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Seasonal occupancy of the thermal plume of a spring tributary to the South Fork Roanoke River, Virginia.

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Seasonal occupancy of the thermal plume of a spring tributary to the South Fork Roanoke River, Virginia.

Abstract

Detection of temperate stream fishes varies widely across seasons as streams teeming with life in summer often appear empty during winter sampling efforts. While much literature documents the disproportionate use of the thermal plumes of spring tributaries by cold water fishes during summer, few studies have investigated occupancy of those habitats by warm water fishes in winter. We conducted quantitative snorkeling observations within the near uniform temperatures (10-14^{o}C) of the thermal plume of a spring tributary to the South Fork Roanoke River across seasons and compared number of fishes observed and species richness to control observations made just upstream of the spring tributary and downstream of the spring tributary outside of the thermal plume. Outside of the thermal plume, species richness and number of fishes observed increased with stream water temperature ranging from 2-25^{o}C. Within the thermal plume of the spring tributary, non-salmonid species richness and number of fishes observed were greater during colder months than during warmer months. This suggests warm water fishes were disproportionately using the thermal plume of the spring tributary during the cold winter months. The warmer water of the plume likely serves as a thermal refuge allowing elevated metabolism that aids feeding, growth, and gamete development when stream water would otherwise leave these ectotherms largely dormant. As such, it appears these spring tributaries are especially important habitats for warm water stream fishes in addition to the well documented importance of these habitats for spring endemics and cold water fishes.

Keywords

Winter, groundwater, springs, warm water fishes, thermal refuge

Cover Page Footnote

We thank Roanoke College for equipment used in this research and for the sabbatical making regular winter sampling possible. We also thank Mr. Homer Duncan for access to our study site throughout this research. Lastly, we thank David Neely and Brett Albanese for thoughtful conversation and sharing their experience sampling streams during winter.

INTRODUCTION

The overwhelming majority of what we know about temperate stream fishes comes from sampling and observations made during warm weather, from March to October. Research describing fish populations and communities mostly focuses on sampling effort during these warmer months (Powers and Ceas 2000, Powers et al. 2003, Lang et al. 2005, Degerman et. al. 2007, Roberts and Hitt 2010, Powers and Spruill 2021). Research projects conducting field work throughout the year often struggle to obtain ample numbers of specimens during colder months, having some of their smallest sample sizes between October and March (Barton and Powers 2010, Holder and Powers 2010, Tarasidis and Powers 2014, Thompson et al. 2016, Powers and Whitlow 2018). While cold weather and often high water levels make for unpleasant field sampling conditions, leading researchers to focus their sampling in warmer months, the above citations of year-round research illustrate that even focused, intentional sampling efforts during cold months are often less successful than comparable efforts in warmer weather. This leaves researchers anecdotally discussing the dearth of fishes in streams during winter and largely wondering where those fishes are. Despite this, very little research has been conducted that investigates the location of temperate stream fishes during winter.

Of the few papers investigating this question, some authors suggest fishes generally move to deeper, slower waters (Cunjak and Power 1986, Cunjak 1996, Gillette et al. 2006, Musselman and Brewer 2009, Dieterman et al. 2018) during winter months. These deeper, slower waters require a lower expenditure of energy compatible with the lower metabolism of fishes in cold water. The occupation of deeper water by fishes also makes them more difficult to detect with normal sampling methods, in part explaining the dearth of observable stream fishes in colder months. Other studies illustrate that fishes variably occupy habitats near groundwater outflows into streams. In some instances, it appears these groundwater outflows provide thermal refugia allowing fishes to avoid ice formation and maintain a higher metabolism and activity level during winter months (Peterson and Rabeni 1996, Power et al. 1999, Brown 1999, Brown et al. 2011). Some research suggests fishes avoid these groundwater outflows as they lack the insulating and stabilizing effect provided by ice (Lindstrom and Hubert 2004, Barrineau et al. 2005). Most of this research has been conducted in cold temperate landscapes (e.g., Alberta, Minnesota, Ontario, Wyoming), where ice plays a much bigger role than it does in streams of the southeastern United States, providing little insight as to the location of warm water fishes during winter in streams of the southeast.

