quality of food available to an individual inhabiting the different environments of the Delta is likely to be highly variable and because food availability affects growth (Wooton, 1990), the growth history of individual fish will differ. Hence, a small old fish may have inhabited a food poor environment prior to being sampled while a relatively young large fish may have inhabited a food rich environment. In habitats as complex as the Okavango Delta, this is likely to result in the large variation in individual growth rates observed in this study.

It is suggested that future research should direct sampling towards increasing the proportion of older fish and younger fish in the sample to obtain a full size and age range of individuals and should adopt a multi model inference approach that encompasses various shapes for growth (Mercier *et al.* 2011). With very large sample sizes, the model may converge to a biologically reasonable L_{∞}.

Longevity

Under the assumption of a single growth ring per year (see marginal zone analysis in Fig 5.2 and Weyl & Booth 2008), this study demonstrated that *C. gariepinus* in the Okavango system were long lived. The estimated maximum age (15 + years) suggests a longer life span than that estimated by Chimatiro (2004) for the same species in the lower Shire floodplain (9 years) and Richardson *et al.* (2009) in Xonxa dam, South Africa (12 years). However this estimate compares well with the longevity estimate for this species in Glen Melville dam (15 years, Weyl & Booth 2008) while it is markedly lower than estimates for Darlington Dam (25years) and Lake Gariep (>35years) (Wartenberg, 2010). Booth *et al.*, (2010) attributed the variation in longevities in the different man made impoundments to the age of the reservoirs. In these temperate reservoirs fishing pressure is low (Weyl *et al.*, 2008) and there are few natural predators, therefore *C. gariepinus* inhabiting these water bodies tend to be considerably longer lived. Therefore, the lower *C. gariepinus* longevity in the Okavango Delta when compared to the reservoirs may partly be ascribed to predation by the sub-adult Nile crocodile population which feeds predominantly on fish (62%) with catfish representing the highest percentage of occurrence (11.3%) in the diet (Wallace, 2006).

A summary on the size reached by yearling *C. gariepinus* in different localities is shown in Table 5.7. It is apparent that the species grows very fast in the first year of life. Fast growth in the first year is typical of organisms that have to go through a succession of different mortality rates (Craig, 1985). These organisms are expected to grow fast during the stage when they are more vulnerable and growth should proceed more slowly by comparison during safer periods (Craig, 1985). McKaye (1986) hypothesized that enhanced growth rate of juvenile catfish (*Bagrus meridionalis*) may reduce their susceptibility to predation. Furthermore, the larger the size of the organism, the better it is protected from changes in the environment (Pianka, 1970). Therefore since *C. gariepinus* exhibits an altricial reproductive strategy (Bruton, 1977), its young are more vulnerable during the early developmental stages due to lack of parental care. When this is coupled with the ephemeral nature of the floodplain habitat on which spawning occurs, the best strategy to ensure increased survival of juveniles and best strategy for survival is to "hurry" in growth through the early developmental stages of life. Moreover a reasonable size may be essential for migration back into the main river channel during the drawdown period (Welcomme, 1979).

TABLE 5.7. The size reached by yearling *Clarias gariepinus* from different localities compared to the Okavango delta population. Rapid growth in the first year is apparent in all populations.

Location	*Sex*	*TL (mm)*	*Time reached*	*Source*
Okavango delta	**M** **F**	**466** **461**	**First year**	**This study**
Lake Liambezi	M+F	480	First year	van der Waal (1976; cited by Bruton & Allanson, 1980)
Shire Valley	M+F	200	First year	Willoughby & Tweddle (1978)
Lake Sibaya	M+F	144	6 months	Bruton & Allanson (1980)
Lake McIlwaine	M F	300 270	First year	Munro (1965; cited by Bruton & Allanson 1980)
Gariep Dam	M+F	287	First year	Hamman (1974; cited by Bruton & Allanson, 1980)
Lake Kariba	M+F	130	9 months	Bowmaker (1973; cited by Bruton & Allanson, 1980)
Elands River	M F	426 414	First year	van der Waal & Schoonbee (1975)

Mortality

A comparison of total mortality of *C. gariepinus* in the Okavango delta to that of other populations elsewhere is presented in Table 5.8. It is evident that there is considerable variability in population mortality for this species.

Using catch curve analysis, Chimatiro (2004) obtained a higher estimate of Z in the lower Shire floodplain for this species compared to this study. Similarly, Mosepele (2000) obtained an even higher estimate of Z using the length based catch curve which was closer to the estimate obtained by Wudneh (1998) in Lake Tana who also used the length based catch curve. It appears that a length based catch curve overestimates *Z* (Table 5.8). This is because length based methods underestimate age in long lived fishes (Damm, 1987). Moreover, when using the age structured catch curve as a control, Pauly *et al.* (1995) found that the length converted catch curve consistently overestimated *Z*. They postulated that the overestimation was caused by the bias introduced by seasonal growth which was corrected for by using a length converted catch curve with seasonality. Chimatiro (2004) attributed the high estimate of Z in the Shire River to high exploitation rates.

The estimate of *Z* from the catch curve was similar to *M* obtained by Hoening's (1983) equation implying that *Z* may be equal to *M*. Therefore considering only the estimate of *M* from Hoening's (1983) equation, there seems to be low fishing mortality on this population in the Okavango Delta. This scenario makes sense because *C. gariepinus* is currently not targeted by commercial fishers and only a very small portion of the floodplain is accessible to fishing.

TABLE 5.8. Comparison of *M* and *Z* for *C. gariepinus* in different localities

Locality	*Estimate*	*Source*
Z		
Okavango delta (Botswana)	**0.25**	**This study**
	1 ▪	Mosepele (2000)
Lower Shire (Malawi)	0.52	Chimatiro (2004)
Lake Tana (Ethiopia)	0.9 ▪	Wudneh (1998)
Darlington Dam (South Africa)	0.30	Weyl *et al.* (2010)
M		
Okavango delta (Botswana)	**0.12□**	**This study**
	0.28○	**This study**
	0.50□	Mosepele (2000)
Xonxa dam (South Africa)	0.26□	Richardson *et al.* (2009)
Lower Shire (Malawi)	0.52□	Chimatiro (2004)
Lake Tana (Ethiopia)	0.40□	Wudneh (1998)
Glen Melville dam (South Africa)	0.80▣	Booth *et al.* (2010)
	0.24○	
Darlington Dam (South Africa)	0.22	Weyl *et al.* (2010)

▪ Z from a length based catch curve □ *M* from Pauly's (1980) equation○ *M* from Hoening's (1983) equation
▣ *M* from adjusted survival probabilities

Conclusion and recommendations

Growth of C. gariepinus appeared to be highly variable resulting in complications in fitting the VBGF. The importance of a sampling strategy and the choice of a growth model in the assessment of growth parameters of a fish stock is emphasised by Mercier *et al.* (2011) who suggest that when there is a small proportion of older fish in the sample, asymptotic models fail to adequately describe the growth of adults. It was therefore interesting to note that despite the availability of fish aged to 15 years in the sample, the VGBF did not converge. It is therefore possible that the VBGF may not be the best model to describe the growth of *C. gariepinus* in the Okavango Delta and elsewhere. This aspect of the study requires further investigation and it is recommended that further research be conducted on this species, focusing particularly on obtaining a larger sample size, particularly from very small and very large individual fishes. Despite this, the estimated growth parameters are currently the best available estimates for growth of this species in the Okavango Delta. As a result, they should be used as first estimates in resource modeling. This is addressed in Chapter 6.

