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Ontogenetic shifts in habitat use by the endangered Roanoke logperch (*Percina rex*)

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SUMMARY

1. Conservation of the federally endangered Roanoke logperch (*Percina rex*, Jordan and Evermann) necessitates protection of habitat that is critical for all age classes. We examined habitat use patterns of individual logperch to determine: (1) if age classes of logperch in the Nottoway and Roanoke Rivers exhibit habitat selectivity, (2) if age classes differ in habitat use, and (3) if ontogenetic patterns of habitat use differ between the Roanoke and Nottoway river populations.
2. In the summers of 2000 and 2001, we observed 17 young-of-year (YOY) logperch [<4 cm total length (TL)], 13 subadult logperch (4–8 cm TL), and 49 adult logperch (>8 cm TL) in the upper Roanoke River, and 40 subadult and 39 adult logperch in the Nottoway River, Virginia.
3. All size classes of Roanoke logperch demonstrated habitat selectivity and logperch used a wide range of habitats in the Roanoke and Nottoway rivers during ontogeny. Habitat use by logperch varied among age classes and between rivers.
4. In the Roanoke River, adult and subadult logperch primarily preferred run and riffle habitat, often over gravel substrate. Subadults were found in lower water velocities and slightly more embedded microhabitats than adults. YOY logperch were found in shallow, stagnant backwaters and secondary channels. In the Nottoway River, both adult and subadult logperch were found over sand and gravel in deep, low-velocity pools and runs. Subadults were observed in slightly more silted, lower velocity habitat than adults. Shifts in habitat use were more distinct between age classes in the Roanoke River than the Nottoway River.
5. Successful conservation of this species will involve sound understanding of spatial variation in habitat use over logperch life history and preservation of the ecological processes that preserve required habitat mosaics.

Keywords: conservation, habitat selection, life history, lotic habitat, ontogeny

Introduction

Among the most pressing goals of conservation biology is the restoration of aquatic biodiversity amidst rapid and pervasive human impacts on aquatic resources (Etnier, 1997; Richter *et al.*, 1997; Williams, Wood & Dombeck, 1997). Degradation of aquatic systems through habitat loss, introduction of

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non-natives, and pollution has contributed to high endangerment and extinction rates among aquatic species (Miller, Williams & Williams, 1989; Williams *et al.*, 1989, 1993; Etnier, 1997), three to eight times the rates for terrestrial birds and mammals (Master, 1990). To reverse declines and restore imperiled populations, managers must understand habitat requirements throughout life histories as well as ecosystem processes that maintain these habitats (Schlosser & Angermeier, 1995; Hartman, Scrivener & Miles, 1996; Labbe & Fausch, 2000; Roni *et al.*, 2002).

Fish species respond to habitat features at multiple scales, particularly through movement of different life-history stages to suitable habitat patches (Labbe & Fausch, 2000). Often a variety of habitat types is required throughout the history for population persistence (Schlosser & Angermeier, 1995; Labbe & Fausch, 2000). Many studies in fishes have documented shifts in habitat use over ontogeny (e.g. Magnan & Fitzgerald, 1984; Werner & Gilliam, 1984; Schlosser, 1987, 1988; Werner & Hall, 1988; L'Abée Lund et al. 1993; Ruzycki & Wurtzbaugh, 1999), presumably related to differences among size or age classes in resource utilisation abilities, predation risk (Kushlan, 1976; Britton & Moser, 1982; Power, 1984, 1987; Werner & Gilliam, 1984; Mahon & Portt, 1985; Schlosser, 1987, 1988; Werner & Hall, 1988), or tolerance of physiological stressors (Tramer, 1977; Mann & Bass, 1997). Effective conservation must, therefore, account for habitat use over the entire life cycle of the target species, particularly younger life stages. Repeated studies have demonstrated that population bottlenecks often occur during the earliest stages in fish life histories (Berkman & Rabeni, 1987; Werner & Gilliam, 1984). Early life stages of fishes are particularly vulnerable to human alterations of stream systems, including sedimentation (Burkhead & Jelks, 2001) and channel straightening or flow regulation (Scheidegger & Bain, 1995; Copp, 1997; Mann & Bass, 1997; Mérigoux & Ponton, 1999; Meng & Matern, 2001).

The life history of logperch is described in Burkhead (1983) and Jenkins & Burkhead (1993) and is based exclusively on data collected in the Roanoke River. The Roanoke logperch (*Percina rex*) is a large darter that occurs only within the Roanoke and Chowan drainages of Virginia (Jenkins & Burkhead, 1993). Its greatest population densities are in the upper Roanoke River (Burkhead, 1983; Jenkins & Burkhead, 1993) and in the Nottoway River drainage (tributary of theChowan River) along the Fall Zone between the Piedmont and Coastal Plain physiographic provinces (Rosenberger & Angermeier, 2002). Because of its limited distribution and the vulnerability of its largest population centres to urban and industrial stressors, Roanoke logperch are federally endangered (U.S. Fish and Wildlife Service, 1992). Roanoke logperch of all age classes are believed to be intolerant to substrates moderate to heavily silted, in the Roanoke River, possibly because of the unique feeding behaviour the subgenus *Percina*. Logperch use their conical snout to flip gravel and feed on exposed invertebrates. This behaviour is effective only in loosely embedded substrate (Burkhead, 1983; Jenkins & Burkhead, 1993).

This study focused on habitat requirements through ontogeny for Roanoke logperch at multiple smaller scales (i.e. pool–riffle series and microhabitat). Knowledge of habitat use at these scales can influence management decisions enhancing preservation of the large-scale processes creating required habitat patches. Further, differences between rivers in available habitat could influence ontogenetic patterns of habitat use. Studies have demonstrated differences in habitat use for different populations of a fish species (Bozek & Rahel, 1992; Freeman, Bowen & Crance, 1997), particularly populations from different regions (Groshens & Orth, 1994). We therefore compared habitat use over ontogeny and between populations to have an insight into limiting factors and generalities for the species as well as its ability to shift habitat use under different regional conditions.

The purpose of this study was to document and quantify ontogenetic shifts in habitat use by endangered Roanoke logperch in the Roanoke and Nottoway rivers. We examined the habitat use of individual Roanoke logperch in three size categories in the Roanoke River and in two size categories in the Nottoway River to determine whether: (1) age classes of logperch exhibited habitat selectivity, (2) age classes differed in habitat use, and (3) ontogenetic patterns of habitat use differ between the Roanoke and Nottoway populations. We use these results to generate hypotheses on the factors that may cause shifts in habitat use through Roanoke logperch ontogeny in both river systems. We discuss the relative importance of these factors in the two river systems and use commonalities in habitat use between the two rivers to form generalised hypotheses about the habitat requirements of this species. Comparison of habitat availability between rivers provides insight into factors contributing to differences in habitat use between the Roanoke and Nottoway rivers. Finally, we discuss conservation and management implications of those ontogenetic habitat shifts and suggest strategies that will preserve habitat mosaics required throughout Roanoke logperch life history for both populations.

