

The predatory impact of invasive alien smallmouth bass, *Micropterus dolomieu* (Teleostei: Centrarchidae), on indigenous fishes in a Cape Floristic Region mountain stream

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Fish populations in the Rondegat River, a mountain stream in the Olifants-Doring system in the Cape Floristic Region, South Africa were surveyed to assess the impact of predatory alien invasive smallmouth bass *Micropterus dolomieu* (Lacepède) on the indigenous fishes. This was the first such attempt to quantify the predatory impacts of *M. dolomieu* within this region. The Rondegat River is home to five species of indigenous fish and is partially invaded by *M. dolomieu*, which has penetrated the lower river up to a waterfall barrier. Seasonal surveys were conducted at five sites above, and five below, the waterfall. Physical habitat was measured at each site. Four of the five indigenous fish species were absent at bass-invaded sites. *Labeobarbus capensis* (Smith), while still present below the waterfall, appeared to have suffered a near-total loss of post-spawning recruits. Analyses of physical habitat quality failed to explain the loss of indigenous fish below the waterfall, although sedimentation may have increased the vulnerability of the catfish *Austroglanis gilli* (Barnard) to *M. dolomieu* predation by obliterating benthic cover. Consequently, predation by *M. dolomieu* was presumed to be the critical mechanism explaining the loss of indigenous fishes in the lower Rondegat River.

Keywords: Cape Floristic Region, diversity, impacts, indigenous fish, invasive fish, *Micropterus dolomieu*, predation

Introduction

The Cape Floristic Region (CFR) of South Africa is a global biodiversity hotspot (Cowling *et al.* 2003). The rivers of this region are notable for their unique and largely endemic fish fauna, which exists within very restricted ranges (Skelton 1983, 1987). Although relatively low in species richness in comparison to the flora, the CFR's fish fauna is arguably the region's most endangered component (Impson *et al.* 1999), with 16 of its 19 species being endemic and 15 listed as threatened (Impson *et al.* 2002). The major threats to indigenous fishes in the CFR are habitat loss (through bulldozing of riverbeds and water abstraction), water quality degradation, and restriction of migration by dams and weirs, as well as the presence of alien invasive fishes (Gaigher *et al.* 1980, Skelton 1987, Impson and Hamman 2000). Of the fish species that have become invasive within the CFR, smallmouth bass (*Micropterus dolomieu* Lacepède) appears to have caused the most damage to the indigenous fish populations (Hamman and Jordaan 1988). Introduced into South Africa from North America in 1937 for angling purposes (Harrison 1952), *M. dolomieu* now inhabits the Berg, Breede and Olifants-Doring river systems in the CFR (De Moor and Bruton 1988), and can be classified

as an invasive alien in this region under the terminology of Occhipinti-Ambrogi and Galil (2004). In the Berg and Breede rivers, it is associated with the disappearance of several endemic cyprinid species and the anabantid *Sandelia capensis* (Cuvier) (De Moor and Bruton 1988, Christie 2002, Shelton 2003).

The Olifants-Doring river system, which includes the Rondegat River, is arguably South Africa's most important catchment for the conservation of freshwater fishes, as eight of its 10 species are both endemic and threatened (Impson *et al.* 2002). Since the introduction of *M. dolomieu* during the 1940s, it has been implicated in the disappearance of six fish species from sections of the Olifants River (Gaigher 1973, De Moor and Bruton 1988). Following a fish survey of the Olifants River, Gaigher (1973) suggested that indigenous fishes were able to survive in the system only above natural barriers where *M. dolomieu* could not penetrate. While studies and surveys like these all produced compelling circumstantial evidence of *M. dolomieu* impacts on fish diversity, they did not compare the impact of *M. dolomieu* to that of other potential factors affecting the distribution ranges of indigenous fishes, such as loss of

