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Habitat associations of three stream fishes on a montane plateau (Nyika Plateau，Malawi)*

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Abstract　This study examined the habitat associations of three stream fishes on a montane plateau，Nyika Plateau，in northern Malawi. Twenty-four sites were sampled over three different periods in three rivers of the plateau. At each site，a riffle and a pool were identified，in a stretch of about 100 m，as separate habitat units，and were sampled for fish and physical habitat. A preference index and logistic regression were used to determine the important habitat variables for each species. The mountain catfish *Amphilius uranoscopus* preferred shallow habitat（< 50 cm）with coarse substrate（pebble and boulder）and moderate flow（0.4 – 1 m/s）. The yellow fish *Labeobarbus johnstonii* was associated with deep habitats（> 50 cm）and moderate and fast flows. The distribution of the exotic trout *Oncorhynchus mykiss* was limited to low temperature（< 20℃）. It was associated with moderate depth，fast flow and high abundance of riparian vegetation. The preferred habitat of trout overlapped with that of the indigenous species. Trout is likely，therefore，to have an impact on the indigenous species，especially the widespread mountain catfish，where they co-occur [*Acta Zoologica Sinica* 54（1）：67 – 76，2008].

Key words　Montane streams，Fish，Habitat unit，Preference index，Logistic regression，Exotic trout

马拉维 Nyika 高原三种溪流鱼类的生境类型*

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摘　要　本研究调查了生活在非洲马拉维北部 Nyika 高原三种溪流鱼类的栖息地。分 3 个时期选择 3 条河流的 24 个地点进行取样，每个样点长 100 m 左右；分急流和回水湾两种生境类型作为独立的栖息地单元取样，据此观察研究对象和物理环境间的关系；用喜好指数和逻辑回归分析每种鱼重要栖息地是否稳定。瞻星平鳍鲇（*Amphilius uranoscopus*）通常喜欢生活在水深小于 50 cm、流速 0.4 – 1 m/s 的缓流河段，这里水色较深，河底多卵石。黄鱼（*Labeobarbus johnstonii*）常被发现在水深大于 50 cm 的河段，河水流速中等或较急。引入种虹鳟（*Oncorhynchus mykiss*）的活动范围常局限在水温低于 20℃的河段，这些河段水深中等，流速较快，沿河多植物。虹鳟栖息地与土著种相似，可能与同域分布的土著种，特别是与广泛分布的瞻星平鳍鲇存在生存竞争 [动物学报 54（1）：67 – 76，2008]。

关键词　溪流鱼类　生境　生存竞争　Nyika 高原　马拉维

Studies on habitat selection by stream fishes usually form the basis for species conservation（Moran-Lopez et al.，2005）. Many of these studies show that local microhabitat variables，such as substrate，depth，velocity and vegetation，form the template to which stream fishes depend on for feeding，breeding and refuge（Leveque，1997；Mattingly and Galat，2002；Moyle and Cech，2004）. The need for such information is essential in southern Africa because many stream fishes are now endangered due to，among other factors，habitat alteration

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(Skelton, 1990; Minshull, 1993), and only a few studies have been done(e.g. Kleynhans, 1999; Kadye and Marshall, 2006).

The understanding of habitat associations is also critical in the context of invasive species. In many countries, invasive alien species have become established at the expense of native species (Cambray, 2003). Classic examples include the displacement from natural home ranges of native mountain galaxias(*Galaxias* spp.) due to predation by trout in Australian and New Zealand rivers (Townsend and Crowl, 1991; Closs and Lake, 1996), and the disappearance of endemic barbs due to the presence of alien trout and bass in headwaters of South African rivers (Kleynhans, 1996). Studies on habitat associations can, therefore, help to reveal habitats that may serve as refugia for native species if they are not preferred or are unavailable for introduced species.

In this study we quantify the habitat selected by two native species, the mountain catfish *Amphilius uranoscopus* and the yellow fish *Labeobarbus johnstonii*, and one introduced species, the rainbow trout *Oncorhynchus mykiss*, in the rivers of the Nyika Plateau, part of the Lake Malawi drainage basin. We identify the major habitat variables that predict the presence or absence of species, and use this information to describe the degree of habitat overlap between the native species and the introduced trout, and habitat characteristics that may limit the colonisation of the invasive trout. The Nyika Plateau has a montane type of climate, which is unique in southern Africa where the climate is tropical. The plateau, protected by a national park, provides an opportunity to study the species under near-natural conditions.

1 Materials and methods

1.1 Study area and species

The Nyika Plateau occupies the area between latitude 10°S and 11°S, and longitude 33°E and 34°E in the northern part of Malawi(Fig.1). Most of the plateau lies at 1800 m a.s.l. Overall altitude in the national park ranges from 600 m a.s.l. in the northwest to 2607 m a.s.l. at Nganda hill on the north-eastern side of the plateau. The climate of the plateau is cool and moist compared to the surrounding region because of its high elevation. Rains fall primarily between the months of November and March. Mean daily temperatures near the centre of the plateau range from 17℃ in November to 10.3℃ in July.

