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The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*)

PETER D. HAZELTON AND GARY D. GROSSMAN
Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. Habitat degradation and biological invasions are important threats to fish diversity worldwide. We experimentally examined the effects of turbidity, velocity and intra- and interspecific competition on prey capture location, reactive distance and prey capture success of native rosyside dace (*Clinostomus funduloides*) and invasive yellowfin shiners (*Notropis lutipinnis*) in Coweeta Creek, North Carolina, U.S.A.

2. Increased turbidity and velocity produced significant decreases in the number of prey captured forward of the fish's location. It is possible that this represents an increase in the amount of energy expended per prey captured.

3. We used Akaike's Information Criterion (AIC) to evaluate competing explanatory models for reactive distance (10 generalised linear models, GLM) and prey capture success (9 generalised linear mixed models, GLMM).

4. Reactive distance decreased by 12% with an increase from 2 to 4 conspecifics, whereas a 10 NTU increase in turbidity reduced reactive distance by 9%. Capture success was affected by velocity, dominance and competition, and varied among species. A 6 cm s^{-1} increase in velocity produced a 28% decline in capture probability; however, dominant fish were 3.2 times more likely to capture a prey item than non-dominant fish. Yellowfin shiners only were 0.62 times as likely to capture a prey item as rosyside dace. Both intra- and interspecific competition reduced capture probability, and fish in high density intraspecific or interspecific trials were 0.46 times and 0.44 times as likely to capture prey, respectively, as fish in two fish intraspecific trials.

5. These results suggest behavioural variables are as important as physical factors in determining reactive distance and capture probability by these minnows.

Keywords: Cyprinidae, habitat degradation, minnow, sediment, water quality

Introduction

Habitat degradation and the presence of invasive species are recognised as the greatest threats to aquatic diversity worldwide (Bruton, 1995; Vitousek *et al.*, 1997; Rahel, 2002). These two factors are correlated, because invasive species frequently are more abundant in degraded habitats (Moyle & Light, 1996; Rahel, 2002; Kennard *et al.*, 2005) and may replace sensitive native species. It is likely that the most frequent cause of habitat degradation in streams is increased fine sediment loads, and these increases have been linked to changes in native aquatic communities in both the northern (Berkman & Rabeni, 1987) and southern hemispheres (Quinn *et al.*, 1992; Richardson & Jowett (2002); Rowe *et al.*, 2003; Townsend *et al.*, 2004). Although ecosystems and species differ with geography, the anthropogenic causes of increased sedimentation in stream sediment are similar worldwide (Harding *et al.*, 1999; Li *et al.*, 2008;

Correspondence: Gary D. Grossman, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, U.S.A. E-mail: grossman@uga.edu

Orioli *et al.*, 2008), including inappropriate agricultural, mining and forestry practices and urbanisation (Brasington & Richards, 2000; Mol & Ouboter, 2004; Bonnet, Ferreira & Lobo, 2008). Fine sediments may negatively affect stream biota through a variety of mechanisms, including (i) interference with migration behaviour (Richardson, Rowe & Smith, 2001), (ii) reduction of reproductive success (Burkhead & Jelks, 2001), (iii) increased vulnerability to predation (Miner & Stein, 1996), (iv) direct physiological damage (Berkman & Rabeni, 1987; Sutherland & Meyer, 2007), (v) reduced foraging success (Berkman & Rabeni, 1987; Rowe & Dean, 1998; Suttle *et al.*, 2004) and (vi) reduced prey availability (Stuart-Smith, Richardson & White, 2004; Rabeni, Doisy & Zweig, 2005; White & Harvey, 2007).

Turbidity is a measure of light scattering caused by suspended solids (Davies-Colley & Smith, 2001). Turbidity is a useful measure of the effects of sediment on stream fish because even small quantities of suspended sediment may negatively affect foraging or reproductive success of fish. By contrast, larger sediment inputs are needed to modify stream geomorphology (Waters, 1995; Davies-Colley & Smith, 2001). Turbidity research primarily has focused on foraging behaviour and prey capture success, because turbidity reduces a fish's ability to visually detect prey (Utne-Palm, 2002). Reactive distance is a common measure of foraging success, and is defined as the distance from the fish's snout to the prey item when the prey is first recognised (Vinyard & O'Brien, 1976; Rowe & Dean, 1998). Nonetheless, turbidity-reactive distance relationships only suggest how suspended sediments might affect fish foraging success (Sweka & Hartman, 2001a,b; Zamor & Grossman, 2007). Consequently, measurements of actual prey capture success also are necessary to assess the true effects of turbidity on foraging success and ultimately individual fitness.

