



FRESHWATER ECOLOGY

Run-of-river dams as a barrier to the movement of a stream-dwelling amphibian

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Abstract. Human activities frequently create structures that alter the connectivity among habitats or act as barriers to the natural movement of animals. Movement allows individuals to access different habitats, connect life history stages, and maintain genetic diversity. Here, we evaluated whether run-of-river (RoR) hydropower projects, an emerging renewable energy source in British Columbia, interrupt the longitudinal connectivity among larval stream amphibians, by altering larval rearing densities, with possible repercussions on growth and survival. In three watersheds, we tested for differences in the average upstream and downstream density of larval coastal tailed frog (*Ascaphus truei*), as well as changes to their longitudinal distribution upstream of the dams, as would be expected if RoR dams or their headponds act as barriers to the natural downstream drift of larvae. We found a 60% decrease in larval densities downstream compared to upstream of dams, consistent with RoR dams interrupting the natural pattern of downstream *A. truei* drift. Larval densities in the first 10 m above RoR headponds were 3 times higher compared to 100 m upstream, and when expressed in terms of relative abundance, we find a similar pattern, with between 2.5 and 3 times more larvae in the first 10 m above of the headpond than expected if larvae followed a uniform distribution. Our results are consistent with the hypothesis that RoR dams alter the spatial connectivity of *A. truei* larvae, leading to an accumulation of larvae directly above the dam, with unknown consequences for larval growth and survival. Our findings suggest caution is warranted when interpreting before–after monitoring studies that are often used to evaluate the impact of dams, whereby we find that reductions in downstream densities could be due to interruptions of downstream movement as opposed to direct mortality.

Key words: *Ascaphus truei*; barrier; connectivity; dam; downstream drift; migration; run of river; small hydropower.

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INTRODUCTION

Human activities, such as the construction of roads, powerlines, railroads, and energy

infrastructure, often interrupt connectivity among habitats and the movement of individual species (Schreiber and Graves 1977, Goosem and Marsh 1997, Ito et al. 2005, Masden et al. 2009,

Clark et al. 2010). The movement of individuals within and between habitats is important to the maintenance of genetic diversity and population viability (Fahrig and Merriam 1985, Dixo et al. 2009), and disruptions can cause genetic drift and local extinction (Templeton et al. 1990, Hanski 1998). For many species with complex life histories, ontogenetic movement is necessary to connect habitats required by different life history stages (Werner and Gilliam 1984, Taylor et al. 1993, Lucas and Baras 2001). Similarly, in river networks connectivity between downstream and upstream reaches, known as longitudinal connectivity, is often essential for population persistence (Fagan 2002) and such movements are often vulnerable to instream structures such as culverts, roads, weirs, and dams (Lucas et al. 2009). Barriers can fracture previously continuous river segments (Jager et al. 2001), make recolonization after stochastic events unlikely (Fagan et al. 2002), alter the spatial distribution of species upstream of a barrier (Favaro and Moore 2015), or act as bottlenecks by allowing only larger species to pass (Warren and Pardew 1998). Hydropower dams are one of the most common forms of instream barriers, with nearly 3000 projects globally (>1 megawatt) estimated to be operational by 2020 (Lehner 2011).

Previous research has established that large hydropower dams act as barriers for many riverine species by preventing upstream movement (Caudill et al. 2007, Lucas et al. 2009, Araújo and Wang 2015), with unintended consequences ranging from increased genetic isolation between upstream and downstream populations (Heggenes and Røed 2006), to local extinction. For example, multiple species of salmonid fishes (Genus *Onchorynchus*) and lamprey (Genus *Lampetra*) have been locally extirpated because hydropower dams prevented access to critical spawning and rearing habitats (Beamish and Northcote 1989, Nehlsen et al. 1991). Additionally, despite their terrestrial life stage, foothill yellow-legged frog (*Rana boylei*) connectivity and genetic diversity have been reduced by large dams and flow regulation in northern California (Peek et al. 2018). Given these unintended but frequent impacts to riverine taxa, research and monitoring efforts associated with large hydropower dams often focus on the effectiveness of mitigation efforts, such as structures built to restore

upstream connectivity of populations (Trussart et al. 2002) and allow migratory species to reach spawning habitats (Gowans et al. 1999, Lucas et al. 2009; e.g., ladders, locks, and the capture and transportation of fish to upstream reaches). However, the consequences of interrupting downstream movement are less frequently the focus of study, but can be equally important to population persistence (Lucas and Baras 2001). For example, when dam mitigation infrastructure only facilitates upstream passage of migratory fish, populations may be trapped in upstream spawning habitats such that larvae or juveniles are prevented from accessing downstream reaches (Mayer and Antonio 2007). Scenarios such as these may be driving population discontinuity in smaller, higher order, mountainous streams as well, which are increasingly the location of new dam construction (Couto and Olden 2018).

