Movements and habitat utilisation of nembwe (*Serranochromis robustus*) in the Upper Zambezi River.

Implications for fisheries management

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Abstract

Økland, F., Hay, C. J., Næsje, T. F., Chanda, B. & Thorstad, E. B. 2002. Movements and habitat utilisation of nembwe (*Serranochromis robustus*) in the Upper Zambezi River. Implications for fisheries management. - NINA Project Report 20: 1-25.

During 4-15 November 2000, 15 nembwe (*Serranochromis robustus* Günther, 1864) (32-49 cm) were tagged with radio transmitters in the Zambezi River in Namibia. The objective was to analyse the behaviour of nembwe for management purposes. The movements and habitat utilisation were recorded and compared during the three periods 1) low water level immediately before the rainy period, 2) increasing water level during the rainy period, and 3) high water level after the rainy period.

The fish were tracked on average every 3.7 day during 23 November-18 May, and individuals were tracked up to 47 times. Mean total distance moved by individual fish was 3,183 m (range 233-11,886 m). The nembwe showed no directional movements up- or downstream, but stayed within defined home ranges. Home ranges were generally small, with a 95% probability of localisation within an average area of 184,563 m^2 (range 621-566,597 m^2). On average, the fish stayed within a river stretch of 1,330 m (range = 24-3,787).

Fish were obviously only recorded in permanently water covered areas during low water. During rising and high water, 67% and 71% of the fish utilised temporary flooded areas, respectively. Most fish were recorded both in permanently and temporary water covered areas during rising and high water. Nembwe did not undertake long-distance migrations onto the floodplains, but utilised the adjacent temporary water covered areas. The utilisation of temporary water covered areas during the spawning period may have been connected to spawning and nursery, but knowledge on the breeding behaviour of nembwe is not yet sufficient to support this.

All the fish were recorded in the mainstream of the river. However, 62% of the fish were recorded in one or more additional main habitat type; 54% of the fish were recorded in side channels, 46% in permanent swamps, 15% in backwaters and 8% in the mouth of backwaters. Although often recorded in the main river channel, nembwe rather stayed closer to shore than in the middle of the river. The fish were recorded on average 58 m from the nearest shore (range 2-416), which constituted 15% of the total width of the river. The fish were also likely to be associated with vegetation, as on average, 78% of the fixes were near or inside/under vegetation. The most frequently recorded habitat type was marginal aquatic anchored vegetation, followed by marginal aquatic floating vegetation.

Water depth where the fish were recorded varied between 1.2 and 7.3 m, and was on average 3.7 m. Water depths where fish stayed were larger during high water than during low and rising water. The fish were mainly recorded on sandy substratum, which is the main substratum type in the Upper Zambezi River.

This is the first study where the behaviour of individual nembwe is followed over time, and much of the data are supplementary information to what is previously known about the species. Based on these results, nembwe seem locally vulnerable to overfishing due to their small movements. Nembwe may potentially be locally overexploited if the local exploitation pressure is high, in contrast to species moving about more widely. The management and regulations are, therefore, important for the local populations of adult nembwe. In rivers bordering to several countries like the Upper Zambezi River, multilateral management regulations are necessary even for stationary species to avoid fish being protected in one country and overexploited in the neighbouring country. The small movements of nembwe also imply that sanctuaries probably will protect adult fish, because they will be staying within the protected area.

Three fish were released more than 1,400 m away from the catch site, and did not show homing to the catch site. Inability to home when displaced over some distance opens the possibility of re-introduction of species in areas with extinct or reduced populations and relocation of fish from surrounding areas to sanctuaries.

Key words: *Serranochromis robustus jallae* - nembwe - radio telemetry - movement - habitat - behaviour - management

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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 nembwe 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

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. The northern perennial river systems border on Angola, Zambia and Botswana. A number of people live near these rivers and are dependent on the fish recourses (MFMR 1995; Tvedten *et al*. 1994). In Namibia, about 50% of the 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).

Inland fisheries are often seasonal and combined with other activities, which tends to reduce the pressure on fish stocks (Sandlund & Tvedten 1992). However, a major concern has been the possible depletion of fisheries resources in the Okavango and Zambezi Rivers as a result of increased subsistence fishing due to the high population growth (Van der Waal 1991; Hocutt *et al.* 1994b; Tvedten *et al.* 1994; Hay *et al.* 1996, 2000). Several other factors may also indirectly influence the fish stocks, such as the effects of overgrazing, soil erosion, deforestation, siltation of the rivers, pollution and low floods (Tvedten *et al.* 1994).

Perceived declining fish stocks have brought about the need to review and improve legislation to protect the environment (Sandlund & Tvedten 1992). Management of a sustainable fishery depends on a better understanding of the fish migrations and habitat preferences in these complex and variable floodplain ecosystems. Most Namibian fish species (78%) are floodplain-dependent for larval and juvenile stages and, thus, dependent on migration between floodplains and the main river (Barnard 1998).

Cichlidae is the largest fish family in Africa with about 870 species described and several more to be described (Skelton 1993). The serranos, or largemouth breams, is a distinct group of large predatory cichlids, which are popular angling species and important in the floodplain fisheries (Skelton 1993). One of these species, the nembwe (*Serranochromis robustus* Günther, 1864), is described by Skelton (1993) as a major angling target with bass-like qualities, and as a valuable commercial and subsistence fishery species. The nembwe attains about 450 mm and about 3.5 kg, but a specimen as large as 6.1 kg has been reported (Skelton 1993). Two subspecies of nembwe are described, and S. *robustus jallae* is the subspecies known from the Upper Zambezi River (Skelton 1993).

The objective of this study was to analyse the behaviour of radio tagged nembwe in the Namibian part of the Zambezi River for management purposes. The movements and habitat utilisation were recorded and compared during the three periods 1) low water level immediately before the rainy period, 2) increasing water level during the rainy period, and 3) high water level after the rainy period.

2 Material and methods

2.1 Study site

The Caprivi Region is a finger-like extension of the north-eastern corner of Namibia, bordering on Botswana, Angola and Zambia. Compared to the rest of Namibia, the Caprivi Region has a relatively high rainfall (760 mm per year). It is a flat area, approximately 1,000 m above sea level. Seasonal flooding during summer creates extensive floodplains, especially in the Eastern Caprivi, where almost 30% of the area can be flooded. Fishery and overgrazing of floodplains are possibly the activities with the highest impact on the environment and fish community in this area. 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).

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 the Eastern 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 this area, with an annual average of 5.2 m (Van der Waal & Skelton 1984). The water level usually rises sharply in January, with one or more peaks in February-April, before a decline in May-June. Thus, the floodplains are annually inundated from February to June (Van der Waal & Skelton 1984). 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, especially of larger cichlids, are 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. 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. Rocky habitats only occur at the rapids at Katima Mulilo and

