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Have Introduced Brown Trout (*Salmo Trutta*) Affected Native Aquatic Vertebrates in Western United States Streams?

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HAVE INTRODUCED BROWN TROUT (*SALMO TRUTTA*) AFFECTED NATIVE
AQUATIC VERTEBRATES IN WESTERN UNITED STATES STREAMS?

by

Nora K. Burbank

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2011

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ABSTRACT

Have Introduced Brown Trout (*Salmo Trutta*) Affected Native Aquatic Vertebrates
in Western United States Streams?

by

Nora Burbank, Master of Science

Utah State University, 2011

Major Professor: Dr. Charles Hawkins
Department: Watershed Sciences

The introduction of exotic species is one of the greatest threats to freshwater biodiversity. Brown trout are native to Eurasia, but have been introduced to much of the rest of the world, including the United States. In other parts of their introduced range, brown trout have caused substantial negative effects to native species' abundances and distributions, and have altered the structure of some aquatic communities. In the United States, studies of some streams and watersheds have shown that brown trout can negatively affect native species, but I found no study that considers the effect of brown trout across a large portion of their introduced range.

For this study, I examined if (1) the abundance and distribution of two ecologically different native fish taxa (sculpins and speckled dace) and (2) the structure of entire stream vertebrate assemblages were negatively associated with the presence and abundance of brown trout. I based my analyses on existing, standardized survey data

collected across streams of the western United States. I found no relationship between brown trout and the abundance, presence-absence, or probability of detection of sculpins or speckled dace. I also found that brown trout were not associated with the structure of native stream vertebrate assemblages. My results imply that native stream vertebrates in western US streams are able to coexist with brown trout across the western United States, despite the negative effects brown trout can have on some taxa in individual watersheds or rivers.

(58 pages)

PUBLIC ABSTRACT

Have Introduced Brown Trout (*Salmo Trutta*) Affected Native Aquatic Vertebrates
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The introduction of exotic species to areas outside of their native range is one of the greatest threats to the biodiversity of native freshwater organisms. Exotic species have outcompeted native species for resources such as food and shelter, and in some cases these interactions have resulted in local extinctions or reductions in abundance of those native species. Brown trout are native to Eurasia, but have been introduced to much of the rest of the world, including the United States. In some parts of their introduced range, brown trout have substantially reduced the abundance and home ranges of some native fish species. In the United States, brown trout have been intentionally stocked in many streams and rivers across the country because they are a desirable sport fish. A few studies have shown that these fish negatively affect some native fish species. However, I found no studies that considered the effect of brown trout on native species across a large portion of their range in the United States.

For my thesis, I examined if the presence and abundance of brown trout have affected (1) the abundance, presence, and distribution of two ecologically different native fish taxa (sculpins and speckled dace) and (2) the composition and relative abundances of entire assemblages of native stream vertebrates in streams across 12 western United States. I found no relationship between brown trout and the abundance, presence or absence, or distribution of either sculpins or speckled dace. I also found that brown trout were not associated with differences in the composition of the native stream vertebrate assemblages. My results imply that native stream vertebrates are able to successfully coexist with brown trout across the western United States, and therefore may not experience the extreme changes in abundance or distribution that some exotic species may cause.

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CHAPTER I

INTRODUCTION

Biological invasions are one of the greatest threats to biodiversity and the persistence of threatened species (Allan and Flecker 1993; Sakai et al. 2001; Dudgeon et al. 2006), and the widespread introduction of exotic species into freshwaters is considered one of the greatest threats to these ecosystems (Dudgeon et al. 2006). Exotic fishes may be introduced by humans unintentionally through accidental releases or intentionally through stocking for either recreation or as biological controls of pest species (Lockwood et al. 2007; Gozlan et al. 2010). Exotic species are often novel predators and competitors in the ecosystems to which they are introduced, and they can be especially threatening because native species often lack the behaviors and adaptations necessary to avoid harm. For example, introduction of piscivorous Nile Perch (*Lates niloticus*) to Lake Victoria contributed to massive declines and extinctions of over 200 endemic cichlid species (Goldschmidt et al. 1993; Kitchell et al. 1997). Two common themes exist in the literature regarding the invasion process and the effects of exotic species on native ecosystems. The first is that the effect of the introduction of new species on the receiving ecosystem is variable. Second, the invasion of an exotic species into a new area is a stepwise process that begins with establishment and can end with major impact.

Species invasions are common although the effects of these species on the native ecosystem are variable. Williamson (1996) argues that of all the species introductions that occur, only 10% will result in successful establishment in the new habitat; and only 10% of those will result in severe negative effects on the receiving ecosystem, a

contention that is supported by other authors (Lodge 1993; Simberloff 2007; but see Jeschke and Strayer 2005 for a contrasting view). Therefore, it is important to understand not only the process by which successful invasions occur, but also the processes that hinder successful invasions.

The invasion of a species into a new area is a stepwise process that begins with initial introduction and has variable end stages (e.g. Williamson 1996; Shea and Chesson 2002; Lockwood 2007; Nentwig 2007). Different authors emphasize different steps as important in their conceptual frameworks of the invasion process. For example, Shea and Chesson (2002) argue that there are two stages of the invasion process: 1) transport of the species to the new area, and 2) establishment and population increase in that new area. Alternatively, Williamson (1996) posits that there are four main stages in the invasion process: arrival and establishment, spread, population equilibrium, and effect on the native ecosystem.

From a management perspective, a useful conceptual framework of the invasion process includes establishment in the new area, interactions with the native ecosystem, and effects on the native ecosystem (Figure 1). Interactions with the native ecosystem are differentiated from major negative effects because while all introduced species will interact with the receiving ecosystem, not all will cause severe negative ecological or economic effects (Williamson 1996; Simberloff 2007). It is important to identify the effect that the introduced species is having on the receiving ecosystem to effectively manage the introduced species and native ecosystem.

Following initial introduction, the first step in the invasion process is establishment in the new area, which occurs if the introduced species forms a self-sustaining population that persists by natural reproduction (Gozlan et al. 2010). The reason few introductions result in establishment is likely associated with the specific factors, both abiotic and biotic, that affect habitat suitability. Once established, the introduced species may also spread to new areas, and become established at those places. Spread can be natural, but is often facilitated by human activities, such as stocking for recreational purposes, such as angling (Taylor et al. 1984).

Although we do not completely understand the relative influence of biotic and abiotic factors in allowing exotic species establishment (Moyle and Light 1996), it is widely recognized that aspects of both the receiving environment and community are important. For establishment to occur, the receiving environment must be suitable for the survival of all life stages, and sufficient food resources must be available (Townsend 1996). Within areas of suitable environmental conditions, some aspects of the receiving community may facilitate establishment. For example, introduced species are more likely to become established in locations that do not already contain potential predators or strong competitors (Townsend 1996; Sakai 2001). Additionally, members of species-poor communities are thought to be maladapted to multiple predators and competitors, thus making these communities more susceptible to invasion (Lodge 1993; Townsend 1996).

Successful invaders often possess several common biological and ecological traits. First, large founding population size appears to promote successful establishment,

especially given multiple introduction attempts (Williamson 1996; Kolar and Lodge 2001). Species with wide native environmental or geographic ranges are thought to be more successful invaders because of a presumed wide tolerance of multiple different habitat conditions (Townsend 1996). Lawton and Brown (1986) also observed a positive correlation between body size and establishment success of vertebrates, which may be due to the fact that larger animals tend to have fewer predators (Townsend 1996).

Animals with broad food niches also tend to be successful invaders, as do those with a high reproductive output and multiple reproductive events per female (Townsend 1996).

Once established, introduced species may interact with the receiving ecosystem in several ways. Exotic species may introduce new parasites and diseases, hybridize with natives (which can reduce fitness of native species), and compete with or predate on natives (Taylor et al. 1984). These interactions may not always be negative, or may be relatively minor, allowing native taxa to coexist with the introduced species. For example, Nasmith et al. (2010) studied the effect of stocked non-native trout on native fish in several lakes in Alberta, Canada. Dace (*Phoxinus* spp.) altered their feeding behavior in the presence of trout, and their size structure in stocked lakes was consistent with size limited predation. However, these effects did not result in any detectable change in the abundance of the dace, prompting the authors to conclude that the stocking of trout can be compatible with the persistence of healthy native fish populations. Thus, some introduced species are able to coexist with native species without causing major negative effects.

