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Habitat associations of imperilled fishes after conservation intervention

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Abstract

The aim of this study was to examine the habitat associations of a native cyprinid community of the recovering Rondegat River in the Cape Fold Ecoregion of South Africa as part of a long-term monitoring project. Relative abundance (MaxN) data was extracted from underwater video camera footage across the longitudinal gradient of the river in three sampling instances. Using multivariate methods we assessed community composition with respect to habitat, protected area and species-specific abiotic predictors of relative abundance. Distance from the uppermost site in the river was the most significant predictor of species abundance, indicating spatial segregation and varying overlap between species. The protected status of sites in the upper reaches, vegetated substrates and size of individual sites were the most important for the endangered fiery redfin *Pseudobarbus phlegethon*. The results of this study indicate that underwater video monitoring is an effective and low-cost approach that can inform conservation recommendations. Reducing agricultural runoff and sedimentation in the lower reaches may be useful further interventions to maintain key habitats of submerged vegetation.

Key words:

Freshwater, habitat, headwater streams, remote underwater video, river restoration, South Africa

Introduction

Freshwater systems are globally threatened as a result of the increasing and multiple stressors acting upon them (Tickner et al., 2020). In particular, climate change, habitat degradation and invasive species have deleterious effects on aquatic biodiversity (Tickner et al., 2020). Impetus is thus on conserving species which are susceptible to anthropogenic disturbance because of endemicity and range restriction as they are constrained in capacity for adaptation. In some cases, restoration interventions can be applied. These include removal of predatory alien invasive species (Slabbert, Jordaan & Weyl, 2014), translocation of populations threatened by habitat change (Hammer et al., 2013), or habitat restoration (Lyon et al., 2019). Threat amelioration allows vulnerable fish species to recover, however, to ensure the success of an intervention robust prior knowledge regarding population dynamics and habitat associations is essential (Van Liefferinge et al., 2019).

In South Africa, a system of primary concern is the Olifants-Doorn water management area. The Olifants River of the Western Cape is home to a relatively high diversity of endemic (and in most cases threatened or endangered) fishes (Ellender et al., 2017). In particular, the Cederberg Mountains within this catchment have been identified as “vulnerability hotspots” within an already vulnerable region (Shelton et al., 2018). Ten of the 19 freshwater fish species endemic to the Cape Fold Ecoregion (CFE) are found in this system (Weyl et al., 2014), highlighting its importance in the conservation of endemic biodiversity. The Rondegat River, a tributary of the Olifants River, is of significant conservation value as it hosts five vulnerable endemic CFE species (Woodford et al., 2005; Weyl et al., 2013). A major conservation intervention was undertaken through 2012 and 2013, when the piscicide

Rotenone was used to remove all alien fishes below the Rooidraai waterfall (Slabbert, Jordaan & Weyl, 2014). The imperilled fish populations have shown considerable recovery within the Rondegat. Two of which, the Clanwilliam yellowfish *Labeobarbus seeberi* (Gilchrist & Thompson, 1914) and the Clanwilliam redfin *Sedercypris calidus* (Barnard, 1938) have reached equilibrium; whereas the Fiery redfin *Pseudobarbus phlegethon* (Barnard, 1938) is yet to (Castañeda et al., 2020a).

Despite the successful removal of the alien species threat, the Rondegat River is susceptible to other pervasive disturbances which need to be assessed to ensure the persistence of the newly recovered community. Long term monitoring with suitable adaptive management after restoration interventions is often neglected which negates the substantial investments in the system (Lintermans, 2013). Within the Rondegat River, habitat change due to agricultural activities and climate related change such as increased fire events and drought are of particular concern. This is compounded by the fish species' limited distributions and the vulnerable status of the still recovering Fiery redfin population (Castañeda et al., 2020a). Now that predatory species have been eliminated it is essential to begin to parse out the abiotic factors which may ensure the continued recovery of the three cyprinid species. The pre-existing data (i.e., prior to intervention and during recovery phase) is not suitable to draw conclusions as the fish assemblage was not in a natural state, and the studies were conducted using methodology with low accuracy or detection probability, such as snorkel surveys or seine netting (Vaughan & Ormerod, 2010).

