Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

Movement patterns and habitat selection of invasive African sharptooth catfish

W. T. Kadye & A. J. Booth

Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa

Keywords
acoustic telemetry; habitat utilization; ecological niche; invasion biology.

Correspondence
Wilbert T. Kadye, Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown 6140, South Africa.
Email: kadyew@yahoo.com

Editor: Jean-Nicolas Volff

Received 12 February 2012; revised 19 July 2012; accepted 23 July 2012

doi:10.1111/j.1469-7998.2012.00960.x

Abstract

Information on the movement behaviour and habitat use by non-native invasive African catfish *Clarias gariepinus* is crucial in understanding and possibly mitigating its potential impacts. The aim of this study was to examine catfish movement and habitat selection within an invaded impoundment in the Eastern Cape, South Africa. Acoustic telemetry data for 10 tagged catfish were analyzed to identify spatial patterns in home ranges and seasonal changes in habitat associations. Long-distance movements were observed for most catfish from common central release point, whereas short-distance movements defined their home ranges and utilization distributions that were categorized as localized within single or multiple habitats. Habitat selection was non-random with most catfish utilizing the shallow river mouth and upper section of the reservoir that were dominated by a rocky substratum interspersed with submerged trees. These localities were likely to be preferred for spawning and/or feeding. Utilization of these habitats by catfish is likely to be associated with probable impact due to predation and interference competition for feeding and breeding grounds with other species. Although most catfish maintained their home ranges throughout the study, seasonal shifts in habitat use, which was reflected by the utilization of deep and silt-dominated habitats, were also observed for some catfish. Non-random habitat use and homing behaviour within single and multiple habitats by non-native sharptooth catfish suggests that its impact within the invaded habitats may be associated with particular habitats both at broad spatial and temporal scales. Protection of habitats from catfish invasion should be considered as a management option to conserve native biota.

Introduction

Evaluating habitat use by fish is crucial in understanding those factors that influence their distribution and resource use. Habitat selection studies, in general, attempt to determine habitat use in relation to its availability (Manly *et al*., 2002; Hirzel *et al*., 2004; Austin, 2007), which in turn depends upon spatial and temporal resource availability (Mauritzen *et al*., 2003; Mosnier *et al*., 2003; Gillies *et al*., 2006). Habitat use by fish is known to vary with prey abundance (Giannico, 2000), habitat availability (Daugherty & Sutton, 2005), presence of predators and competitors (Brown & Moyle, 1991), and varying environmental conditions. Several studies have also shown non-proportional use of certain habitats in response to disproportionate availability of influential resources (Mysterud & Ims, 1998; Gillies *et al*., 2006; Hansen *et al*., 2009).

Within invaded freshwater habitats, information on habitat use is essential as non-native invaders have the potential to influence both resource availability and the distribution of native species (McIntosh, Todd & Townsend, 1994; Bosch *et al*., 2006; Kadye & Magadza, 2008). By understanding habitat selection and movement behaviour of non-native invasive species, potential impacts can be determined and management strategies developed in their mitigation (Carol, Zamora & García-Berthou, 2007; Lapointe, Thorson & Angermeier, 2010). Within the Eastern Cape, South Africa, African sharptooth catfish *Clarias gariepinus* (Burchell, 1822) has become established as an invasive species within many rivers and impoundments (de Moor & Bruton, 1988; Laurenson, Hocutt & Hecht, 1989; Potts, Hecht & Andrew, 2008). Sharptooth catfish occurs in a wide range of habitats and thrives in rivers, lakes and reservoirs of different sizes and trophic status within both its natural and invaded ranges (Teugels, 1986; Bruton, 1988; de Moor & Bruton, 1988). It is hardy species that tolerates water temperatures from 8 to 35°C, salinity of 0–10‰, wide pH ranges (Safriel & Bruton, 1984) and low oxygen concentrations partially due to its possession of an arborescent organ (Van der Waal, 1998). Although sharptooth catfish is considered to be primarily piscivorous (Groenewald, 1964; Willoughby & Tweddle, 1978), it is known to have a wide dietary spectrum (Bruton, 1979a; Teugels, 1986) that includes plant matter, plankton, macro-invertebrates, amphibians and reptiles (Munro, 1967; Bruton, 1979b; Winemiller & Kelso-Winemiller, 1996). Sharptooth catfish has a fast annual growth rate, reaching up to 200 mm standard length within a year and attains sexual maturity within 2 years (Bruton & Allanson, 1980; Skelton, 2001). It grows to a total length of about 1.4 m and mass exceeding 30 kg and has a longevity of at least 15 years (Bruton, 1976; Weyl & Booth, 2008; Booth, Traas & Weyl, 2010).

The biological attributes of sharptooth catfish related to its generalized feeding habits, fast growth, high mobility and ability to survive in a wide range of habitats raises concern over its occurrence as a non-native invasive species (de Moor & Bruton, 1988; Cambray, 2003) particularly due to its predation impact and potential to influence trophic interrelationships (Vitule, Freire & Simberloff, 2009; Kadye & Booth, 2012). In the Eastern Cape, there is concern over the invasion of sharptooth catfish as the region has a depauperate native biota that includes the endemic and endangered fish species such as *Pseudobarbus afer*, *P. asper* and *Sandelia bainsii* (Cambray, 2003). Studies indicate that this catfish is a highly mobile and aggressive predator within invaded habitats (Booth *et al*., 2010). Its movements and habitat use within its natural range have been reported to be driven primarily by its foraging behaviour and reproductive biology (Bowmaker, 1973; Bruton, 1978, 1979*c*; Merron, 1993). Foraging behaviours include solitary feeding, social and organized pack hunting in shallow areas and during spawning migrations (Bruton, 1979*c*; Merron, 1993). Its reproductive movements are often triggered by changes in the photoperiod, temperature and water flow. Sharptooth catfish breeds in summer after the rains, and a large number of sexually active individuals migrate into inundated shallow habitats in lentic habitats and headwaters of lotic habitats to spawn (Bowmaker, 1973; Bruton, 1979*c*; Hocutt, 1989). This species is also known to exhibit both long- and short-distance movements, depending on environmental conditions and food availability, with a varying degree of specialization to specific habitats (Willoughby & Tweddle, 1978; Hocutt, 1989).

While the movement and habitat use by sharptooth catfish have been studied in both lotic (Willoughby & Tweddle, 1978; Cambray, 1985) and lentic environments (Bruton, 1979*a*,*b*; Hocutt, 1989) within its natural range, no information is available for invaded habitats. This study examined the movement and habitat use of catfish using acoustic telemetry within an invaded impoundment in the Eastern Cape Province, South Africa. Telemetry is a convenient tool for assessing movement and habitat use and has been used to study different catfish species within both their natural (Hocutt, 1989; Daugherty & Sutton, 2005; Mitamura *et al*., 2008) and invaded ranges (Carol *et al*., 2007). The objectives of this study were to (1) determine the patterns in movement and habitat use and (2) examine any seasonal changes in habitat use by catfish within the reservoir. These objectives were tested under the null hypotheses that catfish distribution was random, and was not influenced by seasonal changes, especially in temperature, or physical structure such as depth and habitat complexity.