Over half of the world's largest river systems are affected by large hydropower dams (Nilsson et al. 2005). With so many large rivers already dammed, smaller streams are often the focus of new electricity generation using a range of small hydropower technologies, such that globally there are estimated to be 11 small hydropower plants for every large hydropower plant (Couto and Olden 2018). Despite the fact that small hydropower now constitutes 90% of all hydropower projects in the world, there is far less empirical research on their impact to species and river ecosystems. A recent review of hydropower research found that only 5% of published studies specifically examined small hydropower (Couto and Olden 2018). Of the research that has been done, studies have found that small hydropower dams, which are generally considered between one and 50 megawatts in Canada (Natural Resources Canada 2018), have impacts on instream habitat through geomorphological changes both upstream and downstream of small dams with the interruption of sediment transport (Csiki and Rhoads 2010, Fuller et al. 2016), and the alteration flow regimes, decreasing downstream channel width and increasing temperatures (Gibeau et al. 2016, Gibeau and Palen, *unpublished manuscript*). Many of the river networks that these projects are constructed on are thought to serve an important role in current and future watershed stability (Favaro and Moore

2015, Chezik et al. 2017), provide a climate refuge for cold-water species (Isaak et al. 2016), and maintain downstream water quality (Alexander et al. 2007). One form of small hydropower is run of river (RoR), which uses a small dam to create a deep, slow-moving waterbody, termed a headpond, to divert a portion of the river flow into a pipe where it flows downhill and is returned to the watercourse after passing through power generators. Here, we evaluated whether run-of-river dams, and their associated headponds, create discontinuities in the longitudinal distribution of a stream-dwelling amphibian larvae, *Ascaphus truei*, consistent with interrupted downstream movement.

Coastal tailed frog (*Ascaphus truei*) is a stream-associated amphibian ranging from Northern California to Central British Columbia (BC) and is listed as special concern in Canada and California, and sensitive in Oregon (COSEWIC 2012, Oregon Department of Fish and Wildlife 2016, Thomson et al. 2016). *Ascaphus truei* larvae are benthic biofilm grazers that occur in steep montane tributaries with coarse substrate and are adapted to high-velocity stream environments (Mallory and Richardson 2005), displaying strong rheotactic behavior (Altig and Brodie 1972). Many stream organisms employ downstream drift in their life cycle (Brittain and Eikeland 1988), and *A. truei* are thought to employ this life strategy as well, with biased seasonal upstream movement during their terrestrial life stage to compensate for downstream drift (Wahbe and Bunnell 2001, Wahbe et al. 2004, Macedo 2019). Timing of breeding varies depending on elevation and latitude, but females store sperm internally until oviposition, which occurs anywhere from June to August (Sever et al. 2001, Karraker 2006). Eggs are deposited on the downstream side of embedded boulders and cobble in riffles or pools in fast-flowing cobble streams (Karraker 2006), and larvae live in interstitial spaces for one to four years, depending on latitude and elevation (Bury and Adams 1999), before metamorphosing into terrestrial juveniles (Wahbe et al. 2004). *Ascaphus truei* remain juveniles for 3–5 yr after metamorphosis (Matsuda et al. 2006), and once mature, females may move further distances compared to males (Honeycutt et al. 2019). Because of these habitat requirements, *A. truei* have high overlap with current and potential RoR projects throughout their

range in coastal mountains of Northwestern North America.

Pre-construction data from an ongoing before-after-control-impact (BACI) study on RoR rivers suggest that larval *A. truei* densities between upstream and downstream reaches before RoR dam construction are similar regardless of stream position (Appendix S1: Fig. S1). Given these preliminary findings, we conducted surveys of larval *A. truei* in three watersheds with RoR hydropower projects to assess whether RoR dams and their associated headponds alter the spatial distribution of larval *A. truei* by acting as barriers to downstream movement. We predicted that if downstream drift is important for *A. truei* connectivity, larval densities would be lower downstream of RoR dams compared to upstream. Second, we expected that if RoR dams and associated headponds act as barriers to downstream larval *A. truei* movement, we would find peak larval densities directly upstream of the dams, and that densities would decrease with distance upstream.

METHODS

Study system

We surveyed *A. truei* populations in three high-gradient (4–9%) third-order streams (Stokke, Fire, and Tipella Creeks) in Southwestern British Columbia, where each stream includes an operating run-of-river (RoR) hydropower project, all commissioned in 2009 (Fig. 1). Each stream is within the Lillooet and Harrison watersheds and has abundant coastal tailed frogs (*Ascaphus truei*; R. G. Murray, *personal observations*). RoR hydropower projects are typically characterized by the presence of a low-head dam (<17 m), behind which is an excavated area that widens and deepens the stream, resulting in a headpond with little flow and water residence times of <5 d (McManamay et al. 2016). The bypassed reach downstream of the dam remains wetted, but experiences substantially reduced flows. Sediment transport by streams with RoR hydropower is interrupted by the presence of the dam (Fuller et al. 2016), where the precipitous drop in discharge that occurs immediately upstream of the dam results in an alluvial-type deposit of sediment that extends into and upstream of the headpond. We define the

