# Movements and habitat utilisation of tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi River

## Implications for fisheries management

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NO-7485 Trondheim
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Eva B. Thorstad *, Clinton J. Hay**, Tor F. Næsje*, Ben Chanda*** and Finn Økland*



* Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

** Ministry of Fisheries and Marine Resources, Private Bag 2116, Mariental, Namibia

*** Ministry of Agriculture and Co-operatives, Department of Research and Specialised Services, P.O. Box 350100, Chilanga, Zambia.

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Address to contact:
Eva B. Thorstad
NINA
Tungasletta 2
NO-7485 Trondheim
NORWAY
email: eva.thorstad@nina.no
Tel.: +47 73 80 14 00
Fax.: +47 73 80 14 01
http://www.nina.no

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# Abstract

Thorstad, E. B., Hay, C. J., Næsje, T. F., Chanda, B. & Økland, F. 2002. Movements and habitat utilisation of tigerfish (*Hydrocynus vittatus*) in the Upper Zambezi River. Implications for fisheries management. - NINA Project Report 19. 28 pp.

During 6 November - 24 December 2000, 23 tigerfish (*Hydrocynus vittatus* Castelnau, 1861) (30-54 cm) were tagged with radio transmitters in the Zambezi River in Namibia. The main objectives were to record movements and habitat utilisation for management purposes.

The fish were tracked on average every 4.1 day during 23 November-18 May, and individuals were tracked up to 46 times. Mean total distance moved by individual fish was 26,492 m (range 547-105,988 m). Average distance moved between tracking surveys was 1,447 m (range 17-7,210 m).

Two different movement patterns could be described, even though all the fish showed some sort of site fidelity. Approximately half of the fish showed only movements less than 1,000 m between tracking surveys, staying within defined home ranges. The remaining fish showed site fidelity for periods, with long distance movements (> 1,000 m) to new areas between the residency periods. The movements longer than 1,000 m were on average 18,784 m, and 42% were downstream and 58% upstream. Differences in movement patterns among individuals could not be explained by differences in body size, and there seemed to be no seasonality in the long distance movements. It is, therefore, suggested that these movements were not related to spawning, but that they, for example, were related to feeding opportunities.

Home range size varied among individual fish, with a 50% probability of localisation within an average area of 26,464 $m^2$ (range 171-115,564 $m^2$) and 95% probability of localisation within an average area of 276,978 $m^2$ (range 1,041-1,191,836 $m^2$). On average, the fish stayed within a river stretch of 18,836 m (range = 90-71,840).

Fish were obviously only recorded in permanently water-covered areas during low water. During rising water, all the fish (100%) partly or only utilised permanently flooded areas, and during high water, 83%. However, 21% of the fish were also recorded in temporary flooded areas during rising water and 67% during high water. Tigerfish did not undertake long-distance migrations onto the floodplains, but mainly utilised the adjacent temporary water covered areas.

All the fish were recorded in the mainstream of the river, and on average, 81% of the fixes (average of different individuals) were in the main river. However, the tigerfish were to an increasing extent recorded in habitats such as side channels, backwaters and floodplains during rising water level. Although often recorded in the main river channel, tigerfish rather stayed closer to shore than in the middle of the river. The fish were recorded on average 107 m from the nearest shore (69 m during low, 68 m during rising and 356 during high water), which constituted 22% of the total width of the river (25% during low, 23% during rising and 28% during high water). The fish were also likely to be associated with vegetation, but they were never recorded inside or under vegetation. The most frequently recorded vegetation type was marginal aquatic anchored vegetation. Water depth where the fish were recorded varied between 0.5 and 14.0 m, and was on average 3.8 m. Water temperature during the study varied between 20.7 and 30.1 °C.

This is the first study where the behaviour of individual tigerfish is followed over time. Much of the results are new information to what is previously known about the species. Basic information about annual movements, habitat preferences and habitat utilisation of target species are important information and necessary for regulation of fisheries, both locally and regionally among countries. Such information is also needed to regulate exploitation methods and evaluate possible benefits of reserves and sanctuaries. The results in the present study suggest that the exploitation rate of tigerfish may be high, especially during low water, since 26% of the tagged fish were reported recaptured.

Co-ordination of local and regional management regulations are important for the tigerfish populations, to avoid fish being protected in one river section and depleted in the neighbouring river section. In rivers bordering on several countries like the Upper Zambezi River, multilateral management regulations are needed as well, especially for long-distance moving species as the tigerfish. However, tigerfish may be less vulnerable to high exploitation in a specific area than more stationary species. The long distance movements of some individuals makes it likely that a locally depleted population can be re-colonised by tigerfish moving from other areas, even tens of kilometres away.

The stationarity of some of the tigerfish also implies that smaller sanctuaries can protect adult fish, because some of them may be staying in the protected area. However, smaller sanctuaries will not protect the long-distance moving fractions of the tigerfish population, and when management actions to protect tigerfish are needed, gear or effort restrictions may be more effective. A more detailed study of the activity patterns of the fish throughout the day would provide information on the vulnerability of the tigerfish for being caught in passive gears, such as gillnets. The long distance movements also suggest that tigerfish

populations may be vulnerable to dams and other migration barriers.

Key words: *Hydrocynus vittatus* - tigerfish - radio telemetry - movement - habitat - behaviour - management

Tor F. Næsje, Eva B. Thorstad, Finn Økland, Norwegian Institute for Nature Research (NINA), Tungasletta 2, NO-7485 Trondheim, Norway.
tel: +47 73 80 14 00, fax: +47 73 80 14 01

Clinton J. Hay, Ministry of Fisheries and Marine Resources, Private Bag 2116, Mariental, Namibia.

Ben Chanda (*deceased*), Ministry of Agriculture and Cooperatives, Department of Research and Specialised Services, P.O. Box 350100, Chilanga, Zambia.

Corresponding author: **email: eva.thorstad@nina.no**

# Preface

Knowledge on fish migrations and habitat utilisation is imperative when implementing fisheries regulation. The objective of the present study was to analyse the behaviour of radio tagged tigerfish in the Namibian part of the Zambezi River for management purposes.

The study was financed by World Wildlife Fund (WWF), USAID, 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 Kari Sivertsen and Knut Kringstad for help with graphical design and figures.

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| | |
|---|---|
| Clinton J. Hay | Tor F. Næsje |
| Project leader, MFMR | Project leader, NINA |

# Contents



# 1 Introduction

In Namibia, 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 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.* 1994b; Tvedten *et al.* 1994; Hay *et al.* 1996, 2000, Allcorn 1999, Purvis 2001a).

Floodplain rivers, like the Zambezi and Okavango Rivers, experience a characteristic annual sequence of low water during the dry period and early rain, followed by rising and high water during and after the rainy period, inundating large grassland and forest areas. Many fish species have adapted to this cycle by spawning at the beginning of the flood, thereby placing their young in the productive and sheltered areas of the floodplain (e.g. Williams 1971, van der Waal 1996, Hoggarth *et al.* 1999). Management of a sustainable fishery depends on a better understanding of the fish migrations and habitat preferences in these complex and variable floodplain ecosystems.

The tigerfish *Hydrocynus vittatus* Castelnau, 1861 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). This species is a member of the Characidae, which is one of the largest families of freshwater fishes found in Africa (Brewster 1986). Tigerfish are predators throughout life, and they have a reputation as one of the world's most spectacular freshwater game fish species (Skelton 1993). 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 1993, Steyn 1996).

The objective of this study was for management purposes to analyse the behaviour of radio tagged tigerfish in the Namibian part of the Zambezi River. The movements and habitat utilisation were recorded during low water level immediately before the rainy period, during increasing water level during the rainy period, and during high water level after the rainy period.

# 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 (1.45 mill $km^2$). 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 up to 7-8 m in Caprivi, 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).

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 a major concern for the management authorities (MFMR 1995). Pollution in the area is negligible, and large-scale development and urbanisation is not noticeable (Tvedten *et al.* 1994). The local human population lives a rural life style, depending heavily on subsistence fishery as an affordable source of protein. Fish and fisheries in the region are described by e.g. Van der Waal & Skelton (1984), Van der Waal (1990) and Hay *et al.* (1999, 2002).

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. 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 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 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 the fish

Twenty-three tigerfish were captured by rod and line (n = 13) or seine net (n = 10) in the main stream of the Zambezi River 229-611 km downstream from Katima Mulilo in Caprivi, Namibia, during 6 November - 24 December 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 2.2% of the body weight of the smallest fish. The transmitters emitted signals within the 142.043-142.393 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. 16) that was released 600 m downstream from the catch site due to drift of the boat. The water temperatures were 25.4-29.6 °C during catch and tagging.

## 2.3 Tracking of the 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 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 4.1 day during 23 November-18 May, and individual fish were tracked up to 46 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**).

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 rain period, 3: episodic water cover, *i.e.* occasional but not regular during rain period), main habitat type (1: mainstream of river, 2: backwater, 3: mouth of backwater, 4: side channel, 5: tributary, 6: permanent swamp, 7: temporary swamp 7: floodplain), position to vegetation (1: no vegetation, 2: near vegetation, i.e. less than 5 m, 3: at vegetation), and vegetation type if near or at 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

