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Assessing the Predatory Effects of Invasive Brown Trout on Native Rio Grande Sucker and Rio Grande Chub in Mountain Streams of New Mexico, USA

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Abstract: Invasive predators pose a critical threat to native taxa. Body size plays an important role in mediating the interactions of predator and prey. For piscivorous fishes, increased predator body size can be accompanied by the selection of increasingly larger prey or may reflect a mix of small and large prey. Knowledge of such interactions helps determine how predation affects population vital rates. Here, we assessed the predatory effects of invasive Brown Trout (*Salmo trutta*) on populations of native Rio Grande Sucker (*Catostomus plebeius*) and Rio Grande Chub (*Gila pandora*) in streams of the Jemez River watershed (New Mexico, USA). Trout diets were sampled every two weeks during the 2020 growing season. Predator and prey body lengths were measured to examine relationships to better understand patterns of piscivory and quantify the threat Brown Trout pose to populations of Rio Grande Chub and Rio Grande Sucker. Across all streams and sampling dates, 7% of Brown Trout diets contained fish. Predator–prey length relationships reflected a 'wedge' pattern, indicating that Brown Trout consumed an increasing range of prey body sizes as they grew larger. Rio Grande Sucker and Rio Grande Chub comprised 46% of consumed fishes. The findings demonstrated that Rio Grande Sucker and Rio Grande Chub experience constant predation over the growing season by Brown Trout. Moreover, our study provides evidence that these invasive predators pose a threat to the viability of Rio Grande Chub and Rio Grande Sucker populations. Conservation efforts to protect these chub and sucker populations must account for and directly address predation by invasive Brown Trout.

Keywords: biodiversity; invasive species; predation; fish conservation; Rio Grande; Endangered Species Act

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Citation: Ivie, J.; George, O.; Collins, S.F. Assessing the Predatory Effects of Invasive Brown Trout on Native Rio Grande Sucker and Rio Grande Chub in Mountain Streams of New Mexico, USA. *Conservation* **2022**, *2*, 514–525. https://doi.org/10.3390/conservation2030035

Academic Editor: Kevin Cianfaglione

Received: 21 July 2022
Accepted: 17 August 2022
Published: 6 September 2022

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1. Introduction

Interactions between predators and prey help shape the food web and community structure [1–3]. The body sizes of predator and prey strongly mediate these interactions [4–6]. For piscivorous fishes, increased body size can be accompanied by a selection of increasingly larger prey [5]; (Figure 1a) or may reflect a mix of small and large prey (Figure 1b). The latter creates predator–prey length relationships that are asymmetric, or 'wedge' shaped, e.g., [5–7]; (Figure 1b). Although simple in concept, such a distinction has important implications for prey fish population dynamics, because predators may affect parental prey stocks (i.e., select larger prey), prey recruitment (i.e., select smaller prey), or both.

Invasive predators have contributed to declines in biodiversity worldwide [8–13]. Brown Trout *Salmo trutta* are a prime example, as they have been extensively stocked in freshwaters well beyond their native range. Although Brown Trout are prized by anglers for their large size and aggressive feeding behaviors, these same traits have caused ecological harm to freshwater ecosystems across the globe [14,15]. Brown Trout introductions have often been accompanied by strong changes to aquatic food webs, including direct predation on aquatic macroinvertebrates and native fishes [14–16]. Brown Trout undergo

an ontogenetic diet shift from invertebrates to more energetically and nutritionally profitable fish [17,18]. Such a shift is often accompanied by faster individual growth, increased mouth gape, and an expansion in the sizes of consumable prey [19,20]. Notably, these shifts to piscivory do not preclude the continued consumption of aquatic and terrestrial invertebrates, as Brown Trout are generally thought to be opportunistic consumers [21].