Methods

Study sites

The section of the upper Roanoke River targeted by this study extends downstream from the confluence of the North and South forks. The section of the Nottoway River targeted for this study crosses the Fall Line between the Piedmont and Coastal Plain physiographic provinces (Fig. 1). The Roanoke River is a clear, coolwater, high-gradient system, while the Nottoway River in the Chowan drainage is tannin-stained, warmwater and lowland (Jenkins & Burkhead, 1993). The Nottoway River is similar in gradient to the Roanoke River only in the Fall Zone between the Piedmont and Coastal Plain physiographic provinces, where riffle and run habitat similar to that in montane rivers occurs.

We examined habitat use at small scales (i.e. pool–riffle series and microhabitat), where processes such as alluvial transport of water and sediment, presence of woody debris, channel meandering and animal activity (e.g. beaver, cow) can affect habitat availability (Frissell *et al.*, 1986). In the summer of 1999, a reachwide inventory of 10 km of the Roanoke River and 22 km of the Nottoway River was conducted using the Basinwide Visual Estimation Technique (BVET; Dolloff, Hankin & Reeves, 1993). Riffle–run–pool series were systematically selected from these reachwide inventories for quantitative underwater observation for adult and subadult logperch using line-transect snorkeling methods. We considered high gradient areas with

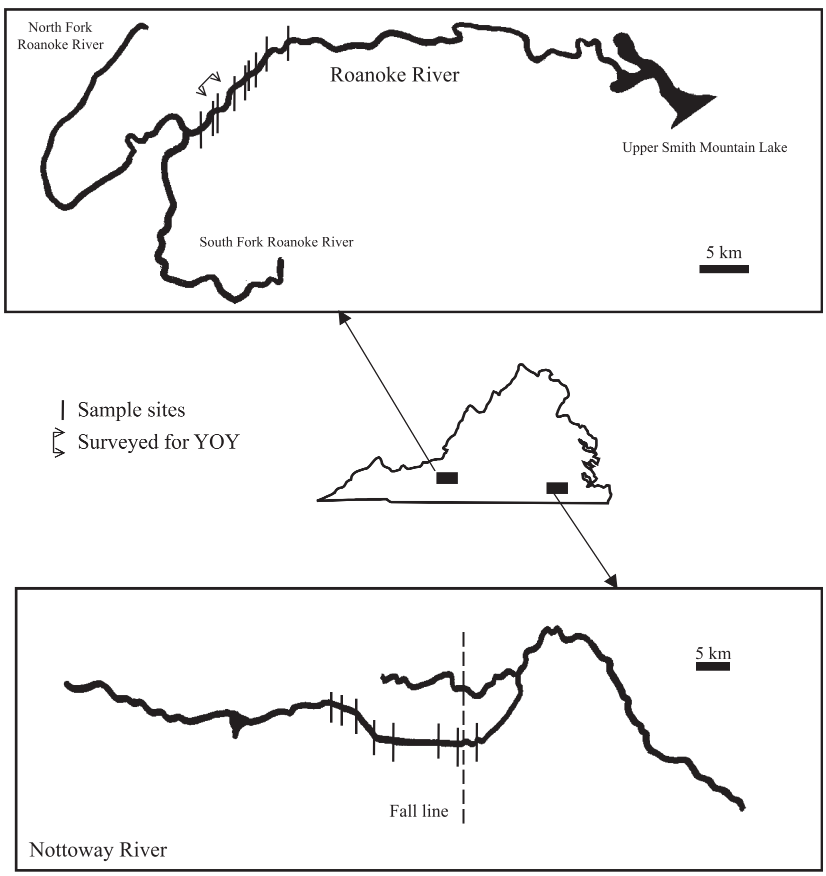

Fig. 1 Map of the Roanoke and Nottoway rivers, Virginia, indicating sites selected for snorkeling surveys and areas surveyed for YOY Roanoke logperch (*Percina rex*).

convex stream bottoms, turbulent water surfaces, and fast water to be riffle habitat. Pools were deep, low gradient, slow-moving areas with concave stream bottoms (Beschta & Platts, 1986). Runs were defined as intermediate gradient areas with flat stream bottoms, fast water, and smooth water surfaces (Vadas & Orth, 1998). Once methods were established for young-of-year (YOY) observations, a 2-km reach of the Roanoke River was selected for visual survey (Fig. 1). This reach was selected based on river access and was centrally located along the inventoried river reach. Data collected using the basinwide technique (Dolloff *et al.*, 1993) indicated that the reach sampled for YOY was representative in terms of the availability of tributaries, backwaters, pools, riffles and runs, and overlapped considerably with unsampled reaches in depth and substrate. Because of logistic and time constraints, we did not attempt to visually survey habitats for YOY logperch in the Nottoway River. Sites were sampled for habitat availability and logperch habitat use during baseflow conditions in both rivers in the summers of 2000 and 2001.

Fish survey methods

Standard survey observations for each riffle–run–pool series were made via line-transect snorkeling methods described in Ensign, Angermeier & Dolloff (1995). One to three parallel lines oriented with river flow were marked with yellow line on the day of sampling. Spacing between lines was a minimum of 1.5 times maximum underwater visibility on the day of sampling. The length of the lines was based on the length of the habitat units but did not exceed 50 m per unit (150 m per site). Visibility was determined by suspending a Secchi disc in the water column in front of a snorkeler. The snorkeler moved away from the disc until the black patterns on the disc were no longer distinguishable from the water. This measurement is a more conservative measure of fish visibility than the standard measure of visibility which is the distance at which the black and white patterns on the disc itself are no longer distinguishable. The distance between the snorkeler and the disc was measured and served as the maximum visibility for that day. Fish sampling was not conducted if maximum visibility was <1.5 m (from Leftwich, Angermeier & Dolloff, 1997).

To minimise effects on fish behaviour, snorkelers did not begin sampling until at least 1 h after placement of the transect lines. Snorkelers entered the water downstream of the area to be sampled and moved slowly upstream along the lines, keeping the centre of the body over the line. Each observer scanned the stream bottom, mid-water and upper-water column directly in front and on both sides of the line of travel. When a logperch was sighted, a numbered weighted marker was placed on the stream bottom precisely where the fish was first spotted. The number codes of markers and size class were recorded on dive slates. Double counting of fish was avoided by simultaneously sampling all three transect lines with snorkelers staying even with each other while moving upstream. Continuous communication between snorkelers also minimised double counting. After the riffle–run–pool sequence was sampled, snorkelers returned to the base of transects to count markers and collect habitat data.

