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Implications of the movement behaviour of African tigerfish *Hydrocynus vittatus* for the design of freshwater protected areas

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Abstract

African tigerfish *Hydrocynus vittatus* (n = 35) were tagged with external radio-transmitters in the Kavango River, Namibia, to determine whether freshwater protected areas could be an effective tool for the management and conservation of this species. They were manually tracked in the core study area of 33 km every *c*. 12 days from July–October 2016 to May 2017 for between 123 to 246 days. In addition, 14 extended surveys were carried out for up to 680 km to determine the total area use of the tagged individuals. Tigerfish displayed at least two behavioural patterns either having high site fidelity with shorter movements or using larger areas with longer movements. Twenty-three (66%) of the tigerfish had high site fidelity using an area of less than 33 km of river, whereas 12 tigerfish (34%) undertook long distance movements of up to 397 km upstream and 116 km downstream from their tagging locations. During the long-distance movements tigerfish crossed the territorial boundaries of Angola, Namibia and Botswana. Of the 35 fish that were monitored, 14 (40%) spent more than 80% of the monitored time in the 33 km study area and 18 (51%) stayed within the study area for at least 50% of the monitored time. These findings suggest that freshwater protected areas may be a useful management tool and we predict that a protected river area of 2–5 km river length could protect 25.9–34.6% of the population for at least 75% of the time whereas protection of 10 km river length could protect at least 50% of tigerfish for at least 75% of the time.

KEYWORDS

area use, behaviour, freshwater protected area, Kavango River, radio tracking, tigerfish

1 | INTRODUCTION

Knowledge about area use by freshwater fishes, such as for feeding, spawning and colonisation of new habitats, is important for managing fish populations (Jungwirth *et al*., 2000). In Africa, there is scant information on area use by most freshwater fish species and this has constrained the effective management of many fishes (Økland *et al*., 2005; Stiassny, 1996). This is of concern as many fish populations

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have come under increasing pressure and declining catch rates, particularly of the larger, more valuable species (Cooke *et al.*, 2016; Tweddle *et al.*, 2015). One of these species is the African tigerfish *Hydrocynus vittatus* Castelnau 1861, a large predatory fish species that is endemic to the African continent (Goodier *et al.*, 2011), is important in small-scale fisheries and, is one of the most sought after species by recreational anglers (Abbott *et al.*, 2015; Cooke *et al.*, 2016).

Freshwater protected areas (FPA) are a promising management and conservation approach for freshwater fishes (Bower *et al.*, 2015). FPAs are modelled on marine protected areas (Hermoso *et al.*, 2016; Suski & Cooke, 2007) where benefits, including the spill-over of fish from protected areas to increase fish biomass and yield in adjacent fished areas, are well documented (Green *et al.*, 2014; Lester *et al.*, 2009, 2017). To be effective, FPAs need to afford protection for a considerable portion of the lifetime of a fish and knowledge of the life-history, movement and migration behaviour of the target species is required if FPAs are to be designed appropriately (Cooke *et al.*, 2012).

Tigerfish are periodic life-history strategists (*sensu* Winemiller & Rose 1992) that attain fork lengths (L_F) of 105 cm and total mass (M_T) of 16.1 kg (IGFA, 2019). Growth is rapid with females attaining lengths >400 mm L_F at *c.* 4 years of age (Gerber *et al.*, 2009; Hay *et al.*, 2000). They are iteroparous and maturity is attained at 4 years of age for both sexes and longevity for this species is *c.* 20 years (Gerber *et al.*, 2009). Fecundity is high with 780,000 ova recorded from 650–700 mm L_F fish (Steyn *et al.*, 1996). Spawning behaviour remains largely speculative, but potamodromous behaviour, with migrations and spawning associated with rising water levels have been reported by several authors (Jackson, 1961; Kenmuir, 1973; Langerman, 1980; Merron & Bruton, 1988). Eggs are negatively buoyant and slightly adhesive for benthic or epibiotic attachment (Steyn *et al.*, 1996). Juveniles are common in floodplains where they feed mainly on zooplankton and small aquatic insects until they become predominantly ichthyophagous at lengths >70 mm total length (L_T; Gaigher, 1970; Holden, 1970; Kenmuir, 1975). In contrast to the relatively comprehensive knowledge on the biology and ecology of this species, information on the movement and migration behaviour of tigerfish is scant. Badenhuizen (1967) and Kenmuir (1973) observed tigerfish migrations up the rivers flowing into the newly constructed Lake Kariba. Økland *et al.* (2005) using radio telemetry in the Zambezi River reported mean total distance moved by individual tigerfish of 26 km and individual means ranged from 0.5 to 105 km.

