PREDATOR-PREY INTERACTIONS BETWEEN INTRODUCED TROUT AND LONG-TOED SALAMANDERS AND WAYS TO MITIGATE NONCONSUMPTIVE EFFECTS

by

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ABSTRACT

Predators can increase prey through mortality, but also have the capacity to alter behavior, morphology, and life history through nonconsumptive effects. In many historically fishless lakes in western North America, trout have been introduced for recreational fishing and are associated with reducing and extirpating populations of amphibians, including long-toed salamanders (*Ambystoma macrodactylum*). Salamanders and trout may coexist in some lakes, as larvae are able to alter foraging behavior by avoiding open water, foraging at night in shallow water, and hiding in cover to avoid predation. However, salamanders may experience nonconsumptive effects due to these behavioral changes. We sought to estimate the nonconsumptive effects of trout on morphology and life history of larval salamanders. We caught salamander larvae using minnow traps in northwestern Montana during the summers of 2012 and 2013 and compared body morphology measurements and size at and timing of metamorphosis between lakes with and without trout. Salamanders in lakes with trout were smaller: they weighed less, had shorter body lengths, and had shorter and narrower tails. Salamanders in lakes with trout were also less likely to metamorphose, did so later in the summer, and had smaller total and tail lengths at metamorphosis. These changes in morphology and life history likely were a result of reduced foraging to avoid predator attacks. We conducted a field experiment in 2013 to investigate whether adding vegetation structure could reduce nonconsumptive effects of trout on salamander larvae by providing refugia and reducing perceived risk of predation. We constructed field enclosures in lakes with and without trout and quantified changes in salamander growth and differences in size at metamorphosis with and without added structure. Salamanders appeared to detect trout cues because they grew more slowly in lakes with trout, even though trout had no ability to consume salamanders. Added vegetation structure did not influence growth rates, but did increase the probability of salamanders that reached metamorphosis. Future research efforts should investigate whether adding vegetation structure to whole lakes can mitigate the nonconsumptive effects of trout, provide a feasible alternative to fish removal, and facilitate coexistence between salamanders and trout.

CHAPTER ONE

INTRODUCTION TO THESIS

Currently, amphibians are experiencing drastic declines globally (Stuart et al., 2004). At least 37% of amphibian species are vulnerable, threatened, or endangered and amphibian populations in the United States are estimated to be declining by 3.7% annually (Alford, 2011; Adams et al., 2013). Declines have been attributed to habitat alteration and loss, pollution, contaminants, climate change, increased UV-B radiation, disease, and introductions of nonnative species (Blaustein et al., 1994; Beebee, 1997; Adams, 1999; Collins and Storfer, 2003; Taylor et al., 2005; Pounds et al., 2006). Introduced predators, especially nonnative fish, prey on all life stages of amphibians and have been a leading cause of declines in some areas (Hayes and Jennings, 1986; Hecnar and M'Closkey, 1997; Knapp and Matthews, 2000; Pilliod and Peterson, 2001; Denoel et al., 2005; Herwig et al., 2013).

In the western United States, fish stocking began in the mid-1900s to increase recreational opportunities for anglers (Bahls, 1992). Introduced trout now exist in 60% of lakes and 95% of all large lakes (>2 ha) historically devoid of fish (Bahls, 1992). Amphibians that breed in historically fishless lakes are more vulnerable to predatory fish, as they often lack chemical or morphological defenses and may be naïve to introduced predators (Kats et al., 1988; Pearl et al., 2003; Welsh et al., 2006; Wells, 2007). Introduced trout have had negative effects on populations of frogs (*Lithobates cascadae*, Joseph et al., 2011; *Rana luteiventris*, Pilliod and Peterson, 2001; *Rana temporaria*, Tiberti and Von Hardenberg, 2012; *Hyla versicolor*, Smith et al., 1999; and *Rana muscosa,* Wake and Vredenburg, 2008; *Pseudacris regilla*, Knapp, 2005), newts (*Notophthalmus viridescens*, Smith et al., 1999; *Triturus vulgaris*, Aronsson and Stenson, 1995; *Taricha torosa,* Gamradt and Kats, 1996), and salamanders (*Ambystoma gracile*, Larson and Hoffman, 2002; *Ambystoma macrodactylum*, Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Hirner and Cox, 2007; Pearson and Goater, 2008). In the western United States, California yellow-legged frogs (*Rana muscosa* and *Rana sierrae*) have been extirpated from >90% of their historic range within the Sierra Nevada Mountains and considerable evidence suggests that the combination of fish stocking and disease have caused these extinctions (Knapp and Matthews, 2000; Vredenburg et al., 2007). Larval populations of the northwestern salamander (*Ambystoma gracile)* are 12 times smaller in lakes with trout compared to populations in fishless lakes (Larson and Hoffman, 2002). Similarly, Columbia spotted frogs (*Rana luteiventris*) and long-toed salamanders (*Ambystoma macrodactylum*) in the Northern Rockies are significantly less abundant in lakes with trout compared to lakes without trout (Pilliod and Peterson, 2001).

Long-toed salamanders (*Ambystoma macrodactylum*) are the most widely distributed amphibian west of the Continental Divide, occupying areas from central California through the Pacific Northwest and extending into southern Alaska (Werner et al., 2004). They are considered to be widespread and abundant by global rankings and are the most common salamander in the state of Montana (Montana State Government, 2014). However, extirpations have occurred in lakes with introduced trout and populations are suspected to be declining despite their secure status within Montana

(Funk and Dunlap, 1999; Pearson, 2004; Werner et al., 2004; Pilliod et al., 2010; Montana State Government, 2014). Larvae often metamorphose in late summer of the same year they hatch, but may remain in lakes at higher elevations to overwinter or when they require more time to initiate metamorphosis (Wilbur and Collins, 1973). Salamanders are palatable to fish during all aquatic stages and may remain in the aquatic environment for as many as 2-3 years before metamorphosis, making them especially vulnerable to predation (Howard and Wallace, 1985; Welsh et al., 2006).

In lakes with trout, survival of larval long-toed salamanders is greatly reduced, populations are less abundant, and the presence of salamanders is negatively correlated with the presence of fish predators (Tyler et al., 1998a; Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Bull and Marx, 2002; Dunham et al., 2004; Welsh et al., 2006; Hirner and Cox, 2007). Salamanders are 44 times less likely to be found in lakes with trout, populations in lakes with trout are $\geq$ 65% less abundant, and the proportion of sites occupied by both trout and salamanders is as low as 0 – 0.15 (Tyler et al., 1998a; Pilliod and Peterson, 2001; Welsh et al., 2006; Hirner and Cox, 2007; Pearson and Goater, 2008).

Larval salamanders are capable of detecting fish through chemical and visual cues and alter behavior to reduce encounter rates with fish, most often by increasing refuge use (Tyler et al., 1998b; for other *Ambystoma* species see: Semlitsch, 1987; Figiel and Semlitsch, 1990; Sih and Kats, 1991, 1994; Storfer and Sih, 1998; Storfer, 1999). Altered behavior can increase salamanders' probability of survival, but these changes may come at a cost. Individuals that reduce the amount of time spent foraging in open water may decrease energy uptake and body size (Semlitsch, 1987; Figiel and Semlitsch, 1990; Tyler et al., 1998b). Smaller body sizes during the larval period and at metamorphosis are associated with reduced survival and reproduction and increased susceptibility to predation, desiccation, and disease as adults (Petranka et al., 1987; Semlitsch, 1987; Figiel and Semlitsch, 1990; Kiesecker and Blaustein, 1998; Tyler et al., 1998b; Gervasi and Foufopoulos, 2008; Warne et al., 2011). Long-toed salamander populations may be at risk of decline and potential extirpation if trout reduce abundance through predation (consumptive effects) or affect survival and reproductive success of adult salamanders to a point that influences recruitment (nonconsumptive effects) (Kats and Ferrer, 2003; Pilliod et al., 2010).

Trout removal has been an effective method to reduce the negative effects of fish predators (Hoffman et al., 2004; Vredenburg, 2004; Knapp et al., 2007; Gross, 2009). Amphibians are able to recolonize sites quickly and increase population size and species diversity (Vredenburg, 2004; Knapp et al., 2007; Gross 2009). Long-toed salamanders were present in five of six lakes where trout had gone extinct, compared to only two of 12 where trout still existed (Funk and Dunlap, 1999). However, this strategy is often unpopular with the public and, like other management efforts (e.g., maintaining buffer zones surrounding breeding sites, creating connectivity between wetlands, or constructing water bodies), can be costly in time, energy, and resources (Semlitsch, 2002; Shulse et al., 2012).

Despite the rarity of coexistence, long-toed salamanders and trout have been found to co-occur in lakes where habitat characteristics such as emergent vegetation and physical barriers from trout are present (Tyler et al., 1998a; Pearson and Goater, 2008; Pilliod et al., 2010; Pilliod et al., 2013). Structural complexity and available refugia are crucial for larval amphibians to persist with predatory fish, as dense vegetation provides protection, while also reducing the maneuverability, visual range, and effectiveness of fish predators (Werner et al., 1983; McNair, 1986; Sih, 1987; Kats et al., 1988; Sih et al., 1988; Figiel and Semlitsch, 1991; Diehl, 1992; Babbitt and Jordan, 1996; Babbitt and Tanner, 1997; Tyler et al., 1998b; Allouche, 2002; Pearson, 2004). However, we are not aware of studies that have experimentally manipulated cover or added structural complexity as a method to enhance amphibian coexistence with trout predators.

Understanding the nonconsumptive effects of introduced trout on long-toed salamanders, the ways in which predator-prey dynamics affect morphology and life history of prey species, and how these effects contribute to prey persistence and coexistence will be important in designing new and effective conservation strategies that help preserve salamander populations without requiring the removal of trout.

Objectives:

We aimed to examine the nonconsumptive effects introduced trout have on long-toed salamander larvae and test the effectiveness of a new conservation strategy intended to facilitate coexistence between these species.

Chapter two is focused on understanding predator-prey interactions and the nonconsumptive effects introduced trout have on long-toed salamander larvae. Specifically, we will investigate morphology, before and at metamorphosis, of salamanders in lakes with and without trout. We will also examine the influence of trout on life history, namely the probability and timing of metamorphosis. Chapter three investigates the efficacy of adding complex vegetation structure to reduce the nonconsumptive effects of trout on larval salamanders. We seek to test the effectiveness of this management strategy and its potential use in conservation efforts for other amphibian populations negatively affected by introduced predators.

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CHAPTER TWO

NONCONSUMPTIVE EFFECTS OF INTRODUCED TROUT PREDATORS ON LONG-TOED SALAMANDERS: CHANGES IN MORPHOLOGY AND LIFE HISTORY

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CHAPTER TWO

NONCONSUMPTIVE EFFECTS OF INTRODUCED TROUT PREDATORS ON LONG-TOED SALAMANDERS: CHANGES IN MORPHOLOGY AND LIFE HISTORY

Abstract

Predators can influence prey directly through consumption or by altering prey behavior, morphology, and life history. Facultative changes to reduce predation often come with a cost, such as expenditure of energy and resources, reduced size, and potentially reduced fecundity and survival. In western North America, trout have been introduced to lakes for recreational fishing, leading to reductions and extirpations of long-toed salamanders (*Ambystoma macrodactylum*). Salamanders and trout may coexist in some lakes, as larvae are able to alter foraging activity and time in refugia. However, salamanders may experience nonconsumptive effects due to these changes in behavior. We sought to investigate the effects of trout on salamander morphology and life history We sampled lakes with and without trout in northwestern Montana during the summers of 2012 and 2013. We captured salamander larvae using minnow traps and compared morphological measurements of non-metamorphosing and metamorphosing salamanders between lakes with and without trout. Salamanders in lakes with trout were smaller: they weighed less, had shorter body lengths, and had shorter and narrower tails. Salamanders in lakes with trout were >20 times less likely to metamorphose and those that did, metamorphosed later and had smaller total and tail lengths. Changes in body morphology

and life history were likely a result of predator-avoidance behavior, such as increased vigilance, reduced foraging, and increased refuge use. Defensive strategies may reduce predation, but may affect reproduction and survival in the long term. Future research should be directed at understanding how nonconsumptive effects experienced during the larval stage translate to survival and reproduction of adult salamanders.