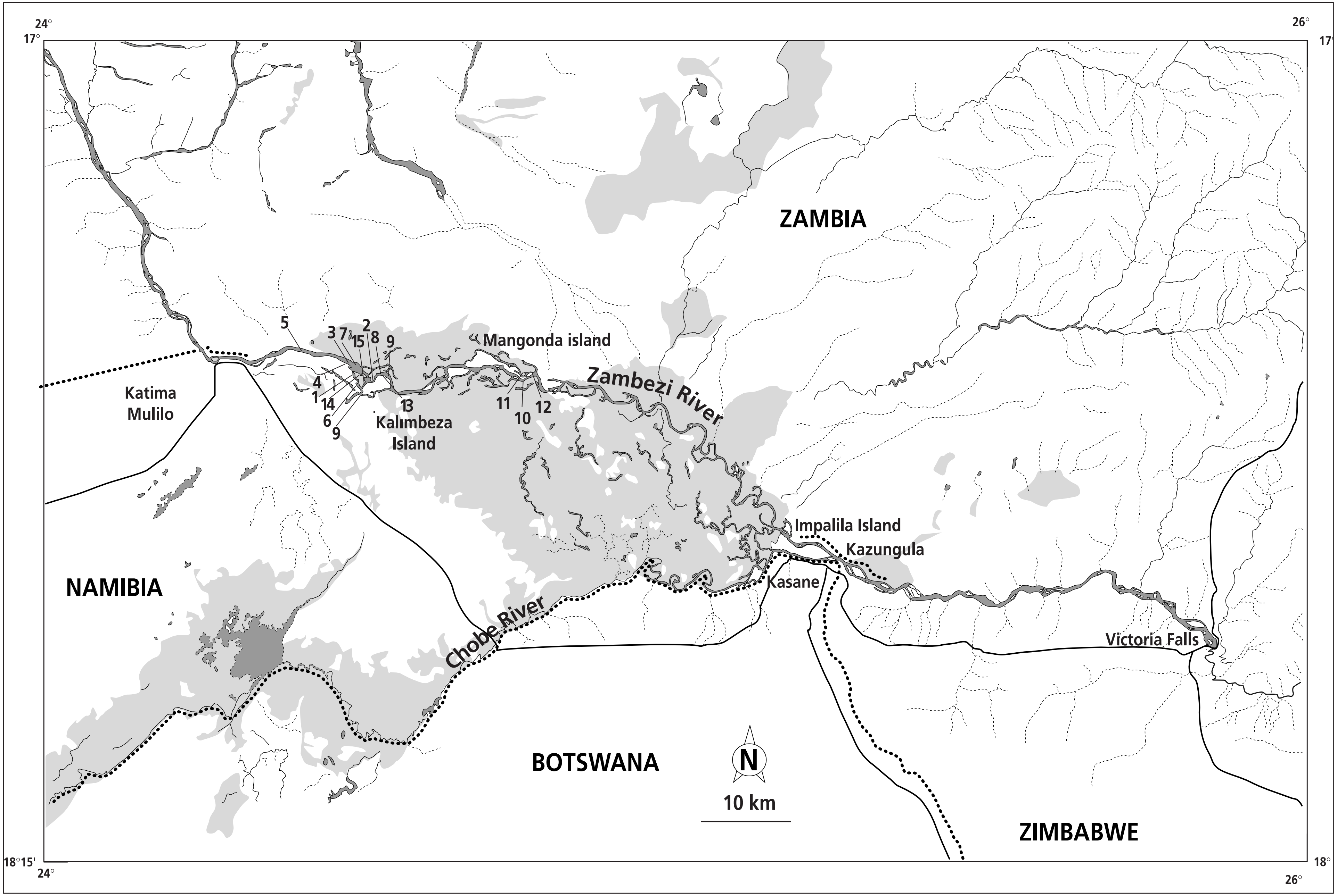


Figure 1. *The upper part of the Zambezi River in north-eastern Namibia. Sites where individual nembwe were radio tagged and released are indicated. Individual fish numbers correspond to the numbers in* ***table 1****. Shaded areas indicate floodplain during high waters.*

Impalila. The water is generally clear with little suspended particles, but with a higher turbidity during floods. The river has ample available cover in the form of overhanging marginial terrestrial vegetation, marginal aquatic vegetation, and inner aquatic vegetation. Marginal terrestrial vegetation can be described as fringing vegetation on riverbanks in the form of terrestrial grass, reeds, overhanging trees and shrubs. Vegetation 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

Fifteen nebmwe were captured by rod and line in two areas in the Zambezi River, namely 22-31 km and 56-60 km downstream from Katima Mulilo in Caprivi, Namibia, during 4-15 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. (ATS), USA, **table 1**) were externally attached to the fish, using the method described in Thorstad *et al.* (2000). During the tagging procedure, which lasted about 2 min, the fish were kept in a water filled tube. Transmitter weight in water was less than 1.3% of the body weight of the fish. The transmitters emitted signals within the 142.004-142.383 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 six fish that were released 118-2,261 m downstream from the catch site due to drift of the boat during handling of the fish, or because they were brought to the tagging boat from another angling boat (**table 1**). The water temperatures were 27.1-29.7 °C during catch and tagging.

2.3 Tracking of the fish

The fish were tracked from boat using a portable receiver (R2100, ATS) connected to a 4-element Yagi antenna. The fish were located with a precision of ± 10 m in the main river. Some of the backwaters were inaccessible by boat, and the location had to be estimated based on the direction and signal strength.

Thoreau & Baras (1997) found reduced activity levels during the first 12-24 hours after anaesthetisation 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 buoy-

Table 1. *Radio tagged nembwe in the Zambezi River, Namibia, during 4-15 November 2000. Release site is given as distance from catch site.*

Fish no.	Tagging date	Body length (cm)	Transmitter model*	Releasesite (m)	Total number of fixes	Number of fixes during each period (low, rising, high water)	Last tracking date
1	04.11.00	45	F2120	0	41	8, 18, 14	08.05.01
2	04.11.00	33	F2040	0	1	1, 0, 0	06.12.00
3	04.11.00	40	F2120	1408	47	11, 18, 14	18.05.01
4	05.11.00	39	F2120	0	38	11, 18, 7	05.04.01
5	05.11.00	37	F2120	0	31	11, 18, 0	06.03.01
6	08.11.00	49	F2120	0	26	11, 13, 0	23.02.01
7	08.11.00	43	F2120	2261	47	11, 18, 14	18.05.01
8	11.11.00	35	F2120	511	45	10, 17, 14	18.05.01
9	11.11.00	32	F2040	0	18	10, 6, 0	18.01.01
10	12.11.00	37	F2040	153	32	12, 17, 1	13.03.01
11	12.11.00	40	F2120	0	45	12, 15, 14	18.05.01
12	12.11.00	32	F2040	118	26	12, 12, 0	13.02.01
13	15.11.00	36	F2120	2000	0	0, 0, 0,	17.11.00
14	15.11.00	45	F2120	0	9	2, 7, 0	06.03.01
15	15.11.00	43	F2120	0	5	5, 0, 0	09.12.00

*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.

ancy 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.

The fish were tracked on average every 3.7 day during 23 November-18 May, and individual fish were tracked up to 47 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 on water cover (1: permanent water cover, 2: temporary water cover, *i.e.* each year during the rain period, 3: episodic water cover, *i.e.* occasional but not regular during rain period), main habitat type (1: 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: inside/under vegetation), and vegetation type if near or inside/under vegetation (1: inner aquatic submerged, 2: inner aquatic floating, 3: inner aquatic anchored, 4: marginal aquatic submerged, 5: marginal aquatic floating, 6: marginal aquatic anchored, 7: marginal terrestrial submerged, 8: marginal terrestrial overhanging). Moreover, recordings were made on water temperature at surface, visibility (1: clear, 2: medium, 3: muddy, 4: high turbidity), depth (only water depth, depth of the fish was unknown, measured by manual sounding and echo sounder), 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.

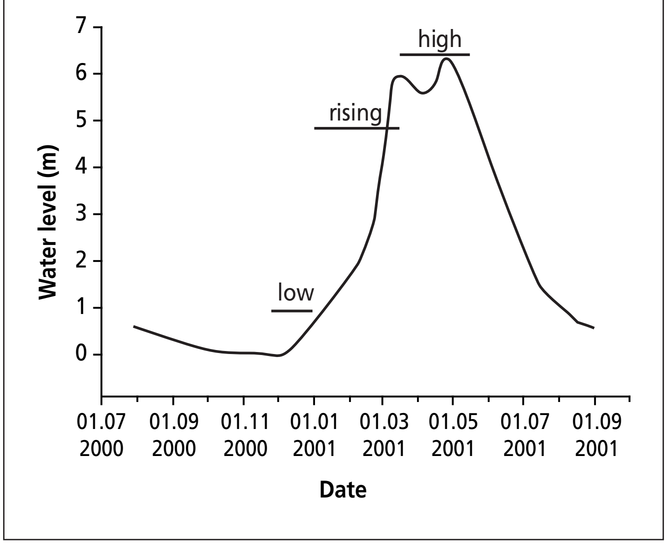


Figure 2. *The water level in the Zambezi River from 1 August 2000 to 31 August 2001. The study periods at low, rising and high water are indicated.*

2.4 Data analyses

Fish no. 2 and 13 disappeared from the study area shortly after tagging (**table 1**), and were not included in the analyses. Descriptive statistics were based on all fish recorded in the referred periods (see **table 1**). However, statistical analyses of behaviour and habitat utilisation among low, rising and high water levels were made by non-parametric paired comparisons, and only fish recorded in all periods under comparison could be included in the analysis. Therefore, results from only six fish were included in the comparisons among all three periods, which were made by Friedman Tests (fish no. 1, 3, 4, 7, 8 and 11, **table 1**). Comparisons between low and rising water were also performed, since the sample size was higher than for comparisons among all three periods. Results from 11 fish were included in the comparisons between low and rising water, which were made by Wilcoxon Signed Ranks Tests (fish no. 1 and 3-12, **table 1**; fish no. 14 were excluded due to few recordings). Descriptive statistics and statistical analyses were based on average values for individual 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 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, except for 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: *Tagging personnel in survey boat with tagging equipment****.***

Lower picture: *Survey team catching nembwe for radio-tagging. All fish were caught with rod and line.*

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

After recovery the nembwes were in very good form when released.

Upper picture: *Survey team tracking radio-tagged nembwe and recording the exact position with GPS. The habitat of nembwe was also described.*

Lower picture: *The main river with vegetated river banks, a common nembwe habitat in the Zambezi River.*

3 Results

3.1 Movements

Mean total distance moved by individual fish during the first 10-22 days after tagging (from tagging to first tracking) was 458 m (SD = 952, range = 14-3 711, only one fish moved more than 560 m away). Five fish had a downstream movement, seven upstream and two sidewise during this period. Of the six fish released away from the catch site (**table 1**), two fish (no. 8 and 10) were later recorded at the catch site.