To contribute towards a better understanding of the movement ecology of tigerfish and inform FPA design, we present results of tracking 35 radio tagged adult individuals within a core study area of 33 km of river and in an extended area of 680 km of the Kavango River, south-west Africa. The purpose of the study was to assess the area use of adult tigerfish in this river and to use the results to determine what size FPAs might be effective in providing adequate protection for this fish.

2 | MATERIALS AND METHODS

This research was conducted under the mandate of the Ministry of Fisheries and Marine Resources of Namibia to improve the sustainable development and utilisation of inland fisheries resources.

2.1 | Study area

The Kavango (Cubango in Angola and Okavango in Botswana) River originates from several headwater streams on the southern slopes of the Angolan highlands and drains a total catchment of 115,000 km^2 (McCarthy *et al.*, 2000). The river meanders south–south east from the Angolan highlands and reaches the Namibian border at Katwitwi (17° 23′ 23″ S, 18° 25′ 17″ E) in the Kavango West region (Figure 1). The river then turns east and forms a 415 km long border between Namibia and Angola (Hocutt & Johnson, 2001). Two major tributaries enter the Kavango River (Figure 1). The Omatako River from the south, which is an ephemeral river that seldom flows and the perennial Cuito River from the north. The Kavango River then turns south for 53 km passing through Popa Falls game park and Bwabwata national park, before it enters the north-west of Botswana forming the Okavango Panhandle. Thereafter the Kavango River terminates in the 15,000 km^2 Okavango Delta (McCarthy & Ellery, 1998).

The Mahangu Game Park is situated on the western bank of the Kavango River and extends for 17 km downstream to the Botswana border. The eastern bank is situated in a protected area (Taylor *et al.*, 2017). The core study area ranged from Popa Falls game park (18° 07′ 03″ S, 21° 35′ 01″ E) downstream to the Botswana border (18° 15′ 16″ S, 21° 47′ 06″ E). This section of the river was 33 km long, 100–200 m wide in the mainstream and had a maximum depth of 7 m in the mainstream during the flood season. The study section of river had mostly sandy substrate, with some rocky areas, especially the area close to Popa Falls game park. This river section also has large backwaters (2.0–3.5 m deep) that are bounded by floodplains (Hay *et al.*, 1996; Taylor *et al.*, 2017).

2.2 | Fish capture and tagging

Radio-tagging of tigerfish was conducted within the Mahangu and Buffalo core areas of Bwabwata national park (Figure 1). Forty-nine tigerfish were caught with standard recreational fishing gear similar to Smit *et al.* (2009) from a boat between 21 June and 22 October 2016 (Table 1). On capture, each fish was guided into a soft weighing sling before being lifted and placed in a 50 l aerated water-filled container into which 2-phenoxy-ethanol, 0.3 ml l^{-1}, had been added as anaesthetic (O'Brien *et al.*, 2012). Once the fish was anaesthetised, it was moved into another 50 l aerated water container with circulating freshwater from the river to start the recovery process. The tagging method was based on Økland *et al.* (2005). While in an anaesthetised state, stainless steel hypodermic needles were inserted through the musculature below the dorsal fin of the fish. Orthopaedic wires (0.65 mm diameter) were threaded through the hypodermic needles