The mountain catfish *Amphilius uranoscopus* is a small benthic species with a widespread distribution on the plateau. This species is likely to be threatened due to predation by exotic trout (Skelton, 1993). Preliminary studies indicate that the catfish occur in disjunct populations in the presence of exotic trout and in sections with sand and silt substrates on the Nyika Plateau(pers. obs.). The yellow fish *Labeobarbus johnstonii* is a large cyprinid endemic to the Lake Malawi drainage basin. It inhabits the shores of the lake, and migrates up rivers in shoals to breed(Tweddle, 1982). It is widely distributed in the North Rukuru River and its tributaries on the Nyika Plateau. Rainbow trout *Oncorhynchus mykiss* is exotic on the plateau, and is widespread at high altitude(> 1800 m a.s.l).

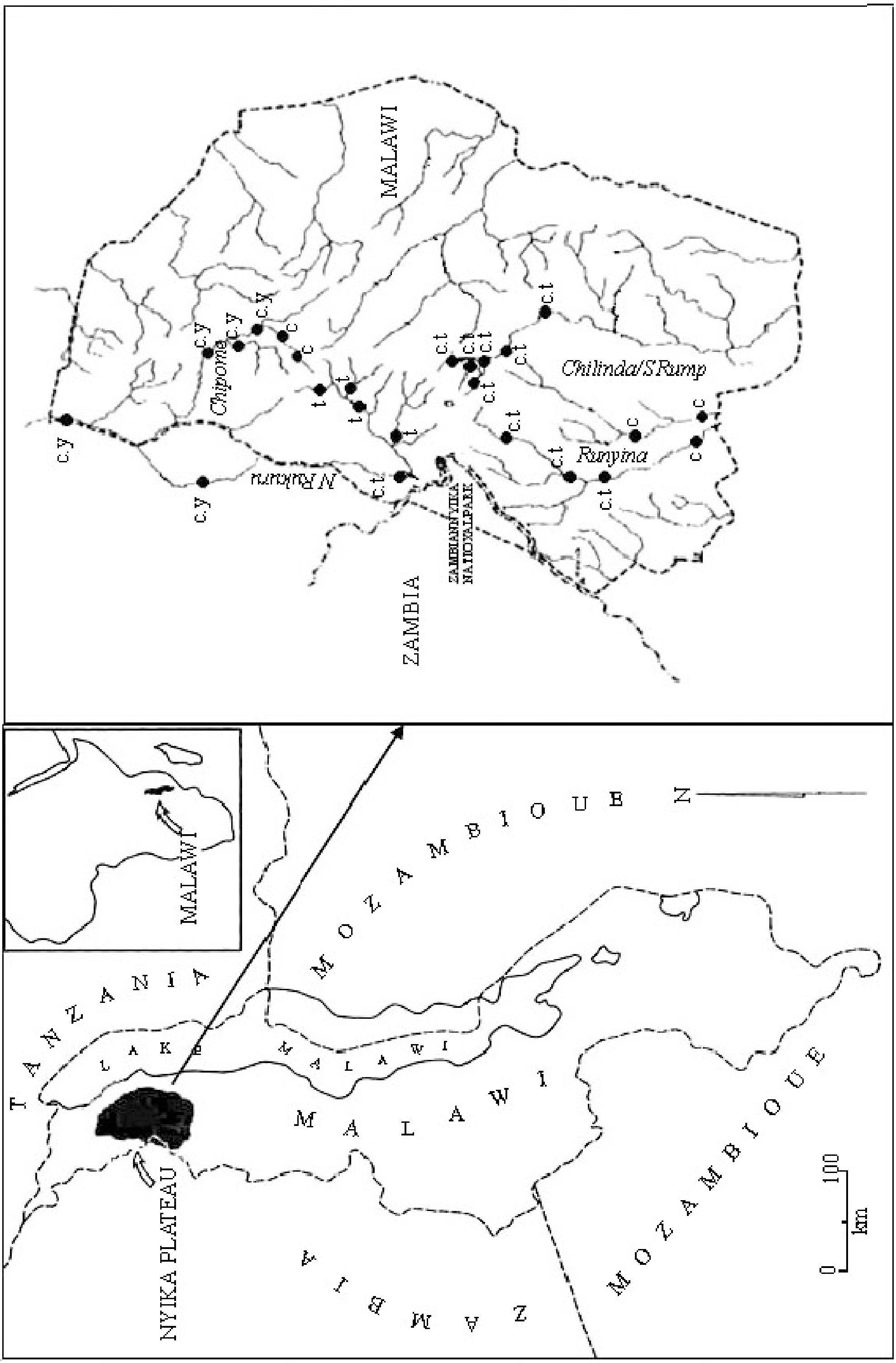
1.2 Data collection

Twenty-four sites were sampled on three rivers of Nyika National Park. Samples were collected in May–June, 2006, October–November 2006 and March 2007. An exception was for five sites that were sampled in the dry and warm and wet and warm months. At each site, a riffle and a pool were identified, in a stretch of about 100 m, as separate habitat units. Each habitat unit was sampled separately to detect the presence or absence of fish, and to collect habitat data. Fish were captured using a DEKA 3000 backpack electrofisher. Electrofishing was conducted in an upstream direction for 10 minutes using 300–500 V, 4–6 A AC.

