

Turbidity, velocity and interspecific interactions affect foraging behaviour of rosyside dace (*Clinostomus funduloides*) and yellowfin shiners (*Notropis lutipinnis*)

Hazelton PD, Grossman GD. Turbidity, velocity and interspecific interactions affect foraging behaviour of rosyside dace (*Clinostomus funduloides*) and yellowfin shiners (*Notropis lutipinnis*). Ecology of Freshwater Fish 2009: 18: 427–436. © 2009 John Wiley & Sons A/S

Abstract – Fish diversity is strongly affected by habitat degradation (e.g., increased turbidity) and invasive species. We examined the effects of turbidity, velocity, length, dominance and intra- and interspecific competition on focal point depth, movement rate, dominance and aggression rate in native rosyside dace (*Clinostomus funduloides*) and invasive yellowfin shiners (*Notropis lutipinnis*) in a southern Appalachian stream (NC, USA). We compared results for intra- and interspecific groups of fishes at two densities (two and four fishes), three turbidity levels (10, 20 and 30 nephelometric turbidity units), and two velocities (12, 18 cm·s⁻¹). Dominance was significantly correlated with length in intraspecific groups of both species, and dominant fish held more profitable foraging positions about 75% of the time. Yellowfin shiners were dominant more often than rosyside dace in interspecific trials. Akaike's Information Criterion indicated that models containing turbidity, velocity, species and intraspecific competition, explained the greatest amount of information in focal point depth data. By contrast, movement and aggression rates were best explained by models based on dominance and velocity. Finally, aggression rate was best explained by models containing fish length and turbidity. These results indicate that habitat degradation, intra- and interspecific interactions influence the foraging behaviour and future success of these species in the Little Tennessee River drainage.

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Key words: turbidity; sediment; dominance; competition; density

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Accepted for publication February 12, 2009

Introduction

Biological diversity faces a variety of threats in the 21st century. For aquatic organisms, increases in both suspended (i.e., turbidity) and depositional fine sediments are two of the most important threats in the northern hemisphere (Waters 1995). Increases in fine sediments in streams, frequently are linked to home construction, road-building and row crop agriculture, when insufficient protection is afforded streams and rivers. Fine sediments in streams have a variety of

negative impacts including (1) destruction of interstitial habitat for macroinvertebrates – the prey base for fishes (Rabeni et al. 2005; Wood et al. 2005), (2) elimination of reproductive habitat for crevice and benthic spawning fishes (Burkhead & Jelks 2001; Sutherland 2007), (3) direct physical damage and physiological stress for both macroinvertebrates and fishes (Newcombe & MacDonald 1991; Sutherland & Meyer 2007) and (4) reductions in the visual ability of fishes to locate and capture prey (Barrett et al. 1992; Zamor & Grossman 2007).

Although, turbidity clearly is an important agent of habitat degradation in streams, there are few studies detailing its effects on noncommercially important species, despite their dominance of stream fish assemblages (Matthews 1998). In addition, most studies focus on the effects of turbidity on foraging success of single species (Sweka & Hartman 2001; Zamor & Grossman 2007), rather than elucidating its effects on intra- or interspecific behavioural interactions. Because many stream fishes are found in multispecific groups, these effects may be particularly important (Freeman & Grossman 1992a; b; Freeman & Grossman 1993; Grossman et al. 1998; Matthews 1998). In one of the few extant studies, Berg & Northcote (1985) showed that turbidities above 20 nephelometric turbidity units (NTU) reduced prey capture success and intraspecific aggression fourfold in both aggressive and nonaggressive juvenile coho salmon (*Onchorychus kisutch*). Dominant coho salmon consistently occupied focal positions at the front of the tank and captured significantly more prey than subordinate individuals (Berg & Northcote 1985). In addition, Vinyard & Yuan (1996) demonstrated that reduced recruitment and growth of lacustrine Lahontan cutthroat trout (*Onchorynchus clarki henshawi*) may be a result of the introduction of Lahontan redbreast (*Richardsonius egregius*) which is a superior forager in turbidities found in the study habitat (Summit Lake, NE). Studies of the effects of turbidity on interspecific interactions are especially important, because habitat degradation produced by increased turbidity also may favour more tolerant invasive species (Scott & Helfman 2001; Scott et al. 2002; Sutherland et al. 2002; Walters et al. 2003; Vogt 2004).

Changes in turbidity and velocity also may affect individual behaviour of fishes, and how they search for prey. Sweka & Hartman (2001) found that rainbow trout (*Onchorynchus mykiss*) increased movement with increases in turbidity. This was attributed to a switch to active prey searching behaviour, and resulted in more prey captures, but increased energy expenditure. Focal point depth (distance to substrate) also is an important microhabitat parameter for drift feeding fishes because it is potentially related to the amount of energy expended per prey captured (Grossman & Ratajczak 1998; Grossman et al. 2002). Furthermore, changes in focal point depth may indicate changes in foraging behaviour, from drift feeding to more active benthic searching behaviour (Piccolo et al. 2007).

