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Spatial behaviour and management of greenhead tilapia (*Oreochromis macrochir*) in the Zambezi River, Namibia

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ABSTRACT

Thorstad, E.B., Hay, C.J., Økland, F., Nickanor, N. & Næsje, T.F. 2007. Spatial behaviour and management of greenhead tilapia (*Oreochromis macrochir*) in the Zambezi River, Namibia. - NINA Report 287. 26 pp.

The large cichlids in the Upper Zambezi River are valuable species in commercial and subsistence fisheries, and are popular among recreational anglers. However, reports of reduced catches are a major concern for the management authorities. To be able to develop local and regional management strategies, information on fish movements and habitat use is fundamental. The aim of this study was, therefore, to provide information on behaviour and habitat use of one of the most important cichlids, the greenhead tilapia (*Oreochromis macrochir*).

Twenty-two greenhead tilapia (body length 25-44 cm) were captured and radio tagged 27-60 km downstream from Katima Mulilo, Namibia, during 18-25 November 2003. They were subsequently tracked on average every 3.3 day (a total of 74 tracking surveys) during a period of rising water level (1 December - 28 March), high water level (29 March - 2 May) and decreasing water level (3 May - 5 August). Five transmitters were returned from local fishermen, giving a minimum exploitation rate of 23% during the study.

Total distance moved by individuals during the study was on average 4,076 m (range 334-19,666 m). Mean distance moved between tracking surveys was 100 m (range 14-518 m), and did not differ among periods. Home ranges were relatively small, with a 50% probability of localisation within an average area of 0.5 km^2 and a 95% probability of localisation within an average area of 3.1 km^2. Home range size did not differ among periods. The length of the river stretch used was on average 2,554 m (range 171-13,697 m). The fish utilised permanently water covered areas only (42% of the fish), alternated between permanently and temporarily water covered areas (50% of the fish), or utilised only temporarily water covered areas (8% of the fish). During rising water, 42% of the fish utilised temporarily flooded areas, during high water 40% and during decreasing water 50%. The proportion of fixes in temporarily flooded areas did not differ among periods.

During the study, 67% of the fish were recorded in the main channel of the river, 63% in side channels, 63% in backwaters, 63% in swamps, 25% on the floodplain and 8% in the mouth of backwaters. (Note that percentages add up to more than hundred because some fish are recorded in more than one habitat type.) The fish were recorded in different positions related to vegetation; 83% of the fish were recorded at no vegetation (> 5 m away from vegetation), 75% near vegetation (≤ 5 m away from vegetation) and 83% inside/under vegetation. Only one fish was never recorded near or inside/under vegetation. Water depth where the fish were recorded varied between 0.3 and 12.7 m, and was on average 4.2 m. The fish were mainly associated with sandy substratum; 92% of the fish were recorded on sandy substratum, 58% on clay and 50% on muddy, soft bottom. Total width of the river where the fish were positioned varied between 30 and 2,000 m, and was on average 322 m. Distance to nearest shore varied between 1 and 1000 m, and was on average 51 m.

In conclusion, there was a large individual variation in movements and habitat utilisation among greenhead tilapia, which emphasises their mobility and association with different habitats. In rivers bordering on several countries such as the Upper Zambezi, fish frequently cross national borders, and multilateral management regulations are needed. Greenhead tilapia may be vulnerable to local overfishing due to their relatively restricted movements. Their residency to defined home ranges implies that protected areas may pro-

tect adult fish, if the area is large enough. Still, there is limited information on movements and habitat use of juveniles.

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CONTENTS

PREFACE

This study on movements and habitat use of radio tagged greenhead tilapia and implications for fisheries management in the Upper Zambezi River is a collaboration between the Namibian Ministry of Fisheries and Marine Resources (MFMR) and the Norwegian Institute for Nature Research (NINA). The study was funded by World Wildlife Fund (WWF), USAID, MFMR and NINA.

We thank Nicoline and Rolly Thompson for extensive help during catch, tagging and tracking of the fish. We also thank Bernard Sezuni, Savage Simulebu and Garth M. Cavanagh and his family for assistance during the project.

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1 INTRODUCTION

Namibia is one of the driest countries in the world, and people strongly depend on the availability of open water bodies for fish to eat and water for domestic and agricultural use (Mendelsohn *et al*. 2002). Perennial rivers are found only along the national borders in the north, north-east and south. The most important rivers are the Kwando, Kunene, Okavango, Orange and Zambezi Rivers, which are all shared with neighbouring countries.

The White Paper "Responsible Management of the Inland Fisheries of Namibia" was finalised in December 1995 (Anon. 1995), and forms the basis for the new Inland Fisheries Resources Act and Regulations concerning fish resources management in the different freshwater systems. When implementing local and regional fisheries regulations for such complex systems, information on the fish resources and their exploitation is essential. A series of studies have, therefore, provided baseline information on occurrence, species diversity, life history and catch per unit effort of numerous fish species in the large, perennial rivers (Hay *et al*. 2000, 2002, Næsje *et al*. 2004, 2007). However, to develop spatial management strategies, information on fish movements and habitat use is fundamental. Therefore, a series of studies using telemetry methods have provided baseline information on movements and habitat use of species such as the common carp (*Cyprinus carpio*), humpback largemouth (*Serranochromis altus*), nembwe (*Serranochromis robustus*), pink bream (previously pink happy, *Sargochromis giardi*), threespot tilapia (*Oreochromis andersonii*) and tigerfish (*Hydrocynus vittatus*) (Økland *et al*. 2000, 2001, 2002, 2005, 2007, Thorstad *et al*. 2001, 2002, 2003a, 2003b, 2004, 2005).

The aim of this study was to follow up previous telemetry studies and provide information on behaviour and habitat use of greenhead tilapia (*Oreochromis macrochir*), which is one of the large cichlid species in the Upper Zambezi River in Namibia. Implications for fisheries management are also discussed. The large cichlids in the Upper Zambezi River are valuable in commercial and subsistence fisheries, and are popular among recreational anglers (Næsje *et al*. 2001, Hay *et al*. 2002). However, reports of reduced catches are a major concern for the management authorities (Anon. 1995).

2 MATERIALS AND METHODS

2.1 Study area

The Caprivi Region in the north-eastern corner of Namibia borders on Botswana, Angola and Zambia. Compared to the rest of Namibia, the Caprivi Region has a relatively high rainfall (760 mm per year). It is a flat area, approximately 1,000 m above sea level. Seasonal flooding during summer creates extensive floodplains, especially in the Eastern Caprivi, where almost 30% of the area may be flooded. Fishery and overgrazing of floodplains are possibly the activities with the highest impact on the environment and fish communities. Pollution in the area is negligible, and large-scale development and urbanisation is not noticeable (Tvedten *et al*. 1994). The local human population has a rural life style, depending heavily on subsistence fishery as an affordable source of protein.