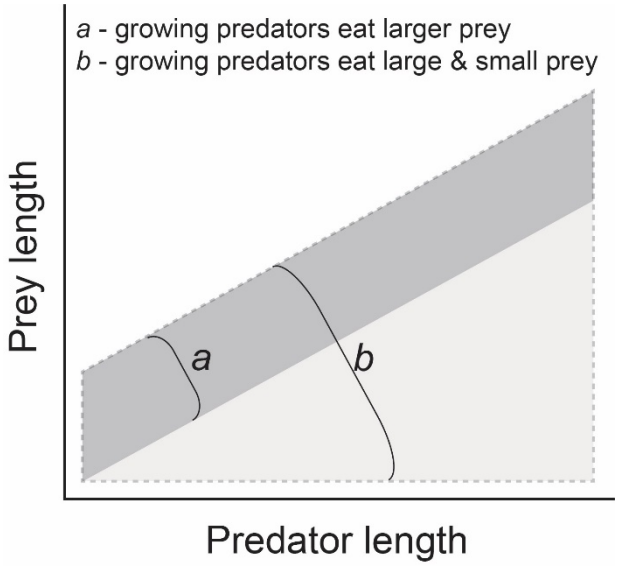

Figure 1. Conceptual prey–predator length relationships: (**a**) piscivores that feed on increasingly larger prey as they grow, and (**b**) piscivores that feed on both large and small prey.

Across the United States, Brown Trout are the third most widely introduced species [22]. Streams of the Upper and Middle Rio Grande Basin were stocked with Brown Trout to create new fisheries in the late 1800s and early 1900s [16]. Self-sustaining populations of Brown Trout can now be found throughout many coldwater mountain streams of the region. Unfortunately, Brown Trout have either replaced or numerically dominated native Rio Grande cutthroat trout *Oncorhynchus clarkii virginalis* and other native fishes in many locations [23]. Rio Grande cutthroat trout are not particularly piscivorous [24–26], especially when compared to Brown Trout. This distinction may have important implications for the trophic dynamics of stream food webs. Although both species are salmonids, their functional roles (e.g., productivity, behaviors, and trophic position) likely vary and should not be assumed to be equivalent [27]. Indeed, the replacement of cutthroats with the more piscivorous Brown Trout has likely affected native stream fishes as they now co-exist with the more aggressive, larger piscivore [28].

Native fishes of the Upper and Middle Rio Grande Basin have declined over the last century [29,30]. Rio Grande Sucker *Catostomus plebeius* (RGS) and Rio Grande Chub *Gila pandora* (RGC) are native to the Rio Grande Basin and were once highly abundant across New Mexico [31]. RGS and RGC have experienced a dramatic range reduction over the past century due to habitat degradation, reduced streamflow, and invasive species [30,32]. Consequently, RGS and RGC face local extirpation and possible extinction. Both species are designated as '*sensitive*' by the state of New Mexico, USA, and listed as a species of conservation concern [32,33]. Moreover, Rio Grande Sucker are listed as '*endangered*' by the state of Colorado, USA [34]. In Texas, RGC is listed as '*State Threatened*' and a species of the greatest conservation need [35]. Recently, both species were petitioned for listing under the Endangered Species Act [36,37]. There has been a concerted effort to protect RGS and RGC in the Rio Grande Basin via a multi-institution conservation agreement [38], with the primary goal of maintaining the long-term viability (i.e., self-sustaining wild populations) of RGS and RGC within their historic range.

Predation by non-native Brown Trout has been hypothesized to be a key factor in the continuing decline of these chub and suckers [28]. Recent syntheses have noted that

fluvial Brown Trout tend to be more piscivorous in their introduced environment and can achieve larger body sizes (and presumably mouth gape) relative to their native range [39]. The degree to which Brown Trout feed on RGS and RGC has not been examined in a quantitative manner. Here, we assessed the predator–prey length relationships (e.g., linear or 'wedge' shaped) as a critical first step in describing how Brown Trout affect populations of sensitive native fishes. Such efforts are needed to better understand patterns of piscivory and quantify the threat Brown Trout pose to populations of RGC and RGS. Our study was conducted in the Jemez River watershed in Northern New Mexico (USA), which is one of the remaining 'strongholds' of RGS and RGC within the Rio Grande. Brown Trout diets were collected during the summer 2020 growing season to document the frequency of piscivory across six streams. Predator–prey length relationships and associations between prey availability, predator size structure, and the frequency of piscivory were examined to assess the threat Brown Trout pose to sensitive fish populations.

