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Spatial extent and consequences of black bass (Micropterus *spp.*) *invasion in a Cape Floristic Region river basin*

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ABSTRACT

1. Black bass (*Micropterus* spp.) are invasive fish that have adversely affected native fish communities in many regions of the world. They are known to threaten native fishes in the Cape Floristic Region of South Africa, a fish endemism hotspot, but the extent of invasion and consistency of impacts at river basin scales are not known.
2. This study investigated the extent of black bass invasions in 41 tributaries in the Olifants–Doorn River basin (ODR) using above-water observations, snorkel surveys and underwater video assessment. Physical barriers that defined the upper limit of black bass distributions in tributaries were measured. Black bass impacts on the densities and diversity of the native fish fauna across the basin were assessed.
3. Black bass were found to have invaded 81% of stream habitat in the basin, with *Micropterus dolomieu* and *Micropterus punctulatus* consistently being blocked by physical barriers in the form of waterfalls, cascades and chutes. These barriers had a minimum height of 49 cm and a median height of 1.09 m.
4. Small-bodied cyprinid minnows (*Barbus calidus* and *Pseudobarbus phlegethon*) were consistently extirpated from black bass-occupied reaches, while larger cyprinid species co-occurred with black bass, but only when they were larger than 10 cm.
5. These findings demonstrate the severe habitat loss to native fishes as a result of black bass invasion, and the prevention of the further spread and removal of black bass from these rivers should be a high conservation priority.
6. The study demonstrates the critical role physical barriers play in preventing the extinction of native fish species and provides a basis for the planning of conservation interventions such as the construction of in-stream invasion barriers.

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KEY WORDS: *Micropterus dolomieu*; *Micropterus punctulatus*; *Micropterus salmoides*; *Pseudobarbus phlegethon*; *Barbus calidus*; impacts; invasion barriers; predation; Mediterranean climate region

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INTRODUCTION

Freshwater game fishes have been moved around the world to create new sport angling opportunities, and have often successfully established alien populations as a result of concerted stocking efforts (Cambray, 2003; Ellender and Weyl, 2014). A result has been the homogenization of freshwater fish faunas around the world, with river systems in many regions today containing more alien than native fish species (Leprieur *et al*., 2008; Marr *et al*., 2010). Predatory and competitive interactions between native and alien fishes appear to be the main reasons for the reduction of native fish densities and diversity in many invaded environments (Cox and Lima, 2006; Castaldelli *et al*., 2013; Ellender and Weyl, 2014). Owing to the dendritic connectivity of freshwater ecosystems, natural barriers to upstream movement can play a critical role in mitigating the process of fish community homogenization (Rahel, 2007), particularly in systems where alien fish are stocked in the lower reaches of river networks (Adams *et al*., 2001). Understanding what constitutes a natural barrier for invasive aquatic species is essential for understanding the extent of invasions, assessing invasion risk and setting priorities for conservation action (Lodge, 1993).

Black bass, a collective term for North American *Micropterus* species, are popular angling species that have been introduced into novel environments in North and South America, Africa, Europe and Asia (Casal, 2006; Loppnow *et al*., 2013; Ellender and Weyl, 2014). While such introductions have resulted in new opportunities for sport fishing, introductions of predatory black bass into previously predator-depauperate environments have resulted in severe impacts on native fish communities (Jackson, 2002; Iguchi *et al*., 2004; Clarkson *et al*., 2005; Weyl *et al*., 2013, 2014). Although assessments are largely limited to isolated case studies (Woodford *et al*., 2005; Ellender *et al*., 2011; Kimberg *et al*., 2014; Shelton *et al*., 2014), it is evident that invasions generally result in the extirpation of small-bodied native fishes (Elvira and Almodovar, 2001; Moyle, 2002; Leunda, 2010; Ellender and Weyl, 2014). Particularly affected are fishes in Mediterranean climate regions, such as California in the USA, the Iberian Peninsula in Southern Europe and the Cape Floristic Region (CFR) in Africa, where high degrees of endemism and small natural distribution ranges make native fishes vulnerable to predation (Moyle, 2002; Leunda, 2010; Weyl *et al*., 2014). Understanding the extent, nature and limits of black bass invasions is therefore of fundamental importance in developing and prioritizing conservation approaches.

The present study aimed at characterizing the nature of natural barriers that limit the distribution of black bass in the Olifants–Doorn River basin (ODR), a large river basin in the CFR, and one of the most important areas of freshwater fish endemism in Africa (Linder *et al*., 2010). The ODR presents an excellent natural experiment with which to assess black bass invasions in the context of a river basin. Three black bass species, *Micropterus salmoides*, *Micropterus dolomieu* and *Micropterus punctulatus* were introduced and became established in the ODR more than 80 years ago (Barnard, 1943; Harrison, 1952; Jubb, 1961; van Rensburg, 1966; Gaigher, 1973; Gaigher *et al*., 1980; Swartz, 2005). Most recorded black bass introductions were into lower mainstream river reaches and impoundments (De Moor and Bruton, 1988), therefore contemporary invasions into sensitive tributaries are primarily upstream processes that are limited by the presence of physical barriers such as cascades and waterfalls (Harrison, 1953; Gaigher, 1973; Weyl *et al*., 2014). By assessing presence or absence of the three black bass species in 41 ODR tributaries and by determining the features that demarcated the upper distribution limit in invaded streams, this study contributes towards a better understanding of invasion processes, an important component of conservation planning. As the ODR contains 10 of the 19 currently described fish species that are endemic to the CFR (Weyl *et al*., 2014), a second aspect of the study was to assess the extent of black bass impacts on native fish communities in this river basin.

