Evidence for overfishing of tigerfish *Hydrocynus vittatus* (Castelnau 1861) in the Kavango River, Namibia

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Abstract

The fishery for the African tigerfish *Hydrocynus vittatus* in northern Namibia makes a substantial contribution to food security and stimulates the local economy through subsistence and recreational fishing. However, local fishers suggested that catch rates of *H. vittatus* have declined and the fish are now smaller. The Namibian Ministry of Fisheries and Marine Resources has conducted annual gill net surveys in the Kavango River from 1994 to 2018. These standardised surveys were used to compare catch per unit effort data and length frequencies of *H. vittatus* between intensively fished areas and a freshwater protected area (FPA). The catch per unit effort in numbers and weight and proportion (56% vs. 10-20%) of mature fish were higher inside the FPA compared to those outside. The *H. vittatus* population both outside and inside the FPA are subject to overfishing, and management actions should be taken to secure this important fisheries resource for subsistence and recreational fishers.

Keywords: inland fisheries, catch per unit effort, length frequency, freshwater protected area, sustainable management

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Introduction

Sustainable fisheries are based on the principle of harvesting the surplus production of a fish stock and should prevent collapse of the target species. The term overfishing is commonly used by managers and scientists, and often expressed in relation to different mechanisms that regulate recruitment (Schaefer 1954; Gulland 1983; Beverton et al. 1994). Gulland (1983) defined two types of overfishing; growth overfishing and recruitment overfishing. Growth overfishing occurs when fish are harvested at an average size that is smaller than the size that would produce the maximum yield per recruit (i.e. individuals that reach sexual maturity). Recruitment overfishing occurs when the rate of fishing causes a significant reduction in the recruitment to the exploitable stock, characterized by greatly reduced spawning stock, decreased proportion of older fish in the catch and low yearly recruitment. Beamish et al. (2006) proposed another type of overfishing, longevity overfishing, which is the elimination of older age classes (i.e. large fecund fish) in a population such that this removal impairs recruitment. They argue that this form of overfishing deserves serious attention as older age classes may have greater resilience to environmental perturbations than younger fish, and that longevity overfishing will hinder a population from rebuilding after periods of overexploitation.

In Namibia the tigerfish *Hydrocynus vittatus* occurs in the Zambezi, Kwando, Chobe and Kavango rivers that are associated with large grassland floodplains and a seasonal cycle of flooding (Jubb 1952; Holtzhausen 1991; Welcomme 1976). These floodplain rivers have complex food webs in which *H. vittatus* is an apex predator, and an important contributor to the transfer of energy from the floodplain into the main river (Bell-Cross 1965, Winemiller and Kelso-Winemiller 1994; Winemiller and Jepsen 1998). *Hydrocynus vittatus* are an important component of artisanal fisheries where they contribute to food security and rural livelihoods (Abbott et al. 2015; Tweddle et al. 2015). In addition, they are popular target fish for recreational anglers, an activity that in northeast Namibia is estimated to contribute up to 70% of the revenue received by tourism lodges (Cooke et al. 2016). Situated mostly in remote areas, these lodges are often the only source of paid employment for local communities and provide an important economic contribution to the local economy and people's wellbeing (Tvedten 1996; Tweddle et al. 2015; Cooke et al. 2016).

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Declines in *H. vittatus* populations have been reported for numerous freshwater ecosystems (Jackson 1961; Kenmuir 1973; Hay et al. 1996), and recently extensive exploitation of tigerfish populations was reported for northern Namibia (Cooke et al. 2016). Given the ecological and socio-economic importance of *H. vittatus* in the region, there is need for implementing measures that promote sustainable utilisation and management of this species to safeguard the livelihoods of communities that are dependent on this resource. In Namibia this is particularly pertinent, as anglers have reported declines in catch rates of *H. vittatus* (Tweddle et al. 2015). A similar negative development was also found in the same rivers in catch rates of the commercially important large cichlids (e.g., *Oreochromis andersonii*, *O. macrochir* and *Coptodon rendalli*) (Tweddle et al. 2015). This decline in the catch rates of the cichlids has been attributed to excessive fishing effort and the use of environmentally destructive and unsustainable fishing methods (Tweddle 2010; Cooke et al. 2016). The status of *H. vittatus*, however, has received less attention. This is problematic as the consequences of overfishing (i.e. decreased catch rates and fish size) are likely to have negative impacts on the livelihoods of local fishing communities as well as the tourism industry (Tweddle et al. 2015; Cooke et al. 2016).

Hydrocynus vittatus are considered a fast growing and long-lived species, and hence, might be vulnerable to longevity overfishing. In the Kavango River, males reach 50% maturity at approximately 180 mm fork length (F_L) and females at 280 mm F_L (Hay et al. 2000). Gerber et al. (2009) used otoliths to age tigerfish in the Okavango River in Botswana and documented that the longevity of this species was up to 20 years. These authors recorded *H. vittatus* up to 7 kg (860 mm total length) in that system. The current Crockango Fishing Club record for the Kavango River in Namibia stands at 8.3 kg (pers. comm. E. Atkinson).

