

Space use and habitat utilisation of tigerfish and the two cichlid species nembwe and threespot tilapia in the Upper Zambezi River

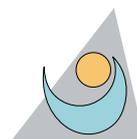
Implications for fisheries management



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Directorate Resource Management
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Namibia



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Space use and habitat utilisation of tigerfish and the two cichlid species nembwe and 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. Space use and habitat utilisation of tigerfish and the two cichlid species nembwe and threespot tilapia in the Upper Zambezi River. Implications for fisheries management. - NINA Project Report 24. 23 pp.

Background and objectives

A successful management of floodplain fisheries, such as in the Caprivi Region in Namibia, depends on a good understanding of the fish migrations and habitat preferences in these complex and variable ecosystems. Therefore, studies of the movements and habitat utilisation of radio tagged fish in the Upper Zambezi River were initiated by the Namibian Ministry of Fisheries and Marine Resources in 1999. The movements and habitat utilisation of tigerfish (*Hydrocynus vittatus* Castelnau, 1861), nembwe (*Serranochromis robustus* Günther, 1864) and threespot tilapia (*Oreochromis andersonii* Castelnau, 1861) were studied in 2000/2001, and the species specific results have been presented in three previous reports. The three species were studied in the same area of the river during the same period, and the results are therefore comparable.

The objectives of this report are to:

- 1) summarise and compare the recorded movements and habitat utilisation of tigerfish, nembwe and threespot tilapia, and
- 2) outline the implications of fish movements and habitat utilisation for fisheries management.

Comparison of movements and habitat utilisation among tigerfish, nembwe and threespot tilapia

Movements and habitat utilisation were recorded for 15 tigerfish (body lengths 30-54 cm), 13 nembwe (body lengths 32-40 cm) and 6 threespot tilapia (body lengths 25-50 cm). Fish were caught and radio tagged during 6 November - 24 December 2000, and they were tracked until 18 May 2001. The tigerfish were positioned on average every 4.1 day, the nembwe every 3.7 day and the threespot tilapia every 4.4 day.

The three species differed in their movement patterns, with nembwe as the most stationary species,

tigerfish as the species with the most extensive movements and threespot tilapia as the intermediate. Average distance moved between tracking surveys was 16 times longer for tigerfish (1447 m) than for nembwe (93 m), and 4 times longer for threespot tilapia (391 m) than for nembwe. Mean length of the river stretch used was 14 times longer for tigerfish (18.8 km) than for nembwe (1.3 km), and 4 times longer for threespot tilapia (5.4 km) than for nembwe.

Most riverine cichlid species are in the literature regarded as having a highly resident life style. Although systematic migratory patterns were not demonstrated in this study, the cichlids were to a relatively large extent moving around, especially the threespot tilapia. Thus, the large riverine cichlids may not be as highly resident as previously suggested.

The tigerfish showed a variable movement pattern, with approximately half of the fish staying within defined home ranges, only performing movements less than 1,000 m between tracking surveys. The remaining tigerfish were resident for periods, but moved over long distances (on average 18,784 m) to new areas between the residency periods. However, home range size (the area with 95% probability of localisation of the fish) was not larger for tigerfish than for the two other species, even though the movements were more extensive.

Approximately half of the individuals of all three species moved to temporary water covered areas during rising and high water levels. The tigerfish differed from the two other species in the utilisation of temporary water covered areas, as they were recorded in temporary water covered areas to a lesser extent during rising water level. However, during high water level, the utilisation of temporary water covered areas was similar for the three species.

The three species seemed more similar in their habitat utilisation than in their movement patterns. All species were much of the time associated with the main river, and stayed in relatively deep, open water bodies at some distance from shore. However, adults of these species are apparently not habitat specialists, and the fish were recorded in a wide range of habitats. Variation in habitat utilisation

tion was relatively large both within and among individuals. The results indicate that adults of all three species were more associated with vegetation than previously assumed, although tigerfish were to a lesser extent associated with vegetation than threespot tilapia and nembwe.

Implications for fisheries management

Coordination of local and regional management regulations is important for the management of tigerfish, nembwe and threespot tilapia, to maintain sustainable fisheries and protect the fish resources. In rivers that flow through or border on several countries such as the Upper Zambezi River, multilateral management regulations are needed; especially for management of long-distance moving species as the tigerfish, and for fish that frequently cross the river, as all the three species studied. However, tigerfish populations may be less vulnerable to high exploitation in a limited area than the more resident species nembwe and threespot tilapia, because it is likely that a locally depleted population can be re-colonised by fish from other areas.

Management regulations are often implemented with the use of gear and fishing effort restrictions, and introduction of sanctuaries and no fishing periods. In the Upper Zambezi River, local stocks of nembwe and threespot tilapia may be depleted if the fishing mortality exceeds their carrying capacity. In addition to gear and effort restrictions, sanctuaries within areas with high fishing pressure can protect adult fish, because some of them may stay within the protected area for longer periods and during variable flow regimes. Threespot tilapia may require larger sanctuaries for protection than nembwe, since they seem to utilise larger river stretches. Small sanctuaries may only to a limited extent protect the long-distance moving fractions of the tigerfish population, and when management actions to protect adult tigerfish are needed, other implementations may be more appropriate.

In general, vulnerability for being caught in passive gears like gillnets depends on the movement patterns of the fish. Based on the present results, the extensively moving tigerfish seem to be more likely caught in wide spread passive gears than the more stationary threespot tilapia and even more stationary nembwe. However, the vulnerability for being

caught in gillnets will also depend on the daily movement patterns, the local activity patterns, and if the gill net fishery targets certain species.