2. Materials and Methods

2.1. Study Area

The field study was conducted in six 2nd–4th order streams located in the Jemez River drainage in Northern New Mexico, USA. The Jemez River watershed (total area: 2688 km^2) is in the Southern Rocky Mountains region and is a tributary of the Middle Rio Grande system. The drainage is dominated by volcanic geologic formations (e.g., basalts, pumice, rhyolites, andesites, and tuffs) and ranges in elevation from 1700 to 3432 m.a.s.l. [40]. The Rio Guadalupe (692 km^2) is a large tributary of the Jemez River and is formed by the confluence of Rio Cebolla and Rio de Las Vacas. Streams in the region have been influenced by logging, recreation, road building, and livestock grazing. Riparian vegetation is typically dominated by alder *Alnus* spp., willow *Salix* spp., and assorted grasses.

2.2. Sampling and Analyses

During each trip, stream discharge was calculated at each stream to track flow conditions (Marsh McBirney Flo-Mate 2000). Rio De Las Vacas became intermittent during the field season, whereas all other streams remained perennial. Fish relative abundance (# per 100 m) was estimated at each stream to determine available prey proportions and to collect Brown Trout for diet samples. Fishes were collected using a backpack electrofisher (Smith-Root, LR-24; 185–275 V, 20–35 Hz, 20% duty cycle). The gut contents of all Brown Trout from each stream were collected during each sample period using non-lethal gastric lavage. Gut contents were collected in a 250 µm mesh sieve and examined for the presence or absence of fish to determine the proportion of piscivorous diets. Samples containing fish were stored in 70% ethanol. In the laboratory, fishes were assigned to species (when possible); then, their body lengths were measured to the nearest millimeter. In some cases, fishes were highly digested and were not assigned to species nor measured. In such cases, data were included in calculations of the percent piscivory but not in predatory–prey length relationships. A histogram was constructed to examine the distribution of consumed prey body lengths. Prey–predator length ratios were calculated by dividing the prey length by predator length, then multiplying by 100. Differences among consumed prey species were examined using a one-way analysis of variance (H_0: no difference among species; significance at $\alpha = 0.05$; $\log_{10}$ transformed). Logistical complications precluded the collection of fish diets at East Fork Jemez River and mainstem Jemez River during the first sampling period. The population size structure was assessed using the proportional size distribution of good-quality Brown Trout [41]; PSD-Q; Stock > 150 mm, Quality > 230 mm at each stream. All individuals lavaged over summer were included in the assessment. Linear regression analysis (H_0: no relationship; $\alpha = 0.05$; $\log_{10}$ transformed) was used to examine relationships between the frequency of piscivory (%, dependent variable), average body length of lavaged trout (independent variable), and the PSD-Q of lavaged trout in two separate analyses.

A general model of predator–prey length relationships between non-native Brown Trout and native fishes was developed using pooled diet data from all streams. Predator–prey length relationships were examined using quantile regression analysis [42,43]. Trends (H_0: no trend) in prey length in relation to predator length across multiple quantiles (τ, 0.1, 0.3, 0.5, 0.7, and 0.9) were assessed. The slopes (β) of each quantile were compared to determine how prey lengths related to predator lengths. Previous studies have noted that scaling differences between lower and upper bounds can lead to polygonal shaped predator size–prey size relationships, e.g., [43]; (Figure 1b). Thus, the slopes of the upper ($\tau = 0.9$) and lower ($\tau = 0.1$) bounds of the prey–predator length relationships were assessed to determine whether they changed at different rates.

To determine whether diet proportions reflected the composition of fishes in a stream, correlation analysis was used. For diets, highly digested (i.e., unidentifiable species) individuals were excluded from estimates of diet proportions. For fish assemblages, we calculated species proportions with and without Brown Trout. With respect to the lattter, incidences of cannibalism were low and isolated to a single stream in our study. Moreover, cannibalism tends to be low for fluvial Brown Trout in general [15,44]. Thus, removing Brown Trout from proportions of possible prey may lead to stronger congruence with diet proportions. For each correlation (i.e., with and without Brown Trout), the intercept was constrained to zero, and tested for significance ($\alpha = 0.05$), and slope terms (β) were compared. If diet proportions match living prey proportions, the pattern should reflect a 1:1 relationship. Thus, the slope closest to 1 should identify the best means of comparing diets to abundances within our data.

