Thermal habitat restricts patterns of occurrence in multiple life-stages of a headwater fish

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Abstract: Our lack of knowledge on the spatiotemporal drivers of the distribution of many freshwater fishes, particularly as they differ among life-history stages, is a challenge to conservation of these species. We used 2-stage hurdle models to investigate drivers of occurrence and abundance of locally threatened adult and juvenile Northern River Blackfish in the upper Condamine River, Queensland, Australia. Different processes drive occurrence and abundance between the 2 life-history stages. Both adult and juvenile occurrences were negatively associated with high-magnitude, extended warming events, suggesting Northern River Blackfish are thermally restricted to cooler headwaters. Juveniles had greater sensitivity than adults to high stream temperatures. In contrast, drivers of abundance differed between life-history stages. Adult fish were negatively associated with increased fine-sediment loads, whereas juveniles were negatively associated with a hydrologically active inverse-distance-weighted grazing metric that accounted for the greater influence of grazed land close to the stream or in areas of high overland flow. Teasing apart environmental drivers affecting multiple life-history stages of a locally threatened headwater species enabled us to provide direct management recommendations for conserving this species and ecologically similar headwater fishes and their associated habitats.

Key words: thermal regime, distribution, environmental drivers, fish ecology, temperature, hurdle model, climate warming

Many freshwater fish populations have declined globally as freshwater habitats have become increasingly fragmented by anthropogenic effects related to thermal regimes, hydrological regimes, dispersal barriers, and habitat degradation (Gregory and Bisson 1997, Dudgeon et al. 2006, Magurran 2009, Fullerton et al. 2010). For species of conservation or commercial interest, understanding the spatiotemporal drivers that influence key life-history processes is a fundamentally important ecological question and a necessity for successful management (Planque et al. 2011). A wide range of biotic and abiotic variables that interact across multiple spatial and temporal scales influence the ecological patterns observed in stream systems (Poff and Allan 1995, Angermeier and Winston 1998, Steel et al. 2010). For example, landscape-scale processes may drive the overall distribution of a species, whereas local or fine-scale processes determine species abundance at any particular location (Kennard et al. 2007, Stewart-Koster et al. 2013). With the exception of many commercially and culturally important species, little

is known about the ecology and spatiotemporal dynamics of a large proportion of the fish populations occupying freshwater streams. This lack of knowledge makes their conservation challenging (King et al. 2013). Our goal was to tease apart the drivers (e.g., thermal magnitude or sedimentation) affecting multiple life-history stages of a locally threatened headwater species to provide ecological information to support conservation of this species and ecologically similar headwater fishes and their associated habitats.

The ability to manage and protect freshwater species requires knowledge of the spatiotemporal factors that most strongly influence their distribution and abundance (Walsh and Webb 2014) at multiple scales, but effective conservation is difficult when little is known about a species (Feist et al. 2010, Stewart-Koster et al. 2013). Influential drivers may shift between life-history stages of fish (Parsley et al. 1993). For example, early life stages require nursery habitats that provide adequate food resources, protection from extreme environmental stressors (i.e., extreme temperatures,

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high sediment, and nutrient loads), and shelter from predators (Koehn and Kennard 2013). In contrast, their requirement for food resources increases but their predation risk decreases with ontogenetic development. Adults also may migrate to habitats that suit their new ecological and physiological requirements (Koehn and Kennard 2013). Thus, understanding how habitat requirements differ between juvenile and adult fishes (Schlosser 1991, Dudgeon et al. 2006) is necessary for sustainable management and conservation of populations.

Headwater streams are integral components of freshwater stream systems because they provide a diverse array of habitats for multiple life stages of aquatic vertebrates and invertebrates (Lowe and Likens 2005, Callahan et al. 2014). Headwater streams often are characterized by high ecological and hydrological variability because relatively fine-scale shifts in local conditions can influence in-stream habitats and biota (Lowe and Likens 2005, Meyer et al. 2007, Callahan et al. 2014). For example, climate change has variable influence in headwater systems in northwestern USA (Isaak et al. 2016). This finding highlights the need to understand how stream biota may be affected locally by global environmental changes and the scales at which environmental variables operate. Many cold-water species that occupy headwater streams are restricted to these habitats because of narrower physiological thermal tolerance at high temperatures compared to tolerances of more generalist species. Current rates of climate warming are likely to alter headwater streams, but the extent and repercussions of changes in climate on juvenile and adult fishes, whose thermal thresholds may differ, are unclear (McCullough 1999). The results of many climate studies suggest that the thermal thresholds of cold-water species may be surpassed in many streams, thereby reducing the amount of thermally suitable habitat available to species (Parmesan and Yohe 2003, Pörtner and Farrell 2008).

The goal of our study was to gain an understanding of the effects of environmental variables and the scales at which they influence the distribution and abundance of adult and juvenile fishes in headwater streams. We have based our case study on the Northern River Blackfish (*Gadopsis marmoratus* Richardson, 1848) (hereafter blackfish) in the upper Condamine River, Queensland, Australia. We wanted to understand: 1) which environmental variables most strongly influence adult and juvenile distribution (presence/absence), 2) given presence, which environmental variables drive local abundance of adult and juvenile fish, and 3) whether the scales at which these environmental effects occur differ between adult and juvenile fish. We used the information gained to make management and conservation recommendations tailored to juvenile and adult life stages of this locally threatened species. In addition, we demonstrate a modeling approach that can be used to answer similar questions about other species with restricted dispersal abilities and diverse habitat needs over multiple life stages.