The use of spring outflows by cold water fishes like trout and salmon during warm months has been well documented and appears key to their survival in marginal habitats or during extreme heat and drought (Matthews et al. 1994, Matthews and Berg 1997, Torgerson et al. 1999, Keefer et al. 2009, Stevens et al. 2011, Greer et al. 2019). Despite the abundance of research on cold water fishes using groundwater outflows during summer, little research beyond Peterson and Rabeni (1996) has investigated the use of groundwater outflows as winter refugia for warm water fishes during cold months in truly ice-free environments. Additionally, nearly all of the above research has focused on how salmonids use these habitats, leaving the hypothesized use of these groundwater outflows by warm water fishes during winter in ice-free environments largely untested. Therefore, the objective of this study was to examine the use of groundwater outflows by warm water fishes for differences in occupation associated with stream temperatures.

METHODS

Study Site

Data were collected in the South Fork Roanoke River in Elliston near the outflow of Big Spring in Montgomery County, Virginia (37.216º N, 80.235º W). At this locality, the South Fork Roanoke River is 16.7-21.4 m wide at normal flows. Our study site was downstream of the USGS streamgage at Shawsville (https://waterdata.usgs.gov/monitoring-location/02053800/#parameterCode=00065&period=P7D&showMedian=false) and all observations were made when flows were 0.85-3.9 m^3/second. On 2 March 2023, habitat of the study locality was quantified at 10 representative points within each snorkel reach. Those reaches were located upstream of, downstream of, and in the thermal plume of the outflow of Big Spring. Habitat was quantified by measuring water depth with a meter stick and current velocity approximately 5 cm above the substrate with a FloWatch flowmeter at each point. Depth of snorkel reaches (Fig. 1) was compared with a one-way analysis of variance (ANOVA), as was current velocity (Fig. 2). The downstream reach was deeper ($p = 0.001$) than the upstream and plume reaches. Current velocity did not vary among snorkel reaches ($p = 0.65$).

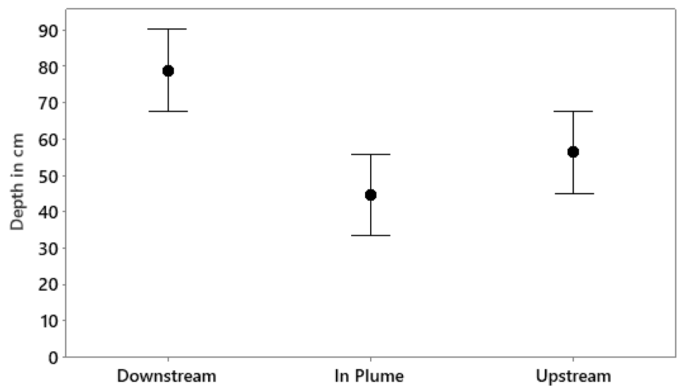

Figure 1. Means and 95% confidence intervals for depth in cm of snorkel reaches in the South Fork Roanoke River in Elliston, VA. Snorkel reaches are in the thermal plume of Big Spring (In Plume), downstream of the thermal plume (Downstream), and upstream of the thermal plume (Upstream).

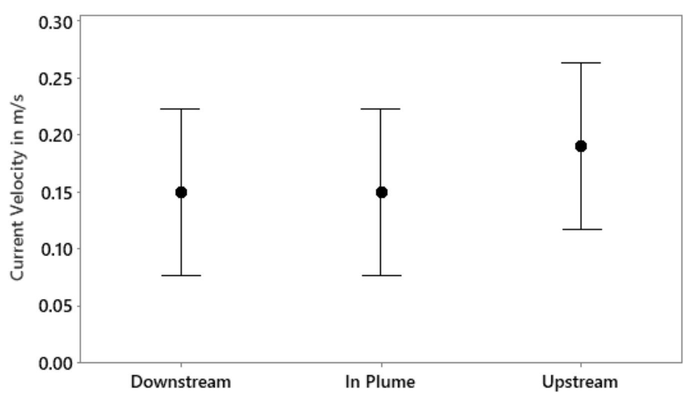

Figure 2. Means and 95% confidence intervals for current velocity in meters per second of snorkel reaches in the South Fork Roanoke River in Elliston, VA. Snorkel reaches are in the thermal plume of Big Spring (In Plume), downstream of the thermal plume (Downstream), and upstream of the thermal plume (Upstream).