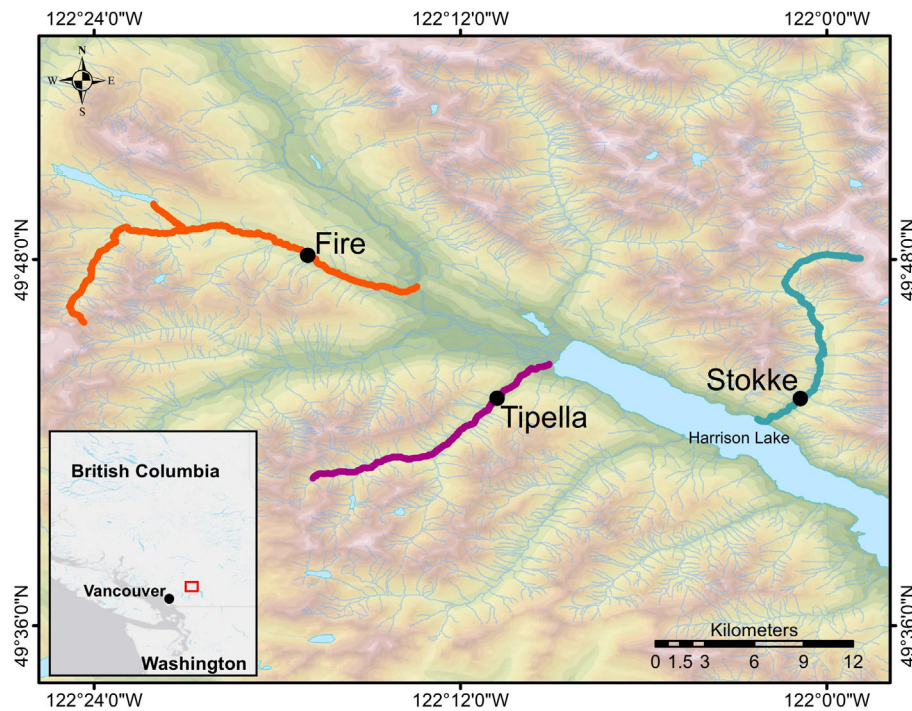


Fig. 1. Study area within the Lillooet River and Harrison Lake drainage in Southwestern British Columbia. Dots represent the location of the dams and associated headponds within the three study streams. Background colors represent elevation above sea level ranging from 6 to 2600 m (from green to pink).

headpond-affected reach as occurring between the upstream extent of the headpond and the upstream edge of the alluvial deposit (study streams ~70–120 m long).

Above–below dam surveys

We hypothesized that RoR dams and their associated headponds create a barrier to the connectivity of *A. truei* larvae by interrupting natural downstream drift. To evaluate this hypothesis, we conducted time-constrained surveys (15 min) of larval density at 12 locations upstream and downstream of dams in each study stream (72 survey locations) during July–August 2015. We randomly selected two 1-m² plots at six distances (100 m, 200 m, 300 m, 400 m, 500 m, and 600 m) upstream and downstream of each RoR dam. Two researchers sampled each plot by lifting and inspecting the cobbles and gravels up to a substrate depth of 5–10 cm, with a small dip net placed on the downstream side to capture dislodged larvae. Additionally, we installed block nets on the three downstream edges of each plot

to capture drifting larvae missed by lifting cobbles and gravel.

Longitudinal upstream surveys

To help determine whether RoR dams act as barriers to the longitudinal distribution of *A. truei* larvae, we mapped environmental characteristics associated with *A. truei* larvae upstream of RoR dams, selecting areas of cobble with low embeddedness, shallow to medium depth, and moderate to high flows (Dupuis and Steventon 1999), in August 2017. We selected 5–10 survey plots (range 2–20 m²) within the headpond-affected reach (range 70–120 m upstream) of each stream, with the total number and size of plots per stream depending on the length of the headpond-affected reach and size of high-quality habitat patches. We searched plots using the same techniques as above, recording the number and age class of all *A. truei* larvae, as well as environmental characteristics expected to influence habitat suitability: mean sediment size (diameter, cm), depth category (1, 2, or 3, shallowest to

deepest), habitat type (run, riffle), fine sediment embeddedness (%), canopy cover (%), distance to wetted edge (m), water flow category (1, 2, or 3, slowest to fastest), and distance upstream from headpond (m). Additionally, we estimated biofilm ash-free dry mass (AFDM) and chlorophyll a content for two rocks per plot as an index of biofilm resources to *A. truei*. To estimate available coastal tailed frog larval habitat and sample plot locations in relation to each headpond, we used aerial drones (DJI Mavic Pro) to photograph georeferenced plot locations (GPS, UTM) for analysis in ArcMap 10.7 (ESRI, Redlands, California, USA). In ArcMap, we created polygons of inferred *A. truei* habitat (area, m²) based on surveys and georeferenced locations, and calculated total area in each 10-m reach from the top of each headpond to the upstream most extent of the headpond-affected area, measured along a midline centered on the stream channel.

Above–below dam analysis

To compare the density of larvae upstream and downstream each of the three dams, we created a general linear model of *A. truei* density as a function of location (above or below dam) and stream (Fire, Tipella, Stokke) with a negative binomial error distribution to account for overdispersion in R (R Core Team 2019), using the package MASS (Venables and Ripley 2002). We competed all possible combinations of the global model, including a stream–location interaction and an intercept-only model (5 total models), using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2003). We used the top AIC_c-ranked model to predict larval densities above and below RoR dams for each stream.