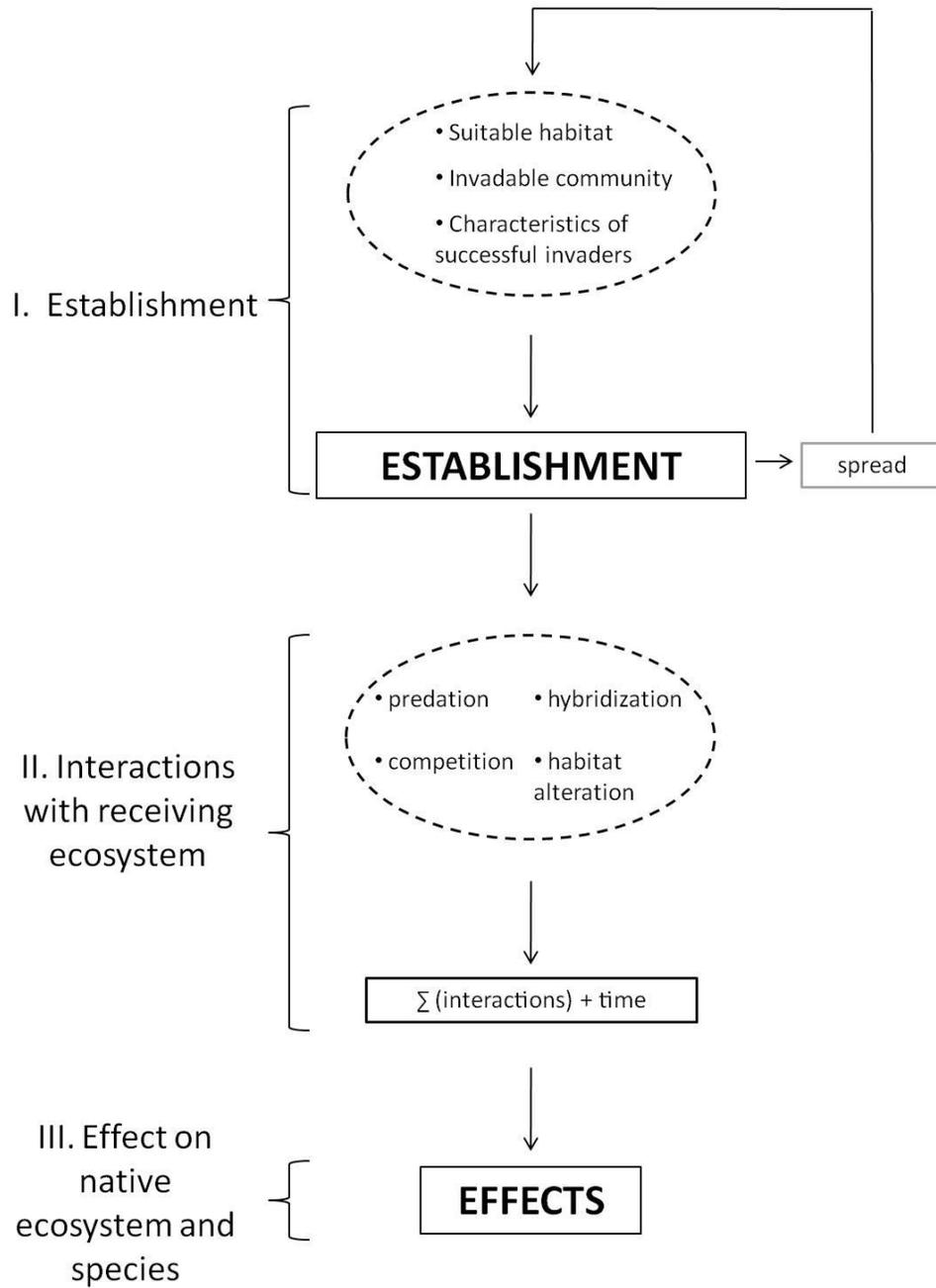


Figure 1. Conceptual framework outlining the invasion process.

In the context of native species conservation, it is important to differentiate between interactions and subsequent effects that allow native species to coexist with introduced species (such as those outlined in the above section) and those that do not allow for coexistence (such as extirpations or substantial reductions in abundance). Population and individual growth rates, abundance, distribution, behavior, and species richness and diversity are commonly measured in studies that assess the potential effect of introduced species on native individuals and communities (Lodge 1993; Williamson 1996; Parker et al. 1999).

Definition of problem

In the United States, freshwater fauna have shown alarmingly high rates of extinction (Miller et al. 1989; Taylor et al. 1996; Ricciardi and Rasmussen 1999) and increasing rates of imperilment (Lannoo 2005; Jelks et al. 2008) over the last century. Threats to freshwater fauna include habitat alteration and destruction, pollution, flow modification, but the introduction of exotic species presents a particularly important threat because once an exotic species has successfully established, there is little hope for eradication (Allan 1995; Richter 1997; Dudgeon et al. 2006).

Brown trout (*Salmo trutta*) are native to Eurasia, but because they are a valued sportfish have become widely established outside of their native range. They are such a successful invader that the World Conservation Union considers them to be one of the world's 30 worst invasive species (McIntosh et al. 2011). They possess many of the biological and ecological attributes that facilitate long-term survival in a new location,

such as a wide native range that includes a variety of suitable habitats, a generalist diet, a high reproductive output (e.g. up to 7,500 eggs per female; Becker 1983), and multiple reproductive events per female (Elliot 1994; Townsend 1996). These characteristics, combined with extensive stocking efforts, have facilitated the widespread introduction and establishment of brown trout in at least 29 countries outside of their native range (McIntosh et al. 2011). Brown trout are aggressive predators (Nillson 1963) that can negatively affect native fauna within their introduced range. Predation by introduced salmonids, including brown trout, has been implicated as a major cause of a decline in some native fishes (family Galaxiidae) in New Zealand (Townsend and Crowl 1991; McIntosh et al. 2010). Additionally, introduced salmonids, including brown trout, have become a majority component of the overall fish biomass and abundance in many Chilean streams (Soto et al. 2006; Arismendi et al. 2009). Native fish were not found in 40% of streams surveyed by Soto et al. (2006), and Arismendi et al. (2009) concluded that predation by introduced salmonids, including brown trout, caused a decline in the abundance of native fishes in six Chilean lakes.

Brown trout were first introduced to the United States in 1883, and through extensive stocking efforts have since become naturalized throughout most of the country (Becker 1983; Behnke 2002). In streams of the western United States, brown trout are now among the most widely distributed and abundant nonnative aquatic vertebrate species and have become incorporated into resident fish assemblages (Schade and Bonar 2005; Lomnický et al. 2007). Despite their widespread distribution, the study of the effect of brown trout on native fishes is relatively new - about 15 years (McIntosh et al.

2011). Brown trout are partially piscivorous in the United States (Hannuksela 1969; Stauffer 1977; He and Wurtsbaugh 1993), and considered superior competitors to some native fishes (McHugh and Budy 2005, 2006; Wang and White 1994). Brown trout have also been associated with reduced growth and abundance of some North American native fish species (Garman and Nielsen 1982; Zimmermann and Vondracek 2006), and have replaced native brook trout (*Salvelinus fontinalis*) in many streams of eastern North America (Waters 1983; Sorensen et al. 1995; Grant et al. 2002). Additionally, mountain yellow-legged frogs (*Rana mucosa*) in California are negatively associated with introduced trout, including brown trout (Knapp and Matthews 2000). These observations, coupled with their widespread distribution, known piscivory in the United States, and consistent negative associations with native fauna elsewhere, suggest that brown trout may be profoundly affecting native aquatic vertebrates across the western United States.

