Trends in Biomass and Relative Weight of Brook Trout in Response to Introduction of Non-native Brown Trout in an Appalachian Mountain Stream

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Abstract: Native brook trout (*Salvelinus fontinalis)* have been declining in many areas of their range partially because of introduction of nonnative salmonids. Brook trout biomass and relative weight in the Conway River, Virginia, were evaluated for 24 years using regression to discern trends potentially associated with colonization of brown trout (*Salmo trutta*). The Rapidan River is adjacent to the Conway River and has brook trout but not brown trout, and thus this river was sampled over similar time intervals and served as a reference stream for this case study. Brook trout biomass in the Conway River varied from 21.8 to 58.5 kg ha^{-1} but displayed no temporal trends throughout the study ($r^2 = 0.01$; $P = 0.81$). Concurrently, brown trout biomass varied from 5.5 to 59.9 kg ha^{-1} and increased during the study ($r^2 = 0.63$; $P < 0.01$). Total salmonid biomass increased from 44 to 61 kg ha^{-1} over 1995–2000 to 80 to 107 kg ha^{-1} over 2014–2019 ($r^2 = 0.39$; $P < 0.02$) suggesting brown trout biomass was additive and did not replace brook trout biomass. Brown trout composed <25% of salmonid biomass in the Conway River from 1995 to 2003 but increased to 40%–55% from 2008 to 2019. Brook trout biomass in the Rapidan River was approximately double that of the Conway River but also displayed no temporal trends during the study ($r^2 = 0.01$; $P = 0.76$). Mean relative weight of brook trout was relatively stable through time in the Rapidan River but appeared to decline in the Conway River ($r^2 = 0.28$; $P = 0.06$), possibly from density-dependent factors due to the increase in total salmonid biomass. In systems such as ours where brook trout do not appear to be negatively affected by brown trout, resource management agencies in eastern North America may wish to consider forgoing intensive eradication of expanding brown trout populations in lieu of brook trout habitat protection measures.

Key words: nonindigenous trout, headwaters, native species

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The Appalachian Mountains in eastern North America harbor substantial native brook trout (*Salvelinus fontinalis)* populations. Many Virginia streams support these fish in the Ridge and Valley and Blue Ridge provinces (Jenkins and Burkhead 1994), but some populations have been extirpated due to poor land management, improper livestock grazing, and other anthropogenic changes (Hudy et al. 2008). These alterations have frequently degraded water quality and streamside conditions resulting in increased water temperatures and siltation. Nonnative salmonids such as brown trout (*Salmo trutta)* also pose considerable conservation threats to brook trout (Eastern Brook Trout Joint Venture 2011). Self-sustaining brown trout populations sympatric to native brook trout occur in many Virginia streams, especially in lower elevation reaches with marginal brook trout thermal habitat.

The exact mechanisms mediating the ability of brown trout to reduce or eliminate brook trout populations are not fully understood but likely vary based on multiple biotic and abiotic variables (Davis and Wagner 2016). Grant et al. (2002) postulated spawning interactions between sympatric brown and brook trout in a Minnesota stream contributed to species replacement by brown trout via disruptive processes, as spawning behavior was not reproductively isolated. In laboratory tests, brown trout demonstrated higher prey capture rates, higher body condition, and less susceptibility to disease than brook trout (DeWald and Wilzbach 1992). The presence of brown trout also resulted in lower brook trout occurrence probability in Pennsylvania streams (Wagner et al. 2013) where Kirk et al. (2018) found that brook trout populations had fewer age-classes and lower population density when sympatric to brown trout compared with allopatric populations. Conversely, McKenna et al. (2013) found only weak evidence of brook trout suppression or elimination by brown trout in New York, and Kelly et al. (2021) asserted there was no evidence that brown trout abundance was inversely related to brook trout occupancy in Iowa. Thus, there is copious literature concerning such interactions between these two species, but it remains unclear if sympatric populations can coexist in relatively undisturbed watersheds without deleterious impacts to brook trout. Jenkins and Burkhead (1994) stated that Virginia brook trout populations appeared to be relatively resistant to invasion, but this has not been empirically tested using long-term datasets.

