Sympatric relationship between redband trout and non-native brook trout in the Southeastern Oregon Great Basin

Stephanie A. Miller · Stephanie Gunckel · Steve Jacobs · Dana R. Warren

Abstract Brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*) have been widely introduced outside their respective ranges within North America causing declines and displacement of native trout. Yet, successful coexistence of native and non-native trout has received little attention. Here we evaluated the effect of introduced brook trout on the size and density of native redband trout in two invaded sub-basins in southeastern Oregon. In a multi-year study, we investigated whether habitat and fish communities differed between streams and stream reaches where redband trout were allopatric versus where redband trout were sympatric with brook trout. We hypothesized that redband trout would be less dense and have smaller total length in sympatry with brook trout than in allopatry, but that total trout density would not differ. We investigated whether differences in habitat existed between sympatric and allopatric locations that would indicate differentiation in site level habitat preferences for each trout species. We found that sympatric locations had more wood but similar fish community structure. Mean length and densities of redband trout were higher at allopatric locations. However, in most years at sympatric locations total trout density was twice that of allopatric redband trout sites. Using comparable data from an eastern United States system where brook trout are native, sympatric sites had lower densities of brook trout; however, total trout density did not differ. We conclude that invading trout negatively impact native trout densities; but in southeastern Oregon system the negative impact is minimized.

Keywords Redband trout · Brook trout · Interactions · Density · Sympatry · Allopatry

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Introduction

Non-native fish may have deleterious effects on aquatic communities, such as decrease on growth and reproductive success of native fish, introduction of pathogens, and modification of the environment (Moyle 1986; Allan and Flecker 1993; Parker et al. 1999). Successful non-native species are often generalists that have greater tolerance to degraded habitat, and are not co-adapted with predators; in these situations the non-native species are often superior competitors (Moyle 1986; Fausch 1988). Introduced salmonids are frequently the ecological analogs of native

salmonids, increasing the potential for direct competitive interaction (Gunckel et al. 2002). Introduced salmonids are therefore frequently implicated in the declines of native salmonids (Dunham et al. 2003; Peterson et al. 2004) with most attention focused on how non-natives displace or replace native salmonids (McGrath and Lewis 2007; Benjamin and Baxter 2010, 2012; Benjamin et al. 2011). Beyond replacement or displacement, little consideration is given to whether the invader can coexist in sympatry with their native analogs with minimal interspecific competition.

Brook trout (Salvelinus fontinalis) are native to eastern North America but have been widely introduced throughout the western United States (Schade and Bonar 2005). In Oregon, brook trout are a popular game fish and have been stocked widely across the state for over 80 years. The naturalization of brook trout can be ecologically devastating to many native trout (Dunham et al. 2003). Brook trout, for example pose a significant risk to the viability of native bull trout (Salvelinus confluentus) (Gunckel et al. 2002) and inland cutthroat trout (Benjamin et al. 2007) populations. In streams with sympatric brook trout and bull trout, competition for resources (as well as hybridization) has been cited as reasons for the decline of bull trout (Dambacher et al. 1992; Ratliff and Howell 1992). Although the impacts of brook trout on displacement of native cutthroat (Oncorhynchus clarkii) and bull trout in the western United States has been well documented, the impacts of brook trout on native rainbow trout (Oncorhynchus mykiss) remain understudied. The potential for non-native brook trout to impact or displace native rainbow trout is particularly interesting because these two species are undergoing reciprocal invasions (Fausch 2008). Rainbow trout have been found to supplant brook trout when introduced into native brook trout streams in the eastern United States (Fausch 2008). While brook trout are present in many western streams where rainbow trout are present, it remains unclear whether brook trout present a similar threat to native resident rainbow trout (O. mykiss). It also is unclear what the effects non-native brook trout have on the resource use, distribution, and performance of rainbow trout. Similarities in food and habitat likely exist.

Trout biomass is typically greatest where two or more species occur. Behnke (1992) hypothesized that each species becomes more specialized to make efficient use of the resources available and minimize competition. While anecdotal information from trout managers across North America concurs with Behnke (Graff and Hollender 1980; McDowell 1986), comparative studies directly measuring native trout in sympatry with a non-native species versus allopatry are limited. The closed basin stream systems in eastern Oregon are particularly well suited to explore these questions. The native rainbow trout in this region, redband trout (O. mykiss newberri), is relegated to a resident life-history in most years (occasional adfluvial forms occur in high water years) and headwater streams are only partially invaded (through intended introductions) by non-native brook trout. Redband trout therefore occur in allopatry and in sympatry with non-native brook trout across a number of streams within a single region allowing us to assess whether a pattern of increased specialization in sympatry holds true for both redband and brook trout in southeastern Oregon.

Our objective was to evaluate the effect of introduced brook trout on the size and reach-scale population density of native redband trout. Size and density were compared between locations where redband trout populations did not co-occur with brook trout and locations where redband trout occur in sympatry with brook trout. Total length and reach-level density were used as measures of competitive success. We hypothesized that, assuming equal carrying capacity, redband trout would be less successful (less dense and smaller total length) in sympatry with brook trout than in allopatry. If both species were truly competing for the same resources, we also hypothesized that total trout density would not differ when these fish exist in sympatry; opposite to the expectation suggested by Behnke's hypothesis. Further, we predicted these pattern would hold true in reciprocal invasions where brook trout are the invader (Oregon Southeastern Great Basin) and those where they are native (Great Smoky Mountain National Park). Finally, we investigated whether differences existed in the physical habitat template and fish community structure between sympatric and allopatric locations that may indicate preferences for each fish species (Jonnson and Jonnson 2011).