Mean total distance moved by individual fish during the entire study period was 3,183 m (SD = 3,061, individual means from 233 to 11,886 m). Average distance moved between tracking surveys was 93 m (SD = 62, individual means from 31 to 258 m), and did not differ among periods (Wilcoxon test comparing low and rising water, Z = 0.89, P = 0.37; Friedman test comparing all three periods, χ^2 = 4.96, P = 0.084). Average distance moved was not dependent on fish body size (linear regression, r^2 = 0.09, P = 0.31).

Fish were obviously only recorded in permanently water-covered areas during low water. During rising water, 67% of the fish utilised temporary flooded areas, and during high water, 71%. Only one fish during rising and four fish during high water were only recorded in temporary covered areas, thus, most fish utilised both permanently and temporary water covered areas during rising and high water (see also **figure 3**). On average, 30% of the fixes during rising water and 61% during high water were in temporary flooded areas. The body size of fish utilising temporary flooded areas were larger than of those staying only in permanently water covered areas during rising water (mean body length 42 cm, range 37-49 cm *versus* mean body length 35 cm, range 32-40 cm, Mann-Whitney Test, U = 3.5, P = 0.028; sample size was too small for comparison during high water).

3.2 Home range

The fish showed no directional movements up- or downstream, but stayed within defined home ranges (**figure 3**). Home ranges were generally small, with a 50% probability of localisation within an average area of 38,595 m^2 (SD = 33,221, range 136 -109,657 m^2) and 95% probability within an average area of 184,563 m^2 (SD = 163,329, range 621-566,597 m^2) (based on average 36 fixes per fish, range 18-47 fixes, and a sample size of 11 fish). Home range size was not dependent on fish body size (linear regression, 95%: r^2 = 0.10, P = 0.34, 50%: r^2 = 0.14, P = 0.26). Distance between the two fixes farthest off from each other in individual fish during the entire study period was on average 1,330 m (SD = 1,240, range = 24-3,787). Home ranges were also analysed separately for low (n = 10), rising (n = 10) and high (n = 5) water level (**figure 3**). The 95% probability home range was on average 69,210 m^2 during low water, 153,236 m^2 during rising water and 56,376 m^2 during high water. The 50% probability home range was on average 19,749 m^2 during low water, 30,463 m^2 during rising water and 12,649 m^2 during high water. The 95% probability home range was larger during rising than during low water, but not the 50% probability home range (Wilcoxon test, n = 9, 95%: Z = -2.55, P = 0.011, 50%: Z = -1.60, P = 0.11, **figure 3**, all three periods were not compared due to a low sample size). Home range size neither during low nor rising water was dependent on fish body size (linear regressions, 95%: r^2 from 0.002 to 0.15, P from 0.26 to 0.90, 50%: r^2 from 0.010 to 0.29, P from 0.11 to 0.78). Proportions of fish with 1, 2, 3 and 4 core areas did not differ among periods (analysed both for 95% and 50% probability, Pearson chi-square tests, χ^2 from 2.44 to 5.86, P from 0.44 to 0.66, **figure 3**).

3.3 Habitat utilisation

All the fish were recorded in the mainstream of the river. However, 62% of the fish were recorded in one or more additional main habitat type; 54% of the fish were recorded in side channels, 46% in permanent swamps, 15% in backwaters and 8% in the mouth of backwaters. (Note that percentages add up to more than hundred because some fish are recorded in more than one habitat type.) On average, 69% of the fixes were in the mainstream of the river (94, 60 and 43% during low, rising and high water), 17% in side channels (3, 17 and 43% during low, rising and high water), 12% in permanent swamps (22, 0 and 14% during low, rising and high water), 1% in backwaters (3, 1 and 0% during low, rising and high water) and 0.2% in mouth of backwaters (0, 0.5 and 0% 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 -1.15 to -0.44, P from 0.25 to 0.66), except that proportion of fixes in the mainstream of the river were lower, and in permanent swamps higher, during rising water (Z = -2.03, P = 0.043; Z = -2.21, P = 0.027). Average proportion of fixes in the different main habitats did not differ when tested among all the three periods (Friedman tests, χ^2 from 1.00 to 5.60, P from 0.061 to 0.61). There was no difference in body size between fish recorded in the mainstream of the river only and fish recorded in additional main habitats (Mann-Whitney U test, U = 12.5, P = 0.28), between fish recorded in side channels and not (U = 18.0, P = 0.73), or between fish recorded in permanent swamps and not (U = 12.5, P = 0.23).

The fish were recorded in different positions related to vegetation; 69% of the fish were recorded at no vegetation, 92% near vegetation and 92% inside/under vegetation. On average, 21% of the fixes were at no vegetation (27, 12 and 43% during low, rising and high water), 25% near vegetation (36, 22 and 0% during low, rising and high water) and 53% inside/under vegetation (38, 67 and 57% during low, rising and high water). Position related to vegetation did not differ among periods (Wilcoxon tests, Z from -1.75 to -0.71, P from 0.08 to 0.48; Friedman tests, χ^2 from 0.44 to 5.44, P from 0.07 to 0.80). There was no difference in body size between those recorded near and inside/under vegetation compared to those not recorded at vegetation (Mann-Whitney U test, U = 9.0, P = 0.20).

Of the fish recorded near or inside/under vegetation (n = 12), 100% were associated with marginal aquatic anchored vegetation, 25% with marginal aquatic floating vegetation, 25% with marginal terrestrial overhanging vegetation and 8% with marginal aquatic submerged vegetation. On average, 92% of the fixes were at marginal aquatic anchored vegetation, 7% at marginal aquatic floating vegetation and 1% at the other vegetation types. There were no differences among periods in which vegetation type the fish were associated with (Wilcoxon tests, Z from -1.34 to -0.37, P from 0.18 to 0.72; Friedman tests, χ^2 from 0.0 to 3.71, P from 0.16 to 1.0).

Water temperature where the fish were positioned varied between 25.3 and 29.5 °C during the study. The water temperature decreased slightly during the study period, and was on average 27.4 °C (range 26.9-29.5) during low water, 27.3 °C (range 26.5-27.9) during rising water and 26.1 °C (range 25.3-27.5) during high water.

All the fish except one, were recorded at both medium water visibility (on average 51% of the fixes) and at high turbidity (on average 49% of the fixes) during the study. During low water, all fixes were at medium visibility. During rising water, on average 8% of the fixes was at medium visibility, and during high water, 51%. The remaining fixes were at high turbidity. Average proportion of fixes recorded at medium visibility differed among periods (Wilcoxon test, Z = -2.95, P = 0.003, Friedman tests, χ^2 = 12.0, P = 0.002).

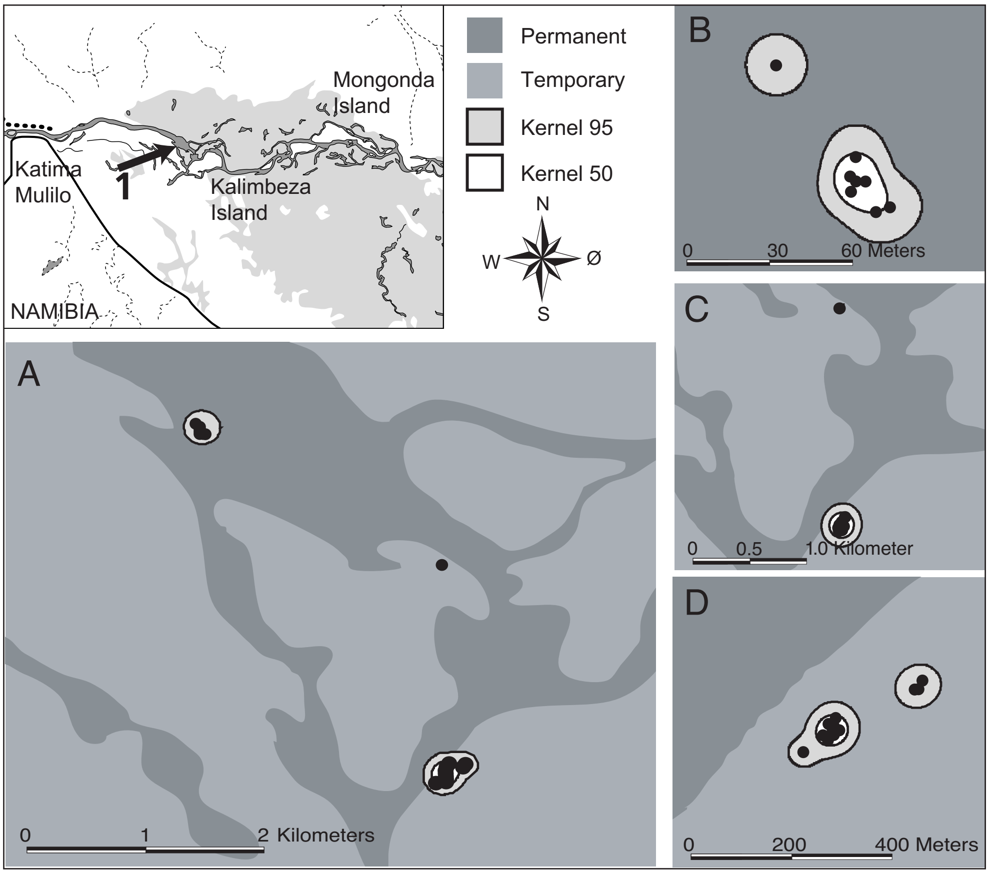
Water depth where the fish were recorded varied between 1.2 and 7.3 m, and was on average 3.7 m (3.5 m during low, 3.3 m during rising and 5.5 m during high water). Water depths did not differ between low and rising water (Wilcoxon test, Z = -0.36, P = 0.72), but differed among low, rising and high water (Friedman tests, χ^2 = 9.3, P = 0.009). Water depth was not dependent on fish body size (linear regression, r^2 = 0.011, P = 0.74).