A common pattern in stream habitats in which turbidity disturbance has occurred is that sensitive native species decline in abundance and tolerant species increase (Gradall & Swenson, 1982; Vinyard & Yuan, 1996). However, the mechanism for this 'replacement' is unclear. For example, does this pattern represent direct replacement where the tolerant species is competitively superior to the sensitive native species in the changed environment, or does the change represent differing responses to a changing physical environment with no direct competition (Rahel, 2002)? Competition for food in fishes is typically manifested via either exploitation competition where one species is better at exploiting a limited resource, or interference competition, where one species excludes the other from the resource (Matthews, 1998). Drift feeding fishes exhibit both intra- and interspecific competitive behaviours linked to foraging success (Freeman & Grossman, 1992a,b; Rincon & Grossman, 1998, 2001). Berg & Northcote (1985) found that turbidities greater than 20 NTU reduced both prey capture success and agonistic interactions in juvenile coho salmon (*Onchorynchus kisutch*, Walbaum). Conversely, Suttle *et al.* (2004) found that increases in deposited sediment increased aggressive encounters in intraspecific groups of rainbow trout (*Onchorynchus mykiss*). Thus the effects of sedimentation on aggression are not yet clear. Furthermore, the combined effect of sedimentation and interspecific competition between two different species has received little attention.

The southeastern United States is home to the highest diversity of freshwater fishes in North America, with many species restricted to just a few catchments (Walsh, Burkhead & Williams, 1995; Warren *et al.*, 2000; Scott & Helfman, 2001). Nonetheless, approximately 46% of these species are imperiled, mostly due to habitat degradation and invasive species (Jelks *et al.*, 2008). Most research on turbidity and freshwater fishes has focused on commercially important species (Vinyard & O'Brien, 1976; Barrett, Grossman & Rosenfeld, 1992; Sweka & Hartman, 2001a,b) despite the fact that these species represent only a small fraction of freshwater fish diversity. Consequently, we examined the effects of turbidity, velocity, intraspecific competition and interspecific competition on foraging success of an endemic species (rosyside dace, *Clinostomus funduloides* Girard) and a species that has recently invaded our sites (yellowfin shiner, *Notropis lutipinnis*, Jordan and Brayton; Grossman & Ratajczak, 1998) in Coweeta Creek, North Carolina, U.S.A.

Methods

Study species

Rosyside dace are found in streams from Georgia to Maryland, USA (Etnier & Starnes, 1993; Warren *et al.*, 2000). The study population occupies Coweta Creek, a tributary of the Little Tennessee River, and may represent a new species (Etnier & Starnes, 1993; Warren *et al.*, 2000; Jelks *et al.* 2008). Rosyside dace are considered to be vulnerable by both the North Carolina Wildlife Resources Commission (Grossman *et al.*, 2002), and the American Fisheries Society (Jelks *et al.*, 2008). Rosyside dace are small, drift feeding minnows [maximum size in Coweta Creek = 91 mm standard length (SL)], that probably reach an age of 4–5 years (G. Grossman, unpubl. data). The species reproduces during late spring and early summer (DeHaven *et al.*, 1992), and is a member of the mid-water column microhabitat guild (Grossman & Ratajczak, 1998). In Coweta Creek, rosyside dace generally occupy focal point velocities that maximise their net energy gain (Grossman *et al.*, 2002).

Yellowfin shiners are native to the eastern slope of the southern Appalachians and Piedmont region of the Southeast United States (Etnier & Starnes, 1993). Until recently, yellowfin shiners were believed to be introduced in the Little Tennessee River drainage (Johnston *et al.*, 1995); however, new genetic data render this status uncertain (Scott *et al.*, 2009). Nonetheless, this species has undergone a tremendous range expansion in the upper portions of the Little Tennessee drainage (Grossman *et al.*, 2002). Yellowfin shiners also are mid-water column guild members in Coweta Creek and probably live to 2–3 years of age (Meffe, Certain & Sheldon, 1988; G. Grossman, unpubl. data). In the Coweta drainage, maximum length is 84 mm SL, and reproduction occurs during late spring/early summer (G. Grossman, pers. obs.). Yellowfin shiners may occupy focal point velocities that maximise energy gain, although this response is weaker than that displayed by rosyside dace (Grossman *et al.*, 2002). Finally, yellowfin shiners are common in habitats dominated by fine substrata and high turbidities (Sheldon & Meffe, 1995; Scott, 2001; Vogt, 2004).

Both rosyside dace and yellowfin shiner compete for drifting prey in experimental flumes (Wagner, 2004) and we assume that this behaviour may occur in Coweeta Creek (G. Grossman, unpubl. data; P. D. Hazelton, pers. obs.). These species display a context-specific competitive relationship, with yellowfin shiner obtaining more prey at slower velocities (10–12 cm s^{-1}) and rosyside dace being the superior forager at faster velocities (18–20 cm s^{-1}, Wagner, 2004). This competitive reversal probably is related to yellowfin shiners' greater aggressiveness which allows it to dominate at low velocities and rosyside dace's superior foraging abilities which allow it to dominate at higher velocities (Wagner, 2004; Rincon, Bastir & Grossman, 2007).

Experimental procedures

A detailed description of the experimental stream, collecting and experimental procedures is presented in Hazelton and Grossman (2009). In brief, we used the 3.0 m (l) × 0.75 m (w) × 1.0 m (h) Plexiglas artificial experimental stream of Zamor & Grossman (2007). We marked the tank with a 1 cm^2 grid to facilitate precise location of the test specimens and used a shroud to minimise observer disturbance (Zamor & Grossman, 2007). We maintained pH near 7 and water temperature between 10 and 12 °C, which represent average pH and spring/autumn stream temperature at Coweta Creek (Grossman & Freeman, 1987; Grossman & Ratajczak, 1998).