Methods

Study area and design

For this study, we identified streams where redband trout were present in allopatry and in sympatry with

brook trout. We limited our analysis to the southeastern Oregon Fort Rock and Chewaucan sub-basins where both salmonids were found in relatively high frequency (Fig. 1). Populations were defined as groups of (or single) streams, within a sub-basin, that were geographically isolated from each other for most of the year with no or limited hydrologic connectivity (Miller et al. 2010). In both sub-basins, brook trout were introduced as a game fish and stocked repeatedly for several years (ODFW unpublished data). The last recorded stocking occurred 1939 in Fort Rock and 1934 in Chewaucan so existing brook trout represent well-established wild populations with no further hatchery supplementation. Historical stocking of brook trout occurred in all populations with the exception of Bridge Creek in the Fort Rock sub-basin. Presence/absence of each species for the entire study area was not available prior to the implementation of this study. Therefore, categorizing sites into sympatry and allopatry was assessed following data collection. Henceforth, sympatry refers to sites where redband trout and brook trout co-occur, and allopatric refers to sites where redband trout do not co-occur with brook trout but do exist with other fish species. Three redband trout populations exist within the Fort Rock sub-basin: Buck, Bridge, and Silver Creeks; Bridge is void of brook trout. Within the Chewaucan sub-basin, three redband trout populations exist: Chewaucan, Crooked, and Willow; the Chewaucan and Crooked populations have areas of established brook trout and redband trout but Willow is void of brook trout. Within these two sub-basins, 84 sites were designated as sympatric (Chewaucan=28; Fort Rock=56) and 150 sites were allopatric with respect to redband trout (Chewaucan=82; Fort Rock=68).

We conducted surveys for four consecutive years, 2007–2010. The sampling frame in each basin consisted of all wadeable stream reaches that contained documented and/or potential summer distribution for redband trout. The identification of suitable redband trout stream reaches was based on documented distribution and the professional judgment of local biologists and other fishery managers. The resulting sample frame, mapped at a 1:24,000 scale, provided the pool of possible locations from which sample sites were selected and represented our scope of inference.

All sites were randomly selected using a Generalized Random Tessellation Stratified (GRTS) design
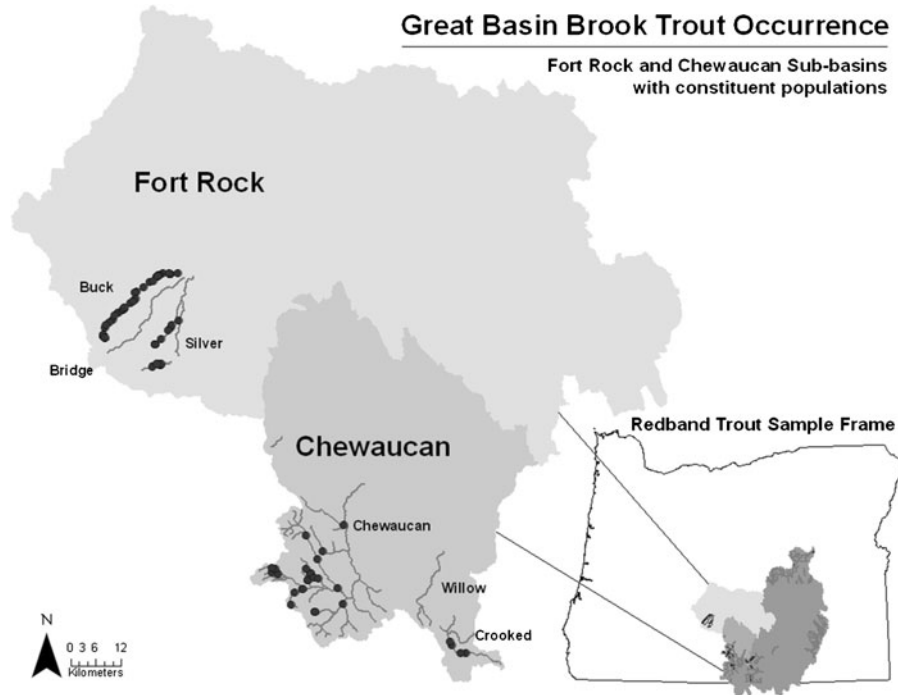

Fig. 1 Map of the Oregon Fort Rock and Chewaucan sub-basins with constituent populations. *Grey lines* represent the redband trout sample frame. *Dots* represent locations of brook trout occurrence

developed by the U. S. Environmental Protection Agency (Stevens and Olsen 2003, 2004). The GRTS sampling design provides a random spatially balanced sample, allowing for statistically rigorous evaluation of status, trend and distribution at multiple scales. The sample frame was further delineated into populations to provide better spatial coverage within a sub-basin and allowed us to allocate samples proportional to the frame size of each population.

The site selection process produced a minimum of 30 spatially balanced sites within the redband trout sampling frame in each sub-basin during 2007, 2008, and 2010, and in 2009 30 sites per population (90 sites per sub-basin). We targeted a minimum sample of 30 sites per year, with additional sites selected as replacements in the event some sites were unsuitable (e.g., located in a dry stream channel or where access to private property was denied). The GRTS design selection process assigns sample sites in a numerical order that maintains the random and spatial structure of the sample. Sites were selected consistent with this order, such that replacement sites had the same design properties as the initial sample.

