

**RELATIONSHIPS BETWEEN TROUT STOCKING
AND AMPHIBIANS IN BRITISH COLUMBIA'S
SOUTHERN INTERIOR LAKES**

by

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ABSTRACT

Stocking lakes with non-native trout to encourage recreational fishing causes changes in lake ecosystems that can negatively affect biodiversity. I examined associations between rainbow trout (*Oncorhynchus mykiss*) and amphibians in small lakes of British Columbia's Southern Interior by comparing abundance, growth, and probability of presence of aquatic breeding amphibians between lakes with and without trout. My evidence suggests that abundance of long-toed salamander (*Ambystoma macrodactylum*), Columbia spotted frog (*Rana luteiventris*), and Pacific treefrog (*Hyla regilla*) larvae may be reduced by 65% or more in lakes with trout. Long-toed salamander larvae were also significantly smaller in lakes with trout. In contrast, western toad (*Bufo boreas*) larvae were more likely to be present and more abundant in lakes with trout. Managers may reduce negative impacts of introduced trout on amphibians by considering overlap between distributions of trout and amphibians and maintaining some troutless amphibian habitat across landscapes.

Keywords: trout stocking; amphibians; freshwater recreational fisheries management; Southern Interior of British Columbia; biodiversity

DEDICATION

To my father John McGarvie, who introduced me at a young age to the biodiversity lurking in tide pools and under rocks on the beach. Thanks for sharing those hidden creatures with me and for sparking my continuing fascination with nature.

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

1.1 Conservation of biodiversity

Loss of biodiversity has raised major scientific and public concern in recent years. Declines in biodiversity at the genetic, population, species, and ecosystem scales have been observed in areas all over the world and have consequences for ecosystem services and human well-being (Chapin et al. 2000; Balmford et al. 2003; Luck et al. 2003; Balmford & Bond 2005). Biodiversity supports ecosystems that provide a variety of goods and services invaluable to humans and other organisms, including food and fuel, water regulation and supply, and cultural and aesthetic benefits such as opportunities for recreational activities (Costanza et al. 1997; SCBD 2000; Balmford et al. 2002). Although much of the value of biodiversity and ecosystem services is outside the marketplace and very difficult to quantify (Nunes et al. 2001), ecosystem goods and services certainly have substantial economic value. One recent estimate of the value of global ecosystem services is \$16-54 trillion (U.S. dollars) per year (Costanza et al. 1997), and the estimated benefit:cost ratio of an effective global program for conservation of remaining wild nature is at least 100:1 (Balmford et al. 2002). The estimated economic and environmental benefits of biodiversity in the United States total approximately \$300 billion annually (Pimentel et al. 2000).

In 1992 over 150 countries, including Canada, signed the Convention on Biological Diversity (CBD) at the Earth Summit in Rio de Janeiro. One of the main goals of the CBD is to achieve a “significant reduction of the current rate of biodiversity loss” by 2010 (SCBD 2006), and under the CBD governments are required to develop national biodiversity strategies and action plans (SCBD 2000). To meet Canadian obligations under the CBD, in 1995 the federal, provincial, and territorial governments of Canada developed the Canadian Biodiversity Strategy, in part to enhance coordination of national efforts aimed at conservation of biodiversity and sustainable use of biological resources (Environment Canada 1995). More recently, the Canadian government passed the Species at Risk Act (SARA), which legally requires that recovery strategies and management plans be put in place to protect imperilled species listed on Schedule 1 of SARA (Schedule 1 is the official List of Wildlife Species at Risk) (Environment Canada 2003b).

British Columbia (B.C.) also made a commitment to conserving biodiversity when it participated in the development of the Canadian Biodiversity Strategy in 1995 and signed the Canadian Accord for the Protection of Species at Risk in 1996. Under the Accord, Canadian federal, provincial and territorial ministers responsible for wildlife committed to a national approach for protecting species at risk, with a goal to prevent species in Canada from becoming extinct as a result of human activity (Environment Canada 2003a). Part of the stated mandate of the B.C. government’s Ministry of Environment is to “maintain and restore the diversity of native species, ecosystems and habitats” in British Columbia (MoE 2006a).

1.2 Introduced species and biodiversity

One of the major threats to biodiversity is introduction of non-native species (also referred to as non-indigenous, alien, exotic, or invasive species), where introduction involves the transfer and/or release of species to geographical areas outside their native range, through direct or indirect human action (definition of 'introduction' based on that of Copp et al. 2005). The spread of non-native species ranks as the second largest threat to imperilled species of plants and animals in the United States, after habitat destruction and degradation, and more than half of the imperilled species in the United States are negatively affected by non-native species (Wilcove et al. 1998). The cost of non-native species in the United States is estimated at approximately \$137 billion (U.S. dollars) per year (Pimentel et al. 2000), which is probably an underestimate given some costs and non-native species left out of the analysis (Lodge & Shrader-Frechette 2003).

Introductions of non-native species appear especially damaging to freshwater ecosystems (Sala et al. 2000), being the leading threat to the viability of aquatic species in the western United States (Richter et al. 1997) and an important threat to aquatic taxa in Canada (Dextrase & Mandrak 2006). Recent and future extinction rates for North American freshwater fauna are estimated five times higher than for terrestrial fauna, and non-native species likely play an important role in many extinctions of native aquatic species (Ricciardi & Rasmussen 1999).

1.3 Trout as an introduced species

Although many introductions of non-native species are accidental, other introductions are intentional. The practice of stocking lakes and rivers with non-native fish to expand and enhance opportunities for recreational fishing is an example of an

intentional introduction. Several trout species have been introduced to a variety of freshwater habitats around the world, which represent one of the world's most widespread introductions of non-native species (MacCrimmon 1971; Lever 1996; Cambray 2003; Dunham et al. 2004). Brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), and rainbow trout (*Oncorhynchus mykiss*) in particular have been introduced hundreds or thousands of kilometers outside their native ranges for the purpose of recreational fishing (MacCrimmon 1971; Lever 1996). For example, brown trout (native to Europe) and rainbow trout (native to western North America) have been introduced to Australia and New Zealand, where these species, especially brown trout, have caused important ecological impacts (Crowl et al. 1992; Flecker & Townsend 1994; Townsend 1996). This practice of stocking non-native sport fish has led to a "globalisation" of certain sport fish and a "homogenisation" of freshwater fish fauna (Rahel 2000; Cambray 2003).

Rainbow trout introductions have been particularly widespread across the globe. The native range of rainbow trout is the west coast of North America, from Alaska to Mexico, mainly west of the continental divide (MacCrimmon 1971; Behnke 1992). However, rainbow trout are now widely established across North America, are found in at least 82 countries, and have been introduced to all continents except Antarctica (MacCrimmon 1971; Cambray 2003). The widespread nature of rainbow trout introductions and the associated negative consequences for native species have led to this species being included on a list of 'One Hundred of the World's Worst Alien Species' (Cambray 2003; ISSG 2006).

Even within their native ranges, trout species are sometimes stocked in lakes that previously lacked trout, and populations established via such introductions are non-native from the perspective of the receiving ecosystems (Dunham et al. 2004). Translocating trout within their native range can have negative impacts similar to those associated with introducing species well outside their natural distribution. For example, golden trout (*Oncorhynchus mykiss whitei*, *O. mykiss aguabonita*), cutthroat trout (*Oncorhynchus clarki henshawi*, *O. clarki seleniris*), and coastal rainbow trout (*Oncorhynchus mykiss irideus*) native to the Sierra Nevada region of California were stocked in fishless headwater areas of the region via interbasin transfers, and have since been associated with the severe decline of at least one species of amphibian (Knapp & Matthews 2000a). Almost all the studies I reviewed on ecological effects of trout stocking do not distinguish between trout introduced to troutless sites within their native range and trout introduced well outside their native range. Thus, for the remainder of this paper, I apply the terms non-native and introduced in a broad sense to include trout introduced to sites both inside and outside their native range.

Trout stocking in mountain lakes of western North America, often in wilderness areas and parks, has attracted particular attention and study (e.g. Knapp et al. 2001a). These lakes were often fishless prior to trout introductions because impassable barriers prevented colonization by downstream fish populations (Donald 1987; Knapp et al. 2001a; Pister 2001). Fishless headwater areas may provide important refuges for native fauna from native predatory fish or from non-native fish introduced downstream, and trout stocked in headwaters can spread downstream relatively easily; thus, stocking headwaters may be particularly damaging (Adams et al. 2001a). Approximately 95% of

an estimated 16,000 high mountain lakes in the western United States were fishless prior to stocking whereas 60% of the total and 95% of deeper (>3 m) and larger (>2 ha) lakes now contain trout (Bahls 1992). Concerns about ecological impacts and the appropriateness of trout stocking in wilderness areas have caused controversy and debate around management of stocking in western North America, especially the western United States (e.g. Landres et al. 2001; Parker et al. 2001; Pister 2001; Wiley 2003; Dunham et al. 2004). Trout stocking was discontinued in most mountain national parks in the western United States and Canada in the 1970s and 1980s (McNaught et al. 1999; Donald et al. 2001; Knapp et al. 2001a; Parker et al. 2001), but remains common and widespread in many other areas (Bahls 1992; Knapp et al. 2001a; Landres et al. 2001).

1.3.1 Ecological impacts of trout stocking

Introduced trout can influence freshwater systems at a variety of ecological levels, from individual organisms to populations and ecosystems (Simon & Townsend 2003). Non-native trout can cause trophic cascades that alter lake and stream food chains, primary production, algal communities, and energy and nutrient cycling (Leavitt et al. 1994; Drake & Naiman 2000; Nyström et al. 2001; Simon & Townsend 2003). For example, predation by introduced trout on benthic and terrestrial prey can regenerate nutrients that otherwise would be unavailable in a naturally fishless lake, and this new source of nutrients could increase algal production (Schindler et al. 2001). Trout stocking can also change animal communities across a landscape by decreasing faunal richness (Knapp et al. 2005).

Aquatic invertebrate communities are particularly sensitive to trout introductions. In general, predation by introduced trout tends to decrease or even eliminate some large

benthic macroinvertebrates and large zooplankton, and reductions in larger taxa are often associated with increases in smaller macroinvertebrates and zooplankton (Vanni 1988; Bechara et al. 1992; Bradford et al. 1998; Carlisle & Hawkins 1998; McNaught et al. 1999; Donald et al. 2001; Knapp et al. 2001b; Knapp et al. 2005). Predation by introduced trout can also lead to behavioural changes in aquatic insects, such as increased refuge seeking in the littoral zone of lakes (Luecke 1990) and decreased grazing on algae in streams (Simon & Townsend 2003).

Introduced trout can also negatively affect native fish. For example, many native fish in Australia and New Zealand have experienced reductions in distribution and abundance in response to introduced trout (Crowl et al. 1992; Townsend 1996). Non-native brook trout and lake trout (*Salvelinus namaycush*) pose a threat to native cutthroat trout (*Oncorhynchus clarki*) in western North America through competition, predation and possibly disease transfer (Ruzycki et al. 2003; Dunham et al. 2004), and declines in cutthroat trout may have negative impacts on their predators and anglers (Koel et al. 2005; Crait & Ben-David 2006). Non-native trout species also threaten native species through hybridization (Allendorf et al. 2001). Even stocking trout within their native range can have negative effects on natural populations of the same species. Hatchery stocks can replace wild stocks, and stocking can mask declines in wild stocks and encourage angling effort at exploitation rates higher than sustainable for wild stocks (Evans & Willox 1991; Post et al. 2002).

1.4 Introduced trout and amphibians

Declining trends in biodiversity have included declines in amphibians from areas throughout the world (Blaustein et al. 1994b; Alford & Richards 1999; Houlihan et al.

2000; Stuart et al. 2004). Although potential causes include climate change, disease, pollution, and in particular habitat destruction and alteration, introduced species are an important factor (Alford & Richards 1999; Blaustein & Kiesecker 2002; Kats & Ferrer 2003). Introduced predatory fish such as trout have been implicated in numerous amphibian population declines and local extinctions (Kats & Ferrer 2003), and can play important roles in determining the distributions of amphibians and the structure of their communities (Hecnar & M'Closkey 1997). Non-native trout have been associated with negative impacts on amphibian species in lentic and lotic habitats throughout the world (Braña et al. 1996; Delacoste et al. 1997; Gillespie 2001; Bosch et al. 2006), but a particularly high proportion of these studies have been done in high elevation mountain lakes in western North America (e.g. Bradford 1989; Tyler et al. 1998a; Funk & Dunlap 1999; Knapp & Matthews 2000b; Pilliod & Peterson 2001; Bull & Marx 2002; Knapp 2005; Welsh et al. 2006).

Introduced trout have been strongly associated with the severe decline and extirpation of mountain yellow-legged frogs (*Rana muscosa*) from wilderness areas in the Sierra Nevada region of California (e.g. Bradford 1989; Knapp & Matthews 2000b; Knapp et al. 2003; Vredenberg 2004; Knapp 2005). The abundance and distribution of Pacific treefrogs (known as *Hyla regilla* and *Pseudacris regilla*, and also called the Pacific Chorus Frog) are also negatively associated with introduced trout in the Sierra Nevada (Bradford 1989; Matthews et al. 2001; Knapp 2005), as well as in other regions of the western United States (Bull & Marx 2002; Welsh et al. 2006). Declines in the mountain yellow-legged frog and possibly other amphibians in the Sierra Nevada have indirectly led to decreases in garter snakes (*Thamnophis* spp.) in the region, because

amphibians are an important component of their prey (Jennings et al. 1992; Matthews et al. 2002; Knapp 2005).

Ambystomid salamanders in western North America are also negatively associated with trout introductions. Northwestern salamanders (*Ambystoma gracile*) and long-toed salamanders (*Ambystoma macrodactylum*) are significantly less abundant in lakes with introduced trout than in troutless lakes (Tyler et al. 1998a; Pilliod & Peterson 2001; Bull & Marx 2002; Larson & Hoffman 2002), and the distribution and probability of presence of long-toed salamanders are negatively associated with trout presence (Funk & Dunlap 1999; Adams et al. 2001b; Welsh et al. 2006). In regions where more habitat is occupied by trout, densities of overwintering long-toed salamander larvae are lower across the landscape, even in troutless sites, than in regions with less habitat occupied by trout (Pilliod & Peterson 2001). This suggests that introduced trout may negatively affect long-toed salamanders at the landscape scale as well as in individual lakes, probably by extirpating salamander populations in lakes with trout and thus reducing sources of immigrants to the remaining troutless sites (Pilliod & Peterson 2001). Thus, trout stocking may lead to the exclusion, severe decline, or extirpation of long-toed salamanders in individual lakes and/or entire drainage basins (Funk & Dunlap 1999; Pilliod & Peterson 2001).

Another amphibian species from western North America negatively associated with introduced trout is the Columbia spotted frog (*Rana luteiventris*). Introduced trout can significantly reduce the abundance of all life stages of Columbia spotted frogs, and can lower spotted frog recruitment even in troutless lakes in drainage basins where introduced trout are more common (Pilliod & Peterson 2000, 2001). Introduced trout are

also suspected to have contributed to the decline of the Cascades frog (*Rana cascadae*) in Northern California (Fellers & Drost 1993; Welsh et al. 2006).

1.4.1 Mechanisms of interaction between trout and amphibians

The most commonly assumed mechanism of interaction between introduced trout and amphibians is predation. Direct predation by trout on amphibian larvae has been observed in western North America (Hoffman et al. 2004; Vredenberg 2004) and Australia (Gillespie 2001), and will directly lead to decreased amphibian abundance if the growth rate of amphibian populations cannot compensate for losses through predation. However, predation may also indirectly affect amphibians by causing changes in amphibian behaviour in response to predation risk. For example, long-toed and northwestern salamander larvae may change their habitat use and activity patterns to avoid predation by trout (Taylor 1983; Tyler et al. 1998b; Hoffman et al. 2004), and observed changes in behaviour may reduce survivorship and growth because of lost foraging opportunities (Tyler et al. 1998b; Lawler et al. 1999; Nyström et al. 2001; Kats & Ferrer 2003).

A less commonly cited mechanism of interaction is competition for food between trout and predaceous amphibians such as salamander larvae (Tyler et al. 1998b). Long-toed salamander larvae are opportunistic carnivores and eat a wide range of invertebrates (Tyler et al. 1998a; Pilliod & Fronzuto 2005) that are also prey for trout. Introduced trout are known to cause changes to aquatic invertebrate communities, such as reductions in large conspicuous taxa (e.g. Bradford et al. 1998; Carlisle & Hawkins 1998; Donald et al. 2001; Knapp et al. 2001b), and these changes may be associated with reductions in food resources for carnivorous amphibians.

Introduced trout can also indirectly influence amphibians. For example, trout introductions may fragment and isolate populations of sensitive amphibian species. The probability of patch occupancy by mountain yellow-legged frog larvae in the Sierra Nevada is an increasing function of the number of nearby troutless lakes and a decreasing function of the weighted distance to nearby frog populations (Knapp et al. 2003). Populations of yellow-legged frogs are now significantly more isolated in the region than they were before trout were introduced (Bradford et al. 1993). Isolation and fragmentation may be particularly problematic for species such as the mountain yellow-legged frog that are highly aquatic during the adult stage (i.e. more likely to use water for dispersal and thus more likely to encounter trout) and/or that do not disperse over long distances (Bradford et al. 1993).

Extinction via natural causes and/or stochastic events becomes more likely in fragmented populations because (1) the probability of recolonization is reduced, (2) isolated populations are often small, and (3) population size of many amphibians is inherently variable and sensitive to fluctuations in the physical environment (Pechmann et al. 1991; Sjögren 1991; Bradford et al. 1993; Blaustein et al. 1994b; Semlitsch 2002). Amphibians often exhibit high site fidelity and limited dispersal, leading to lower rates of recolonization and higher probability of local extinctions (Blaustein et al. 1994b; Funk & Dunlap 1999; Semlitsch 2002). Probability of recolonization is also related to connectivity, and connectivity is reduced by introduced trout when (1) amphibian populations are eliminated by trout presence, and (2) rates of successful dispersal are reduced by greater distances between populations and by the presence of trout (or other predators) along dispersal corridors (Knapp et al. 2003). Habitat fragmentation and

reduced connectivity may have contributed to observed negative associations between trout and mountain yellow-legged frogs (Bradford et al. 1993; Knapp & Matthews 2000b; Knapp et al. 2003) and long-toed salamanders (Tyler et al. 1998a) respectively.

Extirpation of local populations may have a disproportionate effect on amphibians across a landscape if extirpated populations served as ‘sources’ for recolonization of less suitable ‘sink’ habitats (Braña et al. 1996; Pilliod & Peterson 2001). For example, mountain yellow-legged frogs take at least two years to reach metamorphosis and overwintering larvae require deep permanent water bodies that do not dry or freeze completely (Bradford 1989; Knapp & Matthews 2000b; Knapp et al. 2003; Knapp 2005). The presence of trout in many deep permanent lakes in the Sierra Nevada has converted potential source habitats into sink habitats where the population growth rate is negative in the absence of immigration (Knapp & Matthews 2000b). Many remaining fishless water bodies may be sink habitats as well because they are not permanent or are too shallow for good overwinter survival, which may lead to eventual extirpation of frogs from lakes both with and without trout (Knapp & Matthews 2000b). Similarly, in a high-elevation region of Idaho where long-toed salamander larvae and post-metamorphic Columbia spotted frogs require deep lakes for overwintering, frog and salamander densities are lower in drainage basins with a higher proportion of deeper lakes occupied by trout, presumably because lakes with trout are sink habitats (Pilliod & Peterson 2000, 2001). In general, amphibians that typically inhabit permanent water bodies tend to be most vulnerable to introduced aquatic predators (Kats & Ferrer 2003), and amphibians that are able to breed in temporary water bodies where trout cannot persist and that overwinter in troutless areas (e.g. on land) are less vulnerable to trout (Knapp et al. 2001b).

Several other factors also determine the sensitivity of amphibians to trout introductions. Species with large bodies or large egg clutches tend to co-occur more frequently with predatory fish than species with small bodies or small clutch sizes (Hecnar & M'Closkey 1997). Species with higher dispersal abilities and rates are also probably better able to cope with trout introductions (Gillespie 2001). Longer periods of development before metamorphosis, which are more common in species at higher elevations, increase the probability of predation during the vulnerable egg and larval stages (Pilliod & Peterson 2001). Lake characteristics may also be important; for example, the response of amphibians to trout may change with changing lake productivity (Tyler et al. 1998a) or with changing habitat complexity where structural refuges in more complex habitats reduce the foraging efficiency of fish (Anderson 1984; Diehl 1992; Knapp et al. 2005). Characteristics of trout populations may also influence the response of amphibians; for example, evidence suggests that higher densities of trout may be associated with stronger negative responses in amphibians (Tyler et al. 1998a; Welsh et al. 2006).