3. Results

Piscivory was observed at all streams during the 2020 growing season (Table 1). Overall, 7.0% (43 of 611 diets) of Brown Trout diets contained fish. The frequency of piscivory varied among streams and over time, ranging from as low as 0% to as high as 58.3% (Table 1). Notably, Brown Trout were less abundant in some streams, which influenced piscivory percentages. For example, only 12 Brown Trout and their diets were collected in the mainstem Jemez River over the entire season, of which 16.6% of diets contained fish. The frequency of piscivory (%) among streams was strongly related to the Brown Trout size structure (Figure 2a,b). The average body size of lavaged Brown Trout (adj. $R^2 = 0.79$, $p = 0.02$; Figure 2a) and the overall size structure (PSD-Q; adj. $R^2 = 0.92$, $p = 0.006$; Figure 2b) was positively related to the frequency of piscivory. Piscivory was more common in streams with proportionally larger trout (PSD-Q > 20), with values that generally plateaued around 16–18%. Rio De Las Vacas became intermittent midway during the sampling season, resulting in only a few pools, whereas all other streams had sustained flows. Consequently, this stream was treated as an outlier and removed from the linear regression analyses (see differences in plot bubble sizes).

Table 1. Percentage of Brown Trout (*Salmo trutta*) diets containing fish in streams of the Jemez River watershed, New Mexico (USA). Sampling occurred every 14–21 days from 7 July through 1 October of 2020. T = sampling event.

Stream	T1	T2	T3	T4	T5	T6
East Fork Jemez River	–	13.0	3.9	0.0	12.5	0.0
San Antonio	0.0	2.9	3.0	40.0	35.3	0.0
Jemez River	–	16.7	0.0	0.0	50.0	0.0
Rio de las Vacas	2.8	11.1	0.0	0.0	28.6	0.0
Rio Cebolla	1.4	0.0	0.0	0.0	0.0	0.0
Guadalupe	2.8	0.0	8.3	9.1	58.3	36.4

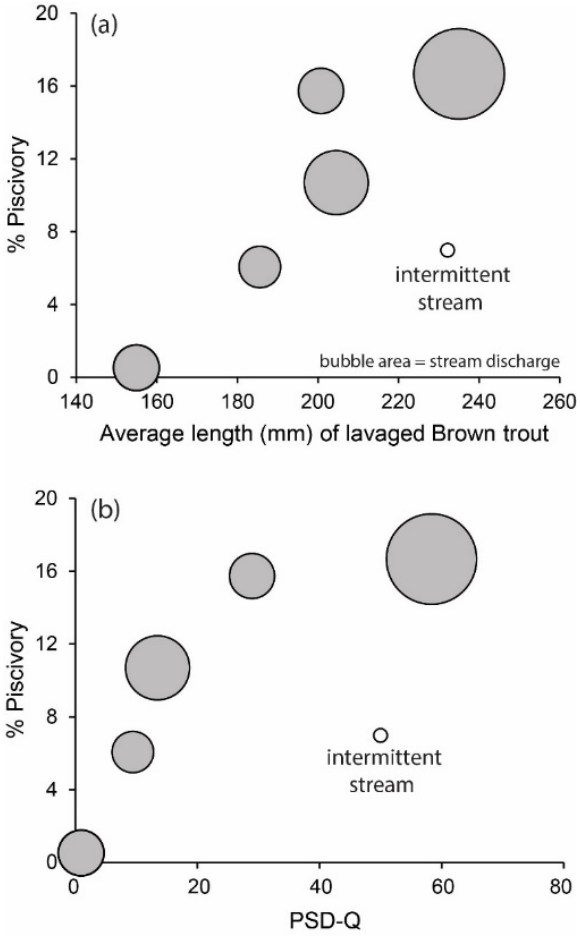

Figure 2. Percentage of piscivory by Brown Trout (*Salmo trutta*) in relation to the (**a**) average body length of lavaged fish and (**b**) population size structure (PSD-Q). Bubble sizes represent average stream discharge among study sites.

The composition of fish prey within the diets of Brown Trout varied among the six streams (Figure 3a). Of all identifiable prey (n = 23), Rio Grande Sucker and Rio Grande Chub were each present in 10 diets. Longnose dace made up 11.6% (5 of 43) of the piscivory samples. Additionally, 37.2% (16 of 43) were too digested to identify to species. Finally, two instances of cannibalism were observed (4.7%) in a single stream. Brown Trout were present in all streams and tended to outnumber native fishes, averaging 44% of individuals within a stream (median of 40%) (Figure 3b).