For the last 25 years we have been studying fish assemblages in the Coweeta Creek drainage of North Carolina, USA. In the mid-1990s we observed the first appearance of yellowfin shiners (*Notropis lutipinnis*) in this system. Although recent genetic studies indicate that yellowfin shiner may be native to the Little

Tennessee River, it has only recently invaded a number of smaller tributaries such as Coweeta Creek (Scott et al. 2008, in press and W. L. McLarney, personal communication). Both rosyside dace (*Clinostomus funduloides*) and yellowfin shiners are small-bodied (maximum length <13 cm), drift-feeding minnows that belong to the mid-water microhabitat guild in Coweeta Creek, NC, USA. (Grossman et al. 1998). The species reproduce during summer and rosyside dace probably reach an age of at least four in Coweeta Creek (G. Grossman, personal communication). By contrast, yellowfin shiner likely only reach an age of 2+ and may die after reproducing (Goforth & Foltz 1998). Rosyside dace are a species of special concern in North Carolina and are distributed from North Georgia to Ohio (Zamor & Grossman 2007). By contrast, yellowfin shiners have a much more restricted distribution and are native to Atlantic slope drainages in both Georgia and North Carolina (Etnier & Starnes 1993), and are more abundant in degraded streams with higher sedimentation rates (Scott et al. 2002; Price & Leigh 2006). Wagner (2004) studied the interspecific interactions between rosyside dace and yellowfin shiner at two velocities (10 and 20 cm·s⁻¹) and found that yellowfin shiner aggressively dominated rosyside dace at both velocities. Dominance in these species resulted in having a move forward position in the tank, and hence, increased access to food. Nonetheless, rosyside dace caught more prey at higher velocities than yellowfin shiners and hence, may be able to coexist because of this ability (Wagner 2004).

Given the characteristics of rosyside dace and yellowfin shiner and increasing environmental change in the study region (Scott et al. 2002; Sutherland et al. 2002), we examined how the combined effects of turbidity and an invader might influence future population status of rosyside dace. Consequently, we conducted a multifactorial experiment in which we examined the effects of physical (turbidity and velocity) and biological factors (length, intra- and interspecific competition) on focal point depth, movement rate, dominance and aggression in native rosyside dace and yellowfin shiner.

Methods

Experimental procedures

Experiments were conducted using the 3.0 m (*l*) × 0.75 m (*w*) × 1.0 m (*h*) Plexiglas artificial flume of Zamor & Grossman (2007), powered by two 36 kg thrust electric trolling motors. However, we reduced the test chamber to 1.6 m × 0.45 m × 0.5 m to facilitate identification of individual fish. This system produced semi-laminar flow, and during experiments

velocities were constantly monitored and varied $<3 \text{ cm}\cdot\text{s}^{-1}$ throughout the water column. Test velocities were average tank velocities measured at 60% depth. The substratum consisted of a 4-cm layer of pebbles (maximum diameter 50 mm), marked with a 1 cm grid for location of test specimens. We held pH and water temperatures at ~ 7.0 and $10\text{--}12 \text{ }^\circ\text{C}$ respectively, which corresponded to spring and fall temperatures in Coweta Creek (Grossman & Ratajczak 1998). We tested fish at two velocities (12 and $18 \text{ cm}\cdot\text{s}^{-1}$) that bracketed the optimal focal point velocities for these species in Coweta Creek (yellowfin shiner = $13 \text{ cm}\cdot\text{s}^{-1}$, rosieside dace = $16 \text{ cm}\cdot\text{s}^{-1}$; Grossman et al. 2002). We tested fish at three turbidities (10, 20 and 30 NTU) using a natural, commercially available local substratum – red clay (see Zamor & Grossman 2007). Turbidity treatments represent moderately impacted to heavily impacted streams in this region (Sutherland et al. 2002; Price & Leigh 2006). To facilitate observations at 30 NTU, the test chamber was reduced to $1.6 \text{ m} \times 0.45 \text{ m} \times 0.5 \text{ m}$. We tested five species \times density combinations: two and four rosieside dace (intraspecific rosieside dace trials), two and four yellowfin shiners (intraspecific yellowfin shiner trials), and two of each species (interspecific competition trial), for a total of 30 treatment combinations. Each treatment was replicated three times, with the exception of four replicates of: four rosieside dace at 10 NTU and $12 \text{ cm}\cdot\text{s}^{-1}$; two rosieside dace at 20 NTU and $12 \text{ cm}\cdot\text{s}^{-1}$; two rosieside dace at 30 NTU and $12 \text{ cm}\cdot\text{s}^{-1}$; four yellowfin shiners at 20 NTU and $18 \text{ cm}\cdot\text{s}^{-1}$; two yellowfin shiners at 30 NTU and $18 \text{ cm}\cdot\text{s}^{-1}$. We conducted a total of 95 trials.

Test specimens were collected from Coweta Creek and other headwater streams within the Little Tennessee drainage between November and April of 2005, 2006 and 2007.

