Effects of rainbow trout (*Oncorhynchus mykiss*) on amphibians in productive recreational fishing lakes of British Columbia

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Abstract: Stocking lakes with trout to enhance recreational fishing can negatively affect native aquatic species. Our objectives were (*i*) to compare presence, relative abundance, body size, and developmental stage of amphibians in lakes with and without rainbow trout (*Oncorhynchus mykiss*) in British Columbia's southern interior, and (*ii*) to estimate the size of trout impact for application to amphibian conservation. Presence of long-toed salamander (*Ambystoma macrodactylum*), Columbia spotted frog (*Rana luteiventris*), and Pacific treefrog (*Pseudacris regilla*) was not significantly different between lake types. In contrast, western toad (*Bufo boreas*) larvae presence and relative abundance were significantly higher in lakes with trout. Relative abundance of salamander larvae was significantly lower in lakes with trout, but hypothesis testing did not provide consistent evidence of significantly lower abundances of spotted frog and treefrog larvae. However, estimated ratios of relative abundance (impact) indicated that larvae of the salamander and two frogs were ≥65% less abundant in lakes with trout. Salamander larvae were significantly smaller in lakes with trout. Although amphibians may currently coexist with trout in our study region, trout stocking policy in British Columbia should consider amphibian conservation because the presence of trout is associated with lower amphibian abundance and body size in individual lakes.

Résumé : L'empoissonnement de lacs avec de la truite pour améliorer la pêche sportive peut affecter négativement les espèces aquatiques indigènes. Nos objectifs sont (*i*) de comparer la présence, l'abondance relative, la taille corporelle et les stades de développement des amphibiens dans des lacs avec et sans truites arc-en-ciel (*Oncorhynchus mykiss*) dans la région intérieure sud de la Colombie-Britannique et (*ii*) d'estimer l'importance de l'impact des truites dans un but de conservation des amphibiens. Il n'y a pas de différences significatives dans la présence de salamandres à longs doigts (*Ambystoma macrodactylum*), de grenouilles maculées du Columbia (*Rana luteiventris*) et de rainettes du Pacifique (*Pseudacris regilla*) entre les types de lacs. En revanche, la présence et l'abondance relative des larves de crapauds de l'ouest (*Bufo boreas*) sont significativement supérieures dans les lacs qui contiennent des truites. L'abondance relative des larves de salamandres est significativement plus faible dans les lacs qui contiennent des truites, mais la vérification de nos hypothèses ne fournit pas de données assez uniformes pour conclure à une abondance réduite des larves de grenouilles et de rainettes. Cependant, les rapports estimés d'abondance relative (impact) indiquent que les larves de salamandres et des deux anoures sont ≥65 % moins abondantes dans les lacs qui contiennent des truites. Les larves de salamandres sont significativement plus petites dans les lacs avec truites. Bien que les amphibiens puissent actuellement coexister avec la truite dans notre région d'étude, les politiques d'ensemencement de la truite en Colombie-Britannique devraient tenir compte de la conservation des amphibiens, parce que la présence de la truite dans les lacs individuels s'accompagne d'une réduction de l'abondance et de la taille corporelle chez les amphibiens.

[Traduit par la Rédaction]

Introduction

Nonnative species introductions are a threat to natural biodiversity and may be particularly damaging to freshwater ecosystems (Sala et al. 2000). Stocking lakes and rivers with trout and char (e.g., *Oncorhynchus* spp., *Salmo trutta*, *Salvelinus* spp.) to enhance recreational fisheries is one of the world's most widespread means of introducing nonnative species to freshwater systems (Cambray 2003). Although trout are often stocked into water bodies within their native ranges, populations established via such introductions are also nonnative from the perspective of the receiving ecosystems (Dunham et al. 2004). Introduced trout can influence aquatic systems at individual, population, community, and ecosystem levels (Simon and Townsend 2003). For example, nonnative trout can decrease faunal richness across a land-

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scape (Knapp et al. 2005), cause trophic cascades that alter aquatic food chains, primary production, and energy and nutrient cycling (Simon and Townsend 2003), and exclude native fish through competition, predation, hybridization, and possibly disease transfer (Allendorf et al. 2001; Dunham et al. 2002).

Trout introductions often have negative impacts on native amphibians. For example, introduced trout are strongly associated with declines and extirpations of mountain yellow-legged frogs (*Rana muscosa*) from California's Sierra Nevada region (e.g., Bradford 1989; Knapp and Matthews 2000; Vredenburg 2004). Although predation is most commonly assumed to cause such declines, competition for food (Tyler et al. 1998*b*) and transfer of pathogens from trout to amphibians (Kiesecker et al. 2001) are also possible. At the landscape scale, introduced trout may reduce connectivity among amphibian populations leading to fragmentation, isolation, and increased probability of local extinctions, even in habitats without trout (Bradford et al. 1993; Pilliod and Peterson 2001; Knapp et al. 2003).

Trout stocking remains an established tool for recreational fisheries enhancement in British Columbia, Canada, where lake fisheries, mainly for rainbow trout (*Oncorhynchus mykiss*), generate approximately 2.8 million angler days in fishing activity each year and contributed $400 million to British Columbia's economy in 2000 (Levey and Williams 2003). The contribution of stocking programs to these fisheries is substantial. For example, although stocked lakes make up less than 1% of the lakes that offer sportfishing opportunities, in 1995 approximately 40% of anglers in British Columbia always or usually fished stocked lakes (Levey and Williams 2003). However, policymakers are concerned about conservation risks associated with stocking, particularly risks to amphibians. Furthermore, policymakers need to define acceptable levels of risk associated with trout stocking in order to design and evaluate management activities aimed at amphibian conservation.