CHAPTER 6

MANAGEMENT OF *C. GARIEPINUS* IN THE OKAVANGO DELTA, BOTSWANA USING PER-RECRUIT ANALYSIS.

6.1. INTRODUCTION

In the Okavango Delta, *Clarias gariepinus* is a by-catch in the commercial gill net fishery which mainly targets large breams. Evidence from the commercial gill net fishery data collected between 1996 and 2005 indicates that the large catfishes *C. ngamensis* and *C. gariepinus* constitute 23 % of the total catch by weight while large cichlids comprised 70 % of the catch (Table 6.1). Catfishes were also the most abundant species group in experimental gill net catches (Chapter 3) and are an important component of the subsistence fishery (Van der Bank & Smit, 2007). They are also an important component of recreational angling where the annual feeding migration is an international tourist attraction (Field, 2009).

TABLE 6.1. The Contribution of large catfishes (*Clarias gariepinus and Clarias ngamensis*) by number and weight to the catch composition of the commercial gill net fishery in the Okavango Delta, Botswana in the period (1996-2005). The species ranked second in terms of both %no and % weight after cichlids. Data source (Department of Wildlife and National Parks-Fisheries Division)

Species	*no*	*% no*	*Weight(tonnes)*	*% Weight*
All bream (cichlids)	358998	52.9	4531.0	69.66
Large clariids	167708	24.7	1503.8	23.12
Hydrocynus vittatus	69960	10.3	284.8	4.38
Others (unspecified)	50352	7.41	119.4	1.84
Schilbe intermedius	32106	4.73	65.8	1.01
Total	679124	100	6504.8	100

As the human population of Ngamiland increases, fish demand will increase and commercial and subsistence fisheries are likely to expand. As a result of this foreseen growth, it is important that the *C. gariepinus* resource is included in a multi-species fisheries management framework. Under such conditions it is important to set exploitation guidelines that ensure long-term biological and socio-economic sustainability of the resource (Richardson *et al.* 2009).

Like in many other developing countries (Weyl *et al.*, 2005), fisheries in the Okavango Delta are considered data limited. While there are numerous studies on the biology and ecology of fishes in this habitat, there are few assessments of the fishery. Catch and effort data are temporally disjunct and there is a lack of age-based catch data. This precludes the use of most stock assessment methodologies such as the application of surplus production models (Schaefer, 1954, 1957; Pitcher & Hart, 1982; Hilborn & Walters, 1992) or age based production modelling (Pope, 1972). This can result in fisheries development preceding stock assessment (Weyl *et al.*, 2005) and often leads in the long term to unsustainable harvest levels and overfishing.

In similar situations, African scientists have utilised per-recruit models (Beverton & Holt, 1957) because per recruit analyses offer biological realism within data limited situations. With per-recruit analyses, alternative management strategies can be tested even when historical information on recruitment for the fish population being studied is limited (Chen *et al.*, 1998). This is a distinct characteristic that has made this analysis particularly appealing to fisheries scientists in Africa (Allison *et al.* 2002; Kanyerere *et al.*, 2005; Weyl *et al.*, 2005; Richardson *et al.*, 2009)

As there was no information on the selectivity of the commercial gear used in the Okavango fishery the aim of this chapter was therefore threefold. First, to use experimental catch data to estimate the selectivity of commonly used gill net mesh sizes. Second, to assess the status of *C. gariepinus* in the Okavango Delta using, Yield Per-Recruit (YPR) and Spawner Biomass Per-Recruit (SBR) analyses (Beverton & Holt, 1957; Ricker, 1975). Thirdly, to use results from these models to investigate the response of the stock to increasing effort using various gill net mesh sizes.

6.2. MATERIALS AND METHODS

Gill net fishing efficiency

Catch per unit effort (CPUE) was calculated for each mesh size to determine the efficiency of each mesh size in capturing *C. gariepinus*. CPUE was calculated in Pasgear II (Kolding & Skaalvik, 2010) as described in Chapter 3.

Gill net Selectivity

For the fisheries of the Okavango Delta, it was assumed that subsistence and recreational harvest patterns would remain fairly constant but that there would be increasing interest to further develop the commercial fishery (Shipton, 2011). For this reason it was important to establish the gill net selectivity patterns. Data used in this Chapter are from the Department of Wildlife and National Parks - Fisheries Division; collected over a period of 8 years from 2001-2009 as described in chapter 3. The gill net fleet comprised of 9 mesh sizes. These mesh sizes were 22 mm, 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 118 mm and 150 mm stretched mesh. The nets were set monthly at Ngarange, Seronga and Guma lagoon in three different habitats (lagoons, main channel and floodplains). Setting time was approximately 12 hours, from 6 pm to 6 am.

In this study, relative selection was used to estimate selectivity. This is because absolute selection is difficult to estimate as it requires full knowledge of the species and size composition in the population (Hovgård, 1996; Hovgard *et al.* 1999; Hovgård & Lassen, 2000). Therefore, most selection studies rely on relative selection which deals with that proportion of the population that comes into contact with the gear (Hovgårt & Lassen, 2000). The population of *C. gariepinus* was reconstructed by length and expected catches compared against observed catches. To do this, selectivity values for different mesh sizes were obtained by manipulating the general selection equation (Hovgård & Lassen, 2000):

$$C_{l,m} = q_{l,m} N_l P_m S_{l,m} E_m + Noise \ , \qquad (6.1)$$

where $C_{l,m}$ is the catch of a given length class l by mesh size m, $q_{l,m}$ is the proportion of the population of length class l that is vulnerable to the mesh m , N_l is the population of a length class l available to the mesh, P_m is the fishing power or efficiency of the mesh at retaining fish of size l, $S_{l,m}$ is the selectivity of m and assumed to be size dependent only, and E_m is the effort under which m is deployed. Noise accounts for aspects such as patchy distribution of fish, variability of fish behavior, gear performance variability and sampling variance (Hovgårt & Lassen, 2000).

The regression framework method (Hovgård & Lassen, 2000) which is a generalization of the methods used by Hovgård (1996) and Hovgård *et al.* (1999) was chosen to model selectivity of brown nets. The method assumes the principle of geometric similarity (Baranov, 1948. *In*

Hovgard & Lassen, 2000) and the stock abundance is derived by using a non-linear minimisation routine (Hovgård, 1996). This procedure is robust and more appealing because of its flexibility. The error structure was accounted for by using a power transformation of the catch data and least squares regression (Equations 6.3 & 6.4) where β takes a value between 0 and 1. If $\beta = 0.5$, poisson distribution is assumed, $\beta > 0.5$ implies a distribution with low contagion and $\beta < 0.5$ implies a contagious distribution (Hovgård & Lassen, 2000). The regression minimises the sum of squared residuals between the observed and expected catch (Equation 6.4) on a log transformed scale (Hovgård & Lassen, 2000). The selection curve (Equation 6.2) was assumed to be log-normal with Poisson distributed errors ($\beta = 0.5$).

$$S_{lm} = \exp\left(\frac{\left(-0.5 * \left(\ln\left(\frac{l}{m}\right) - \ln k\right)^2\right)}{\sigma^2}\right) \tag{6.2}$$

The population per size class was estimated as:

$$qN_l = \left[\frac{\sum_m \left(C_{l,m} E_m P_m S_{l,m}\right)^{\beta}}{\sum_m \left(P_m E_m S_{l,m}\right)^{2\beta}}\right]^{\frac{1}{\beta}}. \tag{6.3}$$

Through this equation, the least-squares estimates for the *qNl's* were generated. Model parameters, the selection factor (*K*) and the variance structure (σ^2) were then estimated using solver by minimizing the least squares sum:

$$L_{sq} = \sum_m \sum_l \left[C_{m,l}^{\beta} - \left(E_m P_m S_{l,m} q N_l\right)^{\beta}\right]^2. \tag{6.4}$$

Since equal effort (*12hrs*) was used per mesh throughout the sampling regime and the fishing power was assumed to be equal among meshes, selection equation parameters P_m and E_m were ignored (Hovgårt & Lassen, 2000).