For experiments, we collected rosyside dace ($n = 312$; SL ± SD = 63.5 ± 9.19 mm; mass ± SD = 3.73 ± 1.0 g) and yellowfin shiners ($n = 343$; SL ± SD = 63.7 ± 7.31 mm; weight ± SD = 3.68 ± 1.2 g) from Coweta Creek and other streams within the Little Tennessee drainage between November and April of 2005–07. Collections were made using a backpack electrofisher at 600–800 V and nets, or nets alone. We visually inspected all fish after collection and only used individuals free from physiological stress or injury. Fish were held for 2 days to recover from the stress of collection and fed meal worms (*Tenebrio molitor*, Linneas) *ad libitum* once daily. After acclimation we anaesthetised fish with MS-222, and weighed (±0.01 g), measured (±1 mm, SL) and tagged them with a unique combination of coloured plastic discs (3.0 mm diameter; Wagner, 2004). Following tagging and a short recovery period, fish were allowed a minimum of 2 days recovery to ensure normal feeding behaviour (Wagner, 2004). Prior to an experiment, we placed subjects in a second holding tank where they underwent a 2-day fasting period to ensure all specimens were in a similar physiological state.

Experimental design and data collection

We quantified the effects of intra- and interspecific competition, turbidity and velocity on (i) capture location, (ii) reactive distance and (iii) capture success of specimens, using five treatments. The treatments were (i) separate trials of either two rosyside dace or two yellowfin shiner (low density intraspecific competition treatment), (ii) separate trials of either four rosyside dace or four yellowfin shiner (high density intraspecific competition treatment), and (iii) two rosyside dace + two yellowfin shiner (interspecific competition treatment). We tested each combination of competition at three turbidity treatments (10, 20, 30 NTU) and two velocities (12 and 18 cm s^{-1}) for a total of 30 treatment combinations (5-competition × 3-turbidity × 2-velocity). We used red clay as a turbidity agent because it is a naturally occurring turbidity agent in the region and has been used in previous studies (Zamor & Grossman, 2007). Turbidity was measured and controlled using a HACH 2100P turbidity meter (see Zamor & Grossman, 2007). We performed a minimum of three replicates of each treatment combination (four replicates of five treatment levels, randomly distributed; Hazelton & Grossman 2009), resulting in a total of 95 trials.

During a trial, we observed and videotaped fish behaviour for later analysis. Thirty seconds after initiating a trial we began measuring the position of each fish at one minute intervals. The location of the fish along the *x*-axis (length from front of tank) and *y*-axis (height from substrate) were measured in 5 cm increments using a scale on the front of the tank. We estimated the *z*-axis position of fish at higher turbidities by dividing the tank into three 15 cm wide feeding lanes (see below), and assigned each fish's position to the midpoint of the lane occupied (Near = 7.5 cm, Middle = 22.5 cm, Far = 37.5 cm). Throughout each trial we recorded agonistic acts between individuals and ranked fish as dominant, subdominant or subordinate assuming a linear hierarchy (Katano, 1990; Ward *et al.* 2006; Hazelton & Grossman 2009).

At two minute intervals we released a single prey item (*Tenebrio molitor* larvae) through one of three randomly chosen, silicon tubes at the front of the experimental chamber. Silicon tubes were spaced 15 cm apart corresponding to the feeding lanes described previously (Tube 1 = 7.5 cm, Tube 2 = 22.5 cm, Tube 3 = 37.5 cm). Tube 1 and Tube 3 were positioned 35 cm above the substrate, and Tube 2 was positioned 22 cm above the substrate to mimic random drift availability in the stream. We used miniature mealworms (8–10 mm, *c.* 0.02 g) as prey because they resembled natural prey, are easily visible at varying turbidity, and are readily consumed by fish in turbidity experiments (Barrett *et al.*, 1992; Zamor & Grossman, 2007). Trials averaged 42 min with a standard error of 25 s ($n = 94$).

We used video tapes from each trial to quantify (i) the behavioural reaction of the fish to the prey, (ii) fish location (x, $y + z$ axes), (iii) time of reaction (0.01 s), (iv) prey location at time of reaction (not always possible at higher turbidities) and (v) capture time (0.01 s) and (vi) capture location. We classified fish as reacting to prey if they oriented directly towards the prey (Vinyard & O'Brien, 1976; Zamor & Grossman, 2007). A capture represented a fish grasping a prey regardless of whether or not the prey was consumed. Typically we released 20 prey items during a trial. However, if fish did not react to the first five prey items, five prey items were added at the end of the trial resulting in 25 total prey.

We measured the location of each prey capture and the reactive distance of fish, and divided capture locations into two categories: forward captures – where the fish moved forward to capture a prey, and lateral captures where the fish caught the prey behind its reaction position. Reactive distance was measured as the distance from the nose of the fish to the prey, at the moment of orientation towards the prey (Barrett *et al.*, 1992; Zamor & Grossman, 2007). We used a three dimensional adjustment of the Pythagorean theorem ($d^2 = x^2 + y^2 + z^2$) to measure reactive distance where d is reactive distance, x is the difference between the fish and prey's position along the x-axis, y is the difference between the fish and prey's position on the y-axis, and z is the difference in the assigned z position of the fish and the prey. We assumed that errors in z-coordinate estimates were randomly distributed.

