The effects of natural disturbances on the Nile crocodile (*Crocodylus niloticus*) in the Mutale River, Limpopo Province

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Introduction

Natural disturbances such as flooding, result in a cascade of physical processes such as erosion, sediment deposition and associated changes of both aquatic and riparian organisms in their habitats (Swanson et al., 1998). Species-specific traits and substrate characteristics including heterogeneity and stability, dictate biotic responses to patch disturbance in a stream (Holomuzki & Biggs, 2000, 2003; Olsen et al., 2007; Townsend et al., 1997). Though regional populations of fauna adapt to the local prevailing climate through physiological and behavioural responses (McMichael et al., 2006), extreme events often stress populations beyond these limits. A variety of aquatic species are thought to be at risk as their ability to adapt through natural selection is limited and because anthropogenic alterations to the environment reduce the dispersal and migration potential of organisms, limiting their ability to find suitable habitat (Angeler, 2007). Moreover, synchronization between life-cycle events and seasonal changes in habitats may be disrupted (Harper & Peckarsky 2006; Winder & Schindler 2004), limiting the ability of organisms to reproduce and persist in the face of climate change.

Freshwater ecosystems are vulnerable to climate change (Alvarez-Cobelas et al., 2005; Carpenter et al., 1992; Firth & Fisher 1992, Magnuson et al., 1997; Lake et al., 2000; Lodge, 2001; McCarthy et al., 2001; Poff et al., 2002; Schindler, 2001; Kundzewicz et al., 2008; Woodward et al., 2010). Global Change Models (GCMs) indicate an anticipated increase in the frequency and severity in extreme weather events such as droughts and flooding (Collier et al., 2008; McMichael et al., 2006). In 2003, the Department of Agriculture indicated that South African rivers are already frequently affected by erratic and unpredictable climatic extremes such as drought and flooding (M'Marete, 2003) and increases in these events would result in heightened flood risk. In the context of my dissertation, flood risk is defined as the combination of the probability of a flood event and its negative consequences. The latter is a function of flood

intensity, exposure and vulnerability of the system to flooding (Angeler, 2007). Worst-case scenarios of climate change depict increased extinction rates and loss of biodiversity resulting from physiological stress, interactions with invading species, habitat conversion and habitat loss (Hughes 2000; Root et al. 2003; Thomas et al. 2004; Vitousek 1994;). Increases in flooding and associated changes in the riverine habitat could result in the reduction or degradation of suitable terrestrial and aquatic habitat being available to Nile crocodiles (*Crocodylus niloticus*). Flooding has been shown to result in direct mortality of crocodile eggs (Magnusson, 1982) and the resultant rise in nest failure, if compounded by decreases in habitat availability, would increase the vulnerability of crocodiles to the effects of climate change.

Excessive alteration of the Mutale catchment occurred in 2000 when high rainfall in Mozambique and the north eastern region of South Africa resulted in flooding of large areas in Limpopo Province (Christie & Halon, 2001). The Mutale River, was altered from a narrow, deep river associated with a gorge and a riparian area, to a flat, shallow river with a multitude of small pools and limited riparian forest growth (pers comm. Bunn, 2012; pers comm. Allan, 2012; Pearcy, *unpublished*). Despite the low likelihood of such an event occurring on multiple occasions in a short time-span, flooding in January 2013 further flattened the Mutale River and altered the river channel while shifting large amounts of sediment downstream (pers. obs.). These changes in channel morphology, and the possibility of increased frequency of floods of this magnitude is likely to result in the degradation of habitat available to Nile crocodiles and may also have cascading effects on water quality.

Rationale

The floods of 2000 and 2013 in the Mutale River resulted in shifts in the locations of optimal crocodile nesting habitat availability and sheltered pools and runs suitable for crèches available to the Nile crocodile (Pearcy*, unpublished*). By investigating the extent and the subsequent effects of flooding, I sought to supplement current knowledge on flooding effects on river quality, including crocodile abundance and distribution outside of a protected area. The emerging patterns can then be used by future studies to model the impacts of flooding on small riverine systems. In addition, the regular collection of river quality data and crocodile population demographics can serve as a useful tool in monitoring river health in this region.

Aims

The aims of my study were fourfold: 1) to investigate changes in river quality, including physiochemical variables such as pH, water temperature and turbidity, as well water quality measured by the South African Scoring System (SASS5) rapid Bioassessment method, 2) to examine pre- and post-flood changes in the riverine landscape, including rapid habit assessments of available habitat to the Nile crocodile and the potential (indirect) effects of land-use change, 3) to assess the abundance of crocodiles and their nests in subsections of the Mutale River and 4) to compare these results to changes in the crocodile population to better understand the overall impact of natural disturbances on the riverine environment. River quality variables were anticipated to fluctuate between seasons, due to changes in insolation and the associate effects of shifts in temperature and water availability (Palmer and Poff, 1997). Land use change effects were hypothesized to increase sandbank presence due to sediment depostion, though these effects could have been curtailed due to seasonal shifts in deposition (Allan, 2006). As the population of crocodiles in the Mutale river occurs outside a protected area, decreases in the population size were anticipated (Pollard et al., 2011).

Methods

Study site

The primary study site for the intermediate and small scale data collection was located in Hamakuya, a cluster of 19 villages in the rural Thulamela Local Municipality of the Vhembe District in Limpopo Province. Sample collections took place from Lamvi, a 7 km section upstream of a 3 km, inaccessible gorge. Collections continued 8 km below the gorge, upstream of the research base (Tshulu, Fig. 11), and 8 km below the gorge, downstream of the base (Fig. 11). Sampling was limited to this area, which is accessible on foot. The gorge itself is not frequently utilized by villagers from the surrounding areas as there is little or no grazing available for livestock and the banks of the river are not suitable for farming. Fishnets observed in the lower stretches of the gorge indicate that it is at least partly utilized and as one moves

away from the gorge, both further up and down-stream, there is a progressive increase in the exposure to direct anthropogenic alterations of the environment.

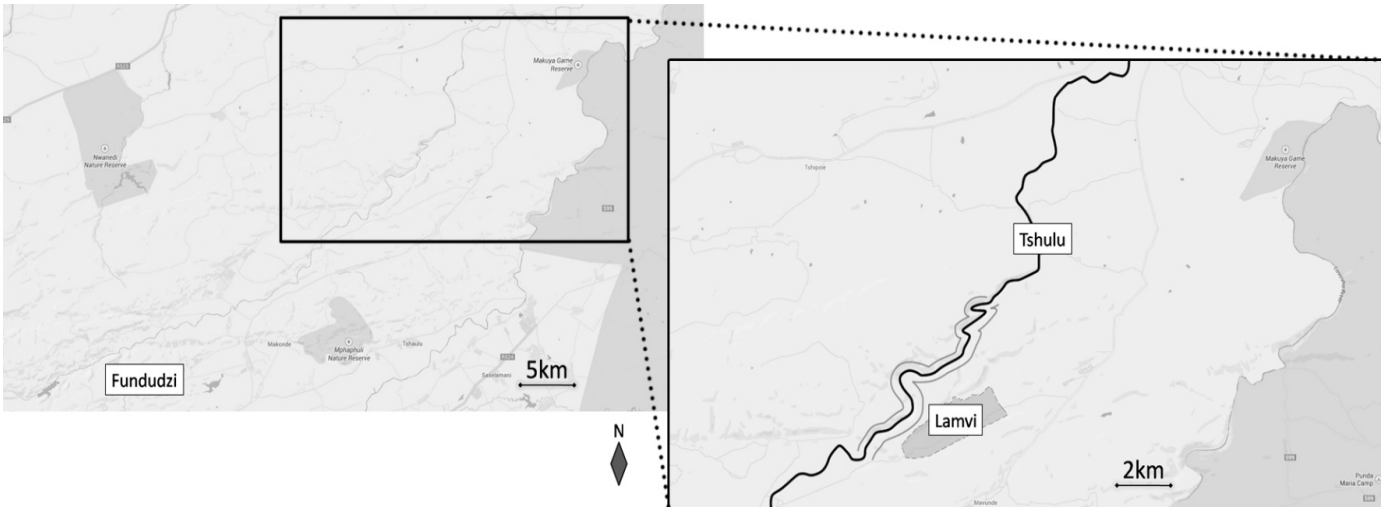


Figure 11: Sections of the Mutale River, Limpopo, covered in seasonal surveys and pre- and post-flood, intermediate and small scale surveys. Surveys and samples were performed along the portrayed section of the river (indicated in black), excluding the three kilometre gorge (indicated in grey).