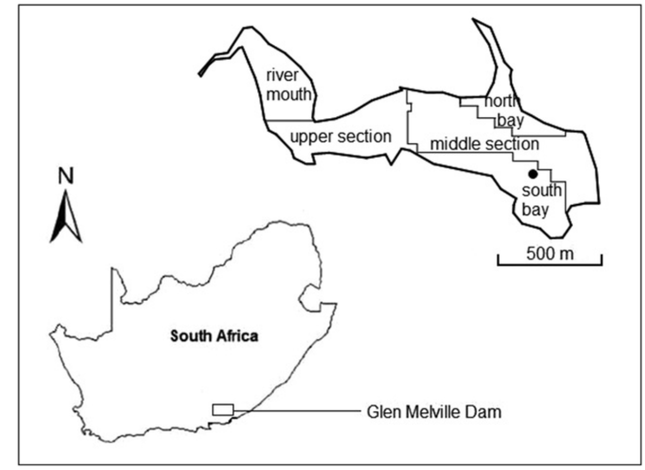

Figure 1 Map of the study area illustrating the main habitat types within the Glen Melville Reservoir, Eastern Cape, South Africa. Increasing intensity in the greyscale inset map indicates decreasing depth. The dot within the south bay represents the joint capture and release point for catfish.

Materials and methods

Study area

Glen Melville Reservoir (33°129 S; 26°409 E) (Fig. 1), constructed in 1992, covers an area of 76 ha and has a maximum depth of 25 m at maximum capacity. The reservoir is regulated by water transferred from the Great Fish River through an inter-basin water transfer scheme. This regulation involves filling of the dam biannually between February and March and between July and August through a water transfer tunnel. The substratum comprises of shale and mud with drowned trees mostly in the former river channel. Water surface temperature ranged from 27°C in February to 14°C in July. Water pH was alkaline and ranged between 8 and 9, and turbidity was relatively high, ranging between 129 and 257 Nephelometric Turbidity Units during the study period. Sharptooth catfish was first introduced into the reservoir through the water transfer tunnel in 1992 and is restricted to the reservoir because there are no other inflowing rivers. Water only exits from the reservoir over the retaining wall during flooding, which did not occur during the study. Other fish species occurring within the reservoir include longfinned eel *Anguilla mossambica*, moggel *Labeo umbratus*, smallmouth yellowfish *Labeobarbus aeneus*, mudfish *Labeo capensis*, common carp *Cyprinus carpio* and mosquitofish *Gambusia affinis*.

Pilot experiment

A pilot experiment was conducted to determine short-term tag loss or expulsion. This was necessary as clariids have been shown to exhibit expulsion of surgical implants (Baras & Westerloppe, 1999). Short-term tag expulsion in catfishes has been observed to usually occur within 12 days of tagging either through the incision or trans-intestinally by formation of a capsule around the implant that adheres to the intestine that is resorbed and then expelled (Baras & Westerloppe, 1999). Three catfish were surgically equipped with dummy tags following methods described by Jepsen *et al.* (2002). The dummy tags were 13 mm in diameter, weighed 5.6 g in water and were identical in size and mass to the acoustic tags. Fish were placed in an anaesthetic bath with clove oil for approximately 2 min until opercula movement was slow. The fish measured 81.9 cm, 65.1 cm and 56.7 cm in total length and weighed 3320 g, 1660 g and 860 g, respectively. Each fish was placed on a V-shaped surgical table and a dummy tag was implanted into the peritoneal cavity through a mid-ventral incision that was positioned posterior to the pelvic girdle. The incision was closed by three separate non-absorbable sutures. The duration of the operation was 2 min. After the operation, fish were placed in a recovery bath with aerated clean water. Recovery time was 5 min. Each catfish was maintained in captivity in a separate concrete tank together with two untagged similar-sized catfish. Fish were fed daily on fish and pellet diet and monitored weekly for 2 months from December 2010 to February 2011. The incisions were observed to heal within 7 to 14 days with the sutures being shed. There was neither evidence of short-term tag expulsion nor signs of deleterious effects of the tags on catfish behaviour or feeding during the pilot experiment.

Habitat classification

Global Positioning System (GPS; Garmin eTrex, Garmin Corporation, Taipei, Taiwan) coordinates outlining the perimeter of the Glen Melville Reservoir and habitat classifications were conducted in February 2011 when the dam was at full capacity. The GPS coordinates of the reservoir map were then transformed into vector coordinates that outlined the surface area of the reservoir as a gridded raster map of 20 × 20 m pixels. Five areas were then identified from the raster map to differentiate and represent spatial heterogeneity. These areas were categorized as river mouth, upper section, middle section, south bay and north bay (Fig. 1). Within each area, depth and substrate composition were sampled at 30 random localities on three transects that were set along the main axis of each area. Sampling was conducted from the boat with an electric motor at irregular intervals on 10 localities along each of the three transects that were set along the main axis within each area. At each locality, depth was measured using a line with depth markings attached to a lead weight. Substrate composition was determined from the lead weight and categorized as either silt (soft bottom) or rock (hard bottom), and the presence of trees (submerged woody debris or drowned trees) noted. Each area was therefore classified based on average depth and the proportions of silt, rock and trees that were determined from the total number of points measured (Table 1). An additional variable, the distance from the joint capture and release point was included in the analyses to investigate possible changes in movement subsequent to each fish's displacement. This was determined based on the Euclidean distance between the capture/release site and each point on the spatial pixel data frame. The reservoir's water level was relatively constant during the study. After being refilled to capacity April 2011, the drawn-down was approximately 1.5 m.

Table 1 Depth and habitat criteria expressed as percentages (%) assessed within each of the sampled spatial areas within Glen Melville Reservoir, Eastern Cape, South Africa

	Depth range (m)	Mean depth (m)	Rock	Silt	Trees
River mouth	0–3	1.6 ± 1.1	60	40	50
Upper section	3–10	6.6 ± 2.3	15	20	85
Middle section	15–25	19.6 ± 3.4	0	100	0
North bay	0–15	8.5 ± 4.2	10	90	15
South bay	0–8	4.9 ± 2.2	27	73	80

Tagging of fish

Prior to fish tagging and tracking in the reservoir, range tests were conducted to determine the minimum detection distance for the acoustic transmitters. This was conducted by detecting three transmitters that were randomly placed within each of the five spatial areas of the reservoir. Within each area, the transmitters were deployed at different depths (i.e. 1 m below the surface, intermediate, and 1 m above the bottom). The minimum detectable distance ranged from about 4 m near the surface to about 8 m near the bottom in the deeper sections of the reservoir.