METHODS
Study site

Our study area is in the upper Condamine River and Spring Creek tributaries of the Condamine River catchment in southern Queensland, Australia (Fig. 1). The regional climate is characterized by hot summers where temperatures can be >40°C and cool winters, where temperatures often are <0°C (Australian Government Bureau of Meteorology 2014). Most rainfall occurs during the austral summer (December–February), when the mean annual rainfall is ~750 mm (Australian Government Bureau of Meteorology 2014). Much of the region is currently used for agriculture (e.g., grazing and cropping) in part because the soils have high fertility. European settlement in the 1840s led to significant agricultural expansion, clearing of riparian areas and woodlands, and consequent erosion and water-quality issues (Carberry 1995). The primary vegetation throughout Spring Creek is open rainforest, with grasslands and eucalypt species prominent in the lower reaches. River she-oak (*Casuarina cunninghamiana*) currently dominates the heavily farmed riparian areas bordering much of the Condamine River. Recent improvements to agricultural practices and habitat restoration efforts have improved riparian-zone health in parts of the catchment (SRB, personal observation).

Study species

Blackfish are benthic-dwelling, nocturnal fish of the Percichthyidae family (Baumgartner 2007). They are carnivorous, generalist feeders that forage for crustaceans, mollusks, small fish, and insects (Jackson 1978a, Lintermans 2007). Blackfish are nonmigratory and highly sedentary, with home ranges that average between 10 and 26 m in length (Khan et al. 2004). Like many cold-water fish species, blackfish are a headwater species because they generally are unable to tolerate high temperatures or high levels of siltation (Koehn and O'Connor 1990). For example, in Victoria, Australia, they are physiologically limited to streams with maximum temperatures of 28°C (Harasymiw 1983), prefer low-velocity streams (<20 cm/s), and show strong affinity for pools (Jackson 1978b, Khan et al. 2004). Blackfish are strongly associated with in-stream cover including undercut banks, large woody debris, snags, boulders, and in-stream vegetation. Blackfish spawning typically occurs from austral spring to early summer when temperatures are >16°C, and females generally lay their eggs in hollow logs or on boulders where water velocities are relatively low (Jackson 1978b, Khan et al. 2004).

Blackfish are distributed throughout most of the Murray–Darling Basin (MDB) and were historically distributed across
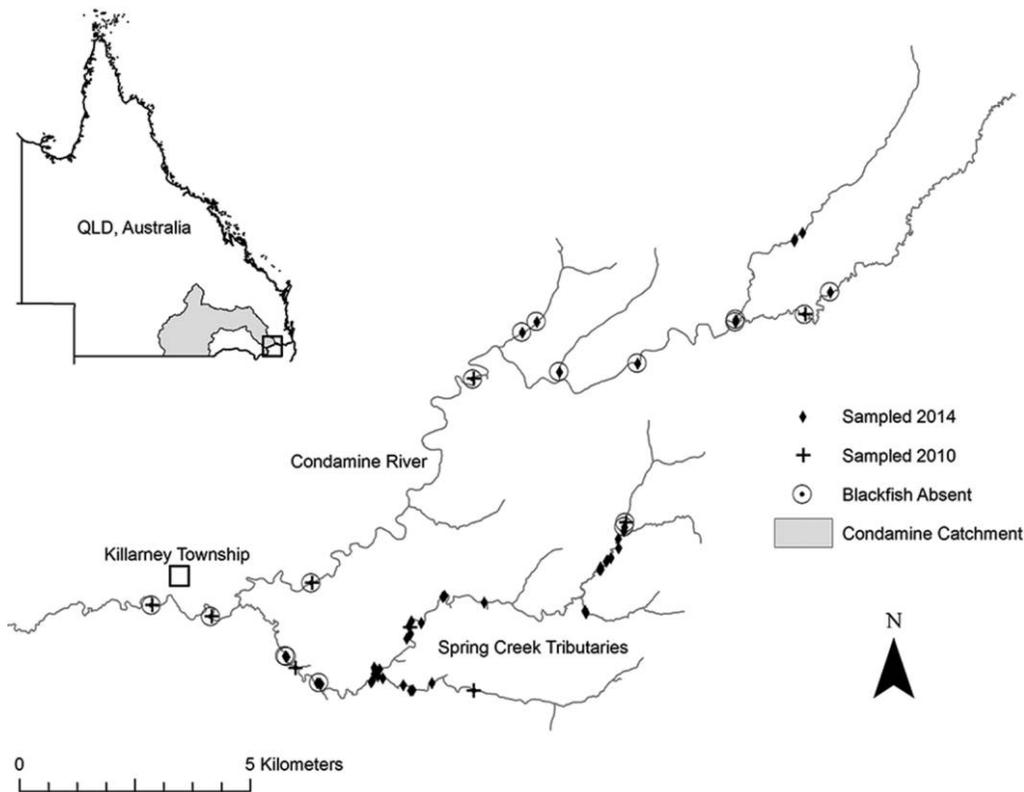
Figure 1. Map showing the location of the Condamine River catchment in southeastern Queensland (QLD), Australia, the locations of 50 sites surveyed for northern River Blackfish in 2014, and the additional 9 sites surveyed in 2010.

the entire upper Condamine River catchment. The population we studied occupies the upper Condamine River and Spring Creek subcatchments of the northern MDB at the northernmost extent of the blackfish range. Recent surveys of this isolated population suggest that these fish may be thermally restricted to their current habitat range (Balcombe et al. 2011a). The species is not listed as threatened, but this population is regarded as locally threatened and is a no-take species (Department of Agriculture and Fisheries 2016).

