AN ABSTRACT OF THE THESIS OF

David E. Rundio for the degree of Master of Science in Fisheries Science presented on July 8, 2002.
Title: Coexistence of Top Predators in Headwater Streams: Pathways of Intraguild Predation between Pacific Giant Salamander Larvae and Cutthroat Trout.

Abstract approved: Deanna H. Olson / Stanley V. Gregory

The coexistence of multiple predators may have important consequences for the structure and function of communities. Interactions between predators may strongly affect their combined direct and indirect effects on prey populations and lower trophic levels. Predators often have size-structured populations, which may result in intraguild predation characterized by complex trophic and behavioral interactions. Coexistence of multiple predators may strongly depend on antipredator defenses of small size classes that reduce their vulnerability to predation.

In Pacific Northwest forested ecosystems, Pacific giant salamanders (Dicamptodon tenebrosus) and coastal cutthroat trout (Oncorhynchus clarki clarki) are the top predators in many perennial headwater streams. Dicamptodon and cutthroat have size-structured populations with roughly corresponding size classes, and interactions between these species appear consistent with intraguild predation. My research objective was to determine the mechanisms contributing to the coexistence of Dicamptodon larvae with cutthroat trout in headwater streams, and...
the effects of this coexistence on factors related to *Dicamptodon* fitness. First, I
tested for two general types of antipredator defenses of young-of-year
*Dicamptodon* larvae against trout. Larvae were palatable to trout during initial and
repeated offerings, which suggests that they may survive few encounters with trout.
However, larvae increased refuge use in response to non-visual, chemical cues
from trout, which likely reduces the probability of encounters with trout and
contributes to their coexistence. Second, I measured the effects of cutthroat trout on
*Dicamptodon* fitness parameters in a field experiment. *Dicamptodon* survival,
growth, and behavior (activity level) did not differ between trout-present and trout-
absent pools, although these results were compromised by unexplained gains or
losses of larvae from most pools. Antipredator behaviors may promote coexistence
of *Dicamptodon* and cutthroat trout, and may contribute to a complex series of
behavioral and trophic interactions affecting lower trophic levels within headwater
stream communities.
Coexistence of Top Predators in Headwater Streams: Pathways of Intraguild Predation between Pacific Giant Salamander Larvae and Cutthroat Trout

by
David E. Rundio

A THESIS
submitted to
Oregon State University

in partial fulfillment of
the requirements for the
degree of
Master of Science

Presented July 8, 2002
Commencement June 2003

APPROVED:

Redacted for privacy

Co-Major Professor, representing Fisheries Science

Redacted for privacy

Co-Major Professor, representing Fisheries Science

Redacted for privacy

Head of the Department of Fisheries and Wildlife

Redacted for privacy

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for privacy

David E. Rundio, Author
ACKNOWLEDGMENTS

I am grateful to a number of people for help during my thesis. I thank my family, Meg and Maya, for making my life full and fun, and understanding when I needed to go out some nights to check on salamanders. I owe a huge debt to Dede Olson for allowing me to develop a project that balanced my family and student lives, and for her support in both—she has been an outstanding mentor. I thank Stan Gregory for his advice and encouragement throughout this project, and I am grateful to Andy Blaustein, Lynne Houck, and John Young for their service on my committee. I thank Lance Campbell for help in the field, thoughtful discussions, and memorable fishing trips, and Chris Sheridan for sharing an office and insights. The involvement of all these people has improved my thinking, writing, and this thesis—thanks!
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Antipredator Defenses of Pacific Giant Salamander Larvae Against Cutthroat Trout</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Methods</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>Results</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Discussion</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Acknowledgments</td>
<td>26</td>
</tr>
<tr>
<td></td>
<td>Literature Cited</td>
<td>27</td>
</tr>
<tr>
<td>3</td>
<td>Effects of Cutthroat Trout on Survival, Growth, and Behavior of Pacific Giant Salamander Larvae</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Methods</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>Results</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>Discussion</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>Acknowledgments</td>
<td>51</td>
</tr>
<tr>
<td></td>
<td>Literature Cited</td>
<td>52</td>
</tr>
<tr>
<td>4</td>
<td>Conclusion</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Bibliography</td>
<td>70</td>
</tr>
<tr>
<td>Figure</td>
<td>Page</td>
<td></td>
</tr>
<tr>
<td>--------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td>1. Potential pathways of intraguild predation between Pacific giant salamander larvae and coastal cutthroat trout in headwater streams</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>2. Sizes of (A) coastal cutthroat trout and (B) <em>Dicamptodon</em> larvae used in the experiment</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>3. Initial sizes of <em>Dicamptodon</em> recovered (light) and lost (dark) from pools</td>
<td>44</td>
<td></td>
</tr>
<tr>
<td>4. Individual daily growth rates of <em>Dicamptodon</em> and cutthroat trout relative to body size (TL for <em>Dicamptodon</em>, FL for cutthroat)</td>
<td>45</td>
<td></td>
</tr>
<tr>
<td>5. Potential pathways of intraguild predation between Pacific giant salamander larvae and coastal cutthroat trout in headwater streams</td>
<td>58</td>
<td></td>
</tr>
<tr>
<td>6. Potential direct and indirect effects of Pacific giant salamander larvae and cutthroat trout in headwater stream communities</td>
<td>59</td>
<td></td>
</tr>
</tbody>
</table>


**LIST OF TABLES**

<table>
<thead>
<tr>
<th>Table</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Physical habitat characteristics of experimental stream pools at the start and end of the experiment</td>
<td>36</td>
</tr>
<tr>
<td>2. Numbers of salamanders stocked and recovered from experimental pools</td>
<td>43</td>
</tr>
<tr>
<td>3. Multiple linear regression analyses for the effects of trout and habitat block on average survival (%), daily growth rate (g/g/d), and nocturnal activity (%) of <em>Dicamptodon</em> larvae in experimental pools</td>
<td>44</td>
</tr>
</tbody>
</table>
## LIST OF APPENDICES

<table>
<thead>
<tr>
<th>Appendices</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Appendices</td>
<td>81</td>
</tr>
<tr>
<td>Appendix A—Effects of Neotenic Pacific Giant Salamanders on Survival and Growth of Cutthroat Trout Fry and Age 1+ (Years) Pacific Giant Salamander Larvae</td>
<td>82</td>
</tr>
<tr>
<td>Methods</td>
<td>82</td>
</tr>
<tr>
<td>Results</td>
<td>88</td>
</tr>
<tr>
<td>Discussion</td>
<td>88</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>89</td>
</tr>
<tr>
<td>Appendix B—Avoidance of Chemical Cues from Potential Predators by Pacific Giant and Southern Torrent Salamander Larvae</td>
<td>90</td>
</tr>
<tr>
<td>Methods</td>
<td>91</td>
</tr>
<tr>
<td>Results</td>
<td>93</td>
</tr>
<tr>
<td>Discussion</td>
<td>94</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>95</td>
</tr>
</tbody>
</table>
Coexistence of Top Predators in Headwater Streams: Pathways of Intraguild Predation between Pacific Giant Salamander Larvae and Cutthroat Trout

CHAPTER 1—INTRODUCTION

Coexistence of multiple predators has important consequences for population- and community-level structure and dynamics (Sih et al. 1998, Peckarsky and McIntosh 1998). The presence of two predators often may reduce prey survival compared with the effect of either predator alone (Rahel and Stein 1988, Soluk and Collins 1988, Krupa and Sih 1998), and in some cases may eliminate an entire assemblage (Kurzava and Morin 1998). Additionally, prey with multiple predators that have different foraging modes may face conflicts with respect to antipredator behaviors (Sih et al. 1998, McIntosh and Peckarsky 1999). Prey behaviors in response to this conflict may influence predation rates (Rahel and Stein 1988, Soluk and Collins 1988, Sih et al. 1998). Separately and in combination, these effects of multiple predators on prey populations and behavior may result in strong indirect effects on lower trophic levels in a community (Spiller and Schoener 1994, Morin 1995, Peckarsky and McIntosh 1998).

The coexistence of multiple predators may depend on interactions among them. Many predators have size-structured populations in which the nature of intra- and inter-specific interactions changes greatly with size and development (Werner and Gilliam 1984, Ebenman and Persson 1988). For example, diet and the identities of potential competitors or predators may differ between size-classes (Werner and
Gilliam 1984, Ebenman and Persson 1988). For such species, coexistence among predators may be influenced by competition with similarly sized individuals and predation by larger individuals. This combination of competition and predation in which each influences the other is termed intraguild predation (Polis and McCormick 1987). For example, competition between small size-classes of two species can be strongly influenced by predation, but competition in small size classes may reduce recruitment to large size classes and affect predation level (Polis 1988). Intraguild predation is common across many habitats and taxa (reviewed by Polis et al. 1989), and often has been described from aquatic systems, particularly from assemblages of fishes (e.g., Johannes and Larkin 1961, Olson et al. 1995, Persson et al. 1999), and amphibians (salamanders: Wilbur 1972, Morin 1983, Stenhouse et al. 1983, Fauth and Resetarits 1991; frogs: Werner et al. 1995).

The many pathways by which species may interact conceptually result in a variety of predicted outcomes between interacting species, and may promote alternative stable states (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997). These hypotheses are supported by experiments involving amphibians (Fauth and Resetarits 1991) and protists (Morin 1999) where outcomes depended on initial densities and nutrient levels, respectively.

Due to the vulnerability of small size classes of predators to predation by other predators, antipredator defenses of small size classes may be important for coexistence among predators (e.g., Kats et al. 1988, Werner and McPeek 1994, Chivers et al. 2001), and may influence the outcome of intraguild predation.
Antipredator defenses can be broadly categorized as either defenses that decrease the probability of encountering predators, or defenses that increase the probability of surviving a predation attempt (Sih 1987, Brodie et al. 1991). Each of these broad categories includes a variety of different, specific behaviors. For example, small size-classes of predators may avoid encounters with their predators by reducing activity levels, altering habitat use, or behaving cryptically (Sih 1987). Alternatively, they may increase the probability of surviving encounters by actively fleeing or fighting, or by producing toxic or noxious compounds that make them unpalatable (Sih 1987). However, the expression of these two general types of defenses toward a particular predator usually is complementary; that is, species that have behaviors to avoid encounters generally lack or show reduced behaviors that increase survival during encounters, and vice versa (Kats et al. 1988, Brodie et al. 1991, Hileman and Brodie 1994).

Salamanders and fishes are top predators in many aquatic habitats, and are characterized by size-structured populations and ontogenetic changes in their ecological interactions (Werner and Gilliam 1984, Ebenman and Persson 1988). Thus, interactions between these taxa may be characterized by intraguild predation. However, despite the potential for intraguild predation to result in multiple outcomes, interactions between fishes and salamanders are consistently and strongly asymmetric in favor of fish. Fish almost universally have negative effects on salamander survival, growth, or distributions (Hairston 1987), while salamanders have not been found to affect fish (Bristow 1991, Resetarits 1991,
1995). Predation by fishes can drastically reduce salamander survival and abundance in ponds (Semlitsch 1987, 1988), lakes (Tyler et al. 1998), and streams (Resetarits 1991, Sih et al. 1992, Resetarits 1995), and can eliminate salamanders from single habitat units (Sih et al. 1992) and large habitat areas (Petranka 1983, Thiesmeier and Schuhmacher 1990). Predatory fishes also can reduce salamander growth by a combination of exploitative competition and induced antipredator behaviors such as reduced activity rates or microhabitat shifts (Semlitsch 1987, Figiel and Semlitsch 1990, Resetarits 1991, Sih et al. 1992). Salamanders that coexist with fishes usually have either type of general antipredator defenses (i.e., behaviors to avoid encounters [refuge use] or to survive encounters [unpalatability]; Kats et al. 1988).