MATERIAL AND METHODS

Study area

The ODR system drains an area of 56 446 km^2 in the Western and Northern Cape Provinces of South Africa and consists of four management areas: the Olifants, Knersvlakte, Doorn and Koue Bokkeveld (DWAF, 2005, Figure 1). The main river is known as the Olifants River with the Doring and Sout Rivers forming the two largest tributaries. The topography varies from flat valleys in the north and east to sandstone mountains with a maximum altitude of 2073 m in the south and west. There is a large range in climatic conditions due to the variation in topography. Most of the rainfall occurs in the winter months (May to August) and is concentrated in the southern and central higher mountain areas of the Cederberg, Groot Winterhoek and Koue Bokkeveld Mountains, with the highest rainfall (>1400 mm year^{-1}) recorded in the Groot Winterhoek Mountains (DWAF, 2005). The geology of these mountain areas is

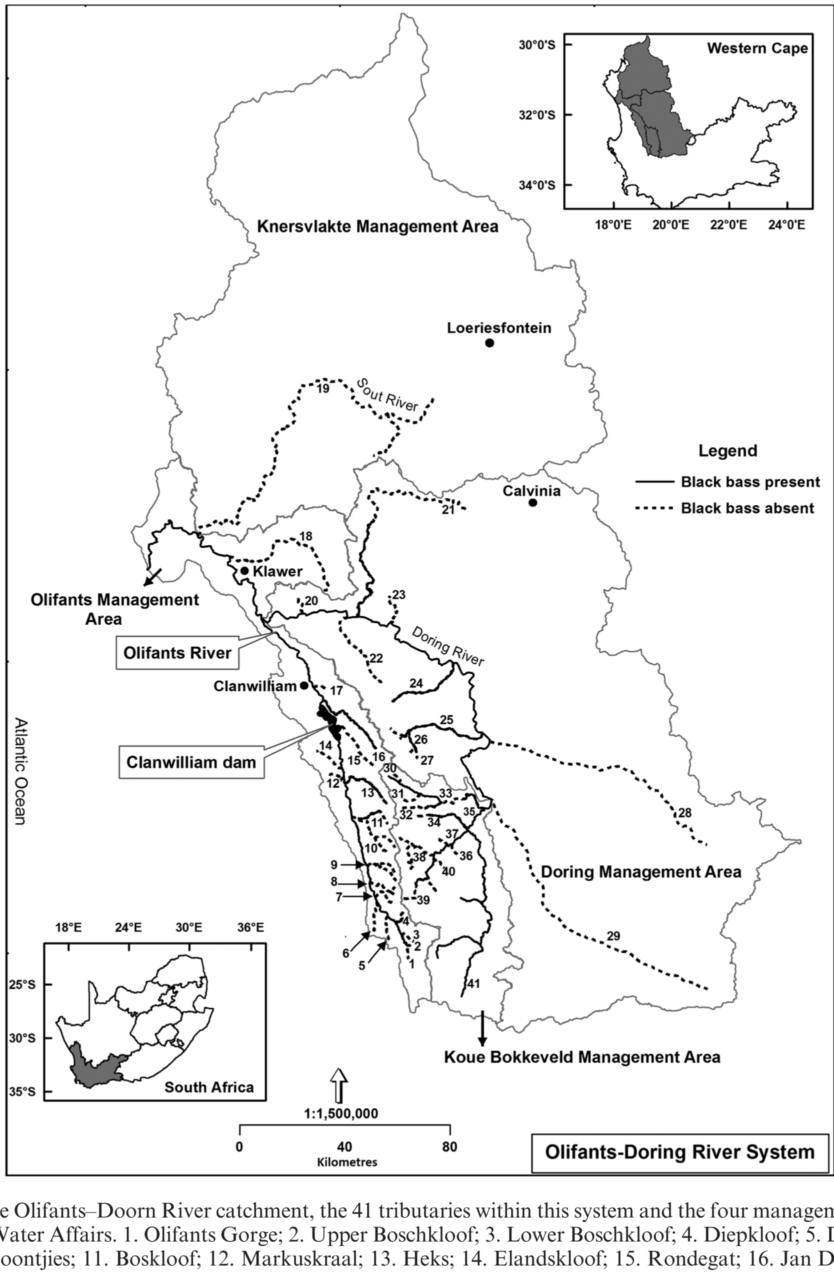

Figure 1. A map showing the Olifants–Doorn River catchment, the 41 tributaries within this system and the four management areas it has been divided into by the Department of Water Affairs. 1. Olifants Gorge; 2. Upper Boschkloof; 3. Lower Boschkloof; 4. Diepkloof; 5. Dwars; 6. Ratel; 7. Oudste; 8. Thee; 9. Noordhoeks; 10. Boontjies; 11. Boskloof; 12. Markuskraal; 13. Heks; 14. Elandskloof; 15. Rondegat; 16. Jan Dissels; 17. Kliphuis; 18. Troe Troe; 19. Sout; 20. Gif; 21. Oorlogskloof; 22. Brandewyn; 23. Kransgat; 24. Biedouw; 25. Tra Tra; 26. Eselbank; 27. Martiensrus; 28. Tankwa; 29. Upper Doring; 30. Driehoeks; 31. Dwars; 32. Krom; 33. Matjies; 34. Breekkrans; 35. Groot; 36. Tuinskloof; 37. Rietkloof; 38. Twee; 39. Leeu; 40. Langkloof; 41. Riet.