The Zambezi River is the fourth largest river system in Africa (2,660 km long, 1.45 mill km^2 catchment area). The river flows through Zambia, Angola, Namibia, Zimbabwe and Mozambique. It forms the north-eastern border between Zambia and the Eastern Caprivi in Namibia from Katima Mulilo to Impalila Island, which is a distance of approximately 120 km (**figure 1**). The annual variation in water level is up to 7-8 m in this area, with an annual average of 5.2 m (Van der Waal & Skelton 1984). The water level usually rises sharply in January, with one or more peaks in February-April, before a decline in May-June. Thus, the floodplains are annually inundated from February to June (Van der Waal & Skelton 1984).

In the study area, the Zambezi River consists of a wide main channel, with bends and deep pools. Small, vegetated islands, sandbanks, bays, backwaters and narrow side streams occur frequently. The water velocity varies from stagnant to fast flowing, varying with water discharge. The only rapids are at Katima Mulilo and Impalila. There are also larger slow flowing channels and isolated pools. In the main channel of the river, sandy bottom substrate dominates. Muddy bottom substrate is often found in isolated pools, bays, backwaters and on floodplains where siltation occurs. Side channels and smaller side streams usually have a sandy bottom substrate. Rocky habitats only occur at the rapids at Katima Mulilo and Impalila. The water is generally clear with little suspended particles, but with a higher turbidity during floods. The river has ample available cover in the form of overhanging marginial terrestrial vegetation, marginal aquatic vegetation, and inner aquatic vegetation. Marginal terrestrial vegetation can be described as fringing vegetation on riverbanks in the form of terrestrial grass, reeds, overhanging trees and shrubs. Vegetation is locally dense, making the riverbank impenetrable. In other areas, grass and terrestrial reeds grow on sandy riverbanks and substitute the dominant dense vegetation of trees and shrubs, which grow on more stable ground. Periodically inundated grassland is the dominant floodplain vegetation.

2.2 Capture and tagging

Twenty-two greenhead tilapia (mean total body length 31 cm, range 25-44 cm) were captured from boat in the Zambezi River; 27-60 km downstream from Katima Mulilo in Caprivi, Namibia, during 18-25 November 2003 (**figure 1, table 1**). The fish were captured by rod and line baited with worms on a single Mustad 2/0 hook. Playing time during capture was 0.5-2.5 min. Most fish were hooked in the upper lip. The fish were anaesthetised by immersion in an aqueous solution of 2-phenoxy-ethanol (EC No 204-589-7, SIGMA Chemical Co., USA, 0.7 ml/l, mean time 2.5 min.). Radio transmitters (Advanced Telemetry Systems, Inc. (ATS), USA, **table 1**) were externally attached to the fish, using the method described in Thorstad *et al.* (2000). During the tagging procedure, which lasted about 2 min., the fish were kept in a water filled tube. Transmitter weight in air was on average 1.9% (range 0.2-

3.5%) of the body weight of the fish. The transmitters emitted signals within the 142.143-142.641 MHz band, and transmitter frequencies were spaced at least 10 kHz apart for individual recognition of the fish. Total body length and mass were recorded, before the fish were placed in a container for recovery (2-5 min.). Fish no. 362 had buoyancy problems due to swim bladder inflation, and the swim bladder was deflated with a needle from the side. The fish was held in the cage for 2.5 h for observation before release. It appeared in good condition at release. All fish were released at the catch site. The water temperature was 25-28 °C during catch and tagging.

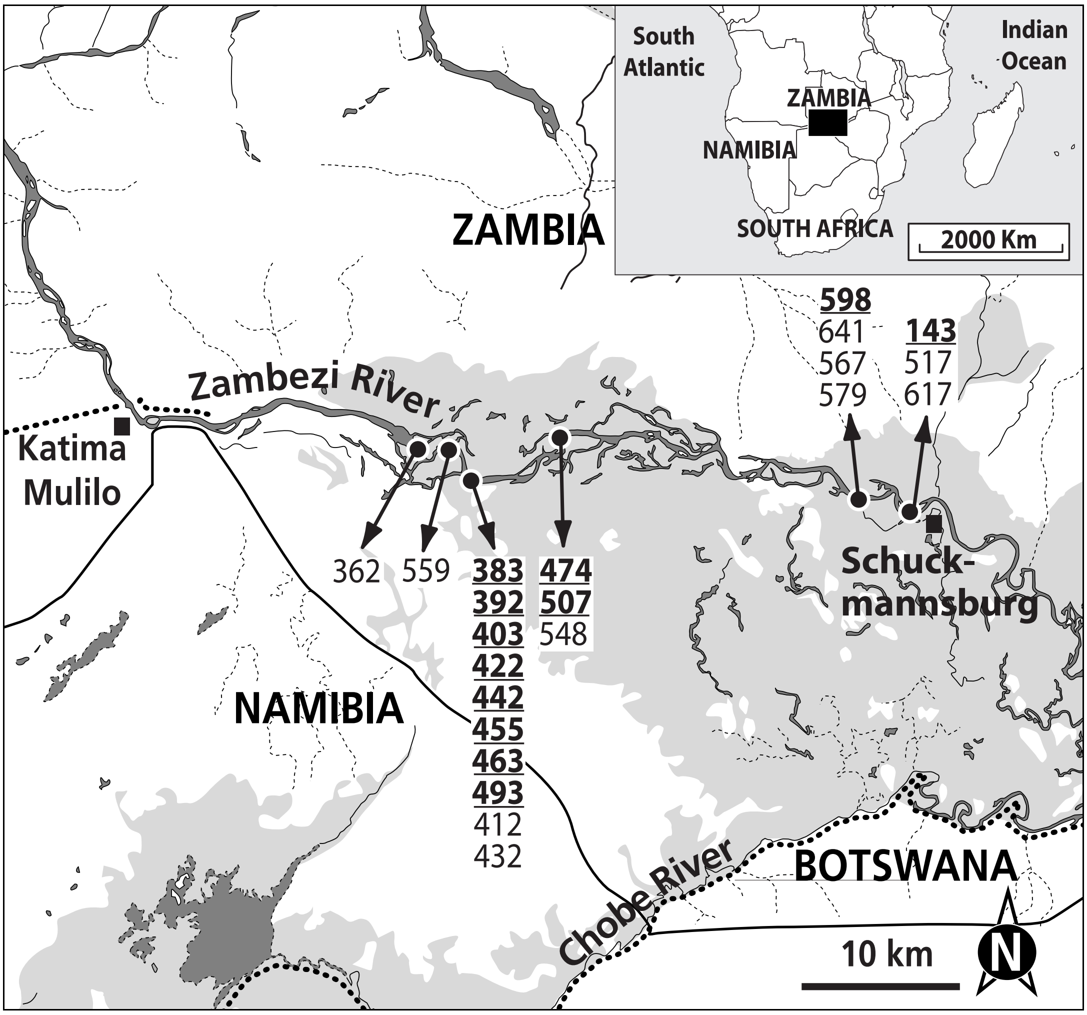


Figure 1. *The upper part of the Zambezi River in north-eastern Namibia. Sites where individual greenhead tilapia were radio tagged and released are indicated. Individual fish numbers correspond to the numbers in table 1. Fish included in result analyses are indicated with bold, underlined numbers.*

2.3 Tracking

The fish were tracked from boat using a portable receiver (R2100, ATS) connected to a 4-element Yagi antenna. The fish were located with a precision of ± 10 m in the main river. Some of the backwaters were inaccessible by boat, and the location was estimated based on signal strength and direction. Approximately 100 km of the main river, including main side channels and backwaters, were searched for tagged fish.