To our knowledge, few studies have investigated relationships between introduced fish and amphibians in Canada, and no published studies have addressed trout stocking specifically. Associations between trout and amphibians in British Columbia's southern interior may differ from those observed elsewhere for several reasons. Lakes in British Columbia's southern interior region are at lower elevations, are generally more productive, and have higher habitat complexity than alpine lakes of western North America where many existing studies focus; all of these factors likely affect trout–amphibian interactions (Tyler et al. 1998*a*; Pilliod and Peterson 2001). In addition, glaciation over most of British Columbia produced a landscape with high densities of lakes, many of which are fishless, that may provide relatively high levels of predator-free amphibian habitat.

We examine the potential impacts of a large-scale rainbow trout stocking program on native amphibians in British Columbia lakes. Our objectives were (*i*) to compare probability of presence, abundance, body size, and developmental stage of four amphibian species between lakes where rainbow trout were present or absent, and (*ii*) to estimate the size of the impact of trout on amphibian abundance, for potential application toward setting and evaluating management objectives related to amphibian conservation. Long-toed sala-

manders (*Ambystoma macrodactylum*), Columbia spotted frogs (*Rana luteiventris*), Pacific treefrogs (*Pseudacris regilla*), and western toads (*Bufo boreas*) use small lakes for aquatic breeding and thus may be affected by introduced trout. Reductions in abundance of the salamander and the two frogs in some other regions of North America are associated with trout (e.g., Tyler et al. 1998*a*; Matthews et al. 2001; Pilliod and Peterson 2001); however, the conservation status of these species remains secure in both the United States (Pilliod and Fronzuto 2005; Reaser and Pilliod 2005; Rorabaugh and Lannoo 2005) and Canada (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2006). Western toads are positively associated (Welsh et al. 2006) or not associated (Bull and Marx 2002) with introduced trout, but laboratory experiments suggest that trout may threaten western toads through transfer of pathogens (Kiesecker et al. 2001). Western toads are a Species of Special Concern under Canada's Species at Risk Act, and severe local declines and extirpations have led to consideration of the toad as endangered in several US states (Muths and Nanjappa 2005).

Materials and methods

All study lakes exist within the North and South Thompson River watersheds in British Columbia's south-central interior where the climate 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). All of the study lakes are located in forested areas with low human population densities, mostly on plateaus, at elevations ranging between 600 and 1500 m (Table 1); no lakes are in grassland or alpine areas. Small forested lakes in the region are generally productive and often have soft organic bottoms and high levels of structural complexity with aquatic vegetation and coarse woody debris (Table 2).

During the summer of 2003, we conducted a pilot study at five lakes to evaluate sampling methods, determine timing of amphibian development, and collect preliminary data for power analyses. We identified live-trapping and visual surveys (Heyer et al. 1994) as logistically practical and effective at providing relative abundance information for larvae (i.e., tadpoles) and metamorphs (i.e., recently transformed juveniles) of all four amphibian species. Trap catch data obtained during the pilot study appeared to follow a negative binomial distribution in which catches of zero individuals were common, but occasional large catches also occurred. We therefore used a simulation approach to power analysis because conventional tests of statistical power can be unreliable with non-Gaussian data (Hilborn and Mangel 1997). The simulation objective was to determine sample sizes (i.e., number of lakes sampled per lake type) required to achieve a minimum 80% probability of detecting a minimum 50% difference in amphibian abundance between lakes with and without trout using trap sampling and a standard two-sample t test with a type I error rate of 0.05. Based on this analysis, minimum sample sizes per lake type were 10 for long-toed salamanders, 14 for Pacific treefrogs, and 25 for Columbia spotted frogs. More than 30 lakes per lake type were

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Table 1. Physical and biological characteristics in British Columbia's southern interior lakes sampled for amphibian density, body size, and developmental stage in 2004.

Lake type	n	Physical characteristics (mean ± SD)				Fish populations		Stocking rate[d]	No. of lakes with fish other than trout[e]
		Elevation[a] (m)	Surface area[b] (ha)	Perimeter (m)	Littoral width[c] (m)	Stocked	Natural		
Troutless	19	1194±236	10.6±8.0	1687±1092	15.1±7.1	0	0	0	2
Trout	19	1208±186	14.4±9.5	1917±839	13.0±5.7	11	8	288±254	3 or 4

Note: SD, standard deviation.

[a]Elevation obtained either from provincial government databases or from on-site GPS.

[b]Lake surface area obtained from provincial government databases.

[c]Mean width of littoral zone based on measurements of the distance from shore to a depth of 1 m at seven randomly chosen sites per lake.

[d]Stocking rate is the mean number of rainbow trout stocked per hectare of lake surface (± SD). Mean calculated from stocking records (Ministry of Sustainable Resource Management (MSRM) 2006) and unpublished data (Paul Askey, University of Calgary, Ecology Division, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada), 1999–2003.

[e]See Materials and methods for description of other fish species.