Amphibian species not negatively associated with trout are often those considered unpalatable or even toxic (e.g. Knapp 2005; Welsh et al. 2006). Other defenses to predatory fish include the ability to detect chemical cues of predators and behaviourally-mediated predator avoidance, such as changes in flight response, habitat use, and levels and timing of activity (Taylor 1983; Kats et al. 1988; Hoffman et al. 2004; Bosch et al. 2006). Amphibians often reduce their activity in response to predators (Kupferberg 1998; Lawler et al. 1999; Nyström et al. 2001; Bosch et al. 2006) and female amphibians may avoid laying eggs in sites with predatory fish (Hopey & Petranka 1994; Binckley &

Resetarits 2003). Evidence suggests that amphibians are more likely to have defenses if they encounter predators more frequently or their distributions naturally overlap with predators (Kats et al. 1988; Kats & Ferrer 2003). However, even when amphibians have predator defense mechanisms, these may be specific to native predators and ineffective against non-native predators (Gillespie 2001; Bosch et al. 2006).

One final indirect mechanism of interaction between amphibians and trout may be disease transfer. Laboratory experiments suggest that rainbow trout can transfer the pathogenic fungus *Saprolegnia ferax* to amphibian embryos directly, or indirectly via infected substrate (Kiesecker et al. 2001), and this fungus appears to have caused mass egg mortality in at least one population of western toads (*Bufo boreas*) in Oregon (Blaustein et al. 1994a). Introduced trout could also influence important host-pathogen interactions by acting as a stressor to host amphibians (Blaustein et al. 1994a; Kiesecker et al. 2001).

1.4.2 Amphibian species included in this study

Four species of amphibians were encountered during this field study: the long-toed salamander, the Columbia spotted frog, the Pacific treefrog, and the western toad. All four species may use small lakes for aquatic-breeding and thus may be affected by the presence of trout. Reductions in abundance and/or probability of presence of the salamander, treefrog and spotted frog have previously been associated with the presence of trout during at least one field study for each species (Bradford 1989; Tyler et al. 1998a; Funk & Dunlap 1999; Adams et al. 2001b; Matthews et al. 2001; Pilliod & Peterson 2000, 2001; Bull & Marx 2002; Knapp 2005; Welsh et al. 2006). In contrast, field studies have found either a positive association between western toads and

introduced trout (Welsh et al. 2006) or no association (Bull & Marx 2002). However, laboratory experiments suggest that introduced trout may threaten western toads through transfer of pathogens (Kiesecker et al. 2001).

All four study species have broad distributions in western North America that extend along the Pacific coast from southeast Alaska to California or northern Mexico, and east into Alberta and/or the western U.S. states of Idaho, Montana, Wyoming and Colorado (Green & Campbell 1984; Leonard et al. 1993; Corkran & Thoms 1996; Russell & Bauer 2000; Lannoo 2005). Columbia spotted frogs were previously considered the same species as Oregon spotted frogs (*Rana pretiosa*), but the two species have recently been separated based on genetic differences (Reaser & Pilliod 2005).

The conservation status of the Columbia spotted frog, Pacific treefrog, and long-toed salamander is generally considered secure. The spotted frog and the salamander were designated Not at Risk by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) in 2000 and 2006, respectively, because these species remain widespread and abundant in Canada (COSEWIC 2006). Although the Columbia spotted frog and long-toed salamander are generally considered secure in the United States, several populations of the spotted frog in the southeastern part of its U.S. range have shown declines of concern (Reaser & Pilliod 2005) and some local populations of the salamander may be threatened (Pilliod & Fronzuto 2005). The Pacific treefrog has not been assessed by COSEWIC, but is considered secure and not at risk of extinction in British Columbia (MoE 2006b). In the United States, Pacific treefrogs are not declining throughout most of their range and are typically one of the most common amphibians where they occur (Rorabaugh & Lannoo 2005).

The conservation status of the western toad is not as secure as the other three species. The western toad was added to Schedule 1 of Canada's Species at Risk Act in January 2005 as a species of Special Concern ("species that may become threatened or endangered... because of a combination of biological characteristics and identified threats"; Environment Canada 2003b) and thus is considered a 'species at risk' throughout its range in Canada. Although the western toad is widespread and locally abundant throughout most of its historic range in Canada, it has experienced population declines and extirpations, and is considered threatened by urban expansion, conversion of habitat for agriculture, habitat deterioration, disease, and introduced exotic predators and competitors (COSEWIC 2002; Wind & Dupuis 2002). Internationally, the IUCN (International Union for Conservation of Nature and Natural Resources) has classified the western toad as Near Threatened because it is probably in significant decline due to diseases such as the fungal disease chytridomycosis (IUCN 2006). Severe declines and extirpations in several areas where the toad was once abundant have led to this species being considered endangered in several U.S. states (Muths & Nanjappa 2005).

1.5 Trout stocking and recreational fishing in British Columbia

The purpose of trout stocking is usually to create, expand and/or maintain recreational fishing opportunities. Trout stocking is also intended to provide a diversity of recreational fishing opportunities to anglers (Bahls 1992). Stocking presumably provides one method that managers can use to control angling quality and respond to angler needs, by offering some measure of control over the distribution, density and types of fish available. Stocking is also sometimes used as a conservation mechanism to restore populations of threatened species (e.g. Young & Harig 2001; FFSBC 2006b). In a

regional context, stocked lakes may be used to divert angler effort away from lakes with wild trout that are more sensitive to increased angler effort (Webb 2006), although stocking should be used cautiously for such a purpose because hatchery trout can also mask declines in wild populations or encourage angling effort on sensitive wild stocks (Post et al. 2002).

Trout stocking is a well-established and important part of recreational fisheries management in British Columbia. The federal Dominion Department of Fisheries began stocking lakes as early as 1909 (Mottley 1932) and a policy of extensive hatchery introductions was established by the provincial Game Commission beginning in the late 1930s (Sport Fishing Institute 1955). Currently, about 1,000 lakes and streams are stocked annually in British Columbia (although the total number stocked is approximately 2500 (MoE 2006c) because not all lakes stocked are stocked every year), and the vast majority of these lakes are stocked with rainbow trout (FFSBC 2006a). The contribution of stocking programs to recreational fisheries in British Columbia is significant. For example, although the number of lakes stocked annually represents less than 1% of the approximately 10,000 lakes in British Columbia that offer sport fishing opportunities, in 1995 more than half of all licensed anglers in British Columbia spent at least some of their fishing effort on stocked lakes and approximately 40% of B.C. anglers always or usually fished stocked lakes (Levey & Williams 2003). Of the 30 lakes that experienced the highest levels of angler effort in the Thompson-Nicola Region of B.C.'s Southern Interior between 2000 and 2004, 29 were stocked (S. Webb, unpublished data).

Freshwater angling provides important recreational and economic benefits in British Columbia, and given that a high proportion of angling effort in B.C. occurs on

stocked lakes, a considerable portion of these benefits are presumably attributable to trout stocking. In 2000 there were almost 350,000 licensed anglers in British Columbia, and a majority (65%) of their effort occurred on open water lakes (Levey & Williams 2003). Freshwater anglers may invest in trip-related expenses, equipment, gear, and other goods in order to practice fishing activities, and in 2000, over \$400 million in expenditures were directly attributable to freshwater recreational fishing in British Columbia (Levey & Williams 2003). Over 71,000 licensed anglers in 2000 were from outside of British Columbia (Levey & Williams 2003), which indicates the importance of freshwater angling to British Columbia's tourism industry. A variety of fishing resorts, lodges, camps, and campgrounds serve freshwater anglers in British Columbia, and other important sectors of B.C.'s recreational fishing industry include fishing guides, bait and tackle shops, and fishing-specific magazines and websites. Businesses not specific to the recreational fishing industry (e.g., hotels, restaurants, gas stations, etc.) may also experience the economic benefits of recreational fishing. Because the majority of recreational fishing opportunities occur outside of British Columbia's major urban centres, the more remote or rural areas in the interior of the province experience substantial economic benefits that would not otherwise exist.

In addition to obvious economic benefits, many benefits of recreational fisheries are non-market in value and difficult to quantify (e.g., social benefits; Rudd et al. 2002). Anglers may receive a wide variety of values such as relaxation, camaraderie, and sport and competition from recreational fishing (Kearney 2002). Recreational fishing may also promote environmental awareness and environmental responsibility among those who fish by getting them outside and appreciating nature, which may partially offset the

ecological costs of trout stocking (Kearney 2002). Anglers in British Columbia recently rated closeness to nature as the top reason for fishing where they did (Levey & Williams 2003).

1.5.1 Study region

This study focused on lakes in the Southern Interior region of British Columbia, where the Southern Interior is defined as the south-central region of the province, excluding the Okanagan Valley but including Kamloops in the south and extending north to the southern Cariboo. Most study lakes were located in the Thompson-Nicola Region (B.C. Ministry of Environment Region 3), but a small number were located in the southeast corner of the Cariboo Region near 100 Mile House (B.C. Ministry of Environment Region 5) (Fig. 1.1; Appendix). All of the study lakes were located in forested areas within the Thompson River watershed, including both the North and South Thompson River watersheds. For more detailed information about the region, watersheds and ecosystems represented by the study lakes, see Section 2.2.1 and the Appendix.

Lakes and angling opportunities in the Southern Interior are diverse, ranging from productive grassland lakes to more remote and pristine forested lakes. Just over 1,000 lakes in the Thompson-Nicola Region are known to contain freshwater game fish (as defined in MoE 2006d) and thus provide sport fishing opportunities (S. Webb, unpublished data). Of a subset of approximately 800 game fish-bearing lakes with detailed records, the majority (93%) are small (<1,000 hectares). Almost all (98%) of the subset are inhabited by rainbow trout and 74% contain rainbow trout as the only fish species (S. Webb, unpublished data).

Although rainbow trout are native to the Southern Interior region, many populations are maintained or augmented by hatchery stocking. Between 2002 and 2005, 228 lakes in the Thompson-Nicola Region were stocked mainly with rainbow trout while kokanee or non-native eastern brook trout made up the balance in a small number (<30) of lakes (S. Webb, unpublished data). Stocking is more common in the southern half of the region where angler effort is highest and lakes are closer to major population centres and transportation routes (S. Webb, unpublished data). Besides lakes currently being stocked, additional lakes in the region have a history of fish introductions. More than 450 lakes in the Thompson-Nicola region have records of stocking (S. Webb, unpublished data) and many of the naturally reproducing rainbow trout populations in land-locked or headwater lakes in the Southern Interior could have been introduced through extensive stocking that occurred in British Columbia during the first half of the 20th century (Mottley 1932; Sport Fishing Institute 1955).

Recreational fishing is both popular and economically important in the Southern Interior. In 2000, approximately 17% of the total angling effort in British Columbia was spent in the Thompson-Nicola Region, which was second only to the Lower Mainland (18%) (which has a much larger population) (Levey & Williams 2003). Approximately 27% of all anglers who fished in B.C. fished in the Thompson-Nicola, making it the most popular region in the province (Levey & Williams 2003). Most (79%) anglers who fished in the Thompson-Nicola came from outside the region (Levey & Williams 2003), providing an important source of tourism for the region.

1.6 Management and policy issues in British Columbia

The government of British Columbia, which is ultimately responsible for managing recreational fisheries and trout stocking in B.C., has obligations to the public and the federal government to protect and conserve biodiversity and species at risk. These obligations may be legally binding in the case of species listed under SARA, but the government also has non-legally binding obligations, such as commitments made through its participation in developing the Canadian Biodiversity Strategy and signing the Canadian Accord for the Protection of Species at Risk. In addition, many members of the general public value and support conservation of biodiversity, perhaps because of the various goods and services that biodiversity provides or simply because they believe that nature has value simply by existing (existence value). To represent all members of the public, the government has obligations to consider these points of view during decision-making. Trout stocking, especially stocking new lakes that are currently troutless, poses a threat to biodiversity protection. However, the provincial government also has a responsibility to encourage economic activity and development in British Columbia, such as that related to recreational fishing and development of new angling opportunities, and many members of the public enjoy non-economic benefits from freshwater recreational fishing. Funding for hatcheries and research on recreational fishing is directly linked to freshwater angling license sales in British Columbia, which creates additional incentives for promoting angling. Trout stocking continues to be one of the main tools used to provide a range of quality angling options and, in the future, stocking lakes that are currently troutless could be used to expand recreational fishing opportunities. Thus, a

potential conflict exists between conservation of biodiversity and trout stocking programs that enhance recreational fishing.

The provincial government currently has no official policy on trout stocking with respect to biodiversity. New stocking proposals go through an ‘enhanced review process’ within the government to ensure that biodiversity values are incorporated in proposal evaluation (G. Jones, personal communication). However, there are no official criteria for decision-making and interested parties outside of management agencies are not necessarily involved. Only a few new lakes have been stocked recently, which is in part due to biodiversity concerns and uncertainty as to how such concerns should be addressed (Quadra Planning Consultants 2001a). Thus, the policy question is: How can biodiversity be conserved without unnecessarily limiting recreational fishing opportunities?

1.7 Study objectives

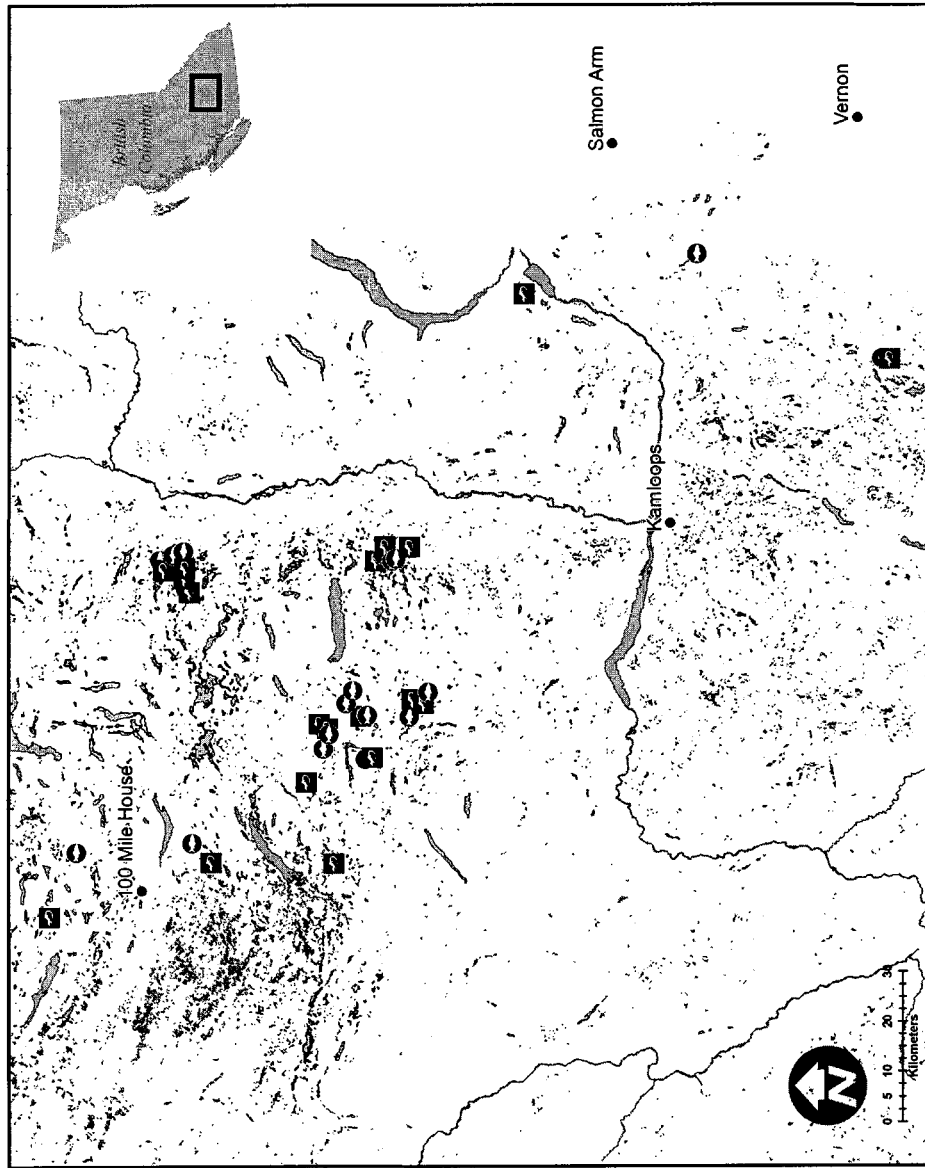
In 2001, a review of small lakes (<400 ha) fish stocking in British Columbia identified (1) understanding and consideration of biodiversity issues, (2) protection for lakes without recreationally important fish species, and (3) monitoring of the impacts of stocking on ecosystems and biodiversity to be lacking within current fish stocking policy and management (Quadra Planning Consultants Ltd. 2001a, 2001b). The review recommended addressing these issues by developing research and monitoring programs to assess the potential impacts of trout stocking on troutless systems in British Columbia. Such programs would provide managers with useful information for designing trout stocking policies that reduce negative impacts of this practice on lakes and native species (Quadra Planning Consultants 2001a).

To my knowledge, associations between rainbow trout and amphibians have not been investigated in British Columbia. Previous studies in other parts of western North America have shown negative associations between introduced trout and amphibians with the strength of relationships varying both within and among amphibian species, as well as regionally. However, there are at least two reasons to expect that associations between trout and amphibians in British Columbia's Southern Interior region may be different than those published in the literature. First, most studies have focused on oligotrophic alpine lakes that were fishless prior to trout introductions and that have little habitat complexity (but see Welsh et al. 2006; Knapp 2005; Knapp et al. 2005). Amphibians may be especially sensitive to introduced trout in such habitats because (1) they evolved without pressure to develop defenses to fish predators, (2) larvae often need to overwinter at higher elevations, which restricts breeding to permanent habitats that are more likely to be occupied by trout, and (3) lower habitat complexity provides less cover from predators (Knapp 2005; Knapp et al. 2005; Welsh et al. 2006). In contrast, forested lakes such as those included in this study in British Columbia's Southern Interior region are generally at lower elevations (~600-1500 m) than those examined in the literature, are probably more productive, and provide relatively high habitat complexity. Second, trout and amphibians occur naturally together in the Southern Interior of British Columbia and their native distributions may overlap to a much larger degree than regions investigated in other studies. Thus, amphibians in British Columbia's Southern Interior lakes may exhibit habitat preferences and behaviours that limit the effects of trout.

The objective of this study is to contribute towards an increased understanding of the ecological impacts of trout stocking in British Columbia by assessing the potential

effects of rainbow trout on four species of amphibians. To accomplish this objective, I examined associations between rainbow trout presence and several characteristics of amphibian populations in small lakes of the B.C. Southern Interior region. The specific research questions addressed are: (1) Is the presence of trout associated with lower relative abundance and/or probability of presence for each amphibian species in the study region?; and (2) Is there a difference in amphibian size and/or stage of development between lakes with and without trout when sampled at the same time and similar location?

1.8 Figures



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Figure 1.1. Location of study lakes in the Southern Interior region of British Columbia. Circles with fish indicate lakes with trout and squares with salamanders indicate troutless lakes. Source: Daniel Himer, Instar GIS Solutions, 2006, by permission.

CHAPTER 2: RELATIONSHIPS BETWEEN RAINBOW TROUT AND AMPHIBIANS IN BRITISH COLUMBIA'S SOUTHERN INTERIOR LAKES

2.1 Introduction

Observed declines in biodiversity from regions around the world, and the potentially serious consequences for ecosystem services and human well-being, have raised considerable public and scientific concern (Chapin et al. 2000; Balmford et al. 2003; Luck et al. 2003; Balmford & Bond 2005). One of the major threats to biodiversity is introduction of non-native species (also called non-indigenous, alien, exotic, or invasive), which may be particularly damaging to freshwater ecosystems (Richter et al. 1997; Sala et al. 2000) where extinction rates are estimated to be much higher than in many terrestrial ecosystems (Ricciardi & Rasmussen 1999). Although many introductions of non-native species are accidental, others are intentional, including stocking of lakes and rivers with non-native trout to expand and enhance opportunities for recreational fishing.

Several species of trout have been successfully introduced to areas outside their native ranges, which represents one of the world's most widespread introductions of non-native species (MacCrimmon 1971; Lever 1996; Rahel 2000; Cambray 2003). Even within their native ranges, trout species are sometimes stocked in water bodies that previously lacked trout, and populations established via such introductions are also non-native from the perspective of the receiving ecosystems (Dunham et al. 2004).

Introduced trout can have a variety of impacts on aquatic environments, at the individual, population, community, and ecosystem levels (Simon & Townsend 2003). Non-native trout can cause trophic cascades that alter aquatic food chains, primary production, and energy and nutrient cycling (Leavitt et al. 1994; Drake & Naiman 2000; Schindler et al. 2001; Simon & Townsend 2003), and can decrease the faunal richness across a landscape (Knapp et al. 2005). Aquatic invertebrate and algae communities can be altered by trout introductions (Bradford et al. 1998; Carlisle & Hawkins 1998; McNaught et al. 1999; Drake & Naiman 2000; Donald et al. 2001; Knapp et al. 2001b; Parker et al. 2001), and introduced trout can harm or exclude native fish through competition, predation, hybridization, and possibly disease transfer (Evans & Willox 1991; Crowl et al. 1992; Allendorf et al. 2001; Ruzycki et al. 2003; Dunham et al. 2004).