Key words: *Hydrocynus vittatus* - *Serranochromis robustus* - *Oreochromis andersonii* - tigerfish - nembwe - threespot tilapia - radio telemetry - 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 and compare the behaviour of radio tagged tigerfish, nembwe and threespot tilapia in the Namibian part of the Upper Zambezi River as background for recommendations to fisheries managers. The report is based on data published in the NINA Project Reports Økland *et al.* (2002), Thorstad *et al.* (2002) and Thorstad *et al.* (2003).

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, and Odd Terje Sandlund for constructive comments on an earlier version of the report.

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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, Thorstad et al. 2001). The movements and habitat utilisation of tigerfish (*Hydrocynus vittatus* Castelnau, 1861), nembwe (*Serranochromis robustus* Günther, 1864) and threespot tilapia (*Oreochromis andersonii* Castelnau, 1861) were studied in 2000/2001, and the species specific results have been presented in three previous reports (Økland et al. 2002, Thorstad et al. 2002, 2003).

The tigerfish is an important species in both the subsistence, semi-commercial and recreational fisheries in the Zambezi River (Næsje et al. 2001, Purvis 2001b, Hay et al. 2002), and has a reputation as one of the world's most spectacular freshwater game fish species (Skelton 2001). Tigerfish are predators throughout life (Skelton 2001). Although widespread in Africa and still common in certain areas, tigerfish have declined in many rivers due to pollution, water extraction and migration barriers, such as weirs and dams (Skelton 2001, Steyn 1996).

Cichlidae is the largest fish family in Africa with about 900 species described and several more to

be described (Skelton 2001). The nembwe is one of the serranos, or largemouth breams, which is a distinct group of large predatory cichlids, which are popular angling species and important in the floodplain fisheries (Skelton 2001). The nembwe is a major angling target with bass-like qualities, and valuable for the commercial and subsistence fisheries (Næsje et al. 2001, Skelton 2001, Hay et al. 2002). The threespot tilapia is, like nembwe, a cichlid important for commercial and subsistence fisheries, and it is a valuable angling species (Næsje et al. 2001, Purvis 2001b, Skelton 2001, Hay et al. 2002). Unlike the predatory habits of tigerfish and nembwe, threespot tilapia graze on diatoms, algae and detritus, but large individuals may take insects and other invertebrates (Skelton 2001).

Tigerfish, nembwe and threespot tilapia were studied with similar methods, in the same area and during the same period in 2000/2001, and the data are therefore directly comparable. The objectives of this report are to:

- 1) summarise and compare the recorded movements and habitat utilisation among tigerfish, nembwe and threespot tilapia, and
- 2) outline the implications of fish movements and habitat utilisation for fisheries management.

For details regarding results and methods for each of the species, previous reports should be consulted (Økland et al. 2002, Thorstad et al. 2002, 2003).

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, passes through Angola, then back into Zambia, before it forms the north-eastern border between Caprivi in Namibia, from Katima Mulilo to Impalila Island, and Zambia, 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 flood peaks in February-April, before it declines 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, back-

waters 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.

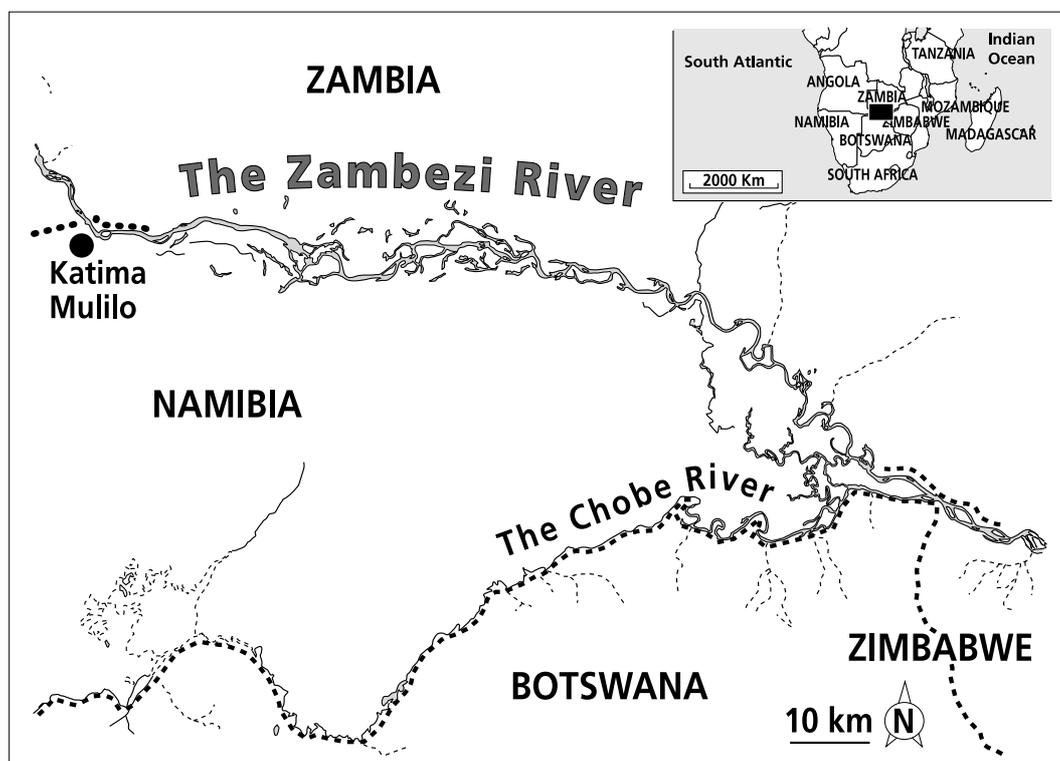


Figure 1. The Upper Zambezi River in Zambia and north-eastern Namibia. The radio tagged tigerfish, nembwe and threespot tilapia were caught and released 25-61 km downstream from (i.e. east of) Katima Mulilo.