Introduction

Predator-prey interactions are viewed most often in terms of consumption (Mittelbach, 2012). However, predator-prey interactions are much more diverse and complex when nonlethal, nonconsumptive effects also are considered (Huang and Sih, 1991; Beckerman et al., 1997; Werner and Peacor, 2003; Joseph et al., 2011). To avoid predation, prey use tactile, visual, or chemical cues to detect predators and respond with appropriate defensive tactics to increase their probability of survival (Kats et al., 1988; Stauffer and Semlitsch, 1993; Lima, 1998). When defenses are not innate (e.g., unpalatable toxins in skin of newts and toads, Daly, 1995), the presence of predators may induce facultative defenses that result in marked changes in prey behavior, morphology, and life history (Gilliam and Fraser, 1987; Ludwig and Rowe, 1990; Brönmark and Miner, 1992; McNamara and Houston, 1994; Lima, 1998; Peckarsky et al., 2001, 2002; Benard, 2004; McPeek, 2004; Mittelbach, 2012).

Although such defensive strategies may reduce the risk of predation, they also can reduce prey energy intake, reproductive success, and survival (Gilliam, 1982; Werner et al., 1983; Gilliam and Fraser, 1987; Ludwig and Rowe, 1990; McNamara and Houston, 1994; Lima, 1998; McPeek and Peckarsky, 1998; Peckarsky et al., 2002; Benard, 2004). For example, when small, bluegill sunfish (*Lepomis macrochirus*) are exposed to predators, they increase foraging activity in vegetated areas that are resource-poor relative to open areas that are resource-rich, which results in a 27% reduction in growth (Werner et al., 1983). Elk (*Cervus elaphus*) spend more time in protected, coniferous forest and less time in grasslands that are rich in foraging resources when wolves are present, which reduces fecundity by 35% (Creel et al., 2005). Similarly, larval dragonflies reared with caged predators have higher levels of mortality and metamorphic failure, despite predators' inability to actually capture and consume prey (McCauley et al., 2011). Thus, predator avoidance tactics confer benefits by reducing predation risk, but prey my may incur costs to growth and survival with such responses (Brönmark and Hansson, 2005).

The standard interplay between predators and prey becomes more complex when predators become established in novel environments (Salo et al., 2007). Unlike prey that have coexisted with native predators over evolutionary time, naïve prey may lack chemical or morphological defenses, be unable to detect predators as a threat, or both (Kats et al., 1988; Kiesecker and Blaustein, 1997; Preisser et al., 2005; Salo et al., 2007). Even prey that are capable of assessing predation risk and responding with altered behavior have reduced growth, are smaller in size, and have higher rates of mortality compared to prey in the absence of introduced predators (Tyler et al., 1998a; Pearson and Goater, 2009). Nonconsumptive effects can be as great or greater than consumptive effects, and together, can influence prey abundance and predator-prey dynamics (Macan, 1977; Werner and Peacor, 2003; Bolnick and Preisser, 2005; Preisser et al., 2005; Finlay and Vredenburg, 2007).

In the western United States, trout have been introduced for recreational fishing to 95% of historically fishless lakes and have replaced native amphibians as top predators within some of these lakes (Bahls, 1992; Dunham et al., 2004). Long-toed salamanders (*Ambystoma macrodactylum*) are considered the most common salamander in Montana, yet populations have decreased and been extirpated in some lakes with introduced trout (Funk and Dunlap, 1999; Pilliod et al., 2010). Salamanders are palatable to trout and are susceptible to predation during all developmental stages from egg to adult (Tyler et al., 1998a; Pearson and Goater, 2009). These salamanders require deep, permanent lakes for overwintering, oviposition, and development during their 1-3 year larval period and infrequently coexist with trout (Tyler et al., 1998b; Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Bull and Marx, 2002; Pearson and Goater, 2008; Pilliod et al., 2010, 2013). In lakes with trout, survival of long-toed salamander larvae is greatly reduced, populations are less abundant, and the presence of salamanders is negatively correlated with the presence of fish predators (Tyler et al., 1998b; Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Bull and Marx, 2002; Dunham et al., 2004; Welsh et al., 2006; Hirner and Cox, 2007). The rarity of coexistence and reduced abundance of salamanders in lakes with trout is primarily thought to be a result of direct predation.

Long-toed salamander larvae are capable of detecting chemical and visual cues of fish predators and use behavioral strategies to avoid predation (Tyler et al., 1998a; Pearson and Goater, 2009). Larvae often increase the use of cover objects or occur in dense vegetation or shallow water, which reduces encounter rates with trout and decreases the maneuverability and visual range of these predators (Werner et al., 1983; Figiel and Semlitsch, 1991; Babbitt and Jordan, 1996). However, increased refuge use is associated with reduced foraging activity (Petranka et al., 1987; Skelly and Werner, 1990; Pearl et al., 2003; Paoletti et al., 2011). Spending more time in refugia can limit the amount of resources acquired and negatively influence growth and size (Petranka et al., 1987; Skelly and Werner, 1990; Tyler et al., 1998b; Nyström et al., 2001; Benard, 2004; Davenport et al., 2013).

Predator-induced changes in behavior also can correspond to changes in life history (Benard, 2004). Increased predation risk in the larval stage may encourage early metamorphosis, so individuals can minimize their exposure to predators and escape environments with high risk of mortality (Ludwig and Rowe, 1990; Rowe and Ludwig, 1991; Abrams and Rowe, 1996; Chivers et al., 1999; Lardner, 2000). Alternatively, anti-predator defenses that result in reduced growth rates may extend larval periods and require more time for larvae to acquire necessary resources for metamorphosis (Wilbur and Collins, 1973; Lardner, 2000; Barnett and Richardson, 2002; Benard, 2004; Skelly, 1992).

We aimed to examine the nonconsumptive effects of introduced trout on long-toed salamander morphology and timing and size at metamorphosis. We used lakes with and without trout as a model system to better understand predator-prey interactions and the nonconsumptive effects incurred by prey. We hypothesized that salamanders in lakes with trout would be smaller in size and that the presence of trout would shorten the larval period of salamanders.

Methods

Study Sites:

Our study took place in permanent lakes in northwestern Montana between the cities of Hungry Horse and Helena, Montana (Figure 2.1). We sampled lakes primarily northeast of Missoula, in the South Fork Flathead River and Swan River drainages; elevation ranged from 953 to 1,988 m and lake perimeters ranged from 140 to 960 m (Table 2.1). In 2012, we sampled 14 lakes for long-toed salamanders, seven lakes with trout and seven without trout. In 2013, we sampled for salamanders in six of the original 14 lakes, three with trout and three without, to increase our trapping effort within each lake. We did not randomly select sites; we considered lakes where previous surveys verified the presence of salamanders, salamanders and trout (B. Maxell, pers. comm.; M. Boyer, pers. comm.), or lakes of similar size that we found with local maps. We identified trout as rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarkia*), or hybrids of the two species based on field observations, recreating anglers, and Montana stocking reports (Montana Fish, Wildlife & Parks, 2004, 2005, 2007, 2010, 2011). We selected lakes for our study based on visual encounter and trapping surveys in 2012 to confirm the presence of salamanders and the presence or absence of trout.

Sampling:

We used minnow traps to capture salamanders as they are especially useful to trap small, cryptic larvae, are associated with little mortality or injury, and capture individuals passively without bait (Adams et al., 1997). We set all traps in the littoral zone around the perimeter of each lake at depths ≤1 m. In 2012, the total number of traps in each lake ranged from 6 to 16 and in 2013, the total number of traps in each lake ranged from 7 to 48. In 2012, we collected measurements of dissolved oxygen, pH, and water temperature using a YSI Pro 1030 meter at each study lake, during each visit, close to the lake shore in water <1 m deep.

We deployed traps for four-day periods from July through August of 2012 and 2013. We visited lakes a total of four times in 2012 and three times in 2013. During each visit, we collected salamanders from traps, anesthetized individuals with MS-222, measured weight, snout-vent length (SVL), total length, tail length, and tail depth (Figure 2.2) with an electronic scale and calipers, and marked individuals with visual implant elastomer in the middle of the tail. We marked individuals uniquely except when we captured >100 salamanders during one visit to a lake, we used batch marks specific to the trap and visit number. Elastomer is a common marking technique for larval salamanders, is long lasting, does not affect survival or metamorphosis, and allowed us to identify individual salamanders if and when we recaptured them (Grant, 2008). We also noted whether individuals had initiated metamorphosis, defined as showing any evidence of gill absorption (Dodd and Dodd, 1976; Arntzen, 1981; Duellman and Trueb, 1986). We released all individuals at their original capture location following data collection (Montana State University Institutional Animal Care and Use Committee protocol 2013-04).

Statistical Analyses:

We compared body morphology (weight, SVL, total length, tail length, tail depth, and tail index) of larvae between lakes with and without trout and made separate comparisons for larvae that were metamorphosing and those that were not. We calculated tail index by dividing tail length by SVL to estimate tail size relative to the body (Arntzen, 1981). We evaluated allometric relationships between weight and SVL, tail length, and tail depth of non-metamorphosing salamanders and compared slopes of these relationships between lakes with and without trout (Arntzen, 1994; Delgado-Acevedo and Restrepo, 2008). We also compared the probability and timing of salamander metamorphosis in lakes with and without trout; these estimates were based on the number of individuals exhibiting signs of metamorphosis out of the total number of individuals captured at each visit. Lastly, we computed the total number of salamanders captured divided by lake perimeter and made comparisons between lakes with and without trout, to assess differences in salamander density.

We used a generalized linear mixed model approach for all analyses, selecting the appropriate distribution and link function for each response variable. We treated lakes as our subjects and included a three-tiered, nested data structure – multiple visits within lakes within years – as random effects in all analyses to account for repeated measurements and variation among lakes (Zuur et al., 2009). We included the presence or absence of trout (trout) as the main effect in our analytical model. We also included year and number of days since the first sampling visit to account for changes over time and to test for interactive effects (trout*day). We removed interactions that did not explain sufficient variation ($\alpha > 0.1$) from models for inference, but kept all simple explanatory variables (i.e., trout, year, and day). We included lake level covariates (i.e., perimeter, elevation, and repeated measures of dissolved oxygen, pH, and temperature) to better account for variation among lakes. We log-transformed response variables when appropriate to meet assumptions. We ran all statistical analyses in program R version 3.0.2 and used packages nlme and MASS (R Developmental Core Team, 2008). We report mean values, percent differences, and 95% confidence intervals in text and tables; we back-transformed these values when appropriate.