We collected fish using a backpack electrofisher (Smith-Root, model LR-24) and nets (Zamor & Grossman 2007). Dip nets also were used to hand capture fish from large pools ($>1.5 \text{ m}$ deep). We discarded all specimens that displayed evidence of physiological stress or collecting injuries. Following collection, we held rosieside dace and yellowfin shiner for 2 days in separate 1150L recirculating systems maintained at $10\text{--}12 \text{ }^\circ\text{C}$, pH of $7.0\text{--}7.2$, and 12 h:12 h, light:dark photoperiod. Fishes were fed meal worms (*Tenebrio molitor*) *ad libitum* once daily. The mean length and mass of specimens were: rosieside dace $N = 152$; $\text{SL} \pm \text{SD} = 65 \text{ mm} \pm 9$; $\text{mass} \pm \text{SD} = 3.7 \text{ g} \pm 1.0$ and yellowfin shiners $N = 150$; $\text{SL} \pm \text{SD} = 64 \text{ mm} \pm 7$; $\text{mass} \pm \text{SD} = 3.7 \text{ g} \pm 1.2$, and we restricted length ranges of fish used in trials to minimise length effects (see below).

After acclimation we anaesthetised (MS-222; Ross & Ross 1999) and tagged fish with unique coloured

plastic discs (3.0 mm diameter, black, white, yellow and clear) located just posterior to the dorsal fin (Wagner 2004). These tags do not affect general or feeding behaviour of the experimental subjects (Wagner 2004), and we found no significant difference in the aggression received by any colour (Hazelton and Grossman, unpublished data). Following tagging and a short recovery period, we returned fish to holding tanks for a minimum of 2 days to ensure adequate posttagging recovery. The holding system was treated with kanamycin sulphate at a dose of $3 \text{ mg}\cdot\text{l}^{-1}$ to reduce infection from tagging (Wagner 2004). Fish were placed in a second holding tank, prior to use in experiments, and fasted for 2 days to ensure that all specimens experienced similar hunger levels. A 2-day period ensured that specimens had evacuated their stomach and intestinal contents (Hazelton, unpublished data). Each specimen was used in only one trial.

Aggression, dominance, position and fish length

In preliminary trials we distinguished four aggressive behaviours exhibited by both species: (1) Flash – behavioural display involving parallel swimming, fin flaring or a positioning of the body by tilting the dorsum towards the recipient (Berg & Northcote 1985), (2) Chase – aggressor pursues a retreating recipient, (3) Charge – aggressor accelerates directly towards a recipient but does not chase or make contact and (4) Nip – aggressor bites recipient, usually on the anal or caudal fin. We used videography to quantify behavioural interactions and recorded the time of each aggressive act to the nearest second.

Although length differences among fish in trials were less than 10 mm, with one exception (15 mm difference), we still examined the relationship between length and aggression. We ranked individuals by length within a trial from smallest (one) to largest (four) in four fish trials and small (one) and large (two) for two fish trials. For each density, we tested whether the per cent of aggressive acts received within the trial was significantly affected by length rank using one-way ANOVA with Tukey's (Honestly Significant Differences HSD) tests (Dowdy et al. 2004). We performed a similar analysis on the per cent of aggressive acts initiated by each length rank. Finally, we tested whether length was related to dominance, because the dominant fish (see below) was not always the most aggressive. We used chi-squared tests for independence (Dowdy et al. 2004) on dominance ranks and length ranks to determine if these two variables were independent within a trial. We analysed two and four fish trials separately.

We constructed linear dominance hierarchies for each trial based on the number of aggressive acts

initiated or received (Grossman 1980; Rincon & Grossman 2001). In brief, a dominant fish initiated more aggressive acts than it received (Grossman 1980; Rincon & Grossman 2001). Assuming that hierarchies are linear, a dominant fish is dominant over all other individuals subordinate to any challenger that it has defeated (De Vries 1998). We used this format to identify three different dominance levels: one – subordinate, two – subdominant and three – dominant. In two fish trials typically there was only a subordinate and a dominant. For four fish trials, there was typically one dominant (three), one subdominant (two) and two subordinates (one). However, in the case of a tie in four fish trials, we assigned both fish to the same rank. We tested whether one species was dominant over another by determining if species and dominance rank were independent in interspecific trials using a chi-squared test.

In four fish trials, we tested whether dominant fish occupied the first (most upstream) position in a group more frequently than expected by chance and whether subordinate fish occupied the positions three and four (most downstream) more frequently than expected by chance. We used chi-squared tests for independence (Dowdy et al. 2004) to test for the independence of position and dominance for both species. We tested data from two and four fish intraspecific trials separately.

Per capita aggression rates, focal point depth and movement rates

To examine the relationships between turbidity, focal point depth, intraspecific aggression and interspecific interactions; we quantified per capita aggression rates

at the trial level by calculating the total number of aggressive acts in a trial divided by number of fish in the trial, and then standardising the result per unit time (acts/fish/min, Wagner 2004). We quantified focal point depth as the distance from an individual fish to the substratum (cm) at 1-min intervals over each trial. We then calculated the mean distance from the substratum for each fish, and used this as the response variable.