Survey methodology

Each site, defined by geographic coordinates, served as the downstream boundary of a survey reach. Field crews located each sample point using Universal Transverse Mercator (UTM) coordinates, maps, and a personal digital assistant (PDA), equipped with a Global Positioning System (GPS) receiver. Stream survey reach lengths were calculated as 30 times the wetted width with a minimum of 30 m and a maximum of 100 m long. Survey reaches included a variety of stream habitat types and typically contained a minimum of three pool-riffle sequences. All side channels within a survey reach were included in the sample. Block nets were installed at the upper and lower site boundaries to prevent fish movement into or out of the site during a survey.

We conducted surveys between mid-June and mid-September using two-person survey crews. We used multiple pass depletion backpack electrofishing to obtain abundance estimates at each site. A minimum of two passes of equal effort were made, beginning at the downstream block net and employing two systematic upstream and downstream sweeps to herd fish toward the lower block net. A single upstream and downstream sweep constituted one pass. Our field criterion targeted redband and brook trout >60 mm, however an effort was made to collect smaller trout and all other species. If the number of redband trout or brook trout in the second pass was greater than 50 % of that in the first pass, two additional passes were completed. For sites where four passes were required, the number of fish captured was summed for passes 1 and 2, and again for passes 3 and 4. A site failed (was not included in our analysis) if the total number of redband or brook trout captured during passes 3 and 4 exceeded 50 % of the total from passes 1 and 2. Sampling was limited to streams with water temperatures <21 °C, measured prior to initiation of sampling.

Following capture, fish were placed in an aerated bucket until they could be processed at the end of the pass. Fish were anesthetized prior to processing using a buffered Tricaine methanesulfonate (MS-222) solution, then identified to species, counted and measured. The fork length (FL) was measured to the nearest millimeter. If large numbers of other species were present, a subsample of 20 of each non-trout species, representing the range of size classes collected, was measured and the remaining individuals were tallied by tens. We processed fish after each pass and released them downstream of the lower block-net before starting the next pass.

Habitat data collection

We collected physical data describing habitat complexity at each survey site. The overall maximum depth and thalweg length were measured at each site. Obstructions that made electrofishing more difficult (e.g., log jams, heavy vegetation, deep undercuts) were counted and classified into categories describing the percent of the sample site obstructed: no obstructions, 0 %–33 %, 33 %–66 %, and 66 %–100 % obstructed. Large wood (at least 10 cm in diameter) within the wetted channel was tallied. Each site was divided into 10 m across-stream transects, beginning five meters upstream from the lower block-net. For sites less than 50 m, five equally spaced transects were used. We measured maximum depth and depth at ¼, ½, and ¾ channel width, and wetted channel width. We recorded dominant substrate and number of pools. We calculated percentage obstructions and substrate types, and total large wood per site length.

Statistical analysis

Length analysis

To determine whether any difference existed in the size of redband trout at allopatric versus sympatric locations we used a mixed linear ANCOVA model, PROC MIXED, in SAS 9.1.3 (SAS Institute 2001). Sites were grouped into one treatment factor with two levels: redband trout at allopatric versus sympatric locations. We modeled the response (average redband trout length) with fixed factors treatment, year, and year x treatment interaction. Redband trout density was used as a covariate to control for size-density dependence (Bohlin et al. 2002; Utz and Hartman 2009). Population nested within sub-basin was the random factor used to assess variability based in differing populations and sub-basins. For individual basin models, the random factor was population. No transformations were necessary as each model met assumptions of normality and homogeneity of variance based on visual inspection of Q-Q plots and of residuals plotted against fitted values.

Density analysis

We grouped sites into a single treatment factor with two levels: redband trout at allopatric versus sympatric locations. We used a mixed linear ANCOVA model, PROC MIXED, in SAS 9.1.3. Fixed factors included treatment, year, and year x treatment interaction. The response variable was redband trout density. To the model we added additional a priori selected continuous covariates and interactions, if appropriate. The covariates selected for two of our models were derived from the literature and based on habitat variables thought to influence trout distribution (Fausch 1988; McMahon et al. 2007). Our third model covariates were selected based on the output from our NMS habitat analysis. Here we selected the three habitat variables most strongly correlated with trout occurrence. Redband trout length was a continuous covariate used to control for size-density dependence.

Candidate models:

Model 1: redband trout density=(year) (treatment) (year*treatment) (average redband trout length) (% gravel) (elevation).

Model 2: redband trout density=(year) (treatment) (year*treatment) (average redband trout length) (wood) (obstructions) (% sand).

Model 3: redband trout density=(year) (treatment) (year*treatment) (average redband trout length) (% cobble) (% sand).

Population nested within each sub-basin was the random factor used to assess variability based on differing populations and sub-basins. Again, individual models for both Chewaucan and Fort Rock were run where the random factor was population. No transformations were necessary as each model met assumptions of normality and homogeneity of variance. To assess whether sympatric sites had overall higher trout densities than allopatric redband sites we used a similar mixed linear ANCOVA model. Here, the response was total trout density, fixed factors were treatment, year, treatment x year, and the average redband trout length was the covariate.