Habitat observations

Microhabitat data included water depth, bottom and mean water velocity, substrate size (using a 9-category Wentworth scale), embeddedness within a 1-m^2 area around the marker [1 ≥ 95% embedded, 2 = 50–94%, 3 = 25–49%, 4 = 1–24%, 5 = 0% (i.e. exposed)], and silt cover within a 1-m^2 area around the marker (1 = 76–100% covered with silt, 2 = 51–75%, 3 = 26–50%, 4 = 1–25%, 5 = 0%). Microhabitat availability was recorded within 24 h of the snorkeling run. Horizontal transects along the wetted width of the river were placed at 10-m intervals along the length of the riffle–run–pool series. Every 3 m along the horizontal transect, depth, mean and bottom water velocity, silt cover, and dominant and subdominant substrate within a 1-m^2 area were recorded.

Young-of-year logperch [<4 cm total length (TL)] were not observed during snorkeling surveys. To observe YOY logperch, 2–3 researchers used polarised glasses and binoculars to survey shallow waters associated with backwaters, secondary channels and river edges. When an individual or group of YOY was observed, the surveyor identified any logperch and placed markers on spots that small logperch were seen foraging. Habitat use and availability data were recorded at the site where each fish was observed using a cross-shaped transect, which was centred on the logperch sighting location. Habitat data were taken along transect arms set at 45°, 135°, 225° and 315° from this centre location. Habitat availability was measured in each transect line 1, 1.5, 2.0 and 3.0 m from the centre point. The following habitat variables were recorded: depth, mean and bottom water velocity, embeddedness and silt cover in a 10-cm^2 area, and substrate size over which the YOY was observed. Data collection methods for adults and subadults differed from data collection for YOY individuals primarily in their scale of measurement (extent and grain). We presumed that small individuals perceive and use habitat at a smaller scale than do larger individuals, thereby justifying comparison among data sets for a subset of the microhabitat measurements.

Data analysis

All data analyses were performed using SYSTAT (Version 9, Copyright © SPSS Inc., 1998). As the scarcity of Roanoke logperch limited our sample size, habitat use and availability data were pooled for the summers of 2000 and 2001. Although no site was

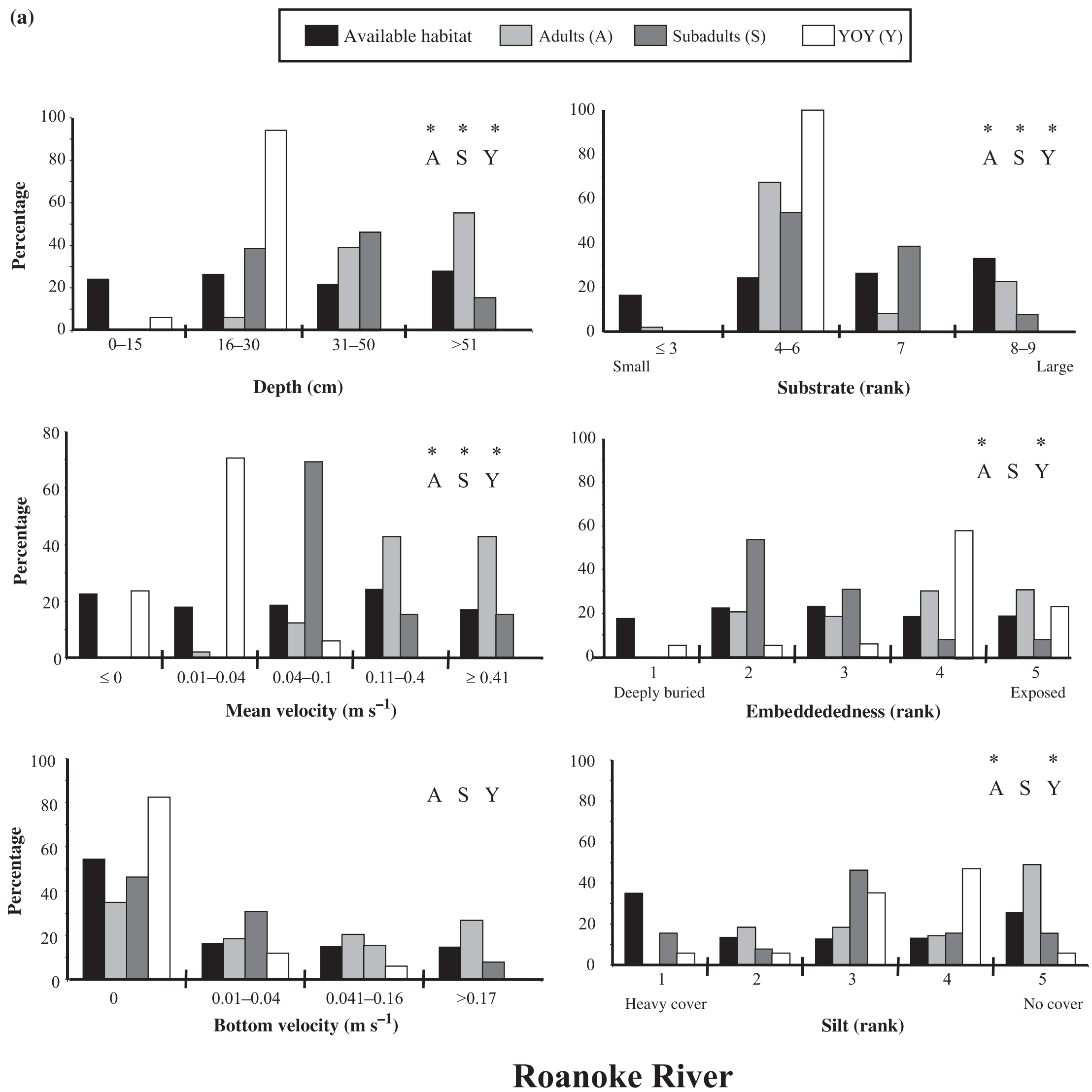

Fig. 2 Percentage abundance of available habitat and proportional occurrence of observed adult, subadult and young-of-year logperch in habitat categories for the (a) Roanoke River and (b) Nottoway River, Virginia. Asterisk indicates a significant *G* test at the 0.02 level (Dunn–Sidak correction for multiple tests). Significance indicates non-random selection of a habitat variable by the age class (A = adult, S = subadult, Y = young-of-year).