Table 2. Habitat variables (mean and range) used in comparison of habitat between lake types.[a]

	Lake type	
Variable	Troutless	Trout
Bedrock (%)	0	0.01 (0–0.3)
Boulder (%)	0.5 (0–3.3)	3.1 (0–10.0)
Cobble (%)	0.8 (0–5.8)	4.1 (0–21.1)
Pebble (%)	0.4 (0–1.6)	3.9 (0–22.5)
Gravel (%)	1.2 (0–11.1)	5.4 (0–31.8)
Sand (%)	1.7 (0–11.6)	3.4 (0–23.0)
Silt–clay (%)	3.5 (0–65.3)	1.2 (0–23.5)
Coarse particulate organic matter (%)	20.5 (0.6–48.5)	22.9 (3.6–57.5)
Fine particulate organic matter (%)	65.4 (0.5–100)	52.8 (0.6–98.8)
Coarse woody debris (CWD) (%)	5.6 (0–23.3)	4.9 (0.2–17.1)
Emergent vegetation (%)	14.7 (0–58.5)	12.7 (0.1–38.0)
Submerged vegetation (%)	23.5 (1.0–91.3)	16.4 (0.2–83.3)
Surface area of water bodies within 100 m buffer (%)	12.4 (0–100.0)	10.2 (0–87.0)
Surface area of water bodies within 1000 m buffer (%)	4.6 (0–16.0)	4.4 (0–16.0)
Stream length within 100 m buffer (m·ha^{-1})	9.3 (0–16.5)	10.0 (0–24.7)
Stream length within 1000 m buffer (m·ha^{-1})	7.1 (2.1–13.0)	8.5 (0–14.5)
Road length within 100 m buffer (m·ha^{-1})	1.6 (0–26.5)	6.8 (0–36.9)
Road length within 1000 m buffer (m·ha^{-1})	5.9 (0–18.8)	8.5 (1.0–27.8)

[a]Water body surface area, stream length, and road length within 500 m buffer were also compared.

required for western toads; however, a 60-lake sampling season was unreasonable given logistic and resource constraints. Therefore, we accepted potentially low power for Columbia spotted frogs and western toads and developed a sampling design using $N = 38$ lakes (19 per lake type).

We used provincial government records of fish surveys (Ministry of Sustainable Resource Management (MSRM) 2006) and local knowledge of fisheries biologists and fishing resort operators to select troutless lakes that were small (<40 ha surface area) and accessible (within 2 km of a road). We then paired each troutless lake with the closest lake containing rainbow trout (MSRM 2006) that was similar in elevation and that met the accessibility and size criteria. We confirmed that trout were present in each trout lake using records of fish surveys and recent stocking and evidence of trout presence during lake sampling (i.e., direct observations of trout and (or) anglers on lakes). We observed no evidence of trout presence at any of the troutless lakes. Trout lakes include lakes with both stocked and natural populations of trout (Table 1). Stocked populations had trout release re-

cords for at least 2 years between 1999 and 2003. Natural populations either had no stocking records or (in one case) had not been stocked for at least 15 years.

A small number of lakes of both types contained fish species other than rainbow trout (Table 1). Two troutless lakes and one trout lake contained redside shiners (*Richardsonius balteatus*). A second trout lake contained peamouth chub (*Mylocheilus caurinus*), and a third trout lake contained unidentified minnows, which were possibly lake whitefish (*Coregonus clupeaformis*) or northern pikeminnow (*Ptychocheilus oregonensis*) based on fisheries inventory records (MSRM 2006). A fourth trout lake contained northern pikeminnow in 1994 according to government records (MSRM 2006), but we did not directly observe fish other than trout in this lake. We assumed that presence of fish other than rainbow trout was not an important confounding factor given the small number of lakes with this issue.

Field sampling took place between late May and mid-August 2004. Each lake was sampled only once and sampling occurred over a 2-day period. We sampled pairs of

trout and troutless lakes at the same time to avoid unequal influence between lake types in location, elevation, season, and weather on amphibian development, abundance, and activity. We sampled lower elevation lakes earlier in the season to decrease variation among lake pairs in stage of amphibian development and to ensure that we sampled lakes between egg hatching and metamorphosis.

On each lake, we set 37 unbaited collapsible funnel traps in the littoral zone at random locations and random depths between 0.15 and 0.50 m. Traps were set and retrieved in the same order so that individual trap soak times were as close to 24 h as possible (mean soak time = 23.14 h, standard deviation (SD) = 1.33 h). Observers recorded the species, snout-vent length (Heyer et al. 1994), and life stage (larva, metamorph, or adult) of each amphibian captured and Gosner developmental stage (Gosner 1960) for anuran (frog and toad) larvae and metamorphs.

Visual surveys were conducted during daylight (0900–1630 h) along strip transects at four randomly chosen sites per lake. We divided these sites into parallel shoreline and shallow water strata and sampled each stratum separately. Within each stratum, observers counted exposed animals along a 30 m × 2 m transect and determined the number, species, and life stage of all amphibians observed. The search time per unit of transect was standardized as much as possible among observers and lakes, and searches were avoided during weather conditions that could limit visibility. We avoided persistent observer biases by randomly allocating observers among lake types. Although we conducted visual surveys at all 38 lakes, we excluded transect data for the first eight lakes sampled because of methodological problems; thus the sample size for transect data was 15 per lake type.

We also recorded counts, species, and life stage for amphibians sighted at any time outside of trapping and visual transect surveys during the 2 days of sampling at each lake (i.e., incidental sightings). However, because incidental sightings were not a result of sampling standardized among lakes, we only included this data in the presence–absence analysis. Amphibians sighted during visual transect surveys at the first eight lakes were included in the incidental sightings data set.