We measured movement as the distance between points travelled by each individual along *x*, *y* and *z* coordinates of the experimental flume, at 2-min intervals. Estimating fish location along the width of the tank (*z* coordinate) was difficult at higher turbidities. To compensate, we divided the tank into three lanes of equal distance across the width of the tank and recorded the lane occupied by each fish. We then assigned a *z* coordinate based on the median value of that lane. Movement rates were calculated by dividing the mean movement by the number of minutes in the trial. These estimates actually underestimated true movement, because they assumed that all movement was linear.

We examined the effects of turbidity, velocity and competition on per capita aggression rate, focal point depth and movement rates of fishes using linear models and Akaike’s Information Criterion. For analyses of focal point depth and movement, we constructed a set of 10 *a priori* conceptual models including: main effects of environmental, behavioural and competition parameters; and interaction effects (Table 1). Environmental variables included: Turbidity – measured as the mean experimental value in the trial in NTU, and Velocity – measured as the treatment level (12, 18 cm·s⁻¹). Competition variables included:

Table 1. Candidate models used to evaluate the relative importance of environmental and behavioural variables affecting foraging behaviour of rosyside dace and yellowfin shiners.

No.	Model name	Hypothesis	Models
1	Global	All main effects and interactions will change response parameter	
2	Environmental	Response is dependent on changes in environmental stimuli	$y = \text{velocity} + \text{turbidity}$
3	Competition	Response is dependent on species and type of competition	$y = \text{species} + \text{interspecific} + \text{intraspecific}$
4	Behavioral	Response is dependent on species, fish length and dominance rank	$y = \text{species} + \text{dominance} + \text{length}$
5	Environmental and Competition	Response is dependent on both environmental and competition factors	$y = \text{velocity} + \text{turbidity} + \text{species} + \text{interspecific} + \text{intraspecific}$
6	Environmental and Behavioral	Response is dependent on species environmental and behavioural factors	$y = \text{velocity} + \text{turbidity} + \text{species} + \text{dominance} + \text{length}$
7	Behavioral and Competition	Response is dependent on species, dominance rank, fish length and type of competition	$y = \text{species} + \text{dominance} + \text{length} + \text{interspecific} + \text{intraspecific}$
8	Species × Environmental	Response is dependent on species and changes with level of environmental factors	$y = \text{species} + \text{velocity} + \text{turbidity} + \text{species} \times \text{velocity} + \text{species} \times \text{turbidity}$
9†	Dominance × Environmental	Response is dependent on dominance rank and changes with level of environmental factors	$y = \text{dominance} + \text{velocity} + \text{turbidity} + \text{dominance} \times \text{velocity} + \text{dominance} \times \text{turbidity}$
10	Species × Competition	Response is dependent on species and changes with type of competition	$y = \text{species} + \text{interspecific} + \text{intraspecific} + \text{species} \times \text{interspecific} + \text{species} \times \text{intraspecific}$

†Model 9 was not used in analysis of per capita aggression because dominance was measured at the focal fish level, and per capita aggression was measured for each trial (group of fish).

Species – binary coded 0 = *C. funduloides*, 1 = *N. lutipinnis*; Intraspecific Competition – binary coded 0 = 2 fishes intraspecific trial, 1 = 4 fishes intraspecific trial; Interspecific Competition – binary coded 0 = intraspecific trials, 1 = interspecific trials; Dominance – binary coded 0 = nondominant fish, 1 = dominant fish; Length – standard length of the focal fish. Because per capita aggression rates were calculated for groups of fish rather than individuals, we omitted Dominance and the model for Species \times Interspecific Competition because these parameters were measured at the focal fish level. We also modified the Length parameter as the mean standard length of all fish in the trial (Mean Length). This resulted in fitting only nine of the candidate models used for the other analyses (Table 1).

We assessed the relative abilities of the competing models to explain information in the data using Akaike's Information Criterion adjusted for small sample sizes (AICc; Hurvich & Tsai 1989). Models with low, Δ AIC values and high Akaike weights (w_i) lose little of the information present in the data, and hence best represent the processes affecting the response variable (Burnham & Anderson 2002; Grossman et al. 2006). To control for multicollinearity, we conducted a Pearson correlation analysis on all pairs of variables and deleted one of each pair that had r^2 values >0.25 . Sex of fish and seasonality of trial did not covary with either response variable, and we therefore excluded them from all analyses. We examined data normality through normal probability plots and found few substantial deviations from normality. Using the criterion of Burnham & Anderson (2002), we interpreted models that had w_i values $>10\%$ of the model with the highest w_i value. Interpretable models were used to calculate model - averaged parameter