Per recruit analyses

Per recruit analyses explore the abundance of a cohort in numbers or weight as it is fished progressively over time in relation to the initial abundance of that cohort (Buxton, 1992). With these analyses, it is possible to make management recommendations without knowing the exact relationship between effort and fishing mortality (Booth & Buxton, 1997). Depending on management objectives, YPR may be used to determine management parameters such as: (1) The selection pattern of fishing gears that optimizes maximum yield per recruit for a given fishing rate; (2) fishing rate that optimizes yield per recruit for a given selection pattern; and (3) biological reference parameters (Chen *et al.*, 1998). Biological reference points are values used to manage a fish stock by establishing its status over a range of these values that are believed to be acceptable (Booth, 2004)

The important assumption of per-recruit analyses is that there is no variability in recruitment, growth and mortality from year to year and therefore the stock is in a steady state (Beverton & Holt, 1957). Under these asssumptions Yield Per Recruit (YPR) and Spawner Biomass Per Recruit (SBR) as a function of fishing mortality (F) were calculated as:

$$YPR_F = \frac{\sum_{a=0}^{\max} w_a S_a F \widetilde{N}_a \left[1 - e^{-(M+S_a F}\right]}{(M + S_a F)\Delta a} \qquad (6.5)$$

and

$$SBR_F = \sum_{a=0}^{\max} \psi_a w_a \widetilde{N}_a \Delta a \ , \tag{6.6}$$

where $\widetilde{N}_a$ is the relative proportion of fish at age *a* and is defined recursively as

$$\widetilde{N}_a = \begin{cases} 1 & if\ a = 0 \\ \widetilde{N}_{a-1^{e-(M+S_{a-1}F)}} & if\ 1 \le a < \max \\ \widetilde{N}_{\max-1^{e-(M+S_{\max-1}F)}} /(1-e^{-(M+S_{\max-1}F)}) & if\ a = \max \end{cases}$$

where S_a is the selectivity at age *a*, *F* is the instantaneous rate of fishing mortality on fully recruited cohorts, *M* is the instantaneous rate of natural mortality and *max* is the maximum recorded age (Weyl *et al.*, 2005). The weight at age was calculated as:

$$W_a = q(l_a)^b \tag{6.7}$$

where l_a is the length-at-age determined from the von Bertalanffy growth equation and *a* and *b* are the parameters describing the length-weight relationship (Weyl *et al.*, 2005).

Input parameters

The fishery parameters, maximum age at selection (t_r) and the variance of age at selection (σ^2_{tr}) were estimated from the back-transformed von Bertalanffy growth function and fitting a normal selection curve to the observed probability of capture at age for the specific mesh size using non-linear least squares regression. Biological parameters obtained from Chapter 4 and 5, and the fishery selectivity parameters estimated from this chapter were used as input for the model. These parameters are summarised in Table 6.2.

TABLE 6.2. Biological and fishery parameters used as input for the application of yield and spawner *biomass* per recruit models on *C. gariepinus* from the Okavango Delta, Botswana

Parameter	*Estimate*
L_{∞} (asymptotic length) (mm TL)	10000
K (Brody growth coefficient) (y^{-1})	0.002
t_0 (age at zero length) (y)	-18.75
a (length-weight parameter) (mm)	0.000011
b (length-weight parameter) (g mm^{-1})	2.9
ψ (age at 50% maturity) (y)	1
δ_{ψ} (inverse rate of maturity curve) (mm y^{-1})	0.1- knife edged
t_r (maximum age at selection) (y)	2.88 (93 mm); 0 (73 mm); 7.52 (118 mm)
σ^{2}_{tr} (variance of t_r) (y^{-1})	1.9 (93 mm); 1.26 (73 mm); 2.63 (118 mm)
M (natural mortality rate) (y^{-1})	0.20 (range: 0.12-0.28)
Z (y^{-1})	0.25
max(maximum age in the population) (y)	15

Biological Reference Points

Five biological reference points were investigated:

(1) F_{max} - fishing mortality that results in the maximum yield

(2) $F_{0.1}$ - the fishing mortality rate at which the slope of the yield per recruit curve is 10% of the slope at the origin

(3) $F_{0.2}$ - the fishing mortality rate at which the slope of the yield per recruit curve is 20% of the slope at the origin.

The $F_{0.1}$ and $F_{0.2}$ reference points are considered to be more conservative than the traditional F_{MSY} (Hilborn & Walters, 1992; Haddon, 2001)

(4) F_{SB40} - the fishing mortality that results in reduction of SBR to 40% of pristine levels.

(5) F_{SB30} - the fishing mortality that results in reduction of SBR to 30% of pristine levels.

Richardson *et al.* (2009) and McCafferty (2009) investigated F_{SB40} and F_{SB30} for *C. gariepinus* and considered them adequate limit reference points for the species. Moreover, Richardson *et al.* (2009) hypothesised that if SBR is reduced to below 30% of pristine levels the stock runs a high risk of reproductive failure.

6.3. RESULTS

Gill net fishing efficiency

CPUE was low (< 0.2 kg/ mesh/ set) for mesh sizes smaller than 57 mm (Fig 6.2). From the 57 mm mesh size, CPUE increased with mesh size to a maximum of 1.4 kg/ mesh/ set in the 93 mm mesh then decreased to 0.7 kg/ mesh/ set in the 150 mm mesh size. The 93 mm and 118 mm mesh sizes were therefore considered most efficient. Of the 1050 *C. gariepinus* caught, these mesh sizes accounted for 44.5 % and 21.8 % of the total catch respectively.

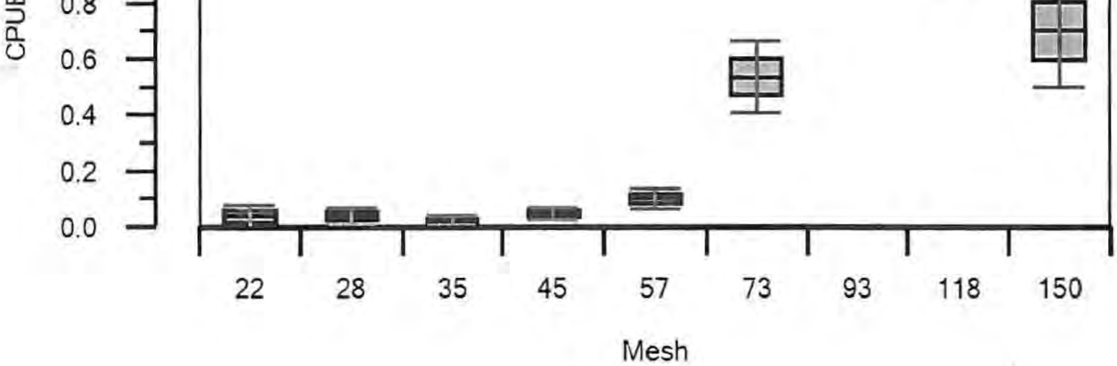

FIG. 6.2. Catch rates (kg)/ mesh/ set of *C. gariepinus* from the different mesh sizes of the brown nets in the Okavango Delta, Botswana. Four mesh sizes (73 mm, 93 mm, 118 mm and 150 mm) show marked fishing efficiency with mesh 93 mm producing the highest catch per set. (Data was provided by the Department of Wildlife and National Parks- Fisheries Division for the period 2001-2009). 1050 fish were caught out of 3126 net settings. S.E = Standard error.