Reduced activity levels during the first 12-24 hours after anaesthetisation and radio tagging of tilapia (*Oreochromis aureus* Steindachner 1864) were recorded by Thoreau & Baras (1997). They suggested that the tilapia need three to four days to completely compensate for the negative buoyancy resulting from anaesthesia and tagging. To ensure that movements due to handling and tagging effects were not included, the greenhead tilapia were not tracked before 1 December (6-13 days after capture and tagging).

The fish were tracked intensively during a period of rising water level (1 December-28 March), high water level (29 March-2 May) and decreasing water level (3 May-5 August) (**figure 2**, **table 1**). A total of 74 tracking surveys were performed; 36 during rising water, 11 during high water and 27 during decreasing water. Hence, the fish were tracked on average every 3.3 day (*i.e.* every 3.3 day during rising water, every 3.1 day during high water and every 3.5 day during decreasing water).

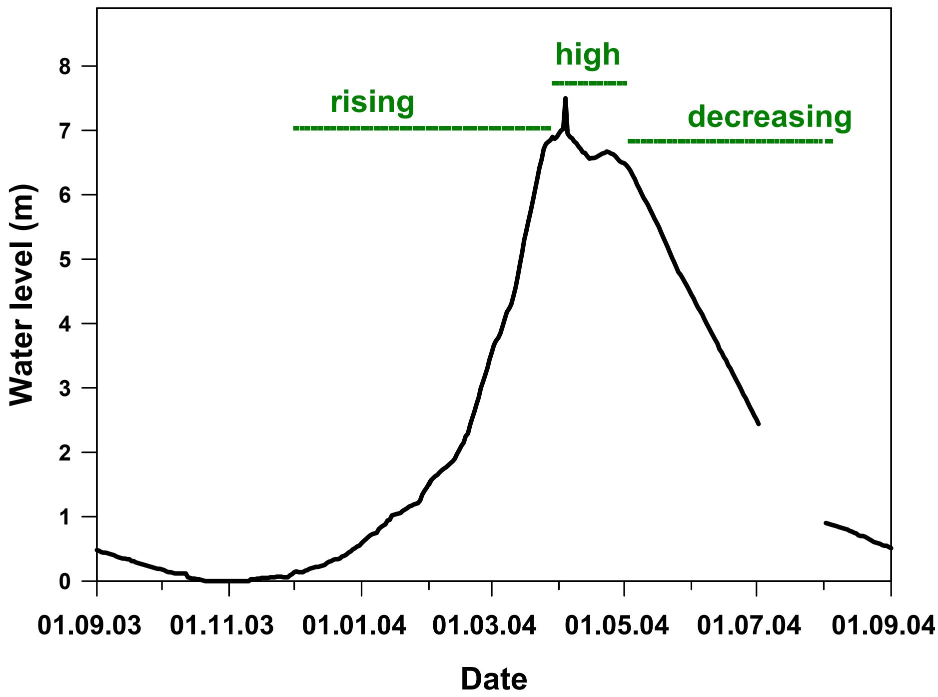


Figure 2. *The water level in the Zambezi River at Katima Mulilo, Namibia, from 1 September 2003 to 1 September 2004. The study periods during rising, high and decreasing water are indicated. Data provided by The Department of Water Affairs in Windhoek.*

Individual fish were tracked until disappearing from the area. Those not recaptured or lost (see below), were tracked until transmitter batteries were running out of power, which happened at slightly different dates (**table 1**). Some of the fish were not found during all tracking surveys. Fish no. 403, 455, 463 and 493 were not found during 1-4 surveys towards the end of the tracking period, probably because transmitter signals were weaker when the transmitter batteries started to run out. Fish no. 422 was not found during 25 surveys during rising water and five surveys during decreasing water. Fish no. 507 was not found during six surveys during rising water, six surveys during high water and 21 surveys during decreasing water. Fish no. 493 was not found during one of the surveys during rising water. On these occasions, the fish probably stayed in areas inaccessible by boat, and maybe in a location with a reduced range (such as deep water, sheltered by solid structures and so on).

Table 1. *Radio tagged greenhead tilapia in the Zambezi River, Namibia, during 18-25 November 2003. Fish included in result analyses are indicated with bold letters.*

Frequency 142.xxx MHz	Fish no.	Tagging date	Body length (cm)	Body mass (g)	Transmitter model*	Sex	Total number of fixes	Number of fixes during each period (rising, high and decreasing water)	Last tracking date	Remarks
143	**62**	**25 Nov**	**43.7**	**1850**	**F1960**	**female**	**15**	**15, 0, 0**	**13.01.04**	
362	37	18 Nov	31.8	624	F2110	male	0	0, 0, 0	-	Deflated swim bladder. Transmitter located under tree on Kalimbeza Island 1 February 2004. The fish had probably been captured and eaten by a fish eagle.
383	**39**	**21 Nov**	**29.6**	**565**	**F2110**	**?**	**74**	**36, 11, 27**	**15.07.04**	
392	**40**	**21 Nov**	**30.6**	**664**	**F2110**	**male**	**9**	**9, 0, 0**	**21.12.04**	**Caught by local fishers in a net. The transmitter was handed in on 24 December 2003.**
403	**41**	**21 Nov**	**30.0**	**652**	**F2110**	**male**	**60**	**36, 11, 13**	**29.06.04**	
412	42	21 Nov	32.3	803	F2110	female	3	3, 0, 0	08.12.04	Caught by local fishers possibly in early December. The transmitter was handed in by Zambian fishers on 9 January 2004.
422	**43**	**21 Nov**	**29.8**	**624**	**F2110**	**male**	**35**	**11, 11, 13**	**02.07.04**	
432	44	21 Nov	26.8	468	F2110	male	1	1, 0, 0	01.12.04	Caught by local fishers in a drag net on 3 December 2003. The transmitter was handed in by a Zambian fisher on 4 December 2003.
442	**45**	**21 Nov**	**30.2**	**672**	**F2110**	**male**	**73**	**36, 11, 26**	**05.08.04**	
455	**46**	**21 Nov**	**28.8**	**606**	**F2110**	**male**	**72**	**36, 11, 25**	**15.07.04**	
463	**47**	**21 Nov**	**25.6**	**498**	**F2110**	**male**	**73**	**36, 11, 26**	**15.07.04**	
474	**48**	**21 Nov**	**25.3**	**340**	**F2110**	**male**	**73**	**36, 11, 26**	**09.08.04**	
493	**50**	**21 Nov**	**27.3**	**378**	**F2110**	**male**	**70**	**35, 11, 24**	**09.08.04**	
507	**51**	**21 Nov**	**31.1**	**693**	**F2110**	**male**	**40**	**30, 5, 5**	**09.08.04**	
517	52	21 Nov	33.5	774	F2110	female	0	0, 0, 0	**-**	Caught by local fishers in a net. The transmitter was handed in on 26 November 2003.
548	54	22 Nov	34.9	980	F2110	female	1	1, 0, 0	02.12.03	Caught by local fishers in a drag net. The transmitter was handed in on 4 December 2003.
559	55	22 Nov	27.0	431	F2110	male	72	36, 11, 25	09.08.04	Stationary from the start, believed to be dead.
567	56	23 Nov	32.2	747	F2110	female	3	3, 0, 0	09.12.03	Transmitter recovered from shore on 12 December 2003. The fish had probably been predated by an otter.
579	57	23 Nov	33.6	995	F2110	female	2	2, 0, 0	04.12.03	Transmitter recovered from shore on 7 December 2003. The fish had probably been predated by an otter.
598	**58**	**24 Nov**	**28.2**	**507**	**F2110**	**male**	**66**	**36, 11, 19**	**05.07.04**	
617	59	25 Nov	37.7	1305	F2110	female	0	0, 0, 0,	**-**	Predated by a tigerfish immediately after release.
641	60	25 Nov	36.4	1185	F2110	female	70	36, 11, 23	23.07.04	Stationary from the start, believed to be dead.