The fish were mainly associated with sandy substratum; 100% of the fish were recorded on sandy substratum, 23% on clay, 8% on muddy, soft bottom, 8% on gravel and 8% on rocks. On average, 93% of the fixes were on sandy substratum (87, 96 and 98% during low, rising and high water), 2% on clay (2, 3 and 2% during low, rising and high water), 1% on muddy bottom (3, 0 and 0% during low, rising and high water), 0.3% on gravel (0, 0.6 and 0% during low, rising and high water) and 3% on rocks (7, 0.5 and 0% during low, rising and high water). Average proportion of fixes recorded on the different substratum types did not differ among periods for any substratum type (Wilcoxon tests, Z from -0.45 to -1.00, P from 0.32 to 0.66; Friedman tests, χ^2 from 0.00 to 2.00, P from 0.37 to 1.00).

Total width of the river where the fish were positioned varied between 40 and 1,033 m, and was on average 342 m (264 m during low, 241 m during rising and 826 m during high water). Total width of the river did not differ between low and rising water (Wilcoxon test, Z = -1.78, P = 0.86), but differed among low, rising and high water (Friedman tests, χ^2 = 9.33, P = 0.009). Total width of the river where fish stayed was not dependent on fish body size (linear regression, r^2 = 0.00, P = 0.97). Distance to nearest shore given as proportion of total river width was on average 15% (6% during low, 18% during rising and 29% during high water). Distance to nearest shore given as proportion of total river width did not differ between low and rising water (Wilcoxon test, Z = -1.51, P = 0.13), but differed among low, rising and high water (Friedman tests, χ^2 = 9.00, P = 0.011).

Distance to nearest shore varied between 2 and 416 m, and was on average 58 m (19 m during low, 22 m during rising and 247 m during high water). Distance to shore did not differ between low and rising water (Wilcoxon test, Z = -1.33, P = 0.18), but differed among low, rising and high water (Friedman tests, χ^2 = 9.3, P = 0.002). Average distance to shore was not dependent on fish body size (linear regression, $r^2 < 0.001$, P = 0.97).

Fish no 1



Fish no 3

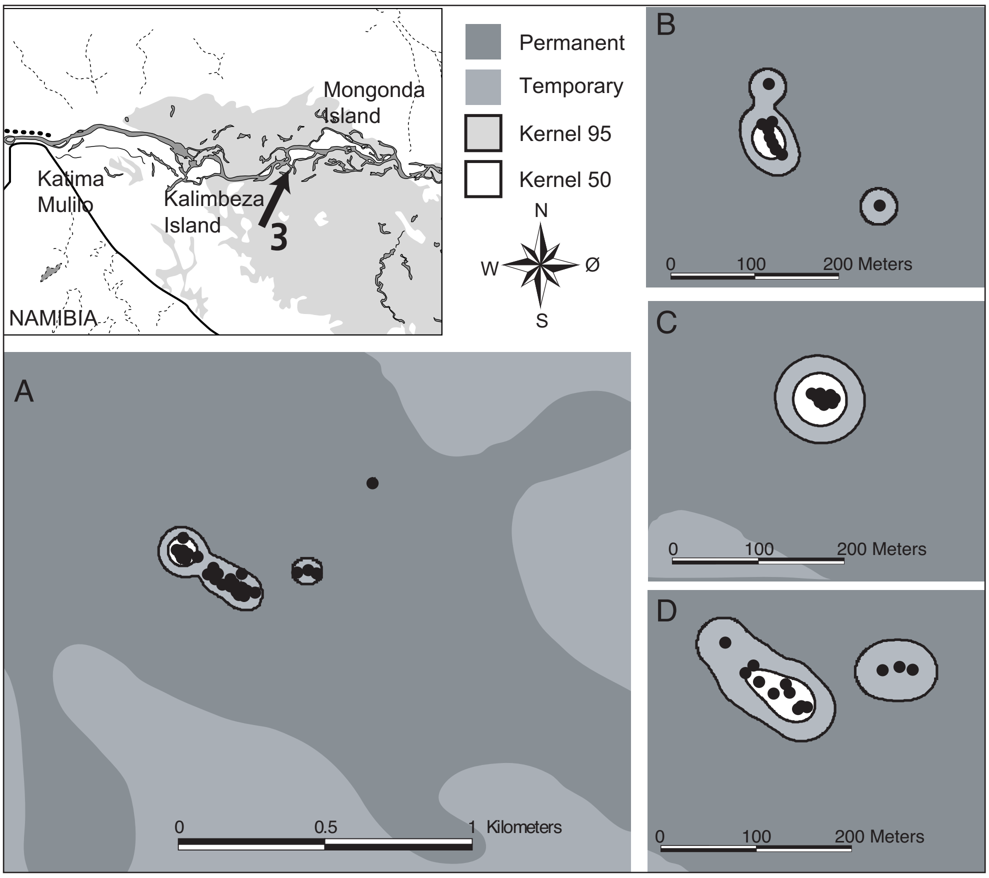
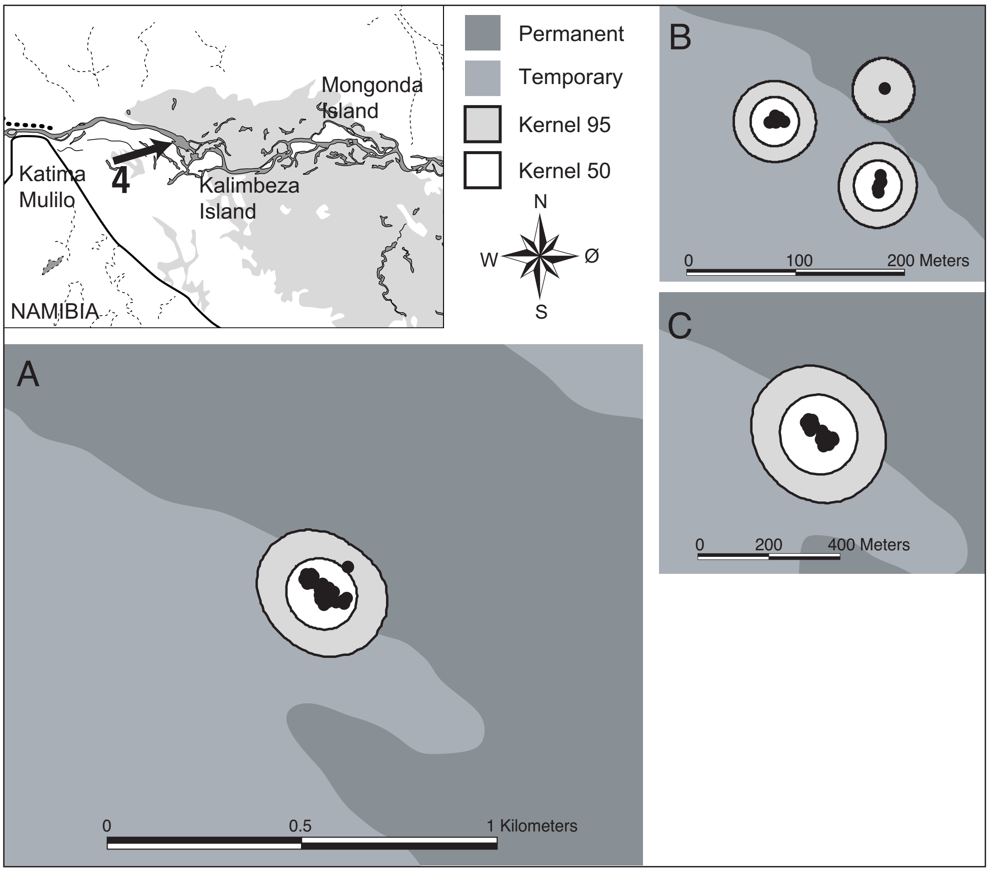