We collected information about the shallow (<0.50 m) littoral habitat of each lake at 20 randomly selected quadrats (1 m^2) per lake (Table 2). We measured percent cover of aquatic vegetation (emergent and submerged), fine (<1 mm) and coarse (>1 mm) particulate organic matter, coarse woody debris (wood >7.5 cm diameter), and inorganic substrates, which were categorized as silt–clay (<0.05 mm), sand (>0.05 mm), pebble (>2 mm), gravel (>16 mm), cobble (>64 mm), boulder (>300 mm), and bedrock. We also used geographic information systems (GIS) analyses of provincial forest tenure road lines (Province of British Columbia 2005) and Watershed Atlas data (MSRM 2005) to calculate the percentage surface area of amphibian habitat (water bodies including wetlands, marshes, swamps, and lakes), density of streams (stream length, in metres per hectare), and density of roads (road length, in metres per hectare) within 100, 500, and 1000 m buffers around each lake. We performed two-sample Wilcoxon rank-sum tests and permutation tests (without pairing) similar to those described below to deter-

mine whether any habitat factors were significantly different between lake types.

Statistical analyses

Although analysis of habitat data showed that, on average, lakes with and without trout were similar for most habitat variables, lakes within an individual pair often differed in habitat factors such as size, aquatic vegetation, and bottom substrate. Analyzing trap and transect data with and without lake pair included as a blocking variable had no effect on statistical significance or our conclusions. Therefore, for analyses of trap and transect data we describe and report only analyses that ignore pairing for presence–absence and abundance data.

We used Fisher's exact test for count data to perform presence–absence analyses under the null hypothesis that the proportion of lakes where each species was present was the same between lake types. We considered a species present if we counted at least one larva, metamorph, or adult in any trap, transect, or incidental sighting. Because incidental sightings were not a result of standardized sampling, we conducted presence–absence analysis both with and without incidental sightings included. We also performed separate analyses for (i) presence of adults, metamorphs, and (or) larvae, and (ii) presence of metamorphs and larvae only. Because we sampled each lake only once and did not sample the entire shoreline of each lake, the detection probability for amphibians was very likely less than one. However, we assumed that the detection probability was the same on average between lake types because (i) sampling (excluding incidental sightings) was standardized among all lakes, and (ii) paired sampling of lakes with and without trout ensured that any effects of location, season, weather, or elevation on amphibian detectability were similar between lake types. Analysis of habitat data showed that, on average, lakes with and without trout were similar for most habitat variables, which suggests that influence of habitat on detectability was also similar between lake types.

We summarized trap and transect data to give two indices of abundance for each species and lake. Both are indices of relative rather than absolute abundance and are theoretically proportional to amphibian density in a lake (number of animals per hectare). Trap catch is the sum of larvae and metamorph counts across all traps, and transect count is the sum of larvae and metamorph counts across all land–water transects. We excluded adult data from trap and transect counts because our sampling methods targeted juvenile amphibians rather than adults and the final adult data set was small. In addition, data for larvae and metamorphs are 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 will be referred to hereafter as larvae or larval data.

Because trap catch and transect count data did not meet all assumptions of the two-sample t test, even after $\log(X + 1)$ transformation, we performed two sample Wilcoxon rank-sum tests on the null hypothesis of no difference between lake types in true means for each of the two abundance indices. We also tested our null hypothesis using permutation

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(randomization) tests (Efron and Tibshirani 1998). The achieved significance level (ASL) of a permutation test based on 5000 randomized test statistics is the proportion of values that are as extreme as or more extreme than the observed value; thus, the ASL has the same interpretation as a conventional p value.

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; thus, using a type I error rate greater than 0.05 may be justified in order to decrease the chances of making a type II error (Peterman 1990). We interpreted the results of all analyses as significant whenever $p \leq 0.10$ because our a priori power analysis predicted low power for some species.

Estimating the size of the impact of a given human activity is also important in environmental management applications. Such estimates can serve as biological reference points, which are increasingly used to define conservation thresholds and management targets for renewable resources (e.g., fisheries; Mace 1994). We estimated the impact of trout on abundance of each amphibian species as $I = \bar{x}_{\text{Trout}} / \bar{x}_{\text{No trout}}$, where $\bar{x}$ is mean trap catch or mean transect count for a given lake type. Although our study was not an experiment and thus cannot establish causation, this ratio can still be used to suggest the potential impact of trout. A ratio close to one suggests little difference in abundance between lake types and thus no impact, whereas values closer to zero suggest a potentially large negative impact. Bootstrap 90% confidence intervals for I were computed using a nonparametric, bias-corrected and accelerated (BC_a) method (Efron and Tibshirani 1998) and 10 000 bootstrap replicates.

We assessed the differences between lake types in (*i*) body size of long-toed salamanders and Columbia spotted frogs, and (*ii*) developmental stage for the Columbia spotted frog. Western toads and Pacific treefrogs were excluded from size and stage analyses because the data sets were too small to be meaningful, and stage analysis was not possible for salamanders because Gosner stages do not apply to salamander larvae. We used analysis of covariance (ANCOVA) to test the null hypothesis of no difference in true mean body size or developmental stage between lake types after accounting for date as a covariate. Date and elevation are both important in determining the progress of amphibian development (Heyer et al. 1994); however, elevation was not included as a covariate because date and elevation were correlated ($n = 38$; Pearson $\rho = 0.75$ and $p < 0.001$) as a result of our sampling design. We used mean snout-vent length (mm) and mean stage per lake as response variables. To account for differences among lakes in the number of observations included in the calculation of means, we used inverse-variance-weighted ANCOVA. Because weighted least squares analyses can sometimes give misleading results when weights are calculated from small numbers of observations (Carroll and Ruppert 1988), we excluded lakes with less than five observations from the analyses. Thus, for analyses of salamander length data we used 11 troutless and 6 trout lakes, and for spotted frog data we used 8 troutless and 4 trout lakes. In each of the three ANCOVA analyses, we included lake type, date, and a date – lake type interaction in the models. We also included a quadratic effect of date (date squared) on

length of spotted frog tadpoles because plots suggested that mean tadpole length in both lake types was highest in the middle of the sampling season. If the interaction between lake type and date was not significant ($p \leq 0.10$), we then fit the same model without the interaction term.