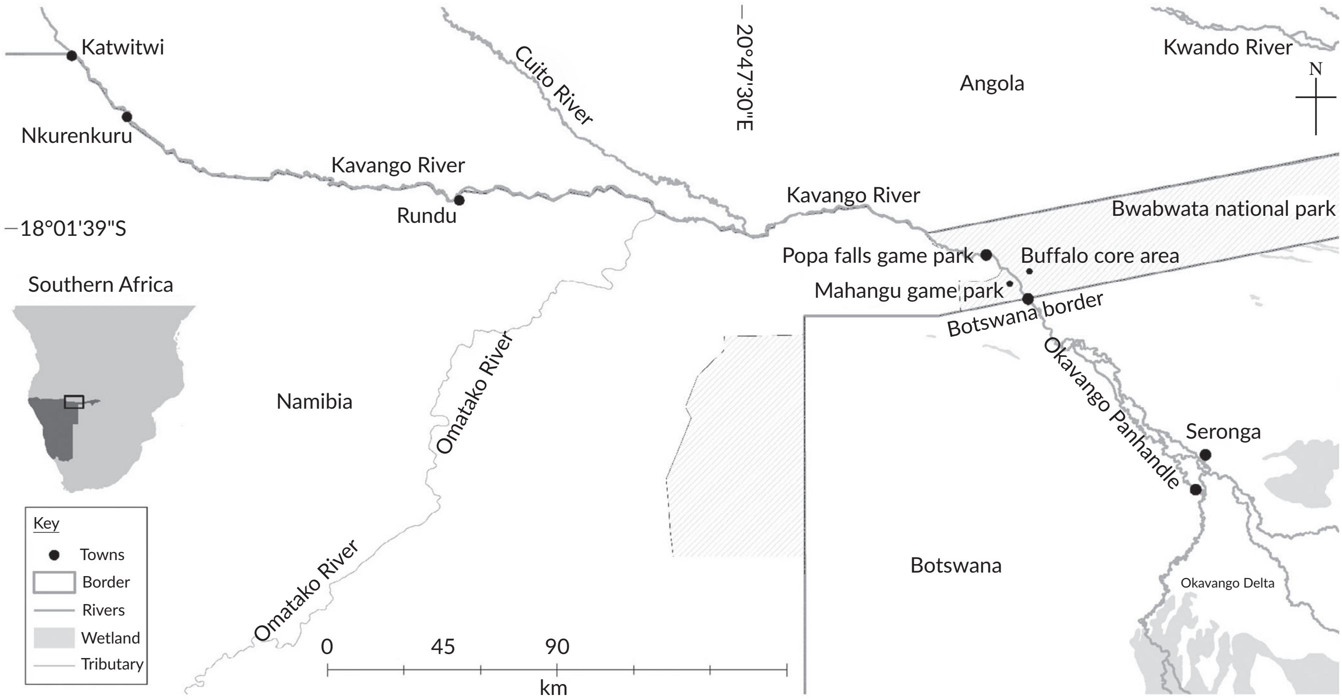

FIGURE 1 The area of the Kavango River, Namibia, were movement of tagged African tigerfish *Hydrocynus vittatus* was studied. Fish were caught, tagged and released in the Mahangu game park and Buffalo core area and tracking was carried out predominantly from Popa Falls game park to the Botswana border. Additional tracking surveys were conducted from Katwitwi in Namibia downstream to the end of the Okavango Panhandle near Seronga in Botswana

and used to firmly secure the external radio transmitters, 16 g in air and 55 × 20 × 11 mm (Model F2120, Advanced Telemetry Systems, Inc.; www.atstrack.com) by twisting and locking the ends of the wire against a plastic back-plate. The tagging procedure lasted about 2 min and total recovery time ranged between 2 and 5 min, which was similar to Økland *et al*. (2005). During the recovery period L_F (mm) and M_T (g) were measured and recorded for each individual. Air exposure was kept to a minimum, never >10 s. Each fish was continuously observed in the recovery container until it exhibited increased tail beats and normal operculum movement. Once this was observed, the fish was transferred back to the river and held loosely by the caudal peduncle. If fish could not swim away, gills were ventilated by moving the fish back and forth until it swam away. All fish were subsequently released at their capture site. It was not possible to sex the tigerfish based on external characteristics.

2.3 | Tracking

Positioning of tigerfish was undertaken during daylight hours and tracking was conducted from a boat using a portable receiver (Model R2100 Advanced Telemetry Systems, Inc.) connected to a four-element Yagi antenna. Fish were located using signal strength triangulation with a precision of *c*. ±10 m; hence, movements <10 m were classified as stationary. The fish were tracked every *c*. 12 days over the same 33 km stretch of river in the core study area from Popa Falls game park to the Botswana border (Figure 1). To find tigerfish that could not be located in the core study area, long distance tracking was undertaken to locate fish beyond the study area to determine the possible fate and total river length that tigerfish used during this study. Long-distance tracking surveys included four surveys from Katwitwi to Rundu (200 km), two surveys from Rundu to Cuito (135 km), six surveys from the Cuito River to Popa Falls Game Park (105 km) and two surveys from the Mahangu game park lower boundary down the Botswana Panhandle (210 km; Figure 1).