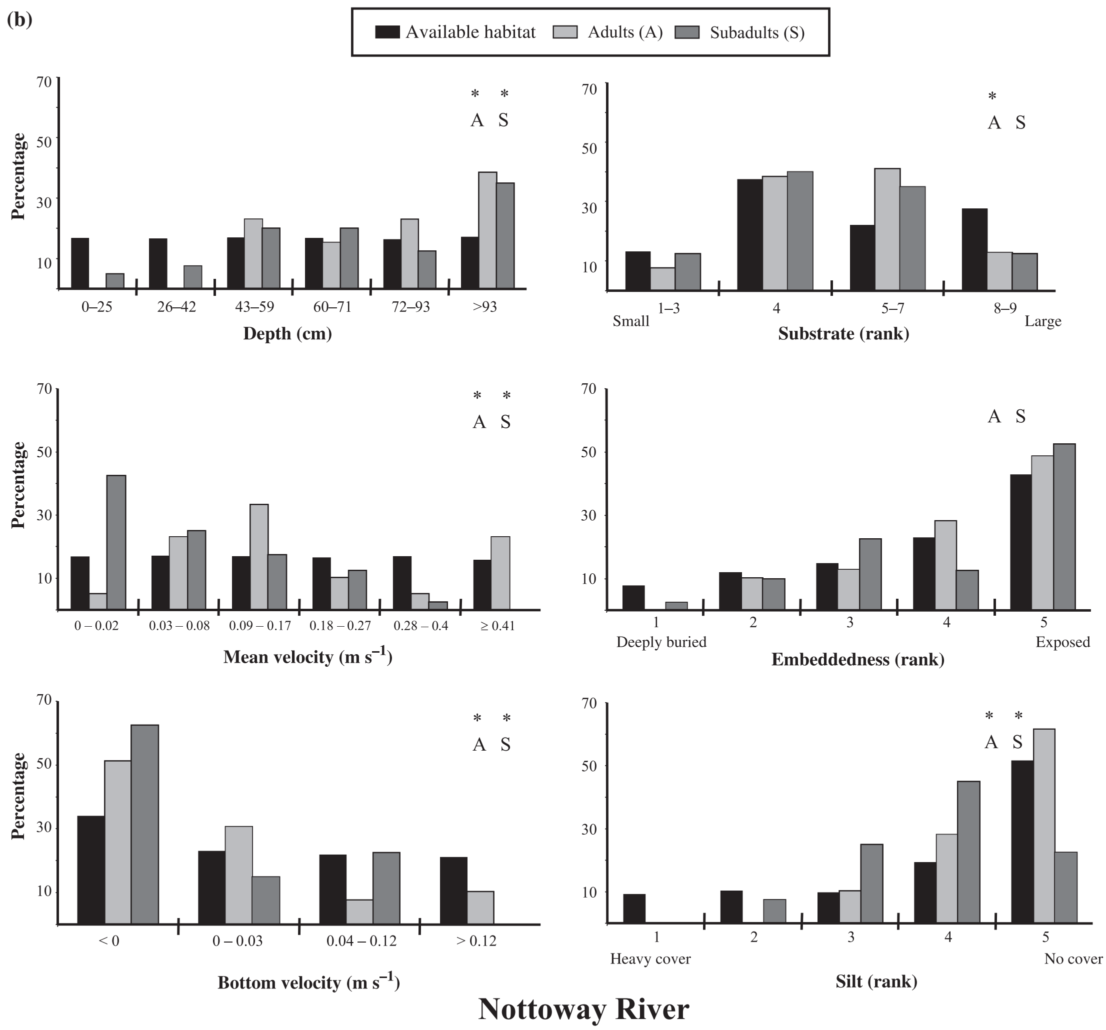

Fig. 2 (*Continued*)

sampled for both years, we took several precautions to ensure that this did not bias the analyses. First, sampling was conducted during base flow summer conditions for both years. Secondly, we used principal components analysis (PCA) to examine if there was any shift in habitat availability between the years that may have affected habitat use. We ordinated habitat use and availability data and found that data from both the years occupied the same area of multivariate space. In addition, we did not observe any appreciable differences between the years in the relative frequency of habitat availability or habitat use data points along multivariate axes (see Fig. 3). We did not perform univariate *t*-tests or Mann–Whitney *U*-tests to examine differences between the years in habitat availability because our availability sample sizes were so large ($n = 937$ for both rivers) that statistical significance would not necessarily indicate biologically meaningful differences between the years. We were unable to test if density-dependent factors may have affected habitat use and caused differences in habitat use patterns between the years, but we feel this is an unlikely scenario because of the scarcity of this species.

Habitat availability data collected in the Roanoke and Nottoway rivers include water depth (cm), bottom and mean water velocity (m s^{-1}), dominant substrate (rank category), embeddedness (rank category), silt cover (rank category) and predator abundance (rank category). Availability data were separated into pool, riffle and run habitat unit categories to examine differences in meso-habitat characteristics between rivers. Univariate *t*-tests were used to compare the two rivers for depth, bottom velocity and mean velocity. We used Mann–Whitney *U*-tests to compare substrate, embeddedness, silt and predator abundance between Roanoke and Nottoway river pools, riffles and runs. Alpha values were adjusted for multiple tests using the Dunn–Sidak correction ($\alpha' = 0.02$).

Microhabitat use data included mean velocity (m s^{-1}), bottom velocity (m s^{-1}), substrate (rank category) embeddedness (rank category), silt cover (rank category), and depth (cm). Logperch were segregated into three age categories based on Burkhead (1983). Individuals <4 cm were classified as YOY. Roanoke logperch mature at 3 years (8–11.4 cm TL, Burkhead, 1983); therefore, individuals between 4 and 8 cm TL were considered subadults between 1 and 2 years of age, and individuals >8 cm TL were considered adults between 3 and 6 years of age. *G*-tests with Williams' correction (Williams, 1976) were used to detect habitat selection by each age class by comparison of actual habitat use with that expected if logperch used habitat randomly. Category ranges were selected such that each category was equally available in a given river; thus category values differed among rivers. Alpha values were adjusted for multiple tests using the Dunn–Sidak correction ($\alpha' = 0.02$). Differences among age classes for each habitat parameter were tested with Kruskal–Wallis tests for the Roanoke River and Mann–Whitney *U*-tests for the Nottoway River. After verification of linearity assumptions, multivariate comparison of logperch habitat use with available habitat was examined with PCA. Habitat availability data were ordinated along two principal axes and locations of habitat use data points along these axes were calculated using the principal components' scoring coefficients. We graphically superimposed these calculated scores on a polygon circumscribing the multivariate space occupied by habitat availability data points to indicate multivariate habitat selection and marked differences among age classes in habitat use.