Furthermore, interactions among same-sized salamanders and fishes are consistently asymmetric in favor of fishes and can decrease salamander growth and survival nearly to the extent of larger fish. For example, up to six species of salamanders coexist with brook trout in headwater streams in Virginia, although densities of most are lower in the presence of trout (Resetarits 1991, 1997). Despite this coexistence, experiments in artificial stream channels revealed highly asymmetric interactions between spring salamander (Gyrinophilus porphyriticus) larvae and brook trout (Salvelinus fontinalis) of the same size: trout reduced salamander survival by 50-60% and growth by 65-90% (Resetarits 1991, 1995). These results demonstrated that coexistence of salamanders with fish does not imply lack of strong interactions (Resetarits 1991), and that interactions among
same-sized predators may have effects comparable to larger predators on smaller predators (compare with Semlitsch 1987).

In Pacific Northwest forested ecosystems, Pacific giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarki clarki*) are the top predators in many perennial headwater streams (Hawkins et al. 1983, Olson et al. 2000). Both species have size-structured populations with roughly corresponding size classes. *Dicamptodon* typically spend 2-3 years as aquatic larvae and show distinct age/size-classes (Nussbaum and Clothier 1973). Larvae usually transform when they reach 110-150 mm total length (TL), but neotenes (reproductively mature, gilled adults) are common and often exceed 200 (and sometimes 300) mm TL (Nussbaum and Clothier 1973). Resident cutthroat trout in headwater streams usually live 3-4 years and reach a maximum length of 150-200 mm (Trotter 1989). Interactions between *Dicamptodon* and cutthroat trout appear consistent with intraguild predation (Fig. 1). Large *Dicamptodon* larvae are known to prey on trout fry (Antonelli et al. 1972, Parker 1993a, 1994), but small larvae may, in turn, be consumed by larger larvae (Parker 1994) and trout (Parker 1992). However, both *Dicamptodon* and trout feed primarily on aquatic invertebrates, and thus are potential competitors (Antonelli et al. 1972, Parker 1994). These predator-prey and competitive interactions have been observed or inferred from diet studies, and it is uncertain how they influence the coexistence of these species. In addition, the role of behavioral interactions in the coexistence of these species is unknown.
FIGURE 1. Potential pathways of intraguild predation between Pacific giant salamander larvae and cutthroat trout in headwater streams. Thin arrows indicate documented predation, block arrows indicate potential interactions. Competition may occur within and among different size classes.
Coexistence of *Dicamptodon* and trout may have important direct and indirect effects in headwater stream communities. Both species feed on a variety of invertebrate and vertebrate prey (Metter 1963, Antonelli et al. 1972, Wilzbach and Hall 1985, Parker 1994, Esselstyn and Wildman 1997) but differ in foraging mode. *Dicamptodon* larvae are primarily benthic feeders (Parker 1994), whereas cutthroat are primarily water column drift feeders (Wilzbach and Hall 1985). This difference in foraging mode potentially presents shared prey with conflicting antipredator decisions that may affect behavior and survival (Soluk and Collins 1988, McIntosh and Peckarsky 1999), which may, in turn, affect lower trophic levels (Peckarsky and McIntosh 1998). Because benthic-feeding predators often have stronger effects on densities of benthic prey than drift-feeding predators (Dahl and Greenberg 1996), interactions between *Dicamptodon* and cutthroat trout that affect *Dicamptodon* populations or behavior may be especially important in headwater streams communities. *Dicamptodon* larvae prey selectively on larger invertebrates (Parker 1993b), and have been shown to alter the composition of benthic invertebrates by directly reducing the abundance of large predatory invertebrates and indirectly increasing the abundance of small invertebrates (Parker 1992). These direct and indirect effects suggest that *Dicamptodon* may initiate trophic cascades (Carpenter et al. 1985) that influence primary production in streams.

My research objective was to understand the mechanisms contributing to the coexistence of *Dicamptodon* larvae with cutthroat trout in headwater streams, and the effects of this coexistence on factors related to *Dicamptodon* fitness. In
Chapter 2, I tested for antipredator defenses of young-of-year Dicamptodon larvae against trout. I tested Dicamptodon both for defenses that might increase the probability of surviving encounters with trout (unpalatability) and for behaviors that might reduce the probability of encountering trout (refuge use and microhabitat selection along a depth gradient). In Chapter 3, I tested the effects of cutthroat trout on survival, growth, and behavior of Dicamptodon in a field experiment. My intent was to determine whether trout and Dicamptodon interacted under natural conditions, and whether these potential trophic and behavioral interactions influenced factors related to Dicamptodon fitness. In Chapter 4, I summarize and integrate the results from Chapters 2 and 3, and present a conceptual model of interactions in headwater stream communities where Dicamptodon and cutthroat trout are top predators. Finally, in Appendices A and B, I describe two ancillary experiments that examined additional aspects of intraguild predation between Dicamptodon and cutthroat trout and the effects of these predators in headwater streams. The first investigated predation by neotenic Dicamptodon on small larvae and cutthroat trout fry, and the second tested behavioral responses of Dicamptodon and southern torrent salamander (Rhyacotriton variegatus) larvae to neotenic Dicamptodon and large cutthroat trout. Rhyacotriton often occur with Dicamptodon in small or intermittent headwater streams where trout are absent (Olson et al. 2000). Rhyacotriton may be an important intermediate predator in these systems, and behavioral responses to Dicamptodon may influence the indirect effects of Dicamptodon on lower trophic levels in headwater stream communities.
Literature Cited


Prey that coexist with potential predators typically have defenses that reduce vulnerability to predation (e.g., Sih 1987, Kats et al. 1988, Azevedo-Ramos and Magnusson 1999). Antipredator defenses can be broadly categorized as either defenses that decrease the probability of encountering predators, or defenses that increase the probability of surviving a predation attempt (Sih 1987, Brodie et al. 1991). Each of these broad categories includes a variety of different, specific behaviors. For example, prey may avoid encounters with predators by reducing activity levels, altering habitat use, or behaving cryptically (Sih 1987).

Alternatively, prey may increase the probability of surviving encounters by actively fleeing or fighting, or by producing morphological (e.g., shell, spines) or chemical (e.g., toxic or noxious compounds) defenses (Sih 1987). Both of these types of defense are common in amphibians (Duellman and Trueb 1986); however, the expression of these two general types of defenses toward a particular predator usually is complementary. That is, amphibians that have behaviors to avoid encounters generally lack or show limited defenses that increase survival during encounters, and vice versa (Kats et al. 1988, Brodie et al. 1991, Hileman and Brodie 1994). Amphibian species that have either type of defense commonly coexist with predators, while species lacking defenses generally do not (Petranka 1983, Kats et al. 1988, Azevedo-Ramos and Magnusson 1999).
Antipredator behaviors appear to be important in mediating predator-prey interactions involving amphibians in forested headwater streams in the US Pacific Northwest (Feminella and Hawkins 1994, Rundio and Olson 2001). Fishes (trout \textit{Oncorhynchus} and sculpin \textit{Cottus}) and giant salamanders \textit{(Dicamptodon)} are top predators in these streams (Hawkins et al. 1983), and potential amphibian prey species show a variety of defenses against them. For example, tailed frog tadpoles \textit{(Ascaphus truei)} differentially alter foraging activity in response to non-visual cues from trout, sculpin, and giant salamanders (Feminella and Hawkins 1994), and larval southern torrent salamanders \textit{(Rhyacotriton variegatus)} are unpalatable to giant salamander larvae (Rundio and Olson 2001). In turn, however, fishes and \textit{Dicamptodon} are vulnerable to predation during early life stages (Antonelli et al. 1972, Parker 1993), yet nothing is known about the antipredator behaviors that might influence these interactions.

I investigated defenses of Pacific giant salamander \textit{(Dicamptodon tenebrosus)} larvae against coastal cutthroat trout \textit{(O. clarki clarki)}. Cutthroat trout occur across the entire geographic range of \textit{D. tenebrosus} (Trotter 1989, Petranka 1998), and these species are abundant together in many forested headwater streams (Hawkins et al. 1983). \textit{Dicamptodon} usually spend at least two years as aquatic larvae (Nussbaum and Clothier 1973), and for most of their first year probably are small enough to be prey for trout. The coexistence of \textit{Dicamptodon} larvae in habitats with trout suggests the presence of an effective antipredator defense (Kats et al. 1988).
My objective was to test young-of-year *Dicamptodon* for both general types of antipredator defenses (i.e., surviving or avoiding predation attempts) against cutthroat trout. First, I tested the palatability of *Dicamptodon* to trout. Unpalatability is a common defense among amphibians (Duellman and Trueb 1986), and adult and older *Dicamptodon* larvae produce noxious skin secretions (Nussbaum et al. 1983, personal observations). I tested palatability during both single and repeated encounters because some fishes immediately reject unpalatable prey, but others learn to avoid unpalatable prey after several predation attempts (Kruse and Stone 1984, Crossland 2001). Second, I tested whether larvae increase refuge use in response to non-visual, chemical cues from trout. Non-visual cues are ubiquitous in aquatic systems (Dodson et al. 1994, Kats and Dill 1998), and I suspected that they might be important to *Dicamptodon* because larvae are nocturnal (Nussbaum et al. 1983). Nocturnal activity alone probably is insufficient defense against trout because trout commonly are active at night (Grunbaum 1996, personal observation). Furthermore, several species of stream salamanders from the eastern US have been shown to increase refuge use in response to fish cues (Petranka et al. 1987, Kats et al. 1988). Finally, I tested whether larvae select shallower microhabitats in response to trout chemical cues. Large cutthroat trout occur primarily in deeper pool habitats in streams (Bisson et al. 1988), and other salamander larvae shift to shallower microhabitats to avoid predatory fish (Resetarits 1991, Sih et al. 1992). I chose to test the last two behaviors

**Methods**

**Palatability trials.** I tested the palatability of *Dicamptodon* larvae to cutthroat trout during initial encounters in paired trials (Brodie et al. 1978) during July–September 2001. I used juvenile western red-backed (*Plethodon vehiculum*) and Dunn’s (*P. dunni*) salamanders as control prey because they appeared to be fully palatable to cutthroat trout during preliminary trials and they were similar in size to young-of-year *Dicamptodon*. I therefore expected that they would serve as a control to demonstrate predation under experimental conditions. I tentatively identified *P. vehiculum* and *P. dunni* to species, and it appeared that 44% were *P. vehiculum* and 56% were *P. dunni*. However, I could not positively distinguish between the species because of the high proportion of melanistic individuals in this area (Nussbaum et al. 1983), and considered them *Plethodon* spp. for the purpose of this experiment. The species did not appear to differ in palatability in preliminary trials or a previous experiment (Rundio and Olson 2001).

I collected trout and salamanders from several small streams in the Oregon Coast Range (Benton Co.). I captured cutthroat trout (mean fork length (FL) = 179 mm, range = 147–212 mm) from Soap Creek and Oak Creek by electrofishing, and placed them into individual experimental tanks. I fed trout one large earthworm every day at 1600-1800 h for 4-6 days prior to trials to allow them to adjust to
experimental conditions and to standardize hunger level. I captured *Dicamptodon* by hand from stream reaches that contain cutthroat trout in Soap Creek, Racks Creek, and Tobe Creek, and collected *Plethodon* from stream banks along Soap Creek and Parker Creek. *Dicamptodon* and *Plethodon* were held for several days prior to trials in separate 40-l flow-through containers placed in the stream.

I conducted trials in eight 60-liter (54 × 36 × 31 cm) clear plastic tanks placed on the stream bottom in Soap Creek, a 2-4 m wide second-order stream in the MacDonald-Dunn Research Forest of Oregon State University, Benton County, Oregon. Each tank received stream water at a rate of 15-20 l/min, and water depth was maintained at 25 cm by screened standpipes (2.5-cm diameter). I closed the tops of tanks with screen lids, and inserted separate water supply and feeding pipes (50 cm × 2.5 cm diameter vertical pipes) through the lids. The feeding pipes and small viewing holes in blinds constructed around the tanks allowed me to feed and observe trout without disturbing them.