***Figure 3**. Kernel home ranges of individual radio tagged nembwe (n = 11) in the Zambezi River in 2000 and 2001 during a) the entire study period, b) low water only, c) rising water only, and d) high water only (figure d is lacking for fish not recorded during high water). Dots show fixes during tracking, 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 4



Fish no 5

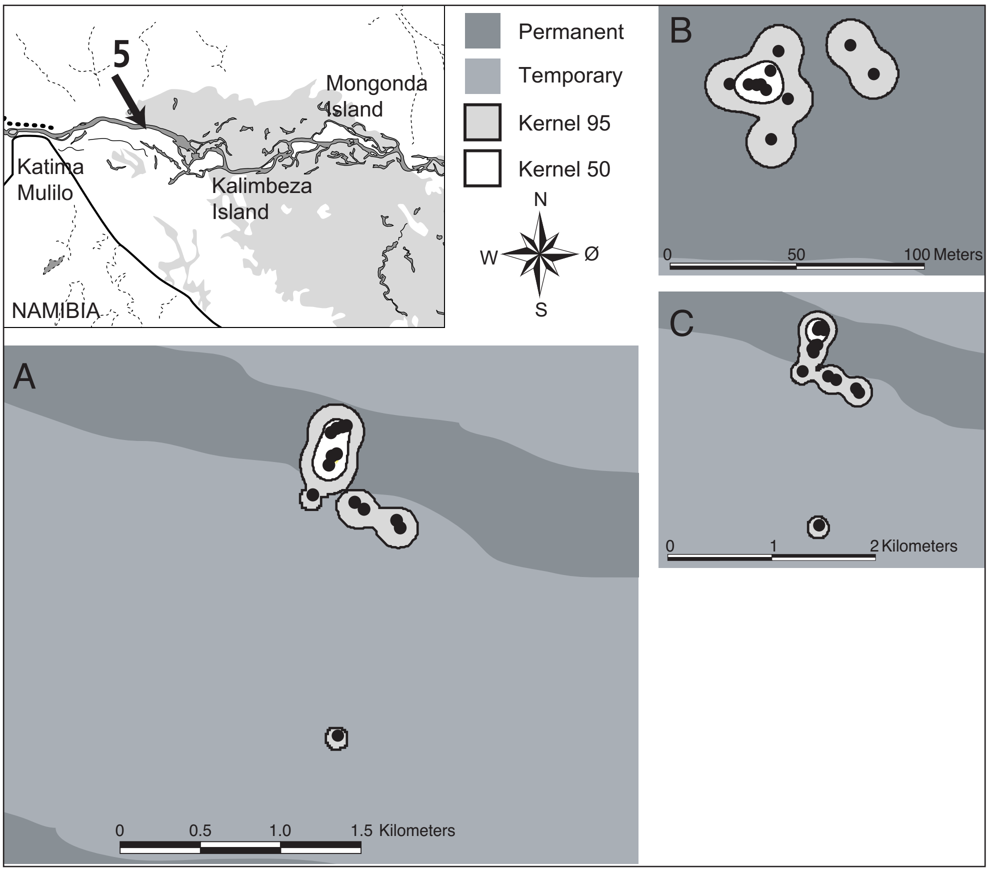
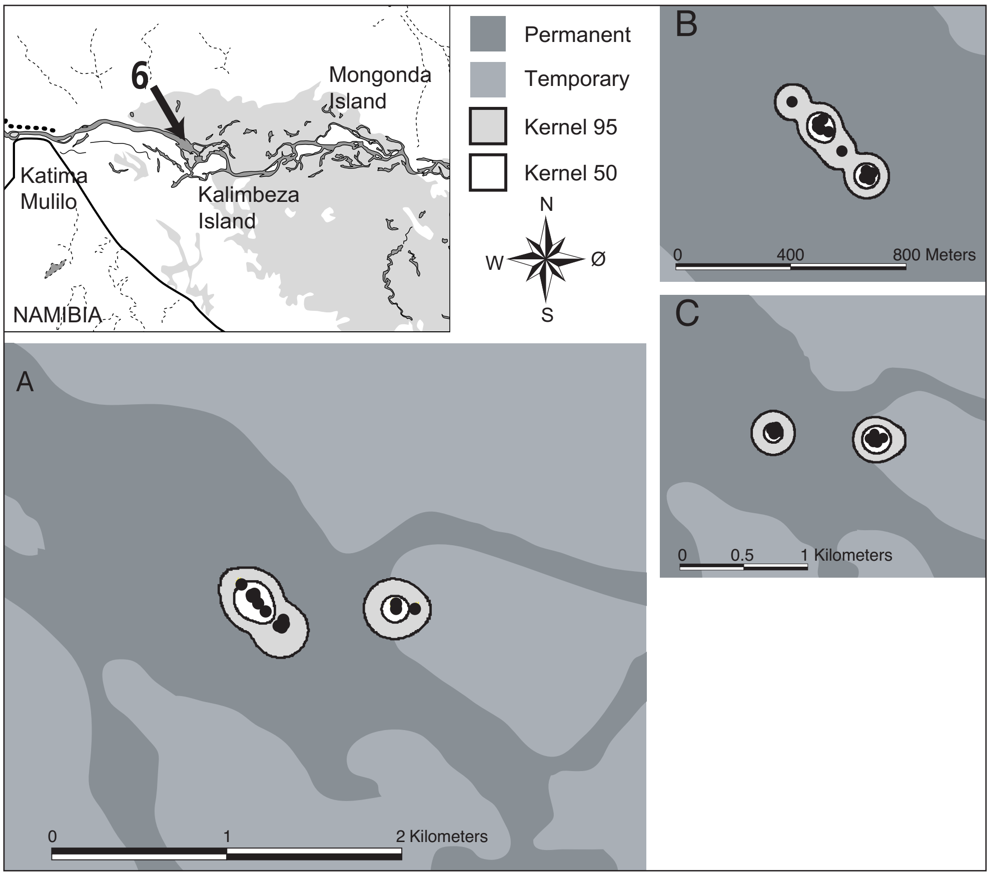