dominated by Table Mountain sandstone and sandstone fynbos vegetation types (Mucina and Rutherford, 2006), while most of the tributaries draining from these areas into the Olifants River (n = 16) are perennial. The water of these mountain tributaries is typically clear, low in nutrients and has a relatively low pH (DWAF, 2005). The northern (Sout River) and western Doring River tributaries are located in a summer rainfall (November – March) area which receives < 200 mm year^{-1} of rainfall and this give rise to seasonal or ephemeral streams (DWAF, 2005). The geology of these two relatively flat areas is dominated by shale that results in more turbid water than in mountain streams. The vegetation of these two arid areas is dominated by succulent vegetation types (Mucina and Rutherford, 2006).

Extent of invasion

The mainstream Olifants River and Doring River are considered fully invaded by black bass (Impson, 1999; Swartz, 2005). The current study therefore focused on the 41 tributaries (Figure 1). Field surveys to determine the distribution of black bass and the location of the barriers that contain their upstream spread within the tributaries were conducted between October 2012 and September 2014. Fish distribution databases held at the South African Institute for Aquatic Biodiversity and CapeNature were used to locate the most current upstream distribution records of black bass in the respective tributary streams. Tributaries were surveyed upstream from the nearest previously recorded black bass locality using: (1) above water observations; (2) snorkel surveys; and (3) observation through underwater video assessment (UVA). In shallow areas, black bass could be detected from the river bank owing to the clarity of the water in the majority of the tributaries. When no black bass were observed from the river bank, snorkel surveys were conducted. For UVA, GoPro Hero 2 video cameras were used to assist with verifying the status of black bass in pools deeper than 2 m when the other two methods failed to detect any black bass. If no black bass were located in pools up to 500 m above a waterfall, cascade or chute, this feature was recorded as a natural black bass barrier and its location was mapped using a Garmin Juno 3d GPS. The survey was then continued upstream in each tributary to determine the upper limit of the native fish distribution (excluding the small cryptic *Galaxias zebratus*) and similarly recorded.

Description and classification of barriers

Each barrier was photographed and measured using standard survey equipment (Pentax AP-120 dumpy level, expandable tripod, 5 m graduated staff and a 50 m tape). The barriers were then categorized using the criteria of Powers and Orsborn (1985) into a waterfall, chute or cascade. According to these criteria a waterfall is a feature where water falls over a ledge and loses contact with the substrate, a chute is a steep section where the water stays in contact with the substrate, and a cascade is a series of falls with breaks and pools that maintains a steep gradient and turbulent water surface. In the case of waterfalls the vertical drop was measured, while for chutes and cascades vertical and horizontal measurements were taken to determine the slope gradient. If there was more than one waterfall into a pool, both waterfalls were measured and the lowest waterfall was regarded as the effective drop. For a cascade, the highest vertical drop was regarded as the effective drop that prevented black bass for getting up the barrier.

Impacts

To assess impacts, all fish were counted in the first three pools directly above and below the located black bass barriers in each tributary. Sampled pools were always located within 500 m of the barrier and were (average ± S.D.) 24.2 ± 15.6 m long, 6.6 ± 3.0 m wide and 0.78 ± 0.3 m deep. All fish identifications and counts were made by the same person in all but one tributary (Rondegat River) using a single-pass snorkel survey. The snorkeller entered pools on the downstream side and then swam upstream in a zigzag pattern to the top of the pool. This minimized the initial disturbance and prevented visibility problems. All fish were counted as the snorkeller passed them to reduce double counting of fish. During these counts fish length was estimated visually using the procedure of Weyl *et al*. (2013).

Data analysis

To determine the length of river invaded by black bass, not invaded, and without fish, the river channel was digitized on Google Earth (KML files) and converted into shape files for Arc GIS 10.1. The river was measured using the path feature on Google Earth. To determine if there was a significant difference in barrier height preventing movements of *M. dolomieu* and *M. punctulatus*, barrier heights were compared using a non-parametric Mann–Witney U-test. An initial assessment of native fish and black bass abundance in each pool sampled demonstrated a binary relationship. Subsequently the impact of *Micropterus* spp. on native fishes was expressed as presence vs. absence of native fishes above and below barriers using a 2×2 contingency table.

RESULTS

Distributions

A summary of native and alien fish in each tributary is provided in Table 1. In total 10 native and nine alien fish species were recorded. One stream was fishless and in the 40 streams containing fish, the total species richness ranged from one to 10 species (average ± S.D., 4.3 ± 2.7). Alien species were present in 28 streams. When present, alien species richness ranged between one and five species (average ± S.D., 2.3 ± 1.3) and on average comprised $44 \pm 22\%$ of species in invaded tributaries. Native fish were present in 38 tributaries. At least one black bass species was present in 22 of the tributaries. A summary of the invasion state of different stream types is provided in Table 2. With the exception of one ephemeral stream all tributaries contained fish (Table 2). Black bass were generally absent from ephemeral, seasonal and first-order streams but were generally present in second- to fourth-order streams (stream order according to Strahler, 1957; Table 2).