A trial consisted of offering a trout one *Dicamptodon* and one *Plethodon*, separately, and recording whether each was rejected or consumed. I randomly determined which prey was offered first, and offered the second prey to the same trout 24 h later; prey were offered between 1600-1800 h. I matched *Dicamptodon* and *Plethodon* sizes as closely as possible within a trial, although total lengths of *Plethodon* were slightly larger on average (mean = 64 mm, range = 47-85 mm) than *Dicamptodon* (mean = 61 mm, range = 52-78 mm). Salamanders that were not eaten were removed from tanks after 0.5 h. I conducted a total of 48 trials, but
analyzed data only from trials in which a trout attacked, and presumably tasted, both prey. Individual trout and salamanders were tested only once, and survivors were released to their site of capture.

Based on the paired design, I used McNemar's test (Sokal and Rohlf, 1995) to test whether the proportion of trials in which *Dicamptodon* was eaten differed from the proportion in which *Plethodon* was eaten.

In a second experiment, I tested whether the palatability of *Dicamptodon* larvae to cutthroat trout varies over multiple encounters. I collected five trout (mean FL = 200 mm, range = 190-215 mm) from Oak Creek by electrofishing and held them in separate 60-l flow-through, clear plastic tanks placed in a 0.76 m-wide, 5 × 4 m oval indoor stream channel at the Forestry Sciences Laboratory, USDA Forest Service and Oregon State University, Corvallis, Oregon. I filled the channel to 0.5 m deep, and controlled the water temperature at 12-13°C and current speed at 6-10 cm/s. Timers on overhead lights maintained a daily photoperiod of 14 L:10 D. I fed trout large earthworms for five days to allow them to adjust to the experimental conditions and to standardize hunger level. To minimize disturbance, I fed trout through via pipes and observed trials through viewing holes in blinds placed over the plexiglass interior wall of the channel. I then offered each trout one *Dicamptodon* larva per day for five days and recorded whether each larva was consumed or rejected. Larvae were collected from sites in Racks Creek that contain trout several days prior to the experiment and held in a 40-l flow through container in a separate channel. Mean total length of larvae was 58 mm (range = 52-61 mm).
Chemical cue trials. I tested whether *Dicamptodon* larvae increase refuge use and select shallower microhabitats in response to chemical cues from cutthroat trout in September 2001. I ran the experiment in eight tank-channel pairs arranged in two rows of four in a shallow riffle in Soap Creek, MacDonald-Dunn Research Forest, Benton County, Oregon. Stream water was piped at a rate (mean ± SE) of 16.8 ± 0.88 l/min to each 20-l plastic tank (33 × 29 × 22 cm) where I isolated trout. Water depth in tanks was maintained at 16 cm by screened standpipes (2.5-cm diameter), which drained to the downstream channels where *Dicamptodon* larvae were held. These channels were 1.35 × 0.48 × 0.25 m plastic livestock feed troughs that drained to the stream by 5.0-cm high standpipes (6.0 cm-diameter, screened with 2 × 1 mm mesh rubberized fiberglass). I filled channels with small gravel (6-10 mm diameter) to a depth of 5 cm, and inclined them to create a shallow half (0-5 cm deep) at the outlet end and a deep half (5-10 cm) at the inlet end. I placed four unglazed clay tiles (15 × 15 × 0.8 cm) about 15 cm apart down the center of each channel, and elevated one edge of each tile about 2 cm to provide a crevice for refuge. In the morning of the experiment, I stocked each channel with benthic invertebrates and organic matter collected by kick-netting a 1 × 0.35 m area of the stream bottom upstream of a 500-μm mesh net. Water temperatures during the experiment were 12-15°C.

I collected eight cutthroat trout from Oak Creek by electrofishing five days prior to the start of the experiment and held them in 60-l flow through containers placed in the stream. Trout ranged from 176 to 213 mm FL (mean = 192) and from
45 to 99 g (mean = 70). I fed them large earthworms daily but stopped feeding 24 h prior to the experiment. Several days prior the experiment, I captured *Dicamptodon* larvae by hand from two sites, Racks Creek and Tobe Creek, that contain trout, and held them in 40-l flow-through plastic containers placed in the stream. Mean total length of larvae was 63 mm (range = 52-77 mm).

I conducted the first set of trials on 20 September 2001. In the morning (1000-1100 h), I stocked the channels with invertebrates, added four *Dicamptodon* larvae to each channel, and placed trout in four randomly selected upstream tanks; the remaining four tanks served as controls. That night, I counted the total number of larvae located outside refugia in the shallow and deep halves of each channel at 2200-2230 h (when nocturnal activity was at a peak) using a flashlight with a red lens. I removed the trout afterward and returned them to holding tanks, and removed larvae the following morning. I then scrubbed and rinsed the tanks and channels, set them up as before, and let them flush with stream water for three days. I repeated the experiment on September 24 with new animals, for a total of eight replicates each of control and trout-cue treatments. I released all animals to their site of capture.

I used a permutation test (Sokal and Rohlf, 1995) to test whether the number of larvae under refuges was higher in the trout-cue treatments than in controls. I chose this non-parametric test due to the binomial structure of the data and small sample size.
Results

Palatability. Palatability during initial encounters was assessed from 22 trials (of 48 total) in which cutthroat trout attacked both salamander prey. Trout consumed *Dicamptodon* larvae in 95% (21 of 22) of trials, and consumed *Plethodon* in all trials. The data did not meet the requirements for McNemar’s test due to the complete consumption of *Plethodon*; thus this analysis was not conducted. Trout attacked prey as soon as they entered the tank, and generally swallowed prey immediately. The single *Dicamptodon* that was rejected died later from severe injuries. During repeated encounters trials, each of five trout consumed all *Dicamptodon* larvae offered.

Chemical cues. The proportion of *Dicamptodon* larvae under refuge was 60% higher in channels receiving trout cues (mean ± SE = 66 ± 9.4%) than in controls (41 ± 6.3%; one-sided \( p = 0.04 \)). In contrast, the proportion of larvae outside refugia that were in the deep half of channels did not differ between control (88 ± 8.8%) and trout-cue (95 ± 5.5%) treatments (one-sided \( p = 0.85 \)).

Discussion

Antipredator defenses of young-of-year *Dicamptodon* larvae appear to be based on avoiding, as opposed to surviving, predation attempts by cutthroat trout. The results from both single and repeated offerings of larvae to cutthroat trout clearly rule out unpalatability as a defense, and suggest that *Dicamptodon* larvae are potentially vulnerable to this predator. However, I have shown that larvae
increase refuge use in response to trout chemical cues in stream water under natural conditions, which likely reduces the probability of encounters and contributes to their coexistence. This antipredator strategy appears to be common among amphibian larvae in general, and stream salamanders in particular, that coexist with fishes (Kats et al. 1988, Resetarits 1991). Furthermore, the expression of only one of the general types of defense (i.e., behaviors to reduce encounters versus behaviors to increase survival) by *Dicamptodon* against trout is consistent with the complementary expression of these defenses toward a particular predator among many amphibians (Kats et al. 1988, Brodie et al. 1991).

Predation risk is context-dependent and varies in response to changes in environmental and ecological conditions (e.g., Lima and Dill 1990, McIntosh and Peckarsky 1999, Sih and McCarthy 2002). Many prey have been shown to assess predation risk and respond differentially according to the level of threat (e.g., fishes: Helfman, 1989; amphibians: Anholt et al. 1996; aquatic insects: McIntosh et al. 1999). Chemical cues from a predator may induce a general antipredator response that may be modified when a prey has additional information about the risk posed by the predator (Chivers et al. 2001). Additional information may come from visual cues about a predator (Chivers et al. 2001), alarm cues released by conspecifics (Chivers and Smith 1998), chemical cues of alternate, preferred prey (Kerby and Kats 1998), or changes in the concentration of predator chemical cues (McIntosh et al. 1999). The flexibility of prey behaviors depending on risk suggests that refuge use by *Dicamptodon* may vary under natural conditions. Thus, although
my results show that larvae detect and respond to non-visual cues from trout, they should not be interpreted as a static estimate of antipredator behavior.

Refuge use by *Dicamptodon* may reduce predation by trout and increase survival, but it also might have a negative effect on other factors affecting fitness. For example, two salamander species with different behavioral responses to brook trout (*Salvelinus fontinalis*) showed contrasting effects on survival and growth in experimental streams (Resetarits 1991). Two-lined salamander (*Eurycea bislineata*) larvae increased refuge use and moved to shallower microhabitats in response to brook trout, and had similar survival between control and trout treatments, but lower growth in the trout treatment. In contrast, spring salamander (*Gyrinophilus porphyriticus*) larvae did not alter behavior and had both lower survival and growth in response to trout (Resetarits 1991). In addition, increased refuge use by anuran larvae in response to predator cues decreased growth and development (Skelly 1992) and size at metamorphosis (Skelly and Werner 1990) in field and laboratory experiments. These studies suggest that increasing refuge use probably decreases *Dicamptodon* growth, although the size of this effect may be reduced if larvae can detect and react to changes in predation risk quickly (e.g., *Ascaphus truei* tadpoles resumed high foraging rates within an hour after brook trout cues were removed [Feminella and Hawkins 1994]).

My results suggest that the availability of refugia may be important for predator avoidance and might influence the distribution and abundance of *Dicamptodon* larvae. This may explain, at least in part, the positive correlation
between *Dicamptodon* density and the amount of large, non-embedded stream substrates (Murphy et al. 1981, Hawkins et al. 1983, Wilkins and Peterson 2000). Rapid (< two months) increases in larval density to experimental manipulation of stone density in a northern California stream (Parker 1991) suggest that this pattern can be produced by behaviors (i.e., microhabitat selection). Changes in population size also may result if survival is higher in habitats with more refuges. Land management activities such as timber harvest and road construction that increase siltation in streams (Waters 1995) may reduce the availability of refugia to *Dicamptodon* and increase vulnerability to predation.

I did not detect an effect of trout chemical cues on habitat selection by larvae along a gradient of water depth, and larvae were observed almost exclusively in the deepest portion of the channels regardless of treatment. However, despite the consistency of this result in this experiment, my results might not accurately represent this behavior in natural habitats. Because the channels were relatively shallow (0-10 cm), the “deep” and “shallow” halves may actually correspond to shallow habitats in natural streams that generally are free of large, predatory trout (Bisson et al 1988). Therefore, larvae may react to trout cues across a more pronounced and natural depth gradient than I presented. Furthermore, habitats in headwater streams are heterogeneous, and include additional environmental gradients (e.g., substrate and current velocity) and habitat types (e.g., riffles and glides) (Gordon et al. 1992) that may provide *Dicamptodon* larvae with additional choices for habitat selection.
Increased refuge use by *Dicamptodon* in response to cutthroat trout may have important direct and indirect effects in headwater stream communities. Refuge use may reduce *Dicamptodon* predation on its prey, directly affecting invertebrate populations and indirectly affecting resources consumed by invertebrates (e.g., algae or other invertebrates). Also, coexistence of *Dicamptodon* and trout presents their mutual prey with predators having different foraging modes (i.e., benthic-feeding *Dicamptodon* and drift-feeding trout). Consequently, this may result in conflicting antipredator behaviors that may influence prey survival (Sih et al. 1998). Additional research is needed to address the way in which *Dicamptodon* behavior in response to trout may contribute to a series of behavioral and trophic interactions potentially affecting lower trophic levels within headwater stream communities (Sih et al. 1998, Peckarsky and McIntosh 1998).

**Acknowledgments**

I thank Lance Campbell for help collecting trout and thoughtful discussions, and Ben Greenough and the Statistical Consulting Service of the Department of Statistics at Oregon State University for statistical advice. Oregon State University granted permission to conduct the experiments in the MacDonald-Dunn Research Forest. Salamanders and trout were collected under Oregon Department of Fish and Wildlife permits 049-01 and 01-108, respectively. This research was approved by the Institutional Animal Care and Use Committee at Oregon State University under
protocol 2590. Funding was provided by the Pacific Northwest Research Station, USDA Forest Service.