Results

Almost no habitat variables were significantly different between lake types (Table 2). Elevation, surface area, perimeter, and littoral distance were not significantly different between lakes with and without trout, nor were percent cover of aquatic vegetation (emergent and submerged), fine and coarse particulate organic matter, coarse woody debris, silt–clay, and bedrock. The amount of aquatic habitat and density of streams (stream length, in metres per hectare) within 100, 500, and 1000 m buffers around each lake were also not significantly different between lake types. Mean percent cover of several nonorganic substrates (boulder, cobble, pebble, and gravel) was significantly higher in lakes with trout ($W \leq$ 99.5, $n = 38$, $p < 0.02$; ASL < 0.03). However, mean percent cover of each nonorganic substrate was very low in both lake types ($\leq 5\%$ in lakes with trout and $\leq 1\%$ in troutless lakes), suggesting that the magnitude of difference between lake types was too small to have an important effect on our results. Road length within the 100, 500, and 1000 m buffers was also significantly higher for lakes with trout ($W \leq 121$, $n = 38$, $p < 0.08$; ASL < 0.09); however, the magnitude of the difference was again very small (≤ 5.2 m·ha^{-1}). Thus, the lack of important differences in habitat (on average) suggests that any observed differences in amphibian presence, abundance, body size, and (or) stage between lakes with and without trout was probably not caused by a systematic difference in habitat between lake types.

Long-toed salamanders and Columbia spotted frogs were present in a relatively high proportion of both lake types, whereas Pacific treefrogs and western toads were present in a relatively low proportion of both lake types (Table 3). Long-toed salamander, Pacific treefrog, and Columbia spotted frog larvae were present slightly more often in troutless lakes, but the differences were not statistically significant. In contrast, western toad larvae were present significantly more often in lakes with trout; however, this difference was no longer significant when we included adult toads in the analysis (Table 3).

Mean trap catch and mean transect count of long-toed salamanders, Columbia spotted frogs, and Pacific treefrogs were lower in lakes with trout (Table 4). Trap catch was positively correlated with transect count for all four species ($n = 30$ lakes; Spearman rank $\rho \geq 0.58$ and $p \leq 0.001$ for all species), suggesting the two sampling methods consistently indicated similar trends in amphibian abundance. Because transect counts presumably had lower power than trap catches because of the smaller sample size ($n = 15$ for transects versus $n = 19$ for traps), we report hypothesis test results only for trap catch, except where transect results differed in statistical significance from those of trapping. Results of Wilcoxon rank-sum and permutation tests both suggest that salamander abundance was lower in lakes with trout ($W = 259$, $n = 38$, $p = 0.02$; ASL = 0.04). However, transect counts of salamanders were not significantly differ-

Table 3. The proportion of British Columbia's southern interior lakes ($n = 19$ per lake type) sampled where only larvae of each species were present and where larvae or adults of each species were present.

	Larvae only			Larvae or adults		
Species	Troutless	Trout	p value	Troutless	Trout	p value
Trap and transect						
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
Pacific treefrog	0.37	0.26	0.73	0.42	0.42	1
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
Pacific treefrog	0.47	0.32	0.51	0.47	0.42	1
Western toad	0.16	0.47	0.08	0.42	0.63	0.33

Table 4. Mean trap catch and transect count of amphibian larvae (including metamorphs) in British Columbia's southern interior lakes in which rainbow trout were present or absent and estimates of the impact size (I) in lakes with trout.

	No. of larvae (mean ± SE)		Impact size	
Species	Troutless	Trout	I ± SE	90% CI
Trap catch ($n = 19$)				
Long-toed salamander	36.89±11.53	9.95±5.57	0.27±0.20	0.09–0.88
Columbia spotted frog	12.74±5.04	4.32±2.01	0.34±0.28	0.10–0.92
Pacific treefrog	7.32±5.58	0.21±0.10	0.03±0.12	0.00–0.17
Western toad	NA	329.11±314.01	NA	NA
Transect count ($n = 15$)				
Long-toed salamander	6.93±3.69	0.93±0.30	0.13±0.36	0.04–0.38
Columbia spotted frog	2.40±1.28	0.47±0.27	0.19±0.61	0.04–0.86
Pacific treefrog	7.93±7.36	0.27±0.21	0.03±0.39	0.00–0.63
Western toad	0.13±0.13	25.27±20.98	194.38±NA	NA

Note: SE, standard error; CI, confidence interval; NA, not applicable.

ent between lake types according to the Wilcoxon test ($W = 129$, $n = 30$, $p = 0.4764$). Trap catch of Pacific treefrogs was significantly lower in lakes with trout according to the permutation test (ASL = 0.10) but not the Wilcoxon test ($W = 188.5$, $n = 38$, $p = 0.759$). However, transect counts of treefrogs were significantly lower in lakes with trout according to the Wilcoxon test ($W = 149$, $n = 30$, $p = 0.06$). We detected no difference in Columbia spotted frog abundance between lake types ($W = 228.5$, $n = 38$, $p = 0.133$; ASL = 0.14).