Data Collection

Snorkel observations were made near the mouth of the outflow of Big Spring in the South Fork Roanoke River. On each snorkeling day, temperature was measured with an alcohol thermometer in the outflow of Big Spring and recorded. Similarly, temperature of the South Fork Roanoke River outside of the thermal plume of Big Spring was measured and recorded. Observations were made on 20 days when the water in the South Fork Roanoke River was 2-9^{o}C (labeled cold) and 20 days when water in the South Fork Roanoke River was 12-25^{o}C (labeled warm). The temperature of the outflow of Big Spring was always 10-14^{o}C. On each snorkeling day, a 10-minute snorkel observation was made within the thermal plume of the spring outflow and species observed and number of individual fishes observed were recorded on a dive slate. Additionally, 10-minute snorkel observations were also made in a reach just upstream of the spring outflow and a reach just downstream of the spring outflow outside of the thermal plume. In each snorkel observation, the snorkeler moved slowly from the most upstream point of the reach toward the downstream end of the reach noting species observed and number of individual fishes observed in each snorkel reach and recorded those data on a dive slate. Fishes that appeared to have already been recorded were not counted a second time. Common and scientific names of Roanoke River fishes follow Bugas et al. (2019).

Statistical Analyses

Species richness during cold water observations was compared among upstream, downstream, and in thermal plume with ANOVA. The number of fishes observed during cold water observations was also compared among upstream, downstream, and in thermal plume with ANOVA. Species richness during warm water observations was compared among upstream, downstream, and in the thermal plume with ANOVA. Lastly, the number of fishes observed during warmwater observations was also compared among upstream, downstream, and in the thermal plume with ANOVA.

Species richness of observations within upstream, downstream, and in the thermal plume snorkel reaches was compared between cold water and warmwater periods with two-sample T-tests. Linear regression of temperature (^{o}C) of the South Fork Roanoke River outside of the Big Spring thermal plume with species richness was conducted within upstream, downstream, and in the thermal plume snorkel reaches. As species richness in the thermal plume of the spring was artificially elevated during warm water by the presence of trout stocked in the Roanoke River, only non-salmonid species richness was used in regression with temperature for that reach. Linear regression of temperature (^{o}C) of the South Fork Roanoke River outside of the Big Spring thermal plume with number of individual fishes observed was conducted within upstream, downstream, and in thermal plume snorkel reaches. All analyses were conducted with Minitab 20.

RESULTS

A total of 23 species were encountered in the upstream reach and in the downstream reach. A total of 20 species were encountered within the thermal plume of Big Spring. *Moxostoma cervinum* (Blacktip Jumprock), *Thoburnia rhothoeca* (Torrent Sucker), and *Lepomis cyanellus* (Green Sunfish) were unique to the upstream reach. *Pimephales notatus* (Bluntnose Minnow) and *Moxostoma collapsum* (Notchlip Redhorse) were unique to the downstream reach. *Moxostoma erythrurum* (Golden Redhorse) and *Oncorhynchus mykiss* (Rainbow Trout) were unique to the within-plume reach. The full list of species for each reach is presented in Table 1.

Table 1. Species encountered in the South Fork Roanoke River, VA during snorkeling observations upstream, downstream, and in the thermal plume of the outflow of Big Spring in Elliston. Total species observed within each snorkel reach is at the bottom of each column. Scientific and common names follow Bugas et al. (2019).

