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Complete List of Authors:	Gibeau, Pascale; Simon Fraser University, Biological Sciences Connors, Brendan; Simon Fraser University; ESSA Technologies Palen, Wendy; Simon Fraser University
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Run-of-River hydropower and salmonids: potential effects and perspective on future research

Gibeau P.[1,2,†], B.M. Connors[3,4,] and W. J. Palen[1,2]

[1]Earth to Ocean Research Group, Simon Fraser University, Burnaby, BC, Canada

[2]Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada; wpalen@sfu.ca

[3]ESSA Technologies, Vancouver, BC, Canada

[4]School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada; bconnors@sfu.ca

[†] pgibeau@sfu.ca, phone: 01-778-266-0142

Abstract

The spatial footprint of individual run-of-river (RoR) hydropower facilities is smaller than reservoir-storage hydroelectric projects and their impacts to aquatic ecosystems are often assumed to be negligible. However, these effects are poorly understood, especially for salmonids whose freshwater habitat often overlaps with RoR hydropower potential. Flow regulation for RoR hydropower is unique in how it influences the seasonality and magnitude of flow diversion, and because low-head dams can be overtopped at high flows. Based on a review of the primary literature, we identified three pathways of effects by which RoR hydropower may influence salmonids: reduction of flow, presence of low-head dams impounding rivers, and anthropogenic flow fluctuations. We synthesized empirical evidence of effects of RoR hydropower on river ecosystems from 31 papers, of which only ten explicitly considered salmonids. We identified key research gaps including impacts of extended low flow periods, anthropogenic flow fluctuations, and cumulative effects of multiple RoR projects. Filling these gaps is necessary to help manage and conserve salmonid populations in the face of the growing global demand for small-scale hydropower.

Résumé

L'empreinte spatiale individuelle des centrales hydroélectriques au fil de l'eau est moindre que celle des centrales hydroélectriques avec réservoirs de retenues et en conséquence, leurs impacts sur les écosystèmes aquatiques sont souvent considérés négligeables. Par contre, leurs effets écologiques sont peu connus, particulièrement pour les salmonidés dont l'habitat en eau douce coïncide souvent avec le potentiel hydroélectrique des centrales au fil de l'eau. La régulation des eaux par les centrales au fil de l'eau est unique par la façon dont elle influence la saisonnalité et l'ampleur de la déviation des eaux, et parce que les barrages de basse-chute peuvent être submergés lors des crues. En se basant sur une revue de la littérature primaire, nous avons identifié trois voies principales par lesquelles la production d'électricité par des centrales au fil de l'eau peut influencer les salmonidés: la réduction du débit dans des segments de rivière, la présence de barrage de basse-chute endiguant les rivières, et la création de fluctuations artificielles du débit en aval des barrages et des centrales. Nous avons synthétisé les résultats empiriques de 31 études portant sur les effets de la production d'hydroélectricité par des centrales au fil de l'eau sur les écosystèmes lentiques, desquels seulement dix ciblent les salmonidés. Finalement, nous soulignons les principales incertitudes dans les connaissances scientifiques actuelles sur l’impact des centrales au fil de l’eau, liées aux périodes prolongées de bas débit, aux fluctuations anthropogéniques de débit et aux effets cumulatifs de l’établissement de plusieurs centrales. Combler ces lacunes est essentiel pour gérer durablement et protéger les populations de salmonidés face à la demande mondiale croissante pour de l'énergie renouvelable et à petite échelle.

Introduction

Rivers are dynamic, disturbance-driven ecosystems, where flow plays a fundamental role in structuring aquatic and riparian communities (Resh et al. 1988; Poff et al. 1997; Murchie et al. 2008). The natural flow regime (NFR) of rivers is defined by the magnitude, frequency, duration, timing, and rate of change of flow events, each of which affect stream-dwelling aquatic organisms over short-term to evolutionary timescales (Poff et al. 1997). Many anthropogenic activities can alter the flow and disturbance regimes of streams, which in turn may affect the survival and fitness of native species (Poff and Ward 1990; Reice et al. 1990; Strayer and Dudgeon 2010). Impoundment of water by dams, either built for irrigation, flood control, or hydroelectricity generation, is one of the greatest anthropogenic drivers of change to NFRs. Over 800,000 dams have been built worldwide since the beginning of the 20th century, collectively influencing more than half of global runoff and intercepting 25% of naturally transported sediment (Vörösmarty and Sahagian 2000; Jackson et al. 2001; Pittock and Hartmann 2011). Storage dams retain water for extended periods in reservoirs, and subsequently release it at times that can be out of phase and frequency with NFRs (Rosenberg et al. 1997; Murchie et al. 2008). Such deviations from NFRs cause flow alterations that have well-documented consequences for river geomorphology, continental runoff, riparian communities, and macroinvertebrate and fish populations (Nilsson et al. 2005; Murchie et al. 2008; Poff and Zimmerman 2010).