*Model F2110 are flat, rectangular transmitters with outline dimensions of 19 x 40 x 9 mm, weight in air of 12 g and guaranteed battery life of 139 days. Model F1960 are flat, rectangular transmitters with outline dimensions of 13 x 29 x 6 mm, weight in air of 3.6 g and guaranteed battery life of 258 days.

Habitat classifications were made each time a fish was positioned. Recordings were made on water cover (1: permanent water cover, 2: temporary water cover, *i.e.* each year during the rain period, 3: episodic water cover, *i.e.* occasional but not regular during rain period), main habitat type (1: main channel of river, 2: backwater, 3: mouth of backwater, 4: side channel, 5: tributary, 6: swamp, 7: floodplain, 8: isolated pool), position to vegetation (1: no vegetation, *i.e.* > 5 m away from vegetation, 2: near vegetation, *i.e.* ≤ 5 m away from vegetation, 3: inside/under vegetation), and vegetation type if near or inside/under vegetation (1: inner aquatic submerged, 2: inner aquatic floating, 3: inner aquatic anchored, 4: marginal aquatic submerged, 5: marginal aquatic floating, 6: marginal aquatic anchored, 7: marginal terrestrial submerged, 8: marginal terrestrial overhanging). Moreover, recordings were made of surface water temperature, depth (water depth measured by manual sounding and echo sounder, depth of fish position was unknown), and substrate (1: muddy, 2: clay, 3: sand, 4: gravel, 5: pebbles, 6: rocks/bedrock). Also the distance to the nearest shore was measured, as well as the total width of the river. A laser range finder (Bushnell BU Yardage 800) was used to record the distances with a precision of ± 1 m. Due to the high water level during the study, resulting in the river being many kilometres wide in much of the study area during the flood peak, the width of the river and distance to shore could no be recorded during the period with the highest flood. Classifications listed here were alternatives in the tracking journal, and fish were not actually recorded in all these habitats (see results). The tracking was carried out during daytime, thus, the data represent the daytime habitat utilisation of the fish.

2.4 Data analyses

Two fish (fish no. 559 and 641) were stationary from the start of the tracking programme, and were believed to be dead or the transmitters had fallen off (**table 1**). These fish were, therefore, not included in the analyses. Further, one fish was predated by tigerfish *Hydrocynus vittatus*, one fish was probably predated by a fish eagle *Haliaeetus vocifer* and two fish were probably predated by otter (African clawless otter *Aonyx capensis*, or spotted-neck otter *Lutra maculicolis*, both species present in the study area) shortly after release (**table 1**). Four fish were caught by local fishermen in November-December and were tracked less than four times each before recapture (one more fish was caught by local fishers later, giving a capture rate by local fishers of minimum 23% during the study period) (**table 1**). Hence, 12 of the 22 tagged fish were left for behaviour analyses (**table 1**). Most of these fish were males (**table 1**), hence, comparisons between the sexes were not performed.

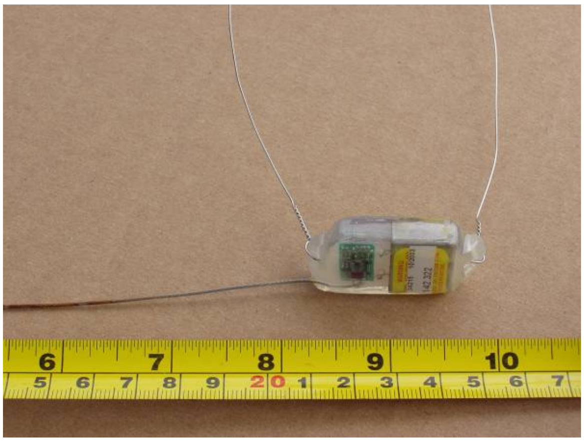
Descriptive statistics and statistical analyses were based on average values for individual fish. Comparisons of behaviour and habitat utilisation among periods of rising, high and decreasing water levels were made by non-parametric paired comparisons, and only fish located ten times or more in each period were included in the analyses. Hence, results from only nine fish were included in the comparisons among periods (**table 1**).

Home ranges were calculated using the non-parametric kernel method and a probability density function (e.g. Worton 1989, Seaman & Powell 1996, Lawson & Rodgers 1997). For the kernel smoothing parameter "*h*", the "*ad hoc*" solution was rejected in favour of the least square cross-validation approach, which is more effective with multimodal distributions (Worton 1989). The utilisation distribution was estimated, in terms of perimeter and area covered, at two different levels of probability (95 and 50%). The catch and release sites were not included in the analyses.

All statistical analyses were performed with SPSS 13.0 for Windows, except for the home range analyses, which were performed with ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.).


Greenhead tilapia were captured for tagging by using rod and line.


Typical greenhead tilapia habitat in the study area in the Upper Zambezi River.




Radio transmitters (left picture) were attached externally to the fish. Individuals could be recognized by using different frequencies. Telemetry has proven to be a suitable method for collecting information about movements and habitat utilisation of cichlids in the Upper Zambezi River.

All photos: Eva B. Thorstad


The fish were anaesthetised before tagging, and were in a good condition at release.


Radio tagged fish were located by manual tracking from boat on average every 3.3 day in the period 1 December 2003 to 5 August 2004.


There was a large individual variation in movements and habitat utilisation among green-head tilapia, which emphasises their mobility and association with different habitats.

All photos: Eva B. Thorstad

3 RESULTS

3.1 Movements

Mean total distance moved by individual fish during the first 6-13 days after tagging (from tagging to first tracking) was 202 m (SD = 93, range = 56-315). Four fish had a downstream movement, seven an upstream and one a sidewise movement during this period.

Total distance moved by individual fish during the entire study period was on average 4,076 m (SD = 5,458, range 334-19,666 m). Mean distance moved between tracking surveys was 100 m, and did not differ among periods (Friedman test, χ^2 = 5.56, P = 0.062) (**table 2 and 3**). Mean distance moved between tracking surveys was not dependent on fish body size (linear regression, r^2 = 0.005, P = 0.82).