Results

Habitat use descriptions

Adult logperch in the Roanoke River were observed most frequently in runs, occasionally in riffles, and rarely in pools (Table 1). Adult logperch primarily used deep water with medium to high water velocities, often directly over gravel in areas dominated by cobble. Subadults in the Roanoke River were observed primarily in runs over moderately embedded gravel in slightly shallower and lower-velocity habitats than the adults. YOY, in contrast, were found in nearly stagnant areas such as backwater habitats, secondary channels, and the shallow edges of pools, riffles and runs. These small individuals were consistently found in water around 20 cm deep with small, slightly embedded substrate. A thick layer of silt covered these areas; however, small logperch foraged in small patches of silt-free, loosely embedded gravel. Adult and subadult logperch in the Roanoke River did not exhibit schooling behaviour, but YOY logperch were observed in mixed-species schools. Small logperch occasionally separated from schools to feed, flipping small gravel. We were unable to observe whether these foraging attempts were successful.

Adult and subadult logperch in the Nottoway River were observed primarily in pools and occasionally in runs. Few adults and no subadults were observed in riffle habitat (Table 1). Both adult and subadult logperch in the Nottoway River were found over sand and gravel in deep, low-velocity habitats. Although both age classes were found over relatively exposed and lightly silted habitats, the subadults were found in slightly more silted habitat with lower velocities. Unlike the Roanoke River, subadults were observed frequently in the Nottoway River (Table 1).

Univariate analysis

Habitat availability differed between the Nottoway and Roanoke River pools, riffles, and runs (Table 2). For all unit types, the Nottoway River was consistently deeper ($t > 2.8$, $P < 0.005$), less embedded and less silted ($\chi^2 > 20.7$, $P < 0.001$) than the Roanoke River. Nottoway River pools and riffles had wider channels than corresponding units in the Roanoke River ($t > 3.2$, $P < 0.001$). Substrate sizes were smaller in Nottoway River runs and pools than that observed in the Roanoke River ($\chi^2 > 25.8$, $P < 0.001$).

All age classes of logperch selected depth in the Roanoke River ($G \geq 10.0$, d.f. = 3, $P < 0.01$, Fig. 2). Adults selected deeper habitats, while subadults selected intermediate depths. YOY consistently selected water depths between 16 and 30 cm. All age

Table 1 Habitat use by Roanoke logperch in the Roanoke and Nottoway rivers, Virginia

	YOY (Y)	Subadult (S)	Adult (A)	Chi-square	*P*	Multiple comparisons
Roanoke River						
Fish length (cm)	<4	4–8	>8			
Meso-habitat unit types (% occurrence)						
Backwaters and secondary channels	100	0	0			
Pools	0	23	16			
Runs	0	54	51			
Riffles	0	23	32			
Mean depth (cm) (± SD)	19.7 ± 3.4	34.2 ± 10.6	52.5 ± 12.7	48.9	<0.001*	Y S A
Mean velocity (m s^{-1}) (± SD)	0.02 ± 0.04	0.19 ± 0.23	0.63 ± 0.70	44.7	<0.001*	Y S A
Mean bottom velocity (m s^{-1}) (± SD)	−0.01 ± 0.02	0.04 ± 0.11	0.16 ± 0.32	3.0	0.06	Y S A
Substrate (mean rank) (± SD)	5.0 ± 0	6.0 ± 1.3	5.8 ± 1.7	3.5	0.10	Y S A
Embeddedness (mean rank) (± SD)	3.8 ± 1.1	2.7 ± 0.95	3.7 ± 1.1	9.8	0.008*	Y S A
Silt (mean rank) (± SD)	4.0 ± 1	3.1 ± 1.3	3.9 ± 1.2	5.5	0.06	Y S A
n	17	13	49			
	YOY	Subadult	Adult	Mann–Whitney *U*	*P*	
Nottoway River						
Fish length (cm)		4–8	>8			
Meso-habitat unit types (% occurrence)						
Pools		60	69			
Runs		40	21			
Riffles		0	10			
Mean depth (cm) (± SD)		81.8 ± 35.7	84.4 ± 27.8	0.36	0.55	
Mean velocity (m s^{-1}) (± SD)		0.07 ± 0.09	0.20 ± 0.17	18.3	<0.001*	
Mean bottom velocity (m s^{-1}) (± SD)		0.0 ± 0.04	0.02 ± 0.09	0.65	0.42	
Substrate (mean rank) (± SD)		4.9 ± 2.3	5.1 ± 2.0	0.19	0.67	
Embeddedness (mean rank) (± SD)		4.0 ± 1.2	4.2 ± 1.0	0.05	0.82	
Silt (mean rank) (± SD)		3.8 ± 0.9	4.5 ± 0.07	13.2	<0.001*	
n	0	40	39			

*Significant difference in habitat use ($\alpha' = 0.02$).
Underlined values are not significantly different (non-parametric multiple comparisons, $\alpha = 0.05$).

classes selected for mean water velocity in the Roanoke River, with individuals proportionally skewed towards higher velocities for adults ($G = 52.9$, d.f. = 4, $P < 0.001$), medium velocities for subadults ($G = 20.1$, d.f. = 4, $P < 0.001$), and very low velocities for YOY ($G = 29.7$, d.f. = 4, $P < 0.001$). There was no apparent selection, however, for bottom water velocity by any age classes ($G \leq 7.1$, d.f. = 3, $P < 0.10$). Adults and subadults selected substrates ranging from sand to cobble ($G \geq 11.2$, d.f. = 3, $P < 0.02$), while YOY selected smaller substrate categories (sand and small gravel, $G = 46.1$, d.f. = 3, $P < 0.001$, Fig. 2). Adults and YOY selected for moderately embedded to exposed substrate with little silt ($G \geq 16.6$, d.f. = 4, $P < 0.005$). No apparent selection for embeddedness or silt categories was observed in subadults in the Roanoke River ($G \leq 10.3$, d.f. = 4, $P > 0.05$).