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The Conway River in northern Virginia is located in the Rapidan Wildlife Management Area (WMA) adjacent to Shenandoah National Park (SNP) and contains a healthy brook trout population. However, brown trout were stocked in this river at lower elevations during the 1970s and were first detected upstream in brook trout habitats in 1987. Conversely, the Rapidan River, adjacent to the Conway River and also located within the Rapidan WMA and SNP, has similar habitat and a brook trout population, but brown trout are not present. Our objective in this study was to use an existing dataset for both rivers to examine any possible temporal changes in biomass and body condition of brook trout in the Conway River that could plausibly be attributed to the presence of brown trout. The Rapidan River was used as a reference stream.

Methods

The Conway and Rapidan river watersheds are forested and have experienced minimal anthropogenic impacts since before the mid-20th century. The Conway River is smaller than, and a tributary to, the Rapidan River. Single, fixed fish community sampling stations were established in the 1970s in upper reaches of both rivers. The Conway River site is at 474 m elevation, and the Rapidan River site is at 562 m elevation, approximately 17.7 km above the confluence with the Conway River. This corresponded with drainage areas above each sample site of 1291 ha and 1832 ha at the Conway and Rapidan river, respectively. Historical sampling on the Conway River occurred sporadically between 1976 and the mid-2000s, and the Rapidan was sampled in alternate years (sometimes annually) between 1997 and 2009. From 2011 to 2019, samples were conducted annually on both rivers with the exception of 2018 which was a flood year. Final data sets used for the study included 13 samples taken in the Conway River from 1995 to 2019 and 16 samples taken in the Rapidan River from 1997 to 2019.

Each sample was collected with three-pass depletion sampling conducted in summer (usually July) using two back-pack electrofishing units with two dippers assigned to each unit (unit operators also dipped fish). Sampling stations were 100 m long, encompassed several pool/riffle/run sequences, and were bounded by gradient barriers at upper and lower ends that were expected to minimize fish movement. Five wetted widths at 20-m intervals were measured during each sampling event; mean wetted width was used to calculate density and biomass estimates. Over the 1995—2019 study period, wetted widths averaged 8.1 m (range 3.2 to 14.0 m) on the Conway River and 7.0 m (range 3.7 to 10.4 m) on the Rapidan River, but the Rapidan had a higher gradient at 12.2% compared to 6.7% on the Conway River. Captured fish were counted, measured (TL, mm), weighed (g), and placed in live cages outside of sampling sites after each run.

Using depletion data, we estimated population size and derived biomass estimates using Microfish 3.0 (Microfish.org, Ogden, Utah; Van Deventer 1989). Linear regression models were used to determine if population biomass of brook trout and brown trout displayed temporal trends (Wilkinson 1997). Biomass and abundance were highly correlated ($r = 0.75$; $P < 0.01$), and biomass was chosen as the dependent model variable because it was determined to be a more comprehensive metric of population health that should minimize short-term bias due to highly variable recruitment and subsequent spikes in collection of age-0 fish (House 1995). Biomass estimates included age-0 trout.

Relative weights (*Wr*) were calculated for adult brook and brown trout as a measure of body condition using equations for each species given in Neumann et al. (2012). Adult trout were considered those fish over 100 mm TL or at least age-1 fish (Sweka and Hartman 2008). Mean *Wr* was compared between species in the Conway River and between brook trout populations in study rivers for years in which paired data existed using *t*-tests. Observed *Wr* distributions for each species-river combination were examined for normality using Kolmogorov-Smirnov tests within the distribution fitting function in Systat 11 (Wilkerson 1997). Results of this latter analysis confirmed that untransformed *Wr* data approximated normal distributions; thus these data were used for comparison. Temporal trends of *Wr* for brook trout in both rivers and brown trout in the Conway River were examined using linear regression as described above. Finally, mean TL of adult brook trout in the Conway River was reviewed with a scatter plot to visually ensure that size structure of this population did not change over the study period.