***Figure 3**. Continued.*

Fish no 6



Fish no 7

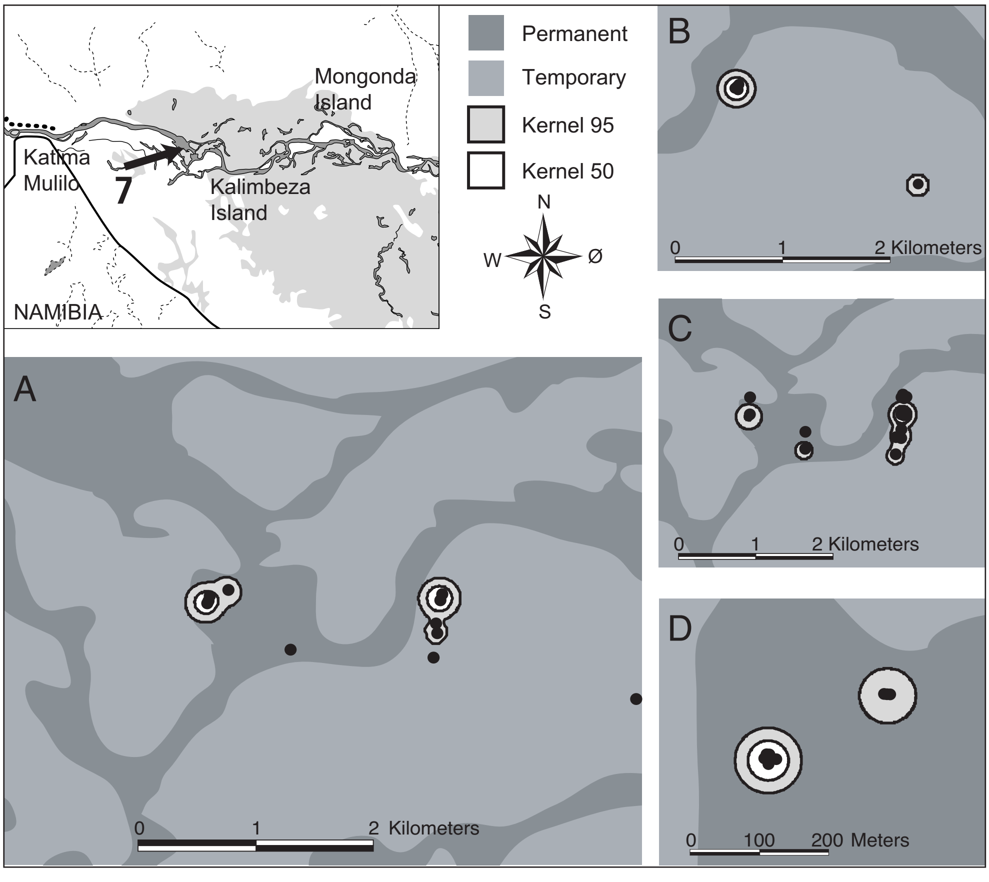
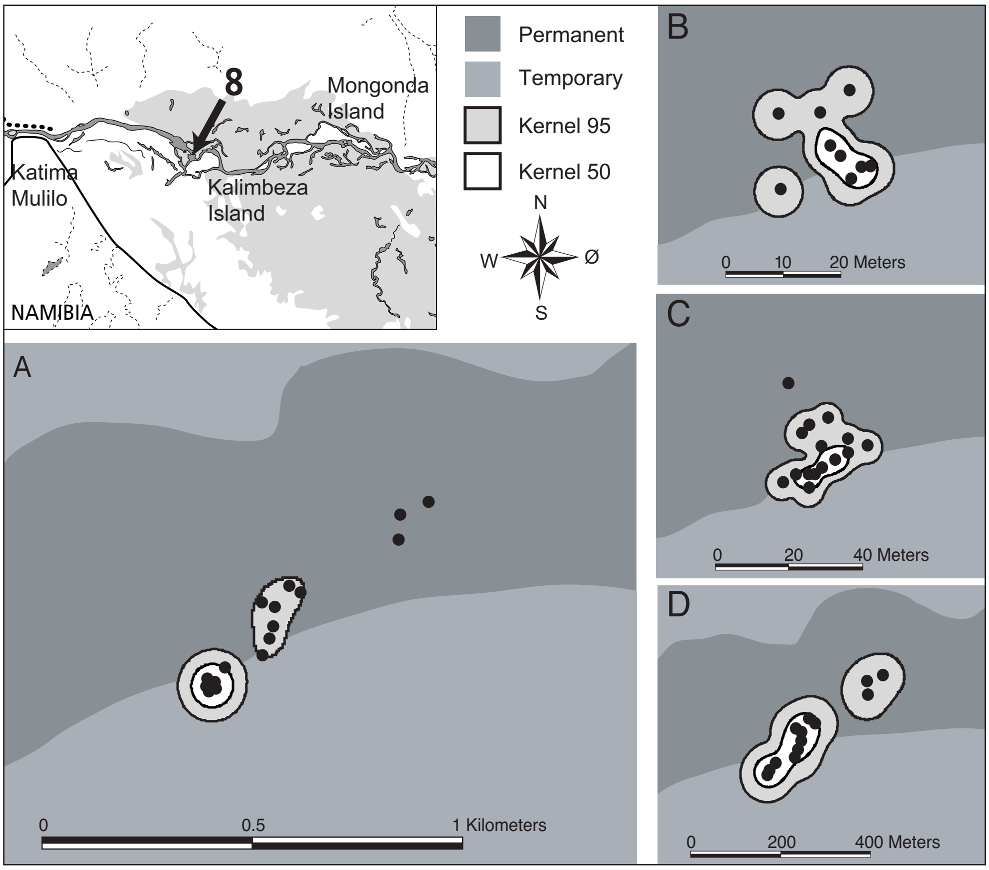


***Figure 3**. Continued.*

Fish no 8



Fish no 9

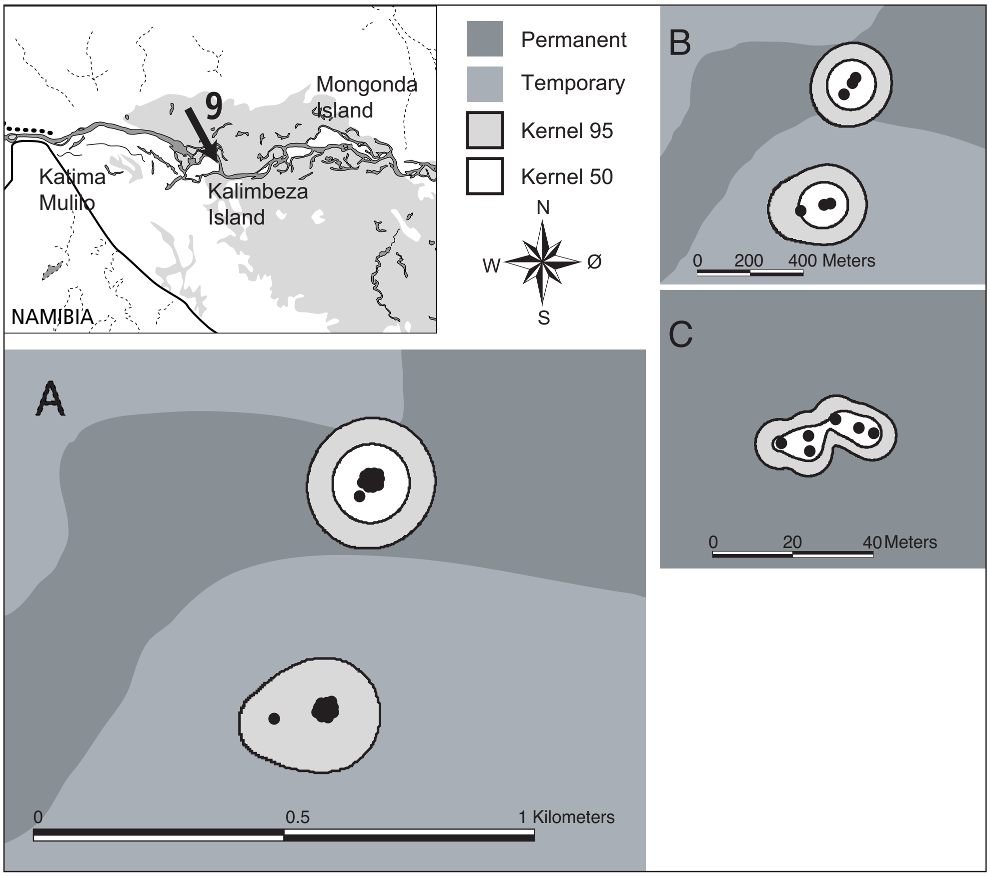
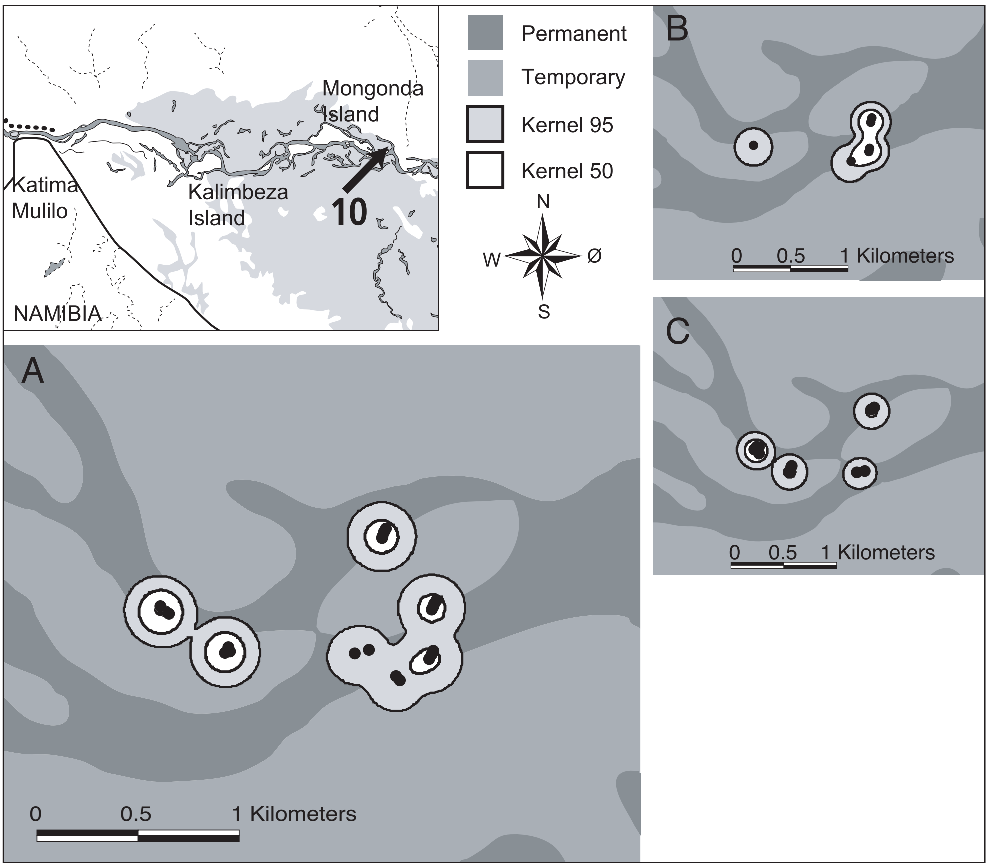


