



Resilience of imperilled headwater stream fish to an unpredictable high-magnitude flood

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Dates:

Received: 04 Nov. 2014

Accepted: 27 Jan. 2015

Published: 22 May 2015

How to cite this article:

Ellender, B.R. & Weyl, O.L.F., 2015, 'Resilience of imperilled headwater stream fish to an unpredictable high-magnitude flood', *Koedoe* 57(1), Art. #1258, 8 pages. <http://dx.doi.org/10.4102/koedoe.v57i1.1258>

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Headwater stream fish communities are increasingly becoming isolated in headwater refugia that are often cut off from other metapopulations within a river network as a result of non-native fish invasions, pollution, water abstraction and habitat degradation downstream. This range restriction and isolation therefore makes them vulnerable to extinction. Understanding threats to isolated fish populations is consequently important for their conservation. Following a base-flow survey, a high-magnitude flood (peak flow of 1245 m³s⁻¹) provided an opportunity to investigate the response of endangered Eastern Cape redbfin *Pseudobarbus afer* populations to a natural disturbance in the Waterkloof and Fernkloof streams, two relatively pristine headwater tributaries of the Swartkops River system within the Groendal Wilderness Area, Eastern Cape Province, South Africa. *Pseudobarbus afer* had limited distributions, occupying 3 km in both the Fernkloof and Waterkloof streams. Fish population assessments before and after the flood event indicated that there were no longitudinal trends in *P. afer* abundance before or after the flood, but overall abundance post-flooding in the Fernkloof stream was higher. There were no noticeable changes in *P. afer* size structure pre- and post-flood. *Pseudobarbus afer* showed resilience to a major flooding event most likely related to evolution in river systems characterised by environmental stochasticity.

Conservation implications: This research provides insight into the population level responses of native headwater stream fishes to unpredictable natural disturbance. Of particular relevance is information on their ability to withstand natural disturbances, which provides novel information essential for their conservation and management especially as these fishes are already impacted by multiple anthropogenic stressors.

Introduction

Headwater stream fishes in South Africa are increasingly being isolated in small fragmented headwater refuges as a result of competition with and predation by non-native fishes, downstream water abstraction, pollution and habitat degradation (Marr *et al.* 2010; Tweddle *et al.* 2009; Weyl *et al.* 2014). Protected areas play an important role in conserving headwater fishes by preserving habitats and preventing non-native fish introductions (Russell 2011). It is increasingly recognised, however, that the persistence of fishes in these environments may be dependent on dispersal between complementary habitats for reproduction, feeding, rearing and disturbance avoidance (Franssen *et al.* 2006; Labbe & Fausch 2000; Schlosser & Angermeier 1995). Isolation may therefore compromise their long-term persistence (Fausch *et al.* 2009). Understanding the vulnerability of isolated refuge populations to natural catastrophic events such as flooding is therefore important for conservation planning.

Headwater streams are considered particularly susceptible to floods because they have small catchments and are easily influenced by relatively minor changes in local conditions (Meyer *et al.* 2007). Unpredictable, infrequent and catastrophic floods can result in slope failures, bank erosion, substrate scouring, and loss of habitat and biota (Resh *et al.* 1988). In fish populations, floods can result in downstream displacements (Cambray 1994), reduced abundance (Magalhaes, Schlosser & Collares-Pereira 2003; Matthews 1986; Nislow *et al.* 2002; Pires *et al.* 2008), recruitment failure (Letcher & Terrick 1998) and alteration in community composition (Matthews 1986; Nislow *et al.* 2002).

Despite the documented impacts of floods on stream fish communities (Letcher & Terrick 1998; Matthews 1986; Nislow *et al.* 2002; Pires *et al.* 2008; Resh *et al.* 1988), fishes also display long-term resilience and have been shown to return to equilibrium fairly rapidly following catastrophic flood events (Dolloff, Flebbe & Owen 1994; Matthews 1986). Under natural conditions, fishes are able to recolonise disturbed stream reaches from metapopulations in undisturbed refuge habitats (Dolloff *et al.* 1994; Matthews 1986; Medeiros & Maltchik 2001).



Isolation is a concern for freshwater fish conservation in South Africa, where many headwater stream fishes are endemic to individual river systems and populations are increasingly fragmented by man-made (dams, weirs) or biological (invasive fish predation) barriers (Ellender, Weyl & Swartz 2011; Tweddle *et al.* 2009). One such species is the Mandela lineage of the endangered Eastern Cape redfin minnow, *Pseudobarbus afer* (Peters, 1864) (Swartz & Impson 2007). Its natural distribution is limited to only three river systems (Sundays, Swartkops and Baakens) in the Eastern Cape Province of South Africa (Swartz, Skelton & Bloomer 2007). Populations are heavily impacted by non-native fish predation (Ellender *et al.* 2011) and only persist in isolated headwater refugia (Ellender 2013). Fortunately, a considerable portion of these headwater refugia are located in two protected areas, the Addo Elephant National Park (Sundays River system) and the Groendal Wilderness Area (Swartkops River system). Whilst these protected areas provide protection from non-native fishes and habitat destruction, the impact of natural catastrophic floods on these isolated populations are unknown.