Ten catfish were captured using a surface set long line that was constructed of polyethylene rope and 1-m nylon snoods with circle hooks. The long line was approximately 100 m in length and had 35 hooks that were baited with chicken livers. The long line was patrolled from the boat and captured fish were noticeable by the movement of long-line floats. All fish were hooked in the corner of the mouth. Captured fish were quickly removed from the hooks, transferred to a water bath and transported to a tagging station on land. The fish were identified as fish 1 to fish 10, and were measured (mean = 76.9 ± 23.2, range = 38.7–100.1 cm total length) and weighed (mean = 3562 ± 2213, range = 520–6320 g; Table 2). Each fish was anesthetized in clove oil and surgically implanted with Low-Power (LP) – 13 acoustic tags (Thelma Biotel, Trondheim, Norway) using the dummy tag surgical procedure. The acoustic tags were 13 mm in diameter, weighed 5.6 g (in water), giving tag-to-body mass ratios <1.08%. The tags had a pulse interval of 1000 ms and a delay rate of 5–15 s. Each tag had a guaranteed life span of 4.2 months and an estimated life span of 6.5 months. The tags transmitted at a frequency of 69 kHz. All captured fish were tagged and, after recovery, released at the capture point on the same day. Since sharptooth catfish reaches sexual maturity from 20–53 cm (Bruton, 1976, 1979*c*; Richardson, Booth & Weyl, 2009; Booth, unpubl. data), the tagged catfish were considered to be mature.

Tracking of fish

Manual tracking of the tagged fish commenced 6 days after tagging. Tracking was conducted during both summer and

Table 2 The number of tagged sharptooth catfish *Clarias gariepinus*, their length and weight, and the number of tracking times and relocations recorded during each tracking day

		Fish 1	Fish 2	Fish 3	Fish 4	Fish 5	Fish 6	Fish 7	Fish 8	Fish 9	Fish 10	Tracking times
Length (cm)		84.0	38.7	40.6	58.0	82.0	95.8	100.1	100.0	91.8	78.0	
Weight (g)		3620	520	680	1230	3380	5520	6320	5960	5430	2960	
Tracking date	26/02/2011	2		1	2	3	4	3	3	4	3	4
	27/02/2011	1	2	2	1	3	1	3	3	2	1	4
	12/03/2011		1	1	3	2	3	4	2	3	3	4
	19/03/2011	1	3	3	2	4	2	3	4	2	2	4
	20/03/2011		2	2	1	2	3	3	2	2	3	3
	29/03/2011	1	3	2	3	3	2	1	2	2		3
	16/04/2011	2	2	2	1	2	3	2	3	3	3	3
	30/04/2011		3	4	3	2	3	4	2	2	1	4
	07/05/2011	3	2	3			2		3	4	2	4
	08/05/2011		1	2	2	1	2	1	2		2	3
	21/05/2011	1	4	2	3	3	3	2	3	2	3	4
	10/06/2011	2				2	3	1	2	2	1	3
	25/06/2011		2	1	1		2		2		1	3
	16/07/2011			2			1		3	1		3
Total relocations		13	25	27	22	27	34	27	36	29	25	

winter using a VEMCO VR60 receiver with a directional hydrophone (VEMCO, Halifax, Nova Scotia, Canada) from February 2011 to July 2011. Catfish were tracked from 05:00 to 19:00 h, and there were between three and four tracking sessions daily. During each tracking session, fish positions were sequentially monitored from the dam wall to the river mouth. When an individual fish was located, the exact position of the fish was located by moving the boat, with a quiet electric motor, slowly towards the direction of the signal to avoid frightening the fish while decreasing the sensitivity of the receiver and determining the location of the greatest signal strength. Each fish's location was recorded using a portable GPS. Each tracking session lasted approximately 2 h and the exercise was repeated after every 3 h to record new relocations and to determine whether the fish displayed any mortality or tag loss signal. Mortality or tag loss signals were considered to be consecutive repeated measurements of a transmitter within 10 m of previously recordings. Temperature was measured using a HANNA HI 98129 Combo meter (HANNA Instruments Inc., Woonsocket, RI, USA) during each sampling occasion.

Data analysis

GPS coordinates for catfish relocations were transformed into Universal Transverse Mercator units. Home range size for individual catfish was determined using minimum convex polygons (MCP) from 50 to 95% of the relocations by calculating the smallest convex polygon that encompasses all relocations (Mohr, 1947). Home range sizes were compared for the summer (temperature > 20°C) and winter (temperature < 20°C) periods. Kernel estimation of the utilization distribution (KUD; VanWinkle, 1975; Worton, 1989) was used to describe the probability density of the relocations. The smoothing parameter (h) for KUD was estimated using least squares cross-validation. Ecological niche factor analysis (ENFA, Hirzel *et al*., 2002) was used to investigate the patterns in habitat selection. ENFA searches for gradients in ecological space that maximizes the differences between the utilized and available habitats or resources (Basille *et al*., 2008). ENFA is based on the concept of marginality and specialization. Marginality measures the magnitude of deviation between the niche (used space) and available space, and specialization measures the narrowness of the niche based on the highest variance of the ratio between available and utilized habitat (Calenge, 2006; Basille *et al*., 2008). A Monte Carlo randomization procedure with 1000 permutations was used to test the significance of marginality and specialization. Compositional analysis (Aebischer, Robertson & Kenward, 1993) was used to test for habitat preference. This was followed by application of Manly *et al*.'s (2002) index, $w_j = \frac{u_j}{a_j}$ to test the selection ratios of the different habitat categories, where u_j is the proportion of use of the habitat category j and a_j is the proportion of availability of this habitat category j. The selection ratios for all habitats were normalized to $B_j = \frac{w_j}{\sum_j w_j}$ (Manly *et al*., 2002). A chi-square test was performed for the Manly's selection ratios to test the null hypothesis of random selection of habitat categories. Comparison between summer and winter habitat selection was conducted using a principal component analysis-based Outlying Mean Index (OMI, Doledec, Chessel & Gimaret Carpentier, 2000) analysis. OMI compares the mean habitat conditions that are used by individuals to the mean habitat conditions of the sampled area. Environmental variables, in proportions, were arcsine transformed prior to ENFA and OMI analyses. All the analysis were conducted within *R* (R