The establishment of freshwater protected areas (FPAs) is fast becoming one of the most promising management and conservation approaches for freshwater fish species worldwide (Abell et al. 2007; Penha et al. 2014; Bower et al. 2015; Wiederkehr et al. 2019). Similar to marine protected areas (MPAs), FPAs are geographical areas that have been recognised for management or conservation of freshwater fish species (Bower et al. 2015; Hermoso et al. 2016; Hannah et al. 2019). The fishery management and conservation benefits of MPAs such

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as increased yields and biomass have been well documented (Lester et al. 2009; Green et al. 2014; Lester et al. 2017), whereas the effectiveness of FPAs have received less attention (Suski and Cooke 2007; Hermoso et al. 2016). In a southern African context, most FPAs exist because protected areas initially were established for wildlife and bird conservation, which, by restricting access to the river, also serves as FPAs protecting fish populations (Abell et al. 2008; Roux et al. 2008). The benefits of FPAs are increasingly being recognised as they have been reported to sustain increased abundances or size classes of freshwater fish species (Sztramko 1985; Sanyanga et al. 1995; Schram et al. 1995; Reid et al. 2001; Suski and Cooke 2007; Penha et al. 2014). Despite this, evidence for their efficacy, particularly in the context of African riverine fishes is scant.

The movement of *H. vittatus* in the Kavango River was recently documented by Jacobs et al. (2020) in relation to the establishment of FPAs. Their study found that 66% of the tigerfish had high site fidelity using an area of less than 33 km of river, whereas 34% undertook long distance movements of up to 397 km. The resident behaviour of some individuals in that study is similar to observations by Økland et al. (2005), showing that not all tigerfish undertake annual large-scale movements. This may indicate that for tigerfish to fulfil their life histories they do not necessarily require vast areas as previously thought.

The aim of the present study was to use annual survey data collected by the Namibian Ministry of Fisheries and Marine Resources (MFMR) from 1994 to 2018 to evaluate whether the tigerfish fishery in the Kavango River is subject to overfishing. We used catch per unit effort and length frequency data collected for populations of this species inside the Mahango FPA in the Kavango River in Namibia, and three unprotected sampling areas in the river to compare the abundance and overall size classes in the FPA and outside the protected area.

Material and methods

Study Area

The Kavango River originates from a series of headwater streams on the southern slopes of the Angolan highlands and drains a total catchment area of 115,000 km^2 (McCarthy and Ellery

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1998). From the sources, streams flow south-south east to form the large mainstream which continues to Namibia where the river flows eastwards to form the 415 km long border between Angola and Namibia (Hocutt and Johnson 2001) (Figure 1). The Cuito River is a major tributary, which enters the Kavango River in Namibia from the north. The Cuito River nearly doubles the annual runoff below the confluence (Smit 1991). After approximately 50 km, the Kavango River now turns south and flows for about 53 km until it crosses the Namibia-Botswana border. The Kavango River in Botswana flows in a south easterly direction in the Panhandle before it terminates in the 15,000 km^2 Okavango Delta (McCarthy and Ellery 1998; Hocutt and Johnson 2001).

In this study we used *H. vittatus* gill net catch data from the Kwetche area within Mahango FPA and three areas, Musese, Rundu and Cuito, outside the FPA (Figure 1). From where the Kavango River enters Namibia at Katwitwi, the sampled areas were located at 90 km (Musese), 210 km (Rundu), 340 km (Cuito) and 470 km (Kwetze) in a downstream direction. Musese, Rundu and Cuito are open access areas with limited fisheries regulations, whereas Kwetze is situated within Mahango National Park (proclaimed in 1989 and 17 km in length) and is closed to fishing and unauthorised boat traffic.

All four sampling areas were regarded as prime habitats for adult *H. vittatus* (Økland et al. 2005). Hay et al. (2000) and Hocutt and Johnson (2001) confirmed spawning areas for *H. vittatus* and recorded abundant juveniles for this species at all sampled sites. The Musese sampling area (17°49’ S, 18°55’ E) is characterized by shallow waters with sandy and rocky substrates that generated numerous well oxygenated rapids. The Musese sampling area was in the mainstream of the Kavango River, and the water was usually clear with reeds present on the riverbank. This sampling area had a width of approximately 100 m, and the depth varied between 0.3 and 3.0 m. The Rundu sampling area (17°53’ S, 19°46’ E) included the densely populated areas around Rundu town. This area contained well developed floodplains with several oxbows and backwaters, although, sampling was conducted predominantly in the mainstream of the river which was approximately 100-200 m wide. The substratum was mostly sandy with some rocky outcrops. The depth varied largely within this area and ranged from relatively shallow rapids (< 1 m) to deep pools (> 12 m). The Cuito sampling area (18°01’ S, 20°47’ E) consisted mostly of rocky, sandy and gravel substrates. Similar to the Rundu area, this area contained well developed floodplains with several oxbows and backwaters. Sampling was conducted predominantly in the mainstream, and the Cuito River confluence where the river was approximately 100-200 m wide. The Kwetze sampling area (18°13’ S, 21°45’E) was situated in the Mahango Game Park where no fishing is allowed. This area is the only designated freshwater protected area (FPA) on the Kavango River. The sampling area was mainly situated in the mainstream which was approximately 100-200 m wide. The mainstream had clear flowing water with a depth of up to 7 m and a sandy substrate, with some rocky areas. This area also contained large nearly stagnant backwaters (2-3.5 m deep) with reeds along the shore.