In the recent study, we aimed to determine the habitat associations and co-occurrence patterns of the recovered Rondegat River fish community. This follows the recommendations by Castañeda et al. (2020a) and compiles evidence to advise and enhance monitoring and restoration efforts in the catchment. The fish assemblage at the time of monitoring may be considered as the nearest proxy for a baseline natural state of the river and ought to be assessed prior to further decision making (Castañeda et al., 2020a). Our specific objectives were to assess 1) how community composition changes with respect to habitat, protected area and 2) species-specific abiotic predictors of relative abundance through multivariate methods. Ultimately, this information could be used to improve further monitoring efforts and provide additional context and focus to conservation efforts.

Materials and Methods

Ethical statement

Entry into a protected area for research purposes and deployment of equipment complied with Western Cape animal welfare laws, guidelines and policies as approved by local authority CapeNature, permit number CN44-28-8357.

Study area

The Rondegat River (32°24’S; 19°05’E) is a 25km long 2nd order perennial tributary of the Olifants River, with the point of confluence at the Clanwilliam Dam (Lowe et al., 2008; van der Walt, 2014) (Figure 1). The river originates as a pristine headwater stream in the

Cederberg Mountains, with the uppermost 4km of the river being classified as a protected area by the local conservation authority CapeNature. In dry season months (October – March), the river is clear, with low turbidity and flow conditions, making it a good candidate for underwater video observations. Submerged vegetation is limited to semi-aquatic sedges and is primarily found in the upper reaches. The river progresses through undisturbed fynbos vegetation and passes through citrus fruit orchards encroached by alien vegetation in the mid- and lower reaches (Woodford, 2005; Lowe et al., 2008). Typical habitat in the Rondegat River ranges from predominantly cobbled and boulder-dominated upper reaches, to sandy and silted substrates in the abstracted farmland lower reaches. The river is divided in part by the natural Rooidraai waterfall, as well as anthropogenic barriers including an invasive fish exclusion weir near to the confluence at the Clanwilliam Dam and various weirs associated with farmland abstraction sites. The catchment area covers approximately 111 km^2 and is characterised by winter rainfall falling primarily from June until August (Lowe et al., 2008). Temperatures in the CFE are hottest in February and coldest in June (de Moor & Day, 2013). Winter rainfall restricts sampling efforts to months of lesser flow for all sampling methods as a result of high water velocity, turbidity and flooding risks (October – April). In early February 2018, a large unseasonal fire and increased rainfall over the winter months is likely to have resulted in high turbidity and altered physical characteristics through the release of a sand plug downstream of burnt areas (Figure 2).

Study species and knowledge prior to recovery

Sedercypris calidus – formerly *Barbus* and *Pseudobarbus calidus* (Skelton, Swartz & Vreven, 2018) – is evaluated as Near Threatened using IUCN Red List criteria (van der Walt, Jordaan & Impson, 2017). This species is only distantly related to the fiery redfin (*Pseudobarbus phlegethon*) with which it co-occurs. In the Rondegat River, *S. calidus* is the more abundant of the two redfins present and has previously been associated with deeper pool habitats via snorkel surveys (Woodford et al., 2005). Occupancy modelling of this species indicates it has a stable population in a relatively recovered state as of 2016 (Castañeda et al., 2020a).

Pseudobarbus phlegethon is endemic to the Olifants River and tributaries (Skelton, 1996, 2001 pp 126). With fewer than ten populations remaining, *P. phlegethon* is listed as Endangered on the IUCN Red List (van der Walt, Impson & Jordaan, 2017). Habitat preferences for this species are thought to be slower flowing pool environments with complex structure. This is based on legacy snorkel survey data and observations of populations in similar Olifants River tributaries, the Thee and Noordhoeks rivers (Gore, King & Hamman, 1991). This species is likely to remain vulnerable to disturbance, as occupancy modelling for this species indicated that it has not yet returned to equilibrium following non-native fish invasion and the subsequent conservation intervention (Castañeda et al., 2020a).