Results

Estimates of brook trout density in the Conway River varied from 797 to 4040 fish ha^{-1} with no temporal trend, whereas estimates of brown trout density in the Conway River varied from 40 to 1128 fish ha^{-1} and increased significantly ($r^2 = 0.59$; $P < 0.01$) over time. Meanwhile, estimates of brook trout density in the Rapidan River followed a similar pattern as in the Conway River with no temporal trend, but densities were higher at 1393 to 7233 fish ha^{-1} (Table 1). Biomass trends mirrored density trends, as estimates of brook trout biomass in the Conway River varied from 21.8 to 58.5 kg ha^{-1} but did not show any temporal trends (Figure 1). During the same period, brown trout biomass varied from 5.5 to 59.9 kg ha^{-1} and increased significantly throughout the study. Brook trout biomass in the Rapidan River was approximately double that of the Conway River, varying from 30.7 to 191.0 kg ha^{-1} during the study and likewise showed no temporal trends (Figure 1). Brown trout composed ≤25% of total salmonid biomass in the Conway River from 1995

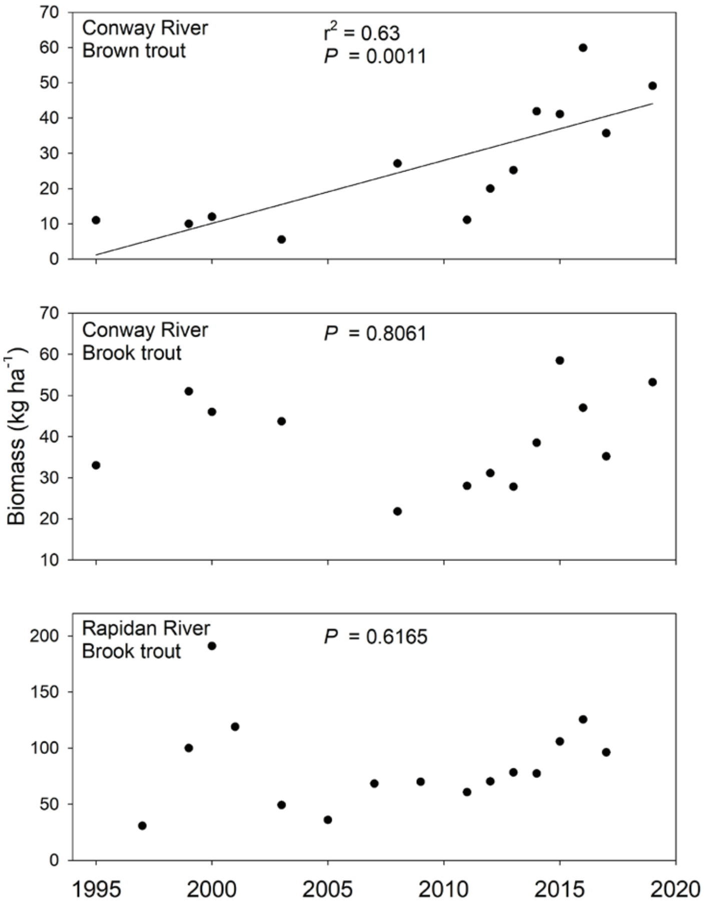

Figure 1. Brook and brown trout biomass estimates from the Conway and Rapidan rivers, Virginia, between 1995 and 2019.

to 2003 but was generally 40%–55% from 2008 to 2019 (Figure 2). Total salmonid biomass was 44 to 61 kg ha^{-1} over 1995–2000 but 80 to 107 kg ha^{-1} over 2014–2019 and increased significantly during the study ($r^2 = 0.39$; $P < 0.02$).

Mean *Wr* of brook trout in the Conway River varied from 85 to 101 over the study but varied from 77 to 95 in the Rapidan River (Table 2). Brook trout mean *Wr* was generally similar between rivers but was higher in the Conway River than in the Rapidan River in three years, and the converse was true in two other years.

Table 1. Estimated density (fish ha^{-1}) of brook trout (BKT) and brown trout (BNT) in the Rapidan and Conway rivers, Virginia, between 1995 and 2019.