2.4 | Environmental data

During the monitoring periods, water temperature was recorded at each individual's location every time it was positioned (Elite-3x echo sounder, Lowrence; ww2.lowrance.com) between July 2016 and May 2017. During the study period the mean (±SD) water temperature was 24.3 ± 3.9°C (median 25.9°C, range 16.2–31.1°C; Figure 2). The study period included the annual flood cycle (Figure 2) and fish were monitored during receding, low, rising and high-water levels. The daily mean (±SD) water-discharge, recorded by the University of Botswana and the Okavango Research Institute, Botswana, at the Mohembo hydrological measuring station *c*. 3.5 km downstream of the core study area, was 243 ± 107 $m^3\ s^{-1}$ (median 237 $m^3\ s^{-1}$, range 82–446 $m^3\ s^{-1}$; Figure 2).

2.5 | Data analyses

Data from 14 of the tagged fish were excluded from the analyses because 11 fish could not be located for the whole period (up to 22 February 2017), a monitoring period necessary to include the

TABLE 1 African tigerfish *Hydrocynus vittatus* tagged in the Kavango River, Namibia, June–October 2016, including tag number (No.), tagging date, fork length (L_F, mm), total mass (M_T, g), total number of positional fixes, monitored period and last tracking date during the study (fish not tracked up to 22 February 2017 or recaptured by anglers are excluded from the table)

No.	Tagging date	L_F (mm)	M_T (g)	Total number of fixes	Monitored period (days)	Last tracking date
1	21/06/2016	510	1750	33	246	04/06/2017
2	21/06/2016	594	3240	39	246	04/06/2017
3	23/06/2016	535	2240	38	244	04/06/2017
4	23/06/2016	590	3540	19	244	03/06/2017
5	23/06/2016	549	3210	17	244	04/06/2017
6	25/06/2016	558	3270	19	242	04/06/2017
7	25/06/2016	490	1950	20	242	03/06/2017
8	25/06/2016	760	6011	14	242	04/06/2017
9	28/06/2016	603	4220	38	239	07/06/2017
10	28/06/2016	570	3320	23	239	04/06/2017
11	16/07/2016	590	3080	39	221	03/06/2017
12	17/07/2016	525	2400	12	220	04/06/2017
13	17/07/2016	530	2300	39	220	04/06/2017
14	19/07/2016	490	2300	15	218	03/06/2017
15	19/07/2016	610	4008	20	218	04/06/2017
16	19/07/2016	483	1980	39	218	04/06/2017
17	19/07/2016	485	1800	39	218	04/06/2017
18	26/07/2016	575	2990	39	211	04/06/2017
19	27/07/2016	510	2420	37	210	22/02/2017
20	27/07/2016	505	2300	10	210	03/06/2017
21	28/08/2016	615	4200	3	178	04/06/2017
22	02/09/2016	485	2200	6	173	04/06/2017
23	10/09/2016	550	2630	26	165	07/06/2017
24	10/09/2016	615	4640	5	165	04/06/2017
25	28/09/2016	495	2200	25	147	04/06/2017
26	28/09/2016	568	3260	23	147	04/06/2017
27	19/10/2016	580	2390	11	126	04/06/2017
28	19/10/2016	570	3130	22	126	02/05/2017
29	19/10/2016	573	3250	11	126	22/02/2017
30	20/10/2016	505	1840	15	125	04/06/2017
31	21/10/2016	568	3800	26	124	07/06/2017
32	21/10/2016	615	3860	11	124	07/06/2017
33	22/10/2016	500	1500	14	123	04/06/2017
34	22/10/2016	530	2720	26	123	04/06/2017
35	22/10/2016	655	3900	26	123	04/06/2017

spawning period. One tigerfish was caught by a crocodile *Crocodylus niloticus* 2 days after it was released (F.J. witnessed attack and retrieved tag) and two more tigerfish were reported recaptured and released by anglers, which might have influenced their behaviour. The final dataset, therefore, comprised 35 individuals (Table 1). To avoid possible effects of the tagging procedure only fish positions recorded 14 days after tagging were used in the dataset (Økland *et al*., 2005). The minimum distance moved for each individual tigerfish was calculated using the locate-features-along-route tool in ArcMap 10.5 (Environmental Systems Research Institute, Inc.; www.esri.com). The movement directions (upstream or downstream) were defined as the direction and shortest distance in the river between two spatial tracking points. It is plausible, therefore, that tigerfish moved further and the recorded distance was considered a minimum total distance moved. Total distance moved was $\log_{10}$ transformed to meet the assumption of normality after testing with Kolmogorov–Smirnov test. A general linear model (ANOVA) was used to test the effect of L_F, number of days monitored, water temperature and water discharge