In the Nottoway River, both adult and subadult logperch selected deep water ($G \geq 13.0$, d.f. = 5, $P < 0.02$, Fig. 3). However, age classes selected different mean water velocities, with adults selecting moderately fast water ($G = 16.1$, d.f. = 5, $P < 0.01$) and subadults selecting slow water ($G = 32.2$, d.f. = 5, $P < 0.001$). Despite these differences, both age classes selected slow bottom velocities ($G \geq 11.3$, d.f. = 3, $P < 0.01$). Adults selected substrate suitable for feeding (gravel or cobble) and sand, the most common substrate category in the Nottoway River ($G = 10.1$, d.f. = 3, $P = 0.02$). Subadults did not appear to select for substrate category, though individuals were frequently observed over sand and gravel ($G = 6.46$, d.f. = 3, $P > 0.1$). Adults and subadults were frequently observed flipping small pieces of organic debris when foraging over sand. Adults and subadults did not appear to select for embeddedness ($G \leq 6.8$,

Table 2 Comparison of habitat characteristics of pools, runs, and riffles in the Roanoke and Nottoway rivers, Virginia

Pool characteristics	Roanoke River	Nottoway River	*t*	*P*
Mean channel width (m) (± SD)	24.8 ± 4.3	33.1 ± 5.7	21.2	<0.001*
Mean depth (m) (± SD)	75.7 ± 45.1	84.9 ± 35.9	2.8	0.005*
Mean bottom velocity (m s^{-1}) (± SD)	0.06 ± 0.24	0.04 ± 0.09	1.9	0.06
Mean velocity (m s^{-1}) (± SD)	0.21 ± 0.45	0.15 ± 0.15	2.1	0.03
			Chi-square	*P*
Dominant substrate (mean rank) (± SD))	5.9 ± 2.5	4.7 ± 2.2	25.8	<0.001*
Subdominant substrate (mean rank) (± SD))	4.8 ± 1.9	4.6 ± 2.4	0.57	0.45
Embeddedness (mean rank) (± SD))	2.5 ± 1.4	3.5 ± 1.3	78.5	<0.001*
Silt (mean rank) (± SD))	2.4 ± 1.5	3.4 ± 1.5	62	<0.001*
Run characteristics			*t*	*P*
Channel width (m (± SD))	28.9 ± 7.8	27.8 ± 5.2	1.8	0.07
Depth (m (± SD))	35.8 ± 21.16	50.7 ± 24.0	7.4	<0.001*
Bottom velocity (m s^{-1} (± SD))	0.08 ± 0.16	0.07 ± 0.13	0.73	0.47
Mean velocity (m s^{-1} (± SD))	0.25 ± 0.31	0.28 ± 0.33	1.2	0.23
			Chi-square	*P*
Dominant substrate (mean rank) (± SD))	7.0 ± 1.7	5.4 ± 2.2	64.3	<0.001*
Subdominant substrate (mean rank) (± SD))	5.9 ± 1.6	5.1 ± 2.1	27.5	<0.001*
Embeddedness (mean rank) (± SD))	3.3 ± 1.3	3.9 ± 1.3	26.6	<0.001*
Silt (mean rank) (± SD))	3.4 ± 1.4	4.3 ± 1.2	56.6	<0.001*
Riffle characteristics			*t*	*P*
Channel width (m (± SD))	26.5 ± 6.1	28.9 ± 8.8	3.2	0.001*
Depth (m (± SD))	26.2 ± 16.3	34.3 ± 21.3	4.4	0.001*
Bottom velocity (m s^{-1} (± SD))	0.16 ± 0.30	0.08 ± 0.19	3.1	0.002
Mean velocity (m s^{-1} (± SD))	0.40 ± 0.44	0.37 ± 0.48	0.82	0.41
			Chi-square	*P*
Dominant substrate (mean rank) (± SD))	7.7 ± 1.0	6.9 ± 2.3	0.86	0.36
Subdominant substrate (mean rank) (± SD))	5.7 ± 1.6	5.6 ± 2.0	0.35	0.56
Embeddedness (mean rank) (± SD))	3.7 ± 1.1	4.3 ± 1.1	33.2	<0.001*
Silt (mean rank) (± SD))	4.0 ± 1.4	4.5 ± 1.0	20.7	<0.001*

*Significance at the 0.02 level for *t*- and Mann–Whitney *U*-tests (Dunn–Sidak correction for multiple comparisons).

d.f. = 4, $P > 0.1$); however, both selected habitat with little to no silt cover ($G \geq 16.9$, d.f. = 4, $P < 0.005$).

Kruskal–Wallis tests indicated that adult logperch used deeper, faster water than subadults and YOY in the Roanoke River ($\chi^2 \geq 44.7$, d.f. = 2, $P < 0.001$). Roanoke River subadults were found in intermediate depths when compared with adults and YOY ($\chi^2 \geq 44.7$, d.f. = 2, $P < 0.001$) and used more deeply embedded habitats ($\chi^2 = 9.8$, d.f. = 2, $P = 0.008$, non-parametric multiple comparisons, $\alpha \leq 0.05$, Table 1). No significant differences among age classes in median habitat characteristics were observed for substrate size, silt cover and bottom water velocity in the Roanoke River ($\chi^2 \leq 8.05$, d.f. = 2, $P \geq 0.02$).

As in the Roanoke River, Nottoway River logperch adults were found in faster velocities than subadults ($\chi^2 = 18.3$, $P < 0.001$). In addition, adults were found in less silted habitats than subadults ($\chi^2 = 13.2$, $P < 0.001$, Fig. 4). No significant differences among age classes in use of habitat characteristics were observed for depth, bottom velocity, substrate and embeddedness in the Nottoway River ($\chi^2 \leq 0.65$, $P > 0.42$).

Habitat use and availability locations in the Roanoke River ordinated through PCA into two primary principal components (Table 3). The first component was loaded heavily by embeddedness, silt, substrate and, mean and bottom water velocities, while the second component was loaded most heavily by depth. One end of the first axis (component 1) represents stagnant, embedded habitats with small substrates, while the other end represents scoured habitats with larger substrate and high water velocities (Fig. 3). The