Habitat comparisons

We used non-metric multidimensional scaling to determine if the collective habitat variables in stream sections with allopatric redband trout differed from sympatric locations (Kruskal 1967; McCune and Meford 1999). We used Proc Corr in SAS 9.1.3 to identify and remove highly correlated variables to reduce multicollinearity. We performed NMS on the reduced habitat variables using Euclidean distances with each variable relativized by adjusting to the standard deviate. We used Monte Carlo simulations with 250 iterations to calculate final stress, stability, and dimensionality of data. Final dimensionality of the ordination was assessed by comparing the results of the final stress for each dimension with that of the randomized data. We chose the ordination where the maximum number of dimensions had significantly lower stress than randomized data based on Monte Carlo text of significance (McCune and Meford 1999). We rotated the ordination such that the maximum variation was loaded on the first axis. We used correlation coefficients of habitat variables to the ordination axes to describe the relationship of redband trout in sympatry and allopatry in habitat space.

In addition to NMS, we used multivariate analysis of variance to identify whether allopatric redband trout locations differed from sympatric redband trout and brook trout locations in terms of wood, obstructions, and amount of sand; these are surrogate habitat variables that are often associated with brook trout occurrence (Fausch 1988). For the multivariate analysis, we

adjusted each habitat variable using a log transformation, to meet the assumption of normality. We performed this analysis on each sub-basin separately.

Fish density and community structure

We calculated fish density (fish/m^2) of age-1+ redband and brook trout in each sub-basin at each sample site (Zippin 1958). To determine whether the collective fish community structure differed in sympatric and allopatric redband trout locations we used non-metric multidimensional scaling (NMS) on the presence or absence of fish at each site, separately for each sub-basin (Kruskal 1967; McCune and Meford 1999). We conducted this analysis using Sorensen's distance measure and a random starting configuration. The data were run 50 times and a Monte Carlo simulation test was conducted using 250 iterations of randomized data to calculate final stress, stability, and dimensionality. We ordinated each sub-basin separately. Each ordination was rotated such that the maximum of the variation was loaded on the first axis. We overlaid a matrix including physical habitat measures of each sample site on this NMS ordination to identify correlations between species composition and habitat characteristics.

Results

Length analysis

The overall model, as well as individual Fort Rock sub-basin model, indicates that the average lengths of age 1+ redband trout were significantly smaller at sympatric locations than in allopat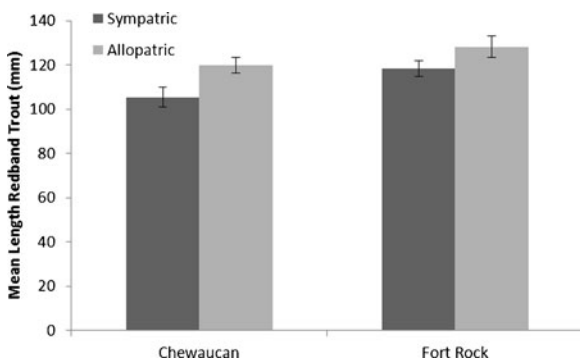ric locations (Fig. 2) (Overall basin-wide model: $F=6.04$, $df=1,55$, $p=0.02$; density of redband: $f=13.75$, $df=1,55$, $p=0.0005$; Individual Fort Rock: $F=4.57$, $df=1, 32$, $p =0.04$; redband density: $F=17.11$, $df=1,32$, $p=0.0002$, respectively). No interaction term in any model was significant. In the Chewaucan sub-basin model, no variable was significant but the variance among the populations was three times the residual variance (population=775 versus residual=247) suggesting there is high variability in the Chewaucan populations. Covariance estimates were large suggesting unmeasured factors were important influences on the length of redband trout besides parameters included in these models.

Density analysis

Across years, densities of age 1+ redband trout were significantly higher at allopatric sites (Fig. 3). Year and treatment were significant factors in models one (Year: $F=9.52$, $df=3,60$, $p<0.0001$; Treatment: $F=5.69$, $df=1,60$, $p<0.0001$) and two (Year: $F=9.37$, $df=3,59$, $p<0.0001$; Treatment: $F=4.59$, $df=1,59$, $p =0.04$). However, only the significant covariates were average length of redband trout ($F=19.39$, $df=1,60$, $p<0.0001$), % gravel ($F=4.82$, $df=1,60$, $p =0.03$) and elevation ($F=6.05$, $df=1,60$, $p =0.02$). In both sub-basins, the largest redband trout were found at sites with the lowest densities (Fig. 4a). No brook trout were found where redband trout average length exceeded 184 mm. Brook trout were present at most elevations (Fig. 4b) and across sites that varied in percentage of gravel (Fig. 4c).

The significance of the interaction terms in overall model three, between sub-basin and percent cobble suggested that this analysis should be performed separately for each sub-basin. In Fort Rock, treatment, year,
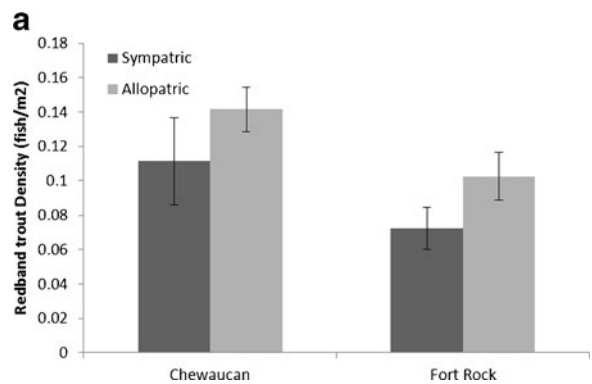

Fig. 2 Mean (SE) total length of redband trout (mm) in locations of sympatry with brook trout versus allopatry for the southeastern Oregon Chewaucan and Fort Rock sub-basins.