Data collection

Catch per unit effort in numbers (CPUE), weight (WPUE), and length frequency data were obtained from 25 years of surveys that were conducted once a year in the months July - November in the period from 1994 to 2018 (Table 1). Gill nets were set at sunset (ca. 18h00) and retrieved at sunrise (ca. 06h00) with a mean fishing time of 12 h. Gill nets had nine multifilament (6 ply) fleets, which comprised 10 m long × 2 m deep panels of stretched mesh 22, 28, 35, 45, 57, 73, 93, 118 and 150 mm. According to the sampling protocol by Ministry of Fisheries and Marine Resources (MFMR), each gill net fleet was deployed at the same location in each sampling area at all sampling occasions. All fish collected were counted, weighed whole (M_T) to the nearest 0.1 g and their length measured to the nearest mm fork length (L_F).

Statistical Analysis

Sampling years and gill net effort varied to some extent at sampling areas, and included surveys to Musese for 21 years (i.e. excluding 2000, 2001, 2007, 2008) and 110 gill net efforts (net nights), Rundu for 20 years (i.e. excluding 1997, 2000, 2007, 2008, 2009) and 121 gill net efforts, Cuito for 20 years (i.e. excluding 1998, 2000, 2001, 2007, 2008) and 107 gill net efforts and Kwetze for 22 years (i.e. excluding 2000, 2007, 2008) and 97 gill net efforts (Table 1). Relative fish abundance was expressed as catch per unit effort, and is expressed in numbers (CPUE: fish/net-night) and in weight (WPUE: kg/net-night), and are calculated as:

$$CPUE = Ci/Ei$$

$$WPUE = Wi/Ei$$

where *Ci* or *Wi* are the catch of *H. vittatus i* (in numbers or weight) and *Ei* is the gill net effort. Catch per unit effort and WPUE were standardised to number or weight of fish per net-night. Pearson's correlation test was conducted to measure the strength of the relationship, or association between CPUE in numbers or weight and the Kavango River water discharge. The CPUE data were tested for normality using a Shapiro-Wilk test and for homogeneity of variance using the Levene's test. The CPUE and WPUE data were not normally distributed for each separate station, and data collected from mainstream and backwater habitats were assessed for differences using the non-parametric Mann-Whitney *U* test. The non-parametric Kruskal-Wallis H test followed by post-hoc multiple comparisons was used to compare the respective abundances, length and weight of *H. vittatus* among the sampled areas. The analyses were done using the statistical program SPSS (IBM, Armonk, NY, IBM Corp.).

To evaluate if there were changes in catches over the sampled years, the CPUE in number of the sites outside the FPA (Musese, Rundu and Cuito) were grouped and the FPA (Kwetze) was evaluated separately. In this analysis a Generalized Additive Model (GAM) technique was used (Chambers and Hastie 1992). This technique allows independent variables to have a nonlinear effect on the dependant variable as determined by a smoothing algorithm (Cieveland 1979):

$$\log(CPUE) = a + lo(t)$$

where *lo(t)* is a regression (LOESS; Chambers and Hastie 1992) smoothing function of the year. In this case the LOESS functions were of degree 1 and span parameter 0.5. We did not progress to further models with additional independent variables, such as environmental variables, because specific, set-by-set data other than catch were not available. The analysis was done in R (R version 3.4.2, R Foundation for Statistical Computing, Vienna, Austria).

Results

The combined fishing effort for all four sampling areas consisted of 435 net nights which yielded a total sample of 926 *H. vittatus* specimens with a weight of 208.35 kg (Table 1). There was no difference in CPUE between the mainstream and backwater habitats in the four areas (Musese: Mann-Whitney U-test 1966.5, $p = 0.677$, Rundu: Mann-Whitney U-test 2500.5, $p = 0.562$, Cuito: Mann-Whitney U-test 1362.0, $p = 0.587$, or Kwetze Mann-Whitney U-test 1002.0, $p = 0.603$). Therefore, mainstream and backwater efforts were combined for all further analyses.

The Kavango River had a mean water discharge of 122 ± 54 m^3/s (median 118 m^3/s, min 26 m^3/s, max 263 m^3/s) over the sampled years, and there was no correlation between water discharge and the CPUE in numbers (Musese $r(108) = 0.04$, $p = 0.05$, Rundu $r(119) = 0.03$, p = 0.06, Cuito $r(105) = 0.03$, $p = 0.78$, Kwetze $r(95) = 0.08$, $p = 0.50$) or WPUE (Musese $r(108) = 0.07$, $p = 0.56$, Rundu $r(119) = 0.08$, $p = 0.51$, Cuito $r(105) = 0.11$, $p = 0.33$, Kwetze $r(95) = 0.13$, $p = 0.22$) in the sampling areas.