habitat or water pollution. The absence of data for alternative impacts makes the decrease in fish diversity in streams difficult to attribute solely to the presence of invasive alien fish (Crivelli 1995). Furthermore, as very few scientific papers (e.g. Gaigher *et al.* 1980) or popular articles (e.g. Hamman and Jordaan 1988) have reported these findings in the past, it has been difficult to convince a sceptical public, including anglers (Kruger 2004), of the severity of the threat posed by *M. dolomieu* to indigenous fish diversity. This study examined the longitudinal changes in the indigenous fish assemblage structure in a mountain stream where only the lower reaches contained *M. dolomieu*, and contrasted the effects of the presence of this invasive predator with changes in physical habitat variables, in order to assess the relative influences these variables may have on fish distributions within the stream.

Materials and methods

Study site

The Rondegat River, a tributary of the Olifants River, Western Cape Province, South Africa, rises in the Cedarberg Mountains and flows into Clanwilliam Dam. It is a relatively short river, spanning about 20km from its source to the reservoir (Figure 1). The upper catchment has a long history of afforestation, though the plantations have for the most part now been removed and, apart from a small human settlement and a dirt road close to the stream, the riparian zone is largely undisturbed. The middle and lower sections of the river flow through farmland, and the riparian zone is impacted by various agricultural factors such as cattle, sheep, citrus orchards and grazing lands which in some places lie adjacent to the river, with little or no riparian buffer present (February 2002). In many parts of the river, the riparian zone is invaded by alien invasive trees, including black wattle (*Acaia mearnsii*), blackwood (*Acacia melanoxylon*) and small patches of bramble (*Rubus sp.*).

The river is currently home to three indigenous cyprinids — the Clanwilliam yellowfish (*Labeobarbus capensis* Smith), the Clanwilliam redfin (*Barbus calidus* Barnard) and the fiery redfin (*Pseudobarbus phlegethon* Barnard) — an indigenous austroglanidid, the Clanwilliam rock catfish (*Austroglanis gilli* Barnard), and an indigenous galaxiid, the Cape galaxias (*Galaxias zebratus* Castelnau). Historically, the indigenous Clanwilliam sawfin (*Barbus serra* Barnard) was also present in the lower reaches of the river (Van Rensburg 1966). Today, however, the lower reaches contain *M. dolomieu*, which appears to have invaded the tributary in the early 1950s (Harrison 1963), and the alien bluegill (*Lepomis macrochirus* Rafinesque). While both *M. dolomieu* and *L. macrochirus* had previously been recorded close to the reservoir (Van Rensburg 1966), at the time of the present study *M. dolomieu* had penetrated upstream as far as a waterfall barrier (Figure 1), about 5km upstream of the reservoir (Bills 1999).

Field procedures

The Rondegat River was visited in October and November 2003 and April 2004. Five sites were selected upstream and downstream of the waterfall, to represent longitudinal