In 17 of the 22 tributaries invaded by black bass, the invaded reach was from the mainstream up to a discernible physical barrier. In four tributaries, the presence of *M. salmoides* above barriers that restricted *M. dolomieu* and *M. punctulatus* was attributed to direct stocking based on interviews with land owners. The extent of black bass invasion in the ODR system is summarized in Table 1 and Figure 1. Some 70% of the 571 km of tributary stream length was invaded by black bass (Table 1). When the invaded Olifants and Doring River mainstreams are included in the analysis, it was estimated that 81% of the available 961 km stream length have been invaded.

Invasion barriers

Natural barriers restricting the upstream movement of *M. dolomieu* and *M. punctulatus* were found in 17 streams. These were classified into 14 waterfalls, two cascades and one chute. Fifteen of the 17 barriers were bedrock waterfalls or chutes and two barriers (Boskloof and Tra Tra Rivers) were formed in association with macrophytes. In the Tra Tra River, the barrier waterfall is a dense bed of palmiet *Prionium serratum* and sandstone cobbles while on the Boskloof River it is a conglomerate of clay and river cobbles among a stand of common reeds *Phragmites australis* (Figure 2).

A summary of barrier heights and locations is provided in supporting Table S1. Two of the black bass barriers consisted of a series of small falls that formed cascades in the Ratel River and Olifants Gorge. The highest vertical fall in the Ratel River cascade (0.8 m) was regarded as the effective drop that prevented the upstream movement of black bass, and in the Olifants gorge the effective drop was considered to be 0.78 m. Only one chute formed a barrier and this was in the Boontjies River where it had a gradient of 0.538° and a total drop of 1.67 m. There was no significant difference between the barrier heights (range 0.49–3.5 m) that restrict the upstream movement of *M. dolomieu* and *M. punctulatus*. Median and average (± S.D.) barrier heights were 1.09 m and 1.21 ± 0.66 m, respectively. The lowest effective drop was a 0.49 m waterfall on the Heks River.

Table 1. Summary of the Olifants–Doorn River tributaries sampled during this study. Tributary ID numbers correspond to those in Figure 1. O = stream order, E = ephemeral, S = seasonal, 1 – first, 2 = second, 3 = third, 4 = fourth order. IL = length inhabited by fish; INV (%) = percentage of IL occupied by black bass. Native fish: AG = *Austroglanis gilli*; AB = *Austroglanis barnardi*; BA = *Barbus anoplus*; BC = *Barbus calidus*; BS = *Barbus serra*; PP = *Pseudobarbus phlegethon*; BE = *Barbus erubescens*; LS = *Labeo seeberi*; LC = *Labeobarbus capensis*; GZ = *Galaxias zebratus*. Alien fish: MD = *Micropterus dolomieu*; MP = *Micropterus punctulatus*; MS = *Micropterus salmoides*; LM = *Lepomis macrochirus*; ST = *Salmo trutta*; OMY = *Oncorhynchus mykiss*; SC* = *Sandelia capensis*; OMO* = *Oreochromis mossambicus*; TS* = *Tilapia sparrmanii*. Alien (%) = alien species richness as a proportion of species richness. * = native to South Africa but alien to the Olifants–Doorn River

River					Native fish										Alien									
ID	Tributary	O	IL (km)	INV (%)	AG	AB	BA	BC	BS	PP	BE	LS	LC	GZ	MD	MP	MS	LM	ST	OMY	SC*	OMO*	TS*	Alien (%)
1	Olifants Gorge	3	10.5	47					1				1		1	1		1	1					67
2	Boschkloof (U)	2	0.3	0					1															0
3	Boschkloof (L)	2	0.0	0										1										0
4	Diepkloof	2	6.6	65				1							1					1				67
5	Dwars	2	2.0	49	1			1	1				1		1									20
6	Ratel	3	7.7	28	1			1	1				1		1	1								33
7	Oudste	1	7.5	0	1			1		1				1										0
8	Thee	3	10.4	49	1	1		1		1			1	1		1							1	25
9	Noordhoeks	3	18.0	0	1	1		1		1			1	1									1	14
10	Boontjies	3	12.4	47	1			1					1		1	1							1	50
11	Boskloof	2	10.7	1	1			1		1			1	1	1	1							1	38
12	Markuskraal	2	1.2	0			1																1	50
13	Heks	3	22.3	95	1	1		1							1									25
14	Elandskloof	2	0.3	0			1																	0
15	Rondegat	2	21.7	6	1			1		1			1	1	1	1							1	38
16	Jan Dissels	3	33.7	94	1			1	1				1	1	1									17
17	Kliphuis	S	0.2	0			1																	0
18	Troe Troe	S	1.1	0			1																	0
19	Sout	E	0.0	0																		1		100
20	Gif	S	4.2	0					1			1											1	33
21	Oorlogskloof	S	71.1	74			1		1			1	1		1	1		1					1	50
22	Brandewyn	S	3.1	0				1					1										1	33
23	Kransgat	S	1.0	0			1					1											1	33
24	Biedouw	S	33.6	97	1			1	1			1	1			1		1						29
25	Tra Tra	3	34.6	99	1			1	1			1	1	1	1	1		1					1	40
26	Eselbank	2	10.8	82	1			1	1				1		1	1								33
27	Martiensrus	S	0.0	0			1																	0
28	Tankwa	E	0.0	0			1																	0
29	Doring (U)	E	0.0	0																				0
30	Driehoek	3	25.7	96				1	1	1			1	1			1							17
31	Dwars	2	0.0	0										1										0
32	Krom	2	8.1	100	1												1	1		1				75
33	Matjies	3	24.5	55	1			1	1			1	1		1	1				1				38
34	Breekkrans	2	23.5	82	1		1	1		1					1	1								33
35	Groot	4	31.7	100									1		1	1								0
36	Tuinskloof	S	0.0	0			1																	0
37	Rietkloof	S	0.1	0			1																	0
38	Twee	3	35.1	3							1		1	1	1	1		1		1	1			67
39	Leeu	3	20.6	100									1		1	1	1	1						80
40	Langkloof	1	3.0	0	1				1															0
41	Riet	S	75.9	100			1										1	1					1	83