This article provides insight into the population level responses of *P. afer* to an unpredictable high-magnitude flood event by comparing the distributions, relative abundance and population structure of *P. afer* in two headwater streams before and after an unpredictable high-magnitude flood. It was hypothesised that the flood would (1) result in displacement and mortality of headwater fishes, resulting in changes in abundance and distribution in headwater streams and (2) that juvenile life history stages of *P. afer* would be more vulnerable to flood disturbance.

Research method and design

Study site

The study was undertaken within the Groendal Wilderness Area on two second-order, episodic headwater tributaries (Fernkloof stream, Waterkloof stream) of the Kwa-Zunga River, a major tributary of the Swartkops River system, Eastern Cape, South Africa (Figure 1). As a result of their entire catchments being situated within the Groendal Wilderness Area (a protected area proclaimed for the protection of indigenous forest and water resources), the Fernkloof and Waterkloof streams are relatively pristine with undammed catchments and intact riparian zones characterised by closed canopy (Fernkloof: $46\% \pm 23\%$ canopy cover; Waterkloof: $33\% \pm 24\%$ canopy cover) tropical coastal forest (Acocks 1975) and mesic grassy fynbos (Campbell 1985). The character of the two streams is typical for episodic headwater streams in the Eastern Cape. Both streams have steep, high profile banks within narrow valleys. In-stream habitat was characterised by isolated pools (Fernkloof [mean \pm s.d.] length: $10.8 \text{ m} \pm 3.2 \text{ m}$; width: $3.6 \text{ m} \pm 0.9 \text{ m}$; depth: $0.7 \text{ m} \pm 0.4 \text{ m}$; Waterkloof [mean \pm s.d.] length: $11.9 \text{ m} \pm 3.7 \text{ m}$; width: $5.5 \text{ m} \pm 4.8 \text{ m}$; depth: $0.7 \text{ m} \pm 0.6 \text{ m}$) connected by subsurface flows, with bedrock, large unconsolidated boulder, cobble and pebble substrates.

Surface flow only connects pools for a few days after heavy sustained rainfall.

Field surveys

Ten sites on each stream were sampled before (May 2010) and two months after (August 2012) a major flooding event (June 2012) by electrofishing using a Samus 725G backpack electrofisher, attached to a 12 V battery with settings standardised at the duration of 0.3 ms and a frequency of 80 Hz. Because flood scouring and filling changed the position of pools within the two streams in the post-flood survey, the nearest pool to the pre-flood sample site was electrofished. Single-pass electrofishing was conducted from the downstream side (tail) of the pool in an upstream direction, covering the entire length of each pool. Upon completion of the pass, fish were identified to species level, measured, counted and released. Electrofishing data were used as an index of relative abundance and catch per unit effort (CPUE) was expressed as fish m^{-3} using volume estimates from the habitat data collected for each sampled pool. Block nets were not used as pools were primarily isolated on the surface because of the episodic nature of the sampled streams.

At each sampling site, temperature, conductivity and pH were measured using a Hanna HI98129 Combo pH and electrical conductivity meter (HANNA Instruments Inc., Woonsocket, USA). Turbidity (NTU) was measured using a Hanna HI 98703 turbidimeter (HANNA Instruments Inc., Woonsocket, USA). To estimate pool volume and habitat diversity, the length ($\pm 0.1 \text{ m}$) of the pool was measured, followed by equally spaced width measurements ($\pm 0.1 \text{ m}$). On each width transect, three depths ($\pm 0.1 \text{ m}$) were measured; the outer two were 0.2 m each from the left-hand and right-hand stream bank and the third measurement taken midstream. At each depth measurement, the habitat type was recorded. Canopy cover was estimated as a percentage of total cover and bankside vegetation type was recorded.

Data analysis

Rainfall and flow

Long-term hydrological and meteorological data were obtained from the Department of Water Affairs hydrology section (DWAF 2012); the locations of the rainfall and gauging stations are presented in Figure 1. These data were used to illustrate rainfall, flow variability and the magnitude of the flood in the headwaters of the Swartkops River system. Because of an absence of long-term flow data for the Fernkloof and Waterkloof streams, flow data were obtained from a representative Swartkops River system headwater tributary, the gauging weir at Wincanton on the Elands River (M1H004) for the period 06 April 1965 – 05 January 2012. Rainfall data were obtained from station M1E001 at Groendal Dam (period: 16 February 1950 – 11 January 2006) and supplemented with data from the nearby station M1E002 at Uitenhage (period: 30 November 2006 – 05 January 2012).