Longitudinal upstream analysis

To describe the change in density of *A. truei* larvae with distance upstream from the headpond, we constructed a count-based general linear model in R with a negative binomial error distribution to accommodate our low number count data and account for overdispersion. We used data from the longitudinal upstream surveys (above dam) to model the number of larvae per plot as a function of distance upstream from the headpond, AFDM, canopy cover, biofilm chlorophyll a content, depth category, embeddedness,

distance from edge, habitat type, mean sediment size, flow category, and stream, and used plot area (m²) as an offset to convert our response to number of larvae per square meter. We standardized and centered the continuous variables by subtracting the mean and dividing by two standard deviations (Schielzeth 2010), and computed a Pearson correlation coefficient (*r*) for each. All variables had an *r*-value of <0.7 and thus remained in the global model. We competed all possible combinations of the global model in an AIC_c framework using the model selection package in MuMIn (Barton), without interaction effects. After finding low support for the top model (AIC *w* = 0.15), we averaged models contained within the top 95% weight of support, as described by Burnham and Anderson (2003), and computed the model-averaged regression coefficients and unconditional standard errors with the MuMIn package (Barton). Among the models included in the model average, we computed relative variable importance (RVI) values for each coefficient by summing the Akaike weights across all models containing each coefficient.

Longitudinal larval abundance

To evaluate how changes in habitat availability due to RoR construction amplify or dampen patterns observed in larval density, we made a first-order estimate of the longitudinal distribution of larval *A. truei* abundance within the headpond-affected reach. We used the model-averaged coefficients described above, computing predictions of average larval density for each 10-m stream segment within the headpond-affected reach for each stream. We computed predictions as a function of distance from headpond for each stream, while fixing all other environmental variables at their mean value, and holding habitat type as riffle, flow as high. We multiplied predictions of larval density for each 10-m stream segment by the area (m²) of inferred *A. truei* habitat to produce abundance estimates and converted those to relative abundance. Using the relationship between surveys of high larval density and drone photographs of those sites, georeferenced in ArcMap, we inferred additional high-quality habitat throughout the remaining headpond area, excluding areas with water depth >50 cm, as those areas were expected to have either very low density or absent *A. truei*. To evaluate the

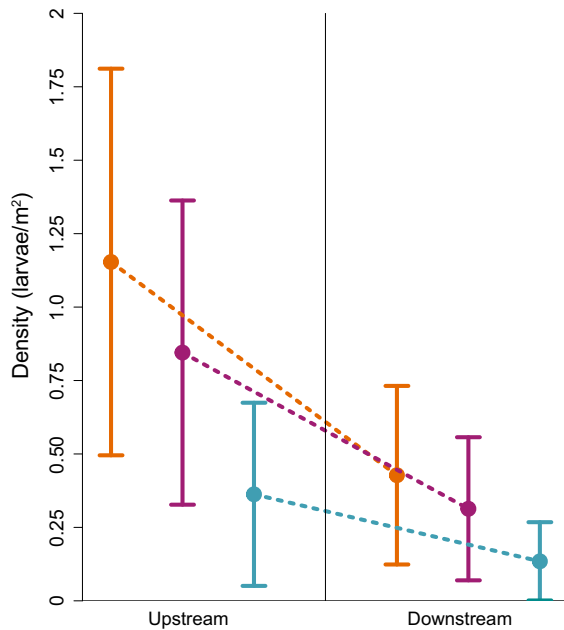


Fig. 2. Comparison of tadpole density upstream and downstream dams with 95% confidence intervals (Fire, orange; Tipella, purple; Stokke, blue). Dashed lines show pair-wise comparisons.

sensitivity of our conclusions to assumptions regarding habitat suitability, we also estimated *A. truei* relative abundance using total wetted area (m²), where all wetted area was assumed to be potential *A. truei* habitat.

RESULTS

Above–below dam

To determine whether dams and associated headponds reduce larval densities downstream of dams by acting as barriers to downstream drift, we compared densities of larvae above and below all three dams studied. We found approximately three times higher larval *A. truei* density above each RoR dam compared to below (Fire = 2.67, Tipella = 2.74, Stokke = 2.77), where Fire Creek had the highest density of larvae with an average of 1.15 larvae/m² upstream and 0.43 larvae/m² downstream (95% CI = ±0.65 upstream, 95% CI = ±0.30 downstream), and Tipella Creek, 0.85 larvae/m² upstream and 0.31 larvae/m² downstream (95% CI = ±0.52, 0.24), and Stokke Creek had the lowest densities, with 0.36 larvae/

m² upstream and 0.13 larvae/m² downstream (95% CI = ±0.31, 0.13; Fig. 2).