Literature Cited


Grunbaum, J. B. 1996. Geographical and seasonal variation in diel habitat use by juvenile (age 1+) steelhead trout (Oncorhynchus mykiss) in Oregon coastal and inland streams. Unpubl. M.S. Thesis, Oregon State University, Corvallis.


Although predation and competition traditionally were considered discrete, independent processes regulating populations and communities (e.g., Menge and Sutherland 1987), in many systems they are intertwined in a complex fashion known as intraguild predation (Polis 1988). Intraguild predation may occur in assemblages with size-structured populations in which the nature of intra- and interspecific interactions changes greatly with size and development (Werner and Gilliam 1984). In these populations, competition between small size-classes of two species can be strongly influenced by predation by larger size-classes. Predation intensity, in turn, may be limited by recruitment to large size-classes, which may be influenced by competition in small size-classes. Intraguild predation is common across many habitats and taxa (reviewed by Polis et al. 1989), and often has been described from aquatic systems, particularly from assemblages of fishes (e.g., Olson et al. 1995, Persson et al. 1999), and amphibians (salamanders: Wilbur 1972, Morin 1983, Fauth and Resetarits 1991; frogs: Werner et al. 1995). The variety of pathways by which species may interact conceptually result in multiple predicted outcomes between interacting species, and may promote alternative stable states (Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997). These hypotheses are supported by experiments involving amphibians (Fauth and Resetarits 1991) and protists (Morin 1999).
Salamanders and fishes are top predators in many aquatic habitats, and are characterized by size-structured populations and ontogenetic changes in their ecology (Werner and Gilliam 1984). Thus, interactions between these taxa may be characterized by intraguild predation. However, despite the potential for intraguild predation to result in multiple outcomes, interactions between fishes and salamanders are consistently and strongly asymmetric in favor of fish. Fish almost universally have negative effects on salamander survival, growth, or distributions (Hairston 1987), while salamanders have not been found to affect fish (Bristow 1991, Resetarits 1991, 1995). Predation by fishes can drastically reduce salamander survival and abundance in ponds (Semlitsch 1987, 1988), lakes (Tyler et al. 1998), and streams (Resetarits 1991, Sih et al. 1992, Resetarits 1995), and can eliminate salamanders from single habitat units (Sih et al. 1992) and large habitat areas (Petranka 1983, Thiesmeier and Schuhmacher 1990). Predatory fishes also can reduce salamander growth by a combination of exploitative competition and induced antipredator behaviors such as reduced activity rates or microhabitat shifts (Semlitsch 1987, Figiel and Semlitsch 1990, Resetarits 1991, Sih et al. 1992).

Furthermore, interactions among same-sized salamanders and fishes are consistently asymmetric in favor of fishes and can decrease salamander growth and survival nearly to the extent of larger fish. For example, up to six species of salamanders coexist with brook trout in headwater streams in Virginia, although densities of most species are lower in the presence of trout (Resetarits 1991, 1997). Despite this coexistence, experiments in artificial stream channels revealed highly
asymmetric interactions between spring salamander (*Gyrinophilus porphyriticus*) larvae and brook trout (*Salvelinus fontinalis*) of the same size: trout reduced the survival of salamander larvae by 50-60% and growth by 65-90% (Resetarits 1991, 1995). These results demonstrated that coexistence of salamanders with fish does not imply lack of strong interactions (Resetarits 1991), and that interactions among same-sized predators may have effects comparable to larger predators on smaller predators (compare with Semlitsch 1987).

In Pacific Northwest forested ecosystems, Pacific giant salamander larvae (*Dicamptodon tenebrosus*) coexist with salmonids (*Oncorhynchus*) and sculpins (*Cottus*) across a broad range of stream sizes, although they overlap principally with coastal cutthroat trout (*O. clarki clarki*) in smaller, higher gradient perennial streams (Hawkins et al. 1983). *Dicamptodon tenebrosus* and coastal cutthroat trout are sympatric at both broad and small spatial scales, which sets-up a potential for interactions. At a broad scale, cutthroat trout occur across the entire geographic range of *Dicamptodon* (Trotter 1989, Petranka 1998). At a finer scale within headwater stream networks, both species are abundant in first-and second-order perennial reaches (Connolly and Hall 1999, Olson et al. 2000). *Dicamptodon* and cutthroat trout have size-structured populations, and interactions between them appear consistent with intraguild predation. Large *Dicamptodon* larvae are known to prey on trout fry (Antonelli et al. 1972, Parker 1993, 1994), but small larvae may, in turn, be consumed by larger larvae (Parker 1994) and trout (Parker 1992). However, both *Dicamptodon* and trout feed primarily on aquatic invertebrates, and
are thus potential competitors (Antonelli et al. 1972, Parker 1994). These predator-prey and competitive interactions are, at present, mostly anecdotal, and it is uncertain how important they are to the population dynamics or distributions of these species.

My goal was to examine several aspects of potential intraguild predation between *Dicamptodon* and cutthroat trout. Specifically, I sought to experimentally quantify the effects of cutthroat trout on survival, growth, and behavior (i.e., activity rates) of *Dicamptodon* larvae of roughly the same size under natural conditions in a headwater stream.

**Methods**

**Study Site.** I conducted the experiment in a 140-m reach of an unnamed tributary to Racks Creek, Benton Co., Oregon (T13S-R8W-S9) in the summer of 2001. I chose this reach for three reasons. First, the underlying stream substrates were sand and very small gravel into which I could bury and seal fences to block experimental stream pools. Second, pools were structurally relatively simple (i.e., no undercut banks or complex wood deposits), and I expected to be able to remove the salamanders and trout initially present and then manipulate densities experimentally. Finally, cutthroat trout were the only fish present, so *Dicamptodon* and cutthroat potentially interacted as the top predators in the system.

The study reach is a second-order channel, at an elevation of 400 m and average gradient of 3.5% (based on a 1:24,000 scale topographic map). The wetted
width of the channel was 1-2.5 m, and maximum pool depths were 50 cm. Water temperature ranged 7-11 °C (mean = 9.4) over the course of the experiment, and discharge (estimated at a culvert 500 m downstream of the study reach) ranged from 8-9 l/s at the start of the experiment to about 1.5 l/s at the end. The basin has a sandstone geology, and substrates were predominantly gravel and cobble (2-10 cm diameter) overlaying sand and fine gravel. The stream flows through an unmanaged, mature stand of Douglas fir (*Pseudotsuga menziesii*) that regenerated after a 1910 stand-replacing fire (Bill Caldwell, US Bureau of Land Management, personal communication). The primary riparian trees and shrubs are red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), and vine maple (*Acer circinatum*). The most common stream vertebrates were Pacific giant salamanders, resident coastal cutthroat trout, and tailed frogs (*Ascaphus truei*). A waterfall on Racks Creek, 3.2 km downstream of the study site, prevents access by anadromous fishes, and resident cutthroat trout were the only fish species present.

**Experimental design.** I manipulated trout and salamander densities in whole stream pools according to a randomized block design consisting of two treatments (trout present and trout absent [= control]) blocked by physical habitat characteristics (i.e., by a combination of pool depth and current speed: deep/slow versus shallow/fast; Table 1). At the start of the experiment, blocks differed significantly in maximum depth (one-sided *t*-test, *p* = 0.003), current speed (*p* = 0.0008), and area (*p* = 0.02); at the end, blocks differed in mean depth (*p* = 0.03), maximum depth (*p* = 0.01), and area (*p* = 0.01). I replicated each treatment-block
TABLE 1. Physical habitat characteristics of experimental stream pools at the start and end of the experiment. Pools are numbered from upstream to downstream. Treatments are cutthroat present (T) and control (C). Blocks are deep/slow (1) and shallow/fast (2).

<table>
<thead>
<tr>
<th>Pool</th>
<th>Treatment</th>
<th>Block</th>
<th>Area (m²)</th>
<th>Mean Depth (m)</th>
<th>Max. Depth (m)</th>
<th>Current Speed (cm s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Start</td>
<td>End</td>
<td>Start</td>
<td>End</td>
</tr>
<tr>
<td>1</td>
<td>T</td>
<td>1</td>
<td>10.4</td>
<td>8.7</td>
<td>0.11</td>
<td>0.11</td>
</tr>
<tr>
<td>2</td>
<td>C</td>
<td>2</td>
<td>3.5</td>
<td>3.0</td>
<td>0.10</td>
<td>0.09</td>
</tr>
<tr>
<td>3</td>
<td>T</td>
<td>2</td>
<td>4.1</td>
<td>3.3</td>
<td>0.08</td>
<td>0.06</td>
</tr>
<tr>
<td>4</td>
<td>C</td>
<td>2</td>
<td>10.1</td>
<td>8.1</td>
<td>0.07</td>
<td>0.05</td>
</tr>
<tr>
<td>5</td>
<td>C</td>
<td>1</td>
<td>8.6</td>
<td>8.5</td>
<td>0.09</td>
<td>0.08</td>
</tr>
<tr>
<td>6</td>
<td>T</td>
<td>1</td>
<td>10.0</td>
<td>9.0</td>
<td>0.12</td>
<td>0.11</td>
</tr>
<tr>
<td>7</td>
<td>T</td>
<td>1</td>
<td>13.5</td>
<td>11.7</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>8</td>
<td>T</td>
<td>2</td>
<td>5.5</td>
<td>4.5</td>
<td>0.09</td>
<td>0.06</td>
</tr>
</tbody>
</table>
combination twice, for a total of eight experimental units. I selected pools that had no deeply undercut banks or complex wood cover that would make capturing animals difficult. Adjacent pools were separated by at least one entire riffle channel unit, and usually ≥ one pool-riffle sequence (distance between pools [mean ± SE ] = 16.2 ± 5.05 m; range = 7.3-35.2 m).

I blocked the upstream and downstream ends of pools with 6-mm mesh plastic fences. I buried the bottom of the fences at least 10 cm deep into the sand of the stream bottom, and supported the fences with metal rebar stakes. I bent the top of the fence toward the pool and fastened it into a U-shaped awning to prevent salamanders from climbing over the fence, and created awnings on the outside of the fences with additional pieces of mesh to prevent salamanders from climbing into the pools. I extended the fences either 2 m into the dry streambank or until I encountered a vertical bank. The advantages of using whole pools blocked with large mesh for experimental units was that they would provide more straightforward interpretation of results than smaller or artificial experimental units (e.g., Peckarsky et al. 1997) and would minimize disturbance to pools and artifacts related to altering physical conditions (Peckarsky and Penton 1990, Parker 1992) or invertebrate exchange (Cooper et al. 1990). However, the large mesh size restricted the experiment to age 0+ and 1+ (years) Dicamptodon larvae because young-of-year larvae, which were rare in the early summer but became more abundant later, were small enough to pass through the fence. I cleaned debris from the fences every
1-3 days, and placed debris gathered from the upstream fence into the pools to maintain the supply of organic matter.

I measured the dimensions and current speed of the pools at the start and end of the experiment (Table 1). I measured length as the thalweg distance from the upstream to downstream net, and I estimated average width from 3-6 (depending on length) systematic transects across each pool. I estimated average depth from measurements at quarterly intervals along each transect, and measured maximum depth from the deepest point within the pool. I calculated mean current speed from three measurements taken along the length of each pool using a Marsh-McBirney electromagnetic flowmeter.