Fig. 3 Mean (SE) Redband trout density (fish/m^2) in locations of sympatry with brook trout versus allopatry for the southeastern Oregon Chewaucan and Fort Rock sub-basins
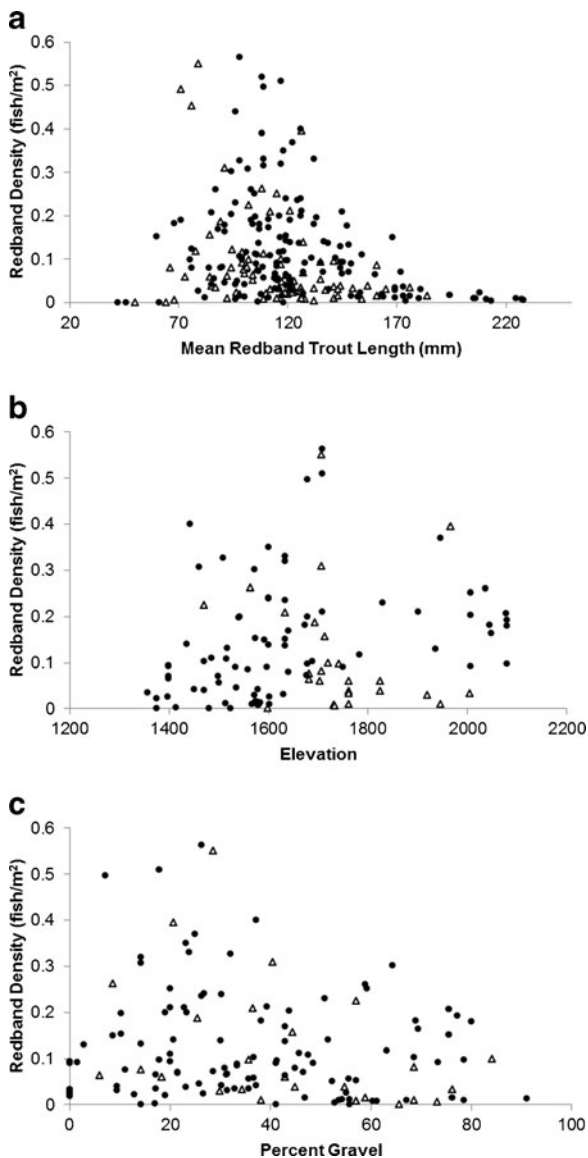
Fig. 4 Scatter plots of redband trout density (fish/m²) for redband trout in allopatry (*black circle*) and in sympatry (*white triangle*) with brook trout and (**a**) mean redband trout total length (mm) for both the Chewaucan and Fort Rock sub-basins in southeastern Oregon, and (**b**) elevation and (**c**) percent gravel for the Chewaucan sub-basin

and average redband trout length were significant in both models (Table 1). No habitat covariates were significant in any model suggesting that the habitat at redband trout locations in the Fort Rock sub-basin was more homogenous than in Chewaucan. In Fort Rock, redband trout densities were significantly higher at sites void of brook trout in all models (Table 1). In the Chewaucan, treatment and year effects were not

significant; only % gravel and elevation in Model 1, average length of redband trout in Model 2, and % cobble in Model 3, were significant (Table 1). Brook trout occurred at range of elevations, though they were not as common at lower elevations (>1,600 m).

Total trout density (age 1+) was greater at sympatric sites in most years of the study, although the magnitude of the difference differed each year (Fig. 5). When the outlier year 2007 was excluded from the analysis, the interaction term was no longer significant. In 2008–2010, densities of the fish at sympatric sites were at least twice that of allopatric sites. Sites with larger fish typically had lower densities. However, within sympatric sites when the response was total trout density, the length of redband and brook trout were not significantly different (Fig. 6). The difference in total trout densities between sympatric and allopatric sites does not appear to be the result of sites being filled with small brook trout.

Habitat comparisons

The final dataset used in this analysis included cross sectional area, wood, aggregates, maximum depth, obstructions, and percentages of sand, gravel, cobble, and boulder. A 3-dimensional solution was realized (final stress: 13.37). Stress between 10 and 20 represent satisfactory solutions, with values closer to 10 being considered better representations (McCune and Meford 1999). Axes 1 and 3 described 68 % of the variability in the data, and the axis 2 an additional 22 %. Axis 2 was represented by obstructions (r^2=0.38) and gravel (r^2=0.38). The variables most strongly correlated with axis 1 were cobble (r^2=0.66) and sand (r^2=0.63), while those for axis 3 were cross-sectional area (r^2=0.46) and aggregates (r^2=0.40). We found no consistent differences (based on visual interpretation of ordination space plots) in habitat between sites in which redband trout occurred alone or co-occurred with brook trout. This pattern held true for individual sub-basin ordinations.