Fish sampling

We used a portable backpack electrofisher (Mk 12 POW set at 300 V, 70 Hz, 4-ms pulse width; Smith-Root, Vancouver, Washington) to sample fish at 50 sites throughout the catchment (Fig. 1) in March 2014. Prior experience suggested that this output is effective for collecting a wide range of fish species across stream and habitat types, while minimizing potential injury to fish (SRB, personal communication). We defined sites as individual hydrologically distinct (i.e., riffle, run, or pool) habitat units in stream reaches. We placed weighted seine nets at either end of the site to reduce the likelihood of fish escaping. We surveyed each site with multiple-pass, spot-fishing techniques as recommended by Pusey et al. (1998) to gain an accurate, quan-

titative estimate of fish species abundance. We sampled from down- to upstream in a zigzag fashion and stunned fish temporarily for ~5 to 10 s until the enclosed area was entirely sampled. This effort was counted as a single electrofishing pass, and we completed 3 passes for each site (Pusey et al. 1998). We collected all stunned fish with a fine-mesh handnet and placed them immediately in a 70-L aerated plastic container containing stream water. Once electrofishing of the site was complete, we weighed and measured captured fish with a measuring board and field balance. Juvenile (young-of-year) blackfish were defined as individuals <70 mm. We returned fish to the study site alive and unharmed ≤1 h after capture. Fish and habitat data collected in March 2010 by Balcombe et al. (2011a) at 9 additional sites were added to the initial data set to increase spatial coverage (n = 59 sites). They used the same electrofishing methods and habitat sampling design as we did. Survey sites were scattered throughout the catchment, but denser sampling occurred along the branches of Spring Creek because of ease of access (Fig. 1).

Environmental predictor variables
Habitat   We conducted habitat surveys according to a standard protocol described by Kennard et al. (2006). Habitat metrics are summarized in Table 1. We measured habitat attributes known to be related to blackfish distribution

Table 1. Environmental predictor variables measured and calculated for hurdle models. LWD = large woody debris, AQMAC = aquatic macrophytes, RM = root mass.

Variable	Description	Unit	Mean (range)
Fines	Fine sediments (mud, sand, silt)	%	33.58 (6.87–97)
Coarse	Coarse gravel	%	47.85 (0–91.1)
B-rock	Bedrock	%	18.44 (0–84.4)
Flow	Stream flow discharge	m^3/s	3.69 (0–48.84)
Str comp	Structural complexity: derived from scaling measures of LWD, AQMAC, and RM and summing to create a measure of functionally structural habitat	Scale (0–15)	3.66 (3–11)
Ucb	Undercut banks	%	24.28 (0–70)
FPC	Foliage projective cover	%	66.4 (0–99.5)
Hab type	Habitat type (pool, run, or riffle)	–	
Hab area	Habitat area = site length × mean wet width × mean depth	m^3	29.2 (3.2–148)
HA-IDW	Hydrologically Active – Inverse Distance Weighted (HA-IDW) grazing metric	%	65.4 (10.6–97.5)
Upbuff	Mean riparian coverage within a 10-m buffer 1 km upstream from a site	%	42.76 (8.4–74.8)
Elev	Elevation	m	675 (505–887)
MWMT	Maximum weekly maximum temperature = highest 7-d moving average of daily maximum temperatures	°C	24.92 (20.32–28.48)
Event Days	The number of successive days stream temperature was >28°C	Count	0.66 (0–4)
Frequency Days	The total number of days in summer on which temperature was >28°C	Count	1.07 (0–11)
Max Change	The maximum temperature change within 3 h at a site	°C	3.96 (1.45–6.17)
wavVar	64-h wavelet variance from a discrete wavelet transformation	–	0.53 (0.17–0.69)

(Jackson 1978b, Davies 1989, Khan et al. 2004, Koster and Crook 2008) at each site immediately after fish surveys. We scaled measures of root masses (RM), large woody debris (LWD), and aquatic macrophytes (AQMAC) from 1 to 5 based on % 2-dimensional cover. These structures have similar ecological functions, so we summed them to create one measure of structural complexity for each site. We calculated one volumetric value for habitat area as mean wetted-stream width × site length × mean site depth and discharge as mean stream velocity × habitat area (m^3/s).

Land use, land cover, and topography   We used a geographic information system (GIS) to create predictor variables that represented aspects of the landscape that were expected to be associated with blackfish distribution (Table 1). Pastoral grazing is the primary land use throughout the upper Condamine River (Department of Science, Information Technology and Innovation 2014) and probably contributes to riparian degradation, which potentially affects fish habitat (Beschta 1997, Isaak and Hubert 2001). We used the 2006 Queensland Land Use Mapping Programme (QLUMP) data set (Department of Science, Information Technology and Innovation 2014) to calculate % grazed area within the catchment at each fish sampling site based on a hydrologically active, inverse-distance-weighted landuse metric (HA-IDW Grazing) (Peterson et al. 2011). We chose to use HA-IDW metrics rather than nonspatial, lumped catchment metrics because HA-IDW metrics account for the greater influence of grazed areas in close proximity to the stream and areas prone to higher overland flows. See Appendix S1 and Peterson et al. (2011) for more details.