Study Design

The methods described below are the same as those used in studies conducted in December 2011, March 2012, October 2012, December 2012 (pre-flood) and March 2013, June 2013, October 2013 and April 2014 (post-flood), in a 23 km subsection of the river. Data were available for a two and a half year period, for the winter and summer seasons. These data were used to compare river quality by indicating 1) crocodile presence, 2) The river quality, assessed using the South African Scoring System (SASS) Version 5 Rapid Bioassessment Method (Dickens & Graham, 2010), 3) changes in the riverine habitat (using rapid habitat assessments) with particular attention to crocodile nesting and potential crèche habitat, and 4) the combined effects of water quality, habitat availability and changes in land-use on the Nile crocodile.

Crocodile surveys

Crocodile surveys were performed using night survey methods. Since crocodiles are active mostly at night, researchers walked along the river to locate crocodiles, starting 30-45 minutes after sunset. Crocodiles were detected based on their distinctive red-eye shine reflection and length of crocodile was estimated based on surrounding objects (e.g. rocks and reed beds). Where located, evidence of crocodile activity such as -slides and nests were also recorded. These assessments were repeated in January, March and October 2012 and in January and June 2013, and again in April 2014. This was done in order to evaluate the population size and demographics of crocodiles in the Mutale River after the January 2013 floods, as well as the effects of seasonality and potential intermediate and small-scale changes in river health and habitat availability. These were performed each night on the return journeys from sample collections (described below), or separately on the nights succeeding days where sampling did not occur.

Habitat Assessment

Habitat assessments were processed over a time-period of three days. Each morning, researchers walked upstream or downstream along the river, (as specified earlier and represented in Fig. 9; black line, excluding grey gorge areas). As they progressed along the bank of the river, the presence, position and length of predetermined habitat types (terrestrial and aquatic) were recorded for the north and south banks, and within the river channel. GPS co-ordinates for each change in habitat were recorded. The habitat types were categorized during the first data collection period (in 2011) and correlated with habitats that could be considered as valuable to crocodiles (such as sandy banks; found to be the primary nesting site for the Nile crocodile; Leslie & Spotila, 2001). Terrestrial habitat types included sand (with more than 70% coverage of sand), rocks (boulders and basking areas were included in this) and unusable areas (including gorge walls, cliff walls and any other areas that would otherwise be inaccessible to crocodiles). Overlap of habitat types was rare, but those which were observed, were recorded; e.g. sand banks interspersed with rock. Terrestrial habitat types recorded along the north and south banks were

limited to a distance of 7 m away from the river. A 7 m zone is the accepted distance from the river edge that crocodiles will lay eggs (Mabuwaya Foundation, 1993) and is the distance away from the water's edge that nests were located along the river. The presence of any exposed sand, rocks and reeds in the river was also included in habitat descriptions.

The distribution of Nile crocodiles of different life-stages is likely influenced by the size of pools and the rate of flow along the length of this river, as these factors impact the spatial distribution of prey items in the river (Palmer & Poff, 1997). Juveniles are likely to remain close to sections with relatively deep, slow moving water as these are ideal fish nurseries (Mosepele et al., 2009) and crocodiles of all sizes tend to actively avoid rapids (Hutton, 1989). As such, riverscaping data included the presence of rapids (white water), runs or pools.

Garmin BaseCamp (2012) was used to measure the lengths of the different habitat areas of the river by calculating the distances between the co-ordinates of the beginning and end point for each specific habitat type (both terrestrial and aquatic). These data were entered in Microsoft Excel (2013) and the proportion of each habitat type was calculated using the total length of distance travelled, compared with the actual distance for each habitat subsection, including overlaps of each individual habitat type.

Water quality

Physiochemical variables including measurements of water temperature, pH, velocity, turbidity, elevation, and depth were recorded every 500 m along the river, for January 2012, March 2012, October, 2012, March 2013, June 2013 and April, 2014. Water temperature was measured with a thermocouple thermometer and elevation with a Garmin GPS System (GPSmap 60CSx). Turbidity was assessed by counting the number of consecutively smaller dots (five) that could be seen through a clear plastic bottle filled with sample water. Velocity was measured by recording the time taken for a meter-long string attached to a water-soaked apple to fully extend. Using a tape-measure to find depth, three randomly selected points were measured as close to the middle of the river as possible. In some instances, it was not possible to wade out to the middle,

due to the presence of crocodiles or the depth of the water. This sometimes precluded us from doing totally random measures. Three macro-invertebrate community samples were collected every kilometre within each survey section of river, in March 2012, October 2012, March 2013, June 2013 and April 2014. For safety, these samples were collected in rapids since Nile crocodiles tend to avoid fast flowing water, but were otherwise collected according to SASS5 guidelines (Dickens & Graham, 2010). The collected taxa were identified using an invertebrate identification guide (Gerber & Gabriel 2002).

The river quality data were assessed using SASS5 Average Score Per Taxon (ASPT). This score was calculated for the samples of macro-invertebrates found in each site. ASPT was used, instead of SASS scores, as a conservative estimate of river quality (Dickens & Graham, 2010), especially since data from previous years were collected during times of varying flow. This allowed for comparison of data across the years with previously collected samples.

Data analysis

Night surveys of Nile crocodiles were analysed using two-sample T-tests in order to determine whether upstream and downstream populations were significantly different, as upstream areas were less frequently utilized by humans, due to the presence of the gorge and less arable farmland, as mentioned before. An Analysis of Variance (ANOVA) was used to test whether the number of crocodiles in each size class was significantly different between months (seasonal observations). In addition, the proportion of total crocodiles found in each habitat type was compared. Findings were assessed by calculating the relative importance of each habitat type, by dividing the relative abundance of crocodiles in each habitat type with the relative abundance of the habitat type, as per the calculation:

$$\frac{Pcroc}{Phab}$$

where $Pcroc$ refers to the proportion of crocodiles found in the habitat and $Phab$ refers to the proportion of the available habitat type. This calculation was performed for terrestrial and aquatic habitat types.

Habitat availability was assessed by calculating the proportion made up by each habitat type. I tested for differences between years using a single-factor ANOVA, with the year as the independent variable, and the habitat type as the dependent variable. In addition, the proportion of terrestrial habitat availability calculated for 2013 was compared with land-use data for 2013.

Land-use data were collected in the same manner as presented in Chapter 2 (within the 500 m polygons), but limited to the section of the river traversed in this study (Fig. 9) and to a single survey (March 2013). Data were compared using GPS location to determine where each habitat type was situated along the banks of the river, within the 7 m polygon directly adjacent to it, and what land-cover type was present within the 500 m polygon on the same bank. Each 500 m polygon for the year 2013 was investigated in this way as this was the most recent aerial survey data available for this region. Within the 500 m polygon, the proportion of each habitat type along the banks of the river was calculated. This measure was repeated along the length of the surveyed section of the river, resulting in 23 comparisons (as each 500 m polygon and corresponding habitat type data was considered a single data entry). This was analysed using a single factor ANOVA, with Land Cover type as the independent variable, and Habitat availability as the dependent variable. As this information was investigated as proportions, all data were first Arcsin transformed to normalise the variables.