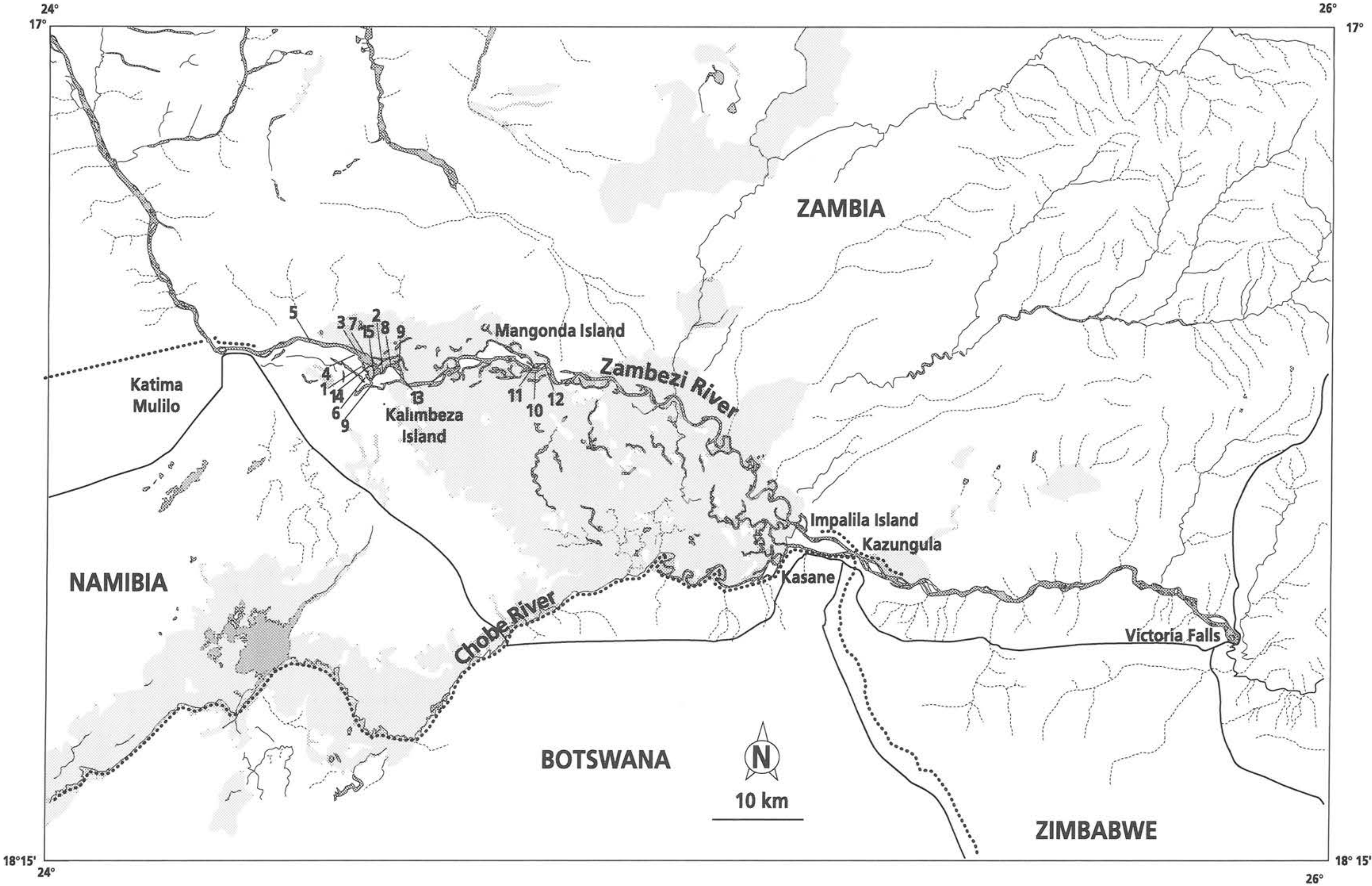



***Figure 1.*** *The upper part of the Zambezi River in Caprivi in north-eastern Namibia. Sites where individual tigerfish were radio tagged and released are indicated. Individual fish numbers correspond to the numbers in* ***table 1***. *Shaded areas indicate floodplain during high waters.*

***Table 1.** Radio tagged tigerfish in the Zambezi River, Namibia, during 6-24 December 2000. Release site is given as distance from catch site.*

| Fish no. skygge | Fish no. date | Tagging (cm) | Body length model* | Transmitter of fixes | Total number during each period (low, rising,high water) | Number of fixes date | Last tracking | Recaptured |
|---|---|---|---|---|---|---|---|---|
| 1 | 6 | 06.11. 00 | 37 | F2040 | 2 | (2, 0, 0) | 30.11.00 | |
| 2 | 7 | 06.11. 00 | 37 | F2120 | 35 | (12, 17, 6) | 31.03.01 | |
| 3 | 8 | 06.11. 00 | 49 | F2120 | 32 | (11, 17, 4) | 26.03.01 | |
| 4 | 9 | 06.11. 00 | 40 | F2040 | 21 | (11, 10, 0) | 03.02.01 | |
| 5 | 10 | 06.11. 00 | 38 | F2040 | 0 | (0, 0, 0) | 07.11.00 | x |
| 6 | 11 | 06.11. 00 | 37 | F2040 | 24 | (11, 13, 0) | 20.02.01 | |
| 7 | 12 | 08.11. 00 | 37 | F2040 | 2 | (2, 0, 0) | 30.11.00 | x |
| 8 | 15 | 10.11. 00 | 39 | F2120 | 16 | (0, 4, 12) | 08.05.01 | |
| 9 | 16 | 10.11. 00 | 39 | F2040 | 18 | (12, 6, 0) | 21.01.01 | |
| 10 | 17 | 10.11. 00 | 39 | F2040 | 22 | (12, 10, 0) | 28.01.01 | |
| 11 | 18 | 10.11. 00 | 43 | F2120 | 37 | (7, 13, 15) | 18.05.01 | |
| 12 | 19 | 10.11. 00 | 49 | F2120 | 46 | (12, 18, 14) | 18.05.01 | |
| 13 | 33 | 14.11. 00 | 37 | F2040 | 0 | (0, 0, 0) | 15.11.00 | x |
| 14 | 34 | 14.11. 00 | 30 | F2040 | 0 | (0, 0, 0) | 23.11.00 | x |
| 15 | 35 | 14.11. 00 | 32 | F2040 | 0 | (0, 0, 0) | 14.11.00 | |
| 16 | 36 | 15.11.00 | 39 | F2040 | 1 | (1, 0, 0) | 21.11.00 | x |
| 17 | 41 | 17.11.00 | 40 | F2120 | 44 | (11, 17, 14) | 18.05.01 | |
| 18 | 42 | 22.11.00 | 32 | F2040 | 18 | (10, 8, 0) | 22.01.01 | |
| 19 | 43 | 22.11.00 | 54 | F2040 | 23 | (10, 13, 0) | 20.02.01 | x |
| 20 | 44 | 16.12.00 | 49 | F2040 | 9 | (2, 7, 0) | 20.02.01 | |
| 21 | 45 | 20.12.00 | 42 | F2040 | 6 | (2, 4, 0) | 08.01.01 | |
| 22 | 46 | 24.12.00 | 38 | F2040 | 12 | (0, 11, 1) | 02.04.01 | |
| 23 | 47 | 24.12.00 | 35 | F2040 | 24 | (0, 15, 9) | 14.04.01 | |

*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.

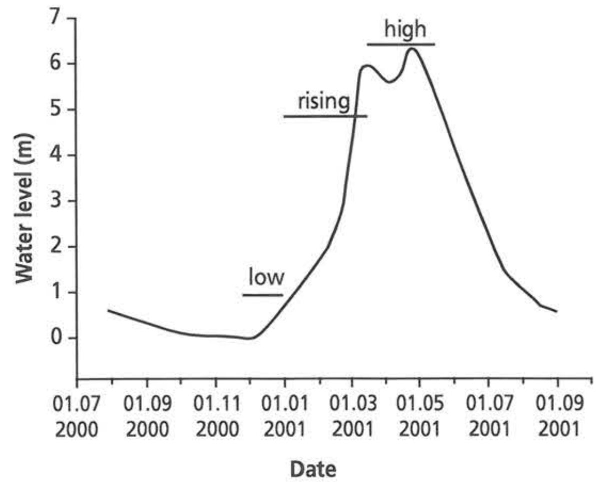



***Figure 2.** The water level in the Zambezi River from 1 August 2000 to 31 August 2001. The study periods at low, rising and high water are indicated.*

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.

## 2.4 Data analyses

Eight fish disappeared from the study area shortly after tagging (**table 1**) and were not included in the analyses. Descriptive statistics for the entire study period was, therefore, based on 15 fish (see **table 1**). Descriptive statistics for each of the periods low, rising and high water were based on fish with more than five fixes in the respective period, which resulted in a sample size of 11 fish during low water, 14 during rising water and six during high water (see **table 1**). Statistical analyses of behaviour and habitat utilisation between periods were performed by non-parametric paired comparisons, which means only fish recorded in all periods under comparison could be included in the analysis. Due to the low number of fish tracked in all three periods, statistical comparisons were made only between low and rising water. Comparisons were made by Wilcoxon Signed Ranks Tests, and included the eleven fish with more than five fixes in both periods (see **table 1**). Descriptive statistics and statistical analyses were based on average values for individual fish. To ensure that we did not include movements due to handling and tagging effects, data from the first week after tagging were not included.

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 too much land areas to be 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%). Home range was not analysed when number of fixes was lower than 10 (see **table 1**), except in the figure showing home ranges (**figure 3**), where all data are included. The catch and release sites were not included in the analyses.

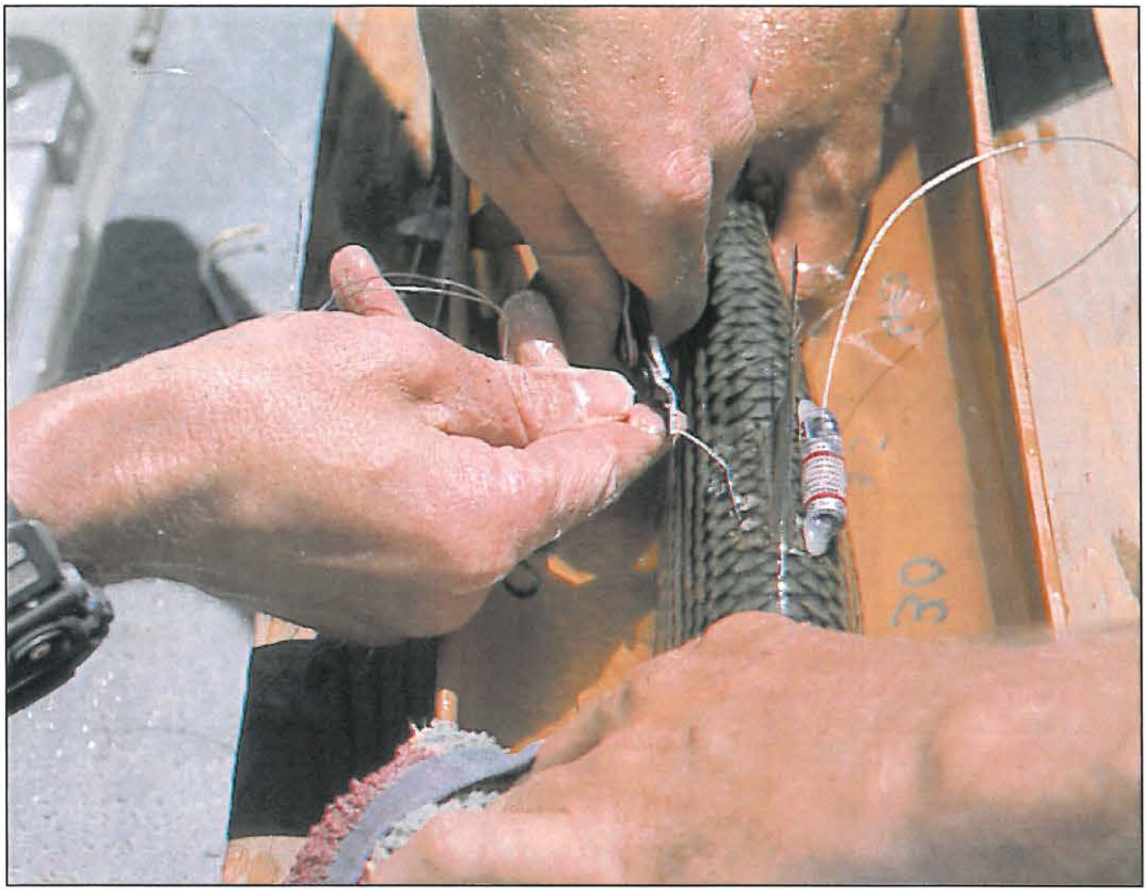
All statistical analyses were performed with SPSS 10.0, except for the home range analyses, which were performed with ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.).