2.2 Studies of tigerfish, nembwe and threespot tilapia

Movements and habitat utilisation were recorded for radio tagged tigerfish ($n = 15$), nembwe ($n = 13$) and threespot tilapia ($n = 6$) in the same area of the Zambezi River during the same period, and the results are, therefore, directly comparable. Nembwe and threespot tilapia were caught in the main river by rod and line, whereas tigerfish were caught by rod and line or seine net. The fish were caught 25-61 km downstream from Katima Mulilo. Mean body length of the tigerfish was on average 40 cm (fork length, range 30-54 cm), of nembwe 39 cm (total length, range 32-40 cm) and of threespot tilapia 32 cm (total length, range 25-50 cm). Fish were caught and tagged during 6 November - 24 December 2000, and tracking continued until 18 May 2001, during low, rising and high water levels (**figure 2**).

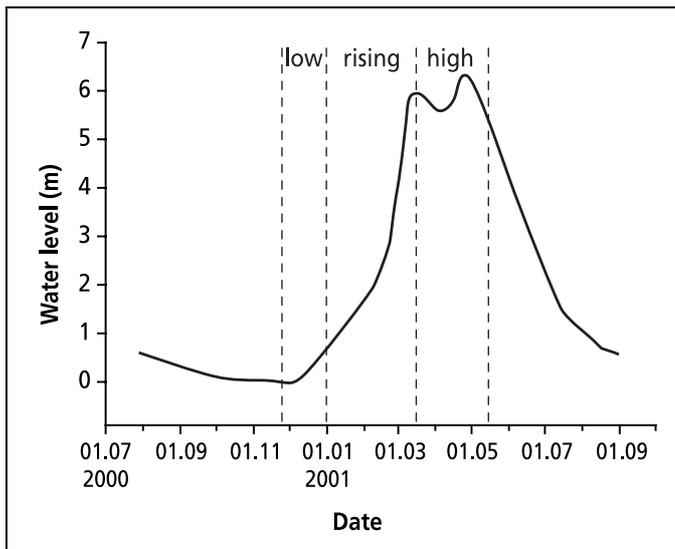


Figure 2. The water level in the Zambezi River from 1 August 2000 to 31 August 2001. The study periods at low, rising and high water levels are indicated.

Individual fish were tracked up to 47 times. The tigerfish were positioned on average every 4.1 day, the nembwe every 3.7 day and the threespot tilapia every 4.4 day. 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.

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/in 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 water temperature at surface, depth (water depth measured by an echo sounder or manually with a rope and weight, depth position 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.

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 area was 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.

Descriptive statistics and statistical analyses were based on proportions of fish or average values for individual fish. A significance level of 0.05 was used. When required, significance levels were adjusted according to sequentially rejective Bonferroni test (Holm 1979) to deal with multiple statistical inference. 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.). For further details on methods and statistical analyses on each species, see descriptions in previous reports (Økland et al. 2000, Thorstad et al. 2002, 2003).

top and bottom:
The studied species are important in both the subsistence and recreational fisheries.





top and bottom:
The studied fish were caught with drag-nets and rod and line.





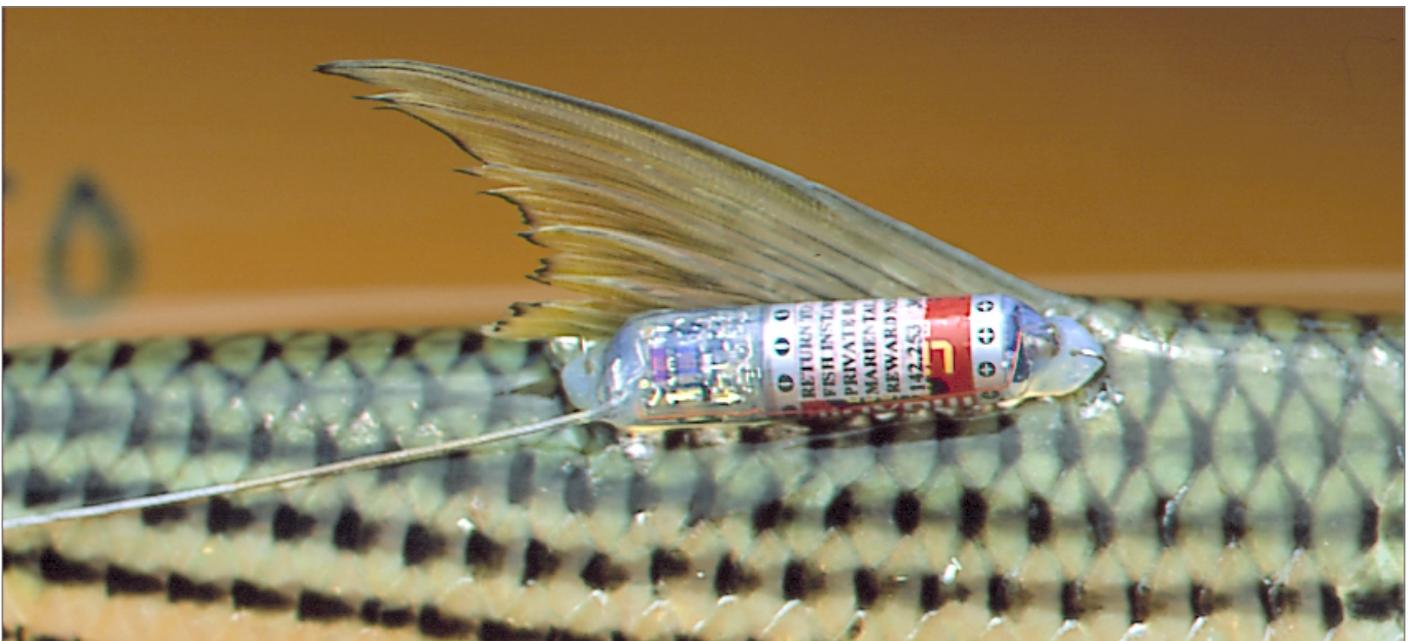
The pictures show the external tagging procedure after anaesthetisation of the fish.