The effects of introduced trout on native amphibians have been the subject of a large amount of research (e.g. Braña et al. 1996; Gillespie 2001; Bosch et al. 2006), especially in high-elevation mountain lakes in western North America (e.g. Bradford 1989; Tyler et al. 1998a; Funk & Dunlap 1999; Knapp & Matthews 2000b; Pilliod & Peterson 2001; Bull & Marx 2002; Welsh et al. 2006). For example, introduced trout are strongly associated with declines and extirpations of mountain yellow-legged frogs (*Rana muscosa*) from wilderness areas in the Sierra Nevada region of California (e.g. Bradford 1989; Knapp & Matthews 2000b; Knapp et al. 2003; Vredenberg 2004; Knapp 2005). Declines in the mountain yellow-legged frog and possibly other amphibians in the Sierra Nevada have indirectly led to decreases in garter snakes (*Thamnophis* spp.) because amphibians are important prey for the snakes (Jennings et al. 1992; Matthews et al. 2002; Knapp 2005).

The most commonly assumed mechanism of interaction between introduced trout and amphibians is predation. Besides causing direct mortality, predation can cause changes in amphibian behaviour (such as increased refuge use) in response to predation risk (Taylor 1983; Sih et al. 1988; Tyler et al. 1998b; Hoffman et al. 2004), leading to reduced growth and survivorship through loss of foraging opportunities (Tyler et al. 1998b; Lawler et al 1999; Kats & Ferrer 2003). Competition for food is possible between predaceous salamander larvae and trout (Tyler et al. 1998b), and introduced trout may transfer diseases to amphibians (Kiesecker et al. 2001). At the landscape scale, introduced trout may reduce the connectivity and probability of successful dispersal among amphibian populations, thus leading to fragmentation, isolation, and increased probability of local extinctions, even in habitats without trout (Bradford et al. 1993; Tyler et al. 1998a; Pilliod & Peterson 2001; Knapp & Matthews 2000b; Knapp et al. 2003).

In this study, I assessed relationships between rainbow trout (*Oncorhynchus mykiss*) and four species of amphibians in small lakes of the Southern Interior region of British Columbia (B.C.), Canada. The long-toed salamander (*Ambystoma macrodactylum*), Columbia spotted frog (*Rana luteiventris*), Pacific treefrog (*Pseudacris regilla*), and western toad (*Bufo boreas*) use small lakes in the region for aquatic-breeding and thus may be affected by the presence of trout. Reductions in the salamander and two frog species have been associated with the presence of trout during at least one previous field study each (Bradford 1989; Tyler et al. 1998a; Funk & Dunlap 1999; Adams et al. 2001b; Matthews et al. 2001; Pilliod & Peterson 2001; Bull & Marx 2002; Knapp 2005; Welsh et al. 2006). In contrast, field studies have found either a positive association between western toads and introduced trout (Welsh et al. 2006) or no

association (Bull & Marx 2002). However, laboratory experiments suggest that introduced trout may threaten western toads through transfer of pathogens (Kiesecker et al. 2001).

Although all four species have broad distributions along the west coast of North America, the western toad is considered a species of Special Concern throughout its Canadian range under Canada's Species at Risk Act, and severe local declines and extirpations have led to consideration of the toad as endangered in several U.S. states (Muths & Nanjappa 2005). Conservation status of the other three species is generally considered secure in North America (Lannoo 2005; COSEWIC 2006; MoE 2006b), although some local populations of the Columbia spotted frog and the long-toed salamander may be declining in the United States (Pilliod & Franzuto 2005; Reaser & Pilliod 2005).

In British Columbia, there is interest in promoting and increasing participation in freshwater recreational fishing, which is an activity that generates over \$400 million annually in direct expenditures in the province (Levey & Williams 2003). Stocking is an established tool for recreational fisheries management in British Columbia (~1,000 lakes are stocked annually), and new lakes may be stocked in the future. However, there is also concern about the ecological impacts of trout stocking, especially in previously troutless lakes. To my knowledge, associations between rainbow trout and amphibians have not been investigated in British Columbia, where these associations may differ from those observed elsewhere for at least two main reasons. First, lakes in British Columbia's Southern Interior region are generally at lower elevations than many of those examined in the literature, and are probably more productive and provide higher habitat complexity,

all of which may change the sensitivity of amphibians to trout (Tyler et al. 1998a; Knapp 2005; Knapp et al. 2005; Welsh et al. 2006). Second, trout and amphibians occur naturally together in many regions of British Columbia and their native distributions overlap to a much larger degree than regions investigated previously, which increases the chances that amphibians have developed antipredator defenses (Kats et al. 1988; Kats & Ferrer 2003).

The objective of this study is to contribute towards an increased understanding of the ecological impacts of trout stocking in British Columbia. To accomplish this objective, I compared abundance, probability of presence, and growth and development of four amphibian species between lakes with and without rainbow trout in British Columbia's Southern Interior region. The specific research questions I addressed were: (1) Is the presence of trout associated with lower relative abundance and/or probability of presence for each amphibian species?; and (2) Is there a difference in amphibian size and/or stage of development between lakes with and without trout when sampled at the same time and similar location?

2.2 Methods

2.2.1 Study area

The Southern Interior region is used in this study to refer generally to the south-central region of British Columbia, including the communities of Kamloops in the south-centre and 100 Mile House in the north. Although the Southern Interior is sometimes considered to include the Okanagan Valley, my study only included areas northwest of the Okanagan Valley. All of the study lakes were located within the Thompson River watershed, including both the North and South Thompson River watersheds (Figure 1.1).

The climate of the study region is dry, with warm to hot summers and cool to cold winters. The landscape ranges from arid valley river basins dominated by grasslands and open forests to forested higher elevation plateaus with many small lakes, low-gradient streams, and shallow wet depressions (Parish et al. 1996). These plateaus have very low human population densities, and the main land uses are forestry, open range cattle grazing, and recreation. All of the study lakes were located in forested areas and most were on the plateaus; none were found in grasslands or alpine areas. Study lakes were usually located at elevations greater than 1,000 m (Table 2.1; Appendix). Small forested lakes in the region are generally eutrophic and have high levels of structural complexity with abundant aquatic vegetation, coarse woody debris, and often soft organic bottoms.

The biogeoclimatic ecosystem classification (BEC) system was developed by the British Columbia Ministry of Forests to classify terrestrial ecosystems according to differences in climate, vegetation, and site conditions using information on vegetation, soils and topography (Meidinger & Pojar 1991; MFR 2006). The biogeoclimatic zones, subzones, and variants (where applicable) represented among lakes with and without trout are presented in Table 2.2 and the Appendix. The majority of study lakes were located in the Interior Douglas-fir (IDF) zone (eight troutless lakes, five lakes with trout), followed by the Sub-Boreal Pine-Spruce (SBPS) (four troutless lakes, seven lakes with trout), Engelmann Spruce-Subalpine Fir (ESSF) (four troutless lakes, three lakes with trout), Sub-Boreal Spruce (SBS) (two troutless lakes, three lakes with trout), and Montane Spruce (MS) (one lake each lake type) zones. All of these zones are dominated by forest rather than grassland or alpine vegetation. For more detailed information about what watersheds and ecosystems are represented by the study lakes, see the Appendix.

Within the Thompson-Nicola region of the Southern Interior (a region that includes most of my study area), just over 1,000 lakes are known to contain freshwater game fish (as defined in MoE 2006d) (S. Webb, unpublished data). Of a subset of approximately 800 game fish-bearing lakes with detailed records, the majority (93%) are small (<1,000 hectares), almost all (98%) are inhabited by rainbow trout, and 74% contain rainbow trout as the only fish species (S. Webb, unpublished data). Although native to the Southern Interior, many rainbow trout populations in the region are maintained or augmented by hatchery stocking. More than 450 lakes in the Thompson-Nicola have a record of hatchery releases, and between 2002 and 2005, 228 lakes in the region were stocked with fish (almost all with rainbow trout) (S. Webb, unpublished data). Besides lakes currently being stocked, many naturally reproducing rainbow trout populations in land-locked or headwater lakes could have been introduced through extensive stocking that occurred during the first half of the 20th century (Mottley 1932; Sport Fishing Institute 1955).

2.2.2 Study design and study lakes

During the summer of 2003, I conducted a pilot study at six lakes (five troutless, one with trout) in the Thompson-Nicola region to test alternative sampling methods, determine the approximate timing of amphibian development, and determine the distributional properties of sampling data for power analyses. I identified live-trapping of amphibians using un-baited collapsible funnel traps set in the water (Shaffer et al. 1994; MELP 1998) and visual encounter survey counts along strip transects (Crump & Scott 1994; MELP 1998) in the water and along the shoreline as the most appropriate sampling methods for this study. Both methods were logistically practical and effective at

providing relative abundance information for larvae and metamorphs (i.e. recently transformed juveniles) of all four species of interest. I used two sampling methods to decrease the influence of biases caused by individual sampling methods on observed trends (i.e. if data from both methods show the same trends, I can conclude with greater confidence that the trends reflect the true situation). Size and more detailed stage information could also be collected through trapping. Although trap catches and strip transect counts are indices of relative rather than absolute abundance, both indices are proportional to population density (number of animals per hectare).

The trap catch data collected during the pilot study were highly aggregated and tended to follow a negative binomial distribution in which catches of zero individuals were very common, but occasional large catches were also observed. I therefore used a simulation approach to power analysis because conventional tests of statistical power can be unreliable with non-Gaussian data (Hilborn & Mangel 1997). The objective of the simulation study was to determine the sample size required to achieve a minimum 80% probability of detecting a minimum 50% difference in amphibian abundance between lakes with and without trout if such a difference exists (given a type I error rate of $\alpha=0.05$). Simulations consisted of generating trap catch data for various sampling regimes differing in number of lakes sampled, where the true abundance of amphibians was 50% less in lakes with trout, and then determining if a hypothesis test using the data could detect the true difference in abundance between lake types. Data were generated through random sampling of appropriate probability distributions parameterized using data from the pilot study. I ran simulations separately for each amphibian species, and analysis of variance was used to test for differences between lake types in each simulated

dataset. Based on this analysis, the minimum sample sizes per lake type were 10 lakes for long-toed salamander, 14 lakes for Pacific tree frog, and 25 lakes for Columbia spotted frog. More than 30 lakes per lake type were required for the western toad. Logistic and resource constraints made a 60 lake sampling season unreasonable; thus, I accepted slightly lower power for Columbia spotted frogs, and potentially quite low power for western toads, and developed a sampling design using $N = 38$ lakes evenly divided between lake types (19 trout and 19 troutless).

2.2.3 Lake selection

The primary criteria used to select study lakes were accessibility (within 2 km of a road) and small size (<40 ha surface area). I first selected troutless lakes that met these criteria using fish survey data available from the British Columbia Fisheries Inventory Summary System (MSRM 2006b), as well as personal communications with provincial biologists and fishing resort operators familiar with the study area. I then paired each troutless lake with the closest lake containing rainbow trout that also met the accessibility and size criteria, and that was similar in elevation. If more than one rainbow trout lake was close by and met the selection criteria, I chose (in order of preference): (1) the lake containing stocked rather than natural populations of rainbow trout; (2) the lake containing only rainbow trout and no other fish species; and/or (3) the lake most similar to the troutless lake in surface area and/or surrounding landscape. I confirmed that trout were present in each trout lake using stocking records and evidence of trout presence during lake sampling (direct observations of trout and/or anglers on lakes).

The number of lakes in the study region that I could confirm were troutless, that met the selection criteria, and that had trout lakes nearby was quite small (approximately

25). As a result, I was forced to use some less than ideal lakes; for example, 8 of 19 trout lakes had naturally reproducing populations of rainbow trout rather than stocked populations (Table 2.1; Appendix). However, some of these naturally reproducing populations likely originated through extensive stocking in the region during the first half of the twentieth century (Mottley 1932; Sport Fishing Institute 1955).

Field studies of amphibian populations are challenged by the complex, multi-stage life cycle of amphibians. The duration and timing of breeding and each stage of development varies among and within species at different elevations, locations, and from year to year (Corkran & Thoms 1996; Lannoo 2005). I sampled lakes within the same trout and troutless pair at the same time and at similar elevations and locations, so that any effects of location, elevation, and time of year on amphibian development, abundance and/or activity were roughly equally represented in the two lake types. Also, because lakes in each pair would have experienced similar weather during sampling, pairing ensured that short-term effects of weather on amphibian activity were also equally represented in lakes with and without trout. This is important because amphibian activity can often be closely related to weather conditions (Heyer et al. 1994; Rorabaugh & Lannoo 2005).

Amphibian field studies must also be timed according to the developmental cycles of the study species. Because amphibians tend to develop earlier and faster at lower elevations, I sampled lower elevation sites earlier in the season and higher elevation sites later. This approach served to decrease variation among lake pairs in the stage of amphibian development at the time of sampling and also ensured that lakes were sampled

during the appropriate development window (i.e. after the majority of eggs had hatched and before the majority of larvae had gone through metamorphosis).

2.2.4 Amphibian data

Sampling of each lake took place over a two day period. A total of 37 traps were set on each lake near shore at random locations and at random water depths within a 0.15-0.50 m range because larvae of the study species tend to live in shallow water around lake edges (Corkran & Thoms 1996). Traps contained floats and were only partially submerged to prevent adult amphibians from drowning. Trap openings were fully submerged except in water shallower than approximately 0.20 m where trap openings could only be partially submerged. Traps were set and retrieved in the same order so that individual trap soak times were as close to 24 hours as possible (mean soak time = 23.14 h , SD = 1.33 h). Observers recorded the species, snout-vent length (Fellers et al. 1994), and life stage (e.g., adult, metamorph, or larva) of each amphibian captured. Observers also determined the Gosner developmental stage (Gosner 1960) for each western toad, Pacific treefrog and Columbia spotted frog (larva or metamorph).

Amphibian relative abundance was also determined using visual surveys along strip transects at four randomly chosen sites per lake. Visual survey sites had a relatively wide (at least 3 to 4 m), shallow littoral areas, and were as free as possible of major impediments to movement and visibility (e.g. large amounts of woody debris or dense vegetation). Each site was divided into shoreline and water strata, which were sampled separately. For shoreline strata, one observer used a low intensity search (only animals exposed on the surface of vegetation were counted) along 30 m long by 2 m wide transects that were centred on the shoreline (i.e., 1 m in the water and 1 m on land). The

observer recorded the number, species, and life stage (larva, metamorph or adult) of all amphibians observed.

Water strata, which were identical in dimension to shoreline strata, were parallel to shoreline transects and at least 2 m from the shoreline. One observer searched each water transect from a small boat, searching a 2 m wide strip centred on the centreline of the boat, while a second person moved the boat forward. Depths along the transect line averaged 0.43 m (SD=0.20 m) and distance from shore averaged 2.73 m (SD=2.54 m). Observers recorded the number, species, and life stage (larva, metamorph or adult) of each individual counted. The level of search intensity was also low for water transects.

The length of time spent searching per unit of transect was standardized as much as possible among observers and lakes for both shoreline and water transects but depended to some extent on water clarity, the complexity of the lake or lakeshore habitat, and the weather conditions. Searches were avoided during poor weather conditions (during rainfall or when wind conditions created ripples on the water) and observers wore polarized glasses to prevent glare from interfering with counts. The time of day for surveys varied but was always during the brightest daylight hours, between 9 AM and 4:30 PM. Pairing of sampling of the two lake types in date and general location ensured that any effects of season and weather on amphibian observability were similar between lakes with and without trout.

Observers also recorded counts, species, and life stage for amphibians sighted at any time outside of trapping and visual transect surveys (i.e. incidental sightings) during the two days of sampling at each lake. However, because incidental sightings were not a result of sampling standardized among lakes, this data was only included in the presence-

absence analysis, which was also done with incidental data excluded (see Section 2.2.5.1).

Several measures were taken during field sampling to ensure that observer biases did not influence patterns observed in the amphibian data. The field staff sampling lakes of each type was varied so that the same staff were not always sampling only lakes of one type, and thus any uncontrolled observer biases were distributed among the data for both lake types. All observers were trained to identify all life stages of all species, and the ability of observers to search for amphibians was compared and standardized among observers. Similarly, the ability of observers to measure and stage amphibians was compared and standardized among observers.

2.2.5 Statistical analyses

Pairs of trout and troutless lakes were pairs only in the sense that they were sampled at the same time and in a similar location, which controlled for general lake characteristics such as location, elevation and weather, and presumably stages of amphibian development. Lakes within a trout-troutless pair were not pairs in any other sense, and often differed in habitat factors such as size, aquatic and lakeshore vegetation, and lake bottom substrate.

I analysed the count data from trapping and transect searches with and without accounting for pairing using t tests, randomization tests, and construction of bootstrap confidence intervals. Although the results of most of these tests were affected to a small extent by pairing, the differences had no effect on statistical significance or my final conclusions. Therefore, for both types of count data I report only analyses that ignored pairing of lakes during sampling. However, pairing was important for the analysis of size

and stage data because date, elevation, and weather are important in determining the progress of amphibian development (Corkran & Thoms 1996; Muths & Nanjappa 2005; Pilliod & Fronzuto 2005; Reaser & Pilliod 2005; Rorabaugh & Lannoo 2005), and all of these variables were similar or the same between lakes within a pair. Therefore, my analyses of size and stage data took pairing into account.

There were problems with the methods used during transect surveys at the first eight lakes sampled (four troutless, four with trout). These problems prevented valid comparison between transect data from the first eight lakes with transect data from all other lakes. Thus, I excluded the first eight lakes from any statistical analyses of transect data, although data from these lakes were included as part of the incidental sightings for the presence-absence analysis.

I also excluded adult data from all analyses other than for presence-absence. Although observers found adults of the toad and two frog species during both trapping and transect sampling, the final adult data set was small. Data for larvae and metamorphs are also a definite indicator of breeding at a given lake, whereas the presence of adults alone does not confirm that breeding took place. Data for larvae and metamorphs were combined for all analyses, and I will refer to this data hereafter as larvae or larval data. All analyses were done separately for each of the four amphibian species. All statistical analyses used two-tailed p -values and were conducted using R statistical computing and graphics software (Version 2.2.0, R Foundation for Statistical Computing, Vienna, Austria).

In environmental management applications, the power of analysis techniques may be low, and the costs of failing to detect an effect when one exists (i.e. a type II error)

may be high (Peterman 1990). In these cases using an α level greater than 0.05 in hypothesis tests may be justified, in order to avoid making costly type II errors. Prospective power analysis predicted potentially low power for some species, so I interpreted the results of all analyses as significant whenever the p -value of a test was ≤ 0.10 .

2.2.5.1 Presence-absence

I used Fisher's exact test for count data to test the null hypothesis that the proportion of lakes where each species was present was the same between lakes with and without trout. I used Fisher's exact test instead of the typical Pearson's chi-square test because many counts in the contingency tables were small (< 5); however, analysis of the same data using Pearson's chi-square test with Yates' continuity correction gave very similar p -values and did not change the significance of the results using $\alpha = 0.05$ or $\alpha = 0.10$. I considered a species present in a lake if it was counted during trapping or transect surveys or was observed incidentally. However, because incidental sightings were not a result of standardized sampling, I conducted presence-absence analysis both with and without incidental sightings included. Analyses were also performed separately for (1) presence of adults and/or larvae, and (2) presence of larvae only.

2.2.5.2 Trapping and transect counts

For each species, I summarized trapping data for each lake by adding up the counts of larvae across all traps to give one number, trap catch, for each species in each lake. Similarly, I summarized transect survey data by adding up the counts of larvae across all surveys within a lake, land and water transects combined, to give one number, transect count, for each species in each lake.

The assumptions of standard statistical tests such as Gaussian (normally) distributed errors, equality of variance among treatment groups, no outliers, and independence of errors, were all violated to some extent by the trapping and transect data for all species. In particular, all count data appeared to violate the assumption of normally distributed errors, even after log-transformation ($X' = \log(X + 1)$). The distribution of counts tended to be positively skewed with a relatively large number of zero counts (especially for the transect count data) and a long right tail, as was observed during the pilot study. Using the ratio of sample standard deviation in the two lake types as an indicator, I found that the assumption of equality of variance between treatment groups (i.e. lake types) was violated in some cases but not others. However, log-transformation solved this problem in all cases except for the western toad transect count data. Most of the data contained outliers in both trap catch and transect count, and some outliers were particularly extreme for the western toad and the Pacific treefrog. For each species, I analysed trap catch and transect count data both with all data included and with the pairs containing the largest outliers for each lake type removed. Outliers were data points that were more than 1.5 times the interquartile range beyond the 25th or 75th percentile.