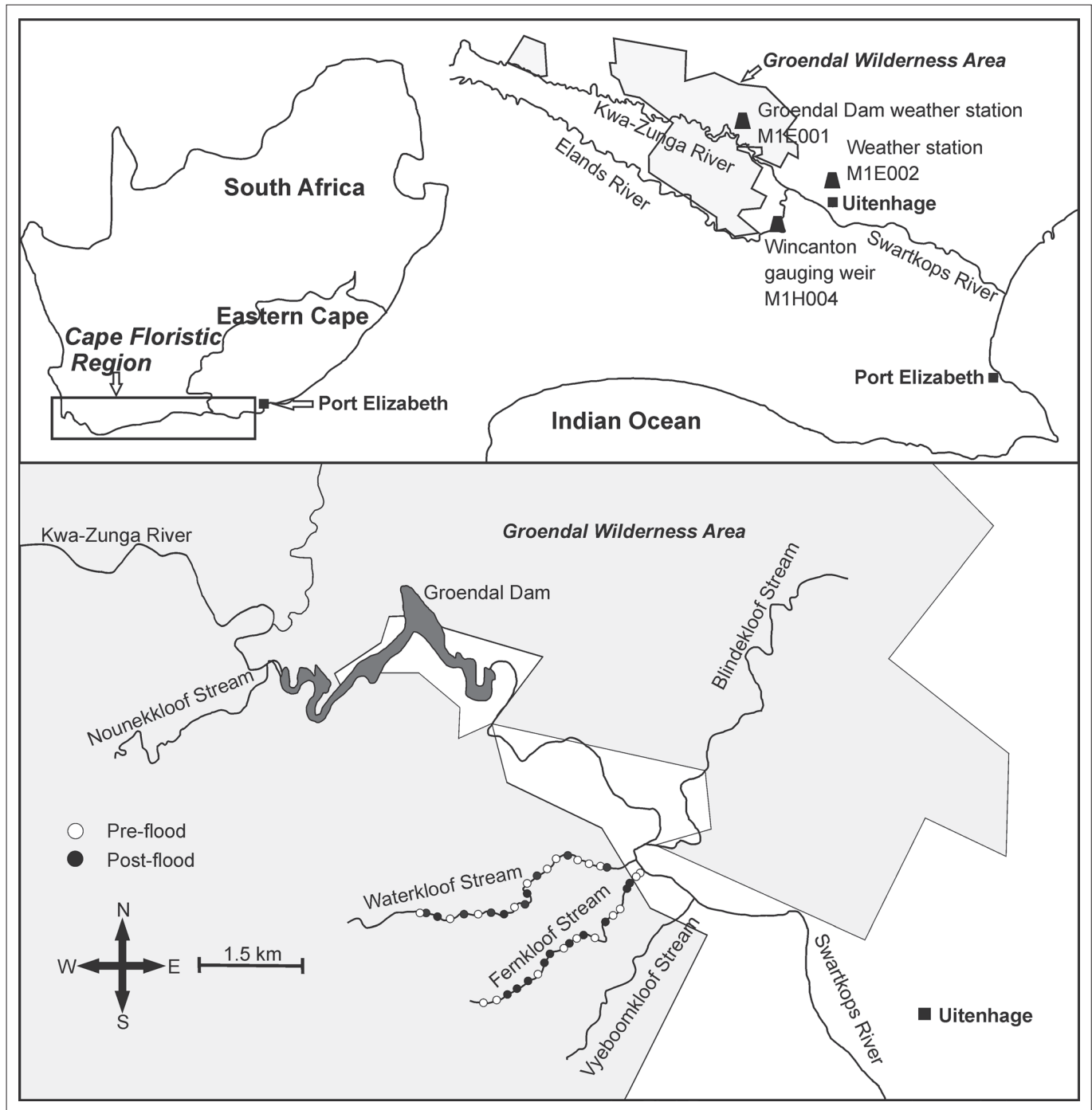


FIGURE 1: The situation and sites sampled on the Fernkloof and Waterkloof streams, headwater tributaries of the Swartkops River system within the Groendal Wilderness Area, Eastern Cape, South Africa. The position of the Wincanton gauging weir (M1H004) on the Elands River and the weather station (M1E001) at Groendal Dam are also noted.

Spearman rank order correlation was used to test for a relationship between rainfall and flow in the Swartkops River system headwater streams at a significance of $p < 0.05$. The following criteria, outlined by Resh *et al.* (1988), were used to classify the magnitude of the flood disturbance as:

any relatively discrete event in time that is characterised by a frequency, intensity, and severity outside a predictable range, and that disrupts ecosystem, community, or population structure and changes resources or the physical environment. (p. 434)

These criteria were applied to peak flow data for the Swartkops River system to verify the magnitude of the flood in June 2012.