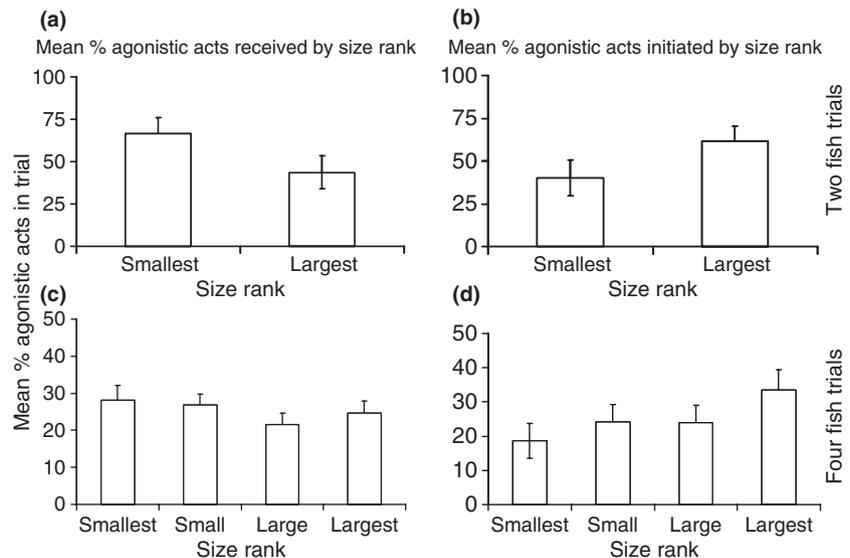
estimates and unconditional standard errors weighted by Akaike weights (Burnham & Anderson 2002). We calculated 95% confidence intervals around these estimates and interpreted parameters with confidence intervals that did not overlap zero (Grossman et al. 2006).

Results

Aggression, dominance, position and fish length

Regardless of species, larger fish initiated a significantly larger proportion of aggressive acts than smaller individuals in two fish trials ($N = 38$ trials, d.f. = 1, $F = 9.05$, $P = 0.0037$), and the same result obtained for the largest and smallest fish in four fish trials (initiated: $N = 71$, d.f. = 3, $F = 2.78$, $P = 0.042$, Fig. 1). In both two and four fish trials we found that larger fish tended to be dominant more often than smaller fish (two fish trials – $N = 38$, d.f. = 1, $\chi^2 = 3.225$, $P = 0.0725$; four fish trials – $N = 56$, d.f. = 6, $\chi^2 = 14.992$, $P = 0.0203$, Fig. 1). The species also exhibited differences in dominance in interspecific trials ($N = 18$, d.f. = 2, $\chi^2 = 7.042$, $P < 0.0296$). In these trials yellowfin shiner were the dominant or subdominant fish 64% of the time as opposed to $\sim 33\%$ for rosyside dace (Fig. 2). The dominant fish occupied the most upstream (i.e., first) position with a significantly greater frequency in all trials for rosyside dace (Fig. 3: two fish trials – $N = 19$, d.f. = 1, $\chi^2 = 6.465$, $P = 0.011$; four fish trials – $N = 19$, d.f. = 6, $\chi^2 = 40.282$, $P < 0.001$) but only in four fish trials for yellowfin shiner (two fish trials – $N = 19$, d.f. = 1, $\chi^2 = 0.444$, $P = 0.505$; four fish trials – $N = 19$, d.f. = 6, $\chi^2 = 44.211$, $P < 0.001$).

Fig. 1. Mean per cent of agonistic acts received and initiated by length in two (top) and four fish trials. Length ranks from 1 to 4, where 1 is smallest fish. Significant differences in the mean percent of acts received by ranks 1 and 2 in two fish trials (a), and a significant difference between ranks 1 and 3 in four fish trials (b). The smallest length rank (1) of fish initiated significantly fewer aggressive encounters than the largest rank in two fish (c) and four fish (d) trials.



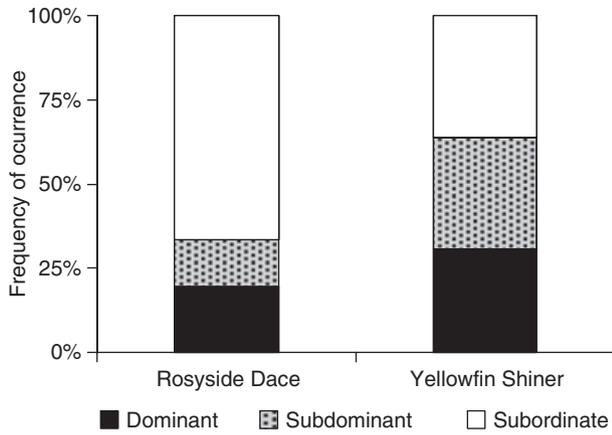


Fig. 2. Frequency of dominance ranks of rosyside dace and yellowfin shiner in interspecific trials. Shiner held Dominant and Subdominant positions significantly more often than dace ($N = 18$, d.f. = 2, $\chi^2 = 7.042$, $P < 0.0296$).

Per capita aggression rates, focal point depth, and movement rate

Across all treatments the mean per capita aggression rate was 1.15 acts/fish/min (SE = 0.094) and there were four interpretable models given the data (Table 2). All four models contained either mean length or turbidity or both factors. Changes in per capita aggression rates were best explained by the Behavioral model (species, mean length and dominance, $w_i = 0.41$), although only mean length and turbidity had confidence intervals that did not overlap zero. The Environmental and Behavioral model had similar explanatory power ($w_i = 0.34$) as the best fitting model. The two remaining interpretable models

(Environmental, and Behavioral and Competition) were approximately 3.4 and 5.9 times less likely to be true given the data, than the Behavioral model. (Tables 2 and 3). Parameter estimates indicated that trials containing fish with a mean length 15 mm greater than other trials would have a 39% increase in per capita aggression (1.60 acts/fish/min) compared to the mean rate. Turbidity had a negative impact on per capita aggression and reduced aggression rates by 17% with an increase of 10 NTU. The remaining model parameters had confidence intervals that overlapped zero and were uninformative.