Year	Rapidan BKT	Conway BKT	Conway BNT
1995		1019	52
1997	1489	–	–
1998	2597	–	–
1999	4075	4040	40
2000	7233	2471	129
2001	5790	–	–
2003	1700	1438	67
2005	1393	–	–
2007	2281	–	–
2008	–	841	400
2009	3835	–	–
2011	1515	392	95
2012	6844	1081	311
2013	2348	797	324
2014	2334	1314	442
2015	3606	2447	659
2016	4178	1744	1128
2017	2043	1229	458
2019	2912	1537	840

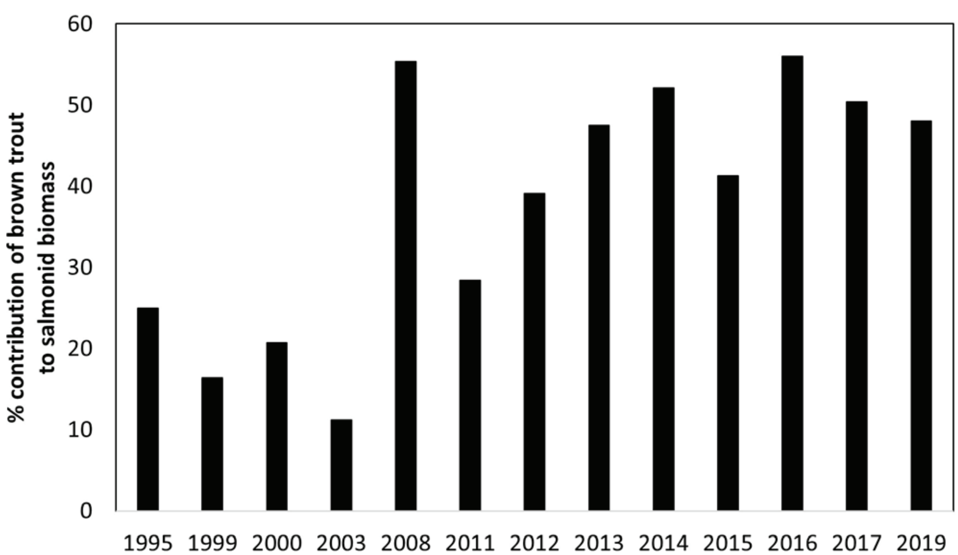

Figure 2. Brown trout percent contribution to salmonid biomass in the Conway River, Virginia, between 1995 and 2019.

Table 2. Mean relative weights of brook trout in the Conway and Rapidan rivers, Virginia, along with *t*-test results examining differences in mean relative weights between rivers each year.

Year	Conway	Rapidan	P	F	df
1999	86.5	82.4	< 0.01	16.21	1, 161
2000	101.0	90.7	<0.01	19.42	1, 107
2011	90.5	89.5	0.33	0.97	1, 91
2012	85.1	88.4	0.03	5.03	1, 77
2013	91.2	88.9	0.18	1.86	1, 90
2014	93.8	94.6	0.48	0.51	1, 122
2015	90.1	90.2	1.00	0.00	1, 146
2016	82.8	86.2	<0.01	10.01	1, 93
2017	90.0	88.7	0.18	1.80	1, 125
2019	83.8	77.4	<0.01	29.00	1, 136

Table 3. Mean relative weights of adult brook trout (BKT) and brown trout (BNT) in the Conway River, Virginia, along with *t*-test results examining differences in mean relative weights between each year. No adult BNT were sampled in 2003.

Year	BKT	BNT	*P*	*F*	*df*
1995	93.4	91.4	0.78	0.08	1, 16
1999	86.5	93.4	0.04	4.41	1, 46
2000	101.0	101.8	0.88	0.02	1, 23
2003	95.9	n/a	–	–	–
2008	95.6	93.4	0.37	0.84	1, 37
2011	90.5	91.5	0.46	0.55	1, 46
2012	85.1	89.9	0.03	5.36	1, 28
2013	91.2	90.8	0.79	0.07	1, 47
2014	93.8	95.6	0.22	1.56	1, 81
2015	90.1	93.4	0.37	0.84	1, 37
2016	82.8	85.9	<0.01	9.34	1, 84
2017	90.0	93.8	<0.01	8.31	1, 71
2019	83.8	88.2	<0.01	7.23	1, 63

Mean *Wr* of brook trout appeared to decline slightly over time in the Conway River ($r^2 = 0.30$; $P = 0.06$), whereas those in the Rapidan River were relatively stable. Mean *Wr* of brown trout was higher than brook trout in 5 of 12 years where comparisons were possible (Table 3). Further, mean *Wr* values were 1–3 units higher for brown trout than brook trout in three other years, although these were not significant. Brook trout mean *Wr* was 1–2 units higher than brown trout in 3 of 12 years, but none were significant (Table 3). Mean size of adult brook trout varied slightly over the study period, but there was no temporal trend (Figure 3).