After fish sampling, 10 transects were set up at each habitat unit to measure physical habitat variables. Measurements were made at three points, two near the edge and one at the centre, along each transect. Habitat data were categorised following Gorman and Karr(1978) and Schlosser(1982) into 5 substrate classes, 4 depth classes, 4 velocity classes and 2 vegetation classes(Table 1). Aquatic vegetation was absent at most of the sites, and was not considered in the analysis. The dominant class was determined from the proportion (%) of all classes for each variable. Each habitat unit was described according to the dominant category for all classes. Velocity was measured at the centre of each transect using an FP201 current metre(Global Water Inc., CA, USA). Water temperature was measured using a Horiba U23 probe(Horiba Ltd, Japan).

1.3 Data analysis

The habitats selected by each species were determined by contrasting the habitat classes in each unit where fish were collected with those available. Manly et al.'s (1993) index, w_i, was used to determine the probability of association of each species to habitat categories of each class. The index is given as: $\hat{w}_i = \frac{o_i}{\pi_i}$ where o_i is the proportion of the sample of used resource units in category i, and π_i is the proportion of available resource units in category i. The standardised selection ratio, $B_i = \frac{\hat{w}_i}{\sum_{i=1}^{n}\hat{w}_i}$, was used to estimate the probability of use of each habitat category. A χ^2 test was performed to test a null hypothesis of random association of species to resources (i.e. no selection). Multiple logistic regressions were used to test the most influential habitat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Chipome
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variables associated with each species. This method is suitable where the analysis involves the relationship between continuous and non continuous variables (Sokal and Rolf, 1995). In this case, the presence/absence of individual species (response variables) was tested against the frequencies of the habitat categories (predictor variables). A forward stepwise method was used for each variable with probabilities of entry of 0.05 and removal of 0.1. χ^2 goodness-of-fit tests were used to asses the fit of each model. The significance of each coefficient (b) was evaluated by the Wald statistic. Odds ratios were used to evaluate the relationship between the predictor and response variable. The odds ratio is the multiplicative factor by which the odds of a habitat occupied change when the variable in question increases by one unit (Quinn and Kenough, 2002). If the value is greater than 1 the odds are increased, and if the value is less than 1, the odds are decreased. The SPSS package was used for the logistic regressions. Rainbow trout *O. mykiss* have been introduced to all major streams of the plateau. In the analysis, it was assumed that all the sampled habitats were available for this species. The mountain catfish *A. uranoscopus* is widespread on the plateau. It was assumed that all the sampled stations were available for this species. An exception was for 5 sites above a waterfall, Chisanga Falls, which was a barrier for upstream migration on the North Rukuru River and sites with trout that were considered not optimum for catfish. *Labeobarbus johnstonni* was collected from the North Rukuru River and its tributary, the Chipome River. All sites from these two streams, except the five sites above the waterfall, were considered available for this species. We considered those variables measured at stations where each species was collected as the used resource units. Each sampling period was considered to yield independent resource unit measures. Logistic regression, with a polynomial function, was used to construct some response curves of the species to each habitat variable.

2 Results

The streams of Nyika Plateau were characterised by moderate to fast flow (Table 1). Gravel and pebble were the dominant substrate types. Most of the sampled sites were shallow (< 50 cm). Riparian cover was present at most sites. Water temperature was < 18℃ for most sites during the sampling period (Table 1).

The mountain catfish *Amphilius uranoscopus* was significantly associated with substrate, depth and velocity ($P < 0.05$). High selection probabilities were for coarse substrate types (pebble and boulder) and shallow depth (< 50 cm) (Fig. 2). Moderate flow and fast flow were the most preferred velocities compared to slow flow. The catfish was generally eurythermal, and the abundance of riparian cover did not significantly influence habitat association. Substrate and depth were significant variables

Table 1 The variables measured in this study and their frequencies for the catfish, yellow fish (y-fish) and trout habitat units

Variable	Class	Catfish	y-fish	Trout
Substrate type (mm)	Silt [sl] (< 0.5)	0	0	6
	Sand [sn] (0.5 – 2)	4	2	14
	Gravel [gr] (2 – 100)	21	18	36
	Pebble [pb] (100 – 300)	18	14	31
	Boulder [bl] (> 300)	11	10	17
Depth (cm)	Very shallow (0 – 20)	8	7	12
	Shallow (20 – 49)	19	17	37
	Moderate (50 – 100)	17	14	33
	Deep (> 100)	10	6	22
Current velocity (ms^{-1})	Static (< 0.05)	1	1	3
	Slow (0.05 – 0.4)	5	6	10
	Moderate (0.4 – 1)	27	20	44
	Fast (> 1)	21	17	47
Riparian vegetation (%)	Absent (0)	6	3	12
	Scarce (0 – 30)	28	25	40
	Moderate (30 – 60)	12	6	24
	Abundant (> 60)	8	10	28
Temperature (℃)	< 15	8	8	22
	15 – 18	16	12	50
	18 – 21	10	8	20
	21 – 24	16	12	8
	> 24	4	4	4

($P < 0.05$) controlling the presence or absence of catfish using multiple logistic regressions (Table 2). The odds ratios show a 1.1 chance of catfish presence for a unit increase in substrate size, and a 0.97 chance of having catfish for an increase in depth. The catfish showed a greater probability of use for a substrate size range of 300 – 400 mm and a depth range of 0 – 40 cm (Fig. 5). The significance of these variables is shown in Table 3.