top:
The fish were in a good condition when released after recovery.

middle:
External attachment of a radio transmitter to the back of a tigerfish.

bottom:
External attachment of a radio transmitter to the back of a cichlid.

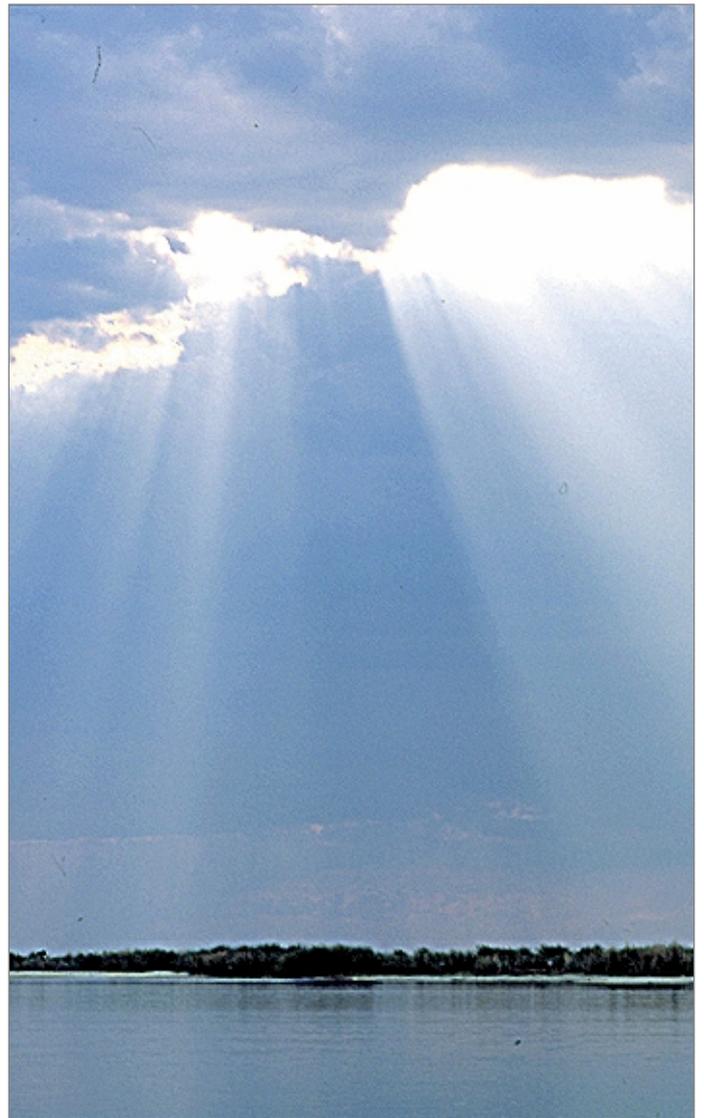


top:

Survey team tracking radio tagged fish and recording the exact position with GPS. The fish habitat was also described.

bottom:

Backwater and main river are important living areas for the studied species in the Zambezi River.



3 Results

3.1 Movements and home range

Average distance moved between tracking surveys was different among the three species (Kruskal-Wallis test, $\chi^2 = 8.0$, $P = 0.18$). The distance moved was different between tigerfish and nembwe (Mann-Whitney U-test, $U = 45.0$, $P = 0.015$) and between threespot tilapia and nembwe ($U = 12.0$, $P = 0.017$), but not between tigerfish and threespot tilapia ($U = 35.0$, $P = 0.47$). Average distance moved between tracking surveys was 16 times longer for tigerfish (1447 m) than for nembwe (93 m), and 4 times longer for threespot tilapia (391 m) than for nembwe (**figure 3**).

All the fish were obviously only recorded in permanently water covered areas during low water. During rising and high water, some of the fish had moved to temporary water covered areas during one or more tracking surveys (**figure 3**). The proportion of fish utilising temporary water covered areas did not differ among species (47% for tigerfish, 67% for nembwe and 50% for threespot tilapia; Pearson chi square test, $\chi^2 = 0.66$, $P = 0.72$). However, the tigerfish utilised temporary water covered areas to a lesser extent than the other two species during rising water (Pearson chi square test, $\chi^2 = 6.1$, $P = 0.047$), but to the same extent during high water (Pearson chi square test, $\chi^2 = 0.95$, $P = 0.62$).