Fish population dynamics

Pre-flood and post-flood comparisons were limited to a single fish species, *P. afer*, as they were ubiquitously distributed from the limit of fish distributions (*P. afer* distribution: Waterkloof = 3 km; Fernkloof = 3 km) in the upper reaches to the confluence with the mainstem Kwa-Zunga River before the flood, allowing longitudinal



analyses. To investigate the impact of a major flooding event on *P. afer* in headwater streams, pre-flood and post-flood electrofishing catch per unit effort (CPUE, fish m^{-3}) estimates were compared within the two streams using a main-effects analysis of variance (ANOVA) at a significance level of $p \leq 0.05$. Specifically, CPUE was tested for longitudinal trends (upper versus lower reaches), as well as flooding impact (pre-flood versus post-flood) and an interaction between the two factors.

Because of complications resulting from differences in sampling months, with the pre-flood survey occurring at the end of the spawning season and the post-flood survey at the beginning of the spawning season (Cambray 1994), *P. afer* juveniles (< 40 mm) and adults (> 40 mm) were analysed separately. To test the vulnerability of the two *P. afer* size classes to the flooding event, the frequency of occurrence (number of sites per stream reach where each size class was present expressed as a percentage of all sites in that reach) by stream reach (upper and lower reaches) was tested for significance by reach and pre-flooding and post-flooding using a chi-squared test of independence. All analyses were undertaken using MS Excel 2007, Microsoft® and Statistica 10.0, StatSoft®.

Results

Rainfall and flow

Mean annual rainfall (mean \pm s.d.) for the period 16 February 1950 – 05 January 2012 was 620.7 ± 212.3 mm yr^{-1} . Rainfall was variable, falling in an unpredictable, erratic pattern (Figure 2). There was a highly significant correlation between rainfall (station M1E001 and M1E002) and peak flow (gauging weir M1H004) (Spearman $r = 0.389$; $Z = 9.45$; $p = 0.000$), highlighting the system's episodic nature. Peak flows between April 1965 and May 2012 were generally low (mean \pm s.d.: $30.3 \text{ m}^3\text{s}^{-1} \pm 202.3 \text{ m}^3\text{s}^{-1}$) and were predominantly $< 25 \text{ m}^3\text{s}^{-1}$ (89%), with a further 8.7%

$< 500 \text{ m}^3\text{s}^{-1}$. During the 47 years on record, there were only four peak flows exceeding $1000 \text{ m}^3\text{s}^{-1}$ (Figure 2). The flooding event with peak flows of $1245 \text{ m}^3\text{s}^{-1}$ (a measure of instantaneous flow at peak discharge) in June 2012 was of a frequency, intensity and severity outside of the predictable range and resulted in changes to the physical environment, which, according to Resh *et al.* (1988), classified the flood as a major disturbance.

Fish responses

The distribution and abundance of fishes from the Fernkloof and Waterkloof streams pre-flood and post-flood are summarised in Table 1. Four species were recorded from the Fernkloof and Waterkloof streams, of which three were shared (native: *P. afer* and Cape kurper *Sandelia capensis* [Cuvier, 1831]; non-native: African sharptooth catfish *Clarias gariepinus* [Burchell, 1822]) and an additional non-native, banded tilapia *Tilapia sparrmanii* A. Smith 1840 was recorded in the Fernkloof stream only. *Pseudobarbus afer* distributions were limited to a 3 km stretch in both the Fernkloof and Waterkloof streams.

There were no significant pre-flood and post-flood longitudinal or interactive effects (stream reach: upper and lower reaches; disturbance: pre-flood and post-flood) in CPUE for *P. afer* in the Waterkloof stream (pre-flood mean \pm s.e.: 1.24 ± 0.33 fish m^{-3} ; post-flood mean \pm s.e.: 2.43 ± 0.40 fish m^{-3}) (Table 2). There was, however, a significant increase in post-flood *P. afer* CPUE in the Fernkloof stream (pre-flood mean \pm s.e.: 1.33 ± 0.49 fish m^{-3} ; post-flood mean \pm s.e.: 6.53 ± 2.12 fish m^{-3}) (Figure 3; Table 2). The frequency of occurrence and length distributions for *P. afer* pre-flood and post-flood are summarised in Table 3 and Figure 4.

The frequency of occurrence for juvenile (< 40 mm) and adult *P. afer* was independent of stream reach and were subsequently grouped by stream (Table 3). The frequency