Longitudinal upstream pattern

To evaluate support for whether the headpond acts as a barrier and causes peak *A. truei* larval density to occur immediately upstream of the headpond, decreasing with distance upstream, we estimated larval densities at increasing distances upstream from headponds on all three streams. We compared the fit of 2048 generalized linear models, consisting of all combinations of 9 different uncorrelated ($r < 0.7$) habitat variables, stream, and distance to headpond. The top AIC_c-ranked model had a weight of 0.15 (out of 1) and contained the variables distance upstream from headpond, stream, flow, embeddedness, Chl *a*, and depth. We found that 187 models made up the top 95% AIC_c weight, with distance upstream from headpond appearing in all top models (Table 1). As expected, our model average confirmed that there are large differences in overall *A. truei* densities among streams (Fire $\beta = 0.41$, Tipella $\beta = 0.30$, Stokke $\beta = 2.60$). Of the remaining variables, distance upstream from headpond had the greatest influence on larval density ($\beta = -1.13$, 95% CI = ±0.48), almost two times greater than the next most influential variable, and also had an RVI of 1.00 (Fig. 3). This translates to a 14.6% decrease in average larval density (95% CI = ±5.53%) for every ten meters upstream of the headpond across all three streams (Fig. 4). Model average coefficients and RVI values revealed that four additional environmental variables have a large influence on *A. truei* larval density—higher densities are found in areas of higher flow ($\beta = 0.67$, CI = ±0.42, RVI = 0.97), at shallower depth ($\beta = -0.46$, 95% CI = ±0.28, RVI = 0.97), less embedded substrate ($\beta = -0.34$, 95% CI = ±0.26, RVI = 0.90), and higher biofilm chlorophyll content ($\beta = -0.39$, 95% CI = ±0.36, RVI = 0.86; Fig. 3).

Longitudinal larval abundance

Changes in larval *A. truei* density could be moderated or amplified by potential changes in habitat availability surrounding RoR headponds. We combined our model average estimates of *A. truei* density as a function of distance upstream of headponds, with the amount of inferred *A. truei* habitat in each 10-m segment and found that the total area of *A. truei* habitat above RoR headponds varied depending

Table 1. AIC model selection results for generalized linear models of *Ascaphus truei* density upstream from headponds on three streams in Southwest British Columbia with RoR hydropower dams, including top-ranked models (<2 ΔAIC_c units), global model, and intercept-only model.

Model variables	df	logLik	ΔAIC_c	w
Chl <i>a</i> + Depth + Embeddedness + Flow + Dist Upstream of Headpond + Stream	9	-72.63	0.00	0.15
AFDM + Chl <i>a</i> + Depth + Embeddedness + Flow + Dist Upstream of Headpond + Stream	10	-72.50	1.72	0.06
Chl <i>a</i> + Depth + Embeddedness + Flow + Dist Upstream of Headpond + Stream + Sediment Size	10	-72.56	1.85	0.06
Chl <i>a</i> + Depth + Dist. to Edge + Embeddedness + Flow + Dist Upstream of Headpond + Stream	10	-72.60	1.93	0.06
Chl <i>a</i> + Depth + Embeddedness + Flow + Dist Upstream of Headpond + Stream + Habitat Type	10	-72.61	1.94	0.06
Canopy Cover + Chl <i>a</i> + Depth + Embeddedness + Flow + Dist Upstream of Headpond + Stream	10	-72.62	1.96	0.05
AFDM + Chl <i>a</i> + Canopy cover + Depth + Distance to edge + Embeddedness + Flow + Distance upstream from headpond + Sediment size + Stream + Habitat type	14	-72.28	9.29	0.00
Intercept-only	1	-105.17	51.06	0

on stream. In both Tipella and Stokke Creeks, inferred larval *A. truei* habitat was the greatest immediately upstream of each headpond, and decreased with distance upstream as the stream channel narrowed (Fig. 4). In contrast, we found that inferred *A. truei* habitat in Fire Creek exhibited two peaks, one immediately upstream of the headpond, and another ~90 m upstream (Fig. 4). We used model average estimates of larval *A. truei* density with distance in each stream combined with mapped high-quality habitat to predict the relative abundance of *A. truei* larvae throughout the headpond-affected reach (Fig. 5). The first 20% of reach length upstream of the headpond contains approximately 60% of larvae in the headpond-affected reach in both Stokke and Tipella Creek and over 50% in Fire Creek (Fig. 5). To examine the sensitivity of our conclusions to assumptions about mapped high-quality habitat, we also calculated the relative *A. truei* abundance using all wetted areas, and found a similar pattern, where the relative distribution of individuals in the headpond-affected reach of all three streams is skewed and highest nearest RoR headponds (Fig. 5). The overall distribution pattern remained the same regardless of whether total wetted area or inferred larval habitat was used to calculate relative abundance (Fig. 5).