Results

Non-metamorphosing Individuals:

Salamander densities were similar between lakes with and without trout, after accounting for year (estimated difference = 6 salamanders/100 m, 95% CI = -22 – 34 salamanders/100 m, $t_{12} = -0.45$, $P = 0.66$). Salamanders were consistently smaller in size in lakes with trout compared to lakes without trout and only some measurements changed over the sampling season (Figure 2.3, Tables 2.2 and 2.3). In lakes with trout, salamander larvae weighed 38% less (95% CI = 3 to 72%), were 24% shorter (6 to 43%) in total length, and had tails 29% shorter (7 to 50%, Figure 2.4); these differences were present at the beginning of the summer and consistent throughout the sampling season. Salamanders in lakes with trout were 19% shorter (-1 to 38%) based on SVL and although SVL of salamanders increased as they grew over the sampling season, these differences persisted (Figure 2.5, Table 2.3). Tail depth changed over time and differences depended on the presence or absence of trout; salamanders in lakes with trout had tails 24% narrower (7 to 41%) at the beginning of the summer, but had comparable tail depths near the end of the summer (Figure 2.5, Table 2.3). Tail index decreased over time and salamanders in lakes with trout had tail length to SVL ratios 0.06 less (0.03 to 0.09, Figure 2.5, Table 2.3). Measurements of body morphology were similar between years (Table 2.2, 2.3)

Allometric relationships between weight and SVL, tail length, and tail depth were positive and linear, and the slopes differed between lakes with and without trout (trout * weight, Figure 2.6, Table 2.4).

Metamorphosing Individuals:

Larval salamanders were >20 times more likely to metamorphose in lakes without trout and they metamorphosed earlier in the summer, compared to larvae in lakes with trout ($t_{1553} = -2.25$, $P = 0.025$, Figure 2.7). Individuals that showed signs of metamorphosis in lakes with trout were 8.8% shorter in total length (95% CI = 3 to 14.9%, $t_6 = -2.98$, $P = 0.02$) and 16.9% shorter in tail length (7.4 to 26%, $t_6 = 3.59$, $P = 0.01$) than salamanders in lakes without trout (Figure 2.8). There was no difference in weight, SVL, and tail depth measurements between metamorphosing salamanders in lakes with and without trout (Table 2.5).

Discussion

Predation, especially by nonnative predators, can reduce or extirpate entire populations of prey (Heyer et al., 1975). Prey may be able to mitigate consumptive effects temporarily, yet they are continually shifting between safe and unsafe states when predators are present (Sih, 1987). By altering the behavior of prey species, through changes in diet or habitat selection, predators also can induce nonconsumptive effects (Huang and Sih, 1991; Schmitz, 1998). Although amphibians occasionally are able to exist with introduced predatory fish, our findings demonstrate that nonconsumptive effects of trout on long-toed salamanders impact larval morphology and timing of metamorphosis.

Salamanders that increase their use of vegetated shallows when predators are detected can successfully coexist with trout, but these behavioral modifications come with costs (Anderson and Williamson, 1974; Taylor, 1983; Stenhouse, 1985; Sih et al., 1988; Babbitt and Jordan, 1996; Tyler et al., 1998b; Van Buskirk and Schmidt, 2000). Salamanders existing in lakes with trout were consistently smaller in size (Figure 2.3). With as much as a 38% reduction in weight and a 24% reduction in total length; these decreases are comparable to California red-legged frog tadpoles (*Rana aurora draytonii*) that weighed 34% less at metamorphosis in the presence of mosquitofish (*Gambusia affinis*) and larval mole salamanders (*Ambystoma talpoideum*) that had 18% reductions in body size in the presence of bluegill sunfish (*Lepomis macrochirus*) in constructed ponds (Semlitsch, 1987; Lawler et al., 1999). Furthermore, variation in allometry relating weight with body and tail measurements suggests different biological scaling relationships for salamanders during larval development. More specifically, in lakes with trout, salamanders increase body and tail shape and size more slowly with increasing weight compared to larvae in lakes without trout. Unless a small size is advantageous to larval salamanders and reduces detection by trout, increases potential refugia in compact spaces, or is genetically selected for in lakes with trout, small sizes likely are a consequence of reduced activity and feeding to avoid predator attacks (Tyler et al., 1998a; Yurewicz, 2004).

Larvae in environments with trout must evaluate the tradeoff between predator-avoidance and procuring resources, which can influence size and timing of metamorphosis (Wilbur and Collins, 1973; Duellman and Trueb, 1986; Semlitsch, 1987; Skelly, 1995; Tyler et al., 1998b; Hirner and Cox, 2007). Salamanders in lakes with trout were less likely to metamorphose and did so later in the summer season. Amphibian metamorphosis is initiated once a minimum body size is attained (Wilbur and Collins, 1973). The significantly smaller size of non-metamorphosing larvae in lakes with trout may have reduced probability of metamorphosis and restricted salamanders to the aquatic environment for longer periods of time, in order to reach adequate sizes for metamorphosis (Wilbur and Collins, 1973; Arntzen, 1981; Bull and Marx, 2002). Much like long-toed salamanders, the larval period of wood frogs (*Lithobates sylvaticus*) is significantly longer in the presence of predatory fish (Davenport et al., 2013). Lengthening the larval periods can increase exposure and susceptibility to trout predation, especially during winter months when larvae must move away from shallow, vegetated areas along the lake perimeter and into open, deep sections of the lake that do not freeze (Emery et al., 1972; Wilbur and Collins, 1973; Scott, 1990). We did not recapture any individuals marked in 2012 in the summer of 2013 and others only have observed second-year larvae in lakes without fish, which may provide evidence of increased predation of individuals that attempt to overwinter (Bull and Marx, 2002).

Timing and size at metamorphosis can also be density dependent and driven by availability of food or permanency of habitat (Wilbur and Collins, 1973; Duellman and Trueb, 1986). Increased density is correlated with smaller size and extended larval periods in permanent bodies of water, whereas reduced resources are related to smaller size and accelerated development (Semlitsch and Caldwell, 1982; Petranka, 1989; Scott, 1990; Van Buskirk and Smith, 1991; Newman, 1994). We did not detect differences in salamander density between lakes with and without trout, but the probability and timing of metamorphosis of salamanders was delayed significantly in lakes with trout.

Relatively small differences in size at metamorphosis can affect reproduction, as the number and size of eggs are positively correlated with size of females (Kaplan and Salthe, 1979; Berven, 1988; Davenport et al., 2013). Mayflies emerge earlier from streams to avoid trout predation, yet, they are 13-20% smaller in size and have a 24-35% reduction in fecundity (McPeek and Peckarsky, 1998; Peckarsky et al., 2001, 2002). A decrease of 3 mm in body length of wood frogs results in a decrease of 90 eggs, which represents a 15% decrease in the mean clutch size (Berven, 1982, 1988). Salamanders that metamorphosed in lakes with trout had smaller total and tail sizes compared to salamanders in lakes without trout. Tail length, in addition to body size, is positively related to clutch size of female golden-striped salamanders (*Chioglossa lusitanica*), as tails serve as food storage and may provide resources for reproduction (Maiorana, 1977; Arntzen, 1981, 1994). Salamanders reproduce as early as one year after metamorphosing from lakes, which provides limited opportunity to compensate for reduced total and tail sizes observed at metamorphosis (Berven, 1988; Boone et al., 2007). Moreover, adult salamanders are able to detect the presence of fish predators and are less likely to oviposit eggs in lakes with trout; if they do, abundance of egg masses, and therefore eggs, are significantly lower compared to lakes without trout, further reducing reproductive success in a population (Bull and Marx, 2002).

Nonconsumptive effects of trout clearly affect larval size, timing of metamorphosis, and size at metamorphosis. Reduced body sizes and delayed metamorphosis of salamanders in lakes with trout provide clear expressions of the morphological and metamorphic costs associated with coexisting with predators. Although remaining in refugia will reduce encounter rates with predators, the resulting changes in body morphology and life history are correlated with lower survival (Smith, 1987; Semlitsch et al., 1988; Beck and Congdon, 1999; Altwegg and Reyer, 2003; Orizaola and Brana, 2005). In addition, the stress associated with predator-induced behaviors can suppress immune function and make amphibians more vulnerable to disease, pathogens, or parasites (Stuart et al., 2004; Gervasi and Foufopoulos, 2008; Warne et al., 2011).

We understand little about whether the nonconsumptive effects of trout we documented persist to affect survival and reproduction of adult salamanders, however small size and increased stress during the larval period are related directly to smaller size at metamorphosis, which can decrease adult survival, mating success, and reproductive potential (Petranka et al., 1987; Semlitsch, 1987; Figiel and Semlitsch, 1990; Kiesecker and Blaustein, 1998; Boone et al., 2007). Further research focusing on the costs prey species incur to coexist with predators could provide better understanding of predator-prey interactions, the importance of nonconsumptive effects relative to consumptive effects, and how introduced predators may influence prey populations.

Tables

Table 2.1: Locations and characteristics of study lakes with (*n* = 7) and without trout (*n* = 7), northwestern Montana, summers 2012 and 2013 (❖ denotes lakes sampled in 2012 and 2013)

Lake	Latitude	Longitude	Trout	Perimeter (m)	Elevation (m)	Salamanders/ 100m
Alpha	48.320911	114.04499	No	365	1811	5
Elk❖	46.849206	113.32387	No	140	1426	57
LL2	47.457973	113.74379	No	180	1264	2
LL3	47.459115	113.75456	No	135	1263	4
Loveboat	47.559311	113.78020	No	245	1113	6
New❖	47.491280	113.77893	No	260	1251	43
Pee❖	47.574885	113.77178	No	180	1104	35
Beta	48.317595	114.02943	Yes	695	1702	9
Elsina❖	47.243857	113.70388	Yes	960	1928	6
Horseshoe	47.024530	113.29864	Yes	600	1180	0.2
Rock❖	46.727317	113.67644	Yes	480	1079	46
Sink	47.267498	113.68732	Yes	180	1694	9
Spook❖	47.073447	113.57002	Yes	960	1723	57
Telegraph	46.465267	112.32396	Yes	110	1988	85

Table 2.2: Factors affecting changes in body morphology of larval salamanders over time in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), northwestern Montana, summers 2012 and 2013

		Weight			Total Length			Tail Length		
Explanatory	*df*	Estimate	*t*	*P*	Estimate	*t*	*P*	Estimate	*t*	*P*
Trout	12	-0.54	-2.13	0.054	-14.32	-2.60	0.023	-8.12	-3.08	0.010
Day	1504	-0.00	-0.04	0.969	0.14	1.44	0.150	-0.02	-0.33	0.745
Year	1504	0.02	0.63	0.527	0.88	1.65	0.100	-0.37	-1.15	0.251

Table 2.3: Factors affecting changes in body morphology of larval salamanders over time in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), northwestern Montana, summers 2012 and 2013

		SVL			Tail Depth			Tail Index		
Explanatory	*df*	Estimate	*t*	*P*	Estimate	*t*	*P*	Estimate	*t*	*P*
Trout	12	-5.77	1.88	0.085	-2.02	-2.70	0.019	-0.06	4.25	0.001
Day	1500	0.15	2.79	0.005	-0.03	-1.22	0.221	-0.00	-5.29	<0.001
Year	1500	0.36	1.28	0.202	0.11	1.37	0.168	-0.02	-2.71	0.007
Trout * Day	1500				0.06	2.11	0.035			

Table 2.4: Allometric relationships, after accounting for time, between weight and SVL, tail length, and tail depth of larval salamanders in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), after accounting for time, northwestern Montana, summers 2012 and 2013

		SVL		Tail Length		Tail Depth	
Explanatory	*df*	*t*	*P*	*t*	*P*	*t*	*P*
Trout	12	0.11	0.912	-0.48	0.640	0.47	0.649
Weight	1486	24.05	<0.001	14.67	<0.001	14.36	<0.001
Trout* Weight	1486	-2.00	0.046	-2.18	0.030	-3.56	<0.001

Table 2.5: Trout effect on body morphology of metamorphosing larval salamanders (means and 95% CIs) in no trout (*n* = 15 salamanders in seven lakes) and trout lakes (*n* = 52 salamanders in seven lakes), after accounting for year, northwestern Montana, summers 2012 and 2013

		Weight		SVL		Total Length		Tail Length		Tail Depth		Tail Index	
Explanatory	*df*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*	*t*	*P*
Trout	6	-0.59	0.578	-0.19	0.853	-2.98	0.025	-3.59	0.012	0.85	0.426	-1.44	0.201
Year	2	-0.46	0.692	0.22	0.846	0.50	0.667	0.89	0.466	0.37	0.749	0.84	0.488