River quality (physiochemistry and SASS data) pre- and post-disturbance was also compared in order to assess the effects of flooding on these variables. Physiochemistry was analysed using a Principle Component Analysis (PCA), performed in Primer (Clarke, 2006), with pH, velocity, water temperature and average depth as inputs. The PCA is considered to be an unbiased method, revealing associations or variations in chemical and physical constituents which could be indicative of seasonal influences on the physiochemical data. Physiochemical variables were compared using Kruskal Wallis analysis of variance, in STATISTICA (StatSoft, 2007) to test for seasonal differences. Macro-invertebrate data were analysed using STATISTICA (StatSoft, 2007), and were subjected to an ANOVA of the ASPT scores when categorized by month, and subsequently using a post-hoc Tukey test in order to determine the difference.

ASPT scores were compared with the habitat availability using the average ASPT scores per habitat type and per location in order to establish whether ASPT changes were significantly influenced by the surrounding habitat type, seasons or flooding effects. All data were discussed in relation to the Nile crocodile.

Results

Crocodile surveys

The average number of Nile crocodiles found in the 23 km stretch of Mutale river was 20.63 p.a. (±2.70). This equates to one crocodile per 1.03 km of river. Crocodiles were seen more frequently during the wet season than in the dry season, but there was no significant difference between years for any size class ($F_{(2,6)}$ = 3.13; $p > 0.05$; Wilks = 0.01) or total numbers between seasons ($F_{(1,4)}$ = 3.03; $p > 0.05$; Wilks = 0.08). Furthermore, no significant differences were found between the population sizes downstream and upstream of Tshulu Camp ($F_{(4,1)}$ = 3.02; Wilks = 0.08; $p > 0.05$), (Fig. 12). The number of crocodiles did not fluctuate significantly from year to year ($F_{(2,6)}$ = 1.37; $p > 0.05$; Fig. 12). Observations of juvenile crocodiles were highest in 2011 (17 Juveniles), though no significant difference was found between years ($F_{(3,2)}$ = 1.93, $p > 0.05$). Adult crocodile population size remained similar between years ($F_{(3,2)}$= 0.27; $p > 0.05$).

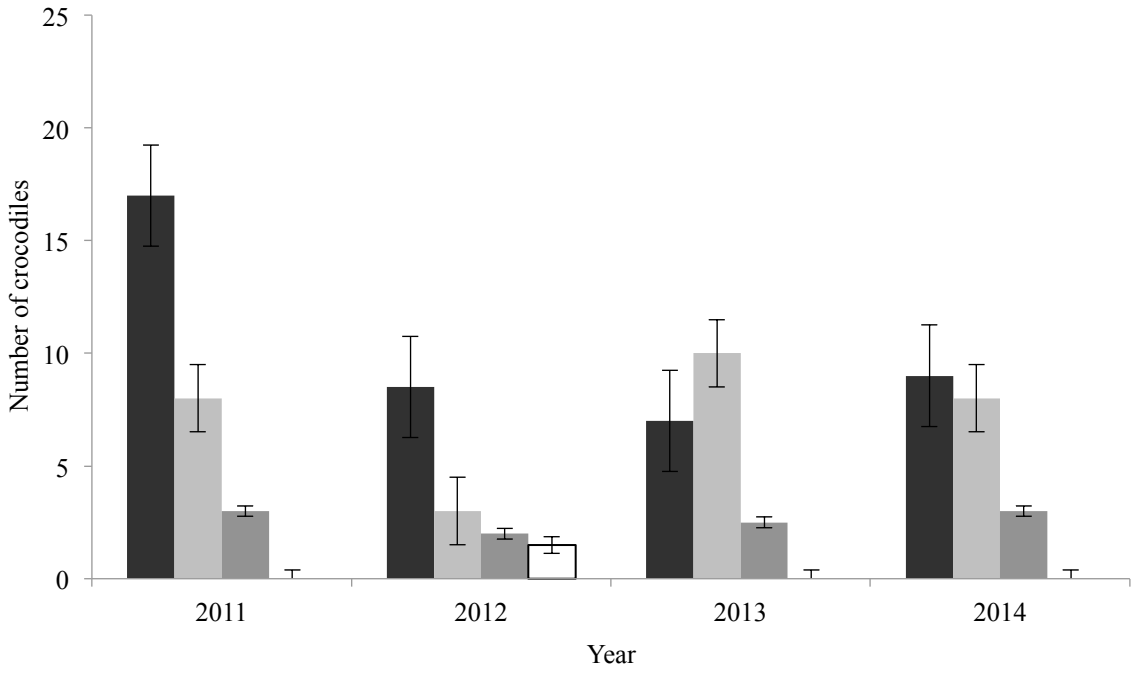


Figure 12: Number of Nile crocodiles sighted in Mutale River, Limpopo Province, during night surveys according to size class (Juvenile, black; Sub-adult, light grey; Adult, dark grey; Unidentified, white.)

Not all terrestrial habitat types were equally favoured by the Nile crocodile in the Mutale River. The majority of crocodiles (72%) were found in sandy areas (Table 3). During the night surveys, crocodiles were also frequently found in rocky areas (20%), and seldom in areas where habitat was considered unusable (8%). The relative habitat importance of sand, was found to be >1, indicating that crocodile distribution in this habitat was not completely random. The proportion of crocodiles found in unusable habitat, and the relative importance of the habitat (<1; Table 3), indicates that crocodiles actively avoided habitats which were considered unusable.

Table 3: Proportion of Nile crocodiles found in each terrestrial habitat type. The proportion of habitat types available and the probability of finding crocodiles in each habitat type in the walked section of the river, in March 2013.

	Proportion of crocodiles	Proportion of habitat available	Relative importance of habitat
Rock	0.20	0.24	0.83
Sand	0.72	0.53	1.36
Unusable	0.08	0.21	0.35

In addition to favouring certain terrestrial habitat types, the Nile crocodile was also found to favour specific aquatic habitat types over others. The majority of crocodiles (72%) were associated with slow-flowing and quite deep runs (Table 4). Only 17% of the crocodiles were found in deep pools, though this is probably a function of pool availability and detectability of crocodiles throughout the river, especially when one considers the relative importance of this habitat (3.4; Table 4). Crocodiles were found to actively avoid rapids (<1; Table 3). They were somewhat evenly distributed in Runs; the most common habitat type (48%).

Table 4: Proportion of Nile crocodiles found in each aquatic habitat type, the proportion of habitat types available and the probability of finding crocodiles in each habitat type in the walked sections of the river in March 2013.

	Proportion of crocodiles	Proportion of habitat available	Relative importance of habitat
Rapid	0.11	0.47	0.23
Run	0.72	0.48	1.5
Pool	0.17	0.05	3.4

Habitat assessment

When comparing land-cover type and the associated percentage of habitat cover, it was found that the proportion of habitat cover for each land-use type was significantly different ($F_{(9, 209.45)} = 4.99$; $p < 0.05$; Fig. 13). Tukey post-hoc comparisons revealed that bare ground and farm encompassed significantly different habitat distributions to areas covered by trees. This is visually represented in Figure 13, in which land-use polygons specified as trees have even distribution of sand, rock and unusable areas.