Length of the river stretch used (i.e. the distance between the two fixes farthest from each other for individual fish) was close to significantly different among the three species (Kruskal-Wallis test, $\chi^2 = 5.6$, $P = 0.060$). Length of the river stretch used was significantly different between nembwe and threespot tilapia (Mann-Whitney U test, $U = 9.0$, $P = 0.007$), but not between tigerfish and nembwe ($U = 61.0$, $P = 0.093$), or between tigerfish and threespot tilapia ($U = 39.0$, $P = 0.64$). Mean river stretch used was 14 times longer for tigerfish (18.8 km) than for nembwe (1.3 km), and 4 times longer for threespot tilapia (5.4 km) than for nembwe (**figure 3**).

Although distance moved and length of river stretch used was different among the species, size of home range was not different (Kernel statistics,

95% probability of localisation within an average area of 398,218 m² for tigerfish, 163,329 m² for nembwe and 245,591 m² for threespot tilapia, Kruskal-Wallis test, $\chi^2 = 1.36$, $P = 0.51$, **figure 3**).

3.2 Habitat utilisation

All the fish were recorded in the mainstream of the river (**figure 4**). However, 40% of the tigerfish, 62% of the nembwe and 67% of the threespot tilapia were during one or more tracking surveys recorded in other habitat types, which was not different among species (Pearson chi square test, $\chi^2 = 1.8$, $P = 0.40$, **figure 4**). The proportion of tracking surveys when individual fish were recorded in the main river was on average 81% for tigerfish, 69% for nembwe and 39% for threespot tilapia, which was also not different among species (Pearson chi square test, $\chi^2 = 4.8$, $P = 0.089$).

Mean total width of the river where fish were recorded was not different among species (529 m for tigerfish, 342 m for nembwe and 493 m for threespot tilapia, Kruskal-Wallis test, $\chi^2 = 4.1$, $P = 0.13$, **figure 4**). Also mean distance to shore as a proportion of total width was not different among species (22% for tigerfish, 15% for nembwe and 31% for threespot tilapia, Kruskal-Wallis test, $\chi^2 = 4.9$, $P = 0.085$) (**figure 4**). However, the mean distance to shore varied among species (107 m for tigerfish, 58 m for nembwe and 158 m for threespot tilapia, Kruskal-Wallis test, $\chi^2 = 4.1$, $P = 0.029$). Mean distance to shore was significantly different between nembwe and threespot tilapia (Mann-Whitney U test, $U = 12.0$, $P = 0.017$), but not between tigerfish and nembwe ($U = 58.5$, $P = 0.072$), or between tigerfish and threespot tilapia ($U = 27.0$, $P = 0.18$).

Tigerfish were to a lesser extent associated with vegetation than nembwe and threespot tilapia (**figure 5**). All the tigerfish (100%) were recorded away from vegetation during some or all tracking surveys, as compared to 69% of the nembwe and 67% of the threespot tilapia, which was close to significantly different among species (Pearson chi square test, $\chi^2 = 5.8$, $P = 0.056$). The proportion recorded near vegetation did not differ among species (60% for tigerfish, 92% for nembwe and 67% for threespot tilapia, Pearson chi square test, $\chi^2 =$