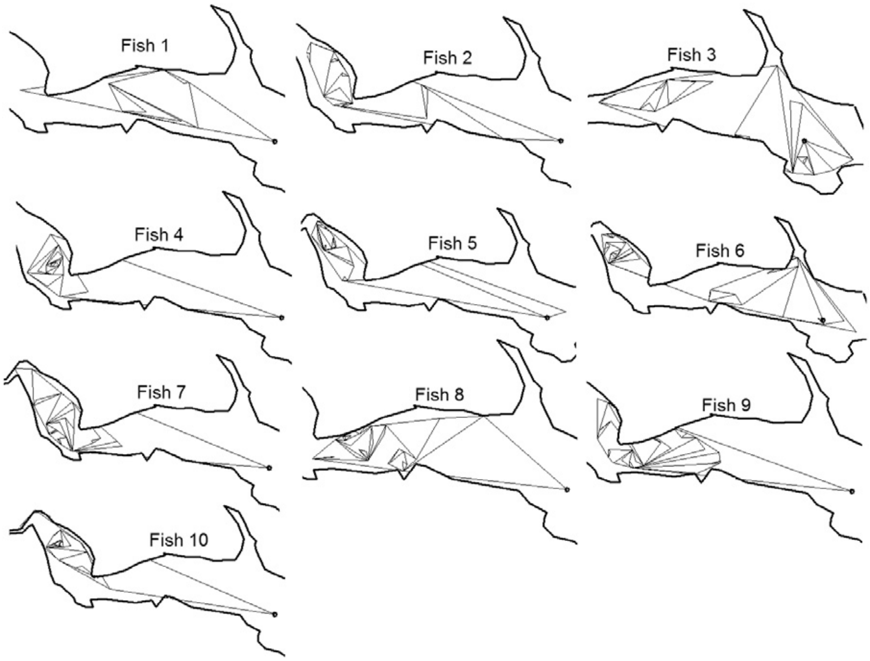

Figure 2 Spatial polygons for individual sharptooth catfish *Clarias gariepinus* relocations within Glen Melville Reservoir, Eastern Cape, South Africa. The dot represents the joint capture and release point for catfish.

Development Core Team, 2012) using the libraries *adehabitatHR* and *adehabitatHS* (Calenge, 2006).

Results

Movement and habitat selection

All tagged catfish were located 265 times during the sampling period. Catfish relocations were characterized by both long- and short-distance movements with most of these relocations being observed further from the common capture and release point (Fig. 2). While the long-distance movements were related to those relocations furthest from the capture and release point, the short-distance relocations were either localized within single localities (fish 4, 5 and 10), widespread within single localities (fish 1, 7, 8 and 9) or localized within multiple localities (fish 2, 3 and 6; Fig. 2). Similarly, the core and extent of individual catfish home ranges were both within single (fish 1, 4, 5, 7, 8 and 10) and multiple (fish 2, 3, 6 and 9) localities (Fig. 3). Tagged catfish exhibited pronounced habitat selection (ENFA axes Monte Carlo randomization test, $P < 0.01$). The optimal space utilized by the catfish was different from that which was available as the centroid of the available habitat differed from that of the utilized ecological niche (Fig. 4). The first two axes of ENFA explained approximately 76% of marginality (48%) and specialization (28%) for the overall catfish niche structure. Substratum types – silt and rock contributed most to the marginality axis, followed by depth (Fig. 4). Similarly, silt, depth and rock contributed most to the specialization axis. Catfish selected habitats that were shallow with a high proportion of rocks and a low proportion of silt that was common in deep habitats. Comparison of habitat preference among the different spatial areas provided evidence of non-random habitat use (compositional analysis $\lambda = 0.16$, $P = 0.01$). Catfish's selection of the different spatial localities was highly dependent ($\chi^2_4 = 211.9$, $P < 0.01$) with the river mouth being the most utilized ($B_j = 0.50$) followed by the upper section ($B_j = 0.33$) of the reservoir, whereas the middle section, north and south bays were the least preferred ($B_j < 0.10$; Table 3).

Temporal patterns in habitat selection

Catfish home range sizes for 95% relocations ranged from 2 (fish 1) to 70 ha (fish 3; Fig. 5). The proportion of home range size for 50–95% relocations was larger during summer compared to those observed during winter. An exception was for three fish (fish 1, 3 and 6) that had large home ranges during winter (Fig. 5). During summer, the first two axes of OMI analysis for habitat selection accounted for 91% and 8%, respectively, for the marginality within the data (Table 4). Six catfish (fish 2, 4, 5, 6, 7 and 10) were associated with the negative values of the first axis based on the samples and species plots that depicted the projection of the resource units (samples) and that of the distribution of utilization weights of individual fish (Fig. 6). Based on the variables plot, the first axis was strongly negatively correlated with the habitat variable – rock (Table 4). Two catfish (fish 8 and fish 9) were strongly associated with the negative values of the second axis on the samples and species plot (Fig. 6), which corresponded to the variable trees (Table 4). Two other catfish (fish 1 and fish 3) were characterized by weak association with either axes. During winter, the first and second axes explained 88 and 10%, respectively, for the marginality in OMI analysis (Table 4).

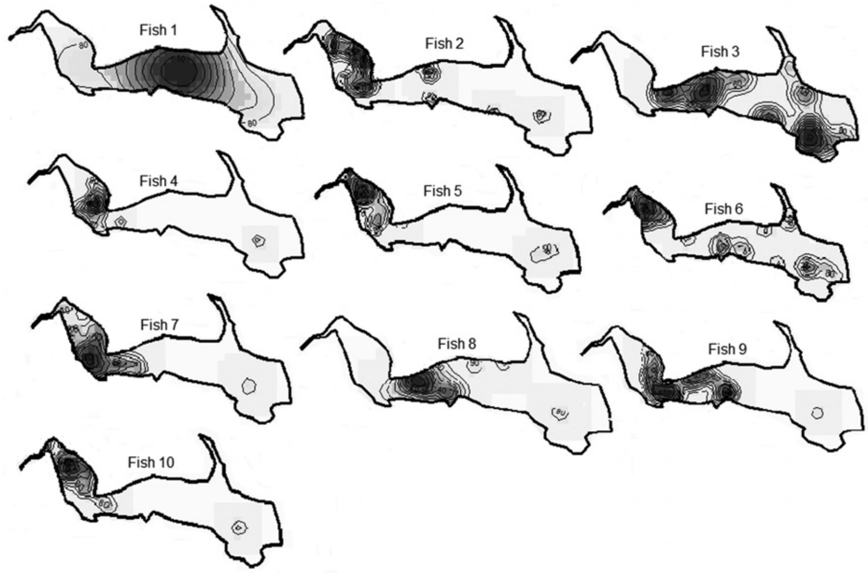

Figure 3 Kernel utilization distribution densities, depicted as raster maps, for individual sharptooth catfish *Clarias gariepinus* within Glen Melville Reservoir, Eastern Cape, South Africa. Contours illustrate home range size at different probability levels.

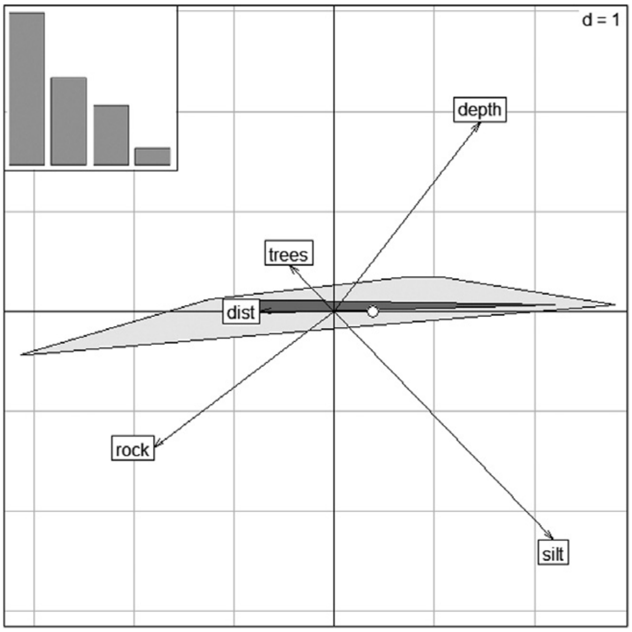

Figure 4 Ecological niche factor analysis (ENFA) for sharptooth catfish *Clarias gariepinus* habitat use within Glen Melville Reservoir, Eastern Cape, South Africa. The plot indicates factorial maps with the dark grey polygon showing the minimum convex polygon (MCP) of used resource units (RUs), whereas the light grey area depicts the projection MCP of the available sites RUs. The abscissa displays the marginality axis of ENFA, whereas the ordinate displays the first specialization axis of ENFA. The white dot along the abscissa corresponds to the centroid of the used habitat. The inserted bar plot shows the overall contribution of each axis to the specialization.