Table 2. Number of tributaries categorized by stream order containing native and alien fish species as well as those containing black bass *Micropterus* spp. in the different tributary categories of the Olifants–Doorn River system, Western Cape, South Africa

	Tributaries			
Stream Order	Total	Native	Alien	Black bass only
Perennial 1st order	2	2	0	0
Perennial 2nd order	12	12	8	7
Perennial 3rd and 4th order	13	12	12	12
Ephemeral	3	1	1	0
Seasonal	11	11	6	3
Total	41	38	27	22

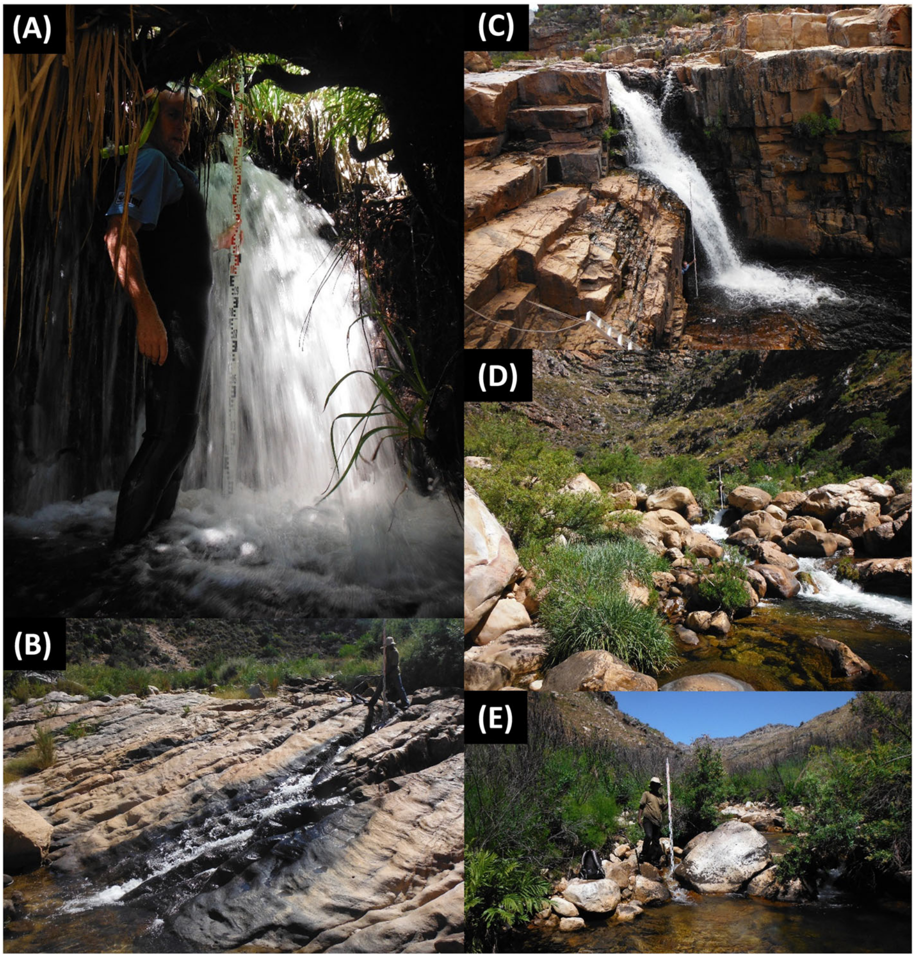

Figure 2. Typical black bass barriers on the Olifants–Doorn River system. (A) A 1.22 m high water fall on the Tra Tra River formed by dense palmiet *Prionium serratum* and sandstone cobbles. (B) A chute with a gradient of 0.54° and a total drop of 1.67 m was the barrier on the Boontjies River. (C) The 7 m high waterfall on the Twee River. (D) The cascade in the Olifants Gorge with an effective drop of 0.78 m. (E) The lowest barrier is the 0.49 m fall on the Heks River.