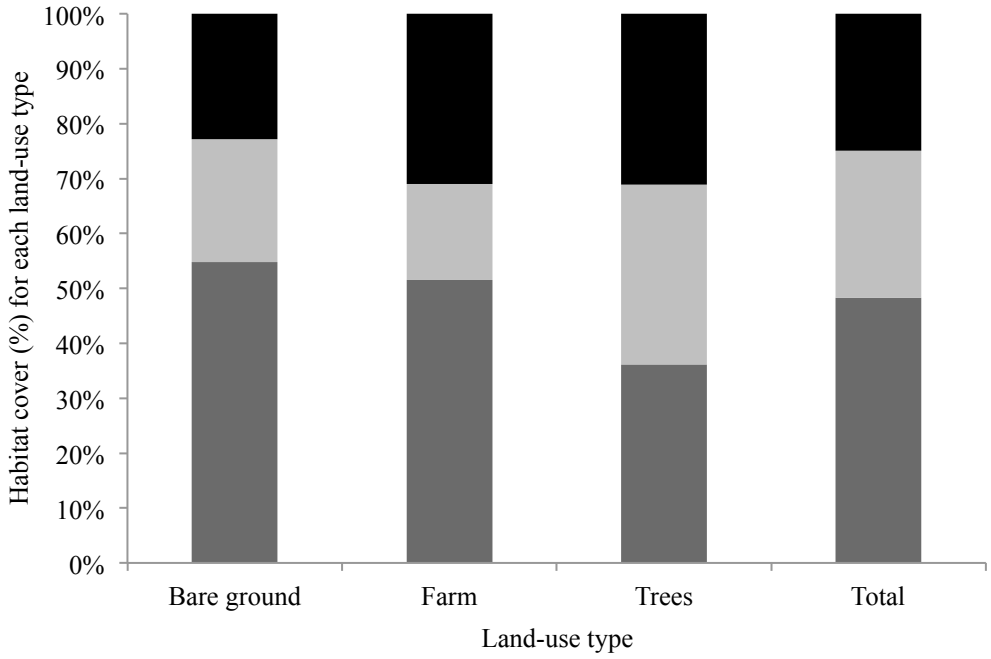


Figure 13: Percentage habitat (%) found under each land-use type on the banks of the Mutale River. Total indicates the average percentage of the river that was covered by the habitat types (Sand, dark grey; Rock, black; Unusable, light grey).

The proportion of terrestrial habitat availability was found to fluctuate over time (Figure 14; Wilks lambda = 0.01; $F_{(12, 8.23)} = 3.08$; $p = 0.06$). Increases in sand coincided with seasonal changes (e.g. October 2012), but a general decrease in sand occurred over time. Rock and unusable habitat showed opposing trends after October 2012, with higher proportions of rock coinciding with lower proportions of unusable territory.

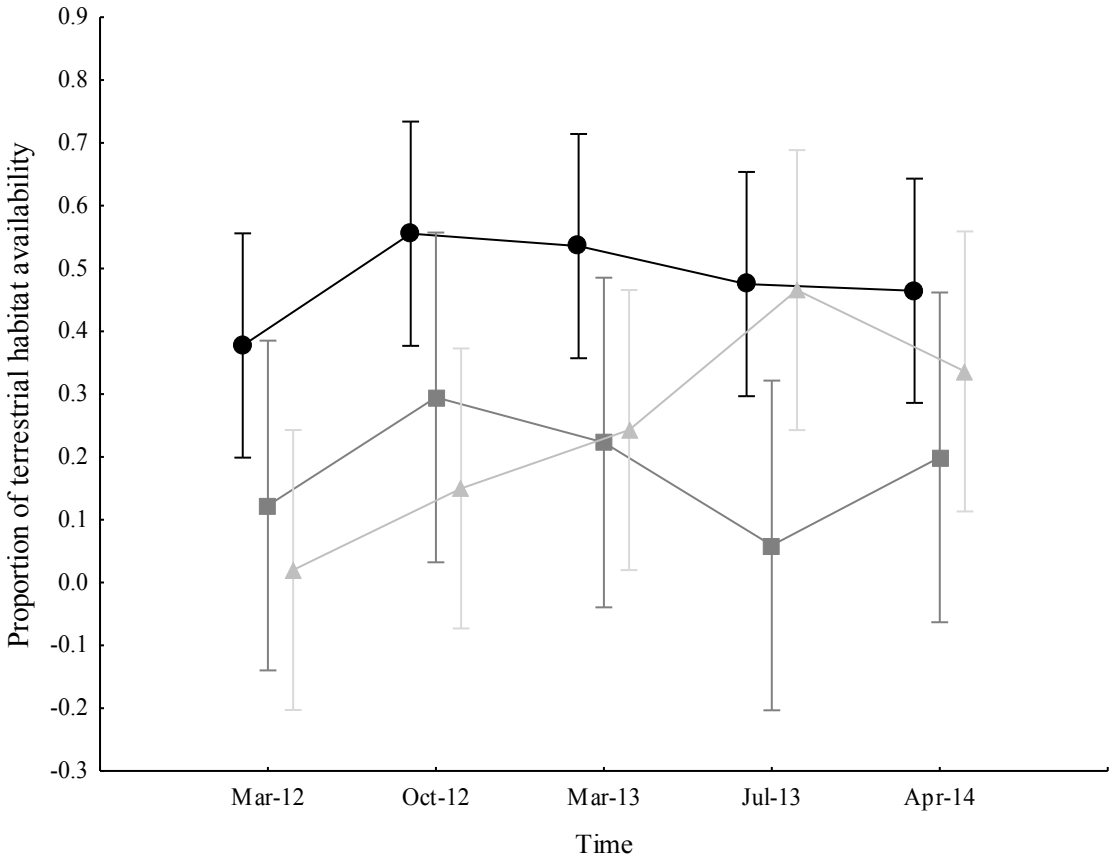


Figure 14: Proportion of terrestrial habitat availability (Sand, black with circles; Unusable, dark grey with squares; Rock, light grey with triangles), over several seasons (March 2012, October 2012, March 2013, July 2013, April 2014), in the Mutale River .Vertical bars denote 95% confidence intervals.

The proportion of aquatic habitat availability along the banks of the Mutale river, was also found to fluctuate over time (Wilks lambda = 0.00, $F_{(12, 8.23)} = 21.93$; $p < 0.05$, Fig. 15). July

2013 showed a marked decrease in rapids; directly after the dry season. Runs fluctuate seasonally as well. A decrease in pools was found after the 2013 flood.