Table 3 Proportion of used and available habitats and the selection ratios based on Manly's index for tagged sharptooth catfish *Clarias gariepinus* in Glen Melville Dam, Eastern Cape, South Africa

Habitat type	Used	Available	w_j	SE (w_j)	P (w_j)	B_j
River mouth	0.44	0.18	2.52	0.18	0.00	0.50
Upper section	0.39	0.24	1.65	0.13	0.00	0.33
South bay	0.10	0.21	0.46	0.09	0.00	0.09
North bay	0.02	0.12	0.19	0.08	0.00	0.04
Middle section	0.05	0.26	0.19	0.05	0.00	0.04

Most catfish were associated with negative values of the first OMI axis with the utilization weights of four catfish (fish 2, 4, 5 and 10) corresponding to habitat variable rock that was typical of the river mouth, whereas the variables – trees and distance corresponded to the utilization weights of three catfish (fish 2, 8 and 9) indicating the utilization of the upper section of the reservoir (Fig. 6). Three catfish (fish 1, 3 and 6) appeared to be associated with increasing depth and high proportion of silt that was typical of the middle and less structured habitat.

Discussion

Habitat use and movements by sharptooth catfish have been investigated in a wide range of environments within its natural range, with studies indicating that its daily and seasonal activities were strongly influenced by foraging and reproductive behaviours (Bruton, 1978, 1979*a*; Willoughby & Tweddle, 1978; Merron, 1993). Telemetry studies have revealed both territorial behaviours related to feeding and long-distance migrations related to spawning runs (Hocutt, 1989). Similarly, during this study, non-native sharptooth catfish exhibited both long- and short-distance movement patterns that defined their home ranges. The homing behaviour of catfish provided

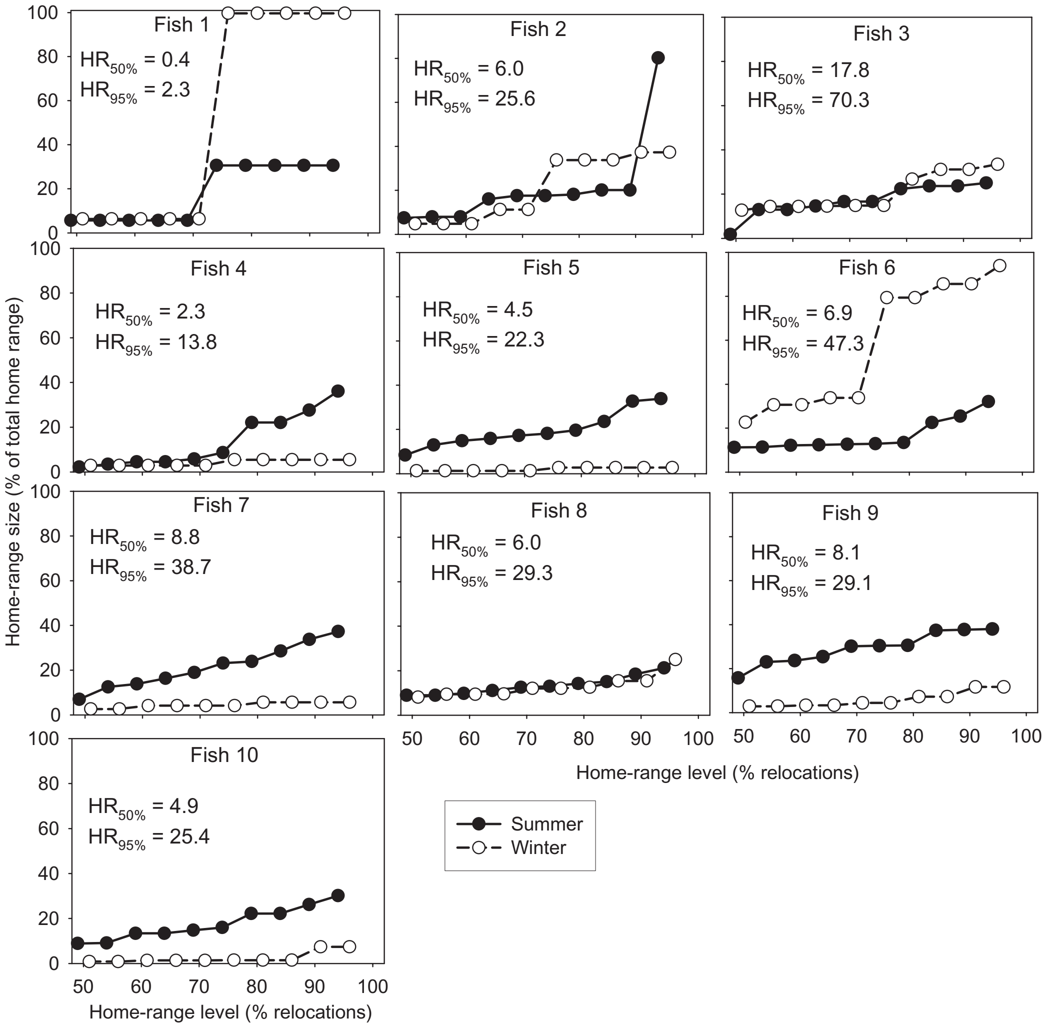

Figure 5 Total home range size (hectares) for 50 and 95% relocations of individual sharptooth catfish *Clarias gariepinus* and the percentage of these relocations during both the summer and winter sampling periods within Glen Melville Reservoir, Eastern Cape, South Africa.