DISCUSSION

We found that RoR dams have the potential to act as a barrier to the downstream movement of

amphibian larvae, and subsequently affect their longitudinal distribution above and below dams. Our empirical data and models of *A. truei* larvae indicate that upstream of three RoR dams, larval densities are almost three times higher than densities found below dams (Fig. 2). Furthermore, longitudinal estimates of *A. truei* density within the headpond-affected area suggest a peak density just above the headpond, decreasing with distance upstream. When these density data are linked to habitat surveys, we estimate that a disproportionately large percentage of individuals (50–60% of total abundance) are located within the first 20% of the headpond-affected reach (Fig. 5), suggesting that the headpond acts as barrier to larval movement. Lower densities downstream of large hydropower systems have frequently been linked to dam-induced changes in environmental conditions, arising from lower growth rates, higher mortality, and decreased population persistence of many riverine taxa (Clarkson and Childs 2000, Jager et al. 2001, Koed et al. 2002). While similar data do not exist for RoR systems, our results give support to another explanation for large differences in densities above and below RoR dams, namely that missing larvae from downstream reaches may be trapped upstream of RoR dams, with undetermined consequences for growth, survival, and population persistence.

While densities and rates of oviposition along the length of a stream are likely to vary within amphibian populations, in free-flowing systems the movement of larvae and simultaneous

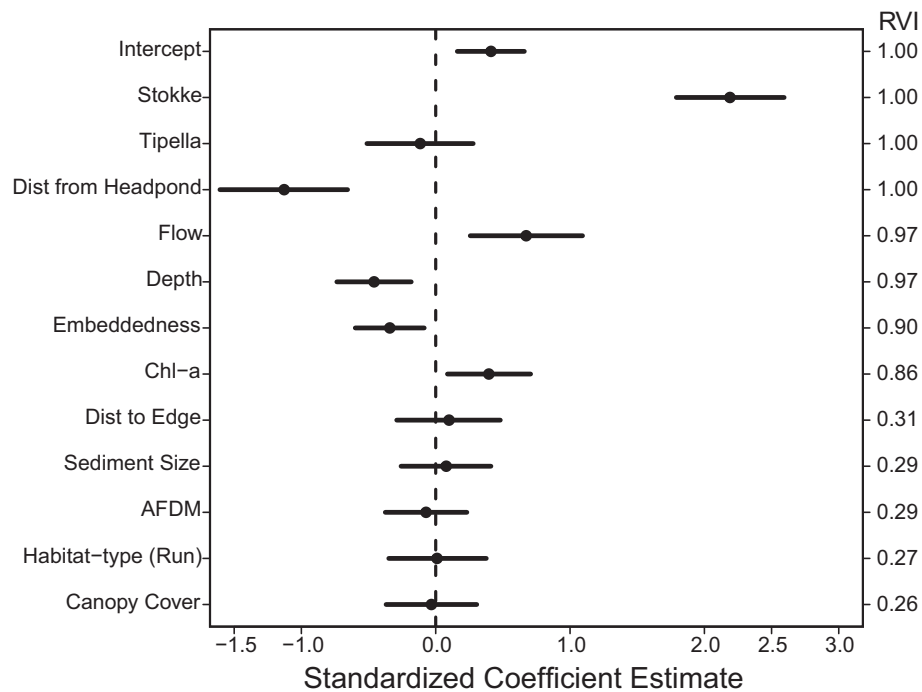


Fig. 3. Standardized coefficients ($\pm 95\%$ CI) from model-averaged output, and relative variable importance (RVI) of parameters influencing larval *Ascapthus truei* density in Fire, Stokke, and Tipella Creeks. Intercept is estimated relative to riffle habitat in Fire Creek.

presence of multiple cohorts are expected to homogenize those differences. The substantially higher larval densities we observed upstream compared to downstream of RoR dams run contrary to what has been observed in free-flowing reaches of similar length ($n = 5$ streams, mean length = $2.21 \text{ km} \pm 1.29 \text{ SE}$). In a BACI study conducted by the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development in the same geographic region (e.g., tributaries to the Fraser R.), pre-construction data analyzed using a negative binomial model of larval density as a function of being above or below a pre-constructed dam, similar to the model used in the above-below comparison of *A. truei* density presented above, indicate that *A. truei* density is similar regardless of location above or below the site of proposed dams (Appendix S1: Fig. S1, Table S2). These data support the interpretation that natural fluctuations in density, or differences in oviposition, are unlikely to explain the threefold change in larval *A. truei* density we observed across three

watersheds, but instead are likely associated with RoR dams (and their headponds). When experimentally entrained in streamflow and flushed into slow-moving eddies, *A. truei* larvae display rheotactic behavior, consistently swimming back toward high-velocity current (Altig and Brodie 1972). Although we were unable to survey the headponds for larvae, we expect that such rheotactic behavior combined with the slow-moving, deep water present in RoR headponds acts as a barrier for *A. truei* larvae.