Scientific Name	Common Name	Upstream	In Plume	Downstream
Cyprinidae/Leuciscidae				
Campostoma anomalum	Central Stoneroller	X	X	X
Exoglossum maxillingua	Cutlip Minnow	X		X
Luxilus albeolus	White Shiner	X	X	X
Luxilus cerasinus	Crescent Shiner	X	X	X
Lythrurus ardens	Rosefin Shiner	X	X	X
Nocomis leptocephalus	Bluehead Chub	X	X	X
Notropis procne	Swallowtail Shiner	X	X	X
Pimephales notatus	Bluntnose Minnow			X
Catostomidae				
Catostomus commersonii	White Sucker	X	X	X
Hypentelium nigricans	Northern Hogsucker	X	X	X
Moxostoma cervinum	Blacktip Jumprock	X		
Moxostoma erythrurum	Golden Redhorse		X	
Moxostoma collapsum	Notchlip Redhorse			X
Thoburnia rhothoeca	Torrent Sucker	X		
Ictaluridae				
Noturus insignis	Margined Madtom	X		X
Salmonidae				
Oncorhynchus mykiss	Rainbow Trout		X	
Salvelinus fontinalis	Brook Trout		X	X
Cottidae				
Cottus caeruleomentum	Blue Ridge Sculpin	X	X	X
Centrarchidae				
Ambloplites rupestris	Rock Bass	X		X
Lepomis auritus	Redbreast Sunfish	X		X
Lepomis. cyanellus	Green Sunfish	X		
Lepomis macrochirus	Bluegill	X	X	
Micropterus dolomieu	Smallmouth Bass	X	X	X
Percidae				
Etheostoma flabellare	Fantail Darter	X	X	X
Etheostoma nigrum	Johnny Darter		X	X
Etheostoma podostemone	Riverweed Darter	X	X	X
Percina nevisense	Chainback Darter	X	X	X
Percina rex	Roanoke Logperch	X	X	X
Percina roanoka	Roanoke Darter	X	X	X
		N=23	N=20	N=23

Snorkel reaches were not equivalent with one another for species richness (Fig. 3) during cold water observations ($p < 0.001$). Mean species richness was higher within the plume (4.15, $SE = 0.41$) than it was upstream (1.25, $SE = 0.24$) and downstream (0.85, $SE = 0.23$). Number of individual fishes observed (Fig. 4) among upstream, within, and downstream of the spring plume also was unequal ($p = 0.003$) during cold water observations. Within plume number of fishes observed (117, SE = 42) was higher than the number of fishes observed in upstream (5.60, *SE* = 2.8) and downstream (11.90, *SE* = 6.8) snorkel reaches.

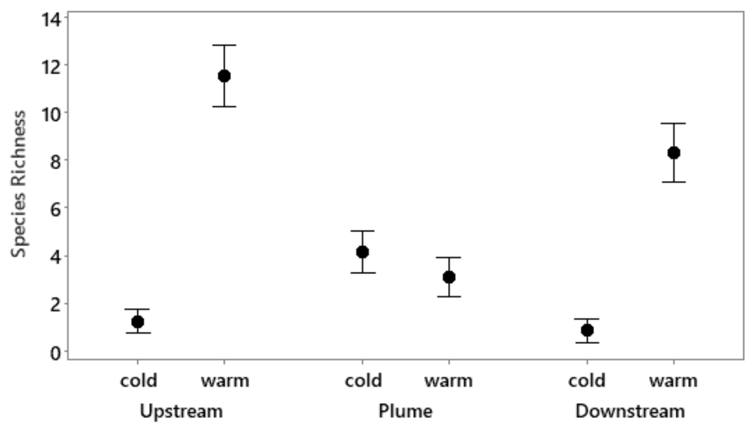

Figure 3. Means and 95% confidence intervals for species richness of snorkel observations in the South Fork Roanoke River in Elliston, VA when water in the South Fork Roanoke River was 2-9ºC labeled “cold” and 12-25ºC labeled “warm.” Snorkel reaches are in the thermal plume of Big Spring (Plume), downstream of the thermal plume (Downstream), and upstream of the thermal plume (Upstream). Each mean and confidence interval is based on a sample size of 20.