Prior to the experiment, I removed all salamanders and trout present within each experimental pool, and retained these animals for use in the experiment. I first made two passes with a backpack electroshocker, and then searched pools by hand by removing all cover objects (rocks and wood) > 5 cm to the stream bank. I next made several more passes with an electroshocker until no additional animals were recovered on two consecutive passes. Finally, I electroshocked each pool on the following day to confirm that all trout and salamanders had been removed, and then replaced all cover objects to the pools. I captured additional animals for the experiment from non-experimental pools in the study reach. *Dicamptodon* and cutthroat trout were held for several days until the start of the experiment in separate 1.5 m² holding nets (6-mm mesh) placed in non-experimental pools.
I added trout and salamanders to the pools on 12 June 2001 according to the randomized block design. To keep densities similar across the range of pool sizes, I added 3-10 *Dicamptodon* larvae to each pool for an average density (mean ± SE) of 0.71 ± 0.03 per m² (Table 2), and added 1-2 trout to the 4 trout-present pools for an average density of 0.19 ± 0.03 per m². Experimental densities were slightly higher than, but within the range of, the mean densities of salamanders (0.58 ± 0.16 per m²) and trout (0.15 ± 0.04 per m²) from 14 pools sampled within the study reach (including the eight experimental pools before fencing). These treatments matched the natural pattern in the study reach, where trout occurred in some pools but were absent from others. Prior to addition to pools, individual trout and salamanders were anesthetized with tricaine methanosulfonate (MS-222), measured to the nearest mm (fork length (FL) for trout, total (TL) and snout-vent (SVL) lengths for salamanders) and weighed to the nearest 0.1 g wet mass using a portable electronic balance. Trout had an average length of 120 mm (range = 111-148 mm; Fig. 2A). Salamander lengths were 75-129 mm TL, and represented the two main size-classes of salamanders in the stream in June (Fig. 2B). Trout and salamanders were then randomly assigned to a pool, with the constraint that the approximately equal numbers of the two salamander size-classes were assigned to each pool. I marked each salamander with a unique toe-clip for individual identification.

To quantify activity levels, I counted the number of larvae that were visible, two hours after sunset, in each pool every five days during the experiment, for a total of 12 observations per pool. Preliminary observations revealed that larvae
FIGURE 2. Sizes of (A) coastal cutthroat trout and (B) *Dicamptodon* larvae used in the experiment.

A) Cutthroat trout

B) *Dicamptodon*
were nocturnal, reaching maximum activity 1.5 – 2 hours after sunset. I approached each pool quietly and counted larvae from the bank using a bright, narrow-beam flashlight. Larvae did not appear to be disturbed by my approach or the light.

I ended the experiment on 12 August, after two months. I recovered animals using the same sequence of electroshocking, removing cover objects, and hand searching as at the start. I anesthetized, identified, measured, and weighed all animals. I also flushed the stomachs of all salamanders and trout using a modified laboratory wash bottle for evidence of predation on *Dicamptodon*. All animals were then released back to the stream.

**Data analysis.** I used multiple linear regression to test for effects of trout and block (i.e., deep/slow or shallow/fast) on salamander survival, growth, and activity rates. First, I fit full models with trout and block as main factors and a term for their interaction. If the interaction term was not statistically significant, it was dropped and the model was refit with only the main factors. Trout and block were categorical variables in all models. I averaged survival and growth for all larvae in a pool, and used these pool averages for analysis. I calculated survival as the proportion of the larvae that were initially stocked in each pool that was recovered at the end of the experiment. I calculated daily growth rate (g) for each larva as:

\[ g = \ln(\text{final mass}/\text{initial mass})/60 \text{ d} \]

and then averaged these values for all larvae recovered in a pool. I calculated activity rates for each pool as the average proportion of larvae recovered at the end of the experiment that was counted on each of the 12 observation nights. Activity
data were arcsine-root transformed prior to analysis (Sokal and Rohlf 1995), but reported as back-transformed values. For all regression analyses, I inspected normal quantile-quantile (QQ) and residual versus fitted values plots to check that assumptions of normality and equal variance were approximately satisfied (Ramsey and Schafer 1997). I estimated the effect size of the trout treatment on each of the three response variables by calculating 95% confidence intervals (CI) for the regression coefficient using a t-distribution. I used $\alpha = 0.05$ for all statistical tests.

**Results**

I recovered all trout and 33 of 46 (72%) of the *Dicamptodon* larvae originally stocked (Table 2). In addition, I captured unmarked larvae from two enclosures; these were age 0+ larvae that were too large (44-65 mm SVL) to pass through the fence. There was no pattern between the *Dicamptodon* size and recaptures (chi-squared test on the numbers of the two size classes stocked versus recovered: $\chi^2 = 0.46$, df = 1, $p = 0.50$; Fig. 3). I did not find larvae in the stomachs of any trout or salamander, although two larvae (110-115 mm TL) from different pools within the trout treatment had new tail bite marks.

There was no evidence that the presence of cutthroat trout reduced the survival, growth rate, or activity rate of salamander larvae (Table 3), after accounting for the blocking variable (i.e., combination of pool depth and current speed). The presence of trout was estimated to reduce the proportion of larvae recovered by 0.95% (95% CI = -37.47 to 35.57%), increase daily growth rate by
0.0004 per day (95% CI = -0.001 to 0.002 per day), and increase the proportion of larvae active outside of cover by 1.62% (95% CI = -5.08 to 21.54%).

*Dicamptodon* growth generally decreased with body size (Fig. 4). All larvae gained mass during the experiment except for one that had a new tail bite mark.

Cutthroat trout growth was more variable, and two of the six trout lost mass (Fig. 4). However, all trout increased in length (mean ± SE increase: 7.7 ± 2.6 mm).

**TABLE 2.** Numbers of salamanders stocked and recovered from experimental pools. Treatments are cutthroat present (T) and control (C). Blocks are deep/slow (1) and shallow/fast (2). “Marked” refers to larvae given unique toe-clips at the start of the experiment; “unmarked” were larvae without toe-clips that were captured at the end of the experiment.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Treatment</th>
<th>Block</th>
<th>No. Stocked</th>
<th>No. Recovered</th>
<th>Density Start</th>
<th>Density End</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>C</td>
<td>1</td>
<td>7</td>
<td>5</td>
<td>0.67</td>
<td>0.57</td>
</tr>
<tr>
<td>2</td>
<td>C</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>0.86</td>
<td>0.67</td>
</tr>
<tr>
<td>3</td>
<td>T</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>0.73</td>
<td>0.91</td>
</tr>
<tr>
<td>4</td>
<td>C</td>
<td>2</td>
<td>7</td>
<td>4</td>
<td>0.69</td>
<td>0.49</td>
</tr>
<tr>
<td>5</td>
<td>C</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>0.58</td>
<td>0.59</td>
</tr>
<tr>
<td>6</td>
<td>T</td>
<td>1</td>
<td>7</td>
<td>5</td>
<td>0.70</td>
<td>0.56</td>
</tr>
<tr>
<td>7</td>
<td>T</td>
<td>1</td>
<td>10</td>
<td>7</td>
<td>0.74</td>
<td>0.77</td>
</tr>
<tr>
<td>8</td>
<td>T</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>0.73</td>
<td>1.11</td>
</tr>
<tr>
<td>total</td>
<td></td>
<td></td>
<td>46</td>
<td>33</td>
<td>mean 0.71</td>
<td>mean 0.71</td>
</tr>
</tbody>
</table>
FIGURE 3. Initial sizes of Dicamptodon recovered (light) and lost (dark) from experimental pools.

TABLE 3. Multiple linear regression analyses for the effects of trout and habitat block on average survival (%), daily growth rate (g/g/d), and nocturnal activity (%) of Dicamptodon larvae in experimental pools. Activity data were arcsine-root transformed. Trout and block are categorical variables where trout = 0 for control, 1 for present, and block = 0 for shallow/fast, 1 for deep/slow. Regression equations follow the form: Response = \( \beta_0 \) (intercept) + \( \beta_1 \) (trout) + \( \beta_2 \) (block).

<table>
<thead>
<tr>
<th>Response</th>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Survival</td>
<td>(intercept)</td>
<td>79.6429</td>
<td>12.3011</td>
<td>0.0013</td>
</tr>
<tr>
<td></td>
<td>trout</td>
<td>-0.9524</td>
<td>14.2041</td>
<td>0.9491</td>
</tr>
<tr>
<td></td>
<td>block</td>
<td>-11.6667</td>
<td>14.2041</td>
<td>0.4488</td>
</tr>
<tr>
<td>Growth</td>
<td>(intercept)</td>
<td>0.0029</td>
<td>0.0005</td>
<td>0.00325</td>
</tr>
<tr>
<td></td>
<td>trout</td>
<td>0.0004</td>
<td>0.0006</td>
<td>0.5546</td>
</tr>
<tr>
<td></td>
<td>block</td>
<td>-0.0008</td>
<td>0.0006</td>
<td>0.2644</td>
</tr>
<tr>
<td>Activity</td>
<td>(intercept)</td>
<td>6.2215</td>
<td>6.8510</td>
<td>0.4055</td>
</tr>
<tr>
<td></td>
<td>trout</td>
<td>7.3105</td>
<td>7.9108</td>
<td>0.3978</td>
</tr>
<tr>
<td></td>
<td>block</td>
<td>12.2805</td>
<td>7.9108</td>
<td>0.1813</td>
</tr>
</tbody>
</table>
FIGURE 4. Individual daily growth rates of *Dicamptodon* and cutthroat trout relative to body size (TL for *Dicamptodon*, FL for cutthroat trout). Data points for *Dicamptodon* are coded by treatment (control or trout present).

Discussion

I investigated several pathways within a broader context of intraguild predation by which cutthroat trout might affect variables related to the fitness of *Dicamptodon tenebrosus* larvae. I found no evidence that trout affected survival, growth, or behavior of *Dicamptodon* larvae in this experiment. This contrasts sharply with most previous studies on fish-amphibian interactions (see introduction), but is consistent with one example from streams. Resetarits (1991,
tested the effects of brook trout (Salvelinus fontinalis) on larvae of two species, two-lined salamanders (Eurycea bislineata) that are much smaller than trout, and spring salamanders (Gyrinophilus porphyriticus) that are about the same size as trout, in an array of artificial stream pools in Virginia. Eurycea survival and growth were unaffected by trout (Resetarits 1991), although larvae reduced activity and moved to shallower microhabitats. In contrast, adult and juvenile trout (tested separately) reduced Gyrinophilus survival by 50-60% and growth by 65-90% (Resetarits 1991, 1995). In addition, green sunfish (Lepomis cyanellus) sharply reduced survival of streamside salamander larvae (Ambystoma barbouri) in an experiment in natural stream pools in Kentucky (Sih et al. 1992). The evidence for the effects of fishes on stream salamanders therefore is mixed at present, and additional experiments are needed before clear patterns (e.g., influence of predator and prey behaviors, habitat complexity, and experimental venue [mesocosm versus field, Skelly and Kiesecker 2001]) may emerge.

The large number of Dicamptodon larvae that were not recovered and the unmarked larvae that were recovered at the end of the experiment suggest that my experimental pools were not closed as expected. This introduces uncertainty to the measure of larval survival and behavior as proportions of the number of larvae originally stocked in each pool. It also may have reduced the accuracy and precision of estimates of larval growth by reducing the already small number of larvae per pool. In addition, the loss or gain of larvae increased the variation in density between pools (Table 2), which may have altered density-dependent
interactions, such as intraspecific competition, and indirectly influenced larval survival, growth, and behavior. These factors may have compromised my tests of the effects of cutthroat trout on *Dicamptodon*.

It is unclear whether the loss of *Dicamptodon* larvae during my experiment was due to predation (by either trout or larger larvae) or to other factors, such as metamorphosis or escape. I did find new tail bite marks on two large larvae from the cutthroat treatment, indicating attempted predation or aggressive interactions during the experiment. However, I did not directly observe predation by trout or cannibalism among larvae, nor did I find remains of larvae in the pools. In addition, I did not find *Dicamptodon* in the stomachs of any trout or larvae at the end of the experiment (only invertebrate prey were found). Furthermore, more than half of the larvae that were not recovered were large (> 110 mm TL, Fig. 2), which suggests that they were not consumed by trout or other larvae. The only other potential predator I detected in the study reach was a garter snake (*Thamnophis* spp.) several weeks prior to the start of the experiment. Thus the predation level posed by other predators during the experiment appeared small.