Diet proportions of native prey eaten by Brown Trout closely reflected the proportions of live prey availability within the stream (Figure 4): correlation including cannibalism (n = 13, F = 56.7, $p < 0.001$); correlation excluding cannibalism (n = 13, F = 49.59, $p < 0.001$). The comparison of slope estimates indicated that proportions excluding Brown Trout (β = 1.009) more closely reflected diet proportions than those that included Brown Trout (β = 0.63); this is likely because cannibalism was only documented in one study stream.

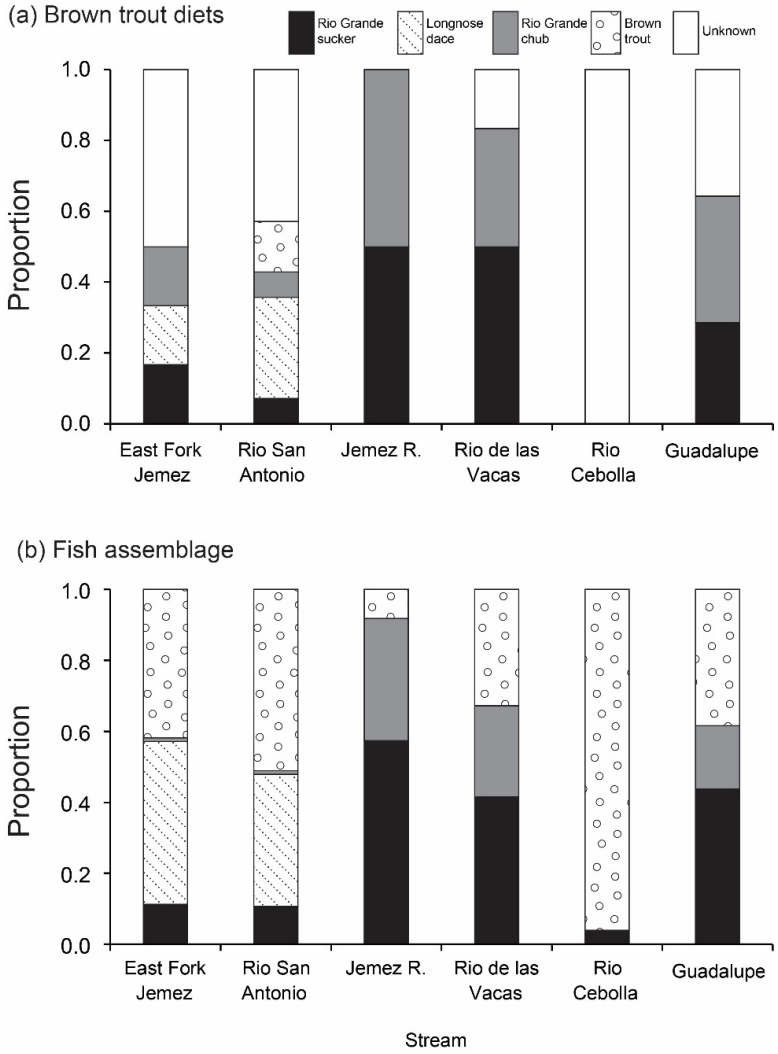

Figure 3. (**a**) Proportion of native fishes within Brown Trout (*Salmo trutta*) diets for all six sites from July to October. Unknown diet items were too digested to identify to species. (**b**) Proportional composition of native fishes sampled in each study stream.

The majority (82%) of consumed fish were between 20 and 60 mm (Figure 5a). The first incidence of piscivory by Brown Trout occurred at a predator size of 101 mm. Although piscivores such as Brown Trout are capable of eating prey of half their body size, we observed that prey were, on average (±SD), 21 ± 7.6% of Brown Trout body lengths. As Brown Trout body sizes increased, we observed a continued increase in the sizes of prey fishes (Figure 5b). This resulted in asymmetrical prey–predator length relationships (Table 2; Figure 5b,c). At the lower bound ($\tau = 0.1$), we detected no relationship ($p = 0.71$; Figure 5c). Moreover, slopes for the 0.3 and 0.5 quantiles ($\tau = 0.3$, $p = 0.03$; $\tau = 0.5$, $p = 0.06$) were greater than that of the lower bound, but lower than those of the 0.7 ($p = 0.02$) and 0.9 ($p < 0.001$) quantiles (Figure 5c). At the upper bound ($\tau = 0.9$), we observed that the sizes of prey increased to the largest extent as the size of Brown Trout increased (Figure 5c). Relative to the lower bound, the rate of increase was 13 times greater (lower $\beta = 0.038$ vs. upper $\beta = 0.504$; Figure 5d).