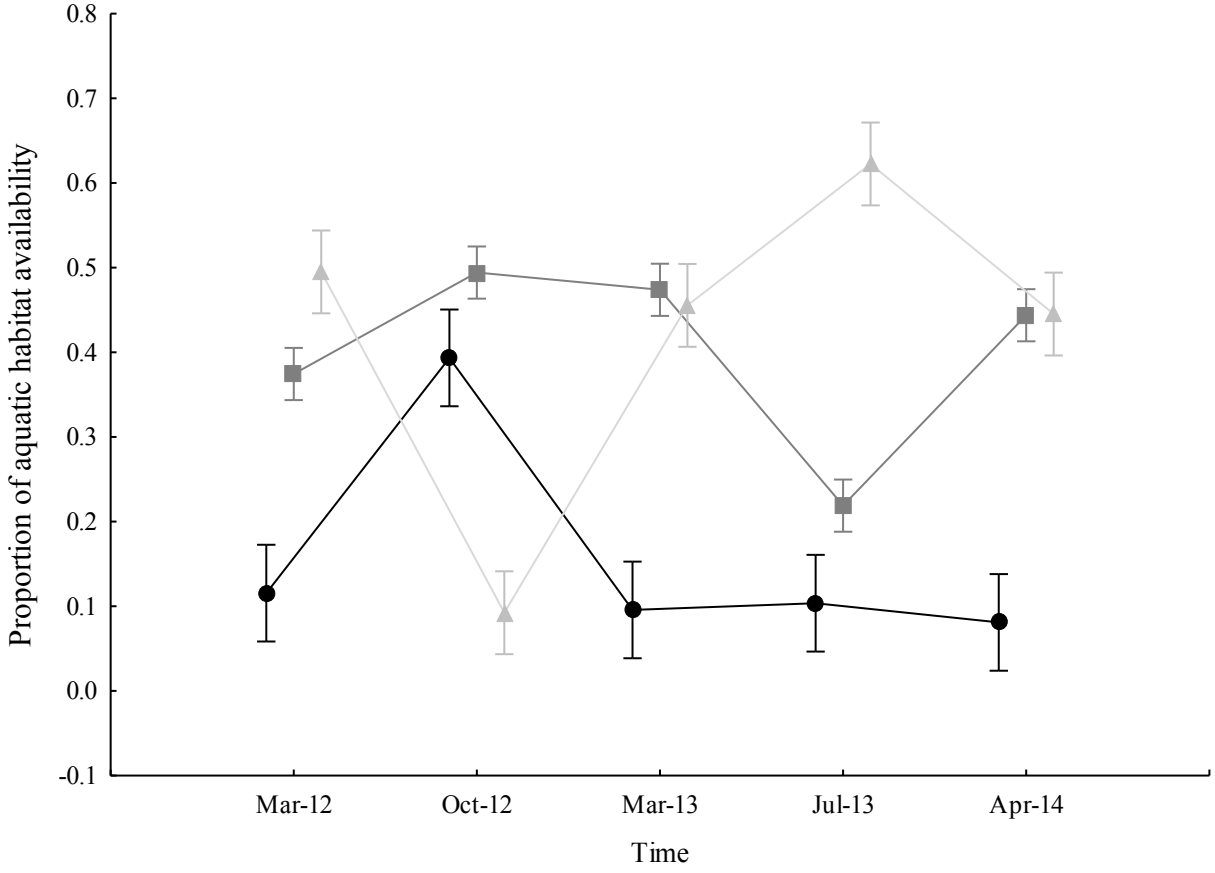


Figure 15: Proportion of aquatic habitat availability (Pool, black circles; Rapid, dark grey squares; Run, light grey triangles) over several seasons in the Mutale River. Vertical bars denote 95% confidence intervals.

River quality

Physiochemical variables

The physiochemical variables investigated in this study (Water temperature, pH, velocity and depth) clustered according to the seasons in which they were recorded (Fig. 16), with significant differences between seasons for each of the variables (Depth: $F_{(5,91)} = 29.76$; $p < 0.001$; pH: $F_{(5,91)} = 20.31$; $p < 0.001$; Velocity: $F_{(5,91)} = 20.31$: $p < 0.001$; water temperature: $F_{(5,91)}$

= 94.73; $p < 0.001$) when analysed using ANOVA. March 2013 data (post-flood) were overlapped with October 2012 data (pre-flood, end of dry season) in the PCA. Post 2013 flood data separated completely from the rest of the data. A potential flood signal was represented in the shift from the riverine physiochemistry in October 2012 to October 2013, as these would be expected to look similar had the river returned to a natural fluctuation. April 2014 data overlapped once more with March 2013 data. PC1 was driven primarily by water temperature (Eigenvector = -0.66), followed by velocity (Eigenvector = -0.58) and pH (Eigenvector = -0.45), thus accumulating a total of 45.1% variation represented by PC1. A further 25.9% of variation was represented by PC2, and was driven primarily by depth (Eigenvector = 0.89).

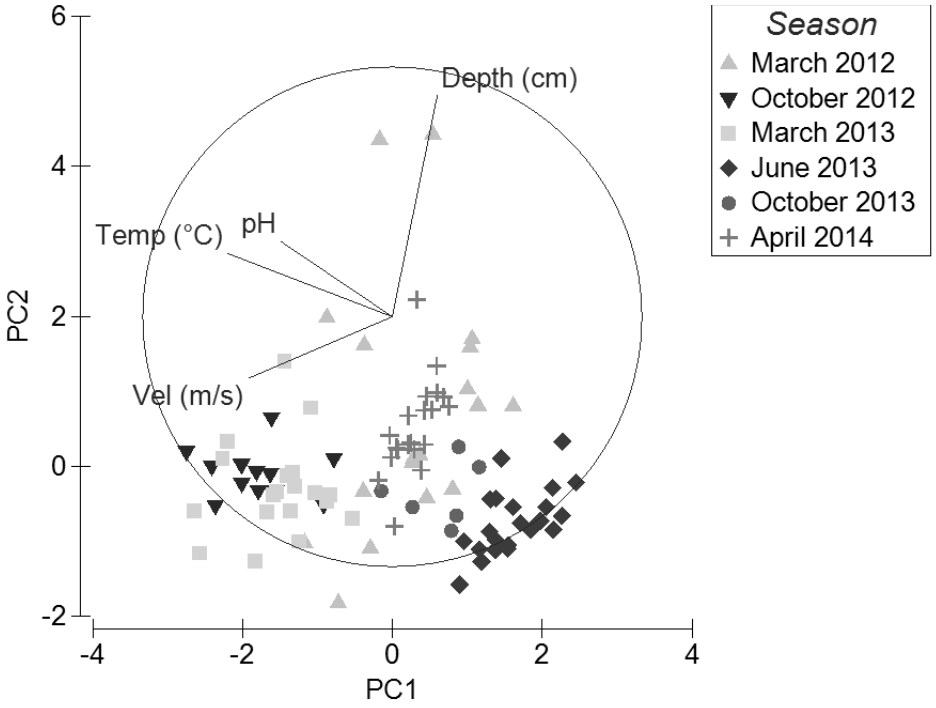


Figure 16: Principle components analysis of physiochemical variables including water temperature (°C), pH, velocity (m/s) and depth (cm) in the Mutale River, Limpopo Province.

Macroinvertebrate assessments

The SASS5 scores revealed that the ASPT along the surveyed sections of the Mutale river differed significantly, in several instances ($F_{(6,19)} = 10.291$, $p = 0.00$) from one another (Fig. 17). The ASPT was found to be higher soon after the flood in March 2013 than in any other

month (Tukey post- hoc; MS = 1.81, df = 59). January 2012 saw significantly lower ASPT scores than other months.

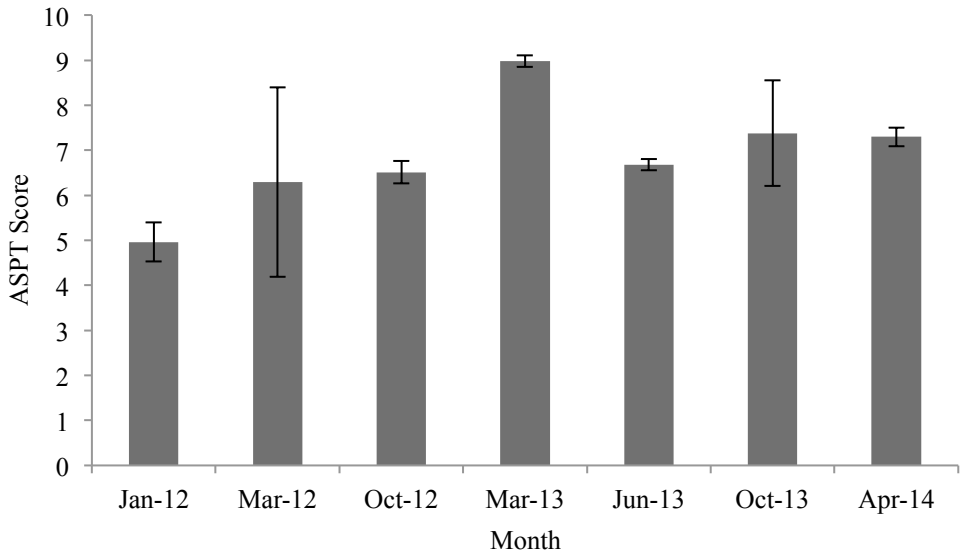


Figure 17: Histogram of the average ASPT scores of the Mutale River, over time (Months, January 2012-April 2014).