For each of the two indices of abundance, trap catch and transect count, I calculated the observed sample mean in each lake type ($\bar{x}_{notrout}$ and \bar{x}_{trout}), the sample difference between the means ($\bar{x}_{notrout} - \bar{x}_{trout}$) and the sample effect size ($\bar{x}_{trout} / \bar{x}_{notrout}$). An effect size of 1.0 represents no difference in mean catch/count between lake types, and thus no effect. I estimated the standard errors of the sample mean (se_{mean}) and the

sample difference between the means ($se_{difference}$) directly from the data using the standard formulas:

$$se_{mean} = \frac{s}{\sqrt{n}} \quad se_{difference} = \sqrt{\frac{s_{NT}^2}{n_{NT}} + \frac{s_T^2}{n_T}}$$

The standard error of the sample estimate of effect size was estimated by non-parametric bootstrapping (Efron & Tibshirani 1998), i.e. the standard deviation of the estimated effect size from 10,000 replicate bootstrap samples, sampled with replacement from the data. I also calculated bootstrap 90% and 95% confidence intervals for effect size and the difference between the means using non-parametric bootstrapping and the BC_a [bias corrected and accelerated] method, which is an improved version of the bootstrap percentile method (Efron & Tibshirani 1998). Plots of the variance of bootstrap estimates of effect size and difference between means with increasing number of bootstrap replicates showed that stable variance was achieved with 10,000 replicates for the trapping and transect data.

I used two-sample t tests with two-sided p -values to test the null hypothesis of no difference between lake types in true means for each of the two indices of abundance. Because both the trapping and transect data did not appear normally distributed and sometimes violated other assumptions as outlined above, I conducted the two-sample t tests with both the untransformed data and the data after $\log(X+1)$ transformation. The $\log(X+1)$ transformation is preferable to the $\log(X)$ transformation based on theoretical grounds (Zar 1999), and was necessary in this study because many counts were zero.

Because the trap catch and transect count data did not meet all of the assumptions of the two-sample t test, even after $\log(X+1)$ transformation, I also used permutation

(randomization) tests (Manly 1991; Efron & Tibshirani 1998) to test the null hypothesis that the distributions of relative abundance indices for each species were the same between lakes with and without trout. The test statistic for the permutation tests was the difference between lake types in mean trap catch or mean transect count ($\bar{x}_{notrout} - \bar{x}_{trout}$). The number of permutations was 4999, with the test statistic calculated for each permutation. These test statistics plus the observed value made a distribution of 5,000 test statistics. Plots of the variance of the test statistic distribution with increasing permutations showed that stable variance was achieved with 5,000 permutations for both the trapping and transect data.

The achieved significance level (ASL) of a permutation test is the proportion of values of the test statistic that are as extreme as or more extreme than the observed value. The ASL is interpreted the same way as the conventional p -value; i.e. the ASL is the probability of observing a test statistic value at least as large as the observed value when the null hypothesis is true (Manly 1991; Efron & Tibshirani 1998). To calculate a two-sided ASL, I compared the absolute value of the observed test statistic with the absolute values of the permutation test statistics using the following equation:

$$ASL_{two-sided} = \frac{\#(|\theta_b^*| > |\hat{\theta}|)}{B}$$

where $\hat{\theta}$ is the observed value of the test statistic, θ_b^* is the permutation value of the test statistic for permutation b , $\#$ is the number of times that the absolute value of the permutation test statistic was greater than the absolute value of the observed test statistic, and B is the total number of permutations plus one to account for the observed value in the test statistic distribution.

2.2.5.3 Size and stage data

To assess whether or not the presence of trout was associated with differences in the development of amphibian larvae, I compared the size and developmental stage of larvae caught during trapping between pairs of lakes with and without trout. Only the long-toed salamander (size data) and the Columbia spotted frog (size and stage data) were included in these analyses. I did not catch any western toad larvae in troutless lakes, and caught very few Pacific treefrog larvae in lakes with trout, making statistical tests for size or stage impossible for these two species. Although the salamander and spotted frog size and stage data violated some of the assumptions of standard statistical tests, none were seriously violated and the data appeared close to being normally distributed. For both species, I analysed size and/or stage data with all data included and with the outlier data points for each lake type removed.

I used linear mixed effects modelling to test the null hypothesis of no difference between lake types in size and/or stage within lake pairs for long-toed salamander and Columbia spotted frog larvae. Pair was included as a random blocking variable in the analysis. Because analysis was only possible when size/stage data existed for individuals in both members of a lake pair, I included only four lake pairs in the analyses of spotted frog size and stage data and only 10 lake pairs in the analysis of salamander size data. I used linear mixed effects modelling instead of analysis of variance because the number of larvae measured in each lake was unbalanced, and linear mixed effects models can better accommodate unbalanced designs. However, the results of this analysis using analysis of variance were the same (in terms of statistical significance) as those from the linear mixed effects modelling.

2.3 Results

2.3.1 Presence-absence

Long-toed salamander larvae were present in a relatively high proportion of both lake types (Table 2.3). The Columbia spotted frog was the next most common in either lake type, particularly when I considered both larvae and adults. The Pacific treefrog and the western toad were present in a relatively low proportion of lakes of both types, especially when I considered larvae only. The overall high degree of absence of treefrogs and toads from both lake types is also reflected in the relatively high proportion of lakes of both types where trap catch and/or transect count were zero (53 to 87% of lakes for the treefrog and 63 to 100% of lakes for the toad). However, when present, toad larvae sometimes occurred in large numbers, which is reflected in the relatively high sample means for trap catch and transect count of toads in lakes with trout (Table 2.4). For example, in one trout lake (Scot Lake) almost 6,000 larvae were captured in 37 traps. However, the next highest total catch in a trout lake was 206 larvae (Lake 997), followed by 27 larvae (Spectacle Lake).

Larvae of the long-toed salamander, Pacific treefrog and Columbia spotted frog were present slightly more often in troutless lakes, but there was not enough evidence to reject the null hypothesis of no difference in presence between lakes with and without trout (Table 2.3). In contrast, there was strong evidence that western toad larvae were present significantly more often in lakes with trout ($p=0.019$). When incidental sightings of toad larvae were included, there was less evidence against the null hypothesis of no difference between lakes types ($p=0.079$) but the result was still significant using $\alpha=0.10$.

However, when counts of adult toads were included in the presence-absence analysis, the difference between lake types was no longer significant.

2.3.2 Indices of abundance

In the thirty lakes where both trapping and transect data could be used for analysis, trap catch and transect count per lake were positively correlated for all four species. Spearman's rank correlation coefficient was greater than 0.58 and the correlation was highly significant ($p < 0.001$) for all species.

The sample mean trap catch and sample mean transect count were greater in troutless lakes than in lakes with trout for all species except the western toad (Table 2.4). This suggests that the presence of trout was associated with reduced abundance of long-toed salamanders, Columbia spotted frogs and Pacific treefrogs, but increased abundance of western toads; however, the results of statistical hypothesis tests provide mixed evidence that these associations truly exist (Table 2.5). The two-sample t test provided relatively strong evidence that true mean trap catch of the long-toed salamander was greater in troutless lakes, regardless of whether or not the data were log-transformed prior to analysis (transformed: $p=0.017$; untransformed: $p=0.042$). The same test provided evidence that true mean trap catch of the Columbia spotted frog was greater in troutless lakes, but only when the data were transformed prior to analysis (transformed: $p=0.081$; untransformed: $p=0.130$). However, the two-sample t test provided little evidence that transect count of the salamander or spotted frog were greater in troutless lakes, regardless of whether or not data were log-transformed prior to analysis (p -values between 0.11 and 0.20). There was also little evidence that true mean trap catch or true mean transect count of the Pacific treefrog were greater in troutless lakes according to the two-sample t test,

regardless of whether or not treefrog data were log-transformed prior to analysis (p -values between 0.13 and 0.31). In contrast, there was strong evidence according to the two-sample t test that true trap catch of the western toad was greater in lakes with trout (transformed data: $p=0.017$), and evidence that true transect count was greater in lakes with trout (transformed data: $p=0.088$). However, this evidence was associated only with the log-transformed toad data (untransformed trap catch: $p=0.302$.; untransformed transect count: $p=0.241$).

The results of the two-sample t tests for all species using either trap catch or transect count, in terms of statistical significance, were robust to removal of the pairs containing the largest outliers, with two exceptions. When outliers were removed, there was no longer enough evidence to reject the null hypothesis of no difference between lakes types in mean trap catch for the Columbia spotted frog (log-transformation, $t=1.571$, $df=32$, $p=0.126$) or in mean transect count for the western toad (log-transformation, $t=-1.417$, $df=26$, $p=0.169$).

Permutation tests provided reasonably strong evidence that trap catch for the long-toed salamander was greater in troutless lakes and evidence that transect count was greater in troutless lakes (trap ASL=0.035, transect ASL=0.094). There was also borderline evidence that trap catch of the Pacific treefrog was greater in troutless lakes, but this evidence was lacking for transect counts (trap ASL=0.103, transect ASL=0.225). The permutation tests did not provide enough evidence to reject the null hypothesis of no difference in trap catch or transect count of the Columbia spotted frog between lake types (trap ASL=0.143, transect ASL=0.210). In contrast, the permutation tests provided very strong evidence that western toad trap catch was greater in lakes with trout, and

borderline evidence that transect count was also greater in lakes with trout (trap ASL=0.008, transect ASL=0.100).

The results of the permutation tests for all species using trap catch or transect count, in terms of statistical significance, were robust to removal of the pairs containing the largest outliers, with a few exceptions. The ASL for the Pacific treefrog trap catch went from 0.103 to 0.229 when I removed outliers from the analysis. When outliers were removed from the total transect count data, the ASL went from 0.094 to 0.194 for the long-toed salamander and from 0.100 to 0.208 for the western toad.

The 95% bootstrap BC_a confidence intervals for differences between lake types in mean trap catch or mean transect count did not overlap zero for any of the species, providing evidence against the null hypothesis of no difference (i.e. a true difference of zero) between lakes types for all species (Table 2.4; Fig. 2.1). However, these confidence intervals did include values close to zero for the Pacific treefrog and the Columbia spotted frog, suggesting that the true difference between lake types in mean trap catch and/or trap total count could be small for these species.

Removing the largest outlier pairs from the data for each lake type did influence to some extent the confidence intervals for the difference between means for all species, but removing outliers changed the interpretation of the results in only a few cases. Removing trap catch outliers resulted in a 95% confidence interval that overlapped zero (95% confidence limits: -0.29, 17.29 larvae per lake) for the Columbia spotted frog; however, the 90% confidence interval for the spotted frog with outliers removed still did not overlap zero (confidence limits: 0.47, 14.82 larvae per lake). Removing the transect count outliers resulted in 95% and 90% confidence intervals that overlapped zero for both

the Pacific treefrog and the Columbia spotted frog (90% confidence limits treefrog: -0.29, 0.64 larvae per lake; 90% confidence limits spotted frog: 0, 1.54 larvae per lake). The transect count data for both species included many zeroes, so removal of one or two non-zero counts strongly influenced the results.

According to the formula I used to calculate effect size ($\bar{x}_{trout} / \bar{x}_{notrout}$), an effect size <1.0 represents a decrease in relative density of larvae in the presence of trout. The sample effect size was less than 0.35 for all species except the western toad for both trap catch and transect count (Table 2.4), representing a >65% reduction in relative density of larvae of the long-toed salamander, Pacific treefrog and Columbia spotted frog in the presence of trout. Using trap catch, the 90% confidence intervals for effect size for the salamander and spotted frog and the 95% confidence interval for the treefrog did not overlap 1.0 (no difference), which provides evidence of a true negative association between trout and abundance of these species (Table 2.4, Fig. 2.2). Using transect count, the 95% confidence intervals for the salamander and treefrog and the 90% confidence intervals for the spotted frog also did not overlap 1.0 (Table 2.4, Fig. 2.2).

Removal of the largest outlier pairs did influence interpretation of estimates of effect size in several cases for the salamander and two frog species. Removal of lake pairs containing the largest trout lake outlier and the largest troutless lake outlier from the trapping data provided stronger evidence of a negative association between trout and long-toed salamander larvae (observed effect size and 95% confidence limits: 0.16, 0.05, 0.51). This suggests strong influence of the largest trout lake outlier on the estimate of effect size for the salamander using the trapping data. When I similarly removed outlier pairs from the Columbia spotted frog trap catch and transect count data respectively, the

90% confidence intervals overlapped 1.0 where they hadn't before, which decreased the evidence of a negative association between trout and the spotted frog (observed effect size and 90% confidence limits: 0.36, 0.07, 1.08 (trapping); 0.25, 0, 1.00 (transects)). Removal of outlier pairs from the Pacific treefrog transect count data also resulted in a large change in the sample estimate of effect size and 95% and 90% confidence intervals overlapping 1.0 (observed effect size: 0.38; 95% confidence limits: 0, 3; 90% confidence limits: 0, 1.80), indicating strong influence of outliers on this result.

I could not calculate the sample effect size for the western toad using trap catch, but the sample effect size was 194.38 using transect count, suggesting a strong positive association between trout and western toad larvae. However, I could not determine the precision of this estimate because the presence of many counts of zero in the data prevented me from calculating bootstrap confidence intervals. Removing the pair containing the largest outlier from the trout lake transect count gave an effect size of 31.96, which shows that the largest transect count strongly influenced the sample estimate of effect size for the western toad.

2.3.3 Size and stage data

Long-toed salamander larvae tended to be smaller in lakes with trout than in troutless lakes sampled on the same or similar dates (Fig. 2.3). There was strong evidence against the null hypothesis of no difference in size between lake types when salamander size was compared between lake pairs ($F_{1,9}=59.60$, $p<0.001$). Analysis with outliers removed from the salamander size data did not change the statistical significance of this result. In contrast, Columbia spotted frog larvae usually were similar in size or developmental stage between lakes with and without trout sampled on the same or similar

dates (Fig. 2.3). There was not enough evidence to reject the null hypothesis of no difference in size between lake pairs ($F_{1,3}=0.17$, $p=0.7049$), and analysis with outliers removed from the spotted frog size data did not change this result. There was borderline evidence of a true difference between lake pairs in developmental stage ($F_{1,3}=5.48$, $p=0.1012$), although this difference was no longer significant ($F_{1,3}=1.62$, $p=0.2930$) when individual outlier data points were removed from the spotted frog stage data, and spotted frog stage was not consistently higher or lower in one lake type over the other (Fig. 2.3). One difference between lake types apparent in Fig. 2.3 is that spotted frog larvae were absent from lakes with trout at the end of the sampling period. The largest mean Gosner stage observed among the trout lakes was 40 (SE=0.31, sampled July 20-21, 2004). In contrast, the largest mean Gosner stage observed among the troutless lakes was 45 (SE= 0, sampled August 4-5, 2004). This difference may indicate low populations of spotted frogs specific to the trout study lakes sampled late in the season, but could also mean that later developmental stages were particularly susceptible to predation or other negative interactions with trout.

2.4 Discussion

The results of this study suggest that trout are negatively associated with the abundance of three species and larval growth of one species of amphibian in the Southern Interior region of British Columbia. Evidence from bootstrapping suggests with at least 90% confidence that trout are negatively associated with the larval abundance of long-toed salamanders, Columbia spotted frogs, and Pacific treefrogs. The implied effect of trout may be large given that sample estimates of effect size suggest that larval abundance may be reduced by more than 65% in the presence of trout for all three of

these species. The results of hypothesis testing show that the abundance of long-toed salamander larvae was significantly reduced in lakes with trout, although the evidence was stronger using trapping data than when using visual transect data. In addition, the size of salamander larvae was significantly reduced in the presence of trout. Reduced growth of long-toed salamander larvae in the presence of trout has previously been demonstrated in an artificial pond experiment (Tyler et al. 1998b), but this is the first study to demonstrate such a relationship in a field setting. Although size and stage of Columbia spotted frogs were not significantly different between pairs of lakes with and without trout sampled at the same time, later developmental stages of spotted frogs were not observed in lakes with trout.

However, although trends in the abundance index data suggest negative associations between the two frog species and trout, observed reductions in abundance were rarely statistically significant using hypothesis tests. In addition, the results of analyses for the two frog species were sensitive to outliers in several instances. The size and developmental stage of spotted frog larvae was not significantly different between lake types sampled on the same or similar dates, although later stages of spotted frog larvae were observed in troutless lakes but absent from lakes with trout.

In contrast to the results for the other three species, results for the western toad indicate that the abundance and probability of presence of toad larvae was significantly higher in lakes with trout. Western toad larvae are unpalatable to trout (Wassersug 1973; Kiesecker et al. 1996) and their larvae are often observed swimming in large conspicuous schools that do not appear to provoke a response from nearby trout (Welsh et al. 2006). However, toad larvae (including those of the western toad) are often palatable to

invertebrate predators (Kruse & Stone 1984; Peterson & Blaustein 1992; Kiesecker et al. 1996) and may even be more susceptible to predation by aquatic insects than other species because of their tendency to remain active even in the presence of predators (Peterson & Blaustein 1992). Therefore, trout may positively influence toads by reducing the abundance of aquatic insects that are predators of toads (Welsh et al. 2006). A similar association exists between bullfrog (*Rana catesbeiana*) larvae and introduced fish, where presence of fish increases bullfrog survival by reducing densities of predatory macroinvertebrates (Smith et al. 1999; Adams et al. 2003).

Long-toed salamander and to a lesser extent Columbia spotted frog larvae were relatively common in both lake types, and the probability of presence of salamander, spotted frog and Pacific treefrog larvae were not significantly lower in the presence of trout. These results suggest that these three amphibians may be able to coexist with trout to some extent in small productive lakes in the Southern Interior of British Columbia. There are several reasons why amphibians may be better able to coexist with trout in this region than in others. Most studies in North America have focused on oligotrophic alpine lakes that were fishless prior to trout introductions and that have little habitat complexity (but see Knapp 2005; Knapp et al. 2005; Welsh et al. 2006). Amphibians may be especially sensitive to introduced trout in such habitats because (1) lower habitat complexity provides less cover from predators, (2) larvae often need to overwinter at higher elevations, which restricts breeding to permanent habitats that are more likely to be occupied by trout, and (3) amphibians evolved without pressure to develop defenses to fish predators (Knapp 2005; Knapp et al. 2005; Welsh et al. 2006). In contrast, lakes in British Columbia's Southern Interior are generally productive with relatively high habitat

complexity and are found at lower elevations (~600-1500 m in this study) than in other studies. At this range of elevations in the Southern Interior it appears that amphibians generally do not overwinter as larvae (even in the highest elevation study lakes sampled in early August, larvae of all species showed signs of metamorphosis). However, it is possible that adults of these species require deep permanent lakes for overwintering, which would increase their susceptibility to negative interactions with trout (Pilliod & Peterson 2000, 2001).

Rainbow trout occur naturally in the Southern Interior of British Columbia, and thus the natural distributions of trout and amphibians may overlap to some extent. This overlap may improve probability of coexistence between trout and amphibians because anti-predator defenses are more likely in amphibians that encounter predators more frequently or whose distributions naturally overlap with predators (Kats et al. 1988; Kats & Ferrer 2003). One obvious form of anti-predator behaviour is avoidance, which may be more feasible in the Southern Interior than in other regions because of relatively high availability of troutless habitat. The Southern Interior of British Columbia appears to have a lower proportion of habitat occupied by introduced trout compared to high elevation areas of the western United States where much of the amphibian-trout literature has originated. Of an estimated 16,000 high mountain lakes in the western United States, approximately 95% were fishless prior to stocking, but 60% of the total number and 95% of deeper (>3 m) and larger (>2 ha) lakes now contain trout (Bahls 1992). Reflecting these high overall levels of stocking, some areas included in previous studies have had 90% or more of the regional total surface area of water bodies occupied by trout (Knapp & Matthews 2000b; Pilliod & Peterson 2001).

In contrast, there are over 12,000 mapped lakes in the Thompson-Nicola region of the Southern Interior (an area approximately 5.77 million hectares in size), and the majority of these lakes are small: 99.4% and 98.5% are less than 100 ha and 40 ha respectively in surface area. Of these 12,000 lakes, only just over 1,000 (approximately 8%) are known to contain freshwater game fish (as defined in MoE 2006d), which in most cases includes rainbow trout (S. Webb, unpublished data). Of the 1,000 game fish-bearing lakes, approximately 450 have a record of hatchery releases and 228 were actively stocked with fish (mostly rainbow trout) between 2002 and 2005 (S. Webb, unpublished data). These data suggest that the amount of troutless habitat available to amphibians in the Southern Interior is high relative to other regions, which may help amphibians to coexist with trout. Amphibians without anti-predator defenses often breed more successfully in ephemeral habitats because of lack of predators (Woodward 1983; Kats et al. 1988; Semlitsch 2002) and may preferentially breed in ephemeral habitats as an anti-predator behaviour (Hopey & Petranka 1994; Binckley & Resetarits 2003). For example, at elevations low enough that larvae develop quickly and do not need to overwinter, long-toed salamanders can be positively associated with small, shallow, ephemeral water bodies with fewer predators such as trout (Pearl et al. 2005; Welsh et al. 2006). Similarly, Pacific treefrogs can breed in a variety of aquatic sites and overwinter on land, which reduces their dependence on permanent water bodies (Bradford 1989; Rorabaugh & Lannoo 2005). In at least some regions, Pacific treefrogs show improved survival in and are positively associated with shallow ephemeral aquatic sites (Adams 2000; Matthews et al. 2001), and the ability of Pacific treefrogs to avoid predators by breeding in ephemeral habitats may explain why this species remains widespread and

common within its range (Kats & Ferrer 2003). A preference for breeding in ephemeral habitats may also explain why treefrog abundance and probability of presence were low in both lake types during this study.