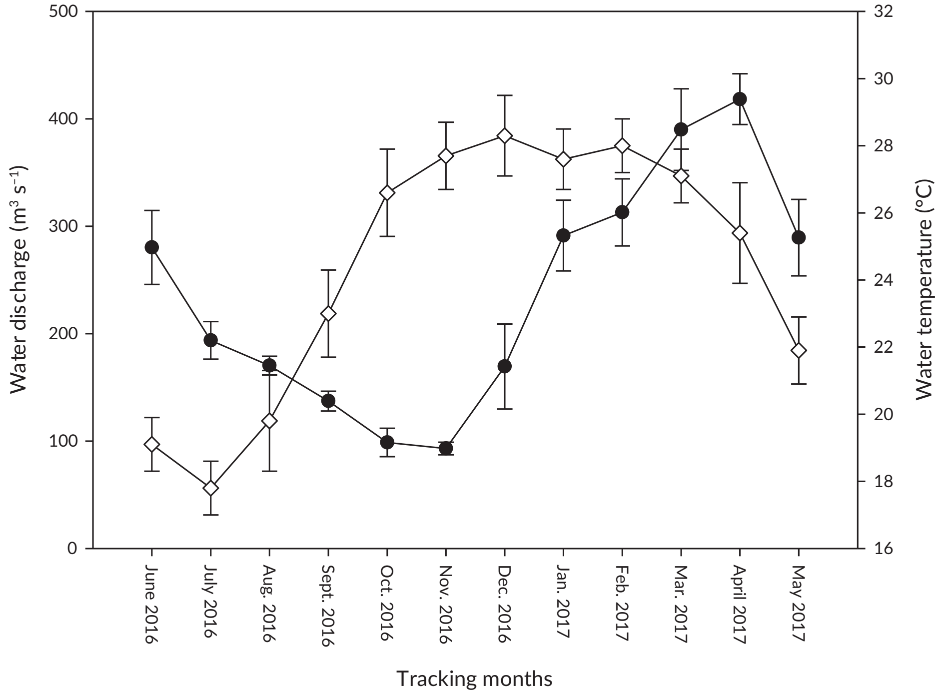

FIGURE 2 The monthly (mean ± SD) water discharge (–●–) and water temperature (–◇–) collected in the Kavango River, Namibia, during the study period from June 2016 to May 2017

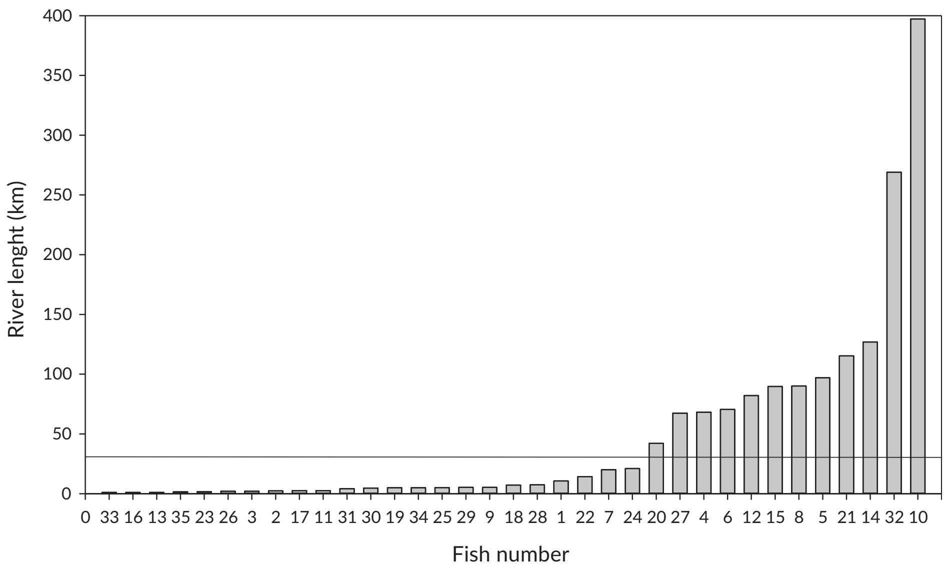

FIGURE 3 The total minimum river length used by individual radio tagged African tigerfish *Hydrocynus vittatus* in the Kavango River, Namibia from June–October 2016 to May 2017. ‐‐, The length of the core study area