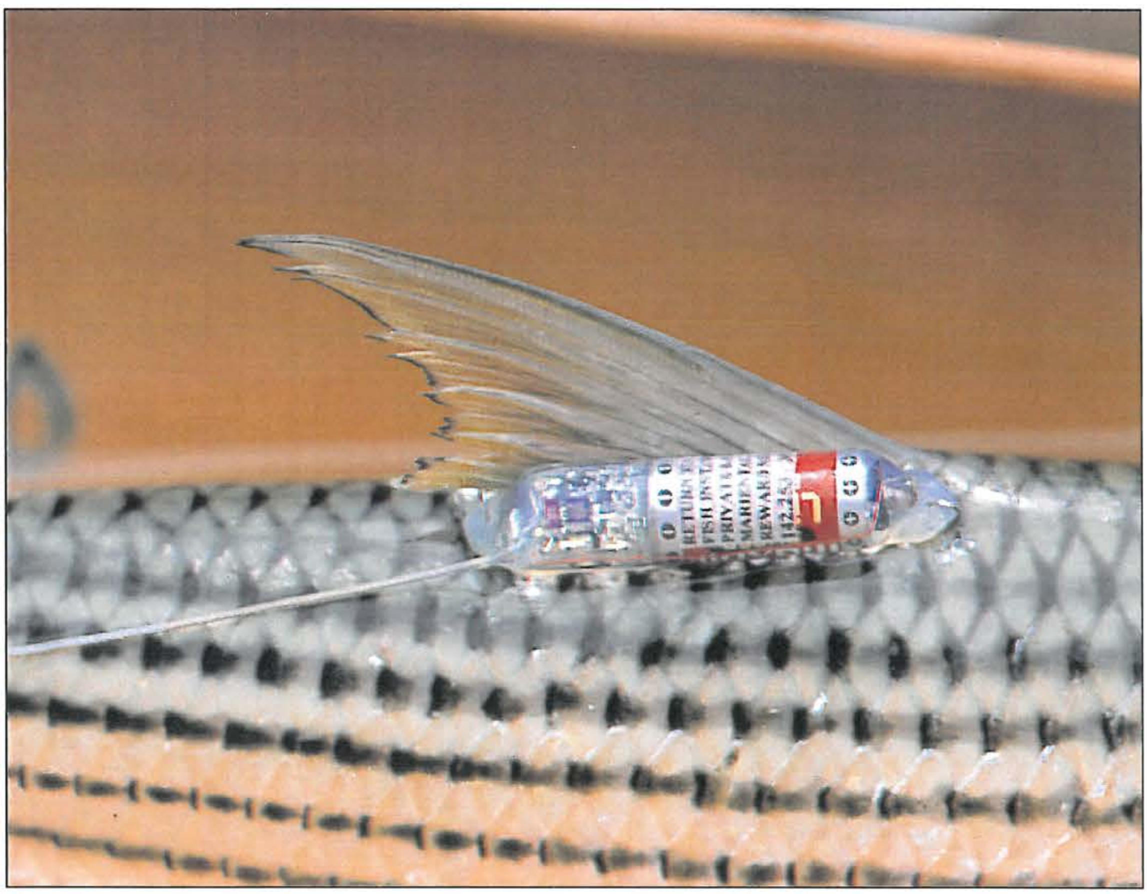

**Upper picture:** *Local fishermen catching tigerfish for radiotagging.*

**Lower picture:** *Survey team catching tigerfish for radiotagging. Tagged fish were caught with drag net or rod and line.*

***Upper picture:*** *Tigerfish for tagging caught on rod and line.*

***Lower picture:*** *Tagging personal in survey boat with tagging equipment.*

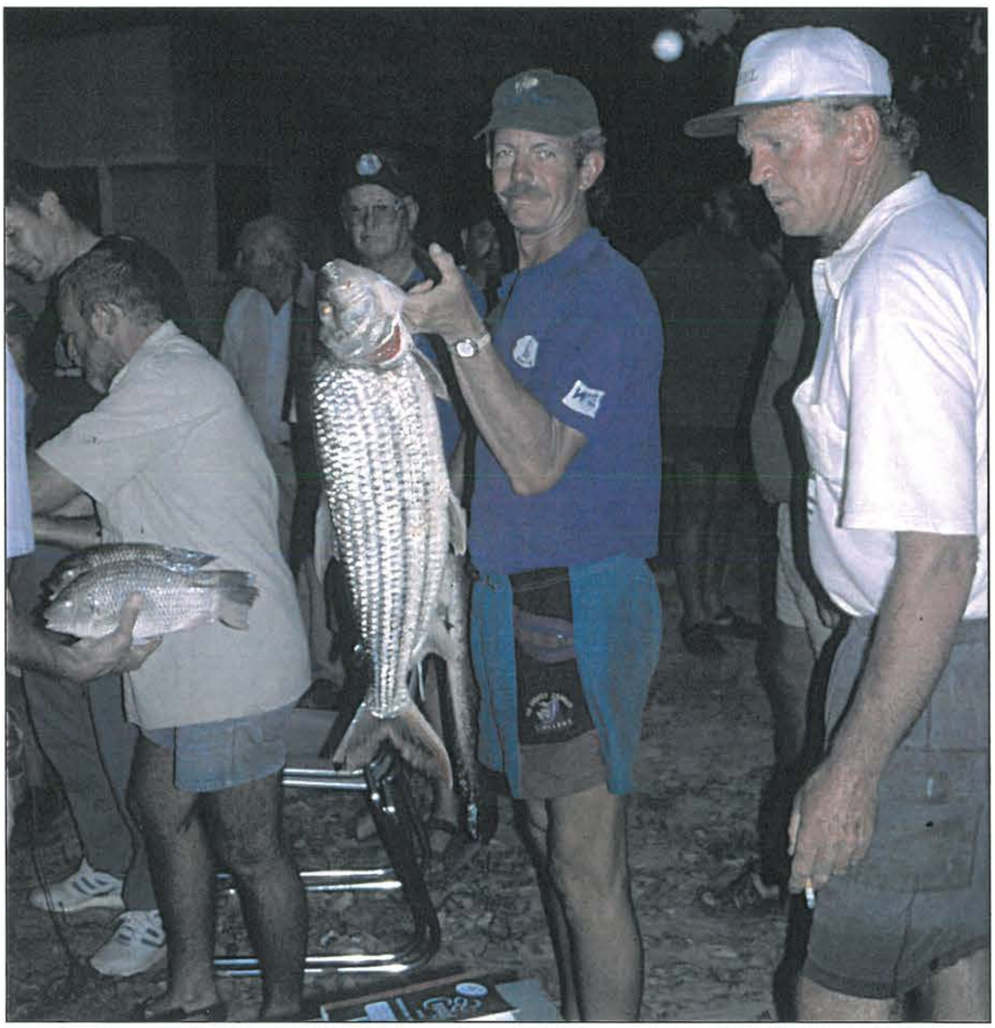




***Upper picture:*** *Radiotagging of tigerfish after anaesthetisation of the fish.*

***Lower picture:*** *External radio transmitter on the back of tigerfish.*

***Upper picture:*** *Survey team tracking radio tagged tigerfish, and recording the exact position with GPS. The habitat of tigerfish was also described.*
***Lower picture:*** *Zambezi main river a common tigerfish habitat.*



***Upper picture:*** *Tigerfish is a common and important catch in the subsistence fishery.*

***Lower picture:*** *Tigerfish is one of the most popular species targeted by recreational fishermen.*

# 3 Results

## 3.1 Movements

Mean total distance moved by individual fish during the entire study period was 26,492 m (SD = 25,468, individual means from 547 to 105,988 m). Average distance moved between tracking surveys was 1,447 m (SD = 2,289, individual means from 17 to 7,210 m), and was larger during low than rising water (Z = -2.85, P = 0.004). Average distance moved was not dependent on fish body length (linear regression, $r^2$ = 0.05, P = 0.42).

Even though average distance moved was 1,447, distance moved between tracking surveys were longer than 1,000 m in only 7% of the occasions (0-36 % for individual fish). Two typical movement patterns were recorded for individual fish: 1) only movements less than 1,000 m between tracking surveys (53 % of the fish), or 2) residency for periods, with long distance movements to new areas between the residency periods (47% of the fish) (**figure 3**). There was no difference in body length between fish with the different movement patterns (Mann-Whitney U-test, U = 18, P = 0.28). The movements longer than 1,000 m were on average 18,784 m, and 42% were downstream and 58% upstream. There seemed to be no seasonality in the long distance movements, as 25% occurred in December, 30% in January, 8% in February, 35% in March and 2% in April. The fastest movement recorded was 39,740 m in six days (fish no. 12), corresponding to an average of 6,623 m $day^{-1}$.

Mean total distance moved by individual fish during the first 1-20 days after tagging (from tagging to first tracking) was 2,990 m (SD = 3,344, range = 149-10,043). Five fish had a downstream movement, eight an upstream movement and two a sideways movement during this period. The individual released 600 downstream from the catch site was recorded at the catch site less than ten minutes after release, and was caught by an angler less than three hours later.

Fish were obviously only recorded in permanently water-covered areas during low water. During rising water, all the fish (100%) partly or only utilised permanently flooded areas, and during high water, 83%. However, 21% of the fish also utilised temporary flooded areas during rising water and 67% during high water (see also **figure 3**). (Note that percentages add up to more than hundred for example when some fish are recorded in more than one habitat type.) On average, 8% of the fixes during rising water and 52% during high water were in temporary flooded areas. The body length of fish utilising temporary flooded areas were larger than of those staying only in permanently water covered areas during rising water (mean body length 49 cm, range 43-54 cm *versus* mean body length 40 cm, range 32-49 cm, Mann-Whitney Test, U = 3.0, P = 0.038).