The catch per unit effort in both number (CPUE) and weight (WPUE) varied among the four sampling areas (Kruskal-Wallis H test, $\chi^2_{(3)} = 36.67$, $p < 0.001$, $\chi^2_{(3)} = 51.08$, $p < 0.001$, respectively) (Figure 2a, b). CPUE was higher at Kwetze (mean rank score 275) compared to Cuito (mean rank score 226, $p = 0.016$), Rundu (mean rank 192, $p < 0.001$) and Musese (mean rank score 186, $p < 0.001$) (Figure 2a). However, there was no difference in CPUE among the three stations outside the FPA (Kruskal-Wallis H test, range $\chi^2_{(3)} = -5.79 – -33.89$, $p = 0.092 – 0.999$). Similarly, WPUE was also highest at Kwetze (mean rank score 290) compared to Cuito (mean rank score 221, $p < 0.001$), Rundu (mean rank 183 $p < 0.001$) and Musese (mean rank score 187, $p < 0.001$) (Figure 2b), which did not differ significantly from one another (Kruskal-Wallis H test, range $\chi^2_{(3)} = 3.766 – -37.87$, $p = 0.112 – 0.999$) (Figure 2b).

The length and weight of *H. vittatus* also varied among the four sampling areas (Kruskal-Wallis H test length: $\chi^2_{(3)} = 189.35$, $p < 0.001$, H test weight: $\chi^2_{(3)} = 183.00$, $p < 0.001$). *Hydrocynus vittatus* was larger in Kwetze (mean rank score 612, mode 170 mm, $n = 364$) compared to Cuito (mean rank score 376, mode 120 mm, $n = 261$, $p < 0.001$), Rundu (mean rank score 335, mode 150 mm, $n = 176$, $p < 0.001$) and Musese (mean rank score 392, mode 125 mm, $n = 125$, $p < 0.001$). There was no difference in *H. vittatus* length among Cuito, Rundu and Musese

(Kruskal-Wallis H test, range $\chi^2_{(3)} = -41.50 – 56.79$, $p = 0.417 – 0.999$). Tigerfish in the gill net catches were also heavier in Kwetze (mean rank score 610, mode 20 g, $n = 261$) compared to Cuito (mean rank score 375, mode 19 g, $n = 261$, $p < 0.001$), Rundu (mean rank score 348, mode 17 g, $n = 261$, $p < 0.001$) and Musese (mean rank score 380, mode 17 g, $n = 261$, $p < 0.001$), but there was no difference in weight among Cuito, Rundu and Musese (Kruskal-Wallis H test, range $\chi^2_{(3)} = -26.23 – 5.19$, $p > 0.05$).

Both the smallest and largest *H. vittatus* were caught in the Kwetze area (min. 55 mm, max. 630 mm) compared with the three samplings areas outside the FPA (Musese: min. 83 mm, max. 573 mm, Rundu: min. 90 mm, max. 585 mm, Cuito: min. 91 mm, max. 605 mm) (Table 1). The length distribution of *H. vittatus* also differed between Kwetze and the three other sampling areas (Figure 3). At Cuito, Rundu and Musese only 9.7-19.5% of the fish were larger than 200 mm, and most fish were between 100 mm and 200 mm. However, at Kwetze fish larger than 200 mm were numerous (65.9%) in the catches, and in this area fish between 300 and 400 mm were also frequently caught, including a few larger fish.

The grouped (Musese, Rundu and Cuito) CPUE and Kwetze CPUE in numbers were fitted with GAM models. The CPUE follows a general U-shape trend with declines in catch rates evident from 1994 to 2005 after which CPUE seems to increase marginally for both inside and outside the FPA. The GAM models show a statistically significant decline of CPUE over the sampled years for both outside ($R^2 = 0.28$, $F = 11.39$, $p < 0.001$) and inside ($R^2 = 0.18$, $F = 7.17$, $p < 0.001$) the FPA with years explaining 20.2% and 31.9% of the deviance respectively (Figure 4).

Discussion

Inland fisheries, including fisheries for the African tigerfish *Hydrocynus vittatus*, make a substantial contribution to food security and stimulation of local economies. Therefore, reports of extensive exploitation of tigerfish populations from northern Namibia have caused concern (Cooke et al. 2016), and it has been suggested that tigerfish populations in these perennial rivers of Namibia have experienced declines in catch rates (Cooke et al. 2016). However, despite the subsistence (Tweddle 2010), commercial (Abbott et al. 2015; Tweddle et al. 2015) and recreational (Cooke et al. 2016) importance of *H. vittatus*, little information is available on the status of *H. vittatus* populations and fisheries in Namibia and elsewhere.

The use of catch per unit effort data from gill net surveys is a common method for assessing fisheries stocks (Maunder et al. 2006). However, gill net fishing is a selective fishing method and catches depend among others on the mesh sizes and twine used, the vulnerability of the species to the gear used, and the size and behaviour of fishes (Maunder et al. 2006). Hay et al. (2000) studied the gill net selectivity of the gears used in the Namibian Ministry of Fisheries and Marine Resources' annual surveys in the Kavango River, and found that gillnets efficiently caught *H. vittatus* between 100 and 450 mm (L_F) with catch probability from 0.81 to 1.0, and the mesh sizes from 22 to 93 mm were the most efficient. We therefore conclude that the catch per unit effort and length frequency data presented in our study are representative for fish larger than 100 mm in the *H. vittatus* populations in the studied areas.