Figures

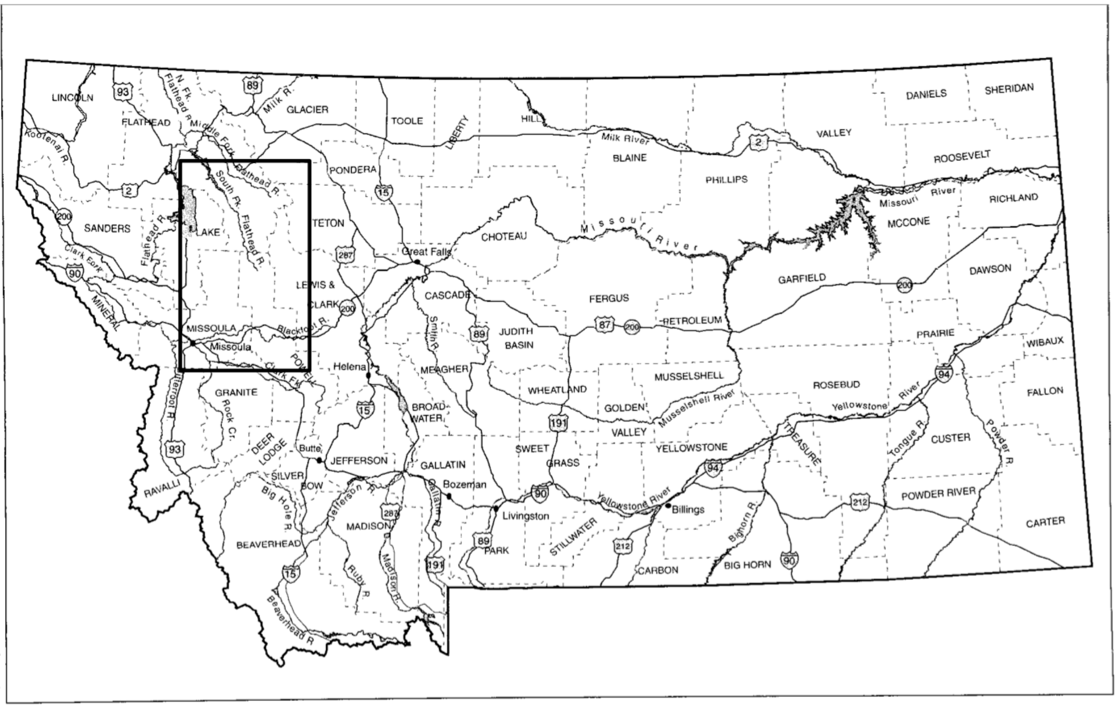

Figure 2.1: Map of Montana, where the black rectangle indicates the location of the 14 study lakes, summers 2012 and 2013 (modified from Robbins, 2005)

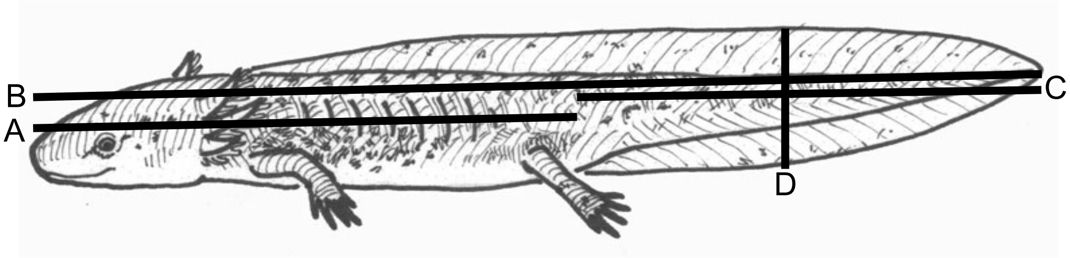

Figure 2.2: Measurements of body morphology for larval salamanders: A) snout-vent length (SVL), B) total length, C) tail length, and D) tail depth (modified from MacDonald, 2004)

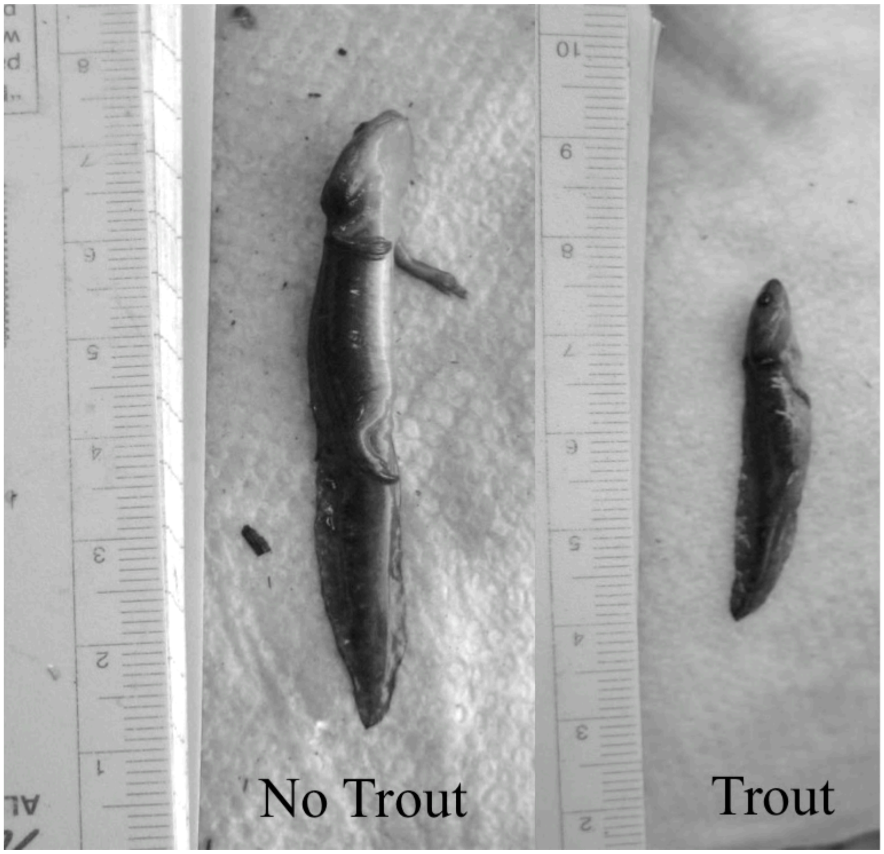

Figure 2.3: Salamanders captured from a lake without trout (left) and a lake with trout (right), each matches the mean estimates of morphology for each lake type and are photographed at equal scales

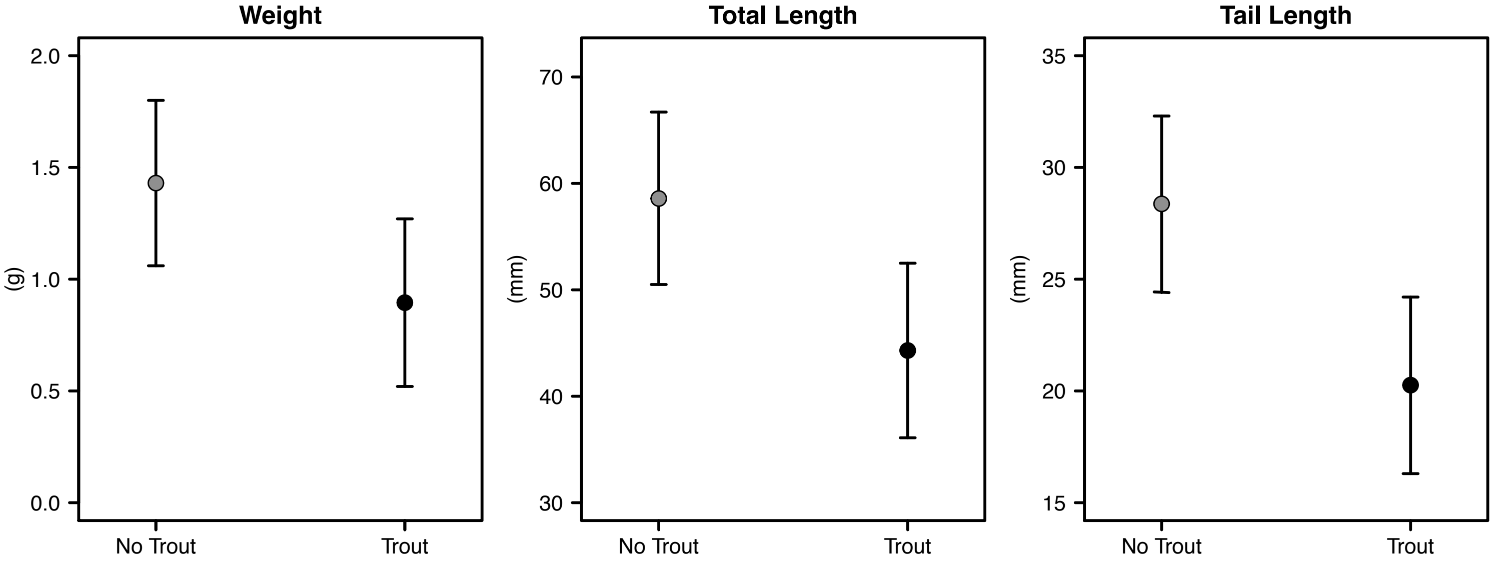

Figure 2.4: Body morphology of non-metamorphosing salamanders (means and 95% CIs) in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), northwestern Montana, summer 2012 and 2013

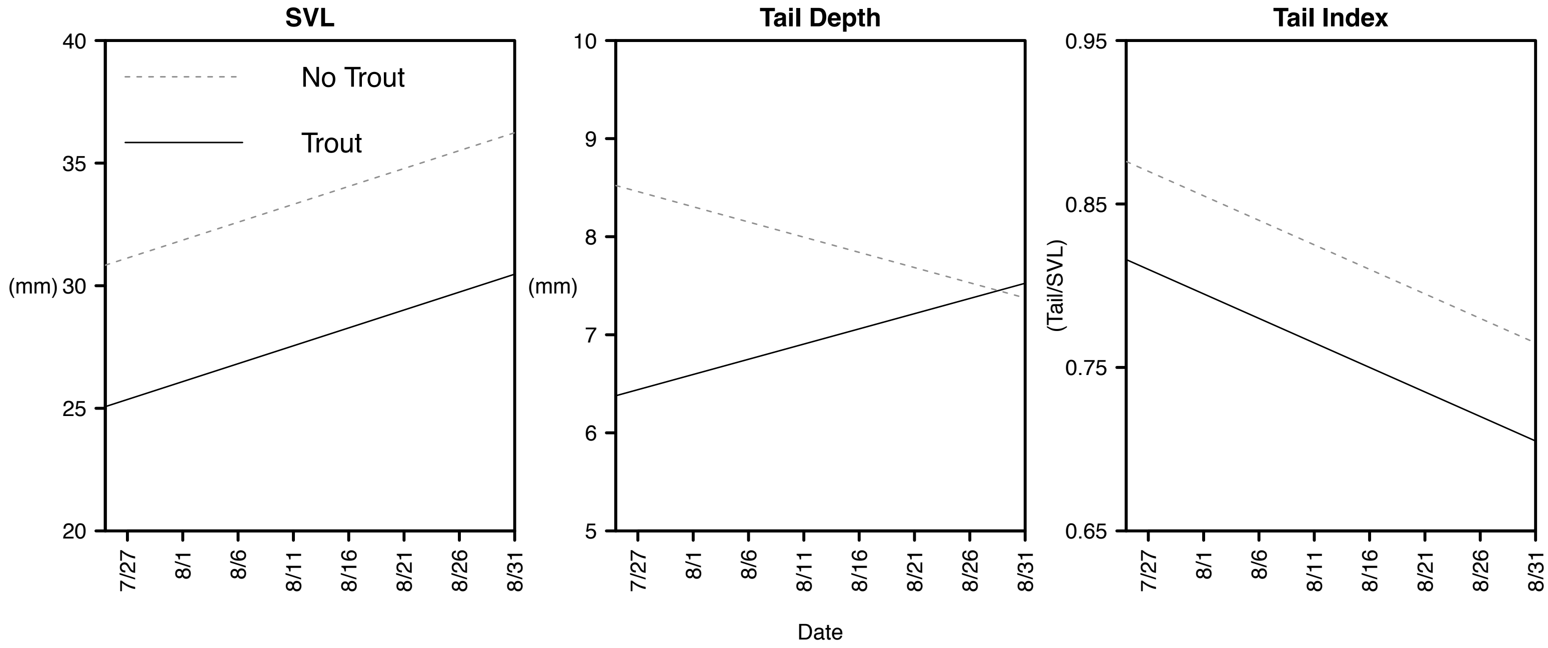

Figure 2.5: Changes in body morphology over time of non-metamorphosing salamanders in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), northwestern Montana, summer 2012 and 2013