## 3.2 Home range

Home ranges varied among individual fish **(figure 3)**, with a 50% probability of localisation within an average area of 26,464 $m^2$ (SD = 34,464, range 171-115,564 $m^2$) and 95% probability of localisation within an average area of 276,978 $m^2$ (SD = 398,218, range 1,041-1,191,836 $m^2$) (based on average 27 fixes per fish, range 13-46 fixes). Home range size was not dependent on fish body length (linear regression, 95%: $r^2$ = 0.12, P = 0.22, 50%: $r^2$ = 0.17, P = 0.15). Distance between the two fixes farthest off from each other in individual fish during the entire study period was on average 18,836 m (SD = 24,568, range = 90-71,840), and was not dependent on body length (linear regression, 95%: $r^2$ = 0.19, P = 0.19).

Home ranges were also analysed separately for low (n = 10), rising (n = 11) and high (n = 4) water level (**figure 3**). The 95% probability home range was on average 104,098 $m^2$ during low water, 72,682 $m^2$ during rising water and 213,382 $m^2$ during high water. The 50% probability home range was on average 19,172 $m^2$ during low water, 13,266 $m^2$ during rising water and 26,168 $m^2$ during high water. Neither the 95% nor the 50% probability home range was different between low and rising water (Wilcoxon test, n = 10, 95%: Z = -0.56, P = 0.58, 50%: Z = -0.26, P = 0.80, **figure 3**). Home range size increased significantly with increasing body length during low water, but not during rising water (linear regressions, low water: 95% $r^2$ = 0.78, P = 0.008, 50% $r^2$ = 0.58, P = 0.01, rising water: 95% $r^2$ = 0.34, P = 0.08, 50% $r^2$ = 0.32, P = 0.09).

## 3.3 Habitat utilisation

All the fish were recorded in the mainstream of the river. However, 40% of the fish were recorded in one or more additional main habitat type; 27% of the fish were recorded in side channels, 7% in permanent swamps, 20% in backwaters, 7% in the mouth of backwaters and 7 % on the floodplain. On average, 81% of the fixes were in the mainstream of the river (95, 77 and 50% during low, rising and high water), 7% in side channels (2, 14 and 8% during low, rising and high water), 2% in permanent swamps (0, 0 and 14 during low, rising and high water), 7% in backwaters (3, 6 and 17% during low, rising and high water), 0.3% in mouth of backwaters (0, 0 and 0.7% during low, rising and high water) and 2% on the floodplain (0, 0.5 and 11% during low, rising and high water). Average proportion of fixes in the different main habitats did not differ between low and rising water (Wilcoxon tests, Z from -1.83 to 0.0, P from 0.068 to 1.0). There was no difference in body length between fish recorded in the mainstream of the river only and fish recorded in additional main habitats (Mann-Whitney U test, U = 19.5, P = 0.39).

Total width of the river (included floodplain) where the fish were positioned varied between 35 and 2,000 m, and was on average 529 m (277 m during low, 320 m during rising and 1,382 m during high water). Total width of the river did not differ between low and rising water (Wilcoxon test, Z = -1.42, P = 0.16), and was not dependent on fish body length (linear regression, $r^2$ = 0.00, P = 0.99). Distance to nearest shore given as proportion of total river width was on average 22% (25% during low, 23% during rising and 28% during high water), and did not differ between low and rising water (Wilcoxon test, Z = -0.62, P = 0.53).

Distance to nearest shore varied between 1 and 1,500 m, and was on average 107 m (69 m during low, 68 m during rising and 356 m during high water). Distance to shore did not differ between low and rising water (Wilcoxon test, Z = -0.45, P = 0.66), and was not dependent on fish body length (linear regression, $r^2$ = 0.02, P = 0.61).

The fish were recorded in different positions related to vegetation; all the fish (100%) were one or more times recorded away from vegetation, 60% near vegetation and 47% at vegetation. On average, 58% of the fixes were at no vegetation (80, 61 and 33% during low, rising and high water), 36% near vegetation (19, 34 and 53% during low, rising and high water) and 6% at vegetation (0.8, 5 and 14% during low, rising and high water). Position to vegetation did not differ between low and rising water (Z from -1.60 to -1.36, P from 0.11 to 0.17). There was no difference in body length between those recorded near and at vegetation compared to those not recorded at vegetation (Mann-Whitney U test, U = 22.5, P = 0.61).

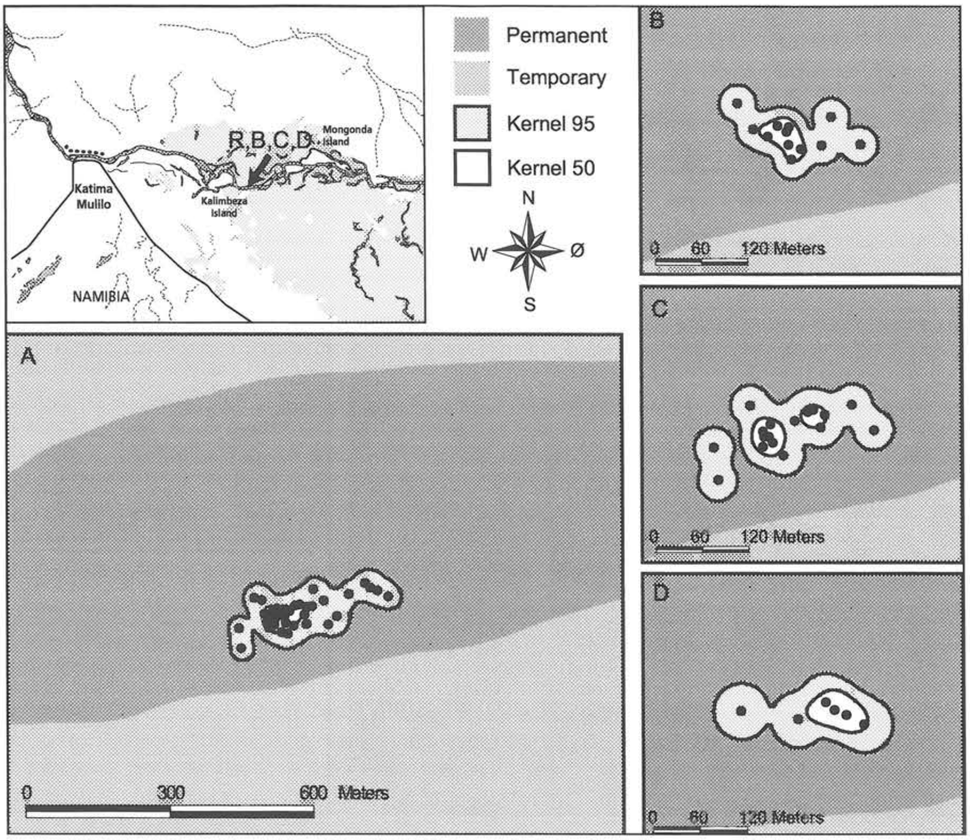
Of the fish recorded near or at vegetation (n = 9), all of them (100%) were one or more times associated with marginal aquatic anchored vegetation, 22% with marginal aquatic floating vegetation, 11% with marginal terrestrial overhanging vegetation, 11% with inner aquatic anchored vegetation and 11% with marginal terrestrial submerged vegetation. On average, 89% of the fixes were at marginal aquatic anchored vegetation, 2% at marginal aquatic floating vegetation, 4% at marginal terrestrial submerged vegetation, 4% at inner aquatic anchored vegetation and 2% at marginal terrestrial overhanging vegetation. There were no differences in which vegetation type the fish were associated with between low and rising water (Wilcoxon tests, all Z = 0.0, all P = 1.0).

Water depth where the fish were recorded varied between 0.5 and 14.0 m, and was on average 3.8 m (3.1 m during low, 3.8 m during rising and 5.1 m during high water). Water depths did not differ between low and rising water (Wilcoxon test, Z = -1.50, P = 0.14), and was not dependent on fish body length (linear regression, $r^2$ = 0.004, P = 0.81).

The fish were mainly associated with sandy substratum; all the fish (100%) were one or more times recorded on sandy substratum, 13% on muddy, soft bottom, 7% on clay and 7% on rocks. On average, 94% of the fixes were on sandy substratum (91, 96 and 100% during low, rising and high water), 4% on clay (6, 4 and 0% during low, rising and high water), 1% on muddy bottom (3, 0 and 0% during low, rising and high water), and 2% on rocks (0, 0, and 0% during low, rising and high water). Average proportion of fixes recorded on the different substratum types did not differ between low and rising water for any substratum type (Wilcoxon tests, Z from -1.61 to 0.0, P from 0.11 to 1.00).

Water temperature at surface where the fish were positioned varied between 20.7 and 30.1 °C. The water temperature decreased slightly during the study period, and was on average 27.1 °C (range 27.0-27.8) during low water, 27.5 °C (range 27.1-28.1) during rising water and 26.0 °C (range 25.5-26.4) during high water.