Our objective was to determine how severely brown trout have affected the abundance and distribution of native aquatic vertebrates in streams of the western United States. We approached this study in two ways. First, we used survey data to determine if the abundance and occurrence of two common native taxa, sculpins (*Cottus* spp.) and speckled dace (*Rhinichthys osculus*), were negatively associated with brown trout occurrence and abundance. These taxa differ in their life histories, behavioral ecology, and geographic distribution, but both are native to streams now occupied by brown trout (see *Sculpins* and *Speckled dace* below). For both taxa, we hypothesized that their abundances and probabilities of detection would be smaller at sites that contained brown

trout. Second, we tested the hypothesis that the structure of entire native aquatic vertebrate assemblages differs between streams with and without brown trout.

CHAPTER II

METHODS

Study area and data

The study area included 12 states in the western United States (Figure 2). We used aquatic vertebrate data collected from perennial streams and rivers by the United States Environmental Protection Agency's Environmental Monitoring and Assessment Western Pilot Project (EMAP). The EMAP project used a probabilistic site selection design and sampled a total of 1,361 sites in streams and rivers to characterize aquatic vertebrate assemblages and their associated local habitat characteristics within the study area (Figure 2; Stoddard et al. 2005; Lomnický et al. 2007). For each of these sites, the EMAP project recorded the completeness of the vertebrate sample as 'Failed', 'Insufficient', 'Yes-partial', or 'Yes-all'. To maximize sample comparability, we only used sites recorded as 'Yes-all,' resulting in a data set of 776 sites. A total of 136 native species were observed at these 776 sites, and counts were available for each species at each site. The species collected were predominantly fish (80%).

Habitat variables

For both the taxon-specific and assemblage-level analyses, we used candidate predictor variables that described physical and climate conditions at each site. The EMAP project collected a suite of habitat variables at each site, and we used 11 of these variables in our analyses (Table 1). In addition to the EMAP variables, we used PRISM climate data (Daly et al. 2000) and STATSGO soils data (Wolock 1997) to calculate 7

additional predictor variables that described precipitation and air temperature for each site's watershed (Table 1). These variables were considered because air temperature is strongly correlated with stream temperature (Mohseni et al. 1998), and fish distributions are often strongly associated with climate conditions (Heino 2002; Buisson et al. 2008; Griffiths 2010). Climate factors are also frequently used to describe and predict the suitability of fish habitat (Eaton and Scheller 1996; Rahel et al. 1996; Steen et al. 2010).

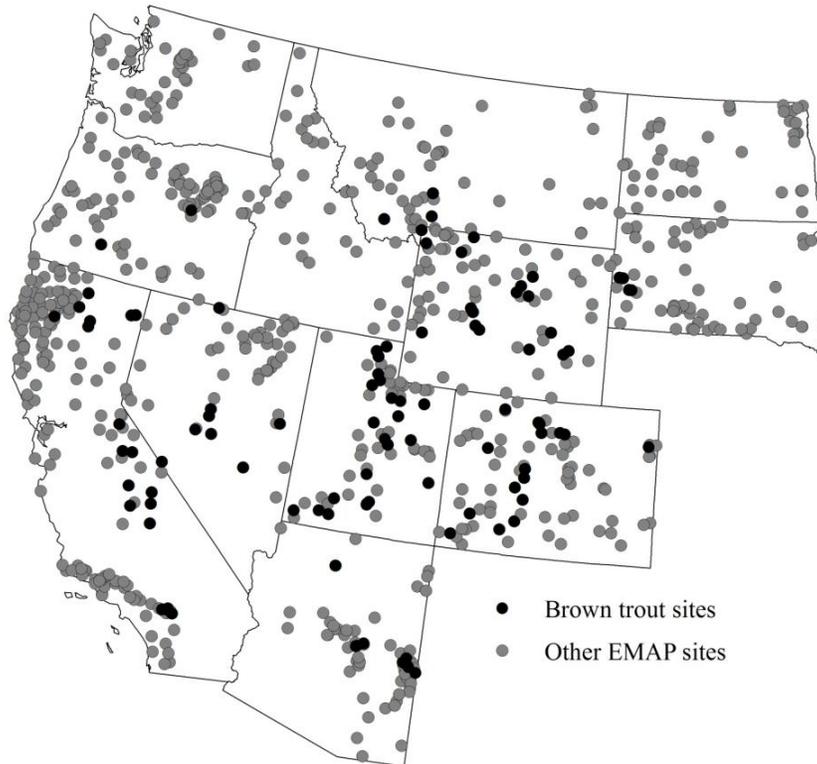


Figure 2. Locations of all 776 EMAP sample sites across the western United States. Black dots indicate sites where brown trout were captured.

Table 1. Description of the 18 habitat variables used in the principal components analysis, random forests models, and PERMANOVA analysis. EMAP variables and descriptions can be viewed and downloaded from http://www.epa.gov/wed/pages/models/EMAP_West_Data.htm; PRISM variables can be viewed and downloaded from <http://www.prism.oregonstate.edu/>; STATSGO variables can be viewed and downloaded from <http://soils.usda.gov/survey/geography/statsgo/>.

Variable	Unit	Description	Source
bankful width	m	Mean bankful stream width	EMAP
bed particle diameter	mm	Estimate of critical bed particle diameter at bankful stage	EMAP
elevation	m	Elevation at center of reach (m)	EMAP
fast habitat	%	% Fast water habitat (riffle and faster)	EMAP
full cover	fraction of reach	Ground, mid-canopy and canopy cover present	EMAP
organic matter	%	% Substrate as wood or detritus	EMAP
sand and fines	%	% Substrate \leq 16mm	EMAP
slope	%	Mean channel slope	EMAP
substrate diameter	mm	Mean streambed particle diameter	EMAP
width	m	Mean wetted width (m)	EMAP
width*depth	m ²	Mean width*depth product	EMAP
width/depth	m/m	Mean channel width-depth ratio	EMAP
woody and vegetation cover	cover	Riparian vegetation canopy cover + mid layer woody cover	EMAP
max temp	°C	Mean 1971-2000 annual maximum monthly air temperature for the watershed	PRISM
mean precip	mm	Mean 1971-2000 average annual precipitation values for the watershed	PRISM
mean temp	°C	Mean 1971-2000 annual average monthly air temperature for the watershed	PRISM
min precip	mm	Mean 1971-2000 minimum annual precipitation values for the watershed	PRISM
min temp	°C	Mean 1971-2000 annual minimum monthly air temperature for the watershed	PRISM
water table depth	m	Average depth to water table	STATSGO

Reduced datasets

Because brown trout are an introduced species, non-detections can represent absences caused by unsuitable habitat, locations where brown trout have not been introduced or established, or sampling error (i.e. a failure to detect their occurrence). Additionally, because brown trout continue to be stocked in the western United States, the detection of brown trout may not represent suitable conditions for brown trout establishment and long-term success. We therefore, restricted our analyses to only sites that had a high potential of being suitable habitat for brown trout. To identify suitable brown trout habitat, we used principal components analysis (PCA) to characterize the environments used by brown trout based on five environmental variables: elevation, long-term mean maximum and mean minimum annual air temperature of the watershed, channel slope and channel width (Table 1). Preliminary analyses demonstrated that these five variables were predictive of brown trout occurrence. Prior to analysis, we checked all variables for approximate normality by inspecting normal probability plots. Channel width was the only variable that required transformation ($\log_{10}(x+1)$). The PCA identified three main axes of habitat variation. These axes were associated with elevation and maximum air temperature (Factor 1), minimum air temperature and channel slope (Factor 2), and channel width (Factor 3). We then used the 102 sites where brown trout were collected to estimate habitat conditions that were likely to be highly suitable, defined here as those sites with factor scores between the 10th and 90th percentiles of factor score values associated with the 102 brown trout presences. This analysis identified 173 sites with a high potential for suitable brown trout habitat, 51 at which

brown trout were observed. This screening eliminated 50% of the sites where brown trout occurred, but should have identified those sites most likely to support established brown trout populations.