The yellow fish *Labeobarbus johnstonii* was significantly associated with depth, velocity and temperature ($P < 0.05$) (Fig. 3). Increasing depth and velocity were more preferred compared to shallow and slow flowing habitats. The yellow fish showed preference for the large substrate type, but this relationship was not significant. No discernable trend was observed for the association with riparian cover (Fig. 3). Depth and velocity were significant variables ($P < 0.05$) determining the presence or absence of the yellow fish from the logistic regressions model (Table 2). There was a 1.1 chance of species presence for a unit increase in depth, and a 0.01 chance of species presence than absence for a unit

Table 2 Multivariate logistic regression model results for the relationship between variables and species

Species	Variable	b	*SE*	Wald	*P*	Odds ratio
A. uranoscopus	Substrate	0.007	0.002	9.331	< 0.05	1.10
	Depth	− 0.070	0.0181	4.778	< 0.05	0.93
L. johnstonii	Depth	0.075	0.030	6.003	< 0.05	1.12
	Velocity	− 9.744	4.420	4.860	< 0.05	0.01
	Temperature	0.821	0.304	7.299	< 0.01	2.27
O. mykiss	Substrate	0.005	0.002	3.915	< 0.05	1.10
	Velocity	2.705	1.331	4.137	< 0.051	4.96
	Riparian cover	0.063	0.018	12.042	< 0.01	1.65
	Temperature	− 0.518	0.175	8.722	< 0.01	0.59

The overall goodness-of-fit tests are as follows: *A. uranoscopus*, $\chi^2 = 14.72$, $P < 0.01$, $r^2 = 0.55$; *L. johnstonii*, $\chi^2 = 37.02$, $P < 0.01$, $r^2 = 0.57$; *O. mykiss*, $\chi^2 = 71.38$, $P < 0.01$, $r^2 = 0.49$. The Wald statistic tests the significance of each coefficient(b).

Table 3 Logistic regression model, with polynomial functions, results

	Variable	Constant	a	b	*P*(a)	*P*(b)	Model *P*
A. uranoscopus	Substrate	− 0.0075	0.0065	− 0.0001	< 0.001	< 0.001	< 0.01
	Depth	0.963	− 0.0016	− 0.0001	< 0.05	< 0.05	< 0.05
L. johnstonii	Depth	− 0.1048	0.0725	− 0.0002	< 0.001	< 0.001	< 0.001
O. mykiss	Substrate	0.4041	0.0028	− 0.0001	< 0.05	< 0.05	< 0.05
	rp. cover	0.0894	0.0221	− 0.0001	< 0.001	< 0.05	< 0.01
	Depth	− 0.1362	0.0282	− 0.0002	< 0.001	< 0.001	< 0.001

Listed are the estimates of constants, a and b, their significance [*P*(a) and *P*(b)], and the model significance(model *P*).

increase in velocity. The yellow fish also showed a 2.3 chance of presence for increasing temperature(Table 2). High and significant probability of use occurred for 60 – 100 cm depth range(Table 3 and Fig.5).

Trout was significantly($P < 0.05$) associated with all habitat variables(Fig.4). The selection probabilities were high for coarse substrate types(pebble and boulder), moderate depth(40 – 80 cm), fast flow(> 1 m/s), increasing riparian cover and low temperature(Fig.4, 5). There was a 14.9 chance of having trout for a unit increase in velocity, a 1.9 chance for a unit increase in the riparian cover and a 1.1 chance for increasing substrate size(Table 2). Increasing temperature was associated with a decrease in odds for the presence of trout (Table 2).

3 Discussion

The streams of Nyika Plateau presented habitat associations that differed among the three species studied. The widespread mountain catfish *A. uranoscopus* preferred shallow habitats with coarse substrate (pebble and boulder). The yellow fish *L. johnstonni* preferred deep habitats with moderate to fast flow. The exotic trout *O. mykiss* was confined to high altitude and low temperature habitats. Its preference was for high riparian cover, fast flow and deep habitat. Trout were generally associated with all substrate types, with a preference or coarse substrate types. We discuss the habitat associations of each species and potential relationships between habitat use, diet and risk avoidance. We then consider the degree to which the invasive trout overlaps with the two native species, and identify refugia where the native species may not interact with the introduced trout.