Labeobarbus seeberi, formerly *L. capensis*, is the largest fish in the system, and is classified as Near Threatened using IUCN classification criteria (Impson, van der Walt & Jordaan, 2017). Prior to alien fish removal *L. seeberi* populations survived in the lower reaches as older, larger individuals in deep over-summering pools with little recruitment success

(Woodford, 2005; Weyl et al., 2013; van der Walt et al., 2016). *Labeobarbus seeberi* is likely to be dependent on these pools for both over-summering refugia as well as important congregation areas for drift and substrate feeding downstream of riffles (Woodford, 2005; Impson, Bills & Wolhuter, 2008). *Labeobarbus seeberi* is a multiple spawning, migratory and riffle-dependent species, making it particularly sensitive to habitat alteration. Like *S. calidus,* occupancy modelling for *L. seeberi* indicated that it has a stable population in a relatively recovered state as of 2016 (Castañeda et al., 2020a).

Sampling methods

Underwater video was chosen as an ideal sampling methodology for imperilled clear water stream species, given fish mortality risks associated with other sampling methods (Ellender et al., 2012; Castañeda, Weyl & Mandrak, 2020). This method has been used in several studies in the CFE (Ellender et al., 2012; Weyl et al., 2013, 2016; Castañeda et al., 2020a), and efforts are underway currently to develop a standardised protocol for the use of this method. Relative abundance (MaxN) data was extracted from underwater video camera footage that was recorded at 51 sites spanning 21 km of the Rondegat River in three sampling instances, the first: 7th - 11th April, second: 21st - 24th October 2018, as well as 30th September – 4th October 2019 (Figure 3; coordinates and general site characteristics are summarised in Table S2). Sampling times were randomised during daylight hours, between 08:00 and 18:00. GoPro® Hero3+® cameras were deployed approximately central to river flow and facing upstream on Perspex platforms. Camera systems were unbaited, to avoid biasing habitat use estimations and allow for natural behaviours to be observed. One system with one camera was used for each deployment at a given site. Cameras were set to record at a resolution of 1920 x 1080p at 30 frames per second and using “wide” field-ofview (127°). Recording time per deployment was 15 minutes, with the initial two minutes excluded from analysis to avoid the effects of disturbance or increased turbidity associated with the deployment. Pilot testing during initial site selection showed that the two-minute exclusion has been found to allow fish to return to normal movement and return to the area within the subsequent 15 minute filming period (Hannweg et al., 2020; CJB pers. obs.). The exclusion period in our study was primarily used to limit the effect of minor turbidity increases from river entry and camera placement. GPS coordinates of each site and photographs of camera placement were taken to minimise differences between sampling instances.

Sites were chosen based on suitability for camera deployment and with deployments alternating between pool and riffle/run habitats. Suitability for camera deployment was determined based on the availability of unobstructed viewing angles and clear visibility of the water volume within a selected site, to avoid biases introduced by obscured areas in the video footage and to maximise comparability between sites. Some sites were selected based on prior knowledge of fish distributions; particularly large pools known to be used as refugia for *L. seeberi*. Beyond these opportunistic deployments (n = 3 of 51), most deployments were randomised and agnostic of any prior knowledge of fish distributions. Distance between deployments was determined by the physical characteristics of the locality; cameras were deployed either side of natural barriers or with 10 to 200m gaps between sites where physical barriers were absent. At each site, physicochemical parameters were recorded using an Aquameter® AM-200 multiprobe device (Aquaread Ltd, Kent, United Kingdom). The substrate type was classified using a modified Wentworth scale (Fisher et al., 2012) to classify the primary substrate of sites as silt, sand, cobble, boulders or bedrock (alternatively classifying sites with high abundances of submerged macrophytes as vegetation). The length of each site (used as a proxy for site size) was measured by means of a tape measure to the nearest cm. Measurements started at the transition zone between reach changes, moving to the next transition (e.g., where a pool became a riffle, or minor physical barriers spanning the width of the river cross-section).

Video footage was analysed by one observer in EventMeasure software (v5.01, SeaGIS, www.seagis.com.au). MaxN counts are defined as the maximum count of individuals per species in a single frame of video footage. This technique avoids the possibility of counting the same individual more than once and gives conservative relative abundance estimates (Ellender et al., 2012; Campbell et al., 2015).

