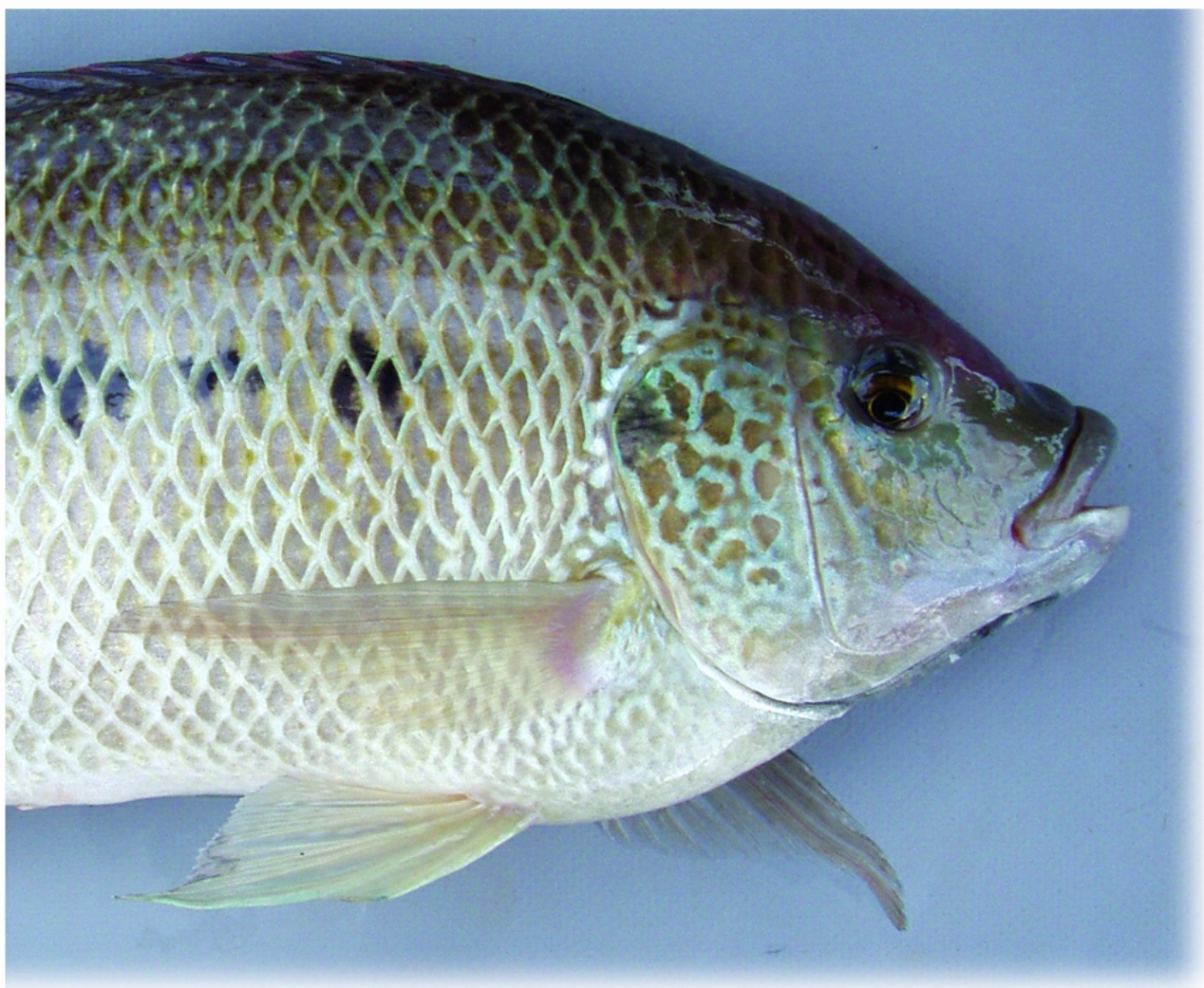


Movements and habitat utilisation of threespot tilapia in the Upper Zambezi River

Implications for fisheries management



NINA Project Report no. 23



Directorate Resource Management
Ministry of Fisheries and Marine Resources
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Namibia



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Movements and habitat utilisation of threespot tilapia in the Upper Zambezi River

Implications for fisheries management

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Abstract

Thorstad, E.B., Hay, C.J., Næsje, T.F., Chanda, B. & Økland, F. 2003. Movements and habitat utilisation of threespot tilapia in the Upper Zambezi River. Implications for fisheries management – NINA Project Report 23. 22pp.

Studies of radio tagged threespot tilapia

A successful management of fisheries in complex and variable floodplain ecosystems, such as in the Caprivi Region in Namibia, depends on a good understanding of the fish migrations and habitat preferences. Studies of the movements and habitat utilisation of radio tagged fish in the Upper Zambezi River were, therefore, initiated by the Namibian Ministry of Fisheries and Marine Resources in 1999. As part of this programme, nine threespot tilapia (*Oreochromis andersonii* Castelnau, 1861) were radio tagged in the Zambezi River in Caprivi during 11-15 November 2000. The objectives of the study were to:

- 1) record movements and habitat utilisation of threespot tilapia, and
- 2) outline the implications of fish movements and habitat utilization for fisheries management.

Three fish disappeared shortly after tagging and were, therefore, excluded from further analyses. The six remaining fish were tracked on average every 4.4 day during 23 November-8 May. Mean total distance moved by individual fish during the study was 13,513 m (range 2,612-44,578 m). Mean distance moved between tracking surveys was 391 m (range = 64-991 m). The fish were not stationary within a small area, but utilised a relatively large river stretch (on average 5,423 m, range = 730-15,360 m). Although to some extent moving around, the fish stayed in defined home ranges, which can be characterised as medium sized (50% probability of localisation within an average area of 48,244 m² and 95% probability of localisation within an average area of 304,645 m²). The threespot tilapia utilised to an increasing extent temporary water covered areas during rising and high water.

The fish utilised a broad spectrum of habitats. On average, 39% of the fish positions during tracking were in the mainstream of the river. The remaining positions were mainly in backwaters, side channels

and permanent swamps, but also on the floodplain during high water level. Total width of the water body where the fish were positioned varied between 8 and 2,000 m, and was on average 493 m. Distance to nearest shore varied between 1 and 1,000 m, and was on average 158 m. The fish seemed to be more closely associated with vegetation than previously described for adults of this species. On average 39% of the fish positions were away from vegetation, 11% near vegetation and 51% along/in vegetation. Water depth where the fish were recorded varied between 0.5 and 10.5 m, and was on average 3.4 m.