At the intermediate scale, despite the absence of common trends, individual changes in terrestrial habitat availability were noteworthy (Fig. 17a). After the January 2013 flood, a 62% increase in the proportion of rocky habitat accompanied a 24% decrease in the sandy habitat availability (October 2012-March 2013). Between March 2013 and July 2013, an increase in rocky habitat coincided with a further decrease in sandy habitat and greater exposure of the rock-bed, which was noticeable after the floods had receded.

Alterations in the aquatic habitat were also notable (Fig. 17b). Between March 2012 and October 2012, decrease in river flow after the dry period resulted in an overall increase in slow-flowing pools. Following the October 2012 dry period, the 2013 floods and wet period resulted in a major increase in the presence of 'runs' (medium to fast flowing water, excluding white rapids). The Mutale River had so much more water flowing through it at this point that in many

deep areas previously classified as pools, the increased velocity altered this classification. Increases in fast flowing water and rapids between October 2012 and April 2014 were likely to result in decreases in the availability of suitable/valuable Nile crocodile habitat. As the proportion of rapids increased by 102% (twice as many rapids between July 2013 and April 2014), there was in the past year an increase in habitat that was actively avoided.

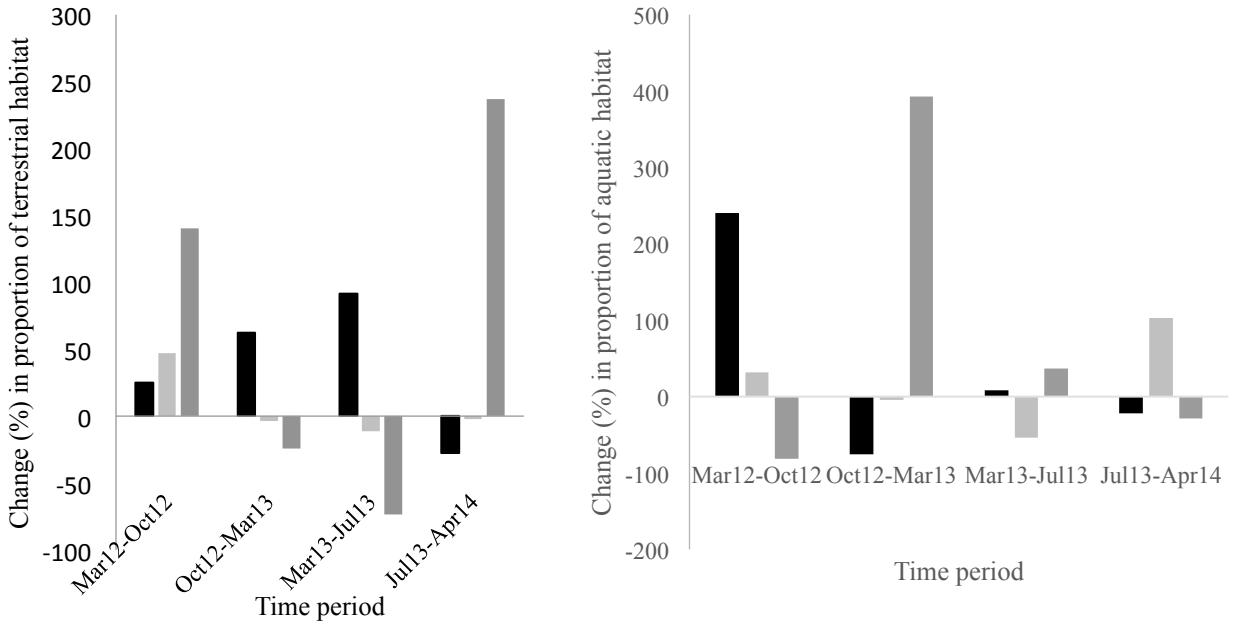


Figure 18: Change (%) in a) terrestrial (rock-black; sand- light grey; unusable- dark grey) and b) aquatic habitat (pool- black; rapid- light grey; run-dark grey) along the surveyed section of Mutale River, including flooding (October 2012-March 2013) and non- flooding (March 2012-October 2012; March 2013-July 2013; July 2013-April 2014) periods.

At the small scale, ASPT scores increased by 37.3% after the January 2013 floods; this increase is likely to have occurred as a result of the initial scouring effect of the flood (Fig. 19). The fluctuating SASS scores indicate that the percentage change is greater in periods of lower

flow than during flooding. This could occur because of a shift in biota associated with seasonality (Wolda, 1988).

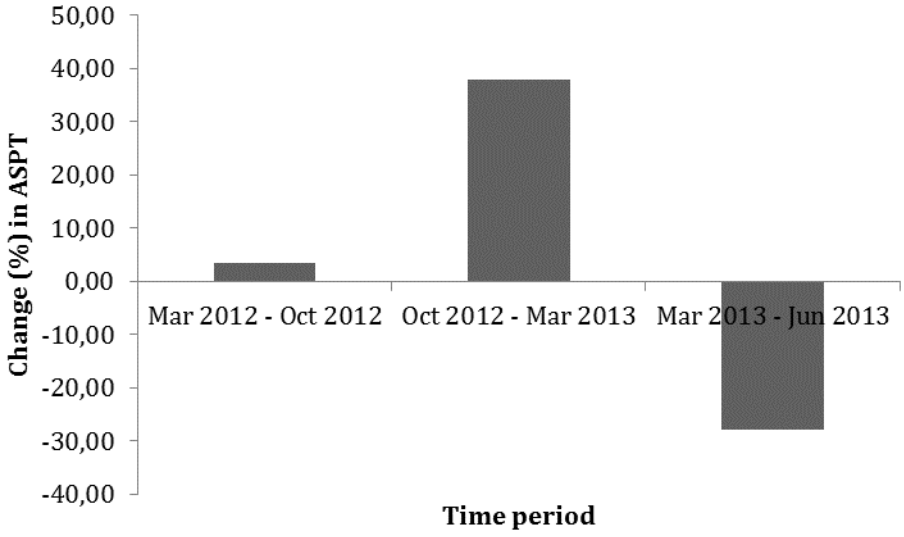


Figure 19: Change (%) ASPT scores along the surveyed section of Mutale River, between flooding (October 2012-March 2013) and non-flooding (March 2012-October 2012; March 2013-June 2013).

Discussion

The density of Nile crocodiles in the Mutale River was one individual per 1.03 km of river traversed. This density is relatively low when compared with populations of crocodiles found elsewhere in South Africa (e.g. the Olifants River; Ashton, 2010). As this population occurs outside a protected area, lower numbers in the population sample were anticipated (Pollard et al., 2011). The results also indicate that the Mutale River population of reproductively active crocodiles has been relatively similar over a short period of time (2011-2014). The adult population did not change during this time period, and the presence of adult individuals in the same areas in every survey, lead to the assumption that the same individuals were found each season. This indicates that the adult crocodile population in this section of the river remained

stable, despite the flooding event in 2013. The high levels of variability in the number of hatchlings found per year was probably due to predation on hatchlings during their most vulnerable life stage (Hutton, 1987). The number of adults remained constant throughout the year as these were resident and less prone to predation. The stability of this crocodile population along the Mutale river was likely also linked to the prevalence of preferred habitat within these areas.