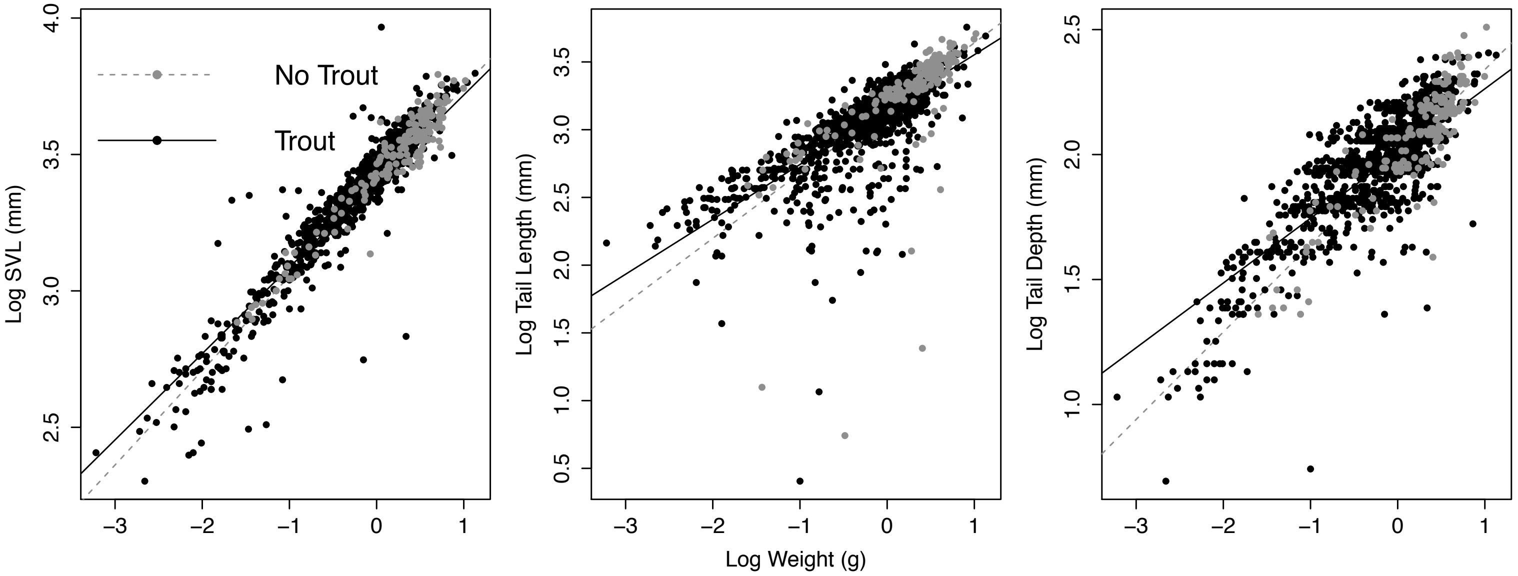

Figure 2.6: Allometric relationships between weight and SVL, tail length, and tail depth for non-metamorphosing salamanders captured in no trout (*n* = 177 salamanders in seven lakes) and trout lakes (*n* = 1372 salamanders in seven lakes), northwestern Montana, summer 2012 and 2013

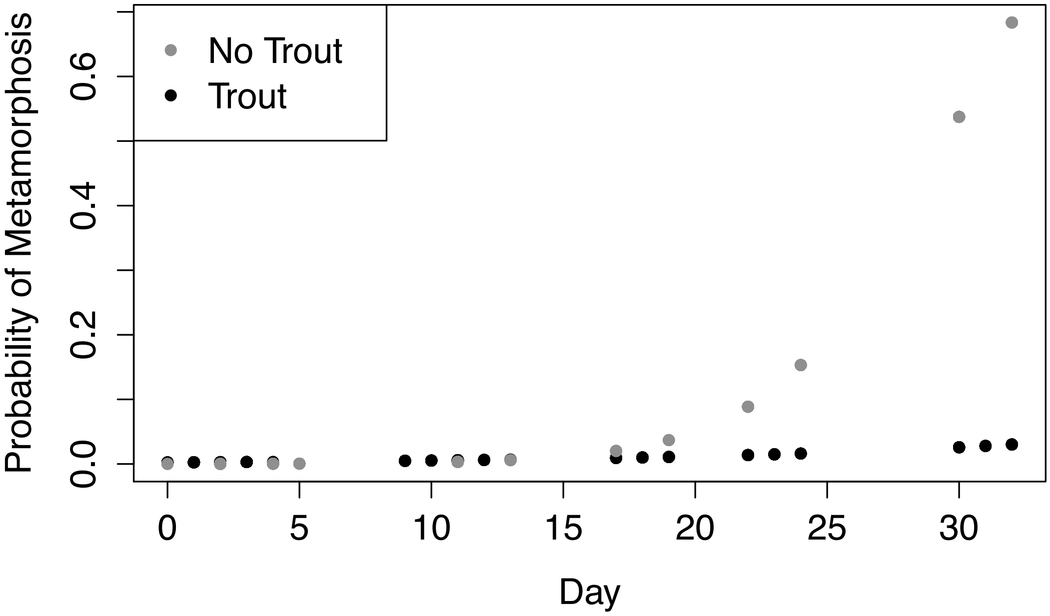

Figure 2.7: The probability of metamorphosing salamanders in trout (*n* = 52 of 1372 salamanders in seven lakes) and no trout lakes (*n* = 15 of 177 salamanders in seven lakes). Estimates are based on the number of metamorphosing individuals relative to the number of individuals captured over time, northwestern Montana, summer 2012 and 2013

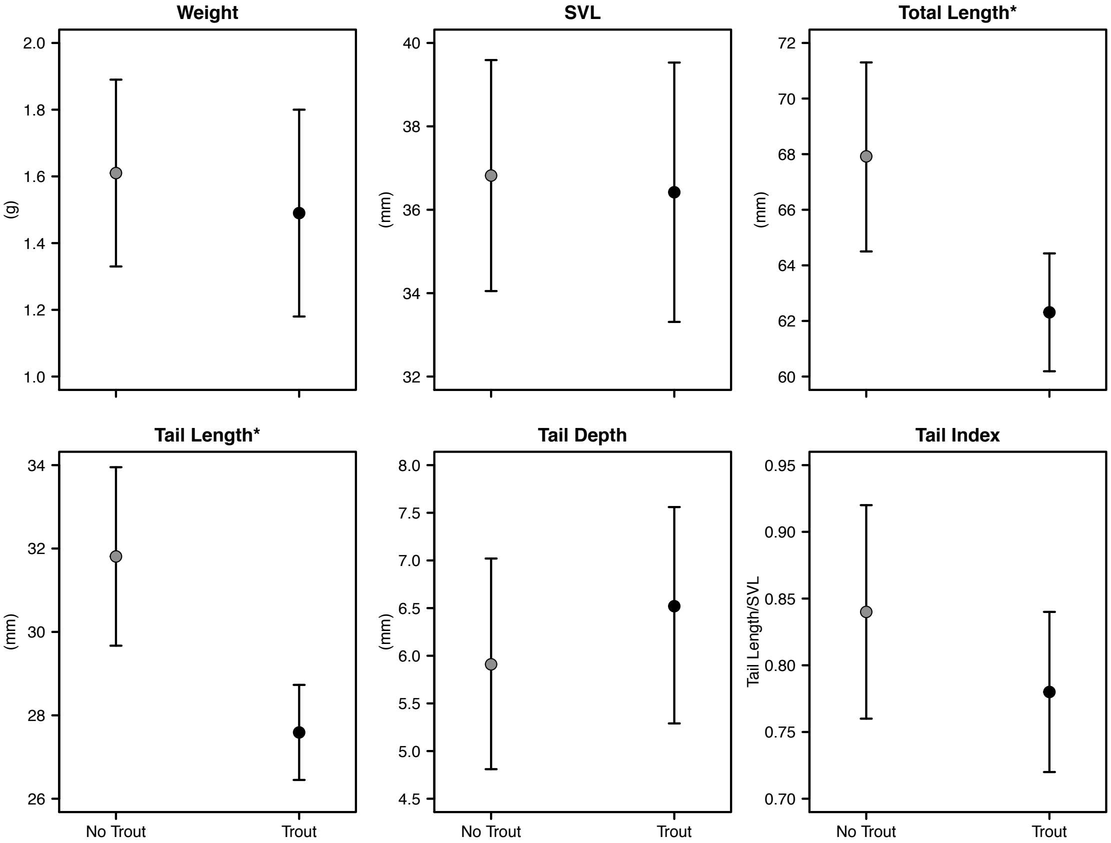

Figure 2.8: Comparisons of body morphology between metamorphosing salamanders (means and 95% CIs) captured in trout lakes (*n* = 16 salamanders in seven lakes) and no trout (*n* = 52 salamanders in seven lakes), northwestern Montana, summer 2012 and 2013 (* denotes significant difference

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CHAPTER THREE

ADDING VEGETATION STRUCTURE TO REDUCE NONCONSUMPTIVE EFFECTS OF INTRODUCED TROUT: A NOVEL METHOD FOR AMPHIBIAN CONSERVATION?

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CHAPTER THREE

ADDING VEGETATION STRUCTURE TO REDUCE NONCONSUMPTIVE EFFECTS OF INTRODUCED TROUT: A NOVEL METHOD FOR AMPHIBIAN CONSERVATION?

Abstract

Predators regulate prey populations, but introduced predators can have a greater impact on native prey. Trout introduced to historically fishless lakes have led to reduced abundance and even local extinctions of amphibian populations. Although uncommon, trout and larval amphibians can coexist in lakes with complex vegetation. Larvae can detect trout cues and rely on increased refuge use to reduce encounter rates with fish predators. However, these behavioral responses can result in decreases in energy uptake and body size, as well as survival and reproduction (nonconsumptive effects). We conducted a field experiment to investigate whether adding vegetation structure can reduce the nonconsumptive effects of trout on long-toed salamander larvae. We constructed field enclosures in lakes with and without trout and quantified changes in salamander growth, probability of metamorphosis, and size at metamorphosis among four treatment types: presence/absence of trout cues and presence/absence of structure. Salamanders appeared to detect trout cues because they grew more slowly in lakes with trout, even though trout had no ability to consume larvae. Added vegetation structure did not influence growth rates, but did increase the probability of salamanders that reached metamorphosis before the end of the experiment. Salamanders did not differ in size at

metamorphosis across all four treatments, but slower growth and reduced probability of metamorphosis may negatively impact persistence of salamander populations. Future research should investigate whether adding vegetation structure to the whole lake can facilitate coexistence and provide a feasible alternative to trout removal.