The catfish *A. uranoscopus* is a small species that feeds on benthic invertebrates(Skelton, 1993). Shallow habitats(< 40 cm) and coarse substrate, to which it was associated in this study, provide both invertebrate supply and refuge, in the form of crevices, from displacement by fast flow. The yellow fish *Labeobarbus johnstonni* on the other hand, was associated with a depth range of 60 – 100 cm. Although the feeding habits of this species are unknown, the position of its mouth, like other *Labeo* species, suggests a scrapping and sucking feeder on periphyton. With their relatively large body size, moderate depth and rocky habitats would provide a feeding habitat and refuge against terrestrial predators. In the North Rukuru River and its tributary, the Chipome River, *A. uranoscopus* and *L. johnstonni* co-occurred at most sites. The co-occurrence for these two native species may be explained by the difference in depth preferences. Patterns associated with co-occurrence of species can be classified as either ecological segregation or habitat segregation(Gray and Stauffer, 1999; Taylor, 2000; Krebs, 2001). These patterns are driven by species-habitat relationships(Peres-Neto, 2004), and may be a result of predation(Gilliam et al., 1993), physiological

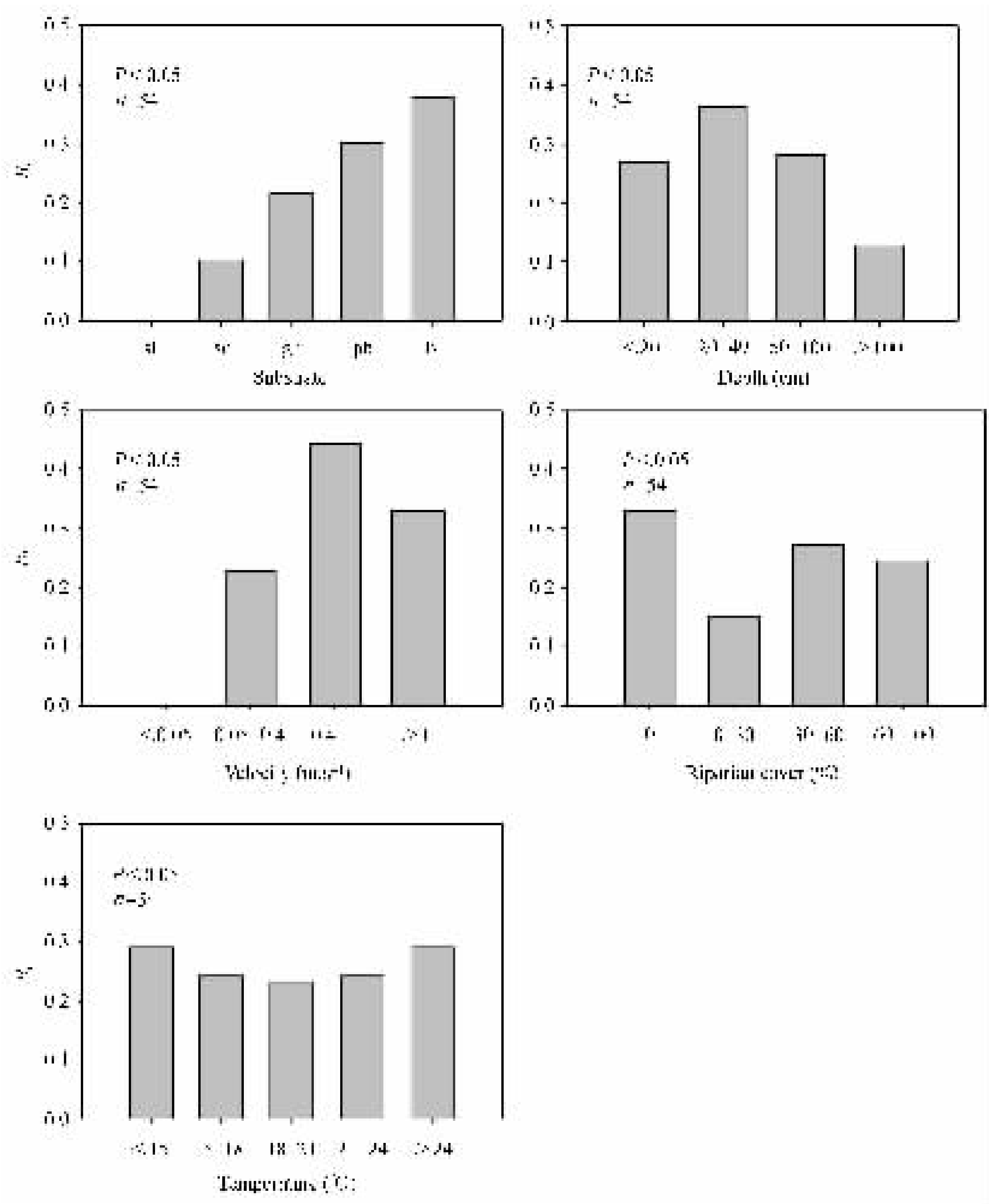

Fig.2 The values for the preference index for the habitat variables associated with *A. uranoscopus*

constraints and stochastic environmental variation (Grossman et al., 1998), and competition for resources (Taniguchi and Nakano, 2000). The important attributes for stream fishes are morphological and physiological adaptations that determine their feeding success and ability to maintain their position in the stream (Moyle and Vondracek, 1985). Body size appears to be the most important factor determining the depth preference for the two native species in this study. The selection of shallow habitats by the catfish and deep habitats by the yellow fish is a reflection of a tradeoff between energy gain and risk avoidance.