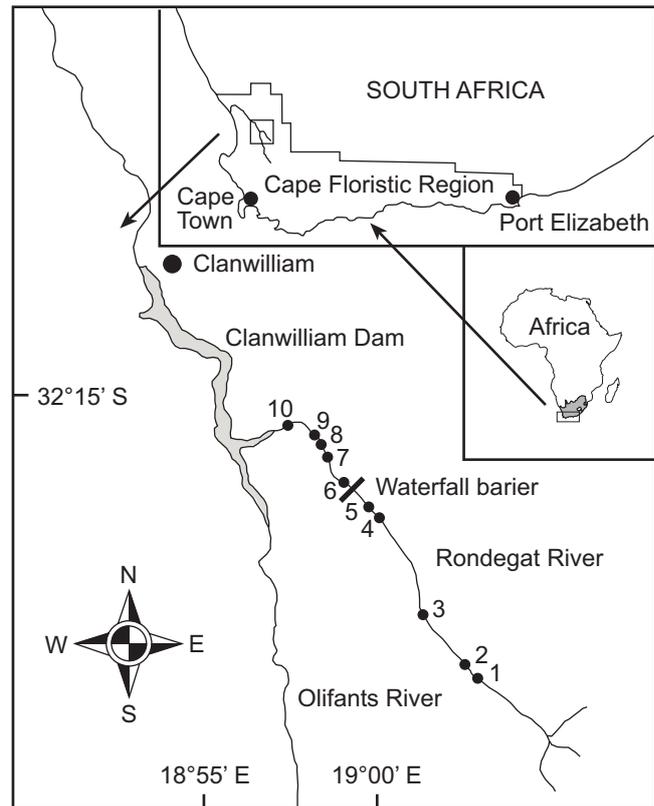


Figure 1: Map of the Rondegat River, showing the position of the waterfall barrier and study sites

Table 1: Physical and biotic characteristics of the riparian zone and invasion status of the river at study sites

Site	Riparian zone/invasion status
1	Near-pristine fynbos/no bass
2	Near-pristine fynbos/no bass
3	Alien trees, campsite/no bass
4	Alien trees, cattle/no bass
5	Alien trees only/no bass
6	Alien trees, cattle/bass present
7	Cattle pasture (no riparian buffer)/bass present
8	Cattle pasture (no riparian buffer)/bass present
9	Cattle pasture (no riparian buffer)/bass present
10	Alien trees only; bass present

changes in the physical and biotic conditions of the river (Table 1). At each site, a pool was chosen for visual underwater surveys, and a riffle (*sensu* Wadeson 1994) for electrofishing. Snorkel surveys were conducted by a single diver moving upstream in a zig-zag motion, to maximise the area covered (after Mullner *et al.* 1998). Three snorkelling passes were made and fish abundance was estimated as the mean number per species per pass. Total length (TL, cm) of each fish was estimated using a 300mm ruler attached to a Perspex writing slate. For electrofishing of riffle habitat, a 20m section was blocked off with block-nets, and an operator using a DEKA 3000 backpack electrofisher

at 600V shocked the riffle in one pass, working downstream. Stunned fish were captured with the cathode-net of the electrofisher and in the downstream block-net, and were pooled per riffle. Captured fish were weighed (g) and measured. Tests of the efficacy of the electrofishing technique (Meador *et al.* 2003) indicated that *L. capensis* and *B. calidus* were probably under-sampled in riffles, while *A. gilli* was never detected during pool surveys, although the species is known to inhabit them (Bills 1999). Despite these inaccuracies, constant sampling effort allowed for separate comparative analysis of species abundance among riffles and pools.

Physical habitat variables of each pool and riffle were measured, following fish surveys. A grid of four longitudinal and five transverse transects was set across the surveyed area and 20 measures were taken for each variable at the intersections of these. Flow velocity (m.s^{-1}), water depth (m) and substrate particle size (mm) were measured at each sampling point. Flow velocity was measured using a Scientific Instruments Mini Flowmeter. Depth and the beta-axis of the substrate particle were measured using a metered pole. If the point lay on a large substrate particle, the embeddedness of the particle (% area of particle covered with sand) was measured (after White and Harvey 2001), whereas, if the substrate was sand or silt, the depth (mm) of the deposit was measured. Density (fronds/ m^2) of woody (branches, roots) and fine (grasses, sedges) debris and overhead cover (%) was estimated within the square metre surrounding each point. While chemical pollution from agricultural run-off was recognised as a potential threat to indigenous fish in the Rondegat River, it was not measured, being beyond the scope of this project to investigate.