Impacts on native fish

Relationships between abundance of black bass and abundance of individual native species across all snorkelled pools are shown in Figure 3. It was evident that the relationship between black bass and native fish abundance is binomial, with only large-bodied native fishes (>10 cm; *Labeobarbus capensis*, *Labeo seeberi* and *Barbus serra*) occasionally co-occurring with black bass. Small minnow species (<10 cm) were generally absent in the presence of

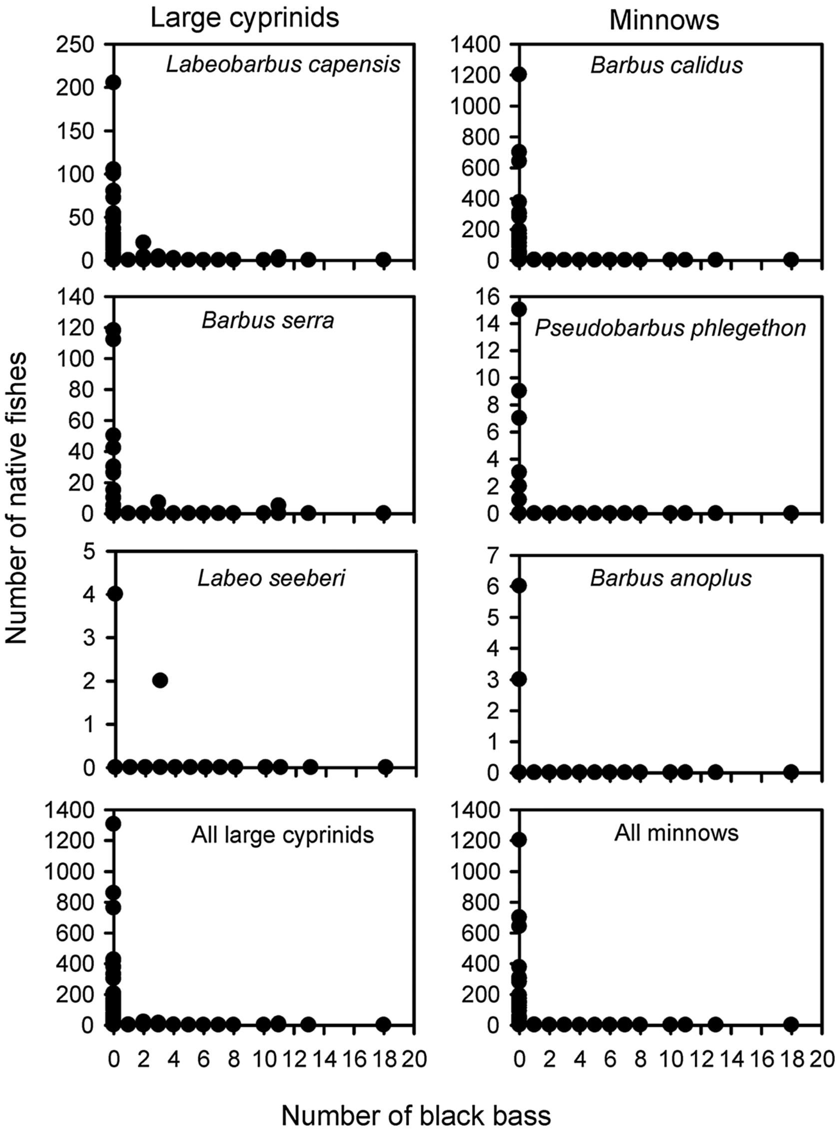

Figure 3. Relationships between abundance of black bass and abundances of individual native species across 96 pools sampled using snorkel surveys on the Olifants–Doorn River system, Western Cape, South Africa.

bass, the only exception being the two *Barbus calidus* observed in a pool that also contained black bass (Figure 3).

The presence and absence of native fishes above and below the 17 invasion barriers identified are presented in Table 3. Only six cyprinid species were used in analyses because the others were either not detected immediately above any barriers despite being present further upstream (*Barbus erubescens*) or because they were inadequately represented in daytime snorkel surveys because they were small and cryptic (*Galaxias zebratus*) or nocturnal (*Austroglanis gilli* and *Austroglanis barnardi*). Results of the contingency table analysis of the presence or absence of native fishes above and below the 17 barriers are provided in Table 3. There was no significant difference in the presence of large cyprinids (*L. capensis*, *B. serra*, *L. seeberi*) above and below barriers. However, the small minnows *B. calidus* ($P < 0.001$) and *Pseudobarbus phlegethon* ($P < 0.05$) were present in a significantly higher proportion of tributaries above barriers than below. In bass-invaded tributaries, *Barbus anoplus* was sampled from one site above the bass barrier

Table 3. Summary of the chi-square 2 × 2 contingency table analysis of the dependence of the presence/absence of native fishes on river reach (below or above invasion barriers) in the Olifants–Doorn River system, Western Cape, South Africa. n = 17 tributaries

Species	Below (present/absent)	Above (present/absent)	Chi square value	Df	*P*
Barbus calidus	1/16	11/6	12.8	1	<0.001
Labeobarbus capensis	5/12	10/7	2.98	1	0.08
Barbus serra	2/15	4/13	0.81	1	0.37
Barbus anoplus	0/17	1/16	1.03	1	0.31
Pseudobarbus phlegethon	0/17	4/13	4.53	1	0.03
Labeo seeberi	1/16	1/16	0	1	1
All small-bodied minnows	1/16	12/5	15.06	1	<0.001
All native fishes	6/11	15/2	10.08	1	0.001

in the Oorlogskloof (one specimen) and Eselbank River (one specimen), respectively.