Our findings may have consequences for the movement and natural connectivity of *A. truei* larvae in RoR impacted streams. Downstream drift is an important part of benthic stream species' life history, including in many stream invertebrates, where both active drift and passive drift with stream flow are used as a means of dispersal (Brittain and Eikeland 1988). Similarly, downstream drift is also known to occur in *A. truei* larvae, where larval drift has been estimated at between 0.3 and 1.3 m per day in streams draining old-growth forests (Wahbe and Bunnell 2001,

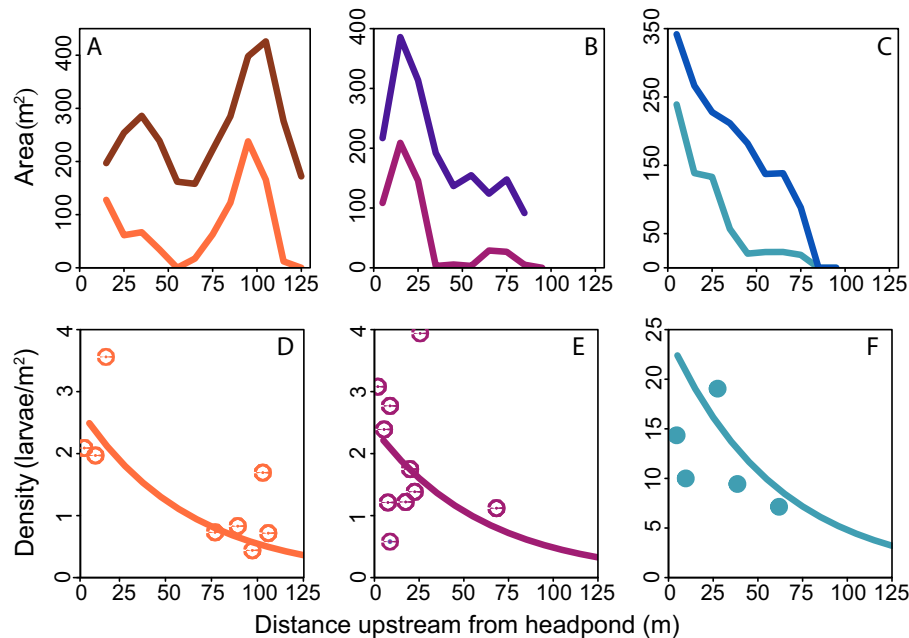


Fig. 4. Panels (A–C) represent high-quality habitat per 10-m section as light lines, and wetted area per 10-m section as darker lines. Panels (D–F) represent the predicted (line) and observed (points) larval *Ascaphus truei* density (number/m²) as a function of distance upstream (m) from RoR headponds in Fire (orange), Tipella (purple), and Stokke (blue) Creeks.

Chelgren and Adams 2017). Using these estimates, over a 4-yr period that characterizes the length of larval residence in our study populations (Bury and Adams 1999), individuals could experience downstream drift between 0.4 and 1.9 km. Uninterrupted downstream drift of larvae below RoR dams, while the remaining population is impeded above the dam, may additionally fragment *A. truei* populations and reduce genetic diversity if the dam, headpond, and related riparian infrastructure are barriers to terrestrial juvenile and adult *A. truei* movement. This can cause a decrease in fitness (Reed and Frankham 2003) and smaller effective population sizes with higher risk of local extinction (Lande 1993). Juvenile or adult *A. truei* movement upstream (Wahbe et al. 2004) from below the dam has the potential to counteract the effect of RoR dams on larval densities we present here, but the degree to which RoR dams are a terrestrial barrier is unknown. Some population structure has been attributed to large hydropower dams in *A. truei* (Grummer and Leaché 2017), and have been found to negatively influence

genetic diversity in *Rana boylei*, another river breeding anuran (Peek et al. 2018).

Our results suggest that direct mortality from RoR dams may not be the primary driver for large differences observed above and below dam reaches; however, increased densities upstream of RoR headponds may have deleterious effects to individuals. In particular, increased larval density has frequently been observed to cause reduced growth and development among larval amphibians (Wilbur 1977, Petranka 1989) and riverine species in particular (Petranka and Sih 1986, Van Buskirk and Smith 1991, Flecker et al. 1999, Gillespie 2002). Whether density-dependent growth or survival in larval *A. truei* could have population-level consequences is still unclear. Many pond-breeding amphibian species exhibit lower population sensitivity to variation in larval survival compared to adult survival (Biek et al. 2002, Vonesh and De la Cruz 2002); however for some lotic species, reductions in larval survival do appear to directly influence adult recruitment and population stability (Kupferberg et al. 2012). Low clutch size and long larval