## Fish no 7




## Fish no 8

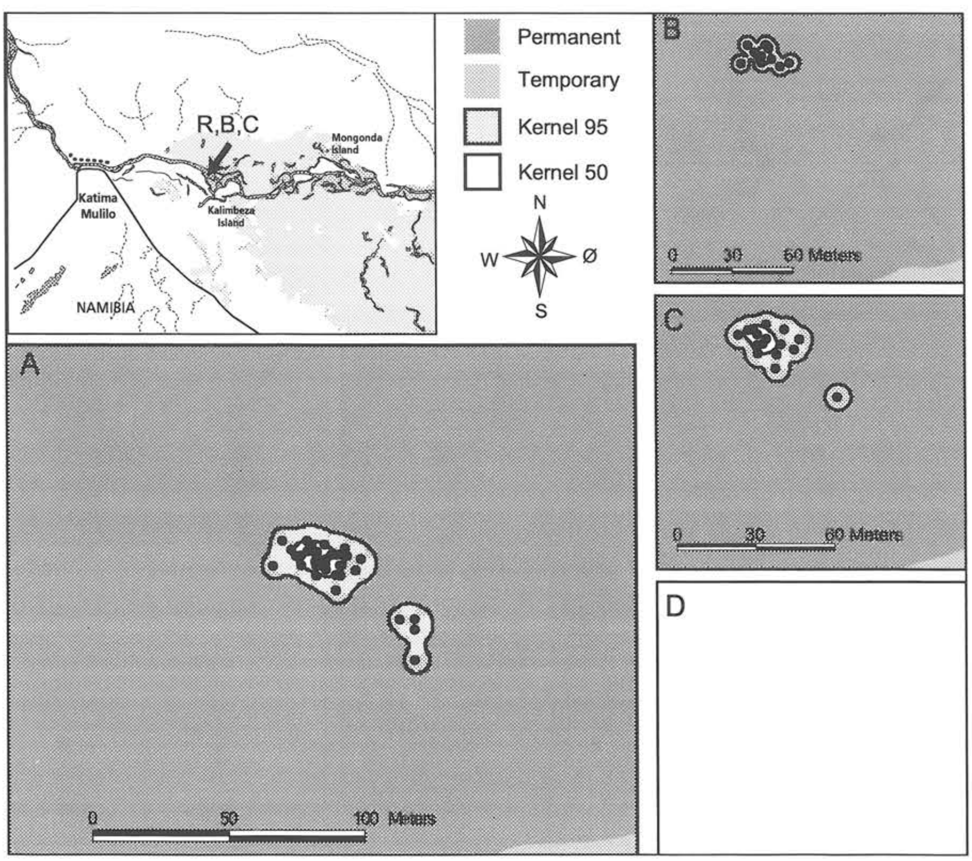
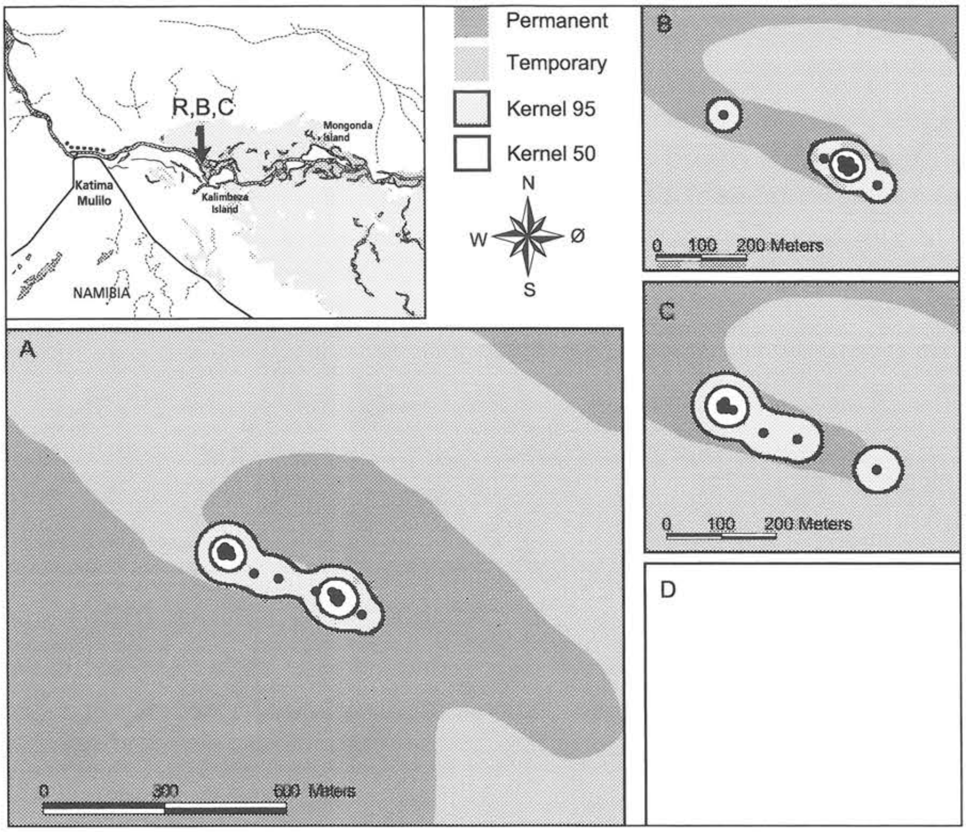



***Figure 3.*** *Kernel home ranges of individual radio tagged tigerfish (n = 15) in the Zambezi River in 2000 and 2001 during a) the entire study period, b) low water only, c) rising water only, and d) high water only (figure b, c or d is lacking for fish not recorded during all periods). Dots show fixes 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 home ranges were recorded and individual fish number, which correspond to the numbers in* ***table 1****.*

## Fish no 9




## Fish no 11

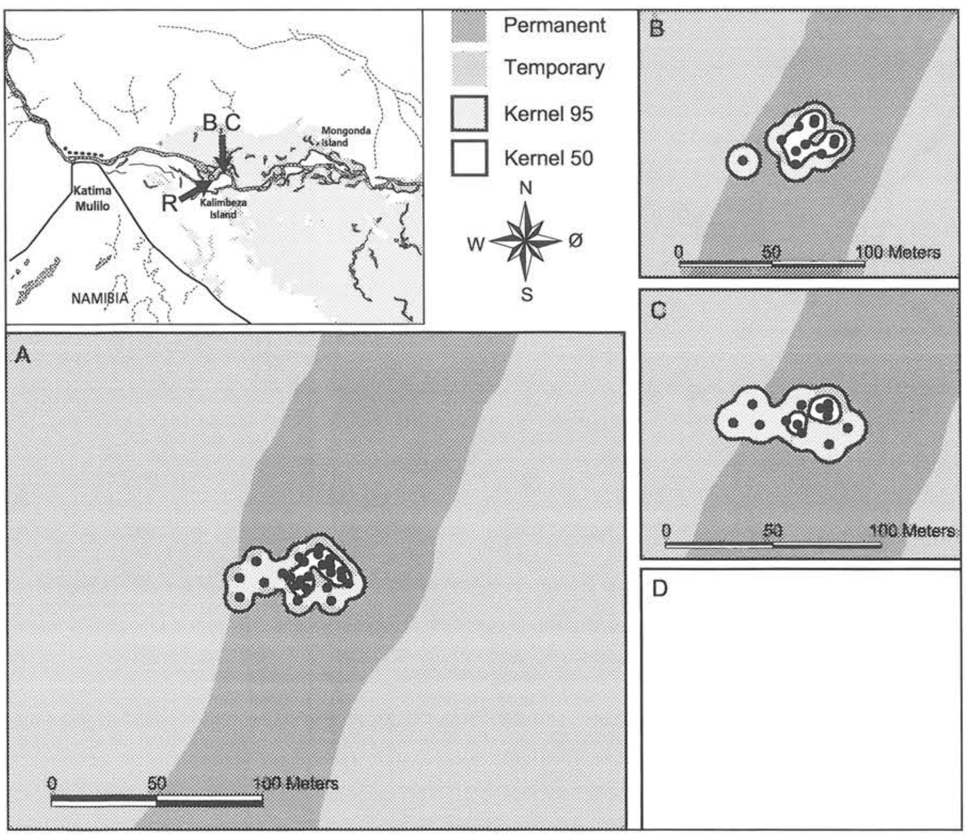
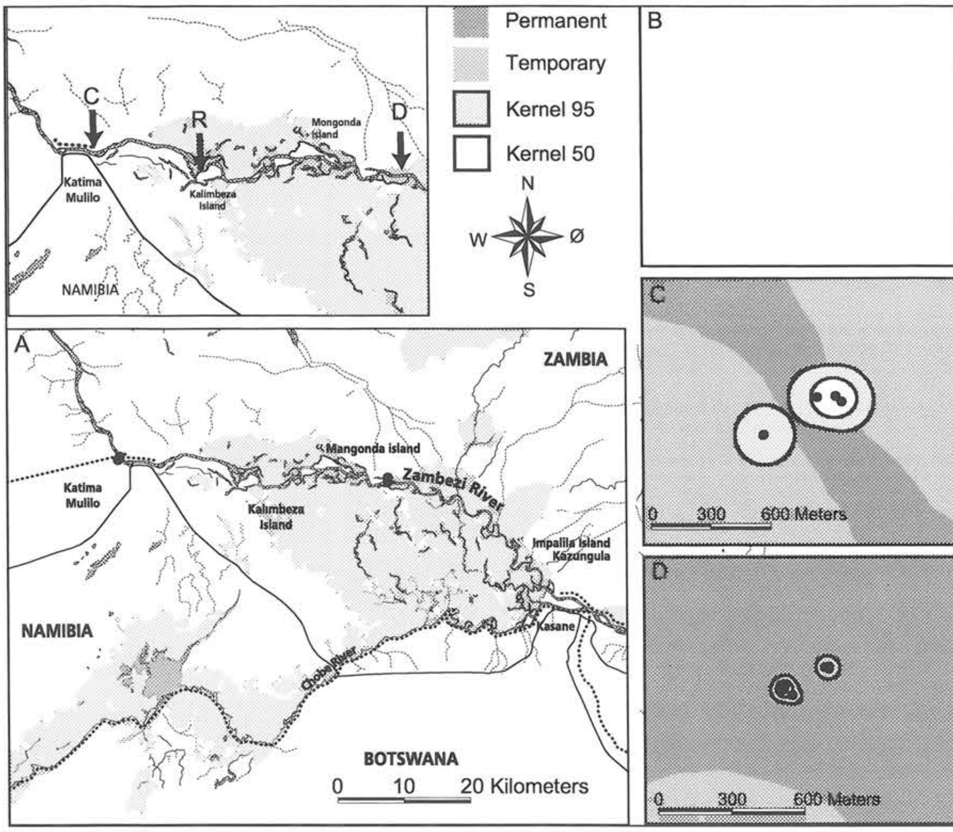