on total distance moved, with total distance as the dependent variable and tigerfish L_F, number of days monitored, temperature and water discharge as the independent variables. To test the effect of temperature and discharge, the percentage of time that tigerfish spent inside the core study area (*i.e.*, Popa Falls game park to Botswana border) was calculated from the total number of days in relation to the total days each individual was monitored. If an individual was not tracked inside the study area at a tracking survey, an assumption was made that the individual had spent half the time since the last tracking survey inside and half of the time outside the study area.

To predict the potential river length needed to design an FPA in the Kavango River from the recorded tigerfish movements, river areas were defined according to lengths of 0–2, 2–5, 5–10, 10–15 and 15–20 km. The total distance each individual moved in relation to their tagging location was calculated using the locate-features-along-route tool in Arc Map 10.5. If the distance was inside a river length of 0–2, 2–5, 5–10, 10–15 and 15–20 km it was given the value 1, if it was outside it was given the value 0. The time between each tracking position was calculated and the days spent inside (value = 1) were calculated by summarising all the days spent inside randomly selected river lengths (*i.e.*, 0–2, 2–5, 5–10, 10–15 and 15–20 km). If an individual moved from one river length to another between two consecutive tracking events, the numbers of days between the tracking were divided between the two river lengths. The percentage of monitored time spent inside an area was calculated by dividing the time spent inside an area divided by total monitoring time, multiplied by 100.

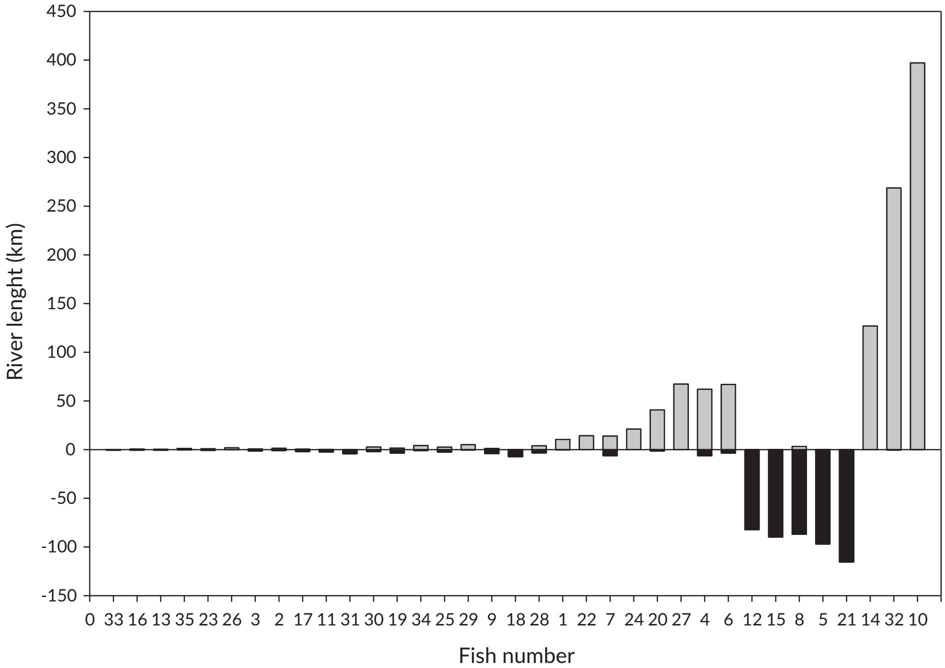

FIGURE 4 Upstream (▭) and downstream (▬) river length used by individual radio tagged African tigerfish *Hydrocynus vittatus* during the radio-telemetry study in the Kavango River, Namibia, June–October 2016 to May 2017