The Nile crocodile has a preference for sandy habitats, with the majority of crocodiles being found in these areas (Table 3; >70%). Crocodiles were found to have a particular preference for sandy terrestrial habitats, as there was a greater proportion of crocodile present than could reasonably be expected from a random distribution. Sand has frequently been recognized as a valuable habitat for nesting and basking (Hutton, 1989; Kofron, 1989). In contrast, few crocodiles were found in areas classified by the observers as 'unusable', indicating active avoidance of these areas, as presence was found to be lower than expected by chance alone. Crocodiles also favoured specific aquatic habitat types. A majority of individuals were associated with runs, however, crocodiles were found to have a greater preference for pools. The absence of any crocodiles in rapids suggests the active avoidance of this habitat type. With increasing flooding anticipated in the future, flooding is likely to induce a higher prevalence of rapid habitat in the river. As rapids are actively avoided, this would be detrimental to the crocodile population.

The prevalence of sand along the Mutale river was found to decrease over time, between March 2012 and April 2014 (Fig. 13). In contrast, the proportion of rock was found to increase (despite seasonal fluctuations) over time (Fig. 14). At the intermediate scale we therefore see the drastic effect of flooding, owing to the shifting of sediment to areas further downstream after high rainfall seasons (March 2013, April 2014). Shifts in sediment and exposure of rock of this magnitude are likely to have a detrimental effect on the Nile crocodile habitat in the Mutale, as rocky areas do not constitute preferred conditions, and more exposure would result in degradation of suitable habitat for the reptiles. Between July 2013 and April 2014, an increase in the proportion of unusable terrestrial habitat was observed to occur as a result of bank erosion

(pers. obs.). Increases in unusable habitat affect the crocodiles as they tend to avoid these areas (Table 2).

These results indicate a decline in preferred Nile crocodile habitat availability post-flood. Although the actively avoided, 'unusable' habitat was found to fluctuate with season (primarily due to the exposure/submergence of rock beds, depending on the season), with no particular increasing or decreasing trend. Rocky habitat, however, is not a particularly favourable habitat, and was found to increase substantially between March 2012 and April 2014, from approximately 12% habitat coverage, to 30% habitat coverage, for the respective years. As mentioned above, Further increases of unusable terrestrial area and rapids in aquatic habitat are likely to impact on crocodiles in the river, due to the unfavorablity of these habitat types.

Riverine systems exhibit seasonal variability in factors such as biotope availability (Armitage et al. 1995; Pardo & Armitage, 1997): hydrology (McElravy et al.,1989), and physiochemical variability such as water temperature (Hawkins et al., 1997). This was reflected in my study as physiochemical variables investigated were found to group together according to seasons (Fig. 15). The overlap in data from pre- and post-flood indicates that flooding resulted in a disturbance in the otherwise natural variation between seasons. Shifts in the physiochemistry directly after the 2013 floods were found to be returning to pre-flood conditions over time. This indicates that the river was returning to a pre-disturbance state. The time taken between the shift in conditions, and the return (approximately 1 year), indicates that this system is sensitive to flooding. Subsequent floods may result in longer restoration periods. This would negatively affect the Nile crocodile because shifts in physiochemistry for extended periods could be detrimental over time. Alterations in land-use on the adjacent river banks are likely to further alter the physiochemistry of the Mutale River. Effluents in the river should also be monitored, as these are likely to affect the physiochemical variables already mentioned.

Seasonal variations in the physiochemistry of the river also influence the variation in the distribution and abundance of benthic macro-invertebrates (Dallas, 2004). This is due to presence of specific habitat requirements, which may only be met in certain seasons. In addition, the seasonal patterns of occurrence and abundance of invertebrates depend on their life history and

behavioural characteristics (Beche et al., 2006; Wolda, 1988) and fluctuations in flow structure (particularly flooding and drying) in stream communities (Beche et al., 2006). This was portrayed in the fluctuating ASPT scores of the Mutale river, as there were differences between macro-invertebrate communities from different seasons, despite the similarity in the habitat type (all data were collected in rapids). A potential reason for this, is that samples were taken only three months after flooding occurred, allowing sufficient time to re-establish the environment to a more pristine, pre- flood state. Subsequent to this, it is likely that ASPT scores decreased due to excess algal growth in sections of the river that had previously produced some of the higher ASPT values (pers. obs.), with only low scoring species persisting in this state. Many of the species contributing to differences between seasons were highly tolerant of pollution (with a low average score per taxon) and physical disturbances. Due to the fact that the dissimilarity was a feature of these highly tolerant species, the results indicate that tolerance is a determining factor in community composition in different seasons. The water quality of the Mutale River was shown to fluctuate over time, and the overall health of this river was found to be somewhat low. The presence of more tolerant species may indicate an increase in pollution within this river. Shifts in community composition and in water quality over time are bound to also affect the Nile crocodile population, as previous studies have shown that increasing pollution has been linked with die-offs in the past (Botha, 2005).

In this study, as in previous studies, it was found that the flooding and seasonal movement of water across the landscape not only influences the biodiversity within the river, but also impacts the ecology of the river across a broad range of spatial and temporal scales (Junk et al., 1989; Poff et al., 1997; Poff & Ward, 1990; Sparks, 1995; Vannote, et al., 1980). The shape and size of river channels, the distribution of rapid and pool habitats, and the stability of the substrate are all largely determined by the interaction between the flow regime and local geology and landform (Cobb et al., 1992; Frissel et al., 1986; Newbury & Gaboury, 1993).

In summary, it was evident at all scales within my study that, excluding the ASPT scores, that there were more changes in the Mutale river during a flooding period, than would normally be the case. At the landscape scale, change increased by as much as four fold compared with inter-flood periods. It is evident that the immediate effects of flooding were often greater than at

a longer scale (e.g. the dramatic shifts in aquatic habitat availability that occurred as a result of the increases in river flow). At the smallest scale, the immediate effects of flooding on ASPT (October 2012-March 2013) were greater than during normal, seasonal fluctuations (March 2012-October 2012). As a long-lived animal, the Nile crocodile is likely to experience both large-scale, long-term changes to the riverine environment, as well as short-term, intermediate and small-scale changes. The crocodile is highly adaptable, but clearly prefers certain types of habitat over others. Overall, results showed that seasonality, intermediate and small-scale flooding will impact the freshwater community. With increases in the occurrence of flooding anticipated with climate change, these shifts in the community may become greater and eventually cause cascading effects across space and time.

References

Alvarez-Cobelas, M., Catalan, J., & García de Jalón, D. (2005). Impacts on inland aquatic ecosystems. In J. M. Moreno (Ed.), *Effects of climate change in Spain* (pp. 113–146).Madrid, Spain: Ministerio de Medio Ambiente.

Angeler, D. G. (2007). Resurrection ecology and global climate change research in freshwater ecosystems. *Journal of the North American Benthological Society, 26*, 12–22.

Armitage, P. D., Pardo, I., & Brown, A. (1995). Temporal constancy of faunal assemblages in 'mesohabitats' - application to management? *Archiv fur Hydrobiologie, 133*, 367–387.

Beche, L. A., McElravy, E. P., & Resh, V. H. (2006). Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean climate streams in California, U.S.A. *Freshwater Biology, 51*, 56–75.

Botha, P. J. (2005*). The Ecology and Population Dynamics of the Nile crocodile (Crocodylus niloticus) in the Flag Boshielo Dam, Mpumalanga Province, South Africa* (Unpublished MSc thesis, University of Pretoria, Pretoria, South Africa).

Carpenter, S. R., Fisher, S. G., Grimm, N. B., & Kitchell, J. F. (1992). Global change and freshwater ecosystems. *Annual Review of Ecology and Systematics, 23*, 119–139.

Clarke, K.R., & Gorley, R.N. (2006). PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Cobb, D. G., Galloway, T. D., & Flannagan, J. F. (1992). Effects of discharge and substrate stability on density and species composition of stream insects. *Canadian Journal of Fisheries, 49,*1788-1795.

Collier, P., Conway, G., & Venables, T. (2008). Climate change and Africa. *Oxford Review of Economic Policy*, *24*, 337-353.