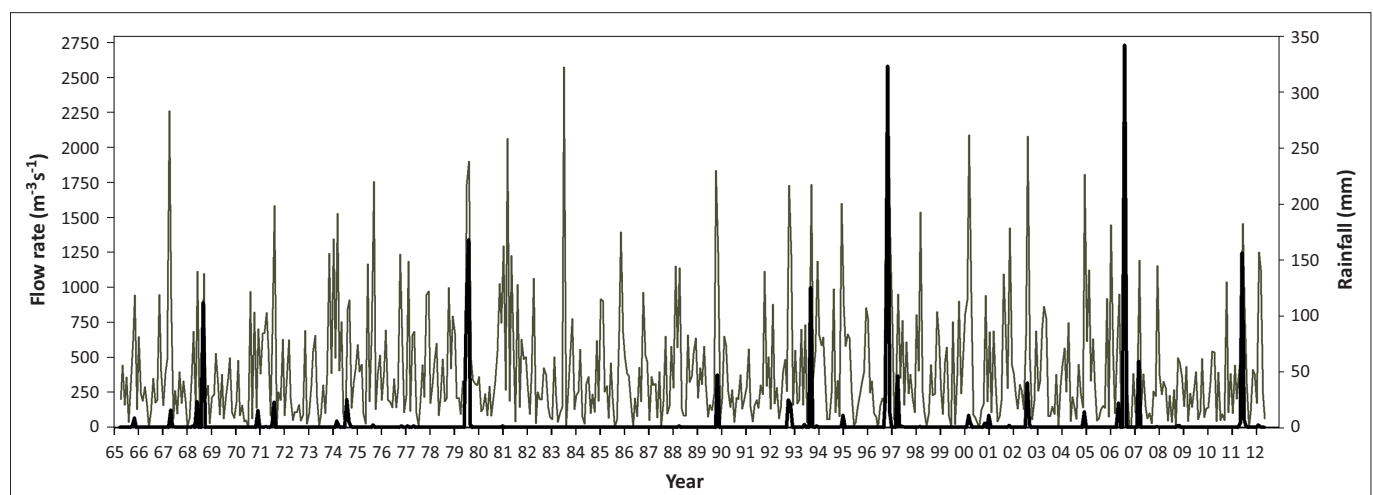


FIGURE 2: Monthly peak flows (black) at the Wincanton gauging weir on the Elands River and total monthly rainfall (grey) at Groendal Dam (16 February – 11 January 2006) and at Uitenhage (30 November 2006 – 05 January 2012) illustrating rainfall and flow variability in the headwater tributaries of the Swartkops River system (flow data are missing for the period April 1981 – September 1986).



TABLE 1: The stream zones (lower reaches, upper reaches), sites (10 sites), distribution, catch per unit effort (fish m⁻³), relative abundance (%) of fishes by site (%), including water-quality variables from site 1 in the lower reaches to site 10 in the upper reaches of the Fernkloof and Waterkloof streams, headwater tributaries of the Kwa-Zunga River within the Groendal Wilderness Area.

Streams	Survey	Lower reaches					Upper reaches				
		1	2	3	4	5	6	7	8	9	10
Fernkloof stream	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudobarbus afer</i>	Pre-flood	0.00	0.03 (33)	0.38 (73)	1.22 (91)	2.15 (80)	1.20 (75)	0.99 (71)	4.36 (100)	3.23 (100)	0.00
	Post-flood	0.10 (10)	0.36 (68)	4.62 (86)	7.67 (88)	11.11 (88)	4.40 (96)	9.87 (100)	4.60 (100)	27.89 (100)	11.25 (100)
<i>Sandelia capensis</i>	Pre-flood	0.15 (100)	0.03 (33)	0.14 (27)	0.12 (27)	0.53 (20)	0.40 (25)	0.39 (29)	0.00	0.00	0.00
	Post-flood	0.93 (90)	0.20 (32)	0.77 (14)	1.02 (12)	1.48 (12)	0.00	0.00	0.00	0.00	0.00
<i>Clarias gariepinus</i> †	Pre-flood	0.00	0.03 (33)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Post-flood	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Tilapia sparrmanii</i> †	Pre-flood	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Post-flood	0.00	0.00	0.00	0.00	0.00	0.17 (4)	0.00	0.00	0.00	0.00
Temperature (°C)	Pre-flood	16.5	16.2	16.2	15.8	16.2	16.1	16.1	15.7	15.4	15.4
	Post-flood	21	21.1	21.4	19.6	19.2	19.2	16.8	16.5	16.4	17.3
Turbidity (NTU)	Pre-flood	0.5	0.43	0.28	0.29	0.35	0.21	0.37	0.43	0.2	0.18
	Post-flood	0.17	-	0.15	0.19	0.41	0.34	0.32	0.17	0.28	0.22
Conductivity (µs/cm)	Pre-flood	302	303	301	301	301	296	304	291	275	260
	Post-flood	230	221	222	222	220	218	214	219	215	213
Waterkloof stream	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudobarbus afer</i>	Pre-flood	0.40 (100)	0.39 (100)	0.44 (71)	0.40 (100)	0.10(89)	1.53 (78)	3.59 (85)	0.99 (87)	1.26 (100)	0.06 (100)
	Post-flood	0.44 (75)	5.21 (96)	2.55 (95)	2.23 (96)	3.16(91)	2.59 (67)	2.69 (100)	3.47 (94)	5.40 (100)	5.60 (100)
<i>Sandelia capensis</i>	Pre-flood	0.00	0.00	0.18 (29)	0.00	0.12(11)	0.44 (22)	0.63 (15)	0.15 (13)	0.00	0.00
	Post-flood	0.15 (25)	0.21 (4)	0.12 (5)	0.09 (4)	0.30(9)	1.29 (33)	0.00	0.22 (6)	0.00	0.00
<i>Clarias gariepinus</i> †	Pre-flood	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Post-flood	0.00	Saw 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Temperature (°C)	Pre-flood	17.4	17.6	17.6	17.9	18.2	15.2	15.5	13.7	14.3	14
	Post-flood	15.9	16	16	15.7	15.7	16.1	15.9	16.5	16.8	17.3
Turbidity (NTU)	Pre-flood	0.41	0.63	0.54	0.44	0.28	0.18	0.47	0.23	0.32	0.31
	Post-flood	0.30	0.43	0.47	0.53	0.21	0.53	0.60	0.33	0.34	0.33
Conductivity (µs/cm)	Pre-flood	267	263	257	259	250	256	250	245	254	234
	Post-flood	212	214	209	209	209	207	206	200	202	216