Implications for fisheries management

Coordination of local and regional management regulations is important for sustainable use of the fish resources and the fisheries. One should try to avoid that fish populations are protected in one part of the river, while seriously depleted in other parts, with the result that the total stock is harmed. In rivers bordering on several countries such as the Upper Zambezi River, multilateral management regulations are needed in addition to the national regulations for species frequently moving across the river, such as the threespot tilapia.

Basic knowledge of fish movements, seasonal migrations, habitat preferences and habitat utilisation is needed to evaluate the possible benefits of reserves and sanctuaries. Furthermore, migration and habitat studies can provide information on where and when important fish species are most vulnerable to exploitation. The residency of threespot tilapia within defined home ranges implies that restricted sanctuaries can protect adult fish, because the fish may be staying within the protected area over longer periods during variable flow regimes. However, a relatively large protected area seems to be required, based on the relatively large river stretch utilised by the fish. The threespot tilapia did not appear as habitat specialists, and protection of one specific habitat type is probably not needed to protect adults of this species. However, they may have special habitat requirements for reproduction. The relatively large movements of threespot tilapia may reduce the vulnerability to high exploitation in a specific area compared to highly resident species, because it is likely that a locally depleted population can be re-colonised by fish from neighbouring areas.

Chances of being caught in passive gears like gill-nets depend on the movement patterns of the fish. Based on the present results, the threespot tilapia is actively moving around, and are, hence, relatively vulnerable for being caught in gillnets widely spread out in the area. However, vulnerability for being caught in gill nets will, for example, also depend on the daily movement patterns of the fish and the distribution of gears.

Key words: *Oreochromis andersonii* - threespot tilapia - radio telemetry - behaviour - movement - habitat - management.

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Preface

Knowledge on fish migrations and habitat utilisation is imperative when implementing fisheries regulations. The objective of the present study was to analyse the behaviour of radio tagged threespot tilapia in the Namibian part of the Upper Zambezi River as background for recommendations to fisheries managers.

The study was financed by World Wildlife Fund (WWF), US Agency for Development (USAID) Namibia Mission, Namibian Ministry of Fisheries and Marine Resources (MFMR), and the Norwegian Institute for Nature Research (NINA). We thank Nicolene and Rolly Thompson for extensive help during catch, tagging and tracking of the fish. We also thank Synnøve Vanvik, Kari Sivertsen and Knut Kringstad for graphical design and figures.

Windhoek/Trondheim October 2003

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1 Introduction

Namibia is considered one of the driest countries in the world, and perennial rivers exist only along the borders in the north, north-east and the south. About 50% of the human population live near the northern perennial rivers, and at least 100,000 people derive most or part of their food, income and informal employment from the inland fish resource (MFMR 1995). A major concern has been the possible depletion of fisheries resources in the Zambezi and Okavango Rivers as a result of increased subsistence fishing due to the high population growth, which has brought about the need to review and improve legislation (Van der Waal 1991, Hocutt et al. 1994, Tvedten et al. 1994, Hay et al. 1996, 2000, Allcorn 1999, Purvis 2001a).

Management of a sustainable fishery depends on a better understanding of the fish migrations and habitat preferences in these complex and variable floodplain ecosystems. Studies of the movements of radio tagged fish in the Namibian part of the Zambezi River was, therefore, initiated by the Namibian Ministry of Fisheries and Marine Resources in 1999 (Økland et al. 2000, 2002, Thorstad et al. 2001, 2002).

Cichlidae is the largest fish family in Africa with about 900 species described and several more to be described (Skelton 2001). The threespot tilapia (*Oreochromis andersonii* Castelnau, 1861) is one of the most important cichlids for commercial and subsistence fisheries, and it is a valuable angling species (Næsje et al. 2001, Purvis 2001b, Skelton 2001, Hay et al. 2002). Threespot tilapia were radio tagged in the Namibian part of the Zambezi River in 2000. The objectives of the study were to:

- 1) record movements and habitat utilisation of threespot tilapia in the Upper Zambezi River during low water level immediately before the rainy period, increasing water level during the rainy period and high water level after the rainy period, and
- 2) outline the implications of fish movements and habitat utilisation for fisheries management.

2 Materials and methods

2.1 Study site

The Zambezi River is the fourth largest river system in Africa, both in length (2,660 km) and catchment area (approximately 1.45 mill km²). The river system is thoroughly described by Davies (1986). The river arises in north-western Zambia, passing through Angola, then back into Zambia, before it forms the north-eastern border between Zambia and Caprivi in Namibia from Katima Mulilo to Impalila Island, a distance of approximately 120 km (**figure 1**). The annual variation in water level is on average 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. Until 1990, the fishing pressure in this section of the Zambezi River was relatively low. However, fishing seems to have increased during the 1990s, and reports of reduced catches are of a major concern for the management authorities (MFMR 1995).

In the study area, the Zambezi River consists of a wide mainstream, with bends and deep pools. Small, vegetated islands, sandbanks, bays, backwaters and narrow side streams occur frequently. The stream velocity varies from stagnant to fast flowing water, varying with the water discharge. The only rapids are at Katima Mulilo and Impalila. There are also larger slow flowing channels and isolated pools. From approximately February until June large floodplains are formed, especially on the Namibian side of the river. In the mainstream 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. The water is clear with little suspended particles during low water. The river has ample available cover in the form of overhanging marginal 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 can be dense in places, 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. Inundated grassland is the dominant floodplain vegetation.

2.2 Catch and tagging of fish

Nine threespot tilapia were captured by rod and line in the main stream of the Zambezi River 25-60 km downstream from Katima Mulilo in Caprivi, Namibia, during 11-15 November 2000 (**figure 1, table 1**). The fish were placed directly into the anaesthetisation bath (5 mg Metomidate per l water, Marinil™, Wildlife Labs., Inc., USA). Radio transmitters (Advanced Telemetry Systems, Inc., USA, **table 1**) were externally attached to the fish, using the method described in Thorstad et al. (2001). During the tagging procedure, which lasted about 2 min, the fish were kept in a water filled tube. Transmitter weight in water was 7-8 g, or less than 2.6% of the body weight of the fish. The transmitters emitted signals within the 142.123-142.361 MHz band, and transmitter frequencies were spaced at least 10 kHz apart. Total body length was recorded, before the fish were placed in a container for recovery (2-5 min). The fish were released at the catch site, except one fish (no. 5) that was released 500 m downstream from the catch site due to drifting of the boat during tagging. The water temperature was 29.1-29.7 °C during catch and tagging.