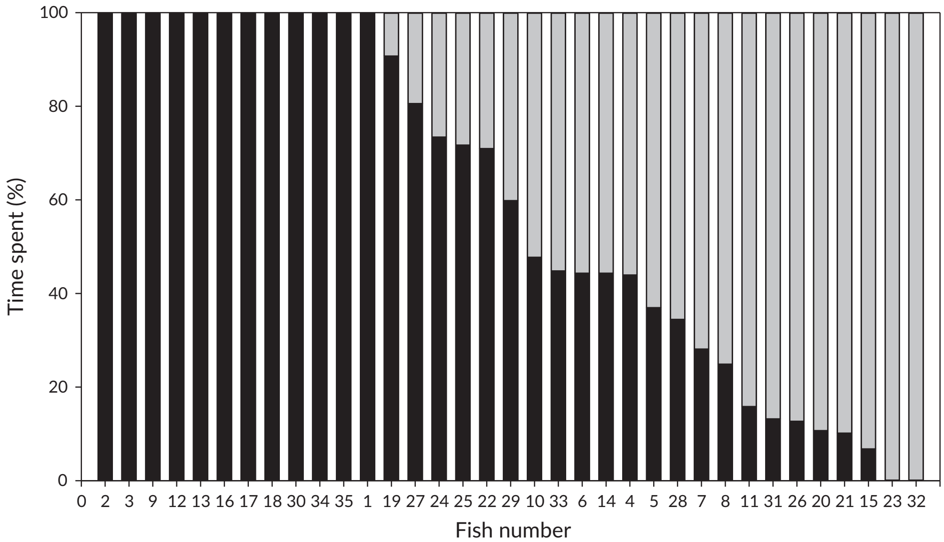

FIGURE 5 The distribution of time spent by individual radio tagged African tigerfish *Hydrocynus vittatus* spent inside (▬) or outside (▭) the 33 km study area from Popa Falls game park to the Botswana border in the Kavango River, Namibia, June–October 2016 to May 2017

TABLE 2 The frequency distribution, by number and percentage of total number (in parentheses), of time spent by tagged and monitored African tigerfish *Hydrocynus vittatus* within designated lengths of the Kavango River, Namibia, June–October 2016 to May 2017

	River length (km)				
Time spent inside area (%)	**2.0**	**5.0**	**10.0**	**15.0**	**20.0**
<25	16 (59.3)	13 (50.0)	7 (29.2)	3 (15.0)	3 (21.4)
25–50	2 (7.4)	7.7 (2)	2 (8.3)	2 (10.0)	2 (14.3)
50–75	2 (7.4)	7.7 (2)	2 (8.3)	2 (10.0)	1 (7.1)
>75	7 (25.9)	9 (34.6)	13 (54.2)	13 (65.0)	8 (57.1)
Total number of fish	27	26	24	20	14

3 | RESULTS

3.1 | Fish samples

The 35 tigerfish used in the analyses measured 555 ± 59 mm L_F (median 550 mm L_F, range 483–760 mm L_F) and M_T = 2954 ± 968 g (median 2800 g, range 1500–6011 g). As their size exceeded the 400 mm L_F at maturity for female fish (Gerber *et al*., 2009), it was assumed that all fish used in this study were adults.

3.2 | River length used

Tagged fish were monitored for between 123 and 246 days, depending on the individual. From the telemetry data, two basic movement patterns were distinguished, sedentary and high mobility, with each tracked fish conforming to one of the two behaviours (Figure 3). Of the monitored 35 tigerfish, 23 individuals (66%) were only found in the smaller (33 km) core study area between Popa Falls game park and the Botswana border. Twelve tigerfish (34%) used a river length larger than the core study area, of which four individuals moved more than three times the length of the study area (range 115.3–397.3 km, mean 227.1 km, median 198.0 km) (Figure 3); with one individual using a minimum upstream river length of 397.3 km. Neither the length of the tracking period (number of days) or L_F had an effect on the size of the total area used by the fish (days vs. area: ANOVA, $F_{1,33}$ = 1.064, $P > 0.05$, R^2 = 0.010; L_F *v*. area: ANOVA, $F_{1,33}$ = 1.949, $P > 0.05$, R^2 = 0.06). Similarly, neither temperature nor water discharge had an effect on the size of the total area used by tigerfish (temperature *v*. area: ANOVA, $F_{1,33}$ = 1.249, $P > 0.05$, R^2 = 0.06; water discharge *v*. area: ANOVA, $F_{1,33}$ = 0.226, $P > 0.05$, R^2 = 0.06).