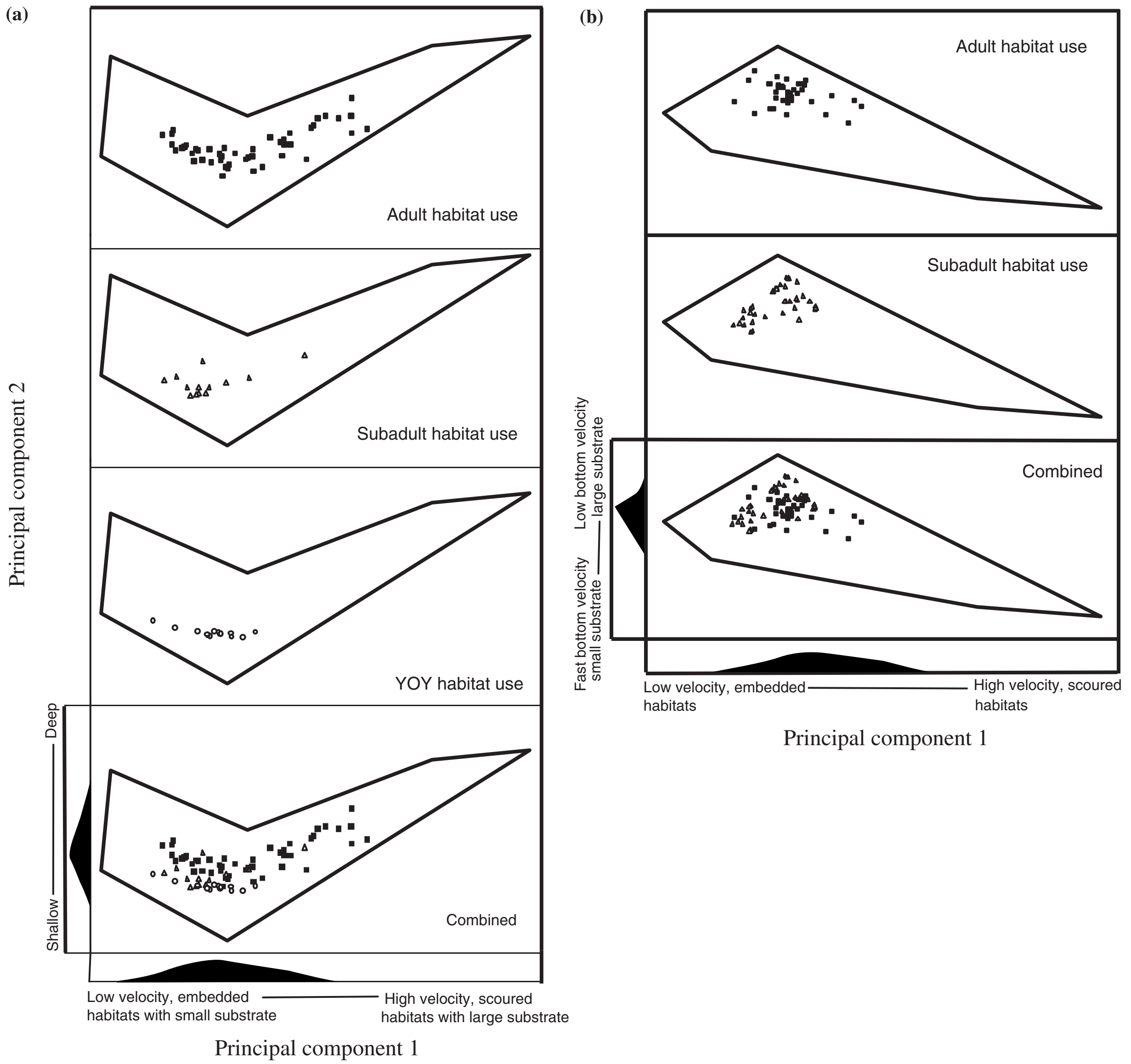

Fig. 3 A graphic presentation of principal component scores for each age class of Roanoke logperch in (a) the Roanoke River and (b) Nottoway River, Virginia. The polygon in each figure circumscribes the area representing available habitat in sampling sites, while the area curves on axes of the bottommost graph represent the relative frequency of availability locations.

two ends of the second axis indicate shallow versus deep habitat.

Plots of logperch locations in the Roanoke River calculated using the components' scoring coefficients onto two-dimensional principal component space illustrate patterns of habitat selection when superimposed on the range of locations representing available habitat (Fig. 3). Segregation among age classes is most marked along the second axis, representing depth characteristics; however, adult logperch spanned a greater range of velocity, substrate, embeddedness and silt characteristics and occupied the more scoured and fast-flowing habitats than other age classes (Fig. 3). Frequency distributions of habitat availability locations along the two axes indicate that scoured and fast-flowing habitat locations are the most rare habitats in the Roanoke River. Although logperch locations do not occupy habitat 'extremes' along the axis, all age classes combined occupy a large portion of available habitat, indicating that a wide

Table 3 Loadings of six habitat variables on the first two principal components and percentage of total variance accounted for by each component based on habitat availability data from the Roanoke and Nottoway rivers, Virginia

	Principal components			
	Roanoke River, VA		Nottoway River, VA	
Principal component	1	2	1	2
Eigenvalues	3.0	1.1	2.4	1.1
Habitat variables				
Depth	−0.245	0.736	−0.412	0.065
Bottom velocity	0.710	0.437	0.636	−0.632
Mean velocity	0.798	0.416	0.710	−0.425
Substrate	0.645	−0.387	0.465	0.558
Embeddedness	0.804	−0.255	0.695	0.448
Silt	0.827	−0.008	0.786	0.202
Percentage variance	48.0	19.0	39.3	19.3

range of habitat types – both common and rare – is used by Roanoke logperch in the Roanoke River through ontogeny (Fig. 3).

Principal components analysis illustrated different patterns of ontogenetic habitat use in the Nottoway River than in the Roanoke River. Habitat availability ordinated into two primary principal components (Table 3). The first component was loaded heavily by velocity characteristics, silt and embeddedness, while the second component was loaded most heavily by bottom velocity and substrate. The ends of the first axis (component 1) represent stagnant, embedded habitats with silt cover versus high velocity, scoured habitats. The extremes in the second axis (component 2) represent fast bottom velocity habitats with small substrate versus slow bottom velocity habitat with large substrate (Fig. 5). Although presence of low bottom velocities and large substrate seems counter-intuitive, it follows that smaller substrates, such as sand, create a smaller velocity boundary layer than larger substrates. Plots of habitat use locations calculated using component scoring coefficients indicate that habitat use of adults were skewed towards the high velocity, scoured extreme of axis 1, while subadults seemed to occupy more low-velocity habitats; however, there is considerable overlap between age classes and only a subtle transition in habitat use between age classes. Relative frequency of habitat availability locations along the two principal axes indicate that logperch occupy habitat configurations that are common in Nottoway River sites.

Discussion

Ontogenetic shifts in habitat use

Roanoke logperch appeared to select specific habitat configurations and used a wide range of habitats in the Roanoke and Nottoway rivers through ontogeny. The shifts in habitat that we observed in the Roanoke and Nottoway rivers may be related to a variety of factors that affect individual survival, growth and reproductive success (Railsback & Harvey, 2002); constraints related to these parameters are likely to change through ontogeny (Werner & Gilliam, 1984; Schlosser, 1987, 1988). Predator–prey interactions associated with different habitat types, among other factors, could play a key role in variation in habitat use over body size (Angermeier, 1992). Fish have low costs of maintenance and can handle some degree of starvation in order to avoid predators; therefore, predation may be more immediately important than food for habitat selection (Power, 1984); however, this relationship can be dynamic because fishes can facultatively change feeding rates in response to changes in predation risk (Werner & Hall, 1988). Hypotheses relating habitat use to predation risk generally state that risk in shallow habitats is from non-gape-limited predators (e.g. wading or diving birds), while risk in deep habitats is mostly from gape-limited predators (e.g. piscivorous fishes) (Magalhães, 1993; Angermeier, 1992; Schlosser, 1987, 1988; Power, 1984). Large predatory fish are rarely observed foraging in shallow water, because of potential risk of aerial predation or decreased maneuverability (Angermeier, 1992). Small YOY, though vulnerable to a variety of aquatic predators, are less likely to be preyed upon by wading or flying predators than larger individuals (Kushlan, 1976). In addition, body size has been directly related to the ability of fishes to maintain position under high water velocities (Mann & Bass, 1997), with larger individuals having greater swimming abilities than small individuals. This phenomenon has been observed in juveniles of fantail darters (*Etheostoma flabellare*) in the Roanoke River (Matthews, 1985).