Gill net selectivity

Parameter estimates (standard deviation σ and the selection factor, *K*) for the log normal selection model fitted to brown nets assuming Poisson distributed errors are shown in Table 6.3. Fig 6.3 shows the model fit to the data. Selectivity curves for the mesh sizes 35 mm, 45 mm, 57 mm, 73 mm, 93 mm, 118 mm and 150 mm are illustrated in Fig. 6.3 (b) with peak relative selectivities found at 190 mm, 240 mm, 310 mm, 390 mm, 500 mm, 640 mm and 810 mm (L_T) for each mesh size respectively.

TABLE 6.3. Parameters for the lognormal selection curve (the standard deviation, σ and the selection factor *K*) fitted to brown nets are shown. The Sum of squared residuals can be used as an indication how good the model fits the data with relation to other models fitted to the same data which was not done in this study.

Parameter	*Estimate*	*Sum of squared residuals*
σ	0.124	
K	0.54	170.65
β	0.5 (for Poisson distributed errors)	

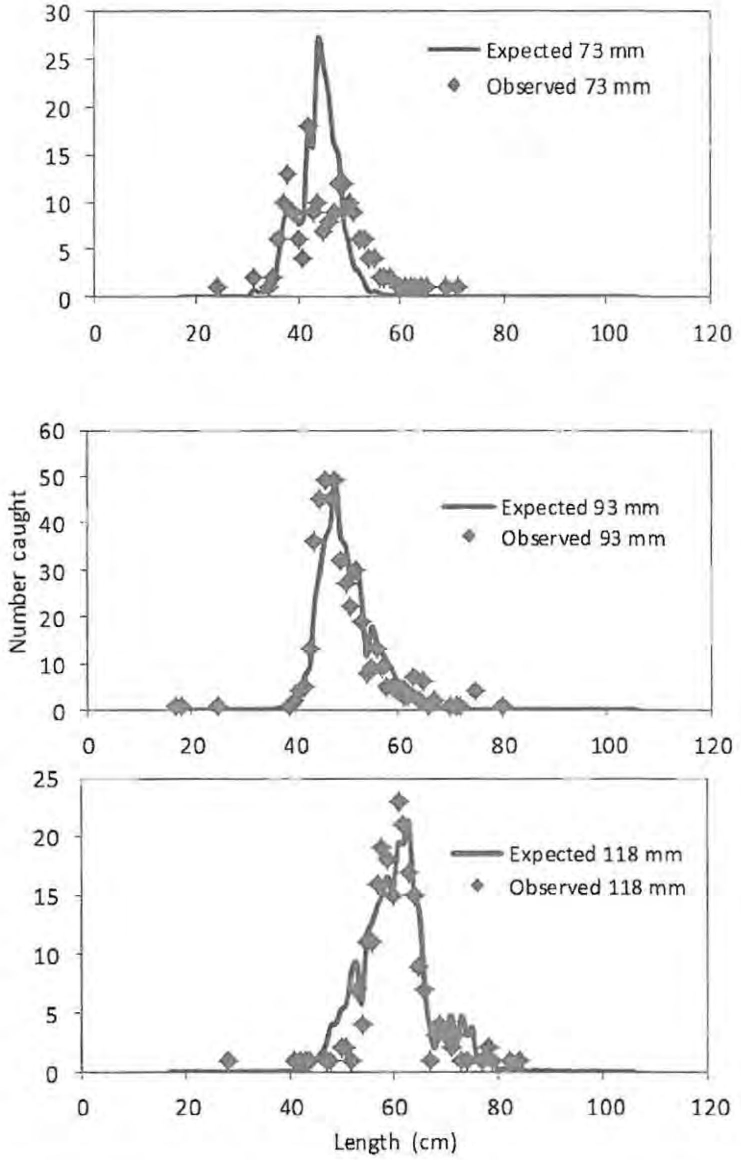

FIG. 6.3. Observed and expected catches of *C. gariepinus* in three mesh sizes of the brown nets (73 mm, 93 mm and 118 mm) that had n>100 catch

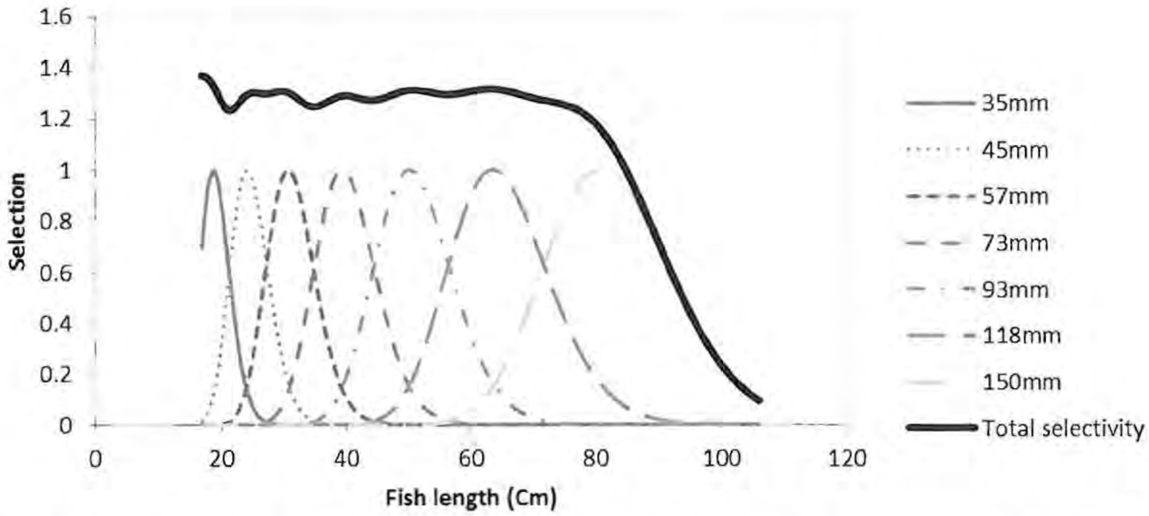

FIG 6.4. Selectivity curves for the mesh sizes (35 mm-150 mm). The thick black line represents total selection for all meshes combined

Per- recruit analyses

The isopleth diagram showing the response of yield per recruit to different fishing mortality rates and age at 50% selection is shown in Fig 6.4. In Fig 6.5, the response of yield per recruit to different fishing mortality rates is illustrated for mesh 73 mm, 93 mm and 118 mm which select at ages of 0, 2.88 and 7.52 years respectively. YPR was maximised when *C. gariepinus* were selected at ages younger than 2.5 years. At harvest ages of less than 2 years, SBR was quickly reduced to below the F_{SB40} BRP. Using 73 mm and 93 mm mesh sizes allowed for YPR to be maximised but at a high risk of stock collapse. The use of gill nets with a mesh size of 118 mm did not result in the reduction of SBR to below 40% of pristine levels at any fishing mortality rate (Fig 6.5). At the age of selection corresponding to the 118 mm mesh YPR was relatively low. From an SBR perspective, the 118 mm mesh would be the most appropriate for the *C. gariepinus* fishery.