2.3 Tracking of fish

The fish were tracked from boat by using a portable receiver (R2100, ATS) connected to a 4-element Yagi antenna. The fish were located with a precision of minimum ± 10 m in the main river. Some of the backwaters and floodplains were inaccessible by boat, and the location had to be estimated based on the direction and signal strength. The fish were tracked on average every 4.4 day during 23 November-8 May, and individual fish were tracked up to 43 times (**table 1**). The fish were tracked intensively during a period of low water (23 November-27 December), rising water (28 December-11 March) and high water (12 March-8 May) (**figure 2, table 1**).

Figure 1. The upper part of the Zambezi River in Caprivi in north-eastern Namibia. Sites where individual threespot tilapia were radio tagged and released are indicated (dots). Shaded areas indicate floodplain during high water levels.

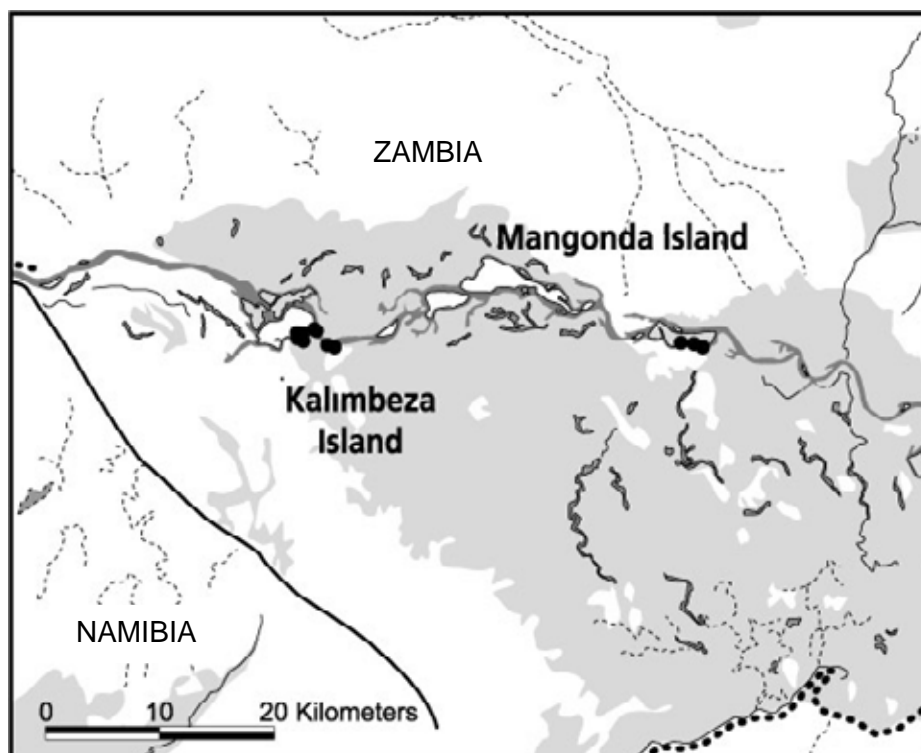


Table 1. Threespot tilapia radio tagged in the Zambezi River, Namibia, 11-15 November 2000.

| Fish no. | Tagging date | Body length (cm) | Transmitter model* | Total number of fixes | Number of fixes during each period (low, rising, high water) | Last tracking date |
|----------|--------------|------------------|--------------------|-----------------------|--|--------------------|
| 1 | 11.11.00 | 28.5 | F2040 | 23 | (6, 8, 9) | 30.04.01 |
| 2 | 11.11.00 | 29.0 | F2040 | 0 | (0, 0, 0) | - |
| 3 | 11.11.00 | 31.0 | F2120 | 33 | (9, 10, 14) | 08.05.01 |
| 4 | 11.11.00 | 25.0 | F2040 | 1 | (1, 0, 0) | 01.12.00 |
| 5 | 11.11.00 | 30.0 | F2120 | 42 | (11, 17, 14) | 08.05.01 |
| 6 | 12.11.00 | 33.5 | F2120 | 43 | (12, 17, 14) | 08.05.01 |
| 7 | 12.11.00 | 50.0 | F2120 | 40 | (12, 17, 11) | 24.04.01 |
| 8 | 12.11.00 | 27.0 | F2040 | 0 | (0, 0, 0)** | - |
| 9 | 15.11.00 | 31.0 | F2040 | 21 | (10, 11, 0) | 08.02.01 |

*Model F2120 are flat transmitters with outline dimensions of 19 x 50 x 9 mm, weight in air of 15 g and weight in water of 7 g. Model F2040 are cylindrical transmitters with diameter of 12 mm, length of 46 mm, weight in air of 10 g and weight in water of 8 g.

**The fish was probably caught by a fish eagle; the transmitter was located five days after tagging under a tree where fish eagles had been observed.

Habitat classifications were made each time a fish was positioned. Recordings were made of water cover (1: permanent water cover, 2: temporary water cover, i.e. each year during the flood, 3: episodic water cover, i.e. occasional but not regular during flood), main habitat type (1: mainstream of river, 2: backwater, 3: mouth of backwater, 4: side

channel, 5: tributary, 6: permanent swamp, 7: temporary swamp, 8: floodplain), position to vegetation (1: no vegetation, 2: near vegetation, i.e. 2-5 m distance, 3: along/in vegetation, i.e. less than 2 m distance), and vegetation type if near or along vegetation (1: inner aquatic submerged, 2: inner aquatic floating, 3: inner aquatic anchored, 4: mar-

ginal aquatic submerged, 5: marginal aquatic floating, 6: marginal aquatic anchored, 7: marginal terrestrial submerged, 8: marginal terrestrial overhanging). Moreover, recordings were made of water temperature at surface, depth (only water depth, which was measured by an echo sounder or manually with a rope and weight, depth of the fish was unknown), and substrate (1: muddy, 2: clay, 3: sand, 4: gravel, 5: pebbles, 6: rocks, 7: 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. 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.

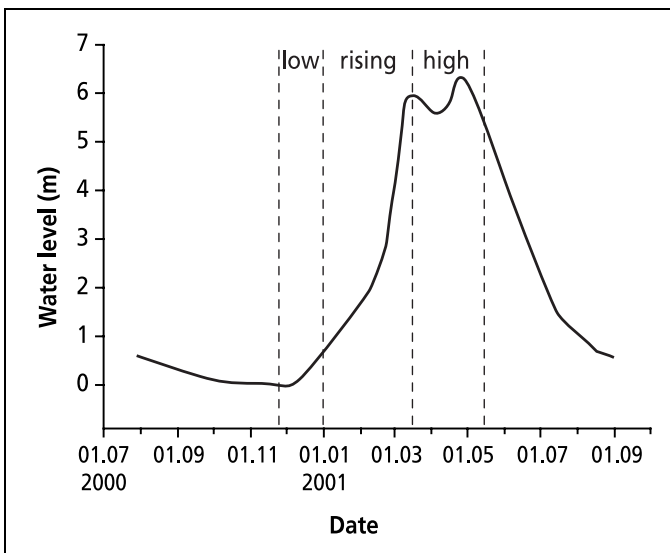


Figure 2. The water level in the Zambezi River from 1 August 2000 to 31 August 2001. The study periods at low, rising and high water levels are indicated.