Table 4 Outlying Mean Index eigenvectors and eigenvalues for first and second principal components for the habitat variables selected by sharptooth catfish *Clarias gariepinus* within Glen Melville Dam, Eastern Cape, South Africa

	Summer		Winter	
	PC1	PC2	PC1	PC2
Depth	0.48	0.08	0.47	–0.05
Rock	–0.55	0.49	–0.44	0.62
Trees	–0.34	–0.85	–0.46	–0.65
Silt	0.49	–0.16	0.43	–0.31
Distance	–0.33	–0.05	–0.43	–0.32
Eigenvalues	4.3	0.4	2.6	0.3
% variation	91.2	7.3	88.4	10.1

evidence of habitat selection and non-random habitat associations among the different spatial areas of the reservoir. In particular, most catfish utilized the river mouth and the upper section, suggesting the importance of structured habitats. Shallow and structured lentic habitats have been observed to be ideal for both catfish feeding and spawning (Bruton, 1979*b*,*c*). Previous studies have also reported that although sharptooth catfish is ubiquitous in many ecosystems, it exhibits its non-random habitat utilization in relation to its feeding behaviour (Bruton, 1979*a*; Hocutt, 1989). While most catfish maintained their home ranges throughout the study, some catfish had multiple home ranges that suggested seasonal shift in habitat utilization. This was particularly reflected by the utilization of the tree-dominated upper section, and deep and silt-dominated habitat by some catfish during winter compared to their summer habitat associations.

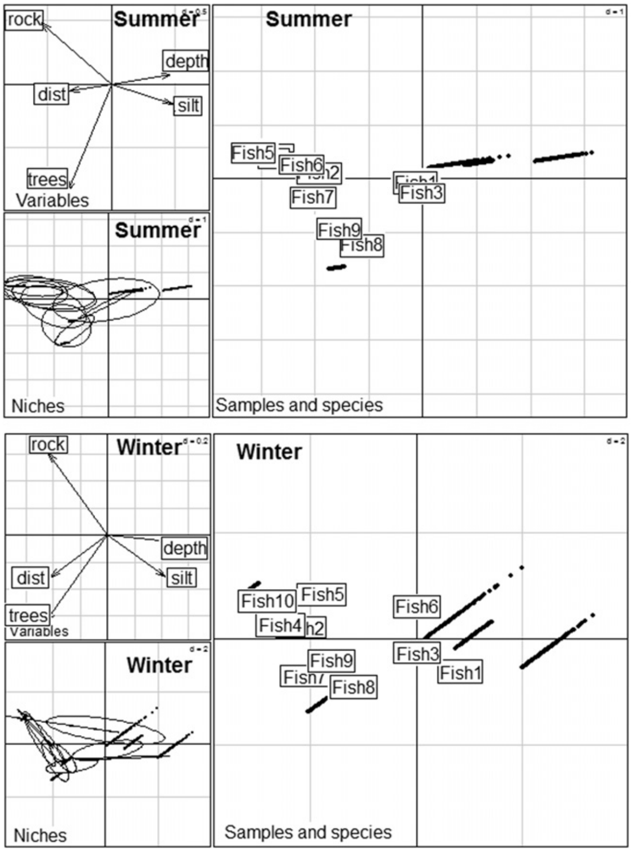

Figure 6 Outlying Mean Index (OMI) analysis indicating patterns in sharptooth catfish *Clarias gariepinus* habitat selection during both the summer (temperature > 20°C) and winter (temperature < 20°C) sampling periods within Glen Melville Reservoir, Eastern Cape, South Africa. The main graphs (samples and species) show the projection of the RUs and the position of the mean of the distribution of utilization weights for each fish. The variables plots (variables) present the scores of the variables on the axes of the analysis and the niche plots (niches) indicates the spatial distribution of utilization range for each fish.

The observed catfish patterns during this study were comparable to those reported within its natural range. For example, Hocutt (1989) described three types of movements in radio-tagged catfish: long-distance movements exceeding 200 m, moderate movements within 40–200 m and local movements not exceeding 40 m within Lake Ngezi, Zimbabwe. Long-distance movements in catfish usually coincide with seasonal activity peaks, such as increasing temperature or flood peaks that induce potamodrometic spawning migrations into either headwaters of rivers (Bowmaker, 1973; Cambray, 1985) or into shallow and inundated marginal habitats in lakes (Bruton, 1979*c*; Hocutt, 1989). During this study, catfish were tagged when the dam was at its maximum capacity. Most catfish exhibited long-distance movement immediately after release and were recorded in the river mouth section and the south bay. Since these movements appeared to be directional for most catfish (i.e. from release point to river mouth) these patterns suggests movement associated with spawning behaviour. Within the reservoir, it is likely that the river mouth section that was shallow and structured would be the most probable spawning habitat for the breeding population of catfish. Catfish is, nonetheless, also known to show localized movements in shallow and marginal habitats for feeding (Bruton, 1979*a*).

In comparison to long-distance movements, short-distance movements defined the home range size and utilization distribution densities for catfish during this study. The short-distance patterns showed that the movements varied from localized relocations on both small and broad spatial scales within single habitats, to localized movements within multiple habitats, which suggest feeding behaviour movements. Hocutt (1989) indicated that local movements were the dominating mode of behaviour in sharptooth catfish, while Bruton (1979*a*) suggested that this catfish engaged in concentrated and intensive searching for prey within a defined area especially where it encounters preferred food sources within lentic habitats. Similar patterns have been inferred for the homing behaviour of the catfish within lotic habitats, such as in the lower Shire River, Malawi (Willoughby & Tweddle, 1978). Telemetry studies have also shown localized home ranges and territoriality in other catfish species, such as the flathead catfish *Pylodictis olivaris* in the St Josephs River, Michigan, USA (Daugherty & Sutton, 2005), and the non-native wels catfish *Silurus glanis* in the Flix Reservoir, Ebro River, Spain (Carol *et al*., 2007). Localized movements in catfishes have been related to high use of particular habitats where fish would typically exhibit multiple displacements within a small but structured habitat (Daugherty & Sutton, 2005). Habitat use and site fidelity within such defined areas typically follows a diurnal pattern that involves high activity associated with intensive search for prey and low activity in areas of refuge when the catfish are less active (Bruton, 1996; Carol *et al*., 2007). Movement studies on sharptooth catfish, nonetheless, indicate both diurnal and nocturnal peaks in response to feeding and risk avoidance behaviours, with its predation impact being high in deep habitats during the day and in shallow areas during the night (Bruton, 1979*b*; Hocutt, 1989; Merron, 1993). During this study, territorial behaviour appeared to be common for most catfish as they maintained their home ranges by exhibiting localized movements either within single or multiple localities. By utilizing defined areas within the invaded habitats, this study suggests that catfish impact may be associated with particular habitats, especially those that are likely to be preferred by its potential prey such as the river mouth. The upper section and river mouth localities were probably the most suitable for refuge and feeding for both the non-native catfish and native species such as moggel *Labeo umbratus*. Utilization of these upstream habitats by catfish suggests a probable impact related to predation and interference competition for feeding and breeding space. Feeding studies indicate that catfish diets are dominated by fish including moggel within the reservoir (Kadye & Booth, 2012).