***Figure 3.*** *Continued.*

## Fish no 15




## Fish no 16

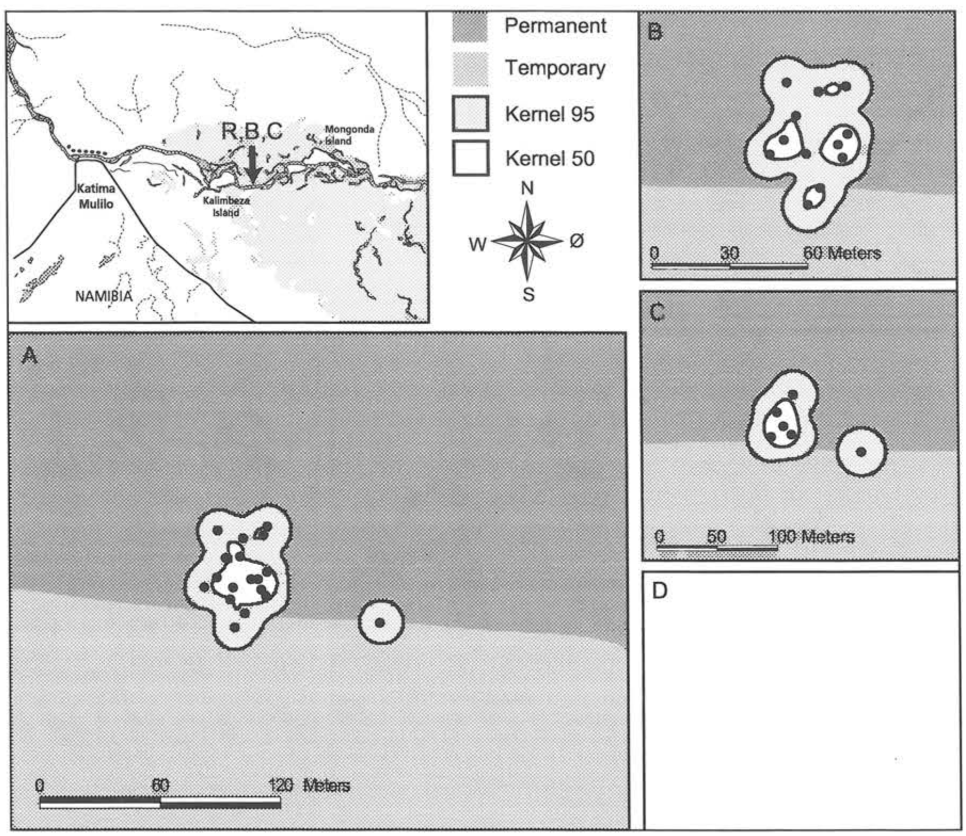
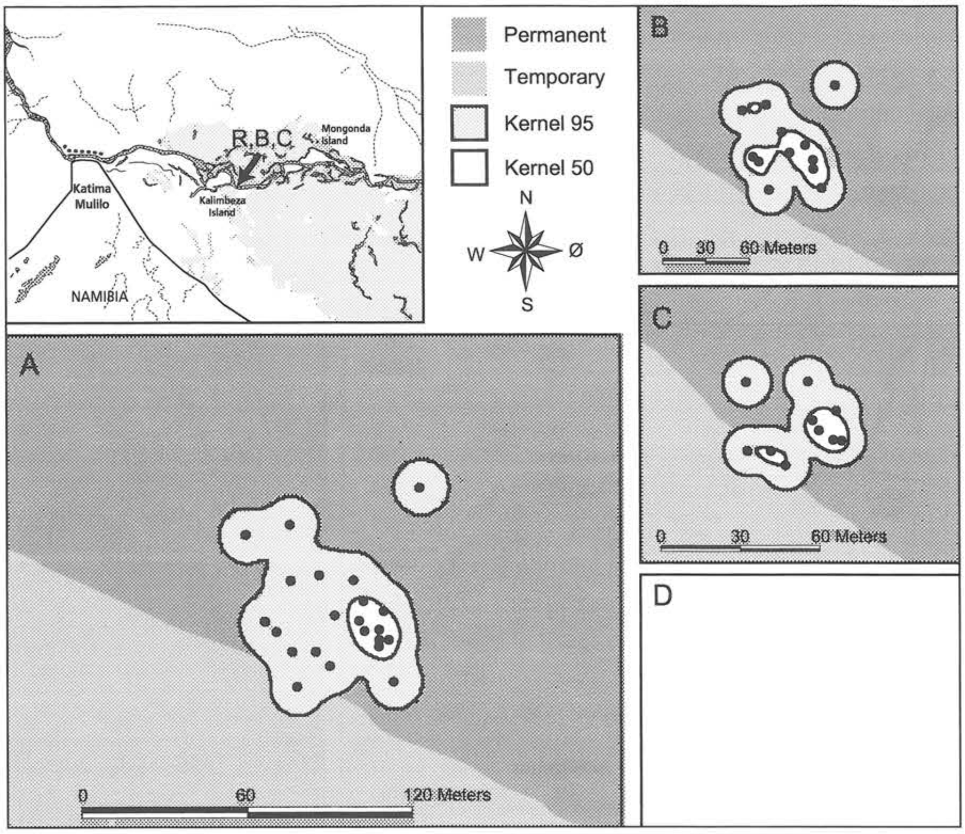



***Figure 3.*** *Continued.*

## Fish no 17




## Fish no 18

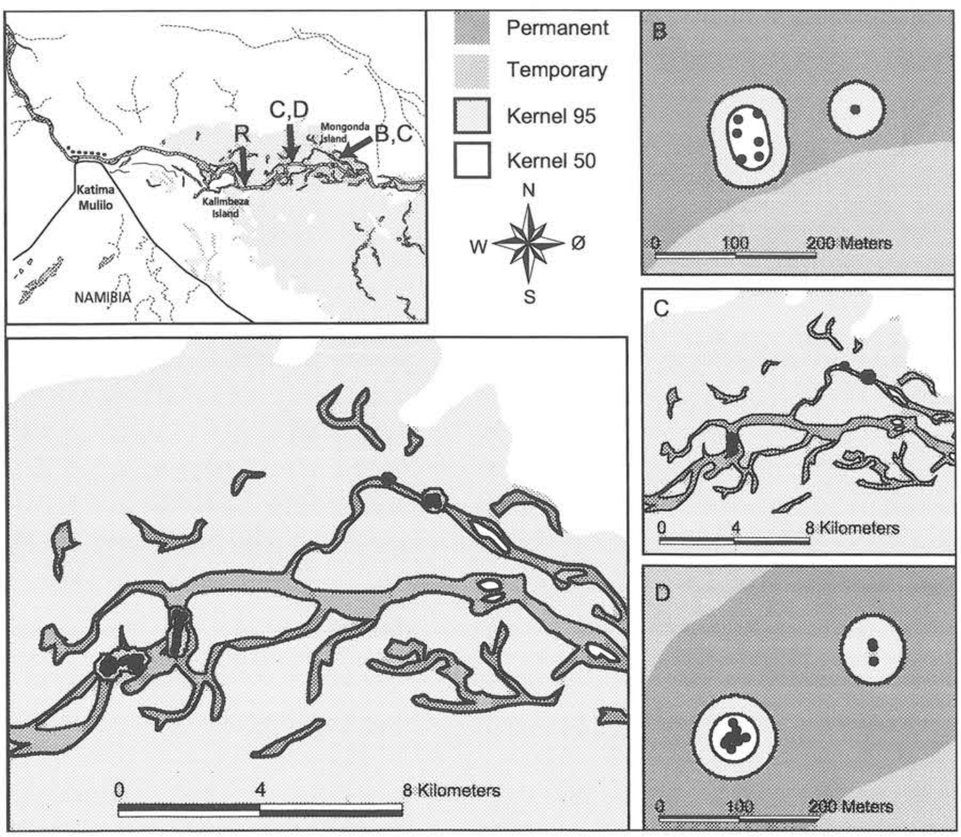
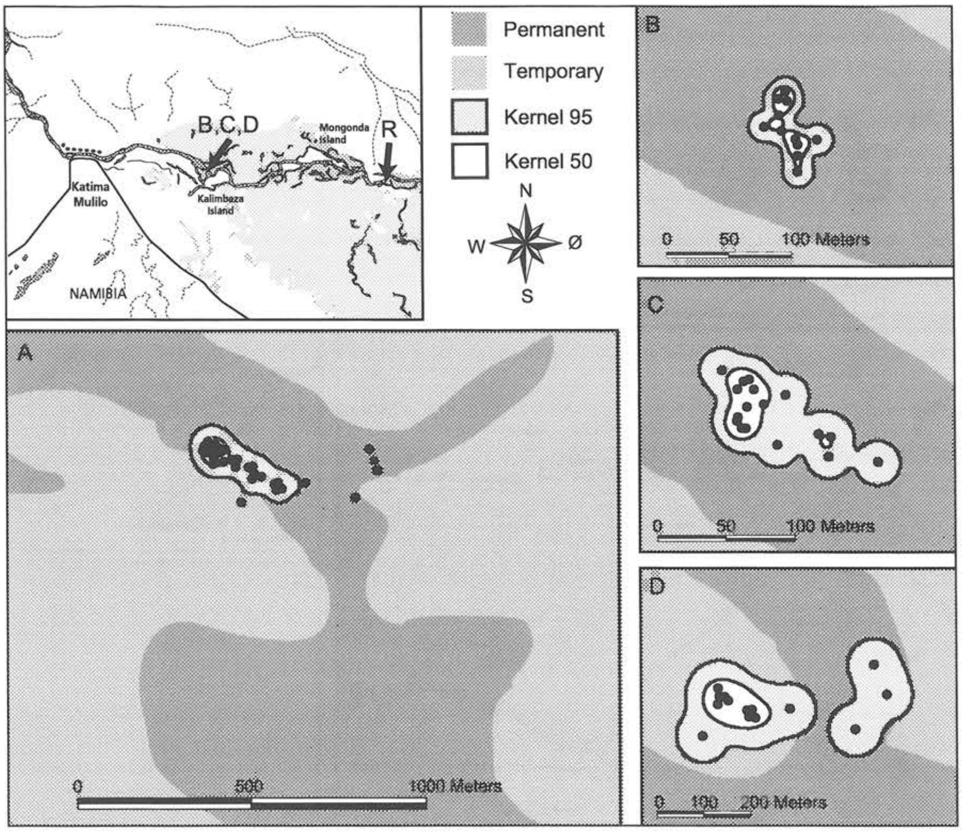