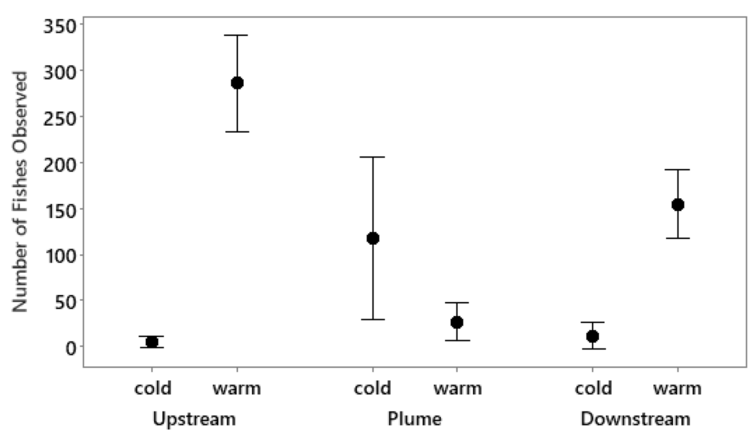

Figure 4. Means and 95% confidence intervals for number of fishes observed during snorkel observations in the South Fork Roanoke River in Elliston, VA when water in the South Fork Roanoke River was 2-9ºC labeled “cold and 12-25ºC labeled “warm.” Snorkel reaches are in the thermal plume of Big Spring (Plume), downstream of the thermal plume (Downstream), and upstream of the thermal plume (Upstream). Each mean and confidence interval is based on a sample size of 20.

Species richness among upstream, within, and downstream of the spring plume (Fig. 3) was also not equal ($p < 0.001$) during warm water observations. Within plume species richness (3.10, *SE* = 0.38) was lower than it was upstream (11.55, *SE* = 2.74) and downstream (8.30, *SE* = 0.59) of the plume. The number of fishes observed among upstream, within, and downstream of the spring plume (Fig. 4) was also not equal ($p < 0.001$) during warm water observation. Within plume number of fishes observed (27.25, *SE* = 9.9) was lower than it was upstream (285.3, *SE* = 25) and downstream (154.6, *SE* = 18) of the spring plume.

Mean species richness of snorkel observations upstream of the thermal plume was 1.25 (*SE* = 0.24) for cold water observations and 11.55 (*SE* = 2.74) for warm water observations (Fig. 3). A t-test comparing species richness between cold and warm observations in the upstream snorkel reach yielded a *p*-value < 0.001. Mean number of fishes observed upstream of the thermal plume during cold water was 5.6 (*SE* = 2.8) and 285 (*SE* = 25) during warm water observations (Fig. 4). A t-test comparing number of fishes observed during cold and warm water observations in the upstream snorkel reach yielded a *p*-value < 0.001. Upstream of the thermal plume, species richness increased with water temperature (Fig. 5) with a *p*-value < 0.001 and an adjusted R^2 value of 0.76. Number of fishes observed upstream of the thermal plume also increased with water temperature (Fig. 6) with a *p*-value < 0.001 and an adjusted R^2 value of 0.81.

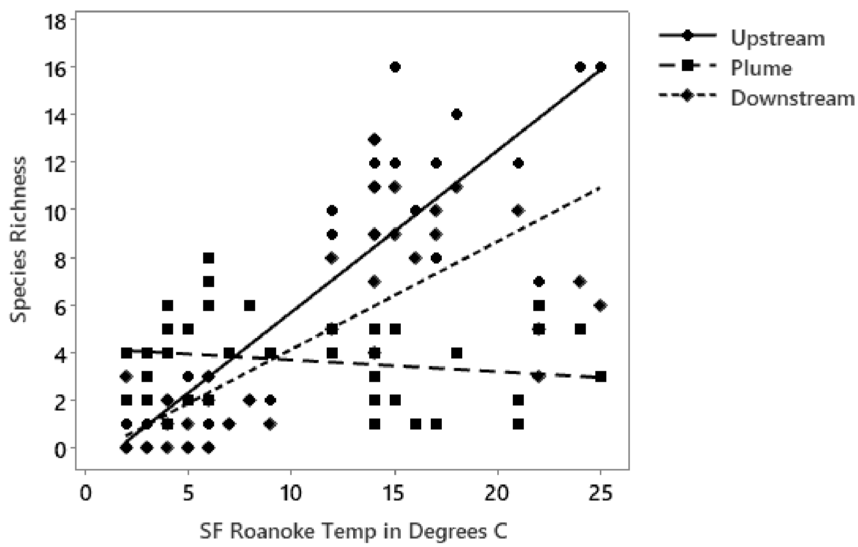

Figure 5. Fitted line plots of temperature (ºC) of the South Fork Roanoke River and the species richness of snorkel observations just upstream of the thermal plume (dots), within the thermal plume (squares), and downstream of the thermal plume (diamonds) at the outflow of Big Spring in Elliston, VA.