Data analysis

All statistical analyses were performed within the R software environment version 3.5.1 (R Core Team, 2020).

Community composition

Focal species relative abundances as the community matrix, and habitat characteristics were visualised using non-metric multidimensional scaling (nMDS) ordination as implemented by the R package ‘vegan’ version 2.5-5 (Oksanen et al., 2019). The nMDS included reach type, substrate type, distance from uppermost site (metres), electrical conductivity (EC, µS), turbidity (ntu), site length (metres) and protected status (factor defined as 1 = site falls within protected area, 0 = outside of protected area). Correlations between variables were checked and the variables EC and distance from uppermost site were retained (Figure S1).

Including protected status as a variable allows assessment of the focal fish community in accordance with the environmental variables thus considering both biotic and abiotic factors driving abundance throughout the river.

PERMANOVA (one-way test using Bray–Curtis non-metric similarity and 1000 permutations), a semi-parametric, permutation-based analogue of traditional ANOVA/MANOVA was used to test for significant effects of habitat characteristics on fish community. The full PERMANOVA model tested the MaxN community data for all three species as response with the variables “substrate type” × “reach type” × “protected status” + turbidity + “site length” + “distance from uppermost site”. Community abundance data were square-root transformed and Wisconsin double standardization was applied as implemented via *vegan::metaMDS*, where ordination stress <0.15 was considered appropriate for a two-dimensional biplot (Cousins, Kennard & Ebner, 2017; Oksanen et al., 2019).

Habitat drivers of relative abundance

To test species specific interactions with abiotic variables, regardless of whole community dynamics, generalized linear mixed models (GLMMs) were constructed for each species with relative abundance (MaxN) per site as the response. Error distributions and zero-inflation terms are outlined in the Supplementary Materials and candidate models are summarised (Tables S1a – S1c). Correlations between variables were checked and the variables EC and distance from uppermost site were retained (Figure S1). Repeated sampling at sites was accounted for by means of a random effect intercept term of site nested in month (*n* = 153 and *n* = 3 respectively), with environmental variables as fixed effects in GLMMs. The environmental predictors included in GLMMs were reach type, substrate type, turbidity, EC, site length, and distance from the uppermost site, as well as interactions between terms. Continuous predictors were centred and scaled prior to analysis. Exhaustive model selection was applied for each species with the final model chosen based on lowest AIC values (Supplementary Materials Tables S1a – S1c). GLMMs were constructed using R package “glmmTMB” version 0.2.3 (Brooks et al., 2017). Checking of model assumptions was performed using “DHARMa” version 0.2.4 (Hartig, 2019). Log-likelihood stepwise model selection was applied using package “buildmer” version 1.1 (Voeten, 2019) and “MuMIn” version 1.43.17 (Bartoń, 2020). Plotting of mixed model terms was facilitated by package “ggeffects” version 0.11 (Lüdecke, 2018).

Results

Seasonal relative abundance

Relative abundances (MaxN counts) of all three species varied between April and October 2018 (Table 1). *Sedercypris calidus* was the most widespread of the three species, being found in 53% and 71% of monitored sites in April and October respectively. *Pseudobarbus phlegethon* and *L. seeberi* were less commonly detected in video samples in April, with both species being detected at very low rates of 27% and 29% respectively. Similarly to the detection rates for *S. calidus*, these species were detected in more sites in October 2018; *P. phlegethon* was detected in 47% of sites while *L. seeberi* detection increased to 53%. Mean MaxN values for the three species reflected the detection rate trends. *Sedercypris calidus* had the highest relative abundance (mean ± standard error: 8.63 ± 1.86 fish^{-1} and 6.59 ± 1.29 fish^{-1} for April and October respectively) while *P. phlegethon* was consistently the least abundant (2.27 ± 1.17 and 0.96 ± 0.20). All three species decreased in relative abundance between April and October but increased in detection rates (Table 1), i.e., fewer fish were found spread across a larger area within the study site, suggesting possible dispersion within the river during winter flooding and increased habitat connectivity. Several sites shifted in primary substrate composition between April and October because of deposition of sediments and hydraulic action over the winter rainfall period. Primarily, sand deposition was high; 16 sites (31%) classified as “sand” in April shifted to 25 sites (49%) in October. However, the number of silted sites decreased from five sites in April to only one in October, indicative of hydraulic scouring. The trend of dispersed distributions continued in October 2019, as all none of the focal species exhibited large aggregations at single sites. Detection rates and mean MaxN for all three species decreased from the 2018 results (Table 1).