These findings may shed light on factors contributing to ontogenetic habitat preferences of Roanoke logperch in the Roanoke River. In the Roanoke River, adult logperch selected deep, high velocity riffles and runs, which provide loosely embedded substrate for feeding and potential spawning habitat (Burkhead, 1983). Subadults in the Roanoke River, however, were found in habitats intermediate in depth with lower velocities, greater silt cover and moderately embedded substrate. For adult logperch, deep, turbulent and fast riffle and run habitats may be silt-free refugia from aquatic and aerial predators. Subadult logperch, however, may be unable to exploit these high velocity areas because of their limited swimming ability. A slight shift into shallower waters may be a defense against predation; however, complicating this is the distribution of heavily silted substrate in the Roanoke River. Habitats with slow water velocities (i.e. pools) are heavily silted (Table 2). As aquatic predators also inhabit these areas, it is difficult to separate the effects of predation from the effects of heavy silt on depth and velocity preferences of subadult Roanoke logperch. Shallow backwater habitats may provide slow water velocities and refugia from aquatic predators; however, subadults may be too large to use these areas effectively and be vulnerable to aerial predation. In addition, these areas were covered with a thick blanket of silt with the exception of very small areas of loosely embedded small gravel that are probably too small to be used by subadult logperch.

Young-of-year logperch in the Roanoke River were observed in low-velocity habitat, yet were not observed in surveys of the river thalweg. Instead, small individuals were found in shallow backwaters and river edges feeding over small patches of loosely embedded, silt-free gravel substrate. YOY logperch in the Roanoke River may find refugia from aquatic predators in backwaters and unit edges and are unlikely targets of wading predators (Kushlan, 1976). They are also small enough to forage in small patches of loosely embedded, silt-free gravel available in these habitats. The schooling behaviour of young logperch may increase their chances of being found in these small patches and also indicates the possibility of some risk of predation, even in shallow habitats. Shifts from shallow to deep water through ontogeny have been observed in other stream fishes (Magnan & Fitzgerald, 1984). Nursery habitat is commonly described as shallow, off-channel habitat that lacks velocities exceeding the swimming abilities of small individuals but offering shelter from large aquatic predators (Copp, 1991, 1997; Leslie & Timmins, 1991; Scheidegger & Bain, 1995; Baras & Nindaba, 1999; Bell, Duffy & Roelofs, 2001; Gadomski *et al.*, 2001).

Roanoke logperch in the Nottoway River occupy habitat that is common and widespread in all sites selected for sampling. This is accompanied by extensive habitat use overlap between the two age classes. Adult and subadult Roanoke logperch in the Nottoway River were found primarily in deep, silt-free, low-velocity pools with sand and gravel substrate and occasionally in runs and riffles. No segregation in depth or embeddedness characteristics was observed; however, as in the Roanoke River, adult and subadult logperch in the Nottoway River segregated by velocity. This supports the notion that subadult logperch have less ability to navigate successfully in fast-moving water than adults. This preference corresponded with a slight increase in silt cover for subadult logperch in the Nottoway River.

Differences between rivers in ontogenetic shifts

Comparison between the two rivers in ontogenetic patterns of habitat use reveals generalities about Roanoke logperch habitat use through life history. Habitat that is free from heavy siltation and contains moderate to loosely embedded substrate is preferentially used in the two systems. Subadults in both rivers were found in slower velocity habitats than adults, indicating that water velocity may be an important limitation for this life stage. The length of the Nottoway River sampled in this study is in relatively pristine condition, and pools without heavy silt loads are common and available for adult and subadult logperch. It is possible that logperch prefer low-velocity, deeper habitats without silt, but that type of habitat is rare in the Roanoke River. Roanoke logperch in the Roanoke River inhabit a range of habitat types from rare to relatively common (Fig. 5). Adults, in particular, seem capable of exploiting rare habitat that is deep, fast moving, and free of silt. In contrast, Roanoke logperch in the Nottoway River occupy widespread and common habitat, accompanied by habitat use overlap between the two age classes. Further, ontogenetic shifts in the Nottoway River were more subtle than shifts in the Roanoke River. This indicates a potential habitat bottleneck in the Roanoke River for juvenile or subadult logperch; because of their requirements for lower velocity habitats, they may be pushed into shallower microhabitats with more embedded substrate, which is suboptimal for foraging. This hypothesis is consistent with subadult logperch being less common in the Roanoke River than in the Nottoway River (Rosenberger & Angermeier, 2002). However, all age classes in both rivers avoided the most embedded habitats.

Conservation and management implications

The Roanoke logperch recovery plan (U.S. Fish and Wildlife Service, 1992) is based primarily on knowledge of the adult stage, ignoring potential for spatial variation in demographic or ecological processes over multiple scales. Each size class of Roanoke logperch selected particular habitat configurations, such that over the course of its life history the species used a wide range of habitats. Successful conservation of this species will involve the preservation of the ecological processes that maintain the connected habitat mosaics required over logperch life history. The distribution of habitat types and pathways of dispersal will be critical for completion of the logperch life cycle. Habitat heterogeneity at multiple scales will contribute to its continued persistence in the Nottoway and Roanoke Rivers, through formation of meso-habitat types such as backwaters, pools, riffles and runs as well as microhabitats with large substrate, silt-free microhabitat and intermediate water velocities.

Microhabitats that contain loosely embedded sediment free of heavy silt cover are critical for this endangered species. Management programmes in the Roanoke River should include protection and restoration of the streambank from agricultural and construction practices that contribute silt loads. Scouring flow during natural floods should also enhance habitat through removal of fine sediments, particularly in backwaters that are rarely exposed to scouring water velocities. Historic and ongoing floodplain development, especially in the Roanoke River, can threaten logperch habitat, particularly backwaters and shorelines that appear to be important for YOY logperch. Management of Roanoke logperch in the Nottoway River should concentrate on preventative programmes to preserve high quality habitat available in this river system. Evidence that Roanoke logperch require a low-silt, complex habitat mosaic over multiple spatial scales indicates that reach-specific management approaches alone will not guarantee the recovery of this species. We instead recommend a watershed-level approach that addresses sediment loading and preserves natural flow regimes that provide the ephemeral, seasonal and persistent types of habitat required throughout logperch life history.

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