2.4 Data analyses

Three fish disappeared from the study area shortly after tagging (**table 1**) and were not included in the analyses. Thus, sample size for all analyses and descriptive statistics were six fish, except for descriptive statistics during high water with a sample size of five fish due to one more fish disappearing (see **table 1**). Statistical analyses of movements and habitat utilisation between periods were per-

formed by non-parametric paired comparisons (Wilcoxon Signed Ranks Tests). Due to only five fish recorded during high water, statistical comparisons were made only between low and rising water. A significance level of 0.05 was used. Descriptive statistics and statistical analyses were based on proportions of fish or average values for individual fish.

Thoreau & Baras (1997) found reduced activity levels during the first 12-24 hours after anaesthesia and radio tagging of tilapia (*Oreochromis aureus* Steindachner 1864), and 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 we did not include movements due to handling and tagging effects, fish were not tracked the ten first days after tagging.

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). When " h " was larger than 100, " h " was set to 100 to avoid that too much land areas were included in the home range. 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 10.0, except for the home range analyses, which were performed with ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.).



left and under:
The treespot tilapia is an important species in both subsistence and recreational fisheries



right and under:
Survey team catching three-spot tilapia for radio tagging. All fish were caught with rod and line either from boat or land.





left and under:
The threespot tilapia were tagged on a surgical table on land (under) or in boat with tagging equipment.



right and under:

After recovery, the threespot tilapia were in a good condition when released back into the river.





top:

The survey team tracking radio tagged threespot tilapia and recording the exact position with GPS.

over and left:

Threespot tilapia were often recorded in the main river in association with vegetation.

3 Results

3.1 Movements

Total distance moved by individual fish during the entire study was on average 13,513 m (SD = 15,567, range = 2,612-44,578 m). Distance moved between tracking surveys was on average 391 m (SD = 336, range = 64-991 m). Distance moved was not different between low and rising water (Wilcoxon test, $Z = -0.94$, $P = 0.35$), and was not dependent on body length (linear regression, $r^2 = 0.12$, $P = 0.51$).

Total distance moved by individual fish during the first 11-20 days after tagging (from tagging to first tracking) was on average 6,060 m (SD = 13,839, range = 16-34,290 m). Two fish had an overall downstream movement, one an upstream movement and three a sideways movement during this period.

Fish were obviously only recorded in permanently water-covered areas during low water. During rising water, all six fish (100%) were recorded in permanently water-covered areas during some or all surveys, but three of the fish (50%) were also recorded in temporary flooded areas (12-45% of the surveys). During high water, two fish (40%) were recorded only in permanently water-covered areas, whereas three fish (60%) were recorded only in temporary flooded areas.

3.2 Home range

Length of the river stretch used (i.e. distance between the two fixes farthest from each other for individual fish) was on average 5,423 m (SD = 5,089, range = 730-15,360 m), and was not dependent on body length (linear regression, $r^2 = 0.086$, $P = 0.57$).

Home range sizes varied among individuals (**figure 3**), with a 50% probability of localisation within an average area of 48,244 m² (SD = 46,795, range = 4,099-133,542 m²) and a 95% probability of localisation within an average area of 304,645 m² (SD = 245,591, range = 24,573-689,732 m²). Home range size did not depend on body length

(linear regression, 95%: $r^2 = 0.28$, $P = 0.28$; 50%: $r^2 = 0.16$, $P = 0.44$).

Home ranges were also analysed separately for low, rising and high water level (**figure 3**). The 95% probability home range was on average 141,376 m² during low water, 168,062 m² during rising water and 108,830 m² during high water. The 50% probability home range was on average 28,651 m² during low water, 31,549 m² during rising water and 22,691 m² during high water. Neither the 95% nor the 50% probability home range was different between low and rising water (Wilcoxon test, 95%: $Z = -0.94$, $P = 0.35$; 50%: $Z = -0.11$, $P = 0.92$, **figure 3**).

3.3 Habitat utilisation

All the fish were recorded in the mainstream of the river. However, four fish (67%) were recorded in one or more additional main habitat type; four fish (67%) were recorded in backwaters, one fish (17%) in the mouth of backwaters, two fish (33%) in side channels, two fish (33%) in permanent swamp and one fish (17%) on the floodplain. (Note that percentages add up to more than hundred due to some fish being recorded in more than one habitat type.)

On average, 39% of the fixes were in the mainstream of the river (50, 33 and 40% during low, rising and high water, respectively), 26% in backwaters (48, 24 and 0% during low, rising and high water), 0.5% in mouth of backwaters (2, 0 and 0% during low, rising and high water), 12% in side channels (0, 14 and 20% during low, rising and high water), 16% in permanent swamps (0, 28 and 20 during low, rising and high water), and 7% on the floodplain (0, 0 and 20% during low, rising and high water).

Total width of the water body where the fish were positioned varied between 8 and 2,000 m, and was on average 493 m (177 m during low, 190 m during rising and 1,088 m during high water). Distance to nearest shore (dry land) given as proportion of total width was on average 31% (22% during low, 36% during rising and 34% during high water). Distance to nearest shore varied between 1 and 1,000

m, and was on average 158 m (48 m during low, 77 m during rising and 384 m during high water).

The fish were recorded in different positions in relation to vegetation; four fish (67%) were one or more times recorded away from vegetation, four fish (67%) near vegetation and four fish (67%) along/in vegetation. On average, 39% of the positions during tracking surveys were away from vegetation (48, 36 and 40% during low, rising and high water), 11% near vegetation (23, 4 and 0% during low, rising and high water) and 51% along/in vegetation (29, 60 and 60% during low, rising and high water).

The fish recorded near or along/in vegetation ($n = 4$) were associated with several types of vegetation. All of them (100%) were during one or more times associated with marginal aquatic anchored vegetation, all (100%) with marginal aquatic floating vegetation, one (25%) with marginal terrestrial overhanging vegetation, two (50%) with inner aquatic anchored vegetation, one (25%) with marginal terrestrial submerged vegetation and one (25%) with inner aquatic submerged vegetation. On average, 39% of the fish positions during tracking surveys were at marginal aquatic anchored vegetation, 38% at marginal aquatic floating vegetation, 13% at marginal terrestrial submerged vegetation, 4% at inner aquatic anchored vegetation, 6% at marginal terrestrial overhanging vegetation and 1% at inner aquatic submerged vegetation.