Environmental constraints associated with species relative abundances

Community composition; Non-metric multidimensional scaling analysis (nMDS)

The three study species separated across dimensions of the nMDS ordination space, indicating differing habitat associations (ordination stress = 0.023; Figure 4). The interaction between substrate (habitat) of a site and reach type significantly affected community composition (Table 2). Other significant factors driving changes in community composition were protected status of sites, distance from the uppermost site, site length and turbidity (Table 2).

The nMDS ordination indicates that the relative abundance of *L. seeberi* was associated with larger distance from the uppermost site (distance), sand and silt substrates and increased turbidity. *Sedercypris calidus* had higher abundances in a variety of environmental features, primarily bedrock, silt, and cobbled substrates. Furthermore, this species was associated with increasing site lengths (i.e., a proxy for larger site areas) and was associated with protected areas, but to a lesser extent than *P. phlegethon* which was strongly associated with the protected area. In addition, *P. phlegethon* was strongly associated with vegetated sites and shorter site lengths, closer distance to the uppermost site and lower turbidity.

Habitat drivers of relative abundance

Habitat characteristics were modelled to determine their significance as drivers of relative abundances, using GLMMs, for the three species. *Sedercypris calidus* was best modelled by a negative binomial mixed effects model with a zero-inflation component; model selection for *P. phlegethon* and *L. seeberi* indicated that negative binomial mixed effects models without zero inflation terms were most suitable (Table S1a – S1c). All species abundances were significantly predicted by distance from the uppermost site, reflecting a longitudinal shift in the fish community distribution between species (Table 3). All species were significantly more abundant in pools and less abundant in run or riffle (i.e., stream) habitats (Table 3). *Sedercypris calidus* relative abundance was predicted by site length in addition to reach type (being associated with pools rather than stream sections) and distance from uppermost site, with higher predicted abundances in longer sites. In addition, this species was more abundant in turbid conditions. *Pseudobarbus phlegethon* abundance was significantly predicted by substrate (habitat) type. This species had a strong association with vegetated and boulder-dominated sites and was very unlikely to be abundant in siltdominated environments. Distance from the uppermost site and pool environments were significant predictors of *L. seeberi* relative abundance, with the predicted abundance of this species increasing with greater distance and in pools as opposed to stream sites (Table 3). The final model for this species included a distance × site length interaction, suggesting a combined role of spatial and physical predictors in *L. seeberi* abundance patterns. There was a disordinal interaction where small sites (low site length) in the upper reaches (i.e., close to the uppermost site) had low abundance and abundance increased with site length. However, in the lower reaches, the opposite was true and *L. seeberi* abundance increased from large sites to smaller sites.

Discussion

Habitat associations and drivers of species abundance are critically important knowledge for conservation purposes. This is particularly important for range restricted and threatened species. We find that several factors affect the distribution and abundance across the longitudinal gradient and determine possible future threats to the recently recovered populations. The data gathered are the most ecologically accurate in the system to date, as much of the biology and baseline ecological knowledge of South African native fishes remains anecdotal (Ellender et al., 2017). We discuss evidence and key areas for developing management initiatives for fish species in a conservation and biodiversity hotspot (Skelton, 2000).