We also restricted our analyses to those sites that the native taxa could also potentially inhabit. To identify these sites, we selected sites from the 173 candidate sites described above that fell within the geographic range of each of the two target taxa. We defined the geographic range of native taxa to include any USGS sub region (Saber et al. 1987) that contained at least one site where the native taxon had been reported. These restrictions resulted in two separate datasets, one for sculpins (n=109 sites, hereafter the sculpin dataset) and another for speckled dace (n=110 sites, hereafter the speckled dace dataset).

Sculpins

Sculpins were widely distributed in the EMAP dataset, and occurred in 122 of the 776 sites. Sculpins are morphologically adapted to benthic environments (e.g. lack of a swim bladder; Fänge 1966), are predators that mainly consume benthic invertebrates but will also consume fish and fish eggs (Fitzsimons et al. 2006), and typically occur in cold waters across North America (maximum tolerable temperature 24.3°C; Eaton and Scheller 1996). We used genus-level data in our analyses because different species have generally similar habitat preferences and feeding strategies and many individuals in the dataset were only identified to genus. In addition, the taxonomy of sculpins is uncertain and there are likely many more individual species than are currently described (Kinziger

et al. 2007). Sculpins are often sympatric with brown trout in North America (Bailey 1952; Brown and Downhower 1982; Quist et al. 2004). Few studies have examined interactions between sculpins and brown trout, but brown trout are known predators of mottled sculpin in the Logan River, Utah (Wood 2008) and are an assumed prey item of brown trout in Lake Ontario, Canada (Jones et al. 1993; Jackson 1997).

Speckled dace

Speckled dace are native to streams and rivers of the western United States and have a wide geographic distribution. Speckled dace are habitat generalists and are found in habitats ranging from small creeks and isolated springs to rivers and in biomes ranging from deserts to mountains, but they prefer cool to cold water (Sigler and Sigler 1987; Moyle 2002). Within their native range, speckled dace often occur in streams and watersheds suitable for brown trout (Holden and Stalnaker 1975; Lanigan and Berry 1981; Erman 1986; Quist et al. 2004), and brown trout are a known predator of speckled dace in the Little Colorado River, AZ (Marsh and Douglas 1997). With the exception of Marsh and Douglas (1997), we are aware of no other studies that have documented interactions between speckled dace and introduced brown trout. However, brown trout predation is one proposed method for controlling populations of another dace-like species, *Phoxinus phoxinus*, which was introduced in Norwegian lakes (Museth et al. 2003). Additionally, predation by introduced trout, including brown trout, is known to negatively affect the growth and habitat use of dace (*Phoxinus* spp.) in several Canadian

lakes (Nasmith et al. 2010). The results of these studies suggest that brown trout have the potential to negatively affect the abundance and distribution of speckled dace.

Niche overlap with brown trout

To ensure that the sites selected in the reduced datasets were suitable for both brown trout and the native taxa, we qualitatively examined the overlap in observed niche space between brown trout and the two target taxa. We used all sites from the full EMAP dataset where sculpins were present, and examined the distribution of sites with and without brown trout in principal component ordination space (PC factors 1 and 2). PCA Factors 1 and 2 were selected because they contained the two temperature variables, and temperature is a strong limiting factor for fish (Eaton et al. 1995). We conducted the same analysis for speckled dace. The niche space of sculpins and brown trout almost completely overlapped (Figure 3), and only a slight difference existed in the niche spaces of brown trout and that of speckled dace (Figure 3).

Brown trout and the abundance and presence-absence of target taxa

To assess the effect of brown trout on the abundance of sculpins and speckled dace, we conducted two-sample t-tests on the abundances of the target taxa at sites where brown trout were present and absent. We first standardized counts as number of fish (i.e. sculpins or speckled dace) caught per meter of stream length. We transformed ($\log_{10}(x+1)$) these values to meet assumptions of normality.

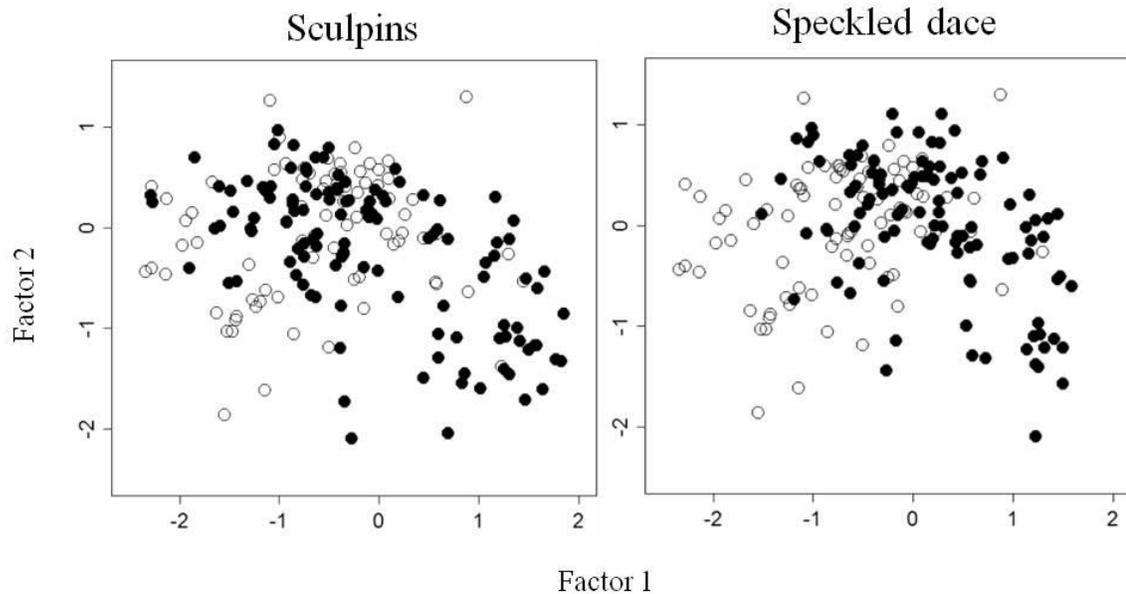


Figure 3. Scatterplots demonstrating the overlap in niche space between brown trout (open circles) and sculpins and speckled dace (black dots) as defined by PCA Factors 1 and 2.

We determined if the presence of each target taxon was associated with the presence of brown trout by testing if the frequencies of occurrence of the target taxa were independent from the occurrence of brown trout (Chi-square test; Zar 1999).

Niche models for target taxa

We used Random Forest (RF) models ('randomForest' package in R; R Core Development Team 2010) to quantify relationships between the probability of detection of the two target taxa and both brown trout counts (standardized as brown trout per meter stream) and habitat predictors. RF models were evaluated based on five performance metrics: percent sites correctly classified (PCC), sensitivity (the percent of presences correctly classified), specificity (the percent of absences correctly classified), Cohen's

kappa (κ), and the area under the receiver operating characteristic curve (AUC). Cohen's kappa is a measure of the agreement between modeled predictions and observations after chance agreement is accounted for, and ranges from -1 to +1, with +1 indicating perfect agreement and values ≤ 0 indicating no agreement better than chance (Cohen 1960). AUC measures the ability of the model to discriminate between sites where the species is present and sites where it is absent (Elith et al. 2006). The statistic ranges from 0 to +1, with +1 indicating perfect discrimination. RF models are especially useful in niche modeling because they capture non-linear and interactive relationships and are difficult to overfit (Cutler et al. 2007). RF output includes a measure of the relative importance of each of the predictor variables, and we used partial dependency plots (Cutler et al. 2007) to depict how the modeled probabilities of detection of the target species varied with each predictor after holding the effects of all other predictors constant.