Immediately following an experiment, fish were removed from the experimental chamber and killed using MS-222. We then determined sex and measured and weighed each fish, using a measuring board (1 mm) and electronic balance (0.01 g), and counted the number of mealworms in the gut via dissection for comparison with visual estimates of captures. A paired t-test demonstrated a lack of significant differences between the number of prey in the gut and visual estimates; hence, our methods can be considered accurate. All experimental procedures conformed to the Institutional Animal Use and Care Guidelines of the University of Georgia.

Statistical analyses

Although our main focus was on reactive distance and capture success, we also examined the effects of turbidity and velocity on the species' prey capture locations using chi-square tests for independence (Dowdy, Weardon & Chilko, 2004). We compared the number of forward and lateral captures across the three turbidity treatments within each velocity treatment. In addition, we performed this analysis over both velocities at a given turbidity. We used the Bonferroni adjustment to recalculate alpha across all nine comparisons ($\alpha = 0.0056$; Dowdy *et al.*, 2004). To evaluate interspecific differences, we compared the frequency of forward and lateral captures between species at each turbidity treatment level. These comparisons were made separately on 12 and 18 cm s^{-1} data, and we adjusted the level of significance for three comparisons in each analysis ($\alpha = 0.017$; Dowdy *et al.*, 2004).

We used the methods of Grossman *et al.* (2006) to construct a series of *a priori* mechanistic models capable of explaining the information content in reactive distance (10 generalised linear models, GLM; Bolker *et al.*, 2009) and capture success (nine generalised linear mixed models, GLMM; Bolker *et al.*, 2009) data using both environmental and competition predictors (see Table 1). Environmental variables included turbidity and velocity. Competition parameters included species of the focal fish (0 = dace, 1 = shiner), intraspecific competition (0 = interspecific trials and 2-fish densities, 1 = addition of 2 conspecifics), interspecific competition (0 = intraspecific trial, 1 = interspecific treatment), and dominance (0 = non-dominant, 1 = dominant). We also included the standard length of the focal fish (length) in our models, even though size ranges in experiments were constrained. We included interaction terms in some models to account for possible differences in responses among species and dominance ranks (e.g. species × turbidity or dominance × turbidity). We avoided multicolinearity by only using variables in our models with *r*-values <0.25.

Reactive distance for analyses was the mean reactive distance of each focal fish and modeled using GLM with a normal distribution (Bolker *et al.*, 2009). We assessed data normality using normal probability plots, and then performed an analysis of variance (ANOVA, $\alpha = 0.05$) on the residuals by focal fish to determine if significant variation existed across trials (Rieman, Peterson & Myers, 2006). Residuals were

Table 1 *A priori*, mechanistic models used to evaluate the relative importance of environmental and community level variables affecting reactive distance and capture probability of rosyside dace and yellowfin shiner

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

normally distributed and the ANOVA indicated no significant random trial effects. Capture success was modeled using a binomial distribution (capture = 1, non-capture = 0), for each fish's response to individual prey items (i.e. logistic regression). Capture probability was significantly influenced by variation among individual fish (inter-individual variation; $F = 4.33$; d.f. = 299; $P < 0.001$); hence we used a GLMM to account for this random effect (Rieman *et al.*,2006; Bolker *et al.*, 2009). Prior to model fitting, all predictor variables in the capture probability dataset were standardised to a mean of 0 and a standard deviation of 1 to facilitate interpretation of relative parameter effect sizes (Hair *et al.* 1984).

We assessed the relative plausibility of each competing model using Akaike Information Criteria adjusted for small sample sizes (AICc; Hurvich & Tsai, 1989; Johnson & Omland, 2004). For each model we calculated the ΔAICc, and Akaike weight (w_i) as measures of the relative performance of the competing models (Burnham & Anderson, 2001; Konishi & Kitagawa, 2008). We only interpreted models with Akaike weights >10% of the model with the best fit (Grossman *et al.*, 2006). To account for model uncertainty in the reaction distance data, we used model-averaged parameter estimates, and calculated 90% confidence intervals (CI) around each estimate (Burnham & Anderson, 2002). Capture probability parameter estimates (and 90% CI) were based on the best fitting model, and are not model-averaged as this is inappropriate for models containing both random and fixed effects (Rieman *et al.*, 2006).

We calculated effect sizes for parameters with confidence intervals that did not overlap zero (Burnham & Anderson, 2002) and did not interpret interaction terms unless both main effects differed significantly from zero. Because reactive distance data were continuous and not standardised, effect sizes were calculated as the parameter estimate multiplied by a unit change in the independent variable (e.g. 10 NTU for turbidity). However, independent variables for capture probability were standardised, and the effect of each parameter is centred on the mean value of the raw measurements of that parameter (Hair *et al.*, 1998). To interpret the effect of predictors on capture probability, we calculated odds ratios from parameter estimates, and the standard deviation of the raw value of the corresponding variable [OR = exp{estimate × {unit change/SD}]; Rieman *et al.*, 2006). For example, a unit change for turbidity = 10, velocity = 6, and binomial variables = 1. Odds ratios less than one are less likely, whereas ratios of one are just as likely, and ratios greater than one are more likely (e.g. OR = 1.5 ~ capture is 1.5 times more likely; Hair *et al.*, 1998). To interpret interaction terms with confidence intervals that did not overlap zero, we plotted the best fitting model at all unit changes for the interaction while keeping all other parameters constant, using the binomial link function $p(\text{capture}) = 1/1 + \exp(\beta_{\text{intercept}} + \beta_i + \beta_{j\ldots n})$, where $\beta_{i\ldots n}$ are the parameter estimates multiplied by standardised unit changes for all parameters in the best fitting model (Hair *et al.*, 1998; Bolker *et al.*, 2009).