Temperature equilibrium in headwaters streams is reached 500 to 1000 m downstream of perturbations that can influence stream temperature (Rutherford et al. 2004). Therefore, we used the Statewide Landcover and Tree Study (SLATS) Foliage Projective Cover (FPC) data set (Kuhnell

et al. 1998) to calculate an upstream shading predictor that represented the mean foliage projective cover within a 10-m riparian buffer continuing 1 km upstream from each sampling site (Appendix S2). Last, we extracted point elevation from a 10-m digital elevation model (DEM) (Department of Natural Resources and Mines 2010) at the midpoint of each fish sampling site because elevation is strongly related to fish distributions throughout Australia (Pusey et al. 2000).

Stream temperature predictors   We calculated a suite of temperature metrics to describe the magnitude, duration, frequency, and variability of heating events likely to affect blackfish across multiple temporal scales throughout the summer period, when extreme temperatures are most likely (Dunham et al. 2005, Isaak et al. 2010). We were unable to install stream temperature sensors at each fish sampling site because of impermeable bedrock in many sites. Therefore, we used hourly stream temperature data collected throughout the upper Condamine catchment and spatial statistical stream-temperature models to predict daily maximum stream temperatures and aggregated stream-temperature metrics at each fish sampling site. We used daily maximum temperatures at observed locations to predict daily maximum temperatures at unsampled sites and then calculated temperature metrics, whereas we produced aggregated metrics by predicting the metrics generated at observed locations (also based on daily maximum temperatures) at unsampled sites. We used aggregated metrics for all but one metric (Frequency Days) because the predictive ability of temperature metrics depends on the method used to generate them (see Turschwell et al. 2016 for further details).

Results from previous studies suggest that blackfish are thermally restricted to temperatures <28°C (Harasymiw 1983). Therefore, we used this temperature to calculate biologically relevant temperature metrics including the maximum weekly maximum temperature (MWMT); successive number of days with temperatures >28°C (Event Days); total number of days with temperature >28°C (Frequency Days); 64-h (2.66-d) wavelet variance (wavVar), which represents the across-day thermal variance at a site (Steel et al. 2016); and the maximum temperature change within 3 h at a site (Max Change). We used a 3-h threshold to examine the acute thermal stress blackfish may experience at a site because a threshold of 100 min (1.66 h) was used to estimate upper and lower tolerance limits for fish survival (Elliott 1991). Wavelet decomposition partitioned overall variance in the time series into independent measures of variability at particular time scales. Higher values of wavVar indicate greater thermal fluctuations at the scale of 2 or 3 d (Steel et al. 2016). We based Wavelet and Max Change metrics on observed hourly data predicted across the 59 sites with stream temperature models. Wavelet metrics were calcu-

lated based on the wavVar function in the *wmtsa* package (Constantine and Percival 2013) whereas MWMTs were calculated in the *zoo* package (Zeileis and Grothendieck 2005) of R statistical software (version 3.1.3; R Project for Statistical Computing, Vienna, Austria). We calculated all other temperature metrics with custom R scripts (Appendix S3).

Statistical methods

Exploratory analyses   The number of ecologically relevant, candidate predictor variables was relatively large compared to the number of observed locations ($n = 59$), so we used machine-learning methods to reduce the number of variables in model selection. We fit random-forest models (Breiman 2001) to adult and juvenile abundance data with the predictor variables in Table 1. We fit models with the *randomForest* package (Liaw and Wiener 2002), with 1000 trees and 6 variables sampled randomly at each split. We began with 17 potential predictor variables and reduced predictors based on variable importance. We fit a total of 4 random-forest models (adult count, adult presence/absence [P/A], juvenile count, and juvenile P/A) to reduce the number of potential predictor variables included in the 2 hurdle models. In each of the 4 random-forest models, we included the top predictors until we saw a clear decrease in variable importance. For count models, variables were kept when permutation of the predictor variable resulted in >12.5% increase in error rate against the out-of-bag predictions. For binomial models, permuted variables that resulted in a mean decrease in accuracy of >15% were included. After random-forest model fitting, we used Spearman's correlation coefficient to test for collinearity among all remaining predictors. When variables had pairwise correlation >0.7, we removed 1 variable based on ecological inference from further analyses (Zuur et al. 2009).

Hurdle models: occurrence vs abundance   Sampling rare species, such as blackfish, often produces data sets with a large proportion of 0 values (i.e., 0-inflated data; Martin et al. 2005, Potts and Elith 2006). Therefore, we applied a hurdle model that accounted for excess true 0s in both adult and juvenile blackfish data. A hurdle model is a 2-part model in which the probability of species presence and abundance, conditioned on presence, are modeled from the same data. We used hurdle models because they allow mechanisms that determine the presence of a species to differ in scale from those that determine abundance (Potts and Elith 2006, Wenger and Freeman 2008, Falke et al. 2013). The P/A component was modeled based on a truncated binomial distribution with a logit link, whereas the abundance component was modeled with a negative binomial distribution and log link. We used the *pscl* package (Jackman 2008) to fit the hurdle models. All statistical analyses were implemented in R.

Model selection and performance We used a 2-stage, backward-stepwise model-selection process for adult and juvenile hurdle models. We began by considering the candidate predictor variables in the binomial model, while fixing the count model to a simple intercept (i.e., no predictor variables). After nonsignificant terms ($\alpha > 0.05$) were removed from the binomial model, we added all potential predictor variables to the count model and used another backward-stepwise selection procedure to reach the final model (Sveegaard et al. 2012), which included only predictors in the count and binomial components that were significant ($\alpha < 0.05$).