The mean distance to the substratum for all experiments was 11.8 cm (SE = 0.30 cm) and our model confidence set included the Species \times Environmental, Global and Environmental and Behavioral models. Given the data, the Species \times Environmental ($w_i = 0.61$) model was slightly <3 times more likely to be true than the Global model ($w_i = 0.23$) and 4.7 times more likely to be true than the Environmental and Behavioral model ($w_i = 0.13$). The intercept (7.67 cm, Table 3) represents the mean distance from substrate of a nondominant rosyside dace at the lowest treatment levels in a two-fish, single-species trial. Velocity had the largest effect size with a $6 \text{ cm}\cdot\text{s}^{-1}$ increase in velocity producing a 1.32 cm increase in focal point depth. The confidence intervals for species and turbidity parameter estimates overlapped zero and hence, were not interpreted, however the Species \times Turbidity interaction indicated that yellowfin shiner were approximately 2 cm closer to the substrate than rosyside dace with each 10 NTU increase in turbidity. A 10 mm increase in standard length resulted in larger fish holding positions one cm closer to the substrate. All

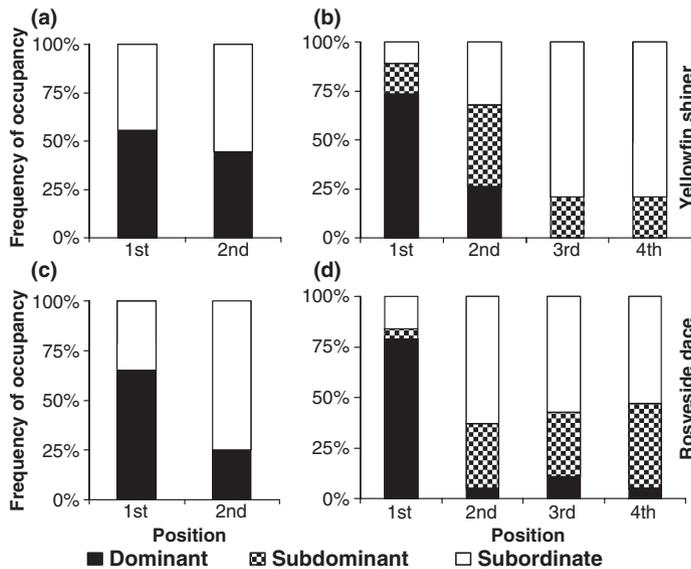


Fig. 3. Frequency of occupancy of positions 1–4 by dominance ranks of rosyside dace and yellowfin shiner in intraspecific two and four fish trials. Dominant individuals (Black), consistently held forward positions in rosyside dace two fish (c) and four fish (d) trials, and yellowfin shiner four fish trials (b) significant at $\alpha = 0.05$ level. Dominant yellowfin shiners held forward positions in two fish trials (a), significant at $\alpha = 0.10$ level.

Dace foraging competition and turbidity

Table 2. Model selection results for competition and environmental parameters on per capita aggression rates, focal point depth and movement rates.

Response	Candidate model	Model number	AICc	Δ AICc	w_i
Per capita aggression rates (acts/fish/min)	Behavioral	4	249.09	0.00	0.41
	Environmental and Behavioral	6	249.48	0.39	0.34
	Environmental	2	251.52	2.43	0.12
Focal point depth (cm)	Behavioral and Competition	7	252.71	3.61	0.07
	Species \times Environmental	8	1770.49	0.00	0.61
	Global	1	1772.49	2.00	0.23
Movement rates (cm \cdot min $^{-1}$)	Environmental and Behavioral	6	1773.61	3.12	0.13
	Dominance \times Environmental	9	1850.57	0.00	0.49
	Environmental and Behavioral	6	1851.82	1.25	0.26
	Global	1	1852.36	1.79	0.20

AICc, Δ AICc, w_i are presented for models included in the confidence set (i.e., $w_i > 10\%$ of best fitting model).

Table 3. Model averaged parameter estimates, 95% confidence intervals and Akaike weights for explanatory variables affecting per capita aggression, fish focal point depth and movement rates.