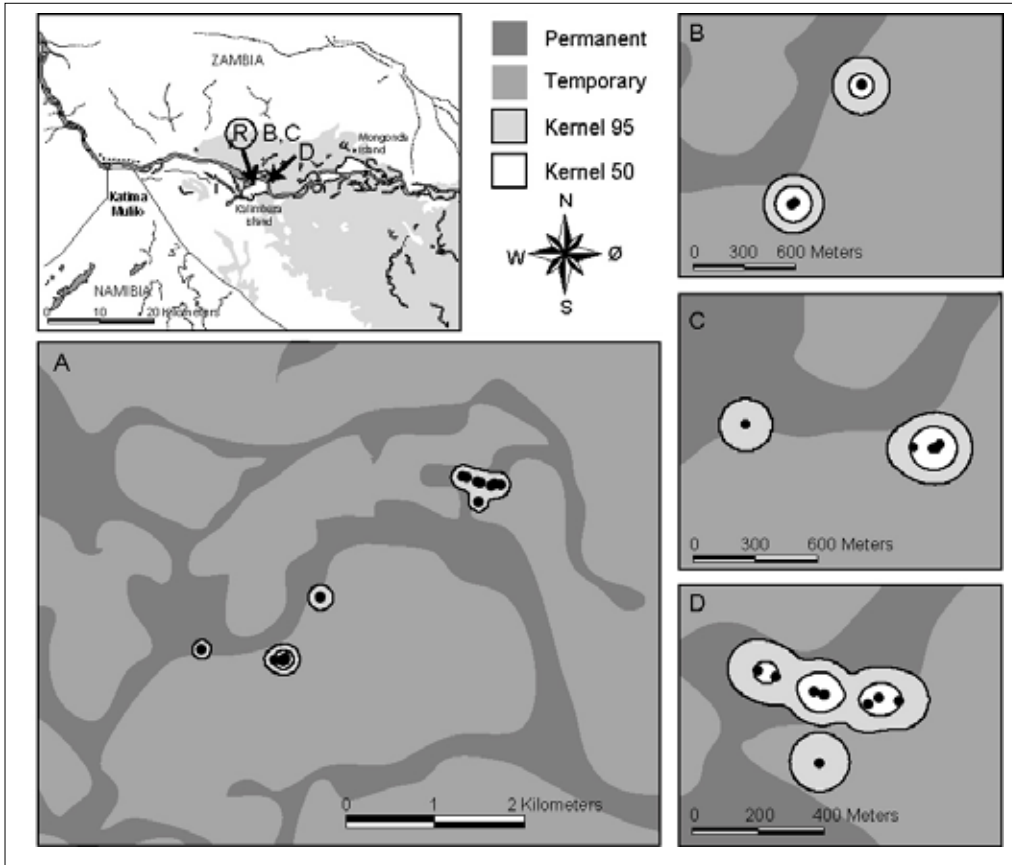
Water depth where the fish were recorded varied between 0.5 and 10.5 m, and was on average 3.4 m (3.2 m during low, 2.8 m during rising and 6.1 m during high water). Water depths did not differ between low and rising water (Wilcoxon test, $Z = -0.31$, $P = 0.75$), and was not dependent on body length (linear regression, $r^2 = 0.006$, $P = 0.88$).

The fish were mainly associated with sandy substratum; all the fish (100%) were one or more times recorded on sandy substratum, three (50%) on muddy, soft bottom and two (33%) on clay. On average, 73% of the fish positions during tracking surveys were on sandy substratum (52, 51 and 100% during low, rising and high water), 6% on clay (10, 12 and 0% during low, rising and high

water) and 21% on muddy bottom (39, 38 and 0% during low, rising and high water).

The water temperature decreased slightly during the study period, and was on average 27.4 °C (range = 26.9-28.3 °C) during low water, 27.6 °C (range = 27.1-28.0 °C) during rising water and 26.2 °C (range = 25.7-26.6 °C) during high water.