In contrast with the other three species, no toad larvae were caught in traps in any troutless lake, and the permutation test indicated that transect counts (ASL = 0.10) of western toad larvae were greater in lakes with trout (Table 4). However, transect counts of toad larvae were not significantly different according to the Wilcoxon test ($W = 88$, $n = 30$, $p = 0.1252$) and were no longer significantly different using the permutation test when the lake pair containing an extremely large outlier was removed (ASL = 0.21).

Sample estimates of impact size for both trap catch and transect count suggest that larval densities were much lower in trout lakes for long-toed salamanders, Pacific treefrogs, and Columbia spotted frogs. Bootstrap 90% BC$_a$ confidence intervals did not overlap 1.0 for any of these species and included zero for Pacific treefrog (Table 4), suggesting a sig-

nificant impact, even though the corresponding results of hypothesis testing were not always significant. Although we could not estimate impact size based on trap catch of western toads (no toads were caught in traps in troutless lakes), the estimate for transect counts indicated much greater western toad abundance in lakes with trout (Table 4). Similar to the results of hypothesis tests described above, when the lake pair containing an extreme outlier was removed, estimated impact for western toad decreased from $I = 194.38$ to $I = 31.96$.

We observed no significant interactions between lake type and date for any of the body size and stage analyses; thus we report ANCOVA results using models fit without the interaction term. Long-toed salamander larvae were significantly smaller in lakes with trout compared with lakes without trout (ANCOVA, $F_{[1,14]} = 9.70$, $p = 0.008$; Fig. 1). Salamander length was also significantly associated with date (ANCOVA, $F_{[1,14]} = 8.31$, $p = 0.012$; Fig. 1). Columbia spotted frog length was significantly associated with date (ANCOVA, $F_{[1,8]} = 4.30$, $p = 0.072$) and date squared (ANCOVA, $F_{[1,8]} = 30.55$, $p = <0.001$) but was not significantly associated with lake type (ANCOVA, $F_{[1,8]} = 0.05$, $p = 0.829$). Similarly, spotted frog stage was significantly associated with date (ANCOVA, $F_{[1,9]} = 16.46$, $p = 0.003$) but not with lake type (ANCOVA, $F_{[1,9]} \leq 0.01$, $p = 0.998$).

Fig. 1. Mean body size (snout-vent length) per lake of long-toed salamander larvae versus sampling date in lakes with trout (▲) and in troutless lakes (○), and regression lines for snout-vent length as a function of date. The broken line is for lakes with trout (length = 0.01 + 0.13(date), R^2 = 0.56, p = 0.003) and the solid line is for troutless lakes (length = 3.62 + 0.13(date), R^2 = 0.56, p = 0.003).
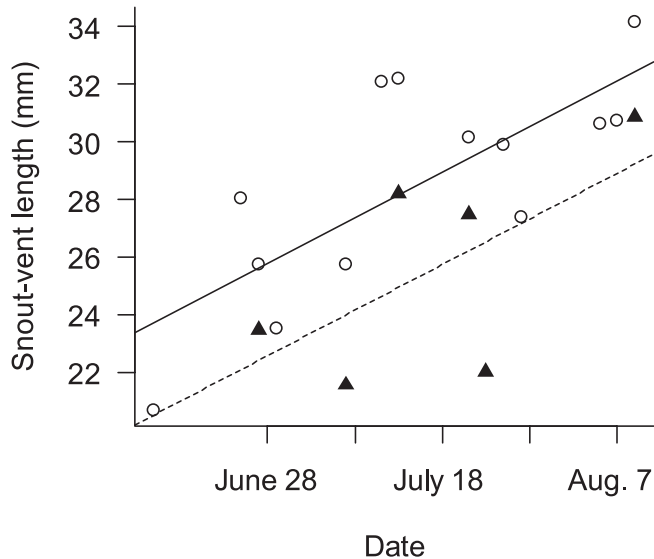
However, Columbia spotted frog larvae were absent from lakes with trout after the third week of July (July 23) but remained present in troutless lakes until the end of the sampling season in August (August 9). The latest stage larva observed in a trout lake was stage 42, even though larval stages 43–46 were observed in troutless lakes.

Discussion

Our results indicate that trout stocking in British Columbia's southern interior lakes has probably not led to widespread extirpations of aquatic-breeding amphibians and that some level of coexistence is currently possible between trout and amphibians in this region. There are several reasons why amphibians may be better able to coexist with trout in British Columbia's southern interior compared with other regions investigated in the literature. Many studies in North America focus on oligotrophic alpine lakes that were fishless prior to trout introductions and that have little habitat complexity. Amphibian production may be especially sensitive to introduced trout in unproductive, low-complexity alpine lakes because (*i*) larvae often need to overwinter at higher elevations, which restricts amphibians to permanent habitats that are more likely to be occupied by trout, (*ii*) lower habitat complexity provides less cover from predators, and (*iii*) amphibians evolved locally without pressure to develop defenses to fish predators (Pilliod and Peterson 2001; Welsh et al. 2006). In contrast, lakes in British Columbia's southern interior are found at lower elevations and are generally productive with relatively high habitat complexity, and natural populations of fish predators do occur in the region.