In the present study the catch per unit effort in number and weight was higher in Kwetze compared to Cuito, Rundu and Musese. Fish caught in the FPA (Kwetze) were larger compared to Cuito, Rundu and Musese, but no differences in weight were found among the fish from Cuito, Rundu and Musese. In addition, both the grouped (Musese, Rundu and Cuito) and Kwetze CPUE in numbers showed a downward trend over the sampled years supporting the hypothesis that these areas are subject to overfishing. The downward trend in the FPA is especially a cause for concern as this area is closed to fishing and by default should not be subject to overfishing.

This study documented differences in the *H. vittatus* populations in the study area inside the FPA versus the areas outside the FPA. Early data in the FPA are indicative of an unexploited fish population, but the documented decline shows that the FPA is negatively affected by exploitation of this species outside the FPA. Jacobs et al. (2020) showed that tigerfish moved from the FPA to other areas of the Kavango River. This indicates that the populations inside and outside of the FPA are connected. Therefore, exploitation of the species outside the FPA will also negatively affect the populations inside of the FPA. The catch per unit effort and length distribution of *H. vittatus* in the three areas outside the FPA indicate that these areas might be affected by overexploitation. In these areas the catch per unit effort indicates reduced populations of *H. vittatus*, and the size distribution indicate a reduction in the number of mature individuals (fish larger than approximately 200-300 mm). The body length at 50% maturity of *H. vittatus* in the Kavango River was approximately 180 mm F_L for males and 280 mm F_L for females (Hay et al. 2000). If as indicated in our study, the proportion of fish outside the FPA larger than 200 mm were approximately a quarter of that inside the FPA (10-20% vs 65%), the spawning population of *H. vittatus* might be severely depleted outside the FPA. This corresponds to what Beamish et al. (2006) describes as longevity overfishing, and possibly also is a sign of recruitment overfishing (Gulland 1983) of these populations.

Telemetry studies of adult *H. vittatus* movements in the Kavango River showed that the fish displayed two behavioural patterns, where 65% of the individuals had high site fidelity utilising areas less than 33 km, while the rest of the individuals undertook longer movements of up to at least 397 km from the tagging site (Jacobs et al. 2020). Hence, some *H. vittatus* tagged in the Kwetze study area in Mahangu FPA moved to all the other areas sampled outside the FPA. Even though *H. vittatus* are highly fecund, fast growing and appear to disperse over large distances (Kenmuir 1973; Steyn et al. 1996; Gerber et al. 2009; Jacobs et al. 2020), the catch per unit effort of *H. vittatus* outside the FPA were significantly lower than inside the FPA, and the fish in the catches were substantially smaller and the proportion of mature fish reduced. This may indicate that the fish are exposed to considerable fishing exploitation in these areas causing negative changes in the fish population structure and its recruitment potential. Pollution, habitat degradation, and environmental changes driven by global warming are considered to have minimal impact at present, but this may change in future due to current developments upstream in Angola.

Jacobs et al. (2020) suggest that freshwater protected areas may be a useful management tool to improve negative consequences of fishing. They found that an FPA of 2–5 km in Kavango River could protect 26-35% of the adult *H. vittatus* population for at least 75% of the time, whereas protection of 10 km river length could protect at least 50% of the *H. vittatus* for at least 75% of the time. Similarly, a no-fishing reserve in Lake Kariba (Zimbabwe) was successful in increasing both the number and size of several freshwater fish species (Sanyanga et al. 1995). Elsewhere, FPAs have also been found to be effective in preserving freshwater fishes (Hermoso et al. 2016). In Cambodia’s Tonle Sap, Hannah et al. (2019) showed that

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management through FPAs could result in increased harvest and greater economic returns in an indiscriminate fishery.

Sustainable management of the Namibian fish stocks, within rivers and floodplains is of utmost importance to safeguard the livelihoods of riparian communities and the associated economic spinoffs from these resources (Tvedten et al. 1996; Welcomme 2011; Youn et al. 2014). The reduction in catch per unit effort in numbers of larger specimens, as documented in our study, is one of the main consequences of overfishing (Welcomme 1999; Allan et al. 2005). This gives reasons for concern as the recorded effects of overfishing are likely to have impact on the livelihoods of local fishing communities as well as the tourist industries, and negatively influence the economy in the rural areas (Tweddle et al. 2015; Cooke et al. 2016).

The major inland fisheries in Namibia are the artisanal fisheries that predominantly utilise gillnets, but also, to some extent, use traditional gears and rod and line (Tvedten et al. 1996; Cooke et al. 2016). In addition, recreational fishing is an important contributor to the local economies as the tourist industry is often the only source of formal employment for local communities (Tweddle et al. 2015; Cooke et al. 2016). Lately, increased use of potentially detrimental fishing practices, such as monofilament gill nets, drag and seine netting, “bashing” in combination with gill netting, have been documented in the nearby Zambezi River (Tweddle et al. 2015; Cooke et al. 2016). The increased fishing effort using these methods depleted the larger bodied fishes such as *H. vittatus* and cichlids which are considered both highly important subsistence and recreational species (Tweddle et al. 2015; Cooke et al. 2016). In Namibia, the increased fishing effort with these gears, driven by the increased commercialisation of the fisheries, has resulted in a 90% reduction in the CPUE of large cichlid species in the Upper Zambezi (Tweddle et al. 2015). This reduction in cichlids has resulted in fishers increasingly targeting *H. vittatus* populations using specialised gear such as drifting gillnets and drag nets (Cooke et al. 2016). Similar increased unsustainable fishing methods of the Kavango River fisheries are evident within this river system and our results indicate that there is an immediate need for more effective management tools to sustain the *H. vittatus* populations. In addition, the fisheries regulation in Namibia states that the minimum gill net mesh size allowed is 45 mm, which puts an increased fishing pressure on larger individuals. In the fisheries regulation there is an effort restriction with regard to number of nets per fisher. However, control of this