We repeated the model-selection process separately for adult and juvenile models for 3 collinear thermal metrics that represented different aspects of the thermal regime (Event Days, MWMT, and Frequency Days). We compared the best subset of predictor variables for each temperature-metric model based on the Akaike Information Criterion corrected for small sample size (AICc; Hurvich and Tsai 1989). We also used leave-one-out cross-validation (Kohavi 1995) to assess the predictive ability of the models. We iteratively removed data from a site, refit the model to the remaining data, and used the fitted model to predict blackfish occurrence and abundance at the missing site (59 sites = 59 models/cross validation). We used the observations and the leave-one-out cross-validation predictions to calculate the root-mean-square prediction error (RMSPE) and squared Spearman's rank correlation coefficient (predictive r^2) for each model. We identified the best 3 adult and juvenile models (3 × predictors, 2 × responses = 6 models) based on the RMSPE, and the predictive r^2 provided an easily interpreted estimate of the predictive ability of the model. Throughout model fitting, we examined standardized residuals in adult and juvenile hurdle models for potentially influential outliers. We also calculated studentized 95% confidence intervals (CIs) for model parameters based on nonparametric resampling (Davison and Hinkley 1997) in the *boot* package (Canty and Ripley 2015).

RESULTS
Exploratory

Variable importance plots generated from the 4 random forest models display the candidate variables included during the hurdle model selection process (Fig. S1). Of the 59 sites included for analysis, 17 had no adults and 31 had no juveniles. Juveniles did not occur at any site without adults, but adults were present without juveniles at 14 sites. Adult abundance ranged from 0 to 60 individuals/site (mean ± SD, 13 ± 15.5), whereas juvenile abundance ranged from 0 to 106 individuals/site (6.1 ± 16.2).

Hurdle models

We pooled sampling years (2010 and 2014) in the final hurdle models because adult and juvenile abundance did not differ between years. We considered using habitat area at a site as an offset in the models because it ranged between 3 and 148 m^3, but we did not do so because we found no statistical relationship between habitat area and adult or juvenile abundance. Blackfish exhibit little movement regardless of life-stage, so we considered adult abundance as an offset based on the assumption that juvenile presence depends on presence of adults in the same habitat. Exploratory analysis indicated that juvenile abundance was not related to adult abundance, so we did not include adult abundance as an offset in the final juvenile model.

MWMT, Event Days, and Frequency Days were highly correlated ($r^2 > 0.7$), but each describes a slightly different aspect of the riverine thermal regime. For the occurrence component of the hurdle models, Event Days provided the best predictive performance based on the RMSPE (Table 2), but the effect of the 3 metrics (Event Days, Frequency Days, and MWMT) was similar (Fig. 2A–C). Each had a significant, negative influence on adult and juvenile blackfish occurrence.

Adult model

The best adult model indicated that the probability of blackfish occurrence was related to 3 thermal metrics. The probability of adult blackfish occurrence at a given site was negatively affected by a high number of Event Days, and positively related to higher wavVar and Max Change. Adult blackfish abundance and wavVar also were positively related in the count component of the adult hurdle model. Adult fish abundance was negatively associated with fine sediments (Fines; Table 3). The RMSPE and predictive r^2 for the best adult model were 14.08 and 0.42, respectively (Table 2).

Juvenile model

The best juvenile blackfish model suggested that the probability of juvenile occurrence was affected by 3 thermal metrics (wavVar, Max Change, Event Days; Table 3). The probability of juvenile blackfish occurrence was negatively

Table 2. Cross-validation results from fitting the 3 collinear temperature metrics to adult and juvenile (3 × predictors, 2 × responses = 6 models) hurdle models. Bold indicates the model with the lowest root mean square prediction error (RMSPE). See Table 1 for variable names.