Multivariate analysis results suggested that the amount of wood, obstructions, and sand differed significantly between sites with allopatric redband trout and sites with sympatric redband trout and brook trout in the Fort Rock sub-basin (wood: F=3.85, df=2, 121, p=0.002; obstructions: F =3.58, df=2, 121, p=0.03; sand: F=5.72, df=2, 121, p=0.004). Within the Chewaucan, the amount of wood appeared to influence analysis outcomes (wood: F=20.03, df=2, 111, p<0.0001) but obstructions and percent sand were

Table 1 Allopatric and sympatric redband trout density analyses were performed for each sub-basin separately. Density of redband trout are calculated from 2-pass depletion surveys and cross-sectional area of the stream. Regression analyses were performed initially to test for the interaction between covariates (redband trout size and habitat characteristics), year, and treatment. Interactions were only significant in the overall model that

combined both basins (results not shown). Since no other interaction was significant (α=0.05) then the interaction was removed from the analysis and we proceeded with an ANCOVA model without the covariate interaction terms. No transformations of the data were necessary since it met assumptions of normality and homogeneity of variance. Bolded values are statistically significant at α =0.05

Effect	DF	F value	Pr > F	Effect	DF	F value	Pr > F
Model 1: Chewaucan				Model 1: Fort Rock			
Year	3,30	0.74	0.542	Year	3,30	15.92	**<.0001**
Treatment	1,20	2.94	0.102	Treatment	1,30	6.4	**0.017**
Treatment × year	3,20	0.11	0.955	Treatment × year	3,30	0.71	0.554
Mean length RT	1,20	3.06	0.096	Mean length RT	1,30	17.05	**<0.001**
Elevation	1,20	10.07	**0.005**	Elevation	1,30	0.03	0.866
Percent gravel	1,20	11.36	**0.003**	Percent gravel	1,30	0.05	0.832
Model 2: Chewaucan				Model 2: Fort Rock			
Year	3,19	1.69	0.202	Year	3,29	14.21	**<.0001**
Treatment	1,19	1.06	0.316	Treatment	1,29	6.11	**0.020**
Treatment × year	3,19	0.11	0.955	Treatment × year	3,29	0.64	0.595
Mean length RT	1,19	4.16	**0.056**	Mean length RT	1,29	19.21	**0.001**
Wood	1,19	0.2	0.662	Wood	1,29	0.14	0.716
Percent sand	1,19	0.89	0.356	Percent sand	1,29	0.25	0.619
Obstructions	1,19	0	0.972	Obstructions	1,29	1.17	0.288
Model 3: Chewaucan				Model 3: Fort Rock			
Treatment	1,20	3.88	0.063	Treatment	1,30	6.57	**0.016**
Year	3,20	1.54	0.235	Year	3,30	15.7	**<.0001**
Treatment × year	3,20	0.11	0.955	Treatment × year	3,30	0.73	0.542
Mean length RT	1,20	3.64	0.071	Mean length RT	1,30	16.92	**0.001**
Percent cobble	1,20	8.56	**0.008**	Percent cobble	1,30	0.4	0.530
Percent sand	1,20	2.86	0.106	Percent sand	1,30	0.04	0.849

non-significant (obstructions: F =2.6, df=2, 111, p=0.12; sand: F=0.25, df=2, 111, p=0.78). Generally,

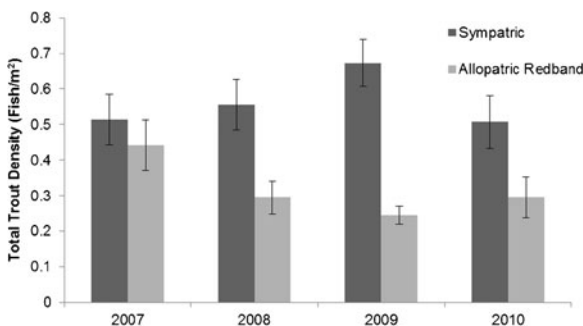in both sub-basins, sympatric sites tended to have more wood (Fig. 7a). Redband trout in allopatry were found

Fig. 5 Mean (SE) total trout density (fish/m^2) of redband and brook trout in sympatry and redband trout and allopatry by year for both Chewaucan and Fort Rock sub-basins of southeastern Oregon combined
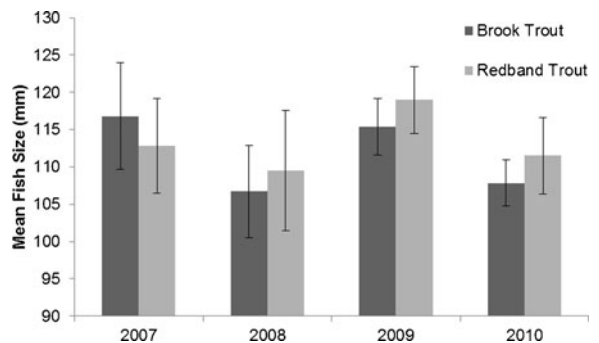

Fig. 6 Mean (SE) trout total length (fish/m^2) of redband and brook trout when in sympatry by year for both Chewaucan and Fort Rock sub-basins of southeastern Oregon combined.

in areas with slightly less wood, obstructions, and percent sand than their sympatric counterparts in the Fort Rock (Fig. 7a–c).