Data on fish length are shown in Figure 4. These data demonstrate that *M. dolomieu* and *M. punctulatus* were predominantly small individuals < 20 cm TL and that all native fishes that were observed together with bass were large (>10 cm TL) specimens. The fish communities at sites above barriers were dominated by small-bodied minnows (mainly *B. calidus* and *P. phlegethon*) and juveniles of the larger *L. capensis* and *B. serra* (Figure 4)

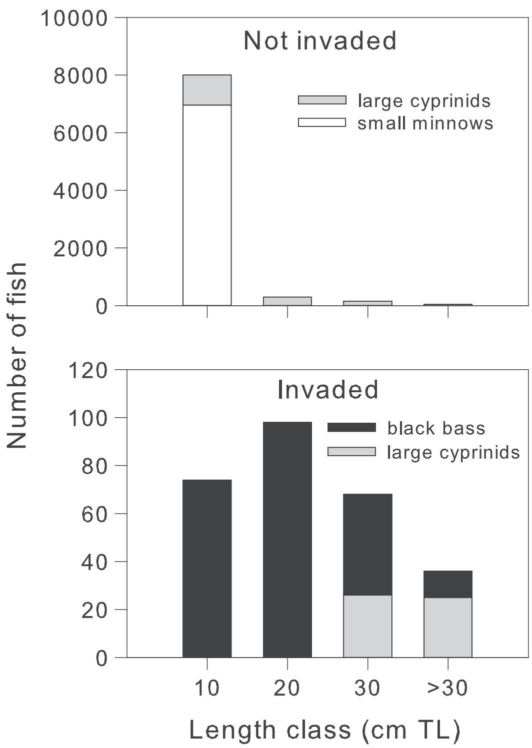

Figure 4. Length structure (10 cm total length groups) of fishes in black bass invaded and non-invaded tributaries in the Olifants–Doorn River basin, Cape Floristic Region, South Africa. Lengths were estimated during snorkel surveys.

DISCUSSION

Black bass have been present in the ODR system for at least 80 years (Harrison, 1952) and because barriers to invasion are generally located in the headwaters of tributaries, 81.5% of the historical native cyprinid range in the ODR system is now invaded by black bass. This is of concern because comparisons of native fish presence/absence, density and length structure above and below the distribution limits of *M. dolomieu* and *M. punctulatus* demonstrate that black bass extirpate smaller native fishes from invaded pools (Figure 4). The small spatial scale of instream observations (assessments 500 m above and below black bass barriers) and the location of study sites in headwater streams where human impacts are negligible, indicates that the main driver explaining native fish abundance across the ODR basin was the presence or absence of black bass, as was previously postulated for individual rivers (Woodford *et al*., 2005; Weyl *et al*., 2013, 2014).

This observation is supported by the rapid recovery of native fishes in a 4 km section of the Rondegat River, after *M. dolomieu* were eradicated as a conservation intervention (Weyl *et al*., 2014). These results are also in agreement with early anecdotal accounts of black bass impacts on CFR fishes (Jubb, 1961; van Rensburg, 1966; Gaigher, 1973), as well as with the results of quantitative assessments of the impact of black bass on minnow populations in other parts of South Africa (Woodford *et al*., 2005; Ellender *et al*., 2011; Kimberg *et al*., 2014; Shelton *et al*., 2014), Japan (Iguchi *et al*., 2004); the western USA (Clarkson *et al*., 2005) and the Iberian Peninsula in Europe (Godinho and Ferreira, 2000).

The extirpation of juveniles (<10 cm TL) of larger cyprinid fishes such as *L. capensis* is also consistent with prior observations of population size structure in parts of the Rondegat River invaded by *M. dolomieu* (Weyl *et al.*, 2013, 2014). An experiment on predation of *M. dolomieu* on hornyhead chub *Nocomus bigutatus*, showed that small chub (6–6.5 cm) were three times more likely to be preyed upon than larger (10–11 cm) chub (Schlosser, 1988), and the results in the present study indicate similar vulnerability. The size structure of native fishes in zones invaded by black bass included only fishes >10 cm while those in non-invaded pools were dominated by fish < 10 cm in length. Although there was co-occurrence of black bass with two other alien species at some sites, *Tilapia sparrmanii* (seven tributaries) and *Lepomis macrochirus* (six tributaries), the consistency of impacts on native cyprinids across all 17 invaded tributaries indicate that bass predation was most likely the primary driver. It is notable that the impact of black bass on small native fishes was both complete and consistent enough across the ODR basin that their absence could be used as an indicator of the presence of bass, whether or not the invader was detected. The effectiveness of black bass at extirpating native fishes is probably exacerbated by the clear water and lack of refuge for native fish in the form of aquatic vegetation within this system. Both clear water and a lack of refuge have been shown to increase black bass hunting success (Takamura, 2007; Brown *et al.*, 2009a, b; Alexander *et al.*, 2014). Understanding the factors that limit black bass occurrence and distribution in invaded river systems is therefore of great importance with regard to conservation planning.