Comparison of habitat utilization on a temporal scale showed that during summer, most catfish were associated with the river mouth that had rock substrate, while few other catfish were in the upper section. This suggests that shallower habitats were most important for catfish during summer compared to deeper habitats and corroborates Bruton's (1979*c*) assessment of catfish movement. Bruton (1979*c*) observed that during summer, catfish preferred shallow inshore littoral habitats both for breeding and feeding. Within these shallow habitats, individuals would display different foraging strategies such as social hunting and surface feeding on floating debris, terrestrial insects, plankton and crustaceans, and organized pack hunting for their preferred fish prey (Bruton, 1979*c*; Merron, 1993). Bruton (1979*b*) also noted diel incursions into the littoral habitats, and concluded that catfish was an efficient nocturnal feeder that is assisted by well-developed non-visual sensors and organs particularly in clear-water habitats. In contrast, Hocutt (1989) reported both diurnal and nocturnal activity in movements, and further suggested that the former was predominant. These studies, nonetheless, suggest that sharptooth catfish's movements and habitat use are likely to vary in response to environmental conditions and may be influenced by seasonality. Although some individual fish maintained their home ranges throughout the study, there were few other individuals that showed localized movements in multiple habitats, which suggest a seasonal shift in home ranges. Seasonal changes in home ranges for catfishes are commonly related to changes in temperature as fish often utilize deeper and warmer habitats during winter (Weller & Winter, 2001). During winter, three catfish were noted to utilize the middle and deep habitats while one catfish was observed to have shifted from the river mouth towards the middle section of the reservoir, suggesting either the influence of seasonality, especially temperature, or changing habitat conditions and food availability for some individuals. Catfish's adaptability and shift in habitat use is primarily related to its alternative life-history style in response to changing internal and external environmental conditions (Bruton, 1996). This suggests that while the risk catfish predation and competition for space may be associated with particular habitats within its invaded range, its impact may be observed both on broader spatial and temporal scales through multiple or seasonal shifts in habitat use.

To conclude, the results of this study provide an assessment of the probable risk associated with invasive catfish. Invasibility of freshwater ecosystems is usually related to the use of critical habitats that provide refuge and food for native species (Lapointe *et al*., 2010). The potential impact in such habitats would be related to competition for both space and resources between the invaders and native species, and the predation risk associated with predatory invaders. Within Glen Melville Reservoir, such risks could be inferred from the utilization of specific habitats, especially the river mouth, by catfish. The river mouth habitat would probably be the ideal habitat for feeding and spawning for native species such as moggel. The movement pattern and use of river mouth habitats of the reservoir could also infer widespread impact of catfish within the invaded mainstream sections and the potential to migrate into the headwater streams that are occupied with native minnows. Management effort should therefore focus on preventing catfish invasions, and, where possible, eradication.

Acknowledgements

We thank the National Research Foundation (NRF) of South Africa and the Rufford Small Grants Foundation who funded this study. The Eastern Cape's Department of Economic Development and Environmental Affairs, through permit number CRO16/10CR and the Rhodes University Ethics committee, through research proposal 2010Q2-1, granted permission for this study. We thank Paul Cowley (SAIAB) who provided a VEMCO receiver and hydrophone for tracking. Olaf Weyl, Amber Childs, Rhett Bennett and Carl Huchzermeyer all gave insightful advice during planning of this study. Warren Bouwer, Stanley Tsarwe, Albert Chakona, Amos Chinomona, Thethela Bokhutlo and Steven Fuchs assisted with field sampling and their help is greatly appreciated. We also thank two anonymous reviewers for their invaluable comments that improved an earlier version of this paper.

References

Aebischer, N., Robertson, P. & Kenward, R. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.

Austin, M. (2007). Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* **200**, 1–19.

Baras, E. & Westerloppe, L. (1999). Transintestinal expulsion of surgically implanted tags by African catfish *Heterobranchus longifilis* of variable size and age. *Trans. Am. Fish. Soc.* **128**, 737–746.

Basille, M., Calenge, C., Marboutin, E., Andersen, R. & Gaillard, J.M. (2008). Assessing habitat selection using multivariate statistics: some refinements of the ecological-niche factor analysis. *Ecol. Model.* **211**, 233–240.

Booth, A.J., Traas, G.R.L. & Weyl, O.L.F. (2010). Adult African sharptooth catfish, *Clarias gariepinus*, population dynamics in a small invaded warm-temperate impoundment. *Afr. Zool.* **45**, 299–308.

Bosch, J., Rincon, P.A., Boyero, L. & Martinez-Salamo, I. (2006). Effects of introduced salmonids on a montane population of Iberian frogs. *Conserv. Biol.* **20**, 180–189.

Bowmaker, A.P. (1973). Potamodromesis in the Mwenda River, Lake Kariba. *Geophys. Monogr.* **17**, 159–164.

Brown, L.R. & Moyle, P.B. (1991). Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Can. J. Fish. Aquat. Sci.* **48**, 849–856.

Bruton, M.N. (1976). On the size reached by *Clarias gariepinus*. *J. Limnol. Soc. S. Afr.* **2**, 57–58.

Bruton, M.N. (1978). The habitats and habitat preferences of *Clarias gariepinus* (Pisces: Clariidae) in a clear coastal lake (Lake Sibaya, South Africa). *J. Limnol. Soc. S. Afr.* **4**, 81–88.

Bruton, M.N. (1979a). The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids. *Trans. Zool. Soc. Lond.* **35**, 47–114.

Bruton, M.N. (1979b). The role of diel inshore movements by *Clarias gariepinus* (Pisces, Clariidae) for the capture of fish prey. *Trans. Zool. Soc. Lond.* **35**, 115–138.

Bruton, M.N. (1979c). The breeding biology and early development of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias* (*Clarias*). *Trans. Zool. Soc. Lond.* **35**, 1–45.

Bruton, M.N. (1988). Systematics and biology of clariid catfish. In *The culture of sharptooth catfish Clarias gariepinus in southern Africa*: 1–10. Hecht, T., Uys, W. & Britz, P.J. (Eds). Pretoria: CSIR. South African National Scientific Program Report No 153.

Bruton, M.N. (1996). Alternative life-history strategies of catfishes. *Aquat. Living Resour.* **9**, 35–41.

Bruton, M.N. & Allanson, B.R. (1980). Growth of *Clarias gariepinus* in Lake Sibaya, South Africa. *S. Afr. J. Zool.* **15**, 7–15.

Calenge, C. (2006). The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516–519.

Cambray, J.A. (1985). Observations on spawning of *Labeo capensis* and *Clarias gariepinus* in the regulated lower Orange River, South Africa. *S. Afr. J. Sci.* **81**, 18–321.

Cambray, J.A. (2003). The need for research and monitoring on the impacts of translocated sharptooth catfish, *Clarias gariepinus*, in South Africa. *Afr. J. Aquat. Sci.* **28**, 191–195.

Carol, J., Zamora, L. & García-Berthou, E. (2007). Preliminary telemetry data on the movement patterns and habitat use of European catfish (*Silurus glanis*) in a reservoir of the River Ebro, Spain. *Ecol. Freshw. Fish* **16**, 450–456.

Daugherty, D.J. & Sutton, T.M. (2005). Seasonal movement patterns, habitat use, and home range of flathead catfish in the lower St. Joseph River, Michigan. *N. Am. J. Fish. Manage.* **25**, 256–269.