Fish community structure

In addition to redband trout and brook trout, species composition of the Chewuacan sub-basin included

Fig. 7 **a** Fort Rock and Chewaucan mean (SE) count of wood, Fort Rock (**b**) mean number of obstructions, and (**c**) mean percentage of sand per site in locations of sympatric redband and brook trout and allopatric redband sites. Site length averaged 70 m

speckled dace (*Rhinichthys osculus*), and tui chub (*Siphateles bicolor thalassinus*); Fort Rock included redband trout, black bullhead (*Ameiurus melas*), brown bullhead (*Ameiurus nebulosus*), brook trout, speckled dace (*R. osculus*), tui chub (*S. bicolor thalassinus*), and largemouth bass (*Micropterus salmoides*). These fishes were used to assess fish community structure in our ordination.

In the Fort Rock and Chewaucan sub-basins, two-dimensional solutions were realized where the axes represented 70 % and 89 %, respectively (final stress: 5.48 Fort Rock, and 6.24 Chewaucan). Though in both ordinations dace (*R. osculus*) were strongly correlated to axis 1 (r^2=0.90) and Tui chub (*S. bicolor thalassinus*) to axis 2 (r^2=0.82), there was no difference in fish community structure between sites with allopatry and sympatry.

Discussion

This study yielded several important insights into the relationship between non-native brook trout and redband trout in the southeastern Oregon portion of the Great Basin. First, consistent with our hypothesis, the mean length and densities of redband trout were larger and higher at locations void of brook trout; though larger fish were typically found in sites with lower trout densities both in sympatry and allopatry. Density-dependence appears to have a large effect in this system, but it is unclear at what life stage these inter-specific (or intra-specific) effects occur and through what mechanism. Second, although redband trout densities were significantly lower in sympatric locations in most years of the study, total trout density in sympatric sites was nearly twice that of locations that supported only redband trout. Competition and predation (both intra and inter specific) are typically coupled with abiotic and biotic factors that influence the dynamics and interactions within a population (Amarasekare 2003; McGrath and Lewis 2007; Pess et al. 2011). Sympatric sites generally have more wood than allopatric sites; however, this pattern was only significant in the Chewaucan sub-basin. Finally, brook trout and redband trout inhabit sites with similar fish community structure regardless of whether they occur in allopatry or in sympatry.

Total trout density was higher in sympatric sites than when redband trout were allopatric of brook trout.
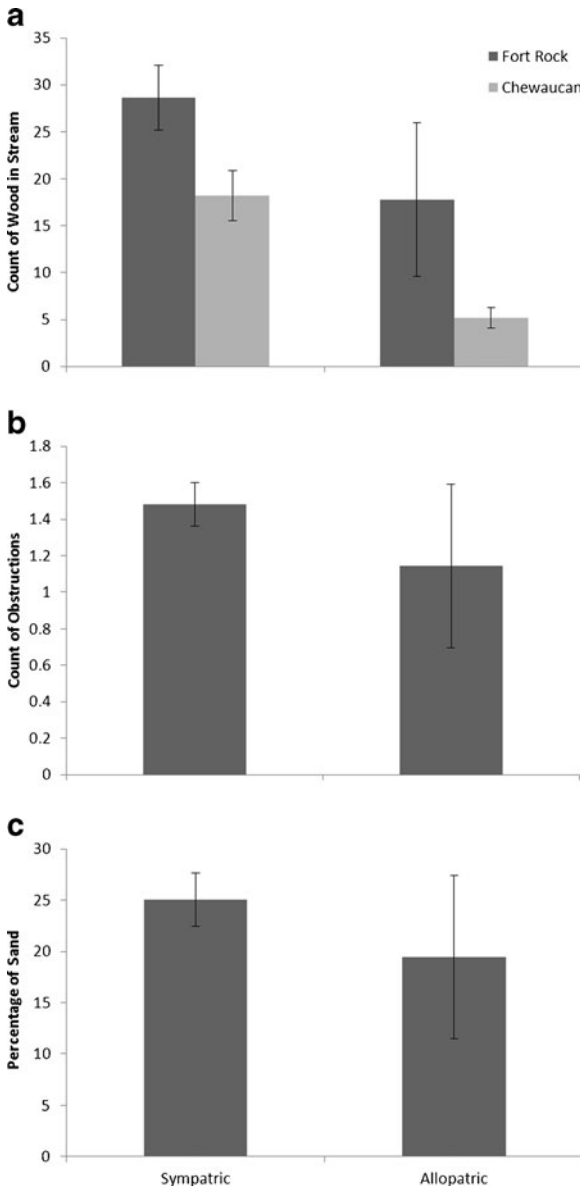
This is consistent with Benhke's (1992) observations of higher overall trout density at sympatric sites and provides some evidence for resource partitioning, or interactive segregation, between species at the micro or macro habitat scale (Bisson et al. 1988). We did not sample microhabitat (e.g., depth, temperature) or macrohabitat features (e.g., pools, riffles) as it correlates to fish density at a scale smaller than reach level. Thus, we can only speculate that segregation is occurring at a level smaller than stream reach. Differences in feeding behavior could account for occupancy of different niches (Mundie 1969). Salmonids typically have similar diets but coevolved species commonly partition resources and occupy different niches. Native sympatric species have evolved mechanisms for partitioning food and habitat resources where each exploits a subset of the available resources thereby reducing the overall potential for direct interaction (Ross 1986). When species are brought together through introductions there is a greater potential for resource use overlap (Fausch 1988) that can result in coexistence through resource partitioning (Amarasekare 2003). Other studies (see Korsu et al. 2009) suggest that establishment of brook trout is mainly due to the availability of niche space, rather than as a result of interspecific competition. Investigation into whether resource partitioning is occurring and if the contributing mechanisms might be diet overlap or underutilization of niche space, or whether it is temporal in nature, could help account for the higher than average total density at these sympatric sites.