Species richness in the thermal plume was not significantly different among cold water and warm water observations (*p* = 0.07) with mean species richness of 4.15 (*SE* = 0.41) for cold water observations and 3.10 (*SE* = 0.38) for warm water observations (Fig. 3). As summer observations in the thermal plume yielded high numbers of stocked trout, non-salmonid species richness and number of fishes observed were calculated and compared among cold and warm water observations in an effort to compare habitat use by the self-sustaining fish community. Non-salmonid species richness was 4.15 (*SE* = 0.41) during cold water observations and 2.75 (*SE* = 0.37) for warm water observations. A t-test comparing non-salmonid species richness during cold and warm water observations in the thermal plume yielded a *p*-value of 0.016. Mean number of non-salmonid fishes observed in the thermal plume during cold water was 117 (*SE* = 42) and 27.3 (*SE* = 9.9) during warm water observations. A t-test comparing number of non-salmonid fishes observed during cold and warm water observations in the thermal plume yielded a *p*-value 0.044. In the thermal plume, non-salmonid species richness decreased with water temperature with a *p*-value of 0.03, and a modest adjusted R^2 value of 0.09. The number of fishes observed in the thermal plume also decreased with water temperature with a *p*-value of 0.034 and a modest adjusted R^2 value of 0.09.

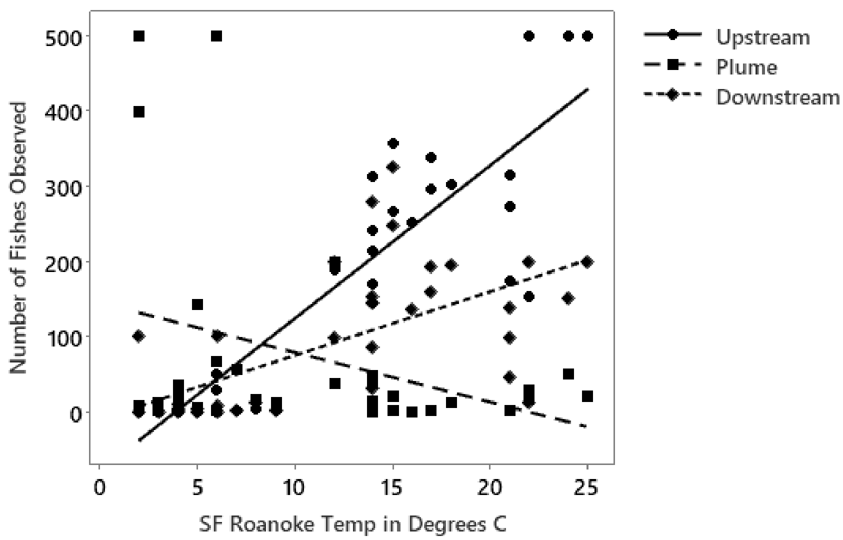

Figure 6. Fitted line plots of temperature (ºC) of the South Fork Roanoke River and number of fishes observed during snorkel observations just upstream of the thermal plume (dots), within the thermal plume (squares), and downstream of the thermal plume (diamonds) at the outflow of Big Spring in Elliston, VA.

Mean species richness of snorkel observations downstream of the thermal plume was 0.85 (*SE* = 0.23) for cold water observations and 8.30 (*SE* = 0.59) for warm water observations (Fig. 3). A t-test comparing species richness between cold and warm observations in the upstream snorkel reach yielded a *p*-value < 0.001. Mean number of fishes observed downstream of the thermal plume during cold water was 11.9 (*SE* = 6.8) and 154 (*SE* = 18) during warm water observations (Fig. 4). A t-test comparing number of fishes observed during cold and warm water observations in the upstream snorkel reach yielded a *p*-value < 0.001. Downstream of the thermal plume, species richness increased with water temperature (Fig. 5) with a *p*-value < 0.001, and an adjusted R^2 value of 0.62. Number of fishes observed downstream of the thermal plume also increased with water temperature (Fig. 6) with a *p*-value < 0.001 and an adjusted R^2 value of 0.41.