***Figure 3.*** *Continued.*

## Fish no 41




## Fish no 43

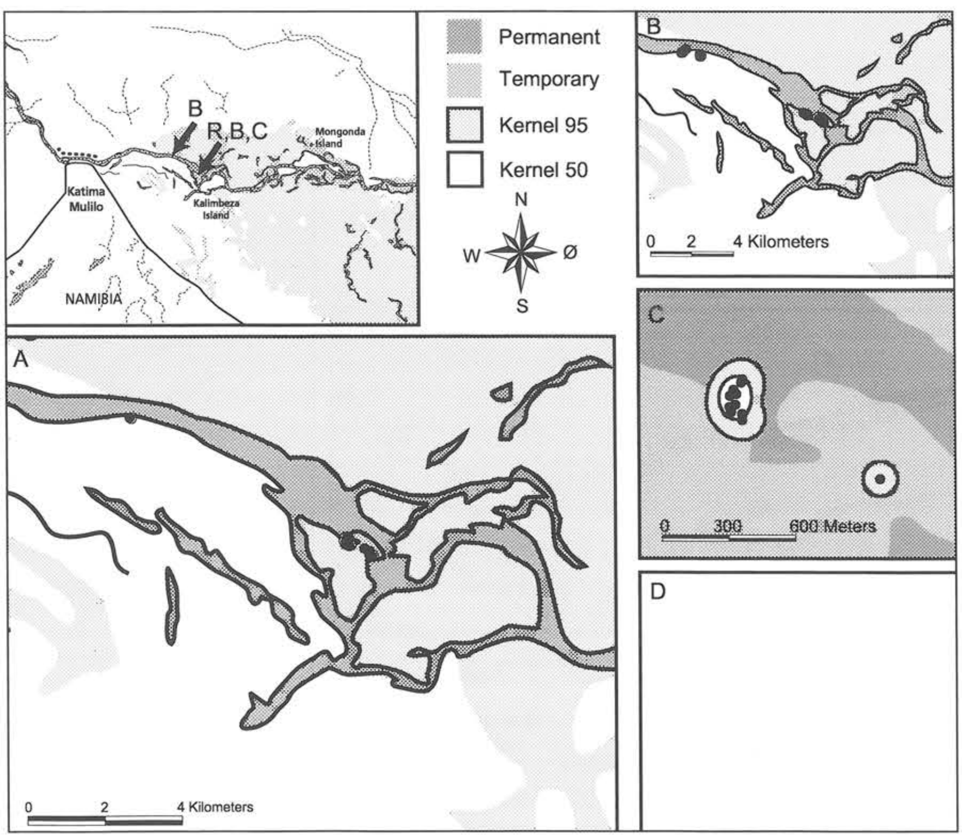
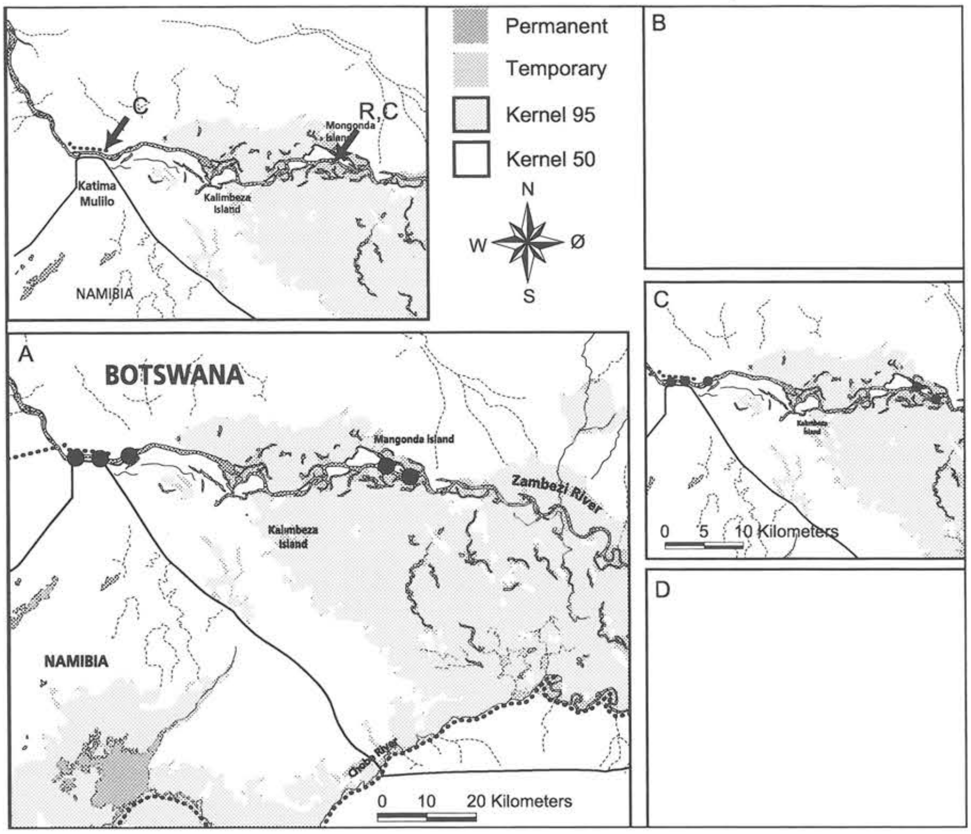



***Figure 3.*** *Continued.*

## Fish no 44




## Fish no 46

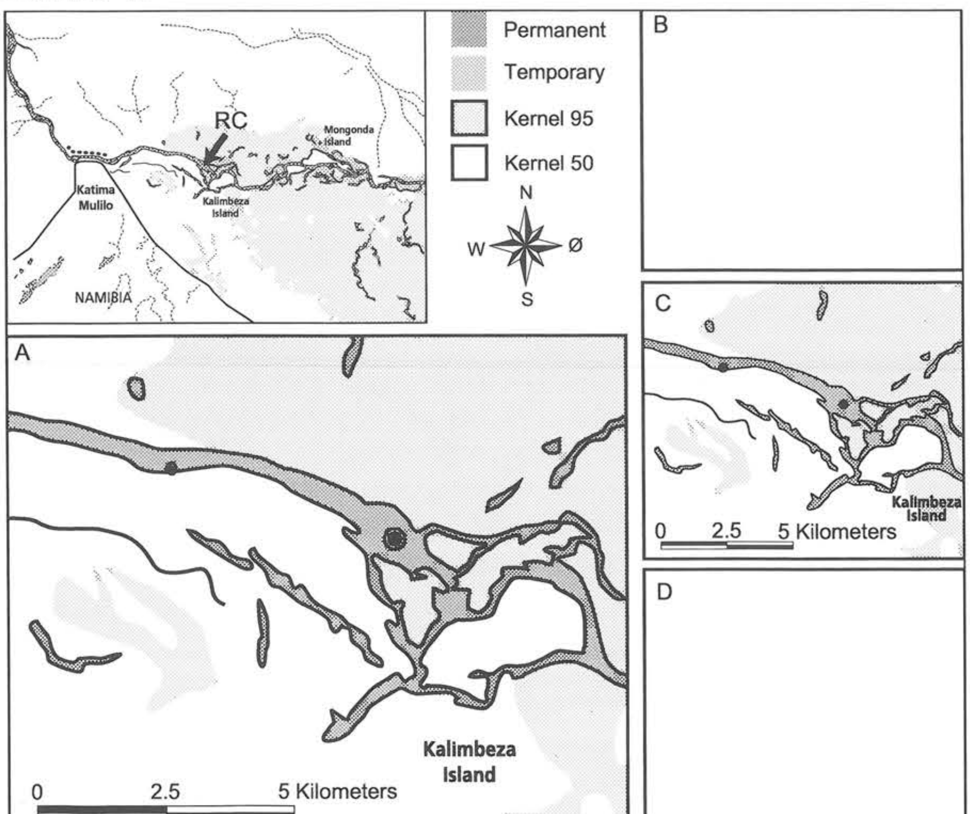



*Figure 3. Continued.*

## Fish no 47

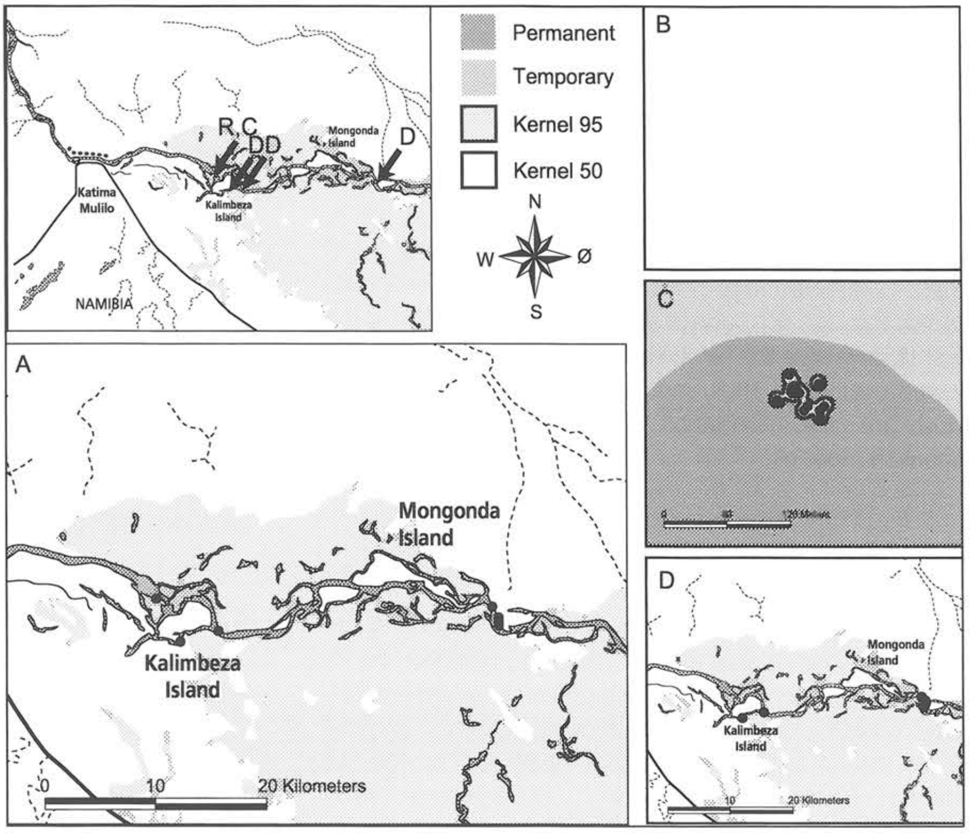



***Figure 3.*** *Continued.*

# 4 Discussion

Tigerfish is one of the most important predatory fishes in African freshwaters (see e.g. Jackson 1961, Lewis 1974, Winemiller & Kelso-Winemiller 1994). Tigerfish have large effects on the fish communities where they are present, both by direct predation and by influences on prey fish behaviour and life history (Jackson 1961, Bell-Cross 1974, Winemiller & Kelso-Winemiller 1994). Most of the information on the ecology of this species is based on collection of fish through fish surveys and anglers reports. This is the first study where the behaviour of individual tigerfish is followed over time. Thus, much of the data in the present study are new information to what is previously known about the species.

## 4.1 Movements and home range

Mean total distance moved by individual fish during the entire study period was more than 26 km, however, the individual variation was large. Two different movement patterns could be described, even though all the fish showed some sort of site fidelity. Approximately half of the fish showed only movements less than 1,000 m between tracking surveys, staying within defined home ranges. The remaining fish showed site fidelity for periods, with long distance movements to new areas between the residency periods. Compared to cichlids studied in the same area at the same time of the year (Thorstad *et al.* 2001, Økland *et al.* 2002), tigerfish had larger home ranges, although the most striking difference was their longer movements.