Analytical procedures

Due to the differing techniques used to sample pools and riffles, analysis of fish abundance was separated into riffle and pool habitats, using total abundance from electrofishing and mean abundance from snorkel passes. All sites were included in one of four groups — non-invaded riffle, non-invaded pool, bass-invaded riffle and bass-invaded pool — for data comparison. Using Statistica 6 (© Statsoft 2003), a forward-stepwise discriminant function analysis (DFA) was performed on the per-site mean values of habitat variables, to explore whether any measured aspect of physical habitat

would discriminate both invaded from non-invaded sites, and riffles from pools. All habitat variables were transformed to meet the assumptions of this analysis. Continuous variables were \log_{10} or $\sqrt{\quad}$ transformed to improve normality, while percentage data were arcsin transformed. Variables that best discriminated between these categories were then used in a canonical analysis, to allow a visual assessment of the separation of sites. In order to assess whether any of the habitat factors measured affected local fish distributions, non-parametric Spearman rank correlations were performed between local abundance of each species and un-transformed habitat variable means at pools and riffles, respectively. This analysis was chosen as the patchiness of the abundance data prevented successful post-transformation normalisation of the data set. Only *A. gilli* and *P. phlegethon* were considered for riffle analyses, due to the suspected under-sampling of the other species.

Results

Field survey data from all seasons combined showed that the indigenous species *G. zebratus*, *B. calidus*, *P. phlegethon* and *A. gilli* were absent from bass-invaded sites (Table 1). Although present in the lower river, *L. capensis* was recorded in lower numbers than at non-invaded sites (Table 2). *Labeobarbus capensis* TL data showed an absence of 2–10cm juveniles from bass-invaded sites (Figure 2). *Micropterus dolomieu* was less abundant at invaded sites

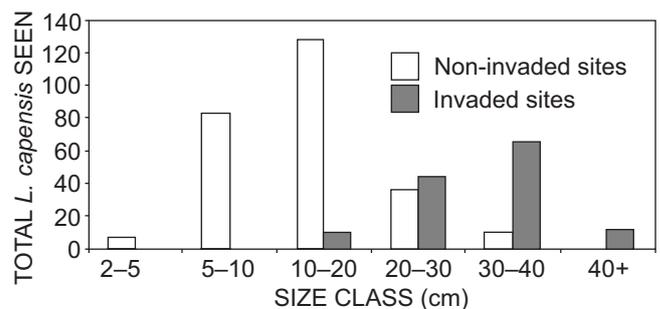


Figure 2: Length frequency distribution of *Labeobarbus capensis* at invaded and non-invaded sites, using combined data from surveys conducted in October and November 2003 and April 2004

Table 2: Species abundance in riffles (total abundance from single-pass electrofishing over 20m) and pools (mean abundance from three snorkel surveys in each pool). October 2003, November 2003 and April 2004 survey data combined

	Pools (mean no. per pool)		Riffles (no. per 20m ⁻¹)	
	Non-invaded	Bass-invaded	Non-invaded	Bass-invaded
Indigenous species				
<i>Labeobarbus capensis</i>	219	126	43	2
<i>Barbus calidus</i>	1 660	-	106	-
<i>Pseudobarbus phlegethon</i>	309	-	109	-
<i>Austroglanis gilli</i>	-	-	312	-
<i>Galaxias zebratus</i>	10	-	-	-
Alien species				
<i>Micropterus dolomieu</i>	-	75	-	26
<i>Lepomis macrochirus</i>	-	3	-	5

than either the cyprinids or *A. gilli* at non-invaded sites (Table 2), while *L. macrochirus* was recorded only at the furthest downstream site, Site 10 (Figure 1).

Forward stepwise DFA selected five habitat variables (Table 3) that discriminated between non-invaded riffles, non-invaded pools, invaded riffles and invaded pools. Canonical analysis indicated that whilst riffles and pools separated completely along Root 1, invaded and non-invaded sites separated only for pool sites along Root 2 (Figure 3).

The three habitat variables that formed the strongest factors in Root 1 were \log_{10} volume and \log_{10} depth, which correlated positively with the root, and \log_{10} velocity, which correlated negatively with the root (Table 4). This indicated that pools were separated from riffles along a gradient of size and velocity, with pools being bigger and deeper, with more slowly flowing water than riffles. The three strongest factors in Root 2 were \log_{10} depth, $\sqrt{\text{particle embeddedness}}$ and \log_{10} sand deposit depth (Table 4), indicating that invaded pools tended to be deeper, with higher sediment loads than non-invaded pools. This could indicate habitat degradation through sedimentation, and may therefore be an additional cause of lowered indigenous fish abundance in the lower Rondegat River.