However, it is important to note that in addition to the 1,000 game fish-bearing lakes, an unknown number of other lakes in the region contain non-game fish (S. Webb, personal communication). Small, native, predatory fish can reduce the abundance of some amphibians (Eaton et al. 2005), so non-game fish in some troutless lakes may reduce the availability of suitable amphibian habitat. In addition, game fish-bearing lakes tend to be concentrated in certain areas of the Southern Interior; for example, stocking is more common in the southern half of the region where angler effort is highest and lakes are closer to major population centres and transportation routes (S. Webb, unpublished data). This uneven distribution of trout could have the benefit of localizing the impacts of trout on amphibians, but where trout are concentrated amphibians are more likely to experience negative effects from trout stocking. Another important consideration is the type of lakes that contain trout. Lakes that support fish are often different from lakes that do not (Dunham et al. 2004) and may be important to amphibians as well as fish (for example, some amphibian species require deep, permanent lakes of the type occupied by trout as overwintering habitat (e.g. Knapp & Matthews 2000b; Pilliod & Peterson 2001)). If the game-fish bearing lakes in the Southern Interior have unique habitat attributes important for supporting amphibians, then the risk of negative interactions between amphibians and trout is increased.

The relatively high productivity of lakes in the Southern Interior may also mediate the effects of trout. For example, long-toed salamanders are more abundant in lakes with

higher productivity, likely because of a higher abundance of food (Tyler et al. 1998a). If productive lakes provide better habitat, amphibian populations may reach higher abundances or otherwise be more resilient to introduced trout. Lakes in the Southern Interior also have relatively high habitat complexity with abundant aquatic vegetation and coarse woody debris. Complex habitat structure may facilitate coexistence between amphibians and trout because it provides refugia from fish predators (Hecnar & M'Closkey 1997). Columbia spotted frogs can apparently breed successfully in water bodies with fish if there is dense emergent vegetation in the littoral zone (Reaser & Pilliod 2005), and refuge use may similarly allow long-toed salamanders or Pacific treefrogs to coexist with trout.

However, although refuge use may decrease the chances of predation by trout, refuge use can also interfere with the ability of amphibians to feed. Long-toed salamanders and other closely related species tend to increase refuge use and change or reduce activity in the presence of trout and other predators (Taylor 1983; Semlitsch 1987; Sih et al. 1988; Figiel & Semlitsch 1990; Tyler et al. 1998a, 1998b; Hoffman et al. 2004; Pilliod & Fronzuto 2005). Long-toed salamander larvae feed on aquatic invertebrates such as zooplankton and insects (Tyler et al. 1998a; Pilliod & Fronzuto 2005), and refuge use may interfere with the ability of salamander larvae to hunt for invertebrate prey, which could slow growth and reduce survival (Semlitsch 1987; Figiel & Semlitsch 1990; Tyler et al. 1998a, 1998b). The significant reductions I observed in both salamander size and abundance in the presence of trout support this hypothesis. Slower growth in the larval stage could decrease survival by decreasing body size at metamorphosis, which could decrease physiological performance, reproduction and survival in the terrestrial

environment. In addition, increased length of the larval period may increase susceptibility to other mortality factors in the aquatic environment (e.g. predation, lake desiccation, or lake freeze) (Tyler et al. 1998b; Nyström et al. 2001; Semlitsch 2002). Thus refuge use does not necessarily protect amphibians from sublethal effects of trout or ensure long-term survival (Tyler et al. 1998a, 1998b; Nyström et al. 2001).

The evidence of a negative association between trout and the long-toed salamander was stronger than for the treefrog and spotted-frog, in terms of consistency of significant results and sensitivity to outliers, and the fact that the salamander was the only species to show significantly reduced size in the presence of trout. These results suggest that long-toed salamanders are particularly sensitive to interactions with trout, which may be linked to differences in feeding habits between anurans (frogs and toads) and salamanders (Welsh et al. 2006). Larvae of the spotted frog, treefrog and toad feed on algae and detritus (Muths & Nanjappa 2005; Reaser & Pilliod 2005; Rorabaugh & Lannoo 2005) rather than invertebrates. Because salamander larvae must hunt for their food, which may require activity in deeper, more exposed habitats where invertebrate prey are often more abundant (Figiel & Semlitsch 1990), salamanders may expose themselves to greater predation risk (Sih et al. 1988). Salamanders may also compete with trout for food because trout and salamanders likely eat similar invertebrates (Figiel & Semlitsch 1990). Long-toed salamanders may also be particularly vulnerable to trout introductions because they have relatively small home ranges and dispersal distances and tend to return to the same locations to breed (Pilliod & Peterson 2001). Thus, salamanders may be less likely than other species to avoid interactions with trout by changing breeding sites following trout introductions. Finally, long-toed salamanders in

Oregon tend to lay their eggs in deeper water further from shore than Pacific treefrogs, Columbia spotted frogs and western toads (Bull & Marx 2002), and such behaviour could expose salamanders of all life stages to increased levels of trout predation.

Even though some degree of coexistence between trout and amphibians may be possible in lakes of the Southern Interior of British Columbia, my results also suggest that amphibian abundance may be substantially reduced where amphibians and trout do coexist. The sample estimates of effect size suggest that the presence of trout may reduce larval abundance by 65% or more for the long-toed salamander, Columbia spotted frog and Pacific treefrog. This represents at least a 65% reduction in recruitment to the adult population for these species when trout are present. Success at the population level for amphibians is determined primarily by the number and quality of metamorphosing larvae that recruit to the adult stage, and recruitment failures over multiple years can lead to decline and eventual extinction of local populations (Semlitsch 2002). In addition, reductions in recruitment are likely important both to populations in individual lakes as well as those in other water bodies nearby. Amphibian populations are often spatially structured by processes of migration, gene flow, extinction, and colonization, and such metapopulation dynamics should be considered when planning amphibian conservation (Sjögren 1991; Bradford et al. 1993; Alford & Richards 1999; Semlitsch 2002). For example, a 65% reduction in larval recruitment represents a 65% reduction in individuals available as immigrants to other water bodies. Thus, the proportion of lakes and amphibian populations affected by trout may be higher than the proportion of lakes that contain trout.

Population reductions would be particularly important where a population reduced by introduced trout served as a 'source' for recolonization of less suitable 'sink' habitats, where the local population is maintained mainly through immigration (Braña et al. 1996; Knapp & Matthews 2000b; Pilliod & Peterson 2001). Introducing trout could change a lake from a source to a sink, which could lead to extinction of local populations, population fragmentation, decreased connectivity among habitats, and declines of amphibians on a landscape scale, even in troutless habitats (Bradford et al. 1993; Tyler et al. 1998a; Knapp & Matthews 2000b; Pilliod & Peterson 2001; Knapp et al. 2003). In fact, the conversion of lakes from source into sink habitats by introduced trout is considered an important factor in landscape-scale declines of long-toed salamanders and Columbia spotted frogs in Idaho (Pilliod & Peterson 2001). If dispersal of amphibians is density dependent (i.e. the probability of emigration increases with increased density of the local population), even a moderate decrease in amphibian recruitment in lakes with trout could lead to a disproportionately large decrease in immigration from lakes with trout to other habitats.

The existence of metapopulation dynamics in amphibians also means that evidence of amphibian breeding does not guarantee a successful breeding population (Pilliod & Peterson 2000, 2001). Breeding by immigrants from other local populations can augment the number of larvae observed in a particular lake, cause time lags in observed responses of amphibians to trout, and mask the effects of trout on amphibians (Sjögren 1991; Knapp & Matthews 2000b; Pilliod & Peterson 2001; Vredenburg 2004). Such effects may have been more apparent if I had considered recruitment of larvae into the adult population and/or had estimated survival of amphibians over time.

Ecological impact studies often have low statistical power, but the consequences of not detecting an effect when it actually exists can be high when results are used to make management decisions (Peterman 1990). Thus, power should always be considered and reported when interpreting the results of ecological research. My *a priori* power analysis suggested that the trap sampling design did not have enough power to detect a 50% or lower decrease in abundance in the presence of trout for the Columbia spotted frog and the western toad. Although I did not conduct power analysis for the transect sampling design, the lower number of lakes in the transect data (n=15 per lake type versus n=19 for trap sampling) probably led to lower statistical power than for the trapping data. In addition, the scale of this study, in terms of number of lakes sampled and temporal scale, was fairly small, especially compared to some previous studies that have included the same amphibian species (e.g. Pilliod & Peterson 2001; Welsh et al. 2006). My results were sometimes sensitive to the removal of outliers, especially for the Columbia spotted frog and the Pacific treefrog, which also suggests that including more lakes in the study would have improved power considerably. Because the power of my study was relatively low, the fact that hypothesis testing did not detect consistently significant associations between trout and amphibians, especially for the two frog species, does not necessarily mean trout do not have an important effect on these species. These species have all been negatively associated with trout in other studies (Bradford 1989; Tyler et al. 1998a; Funk & Dunlap 1999; Adams et al. 2001b; Matthews et al. 2001; Pilliod & Peterson 2001; Bull & Marx 2002; Knapp 2005; Welsh et al. 2006), and the results of bootstrapping analyses did provide significant evidence for negative associations between trout and two frog species.

Evidence for significant associations tended to be weaker using the transect data than when using the trapping data, probably at least in part because of decreased statistical power due to the smaller number of lakes included in the transect data set. In addition, transect sampling may have been less effective than trapping (and less effective than visual sampling in previous studies) because the littoral and shoreline areas of many lakes had high habitat complexity which is known to reduce effectiveness of visual surveys (Pilliod & Peterson 2000). Aquatic and shoreline vegetation was sometimes dense and the complexity and colour of the lake bottom may have decreased detection of amphibians. Thus my results from trapping should be considered more reliable than those from transects. However, the fact that trapping and transect data exhibited similar trends for all species, even if these trends were not always statistically significant, adds weight to the overall evidence for associations between trout and each amphibian species.

Field studies of amphibian populations are often complicated by large natural fluctuations in numbers, which may even occur within one year at a particular site (Pechmann et al. 1991; Blaustein et al. 1994b; Alford & Richards 1999; Pilliod & Peterson 2000; Semlitsch 2002). Ideally, studies of amphibian populations should include multiple site visits within and between years to increase the reliability of data, account for seasonal movements, and estimate overwinter survival and recruitment of larvae into the adult population (Pilliod & Peterson 2000). For example, during a study of mountain lakes in Montana, Columbia spotted frog larvae were relatively common in lakes with trout, but surveys of yearlings and adults the following spring revealed poor overwinter survival related to trout presence, because spotted frogs in the region require deep lakes for overwintering and these lakes are often occupied by trout (Pilliod &

Peterson 2000, 2001). I do not know if adult spotted frogs in the Southern Interior of British Columbia similarly require deep permanent waters for overwintering, and it is possible that I missed effects such as those observed in Montana by sampling only one life stage and each lake only once. For example, if I had sampled all study lakes several times during the 2004 sampling season, I may have been able to determine whether the absence of spotted frogs from the last five trout lakes sampled was due to low populations of spotted frogs in these lakes or because later developmental stages were particularly susceptible to negative interactions with trout. The Gosner developmental stages that were absent from lakes with trout are the stages during which frogs are developing front legs and their tails are shrinking (Gosner 1960). These changes could lead to lower mobility than at earlier developmental stages, and thus could increase the susceptibility of spotted frog larvae to predation.

However, random variation in population size should have had limited influence on my results. Although amphibian population size within one lake may be highly variable from year to year and population dynamics of lakes close to one another may be positively correlated (Ranta et al. 1997; Koenig 1999; Knapp et al. 2003), natural variation in population size is probably random and not correlated among lakes within each lake type. By sampling many lakes across the Southern Interior region, the effect of year and random variation in population size should average out. In addition, the paired sampling of lake types in time and general location increased the chances that variation caused by season, location, and weather was similar between the lake types.

Abundance of some amphibians can be reduced by small, native predatory fish (Eaton et al. 2005), and fish species other than rainbow trout were present in a small

number of lakes of each type (3-4 with trout, 2 troutless). However, fish other than rainbow trout were probably not an important confounding factor given the small number of lakes with this issue. It is interesting that the three trout lakes with confirmed presence of fish species other than rainbow trout had no larvae of any species detected. However, Columbia spotted frog larvae were observed in one and long-toed salamander larvae in both troutless lakes that contained the redbreasted sunfish (*Richardsonius balteatus*), a small native predatory fish.

The results of my study cannot necessarily be generally applied to other regions of British Columbia. For example, the amphibian species present in other regions may differ in their susceptibility to trout. Also, the biogeoclimatic ecosystem classification zones, subzones and variants represented by my study lakes do not represent all the zones in British Columbia, or even all the zones in the Southern Interior (for example, the grassland and shrub-steppe dominated Bunchgrass (BG) zone, which is found within the Southern Interior, was not represented among my study lakes). Zones, subzones and variants differ in climate, vegetation, topography and soils, and these differences could cause the responses of amphibians to trout to differ among ecosystem types, as represented by the BEC categories. For example, lakes in some BEC categories not included in this study may be less productive and/or have less habitat complexity than my study lakes, which would decrease the refugia available for avoiding trout predation and thus increase the risk of negative interactions with trout. Investigating how the responses of amphibians to trout may differ among BEC categories may be an area for further research in British Columbia. However, given the consistency in the literature of observed negative associations between trout and many amphibians across many regions

and studies, a precautionary approach would be to assume negative effects of trout on amphibians until it can be shown otherwise.

2.4.1 Conclusions

This study shows that trout are associated with reduced abundance of several species of amphibians in British Columbia, and provides new field evidence for sublethal effects of trout on amphibian growth. However, evidence from this study and the literature also suggests that amphibians may be better able to coexist with trout in (1) lakes with higher habitat complexity, (2) regions with higher natural overlap between the distributions of trout and amphibians, and (3) regions with lower levels of aquatic habitat occupied by trout. Because these conditions appear to exist in the Southern Interior of British Columbia, there may be increased flexibility (relative to other regions of western North America) to make trade-offs between protecting amphibians and managing recreational fishing using trout stocking. However, where trout and amphibians coexist, trout may cause large reductions in larval abundance, which could also cause population reductions in adjacent troutless habitats through reduced immigration. Such reductions in exchange of individuals between local populations could have longer-term implications for metapopulation dynamics. My results combined with the weight of evidence in the literature provide a strong case for incorporating measures to protect amphibians into trout stocking policy in British Columbia. Assuming that conservation of amphibians is a management goal, decisions about stocking should include consideration of the regional status of amphibian populations and provisions to preserve a range of troutless aquatic habitats across the landscape to reduce impacts on amphibian metapopulation dynamics. On-going monitoring of the relationships between amphibians and trout in productive,

lower-elevation lakes such as those in the Southern Interior would also be useful to determine whether or not trout and amphibians are better able to coexist over the long term in these types of lakes.

2.5 Tables and figures

Table 2.1. Physical and biological characteristics of the study lakes.

Lake type	Elevation ^a (m)		Lake surface area ^b (ha)			Width of littoral area ^c (m)			Rainbow trout populations ^d					
	Number sampled	Mean (SD)	Max	Min	Mean (SD)	Max	Min.	Mean (SD)	Max.	Min.	Number of lakes with fish species other than rainbow trout	Number natural	Number stocked	Mean annual stocking density (no. trout per ha) (SD) ^e
Troutless	19	1,194 (236)	1,533	634	10.6 (8.0)	36.0	2.3	15.1 (7.1)	30	7.6	2 ^f			
Trout	19	1,208 (186)	1,498	826	14.4 (9.5)	34.0	4.2	13.0 (5.7)	25.2	4.9	3 or 4 ^g	8	11	288 (254)

^a Elevation came from either provincial government databases or from a GPS used in the field.

^b Lake surface area came from provincial government databases.

^c Width of littoral area came from field measurements at seven sites per lake, where width of the littoral area was the distance from the shore to a depth of 1 m.

^d Natural populations were rainbow trout populations with no stocking records, or in one case, a population that has not been stocked for at least 15 years. All of the stocked populations were stocked at least twice in the five years prior to the study.

^e The mean was calculated using stocking data from the five years prior to the study. The average number of trout stocked per year was divided by the surface area of the lake to give mean annual stocking density. Stocking data came from provincial government records in most cases (MSRM 2006b), except for two lakes where stocking was part of a university research project, and data came from the researcher (P. Askey, unpublished data).

^f During minnow trapping redside shiners (*Richardsonius balteatus*) were caught in two troutless lakes.

^g During minnow trapping redside shiners were caught in one trout lake, peamouth chub (*Mylocheilus caurinus*) in a second trout lake, and unidentified minnows (probably lake whitefish (*Coregonus clupeaformis*) or northern pikeminnow (*Ptychocheilus oregonensis*) based on previous records [MSRM 2006b]) in a third trout lake. There is a record from 1994 (MSRM 2006b) of northern pikeminnow in a fourth trout lake.

Table 2.2. Biogeoclimatic ecosystem classification^a of study lakes.

Zone	Biogeoclimatic Ecosystem Classification		Number of lakes sampled per lake type	
	Subzone	Variant ^b	Troutless	Trout
ESSF (Engelmann Spruce-Subalpine Fir)	dc (Dry Cold)	2 (South Thompson)	4	3
IDF (Interior Douglas-fir)	dk (Dry Cool)	1 (Thompson)	1	1
		2 (Cascade)	0	1
		3 (Fraser)	6	3
	mw (Moist Warm)	2 (Thompson)	1	0
MS (Montane Spruce)	dm (Dry Mild)	2 (South Thompson)	1	1
SBPS (Sub-Boreal Pine --Spruce)	mk (Moist Cool)		4	7
SBS (Sub-Boreal Spruce)	mm (Moist Mild)		2	3

^a Meidinger & Pojar 1991; MFR 2006.

^b There is no separation into variants within SBPSmk and SBSmm.

Table 2.3. Results of presence-absence analysis showing the proportion of lakes in which each species was present.

Species	Larvae only			Larvae and/or adults		
	Troutless (n=19)	Trout (n=19)	<i>p</i> -value*	Troutless (n=19)	Trout (n=19)	<i>p</i> -value*
Trap and transect counts						
Long-toed salamander	0.84	0.63	0.27	0.84	0.63	0.27
Columbia spotted frog	0.58	0.47	0.75	0.74	0.74	1.00
Pacific treefrog	0.37	0.26	0.73	0.42	0.42	1.00
Western toad	0.05	0.42	0.02	0.26	0.53	0.18
Trap, transect, and incidental sightings combined						
Long-toed salamander	0.84	0.68	0.45	0.84	0.68	0.45
Columbia spotted frog	0.58	0.47	0.75	0.74	0.79	1.00
Pacific treefrog	0.47	0.32	0.51	0.47	0.42	1.00
Western toad	0.16	0.47	0.08	0.42	0.63	0.33

* The *p*-value indicates the consistency of the data with the null hypothesis of no difference in proportions between lakes with and without trout, and was calculated using Fisher's exact test.

Table 2.4. Summary statistics for relative abundance indices.

Species	Sample mean # of larvae (SE)		Difference between means				Effect size	
	Troutless	Trout	$\bar{x}_{notrout} - \bar{x}_{trout}$ (SE)	95% CI ^a	90% CI ^a	$\bar{x}_{trout} / \bar{x}_{notrout}$ (SE ^b)	95% CI ^a	90% CI ^a
Trap catch (n=19 both lake types)								
Long-toed salamander	36.89 (11.53)	9.95 (5.57)	26.95 (12.80)	5.84 56.16	9.16 50.74	0.27 (0.20)	0.07 1.11	0.09 0.88
Columbia spotted frog	12.74 (5.04)	4.32 (2.01)	8.42 (5.43)	0.42 22.58	1.47 19.84	0.34 (0.28)	0.06 1.13	0.10 0.92
Pacific treefrog	7.32 (5.58)	0.21 (0.10)	7.11 (5.58)	0.89 29.95	1.21 24.32	0.03 (0.12)	0 0.21	0 0.17
Western toad	0 (0)	329.11 (314.01)	-329.11 (314.01)	-1595.89 -6.47	-1293.47 -13.16	NA ^c	NA ^c	NA ^c
Transect count (n=15 both lake types)								
Long-toed salamander	6.93 (3.69)	0.93 (0.30)	6.00 (3.70)	1.13 17.53	1.67 15.07	0.13 (0.36)	0.03 0.48	0.04 0.38
Columbia spotted frog	2.40 (1.28)	0.47 (0.27)	1.93 (1.30)	0.07 5.67	0.33 4.80	0.19 (0.61)	0.02 1.25	0.04 0.86
Pacific treefrog	7.93 (7.36)	0.27 (0.21)	7.67 (7.37)	0.13 37.2	0.20 29.87	0.03 (0.39)	0 0.78	0 0.63
Western toad	0.13 (0.13)	25.27 (20.98)	-25.13 (20.98)	-126.20 -1.93	-94.27 -3.80	194.38 (NA ^c)	NA ^c	NA ^c

^a CI=confidence interval; calculated using the bootstrap BC_a method (bias-corrected and accelerated) (Efron & Tibshirani 1998) and 10,000 bootstrap replicates.