Response	Parameter	Estimate	95% Confidence limit		w_i
			Lower	Upper	
Per capita aggression rates	Intercept	-0.20	-2.09	1.70	1.00
	Species	0.26	-0.11	0.62	0.88
	Mean length	0.03	0.01	0.05†	0.81
	Turbidity	-0.02	-0.04	0.00†‡	0.50
	Velocity	-0.01	-0.04	0.02	0.50
	Interspecific competition	-0.03	-0.48	0.43	0.12
	Intraspecific competition	-0.25	-0.62	0.12	0.12
	Species \times turbidity	-0.03	-0.07	0.01	0.02
	Species \times velocity	-0.03	-0.09	0.03	0.02
	Species \times intraspecific	0.30	-0.38	0.98	0.01
Focal point depth	Intercept	7.67	2.04	13.30	1.00
	Turbidity	0.07	-0.02	0.16	1.00
	Species	0.29	-3.68	4.26	1.00
	Velocity	0.22	0.09	0.35†	1.00
	Species \times turbidity	0.20	0.09	0.31†	0.84
	Species \times velocity	-0.02	-0.20	0.16	0.84
	Dominance	-1.00	-4.61	2.61	0.35
	Length	-0.09	-0.15	-0.03†	0.35
	Interspecific Competition	0.26	-1.44	1.97	0.26
	Intraspecific Competition	-1.29	-2.75	0.17	0.26
	Dominance \times turbidity	-0.03	-0.14	0.09	0.23
	Dominance \times velocity	0.20	0.01	0.38†	0.23
	Species \times interspecific	-0.13	-2.58	2.32	0.23
	Species \times intraspecific	0.17	-1.92	2.26	0.23
Movement rate	Intercept	9.59	4.58	14.61	1.00
	Turbidity	0.05	-0.05	0.14	1.00
	Velocity	0.28	0.15	0.41†	1.00
	Dominance	1.87	-3.42	7.16	0.96
	Dominance \times turbidity	-0.10	-0.24	0.03	0.69
	Dominance \times velocity	-0.20	-0.42	0.01	0.69
	Species	0.48	-2.04	3.00	0.48
	Length	-0.05	-0.12	0.01	0.47
	Species \times turbidity	-0.14	-0.26	-0.01†	0.21
	Species \times velocity	-0.01	-0.21	0.19	0.21
	Interspecific competition	-0.46	-2.46	1.55	0.21
	Intraspecific competition	-1.04	-2.83	0.76	0.21
	Species \times interspecific	1.96	-0.88	4.79	0.20
	Species \times intraspecific	4.09	1.68	6.49†	0.20

Focal point depth (cm) and movement rates (cm/min) were measured at the focal fish level. Per capita aggression rates (acts/fish/min) were measured at the trial level (group of fish).

†Denotes a confidence interval that does not overlap zero.

‡Actual value is -0.003.

other parameters in the confidence set models had confidence intervals that overlapped zero and were uninterpretable.

Across all treatments the mean movement rate was 12.48 cm \cdot min $^{-1}$ (SE = 0.32 cm \cdot min $^{-1}$). Movement rate was best explained by the Dominance \times Environ-

mental model ($w_i = 0.49$), followed by the Environmental and Behavioral ($w_i = 0.26$) and Global models ($w_i = 0.20$, Table 2). The best fitting model was 1.9 and about 2.5 times as likely to be true given the data as the Environmental and Behavioral and Global models respectively. Parameter estimates indicated that only velocity and the species \times turbidity and species \times intraspecific competition interaction terms had confidence intervals that did not overlap zero (Table 3). Velocity had the highest effect size on movement and an increase in velocity from 12 to 18 $\text{cm}\cdot\text{s}^{-1}$ increased movement rates by 1.68 $\text{cm}\cdot\text{min}^{-1}$ (Table 3). Species \times turbidity and species \times intraspecific competition, both were interpretable, however the confidence intervals of the individual main effects overlapped zero and were viewed as not interpretable.

Discussion

Our data show that physical and behavioural factors best explain variation in dominance, access to prey, aggression, focal point depth and movement rate of native rosyside dace and invasive yellowfin shiner. Specifically, the main effects of turbidity, velocity, length and interactions involving species and intraspecific competition all were capable of explaining information contained in the data set. In some cases the species displayed similar patterns with larger fish: (1) being dominant, (2) moving less and (3) occupying more profitable foraging positions. Nonetheless, despite being matched for length, yellowfin shiners dominated rosyside dace in behavioural interactions. Dominant fish typically occupied better foraging positions; therefore the invasive species has the potential to negatively affect the native via interspecific competition.

Changing physical conditions may affect the foraging behaviour of stream fishes (Matthews 1998). Yellowfin shiners are less efficient drift feeders than rosyside dace at 20 $\text{cm}\cdot\text{s}^{-1}$ and presumably also at higher velocities (Wagner 2004; Rincon et al. 2007). In a previous study, we did not observe significant differences in capture success between these species at velocities up to 18 $\text{cm}\cdot\text{s}^{-1}$ (Hazelton & Grossman 2009). Nonetheless, our results indicate that fish held positions farther from the substratum at higher velocities, and higher velocities were linked with increases in movement rates. These shifts could subject rosyside dace and yellowfin shiners to increased focal point velocities and increased energy expenditures while foraging (Hill & Grossman 1993; Grossman et al. 2002). In fact, we observed yellowfin shiners holding closer to the substratum and acquiring more old prey items from the bottom (P. D. Hazelton, personal communication). Sweka & Hartman (2001) found that

high turbidities produced similar shifts in brook trout foraging behaviour, as well as weight loss.