Relationship between assemblage groups and brown trout

For the analysis of the association between native aquatic vertebrate assemblages and brown trout we also restricted the data to include only those sites with potentially suitable brown trout habitat. We defined assemblages as the native aquatic vertebrates, primarily fishes, that collectively inhabit a stream reach. We identified groups of biotically-similar sites by clustering (flexible beta UPGMA) sites based on similarity (Sorensen index) in taxon presence-absences. Prior to clustering, we removed rare taxa (<5 sites) because rare taxa generally produce noise in such analyses (McCune and Grace

2002). After selecting sites suitable for brown trout and removing rare taxa, the dataset consisted of 132 sites containing 17 taxa; 16 fishes and the tailed frog, *Ascaphus truei*. Brown trout were observed at 33 of these sites.

We used multivariate analysis of variance with permutations (PERMANOVA) to determine if the structure of the six assemblage groups was associated with the presence of brown trout. For each of the six assemblages, we tested if the assemblages observed at the sites were significantly different in the presence and absence of brown trout. We used the 'adonis' function in the vegan R statistical software package for this analysis (R Core Development Team 2010).

CHAPTER III

RESULTS

Brown trout and the abundance and occurrence of the target taxa

We found no relationship between brown trout presence and either the abundance or occurrence of the target taxa. Neither the two-sample t-test based on the abundances of the two target taxa (Table 2) nor the contingency table based on the presence-absence of brown trout and the presence-absence of the two target taxa (Table 3) were significant.

Brown trout and the target taxa niche models

Brown trout abundance was also not an important predictor of the probability of detecting either target taxon. The RF models for the two target taxa had similar performance, though they differed in the relative importance of habitat predictors (Table 4, Figure 4). Five habitat predictor variables were included in the final RF model for sculpins: channel width, width to depth ratio, mean annual air temperature, minimum annual air temperature, and percent of organic matter in the substrate (Figures 4 and 5, Table 1). When brown trout abundance was included in the model it was the least important predictor and did not improve model performance, as evident in its partial dependence plot (Figure 5).

For speckled dace, eight habitat predictor variables were included in the final RF model: mean annual precipitation, mean annual air temperature, maximum annual air

Table 2. Results of the two-sample t-tests on sculpin and speckled dace abundances including means (\log_{10} number/m), standard deviations (s.d.), number of sites (n), and p values.

		Mean	s.d.	n	p value
Sculpins	Brown trout	-1.47	1.1	27	0.69
	No brown trout	-1.56	0.9	82	
Speckled dace	Brown trout	-1.95	0.8	31	0.12
	No brown trout	-1.70	0.9	79	

Table 3. 2x2 contingency tables used to test the dependence of sculpin (a) and speckled dace (b) presence or absence on brown trout presence or absence. Chi square tests were not significant for either sculpin ($p=0.17$) or speckled dace ($p=0.80$).

a)

		Brown trout	
		Absent	Present
Sculpins	Absent	42%	10%
	Present	33%	15%

b)

		Brown trout	
		Absent	Present
Speckled dace	Absent	53%	20%
	Present	19%	8%

Table 4. Measures of prediction accuracy for the sculpin and speckled dace random forest models.

	PCC (%)	Specificity (%)	Sensitivity (%)	Kappa	AUC
Sculpins	77	76	78	0.54	0.81
Speckled dace	81	91	53	0.48	0.84

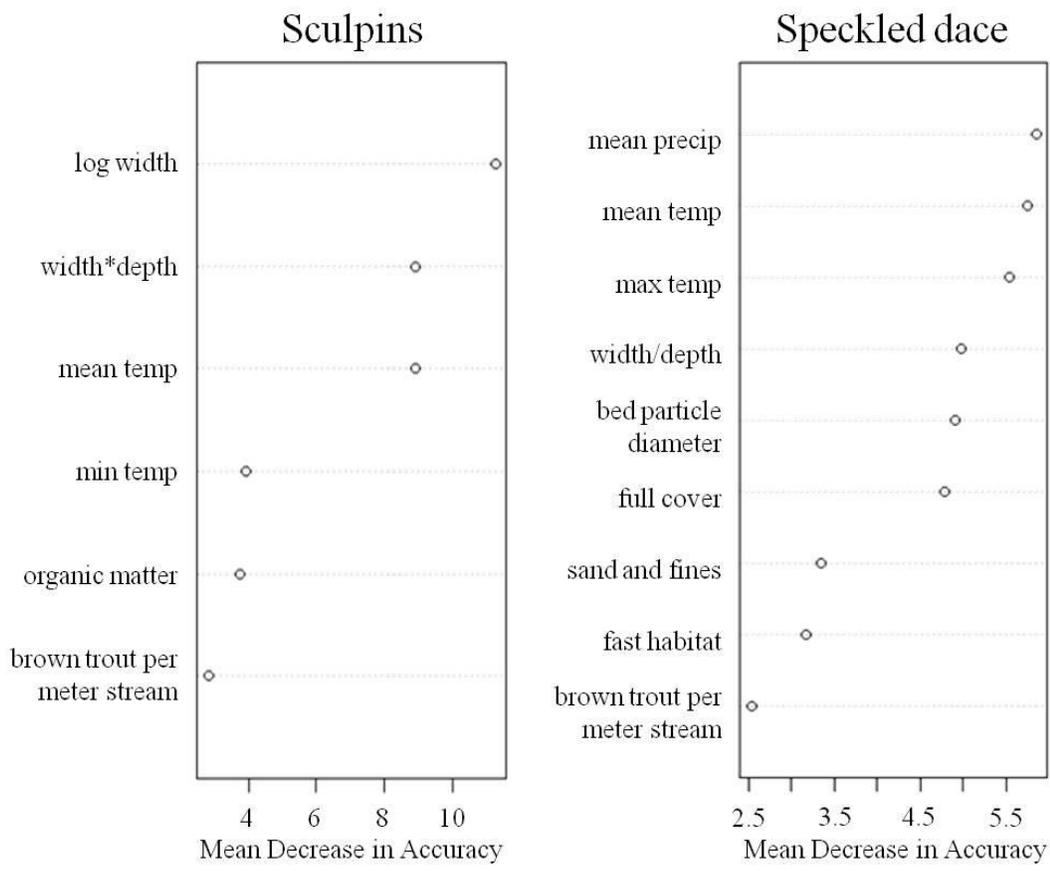


Figure 4. Variable importance plots for the predictor variables from the random forests models for sculpins and speckled dace. A higher mean decrease in accuracy indicates greater error when the variable is excluded from the model.