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effort regulation is poor. A further complication for fisheries management of the Kavango River in Namibia, is the sharing of the river and fisheries resources with Angola and to some extent with Botswana. *Hydrocynus vittatus* moves between the countries (Jacobs et al. 2020), while management regulations and fisheries control are not consistently enforced. Hence, overexploitation of fish species in one country will also affect the fisheries in the other countries.

To conclude, *H. vittatus* populations are declining in exploited areas, and the results from this study show evidence of overfishing. *Hydrocynus vittatus* is considered a key ecological species and important for the food-web ecology. Hence, a population decline from longevity overfishing can result in major changes in the fish communities and potential loss of ecosystem services. Based on the negative consequences of longevity overfishing and non-sustainable fisheries for the local communities, we recommend that immediate actions should be taken to implement sustainable management of the valuable fisheries resources of the larger and more long-lived species in the Kavango River in particular, and the perennial rivers in northern Namibia in general.

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Resources of Namibia to improve the sustainable development and utilization of inland fisheries resources. We are grateful for the constructive comments of the reviewers.

Conflict of interest

The authors declare no competing financial interests.

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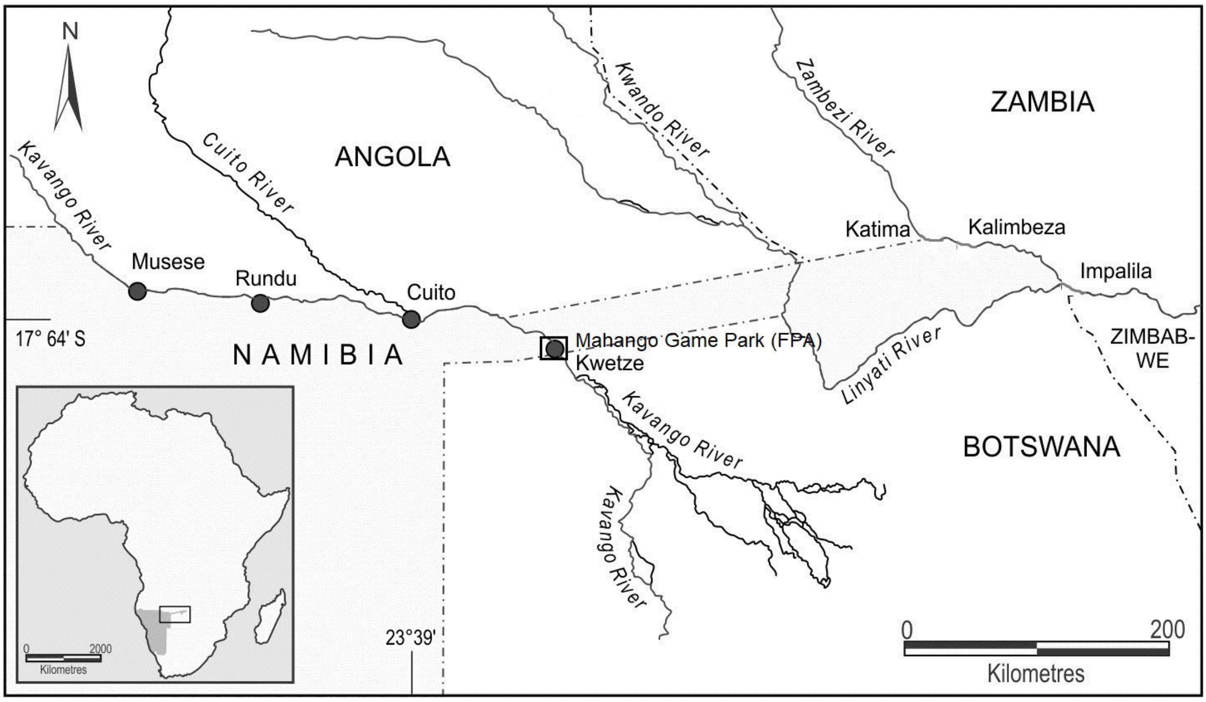

Figure 1: Locations of sampling areas for the annual gill net surveys of *Hydrocynus vittatus* in the Kavango River in Namibia from 1994 to 2018. The four areas were sampled were the Musese, Rundu, Cuito and Kwetze.