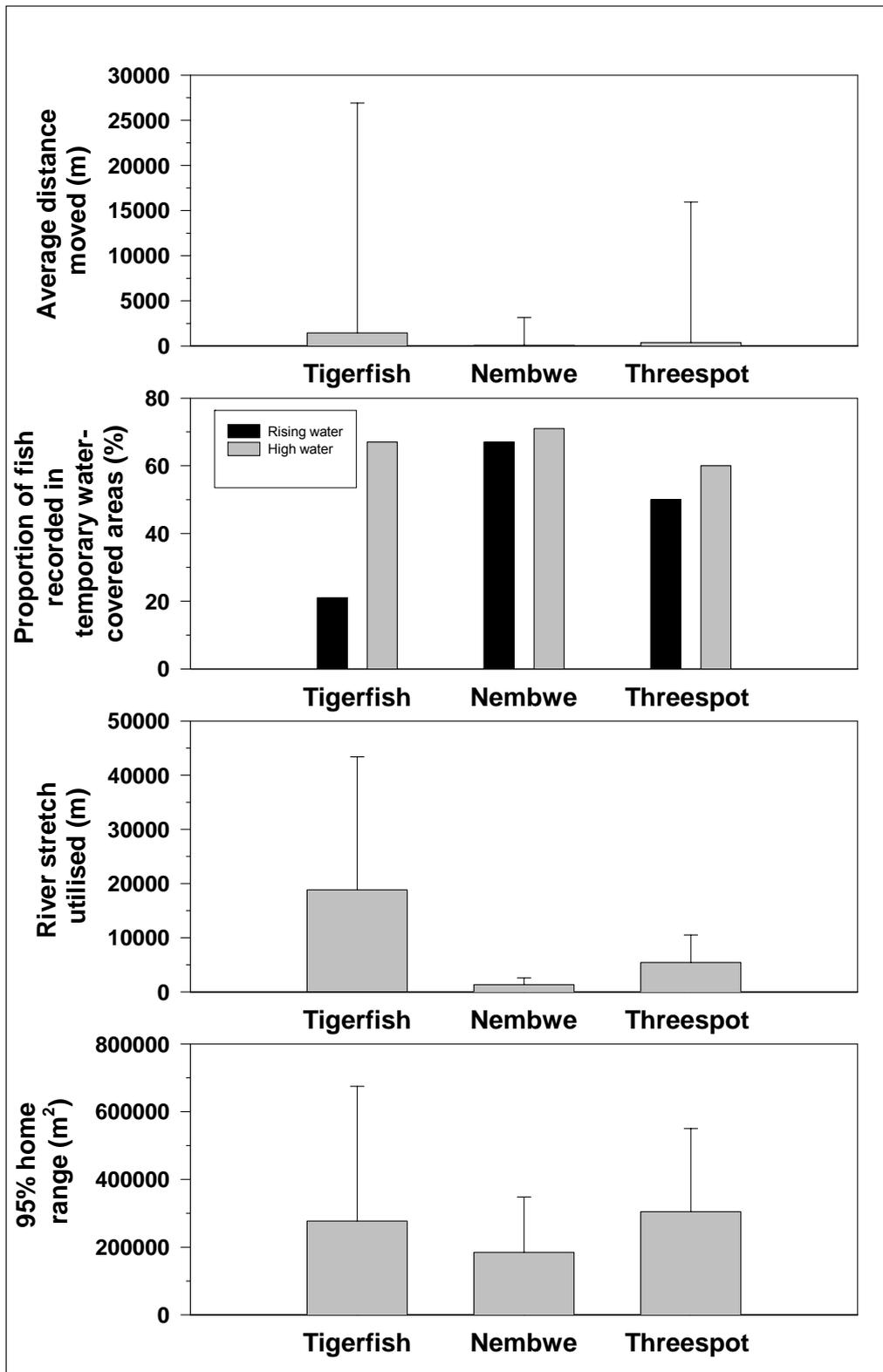
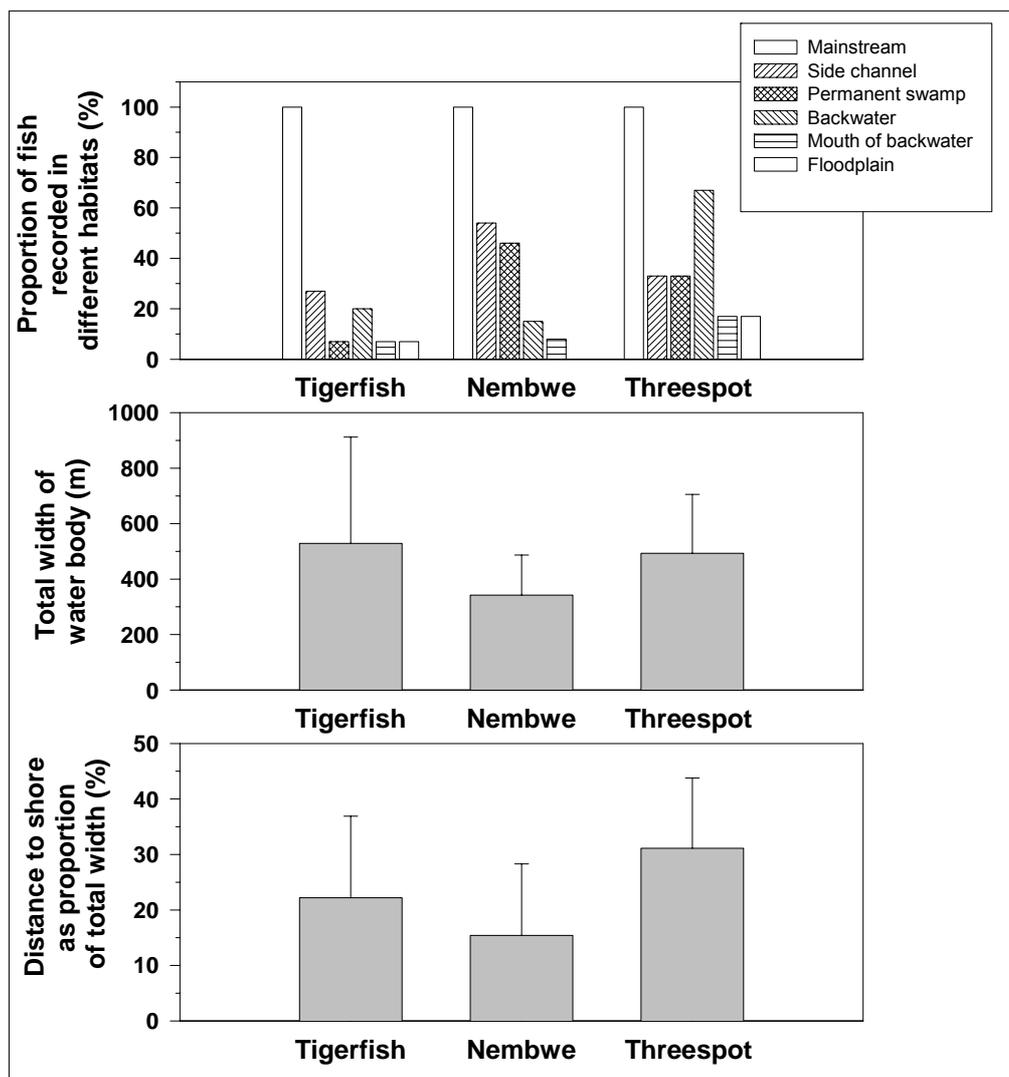


Figure 3. A comparison of radio tagged tigerfish ($n = 15$), nembwe ($n = 13$) and threespot tilapia ($n = 6$) in the Upper Zambezi River during November 2000 to May 2001. Figures show average distance moved between tracking surveys, proportion of fish recorded in temporary water covered areas during rising and high water level, average length of river stretch used (i.e. the distance between the two fixes farthest from each other during the study), and average size of their home range (95% probability of localisation within the area, Kernel statistics). Error bars indicate standard deviation.