The fish utilised permanently water covered areas only (42% of the fish), alternated between permanently and temporarily water covered areas (50% of the fish), or utilised only temporarily water covered areas (8% of the fish). On average, 72% of the fixes were in permanently flooded areas, whereas the remaining 28% of fixes were in temporarily water covered areas (**table 2**). During rising water, 42% of the fish utilised temporarily flooded areas, during high water 40% and during decreasing water 50% (**table 3**). The proportion of fixes in temporarily flooded areas did not differ among periods (Friedman test, χ^2 = 1.6, P = 0.45, **table 3**). There was no difference in body length of fish utilising temporarily flooded areas and those that did not (Mann-Whitney Test, U = 12.0, P = 0.37).

3.2 Home range

Home ranges were relatively small, with a 50% probability of localisation within an average area of 475,648 m^2 (≈ 0.5 km^2) and a 95% probability of localisation within an average area of 3,121,288 m^2 (≈ 3.1 km^2) (**table 2, figure 3**). Home range size did not differ among periods (Friedman tests, 50%: χ^2 = 2.9, P = 0.24, 95%: χ^2 = 0.89, P = 0.64, **table 3**) and was not dependent on fish body size (linear regression, 50%: r^2 = 0.005, P = 0.83, 95%: r^2 = 0.005, P = 0.83). The length of the river stretch used (*i.e.* distance between the two fixes farthest from each other during the entire study period) was on average 2,554 m (SD = 3,904, range 171-13,697 m).

3.3 Habitat utilisation

During the study, 67% of the fish were recorded in the main channel of the river, 63% in side channels, 63% in backwaters, 63% in swamps, 25% on the floodplain and 8% in the mouth of backwaters. (Note that percentages add up to more than hundred because some fish were recorded in more than one habitat type.) On average, 46% of the fixes were in the main channel of the river, 24% in side channels, 14% in backwaters, 4% in swamps, 11% on the floodplain and 1% in the mouth of backwaters (**table 2**). There was no difference in the proportion of fixes in the main channel of the river, side channels, backwaters, swamps or on the floodplain among periods (Friedman tests, main channel: χ^2 = 3.5, P = 0.18, side channels: χ^2 = 0.0, P = 1.0, swamps: χ^2 = 4.8, P = 0.092, floodplain: χ^2 = 5.0, P = 0.082) (**table 3**). In contrast, the proportion of fixes in backwaters differed among periods (Friedman test, χ^2 = 6.0, P = 0.05). However, when testing two and two periods, no differences in the proportion of fixes in backwaters were found between periods (Wilcoxon signed ranks tests, rising *vs*. high: Z= -1.6, P = 0.11, rising *vs*. decreasing: Z= -1.6, P = 0.11, high *vs*. decreasing: Z= -0.0, P = 1.0) (**table 3**).

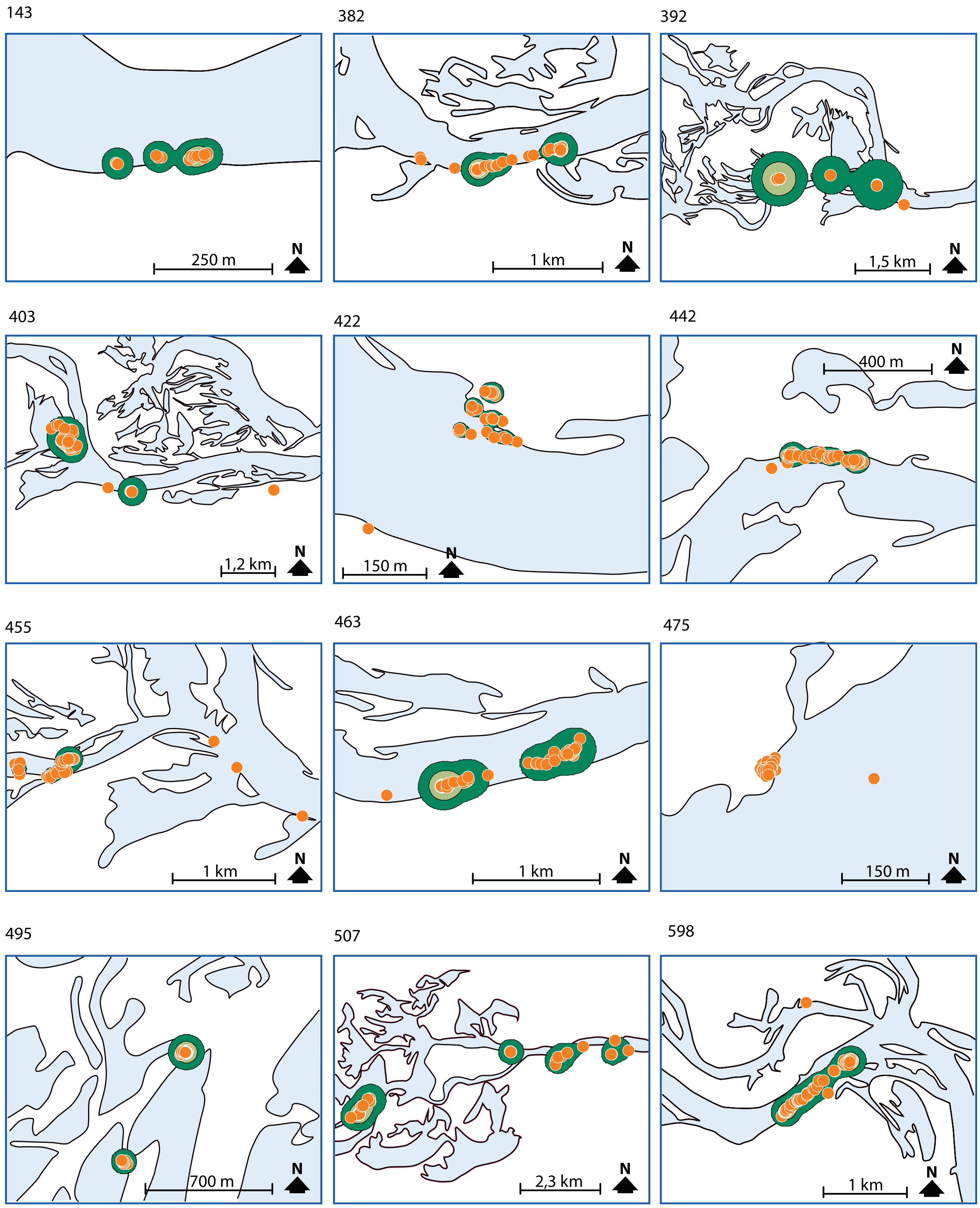


Figure 3. *Kernel home ranges of individual radio tagged greenhead tilapia (n = 12) in the Zambezi River in 2003-2004. Orange dots show fixes during tracking, and the green contours of home ranges refer to two different levels of probability (dark green shows 95% probability and and light green 50% probability). Individual fish numbers correspond to the numbers in table 1.*

The fish were recorded in different positions related to vegetation; 83% of the fish were recorded at no vegetation (> 5 m away from vegetation), 75% near vegetation (≤ 5 m away from vegetation) and 83% inside/under vegetation. Only one fish was never recorded near or inside/under vegetation during the study. On average, 41% of the fixes were at no vegetation, 40% inside/under vegetation and 19% near vegetation (**table 2**). The proportion of fixes at no vegetation and inside/under vegetation did not differ among periods (Friedman tests, no vegetation: χ^2 = 0.86, P = 0.65, inside/under vegetation: χ^2 = 0.58, P = 0.75, **table 3**). However, the proportion of fixes near vegetation differed among periods (Friedman tests, χ^2 = 7.9, P = 0.019), and was higher during rising than during high water (Wilcoxon signed ranks tests, rising *vs*. high: Z= -2.4, P = 0.018, rising *vs*. decreasing: Z= -1.5, P = 0.13, high *vs*. decreasing: Z= -1.3, P = 0.18) (**table 3**).