Introduction

Predator-prey interactions have the capacity to shape population dynamics, species distributions, community composition, and ultimately, regulate ecosystem function (Menge and Sutherland, 1976; Kerfoot and Sih, 1987). Depending on the efficiency of a predator at capturing and consuming prey, predator and prey populations can oscillate in an unstable manner over time (Rosenzweig and MacArthur, 1963). Instability in predator-prey interactions can lead to population booms or increased risk of extinction for prey, predators, or both (Stiling, 2002). Nonnative predators can have a much greater impact on prey compared to native predators, exacerbating this instability (Salo et al., 2007).

The introduction of nonnative species has been associated with global amphibian declines and is considered the greatest threat to freshwater ecosystems (Collins and Storfer, 2003; Kats and Ferrer, 2003). Native prey species are especially vulnerable because they often are naïve to nonnative predators, may not be able to detect introduced predators or do not possess effective adaptations or learned behavior to avoid predation (Kiesecker and Blaustein, 1997; Kats and Ferrer, 2003). Pacific treefrogs (*Pseudacris regilla*), for example, respond to native fish predators by increasing refuge use, but are unable to detect chemical cues of nonnative fish and don't increase time spent under cover (Pearl et al., 2003). Red-legged frog (*Rana aurora*) tadpoles that are naïve to bullfrogs (*Rana catesbeiana*), do not alter behavior when exposed to bullfrogs and are more likely to be depredated, whereas syntopic tadpoles decrease activity and increase refuge use in response to bullfrog larvae and adults (Kiesecker and Blaustein, 1997). Neurotoxins in the skin of adult newts (*Taricha torosa*) are effective defenses against native predators, but are insufficient to protect against predation by introduced crayfish (*Procambarus clarkia*, Gamradt et al., 1997). Without appropriate responses to introduced predators, populations of amphibians are more likely at risk of decline (Pearl et al., 2003).

Throughout much of the western United States, trout have been introduced to historically fishless lakes for recreational purposes (Bahls, 1992). These introductions have resulted in decreases in abundance and even extirpations of populations of amphibians in lakes where trout exist (Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Bull and Marx, 2002). Trout prey on eggs, larvae/tadpoles, juveniles, and occasionally adult amphibians (Matthews et al., 2001; Welsh et al., 2006; Wells, 2007). Most amphibian larvae are capable of detecting fish predator cues, but must rely on changes in behavior to reduce predation risk when they lack chemical or morphological defenses (Petranka et al., 1987; Tyler et al., 1998a; Pearson, 2004). When exposed to introduced trout, larval amphibians increase refuge use and decrease time spent in open water to reduce encounter rates (Petranka et al., 1987; Kats et al., 1988; Tyler et al., 1998a). Although these changes in behavior may increase amphibian survival and reduce predation, fish predators still can have nonconsumptive effects on larvae (Tyler et al., 1998a; Hirner and Cox, 2007; Chapter 2).

As individuals increase the amount of time spent in refugia, foraging activity decreases, with concomitant decreases in energy uptake and body size (Semlitsch, 1987; Figiel and Semlitsch, 1990; Skelly and Werner, 1990; Tyler et al., 1998a; Chapter 2). Smaller body sizes during the larval period and at metamorphosis are associated with reduced survival and reproduction and increased susceptibility to terrestrial threats such as predation, desiccation, and disease (Petranka et al., 1987; Semlitsch, 1987; Figiel and Semlitsch, 1990; Kiesecker and Blaustein, 1998; Tyler et al., 1998a; Gervasi and Foufopoulos, 2008; Warne et al., 2011).

The long-toed salamander (*Ambystoma macrodactylum*) is the most widely distributed amphibian west of the Continental Divide, extending from central California as far north as southeast Alaska, and is the most common salamander in the state of Montana (Werner et al., 2004). However, this species is especially vulnerable to introduced fish due to their palatability, lack of chemical defenses, 1-3 year larval period, and reliance on deep lakes for overwintering (Howard and Wallace, 1985; Pilliod and Peterson, 2000; Werner et al., 2004). Salamander larvae respond to predator cues by increasing use of refugia to avoid predation, yet in lakes with trout, abundance of salamander egg masses is lower, larvae are >65% less abundant, and some populations have been extirpated (Tyler et al., 1998b; Funk and Dunlap, 1999; Pilliod and Peterson, 2001; Bull and Marx, 2002; Hirner and Cox, 2007; Pearson and Goater, 2008).

Furthermore, salamander occupancy is negatively correlated with fish presence and coexistence between trout and salamanders occurs rarely (Pilliod et al., 2013).

Removing fish from historically fishless lakes may be the most effective way to reverse effects on long-toed salamander populations. When fish are removed from lakes, amphibians recolonize sites and population sizes increase rapidly, reducing the risk of local extinction (Funk and Dunlap, 1999; Knapp et al., 2001; Hoffman et al., 2004; Vredenburg, 2004). However, alternative conservation strategies are needed, given that removing trout often is unrealistic due to high costs and effort, in addition to being unpopular with the public.

Dense or structurally-complex vegetation or cover objects provide protection from predators and can facilitate coexistence between predators and prey (Sih, 1987; Allouche, 2002). Complex structure reduces the maneuverability, visual range, and effectiveness of fish predators and has been correlated with increased prey survival (Werner et al., 1983; McNair, 1986; Sih, 1987; Kats et al., 1988; Figiel and Semlitsch, 1991; Diehl, 1992; Babbitt and Jordan, 1996; Babbitt and Tanner, 1997). Despite the rarity of coexistence, long-toed salamanders and trout have been found to co-occur in lakes where habitat characteristics such as emergent vegetation and physical barriers from trout are present (Tyler et al., 1998a; Pearson and Goater, 2008; Pilliod et al., 2010; Pilliod et al., 2013). Therefore, adding complex vegetation structure, such as woody debris, to lakes with trout could provide an alternative strategy for conservation of salamanders. Previous amphibian conservation projects have been directed at maintaining buffer zones surrounding breeding sites, creating connectivity between wetlands, or constructing and restoring water bodies (Semlitsch, 2002; Shulse et al., 2012), yet, adding complex structure may create refugia that can reduce exposure to predators, provide protected areas to forage, and dampen nonconsumptive effects of trout, potentially increasing fitness of terrestrial adults (Bull and Marx, 2002; Relyea, 2007; Shulse et al., 2012).

We sought to understand how adding complex vegetation structure affects growth, body size, and timing of metamorphosis of larval long-toed salamanders in lakes with and without trout. We aimed to determine if this strategy could reduce the nonconsumptive effects of introduced trout and provide an alternative conservation strategy to fish removal. We hypothesized that salamanders would grow faster and be larger at metamorphosis in lakes without trout, but that salamanders in lakes with trout and added structure would be comparable in size. Additionally, we hypothesized that the timing of salamander metamorphosis would be earlier in lakes without trout and that salamanders in enclosures with added structure would metamorphosis faster than those without. If salamanders can grow and metamorphose early and at larger sizes, adults may have higher rates of survival and reproduction, ultimately increasing size of salamander populations. We know of no other studies that have experimentally manipulated cover to assess if added structural complexity could enhance amphibian coexistence with trout predators. We seek to test the effectiveness of this management strategy and its potential use in conservation efforts for other amphibian populations negatively affected by introduced predators.

Methods

Study Sites:

We conducted a field experiment during the summer of 2013 in five permanent lakes, two lakes with trout and three without trout. Lakes were located in northwestern Montana, in the Flathead National Forest between the Swan and Mission Mountain ranges; mainly between Condon and the town of Seeley Lake, with one lake located closer to Missoula, Montana (Table 3.1). We selected all lakes during previous visual encounter and trapping surveys in 2012 that confirmed the presence of salamanders and the presence or absence of trout (Chapter 2).

Field Experiment:

We constructed experimental field enclosures with PVC pipe and fiberglass window screening (2 x 1 x 1 m, LWH) (Sredl and Collins, 1991; Kiesecker and Blaustein, 1998). Experimental treatments were based on a 2 x 2 factorial arrangement: 1) presence or absence of trout cues (i.e., enclosures in lakes with trout compared to those without trout) and 2) presence or absence of added vegetation structure. This design exposed salamanders to the chemical or visual signals of predators, but protected them from direct predation. We randomly assigned treatments to enclosures.

We constructed complex vegetation structures by binding roughly 20 dry, dead sticks with 20 living, leafy branches (i.e., aspen or other littoral vegetation) with twine in an inverted funnel shape (Schneider and Winemiller, 2008, Figure 3.1). Vegetation structures were close to 1 m in circumference at the base and 50–60 cm tall. We placed two vegetation structures in enclosures assigned added structure treatments, one structure at each end of the enclosure, and secured them in place with a large rock.

We placed enclosures along the north-facing edge of each lake in the littoral zone. We positioned enclosures so that depth, distance between enclosures, and distance from shore was equal for all enclosures (Sredl and Collins, 1991). We also added ~10 L of lake substrate to the bottom of each enclosure to incorporate natural sediments. Lakes with trout had 4 replicates of each of the 2 treatments (trout cues, with and without added vegetation structure), for a total of 8 enclosures per lake. Lakes without trout had 2 replicates of each of the 2 treatments (absence of trout cues, with and without added vegetation structure), for a total of 4 enclosures per lake.

We used minnow traps to capture salamanders to add to experimental enclosures during June and July 2013. We used minnow traps, as they are especially useful in trapping small, cryptic larvae and are associated with little mortality or injury (Adams et al., 1997). We anesthetized salamander larvae with MS-222, measured weight, snout-vent length (SVL), total length, tail length, and tail depth with an electronic scale and calipers, and marked each individual uniquely with visual implant elastomer in the middle of their tail. We randomly assigned 20 salamanders to each enclosure; salamanders were comparable in size, >0.2 g, and we marked and measured individuals before adding them to enclosures. We selected this density of salamanders as it was comparable to previous studies that did not observe cannibalism and where adequate amounts of food persisted throughout study periods (e.g., Clark, 1986; Semlitsch, 1987; Tyler et al., 1998a; Pearson and Goater, 2009). Although we expected zooplankton and other small crustaceans to be able to pass through enclosure screen, we added ~10 L of lake water to enclosures at each visit to provide additional food resources (Stenhouse, 1985; Tarr and Babbitt, 2002).

After adding salamanders to enclosures, we visited enclosures four additional times during July and August 2013. At each visit, we captured individual larvae with hand nets, recorded measurements of body morphology (i.e., weight, SVL, total length, tail length, and tail depth), noted whether salamanders were metamorphosing, which we defined as any evidence of gill absorption (Dodd and Dodd, 1976; Arntzen, 1981; Duellman and Trueb, 1986), and released them back into assigned enclosures. We were unable to accurately measure survival, as we couldn't distinguish with certainty whether salamanders missing from enclosures escaped or died from predation by invertebrates, conspecific cannibalism, or natural causes. We terminated the experiment at the end of August, released all remaining individuals, and removed enclosures. We anesthetized, marked, and handled all captured individuals in accordance with Montana State University Institutional Animal Care and Use Committee protocol 2013-04.

Statistical Analyses:

We assessed the effects of trout cues on salamanders in enclosures with and without added vegetation structure by comparing changes in morphological measurements over time among all four treatments: 1) presence of trout cues (i.e., lakes with trout) and added structure, 2) presence of trout cues and no added structure, 3) absence of trout cues (i.e., lakes without trout) and added structure, and 4) absence of trout cues and no added structure. We also examined differences in the probability of metamorphosis, timing of metamorphosis, and size of salamanders at metamorphosis among all four treatments.