Figure 4. A comparison of radio tagged tigerfish ($n = 15$), nembwe ($n = 13$) and threespot tilapia ($n = 6$) in the Upper Zambezi River during November 2000 to May 2001. Figures show proportion of fish recorded in different habitats, mean total width of the water body where the fish were localised, and mean distance to shore as proportion of total width of the water body. Error bars indicate standard deviation.



3.9, $P = 0.14$), but the proportion recorded along/in vegetation differed (47% for tigerfish, 92% for nembwe and 67% for threespot tilapia, Pearson chi square test, $\chi^2 = 6.6$, $P = 0.036$). These results were supported when analysing the average proportion of tracking surveys that the fish were recorded in different positions related to vegetation. The proportion of surveys recorded away from vegetation was different among the species (Kruskal-Wallis test, $\chi^2 = 7.4$, $P = 0.025$). The tigerfish were to a larger extent recorded away from vegetation than both nembwe and threespot tilapia, whereas there was no difference between nembwe and threespot tilapia (Mann-Whitney U tests with Bonferroni test). The average proportion of positions near vegetation was not different among species (Kruskal-Wallis test, $\chi^2 = 1.3$, $P = 0.52$), but the proportion of positions along/in vegetation differed (Kruskal-Wallis test, $\chi^2 = 14.0$, $P =$

0.001). The tigerfish were to a lesser extent recorded along/in vegetation than both nembwe and threespot tilapia, whereas there was no difference between nembwe and threespot tilapia (Mann-Whitney U tests with Bonferroni test).

The mean water depth where fish were recorded did not differ among species (3.8 m for tigerfish, 3.7 m for nembwe and 3.4 m for threespot tilapia, Kruskal-Wallis test, $\chi^2 = 0.9$, $P = 0.64$, **figure 5**). All the fish were recorded on sandy substratum. However, 20% of the tigerfish, 54% of the nembwe and 67% of the threespot tilapia were during one or more tracking surveys recorded on other substratum types (**figure 5**), which was not different among species (Pearson chi square test, $\chi^2 = 5.3$, $P = 0.073$).