Raleigh et al. (1984) described the optimal river habitats for rainbow trout *O. mykiss* as clear and cold water, silt-free rocky habitats, vegetated stream banks, abundant in-stream cover and a relatively stable flow. This study generally confirmed this description of trout's habitat. Trout preferred coarse substrates, moderate depth and higher velocities in this study. Trout, a cold water species, preferred temperatures < 20℃ and habitat units with abundant riparian cover on the streams of the Nyika Plateau. The importance of riparian vegetation in the functional ecology of streams is documented. It provides, among other functions, shade and cover, and a supply of terrestrial invertebrate food items (Growns et al., 2003). Trout are opportunistic predators relying on fish and both drift and aquatic invertebrates (Raleigh et al., 1984). The biomass of trout has been found to increase in areas

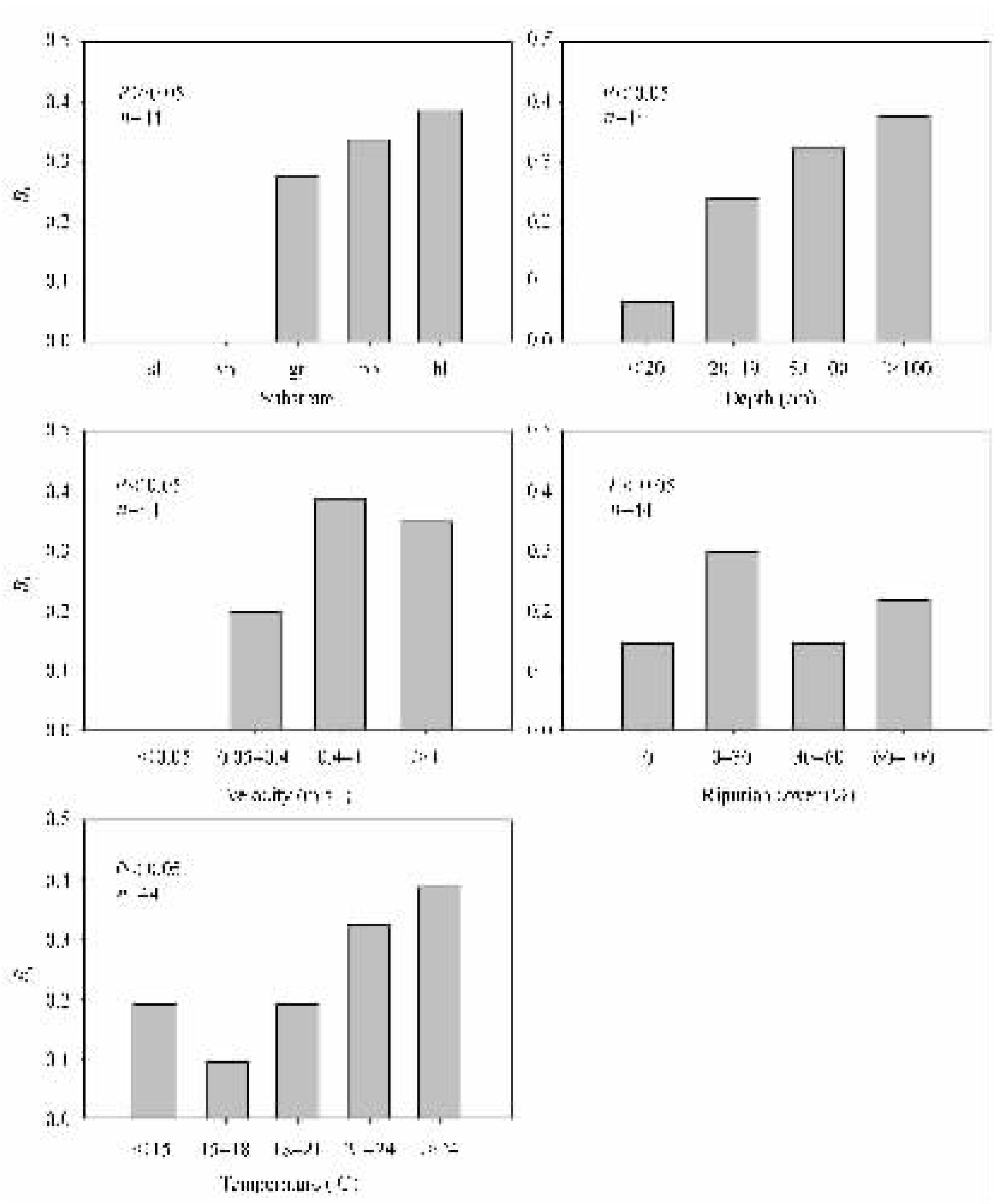

Fig.3 The values for the preference index for the habitat variables associated with *L. johnstonii*

with abundant riparian cover due to the input of terrestrial insects（Kawaguchi and Nakano，2001）.