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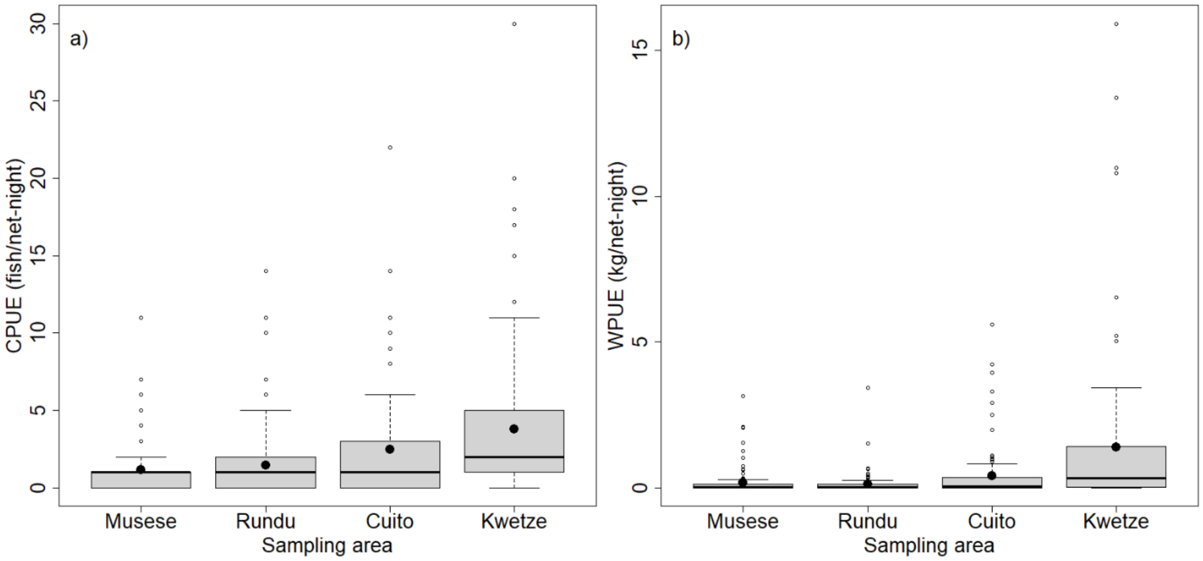

Figure 2: Catch per unit effort in (a) number (CPUE) and (b) weight (WPUE) of *Hydrocynus vittatus* caught in the annual gill net surveys of Musese, Rundu, Cuito, and Kwetze areas in the Kavango River over the period 1994 – 2018. The bottom and top of the box represent the 25th and 75th percentiles (i.e. the boxes include the middle 50% of the observations). The whiskers span to the most extreme data point, which was no more than 1.5 times the interquartile rage, the bold horizontal line represents the median value, and the black point represents the mean value.