The loss of large larvae suggests that metamorphosis may have occurred. Although I incidentally found a newly metamorphosed *Dicamptodon* (200 mm TL) in the study reach when I ended the experiment, I did not find any evidence of metamorphosis by larvae in the experiment. I carefully searched the streambanks and did not find any other metamorphosed salamanders, nor did any of the larvae I recovered show signs of beginning metamorphosis (e.g., reduced gills or change in
head shape). Therefore metamorphosis seems unlikely to explain the loss of many larvae.

Larvae may have escaped from the enclosures, or I may have failed to recover all larvae. On several occasions I observed larvae climbing the fences, but in these cases they were stopped from escaping by the awnings, and I never saw larvae on the bank attempting to crawl around the fences. In addition, I did not find any marked larvae during extensive sampling of the study reach after the experiment. However, I found unmarked larvae in two of the enclosures: either I failed to remove these from these enclosures at the start of the experiment, or they entered the pools during the experiment. If they entered, then presumably larvae also might have found a way out. Considering the high survival (> 96%) and low rate of metamorphosis (< 7%) of the same age classes of *Dicamptodon* larvae for three months in nearly identical enclosures in northern California (Parker 1992), escape, either out of the blocked pools or into areas of the pools where I could not recover them, seems to be the most plausible explanation for most of the losses in this experiment.

The behavior of *Dicamptodon* larvae in this experiment differed from previous studies in both overall activity level and response to trout. First, the average activity rate of larvae in this experiment (grand mean [combining all treatments and blocks] = 15%) was many times lower than in other field (65-75%; Parker 1992) or microcosm (61-79%, Parker 1992; 34-59%, Chapter 2) observations. In my experiment, exposed larvae were clearly visible due to the
shallowness of the stream, relative simplicity of habitat, and contrast in coloration between larvae and the substrate; thus the lower comparative activity level does not appear to reflect a lower probability of observing larvae during my experiment. More observations of *Dicamptodon* activity from a variety of sites are needed to assess whether the present results are an anomaly or within the natural range of variation of activity levels.

In addition to low overall activity levels, *Dicamptodon* larvae did not reduce activity (i.e., increase refuge use) in the presence of trout. In fact, I frequently observed larvae of both size classes active on the bottom when trout were nearby or even directly overhead; larvae had no apparent reaction to the trout. This contrasts strongly with the 60% increase in refuge use by young-of-year larvae (many from the same stream reach) in response to non-visual cues from trout in artificial pools (Chapter 2). These differing results might be explained by threat-sensitive predator avoidance in which larvae assess their predation risk and modify their behavior accordingly (Helfman 1989). Differences in larvae and trout size and the kinds of information about the predator (i.e., chemical or visual cues) between experiments may have contributed to the different responses. My findings that young-of-year larvae increased refuging in response to trout cues (Chapter 2), but two older age classes did not (this experiment), is consistent with reports that prey can assess vulnerability according to their size relative to a predator, and that smaller individuals will show a greater antipredator response than larger individuals (e.g., lobsters: Wahle 1992; whelks: Rochette and Himmelman 1996;
treefrog tadpoles: Puttlitz et al. 1999). In addition, the nature of the predator cues available in each experiment may have altered the ability for larvae to assess and thus respond to threat level. In the absence of visual cues in the artificial pools, larvae may have reacted to trout chemical cues in a general, non-threat-sensitive way, whereas larvae in this experiment may have used visual cues in addition to chemical cues to respond in a threat-sensitive manner (i.e., shown no response to trout that were not much larger than they were; Chivers et al. 2001).

Logistical constraints of manipulating Dicamptodon larvae and cutthroat trout in natural stream pools limited study site selection, experimental design, and the conclusions that can be drawn from this study. Most importantly, I was unable to test for effects of trout on young-of-year Dicamptodon larvae because they were small enough to pass through the 6-mm mesh fences, and finer mesh was impractical (it clogged too quickly). Young-of-year larvae potentially should be most affected by trout because they are vulnerable to predation and show antipredator behavior (Chapter 2) that might reduce feeding opportunity and growth. Thus the lack of effect of trout on the older age classes I used does not imply that interactions with trout are unimportant for Dicamptodon in general. In addition to constraints on which age-classes of larvae I could use, I also was unable to replicate the experiment in several streams, to randomly select experimental pools within the study reach, or to add treatments representing the range of densities of salamanders and trout. Thus, inferences from my study results are
limited to the particular pools and average densities of these organisms within the stream I studied.

In summary, cutthroat trout did not affect *Dicamptodon* larvae under the experimental conditions of this study. However, the large proportion of *Dicamptodon* larvae that was not recovered and the unmarked larvae that were recovered at the end of the experiment suggest that experimental pools were not closed as expected, which may have compromised tests. Placing these results in the context of intraguild predation suggests that the effects of trout on *Dicamptodon* may vary depending not only on the age-classes involved, but also on densities (Fauth and Resetarits 1991) and environmental conditions (Morin 1999). This underscores the complexity of interactions between organisms with size-structured populations, and cautions against drawing general conclusions from single experiments.

**Acknowledgments**

I am grateful to Doug Bateman for recommending the study site, Lance Campbell for help collecting animals, and Lance Campbell and Chris Sheridan for thoughtful discussions. Ben Greenough and the Statistical Consulting Service of the Department of Statistics at Oregon State University provided statistical advice. Funding was provided by the Pacific Northwest Research Station, USDA Forest Service.
Literature Cited


Parker, M. S. 1992. Feeding ecology of the Pacific giant salamander (Dicamptodon tenebrosus) and their role as top predator in a headwater stream benthic community. Unpubl. PhD. Dissertation, University of California, Davis.


CHAPTER 4—CONCLUSION

The coexistence of multiple predators may have important consequences for the structure and function of communities (Sih et al. 1998). Interactions between predators may determine their ability to coexist, as well as strongly affect their combined direct and indirect effects on prey populations and lower trophic levels (Wissinger and McGrady 1993, Spiller and Schoener 1994, Peckarsky and McIntosh 1998). Predators often have size-structured populations (Ebenman and Persson 1988), which may result in intraguild predation characterized by complex trophic and behavioral interactions (Polis et al. 1989). Coexistence of multiple predators may strongly depend on antipredator defenses of small size classes that reduce their vulnerability to predation (Kats et al. 1988, Fauth and Resetarits 1991, Resetarits 1991).

In this thesis, I investigated several interactions that are part of potential intraguild predation between the top predators in headwater streams in western Oregon, Pacific giant salamander (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarki clarki*). I focused on interactions that may be important to the coexistence of *Dicamptodon* larvae with trout. The main findings of my research were:

- Young-of-year *Dicamptodon* larvae were palatable to trout during initial and repeated offerings;
- Young-of-year *Dicamptodon* larvae increased refuge use by 60% in response to non-visual, chemical cues from trout;
• Young-of-year *Dicamptodon* larvae did not select shallower microhabitats in response to trout chemical cues, but this result may have been an artifact of the shallow depth of the stream channels I used;

• Trout did not affect survival, growth, or behavior of similarly-sized, age 0+ and 1+ (years) *Dicamptodon* larvae in natural pools, although these results may have been compromised by unexplained gains or losses of larvae from experimental pools.

These results suggest that antipredator behaviors (i.e., refuge use) may contribute to the coexistence of young *Dicamptodon* with cutthroat trout, but that interactions between similarly-sized, intermediate age-classes of *Dicamptodon* and trout may be weak. However, *Dicamptodon* and cutthroat trout co-occur across a large geographic area, and interactions between them may vary depending on their densities, physical habitat characteristics, and the composition of other species in these headwater stream communities (e.g., Fauth and Resetarits 1991, Morin 1999, Walls and Williams 2001). Moreover, interactions involving different age-classes of *Dicamptodon* and cutthroat trout than I studied may be stronger.

My research addressed only a few of many possible interactions between *Dicamptodon* and cutthroat trout (Fig. 5). Below, I describe the broader potential interactions between these species, and possible community-wide effects of these top predators in headwater streams (Fig. 6). The following ideas present testable hypotheses for future research.
FIGURE 5. Potential pathways of intraguild predation between Pacific giant salamander larvae and cutthroat trout in headwater streams. Thin arrows indicate documented predation, filled block arrows indicate interactions tested in this thesis, and the open block arrow indicates potential, untested interactions.
FIGURE 6. Potential direct and indirect effects of Pacific giant salamander larvae and cutthroat trout in headwater stream communities. Intermediate predators shown are southern torrent salamander (left) and stonefly (right); herbivores shown are tailed frog tadpole (left), mayfly (above), and midge (right). Numbers in text boxes refer to order of discussion in text.
Potential interactions between *Dicamptodon* and cutthroat trout

Interactions between *Dicamptodon* larvae and cutthroat trout may include predation, competition, and facilitation (Figs. 5 and 6 [box 1]). Predation by each species on the other has been documented (Antonelli et al. 1972, Parker 1992, 1993a, 1994), and while each species is rare in the diet of the other relative to invertebrate prey, they may represent large, energetically important items (Parker 1993a). However, the effect of predation on individuals and populations of each species is unknown. Antipredator behaviors likely are important to the survival of vulnerable size classes of each species, but may indirectly affect their growth. For example, increased refuge use by young-of-year *Dicamptodon* in response to trout cues (Chapter 2) may reduce foraging time and growth (e.g., Resetarits 1991, Skelly 1992).

Exploitative competition between *Dicamptodon* and cutthroat trout may occur under some conditions. Both species feed primarily on aquatic invertebrates, and *Dicamptodon* at least has been shown to reduce the abundances of certain invertebrate species (Parker 1992). Food resources for these species possibly may be limited under some conditions, and may lead to exploitative competition. In contrast to predation, which occurs between different size-classes, competition may occur within and between size-classes because there is high dietary overlap among size-classes of both *Dicamptodon* (Parker 1994) and cutthroat trout (Bozek et al. 1994). However, exploitative competition may be reduced by inputs of terrestrial prey from adjacent forests, which may create spatially-subsidized food webs (Polis
et al. 1997) in headwater streams (Fig. 6 [box 2]). Terrestrial prey tend to form a greater proportion of trout diets than *Dicamptodon* diets (Antonelli et al. 1972, Parker 1994), and this difference in diet may reduce competition (Antonelli et al. 1972). However, inputs of terrestrial prey vary seasonally (Cloe and Garman 1996, Wipfli 1997, Nakano and Murakami 2001), and the potential for exploitative competition between *Dicamptodon* and trout may be greatest when terrestrial inputs are low, usually in winter (Cloe and Garman 1996, Nakano and Murakami 2001). For example, experimental elimination of terrestrial inputs to a Japanese stream increased trout predation on aquatic invertebrates and reduced densities of benthic invertebrates (Nakano et al. 1999).

Predation and competition may influence each other via intraguild predation in a variety of ways. Predation may alleviate competition between small size classes by reducing *Dicamptodon* and cutthroat densities (e.g., Wilbur et al. 1983, Morin 1983). Conversely, predation may increase competition when prey respond to a predator by increasing refuge use, and prey may compete for a limited number of refuges or for limited food resources under refuges where they are concentrated (Morin 1986). Young-of-year *Dicamptodon* increase refuge use in response to trout cues (Chapter 2), and I frequently observed cutthroat trout fry under rocks in several streams, so these species may compete for refuges from predators. Competition, in turn, may reduce recruitment to large size classes and reduce the abundance of potential predators. Strong limitation of recruitment to predatory size classes by competition among juveniles often occurs in fishes (i.e., competitive
juvenile bottlenecks: Persson and Greenberg 1990, Byström et al. 1998). However, exploitative competition of this intensity between *Dicamptodon* and cutthroat trout appears unlikely because their diet overlap is reduced by differential use of terrestrial prey (Antonelli et al. 1972).