The results show an overlap for the catfish and trout in substrate and velocity preferences at the 30 – 60 cm depth range. The catfish is，therefore，likely to be displaced from its most preferred depth range due to both competition and predation by the exotic trout. The displacement of native species by exotic trout has been observed in many studies. McIntosh et al.（1994）noted a change in microhabitat use by galaxias，from fast flowing sites with trout to slow flowing sites due to both competition and predation in New Zealand rivers. Townsend and Crowl（1991）also observed that the distribution of native galaxias and exotic trout were non-overlapping with the former being found at sites that were not accessible to trout. On the Nyika Plateau，habitats with very shallow depth would be least preferred by trout and may serve as refugia for the mountain catfish. Such refugia may be found in most of the first order streams and some sections of the streams with extensive riffles. While habitats with less riparian cover may also act as temporary refugia for the catfish，some studies show that active predators such as trout can shift from drift feeding to picking food from the substrate（Fausch et al.，1996）. Sections with less riparian cover may，therefore，only serve as refugia when there is an abundant supply of terrestrial insects. Although there is an overlap in substrate and depth preference，trout are unlikely to have

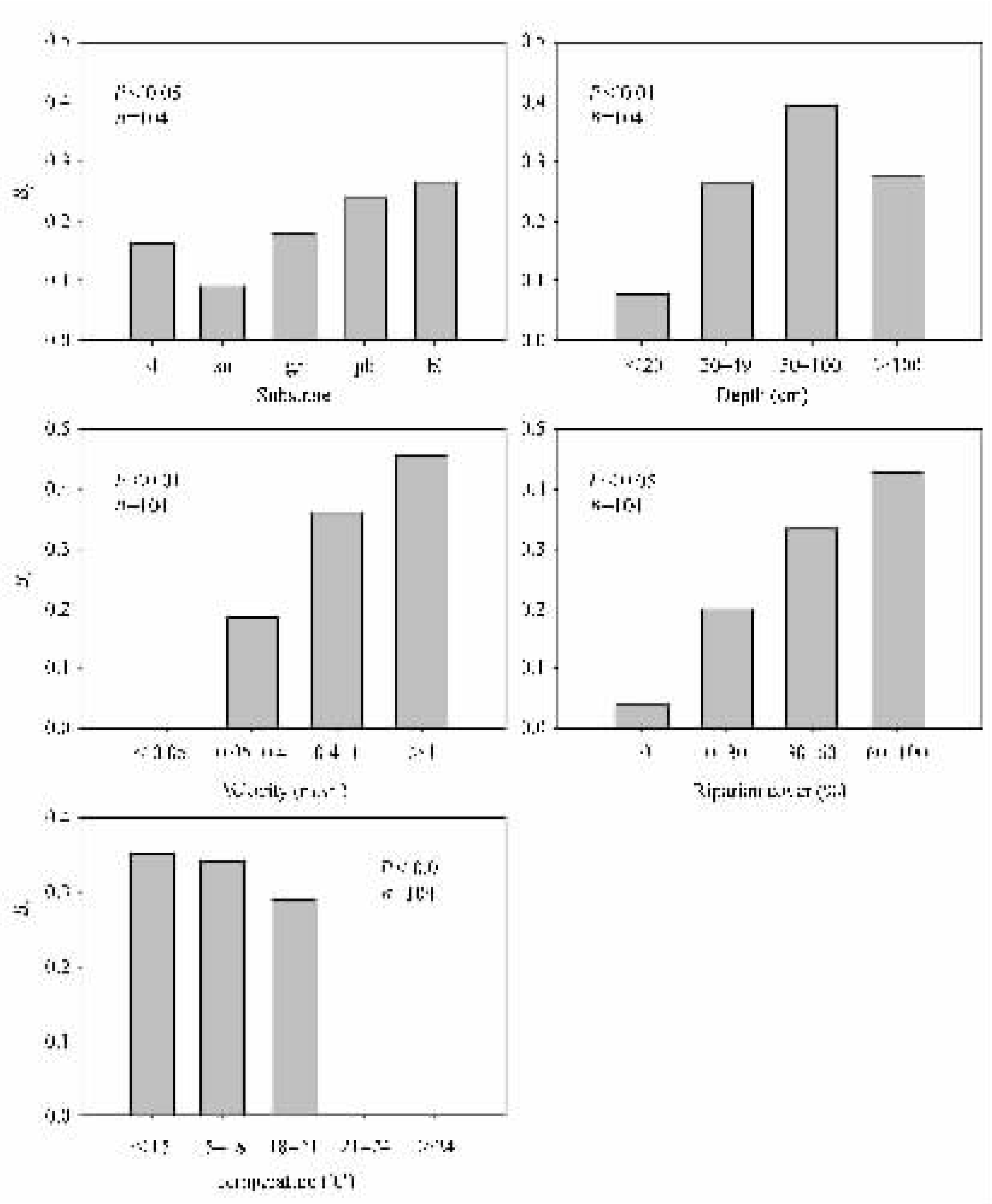

Fig.4 The values for the preference index for the habitat variables associated with *O*. *mykiss*

an impact on the yellow fish *L.johnstonii* due to differences in temperature preference. Trout is a cold water species and preferred temperatures < 20℃ on the plateau. The yellow fish, on the other hand, preferred warmer water temperatures on the plateau. While little is known about the breeding habits of the yellow fish, clean coarse substrate and well oxygenated fast flowing water may be essential for breeding of the yellow fish. The yellow fish migrates form Lake Malawi in summer to breed in rivers, including the North Rukuru River (Tweddle, 1982).