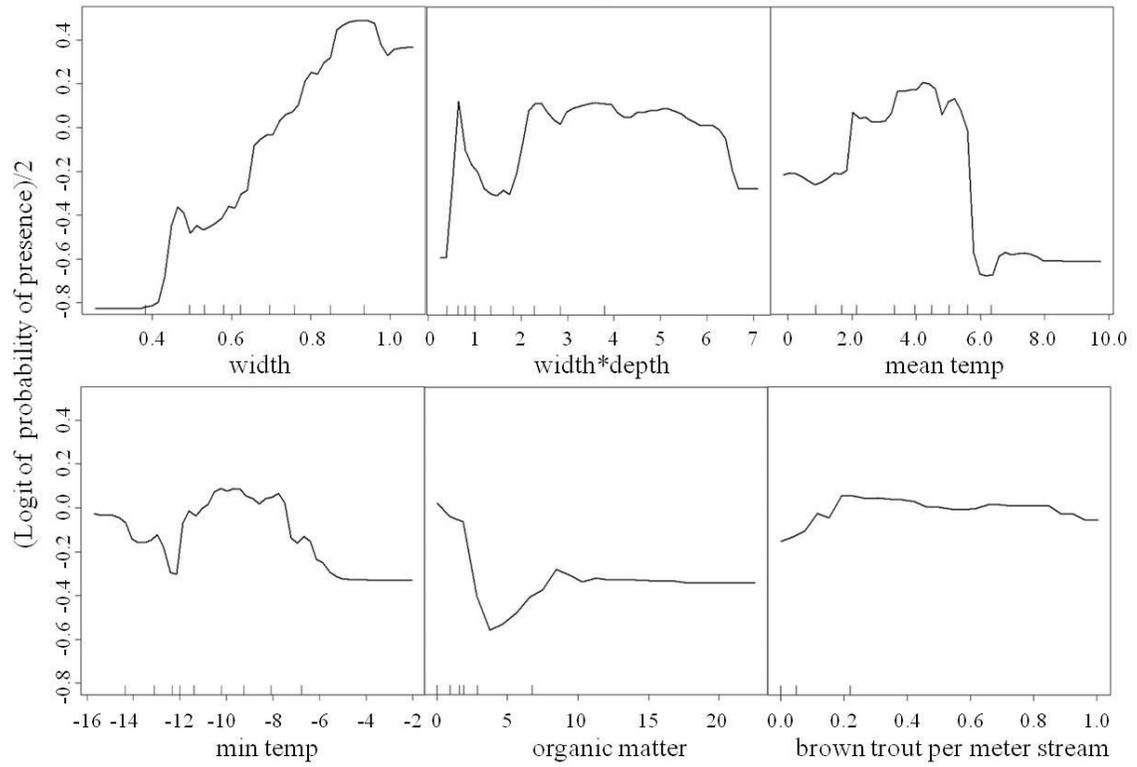


Figure 5. Partial dependence plots for the probability of detection for sculpins based on all predictor variables after averaging out the effects of the other predictor variables in the model.

temperature, mean width to depth ratio, bed particle diameter, riparian vegetation composition, percent sand and fine particle substrate, and percent fast-water habitat (Figure 4, Table 1). Brown trout abundance did not improve the performance of the speckled dace model and was the least important predictor. The partial dependence plot for speckled dace confirmed that there was no relationship between brown trout and the probability of detection of speckled dace (Figure 6).

Assemblage structure analysis

From the cluster analysis, we visually identified six groups of taxa that were associated with one another. The groups varied in terms of both species richness and composition (Table 5), and showed modest spatial coherence (Figure 7). Group 1 consisted of sites typically found in southwestern, arid regions. Speckled dace was the most frequently occurring species in this group. Group 3 consisted of sites found in the high plains east of the Rocky Mountains, and longnose dace (*Rhinichthys cataractae*) and white sucker (*Catostomus commersoni*) were the two most common species in this group. Group 4 consisted of sites in high-elevation streams, and cutthroat trout (*Oncorhynchus clarkii*) was the most prevalent species in this group, occurring at all sites. Groups 2 and 6 consisted of sites widely distributed in mountainous areas, and cutthroat and rainbow trout were the most common species in these two groups, respectively. Group 5 also consisted of sites in mountainous areas, and mottled sculpin (*Cottus bairdii*) occurred at all of these sites.

Brown trout occurred in at least two sites in all six groups, with a similar prevalence (0.22-0.33) in Groups 1-3, 5 and 6, and a lower prevalence (0.13) in Group 4 (Table 5). No relationship was detected between brown trout counts and variation in taxonomic composition among assemblage groups ($p = 0.29$).

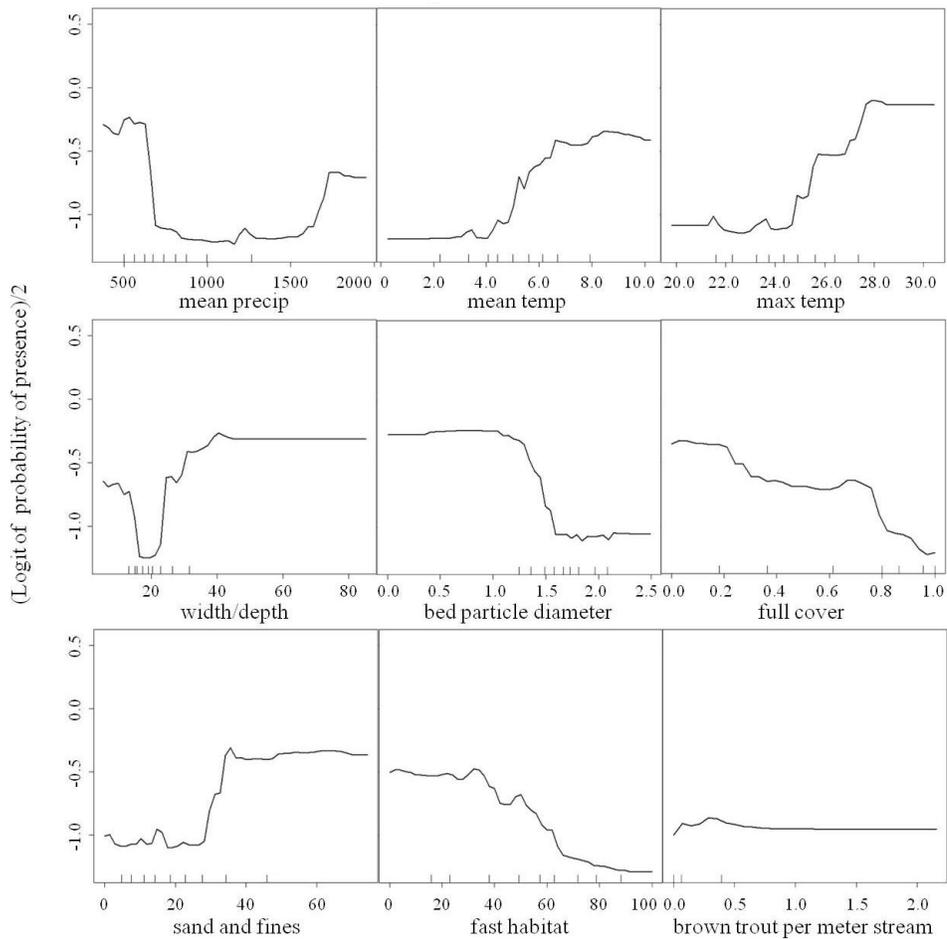


Figure 6. Partial dependence plots for the probability of detection for speckled dace based on all predictor variables after averaging out the effects of the other predictor variables in the model.

Table 5. Prevalence of each species in each of the assemblage groups derived from the cluster analysis.

Species	Group and number of sites					
	1 (27)	2 (18)	3 (13)	4 (16)	5 (12)	6 (46)
Brown trout	0.30	0.22	0.31	0.13	0.33	0.24
Creek chub	0	0	0.46	0	0	0
Cutthroat trout	0	0.39	0	1.00	0.67	0.24
Desert sucker	0.19	0	0	0	0	0
Fathead minnow	0.07	0.06	0.23	0	0	0
Longnose dace	0	0.06	0.85	0	0.17	0.02
Longnose sucker	0	0	0.23	0	0.08	0.07
Mottled sculpin	0	0.06	0	0	1.00	0.28
Mountain sucker	0.11	0.17	0.31	0	0.17	0.02
Mountain whitefish	0	0.06	0.08	0.06	0.17	0.07
Paiute sculpin	0.11	0	0	0.13	0	0.07
Rainbow trout	0.33	0.28	0.15	0	0	1.00
Redside shiner	0.11	0.11	0	0	0	0
Shorthead sculpin	0	0.28	0	0	0	0.04
Speckled dace	1.00	0.06	0	0	0.17	0
Tailed frog	0	0.28	0	0	0.08	0.11
Utah sucker	0.04	0.17	0	0	0.17	0
White sucker	0	0	0.77	0	0	0