Doledec, S., Chessel, D. & Gimaret Carpentier, C. (2000). Niche separation in community analysis: a new method. *Ecology* **81**, 2914–2927.

Giannico, G.R. (2000). Habitat selection by juvenile coho salmon in response to food and woody debris manipulations in suburban and rural stream sections. *Can. J. Fish. Aquat. Sci.* **57**, 1804–1813.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E. & Jerde, C.L. (2006). Application of random effects to the study of resource selection by animals. *J. Anim. Ecol.* **75**, 887–898.

Groenewald, A.A.V.J. (1964). Observations on the food habits of *Clarias gariepinus* Burchell, the South African freshwater barbel (Pisces: Clariidae) in Transvaal. *Hydrobiologia* **23**, 287–291.

Hansen, B.B., Herfindal, I., Aanes, R., Saether, B.E. & Henriksen, S. (2009). Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos* **118**, 859–872.

Hirzel, A.H., Hausser, J., Chessel, D. & Perrin, N. (2002). Ecological-Niche Factor Analysis: how to compute habitat-suitability maps without absence data? *Ecology* **83**, 2027–2036.

Hirzel, A.H., Posse, B., Oggier, P.A., Crettenand, Y., Glenz, C. & Arlettaz, R. (2004). Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. *J. Appl. Ecol.* **41**, 1103–1116.

Hocutt, C.H. (1989). Seasonal and diel behaviour of radiotagged *Clarias gariepinus* in Lake Ngezi, Zimbabwe (Pisces: Clariidae). *J. Zool.* **219**, 181–199.

Jepsen, N., Koed, A., Thorstad, E.B. & Baras, E. (2002). Surgical implantation of telemetry transmitters in fish: how much have we learned? *Hydrobiologia* **483**, 239–248.

Kadye, W.T. & Booth, A.J. (2012). Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharptooth catfish *Clarias gariepinus*. *Biol. Invasions* **14**, 779–795.

Kadye, W.T. & Magadza, C.H.D. (2008). Trout induces a shift from preferred habitat types for indigenous species: the example of the indigenous catfish, *Amphilius uranoscopus* (Pfeffer, 1889), on an African montane plateau. *Hydrobiologia* **614**, 329–337.

Lapointe, N.W.R., Thorson, J.T. & Angermeier, P.L. (2010). Seasonal meso- and microhabitat selection by the northern snakehead (*Channa argus*) in the Potomac river system. *Ecol. Freshw. Fish* **19**, 566–577.

Laurenson, L.B.J., Hocutt, C.H. & Hecht, T. (1989). An evaluation of the success of invasive fish species of the Great Fish River. *J. Appl. Ichthyol.* **5**, 28–34.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002). *Resource selection by animals. Statistical design and analysis for field studies*. 2nd edn. Dordrecht, The Netherlands: Kluwer Academic.

Mauritzen, M., Belikov, S.E., Boltunov, A.N., Derocher, A.E., Hansen, E., Ims, R.A., Wiig, Ø. & Yoccoz, N. (2003). Functional responses in polar bear habitat selection. *Oikos* **100**, 112–124.

McIntosh, A.R., Todd, A.C. & Townsend, C.R. (1994). Size related impacts of introduced brown trout on the distribution of native common galaxies. *N. Z. J. Mar. Freshw. Res.* **28**, 135–144.

Merron, G.S. (1993). Pack-hunting in two species of catfish, *Clarias gariepinus* and *C. ngamensis*, in the Okavango Delta, Botswana. *J. Fish Biol.* **43**, 575–584.

Mitamura, H., Mitsunaga, T., Arai, N. & Viputhanumas, T. (2008). Movements of immature hatchery-reared Mekong giant catfish *Pangasianodon gigas* released in the Mekong River, measured using acoustic telemetry. *Fish. Sci.* **74**, 1034–1039.

Mohr, C. (1947). Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**, 223–249.

de Moor, I. & Bruton, M.N. (1988). *Atlas of alien and translocated indigenous aquatic animals in southern Africa*. South African National Scientific Program Report No 144, CSIR, Pretoria, South Africa. 414–423.

Mosnier, A., Ouellet, J.-P., Sirois, L. & Fournier, N. (2003). Habitat selection and home-range dynamics of the Gaspe caribou: a hierarchical analysis. *Can. J. Zool.* **81**, 1174–1184.

Munro, J.L. (1967). The food of a community of East African freshwater fishes. *J. Zool.* **151**, 389–415.

Mysterud, A. & Ims, R. (1998). Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* **79**, 1435–1441.

Potts, W.M., Hecht, T. & Andrew, T.G. (2008). Does reservoir trophic status influence the feeding and growth of the sharptooth catfish, *Clarias gariepinus* (Teleostei: Clariidae)? *Afr. J. Aquat. Sci.* **33**, 149–156.

R Development Core Team (2012). *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Richardson, T.R., Booth, A.J. & Weyl, O.L.F. (2009). Rapid biological assessment of the fishery potential of Xonxa Dam near Queenstown, South Africa. *Afri. J. Aquat. Sci.* **34**, 87–96.

Safriel, O. & Bruton, M.N. (1984). *Aquaculture in South Africa: a cooperative research programme – a report of the working group for Aquaculture National Programme for Environmental Sciences*. South African National Scientific Programmes Report No. 89.

Skelton, P.H. (2001). A *complete guide to the freshwater fishes of southern Africa*. 2nd edn. Cape Town, South Africa: Struik.

Teugels, G.G. (1986). *A systematic revision of the African species of the genus* Clarias *(Pisces; Clariidae)*. Annales Musée Royale de l'Afrique Centrale Sciences Zoologiques. 247.

Van der Waal, B.C.W. (1998). Survival strategies of sharptooth catfish *Clarias gariepinus* in desiccating pans in the northern Kruger National Park. *Koedoe* **41**, 131–138.

VanWinkle, W. (1975). Comparison of several probabilistic home-range models. *J. Wildl. Manage.* **39**, 118–123.

Vitule, J.R.S., Freire, C.A. & Simberloff, D. (2009). Introduction of non-native freshwater fish can certainly be bad. *Fish Fish.* **10**, 98–108.

Weller, R.R. & Winter, J.D. (2001). Seasonal variation in home range size and habitat use of flathead catfish in Buffalo Springs Lake, Texas. *N. Am. J. Fish. Manage.* **21**, 792–800.

Weyl, O.L.F. & Booth, A.J. (2008). Validation of annulus formation in otoliths of a temperate population of adult African sharptooth catfish *Clarias gariepinus* using fluorochrome marking of wild fish. *J. Fish Biol.* **73**, 1033–1038.

Willoughby, N.G. & Tweddle, D. (1978). The ecology of the catfish *Clarias gariepinus* and *Clarias ngamensis* in the Shire Valley, Malawi. *J. Zool.* **186**, 507–534.

Winemiller, K.O. & Kelso-Winemiller, L.C. (1996). Comparative ecology of catfishes of the upper Zambezi River floodplain. *J. Fish Biol.* **49**, 1043–1061.

Worton, B. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168.