Discussion

Brook trout biomass exhibited no detectable trend in either the Rapidan River, where brown trout were not present, or the Conway River, suggesting there were relatively minor impacts to the Conway River brook trout population as a consequence of brown trout presence. It was possible our temporal scale was too short to observe a significant response to the introduction of a nonnative competitor. Interactions of nonnative and/or invasive species can often take a decade or more to be fully realized, but time frames can be highly variable. For example, Greenlee and Lim (2011) asserted that after 35 years, blue catfish (*Ictalurus furcatus*) had not reached equilibrium in Virginia rivers, but in a North Carolina reservoir, it took only a decade for Alabama bass (*Micropterus henshalli*) to replace largemouth bass (*M. salmoides*) as the dominant black bass species in the main reservoir channel (Dorsey and Abney 2015). Waters (1983) found it took only 15 years in a Minnesota stream for brown trout to replace brook trout as the dominant salmonid. Waters (1983) documented an 88% reduction in brook

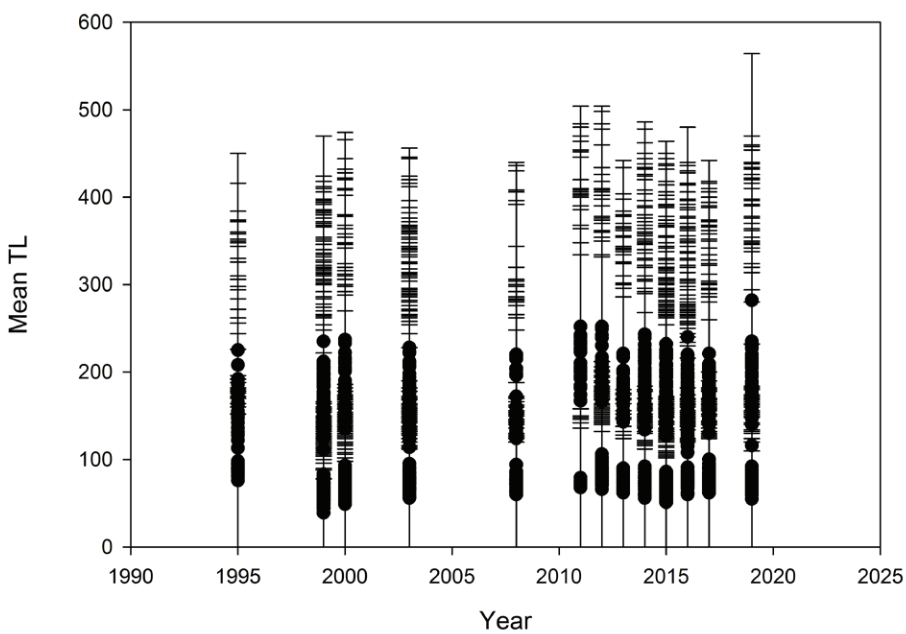

Figure 3. Mean total length of brook trout adults in the Conway River, Virginia, between 1995 and 2019.

trout biomass during a 15-yr period in which brown trout became established. After 32 years of establishment in the Conway River as evaluated in our study, declines in brook trout biomass due to brown trout presence would be expected to have been realized. Brown trout were sometimes the dominant contributor of salmonid biomass in the Conway River by 2008, but this dominance was inconsistent thereafter.