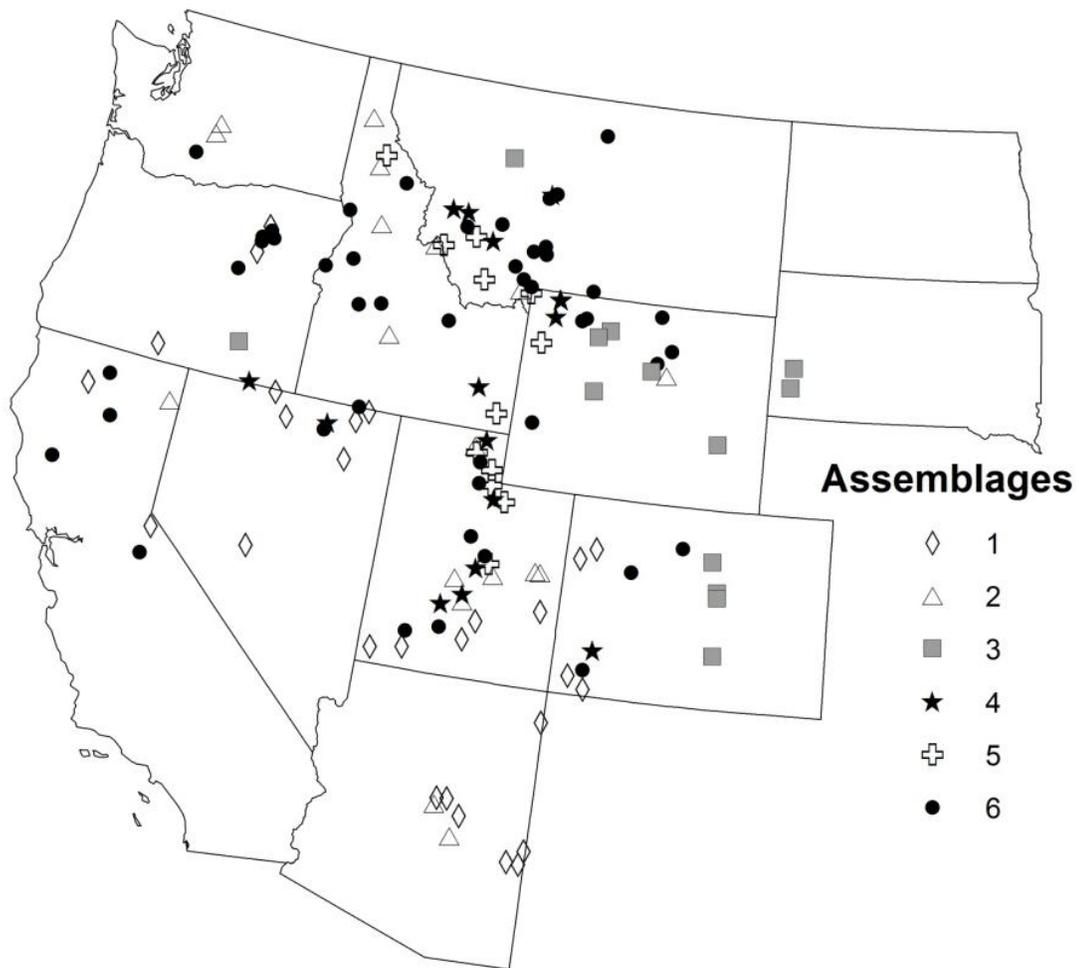


Figure 7. Locations of sites assigned to each of the six assemblage groups.

CHAPTER IV

DISCUSSION

Considerable research has been conducted worldwide that analyzes the effect of introduced brown trout on native fishes, indicating that there is general concern about the possible negative effects of these predators. The results of our study stand in marked contrast to that view and the conclusions drawn from several other studies. There are several possible explanations for the lack of associations in our study. First, our study design and analyses may have been incapable of detecting real effects (i.e. the design or analyses produced type II errors of inference). Second, the severity of effects of brown trout on native fauna may be dependent on other factors that mitigated potentially negative effects in western United States streams. Finally, native aquatic vertebrates in the western United States may be less susceptible to predation and competition by brown trout than in previously studied systems.

We do not think that the design of our study or our analyses suffered from larger Type II errors than occurred in previous studies. Although the data were not collected specifically to assess effects of brown trout, they spanned a wide range of abiotic and biotic conditions. In addition, the site selection criteria used by the EMAP project made the dataset robust to the statistical analyses that we used. Electrofishing was the primary fish sampling technique used by EMAP project crews, and sein nets were rarely used. Small fish, such as sculpins and speckled dace, are not as effectively captured by electrofishing as larger bodied fish, which probably resulted in underestimates of the

counts of such fish at each site. However, any bias introduced by sampling methods should have been consistent across sites, thus making comparisons between sites valid. The strength of the effect of brown trout on other native species has been shown to be dependent on interactions between multiple variables (McIntosh 2000) which could have obscured negative effects. However, the RF analysis should have detected such interactions (Cutler et al. 2007), but inspection of the bivariate partial dependence plots showed no interaction between brown trout counts and other predictor variables on the detection of the two target taxa.

Instead of errors in study design and analyses, we think a more likely explanation for the observed lack of association is that native aquatic vertebrate species in the western United States possess behaviors and other adaptations that better allow them to coexist with brown trout than native taxa in other regions. Introduced species are thought to have the greatest effects when they represent an entirely novel member of the community (Ruesink et al. 1995; Parker et al. 1999). Native aquatic vertebrates in the western United States have coevolved alongside other piscivorous salmonids (e.g. cutthroat and rainbow trout), and currently coexist with those species. Thus, although brown trout are known predators of many native aquatic vertebrates, their establishment may not represent a significantly novel stress. Much of the evidence that implicates brown trout as a threat to native fauna comes from studies conducted in New Zealand, which, prior to the introduction of brown and rainbow trout, lacked any salmonid-type piscivore (McDowall 2006).

Co-occurrence within the sample reaches may also have been facilitated if native

taxa and brown trout used different habitats within those reaches. For example, native brown trout and Siberian sculpin (*Cottus poecilopus*) occupy different microhabitats in stream reaches that both inhabit (Hesthagen and Heggenes 2003; Hesthagen et al. 2004). Therefore, although the two species coexisted in the same stream reach, their microhabitat preferences may limit the opportunities for interactions between the two. A separation of microhabitat use is especially pronounced between brown trout and benthic species, such as sculpins, because brown trout are primarily drift feeders that infrequently consume benthic organisms (Bachman 1984). Although it is possible that brown trout altered the microhabitat use of some native fish species (e.g. Olson and Belk 2005), we could not test for this effect with this data set.

Brown trout may also be affecting native fish in other ways that we were unable to detect. Through size-selective predation, brown trout could alter the size structure of native species (e.g. Nasmith et al. 2010), an effect we could not test for without fish length data over time. Similarly, brown trout may be exploiting resources in such a way that they affect the growth of resident native species, another effect that we could not detect. Data sets that contain information on resident fish species before, during, and after the invasion of brown trout are needed to address these effects.

The potential for brown trout to negatively affect native species may also depend on other factors. Trout are thought to become piscivorous when they reach lengths of 130 mm to 160 mm (Mittelbach and Persson 1998), and others have reported strong effects of brown trout on other species when suitable habitat is available and large (>150 mm) brown trout are resident (McIntosh 2000; Olav Vik et al 2001). We did not consider

size-related effects of brown trout because fish length data from EMAP was not readily accessible.

Considering our results together with evidence from other studies implies that brown trout have variable effects on native species. We expected that the severity of the effect brown trout have on native species may depend on either the type of taxa or ecosystem exposed to brown trout (Figure 8, Table 6). For example, predation is thought to be a common mechanism by which brown trout negatively affect native species. However, as predominantly drift feeders (Bachman 1984), brown trout would be expected to have negligible direct effects on those species associated with the streambed or bottom of a lake compared with species that reside in the water column. This idea appears to be too simplistic, though. Some bottom-oriented species have been severely affected by brown trout (e.g. Arismendi et al 2009, Soto et al 2006), and some water-column oriented species are only moderately affected (e.g. Nasmith et al 2010).

In contrast, brown trout appear to more severely affect other salmonid species than non-salmonid species (Figure 8), which implies that they more strongly affect species with similar overall niches. Brown trout are considered more aggressive than other salmonids (Nilsson 1963; Haswega et al. 2004), and some studies consider brown trout to be a superior competitor than native salmonid species (Wang and White 1994; Harwood et al. 2001; McHugh and Budy 2005, 2006; McHugh et al. 2008). In these cases, brown trout may be acting as a novel competitor with native salmonid species for either limited food or space resources.