Behavioural factors such as dominance also affected foraging behaviour and interacted with physical factors. Dominant fish had higher movement rates and higher capture success than subordinates regardless of species (Hazelton & Grossman 2009). Whether this results in an increase in net energy gain is unknown. When both turbidity and velocity increased, both species captured fewer prey by via forward movement, and captured greater numbers of prey via lateral or downstream captures. This likely resulted in an increase in energy expended per prey captured, because fish exposed their lateral profile to the current rather than their cross-section (Hazelton & Grossman 2009). Consequently, increased turbidity probably will reduce individual fitness in these species via increased foraging costs. We are assuming that mealworms adequately represented natural prey, but both species are opportunistic feeders (Etnier & Starnes 1993) and it is likely that similar patterns are manifested in with natural prey (Freeman & Grossman 1992b).

Previous research on the effects of turbidity and velocity on foraging behaviour of stream fishes has shown that both moderate and high turbidities (Barrett et al. 1992; Zamor & Grossman 2007) and velocities (Piccolo et al. 2008) may negatively affect foraging success of stream fishes. Zamor & Grossman (2007) found that reactive distance of rosyside dace was significantly reduced from ~ 45 to 30 cm with an increase in turbidity from 0 to 10 NTU. Wagner (2004) found that dominant rosyside dace and yellowfin shiners had higher prey capture rates in intraspecific trials, however, yellowfin shiner were more aggressive and dominated rosyside dace at lower velocities (Wagner 2004). Nonetheless, at higher velocities rosyside dace captured more prey than yellowfin shiners (Wagner 2004). With increases in turbidity found in moderately impacted streams in the region (Sutherland et al. 2002; Price & Leigh 2006), the competitive balance between these species may shift so that yellowfin shiners will be dominant regardless of velocity. Our results also may explain why rosyside dace are often absent from disturbed watersheds in the region (Sutherland et al. 2002; Vogt 2004; Scott 2006). These streams typically have increased turbidities as well as lower velocities (Sutherland et al. 2002; Vogt 2004; Scott 2006) and generally maintain substantial populations of more tolerant species including yellowfin shiner (Vogt 2004; Scott 2006). Our results suggest that the combination of reduced velocities and higher turbidities may limit rosyside dace, and give yellowfin shiner a competitive advantage.

Fine sediments also may harm stream fishes via diverse mechanisms including: (1) reducing prey

availability, (2) direct physical harm (Berkman & Rabeni 1987), (3) increased predation risk (Miner & Stein 1996) and (4) reduced breeding success (Burkhead & Jelks 2001; Sutherland 2007). However, the sediment loads necessary to produce these effects are likely to be larger than those associated with reduced foraging ability (Berkman & Rabeni 1987). As a consequence, studies of the effects of turbidity on the foraging behaviour of stream fishes may yield insights into the potential population-level effects of increased sedimentation in a watershed, long before prey populations crash or reproductive habitat is filled.

Our results may yield insights into the future distributions of yellowfin shiners and rosyside dace in this region. It is unlikely that increased predation pressure would differentially affect these species because they have similar morphologies and ecologies (Grossman et al. 2002; Rincon et al. 2007). Similarly, both species are nest associates of nest-building fishes such as *Nocomis*, *Campostoma* and *Semotilus*, so they are unlikely to be differentially affected by sedimentation of reproductive habitat (Etnier & Starnes 1993). In addition, one nest builder creek chub (*Semotilus atromaculatus*) increases in abundance in degraded streams in the region (Scott 2001; Vogt 2004). Consequently, we cannot predict how this interaction will play out across the region, even though yellowfin shiners appear to dominate rosyside dace under some conditions. Conversely, as shown by Wagner (2004) rosyside dace may always have a refuge in higher velocity microhabitats in regional streams, as long as turbidities are relatively low.

We have demonstrated that multiple physical, behavioural and competitive factors can explain variation in foraging behaviour of native rosyside dace and invasive yellowfin shiners. Although, the turbidities used in experiments occur only during storm events in lightly disturbed streams in the Little Tennessee drainage region, they are common in disturbed streams (Bolstad & Swank 1997; Sutherland et al. 2002; Price & Leigh 2006). We suggest that the negative impacts of turbidity on foraging behaviour of native south-eastern stream fishes may be partially responsible for their declines in disturbed habitats, especially given that more tolerant species are abundant in these habitats (Scott et al. 2002; Sutherland et al. 2002; Walters et al. 2003). It is clear that controlling stream sedimentation and other aspects of habitat degradation will be necessary to maintain habitat for rosyside dace and other sensitive native species in the southern Appalachian region.

Acknowledgements

Financial support of this project was provided by the USDA Forest Service McIntire-Stennis program (grants GEO-00114-

MS and GEO-00144-MS) and the National Science Foundation (DEB-2018001). Additional support was provided by the Daniel B. Warnell School of Forestry and Natural Resources. The project would not have been possible without the assistance of Robert Ratajczak, Duncan Elkins, Megan Hill, Rich Zamor and numerous student workers in the Grossman lab. Earlier drafts of this manuscript were improved by the comments of Jim Peterson and Rhett Jackson.

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