Factors associated with negative effects of brown trout on brook trout populations observed in other studies may have been absent in our system. Land cover of the Conway River watershed was exclusively forest, and this may have facilitated brook trout persistence thus far during establishment of brown trout. Brook trout have been found to fare better in streams with greater forest cover in the watershed (McKenna et al. 2013, Kelly et al. 2021). Wagner et al. (2013) and Waters (1983) also postulated environmental stressors acting as precursors could facilitate negative impacts to brook trout populations existing in sympatry with brown trout. Landscape alterations described in other studies, such as increases in impervious surfaces and agricultural operations, may have allowed brown trout to gain a competitive advantage as water quality parameters more favorable to brook trout declined. For example, Fausch (2007) found environmental disturbances and perturbations were avenues for successful trout invasions whereby one nonnative salmonid could replace another through competitive interactions. Mitro (2016) concluded that brook trout population declines in a Wisconsin stream were likely due to the presence of naturalized brown trout combined with stochastic precipitation patterns and thermal regimes less favorable to brook trout but conducive to an epizootic of an ectoparasitic copepod which infected brook trout but not brown trout. Similar parasites are found in some Virginia trout waters, but they were not observed in our study rivers.

Watershed areas of our study streams were larger than those in a study by Kirk et al. (2018) where sympatric brown trout appeared to suppress brook trout in Pennsylvania streams. However, elevations at our study streams were also substantially higher, suggesting streams in Pennsylvania were not comparable to ours and likely had other contributing variables driving brook trout response to brown trout presence. Davis and Wagner (2016) stressed the need to consider spatial scales when investigating sympatric relationships between naturalized brown trout and brook trout. They also described habitat partitioning occurring between the two species, with brook trout selecting deep residual pools more often than brown trout. Similarly, Benjamin and Baxter (2010) noted that replacement of native cutthroat trout *(Oncorhynchus clarkii*) by nonnative brook trout in Idaho appeared to be habitat dependent. Although we did not measure available habitat types in our study, it is possible based on the higher elevation and relatively steep gradient of the Conway River that multiple pool habitat types may have existed allowing both species access to preferred areas.

Brook trout *Wr* was relatively stable in the Rapidan River but appeared to decline in the Conway River during our study. Relative weight has been used in other studies as a surrogate for growth and food availability (Guy and Willis 1995, Hartman and Margraf 2006). Although brook trout are primarily insectivorous, stream-dwelling brown trout often consume crayfish and fish as well as insects (Garman and Nielsen 1982, Stolz and Schnell 1991, Ward and Morton-Starner 2015). Appalachian streams are relatively unproductive, and allopatric brook trout can have difficulty gaining nutrition even without added competitors (Ensign et al. 1990), thus competition by brown trout may have resulted in reduced *Wrs* of Conway River brook trout. Furthermore, the broader diet niche of brown trout may have allowed them to maintain higher condition even as total salmonid biomass increased. Interestingly, in the three years brook trout relative weights were significantly higher in the Conway River, the Rapidan River had above average biomasses including the two highest years (2000 and 2019). Thus, it is possible density-dependent mechanisms via intraspecific competition were at work suppressing Rapidan River brook trout relative weights those years.

Although it should be recognized that our study lacked spatial replication or experimental control, our results suggest that sympatric brook trout and brown trout may be able to coexist in the Conway River and possibly other Virginia headwater streams without deleterious impacts to brook trout. Such streams in relatively pristine forested watersheds with elevations and gradients similar to the Conway River may provide enough habitat diversity and forage to allow both species to prosper, at least for a time. Josephson (1982) posited that brook trout may, under certain conditions, be able to compete successfully with brown trout for stream resources: brook trout in that study showed an apparently more favorable adaptive response to environmental conditions in headwaters similar to ours than did brown trout.

Resource management agencies in eastern North America have sometimes responded to the invasion of brook trout waters by nonnative salmonids with eradication efforts (Kulp and Moore 2000). However, the lack of overt, quantifiable impacts to the brook trout population in the Conway River in the presence of an expanding brown trout population over several decades suggests that agencies, in some cases, may wish to avoid expensive nonnative removal campaigns and instead expend limited resources on habitat protection measures, such as culvert retrofits, to avoid population fragmentation (Whiteley et al. 2013, Rogers et al. 2021). Further, in a situation such as the Conway River where no nongame species of concern are present, managers may give more consideration to the potential for brown trout to provide enhanced angling opportunities for constituents.

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