Although predation and competition between *Dicamptodon* and cutthroat trout may have a negative effect on one or both species, these species also may positively affect one another (i.e., facilitation). Facilitation may occur when behavioral responses of a shared prey to one predator increase its vulnerability to the other, and has been demonstrated in other pairs of predators in streams (Soluk and Collins 1988, Soluk and Richardson 1997) and ponds (Rahel and Stein 1988). For example, behavioral responses of mayflies to avoid benthic-feeding stoneflies increased capture rates by sculpin in laboratory streams (Soluk and Collins 1988), and avoidance of crayfish by darters resulted in higher capture rates by bass in artificial ponds (Rahel and Stein 1988). Increased growth by cutthroat trout in the presence of stoneflies in artificial stream channels was attributed to this mechanism (Soluk and Richardson 1997).

**Potential effects of *Dicamptodon* and cutthroat trout on headwater stream communities**

Individually, *Dicamptodon* and cutthroat trout both may have important effects on prey populations and behaviors in headwater streams. *Dicamptodon* larvae have been shown experimentally to reduce the densities of some benthic
invertebrates, and thereby alter the species composition and trophic structure of this assemblage (Parker 1992). The effects of cutthroat trout on benthic invertebrates are unknown, but other species of trout have been shown to reduce the densities of benthic invertebrates (Flecker and Townsend 1994, Nakano et al. 1999, but see Allan 1982). In addition to reducing prey populations, salamanders and trout may induce antipredator behaviors in prey. Non-visual cues from both *Dicamptodon* and cutthroat trout caused tailed frog (*Ascaphus truei*) tadpoles to reduce foraging activity, although the response was strongest to trout (Feminella and Hawkins 1994). Behavioral responses of other prey are unknown but appear likely.

Invertebrates (crayfish and isopods) reduced activity levels or increased refuge use in response to other species of stream salamanders (Huang and Sih 1991, Resetarits 1991), and invertebrate predators and herbivores commonly alter activity level, position in the substrate, or drift patterns in response to other trout species (e.g., McIntosh and Townsend 1996, Peckarsky and McIntosh 1998, Huhta et al. 1999).

The coexistence of *Dicamptodon* and cutthroat trout may alter their individual effects on shared prey in several ways. *Dicamptodon* and trout may have additive effects on survival of shared prey in which survival is lower where these predators coexist than where either occurs alone (e.g., Rahel and Stein 1988, Soluk and Collins 1988, Krupa and Sih 1998). Alternatively, when the presence of a second predator modifies the behavior of a more efficient predator, prey survival may be higher with both predators than with the more efficient predator alone (Huang and Sih 1991, Eklöv and Werner 2000). For example, if benthic-feeding
Dicamptodon have stronger effects on benthic invertebrates than drift-feeding trout (e.g., Dahl and Greenberg 1996), reductions in Dicamptodon populations or foraging behavior by trout may have a positive impact on the benthic invertebrate assemblage. Finally, the cumulative effect of Dicamptodon and trout on shared prey will depend on how prey respond to potentially conflicting choices of antipredator behaviors for avoiding benthic-feeding salamanders and drift-feeding trout (e.g., Sih et al. 1998, McIntosh and Peckarsky 1999). Prey behaviors probably will depend on the relative risks posed by these two predators, and may be flexible as environmental conditions alter these risks (McIntosh and Peckarsky 1999).

These potential effects of Dicamptodon and cutthroat on prey populations and behaviors may produce trophic cascades with community-wide effects (e.g., Carpenter et al. 1985; Fig. 6 [box 3]). However, it is difficult to predict whether the effect on primary producers (i.e., periphyton) will be positive or negative because Dicamptodon and trout feed on at least two lower trophic levels. If predation is primarily on herbivores, such as tailed frog tadpoles and grazing invertebrates, salamanders and trout should have a positive effect on periphyton through a 3-level trophic cascade (e.g., Forrester et al. 1999). In contrast, if predation is primarily on intermediate predators, such as stoneflies, herbivore densities should increase and periphyton abundance decrease through a 4-level trophic cascade (e.g. Power 1990).

A further difficulty in predicting community-wide effects of Dicamptodon and cutthroat trout is that indirect effects may be mediated by prey behaviors (Fig.
6 [box 4]). For example, antipredator defenses may reduce the effects of predators on prey populations and weaken indirect effects to lower trophic levels. This may be especially true for defenses such as unpalatability that may not affect prey foraging (Kats et al. 1988). Unpalatability of southern torrent salamander larvae (Rhyacotriton variegatus) to Dicamptodon larvae (Rundio and Olson 2001), for example, may be a defense that dampens indirect effects in these headwater communities. In contrast, alterations in prey behavior alone may produce trophic cascades (Schmitz et al. 1997, Peckarsky and McIntosh 1998), so antipredator behaviors that reduce foraging may produce strong indirect effects despite high prey survival, or may add to magnitude of cascades caused by reductions in prey densities. Decreased foraging activity by herbivorous tailed frog tadpoles in response to non-visual cues from Dicamptodon and trout (Feminella and Hawkins 1994) represents a behavior that might produce this type of indirect effect.

In summary, Pacific giant salamanders and cutthroat trout potentially interact through a complex combination of predation, competition, and facilitation. Antipredator behaviors by young-of-year Dicamptodon larvae in response to trout (Chapter 2) and lack of effect of trout on factors related to fitness of intermediate age-classes of larvae (Chapter 3) may promote coexistence of Dicamptodon with cutthroat trout. This coexistence may have important consequences for populations of shared prey and lower trophic levels in headwater stream communities. Headwater streams where Dicamptodon and cutthroat trout are top predators offer an excellent opportunity for studying complex interactions such as intraguild
predation, trophic cascades, behavioral and ecological consequences of multiple predators, and the influence of spatially-subsidized food webs on biotic interactions and community structure.

**Literature Cited**


Parker, M. S. 1992. Feeding ecology of the Pacific giant salamander (Dicamptodon tenebrosus) and their role as top predator in a headwater stream benthic community. Unpubl. PhD. Dissertation, University of California, Davis.


trophic cascades: effects of predation risk on food web interactions.
Ecology 78:1388-1399.


Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and
stoneflies: facilitation and interference among stream predators. Oikos 52:
94-100.

growth of trout: a test of the importance of predator-predator facilitation


Walls, S. C., and M. G. Williams. 2001. The effect of community composition on
persistence of prey with their predators in an assemblage of pond-breeding

Wilbur, H. M., P. J. Morin, and R. N. Harris. 1983. Salamander predation and the
structure of experimental communities: anuran responses. Ecology 64:1423-
1429.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources
in streams: contrasting old-growth and young-growth riparian forests in
southeastern Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic
Sciences 54:1259-1269.

Wissinger, S., and J. McGrady. 1993. Intraguild predation and competition among
larval dragonflies: direct and indirect effects on shared prey. Ecology
74:207-218.


APPENDICES
Pacific giant salamanders (\textit{Dicamptodon tenebrosus}) and coastal cutthroat trout (\textit{Oncorhynchus clarki clarki}) are the top predators in forested headwater streams in the Pacific Northwest (Murphy et al. 1981, Hawkins et al. 1983). These species have size-structured populations, and their coexistence potentially is influenced by mutual predation (Antonelli et al. 1972, Parker 1992, 1993a). \textit{Dicamptodon} are more abundant than cutthroat in many headwater streams (Murphy et al. 1981, Hawkins et al. 1983), and predation by large larvae or neotenes (reproductively mature, gilled adults) on trout fry and smaller conspecifics may be especially common in these systems (Parker 1992, 1993a, personal observations). My objective was to quantify the effects of neotenic \textit{Dicamptodon} on the survival and growth of coastal cutthroat trout (\textit{O. clarki clarki}) fry and small (age 1+ years) conspecifics under natural conditions in a field experiment.

\textbf{Methods}

\textit{Experimental design}. I conducted the experiment in four pools in a 100-m reach of an unnamed tributary to Racks Creek, Benton Co., Oregon (see Chapter 3 for full description of study site). Treatments were the presence or absence (= control) of one \textit{Dicamptodon} neotene per pool. Each treatment was replicated twice, and treatments randomly assigned to pools. Study pools were the four pools
used in Chapter 3 that belonged to the deep/slow current speed habitat block.

Adjacent pools were separated by at least one entire riffle channel unit (mean ± SE distance between pools = 12.4 ± 4.1 m; range = 7.3-28.5 m). Area, mean depth, maximum depth, and mean current speed did not differ between pools assigned to the two treatments (two-sided \( p \geq 0.3 \) from \( t \)-tests for all comparisons; Table 1).

Water temperature (mean ± SE) during the experiment was 10.2 ± 0.02 °C.

I blocked the upstream and downstream ends of pools with 6-mm mesh plastic fences. I buried the bottom of the fences at least 10 cm deep into the sand of the stream bottom, and supported the fences with metal rebar stakes. I bent the top of the fence toward the pool and fastened it into a U-shaped awning to prevent salamanders from climbing over the fence, and created awnings on the outside of the fences with additional pieces of mesh to prevent salamanders from climbing into the pools. I extended the fences either 2 m into the dry streambank or until I encountered a vertical bank. I cleaned debris from the fences every 1-3 days, and placed debris gathered from the upstream fence into the pools to maintain the supply of organic matter.

I measured the dimensions and current speed of the pools at the start and end of the experiment (Table 1). I measured length as the thalweg distance from the upstream to downstream net, and I estimated average width from 3-6 (depending on length) systematic transects across each pool. I estimated average depth from measurements at quarterly intervals along each transect, and measured maximum depth from the deepest point within the pool. I calculated mean current speed from
TABLE 1. Physical habitat characteristics of experimental stream pools at the start and end of the experiment. Pools are numbered from upstream to downstream. Treatments are neotene present (N) and control (C). ND = not detectable using electromagnetic flowmeter.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Treatment</th>
<th>Area (m^2)</th>
<th>Mean Depth (m)</th>
<th>Max. Depth (m)</th>
<th>Current Speed (cm s^-1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Start</td>
<td>End</td>
<td>Start</td>
<td>End</td>
</tr>
<tr>
<td>1</td>
<td>C</td>
<td>8.7</td>
<td>7.8</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>5</td>
<td>C</td>
<td>8.5</td>
<td>7.5</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>6</td>
<td>N</td>
<td>9.0</td>
<td>7.9</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>7</td>
<td>N</td>
<td>11.7</td>
<td>10.4</td>
<td>0.07</td>
<td>0.07</td>
</tr>
</tbody>
</table>

three measurements taken along the length of each pool using a Marsh-McBirney electromagnetic flowmeter.

Prior to the experiment, I removed all salamanders and trout present within each experimental pool, and retained these animals for use in the experiment. I first made two passes with a backpack electroshocker, and then searched pools by hand by removing all cover objects (rocks and wood) > 5 cm to the stream bank. I next made several more passes with an electroshocker until no additional animals were recovered on two consecutive passes. Finally, I electroshocked each pool on the following day to confirm that all trout and salamanders had been removed, and then replaced all cover objects to the pools. I captured additional animals for the experiment from non-experimental pools in the study reach. Age 1+ *Dicamptodon* and cutthroat trout were held for several days until the start of the experiment in separate 1.5 m$^2$ holding nets (6 mm mesh) placed in non-experimental pools, and neotenes were held in 20-l flow-through buckets.

I randomly added *Dicamptodon* neotenes, trout fry, and age 1+ *Dicamptodon* larvae to the pools on 18 August 2001. Densities were 0.10 ± 0.01 neotenes per m$^2$ (1 per pool), 1.0 ± 0.01 trout fry per m$^2$ (9-12 per pool), and 0.85 ± 0.02 age 1+ larvae per m$^2$ (7-10 per pool). These densities were within the range of natural densities in the study reach. Prior to addition to pools, individual trout and salamanders were anesthetized with tricaine methanosulfonate (MS-222), measured to the nearest mm (fork length (FL) for trout, total (TL) and snout-vent (SVL) lengths for salamanders) and weighed to the nearest 0.1 g wet mass using a portable
electronic balance. The two neotenes used in the experiment were 208 and 230 mm TL. Trout fry had a mean length of 53.3 mm (range = 47-60 mm; Fig. 1A), and age 1+ larvae had a mean length of 90.5 mm (range = 78-102 mm; Fig. 1B). Each trout fry and salamander larva was given a unique mark (fin clip for trout, toe-clip for salamanders) for individual identification.