We analyzed all measurements of body morphology: weight, SVL, total length, tail length, and tail depth as separate response variables for non-metamorphosing and metamorphosing salamanders. We used generalized linear mixed models, random slopes and intercepts, and a three-tiered, nested data structure – multiple measurements of salamanders within enclosures within study lakes – to account for repeated measurements and variation among lakes (Zuur et al., 2009). We included our experimental treatments – presence/absence of trout (trout) and presence/absence of vegetation structure (structure) – as simple effects in analytical models. We also included time in models as number of days since the first sampling visit (day), as we hypothesized that changes in morphological measurements over time might differ based on vegetation structure and trout condition. We considered all possible 2-way interactions between treatment factors and time (trout * structure, trout * day, structure * day) in models of larval morphology and probability of metamorphosis. We assessed evidence of effects of trout and structure on size at metamorphosis by examining simple (trout, structure) and interactive effects (trout * structure). We removed interactions that did not explain sufficient variation ($\alpha > 0.1$) from models for inference, but kept all simple explanatory variables in the model. We calculated relative difference over time by dividing the average rate of growth in enclosures without trout cues over the average rate of growth in enclosures with trout cues. We report estimates of changes in morphological measurements over time and average size at metamorphosis, and include 95% confidence intervals for all estimates.

Results

At the beginning of the experiment, salamanders were similar in size among treatments (see differences in intercepts of trout and structure, Table 3.2). All body morphology measurements of non-metamorphosing salamanders increased over time (trout * day, Table 3.2). Changes in all morphological measurements were greater in lakes without trout compared to lakes with trout and did not depend on structure (trout * structure, Figure 3.2) On average, growth rates for salamander in enclosures without trout increased faster by 2.9 times for weight, 2.2 times for SVL, 2.4 times for total length, 2.3 times for tail length, and 6.7 times for tail depth (Figure 3.2, Table 3.3). Adding vegetation structure was not influential for most of the body morphology measurements, but did slow the growth of tail depth in enclosures with and without trout cues (structure * day, Figure 3.3, Table 3.2).

Weight, SVL, total length, or tail depth of metamorphosing salamanders were similar with and without trout cues and with and without vegetation structure (Table 3.4). However, salamanders in enclosures with added structure had tail lengths that were 4.6% shorter (95% CI = 0.5 – 8.7%) than salamanders without added structure, regardless of the presence or absence of trout cues (Table 3.4). Although salamanders were similar in size, the probability of metamorphosis over time did differ among treatments (Table 3.5). Adding structure to enclosures with trout cues increased the probability of metamorphosis to be similar to enclosures without trout cues; probability of metamorphosis was lowest in enclosures with trout cues that did not have added structure (Figure 3.3).

Discussion

Structural complexity is important in mediating species interactions and facilitating the coexistence of predators and prey (Murdoch and Oaten, 1975; Sih, 1987; Diehl, 1992). Coexistence between trout and salamanders is uncommon, often only occurring in lakes with emergent vegetation and shallow littoral zones, areas that provide adequate separation and refuge from fish predators (Tyler et al., 1998b; Pearson and Goater, 2008; Pilliod et al., 2010, 2013). The presence of refugia can stabilize predator-prey interactions, as increased complex vegetation reduces the frequency and success of predator attacks on prey. However, prey still can incur nonconsumptive costs with the use of refugia (Rosenzweig and MacArthur, 1963; Diehl, 1988). We provide evidence that trout chemical cues induce nonconsumptive effects that alter long-toed salamander growth and these effects are more influential on the size of salamanders than the addition of complex vegetation structure.

Trout clearly influenced salamander growth in our study, as larvae grew more slowly in lakes with trout compared to lakes without trout (also see Chapter 2). Even without the physical risk of predation, chemical, visual, or both types of trout cues are sufficient for salamanders to detect and respond with predator avoidance behaviors, such as reduced foraging (Stauffer and Semlitsch, 1993). Tadpoles subjected to the presence of a caged predator or fish chemical cues demonstrate as much as a 41% reduction in foraging or a 68% reduction in time spent outside of refugia (Petranka et al., 1987; Skelly and Werner, 1990). Persisting in environments with fish that are perceived as high-risk not only reduces salamanders’ ability to acquire resources, but also increases stress levels, which can inhibit food intake, suppress appetite, and ultimately, reduce size and growth over the larval period (Crespi and Denver, 2005).

Although vegetation complexity is important for, and increases the likelihood of coexistence (Sih, 1987), adding vegetation structure did not mitigate the effects of trout cues on larval growth or size at metamorphosis in our experiment. However, adding structure to enclosures with trout cues did increase the probability of metamorphosis. Decreased activity in the presence of predators can reduce growth rates and lengthen larval periods (Nicieza, 2000; Babbitt, 2001; Johansson et al., 2001; Altwegg, 2002). Organisms often metamorphose when greater resources can be acquired and increased fitness can be achieved as an adult rather than larvae, but a minimum size must be reached before metamorphosis can be initiated (Wilbur and Collins, 1973; Gilliam, 1982; Benard, 2004). Early metamorphosis can occur under heighted risk of predation, for example western toads shortened their time to metamorphosis by ~10 days when exposed to predatory cues of backswimmers (*Notonecta spp.*, Chivers et al., 1999). Alternatively, in our study, reduced probability of metamorphosis in enclosures with trout cues but without added structure suggests that salamanders may detect risks associated with trout, become more vigilant without adequate sources of refuge but are less likely to leave the aquatic system as early as salamanders without trout cues or with added structure (Nicieza, 2000; Babbitt, 2001; Altwegg, 2002).

Salamanders did not differ in size at metamorphosis, despite differences in the probability of metamorphosis. Southern leopard frogs, wood frogs, and water frogs extend their larval period when exposed to insect predators, but metamorphose at equal sizes (Relyea, 2001; Babbitt, 2001; Van Buskirk and Saxer, 2001). Similarly, long-toed salamanders have longer larval periods and reduced growth rates when in the presence of cannibalistic conspecifics, yet are similar in size at metamorphosis to larvae not exposed to predators (Wildy et al., 1999). Salamanders that remain in their larval period longer in lakes with trout may increase their exposure to predators, reducing the number of individuals that leave the pond and successfully enter into the terrestrial system as adults. The combination of nonconsumptive and consumptive effects of trout ultimately may influence populations if reductions in adult survival and reproduction limit recruitment (Kiesecker and Blaustein, 1998; Nicieza, 2000).

Future research should focus on whether adding complex vegetation structure at a whole-lake level can be effective at reducing the nonconsumptive effects of trout. By adding vegetation structures to lakes, instead of the restricted space of an enclosure, and allowing structures to remain over sufficient time for invertebrate prey to establish, we might be able to create highly productive, food-rich microhabitats for larval amphibians (Diehl, 1992; Hartel, 2004). Habitat features such as rocks, woody material, and vegetation are effective protection from fish predators that also are associated with increased density and species richness of invertebrates (Stenhouse, 1985; Babbitt and Jordan, 1996; Tyler et al., 1998b; Hartel et al., 2007). These areas of structural and vegetative complexity may provide food as well as safety from predators during larval development, which may mitigate nonconsumptive effects of trout even when predator avoidance behaviors are used.

Alternative strategies to reduce the effects of introduced trout are essential, especially as the number of amphibian species that are threatened and endangered continue to increase and populations of the even most common species decrease in size (Adams et al., 2013). Changes to amphibian populations can alter community composition and lead to disruptions of food webs in both the aquatic and terrestrial system (Kats and Ferrer, 2003). Introduced trout in the Sierra Nevada Mountains reduce the availability of aquatic insect prey emerging from lakes, resulting in decreases in the abundance of foraging frogs, and subsequent decreases in abundance of native garter snakes (Matthews et al., 2002; Kats and Ferrer, 2003; Finlay and Vredenburg, 2007). With additional research, adding vegetation complexity has the potential to efficiently improve persistence of amphibian species, facilitate coexistence between introduced predators and native prey, and preserve the function of terrestrial and aquatic ecosystems without requiring removal of fish.

Tables

Table 3.1: Locations and characteristics of study lakes with (*n* = 2) and without trout (*n* = 3), northwestern Montana, summer 2013

Lake	Latitude	Longitude	Trout	Perimeter (m)	Elevation (m)
Elk	46.849206	113.32387	No	140	1426
New	47.491280	113.77893	No	260	1251
Pee	47.574885	113.77178	No	180	1104
Rock	46.727317	113.67644	Yes	480	1079
Spook	47.073447	113.57002	Yes	960	1723

Table 3.2: Factors affecting measurements of body morphology of salamanders, 20 per enclosure with repeated measures, in experimental enclosures without trout cues or added structure (*n* =6 enclosures), without trout cues, but with added structure (*n* = 6 enclosures), with trout cues, but without added structure (*n* = 8 enclosures), and with trout cues and added structure (*n* = 8 enclosures), and northwestern Montana, summer 2013

		Weight		SVL		Total Length	
Explanatory	*df*	*t*	*P*	*t*	*P*	*t*	*P*
Trout	3	0.98	0.400	1.03	0.379	1.16	0.329
Structure	22	-0.18	0.862	-0.36	0.723	-0.55	0.585
Day	1271	8.34	<0.001	10.99	<0.001	10.20	<0.001
Trout * Day	1271	-3.44	0.001	-3.88	<0.001	-3.83	<0.001

		Tail Length		Tail Depth	
	df	*t*	*P*	*t*	*P*
Trout	3	1.05	0.371	0.74	0.513
Structure	22	-0.41	0.683	1.18	0.252
Date	1271	7.74	<0.001	17.87	<0.001
Trout * Day	1271	-2.87	0.004	-13.18	<0.001
Structure * Day	1271			-2.74	0.006

Table 3.3: Estimated change in salamander body morphology over time (means and 95% CIs) in enclosures with/without trout cues (+/−) and with/without added structure (+/−), northwestern Montana, summer 2013

Response	Weight (Δ g/10 days)	SVL (Δ mm/10 days)	Total Length (Δ mm/10 days)	Tail Length (Δ mm/10 days)	Tail Depth (Δ mm/10 days)
+ Trout + Structure	0.10 (0.01 − 0.19)	1.51 (0.75 – 2.27)	2.68 (1.13 – 4.23)	1.33 (0.37 – 2.28)	0.04 (-0.02 − 0.09)
+ Trout − Structure	0.12 (0.03 − 0.21)	1.71 (0.95 – 2.47)	2.87 (1.31 – 4.41)	1.35 (0.39 – 2.31)	0.14 (0.08 − 0.20)
− Trout + Structure	0.31 (0.23 − 0.38)	3.43 (2.78 – 4.08)	6.54 (5.23 – 7.86)	3.11 (2.29 − 3.93)	0.55 (0.48 − 0.61)
− Trout − Structure	0.33 (0.25 − 0.40)	3.63 (2.98 – 4.28)	6.74 (5.41 – 8.06)	3.13 (2.31 − 3.96)	0.65 (0.58 − 0.72)

Table 3.4: Factors affecting body morphology of salamanders at metamorphosis in experimental enclosures without trout cues or structure (n = 18 salamanders in six enclosures), without trout cues, but with added structure (n = 24 salamanders in six enclosures), with trout cues, but without structure (n = 36 salamanders in eight enclosures), and with trout cues and added structure (n = 47 salamanders in eight enclosures), northwestern Montana, summer 2013

		Weight		SVL		Total Length	
Explanatory	*df*	*t*	*P*	*t*	*P*	*t*	*P*
Trout	3	-0.65	0.563	-0.38	0.727	-0.79	0.488
Structure	124	-0.79	0.427	0.07	0.942	-1.40	0.163

		Tail Length		Tail Depth	
	df	*t*	*P*	*t*	*P*
Trout	3	-0.94	0.419	-0.34	0.756
Structure	124	-2.20	0.029	-1.20	0.231