Results

Capture location

Both increased turbidities and velocities resulted in both species capturing more prey in a lateral rather than a forward location (Fig. 1). At 18 cm s^{-1} and 10 NTU rosyside dace had proportionately more forward prey captures ($\alpha = 0.0056$) than lateral captures (77 of 141). However, the opposite was true at 18 cm s^{-1} and 30 NTU (36 of 113; $\chi^2 = 13.42$, $P = 0.001$, d.f. = 2). Yellowfin shiner had proportionately fewer forward captures at 20 and 30 NTU in 12 cm s^{-1} trials (28 of 109, 34 of 103 respectively; $\chi^2 = 12.32$, $P = 0.002$, d.f. = 2), and proportionately fewer forward captures at all three turbidities at 18 cm s^{-1} (10 NTU = 40 of 102, 20 NTU = 35 of 107, 30 NTU = 16 of 90; $\chi^2 = 10.79$, $P = 0.005$, d.f. = 2). Rosyside dace captured more prey ($n = 877$) than yellowfin shiner ($n = 643$) across all turbidity and velocity treatments. Differences in the frequency of forward captures between the species were significant ($\alpha = 0.017$) at 20 NTU and 12 cm s^{-1} (rosyside = 82 of 170 forward, yellowfin = 28 of 109; $\chi^2 = 14.14$, $P < 0.001$, d.f. = 1), and nearly significant at 10 NTU and 18 cm s^{-1} (rosyside = 77 of 141, yellowfin = 40 of 102; $\chi^2 = 5.62$, $P = 0.018$, d.f. = 1), and 30 NTU and 18 cm s^{-1} (rosyside = 36 of 113, yellowfin = 16 of 74; $\chi^2 = 5.21$, $P = 0.022$, d.f. = 1).

Reactive distance

We observed 2401 reactions to prey by fish. Mean reactive distances for rosyside dace and yellowfin shiners were 31.8 cm (SD = 6.9 cm, $n = 69$) and

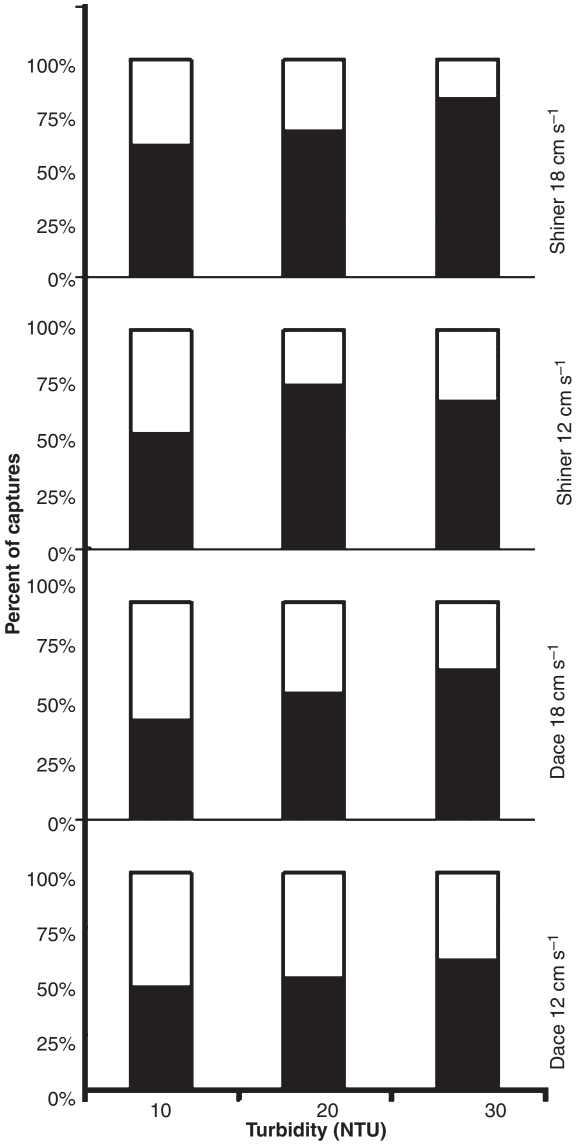

Fig. 1 Effects of turbidity and velocity on the frequency of forward (white) and lateral (black) captures of rosyside dace and yellowfin shiner. Yellowfin shiners (top) had significantly fewer forward captures with increased turbidity (20 and 30 NTU) at low velocity (12 cm s^{-1}), and significantly fewer forward captures than expected at all turbidities at high velocity (18 cm s^{-1}). Rosyside dace had fewer forward captures than expected at 20 and 30 NTU at 18 cm s^{-1}. Rosyside dace also displayed a significantly higher proportion of forward captures than yellowfin shiner at 20 NTU and 12 cm s^{-1}, 10 NTU and 18 cm s^{-1}, and 30 NTU and 18 cm s^{-1}.