Our data suggest that amphibians in the southern interior do not overwinter as larvae in lakes at the elevations included in this study and thus do not necessarily depend on deep permanent lakes for breeding. For example, even in our highest elevation lakes (<1400 m), larvae of all species showed signs of metamorphosis toward the end of the growing season (early August). Although it is possible that adult amphibians may require permanent lakes for overwintering and thus may be negatively affected by trout (Pilliod and Peterson 2001), because amphibians do not depend on permanent lakes for breeding and trout can not survive in temporary water bodies, abundant ephemeral habitats may help amphibians to coexist regionally with trout by providing opportunities to avoid trout, at least during breeding. We did not quantify ephemeral habitats within our study region, but we observed abundant wet depressions and other small water bodies in many areas. Amphibians without antipredator defenses often breed more successfully in ephemeral habitats because of the lack of predators (Woodward 1983; Kats et al. 1988; Semlitsch 2002) and may preferentially breed in ephemeral habitats as an antipredator behaviour (Binckley and 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 and Lannoo 2005). In at least some regions, Pacific treefrogs show increased presence and survival in shallow ephemeral sites (Adams 2000; Matthews et al. 2001). A preference for breeding in ephemeral habitats may explain why treefrog abundance and probability of presence were low in both lake types during this study.

The productive and complex nature of lakes in our study region may also increase the probability of coexistence between amphibians and fish. Amphibians may be more abundant in lakes with higher productivity, likely because of higher food abundance (Tyler et al. 1998*a*), which could increase resiliency to trout. Complex habitat structure in our lakes (abundant organic matter, aquatic vegetation, and coarse woody debris) may provide larval amphibians greater refuges from fish predators (Hecnar and M'Closkey 1997) and reduce the foraging efficiency of fish (Diehl 1992). For example, Columbia spotted frogs can apparently breed successfully in water bodies with fish if there is dense emergent vegetation in the littoral zone (Reaser and Pilliod 2005). However, studies that included some lakes with habitat similar to ours show negative interactions between trout and some amphibians (including Pacific treefrogs), even after taking variation due to habitat into account (Knapp 2005; Knapp et al. 2005). Thus habitat complexity may not always prevent negative interactions between amphibians and trout.

Because rainbow trout occur naturally in British Columbia's southern interior, the natural distributions of trout and amphibians overlap considerably, which may improve probability of coexistence because antipredator defenses are more likely in amphibians that encounter predators more frequently (Kats et al. 1988). On the other hand, amphibians may have many opportunities to avoid predators in British Columbia's southern interior because troutless lakes are quite common. There are more than 12 000 mapped lakes in the Thompson–Nicola region of British Columbia, which is a 5.77 million

hectare area encompassing most of our study lakes. Approximately 98% of these lakes are less than 40 ha in surface area, only 8% (1000 lakes) are known to contain freshwater game fish, about 4% have at least one record of hatchery releases, and only 2% (228 lakes) were actively stocked with fish (mostly rainbow trout) between 2002 and 2005. Thus, much of the habitat for amphibians in this region is currently troutless, which may help amphibians coexist with trout either through preferential breeding in troutless habitats (Binckley and Resetarits 2003) or immigration from troutless habitats to lakes with trout (Sjögren 1991).

Higher western toad abundance and probability of presence in lakes with trout is consistent with existing field studies that show either a positive or no association between western toad presence and (or) abundance and introduced trout (Bull and Marx 2002; Welsh et al. 2006). As in other *Bufo* species with larvae that are unpalatable to fish (Kruse and Stone 1984), western toad larvae are unpalatable to trout and remain active in their presence (Kiesecker et al. 1996), often swimming in large schools that do not appear to provoke a response from nearby trout (Welsh et al. 2006). However, because western toad larvae are often palatable to invertebrate predators (Peterson and Blaustein 1992; Kiesecker et al. 1996), trout may positively influence toads by reducing predatory invertebrate abundance (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 (Adams et al. 2003). Toads may be particularly susceptible to predation by aquatic insects relative to other species because of their tendency to remain active even in the presence of predators (Peterson and Blaustein 1992).

Even though our results suggest that introduced trout and amphibians may currently coexist in British Columbia's southern interior lakes, our results also suggest that trout may have important effects on amphibian population abundances, which may have implications for population dynamics and may decrease the ability of amphibians to coexist with trout in the future. In spite of potentially low power, our results provide some evidence of lower larval abundance in the presence of trout for long-toed salamanders, Columbia spotted frogs, and Pacific treefrogs, with particularly strong evidence for the long-toed salamander. In addition, the estimated impact ratios for these species were lower than 0.35, which represents 65% lower abundance in the presence of rainbow trout. The number and quality of metamorphosing larvae that recruit to adult stages can be important to amphibian population dynamics (Beebee et al. 1996; Semlitsch 2002), and poor recruitment over multiple years can lead to decline of local populations (Semlitsch et al. 1996; Semlitsch 2002). Lower recruitment is also likely important to adjacent water bodies because many amphibian populations are considered spatially structured as metapopulations (Alford and Richards 1999), and processes of migration, extinction, and recolonization are important to amphibian population dynamics (Gill 1978; Sjögren 1991). Differences in larval output of the magnitude we estimated could cause population role reversals in which "source" amphibian populations become "sink" populations that are maintained mainly through immigration (Knapp and Matthews 2000; Pilliod and Peter-

son 2001). For example, conversion by trout of deep permanent lakes from sources to sinks is the likely cause of landscape-scale declines of long-toed salamanders and Columbia spotted frogs in a high elevation area of Idaho, where these species require deep permanent lakes for overwintering, but introduced trout occupy the majority of deep, permanent lakes (Pilliod and Peterson 2001). Such source–sink reversals increase the probability of local extinction and may lead to declines in amphibian abundance at a landscape scale, including troutless habitats, because of increased population fragmentation and isolation (Bradford et al. 1993; Knapp and Matthews 2000; Pilliod and Peterson 2001). It is therefore possible that the proportion of amphibian populations affected by trout stocking in British Columbia is higher than the proportion of lakes that are regularly stocked with trout.