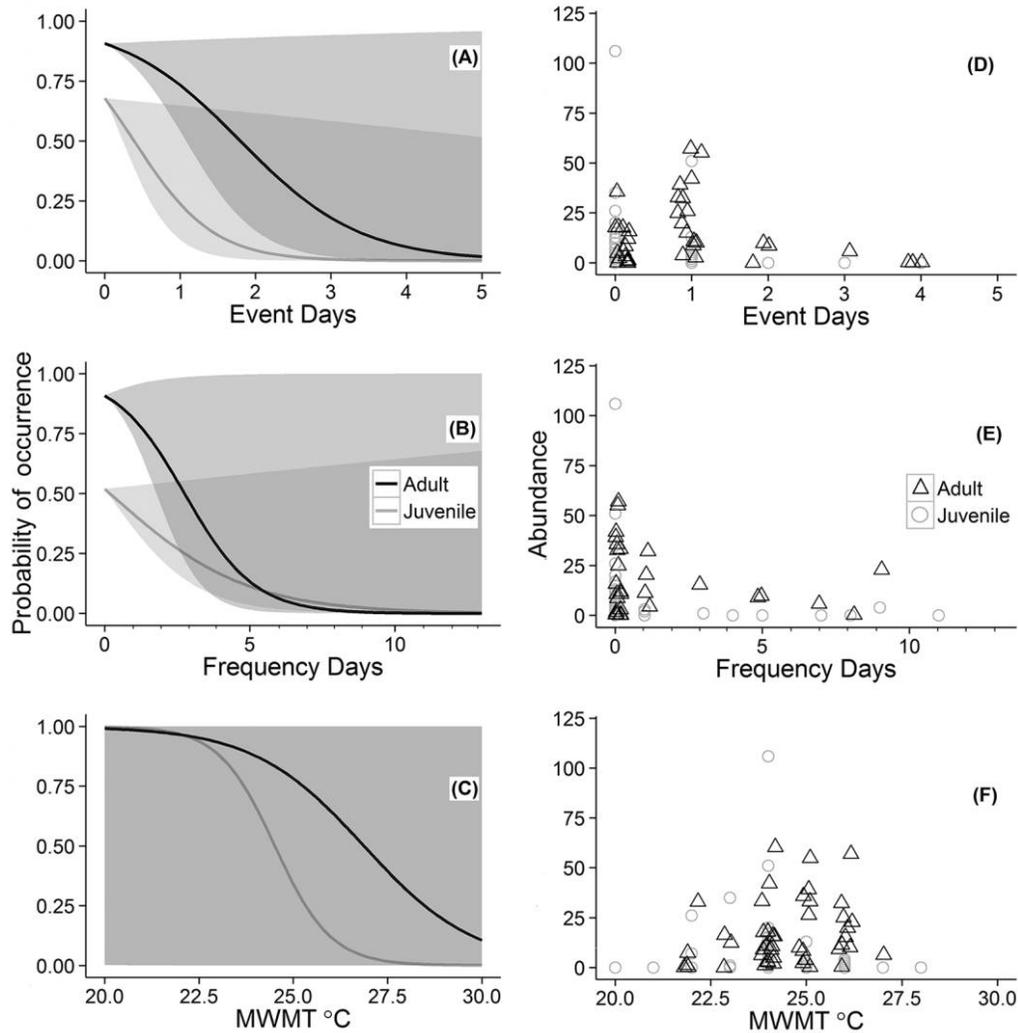| Response	Predictor	RMSPE	Predictive r^2
Adult model	MWMT	14.24	0.37
	Event Days	**14.08**	0.42
	Frequency Days	14.34	0.35
Juvenile model	MWMT	58.35	0.16
	Event Days	**34.12**	0.12
	Frequency Days	35.61	0.17

Figure 2. Relationships between probability of occurrence (A–C) and abundance (D–F) of adult and juvenile River Blackfish and the number of successive days stream temperature was >28°C (Event Days) (A, D), the total number of days in summer on which temperature was >28°C (Frequency Days) (B, E), and the highest 7-d moving average of maximum weekly maximum temperature (MWMT) (C, F) estimated from 3 separate hurdle models for an average site where all predictors in the final model were held at mean values. Shaded areas are 95% confidence intervals.

related to Event Days and positively related to wavVar and Max Change. The effect of Event Days was stronger for juveniles than adults, whereas the relationship between wavVar and Max Change was weaker for juveniles than adults. Our results suggest that juveniles are more susceptible to high-magnitude, extended warming events (Event Days, Frequency Days, MWMT) than adults, which have a higher probability of occurrence than do juveniles at sites with higher maximum temperatures and extended periods of warming (Fig. 2A–C). The count component of the best juvenile model suggested a positive relationship between abundance and elevation at a site and a negative relationship between abundance and HA-IDW grazing (Fig. 3, Table 3). The RMSPE and predictive r^2 of the best juvenile model were 34.12 and 0.12, respectively (Table 2).

Two outliers were identified in the exploratory analyses for the juvenile models, but we made a decision to leave these data in the final model because they are true observations that are representative of local conditions. One outlier occurred at a site with a high level of grazing and higher-than-average juvenile counts, whereas another occurred at a site with lower-than-average elevation and a highly disproportionate number of juveniles compared to adults. Models refit without these data had slightly altered model coefficients and standard errors, but the direction of the relationships between predictor variables and response did not change, so our interpretation remained the same. When these data were excluded from the model, the RMSPE decreased from 34.12 to 29.15, and the predictive r^2 improved marginally from 0.12 to 0.15.

Table 3. Parameter estimates (SE) for adult and juvenile black-fish hurdle model coefficients. Log(theta) = the overdispersion parameter in the negative binomial model component. See Table 1 for variable names. * = $p < 0.05$, ** $p = < 0.01$.

Model	Count (truncated negative binomial)	Zero (binomial)
Adult		
Intercept	1.085 (1.202)	−8.51 (2.67)**
wavVar	4.047 (2.026)*	9.85 (3.77)**
Fines	−0.020 (0.006)**	
Log(theta)	0.637 (0.277)*	
Max Change		1.41 (0.53)**
Event Days		−1.27 (0.49)**
Juvenile		
Intercept	0.953 (1.692)	−8.26 (2.75)**
Elev	0.009 (0.003)**	
HA-IDW	−0.078 (0.020)**	
Log(theta)	−0.857 (0.688)	
Event Days		−1.91 (0.66)**
wavVar		8.86 (4.10)*
Max Change		1.09 (0.45)*

Model comparisons

We examined the mean relationship between the probability of adult and juvenile occurrence for each of the 3 temperature metrics in an attempt to identify differences between life stages. In Event Days and Frequency Days models (Fig. 2A, B), juveniles were less likely than adults to occur at sites that repeatedly were >28°C. However, these relationships carried a significant amount of uncertainty, which probably occurred for several reasons. When Event Day and Frequency Day values were relatively high (>1 and >3, respectively) relatively few juvenile and adult fish were present (Fig. 2D, E). Our relatively low sample size ($n = 59$) in conjunction with few observations at these higher temperature-metric values creates greater uncertainty in our model predictions and subsequent CIs. A great deal more uncertainty was present in the relationship between MWMT and juvenile or adult occurrence because the CIs completely overlapped between adult and juvenile models (Fig. 2C). However, this overlap was not surprising given that both adults and juveniles were found between ~22 and 27°C (Fig. 2F).