^b The standard error of the sample estimate of effect size was a bootstrap estimate (Efron & Tibshirani 1998) from 10,000 replicate bootstrap samples.

^c I could not calculate effect size for the western toad because the sample mean total catch in troutless lakes was zero and thus effect size was undefined.

Table 2.5. Summary of statistical analyses comparing larval abundance in lakes with and without trout for each type of data.

Species	Data	Two-sample <i>t</i> test ^a				Permutation test		
		Untransformed data		Log-transformed ^b data		Assigned significance level (ASL)	<i>p</i> -value	
<i>t</i>	df	<i>p</i> -value	<i>t</i>	df	<i>p</i> -value			
Long-toed salamander	Trapping	2.105	36	0.042	2.493	36	0.017	0.035
	Transects	1.621	28	0.116	1.437	28	0.162	0.094
Columbia spotted frog	Trapping	1.551	36	0.130	1.794	36	0.081	0.143
	Transects	1.482	28	0.150	1.321	28	0.197	0.210
Pacific treefrog	Trapping	1.273	36	0.211	1.525	36	0.136	0.103
	Transects	1.041	28	0.307	1.551	28	0.132	0.225
Western toad	Trapping	-1.048	36	0.302	-2.497	36	0.017	0.008
	Transects	-1.198	28	0.241	-1.769	28	0.088	0.100

^a The null hypothesis for the two-sample *t* test was no difference in true mean catch/count between lakes with and without trout.

^b The log-transformation used was $X' = \log(X + 1)$.

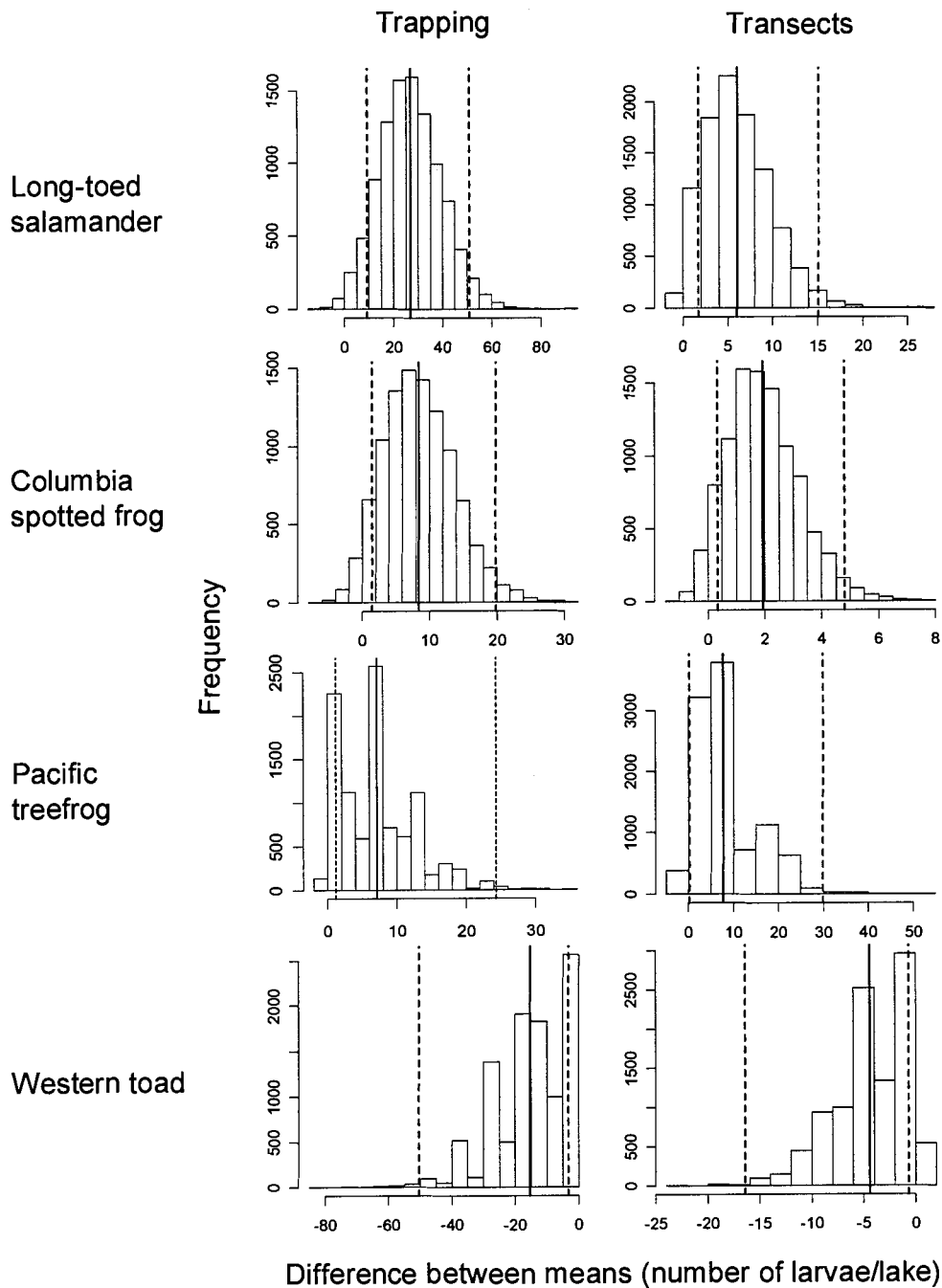


Figure 2.1. Bootstrap distributions of difference in mean trap catch and transect count between lakes with and without trout ($\bar{x}_{diff} = \bar{x}_{notrout} - \bar{x}_{trout}$). Solid vertical lines indicate observed mean difference and dashed vertical lines show 90% bootstrap BC_a confidence limits. The distributions represent estimates from 10,000 bootstrap samples. For clarity of presentation, the bootstrap distributions and sample estimates for the western toad (trap and transect data) were created using data sets with the pair containing the largest outlier removed. For the sample estimate and confidence limits with the outliers included see Table 2.4.

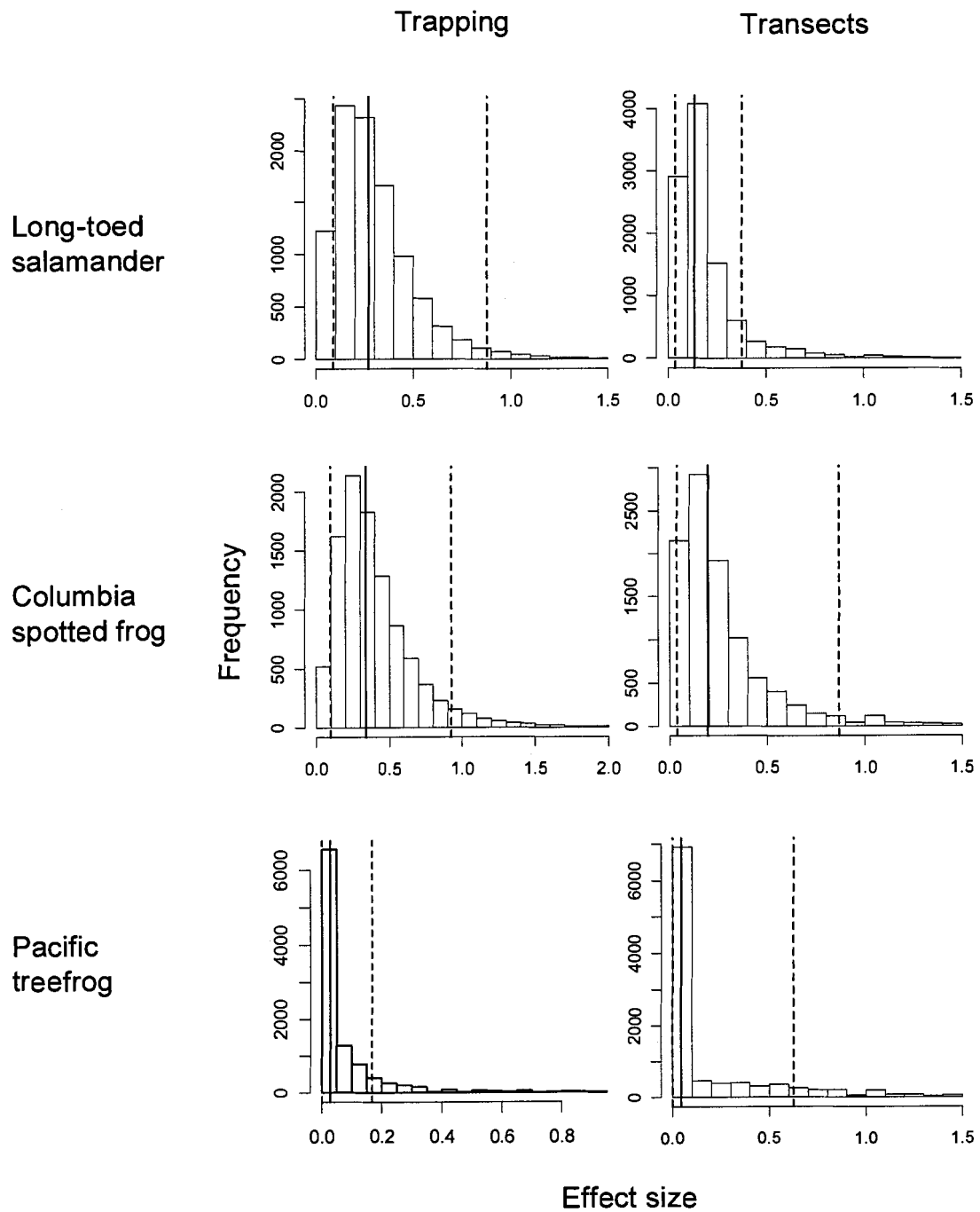


Figure 2.2. Bootstrap distributions of effect size, where effect size is the sample mean catch/count in trout lakes divided by the sample mean catch/count in troutless lakes ($\bar{x}_{trout} / \bar{x}_{noirout}$). Solid vertical lines indicate observed mean effect size and dashed vertical lines show 90% bootstrap BC_a confidence limits. The distributions represent estimates from 10,000 bootstrap samples.

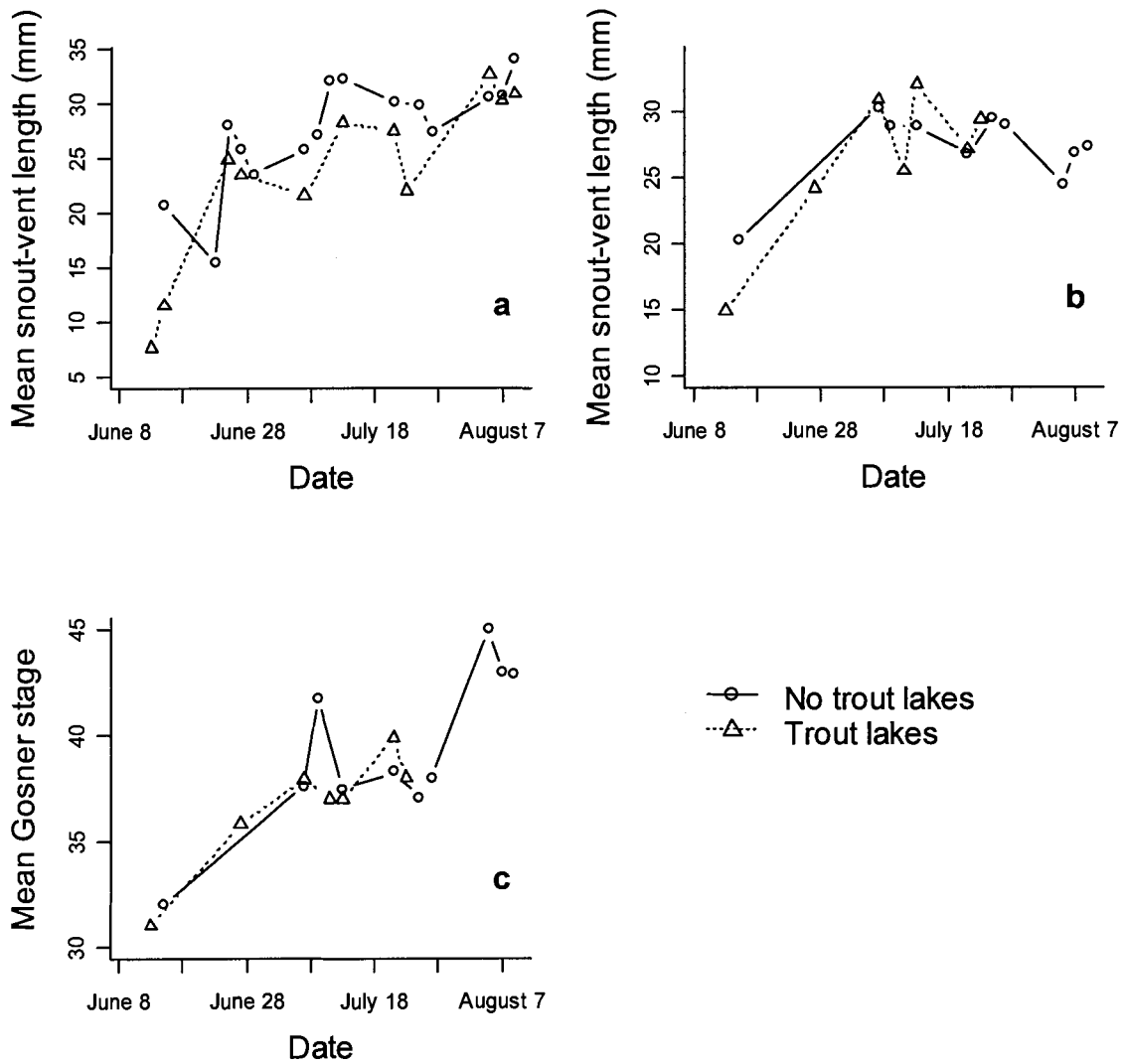


Figure 2.3. Size (mean snout-vent length [mm] per lake) of (a) long-toed salamander larvae and (b) Columbia spotted frog larvae, and (c) developmental stage (mean Gosner stage per lake) of Columbia spotted frog larvae, versus sampling date in lakes with and without trout. Lakes of each type sampled on the same date were lake pairs.

CHAPTER 3: MANAGEMENT IMPLICATIONS AND RECOMMENDATIONS

Management decisions about trout stocking are based on information, perceptions, and judgments about the costs and benefits of stocking. Decisions-makers must consider various political, economic, social and ecological issues. Continuing or increasing stocking may benefit the recreational fishing industry and anglers. Stocking is also an established tool for managing recreational fisheries in British Columbia. On the other hand, evidence suggests there are potential ecological costs associated with trout stocking. In addition, there are increasing political and social pressures to conserve biodiversity. Thus, there is a case for considering ecological values such as those related to amphibians when making decisions about when, where, and how to stock lakes with trout. Assuming that the management objective is to find an acceptable balance between the socio-economic benefits of stocking and the ecological and economic costs, the challenge for managers is to decrease threats to native species such as amphibians without unreasonably limiting opportunities for recreational fishing.

This chapter contains recommendations for reducing impacts of trout stocking on amphibians and incorporating amphibian values into management decisions with special reference to the amphibians of the Southern Interior and British Columbia. For further reference, Pilliod & Peterson (2000) provide excellent recommendations for helping managers design and conduct studies of how trout stocking affects amphibian populations

within a landscape. Dunham et al. (2004) also provide a perspective on managing trout stocking to decrease impacts on native species generally.

3.1 Factors to consider when planning stocking

3.1.1 Consider the amphibian species potentially affected

One of the first steps in evaluating the risk of negative interactions between trout stocking and amphibians in a given lake, watershed or region is to determine which amphibian species occur there, and whether or not they may interact with trout during any life stage (Pilliod & Peterson 2000). All aquatic-breeding amphibians can potentially interact with trout, but species that breed terrestrially and do not use lakes during any life stage are unlikely to be directly affected. The life history of species can also determine the probability of interaction with trout and degree of susceptibility. In general, amphibians that breed primarily in ephemeral water bodies and overwinter on land are less likely to interact with trout than those that breed and/or overwinter in permanent water bodies (Pilliod & Peterson 2000). The susceptibility of each species to introduced trout can be checked using scientific literature (especially any direct studies of associations with trout) and life history accounts. See Section 1.4 for information on attributes that influence susceptibility. General reviews of life history for species occurring in British Columbia are included in Green & Campbell (1984), Leonard et al. (1993), Corkran & Thoms (1996), Russell & Bauer (2000), and Lannoo (2005).

The status and distribution of each species, locally and more broadly, also need to be considered. Amphibians considered imperilled in some way, especially those that have been formally listed as Species at Risk, are generally higher priorities for conservation action. For species not considered imperilled and with large distributions,

stocking within one small area should pose less of a risk than for species that are imperilled and/or have small distributions. Current conservation status in British Columbia and Canada can be checked with the B.C. Conservation Data Centre (<http://www.env.gov.bc.ca/cdc/>; MoE 2006b), COSEWIC (<http://www.cosewic.gc.ca/>) and SARA (http://www.speciesatrisk.gc.ca/search/default_e.cfm), and internationally with the IUCN (<http://www.iucnredlist.org/>) and NatureServe (<http://www.natureserve.org/explorer/>). In the United States information on threatened or endangered species is maintained by the U.S. Fish and Wildlife Service (<http://www.fws.gov/endangered/>), and Lannoo (2005) provides an excellent recent review of the status of all amphibians occurring in the United States. The sources already listed for life history information also provide general information on distributions.

Another important source of information is historical records, which are particularly useful to establish if the distribution or status of a species in an area has changed over time (Kats & Ferrer 2003). Sources of historical records may include government databases, grey literature, and museum records, such as at the Royal B.C. Museum. Biologists specializing in amphibians in government, academia and the consulting industry are also useful sources of information. In particular, any herpetologists working in the region should be consulted for local and up-to-date information (Pilliod & Peterson 2000).

3.1.1.1 Considerations for the Southern Interior and British Columbia

All four of the amphibian species included in my study have broad distributions along the west coast of North America. The conservation status of the long-toed salamander, Columbia spotted frog and Pacific treefrog is considered secure throughout

most of each species' range. However, the status of the western toad is less secure in Canada and in several areas of the United States (Lannoo 2005; MoE 2006b; COSEWIC 2006), and the toad is listed on Schedule 1 of SARA as a Species of Special Concern in Canada. For more details on conservation status of these species see Section 1.4.2.

Evidence from my study and the literature suggests that the long-toed salamander may be the most susceptible of the four species to declines following trout introductions, although the Columbia spotted frog and Pacific treefrog can also be negatively affected by introduced trout. For more on the susceptibility of these species see Sections 1.4.2 and 2.4. Western toads are probably not directly susceptible to declines following trout introductions because they are unpalatable to trout (Wassersug 1973; Kiesecker et al. 1996), although stocking may indirectly influence western toads through transfer of pathogens (Kiesecker et al. 2001) which have been implicated in past mass-mortality events among western toads (Blaustein et al. 1994a).

Given the broad distributions of the four amphibians studied, stocking in a small portion of that distribution will not likely threaten these species as a whole, although local populations may be threatened. The evidence from my study suggests that amphibians may be able to coexist to some extent with trout in the Southern Interior, perhaps because of: (1) high structural complexity and (2) high productivity in lakes; (3) the ability of larvae to avoid overwintering in lakes by reaching metamorphosis in one growing season; (4) relatively high natural overlap between the distributions of amphibians and natural populations of trout; and/or (5) relatively high availability of troutless habitat (see Section 2.4). Thus, although negative associations exist between trout and some amphibians in the Southern Interior, trout stocking may not be as serious a

threat to amphibian persistence as it is in other regions. However, where trout and amphibians coexist in the Southern Interior, the abundance of amphibians may be substantially reduced, which may have long-term implications for metapopulation dynamics. In addition, local amphibian populations in watersheds where trout are widespread may be relatively highly threatened. The fact that the western toad (the one species in the region with conservation status of concern) does not appear negatively associated with trout decreases the risk of unacceptable negative impacts of trout stocking in the Southern Interior. However, the potential for introduced trout to transfer disease to western toads (and potentially other amphibians) suggests that highly cautionary measures should be taken to avoid stocking trout infected with pathogens that could be transferred to amphibians. Even fish with no obvious symptoms may act as vectors of disease (Kiesecker et al. 2001), increasing the need for caution.