The fact that hypothesis testing did not consistently detect significant associations between trout and Columbia spotted frogs and Pacific treefrogs suggests either a relatively small effect of trout on these species or low statistical power. Our a priori power analysis indicated that the trap sampling design did not have adequate power to detect a 50% or smaller decrease in abundance of spotted frogs in the presence of trout. Although predicted power appeared adequate for Pacific treefrogs, the power analysis was based on a small sample of lakes that likely did not capture the full range of variability in treefrog abundance, so power may have also been an issue for the treefrog. We sampled a relatively small number of lakes compared with several larger-scale studies that do show significant negative associations with trout for the two frogs and the salamander (e.g., Matthews et al. 2001; Pilliod and Peterson 2001; Welsh et al. 2006). Because the power of our study was relatively low, the fact that hypothesis testing did not detect consistently significant associations between trout and amphibians does not necessarily mean that trout do not have an important effect in our study region, especially given that the literature suggests that three of the four species are at least sometimes negatively associated with trout.

It is possible that the observed patterns of lower abundance and lower presence in lakes with trout could have resulted from amphibians hiding more or being less active in lakes with trout, thus lowering the probability of detecting amphibians relative to troutless lakes. Increased refuge use and decreased activity in the presence of fish predators has been observed among amphibians, including the long-toed salamander (Figiel and Semlitsch 1990; Tyler et al. 1998b). However, even if such changes in behaviour were responsible for the trends observed in our data, these changes could still be considered negative effects of trout on amphibians, because increased refuge use and decreased activity could interfere with feeding, which could ultimately have negative effects on body size and (or) survival (Semlitsch 1987; Figiel and Semlitsch 1990; Tyler et al. 1998b).

Our results show that body size of long-toed salamanders was smaller in the presence of trout. Smaller body size at metamorphosis may have negative carry-over effects on adult amphibians in the terrestrial environment (Semlitsch 2002), such as decreased survival and decreased ability to disperse (Chelgren et al. 2006). One hypothesis to explain smaller size in lakes with trout is that salamander growth

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rates are lower because of food competition with trout. Long-toed salamander larvae feed on aquatic invertebrates such as zooplankton and insects (Pilliod and Fronzuto 2005) and such a diet overlaps substantially with that of rainbow trout occupying British Columbia's southern interior lakes (Post et al. 1999). Our observation that Columbia spotted frog larvae, which feed on algae and detritus (Reaser and Pilliod 2005), were not significantly smaller in lakes with trout further supports this hypothesis. Another hypothesis to explain decreased body size in salamanders is that increased refuge use in the presence of predators appears to interfere with the predatory feeding activity of long-toed salamander larvae, which could also reduce body size (Semlitsch 1987; Figiel and Semlitsch 1990; Tyler et al. 1998b) even if no diet overlap existed between salamanders and trout.

Although the timing of developmental stages of Columbia spotted frogs was similar between lakes with and without trout, later developmental stages were absent in trout lakes toward the end of the growing season. Although this could be an artefact of sampling particular lakes later in the season, it could also indicate that later developmental stages of spotted frogs are particularly susceptible to interactions with trout. For example, Gosner developmental stages that were missing from lakes with trout are stages during which larval tails are shrinking and front legs are developing (Gosner 1960). These changes could lead to lower mobility than at earlier developmental stages, which could increase susceptibility of Columbia spotted frog larvae to predation. These results also suggest that trout could have a negative effect on spotted frog recruitment, even though breeding may occur in the presence of trout. Such effects may have been more apparent if we had considered recruitment of larvae into the adult population or if we estimated amphibian survival. Metapopulation dynamics suggest that breeding by immigrants from other local populations can augment the number of larvae observed in a particular lake (Sjögren 1991), which could maintain amphibian presence even where conditions are not favourable for recruitment (Pilliod and Peterson 2001). Such "rescue" effects (Sjögren 1991) could lead to more gradual and more difficult to detect declines in amphibians in response to trout (Knapp and Matthews 2000; Pilliod and Peterson 2001; Vredenburg 2004).

Our results indicate that although amphibians currently appear to coexist with trout in British Columbia's southern interior, abundance and body size of at least some amphibian species may be significantly lower in lakes with trout. This conclusion is consistent with most trout–amphibian studies in North America that also show some degree of negative association between trout and amphibians. Therefore, we suggest that explicit amphibian conservation measures be incorporated into trout stocking policy in British Columbia, especially where trout stocking is widespread or where expansion of trout stocking is proposed. Clearly, the high value of recreational fisheries on British Columbia's lakes requires that trade-offs be made between amphibian conservation and trout stocking. To conserve amphibians, stocking policies should aim to preserve a range of troutless aquatic habitats across the landscape to reduce potential impacts on amphibian metapopulation dynamics. In addition, trout stocking impacts on amphibians should be periodically monitored and evaluated against quantitative biological reference points

such as the impact size ratio we describe. For example, periodic amphibian surveys could be evaluated against guiding policy statements such as (hypothetically) "maintain at least a 90% probability that mean larval amphibian abundance in 50% of stocked lakes does not fall below 30% of the average in similar troutless lakes over a 10 year period". Further research incorporating amphibian population dynamics, short- and long-term climatic effects, variable stocking rates, and the value of stocking would help to specify target reference points and probabilities that achieve an appropriate balance between amphibian conservation and recreational fishery value.

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