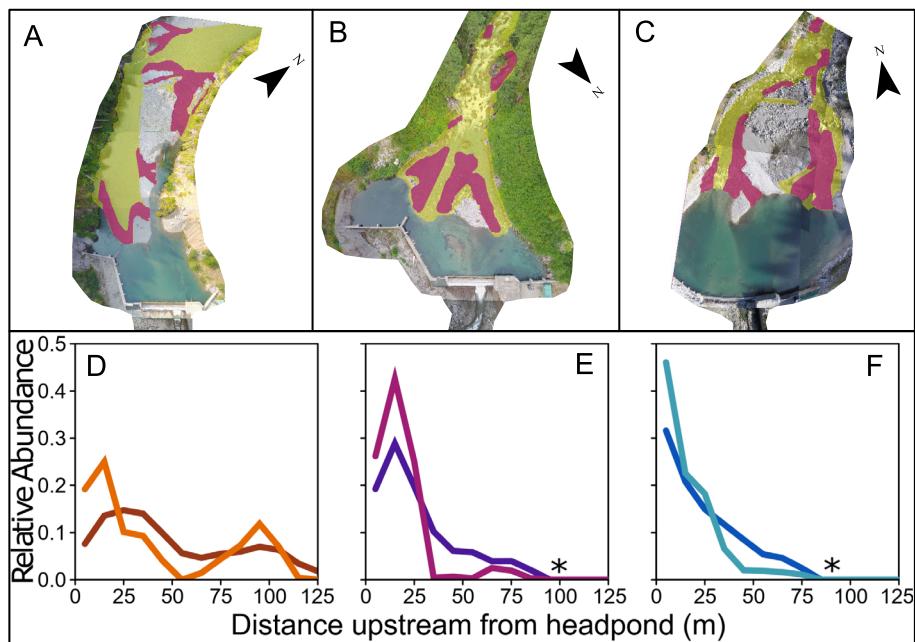


Fig. 5. Panels (A–C) contain drone photography of each headpond area, with purple shaded areas representing high-quality habitat, yellow shaded areas representing flowing water, and all panels orientated so that each dam is at the bottom on the panel. For scale, the front portion of the Fire, Tipella, and Stokke dams is 67, 81, and 66 meters fully across, respectively. Panels (D–F) are estimated larval *A. truei* relative abundance per 10-m section with distance upstream of headpond (m) in Fire (orange), Tipella (purple), and Stokke (blue) Creeks. Asterisks (*) indicate the upstream extent of the headpond-affected reach in each stream, beyond which relative abundance was not estimated. The light lines of the graph represent estimates using high-quality habitat, while darker lines represent estimates using total wetted area.

duration in *A. truei* support the possibility that decreased larval growth or survival could be important to population growth (Karraker 2006). Future research on larval survival rates in reaches below and above RoR dams would help determine the consequences of the patterns we identified.

Dam construction typically results in widened upstream stream channels and inundated riparian areas (Magilligan et al. 2003), changing the natural distribution of habitat types, as well as creating a discontinuity in otherwise continuous aquatic habitats and riparian corridors (Hall et al. 2011). Consistent with this pattern, we found that the amount of inferred larval *A. truei* habitat directly upstream of the dams was highest at the headpond (Fig. 4), and the upstream distribution of abundance deviates from a uniform null expectation (Fig. 5). We combined our estimates of larval *A. truei* density and inferred

habitat in the headpond-affected reach and found that 50% of the larval population occurs in the first 20% of the area upstream of the headpond (Fig. 5). In order to evaluate the sensitivity of our conclusions regarding population distribution to potentially subjective assumptions about high-quality inferred *A. truei* habitat, we re-calculated relative abundance using total wetted area, a less subjective measure, and found the same longitudinal pattern (Fig. 5). Though our relative abundance estimates are subject to several assumptions, our general findings add support to the hypothesis that RoR headponds are likely acting as barriers to the downstream movement of *A. truei* larvae. Though higher availability of larval *A. truei* habitat in the headpond area may confer some benefit to *A. truei* populations, higher concentrations of individuals directly upstream of the headpond may also expose individuals to instream maintenance

activities. For example, in many watersheds, periodic dredging of large amounts of accumulated sediment from headponds is required to maintain the operational efficiency of RoR power production (Fuller et al. 2016). This could pose a major threat to larvae within the headpond area if tadpoles are not relocated before dredging occurs.

This study shows a previously unexplored pathway for RoR impacts on *A. truei* tadpoles. Such impacts are commonly evaluated using before-after-control-impact (BACI) studies, and are designed to detect population-scale differences (e.g., changes in abundance, density, age classes, or size classes) by comparing data from before and after project construction in both impacted and control sites (downstream and upstream of dams, respectively, in our systems; Green 1979, Maloney et al. 2008, Wu et al. 2009, Bilotta et al. 2016). In addition to BACI studies, pre-construction longitudinal distribution surveys of amphibian larvae that encompass both the future headpond and dam sites would aid in predicting how project infrastructure may impact population stability and connectivity. Such analyses are urgently needed as the basis for developing avoidance and mitigation measures. The success of such an approach rests on adequate pre-construction baseline monitoring, and long-term post-construction monitoring data, to determine the effectiveness of mitigation measures, and to recommend adaptive solutions for current and future projects.

Instream infrastructure often alters or interrupts the movement of lotic organisms. This study demonstrates that RoR dams are likely to act as barriers to the natural downstream drift of *A. truei* larvae. Here, differences in larval *A. truei* densities between un-impacted upstream and impacted downstream reaches are consistent with a change in spatial distribution from RoR dams acting as barriers to downstream movement. Because our study is unable to evaluate direct mortality of a *truei* due to RoR dams, we cannot conclude there are no deleterious effects on the populations, with density-dependent growth, reduced population connectivity, and exposure to headpond maintenance being possible threats to these populations. In cases where proposed RoR infrastructure overlaps with *A. truei* populations, it will be important that

monitoring during the planning, pre-construction, and post-construction phases of the project include data to evaluate changes in larval connectivity and the effects of increased density on larval survival.

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