Table 3.5: Factors affecting the probability of metamorphosis in experimental enclosures without trout cues or structure (*n* = 18 salamanders in six enclosures), without trout cues, but with added structure (*n* = 24 salamanders in six enclosures), with trout cues, but without structure (*n* = 36 salamanders in eight enclosures), and with trout cues and added structure (*n* = 47 salamanders in eight enclosures), northwestern Montana, summer 2013

		Probability of Metamorphosis	
Explanatory	*df*	*t*	*P*
Trout	4	1.94	0.125
Structure	608	-2.02	0.044
Day	1347	13.19	<0.001
Trout * Structure	608	-1.38	0.167
Trout * Day	1347	-6.72	<0.001
Structure * Day	1347	1.37	0.171
Trout * Structure * Day	1347	2.08	0.038

Figures

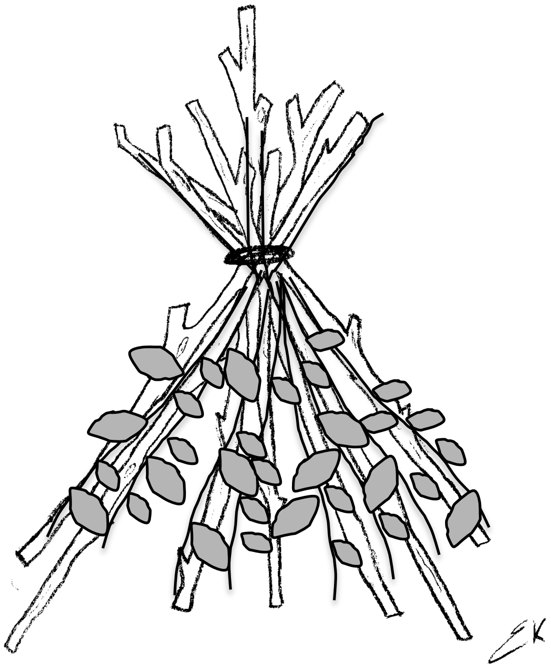

Figure 3.1: Vegetation structure constructed for enclosures, made with dead and living plant materials and secured with twine

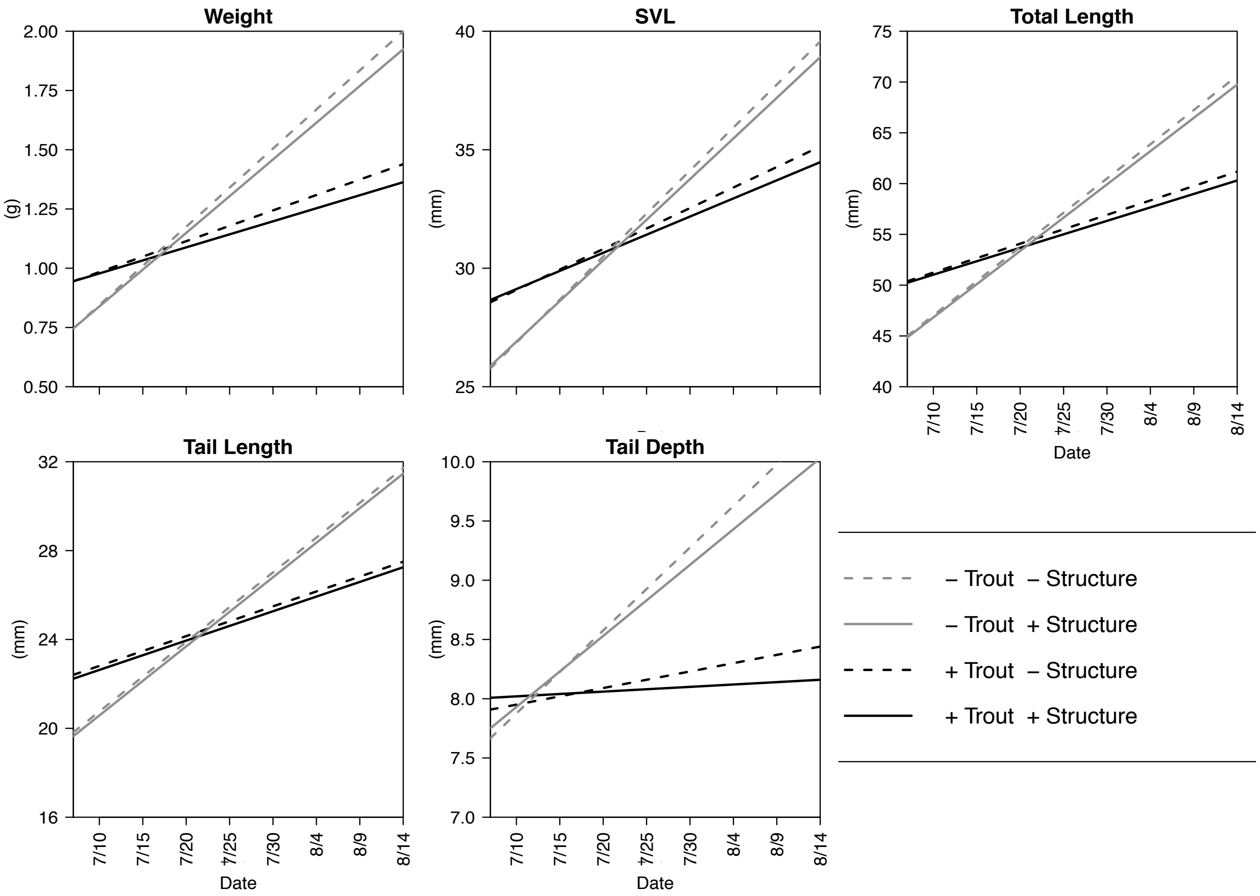

Figure 3.2: Changes in body morphology of salamanders in enclosures over time in lakes without trout or added structure (– Trout – Structure, *n* = 120 salamanders in six enclosures), without trout, but with added structure (– Trout + Structure, *n* = 123 salamanders in six enclosures), with trout, but without added structure (+ Trout – Structure, *n* = 160 salamanders in eight enclosures), and with trout and added vegetation structure (+ Trout + Structure, *n* = 160 salamanders in eight enclosures), northwestern Montana, summer 2013. (Salamanders are similar in size at the start of the experiment)

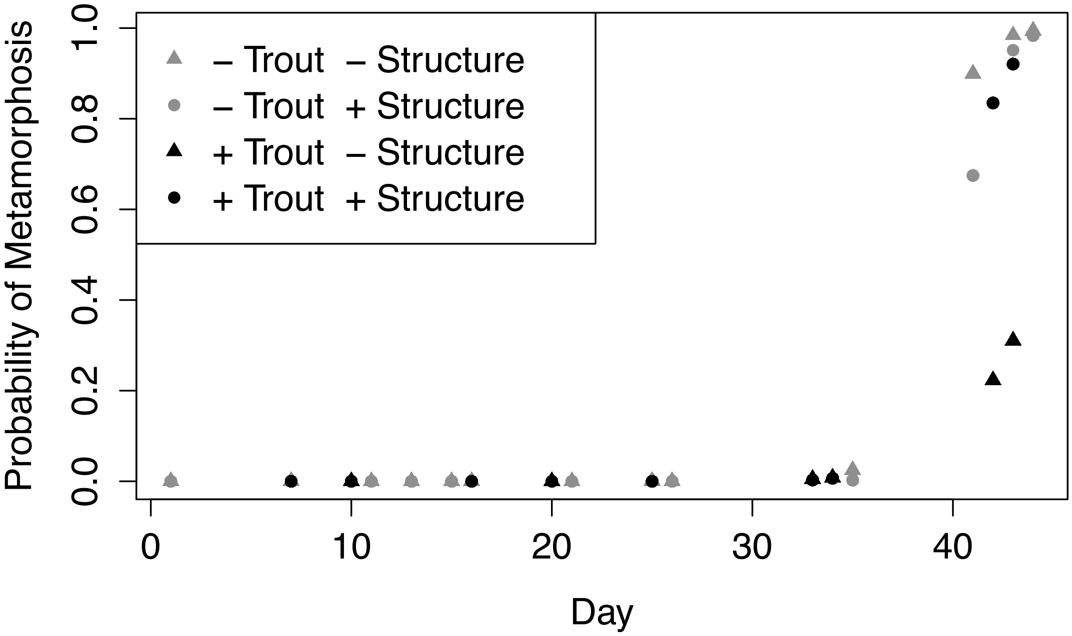

Figure 3.3: Probability of metamorphosis over time of salamanders in lakes without trout or added structure (–Trout –Structure, *n* = 18 of 120 salamanders), lakes without trout and with added structure (–Trout +Structure, *n* = 24 of 123 salamanders), lakes with trout, but without added structure (+Trout –Structure, *n* = 36 of 160 salamanders), and lakes with trout and added structure (+Trout +Structure, *n* = 47 of 160 salamanders), northwestern Montana, summer 2013

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CHAPTER FOUR

CONCLUSIONS

Predators can influence prey directly through consumption or by altering behavior, morphology, and life history of prey (nonconsumptive effects). Salamanders that successfully use anti-predator strategies can coexist with trout; however, behavioral changes to avoid predation can come with costs (Van Buskirk and Schmidt, 2000). By increasing refuge use, prey can reduce encounter rates with predators, but prey must evaluate tradeoffs between foraging and high risk of predation or reduced activity and temporary safety (Werner et al., 1983). We sought to better understand predator-prey interactions between introduced trout and larval long-toed salamanders, the nonconsumptive effects of these fish predators, and discover ways coexistence could be facilitated.

We found salamanders in lakes with trout were thinner and shorter compared to salamanders persisting in lakes without trout. Furthermore, salamanders in lakes with trout were less likely to metamorphose and those that did, metamorphosed later and had smaller total body and tail lengths. The differences we observed in morphology and life history are likely consequences of reduced foraging activity and energy uptake while avoiding predator attacks (Yurewicz, 2004). Changes in body morphology can have long-lasting consequences on fitness at and following metamorphosis; reduced body sizes are correlated with reduced survival, reproductive potential, and increased susceptibility to terrestrial threats, such as predation and desiccation (Petranka et al., 1987; Semlitsch, 1987; Figiel and Semlitsch, 1990; Kiesecker and Blaustein, 1998; Tyler et al., 1998; Relyea, 2007). Additionally, delayed metamorphosis increases the exposure time of larvae to predatory fish, further increasing risk during the aquatic stage.

Although trout and long-toed salamanders do coexist in some lakes, usually with the presence of emergent vegetation and physical barriers from trout, the findings from our field experiment demonstrated that adding complex vegetation structure is not sufficient to mitigate nonconsumptive effects of trout. Added vegetation structure did increase the probability of salamanders that reached metamorphosis before the end of the experiment, but added structure did not influence salamander growth or size at metamorphosis. Changes in body morphology we observed, even without the physical risk of predation, provides evidence that trout can induce nonconsumptive effects and chemical, visual, or both types of cues are sufficient for salamanders to detect predators.

Future research should be focused on whether nonconsumptive effects persist to affect survival and reproduction of adult salamanders. Additionally, research should be directed towards investigating the effectiveness of adding complex vegetation structure at a whole-lake level and examining responses of salamanders over longer periods of time. Added larger vegetation structure, such as logs or treetops, throughout a lake may provide habitat for invertebrate prey as well as refugia for prey. Such large scale cover manipulation could serve as an effective management strategy to allow coexistence between trout and salamanders and other larval amphibians negatively affected by introduced predators. Developing ways to mediate the nonconsumptive effects of trout is extremely important for amphibian conservation, especially as the number of amphibian species that are threatened and endangered continue to increase (Adams et al., 2013). Amphibians are crucial to food web dynamics and nutrient cycles in terrestrial and aquatic systems, therefore, conserving these species will also aide in conserving ecosystem function.

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