From a practical point of view, studying species-habitat associations offers an opportunity for the conservation of stream fish. Generating models from readily measurable attributes in streams is useful in detecting the absence of species where their presence is likely, given certain conditions (Moran-Lopez et al., 2005) as was shown in this study. The alteration of habitats in particular and hydrological regimes in general can result in population losses of stream fish since they prefer specific habitats. In Malawi for instance, the endemic lake salmon *Opsaridium microlepis* is now endangered in most rivers where it breeds due to siltation (Tweddle, 2001). Furthermore, losses can occur due to diminishing water levels and discontinuity in stream habitats. For example, damming and water abstraction without due consideration of ecological flow requirements can reduce habitat availability and quality (Moran-Lopez

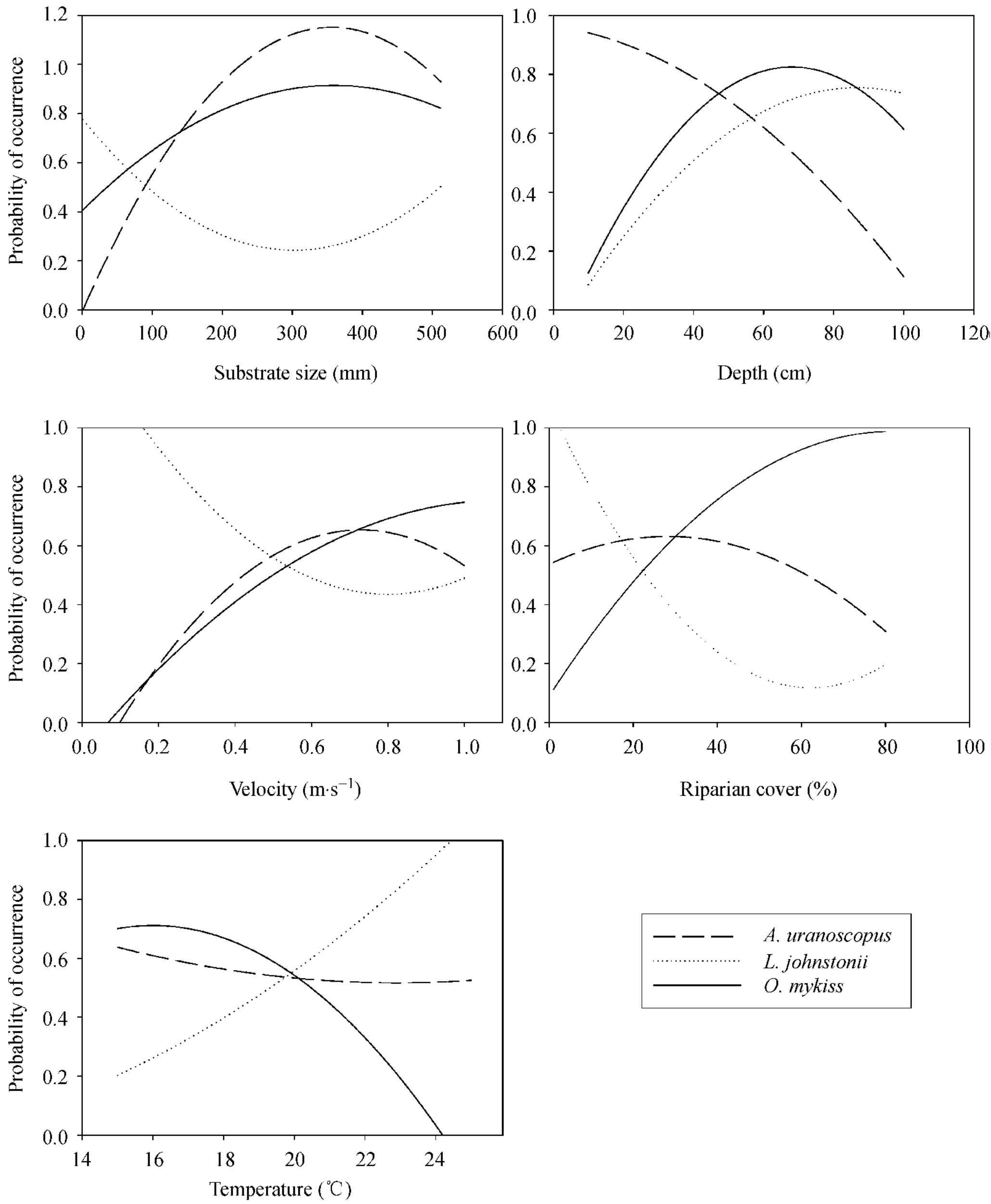

Fig.5 The response curves for the probability of occurrence for the three species in relation to the variable measured

et al., 2005). The headwaters of Nyika Plateau streams inside the national park, especially the Chipome River, may serve as important breeding habitats for the potamodramous yellow fish. Maintenance of clean and silt-free habitats and continuous flow is essential to mitigate against the impact of exotic trout and to provide refugia for the indigenous species on the plateau.

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