Of the fish recorded near or inside/under vegetation (n = 11), 82% were associated with marginal aquatic anchored vegetation, 64% with marginal terrestrial submerged vegetation, 36% with inner aquatic anchored vegetation, 27% with marginal aquatic submerged vegetation, 18% with marginal terrestrial overhanging vegetation and 9% each with inner aquatic submerged vegetation, inner aquatic floating vegetation and marginal aquatic floating vegetation. On average, 59% of the fixes were at marginal aquatic anchored vegetation, 29% at marginal terrestrial submerged vegetation, 5% at both inner aquatic anchored and marginal terrestrial overhanging vegetation, and the remaining 2% of the fixes at the other vegetation types (**table 2**). Different individuals were recorded near or inside/under vegetation during the different periods, and comparisons regarding vegetation type during the different periods were, therefore, not made. However, it is notable that all five fish associated with vegetation during high water were only associated with marginal aquatic anchored vegetation (**table 3**).

Water temperature where the fish were positioned, varied between 16 and 30 ºC during the study. The water temperature decreased during the study period, and was on average 27 ºC during rising water, 26 ºC during high water and 19 ºC during decreasing water (**table 3**).

Water depth where the fish were recorded varied between 0.3 and 12.7 m, and was on average 4.2 m (**table 2**). Water depths differed among periods (Friedman tests, χ^2 = 7.8, P = 0.21), with water depth being larger during high water than during rising and decreasing water (Wilcoxon signed ranks tests, rising *vs*. high: Z= -2.4, P = 0.017, rising *vs*. decreasing: Z= -1.0, P = 0.31, high *vs*. decreasing: Z= -2.4, P = 0.017) (**table 3**). Water depth where the fish were recorded was not dependent on fish body size (linear regression, r^2 = 0.077, P = 0.38).

The fish were mainly associated with sandy substratum; 92% of the fish were recorded on sandy substratum, 58% on clay and 50% on muddy, soft bottom. On average, 63% of the fixes were on sandy substratum, 19% on clay and 18% on muddy bottom (**table 2**). Proportion of fixes on sandy substratum differed among periods (Friedman test, χ^2 = 7.6, P = 0.023), being lower during rising than during high water level (Wilcoxon signed ranks tests, rising *vs*. high: Z= -2.2, P = 0.028, rising *vs*. decreasing: Z= -1.9, P = 0.063, high *vs*. decreasing: Z= -0.73, P = 0.47) (**table 2**). However, proportion of fixes on clay and muddy bottom did not differ among periods (Friedman tests, clay: χ^2 = 2.5, P = 0.29, muddy bottom: χ^2 = 4.7, P = 0.097, respectively) (**table 3**).

Total width of the river where the fish were positioned varied between 30 and 2,000 m, and was on average 322 m (**table 2**). Total width of the river was not dependent on fish body size (linear regression, r^2 = 0.022, P = 0.64). Distance to nearest shore given as proportion of total river width was on average 16%. Distance to nearest shore varied between 1 and 1000 m, and was on average 51 m (**table 2**). Average distance to shore was not dependent on fish body size (linear regression, $r^2 = 0.18$, $P = 0.17$). Note that these figures are underestimates since the river width and distance to shore could not be recorded during the highest flood (see methods).

Table 2. *Results from tracking of radio tagged greenhead tilapia in the Zambezi River, Namibia. Results are given for the entire study period (n = 12 fish). s.d. = standard deviation.*

	Entire study period		
	mean	**range (min-max)**	**s.d.**
Distance moved between tracking surveys (m)	**100**	14-518	146
% fixes in permanently water covered areas	**72**	0-100	35
% fixes in temporarily water covered areas	**28**	0-100	35
Home range size, 50% probability (m^2)	**475,648**	150-4,807,453	1,369,784
Home range size, 95% probability (m^2)	**3,121,288**	603-32,791,143	9,366,498
% fixes in the main stream of the river	**46**	0-100	48
% fixes in side channels	**24**	0-100	41
% fixes in backwaters	**14**	0-100	31
% fixes in swamps	**4**	0-24	7
% fixes on the floodplain	**11**	0-64	24
% fixes in the mouth of backwater	**1**	0-11	3
% fixes at no vegetation	**41**	0-100	44
% fixes near vegetation	**19**	0-67	22
% fixes inside/under vegetation	**40**	0-100	40
% fixes at marginal aquatic anchored vegetation	**59**	0-97	33
% fixes at marginal terrestrial submerged vegetation	**29**	0-100	38
% fixes at inner aquatic anchored vegetation	**5**	0-29	9
% fixes at marginal terrestrial overhanging vegetation	**5**	0-44	14
Water temperature where the fish were positioned (ºC)	**24.8**	23.8-27.2	1.3
Water depth where the fish were positioned (m)	**4.2**	1.8-8.0	2.1
% fixes on sandy bottom (%)	**63**	0-100	33
% fixes on clay (%)	**19**	0-78	25
% fixes on muddy, soft bottom (%)	**18**	0-89	31
Total width of the river where fish were positioned (m)	**322**	111-756	159
Distance to nearest shore (% of total river width)	**16**	3-32	8
Distance to nearest shore (m)	**51**	4-132	33

Table 3. *Results from tracking of radio tagged greenhead tilapia in the Zambezi River, Namibia. Results are given for each of the periods rising, high and decreasing water level (n = 9 fish, see methods). s.d. = standard deviation.*