I ended the experiment after 34 days, on 21 September 2001. I recovered animals using the same sequence of electroshocking and hand searching as at the start. I anesthetized, identified, measured, and weighed all animals. I also flushed the stomachs of neotenes using a modified laboratory wash bottle for evidence of predation on trout and age 1+ larvae. I then released all animals back to the stream.

Data analysis. I tested for differences in survival and growth of trout fry and age 1+ larvae between control and neotene-present pools using t-tests. I averaged survival and growth for all larvae in a pool, and used these pool averages for analysis. I calculated survival as the proportion of fry or larvae that were initially stocked in each pool that was recovered at the end of the experiment. I calculated daily growth rate (g) for each fry and larva as:

$$g = \ln(\text{final mass}/\text{initial mass})/34 \text{ d}$$

and then averaged these values for all fry or larvae recovered in a pool. I inspected data graphically to check that assumptions of normality and equal variance were approximately satisfied (Ramsey and Shafer 1997). I used $\alpha = 0.05$ for all statistical tests.
FIGURE 1. Sizes of (A) coastal cutthroat trout fry and (B) *Dicamptodon* larvae used in the experiment.

A) Cutthroat trout

B) *Dicamptodon*
Results

I recovered 95% (37 of 39) of the cutthroat trout fry and 91% (29 of 32) of the age 1+ *Dicamptodon* larvae that were originally stocked. However, I recovered the neotene from only one of the two treatment pools, which meant that the neotene treatment was unreplicated and prevented statistical comparisons. However, survival and growth of trout fry and age 1+ larvae between the control pools and the single neotene-present pool appeared similar. Survival of trout fry (mean ± SE) was 94 ± 6% in controls pools and 100% in the neotene pool. Daily growth rate of fry was 0.0069 ± 0.0004 in control pools and 0.0059 in the neotene pool. Survival of age 1+ *Dicamptodon* larvae was lower in the neotene pool (80%) than in the control pools (93 ± 7%), but growth was similar between controls (0.0027 ± 0.0002 per day) and the neotene pool (0.0025 per day).

Discussion

Neotenic *Dicamptodon* did not appear to affect the survival or growth of coastal cutthroat trout fry or age 1+ *Dicamptodon* larvae in this experiment. However, the experiment was severely compromised by the loss of one of the neotenes, which resulted in an unreplicated treatment and prevented statistical tests. Possible causes for the loss of the neotene are escape, metamorphosis, or predation, although I did not detect any potential predators in the study reach that were large enough to consume a neotene. The gain and loss of *Dicamptodon* larvae from the same experimental pools in Chapter 3 suggests that the neotene may have escaped,
although I recovered a high proportion of larvae from the present experiment. I incidentally found what appeared to be a newly transformed neotene (200 mm TL) in the study reach prior to the experiment in early August, which suggests that neotenes may be capable of metamorphosis. Despite the loss of the neotene, the recovery of nearly all cutthroat fry and age 1+ Dicamptodon suggests that this experimental approach is feasible for investigating interactions among these species under natural conditions.

**Literature Cited**


Parker, M. S. 1992. Feeding ecology of the Pacific giant salamander (Dicamptodon tenebrosus) and their role as top predator in a headwater stream benthic community. Unpubl. PhD. Dissertation, University of California, Davis.


APPENDIX B—AVOIDANCE OF CHEMICAL CUES FROM POTENTIAL PREDATORS BY PACIFIC GIANT AND SOUTHERN TORRENT SALAMANDER LARVAE

The ability for prey to detect and respond to potential predators may be important for their survival and persistence with predators (Sih 1987, Kats et al. 1988, Kats and Dill 1998). The use of non-visual, chemical cues to detect predators is pervasive in aquatic environments (Dodson et al. 1994, Kats and Dill 1998). Prey show a variety of responses to predator cues, including decreased activity, increased refuge use, and avoidance of water containing cues (Petranka et al. 1987, Kats et al. 1988, Kats and Dill 1998). Pacific giant salamanders (*Dicamptodon tenebrosus*) and coastal cutthroat trout (*Oncorhynchus clarki clarki*) are the top predators in forested headwater streams in the Pacific Northwest (Hawkins et al. 1983). Chemical cues from these predators have been shown to elicit behavioral responses by amphibians (Feminella and Hawkins 1994, Chapter 2). For example, tailed frog (*Ascaphus truei*) tadpoles reduced foraging activity in response to cues from cutthroat trout and *Dicamptodon* (Feminella and Hawkins 1994), and young-of-year *Dicamptodon* increased refuge use in response to cutthroat cues (Chapter 2).

In this experiment, I investigated behavioral responses between additional predator-prey pairs in headwater streams. As a follow-up to the experiments in Chapter 2, I tested whether young-of-year *Dicamptodon* avoid chemical cues from cutthroat trout and neotenic conspecifics. I also tested whether southern torrent
salamander (*Rhyacotriton variegatus*) larvae avoid cues from neotenic *Dicamptodon*. *Rhyacotriton* are common in small or intermittent headwater streams where trout are absent and *Dicamptodon* are the main potential predator (Olson et al. 2000), although they are unpalatable to *Dicamptodon* (Rundio and Olson 2001).

**Methods**

I conducted trials in a gravitational flow-through system of tanks after Petranka et al. (1987). Tanks were arranged at different heights on a laboratory bench so that water flowed between adjacent tanks at a rate of about 0.5 l/min through 4-mm (inside diameter) plastic aquarium tubing. Two uppermost 50-l plastic tanks served as reservoirs and flowed separately to two 50-l tanks. One of these held only water and served as a control source, and the other held a predator and was the source for predator cues. These tanks flowed to separate sides of a 75-l aquarium. The aquarium was divided so that the control and predator-cue water flowed to 52 cm long × 15 cm wide chambers, which in turn flowed through a perforated plexiglass plate to the 8 cm long × 30 cm wide experimental chamber at the far end of the aquarium. Two outlet tubes in the experimental chamber drained to an empty catchment tank. I filled all tanks except the catchment with 20 l of water, and the aquarium with 10 l of water. The water supply was a 0.76 m-wide, 5 × 4 m oval indoor stream channel at the Forestry Sciences Laboratory, Oregon State University, Corvallis, Oregon, filled with de-ionized water that was allowed to mineralize for several days from the gravel and rock substrates in the channel.
Tests with food coloring revealed that a stable gradient of predator cues was established in the experimental chamber 5-6 min after flow was initiated between tanks. I placed blinds around the tanks and aquarium and observed trials using by a small mirror suspended 1 m over the aquarium to eliminate visual stimuli to the predators and prey.

Prior to a trial, I filled the tanks and aquarium with water but clamped the connecting tubes to prevent flow between them. I added a predator to a randomly selected tank to condition the water with predator cues for 30 minutes. I then added one salamander larva to the center of the experimental chamber, and initiated flow between tanks. After allowing 10 minutes for a gradient of predator cues to develop, I recorded whether the larva was in the half of the chamber receiving control water or the half receiving predator cues every minute for 10 minutes. At the end of a trial, I removed animals and rinsed the tanks and aquarium repeatedly with clean water.

I conducted trials with young-of-year *Dicamptodon* as prey and cutthroat trout and neotenic *Dicamptodon* as predators in October 2001. I collected animals from several streams in the Oregon Coast Range (Benton Co.) where they co-occur. I collected 20 *Dicamptodon* larvae from Racks Creek by hand, and 5 cutthroat trout from Oak Creek and 5 neotenic *Dicamptodon* from Parker Creek by electrofishing. Larvae had a mean total length of 61 mm (range = 53-73). Trout had a mean fork length of 200 mm (range = 190-213) and a mean mass of 81.0 g (range = 63.6-98.7). Neotenes had a mean TL of 208 mm (range = 188-225) and a mean mass of
62.4 g (range = 52.0-73.0). *Dicamptodon* larvae were held in a flow-through container in the stream channel serving as the water supply, and trout and neotenes were held in separate containers in a second stream channel. Larvae, trout, and neotenes were randomly assigned to trials. Ten trials were run using trout as predators, and another ten were run using neotenes. Each larva was used only once, but trout and neotenes were used in two trials each.

I conducted trials using *Rhyacotriton* as prey and neotenic *Dicamptodon* as predators in November 2001. I collected 10 *Rhyacotriton* larvae (mean TL = 52, range = 45-65) from Parker Creek by hand, and used the five neotenes from the previous trials. Prior to these trials, I drained the stream channel providing the water supply and refilled it with de-ionized water. *Rhyacotriton* were held in this channel. I ran 10 trials using each larva once and each neotene twice.

I summarized the observations for each trial as the proportion of observations in which the larva was in the half of the chamber receiving predator-cues. I tested for avoidance of predator cues by comparing the data against the null hypothesis that larvae spent equal amounts of time in each half of the chamber using *t*-tests on arcsine-root transformed proportions (Sokal and Rohlf 1995).

**Results**

Young-of-year *Dicamptodon* larvae tended to spend a lower proportion of time in the half of the experimental chamber receiving cutthroat trout cues (mean = 26%, 95% confidence interval [CI] = -7–78%) than in the side receiving
unconditioned water, but this difference was not statistically significant (one-sided \( p = 0.13 \)). Neither *Dicamptodon* nor *Rhyacotriton* larvae appeared to avoid cues from neotenic *Dicamptodon*. *Dicamptodon* larvae were observed in the half of the chamber receiving neotene cues 53% of the time (95% CI = 5–97%; one-sided \( p = 0.55 \)), and *Rhyacotriton* larvae 52% of the time (95% CI = 13–90%; one-sided \( p = 0.55 \)).

**Discussion**

The results of these laboratory trials seem to corroborate my findings in Chapter 2 that young-of-year Pacific giant salamander larvae can detect and respond to non-visual, chemical cues from cutthroat trout, although the response was not statistically significant in this experiment. In contrast, *Dicamptodon* and *Rhyacotriton* larvae either did not detect or did not respond to cues from neotenic *Dicamptodon*. Several previous studies have shown lack of response by amphibian larvae to some predators despite responses to others (Kats 1988, Feminella and Hawkins 1994), although *Dicamptodon* have been shown to induce responses in tailed frog (*Ascaphus truei*) tadpoles (Feminella and Hawkins 1994). The lack of response by *Dicamptodon* and *Rhyacotriton* to neotenes may reflect neotene diet. Some prey respond to predators only if the predator has recently consumed a conspecific of the prey (e.g., Crowl and Covich 1990, Wilson and Lefcort 1993). In the present experiment, neotenic *Dicamptodon* were fed worms, and conspecific cues of prey in the diet were thus absent. In addition, the lack of response by
Rhyacotriton may be a result of its unpalatability to Dicamptodon (Rundio and Olson 2001). Other unpalatable amphibian larvae have been shown to lack or have reduced behavioral responses to predator cues (Kats et al. 1988, Hileman and Brodie 1994).

The absence of refuges may have affected the responses by salamander larvae in this experiment. For example, small-mouthed salamander (Ambystoma barbouri) larvae responses to cues from green sunfish (Lepomis cyanellus) depended on the availability of refuges (Sih and Kats 1991). Larvae waited longer to move when refuges were absent than when refuges were present, and when refuges were absent larvae moved less when presented with fish cues than in controls (Sih and Kats 1991). Movement rates by larvae in the present experiment generally were low, and may reflect an alternative behavioral defense to predator cues (i.e., “freezing”) in the absence of refuges. This may have confounded my ability to detect avoidance of predator cues that required movement by larvae.

**Literature Cited**