Spearman rank correlations performed between per-site fish abundance and corresponding mean habitat variable in pools showed that the abundances of *B. calidus* and *P. phlegethon* correlated significantly and positively with habitat depth. Abundance of *P. phlegethon* and *L. capensis* also correlated significantly and positively with density of woody debris (Table 5). In riffles, abundance of *A. gilli* did not correlate significantly with any habitat variable, whilst *P. phlegethon* correlated positively with density of fine debris, and negatively with water velocity (Table 6). No species in either riffles or pools correlated significantly with sand deposit depth or substrate particle embeddedness, suggesting that habitat sedimentation did not affect fish distributions upstream of the bass barrier.

Discussion

The data indicated a marked reduction in indigenous fish abundance and diversity at sites invaded by *M. dolomieu*. It is unclear whether *G. zebratus* ever occurred in the lower river. In this study, it was found only in small numbers at the uppermost Sites 1 and 2, although it is a very difficult species to detect either by daylight snorkelling or electrofishing. Logistical and safety issues prevented the employment of night snorkelling to assess *G. zebratus* distribution. The

absence of *A. gilli*, *B. calidus* and *P. phlegethon* appears to be the result of genuine extirpation, as these species are known to have inhabited the Olifants River mainstem into which the Rondegat feeds (Gaigher 1973, Skelton 1987). Both *B. calidus* and *P. phlegethon* are thought to have disappeared from the Olifants River prior to 1958, and have not been recorded there (Gaigher 1973). Both alien fish and habitat degradation are thought to have contributed to the loss of these species in the Olifants River, although the impact of *M. dolomieu* and its relative, the introduced largemouth bass (*Micropterus salmoides* Lacepède), has long been considered the primary cause (Skelton 1987). The apparent loss of these species, as well as juvenile *L. capensis* recruits at bass-invaded sites, strongly suggests direct predatory impacts. Furthermore, it appears that predation by *M. dolomieu* has caused a collapse in the recruitment of *L. capensis* in the lower river, and that the lower population now sustains itself only through immigration of adults from upstream of the waterfall barrier.

Micropterus dolomieu has been implicated in the loss of indigenous fishes in several Canadian lakes, where it has reduced the diversity of small cyprinids through predation (MacRae and Jackson 2001). It has, however, not attained the international notoriety of its close relative *M. salmoides*, which has been implicated in the loss of indigenous fish in Europe (Godinho and Ferreira 2000), Japan (Maezono and Miyashita 2003) and southern Africa (De Moor and Bruton

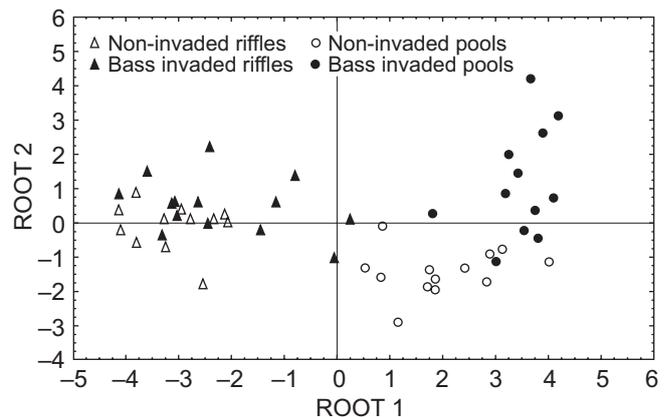


Figure 3: Canonical analysis of discriminant function analysis model discriminating non-invaded riffles and non-invaded pools from bass-invaded riffles and bass-invaded pools. Canonical roots generated from discriminating habitat factors, as shown in Table 3