DISCUSSION

Our results suggest that adult and juvenile blackfish inhabit a similar thermal niche, but that juveniles may be more sensitive than adults to chronic exceedance of thermal tolerance thresholds. We acknowledge significant uncertainty in these relationships. We think similar processes

drive occurrence in adults and juveniles because of the limited dispersal patterns of blackfish (Khan et al. 2004, Huey et al. 2017). Juveniles tend to live in close proximity to adults because blackfish lay adhesive eggs on various substrates in the same general area that they inhabit (Khan et al. 2004, Lintermans 2007) and do not undergo spawning migrations like those of salmonids (Groot and Margolis 1991). Thermal optima often differ between adult and juvenile freshwater fishes (McCullough 1999), but increased stream temperatures can lead to early onset spawning and resource mismatches (Crozier et al. 2008). In extreme cases, increased temperatures may result in a complete inhibition of spawning (Dorts et al. 2012), which may result in habitats occupied only by adults. Additional sampling might reveal that adults and juveniles occupy sites with higher MWMTs, Event Days, and Frequency Days than we observed. However, additional sampling also might confirm that 28°C is a biologically driven thermal threshold as suggested by Harasymiw (1983), who found that the upper thermal thresholds for blackfish were between 27 and 29°C. Thus, further sampling is required to clarify these relationships, especially at large metric values for which few observations exist.

Uncertainty was present in the relationships we found, but the predicted probabilities of occurrence for the 3 thermal metrics derived from our final models are based on the best data available for blackfish in our study region. Based on our results, anecdotal evidence raised in previous studies (Balcombe et al. 2011a, b), and modeled data on blackfish populations in Victoria, Australia (Bond et al. 2011), we think the thermal habitat in parts of the upper Condamine River has been altered to the degree that temperatures exceed the thermal tolerance of juveniles, but not
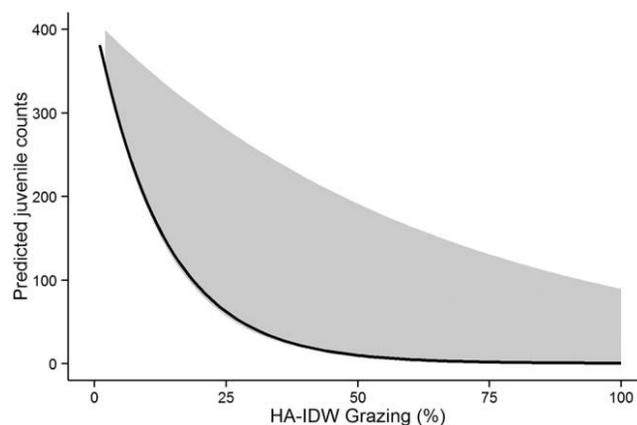

Figure 3. Predicted juvenile blackfish abundance as a function of hydrologically active, inverse-distance-weighted (HA-IDW) grazing (%) in the catchment for an average site, where all predictors included in the final model were held at mean values. Shaded area is 95% confidence interval.

of adults. Furthermore, unlike Isaak et al. (2016), we think the rate of warming is unlikely to be significantly slower in these headwater streams than in lowland regions because of the absence of snow melt and of significant elevational changes between lowland and headwater areas. If we are correct, juvenile blackfish may be more vulnerable than adults to increased climate warming in the upper Condamine River. Increasing air temperatures, which are related to increasing stream temperature (Crisp and Howson 1982, Isaak and Hubert 2001), may lead to changes in survival and recruitment that have population-wide consequences (Ficke et al. 2007).

The strongly positive relationships between adult and juvenile occurrence and temperature metrics associated with variability (wavVar and Max Change) were unexpected, but were understandable when we examined the spatial distribution of measurements. Most sites where blackfish were present were of lower stream order (narrower and shallower streams). Narrow, shallow, low-order streams often have reduced thermal buffering (Poole and Berman 2001, Caissie 2006). Thus, these sites are inherently more susceptible than sites in higher-order streams to thermal fluctuations and increased thermal variability. The implications of increased thermal variability on fish physiology and stress are not well understood (McCullough et al. 2009), but Steel et al. (2012b) experimentally manipulated thermal regimes and found that thermal variance affected the timing and development at emergence of Chinook Salmon (*Oncorhynchus tshawytscha*). We do not think that blackfish benefit from high thermal variability. Rather, variances tend to be higher in the cooler headwater tributaries, where blackfish are more common and abundant, than in the Condamine River, which is a larger stream. Nevertheless, blackfish historically were present throughout the Condamine River. Therefore, we think the current thermal conditions in the Condamine River exceed the physiological tolerances of blackfish, thereby limiting populations to the cooler, more variable headwaters. We also found a strong positive correlation between abundance of adult blackfish and wavVar, and we think the most logical explanation for this result also is the spatial distribution of blackfish in smaller headwater streams, rather than a positive effect of increased thermal variability. Nevertheless, this finding is interesting because it suggests that both adult and juvenile blackfish are tolerant of high thermal variability when the habitat is suitable and within their optimal physiological range.