Dallas, H. F. (2004). Seasonal variability of macroinvertebrate assemblages in two regions of South Africa: implications for aquatic Bioassessment. *African Journal of Aquatic Science, 29,*173–184.

Dickens, C. W. S., & Graham, P. M. (2010). The South African Scoring System (SASS) Version 5 Rapid Bioassessment Method for Rivers. *African Journal of Aquatic Science,* 27, 1–10.

Excel, I. (2013). Microsoft Excel 2007.

Firth, P., & Fisher, S. G. (1992). *Global climate change and freshwater ecosystems.* New York: Springer Verlag.

Frissel, C. A., Liss, W. J., Warren, C. E., & Hurley, M. D. (1986). A hierarchical framework for stream habitat classification: Viewing streams in a watershed context. *Environmental Management, 10*, 199–214.

Garmin BaseCamp. 2012. Version 4.0.1 Garmin Ltd.

Gerber, A., & Gabriel, M. J. M. (2002). *Aquatic Invertebrates of South African Rivers, version 2.* South Africa: Institute for Water Quality Studies, Department of Water Affairs and Forestry.

Harper, M. P., & Peckarsky, B. L. (2006). Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. *Ecological Applications, 16*, 612–621.

Hawkins, C. P., Hogue, J. N., Decker, L. M., & Feminella, J. W. (1997). Channel morphology, water temperature, and assemblage structure of stream insects. *Journal of the North American Benthological Society*, *16*, 728–749.

Holomuzki, J. R., & Biggs, B. J. (2000). Taxon-specific responses to high-flow disturbance in streams: implications for population persistence. *Journal of the North American Benthological Society*, 670-679.

Holomuzki, J. R., & Biggs, B. J. (2003). Sediment texture mediates high-flow effects on lotic macroinvertebrates. *Journal of the North American Benthological Society*, 22, 542-553.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution, 15*, 56–61.

Hutton, J. M. (1987). Growth and feeding ecology of the Nile crocodile (*Crocodylus niloticus*) at Ngezi, Zimbabwe. *Journal of Animal Ecology*, *56*, 25-38.

Hutton, J. M. (1989). Movements, home range, dispersal and the separation of size classes in Nile crocodiles. *American Zoologist, 29*, 1033-1049.

Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The floodpulse concept in river-floodplain systems. In D. P. Dodge (Ed.), PROCEEDINGS of the international large river symposium (pp. 110–127).

Kofron, C. P. (1989). Nesting ecology of the Nile crocodile (*Crocodylus niloticus*). *African Journal of Ecology*, *27*, 335–341.

Lake, P. S., Palmer, M. A., Biro, P., Cole, J., Covich, A. P., Dahm, C., Gibert, J., Goedkoop, W., Martens, K., & Verhoeven, J. (2000). Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. *BioScience, 50*,1099–1107.

Leslie, A. J., & Spotila, J. R. (2000). Osmoregulation of the Nile crocodile (*Crocodylus niloticus*) in Lake St. Lucia, KwaZulu-Natal, South Africa. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *126*, 351-365.

Leslie, A. J. (1997). *The ecology and physiology of the Nile crocodile (Crocodylus niloticus) in Lake St Lucia, South Africa* (PhD thesis, Drexel University, PA, USA).

Lodge, D. M. (2001). Responses of lake biodiversity to global changes. In O. E. Sala, F. S. Chapin, & E. Huber-Sannwald (Eds.), *Future scenarios of global biodiversity* (pp. 277–313). New York: Springer Verlag.

M' Marete, C.K. (2003). Climate and water resources in the Limpopo Province. In A. E. Nesamvuni, S. A. Oni, J. J. O. Odhiambo, & N. D. Nthakheni (Eds.), *Agriculture as the Cornerstone of the Economy in the Limpopo Province* (pp. 1-49). Limpopo: Department of Agriculture.

Mabuwaya Foundation. (1993). http://www.mabuwaya.org/. Accessed 03/03/2013

Magnusson, W. E. (1982). Mortality of eggs of the crocodile *Crocodylus porosus* in northern Australia. *Journal of Herpetology*, *16,* 121-130.

Magnuson, J. J., Webster, K. E., Assel, R. A., Bowser, C. J., Dillon, P. J., Eaton, J. G., Evans, H. E., Fee, E. J., Hall, R. I., Mortsch, L. R., Schindler, D. W., & Quinn, F. H. (1997).

Potential effects of climate changes on aquatic ecosystems: Laurentian Great Lakes and Precambrian Shield region. *Hydrological Processes, 11*, 825–871.

McCarthy, J. J., Canziani, O. V., Leary, N. A., Dokken, D. J., & White, K. S. (Eds.). (2001). *Climate change 2001: impacts, adaptation, and vulnerability. Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge, UK: Cambridge University Press.

McMichael, A. J., Woodruff, R. E., & Hales, S. (2006). Climate change and human health: present and future risks. *The Lancet*, *367*, 859-869.

McElravy, E. P., Lamberti, G. A., & Resh, V. H. (1989). Year-to-year variation in the aquatic macroinvertebrate fauna of a northern California stream. *Journal of the. North American Benthological Society, 8*, 51–63.

Mosepele, K., Moyle, P. B., Merron, G. S., Purkey, D. R., & Mosepele, B. (2009). Fish, floods, and ecosystem engineers: aquatic conservation in the Okavango Delta, Botswana. *Bioscience, 59*, 53–64.

Newbury, R., & Gaboury, M. (1993). Exploration and rehabilitation of hydraulic habitats in streams using principles of fluvial behaviour. *Freshwater Biology, 29*, 195–210.

Olsen, D. A., Matthaei, C. D., & Townsend, C. R. (2007). Patch history, invertebrate patch dynamics and heterogeneous community composition: perspectives from a manipulative stream experiment. *Marine and Freshwater Research, 58*, 307–314.

Pardo, I., & Armitage, P. D. (1997). Species assemblages as descriptions of mesohabitats. *Hydrobiologia, 344*, 111–128.

Poff, N. L., & Ward, J. V. (1990). Physical habitat template of lotic systems: Recovery in the context of historical patterns of spatiotemporal heterogeneity. *Environmental Management, 14*, 629–645.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *BioScience, 47*, 769–784.

Poff, N. L., Brinson, M. A., & Day, J. W. (2002). *Aquatic ecosystems and global climate change: potential impacts on inland freshwater and coastal wetland ecosystems in the United States*. Arlington, Virginia: PEW Center on Global Climate Change.

Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. J., & Pounds, J. A. (2003). Fingerprints of global warming on wild animals and plants. *Nature, 4,* 57–60.

Schindler, D. W. (2001). The cumulative effects of climate warming and other stresses on Canadian freshwaters in the new millennium. *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 18–29.

Sparks, R. E. (1995). Need for ecosystem management of large rivers and floodplains. *BioScience, 45*, 168–182.

StatSoft, Inc. (2007). STATISTICA (data analysis software system). Version 8.0.

Swanson, F. J., Johnson, S. L., Gregory, S. V., & Acker, S. A. (1998). Flood disturbance in a forested mountain landscape. *BioScience, 48,* 681–689.

Thomas, C. D., Cameron, A., Green, R. A., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature, 427*, 145–148.

Townsend, C. R., Scarsbrook, M. R., & Dole´dec, S. (1997). The intermediate disturbance hypothesis, refugia, and bio-diversity in streams. *Limnology and Oceanography, 42*, 938–949.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. R., & Cushing, C. E. (1980). The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*,130–137.

Vitousek, P. M. (1994). Beyond global warming: ecology and global change. *Ecology, 75*, 1861–1876.

Winder, M., & Schindler, D. E. (2004). Climatic effects on the phenology of lake processes. *Global Change Biology, 10*, 1844–1856.

Wolda H. (1988). Insect seasonality: why? *Annual Review of Ecology and Systematics, 19*, 1–18.

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