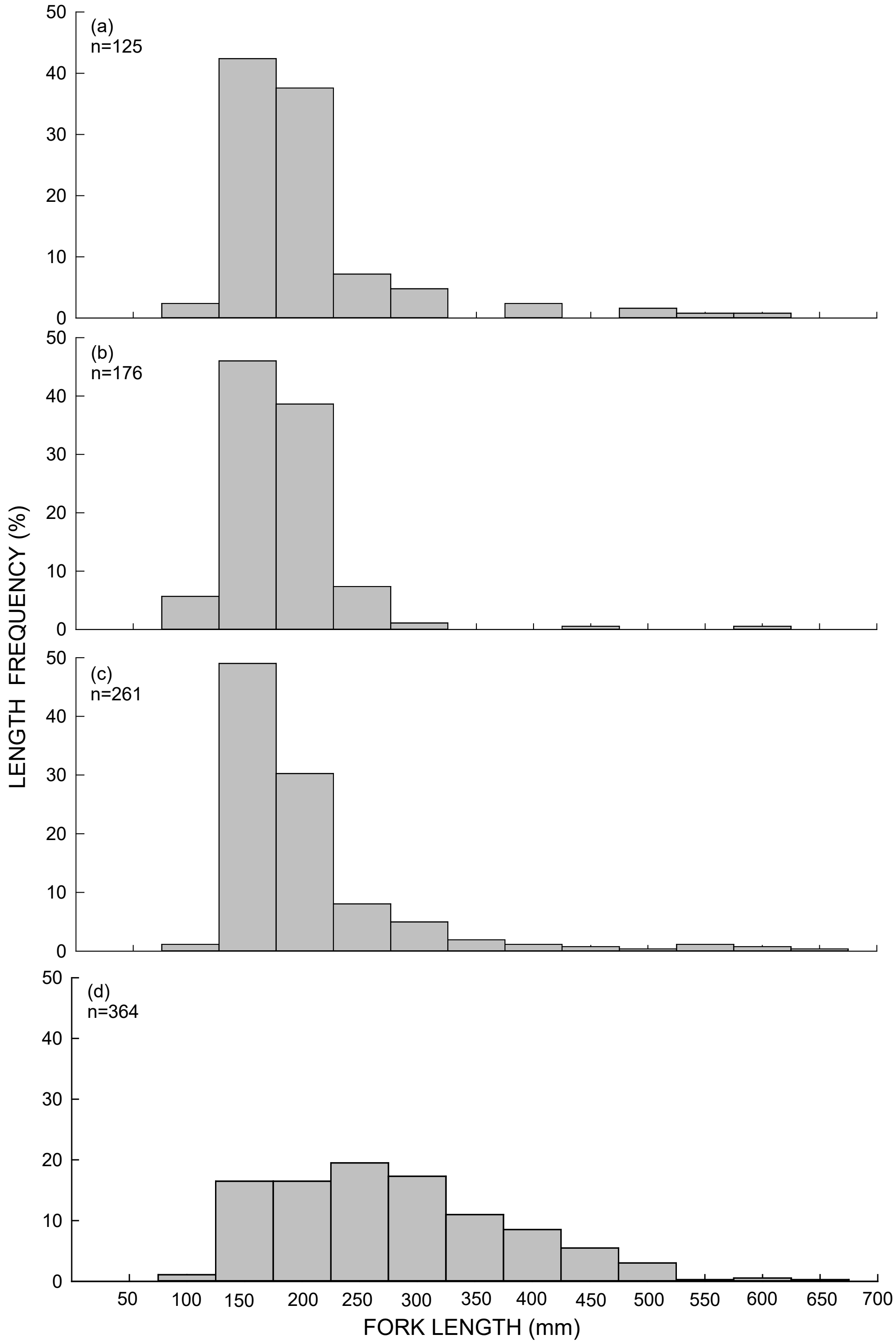

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Figure 3: Length frequency histograms for *Hydrocynus vittatus* caught during the annual gill

580 net surveys at (a) Musese, (b) Rundu, (c) Cuito, and (d) Kwetze areas in the Kavango River

over the period 1994 – 2018.

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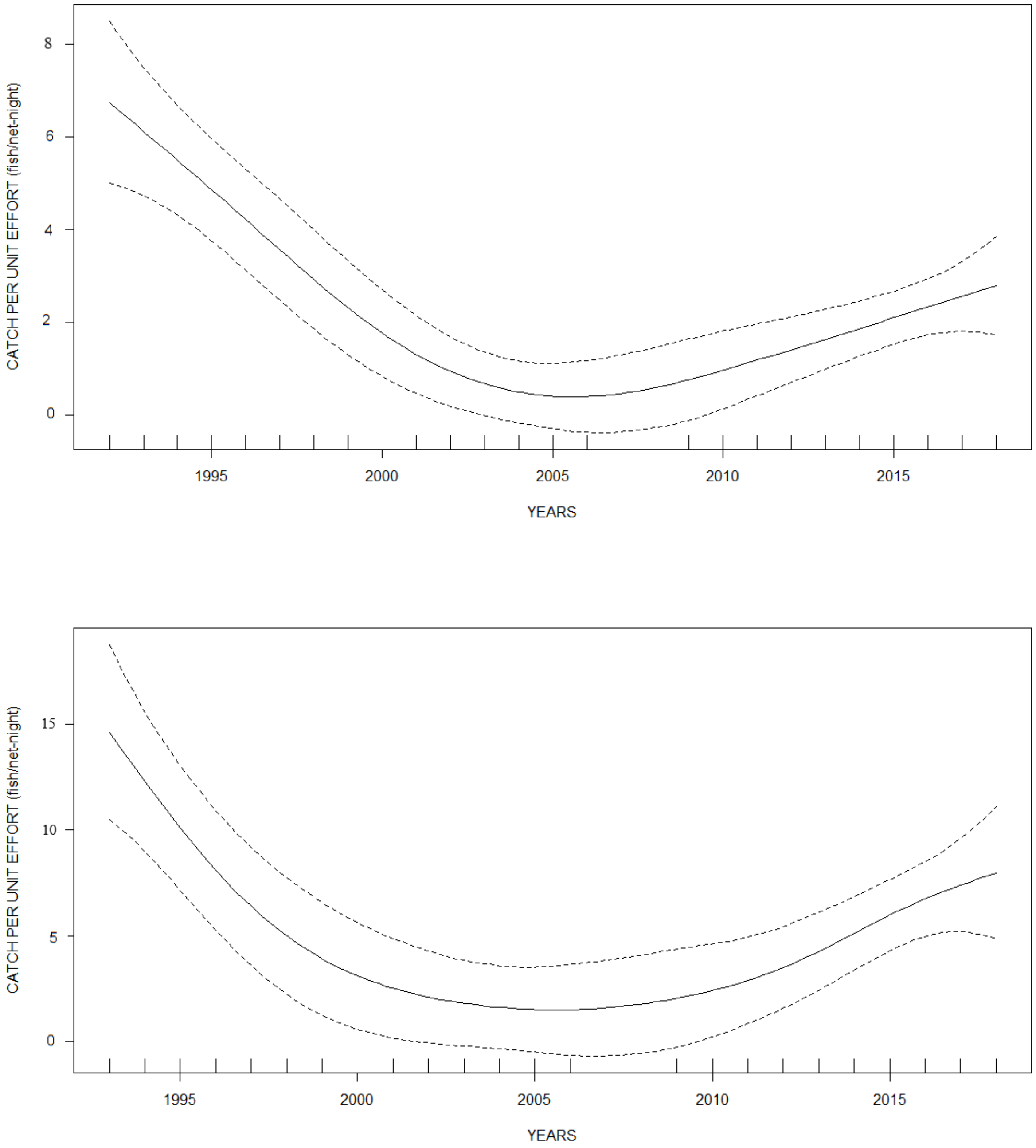

Figure 4: General additive model of the catch per unit effort in number (CPUE) for *Hydrocynus vittatus* caught during the annual gill net surveys for: (a) outside the Freshwater Protected Area (i.e. Musese, Rundu and Cuito combined), and (b) inside the Freshwater Protected Area (Kwetze) over the period 1994 – 2018.

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