Fish no. 1



Fish no. 3

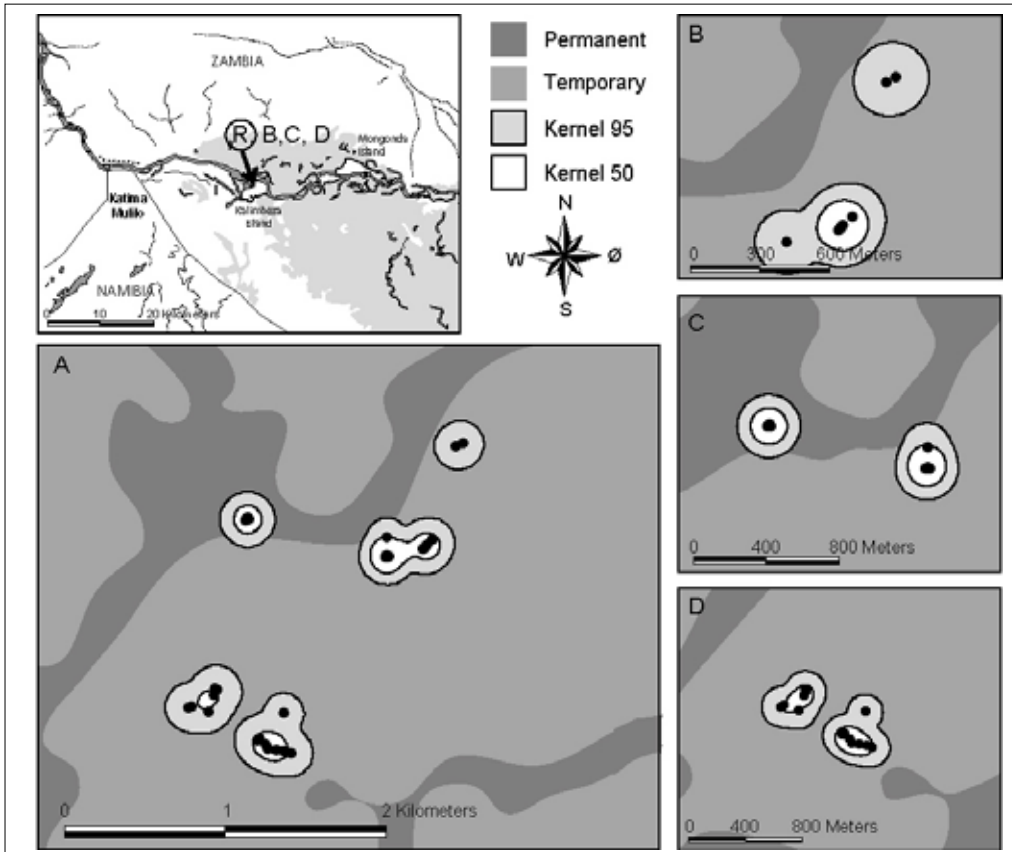
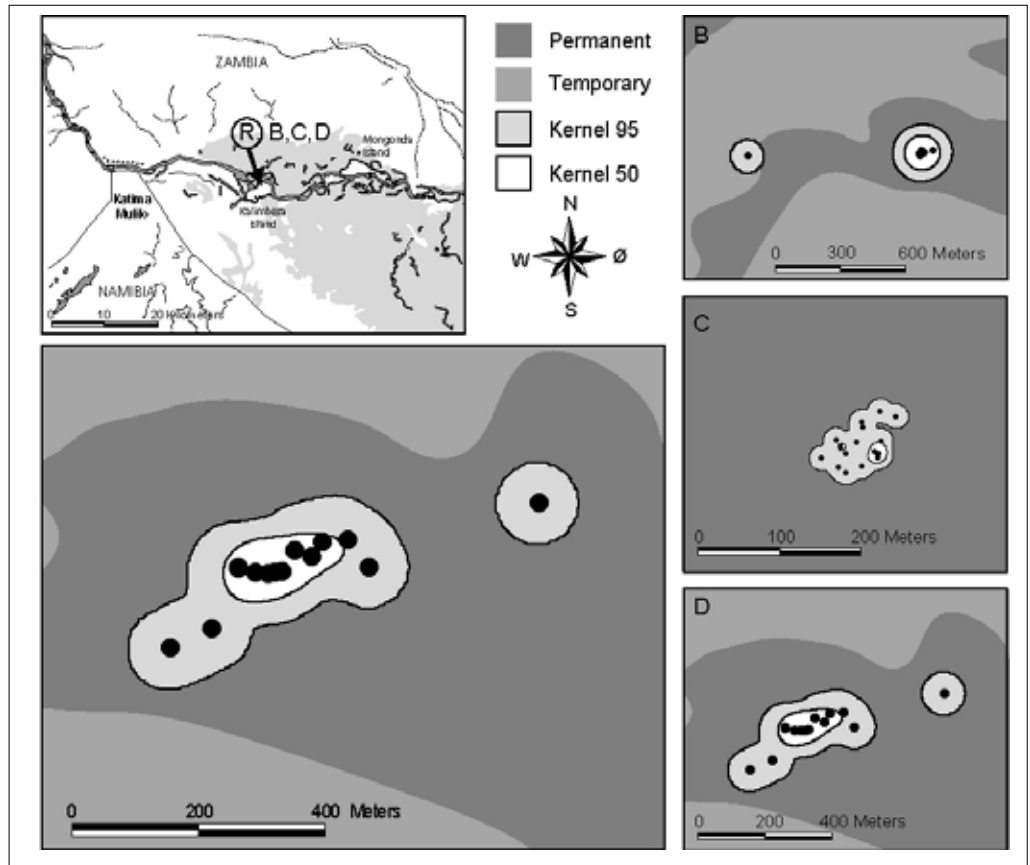


Figure 3. Kernel home ranges of individual radio tagged threespot tilapia ($n = 6$) in the Zambezi River in 2000 and 2001 during a) the entire study period, b) low water only, c) rising water only, and d) high water only (figure d is lacking for the fish not recorded during the high water period). Dots show fish positions during tracking, and the contours of home ranges refer to two different levels of probability (95 and 50%). Landscape contours refer to permanent and temporary water covered areas. Upper left figure indicates where in the Zambezi River the fish were released (R) and where home ranges were recorded. Individual fish number corresponds to the numbers in **table 1**.