NTU, nephelometric turbidity units.

†, non-native species.

TABLE 2: A summary of pre-flood and post-flood longitudinal (upper and lower stream reaches) and disturbance (pre-flood and post-flood) main-effects ANOVA results for *Pseudobarbus afer* CPUE (fish m⁻³) from the Waterkloof and Fernkloof streams, headwater tributaries of the Kwa-Zunga River within the Groendal Wilderness Area.

Streams	DF	MS	F-statistic	p-value
Fernkloof stream				
Site	9	28.1854	1.45811	0.291616
Pre/Post	1	135.4398	7.00667	0.026606
Site*Pre/Post	-	-	-	-
Error	9	19.3301	-	-
Waterkloof stream				
Site	9	1.15082	0.71742	0.685614
Pre/Post	1	7.03571	4.38604	0.065725
Site*Pre/Post	-	-	-	-
Error	9	1.60412	-	-

CPUE, catch per unit effort; DF, degrees of freedom; MS, mean square.

of occurrence of juvenile and adult *P. afer* was independent of flooding for the Waterkloof (pre-flood versus post-flood: $\chi^2 = 0.027$, $df = 1$, $p = 0.87$) and Fernkloof streams (pre-flood versus post-flood: $\chi^2 = 0.044$, $df = 1$, $p = 0.83$) (Table 3).

In the Waterkloof stream, *P. afer* size distributions were similar between stream reaches and pre-flooding and post-flooding (pre-flood lower mean, range: 43.7, 22 mm – 74 mm fork length (FL); pre-flood upper mean, range: 40.7,

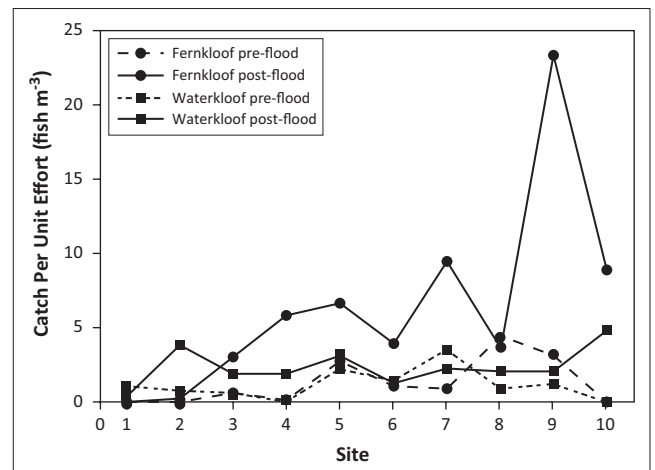


FIGURE 3: Pre-flood and post-flood longitudinal abundance trends for *Pseudobarbus afer* catch per unit effort (fish m⁻³) from the Waterkloof and Fernkloof streams, headwater tributaries of the Kwa-Zunga River within the Groendal Wilderness Area, Eastern Cape, South Africa.

16 mm – 71 mm FL; post-flood lower mean, range: 42.8, 21 mm – 67 mm FL; post-flood upper mean, range: 47.2, 28 mm – 81 mm FL) (Figure 4). In the Fernkloof stream, the mean length of *P. afer* was larger in the lower reaches but similar before and after the flood (pre-flood lower mean, range: 53.0, 11 mm – 96 mm FL; pre-flood upper mean, range: 43.0, 24 mm – 72 mm FL; post-flood lower mean, range: 52.0,



30 mm – 87 mm FL; post-flood upper mean, range: 46.3, 21 mm – 100 mm FL).

TABLE 3: The frequency of occurrence (% of sites containing *Pseudobarbus afer*) of juvenile (< 40 mm) and adult (> 40 mm) *Pseudobarbus afer* pre-flood and post-flood separated by stream reach (lower and upper) for the Fernkloof and Waterkloof streams headwater tributaries of the Kwa-Zunga River within the Groendal Wilderness Area.