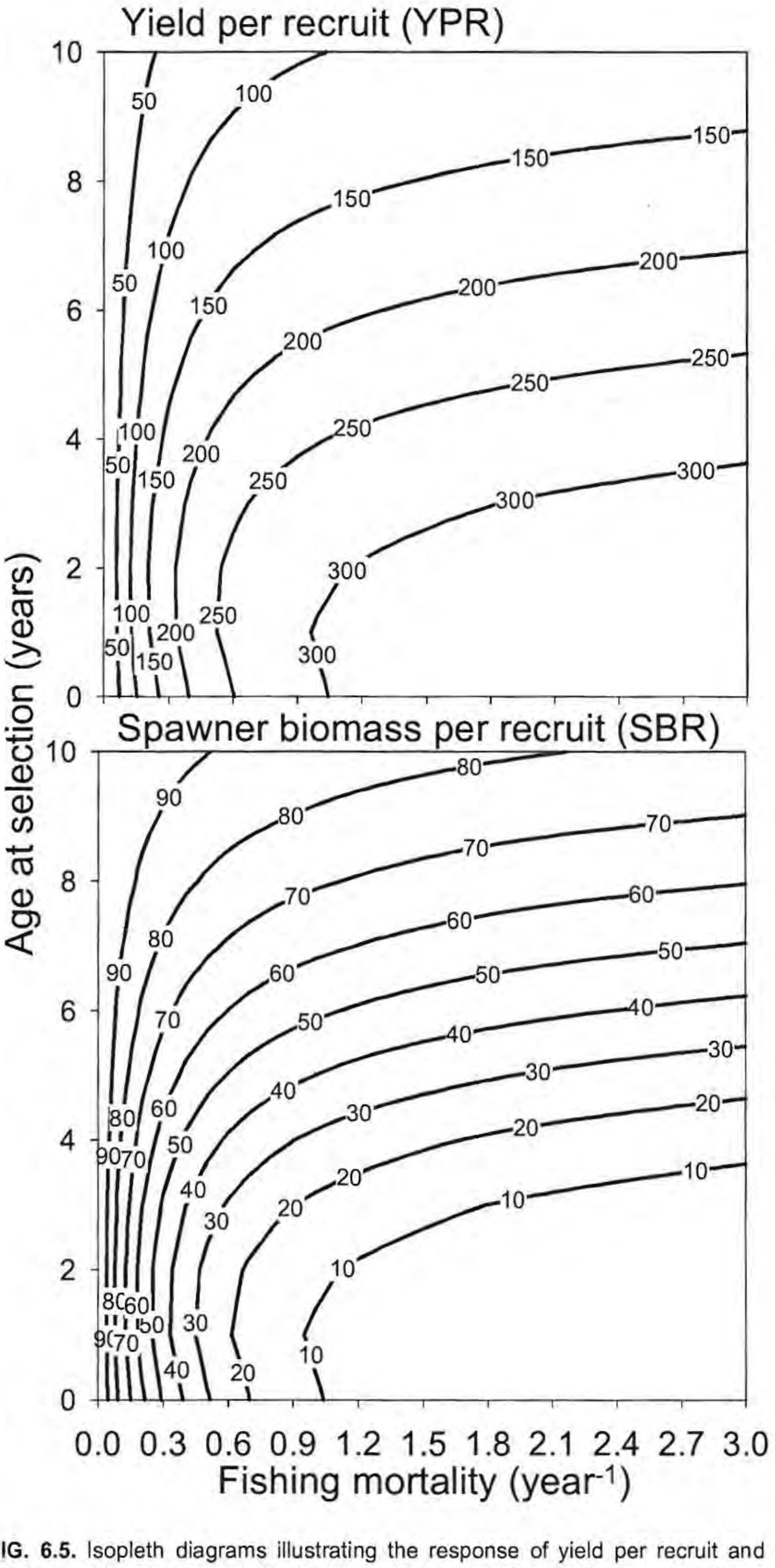

FIG. 6.5. Isopleth diagrams illustrating the response of yield per recruit and spawner biomass per recruit for *Clarias gariepinus* from the Okavango Delta to different fishing mortalities and age at 50% selection. The simulation was performed at a natural mortality rate of 0.2 yr $^{-1}$.

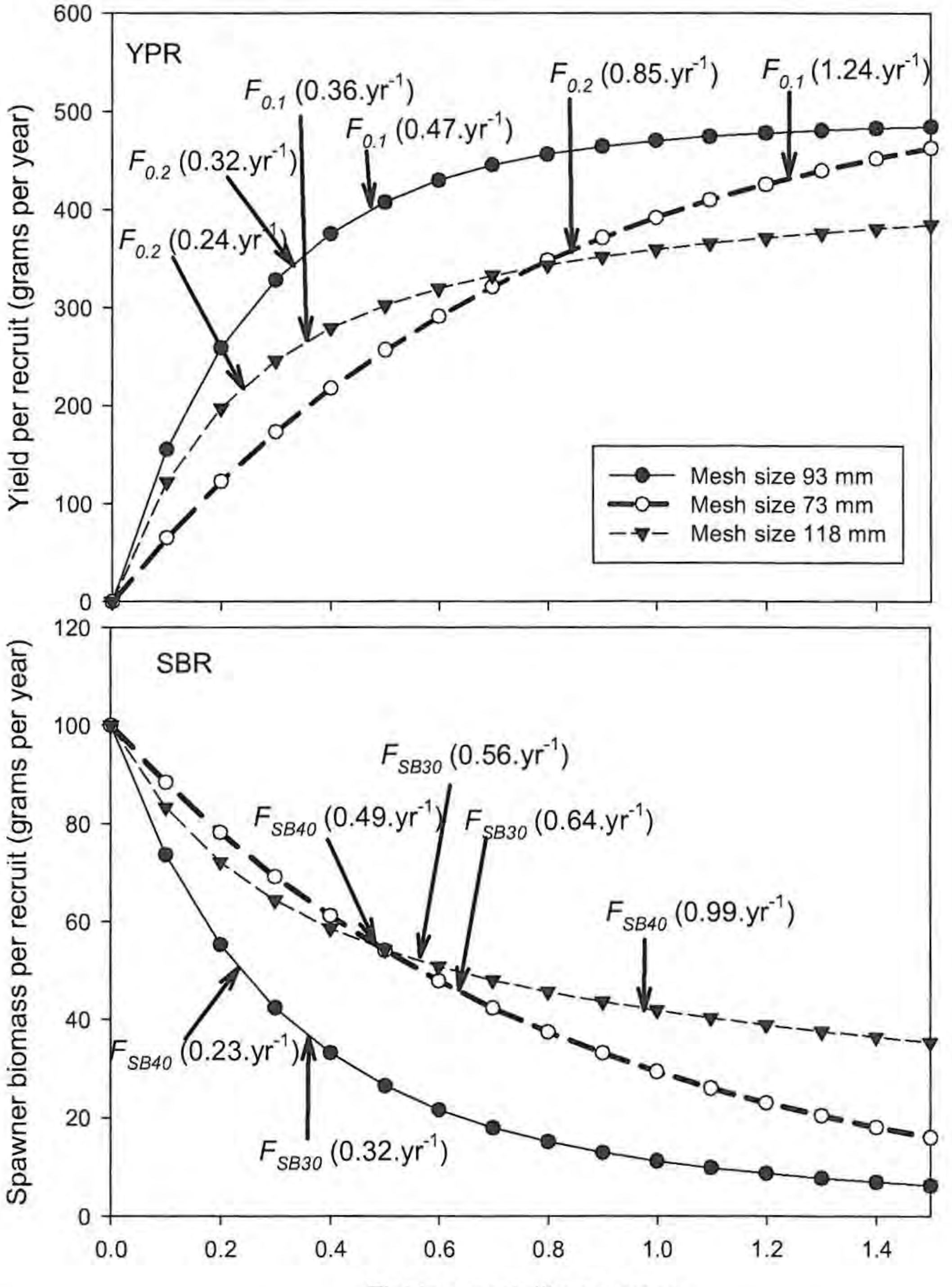

Fig 6.6. The response of yield per recruit and spawner biomass per recruit for *Clarias gariepinus* in the Okavango Delta, Botswana. Analysis was conducted for mesh sizes 73 mm, 93 mm and 118 mm, which select at 0, 2.88 and 7.52 years respectively. Point estimates of five reference points are shown in parenthesis.