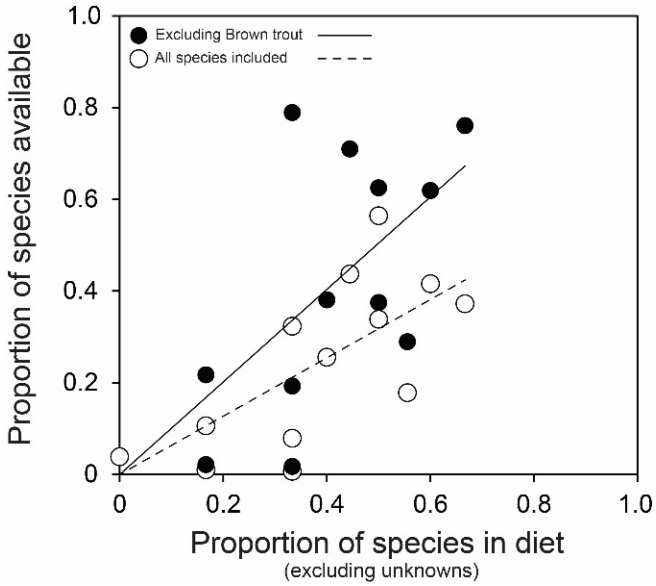

Figure 4. Correlations examining the proportion of a prey species in the diet of Brown Trout (*Salmo trutta*) in relation to proportional availability in the stream. We considered that cannibalism may affect these values; therefore, separate correlations were conducted with and without Brown Trout as a prey item. Closed circles are values in which BRT were excluded, and open circles included all species.

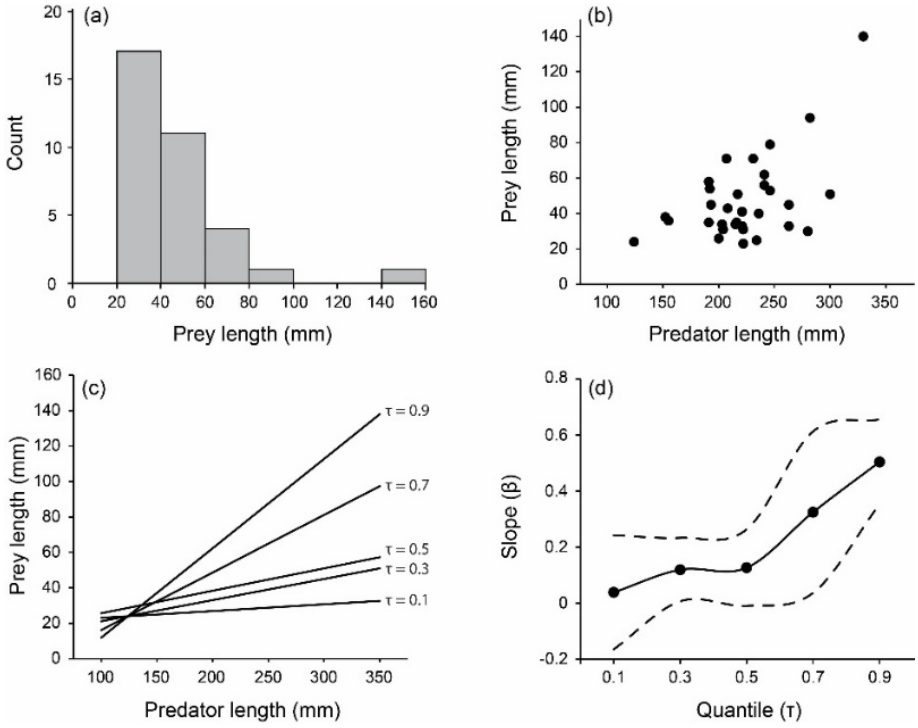

Figure 5. (**a**) Length frequency distribution of fish prey found in the stomachs of Brown Trout (*Salmo trutta*) across all six tributaries of the Jemez River watershed, New Mexico, from July to October 2020. (**b**) Prey lengths in relation to the lengths of Brown Trout that ate them. Each point represents a unique predator–prey interaction. (**c**) Line of best fit describing predator–prey length relationships across 0.1–0.9 quantiles (τ). For this study, we considered 0.1 and 0.9 τ to be the lower and upper bounds, respectively. (**d**) Slope coefficients (β, black dots) and 95% confidence intervals (dashed lines) for each quantile regression model.