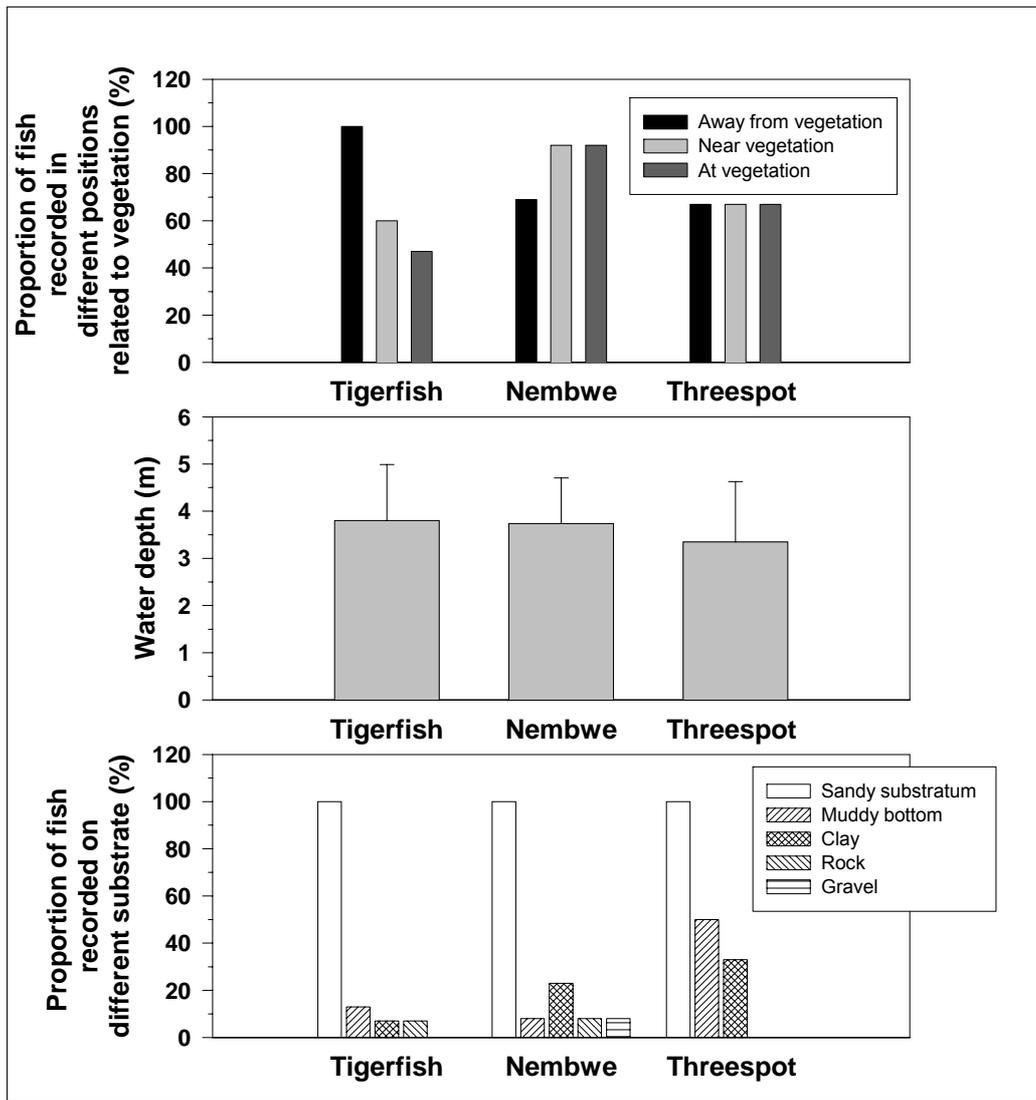


Figure 5. A comparison among radio tagged tigerfish ($n = 15$), nembwe ($n = 13$) and threespot tilapia ($n = 6$) in the Upper Zambezi River during November 2000 to May 2001. Figures show proportion of fish recorded in different positions related to vegetation, mean water depth where the fish were localised, and proportion of fish recorded on different substrate types. Error bars indicate standard deviation.

4 Discussion

4.1 Comparison of movements and habitat utilisation

4.1.1 Movements and home range

Tigerfish, nembwe and threespot tilapia differed in their movement patterns, with nembwe as the most resident species, tigerfish as the species with the most extensive movements and threespot tilapia as the intermediate. The tigerfish showed a variable movement pattern (see Thorstad et al. 2002), with approximately half of the fish staying within defined home ranges, only performing movements less than 1,000 m between tracking surveys. The remaining tigerfish were resident for periods, but moved over long distances (on average 18,784 m) to new areas between the residency periods. The long distance movements were both up- and downstream, and it was suggested that these movements were not related to spawning, but for example, to feeding opportunities (Thorstad et al. 2002). Home range size (the area with 95% probability of localisation of the fish) was not larger for tigerfish than for the two other species, even though the movements were more extensive.

Approximately half of the individuals of all three species moved to temporary water covered areas during rising and high water levels. The tigerfish, however, differed from the two other species in that they utilised temporary water covered areas to a lesser extent during rising water level. However, during high water level, the utilisation of temporary water was similar for all three species.

The creation of extensive floodplains during the rainy season affects the habitat availability for the fish. Changes in behaviour in connection with flooding may be linked to the reproductive behaviour. 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). All the fish in the present study were, according to their body size, mature fish, and the reproduction period for at least nembwe and threespot tilapia probably occurred during the

study period. Although some fish utilised temporary water-covered areas, a migration onto the classical floodplain habitat with submerged grassland and low gradients was not observed. Only one tigerfish and one threespot tilapia were ever recorded on the floodplain. However, some of the fish lost during the study might have moved far into the floodplain and, hence, stayed in shallow areas inaccessible for the tracking boat.

Most cichlid species have a highly resident life style, according to Lucas & Baras (2001), but they emphasise that although cichlids can be regarded as having very limited migratory habits, detailed information is lacking for most, and especially riverine, species. Results from both nembwe and threespot tilapia showed that even if clear migratory habits were not found, the adult fish were actively moving around. Thus, the large riverine cichlids may not be as resident as previously expected.

4.1.2 Habitat utilisation

The three species seemed more similar in their habitat utilisation than in their movement patterns. All species were much of the time associated with the main river, and stayed in relatively deep, open water bodies at some distance from shore, which is in accordance with for example Skelton (2001). However, adults of these species are apparently not habitat specialists, and the fish were recorded in a wide range of habitats. The variation in habitat utilisation was relatively large both within and among individuals. The fish were recorded at different distances from shore, at different water depths and in different positions to vegetation. It seems that all species were more associated with vegetation than previously assumed (Skelton 2001), although tigerfish were to a lesser extent associated with vegetation than nembwe and threespot tilapia.

4.2 Implications for fisheries management

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

Co-ordination of local and regional management regulations is important to maintain fish populations and fisheries, and 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, multilateral management regulations are needed in addition to the national regulations, especially for long-distance moving species such as the tigerfish, and for species frequently moving across the river, such as all three species studied. However, our results indicate that tigerfish populations may be less vulnerable to high exploitation in a limited area than the more resident nembwe and threespot tilapia.

The residency of nembwe, threespot tilapia and some of the tigerfish within defined home ranges implies that restricted sanctuaries can protect adult fish, because individuals may be staying within the protected area over longer periods and variable flow regimes. Threespot tilapia may require larger sanctuaries for protection than nembwe, since they seem to utilise larger river stretches. The long distance moving fraction of the tigerfish population may not benefit from small sanctuaries. Protection of specific habitat types is probably not needed to protect adults of these three species. However, these species may have special habitat requirements for reproduction.

For all three species, however, benefits from sanctuaries should be evaluated against gear and effort regulations. Chances of being caught in passive gears like gillnets depends on the movement patterns of the fish. Based on the present results, the

extensively moving tigerfish may be more frequently caught in widely distributed passive gears than the more stationary threespot tilapia and nembwe. However, vulnerability for being caught in gillnets may also depend on daily movement patterns of the fish, local activity patterns and the distribution of the gears.

It must be emphasised that a relatively small number of fish were recorded in this study, and the full annual cycle was not followed. 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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