Considering the reciprocal case of rainbow trout invasion in the native range of brook trout, Moore et al. (1983) studied the standing crop of brook trout in sympatry and allopatry with non-native rainbow trout in streams of Great Smoky Mountain National Park. This study was undertaken as a management action to determine the feasibility and effectiveness of rainbow trout removals as a native species stream rehabilitation program. Here they found that removal of non-native rainbow trout allowed for an increase in standing crop of brook trout. Although the data from the Moore et al. 1983 study are limited (10 sites), a comparison of standing crop (kg/ha) of sympatric to allopatric sites suggest no difference between these stream sections. Here no significant difference was detected in the mean standing crop (kg/ha) of rainbow and brook trout when in sympatry in selected sections of Great Smokey Mountain National Park streams

(1978–1979) (t-test: $df=10$, $p=0.37$). Current data from Smoky Mountain National Park (unpublished data, Moore and Kulp) comparing allopatric brook trout sites from sites sympatric with rainbow trout further suggest that brook trout densities were significantly lower in sympatric sites (ANOVA $F=23.15$; $df=1$, 51; $p=0.0008$) but did not differ in total trout density ($p=0.26$). These results differ from ours and suggest that reciprocal systems undergo a different pattern or process of species interactions. In this reciprocal system rainbow trout displace native brook trout and little resource partitioning appears to occur. Benhke's (1992) hypothesis of increased standing crop of trout, while well supported in western systems, may not reflect a true generalization to all North American trout streams. In the case of non-native rainbow trout introduced into native brook trout streams, habitat may play a more important role in the relationship of these fishes.

We found evidence for differences in site-level macro-habitat use (wood) between redband and brook trout but no evidence for differences in fish community composition based on fish presence/absence data. Neither region-wide nor sub-basin level ordinations yielded strong evidence of differences in habitat use between the species. However, smaller sub-basin level multivariate analysis suggested sympatric locations generally had higher counts of wood in both sub-basins. Several studies (see Cunjak and Green 1983; Butler and Hawthorne 1968) suggest that brook trout tend to prefer low velocity pools (e.g., higher percentages of sand) adjacent to cover (e.g., more obstructions and wood) more than rainbow trout (Smith and Li 1983). In small streams during low flow, water depth and distance to cover are therefore likely factors that differentiate between brook and rainbow trout habitat selection (Magoulick and Wilzback 1997). Coexistence in more homogenous environments often occurs via mechanisms independent of spatial variation and likely operates at smaller scales where differences in the biotic or abiotic community tend to exist (Amarasekare 2003; Pess et al. 2011). However, our sampling methods did not have the resolution to capture microhabitat or macrohabitat level differences that were present.

While it is clear that brook trout and redband trout can tolerate a sympatric existence, both species may have different life history strategies that would

encourage spatially and temporally different habitat selection and preference at different life stages. Though we did not find larger scale habitat use patterns this could be based simply on the possibility that we were looking at a life stage where the impacts of competition between species occur is less evident (Peterson and Fausch 2003a). During invasions of rainbow trout into native brook trout systems, early life stage dynamics, including density dependence, appear to be the key to understanding mechanisms of competitive exclusion in brook trout (Clark and Rose 1997). However, it is equally likely that patterns of habitat use become more distinct as trout age. Focusing on sexually mature fish may elucidate these patterns. Allopatric redband trout locations in Buck and Silver creek sites in the Fort Rock and the Chewaucan River sites in the Chewaucan may still have indirect effects from brook trout in adjacent areas; absence does not expressly imply that brook trout are not there in other times of the year or at different life stages. Here we only infer the effects of age 1+ brook trout during the summer distribution of redband trout. Further investigation into early life stage dynamics and competitive studies may help to elucidate density-dependence processes at work in this system.

Evolutionary theory predicts that native species should be better adapted to local conditions in the native range than species that are introduced (Poff 1997). Yet, non-native species often displace native species with a long evolutionary history to the local environment (Fausch 2008). Brook trout displace native cutthroat trout in western inland waters but are displaced by non-native rainbow trout in southeastern US. It appears that, at the limits of their range, native species are poorly adapted to disturbance that, by chance, the non-native is pre-adapted to (Fausch 2008). While brook trout are particularly effective invaders in western US streams (Behnke 1992; Peterson et al. 2004), after over 70 years of naturalization their invasion did not result in extirpation of redband trout through the entire range they were introduced. They do however influence native redband trout by reducing local size and abundance. Mechanisms that drive stream salmonid populations likely operate at large spatio-temporal scales (Gowan and Fausch 1996; Rieman and Dunham 2000; Fausch et al. 2002; Wenger et al. 2011). Thus, studies performed at the level of individual sites may not explain population level patterns. Large-scale studies of in stream fish are challenging due to variations in behavior, age-structure and longevity of fish –large-scale longer-term experiments are needed to measure and understand their impacts on native fish (Peterson et al. 2004). Based on our large-scale four year study, we conclude that although brook trout and redband trout can survive in sympatry and that these species are clearly able to reduce their overlap in resource use in some cases, brook trout do indeed have a negative effect on redband trout size and density.

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