***Figure 3**. Continued.*

Fish no 10



Fish no 11

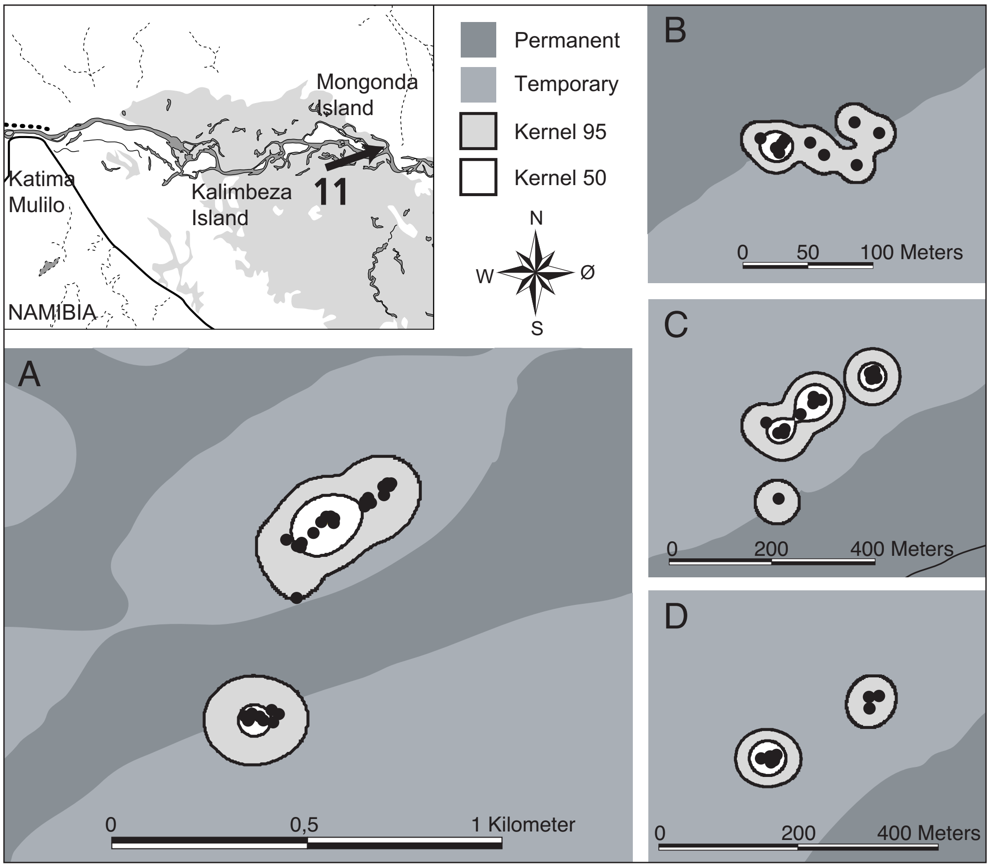


Figure 3. *Continued.*

Fish no 12

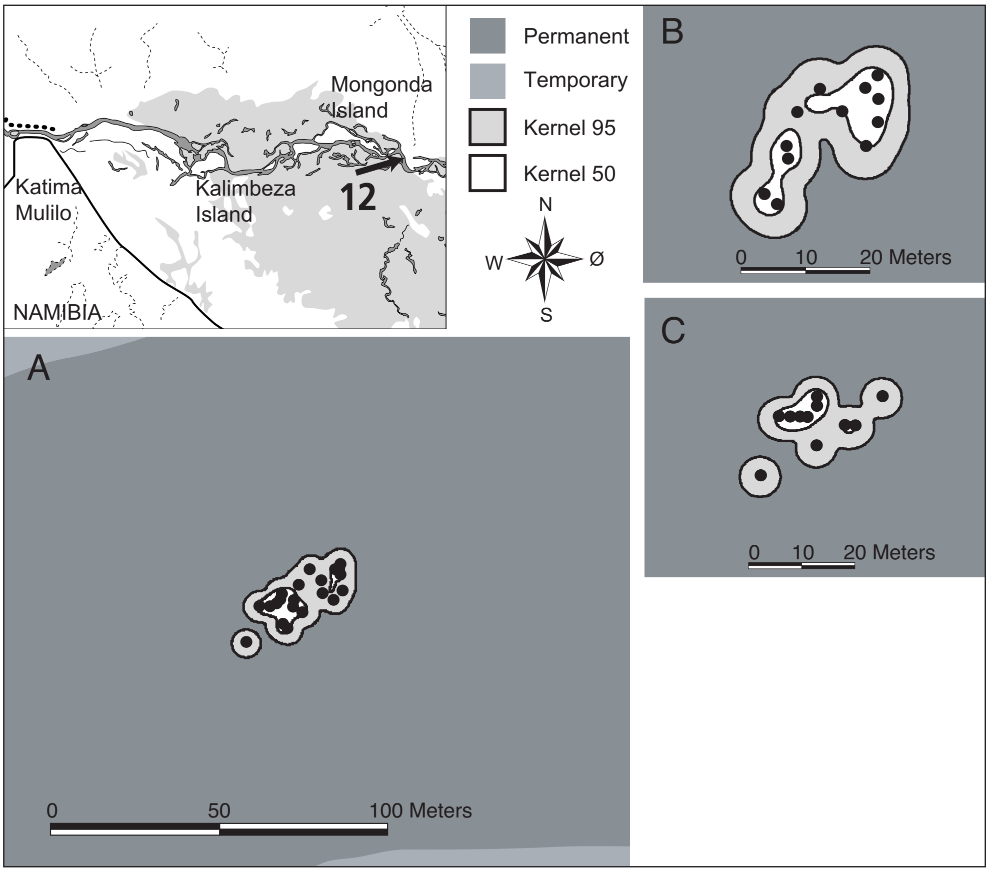


Figure 3. *Continued.*

4 Disscussion

4.1 Movements and home range

Despite the widespread distribution of the *Serranochromis* species in southern and central Africa and their importance in commercial and subsistence fisheries, few ecological data for the group have been published (Winemiller 1991). Previous data are based on fisheries surveys and sports fishermen's reports, and this is the first study where the behaviour of individual nembwe is followed over time. Thus, much of the data in the present study are supplementary information to what is previously known about the species.

This study showed that the tagged nembwe were rather stationary and stayed within an average area of 1,330 m. However, they utilised a larger area than threespot tilapia *Oreochromis andersonii* Castelnau, 1861 and pink happy *Sargochromis giardi* Pellegrin, 1903, which mainly remained resident within a small average area of 540 and 220 m, respectively, during a previous study in the same part of the Zambezi River (Thorstad *et al.* 2001). The nembwe resided in small home ranges, although they were to a larger extent moving about compared to the threespot tilapia and pink happy, which were tracked in approximately the same period of the year (5 October - 1 March) (Thorstad *et al.* 2001). 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, especially riverine, species.

Six fish were released 118 to 2,261 m away from the catch site. Two of three fish released less than 515 m away were later recorded at the release site, whereas the three fish released more than 1,400 m away did not show homing to the catch site. Also displaced individuals of threespot tilapia and pink happy did not show homing to the catch site (Thorstad *et al*. 2001). Homing behaviour for displaced fish has been demonstrated, for example, for displaced carp *Cyprinus carpio* L. (Reynolds 1983; Schwartz 1987), dusky grouper *Epinephelus marginatus* Lowe 1834 (Lembo *et al.* 1999) and pike *Esox lucius* L. (Jepsen *et al.* 2001).

4.2 Habitat utilisation

All the fish were recorded in the mainstream of the river, and on average, 69% of the fixes were in the main river. According to Skelton (1993), the larger specimens of nembwe prefer deep main channels and permanent lagoons, whereas smaller fish occur mainly in lagoons and secondary channels. This was confirmed in a survey of the Barotse area of the Zambezi River, where large size classes of nembwe were encountered primarily in the main river channel during low water, whereas juveniles were captured most frequently in the lagoon and canal habitat (Winemiller 1991). The results in the present study agrees with these previous findings that larger nembwe most often are associated with the main river, but emphasises their mobility and association with other habitats, as most individuals were recorded in one or more additional habitat type during the study, especially side channels and permanent swamps.