Sedercypris calidus is clearly a dominant player in the system, being both the most widely distributed and most abundant of the three cyprinids present. This pattern has been observed in prior studies using underwater video, traditional fyke netting and snorkel surveys (Weyl et al., 2013; Castañeda, Weyl & Mandrak, 2020). Unlike *P. phlegethon* and *L. seeberi, S. calidus* was detected in high abundance throughout the longitudinal gradient of the stream and within all measured habitat types. This species was found to be in greater abundance in larger sites (increased site length); this is possibly indicative that *S. calidus* is responsive to site length in terms of greater volume for larger shoal sizes (i.e., local carrying capacity) as a species that is generally more abundant and appears to have a strong shoaling preference (Woodford et al., 2005; Weyl et al., 2013; Castañeda et al., 2020a). Woodford et al. (2005) found that *S. calidus* was more strongly associated with deeper pools, a result in agreement with the present study.

Pseudobarbus phlegethon is the most vulnerable fish in the system, is only abundant in the protected upper reaches, and is highly unlikely to occur in the lower reaches. In contrast *S. calidus* increased in detection across more sites throughout the monitoring period. All analyses indicated that *P. phlegethon* is the most habitat-dependent and sensitive to disturbed habitats. Sensitivity can be inferred from the changes in this species distribution and abundance between April and October, and the concurrent fire disturbance over that time frame which caused a transition in substrate from silt to sand (i.e., 16 sites classified as "sand" in April shifted to 25 sites in October). The sub-terminal mouth of *P. phlegethon* indicates a preference for substrate foraging on detritus attached to rocky substrate which may be disrupted by excessive sedimentation (Skelton, 1996; Whitehead, Weyl & Bills, 2007). Further evidence of habitat sensitivity is *P. phlegethon's* strong association with vegetated and boulder-dominated habitats which proliferate in the upper reaches.

We found signals in all analyses suggesting that *L. seeberi* only proliferates in the lower reaches of the stream. Exclusion from the uppermost reaches is likely caused by a natural barrier close to the Algeria campsite. However, below the barrier, occurrence and abundance of *L. seeberi* changed considerably between the sampling events. Large aggregations primarily in the larger pools of the lower reaches characterise the late summer April sample, shifting to more widely distributed smaller groups in October. The spawning behaviour and migratory nature of this species could be an explanatory factor in this late-year pattern (Impson, Bills & Wolhuter, 2008; Impson, van der Walt & Jordaan, 2017). The interaction of distance from uppermost site and site length suggests that in the upper reaches *L. seeberi* has lower abundance in general and that small sites are particularly unsuitable.

Major fire events can have severe effects on the suitability of river habitat, in addition to the formation of sand plugs because of vegetation loss and bank erosion. It is unclear whether shifts in all species detection rates were a natural annual phenomenon or were driven/exacerbated by a major fire event in February 2018. We recorded an increase in sandy substrates in October following the winter rainfall. Species which have evolved within the stochastic CFE fynbos ecosystem (i.e., fire adapted) are resilient to unpredictable conditions (Ellender & Weyl, 2015) and it can be assumed that this event was not the main driver of seasonal change in fish abundance. Turbidity affected community composition overall (per PERMANOVA) and turbid conditions seem to increase *S. calidus* abundance (per the GLMMs). This may be linked to high abundance in a small number of larger, downstream pool sites, which tend to be more turbid than small stream sites in the upper reaches (evidenced by the collinearity of turbidity and distance from uppermost site; see

Supplementary Materials Figure S1). When considering aggregative species which accumulate in specific individual sites, abundance metrics alone should be complemented with other multivariate models (i.e., NMDS, CCA etc) to avoid erroneous conclusions. The upper ~4 km of the river runs within a formally protected area that did not burn in the 2018 fire event. This stretch of the river is free from agricultural runoff and has limited anthropogenic influence on the river conditions. This species was strongly associated with submerged vegetation, which was only found commonly in the upper reaches. Submerged vegetation and woody debris were found to be positively correlated with this species' abundance in a previous study (Woodford et al., 2005). Furthermore, *P. phlegethon* was associated with shorter site lengths, indicating a preference for smaller runs between riffles over the large, deep pools. This finding contrasts with those of Woodford (2005), who found a preference for deeper pools in this species. This discrepancy may reflect the use of snorkel surveys in previous studies, which may not adequately sample shallower runs where snorkelling could not be carried out. In contrast, the use of underwater video in the present study allowed for sampling of these sites. It is unclear whether the protected status of the upper reaches or the natural characteristics (high submerged vegetation, riparian integrity, boulders) is facilitating the abundance of *P. phlegethon*. This species appears to have a stronghold in this section of the river, while elsewhere in the river it is clearly in low abundance and has previously been identified as the most vulnerable of the fish assemblage (van der Walt, Impson & Jordaan, 2017).