Fish no. 5



Fish no. 6

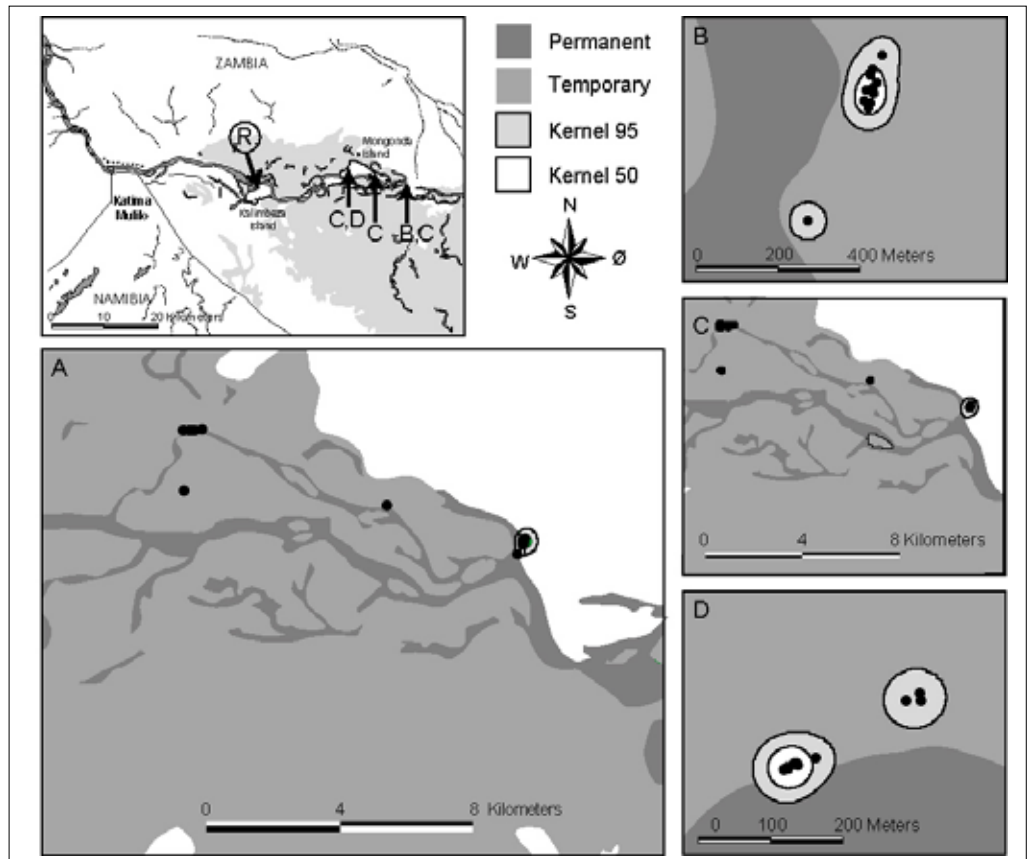
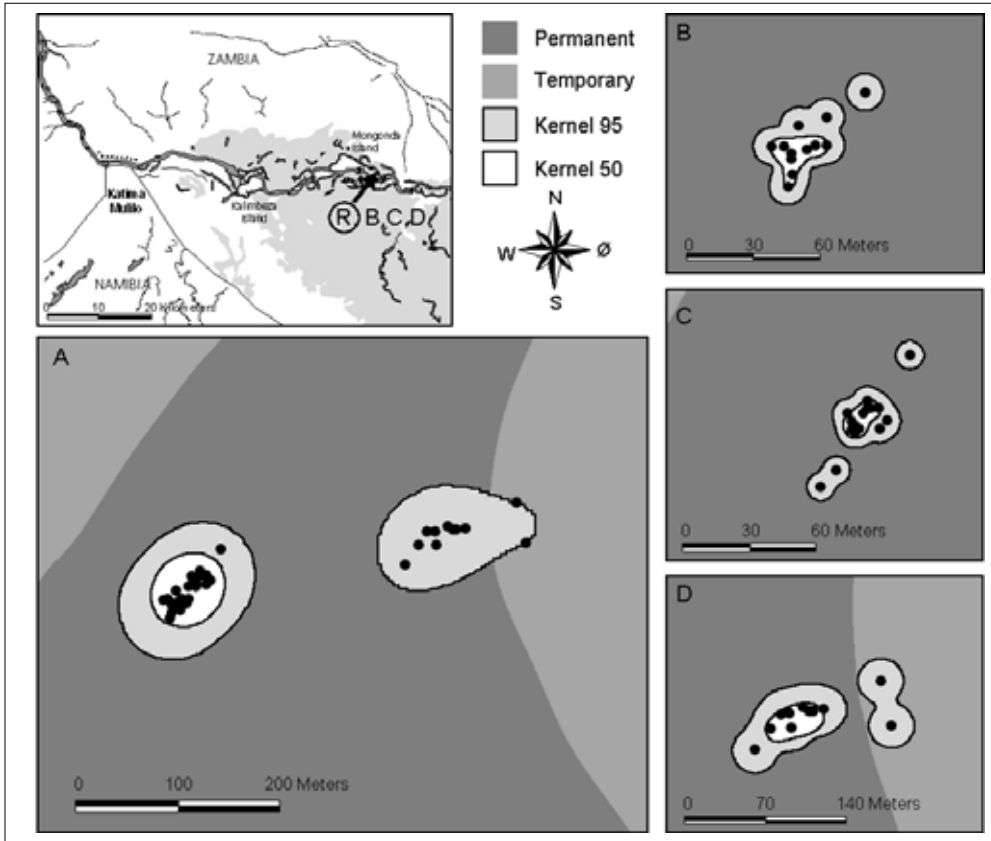


Figure 3. Continued

Fish no. 7



Fish no. 9

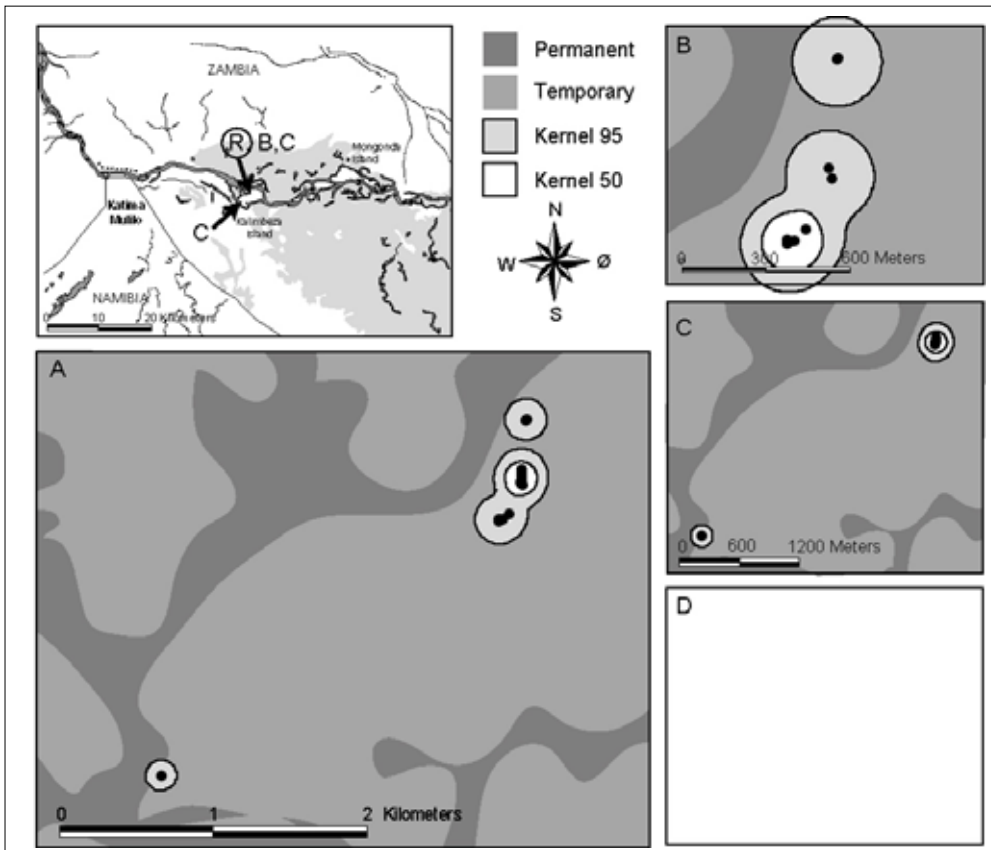


Figure 3. Continued

4 Discussion

4.1 Movements and home range

The threespot tilapia were not stationary within a small area, but moved around and used a relatively large river stretch during the study (on average 5.4 km). The movements were more extensive and the river stretch used larger than for eight radio tagged threespot tilapia in a previous study in the same area in 1999/2000. In the previous study, the fish utilised an average river stretch of only 220 m (Økland et al. 2000, Thorstad et al. 2001). The differences between the two studies seems to be real as the fish were within the same body size range, the tracking intensity comparable, and the time of the year approximately the same (the present study were from November to May and the previous study from October to March). The differences in movement patterns may be linked to differences in the flood cycle, as the rise in water level was much steeper in 2000/2001 than in 1999/2000. Both years, the rise in water level started around 1 December. However, in the middle of March 2000, the water level had still not reached 2 m, whereas at the same time in 2001, the water level had passed 6 m and was almost at its peak. When the flood rises, the main channel and backwaters are first filled with water, and the floodplain is only starting to get flooded at water levels higher than 2 m. Thus, the increased movements in threespot tilapia in 2000/2001 may be connected to the steeper rise in water level.