The results of my study cannot necessarily be generally applied to other regions of British Columbia. For example, the amphibian species present in other regions may differ in their susceptibility to trout. Also, the biogeoclimatic ecosystem classification (BEC) zones, subzones and variants represented by my study lakes do not represent all the zones in British Columbia, or even all the zones in the Southern Interior (for example, the grassland and shrub-steppe dominated Bunchgrass (BG) zone, which is found within the Southern Interior, was not represented among my study lakes). Zones, subzones and variants differ in climate, vegetation, topography and soils, and these differences could cause the responses of amphibians to trout to differ among ecosystem types, as represented by the BEC categories. However, given the consistency in the literature of observed negative associations between trout and many amphibians across many regions

and studies, a precautionary approach would be to assume negative effects of trout on amphibians until it can be shown otherwise. Certainly the conservation status of amphibians in some regions of British Columbia will be less secure than for the species included in this study, and this should be considered in trout stocking management. For example, tiger salamanders (*Ambystoma tigrinum*) in the Okanagan are listed as endangered on Schedule 1 of the Species at Risk Act, and as aquatic breeders may experience negative interactions with trout. Because tiger salamanders are at high risk of extinction in British Columbia, to protect this species stocking should be avoided where interactions could occur between this species and trout.

The habitat available to amphibians may also differ between the ecosystem types represented by this study and those found in other regions of BC, which will also influence the susceptibility of amphibians to trout in each region. Lakes in other regions of the province may be less productive and/or have less habitat complexity than Southern Interior lakes, which would decrease the refugia available for avoiding trout predation and thus increase the risk of negative interactions with trout. Amphibians in other regions, especially at higher elevations, may overwinter in lakes as larvae or adults, which would also increase the risk of negative interactions with trout. There may be less overlap between the natural distributions of amphibians and trout in other regions, which may increase the susceptibility of amphibians to trout because they have not developed anti-predator defenses. Finally, the amount of troutless amphibian habitat available may be lower in other regions, which would increase the risk of negative effects of trout stocking on amphibian populations in these regions. This may be particularly important in the highly populated and developed regions of British Columbia, such as the

Okanagan, Lower Mainland, and east coast of Vancouver Island. In these areas amphibian habitat is not only threatened by introduced trout but also urbanization and pollution, and thus adding trout to a lake where few undeveloped lakes are available may have a disproportionate impact on amphibian populations in the region. See also Section 3.1.2.

3.1.2 Consider the distributions of amphibians, trout and lake types at the landscape scale

When deciding whether or not to stock a lake, managers need to consider more than just the impacts of trout on that particular lake. Amphibians often exist as metapopulations, which are sets of local populations connected by processes of migration, gene flow, extinction and colonization (Semlitsch 2002). Lakes stocked with trout may become population ‘sinks’ where population growth is negative in the absence of immigration from other ‘source’ populations (Knapp & Matthews 2000b). The declines in local populations and decreased population exchange that may result from trout introductions can lead to population fragmentation, decreased connectivity among habitats, extinction of local populations, and declines of amphibians on a landscape scale, even in troutless habitats (Bradford et al. 1993; Tyler et al. 1998a; Knapp & Matthews 2000b; Pilliod & Peterson 2001; Knapp et al. 2003). Preserving troutless aquatic habitats in a network across a landscape will improve connectedness among local amphibian populations and may mediate the impacts of trout on amphibians (Sjögren 1991; Bosch et al. 2006) and other flora and fauna (Drake & Naiman 2000). To maintain connectivity, troutless water bodies should be relatively close together (e.g. less than 1 km apart) because individual amphibians generally do not migrate long distances (Sjögren 1991; Blaustein et al. 1994b; Semlitsch 2002).

The diversity of lake types that are troutless within a watershed is also important for amphibian conservation. Lakes that support fish are often different from lakes that do not (Dunham et al. 2004) and may be important to aquatic fauna besides introduced trout (for example, some amphibian species require deep, permanent lakes of the type occupied by trout as overwintering habitat (e.g. Knapp & Matthews 2000b; Pilliod & Peterson 2001)). On the other hand, shallow ephemeral water bodies and wetlands often play an important role in maintaining amphibian populations across a landscape, especially for species that prefer such habitats for breeding (Semlitsch 2002), and having these water bodies available can dampen the landscape effects of trout on amphibians that do not depend on permanent lakes for part of their life cycle.

To plan management of trout stocking in a landscape context, Pilliod & Peterson (2000) recommend assessing the distribution of amphibians and introduced trout on the scale of watersheds. Ideally, each watershed would be surveyed in detail to determine the distribution of trout, identify amphibian source populations, and target critical habitats for amphibian conservation through protection from stocking (Pilliod & Peterson 2000). A detailed survey could also include assessment of variation in lake physical, chemical, and biological characteristics, and the distribution of lake types across the landscape, which managers could use to ensure that lakes left troutless are representative of the range of natural conditions occurring in the watershed. However, detailed surveys may be demanding in resources and may not be possible. Determining which sites are 'critical habitats' will be difficult beyond identifying sites that support large populations of amphibians, and even this task may be challenging given the natural variability of amphibian populations (Pechmann et al. 1991).

In the absence of detailed survey information, managers should at least consider the distribution of trout, trout stocking and different sizes and types of water bodies (e.g. lakes versus wetlands) within a watershed, which should be relatively easy using existing provincial government data and geographic information systems (GIS). The total surface area of troutless versus trout-occupied habitat should be considered along with the number of water bodies, because the surface area occupied by trout may be much higher than the number of water bodies suggests (Pilliod & Peterson 2001). Watersheds with higher proportions of habitat occupied by trout have a higher probability of negative impacts on amphibians than watersheds with various sizes of troutless habitats in a network across the landscape. Spatial analyses looking at distance between water bodies could be used to quantify connectedness among troutless habitats (e.g. Knapp et al. 2003), so that managers can determine how troutless habitats are distributed across the watershed in order to maintain connectivity among amphibian habitats.

In watersheds with low connectedness and/or high proportions of habitat occupied by trout, managers may want to avoid stocking new lakes or decrease levels of stocking. Creating (or maintaining) a few troutless lakes in a watershed may disproportionately reduce the threats of trout stocking to amphibian persistence; for example, having two amphibian source populations in a watershed instead of one may increase the probability of amphibian persistence by an order of magnitude (Pilliod & Peterson 2000). However, an alternative strategy on a larger scale might be to maintain high levels of trout presence in some watersheds while maintaining other watersheds in a trout-free condition, in which case managers might prefer to stock the watershed that already has high levels of trout presence. Which strategy is better for amphibians depends on the distribution of

amphibians regionally, the distribution of watersheds with high levels of trout presence, and the importance or uniqueness of the watershed in providing amphibian habitat. If amphibians are broadly distributed in a region (i.e. abundant in many watersheds), the watershed does not provide unique or rare types of lakes, and/or adjacent watersheds have relatively low levels of trout presence, the latter strategy may be acceptable. If amphibians have restricted distributions, the watershed is unusual in providing rare habitats or high levels of amphibian production, and/or other adjacent watersheds also have high levels of trout presence, the first strategy is probably more appropriate.

Managers should also consider land use and human development in a given region or watershed. Habitat modification, destruction and pollution are important causes of amphibian declines (Alford & Richards 1999; Blaustein & Kiesecker 2002), and these are more likely in areas with higher human populations and higher levels of human activity. Human activities may decrease the number of lakes, marshes and wetlands available to amphibians through elimination of these habitats or by reducing the quality of these habitats (e.g. through reductions in water quality, elimination of suitable terrestrial habitat nearby, etc.). In areas with high levels of human activity, introduced trout may be more likely to accelerate declines in amphibian populations already under stress from other human-caused factors. Thus, managers should keep in mind that amphibian populations in areas with high levels of human development and low amounts of suitable habitat are more likely to be negatively affected by trout presence, and the quality of available habitat should be evaluated as well as the quantity. This is particularly important in highly populated regions of British Columbia such as the Lower Mainland and the east coast of Vancouver Island (see also Section 3.1.1.)

3.1.2.1 Considerations for the Southern Interior

Although I did not conduct any detailed analyses of the distribution of lakes with and without trout within watersheds, I can comment that in the Thompson-Nicola Region generally, the proportion of water bodies that contain freshwater game fish (as defined in MoE 2006d) is relatively low. There are over 12,200 lakes, 5,800 wetlands and 1,000 marshes mapped in the Thompson-Nicola Region. Most of the lakes are small: 99.4% and 98.5% are less than 100 ha and 40 ha respectively in surface area. However, only just over 1,000 lakes (~8% of the total) in this region are known to contain freshwater game fish (including rainbow trout in most cases) (S. Webb, unpublished data). Of these lakes, more than 450 have a record of hatchery releases and 228 were actively stocked with fish (mostly rainbow trout) between 2002 and 2005 (S. Webb, unpublished data). Human population density and development is low throughout much of the Southern Interior, excluding major population centres located mainly in the south, such as Kamloops. However, cattle grazing and forestry are widespread even in relatively remote areas.

Having a relatively low proportion of lakes occupied by trout decreases the probability of negative interactions between trout and amphibians across the Southern Interior, especially relative to other areas of North America where as much as >90% of aquatic habitat may be occupied by trout (Bahls 1992; Knapp & Matthews 2000b; Pilliod & Peterson 2001). However, it is important to note that in addition to the 1,000 game fish-bearing lakes, an unknown number of other lakes in the region contain non-game fish (S. Webb, personal communication). Small, native, predatory fish can reduce the abundance of some amphibians (Eaton et al. 2005), so non-game fish in some troutless

lakes may reduce the availability of suitable amphibian habitat. In addition, if the game-fish bearing lakes in the Southern Interior also have unique habitat attributes important for supporting amphibians, then the risk of negative interactions between amphibians and trout is increased because an important amphibian habitat is being occupied by trout. Finally, the distribution of lakes with trout is potentially uneven within the Southern Interior region, which may put some amphibians populations at higher risk. For example, stocking is more common in watersheds in the southern half of the Thompson-Nicola Region (S. Webb, unpublished data), which is also where higher population densities and higher levels of human development exist. This combination of a higher degree of trout presence and higher levels of human development likely puts amphibian populations in these watersheds at higher risk of decline. If these watersheds contain unique lake types, these types will be relatively poorly represented among troutless habitats in the region.

3.1.3 Consider geography and invasibility

Decisions about when and where to stock should also take into account the ability of trout to establish naturally reproducing populations and/or to colonize areas beyond where they are initially introduced. In areas where spawning habitat is widely available, introduced trout may become widely established. For example, naturally-reproducing populations of rainbow trout in the Nehalliston watershed of the Southern Interior are thought to have been established by trout introduced in the 1940s that have since spread throughout the watershed.

The extent of area invisable from a stocked lake strongly depends on drainage basin morphology, specifically the locations of barriers to upstream dispersal and the density and distribution of lakes (Adams et al. 2001a). Barriers to downstream dispersal

are less likely to prevent the spread of introduced trout. For example, brook trout are able to disperse downstream even over steep slopes and waterfalls capable of preventing upstream invasion (Adams et al. 2001a). Thus stocking headwater lakes increases the potential for stocked trout to spread because of the potential ease of downstream dispersal. In addition, stocking headwater areas may be particularly damaging to native species because headwaters may provide important refuges from indigenous or non-indigenous predatory fishes (Adams et al. 2001a).

Given these issues, stocking headwater lakes creates a higher risk of negative impacts on amphibians than stocking lakes lower in a watershed, especially if good spawning habitat exists in these headwaters, which could allow establishment of naturally reproducing populations of trout. In any lake, located in headwaters or otherwise, the amount of suitable spawning habitat will determine whether reproducing populations of trout will establish. For example, the probability of trout populations becoming established may be positively related to the size of the lake outlet, presumably because larger outlets increase the amount of spawning habitat available (Donald 1987). Stocking sterile or all-female fish can prevent introduced trout from establishing reproducing populations, but even without reproduction, stocked trout may temporarily invade new areas. For lakes lower in a watershed, stocking lakes with barriers to upstream movement decreases the risk of trout spreading into headwaters. If there is high potential for introduced trout to disperse within several adjacent drainage basins, stocking multiple lakes in one drainage basin may be a better strategy than stocking one lake in each of the adjacent basins, in order to minimize the area and number of drainage basins impacted by introduced trout (Adams et al. 2001a).

3.2 Management options

Pilliod & Peterson (2000) list the following possible management actions for reducing threats to amphibians from introduced trout: (1) discontinue stocking; (2) discontinue stocking and possibly remove trout from some lakes; (3) reduce stocking frequency and density; (4) reduce naturally reproducing populations of trout by restricting access to spawning areas and /or gill netting; (5) change species stocked; (6) stock sterile trout; or (7) make no changes in stocking practices if fisheries threats to amphibian persistence are negligible.

3.2.1 Discontinuing stocking and fish removal

Discontinuing stocking in one lake or an entire area will lead to elimination of trout where adequate spawning habitat does not exist (Armstrong & Knapp 2004). In areas where natural reproduction is possible, discontinuing stocking may reduce impacts even if trout continue to reproduce, because stocking may lead to higher densities of trout, which tend to increase the intensity of effects of trout on native ecosystems (Liss et al. 1998; Tyler et al. 1998a; Donald et al. 2001; Schindler et al. 2001; Knapp et al. 2005; Welsh et al. 2006). Lower densities of trout may also lead to larger fish in better condition, potentially resulting in benefits for anglers as well as native species (Pilliod & Peterson 2000; Welsh et al. 2006). Even in the absence of decreases in density, naturally reproducing introduced trout may show increased growth rates where stocking has been discontinued (Armstrong & Knapp 2004). However, natural reproduction will not always lead to lower densities of trout and reduced impacts on native species. Tyler et al. (1998a) found higher densities and a more complex age structure of trout in lakes with

natural reproduction, and corresponding larger reductions in long-toed salamanders, than in lakes with low stocking densities and no reproduction. See also Section 3.2.2.

Another more intensive and potentially more controversial management option is to physically remove naturally reproducing introduced trout from lakes. This option has been used in California (Knapp & Matthews 1998; Sarnelle & Knapp 2004; Vredenburg 2004), Washington (Hoffman et al. 2004), and at least one lake in Banff National Park, Alberta (Parker et al. 2001). Introduced trout can be eliminated with gill nets alone in small shallow lakes (≤ 3 -10 ha surface area and ≤ 10 m deep) (Knapp & Matthews 1998; Parker et al. 2001). However, removal may be more difficult and/or controversial in other lake types, especially in large and/or deep lakes, lakes with inflows and outflows, or lakes where non-target species may be sensitive to removal efforts (Parker et al. 2001). Other removal methods include electrofishing, disturbing spawning habitat and use of piscicides (Parker et al. 2001). In the Southern Interior region, intensive efforts to eliminate fish may not be necessary in many lakes because suitable spawning habitat is often lacking from small lakes, and simply stopping stocking may be enough. However, monitoring would be required to confirm reduction or extinction of trout following discontinuation of stocking, because introduced trout populations may persist at higher rates than expected (Armstrong & Knapp 2004).

Several studies have assessed the ability of amphibians and other fauna and flora to recover following trout removal or extinction of introduced trout (e.g. Drake & Naiman 2000; Donald et al. 2001; Parker et al. 2001; Sarnelle & Knapp 2004; Vredenburg 2004; Knapp et al. 2005). Most fauna and flora appear to respond positively after trout disappear (but see McNaught et al. 1999; Drake & Naiman 2000; Sarnelle &

Knapp 2004), although recovery may take a long time. Recovery times vary, but most organisms recover within the span of one or two decades, and some taxa respond much more quickly. For example, mountain yellow-legged frogs may recover in as little as 3 years (Vredenburg 2004), but long-toed salamanders may take about 20 years to recolonize mountain lakes following extinction of trout (Funk & Dunlap 1999). The length of time to recovery for amphibians depends on proximity of a lake to other source populations and the dispersal abilities of the amphibian species (Knapp et al. 2001b; Vredenburg 2004; Knapp et al. 2005).

Lakes for discontinuation of stocking or removal of introduced trout should be chosen based on their potential for amphibian recolonization and their importance as amphibian habitat (Pilliod & Peterson 2000). For trout elimination, Pilliod & Peterson (2000) recommend targeting: (1) stocked lakes that already have some amphibian breeding (leads to faster recovery); (2) lakes that provide deep-water overwintering habitat for amphibians in surrounding shallow, fishless lakes; (3) lakes that have low or no natural trout reproduction (reduces the need for invasive fish removal practices); and (4) lakes that are the least important for recreational anglers. To maximize benefits for amphibians, the first three of these recommendations should take priority over the last, because stopping stocking in only lakes with low importance for anglers may not target the lakes most important for amphibians (Pilliod & Peterson 2000). Another important consideration includes proximity of the lake to source populations of amphibians. A lake isolated from other water bodies may not be the best candidate for reduction or elimination of stocking, unless it supports important populations of taxa that are sensitive

to trout, or if it is close enough to other populations to serve as a 'stepping stone' for movements among populations (Alford & Richards 1999).

Discontinuing stocking and removal of trout will certainly be unpopular with some anglers, but there are indications that other anglers may support a decrease in stocking. An informal survey showed that several angler advocacy groups in the United States do not support stocking of lakes that were historically fishless (Pister 2001). One of these groups, Trout Unlimited (both the Canadian and American chapters), has officially advocated that "naturally fishless waters of natural diversity value not be stocked with non-native species at present or in the future. Further, where a body of scientific evidence shows that stocking in historically non-salmonid waters adversely affects native biodiversity..., such stocking should cease. In all cases where stocking occurs, the burden of proof should lie with the state or federal agencies (or other proponents) to demonstrate that stocking does not cause ecological harm" (p. 29, Trout Unlimited 1997).

Decreased stocking could also have negative economic impacts on businesses that depend on recreational fishing such as fishing guides and resort operators, but economic impacts may be less than expected in some situations. Trout stocking costs money, and some analyses suggest that the benefits of stocking do not always justify the monetary costs, excluding any considerations of ecological costs (Johnson et al. 1995; Loomis & Fix 1999; Dunham et al. 2004). Lakes where it is obvious that economic costs outweigh economic benefits are good candidates for discontinuing stocking, and there will be economic savings as well as potential ecological benefits. Especially in areas where effort is low, the success of stocking is low, the costs of stocking are high, and/or there

are few spin-off benefits of angling such as resort use and tourism, managers should consider whether the benefits of stocking outweigh the economic costs. Marginal as well as total costs and benefits should be considered; i.e. what are the costs and benefits associated with adding or removing one stocked lake, and how do they contribute to the total value of recreational fishing in an area as a whole? For example, the marginal benefit of stocking a lake may be small in an area with many recreational fishing opportunities, because angler demand may be satisfied by the opportunities that already exist. Reducing stocking in this situation may have low marginal costs. On the other hand, in an area with few recreational fishing opportunities, stocking a lake may provide a large additional benefit to the area by satisfying or creating angler demand. Finally, although potentially difficult to quantify, the value per unit effort should also be considered. For example, a lake that receives low effort may still have high value per angler to the small number of anglers who use the lake.

3.2.2 Alter stocking practices

Changing the frequency, density, species and/or fertility of stocked trout are relatively easy but largely untested options for managing the impacts of trout on amphibians and other native species (Pilliod & Peterson 2000). As already stated, several studies have found that lower densities of trout tend to have less impact on native species (Liss et al. 1998; Tyler et al. 1998a; Donald et al. 2001; Schindler et al. 2001; Knapp et al. 2005; Welsh et al. 2006), and lower densities may also benefit anglers by leading to larger fish in better condition (Pilliod & Peterson 2000; Schindler et al. 2001; Welsh et al. 2006). For example, Welsh et al. (2006) found that abundance of three species of amphibian (including the Pacific treefrog and long-toed salamander) decreased and the

length and condition of trout deteriorated with increasing relative density of trout. Decreasing stocking densities in combination with decreasing stocking frequency could reduce trout to provide troutless or near troutless habitats for intervals of several years, allowing amphibians to produce successful cohorts and sustain long-lived populations, although the inherent variability of amphibian populations and their sensitivity to stochastic variables may decrease the chances of this strategy working (Pilliod & Peterson 2000). Other potential problems associated with lower densities of trout include the fact that larger trout at lower densities may consume more amphibians and be better predators because of their larger gape (Semlitsch & Gibbons 1988; Pilliod & Peterson 2000), and natural reproduction may confound efforts to control trout density and size structure (Pilliod & Peterson 2000). Monitoring the effects of different densities of trout on amphibians and whether or not densities can be closely controlled through stocking would better establish whether manipulating trout density is a viable tool for reducing negative impacts of introduced trout.

Different species of trout may also have different impacts on native species (e.g. Crowl et al. 1992). For example, some studies cited by Pilliod & Peterson (2000) suggest that eastern brook trout may have stronger effects on zooplankton and amphibians than other trout species, although another study suggests that feeding behaviours of brook trout on invertebrates are similar to other trout species (Carlisle & Hawkins 1999). Eastern brook trout were stocked in 22 lakes in the Thompson-Nicola region in 2005 and 2006 (S. Webb, unpublished data) and in a small number of lakes in other regions of British Columbia (FFSBC 2006a). Given that eastern brook trout are not indigenous to British Columbia and some evidence suggests they are especially damaging to native

species, managers may want to monitor the impacts and limit stocking of this species in particular.