With the exception of Sout River where salinity (37 ppt) exceeded black bass tolerances (17 ppt for *M. salmoides*, Brown *et al.*, 2009b), the reason for the absence of black bass from 18 other tributaries is uncertain because temperature and turbidity were generally within the preferred range of the three black bass species (De Moor and Bruton, 1988; Sweka and Hartman, 2003; Impson *et al.*, 2007; Brown *et al.*, 2009a). It is possible, however, that flow consistency may well be the limiting factor as ephemeral and seasonal tributaries generally did not contain black bass (Table 1) and in the three seasonal tributaries where they occurred (Riet River, Biedouw River and Oorlogskloof River), deep pools provide refugia during the dry season (December–April). This was similar to observations on the occurrence of *M. salmoides* and *M. dolomieu* in the episodic Blindekloof River, Eastern Cape Province, South Africa (Ellender *et al.*, 2011).

Observation data from the present study suggests differences in invasiveness between the black bass species in the ODR. *Micropterus dolomieu* and *M. punctulatus* have invaded upstream to discernible barriers in the larger tributaries, while *M. salmoides* was more localized, occurring only in four headwater plateau reaches where flows are slow. The lack of *M. salmoides* in most tributaries may be because the high-gradient streams with bedrock-dominated morphology, fast-flowing turbulent water and sparse aquatic vegetation are not preferred habitat for *M. salmoides*, which inhabit wide, slow-moving waters with aquatic vegetation (Brown *et al.*, 2009b). Where *M. salmoides* were present in headwater streams above barriers, this was always as a result of direct introduction into farm ponds in headwater plateaux from where they had escaped to establish populations (Paxton, 2008; Marr *et al.*, 2012). It is therefore important that stocking of off-channel ponds in headwater catchments be regulated as escapees from such ponds could facilitate invasions of *M. salmoides* into reaches from which they would otherwise have been excluded.

Invasion barriers

Natural barriers to upstream movement play a critical role in mitigating the impacts of invasions by alien fishes (Adams *et al.*, 2001; Rahel, 2007). In the case of introduced brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) for example, the presence of natural or artificial barriers has mitigated their harmful impacts on native fish biodiversity in South Africa (Shelton *et al.*, 2015), Australia (Jackson *et al.*, 2004), New Zealand (Woodford *et al.*, 2011) and North America (Bjornn and Reiser, 1991; Fausch *et al.*, 2008). These barriers, however, can present a conservation dilemma, in that while protecting headwater stream species from invasive fish incursions, they could also hamper conservation if the threatened species require access to the invaded reaches for part of their life cycles (Fausch *et al*., 2008; Gangloff, 2013; Rahel, 2013). Information on what constitutes effective barriers for invasive fishes is therefore important for identifying approaches for developing selective barriers that prevent the passage of unwanted alien species while potentially allowing movements of native biota (Rahel, 2013).

In the ODR basin, black bass invasions are the primary conservation concern facing native species, so the barriers restricting their upward expansion represent indisputable tools for conservation management. Understanding what constitutes a natural barrier for invasive black bass in this system will assist in assessing invasion risk and identifying priorities for conservation action (Lodge, 1993) in other CFR streams. The results of this study demonstrated that in the ODR, both *M. dolomieu* and *M. punctulatus* invasions were limited by similar barriers. Although there is a general paucity of literature on what constitutes a natural black bass barrier, some literature suggests what heights of artificial barriers prevent black bass movements. Gomez and Wilkinson (2008), considered a vertical drop of 46 cm as a barrier to *M. dolomieu* movement and Meixler *et al*. (2009) modelled their jumping ability (using maximum darting speed 3.42 m s^{-1} and average 38 cm TL) at 60 cm. These measurements correspond with the results of this study, as the lowest natural black bass barrier was 0.49 m. However, the Hex River was the only barrier at this low height and black bass were recorded above barriers of 50 cm height in at least three of the other surveyed tributaries (Biedouw River, Jan Dissels River and Breekkrans River). As a result the median of 1.09 m is a more appropriate barrier height for identifying natural black bass invasion barriers in other systems. This height should not be considered a generalized barrier height for all invasive fish species in South African streams, as rainbow trout were found upstream of a barrier 1.44 m high in this study (Diepkloof River, Table 1).

RECOMMENDATIONS

This study has demonstrated black bass to be a driving force behind the restricted ranges of native endemic fish species in the ODR catchment, and that preventing the further spread of these invasive predators will be critical to the continuing survival of threatened fishes within this catchment. The study also highlighted the importance of natural barriers as important conservation tools to prevent total stream occupation by alien fish. The focus of conservation efforts in future should be to prevent the human assisted movement of black bass above natural barriers. The eradication of bass in tributaries where appropriate should be considered as a management priority to increase the range of the threatened native species across the ODR catchment, and in similar basins across the CFR (Weyl *et al*., 2014). The information on what constitutes a natural barrier to black bass invasions in the ODR should therefore be incorporated in the planning of conservation interventions such as the construction of instream invasion barriers.

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