Table 2. Quantile regression model estimates from the examination of predator–prey length relationships. Models reflect the relationship between Brown Trout (*Salmon trutta*) length (mm) and the lengths of their fish prey (mm). L95% = lower 95% confidence interval; U95% = upper 95% confidence interval.

Quantile	Term	Estimate	SE	*p*-Value	L95%	U95%
0.1	intercept	19.23	23.6	0.416	−27.14	65.61
	predator length	0.03	0.1	0.711	−0.16	0.24
0.3	intercept	9.17	13.1	0.486	−16.63	34.98
	predator length	0.12	0.05	0.038	0.007	0.23
0.5	intercept	13.02	15.8	0.412	−18.10	44.15
	predator length	0.12	0.07	0.069	−0.01	0.26
0.7	intercept	−16.27	33.5	0.628	−82.06	49.51
	predator length	0.32	0.1	0.027	0.03	0.61
0.9	intercept	−38.53	17.5	0.029	−73.02	−4.05
	predator length	0.50	0.07	<0.001	0.35	0.65

4. Discussion

Results from our study indicate that Rio Grande Sucker and Rio Grande Chub experience constant predation by Brown Trout, affirming concerns that this invasive piscivore poses a threat to the viability of native fish populations, e.g., [28,30]. Overall, seven percent of all Brown Trout diets contained fish, with values ranging from 0 to 58% depending on the number and size of the trout sampled. We documented at least one incidence of piscivory during each sampling period—usually at multiple streams—with values similar to those in other studies ([45], <0.5%; [46], 21%; [25], 10–33%). Although 7% may initially seem low, these values reflect an instantaneous snapshot of predator–prey interactions across a range of sites and dates. Given the relative consistency of these percentages across sample periods, we can safely assume similar values between sampling dates. Thus, these values are particularly concerning due to daily 'turnover.' Using the average, 7 in every 100 Brown Trout will eat a fish within the study reach each day. Naturally, these percentages will vary. Nonetheless, the daily turnover and cumulative effects of predation over time will negatively affect RGS and RGC populations, especially if recruitment cannot match exploitation plus mortality by other factors. Indeed, piscivory and population vital rates must be examined together to determine whether predation pressure exceeds the rate of replacement, and thus, population viability. Additionally, factors including competition and behavioral modifications (i.e., predator avoidance; reduced foraging activity) may also influence the productivity of chub and sucker populations [23,28,30,32]. The examination of these bottom-up factors are needed to complement the top-down perspective presented in this study, as both processes influence the productivity of fish populations.

Predator–prey length relationships produced a 'wedge' pattern [*sensu* 5], indicating that Brown Trout consumed an increasing range of prey body sizes as they grew larger. At the upper bound (i.e., 90th percentile), a 10 mm increase in Brown Trout body length corresponded with a 5 mm increase in prey body length. Surprisingly, Brown Trout as small as 101 mm were capable of piscivory, which is smaller than other examples (130–171 mm total length; [7,46]). Unfortunately, the specimen was too digested to identify or measure, but based on the predator–prey length ratios, we predicted the fish to be 15–20 mm in length. Although large Brown Trout ate larger prey, many continued to eat small prey, indicating that predation was opportunistic. Additionally, diet proportions matched prey availability across streams, further indicating that Brown Trout were eating whatever was most readily available. The findings indicate that Brown Trout in the Jemez River watershed are opportunistic generalists, as observed elsewhere [47].