30.9 cm (SD = 7.0, n = 55) respectively. Two interpretable models were included in the confidence set, namely the environmental and competition (w_i = 0.85) model and the global model (w_i = 0.09), and the environmental and competition model had 9.4 times the explanatory evidence of the global model (Table 2). Two parameters (turbidity and intraspecific competition) in the environmental and competition model had model-averaged parameter estimates with CIs different from zero (Fig. 2, Table 3). Intraspecific competition produced the greatest reduction in reactive distance, such that an increase from two to four fish of the same species reduced reactive distance by 4.57 cm on average. Turbidity also reduced reactive distance by 3.5 cm for every 10 NTU increase. The intercept represents the mean reactive distance of rosyside dace tested at low densities, and no interspecific competition (i.e. species = 0, intraspecific competition = 0, interspecific competition = 0).

Capture success

We recorded 1407 prey captures by both rosyside dace and yellowfin shiners. Raw data distributions of main effects include: Species, mean = 0.5, standard deviation (SD) = 0.50; Dominant, mean = 0.31, SD = 0.46; Intraspecific competition, mean = 0.51, SD = 0.50; Interspecific competition, mean = 0.24, SD = 0.43; Length, mean = 64.23, SD = 7.95; Turbidity, mean = 19.83, SD = 7.99; Velocity, mean = 15.01, SD = 3.00. The analysis identified two interpretable models, given the data, namely the global model and the behavioural and competition model. Given the data, the global model had approximately 10 times the explanatory evidence (w_i = 0.91) of the behavioural and competition model (w_i = 0.09) (Table 2). Precision of parameter estimates (log odds) varied across descriptive variables (Table 3). However, capture success appeared to depend on environmental, competition and behavioural predictors. Velocity was the only informative environmental parameter (Fig. 3), and a 6 cm s^{-1} increase in velocity reduced capture success to 0.72 times the level observed at 12 cm s^{-1} (OR = exp{−0.16 x {6.0/3.0}}). Dominance had the greatest impact on capture probability, and dominant fish were 3.2 times more likely to capture prey item than non-dominant fish. We also observed species differences and yellowfin shiners were only 0.62 times as likely to capture a given prey item as rosyside dace. Both intraspecific competition and interspecific competition reduced capture probability, and fish in either four fish single species trials or interspecific trials were 0.46 times and 0.44 times as likely to capture prey as fish in two fish intraspecific trials. The

Table 2 Model selection results for linear regression analysis of reactive distance and logistic regression analysis of capture probability for rosyside dace (*Clinostomus funduloides*) and yellowfin shiner (*Notropis lutipinnis*)

Response	Candidate model	Model number	AICc	ΔAICc	w_i
Reactive distance	Environmental & competition	5	816.32	0.00	0.85
	Global	1	820.80	4.49	0.09
Capture probability	Global	1	5449.70	0.00	0.91
	Behavioural & competition	7	5454.34	4.65	0.09

Table 3 Model averaged parameter estimates, 90% confidence intervals, and AICc importance weights for parameters in interpretable models explaining variation in reactive distance (linear GLM) and capture probability (binomial GLMM). Parameter estimates for reactive distance are based on raw data and were averaged across models included in confidence set. Estimates for capture probability are log odds based on standardised data

	Reactive distance				Capture probability			
		90% CI				90% CI		
Parameter	Estimate	Lower	Upper	w_i	Estimate	Lower	Upper	w_i
Inter-individual variation*					1.31	1.17	1.45	1.00
Intercept	39.42	33.36	45.48	1.00	−1.66	−1.82	−1.51	1.00
Species	−2.09	−4.96	0.79	1.00	−0.24	−0.39	−0.09[†]	1.00
Dominant	0.25	−7.45	7.95	0.11	0.54	0.39	0.68[†]	1.00
Intraspecific competition	−4.57	−6.85	−2.28[†]	1.00	−0.39	−0.57	−0.21[†]	1.00
Interspecific competition	0.61	−2.56	3.77	1.00	−0.35	−0.53	−0.17[†]	1.00
Turbidity	−0.35	−0.52	−0.17[†]	0.94	−0.02	−0.17	0.12	0.91
Velocity	−0.09	−0.32	0.14	0.94	−0.16	−0.31	−0.02[†]	0.91
Length	0.10	−0.03	0.22	0.11	−0.04	−0.19	0.12	1.00
Species × velocity	−0.12	−0.54	0.29	0.09	−0.01	−0.15	0.14	0.91
Species × turbidity	0.20	−0.16	0.57	0.09	−0.03	−0.18	0.12	0.91
Species × interspecific comp.	7.49	2.17	12.81[†]	0.11	−0.09	−0.27	0.08	0.91
Species × intraspecific comp.	2.39	−1.98	6.76	0.11	0.13	−0.04	0.31	0.91
Dominant × turbidity	0.18	−0.16	0.52	0.09	0.33	0.18	0.47[†]	0.91
Dominant × velocity	−0.34	−0.76	0.08	0.09	0.02	−0.12	0.16	0.91

w_i is the parameter importance weight – sum of Akaike importance weights for all models including that variable.
Intercept: is the mean response for a non-dominant rosyside dace in a two fish trial, at 10 NTU, and 12 cm s^{-1}.
Binomial independant variables: *Species* (0 = dace, 1 = yellowfin), *Dominant* (0 = dominant, 1 = non-dominant), *Intraspecific Competition* (1 = 4 fish intraspecific trial, 0 = all other treatments), *Interspecific competition* (1 = both species present, 0 = intraspecific trials).
*A random effect variable estimating the total variance that exists between individual fish across all treatments.
[†] An interpretable parameter estimate with 90% confidence intervals (CI) not including zero.