The present study used underwater videos to demonstrate the utility of such a non-invasive and low-cost method to understand how a recovering and vulnerable cyprinid assemblage interacts with the abiotic variables in the Rondegat River, South Africa. The utility of underwater video monitoring in aquatic environments has been pioneered in marine community assessments and is increasingly being adopted in freshwater settings (Ebner et al., 2014). As a result, many protocols and statistical approaches to monitoring have been established and overcome (Harvey & Mladenov, 2001; Cappo et al., 2003; Coghlan et al., 2017). We were able to determine detection rates between seasons and maximise the data to include habitat characterisation. Thus, we would consider that underwater video makes an ideal candidate for long-term low-cost monitoring initiatives which can be archived for posterity and used in future research (e.g., behavioural analysis). The data collected provide a unique insight into behavioural and ecological aspects of aquatic communities under natural conditions (Ebner et al., 2009, 2014), increasing the scientific value of monitoring programmes beyond those currently possible with other monitoring techniques.

Overall, our results show clear habitat preferences in *P. phlegethon* and *L. seeberi* whereas *S. calidus* is a generalist throughout the stream. All three species can co-occur, but the extent is mediated by abiotic factors. Maintaining habitat integrity for *P. phlegethon* by reducing runoff and sedimentation to promote submerged vegetation in the lower reaches may be a constructive advance and drive population equilibrium. Future extreme drought and fire events are likely to continue to reduce flow and promote sand slugs which threatens *L. seeberi* persistence and reproduction. Thus, measures in the lower reaches should include identifying crucial stretches of the stream which include as many key habitats as possible to limit agricultural activities such as irrigation pumping to maintain water depth and natural flow regimes. By prioritising the species constrained to either extreme of the stream gradient will benefit *S. calidus* coincidently. To gain a more holistic picture, more research should be carried out to determine the biotic interactions which interact with the abiotic factors documented in this study to drive species abundance and distribution trends. Combining traditional survey methods with contemporary video and telemetry approaches may give more conclusive results on fish movement and habitat in the river. Consistent underwater video surveys are feasible to inform whether these actions cause a positive change and can be carried out by both environmental managers and citizen scientists, as local farmers should be engaged in the process.

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Author's contributions

CJB and OLF conceived the ideas and designed methodology; CJB and JS collected the data; CJB analysed the data; CJB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Figure captions

Figure 1 Map of the study system (Rondegat River, Cederberg, South Africa). White areas indicate elevation of 200 – 400 m, grey areas show areas of elevation >400 m. Camera deployment sites are indicated by black dots.

Figure 2 Photographs of the study species and habitats of the Rondegat River. (a) fiery redfin *Pseudobarbus phlegethon* (b) Clanwilliam redfin *Sedercypris calidus* (c) Clanwilliam yellowfish *Labeobarbus seeberi* (d) typical vegetated habitat of the upper reaches (e) the fire-affected banks showing the effects on riparian vegetation (f) a section of river in the middle reach, severely altered by a sand plug following fire-assisted erosion, which was previously inhabited by all three species.

Figure 3 Longitudinal profile of the distribution of study sites and temperature loggers. Stars indicate the location of temperature loggers, circles show the sampled sites. Parallel vertical lines indicate the position of the Rooidraai waterfall, the upper limit of non-native fish invasion. Elevation ranged from 120m to a maximum of 521m above sea level, and sampling covered 21km of the Rondegat River. The camera monitoring sites for collection of relative abundance and distribution data in April and October 2018 are depicted.

Figure 4 Biplot of the nMDS analysis relating environmental constraints and species relative abundances. Species MaxN (abundance) score centroids are shown, while standard ellipses containing 40% of the ordinated data denote the primary habitat types. Overlaps are considered to be non-significant. Site status as “protected” or “unprotected” areas is shown using convex hulls.