In British Columbia, different strains, ages and types (e.g. sterile versus reproductive) of trout are available for stocking, and knowledge exists about many aspects of the biology and ecology of different strains (FFSBC 2004). It is possible that the strain/age/type of trout stocked could influence associations between trout and amphibians or other fauna, but to my knowledge this option has not been researched. However, there are several known factors that could affect the impacts of different types of trout. Stocking sterile trout reduces the probability of unintended dispersal and prevents hybridization with natural populations of trout. As previously stated, larger trout may consume more amphibians and may be better predators on amphibians because their larger gape allows them to consume a wider range of amphibian sizes and life stages (Pilliod & Peterson 2000; Semlitsch & Gibbons 1988). In terms of the strains of rainbow trout most commonly stocked in the Southern Interior, the Blackwater strain may be a greater threat to amphibians than the Pennask strain, because Blackwater trout reach larger sizes and preferentially feed in shallow shoal areas, and Pennask trout are smaller and prefer deep open waters (FFSBC 2004) where amphibians are less likely to occur. More exploration of the literature on mechanisms of interaction between amphibians and fish generally may yield information useful for building hypotheses about whether the characteristics of certain strains/ages/types of trout may increase their likelihood of negatively affecting amphibians. However, these hypotheses should be tested before being widely adopted as management practice.

3.3 Further research and monitoring

General monitoring of the distribution and abundance of amphibians across landscapes and over time will help determine the on-going regional status of amphibians. Landscape-scale monitoring over a longer term is especially important for amphibians because of their natural population fluctuations and metapopulation dynamics (Blaustein et al. 1994b). To decrease the resources required for monitoring, amphibian surveys could be done in conjunction with fisheries surveys, although surveys of only fish-bearing lakes gives an incomplete picture of regional amphibian population dynamics (Pilliod & Peterson 2000). Investigating how the responses of amphibians to trout may differ among BEC categories may be an area for further research in British Columbia. More information on the distribution of different types of lakes, in terms of biological, physical, and chemical characteristics, would be useful for ensuring that troutless lakes represent the full range of lake types across a landscape.

As stated in the previous section, research into responses of amphibians to varying densities of trout could help develop more specific methods for managing the effects of trout on amphibians, as could research on interactions between different strains/ages/types of trout and amphibians. If trout are introduced to new lakes, eradicated from a lake, or stocking is discontinued, before and after monitoring would yield more information on interactions between introduced trout and native species. Setting up monitoring as an adaptive management experiment (Walters 1986; Johnson 1999) would be particularly useful. Longer-term monitoring and research are best, especially given the natural variability in amphibian population dynamics (Pechmann et al. 1991; Blaustein et al. 1994b), and that impacts of trout on amphibians may take years

to become apparent because of metapopulation dynamics that maintain amphibian populations even where the population growth rate is negative in the absence of immigration (Knapp & Matthews 2000b; Pilliod & Peterson 2001; Vredenburg 2004).

Managers may also want to explore formal decision analysis as a tool for guiding stocking policies. Among other uses, decision analysis: (1) helps in making decisions in situations with multiple, potentially conflicting objectives; (2) helps decision makers to explicitly identify and define management objectives, decision rules and alternative management actions; (3) allows explicit incorporation of uncertainty into the decision making process; and (4) shows explicitly the trade-offs being made under each potential management action (Keeney 1982; Maguire & Boiney 1994; Reckhow 1994). Decision analysis using Bayesian statistics to quantify uncertainty could be applied in trout stocking management. Bayesian statistics can be used to make inferences about the probability of different hypotheses or outcomes, which can be particularly useful in environmental decision making (Ellison 1996; Wade 2000). For example, future research could calculate Bayesian probability distributions for the level of effect of trout on different amphibian species. These probability distributions could be used to evaluate different management actions by calculating the risk of unacceptable negative effects on amphibians under each action.

One final important task for managers is defining what the management objectives are for trout stocking management in the Southern Interior and other regions of British Columbia. I based the recommendations in this chapter on the assumption that (1) amphibian conservation and (2) maintenance of some degree of trout stocking are both management objectives. These management objectives likely reflect the types of

objectives that managers will have to balance, but objectives will probably need more specific definition in order to make real-trade offs between amphibian conservation and trout stocking. Objectives may also need to be adjusted for different contexts. For example, what level or risk of effect of trout stocking on amphibians is acceptable for a given amphibian species in a particular area? Is a reduction in trout stocking acceptable and if so, how much of a reduction? Ideally the management objectives would be created through consultation with a range of appropriate stakeholders such as angling groups, fishing resort operators, representatives of all levels of government, and biologists specializing in amphibians. Without well-defined objectives managers will have difficulty creating and evaluating management plans, because they will not know what exactly they are trying to achieve and thus will have no way of measuring success.

3.4 Conclusions

Although there are many lakes with trout and trout stocking in the Southern Interior, there are also many troutless lakes and wetlands in the region, and the proportion of water bodies occupied by trout is lower than in many other regions of western North America. Other conditions in Southern Interior lakes, including relatively high productivity and high habitat complexity, may also help amphibians coexist with trout in the region. The three aquatic-breeding amphibian species that showed evidence of negative associations with trout during this study have broad distributions and a secure conservation status. Given the information above, trout stocking may be less of a threat to amphibian persistence than in other areas of western North America, and discontinuing stocking or eliminating trout from lakes may not be as crucial for amphibian persistence as in other regions. However, where trout and amphibians coexist in the Southern

Interior, the abundance of amphibians may be substantially reduced, which may have long-term implications for metapopulation dynamics. The existing weight of evidence from my study and the literature showing negative associations between trout and amphibians provides justification for a cautious approach to trout stocking that considers and incorporates the needs of amphibians in management decision making. In addition, increasing awareness of biodiversity concerns and amphibian declines, and publicity surrounding negative associations between trout and native species in other regions (e.g. Forstenzer 2000; The Associated Press 2001; Barbassa 2006), will probably increase pressure to limit stocking, especially stocking new lakes.

Trout stocking is currently an important part of recreational fisheries management in British Columbia. Given scientific evidence of negative effects of stocking and social pressures, non-fishery related values such as amphibians and other native species should be explicitly factored into management decisions and planning in order for trout stocking to remain viable in the future. Because the threat of trout stocking to amphibian populations in the Southern Interior is potentially less than elsewhere, managers may have relative flexibility to make trade-offs between protecting amphibians and encouraging recreational fishing using stocking. However, what kind of trade-offs are made will depend on the management objectives and the context and factors influencing each situation (e.g. where amphibian conservation is a management objective and amphibian populations are highly threatened by trout presence, trout stocking will be more strongly limited). As stated at the beginning of this chapter, presumably the challenge for managers is to balance the benefits and costs of trout stocking in a way that decreases threats to amphibians to an acceptable level without unreasonably limiting

opportunities for recreational fishing. The contents of this document hopefully provide a starting point for meeting this challenge.

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APPENDIX: DESCRIPTION OF STUDY LAKES

Table A.1. General descriptive characteristics of troutless study lakes.

Lake ^a	Pair #	Waterbody ID number ^b	Watershed Group ^c	Region ^d	Sampling dates (2004)
Marsden	1	00412BONP	Bonaparte River	3	8-9 June
Lake in the Gap	2	00407BONP	Bonaparte River	3	10-11 June
No Name	3	00332BONP	Bonaparte River	3	12-13 June
Home	4	01967GRNL	Green Lake	3	14-15 June
Dead Car	5	01323STHM	South Thompson	3	22-23 June
Banshee	6	00856ADMS	Adams River	3	24-25 June
Semlin	7	00260DEAD	Deadman River	3	26-27 June
Rock	8	00348DEAD	Deadman River	3	28-29 June
Bog Junior	9	00009DEAD	Deadman River	3	6-7 July
Larsen	10	01680SAJR	San Jose River	5	8-9 July
Parting (west)	11	00983BRID	Bridge Creek	5	10-11 July
Moosehorn	12	00889BONP	Bonaparte River	3	12-13 July
Tanker	13	00357LNTH	Lower North Thompson	3	20-21 July
Log	14	00352LNTH	Lower North Thompson	3	24-25 July
Flying Ant	15	00287LNTH	Lower North Thompson	3	26-27 July
Francis	16	02103MAHD	Mahood Lake	3	24-25 July
Lake #208	17	01245LNTH	Lower North Thompson	3	4-5 August
Border	18	01181LNTH	Lower North Thompson	3	6-7 August
Hike	19	01162LNTH	Lower North Thompson	3	8-9 August

^a Names are gazetted names or aliases used in the British Columbia Fisheries Inventory Summary System (FISS) database (MSRM 2006b), a local name not recognized by the database, or a name made up for this project. When available FISS names were always used.

^b Waterbody id number is the unique lake identifier used in the FISS database (MSRM 2006b).

^c Watershed group as defined in the FISS database (MSRM 2006b).

^d Region is the BC Ministry of Environment management region. Region 3 is the Thompson-Nicola Region and Region 5 is the Cariboo Region.

Table A.2. General descriptive characteristics of trout study lakes.

Lake ^a	Pair #	Waterbody ID number ^b	Watershed Group ^c	Region ^d	Sampling dates (2004)
Moose	1	00365BONP	Bonaparte River	3	8-9 June
Spectacle	2	00414BONP	Bonaparte River	3	10-11 June
Little Scot	3	00638BONP	Bonaparte River	3	12-13 June
Scot	4	00694BONP	Bonaparte River	3	14-15 June
Beautiful	5	01314STHM	South Thompson	3	22-23 June
Joyce	6	00350STHM	South Thompson	3	24-25 June
Fatox	7	00389DEAD	Deadman River	3	26-27 June
Allie	8	00235DEAD	Deadman River	3	28-29 June
Bog	9	00013DEAD	Deadman River	3	6-7 July
Lower	10	00064BRID	Bridge Creek	5	8-9 July
Irish	11	00783BRID	Bridge Creek	5	10-11 July
Burn	12	00817BONP	Bonaparte River	3	12-13 July
Beattie	13	00351LNTH	Lower North Thompson	3	20-21 July
Donna	14	00279LNTH	Lower North Thompson	3	22-23 July
Wineholt	15	00321LNTH	Lower North Thompson	3	22-23 July
Lorenzo	16	02102MAHD	Mahood Lake	3	26-27 July
Lake #997	17	01220LNTH	Lower North Thompson	3	4-5 August
Lake #1227	18	01176LNTH	Lower North Thompson	3	6-7 August
Today	19	01201LNTH	Lower North Thompson	3	8-9 August

^a Names are gazetted names or aliases used in the British Columbia Fisheries Inventory Summary System (FISS) database (MSRM 2006b), a local name not recognized by the database, or a name made up for this project. When available FISS names were always used.

^b Waterbody id number is the unique lake identifier used in the FISS database (MSRM 2006b).

^c Watershed group as defined in the FISS database (MSRM 2006b).

^d Region is the BC Ministry of Environment management region. Region 3 is the Thompson-Nicola Region and Region 5 is the Cariboo Region.

Table A.3. Biological and physical characteristics of troutless study lakes.

Lake	Pair #	Fish species present	BEC Zone, Subzone, Variant ^a	Ecoprovince ^b , ecoregion ^c , ecosection ^d	Land use ^e	Elevation (m)	Area (ha)
Marsden	1		IDFdk3	CEI, FAP, CAB	1, 2	1055	13.12
Lake in the Gap ^f	2		SBPSmk	CEI, FAP, CAP	1	977	7.05
No Name	3		SBPSmk	CEI, FAP, CAP	1, 2	1022	12.11
Home	4		SBPSmk	CEI, FAP, CAP	2, 1, 4	1109	13.63
Dead Car	5		IDFdk1	SOI, TOP, NIB	1, 2	1130	10.98
Banshee	6		IDFmw2	SOI, TOP, NTU	1	634	13.02
Semlin	7		IDFdk3	SOI, TOP, TRU	1, 2	1137	13.04
Rock ^g	8		IDFdk3	SOI, TOP, TRU	1	1105	2.69
Bog Junior	9		SBPSmk	CEI, FAP, CAP	1	1250	7.82
Larsen	10	RSC ^h	IDFdk3	CEI, FAP, CAB	1, 4	857	14.21
Parting (west)	11	RSC ^h	IDFdk3	CEI, FAP, CAB	1	1163	35.99
Moosehorn	12		IDFdk3	CEI, FAP, CAB	1	1167	20.44
Tanker	13		SBSmm	CEI, FAP, CAP	1	1334	3.31
Log	14		SBSmm	CEI, FAP, CAP	1	1376	3.42
Flying Ant	15		ESSFdc2	CEI, FAP, CAP	1	1450	2.30
Francis ⁱ	16		ESSFdc2	CEI, FAP, CAP	1	1429	5.20
Lake #208	17		ESSFdc2	SOI, TOP, TRU	1	1533	4.35
Border	18		ESSFdc2	SOI, TOP, TRU	1	1501	13.11
Hike	19		MSdm2	SOI, TOP, TRU	1	1461	5.54

^a Biogeoclimatic Ecosystem Classification (BEC) zone; ESSF=Engelmann Spruce-Subalpine Fir, IDF=Interior Douglas-fir, MS=Montane Spruce, SBPS=Sub-Boreal Pine-Spruce, SBS=Sub-Boreal Spruce. For an explanation of the BC BEC System and definition of subzones and variants see MFR (2006).

^b Ecoprovince, from the Ecoregion Classification system (MSRM 2006a). CEI=Central Interior, SOI=Southern Interior.

^c Ecoregion, from the Ecoregion Classification system (MSRM 2006a). FAP=Fraser Plateau, TOP=Thompson-Okanagan Plateau

^d Ecosection, from the Ecoregion Classification system (MSRM 2006a). CAB=Cariboo Basin, CAP=Cariboo Plateau, NIB=Nicola Basin, NTU=Northern Thompson Upland, TRU=Tranquille Upland.

^e Dominant land use(s); 1=Forestry, 2=Agriculture (cattle grazing), 3=BC Forest Recreation camp site, 4=Cabins or residences. Note that although cattle were found to some extent in the forest throughout the study region, lakes where agriculture is listed as a land use were lakes where there was obvious evidence of cattle use around the lake shore.

^f Lake in the Gap was stocked with rainbow trout in 1994 (MSRM 2006b). However, winterkills had eliminated trout from Lake in the Gap several years before 2004.

^g Rock Lake was stocked with rainbow trout between 1986 and 1991 (MSRM 2006b). However, winterkills eliminated trout from Rock Lake several years before 2004.

^h Redside shiners (RSC) (*Richardsonius balteatus*) were caught in minnow traps during sampling.

ⁱ One record of rainbow trout exists for Francis Lake from 1978 (MSRM 2006b). However, Francis Lake had been fishless for many years by 2004.

Table A.4. Biological and physical characteristics of trout study lakes.

Lake	Pair #	Trout type? ^a	Other fish species	BEC Zone, Subzone, Variant ^b	Ecoprovince ^c , ecoregion ^d , ecosection ^e	Land use ^f	Elevation (m)	Area (ha)
Moose	1	Natural		SBPSmk	CEI, FAP, CAP	1, 3	1134	15.78
Spectacle	2	Stocked	NSC ^g	SBPSmk	CEI, FAP, CAP	1, 2	1023	12.74
Little Scot	3	Natural		SBPSmk	CEI, FAP, CAP	1, 3	1203	7.62
Scot	4	Natural		SBPSmk	CEI, FAP, CAP	1, 3	1228	33.80
Beautiful	5	Stocked		IDFdk1	SOI, TOP, NIB	1, 2	1076	12.24
Joyce	6	Stocked		IDFdk2	SOI, TOP, SHB	1, 3	826	6.41
Fatox	7	Stocked		SBPSmk	CEI, FAP, CAP	1	1138	14.06
Allie	8	Natural	PCC ^h	IDFdk3	SOI, TOP, TRU	1, 4	1052	11.19
Bog	9	Stocked		SBPSmk	CEI, FAP, CAP	1, 3	1230	33.99
Lower ⁱ	10	Stocked	RSC ^j	SBPSmk	CEI, FAP, CAP	1, 3	929	15.07
Irish ⁱ	11	Stocked		IDFdk3	CEI, FAP, CAB	1, 4	1174	23.44
Burn	12	Stocked		IDFdk3	CEI, FAP, CAB	1	1178	28.51
Beattie	13	Natural		SBSmm	CEI, FAP, CAP	1	1246	6.99
Donna	14	Natural		SBSmm	CEI, FAP, CAP	1	1329	4.22
Wineholt	15	Stocked		SBSmm	CEI, FAP, CAP	1	1281	5.71
Lorenzo	16	Natural	LW, NSC ^k	ESSFdc2	CEI, FAP, CAP	1	1423	20.49
Lake #997	17	Stocked		MSdm2	SOI, TOP, TRU	1	1490	6.22
Lake #1227	18	Natural		ESSFdc2	SOI, TOP, TRU	1	1487	9.61
Today	19	Stocked		ESSFdc2	SOI, TOP, TRU	1	1498	5.13

^a Natural populations are trout populations with no stocking records, or in the case of Allie Lake, a population that has not been stocked for at least 15 years.

^b Biogeoclimatic Ecosystem Classification (BEC) zone; ESSF=Engelmann Spruce-Subalpine Fir, IDF=Interior Douglas-fir, MS=Montane Spruce, SBPS=Sub-Boreal Pine-Spruce, SBS=Sub-Boreal Spruce. Biogeoclimatic Ecosystem Classification (BEC) zone. ESSF=Engelmann Spruce-Subalpine Fir, IDF=Interior Douglas-fir, MS=Montane Spruce, SBPS=Sub-Boreal Pine-Spruce, SBS=Sub-Boreal Spruce. For an explanation of the BC BEC System and definition of subzones and variants see MFR (2006).

^c Ecoprovince, from the Ecoregion Classification system (MSRM 2006a). CEI=Central Interior, SOI=Southern Interior.

^d Ecoregion, from the Ecoregion Classification system (MSRM 2006a). FAP=Fraser Plateau, TOP=Thompson-Okanagan Plateau

^e Ecosection, from the Ecoregion Classification system (MSRM 2006a). CAB=Cariboo Basin, CAP=Cariboo Plateau, NIB=Nicola Basin, SHB=Shuswap Basin, TRU=Tranquille Upland

^f Dominant land use(s); 1=Forestry, 2=Agriculture (i.e. evidence of cattle grazing), 3=BC Forest Recreation camp site, 4=Cabins or residences.

^g One record northern pikeminnow (NSC) (*Ptychocheilus oregonensis*) from 1994 (MSRM 2006b).

^h Peamouth chub (PCC) (*Mylocheilus caurinus*) were caught in minnow traps during sampling of Allie Lake.

ⁱ Brook trout (*Salvelinus fontinalis*) were stocked in Irish Lake 1963-1968 and Lower Lake 1986-1982. No records exist for this species in either lake since stocking ended (MSRM 2006b).

^j Redside shiners (RSC) (*Richardsonius balteatus*) were caught during minnow trap sampling of Lower Lake.

^k One record of each of lake whitefish (LW) (*Coregonus clupeaformis*) (from 1977) and northern pikeminnow (from 2000) exist for Lorenzo Lake (MSRM 2006b). I caught unidentified minnows during minnow trap sampling of Lorenzo Lake, which I assume were either juvenile pikeminnow or whitefish.

Table A.5. Information on stocking of trout study lakes stocked with rainbow trout.

Lake	Pair #	Last date stocked prior to study	Mean annual stocking density (no. trout per ha) ^a	Stage stocked	Timing of stocking	# of years stocked in previous five ^b
Spectacle	2	September 2003	392 (2003-1999)	Fry	Fall	5
Beautiful	5	September 2003	245 (2003-1999)	Fry	Fall	5
Joyce	6	May 2004	914 (2004-2000)	Yearling	Spring	5
Fatox	7	October 2003	199 (2003-1999)	Fry	Fall	5
Bog	9	October 2003	53 (2003-1999)	Fall fry	Fall	5
Lower	10	April 2004	239 (2004-2000)	Yearling	Spring	4 (2001-2004)
Irish	11	September 2003	555 (2003-1999)	Fry in fall, yearlings in spring	Fall (2002-2003); Spring (1999-2001)	5
Burn	12	September 2002	32 (2003-1999)	Fry	Fall	2 (2000; 2002)
Wineholt	15	September 2002	158 (2003-1999)	Fry	Fall	3 (1999; 2001-2002)
Lake #997 ^c	17	June 2004	194 (2004-2000)	Yearlings in early June, fry in early August	Early June and early August (all years)	3 (2002-2004)
Today ^c	19	June 2004	185 (2004-2000)	Yearlings in early June, fry in early August	Early June and early August (all years)	3 (2002-2004)

^a The mean was calculated using stocking data from the five years prior to the study. Stocking data came from provincial government records in most cases (MSRM 2006b), except for two lakes where stocking was part of a university research project, and data came from the researcher (P. Askey, unpublished data). The average number of trout stocked per year was divided by the surface area of the lake to give mean annual stocking density. The range of years over which the mean was calculated is in brackets; however, not every lake was stocked every year within that date range (see far right-hand column in table and next footnote).

^b If the number of years stocked is less than five, numbers in brackets are years when stocking occurred.

^c Stocked 2002-2004, as part of a University of Calgary research project. Lakes were not stocked prior to 2002 but had naturally reproducing populations of rainbow trout (P. Askey, personal communication).