interpretable dominant × velocity interaction term indicated that the relationship between capture success and dominance level varied with velocity (Fig. 4). Probability of capture increased with increased velocity for dominant fish, although subordinate fish showed the opposite pattern.

Discussion

Different factors affected reactive distance and capture success for rosyside dace and yellowfin shiner, confirming the importance of measuring both variables when quantifying foraging responses to environmental and behavioural factors. Turbidity affected reactive distance for both species; however, both reactive distance and capture success were more strongly affected by intraspecific competition than by environmental parameters. In addition, interspecific effects were apparent, with rosyside dace capturing more prey on average than yellowfin shiners. Furthermore, although yellowfin shiner displayed smaller reactive distances than rosyside dace, they had larger reactive distances in trials when tested in interspecific groups. This suggests that the presence of competitors may increase awareness of prey. Our results are some of the first to document the complex interactions between changes in turbidity and biotic factors such as intra- and interspecific competition.

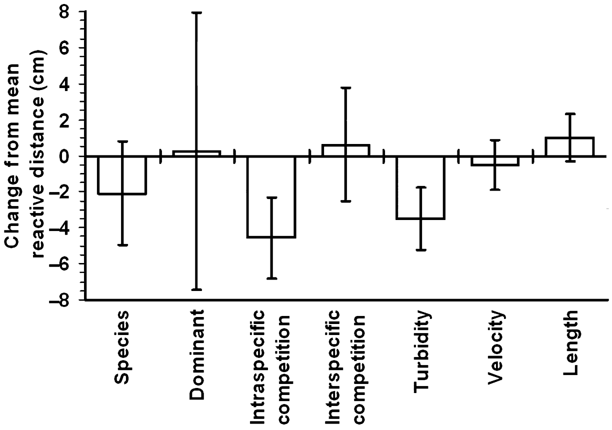

Fig. 2 Scaled effects of environmental and competition variables on reactive distance of rosyside dace and yellowfin shiner. Data are represented as the scaled change (cm) in reactive distance (RD) caused by one unit change, from mean rosyside RD in a two fish trial, holding environmental variables constant (i.e. 0). One unit change = 1 for binomial parameters (Species, Dominant & Competition), 10 NTU for Turbity, 6 cm s^{-1} for Velocity, and 10 mm for Length. Error bars represent 90% confidence intervals.

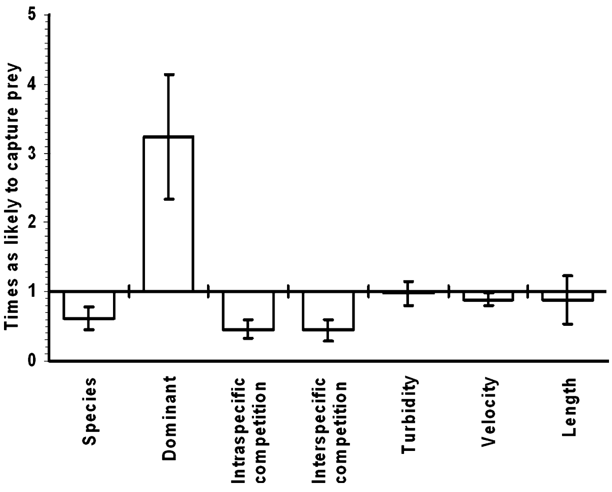

Fig. 3 Scaled odds ratios of the effects of environmental and competition variables on capture probability. Odds ratios (±90% confidence interval) were calculated from log odds parameter estimates from generalised linear mixed model. Odds rations for parameters indicate the differential effect of the parameter on capture probability when compared to results for a non-dominant rosyside dace in a two fish trial. If the odds ratios is >1 then the variable has a positive effect on capture probability whereas values <1 represent decreased probability of capture. Effect size is based on unit change of each independent variable: i.e. 1 for binomial parameters (species, dominant and competition), 10 NTU for Turbity, 6 cm s^{-1} for Velocity, and 10 mm for Length. Error bars represent 90% confidence intervals.