Sensitivity analysis

Since the instantaneous rate of natural mortality is generally a difficult parameter to estimate (Weyl *et al.* 2005), sensitivity analysis (Majkowski, 1982; King, 1995) was conducted using a range of natural mortality values obtained from the equations of Pauly (1980), Hoening (1983) and the average of the two estimates. The analysis was conducted at a selectivity of 2.88 years. Change in *M* resulted in marked change in YPR. Low *M* produced higher YPR while high *M* produced low YPR (Fig. 6.6). Increased *M* resulted in accelerated depletion of SBR. The range of all BRPs for the different *M* scenarios is presented in Table 6.4. Irrespective of mortality level, all the BRPs were considerably higher than the estimated current fishing mortality of $F = 0.05\ y^{-1}$.

The fishery could therefore be at least doubled before the most conservative BRP (F_{SB40}) would be attained and the fishery could be increased 6 times before reaching the F_{SB30} BRP.

TABLE 6.4. Estimates of Biological reference points for *Clarias gariepinus* from the Okavango Delta under different natural mortality rates. Analysis was conducted at a selectivity of 2.88 years.

M	F_{cur}	$F_{0.1}$	$F_{0.2}$	F_{max}	F_{SB40}	F_{SB30}
0.12	0.13	0.50	0.35	1.23	0.25	0.34
0.20	0.05	0.58	0.40	3.06	0.29	0.39
0.28	0	0.69	0.45	4.80	0.33	0.46

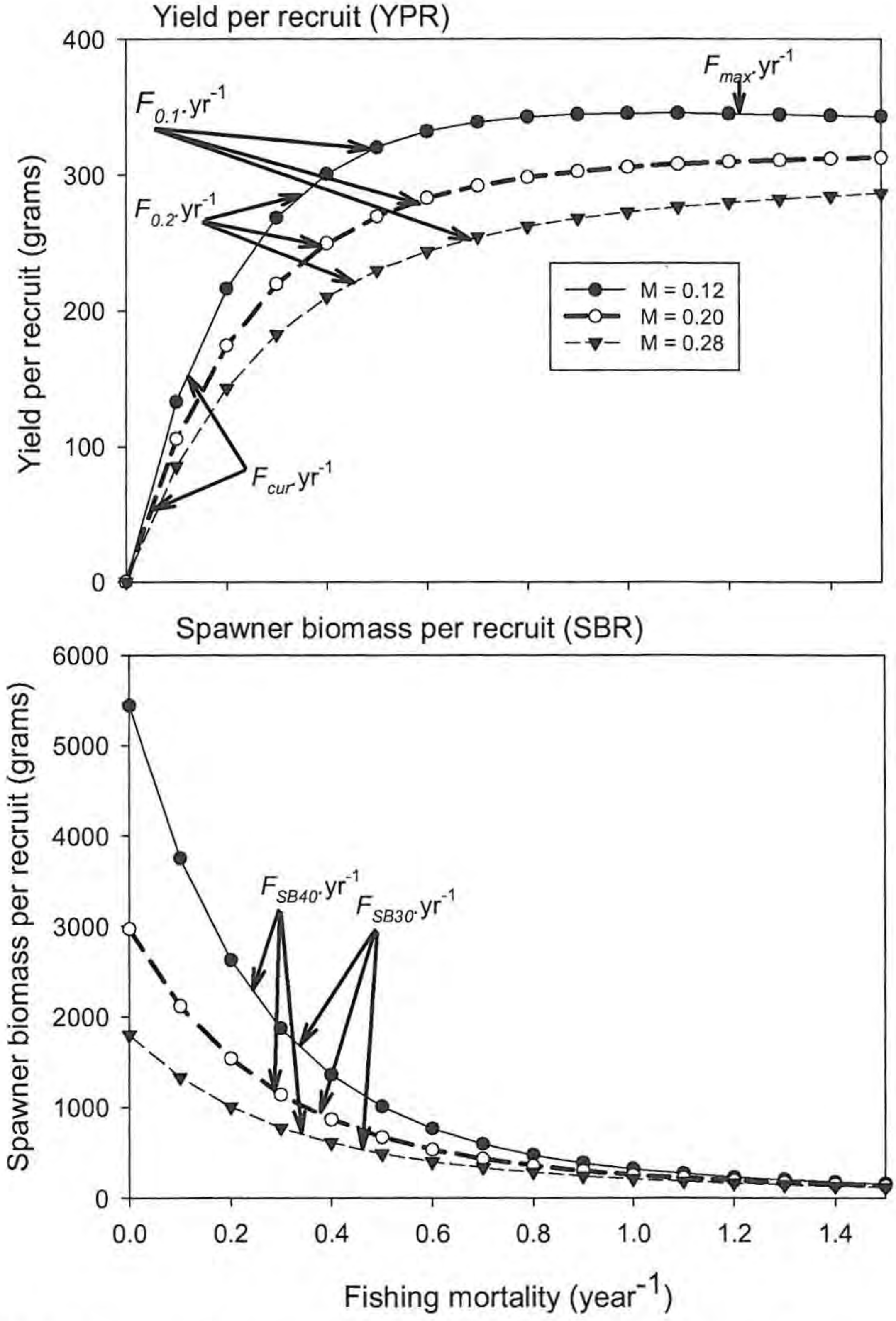

FIG. 6.6. Yield per recruit and spawner biomass per recruit for *Clarias gariepinus* from the Okavango Delta at different rates of fishing mortality under different levels of natural mortality. Age at capture was fixed at 2.88 years mimicking the harvesting pattern of the 93 mm gill net. Point estimates for $F_{0.1}$, $F_{0.2}$, F_{max}, F_{SB40} and F_{SB30} harvesting strategies are shown.

6.4. DISCUSSION

The commercial fishery in the Okavango Delta was established in the late 1980's (Shipton, 2011). Since that time, the fishery has been open access. Even though the Fisheries Act has been in place since 1975, it could not be implemented due to lack of supporting regulations. In 2008, the fisheries regulations were gazetted (Shipton, 2011). These regulations are only targeting commercial fishers while subsistence fishers are not regulated. In the regulations, a commercial fisher is equivocally defined as anybody who uses a factory made gill net. Therefore from the fishery exploitation perspective, the purpose of these regulations is to limit gill net effort. However, there is no mesh size regulation. This allows for harvesting of all size and age ranges of all species. This management strategy is touted as appropriate in a dynamic multi species fishery because it allows for harvesting of a resource that would otherwise not be utilized, thus optimizing yield while maintaining the ecosystem structure (Kolding & Zwieten, 2006; Shipton, 2011).