Streams	Juvenile (< 40 mm) (%)	Adult (> 40 mm) (%)	Mean length (range) mm FL
Waterkloof stream pre-flood	-	-	-
Lower reaches	100	100	43.7 (22–74)
Upper reaches	100	100	40.7 (16–71)
Waterkloof stream post-flood	-	-	-
Lower reaches	100	100	42.8 (21–67)
Upper reaches	80	100	47.2 (28–81)
Fernkloof stream pre-flood	-	-	-
Lower reaches	40	60	53.0 (11–96)
Upper reaches	80	80	43.0 (24–72)
Fernkloof stream post-flood	-	-	-
Lower reaches	80	80	52.0 (30–87)
Upper reaches	100	100	46.3 (21–100)

FL, fork length.

Discussion

Flood-related disturbances typically elicit a variety of responses from fishes in stream environments, the nature of which are related to the predictability, magnitude/intensity and duration of the event (Lytle & Poff 2004) as well as the specific adaptations of the fishes to the abiotic conditions of that environment (Franssen *et al.* 2006; Lytle & Poff 2004). In the Fernkloof and Waterkloof streams, *P. afer* demonstrated resilience to a major flooding event.

In both small streams, there were no longitudinal trends in *P. afer* abundance before or after the flood, but overall abundance post-flooding in the Fernkloof stream was higher. This may have been the result of the inability to sample the exact sites before and after the flood as some pools were filled up by flood deposition. The nearest pool to the pre-flood site was sampled, which may have resulted in sampling a refuge pool where post-flood abundances were high as a result of collection of fishes from that stream segment. Good recruitment during the 2010/2011 spawning season might also have led to the observed increase in abundance as during this period rainfall was higher than