Water depths where fish were recorded varied between 1.2 and 7.3 m, but it is not known from the present study at which depths above bottom the fish stayed. Winemiller (1991) reported that large nembwe frequently were taken by hook and line and gillnet in the deepest regions near the bottom and close to high sandbanks, indicating that nembwe may prefer to stay near the bottom.

Although often recorded in the main river channel, nembwe rather stayed closer to shore than in the middle of the river. The fish were recorded on average 58 m from the nearest shore, which constituted 15% of the total width of the river. The fish were also likely to be associated with vegetation, as on average, 78% of the fixes were near or inside/under vegetation. The most frequently recorded habitat type was marginal aquatic anchored vegetation, followed by marginal aquatic floating vegetation. This is in accordance with Jackson (1986), who describes nembwe as a species that lives with equal facility in weed beds and the open and often deep water.

The nembwe were almost always found on sandy substratum, and only occasionally on clay, muddy bottom, gravel and rocks. The association of nembwe with sandy substratum may not be a preference for sandy substratum, but simply a result of the widespread occurrence of sandy bottom in this area of the Zambezi River. The Upper Zambezi River is a typical "sand-bank" river, mainly with sandy bottom (Van der Waal & Skelton 1984). Van der Waal (1985) found nembwe to be common and abundant during surveys in the Caprivi region, and found them in streams with sandy substrate, in deep, standing water and in shallow swamp.

The presence of predators and availability of food may be among the important factors for the habitat selection of animals. Adult size classes of the deep-bodied nembwe appear to be beyond the size range of fishes that for instance, large tigerfishes can swallow whole (Jackson 1961; Lewis 1974). The behaviour and habitat selection of nembwe in the present study was, therefore, probably not influenced by avoiding predation from other fishes. Nembwe themselves are predators, preying on fish (Bell-Cross 1974, Winemiller 1991, Skelton 1993, Gratwicke & Marshall

2001). In the Barotse area, adult nembwe consumed mostly immature squeakers (*Synodontis* species) (Winemiller 1991). The squeakers are generally protected against predators by their bony skull and large sharp dorsal and well-barbed pectoral fin spines. However, nembwe with their massive jaws, numerous blunt jaw teeth, and massive pharyngeal plates are apparently able to crush the bony head and spines of the squeakers. *Synodontis* species may be found in a variety of habitats, typically feeding on detritus, algae and benthic invertebrates (Skelton 1993). This implies that *Synodontis* are associated with bottom and vegetation, at least when feeding, which fits with the observations of nembwe as staying in deeper water at some distance from the shore, but associated with vegetation. However, Bell-Cross emphasise (1974) that nembwe is a catholic feeder, also feeding on shrimps, insects, gastropods and bivalve molluscs.

The creation of extensive floodplains during the rainy season obviously affects the habitat availability for the fish. Nembwe in the present study, utilised to an increasing extent temporary water covered areas during rising and high water. Individuals utilising temporary water covered areas were larger than those remaining in the permanently water covered areas, which could be a differences between mature and juvenile fish. Although nembwe utilised the temporary water covered areas, the recorded fish did not move out onto the classical floodplain habitat with submerged grassland and low gradients.

Changes in behaviour in connection with flooding may be linked to the reproductive behaviour of the fish. It has been suggested that some riverine cichlids probably 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). Size of sexual maturation for nembwe is 28-30 cm for males and 25-28 cm for females (Winemiller 1991). In the Namibian part of the Zambezi River, mature females down to 22 cm and mature males down to 27 cm have been recorded (C. J. Hay, unpublished data). Thus, most of the fish in the present study had probably reached sexual maturity. Nembwe began to show ripe gonads in Barotse in September, and the fraction increased between September and December, and it was concluded that they appeared to be preparing for initiation of spawning prior to flooding (Winemiller 1991). Also in the Namibian part of the Zambezi River, females with fully developed eggs were collected from the end of September, but sample size was small (C. J. Hay, unpublished data). In the Lake Liambezi, Namibia, ripe females were collected in January and March (Van der Waal 1985). Thus, it is possible that fish in the present study spawned during rising water in January-March.

Nembwe is a female mouth brooder, with the males attracting females to a nest where the eggs are deposited (Merron & Bruton 1988; Ribbink 1977). Nests are built along vegetated fringes of mainstreams according to Skelton (1993), and amongst dense submerged vegetation on sandy substrate in shallow water of only 40 cm, as observed by Van der Waal (1985) in the Lake Liambezi. The females may not necessarily stay in the nest until the juveniles are large enough to be released, but may transport their offspring to the floodplain where they are later released, as speculated by Winemiller (1991). Nembwe is a multiple spawner, and based on experimental breeding, they may spawn twice or three times during the rains with intervals of 3-5 weeks between spawnings (Bell-Cross 1974).

Based on the results in the present study, nembwe did not undertake long-distance migrations onto the floodplains, but utilised the adjacent temporary water covered areas to an increasing extent during rising and high water. Van der Waal (1996) similarly concluded that large-scale migrations of cichlids did not seem to occur in the Namibian part of the Zambezi River. The utilisation of temporary water covered areas during the spawning period in the present study may have been in connection with spawning and nursery, but knowledge on the breeding behaviour of nembwe is not yet sufficient to support this. Temporary water covered areas may also be productive areas, attracting prey of nembwe, and thereby also attracting nembwe.

4.3 Methods

Knowledge on fish migrations and habitat utilisation is imperative when implementing fisheries regulation. The best method to obtain repeated behavioural data on individual fish is by use of radio telemetry. Few telemetry studies have been conducted in tropical rivers (Hocutt *et al.* 1994a), and even fewer in large rivers like the Zambezi River. This study and a previous study (Thorstad *et al.* 2001) 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; all fish were alive as long as they were tracked, and no transmitter-loss was recorded. However, effects of tagging on factors such as growth, swimming capacity and reproduction should be studied thoroughly. Two fish disappeared immediately after tagging, and several fish as the study proceeded. It is unknown whether they moved out of the study area, were recaptured or the transmitter failed. Therefore, longer migrations by nembwe may have been underestimated by the present study, as only those remaining in the study area were tracked. However, most of the fish that disappeared did so during high water level, towards the end of the study, when the transmitter batteries should run out of power.

In a previous study of threespot tilapia and pink happy, many of the fish showed downstream movements immediately after tagging, which was regarded as a behavioural reaction to handling and tagging (Thorstad *et al.* 2001). 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 only moved on average 458 m away from the release site when tracked 10-22 days after release, and they had moved both downstream, upstream and sidewise.

4.4 Fisheries management

Nembwe are caught both in the commercial, subsistence and sport fishery in the Namibian part of the Upper Zambezi. It was the dominant species caught during an angling competition in this area (Næsje *et al.* 2001), which indicates that it is vulnerable towards angling, or that it is very abundant. In experimental gill net catches performed by the Ministry of Fisheries and Marine Resources in Namibia, nembwe was the twenty-second most important species, and in catches with other gears during these surveys it was the thirty-fourth most important species (Hay *et al.* 2002). Basic information on migrations and habitat utilisation has been lacking both for the nembwe and for other important species in this area.

Based on the results in the present study, nembwe seem locally vulnerable to overfishing, due to their small movements. Nembwe may potentially be locally overexploited if the local exploitation pressure is high, in contrast to species moving about more widely. The management and regulations are, therefore, important for the local populations of adult nembwe. In rivers bordering on several countries like the Upper Zambezi River, multilateral management regulations are necessary even for stationary species to avoid fish being protected in one country and overexploited in the neighbouring country. The small movements of nembwe also imply that sanctuaries probably will protect adult fish, because they will be staying within the protected area. Their seemingly inability to home when displaced over some distance opens the possibility of re-introduction of species in areas with extinct populations and relocation of fish from surrounding areas to sanctuaries. However, it must be emphasised that only fifteen adult fish were tagged in the present study, and that the full annual cycle was not studied. Juvenile nembwe may, for example, behave differently from adult fish. These limitations must be considered when using the present data for management recommendations.

Basic information about annual movements, habitat preferences and habitat utilisation of target species is needed to regulate the fishery among the different countries sharing the same resources and exploitation methods used (Hocutt *et al.* 1994a), and to evaluate the possible benefits of reserves and sanctuaries. Migration and habitat studies can provide information on which fish are most vulnerable to exploitation and when. In the Zambezi River, fish migrations are probably linked closely to the annual flood cycle. Any changes to the flood regime caused by factors such as water abstraction, impoundment, canalisation and construction of roads on the floodplains may have a serious negative effect on the functioning of the floodplain system. Even an increase in the silt load as result of erosion or increase in nutrient load, affecting aquatic vegetation growth and thus water movement, may impact on the migrational patterns of fish. The Upper Zambezi is presently still relatively undisturbed by human impacts. For that reason alone, this system should be better studied to provide a baseline in case of future manipulations, as pointed out by Van der Waal (1996).

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