DISCUSSION

The greater species richness during warm water compared to cold water periods in both the upstream and downstream (Fig. 3) snorkel reaches illustrates the general paucity of observable fishes during cold months in localities where they are quite visible in warmer months. A similar comparison of total fishes observed in upstream and downstream (Fig. 4) snorkel reaches also illustrates areas outside of the thermal plume of Big Spring teeming with fishes during warm water periods nearly devoid of observable fish during cold water periods. This is further reflected in the strong positive relationship of species richness with water temperature in the upstream and downstream snorkel reaches (Fig. 5). Lastly, total fishes observed show the same trend of a strong positive relationship with water temperature in both the upstream and downstream (Fig. 6) snorkel reaches. Collectively, these results show a clear pattern, and this dearth of observable fishes during cold months helps explain the difficulty obtaining adequate sample sizes during winter months in projects across all seasons as fishes appear to be largely absent from their warm weather habitats easily sampled during cold periods (Barton and Powers 2010, Holder and Powers 2010, Tarasidis and Powers 2014, Thompson et al. 2016, Powers and Whitlow 2018). As none of the species encountered in this study (Table 1) are known for widespread, long range seasonal migrations (Jenkins and Burkhead 1994), their absence must be explained on a more local scale. As other research suggests fishes generally move to deeper, slower waters (Cunjak and Power 1986, Cunjak 1996, Gillette et al. 2006, Musselman and Brewer 2009, Dieterman et al. 2018) during winter months, the deeper water of our downstream snorkel reach showed the same dearth of fishes as our upstream snorkel reach. Therefore, our data do not support the hypothesis that fishes move into deeper water during cold water periods. As our study was not designed specifically to test the hypothesis of fishes inhabiting deeper waters in winter, our finding should be considered with appropriate caveats.

Within the thermal plume of the outflow of Big Spring, fishes showed the opposite pattern of occupation to that shown by observations in the upstream and downstream snorkel reaches. The greater species richness (Fig. 3) and total fishes (Fig. 4) observed during cold water compared to warm water periods suggests fishes are utilizing this nearly constant 10-14^{o}C water as a thermal refuge during winter. The modest inverse relationship of water temperature with non-salmonid species richness and total fishes observed also suggests warm water fishes are utilizing this thermal refuge when water temperatures in the South Fork Roanoke are below that of the thermal plume of the outflow of Big Spring. Thus, as temperature in the South Fork Roanoke River drops to near freezing, more warm water fishes appear to be utilizing the warmer waters in the outflow of Big Spring.

Numerous studies document the response of warm water fishes to cold temperatures, but those studies do not show clear consensus on causes for this response. The winter dormancy of *Tautogolabrus adspersus* (Cunner) appears to be the result of inactivity to conserve energy during periods of low food availability rather than a depression of metabolic rate during winter (Speers-Roesch et al. 2018). Lemons and Crawshaw (1985) reported a monotonic, exponential decrease in metabolic rate of *Micropterus salmoides* (Largemouth Bass) with temperature and a reduction of food consumption in water below 10^{o}C even when availability of food did not change. The activity level of *M. salmoides* experienced a precipitous drop below 7^{o}C suggesting dormancy below this temperature preventing consumption of enough food to keep up with metabolic requirements. Crawshaw et al. (1982) found a similar response in *Ameiurus nebulosus* (Brown Bullhead), which seek temperatures of 11-13^{o}C for overwintering. When held at temperatures of 3^{o}C, both *M. salmoides* and *A. nebulosus* sought out warmer water when given the opportunity (Crawshaw 1984). Sayer and Davenport (1996) showed similar declines in activity and metabolism at water temperatures approaching 4^{o}C for *Ctenolabrus rupestris* (Goldsinny Wrasse) suggesting these declines are fairly widespread in warm water fishes. As the nervous system of fishes appears to be especially sensitive to cold temperatures, declines in activity are likely attributable to low temperature dormancy (Prosser and Nelson 1981).

At first glance, it is easy to think of food in streams declining in winter months, making dormancy during cold water periods an effective strategy for survival. However, literature regarding seasonal biomass of streams does not clearly document lower aquatic insect biomass in winter. Some studies have found a lower aquatic insect biomass during winter (Bradt 1977, DeHoney and Gaud 1983), but others show no clear trends in aquatic insect biomass seasonally (Mackay and Kalff 1969, Munoz 2003, Buria et al. 2010, Junker and Cross 2014). Lastly, some studies have found greater biomass and/or abundance for at least some macroinvertebrates during winter than other times of year (Minshall 1981, Berg and Hellenthal 1992, Robinson et al. 1993, Jiang et al. 2017). Therefore, it does not appear food is necessarily lower in availability during cold months. This suggests dormancy during cold months offers little real advantage energetically and is unlikely brought on by a lack of food in streams.