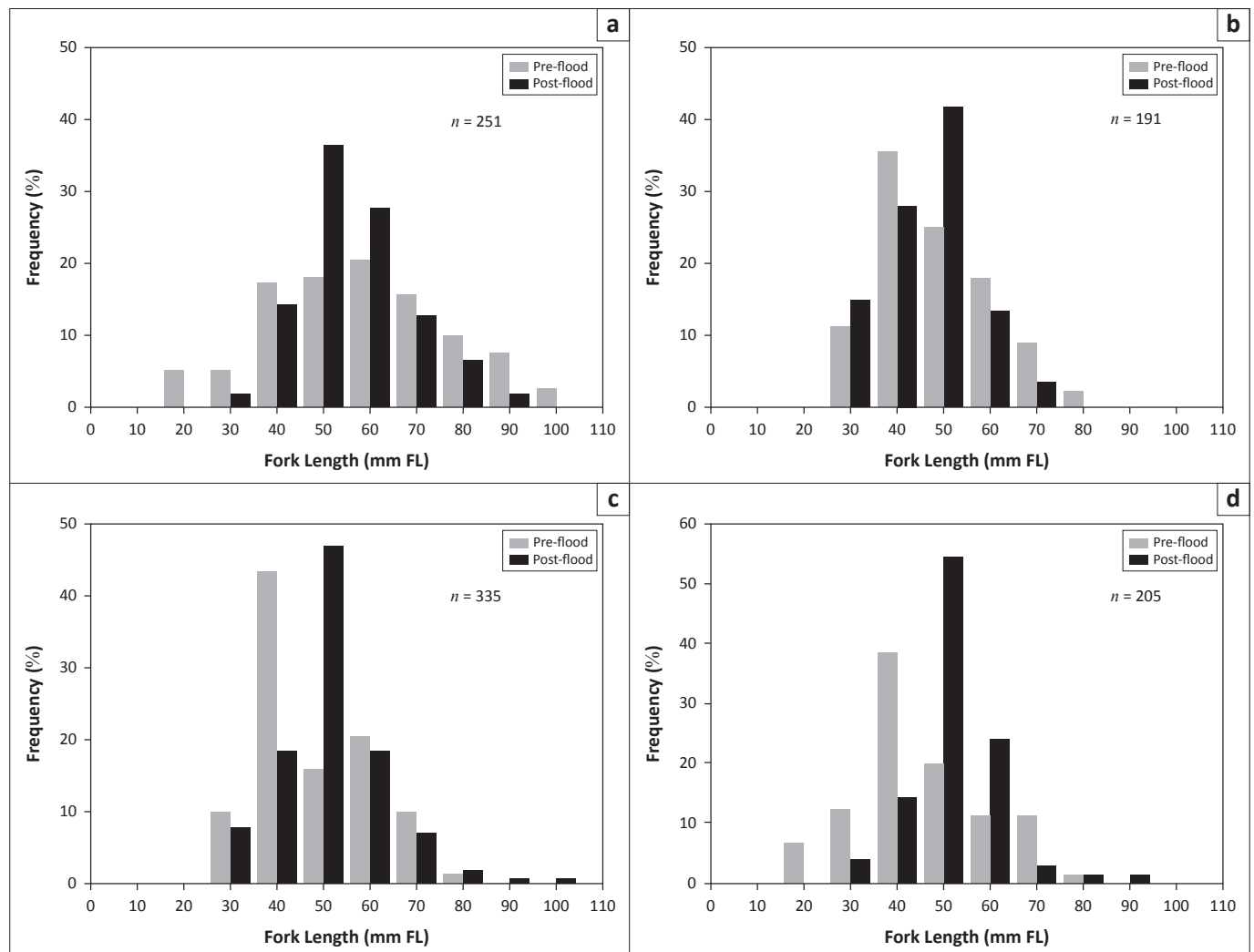


FIGURE 4: Pre-flood and post-flood length frequency distribution for *Pseudobarbus afer* from the upper and lower reaches of the Fernkloof (a = lower; c = upper) and Waterkloof (b = lower; d = upper) streams, headwater tributaries of the Kwa-Zunga River within the Groendal Wilderness Area, Eastern Cape, South Africa.



the preceding two spawning seasons. Increased recruitment during periods of good flow was recorded by Franssen *et al.* (2006) for intermittent prairie stream fishes in north-eastern Kansas, USA. However, the *P. afer* length frequency data from the Waterkloof and Fernkloof streams do not support this, as size structuring before and after the flood was similar.

The vulnerability of stream fishes to flood disturbance is not always clearly evident from overall abundance trends, but in some cases certain life history stages of particular species may be more vulnerable to disturbance than others (Gasith & Resh 1999; Letcher & Terrick 1998; Lytle & Poff 2004). In New England streams in the USA, a massive localised flood caused an age-0 year-class failure in brook trout *Salvelinus fontinalis* (Mitchill, 1815) and brown trout *Salmo trutta* Linnaeus 1758 and a large decrease in abundance of Atlantic salmon *Salmo salar* Linnaeus 1758 (Letcher & Terrick 1998). Similar results have been recorded for other species after catastrophic flood events (Dolloff *et al.* 1994; Harvey 1987; Matthews 1986; Nislow *et al.* 2002).

This was not the case for *P. afer* as there were no significant changes in the occurrence of either juvenile or adult *P. afer* following the flood. Both life history stages were distributed throughout both streams from their confluence with the mainstream Kwa-Zunga in the lower reaches, to the limit of *P. afer* distribution in the upper reaches. The susceptibility of juvenile fishes to flood displacement and mortality has been documented to decrease rapidly with a small increase in length (Harvey 1987) and *P. afer* may show similar trends in changing vulnerability with size. In the nearby Wit River, a headwater tributary of the Gamtoos River system, Cambray (1994) reported that late free embryos and early larvae drift out of the areas where they were spawned. During the current study, the flooding event took place 3–5 months after the peak spawning season of *P. afer* (Cambray 1994), perhaps allowing young-of-the-year fish time to grow out of the most vulnerable life history stages.

Distribution and movement of non-native species indicated species-specific and stream-specific flood response. For example, after the same flood, Ellender, Woodford and Weyl (2015) noted that the flood event appeared to have flushed *C. gariepinus* out of the Fernkloof stream but facilitated its penetration into the Waterkloof stream. Temporal longitudinal movement was also noted in the Blindekloof stream, another Kwa-Zunga River tributary, during a period of prolonged flow (± 5 months) following the June 2012 flood, when *C. gariepinus* penetrated 5 km upstream from the mainstem (Ellender *et al.* 2015).

In conclusion, the observed resilience of *P. afer* populations to a major flooding event is most likely related to their evolution in river systems characterised by environmental stochasticity (Dolloff *et al.* 1994; Magalhaes *et al.* 2003; Pires *et al.* 2008). The long-term persistence of *P. afer* in relatively pristine isolated headwater refugia may therefore not be threatened by flood disturbances of the observed magnitude

and intensity. The biggest long-term threat may be the flood-facilitated penetration of headwater refugia by non-native species.

Acknowledgements

B.R.E. received financial support from: the South Africa–Netherlands Research Programme on Alternatives in Development (SANPAD project 10/06), the National Research Foundation of South Africa (NRF), Rhodes University, the DST/NRF Centre of Excellence for Invasion Biology and the Water Research Commission (WRC Project No. K5/1957/4, K5/2039 and K5/2261). Eastern Cape Parks Board and staff of the Groendal Wilderness Area are thanked for access and for their logistical assistance. Geraldine Taylor and Patrick Gourley are thanked for field assistance. Research was conducted following SAIAB animal ethics guidelines. Research permits were issued by the Eastern Cape Department of Economic Development and Environmental Affairs (DEDEA) and Eastern Cape Parks.

Competing interests

The authors declare that they have no financial or personal relationships which may have inappropriately influenced them in writing this article.

Authors' contributions

B.R.E. (South African Institute for Aquatic Biodiversity) was responsible for study conceptualisation, data collection, analyses, writing and editing the manuscript. O.L.F.W. (South African Institute for Aquatic Biodiversity) contributed to conceptualising the study, writing and editing the manuscript.

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