	Rising water level			**High water level**			**Decreasing water level**		
	mean	**range (min-max)**	**s.d.**	**mean**	**range (min-max)**	**s.d.**	**mean**	**range (min-max)**	**s.d.**
Distance moved between tracking surveys (m)	**95**	15-387	121	**135**	7-1050	323	**103**	3-798	245
% fixes in permanently water covered areas	**75**	0-100	33	**61**	0-100	51	**53**	0-100	50
% fixes in temporarily water covered areas	**25**	0-100	33	**39**	0-100	51	**47**	0-100	50
Home range size, 50% probability (m^2)	**188,049**	171-1,376,441	421,234	**164,787**	19-1,555,842	489,040	**230,724**	7-2,292,250	724,349
Home range size, 95% probability (m^2)	**878,895**	962-6,043,626	1,894,396	**598,120**	147-5,494,241	1,722,631	**815,600**	54-8,062,199	2,546,233
% fixes in the main stream of the river	**45**	0-100	47	**40**	0-100	52	**53**	0-100	51
% fixes in side channels	**20**	0-100	41	**20**	0-100	42	**20**	0-100	42
% fixes in backwaters	**20**	0-100	34	**10**	0-100	32	**10**	0-100	32
% fixes in swamps	**10**	0-80	24	**2**	0-20	6	**0**	0-0	0
% fixes on the floodplain	**5**	0-41	12	**28**	0-100	45	**18**	0-100	37
% fixes in the mouth of backwater	**0**	0-0	3	**0**	0-0	0	**0**	0-0	0
% fixes at no vegetation	**41**	0-100	46	**51**	0-100	52	**55**	0-100	47
% fixes near vegetation	**18**	0-68	25	**0**	0-0	0	**5**	0-40	13
% fixes inside/under vegetation	**41**	0-100	38	**49**	0-100	52	**40**	0-100	50
% fixes at marginal aquatic anchored vegetation	**45**	0-100	37	**100**	100-100	0	**93**	80-100	9
% fixes at marginal terrestrial submerged vegetation	**41**	0-100	45	**0**	0-0	0	**3**	0-17	7
% fixes at inner aquatic anchored vegetation	**9**	0-36	13	**0**	0-0	0	**3**	0-20	8
% fixes at marginal terrestrial overhanging vegetation	**1**	0-12	4	**0**	0-0	0	**0**	0-0	0
Water temperature where the fish were positioned (ºC)	**26.9**	26.7-27.2	0.2	**25.5**	25.3-25.6	0.1	**19.3**	17.8-20.7	0.8
Water depth where the fish were positioned (m)	**3.8**	1.5-7.2	2.0	**6.3**	0.3-10.3	3.6	**4.5**	2.0-9.2	2.6
% fixes on sandy bottom (%)	**57**	0-100	38	**79**	0-100	36	**84**	0-100	32
% fixes on clay (%)	**17**	0-76	33	**9**	0-45	19	**2**	0-20	6
% fixes on muddy, soft bottom (%)	**26**	0-93	37	**11**	0-60	24	**14**	0-100	32
Total width of the river where fish were positioned (m)	**339**	159-756	169	**-**	-	-	**293**	63-508	137
Distance to nearest shore (% of total river width)	**16**	5-28	7	**-**	-	-	**31**	9-70	25
Distance to nearest shore (m)	**52**	20	35	**-**	-	-	**66**	25-109	34

Study area in the Upper Zambezi River. *Photos Eva B. Thorstad*

4 DISCUSSION

Greenhead tilapia is a valuable species for subsistence fisheries and recreational angling (Van der Waal 1990, Næsje *et al*. 2001, Skelton 2001, Hay *et al*. 2002). It was the fifteenth most important species in survey catches in the Upper Zambezi in 1997-2000 (Hay *et al*. 2002). In a fishing competition for recreational anglers, it was the tenth most important species (Næsje *et al*. 2001). However, only limited ecological data for this species has been published, and this is the first study where the behaviour of individual greenhead tilapia is followed over time.

4.1 Movements and home range

The greenhead tilapia were relatively stationary and stayed within a river stretch of mean length 2,554 m. However, they utilised a larger stretch than threespot tilapia and pink bream during a previous study in the same part of the Zambezi River (5 October - 1 March 1999, *i.e.* three months shorter study period than the present study, Økland *et al*. 2000, Thorstad *et al.* 2001). Threespot tilapia and pink bream remained mainly resident within a stretch of mean length 540 and 220 m, respectively. However, annual differences in the flood cycle may affect movement patterns, and threespot tilapia utilised a much larger stretch (average 5,423 m) in a later year when the rise in the water level was steeper (Thorstad *et al*. 2003a, Økland *et al*. 2007). The greenhead tilapia also utilised a larger stretch than nembwe in the same study area; with nembwe utilising a mean stretch of 1,300 m (23 November - 18 May 2000, *i.e.* two months shorter study period than the present study, Thorstad *et al*. 2002, 2005). Hence, the present study and previous radio telemetry studies in the same area indicate that some of the cichlid species do not have such a highly resident life style as previously assumed for cichlids (Lucas & Baras 2001), and that they utilize areas extending over several hundred metres or a few kilometres. The present study took place when the Zambezi River water level reached its highest level in more than 20 years. This might affect the movements and habitat utilisation of the fish, making it difficult to interpret whether differences between greenhead tilapia in the present study and other cichlids in previous studies were due to species differences or annual differences in the flood cycle. Furthermore, the study period in the present study was slightly later in the year, covering rising, high and decreasing water levels instead of low, rising and high water levels in previous studies. The present study also covered a slightly longer time period.

4.2 Habitat utilisation

The greenhead tilapia were recorded in the main channel of the river, in side channels, back waters and on the floodplain. This is in accordance with Skelton (2001), stating that adult greenhead tilapia are found in quiet waters along river margins and backwaters, in floodplain habitats and impoundments. Similarly, Winemiller & Kelso-Winemiller (2003) found that greenhead tilapia were more common in lagoons than in the river channel. The cichlids nembwe and threespot tilapia were more often recorded in the main river (Thorstad *et al*. 2002, 2003a, 2005, Økland *et al*. 2007) than the greenhead tilapia in the present study.

The fish were often associated with vegetation (59% of fixes near or inside/under vegetation), and were often recorded near the shore (average distance from shore 51 m, constituting 16% of the total river width). Compared to nembwe, greenhead tilapia were less often associated with vegetation, but recorded at a similar distance from shore (for nembwe: average 78% of the fixes associated with vegetation, average distance from shore 58 m, constituting 15% of the total river width, Thorstad *et al*. 2002, 2005). Compared with threespot tilapia, greenhead tilapia were to a similar extent associated with vegetation, but were recorded closer to shore (for threespot tilapia: average 62% of the fixes associated with vegetation, average distance from shore 158 m, constituting 31% of the total river width, Thorstad *et al*. 2003a, Økland *et al*. 2007).

Water depths where greenhead tilapia was recorded varied between 0.4 and 12.7 m, but it is not known from the present study at which depths above bottom the fish stayed. Greenhead tilapia were less often recorded on sandy substratum and more often recorded on clay and muddy, soft bottom than nembwe and threespot tilapia (Thorstad *et al*. 2002, 2003a, 2005, Økland *et al*. 2007). This may be linked to the more frequent utilisation of other main habitats than the main river, and with their bottom feeding behaviour. Greenhead tilapia mainly feed on microscopic foods such as algae, diatoms and detritus taken from the bottom (Skelton 2001, Van der Waal 1985, Winemiller & Kelso-Winemiller 2003), in contrast to nembwe that are fish predators (Skelton 2001). Greenhead tilapia and threespot tilapia have a high dietary overlap (Winemiller & Kelso-Winemiller 2003), such that differences in habitat use between these two species might not be expected due to different feeding preferences. Yet, a high proportion of the positional fixes for greenhead tilapia were also on sandy bottom, which can be linked to the widespread occurrence of sandy bottom in this area of the Zambezi River. The Upper Zambezi River is a typical "sand-bank" river, mainly with sandy bottom (Van der Waal & Skelton 1984).