It would appear warm water fishes benefit from maintaining a higher body temperature than the surrounding stream water as it approaches freezing temperatures. The higher body temperatures deter the onset of dormancy (Crawshaw et al. 1982, Lemons and Crawshaw 1985) allowing for continued feeding through winter and increased functioning of their nervous systems sensitive to low temperatures (Prosser and Nelson 1981). The increased species richness and number of fishes observed during cold water periods in the thermal plume contrasting with those values in snorkel reaches outside of the thermal plume suggest warm water fishes disproportionately occupy this nearly uniform temperature water of 10°C or greater found in the thermal plume and gain physiological advantages in doing so.

A few studies have investigated the use of groundwater outflows by fishes during winter. Consensus on their importance is generally lacking as some work suggests these nearly uniform temperature habitats provide important refugia for fishes when stream water is likely to form anchor ice (Brown 1999, Power et al. 1999, Brown et al. 2011). Other research suggests fishes avoid groundwater outflows as they prevent the formation of surface ice which protects and stabilizes waters beneath (Lindstrom and Hubert 2004, Barrineau et al. 2005). As these investigations were conducted in much higher latitudes and elevation than found in Virginia, they likely have little relevance to the South Fork Roanoke River as ice formation is restricted to the very margins of the Roanoke River and its larger tributaries even during the coldest winters. Furthermore, these studies are disproportionately concerned with cold water species such as *Oncorhynchus clarkii* (Cutthroat Trout). In a study conducted at more similar latitude and elevation, Peterson and Rabeni (1996) found biomass of several warm water species higher in a spring run adjacent to Jacks Fork River, MO during cold water periods. Combined with our findings, those of Peterson and Rabeni (1996) suggest that warm water fishes do use groundwater outflows as thermal refugia during winter helping to at least partially explain the general scarcity of warm water fishes in temperate streams during winter. The modest inverse relationships of species richness and total fishes observed with temperature in the South Fork Roanoke River does not fully explain the winter paucity of fishes in normal stream habitats but along with other documented winter habitats like deeper, slower waters (Cunjak and Power 1986, Cunjak 1996, Gillette et al. 2006, Musselman and Brewer 2009, Dieterman et al. 2018) help elucidate the winter habitats of warm water stream fishes. Additionally, future investigation of anecdotally identified important winter habitats like leaf packs (David Neely, pers. comm.) and beneath large rocks and debris (Brett Albanese, pers. comm.) may further help solve the mystery of winter habitats for warm water fishes.

The disproportionate occupation of groundwater outflows during cold water periods by warm water fish documented in this study and Peterson and Rabeni (1996) suggest these are especially important winter habitats for warm water fishes. The use of spring outflows by cold water fishes during warm water periods has been well documented and appears key to the survival of salmonids in marginal conditions (Matthews et al. 1994, Matthews and Berg 1997, Torgerson et al. 1999, Keefer et al. 2009, Stevens et al. 2011, Greer et al. 2019). Additionally, spring-dwelling fishes like *Forbesichthys agassizii* (Spring Cavefish), *Cottus paulus* (Pygmy Sculpin), *Fundulus* *julisia* (Barrens Topminnow), *Elassoma alabamae* (Spring Pygmy Sunfish), and others rely on these groundwater outflows year-round (Etnier and Starnes 1993, Boschung and Mayden 2004). Thus, it would appear the conservation of these unique habitats where groundwater outflows connect to surface streams may be especially key in the conservation of the diverse fish fauna of the southeastern United States.

ACKNOWLEDGEMENTS

We thank Roanoke College for equipment used in this research and for the sabbatical making regular winter sampling possible. We also thank Mr. Homer Duncan for access to our study site throughout this research. Lastly, we thank David Neely and Brett Albanese for thoughtful conversation and sharing their experience sampling streams during winter.

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