Table 3: Habitat variables selected by forward-stepwise discriminant function analysis for a model to discriminate significantly between invaded pools, invaded riffles, non-invaded pools and non-invaded riffles ($P < 0.05$)

Step	Variable	Wilks' Lambda	F-remove (3, 42)	p-level
1	\log_{10} volume (m^3)	0.058	3.76	0.01
2	\log_{10} $\sqrt{\text{velocity}}$ ($\text{m}\cdot\text{s}^{-1}$)	0.084	11.93	0.00009
3	\log_{10} depth (m)	0.071	7.89	0.0002
4	$\sqrt{\text{embeddedness}}$ (%)	0.076	9.23	0.00008
5	\log_{10} sand deposit depth (m)	0.073	8.50	0.0001
6	\log_{10} woody debris ($\text{fronds}\cdot\text{m}^{-2}$)	0.049	1.16	0.33

1988, Gratwicke and Marshall 2001). *Micropterus salmoides* has heavily impacted fish diversity in rivers in Zimbabwe (Gratwicke and Marshall 2001), where in some tributaries its presence corresponded to a 99% reduction in cyprinid abundance. This species has also eradicated all indigenous fish in an invaded section of the Blindekloof River in the Eastern Cape (Skelton 1993). *Micropterus dolomieu* appears to have been less successful than *M. salmoides* in South Africa's summer-rainfall regions outside of the water-rainfall CFR, although *M. dolomieu* has established in tributaries of the Limpopo system and is thought to have had a negative impact on indigenous fish there (De Moor and Bruton 1988).

Although no bass captured during this study were found to have recently eaten indigenous fishes, Shelton (2003) captured specimens of *M. dolomieu* with the Breede River redbfin (*Pseudobarbus burchelli* Smith) in their stomachs. The lack of indigenous fish in *M. dolomieu* stomachs in the Rondegat River is probably a reflection of the length of time since they disappeared from the lower river, as Skelton (1993) concluded when he examined the fish-less stomachs of *M. salmoides* captured in the Blindekloof River.

Enquiry into additional causes of fish losses in the lower river found increased sedimentation to be a physical disturbance that partly characterised the lower, bass-invaded sites. Siltation from bank erosion has long been seen as a major threat to fish communities in the United States, where the chief impacts on fish are listed as physical alteration of stream habitat and decreased survival of eggs and larvae (Walser and Bart 1999). Sedimentation removes benthic refugia for fish and insects, as well as reducing productivity in the stream, and was mentioned by Skelton (1987) and Gaigher *et al.* (1980) as being a potential threat to indigenous fishes in the CFR.

Canonical analysis of the DFA results indicated that there

was a gradient of increasing sedimentation from upstream to downstream sites, particularly in the pools. In contrast, the riffles did not separate out well in the canonical analysis, indicating that their physical attributes did not change much along the length of the river. The increased sedimentation at invaded pools may be linked to a naturally decreasing river gradient, which would raise the amount of sediment deposited in these slower habitats during floods. It could also be linked to increased transformation of the riparian zone at sites in the middle reaches by alien invasive *Acacia* species, which are known to increase sediment levels in rivers through bank destabilisation (Rowntree 1991, Ractliffe *et al.* 2003), or by cattle at sites in the lower reaches, which increase sedimentation by trampling the riverbank (Belsky *et al.* 1999). Interestingly, the abundance and distribution of fish in this study indicate that alien riparian trees have had little, if any, impact on indigenous fish assemblages and may, in fact, benefit some species by increasing availability of undercut banks and woody snags, which the fish utilise for instream cover. This supposition is supported by data gathered on *L. capensis* and *P. phlegethon*, as these species' abundance correlated positively with density of woody debris in pools.