The water temperature decreased during the study period, and was on average 26.9 ºC during rising water, 25.5 ºC during high water and 19.3 ºC during decreasing water. The optimum temperature range for greenhead tilapia is 23-24 ºC, but they can tolerate temperatures as low as 11 ºC, and temperatures in their native range vary between 18 and 35 ºC (de Moor 1996 and references therein). The water temperature where the fish were positioned varied between a minimum of 16 ºC and a maximum of 30 ºC during the study; hence, they experienced conditions within their temperature optimum as well as relatively far from the optimum.

The creation of extensive floodplains during the rainy season greatly affects the habitat availability for the fish (Winemiller & Jepsen 1998). Greenhead tilapia moved on to temporarily water covered areas when the water was rising, with almost one third of the fixes in temporarily water covered areas. Three fish (25%) also moved out onto the classical floodplain habitat with submerged grassland and low gradients. Changes in behaviour in connection with flooding may be linked to the reproductive behaviour of the fish. It has been suggested that some riverine cichlids, including greenhead tilapia, undertake longitudinal and lateral seasonal migrations onto the inundated floodplain where their young may find favourable environments for fast growth, before returning to the river under receding waters (e.g. Bell-Cross 1974, Winemiller 1991, Van der Waal 1996). Minimum size of sexual maturation for greenhead tilapia is 18 cm for males and 22 cm for females in the Namibian part of the Zambezi River (Hay *et al*. 2002), 15 cm for females and 14 cm for males in the Lake Liambezi in the Zambezi River system (Van der Waal 1985), 21 cm for females in the Zambian part of the Zambezi River (Winemiller & Kelso-Winemiller 2003) and 16 cm for females in Lake McIlwaine in Zimbabwe (Marshall 1979). Thus, most of the fish in the present study had probably reached sexual maturity. Females seem to spawn at least 2-4 times a year (Bell-Cross 1974, Van der Waal 1985). Greenhead tilapia in the Upper Zambezi River in Zambia breeds at least once before the floods, and at least once again during the floods (Bell-Cross 1974). Under artificial conditions in fish ponds, greenhead tilapia usually spawn between September and February (Bell-Cross 1974), and in aquaria between August and April (Schwanck 1994). In Lake Liambezi, greenhead tilapia showed a very long spawning season, and ripe females were found from August to March, but with a clear peak in November-December (Van der Waal 1985). In Lake McIlwaine in Zimbabwe, main breeding took place in September-February (Marshall 1979). Thus, the greenhead tilapia in the present study may have participated in breeding from the start of the study until February-March. Greenhead tilapia is a female mouth brooder, with the males attracting females to a saucer and mound type nest in shallow water where the eggs are deposited (Van der Waal 1985, Skelton 2001). The utilisation of temporarily water covered areas and floodplains during the spawning period in the present study may, therefore, have been in connection with spawning and nursery. However, temporarily water covered areas may also provide abundant food for greenhead tilapia.

In conclusion, the present study and previous telemetry studies of cichlids in the same part of the Upper Zambezi River (Økland *et al*. 2000, 2002, 2005, 2007, Thorstad *et al*. 2001, 2002, 2003a, 2003b, 2004, 2005) demonstrated that there is a large individual variation in movements and habitat utilisation among cichlids, and emphasise their mobility and association with different habitats.

4.3 Fisheries management

Basic information of annual movements, habitat preferences and habitat utilisation of target species is needed to regulate the fisheries and exploitation methods used among the different countries sharing the same resources (Hocutt *et al.* 1994), and to evaluate the possible benefits of reserves and sanctuaries. Migration and habitat studies can provide information on which fish are most vulnerable to exploitation and when.

A relatively high exploitation rate was recorded for the greenhead tilapia, with at least 23% of the tagged fish recaptured by local subsistence fishers. All recaptures were done during November and December, indicating that the high water levels later in the season protected the fish against being caught. However, it must be emphasized that calculating exploitation rate based on such a low number of fish is uncertain.

Based on the results in the present study, greenhead tilapia may be locally vulnerable to overfishing, due to their small movements. Greenhead tilapia may potentially be locally overexploited if the local exploitation pressure is high, in contrast to species moving about more widely. The management and regulations are, therefore, important for the local populations of adult greenhead tilapia. In rivers bordering on several countries like the Upper Zambezi River, multilateral management regulations are necessary even for stationary species to avoid fish being protected in one country and overexploited in the neighbouring country. The small movements of greenhead tilapia also imply that reasonably large sanctuaries will probably protect adult fish, because fish will be staying within the protected area. However, it must be emphasised that only twenty-two adult fish were tagged in the present study, and that the full annual cycle was not studied. Juvenile greenhead tilapia may, for example, behave differently from adult fish. These limitations must be considered when using the present data for management recommendations.

Trophy fishing for large cichlids and tigerfish is popular in this area, and catch-and-release angling is common during both ordinary angling and fishing competitions, with fish being released alive into the river after being angled (Næsje *et al*. 2001). The predation of four of the tagged fish (18%) by tigerfish, fish eagle and otter emphasises that there is an increased predation risk after catch-and-release angling, since the fish in this study were captured by ordinary angling methods. Another two fish either died or lost their transmitter immediately after release, further indicating possible negative effects by catch-and-release angling (giving a possible mortality rate after catch-and-release angling of 27%). Cichlids might suffer buoyancy problems due to swim bladder inflation when they are brought from several meters depth during catch (own observations). One fish with buoyancy problems had the swim bladder punctured in the present study, but seemed to be in a good condition at release. However, this was on of the fish that were likely predated, and one might suspect that it was an easier prey due to a reduced condition after release.

The angling procedures in this study were slightly different from procedures performed by the local anglers, since the fish were anaesthetised and radio tagged. It may, therefore, be argued that they were in a poorer condition at release, and therefore more vulnerable to predation and other negative effects. However, on the contrary, our impression was that the fish in this study appeared in a better condition at release that many of those released by the local anglers. The reasons may be that the fish in this study were played for a short time, handled as carefully as possible by experienced researchers, and released as soon as possible after recovery. Further, radio-transmitters were small compared to the fish size. Local anglers may keep the fish in live wells in the boat for hours before release, they may release the fish in an area and habitat far from where they were caught, and handling of the fish is not always optimal. We therefore believe that the fish under normal catch-and-release angling in this area is not less vulnerable to predation and other negative effects than the fish in this study. To reduce the negative effects by catch-and-release angling there is need for educating anglers in optimal handling of the fish. Further, little is generally known of which factors are likely to increase predation and general mortality risk after catch-and-release angling. In a previous study of catch-and-release angling of nembwe and threespot tilapia, almost no mortality was recorded (4%, Thorstad *et al.* 2004). Hence, there is need for studies identifying the most important factors that are likely to increase the mortality risk to be able to develop recommendations and guidelines for fish handling.

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