Data from the commercial gill net fishery collected between 1996 and 2005 indicates that large catfishes (*C. gariepinus and C. ngamensis*) are harvested as by-catch and constitute a considerable proportion of the total catch. This observation is corroborated by CPUE from the experimental gill nets which indicated that *C. gariepinus* was the most abundant species in the Okavango Delta (Table 3.2, Chapter 3) making up 37.39 % of the catch composition by fresh weight. At the estimated current fishing mortality rate, SBR was ≥ 90% of pristine levels. *Clarias gariepinus* population can therefore be categorised as lightly exploited to unexploited, warranting assessment for potential establishment of a directed commercial fishery.

Per recruit analyses indicate that to reach F_{SB40} the current fishing mortality can be doubled at $M = 0.12$, increased 6 times at $M = 0.20$ and increased infinitely at $M = 0.28$. Therefore there is ample room for expansion of the fishery. This agrees with Mosepele (2000) who could estimate MSY only for *Oreochromis andersonii*, *Tilapia rendalli* and *Serranochromis robustus*. For the rest of the species, including large catfishes, MSY could not be reached and Mosepele (2000) concluded that the stocks were underutilized.

Evidence from experimental gill net surveys indicates that mesh 118 mm maintains SBR at levels higher than 40% of pristine levels even at very high fishing mortality rates. However, maximum YPR could not be attained with this mesh size because it selects for old fish. Bokhutlo *et al.* (2007) postulated that overfishing in the Okavango Delta was localised with replenishment invariably occurring from other parts of the system that are not accessible to fishers. In addition, large parts of the Delta are in protected areas where fishing is prohibited (Fig 6.7). Therefore the protected population could replenish the exploited population. Therefore to maximise YPR, a mesh size of 93 mm, which selects at 2.88 years may be used in the early stages of the new fishery with close monitoring of the response of the stock as the fishery develops.

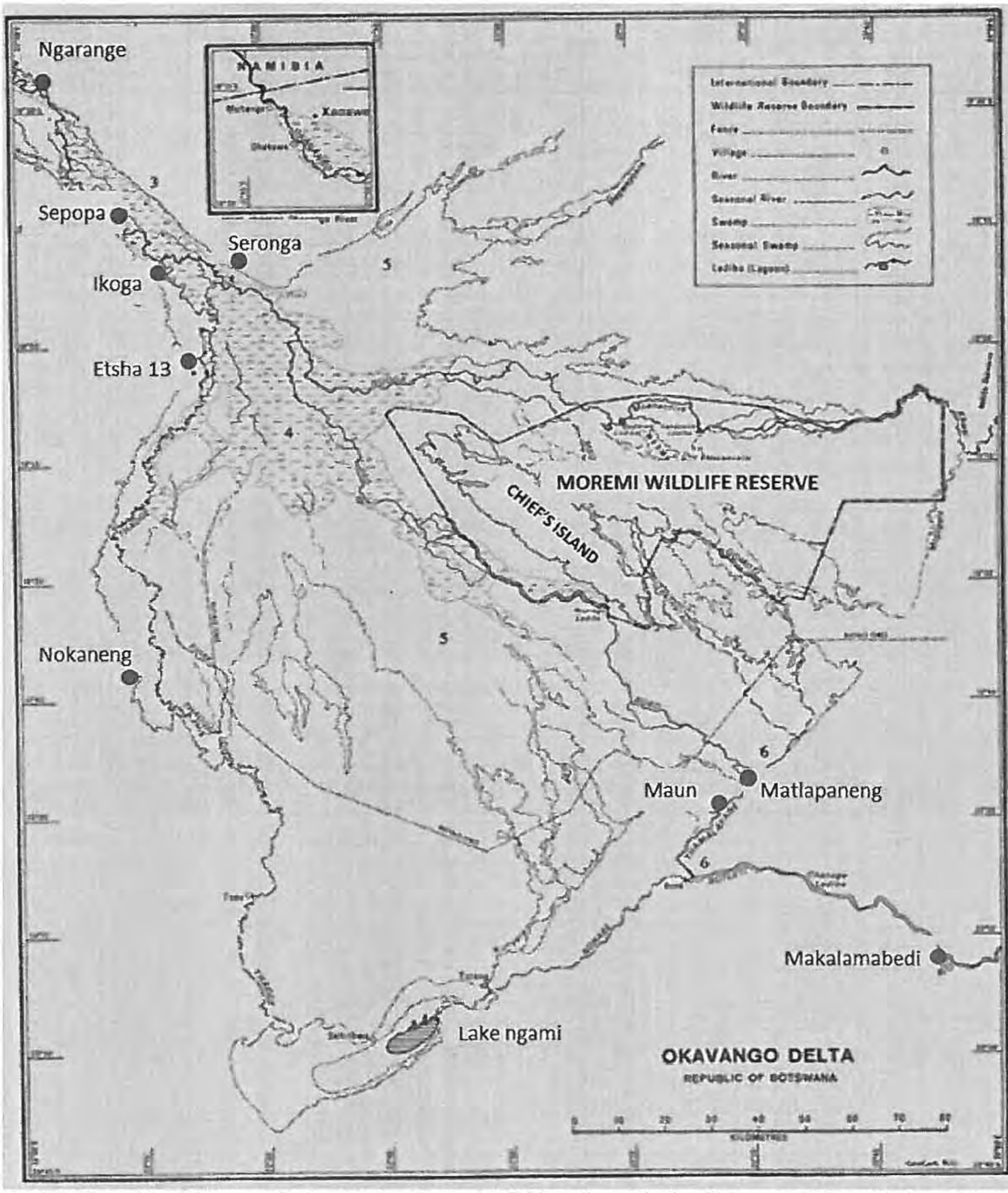

Fig 6.7. Map of the Okavango Delta showing the major fishing villages in the Okavango Delta and Moremi Game reserve (a protected area) covering almost a 1/3 of the Delta's surface area (source: Mosepele, 2000). Fishing is not allowed in Moremi Game reserve and this offers an important refuge for fish biomass which can repopulate exploited habitats.

In conclusion, Per-recruit analyses indicate that the population of *C. gariepinus* in the Okavango Delta is underutilized and forms a potential resource for establishment of a viable commercial fishery. Mesh 93 mm is the most efficient in capturing this species and produces the highest YPR at low fishing mortality rates while selecting fish after maturity. Therefore even though this mesh size could result in recruitment overfishing at very high effort levels, it should be used to optimise yield. This is because large portions of the Okavango Delta are currently not accessible to fishers and large portions of the stock are likely to be protected. In this manner, the fishery is likely to self-regulate as long as the spatial refugia for the adult population are maintained. The most commonly used mesh size in the gill net fishery is currently 100 mm (Chapter 1). Since the 100 mm mesh size harvesting strategy approximates that of mesh 93 mm, recommendations for the 93 mm mesh size are therefore valid for the fishery. It is also important to note that in multispecies fisheries, management may need to focus on the less resilient species such as the cichlids. Finally, developing a catfish based gill net fishery would fall under the current legislation.

CHAPTER 7

GENERAL DISCUSSION AND MANAGEMENT RECOMMENDATIONS FOR THE *C. GARIEPINUS* FISHERY IN THE OKAVANGO DELTA, BOTSWANA.