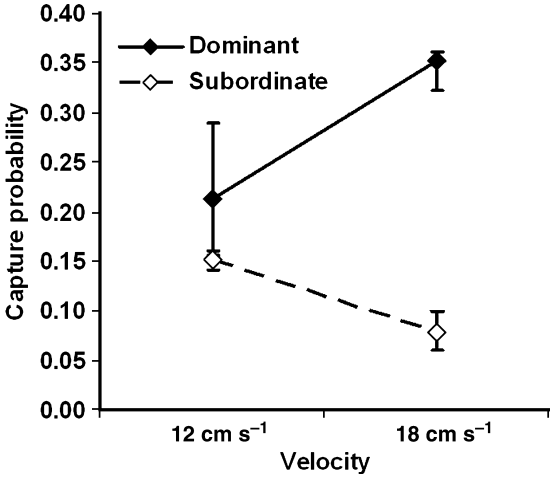

Fig. 4 Modeled interaction effect of dominance × velocity on prey capture probability. The figure represents the capture probabilities for dominant and subordinate rosyside dace (SL = 55 mm), at 10 NTU, in a 4-fish intraspecific group. Error bars represent 90% confidence intervals.

Our treatments were based on the range of conditions observed in Coweta Creek and other streams in the Little Tennessee drainage. For example, rosyside dace and yellowfin shiners are found at focal point velocities ranging from 12–18 to 8–14 cm s^{-1} respectively (Grossman *et al.*, 2002). During base flow conditions, turbidities in relatively undisturbed streams generally would not reduce foraging success of either species; however, this does not hold for moderately disturbed streams in the drainage (Bolstad & Swank, 1997; Sutherland, Meyer & Gardiner, 2002; Price & Leigh, 2006a,b). In addition, development within the southern Appalachian region is increasing in many areas due to second home and resort construction, and these activities frequently increase fine sediments in streams (Bolstad & Swank, 1997). Contrary to our predictions, we found that the endemic rosyside dace captured more prey across all turbidities and velocities. Therefore, interspecific competition for prey is unlikely to explain their distribution in degraded streams of the Little Tennessee River catchment.

Fishes may modify their foraging behaviour in response to changing environmental conditions. Yellowfin shiners are less efficient drift feeders than rosyside dace at higher velocities (Wagner, 2004; Rincon *et al.*, 2007). Velocity was not included in any of our explanatory models for reactive distance; however, there was an interaction between dominant fish and velocity that suggests dominant individuals are more effective at higher velocities than subordinates. Several researchers have reported shifts in fish foraging behaviour at higher turbidities (Gradall & Swenson, 1982; Berg & Northcote, 1985; Sweka & Hartman, 2001a,b). At higher turbidities, rainbow trout (*Oncorhynchus mykiss*) shift from stationary feeding positions to active searching for prey, and expend greater effort capturing prey (Sweka & Hartman, 2001b). In addition, intraspecific groups of rainbow trout also had reduced growth rates and greater rates of movement when exposed to increased sediment deposition (Suttle *et al.*, 2004). Although reactive distance was reduced by turbidity, capture success was not. Nonetheless, both species showed a significant increase in lateral versus forward captures with increased turbidity and velocity, an effect observed in other drift feeding fishes (Hughes *et al.* 2003; Piccolo, Hughes & Bryant, 2008). This may result in greater energy expenditure per prey captured, because it probably takes more energy to capture prey by moving perpendicular to the current than when moving forward. In addition, lateral captures also included downstream captures and these are energetically costly because the fish has to swim both downstream for the capture then back upstream to regain its position (Piccolo *et al.*, 2008).

There are few studies on the effects of turbidity on intra- or interspecific competition. Suttle *et al.* (2004) found that deposited sediment increased aggression rates of rainbow trout. Increased aggression rates, along with a rise in movement rates and decreased prey availability, resulted in reduced growth rates and potentially greater mortality (Suttle *et al.*, 2004). Gradall & Swenson (1982) found that brook tout and creek chub in turbid conditions (4.5–8 Formazin Turbidity Units, FTU) were less likely to be near cover or substrate and were more active than fish in clear water. Increased activity in turbid water probably results in a greater energetic cost per prey, a response similar to our findings on differences in prey capture locations by rosyside dace and yellowfin shiners. Vinyard & Yuan (1996) also observed reductions in capture success for both native cutthroat trout and introduced Lahontan redsides (*Richardsonius egregius*, Girard) from Summit Lake, Nevada, USA at higher turbidities. However, Lahontan redsides were slightly better at capturing larger *Daphnia* at higher turbidities (20–25 NTU) than trout. Nonetheless, because fish only were tested in intraspecific groups, the effect of turbidity on interspecific competitive interactions is unknown.

In conclusion, increased turbidity is a major problem for lotic systems worldwide (Mol & Ouboter, 2004; Li *et al.*, 2008; Orioli *et al.*, 2008), yet little is known about its direct effects on foraging success and biotic interactions in stream organisms. We have demonstrated that increases in turbidity and velocity along with increased competition significantly reduce the foraging success of rosyside dace and the invasive yellowfin shiner. Our results are consistent with the field distributions of these species, which suggest an inverse relationship between rosyside dace and fine sediments in southern Appalachian streams (Scott, 2001; Scott & Helfman, 2001; Sutherland *et al.*, 2002; Vogt, 2004). By contrast, yellowfin shiners frequently occupy habitats with large quantities of fine sediments (Scott & Helfman, 2001; Vogt, 2004). Our findings also suggest that both physical and biological factors (i.e. turbidity and competition) affect foraging success of rosyside dace and yellowfin shiners, both of which should be considered by managers when developing management strategies for endemic species.

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