No significant correlations were detected between indigenous fish abundance and measures of sedimentation at non-invaded sites, even though some of the lower non-invaded sites were just as sandy as sites below the barrier. This result strongly suggests that sedimentation had no direct impact on local abundance of indigenous fish in the Rondegat River. Sedimentation may, however, have had an indirect impact on *A. gilli*, by removing benthic cover in which to hide from predators such as bass. Bills (1999) found *A. gilli* and its close relative *Austroglanis barnardi* (Skelton) to co-exist with *M. dolomieu* in rivers with complex rocky substrates, but not in sandier rivers, and surmised that sedimentation increased the predatory impact of

Table 4: Factor structure matrix for canonical roots generated by discriminant function analysis; r-value indicates linear correlation of variables to canonical roots. The three strongest factors in each root are shown in bold type

	Root 1 r-value	Root 2 r-value
\log_{10} volume (m ³)	0.68	0.08
\log_{10} $\sqrt{\text{velocity}}$ (m.s ⁻¹)	-0.44	0.01
\log_{10} depth (m)	0.67	0.45
$\sqrt{\text{embeddedness}}$ (%)	0.15	0.20
\log_{10} sand deposit depth (m)	0.17	-0.13
\log_{10} woody debris (fronds.m ⁻²)	0.19	0.08

Table 5: Spearman rank correlations between species abundance and habitat variables in pools. Only significant ($p < 0.05$) correlations are shown

	n	Spearman rank (R)	r ²	p
<i>Barbus calidus</i> and volume	13	0.62	0.39	0.02
<i>Barbus calidus</i> and depth	13	0.69	0.47	0.008
<i>Pseudobarbus phlegethon</i> and volume	13	0.65	0.43	0.01
<i>Pseudobarbus phlegethon</i> and woody debris	13	0.69	0.47	0.008
<i>Labeobarbus capensis</i> and woody debris	13	0.61	0.37	0.02

Table 6: Spearman rank correlations between species abundance and habitat variables in riffles. Only significant ($P < 0.05$) correlations are shown

	n	Spearman rank (R)	r ²	P
<i>Pseudobarbus phlegethon</i> and velocity	12	-0.73	0.54	0.006
<i>Pseudobarbus phlegethon</i> and fine debris	12	0.75	0.56	0.004

M. dolomieu on *A. gilli*. Synergy between the loss of benthic cover and predation pressure from alien predators, resulting in the extirpation of benthic indigenous fish, was considered a likely factor behind the severity of alien nembwe (*Serranochromis robustus* Boulenger) predation on benthic catfish (*Chiloglanis* spp.) in Zimbabwe (Gratwicke and Marshall 2001), and has been suggested by Skelton (1987) to occur in the CFR.

The results presented here demonstrate the dramatic impact that *M. dolomieu* can have on indigenous fish abundance in the CFR. The results also indicate that, whilst sedimentation may have enhanced the predatory impact of *M. dolomieu* on *A. gilli*, changes in physical habitat within the Rondegat River could not explain the loss of small cyprinids at bass-invaded sites. This makes it very likely that *M. dolomieu* has been the main cause of the losses of indigenous fish species in other invaded tributaries of the Olifants River (Skelton 1987, De Moor and Bruton 1988), as these rivers all have similar physical characteristics (Bills 1999). With this in mind, controlling the further spread of *M. dolomieu* within the CFR must be seen as a conservation priority. A further step towards ensuring the survival of native fish in this fish diversity hotspot should be targeted eradication programmes designed to remove *M. dolomieu* and other invasive alien fish from the tributaries of the Olifants River, in order to increase the range and conservation status of the indigenous fish. Projects of this nature have been successfully carried out in America (Gresswell 1991) and Australia (Lintermans 2000), using piscicides. In attempting to manage our indigenous fishes, it is critical that we examine all potential threats to a species' survival, and do not ignore secondary threats such as sedimentation, which may exacerbate the primary threat of predation from alien fish. Only then will we be able to develop effective and sustainable rehabilitation programmes.

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