With regard to the status of inland waters and their species, the media and conservation groups have accorded little attention to the threats facing freshwater fisheries and associated biodiversity (Allan *et al.*, 2005). According to Winemiller & Jepson (1998), tropical rivers and their associated floodplains are dynamic habitat mosaics to which fishes are challenged to respond in an adaptive manner. There are also schools of thought that purport that floodplain fisheries cannot be overexploited (Ahmed, 2008; Abbot & Campbell, 2009). The argument is based on the inherent variability of the floodplain environment which defies the simple diagnosis of over fishing based on changes in effort and methods or livelihood (Abbot & Campbell, 2009). Other reasons (not overexploitation) have been suggested for the decline of fish populations in fresh water bodies. For instance, Kolding *et al.* (2008) posit that in Lake Victoria, continued eutrophication presents a much graver risk to the resource base than fishing pressure while Pitcher &Pauly (1998) argue that sustainability in fishery management is a deceptive goal.

These intriguing and dichotomous viewpoints serve as a reference point for the need to manage fresh water fisheries, especially floodplain fisheries with insights drawn from sound empirical data. Moreover, our understanding of naturally functioning river-floodplain ecosystems leaves much to be desired (Bayley, 1995). For these reasons, continued monitoring and assessment of floodplain fisheries are essential.

The Okavango Delta fishery is multispecies and multi gear, representing an intricate mosaic of the interaction between different harvesting regimes. The fishery comprises of three major sectors: (1) the commercial fishery, which uses factory made gill nets; (2) the subsistence fishery which uses traditional gear such as fishing baskets and (3) the recreational fishery which uses hook and line (Mosepele, 2000, 2001; Bokhutlo *et al.*, 2007; Shipton, 2011). This makes it difficult to assess the impact of exploitation on the status of fish stocks in the short to medium term. From a socio-economic perspective, the three fisheries are prone to conflicts due to the limited accessible fishing grounds and different objectives pertaining to realized benefits from the resource (see Chapter 1). Therefore management should be aimed at minimizing conflicts while maximizing sustainable benefits for all fisher groups.

From a biological perspective, management of such a fishery is by no means trivial due to the confounding effects brought about by the unpredictability and the fluctuating nature of the floodplain environment. Fish population abundance varies from year to year depending on the timing and magnitude of the flood pulse (Chapter 3).

Life-history strategies of *C. gariepinus* from the Okavango Delta (Chapter 4 & 5) failed to fit the conventional r-K continuum of Pianka (1970). Similar observations were made in Lake Malawi by Kaunda (2002) for *Bathyclarias nyasensis* which is closely related to *C. gariepinus*. Kaunda (2002) observed that *B. nyasensis* was more compliant with the periodic life-history style suggested by Winemiller & Rose (1992). However, in the Okavango Delta, *C. gariepinus* did not fit the periodic life history style entirely. The population demonstrated an overlap between the opportunistic and periodic life-history styles. The species is relatively large, matures early at a medium size with high fecundity and a small egg size (Bruton, 1977). Juvenile growth is rapid, the reproductive season is long (Chapter 4 & 5) and there is no parental care (Bruton, 1977). Kolding & Zwieten, (2006) suggest that primary management strategies for such life-history traits should be geared towards maintaining critical spawning biomass and appropriate age structure while protecting the species against prolonged disturbances that occur on a large scale.

The present study showed that *C. gariepinus* was the second most abundant species in the commercial gill net fishery. This resource appears underutilized from a per-recruit perspective (Chapter 6). It can therefore be concluded that the species could support increased effort in the commercial gill net fishery. With respect to *C. gariepinus*, the development of this fishery can proceed under the current management regime and there is no need to regulate current mesh size because the species is recruited into the population at a medium size, after maturity. This implies that chances of growth overfishing are low. Moreover, the efficiency of smaller mesh sizes in capturing *C. gariepinus* was very low (Chapter 6). The current closed season over January and February coincides with the peak breeding season for *C. gariepinus* (Chapter 4) and therefore it is relevant for this species.

Catch rates of *C. gariepinus* in the Okavango Delta have been shown to increase during the drawdown period between July and November. This coincides with the annual pack-hunting event (Merron, 1993). It has been hypothesized (Chapter 5) that among other things, pack-hunting may be a preparatory activity for gonadal recrudescence prior to spawning in the upper Delta when the floods arrive. Therefore, all individuals taking part in this event are adults that may comprise the spawner biomass of this species. For this reason, it would be prudent to prevent harvest of this species during this time because recruitment overfishing may occur due to increased vulnerability of the spawner biomass to gill net capture during mass aggregation and increased foraging movement. *Labeo cylindricus* exhibits a similar predictable aggregation behavior prior to spawning in Lake Chikamba, Mozambique and Booth & Weyl (2004) warn that harvesting the species during this time could lead to considerable reduction of spawner biomass each year

The feeding run is a major tourist attraction to the Okavango Delta and it should continue to be promoted as such. Commercial gill net fishing, if allowed over this period, may conflict with recreational angling. Commercial gill net fishing should therefore be prohibited in the main channel and this should only apply for the duration of the feeding run which may vary from year to year. Therefore this should not be confused with the current closed season which protects not only *C. gariepinus* but also other target species in the fishery such as *H. vittatus* and the large cichlids such as *O. andersonii*, *T. rendalli* and *S. robustus*.

At present, the Okavango Delta has large portions that are not accessible to fishers. As a result management should be directed towards maintaining the status quo because these areas act as refuges on a spatial scale. Closed areas have been used successfully in temperate marine systems (Murawski, 2000). Gell & Roberts (2003) suggest that this management style is the most conservative and could reverse the global fisheries declines while protecting marine species and their habitats. At the local scale, management could adapt rotational harvest strategy (Hilborn & Walters, 1992). With this strategy, fishers would be allowed to fish a particular area hard until the stocks are locally depleted after which they would move to another area that had previously not been fished thus allowing the depleted area to recuperate. Close monitoring will be necessary to assess how "elastic" the fishery can be for maintenance of spawning biomass at appropriate levels. However, the designated areas for rotational harvesting should not be those shared with subsistence fishers or those that are easily accessible by traditional dugout canoes. This will ensure protection of subsistence fishers' livelihoods.

It is of paramount importance to note that these management recommendations are tentative. Therefore emphasis is directed towards monitoring with a proper research design to accrue sufficient data of the right type. This would allow for mutability of management strategies as the fishery develops. Initially, regular catch assessment surveys (monthly) may be conducted at the major landing sites to collect biological and fishery data from the commercial gill net fishery. These surveys are cheaper than the experimental gill net surveys and information is obtained directly from the fishery. The intensity of the surveys may be reduced as more insight is gained from the periodic assessments. However, experimental gill net fishing should continue parallel to these surveys. The single species approach used in this study does not take into account the impact of this fishery on cichlids. Therefore comprehensive separate stock assessments will be necessary in future so that multispecies interactions can be included in the management framework.

Recommendations for future research

While the current study provided insight into the life history of *C. gariepinus*, there are still some considerable knowledge gaps. Another research into the reproductive biology and age and growth is necessary. During the assessment of age and growth, it was found that the conventional VBGF could not adequately describe the growth of *C. gariepinus* in the Okavango Delta (Chapter 5). This was most likely a result of the spatial and temporal variability of the floodplain habitat which results in fish of the same age experiencing different environmental conditions and resource availability which subsequently results in different growth rates. For highly mobile species such as *C. gariepinus*, fish from the different micro habitats are constantly mixing. To improve estimates of growth parameters it is recommended that sampling should be directed towards increasing the sample size for all age classes, particularly juvenile fish so that a full range of sizes and ages is assessed. A larger sample size may enable the VBGF model to converge to biologically reasonable asymptotic lengths. Moreover, the migration of *C. gariepinus* should be studied to establish the distance covered by the species during the feeding run.

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