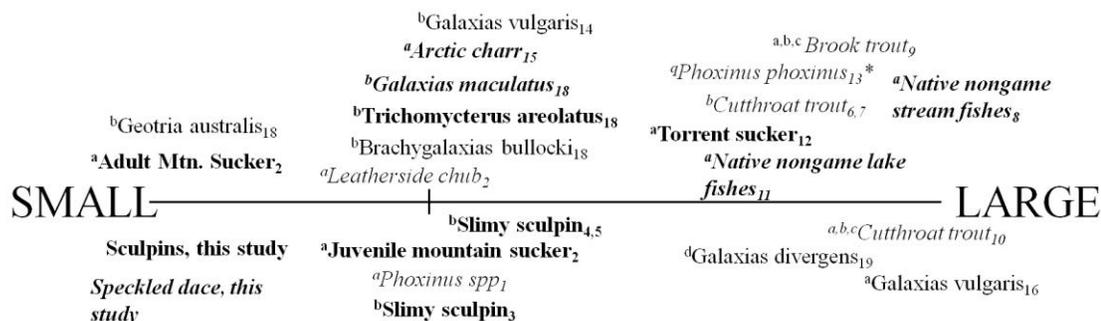


Figure 8. Conceptual representation of the variable effects of brown trout on native fishes. A small effect was inferred when a study did not detect any measureable effect, a moderate effect (marked by the vertical line) was inferred as a measurable change that still allowed the species to coexist with brown trout (in growth, habitat or diet selection), and a large effect was inferred as a change in growth or survival that makes coexistence with brown trout difficult or not possible. Benthic taxa are shown in bold font, and water column species are shown in italics. Superscripts refer to the type of interaction: ^apredation, ^bcompetition, and ^cother. One species (*) was introduced to the native range of brown trout. Subscripts identify the sources of information, which are given in Table 6.

To understand the overall effect of an introduced species, the specific interactions thought to harm native species should be identified. In the case of brown trout, competition for resources with native salmonids species has been demonstrated to negatively affect those native species (Wang and White 1991; McHugh and Budy 2005, 2006). For native non-salmonid species, particularly potential prey species, these interactions are less well defined and understood. While negative effects are often assumed to be asymmetrical, results from other studies suggest that some non-salmonid prey species can negatively affect brown trout through competition (e.g. Hesthagen and Heggenes 2003).

Table 6. Sources used to construct Figure 8.

	Effect Measured	Citation
1	growth, abundance	Nasmith 2010
2	habitat use	Olson and Belk 2005
3	diet composition	Zimmerman 2005
4	growth	Zimmerman and Vondracek 2006
5	growth	Ruetz et al. 2003
6	condition, growth	McHugh and Budy 2005
7	growth, diet composition, movement	McHugh and Budy 2006
8	biomass, presence/absence	Soto et al. 2006
9	presence/absence, distribution	Waters 1983
10	presence/absence, distribution	Moyle and Vondracek 1985
11	relative abundance	Arismendi et al. 2009
12	abundance	Garman and Nielsen 1982
13	biomass loss	Museth et al. 2003
14	habitat space	McIntosh et al. 1992
15	habitat use	L'Abee-Lund et al. 1993
16	distribution	Townsend and Crowl 1991
17	abundance	Death and Death 2005
18	habitat use	Penaluna et al. 2009

It is also important to understand the spatial scale over which negative effects on native species occur. The bulk of studies that consider the effects of brown trout on native species have focused on local effects. These local studies reveal the potential effects brown trout might have throughout its introduced range, but large-scale studies are needed to assess regional impacts. The results of this study imply that brown trout may not be having widespread negative effects on native aquatic vertebrate species in streams of the western United States. Future work should focus on integrating local- and regional-scale studies to better understand the environmental and ecological contexts that lead to variable effects of introduced species such as brown trout on native species.

CHAPTER V

CONCLUSIONS

The introduction of exotic species is considered one of the greatest threats to global biodiversity and the conservation of endangered species (Allan and Flecker 1993; Sakai et al. 2001; Dudgeon et al. 2006). Exotic species have caused extirpations or substantial reductions in native species abundance (Kitchell et al. 1997; McIntosh et al. 2010). But, it is widely held that of the many species introductions made annually, few will result in successful establishment; and only some of those will result in severe negative effects on the receiving ecosystem (Lodge 1993; Williamson 1996; Simberloff 2007). To develop appropriate management plans for any established exotic species, it is important to understand how the magnitude of the effect that introduced species have vary among ecosystems.

For my thesis, I used a data set that spanned a wide portion of the introduced range of brown trout in North America to examine its effect on both individual prey species and entire assemblages of aquatic vertebrates. I used data collected during the EPA's Environmental Monitoring and Assessment Western Pilot Project that provided a dataset that spanned a wide portion of the range of brown trout and native western United States stream fish. Sites were located across the western United States and encompassed a wide range of abiotic conditions. The methods I used to assess the effect of brown trout on native taxa abundance and presence and absence provided easily interpretable results. I used predictive modeling to examine if the likelihood of detecting two target taxa varied

with the presence of brown trout, a method that has previously been used to document effects of brown trout on native species (Townsend and Crowl 1991). The lack of association between native species and brown trout in this study compared with strong negative associations observed elsewhere implies that the effect of brown trout on native fishes may be contingent on the physical and biological structure of the area of interest. In the rest of this chapter, I describe the context-dependent aspects of my study that may have led to my results and outline future research needs.

The intent of this research was to determine if brown trout have severely affected native fishes within a large portion of their introduced range. Although brown trout have been shown to harm native stream fishes in individual watersheds or rivers (e.g. Garman and Nielsen 1982; de la Hoz Franco and Budy 2005), the lack of any detected relationship between native stream vertebrates and brown trout in this study suggests that the presence of brown trout does not always cause negative effects.

Because brown trout are ecologically similar to native trout species, they may not be performing an entirely novel function in western United States streams. Many native non-salmonid fish species coexist with native piscivorous trout (e.g. cutthroat and rainbow trout). Thus, the non-salmonid taxa I studied may already possess behaviors or other traits that allow them to coexist with brown trout. In contrast, native trout are probably highly vulnerable to introduced brown trout because of the high ecological similarity among salmonid species that causes them to compete for resource with each other (Waters 1983; McHugh and Budy 2005, 2005).

Although I did not observe negative effects of brown trout on other species in this study, brown trout could be affecting native species in ways I could not detect. For example, the effect of brown trout on native fishes has been shown to be size-dependent (Garman and Nielsen 1982; McIntosh 2000). Large adult brown trout are considered to be primarily piscivorous (Belica 2007), thereby making them potentially more dangerous to prey species. Additionally, brown trout are gape-limited predators (Jensen et al. 2004), so prey size may also affect the severity of the overall impact of brown trout on resident native species. Despite the potential for size-related effects of brown trout, I was unable to consider this relationship because I did not have length data for individual fish. In addition, it is possible that although brown trout and native species occupy the same reaches of streams, they use different microhabitats within those reaches. For example, southern leatherside chub and juvenile mountain sucker in Utah occupied different microhabitats in stream reaches that contained brown trout than others that did not contain brown trout (Olson and Belk 2005). This effect was not detectable with the EMAP dataset, however.

The current distribution and assemblage structure of western United States fishes may represent a relative equilibrium between brown trout and native species. As previously discussed, native species, such as sculpins, may already possess behaviors that allow them to coexist with brown trout. Brown trout may have coexisted with other native species for a sufficient amount of time for those species to evolve new antipredator behaviors (e.g. 30 generations; O'Steen et al. 2002). Additionally, brown trout may have caused extirpations of other species, especially competitors, in some parts of the western

United States. A combination of these scenarios may explain the patterns observed in native species assemblages and distributions in western United States streams.

I suggest that the reason that I did not detect a negative association between brown trout and sculpins or speckled dace is due to the behaviors or adaptations that both taxa possess that allows them to coexist with other piscivorous native trout species. It would be useful to identify such behaviors or adaptations that facilitate such coexistence. Studies that focus on areas where brown trout coexist with native species could help identify such behaviors or other adaptations that allow this coexistence.

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