Several notable differences were observed between habitats associated with higher levels of adult vs habitats associated with higher levels of juvenile abundance. Deposited fine sediment at a site was negatively associated with adult blackfish abundance. Sedimentation throughout the MDB has been identified as a major cause of range reduction of blackfish across the basin and within the Condamine River catchment because of smothering of spawning sites and

eggs (Lintermans 2007). Furthermore, fine sediment deposition often leads to substrate smothering and negatively affects available surface area for algal and biofilm growth, which can lead to negative, bottom-up trophic effects through food webs (Allan 2004, Bond and Lake 2004). We think the negative relationship between grazed land in close proximity to the stream (HA-IDW Grazing) and juvenile abundance is indicative of coarse-scale degradative effects of grazing within the catchment. Increased sedimentation at a site often is associated with grazing, but sediments generated locally are likely to be entrained in the flow and deposited in lower velocity habitats at sites downstream (Whiting et al. 2005). Thus, high grazing pressure close to the stream or in areas with increased potential for overland flow is most likely to affect juvenile abundance through processes like soil pugging. Pugging occurs when hooved animals graze in moist soils and causes severe compaction of the soil, which may subsequently damage riparian vegetation and increase fine sediment loads (Bilotta et al. 2007). Riparian grazing also can lead to increased nutrient loads through direct deposition or washing of animal feces and urine into the stream (Neilen et al. 2016). This grazing leads to further riparian degradation, which negatively affects local habitat quality (Allan 2004, Sheldon et al. 2012). Our models suggest that predicted juvenile abundance decreased to almost 0 when the % catchment grazing was >65%. These findings indicate that under current management practices, even small increases in grazing in riparian areas or areas with a high potential for overland flow may negatively affect juvenile blackfish survival and recruitment.

Patterns of occurrence and abundance in stream fishes often can arise from ecological processes acting at various spatiotemporal scales (Wenger and Freeman 2008, Steel et al. 2012a, Falke et al. 2013), and disentangling these processes is of substantial ecological and conservational interest. Our results suggest that blackfish occurrence and abundance are influenced by different processes and that drivers of abundance differ between adults and juveniles. Falke et al. (2013) found different drivers of occurrence and abundance in threatened populations of Steelhead (*Oncorhynchus mykiss*). The predicted occurrence of spawning Steelhead increased with higher proportions of suitable substrate grain size, whereas abundance was determined primarily by the thermal regime and frequency of scouring flows in the John Day River, USA. Our results highlight the need to consider the environmental requirements of species at different life-history stages. This consideration is especially critical if size classes are pooled in survey data sets because the conclusions drawn from studies based on such data may not capture the ecological processes underpinning particular life-history stages of the target species (Parsley et al. 1993, Dudgeon et al. 2006). Such pooling can lead to management decisions that benefit a particular life-history stage, but fail to ensure that populations persist over time.

Ecologists often are interested in modeling relationships between distribution and abundance and habitat structure (Elith and Leathwick 2009). The ability of these models to relate abundance and occurrence to environmental and biological processes depends on the ecologist's ability to capture environmental variability at the scales relevant to the species and system in question (Falke et al. 2013). Our model predictions were highly uncertain. The adult model had much better predictive ability than the juvenile models, which described only a small amount of the total variation in blackfish abundance and occurrence. Nevertheless, our results establish a baseline upon which future studies can build. For example, fine-scale nutrient and chemical analyses and seasonal blackfish and habitat sampling may provide additional information about the spatiotemporal drivers of blackfish distribution and abundance. Moreover, we need to understand when or why recruitment failures occur at sites where adults are present without juveniles because our study did not capture these particular processes.

Our results do enable us to provide management recommendations for blackfish that are relevant for other ecologically similar headwater species facing comparable environmental stressors in degraded landscapes. Based on the evidence to date, we think the most sensible restoration strategy is to re-establish and regenerate riparian zones. Most degradation occurs in these hydrologically active regions and, thus, rapid and effective restoration and rehabilitation planning is needed (Poole and Berman 2001). Riparian restoration and grazer exclusion probably would reduce the effects of grazing on in-stream fauna, provide in-stream habitat, filter nutrient-rich runoff, and reduce fine particulate runoff into streams (Tabacchi et al. 1998). All of these grazing effects threaten blackfish (Lintermans 2007). Furthermore, management actions that promote revegetation will help buffer headwater streams against extreme summer temperatures, especially during the extended high-magnitude temperature events (Isaak and Hubert 2001, Rutherford et al. 2004, Caissie 2006, Davies 2010) that are most likely to affect blackfish survival (Balcombe et al. 2011b). Depending on the degree of habitat degradation, 5 to 15 y may be needed for rivers to recover their natural thermal regime after vegetative regrowth (Edmonds et al. 2000). This solution may not seem rapid, but the predicted increase in maximum daily temperatures for the region is 1.17°C by 2030 based on a climate-projection tool (Clarke et al. 2011). Thus, when viewed within the context of climate change, revegetation is a highly achievable management goal. With adequate planning, this action could be an effective way to manage thermally threatened headwater species (Caissie 2006, Isaak et al. 2010).

Conclusions

Little research has been done to provide direct information on the drivers of locally threatened northern River Blackfish populations within the upper Condamine River. We have demonstrated that different environmental processes may be driving blackfish distribution and abundance, and adult and juvenile abundance may have different drivers. We have focused on gaining a better understanding of the ecology and status of 1 threatened headwater species, but the methods we used are applicable to a wide range of species. We think that having the appropriate information about conditions closely linked to fish occurrence and abundance at the appropriate ecological scales can be of great use for effective conservation actions.

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