The fish in this study had probably reached sexual maturity, because the minimum size for sexually mature threespot tilapia is approximately 25-27 cm in this area (Van der Waal 1976, own unpublished data). Females containing ripe ovaries have been found in the Caprivi between November and March (Van der Waal 1976, 1985), hence, reproduction most likely occurred during the study period. The males are building saucer shaped nests where the eggs are laid and picked up by the females (Merion & Bruton 1988, Skelton 2001). Females are mouthbrooding the eggs, and may raise multiple broods during the warmer months (Van der Waal 1976, Skelton 2001). It has been suggested that some riverine cichlids undertake longitudinal and lateral seasonal migrations onto the inundated

floodplain where their young may find favourable environments for fast growth, and then returning to the river under receding waters (e.g. Winemiller 1991, Van der Waal 1996). The threespot tilapia utilised to an increasing extent temporary water covered areas during rising and high water, and one fish moved out onto the classical floodplain habitat. The utilisation of temporary water covered areas and floodplain habitat may be linked to the reproductive behaviour of the fish.

Although to some extent moving around in the river, the threespot tilapia stayed within what can be characterised as medium sized home ranges (95% probability of localisation within an average area of 0.3 km²). However, the individual variation was large, with the largest home range 28 times larger than the smallest.

4.2 Habitat utilisation

All the fish were recorded in the mainstream of the river, and on average, 39% of the fish positions during tracking were in the main river. The remaining positions were mainly in backwaters, side channels and permanent swamps, but also on the floodplain during high water level. This large variation in habitats used, but with a predominance of positions in habitats with slow-flowing or standing water, is in accordance with other studies. According to Skelton (2001), threespot tilapia prefer slow-flowing or standing water such as in pools, backwaters and floodplain lagoons. Van der Waal & Skelton (1984) found that threespot tilapia were abundant in deep, standing waters, common in streams with sandy substrate and regular in shallow swamps. Bell-Cross (1974) reported that threespot tilapia were found in all main habitat types in the Upper Zambezi River.

According to Skelton (2001), adult threespot tilapia occupy deep open waters, whereas juveniles remain inshore among vegetation. The results in the present study call attention to a more variable habitat utilisation by adult fish than this description. In accordance with Skelton (2001), the fish mainly occupied open waters, as the fish were recorded on average 158 m from the nearest shore, which constituted 31% of the total width of the water body. However, some of the adult fish were also

recorded closer to the shore (down to 1 m) and were recorded in narrower water bodies (down to 8 m wide). The adult fish were also often associated with vegetation, as 62% of the fixes were near or along/in vegetation.

Water depths where fish were recorded varied between 0.5 and 10.5 m, but it is not known at which depths above bottom the fish stayed. Threespot tilapia are reported both as filter and bottom feeders, and also feeding on the surface film (Van der Waal 1985, Skelton 2001). These feeding habits indicate that threespot tilapia may stay at different depths in the water column.

The threespot tilapia were mainly found on sandy substratum, but also on mud and occasionally on clay. The association with sandy substratum may not be a preference for sandy substratum, but simply a result of the widespread occurrence of sandy bottom in the study area of the mainstream Zambezi River. The Upper Zambezi River is a typical "sand-bank" river, mainly with sandy bottom (Van der Waal & Skelton 1984).

4.3 Methods

Anaesthetisation and tagging procedures seemed to be acceptable, as all threespot tilapia both in the present and a previous study (Thorstad et al. 2001) were alive as long as they were found during tracking surveys, and no transmitter-loss was recorded.

In a previous study of threespot tilapia and pink happy, many of the fish showed downstream movements immediately after tagging (Thorstad et al. 2001), which was regarded as a behavioural reaction to handling and tagging. Such behaviour immediately after release is also in other studies regarded as abnormal behaviour due to the treatment of the fish (e.g. Mäkinen et al. 2000). In the present study, the threespot tilapia had moved on average 6.1 km away from the release site when tracked for the first time 11-20 days after release, which seems far compared to the average movement of 0.4 km between tracking surveys every 4.4 day later in the study. The excessive movements immediately after tagging were both downstream, upstream and sidewise, but they might still have

been a response to catch and tagging. Therefore, data from this period were omitted from the analysis.

Three fish disappeared from the river immediately after tagging. One of them was probably caught by a fish eagle. It is unknown whether the remaining missing fish moved out of the study area, were recaptured without being reported, or the transmitter failed. Transmitter failure is the least likely explanation, as these transmitters earlier have proven reliable.

4.4 Implications for fisheries management

Basic knowledge of fish movements, seasonal migrations, habitat preferences and habitat utilisation is important for sustainable management of fisheries both locally and regionally among countries. Such information is also needed to evaluate the possible benefits of reserves and sanctuaries. Furthermore, migration and habitat studies can provide information on where and when important fish species are most vulnerable to exploitation.

Coordination of local and regional management regulations is important for fish populations and fisheries. One should try to avoid that fish populations are protected in one part of the river, while seriously depleted in other parts, with the result that the total stock is harmed. In rivers bordering on several countries such as the Upper Zambezi River, multilateral management regulations are needed in addition to the national regulations for species frequently moving across the river, such as the threespot tilapia.

The residency of threespot tilapia within defined home ranges implies that restricted sanctuaries can protect adult fish, because the fish may be staying within the protected area over longer periods and during variable flow regimes. However, a relatively large protected area seems to be required, based on the relatively large river stretch utilised by the fish. The threespot tilapia did not appear as habitat specialists, and protection of a specific habitat type is probably not needed to protect adults of this species. However, they may have special habitat requirements for reproduction.

The relatively large movements of threespot tilapia may reduce the vulnerability to high exploitation in a specific area compared to highly resident species, because it is likely that a locally depleted population can be re-colonised by fish from neighbouring areas.

Chances of being caught in passive gears like gillnets depend on the movement patterns of the fish. Based on the present results, the threespot tilapia is actively moving around, being relatively vulnerable for being caught in widely distributed gillnets. However, vulnerability for being caught in gill nets will also depend on the daily movement patterns of the fish and the distribution of gears.

It must be emphasised that a relatively small number of fish were recorded in this study, and the full annual cycle was not studied. These limitations must be considered when applying the present data for management recommendations. Management actions should also take into consideration the requirements of juveniles of the species.

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