Differences in movement patterns among individuals could not be explained by differences in body size, and there seemed to be no seasonality in the long distance movements. It is, therefore, suggested that these movements were not related to spawning, but that they, for example, were related to feeding opportunities. Van der Waal (1996) observed concentrations of predatory fish such as the tigerfish in the Upper Zambezi River at the end of the flood season and early spring outlets of drainage channels from the floodplains, implying local migrations related to feeding opportunities. Tigerfish usually form roving schools of likesized fish (Skelton 1993), but it is difficult to tell whether whole schools participated in the long distant movements, or whether individuals may undertake such movements on their own.

Several publications mention different types of migrations in tigerfish, although there seem to be a lack of data documenting such migrations. Bell-Cross (1974) found that tigerfish were resident during the dry season based on tagging and recaptures in the Upper Zambezi River, but speculated that tigerfish move upriver during the flood season and return after the floods have receded. Tigerfish is a warm-water species, and in South Africa it is reported that tigerfish migrate downstream to lower-lying reaches of the river during the winter, where the water temperature is higher and more stable (Van Loggerenberg 1983). According to Skelton (1993), tigerfish migrate up- or downstream to suitable spawning sites along flooded river banks and lake shores. Jakcson (1961) mention that tigerfish migrate to floodplains and flooded streams during rains, and that tigerfish in Lake Tanganyika annually migrate up large rivers to spawn. Based on the results in the present study and information from previous publications (as referred to above), it seems that generally applied migration patterns can not be described for tigerfish, but that tigerfish may show opportunistic migration patterns related to for example spawning, feeding and water temperatures depending of the conditions where they reside.

## 4.2 Habitat utilisation

All the fish were recorded in the mainstream of the river, and on average, 81% of the fixes were in the main river. This is in accordance with several other studies reporting that river-dwelling adult tigerfish is mainly found in the open water of main river channels and in large tributaries (Jackson 1961, Bell-Cross 1974, Skelton 1993, Winemiller & Kelso-Winemiller 1994). However, the present study also showed that tigerfish to an increasing extent were recorded in habitats such as side channels, backwaters and floodplains during rising water level.

Although often recorded in the main river channel, tigerfish rather stayed closer to shore than in the middle of the river. The fish were recorded on average 107 m from the nearest shore, which constituted 22% of the total width of the river. The fish were also likely to be associated with vegetation, but they were never recorded inside or under vegetation. When recorded near or at vegetation, they seemed to prefer the shadow from the vegetation (R. Thompson, pers. comm.). Also Bell-Cross (1966) and Balon (1971) observed some adult tigerfish towards the shore and in shallow water, especially in the evening.

Adult tigerfish are almost exclusive fish feeders (Jackson 1961, Matthes 1968, Lewis 1974, Takano & Subramaniam 1988, Skelton 1993, Winemiller & Kelso-Winemiller 1994). It is suggested that the pursuit method of attack used by tigerfish is poorly-suited for capturing prey in lentic habitats containing much aquatic vegetation, in contrast to the ambush habit of African pike *Hepsetus odoe* (Bloch, 1794), which is more suited in densely vegetated habitats (Jackson 1961, Winemiller & Kelso-Winemiller 1994). It is likely that the habitat preferences and movements seen by the tigerfish in the present study was largely determined by availability of prey in different areas combined with a higher foraging efficiency in open water habitats than in vegetated habitats. A detailed study of the behaviour of an individual tigerfish *Hydrocynus brevis* Günther 1864 was undertaken in the River Niger by Baras *et al.* (2002). This individual showed home range behaviour during the study, and hunting activity was observed during daytime, followed by decreased activity in shallower areas during the night (Baras *et al.* 2002). A study with frequent tracking throughout the day could reveal whether the recordings of *H. vittatus* close to shore and in the shadow from vegetation also are related to resting and taking refuge between hunting sequences, spawning activity (see below) or whether they are actively hunting also in these areas.

Water depths where fish were recorded varied between 0.5 and 14 m, but it is not known from the present study at which depths above bottom the fish stayed. Tigerfish is reported to patrol the surface layers (Bell-Cross 1974, Skelton 1993), but they are also observed down to 35 m depth in the Lake Kariba (Matthes 1968).

The tigerfish were almost always found on sandy substratum, and only occasionally on clay, muddy bottom and rocks. The association of tigerfish 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).

The creation of extensive floodplains during the rainy season obviously affects the conditions for the fish. The tigerfish utilised to an increasing extent temporary water covered areas during rising and high water, although only one fish moved out onto the classical floodplain habitat. Individuals utilising temporary water covered areas were larger than those remaining in the permanently water covered areas. Average distance moved between tracking surveys was shorter during rising than low water. Unfortu-nately, it is not known whether these differences were linked to changes in factors such as prey availability or spawning.

Minimum size of sexual maturation for tigerfish is 26 cm for males and 15 cm for females in the same area of the Zambezi River as the present study was carried out (Hay *et al.* 2002). Fifty percent of the males were mature at 26 cm length and of the females at 28 cm length (Hay *et al.* 2002). Thus, most of the fish in the present study had probably reached sexual maturity. The timing of spawning is uncertain. In Incomati River in South Africa, spawning presumably takes place in December and January (Steyn *et al.* 1996). In Cahora Bassa in the Lower Zambezi River, spawning takes place only once a year during the rainy season, and is over in January (Vostradovsky 1984). In Lake Kariba in the Middle Zambezi River, gonad ripening continued from October until March (Kenmuir 1973), and in the Upper Zambezi River in Zambia breeding probably occurs during the floods (Bell-Cross 1974). Thus, it is not known when the fish in the present study could have spawned, but it is likely that spawning occurred before or in the beginning of the study, because ripe running males have been observed in this area of the Zambezi River in late October and early November (C. Hay, pers. obs.). Spawning sites are along flooded riverbanks and lake shores (Skelton 1993), and it seems tigerfish spawns on a sandy substrate in the vicinity of aquatic vegetation (Steyn *et al.* 1996). Fecundity is extremely high (Skelton 1993), and the negatively buoyant eggs are slightly adhesive for benthic or epibiotic incubation (Steyn *et al.* 1996). Tigerfish are not guarding their eggs (Steyn *et al.* 1996), but apart from this, little is known about their reproductive behaviour. It is, therefore, not known to what extent reproduction may have affected movements and habitat utilisation in the present study.

## 4.3 Methods

Few telemetry studies have been conducted in tropical rivers (Hocutt *et al.* 1994a), and even fewer in large rivers such as the Zambezi River. This study and previous studies (Thorstad *et al.* 2001, Økland et al. 2002) showed that telemetry is a suitable method for collecting information about movements and habitat utilisation of cichlids in the Zambezi River system. Anaesthetisation and tagging procedures seemed to be acceptable, as all tigerfish were alive as long as they were tracked, and no transmitter-loss was recorded. The behaviour of the individual released 600 m downstream from the catch site indicated a fast recovery after tagging, based on the immediate return to the catch site and the strike on an anglers spoon bait less than three hours later. However, knowledge on the effects of tagging on factors such as growth, swimming capacity and reproduction are lacking for this species.

Eight fish disappeared from the river immediately after tagging, and several fish as the study proceeded. Six of these were reported recaptured. It is unknown whether the remaining missing fish moved out of the study area, were recaptured without being reported or the transmitter failed. However, most of the fish that disappeared did so during high water level towards the end of the study, and it is likely that the transmitter batteries started to run out during this period. It is also likely that some fish were recaptured without being reported.

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. Downstream movements immediately after release are also in other studies regarded as abnormal behaviour due to the treatment of the fish (e.g. Mäkinen *et al.* 2000). Such a distinct reaction to handling and tagging was not seen in the present study. The fish had moved on average 3.0 km away from the release site when tracked for the first time 1- 20 days after release, which is comparable to the average movement of 1.5 km between tracking surveys every fourth day later in the study. Moreover, movements immediately after tagging were both downstream, upstream and sidewise.

## 4.4 Fisheries management

Basic information about fish movements, seasonal migrations, habitat preferences and habitat utilisation of target species is needed to regulate fisheries locally and regionally among countries, and the exploitation of the fish resources. Such information is also needed to evaluate the possible benefits of reserves and sanctuaries. Furthermore, migration and habitat studies can provide information on which fish are most vulnerable to exploitation and when.
Tigerfish are important both in the semi-commercial, subsistence and recreational fisheries in the Namibian part of the Upper Zambezi River. Tigerfish was the third most dominant species caught during an angling competition in this area (Næsje *et al.* 2001). In experimental gill net catches, it was also the third most important species, and in catches with other gears than gill nets during these surveys, it was the seventh most important species (Hay *et al.* 2002). Tigerfish is among the six main species caught by local fishermen in the area (Purvis 2001b). The results in the present study suggest that the exploitation rate of tigerfish may be high, especially during low water, since 26% of the tagged fish were reported recaptured. It is likely that some catches were not reported, such that this is a minimum estimate.

Co-ordination of local and regional management regulations are important for the tigerfish populations, to avoid fish being protected in one river section and depleted in the neighbouring river section. In rivers bordering on several countries such as the Upper Zambezi River, multilateral management regulations are needed as well, especially for long-distance moving species as the tigerfish. However, tigerfish may be less vulnerable to high exploitation in a specific area than more stationary species. The long distance movements of some individuals makes it likely that a locally overexploited area can be re-colonised by tigerfish moving from other areas, even tens of kilometres away. In this aspect, an interesting question is whether the two different movement patterns observed in tigerfish, with some stationary individuals and some showing long-distance movements, reflects environmental or genetic differences among individuals. If genetically induced, a locally high fishing pressure may be detrimental for a genetically unique stationary tigerfish population.

The stationarity of some of the tigerfish also implies that smaller sanctuaries can protect adult fish, because some of them may be staying within the protected area. However, smaller sanctuaries will not protect the long-distance moving fractions of the tigerfish population, and when management actions to protect tigerfish are needed, gear or effort restrictions should also be considered. A more detailed study of the activity patterns of the fish throughout the day would provide information on the vulnerabibity of the tigerfish for being caught in passive gears, such as gillnets. The long distance movements also suggest that tigerfish may be vulnerable to dams, weirs and other migration barriers, although the reasons for these movements in the Upper Zambezi River are not understood.

It must be emphasised that only fifteen fish were recorded in the present study, and the full annual cycle is not studied. These limitations must be considered when using the present data for management recommendations.

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