3.3 | Time spent inside the core study area

The 35 tagged tigerfish used both upstream and downstream areas from the tagging point (Figure 4). Individual fish that used areas larger than the 33 km core study area displayed a directional movement, using areas either upstream or downstream of the tagging site. The time that the tigerfish spent inside the core study area of 33 km (Figure 1) ranged from 0 to 100%. Of the 35 fish monitored, 11 (31%) were never recorded outside the core study area (Figure 5). Fourteen (40%) spent more than 80% of the time monitored in this area and 18 (51%) stayed within the area at least 50% of the monitored time (Figure 5). None of the monitored fish returned to the core study area of 33 km after having left the area.

3.4 | Length of protected area *v*. area use

To predict the potential design of an FPA based on various river lengths, the percentage of time tigerfish spent inside various lengths of the river during the study period (123 to 246 days) was calculated. Based on the results an FPA of 2–5 km will provide protection for 26–35% of the tigerfish for at least 75% of the time and a 10 km long FPA will provide protection for at least 50% of the tigerfish for at least 75% of the time (Table 2).

4 | DISCUSSION

4.1 | River use

Individual tigerfish monitored during this study either, remained within the well-defined core area of the study (<33 km of the river), or they undertook longer movements of up to 379 km upstream and 116 km downstream from their tagging sites. Therefore, the total length of river used by tigerfish during this study was 513 km. This substantially exceeds the previous estimate of individual means that ranged from 0.5–105.9 km river length recorded by Økland *et al*. (2005) for this species in the Zambezi River. As individual fish were located in both upstream and downstream areas from the sampling location and therefore did not follow a clear directional and synchronised movement pattern, their movements do not conform to the definition of migrations (Northcote, 1978) but rather dispersal to find better resources and conditions (Lucas *et al*., 2001).

In the context of the current study, the fish moved between river sections in Angola, Namibia and Botswana, which highlights the need for international cooperation in the management of this species. The resident behaviour of some individuals in this study is similar to observations by Økland *et al*. (2005), showing that not all tigerfish undertake annual large-scale movements. Badenhuizen (1967), Kenmuir (1973) and Bowmaker (1973), however, observed migrations of tigerfish from the man-made Lake Kariba into inflowing rivers during summer, which suggests that in lentic environments this species may undertake coordinated spawning migrations. Although the current study included the spawning period (austral summer), no inference could be made regarding spawning migrations as coordinated mass-movement was not observed. It may be possible that tigerfish, being long-lived and iteroparous, may not spawn every year. This skip-spawning is documented in several other fish species such as walleye *Sander vitreus* (Mitchill 1818) (Johnston & Leggett, 2002), whitefish *Coregonus albula* (Linnaeus 1758) (Sandlund *et al*., 1991) and *Labeo cylindricus* Peters 1852 (Weyl & Booth, 1999), but has not been explored in tigerfish.

4.2 | Relevance to freshwater protected areas

Although this study was limited to movement of adult tigerfish in the Kavango River, the data indicate that a protected area of 2–5 km could protect 26–35% of the studied population for at least 75% of the time, whereas 10 km could protect at least 50% of the studied population for at least 75% of the time. This suggests that FPAs would provide some protection to at least a portion of the tigerfish population in the river. The positive effects that FPAs can have on freshwater biodiversity (*i.e*., increased local abundance or size classes) have been widely reported (Penha *et al*., 2014; Reid *et al*., 2001; Sanyanga *et al*., 1995; Schram *et al*., 1995; Suski & Cooke, 2007; Sztramko, 1985). For FPAs to be considered effective, it is essential that FPAs incorporate the lateral and longitudinal connectivity of the river system required for a species to access habitats required for spawning and feeding and, accounts for the human activities in the area under consideration (Bower *et al*., 2015; Hermoso *et al*., 2016; Wiederkehr *et al*., 2019). In this regard, we note that the recommendations of the current study are limited to recommending the size of potential FPAs based an assessment of area use by tigerfish. Ultimately, recommendations on the optimal design and placement of FPAs will require additional research to elucidate on the linkages between the biological habitat requirements of tigerfish (*e.g*., for spawning and feeding), their movement biology and, the risk of that interactions with human activities pose to the maintenance of these biological processes (Hermoso *et al*., 2016).

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

F.J.J. conceived paper with T.N., E.U., O.W., D.T., C.H., G.O.B. and C.T.D. F.J.J. collected and analysed data and wrote the paper. T.N., E.U., O.W., C.H., G.O.B. and C.T.D. contributed to analyses and writing of the manuscript.

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