Although it is evident that Brown Trout consume RGS and RGC, the degree to which predation affects chub and sucker mortality rates, recruitment, or year class strength remains unclear. Most fish prey (82%) was 20–60 mm in length, suggesting that predation

is more likely to affect recruitment. Yet, Brown Trout also ate prey as large as ~140 mm. For RGS and RGC, these sizes represent mature adults [48–50]. Given that Brown Trout were opportunistically feeding on prey, these predators may affect vital rates of RGS and RGC populations. By reducing stocks of mature adults, less reproduction would occur. By affecting recruitment and reproduction, Brown Trout may greatly limit native fish populations. Our study was not designed to examine such stock-recruitment processes. Nevertheless, we hypothesize that Brown Trout could contribute to the decline in Rio Grande Sucker and Rio Grande Chub populations by altering the stock-recruitment dynamics.

Production-based approaches are needed to examine the degree to which Brown Trout exploit basal food resources, reduce native fish via competition, and directly consume prey (i.e., production vs. consumption; [51–53]). As Brown Trout can both compete with and eat their native competitors, the full extent of their impacts cannot be understood nor appreciated until production-based approaches are used to model these co-occurring processes. This study provides a necessary first step in describing the top-down effects of Brown Trout on RGS, RGC, and other native fishes. However, a bottom-up perspective is needed to complement the top-down focus of this study.

Freshwater fishery management in North America has a strong bias towards a small number of 'popular', economically important fishes [11,54]. The stocking or sustained management of exotic game fishes often comes at the direct expense of many native fishes [11,55,56]. Our findings show that Brown Trout are a credible threat to New Mexico's native fishes. The management of Brown Trout as a sportfish may directly contradict the conservation and protection of these native fishes, as RGC and RGS are species of greatest conservation need at the state level in New Mexico, and RGS are endangered in Colorado. Rio Grande Cutthroat trout coexisted and co-evolved with RGS and RGC. The replacement of cutthroats with the more piscivorous Brown Trout has disrupted the trophic dynamics of these stream fish assemblages. Moving forward, prudent conservation and management measures must consider the benefits of the removal and replacement of Brown Trout with Rio Grande cutthroat trout in order to (1) re-establish and sustain the Rio Grande native fish complex (i.e., Rio Grande chub, sucker, and cutthroat), which would (2) re-balance the trophic dynamics of these stream systems [23,24,26], while also (3) maintaining a recreational fishery unique to New Mexico and other states. Whereas Brown Trout can be caught most anywhere, Rio Grande cutthroat trout are a species unique to a small geographic area.

There is a pressing need to 'bend the curve' of fish biodiversity declines through local conservation actions [9,10,12,13]. Reversing freshwater degradation through such efforts requires the translation of good intentions and aspirations into action [12]. Elsewhere, the removal of invasive Brown Trout from streams allowed natives to recolonize and establish a breeding population [57,58]. Whether such actions are warranted in montane streams of New Mexico depends on the values placed on invasive and native fishes. Although there remains much to learn about the factors affecting the productivity of RGS and RGC populations, it is evident from our study that any conservation strategy must directly address invasive Brown Trout.

Author Contributions: Conceptualization, S.F.C.; methodology, S.F.C. and O.G.; formal analysis, S.F.C., O.G. and J.I.; resources, S.F.C.; data curation, S.F.C.; writing—original draft preparation, S.F.C., O.G. and J.I.; writing—review and editing, S.F.C., O.G. and J.I.; visualization, S.F.C., O.G. and J.I. All authors have read and agreed to the published version of the manuscript.

Funding: Funding and support was provided by the Department of Natural Resources Management, along with the Davis College of Agricultural Science and Natural Resources at Texas Tech University. The TTU Center for Transformative Undergraduate Experiences (TrUE) provided funds for materials to help support the undergraduate research.

Institutional Review Board Statement: This study was approved by the Animal Care and Use Committee (IACUC) of Texas Tech University (20016-03).

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available at http://doi.org/10.18738/T8/6QGIFC.

Acknowledgments: J.I. was supported by the TTU Center for Transformative Undergraduate Experiences (TrUE). S.F.C., O.G. and J.I. were supported by the Department of Natural Resources Management and Texas Tech University. We thank T. Ausec, A. Norton, and B. Robertory for their help in the field. This manuscript benefitted greatly from feedback provided by J. Rogosch (TTU, USGS Cooperative Research Unit) and J. Hatt (New Mexico Department of Game and Fish).

Conflicts of Interest: The authors declare no conflict of interest.

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