In recent decades, small-scale hydropower production, consisting primarily of Run-of-River (RoR) hydropower, has emerged as an alternative to the construction of new reservoir-storage dams because of their perceived lower economic, social, and environmental costs (Postel et al. 1996; Abbasi and Abbasi 2011; Anderson et al. 2014). For example, the contribution of small hydropower to global power generation nearly doubled from 2001 to 2010, increasing from

32,000 to 45,000 megawatts (MW) (Abbasi and Abbasi 2011), as many regions have developed new RoR hydropower facilities (e.g., Canada: Cyr et al. 2011; Sopinka et al. 2013; Indian Himalaya: Grumbine and Pandit 2013; China: Wang et al. 2010; Thailand: Aroonrat and Wongwises 2015; Africa: Chiyembekezo 2013; Central America: Anderson et al. 2006; Europe: Anderson et al. 2014; Spänhoff 2014). Although no universally accepted definition exists, RoR hydropower typically includes low-head diversion dams with energy output up to 25 MW (Abbasi and Abbasi 2011). However, some countries like China and Canada consider facilities with installed capacities less than 50 MW as small hydropower (Cyr et al. 2011; Kibler 2011). Despite the increased development of RoR hydropower, there is a paucity of peer-reviewed research into the effects of RoR hydropower on aquatic ecosystems in which they occur, leading to knowledge gaps about the effects to aquatic species (but see Abbasi and Abbasi 2011 and Anderson et al. 2014 for recent reviews). Here we provide the most comprehensive global synthesis of observed and potential effects from RoR hydropower on salmonid fishes. We focus our review on salmonid fishes because of their unique ecological, cultural, and economic importance (Naiman et al. 2002) as well as their near-global distribution in coastal and inland rivers. Based on the unique characteristics of flow diversion created by RoR hydropower, we synthesized empirical peer-reviewed literature and expanded upon information from previous reviews to hypothesize three main pathways of effect (e.g. altered ecological mechanisms, linking causes to effects) by which RoR hydropower operations could impact salmonids: the reduction of flow in river reaches, the presence of low-head dams impounding rivers, and the creation of anthropogenic flow fluctuations. We evaluated the evidence in support of these pathways based on a comprehensive search of the peer-reviewed literature on RoR hydropower (n = 31 empirical studies), as well as relevant literature from other forms of flow regulation similar to RoR hydropower. Importantly, our synthesis excludes the effects of ROR hydropower on riparian ecosystems, as such effects are expected to be very similar to those produced by other industrial activities (e.g. terrestrial footprint of facilities, construction of roads and powerlines, etc.) and reviewed elsewhere (e.g., Smith et al. 1991; Weltman-Fahs and Taylor 2013; Abbasi and Abbasi 2011). The specific goals of our review are to: 1) categorize the unique characteristics of flow diversion by RoR hydropower operation, 2) evaluate the support from the peer-reviewed literature for three main pathways of effect on salmonid fishes, and 3) identify critical knowledge gaps that can be used as priorities to guide future research. We organize the findings of existing peer-reviewed studies into a framework under the NFR paradigm, and maintain a broad geographic scope to maximize the extent of the synthesis. We hope these unique characteristics of our review make its findings and conclusions applicable to as many contexts as possible, and help focus new research on filling the highest priority knowledge gaps.

Methods: Literature synthesis of RoR hydropower

To identify peer-review literature examining the effects of RoR hydropower on salmonid fishes, we searched the Web of Science and Aquatic Sciences Fisheries Abstracts databases through April 2016 for combinations of the keywords: "run of river", "small hydro", "small hydropower", "water diversion" crossed with the keywords "salmonid", "trout", and "fish". We also used the literature cited by each paper, as well as high-quality grey literature sources (e.g. Robson et al. 2011), to identify additional peer-reviewed literature related to the effects of RoR hydropower on salmonid fishes. We screened the peer-reviewed papers to include only those focused on RoR hydropower technology (i.e., low-head dams producing hydroelectricity), but information from low-head dams build for purposes other than hydropower (e.g. irrigation, municipal uses) was used to substantiate pathways where possible. We identified 47 peer-reviewed studies specific to the effects of RoR hydropower, of which 31 empirical studies covered impacts of RoR hydropower on fishes, invertebrates, or river habitat (Table 1, Figure 1). Of these 31 empirical papers, 17 examined the effects of RoR hydropower on fish, but only 10 specifically addressed salmonid fishes (Table 1). A total of 14 other papers were related to economics, energy policy, geopolitics, and the geography of RoR hydropower (n=9), or covered related topics such as comparison between small and large dams or cumulative impacts (n=3), engineering (n=1), and dam classification or removal (n=1) (Appendix 1). In addition to these empirical papers, we identified two recent reviews, one focused on the history of RoR hydropower technology that challenges the perception that ecological impacts are minimal (Abbasi and Abbasi 2011), and a second that included a brief overview of two pathways of impact by which RoR hydropower may affect the physical and ecological conditions of rivers, but did not address impacts to fish or salmonids (Anderson et al. 2014). The papers included here encompass a near global geography in order to compensate for the general paucity of peer-reviewed studies on this topic, and to help inform our understanding of the potential effects of RoR hydropower on river ecosystems using all available information.

Characteristics of flow diversion for RoR hydropower and interactions with salmonids

RoR hydropower projects can take on a variety of designs, however, the majority occur in high-gradient, mountainous rivers where kinetic energy, produced from the drop of water over a sharp elevation gradient, creates a hydraulic head for electricity production (Abbasi and Abbasi 2011; Anderson et al. 2014). High-gradient RoR hydropower projects, called high-head schemes (Anderson et al. 2014), are characterized by a low-elevation dam (henceforth called low-head dam) that creates an upstream impoundment (headpond) with little storage capacity (Figure 2). We found that 77% of the empirical papers we reviewed focused on such hydropower schemes, while 17% provided no clear description of the RoR designs (see Table 1). Low-head dams create relatively small headponds with limited water storage capacity, creating the expectation that flow regimes in rivers regulated by RoR hydropower will more closely mimic NFR than reservoir-storage systems (Poff and Hart 2002; Shaw 2004; Kibler and Tullos 2013). Low-head dams divert existing flow through intake structures into a pipe (penstock) running parallel to the river for several kilometers until reaching a powerhouse where turbines are rotated to generate electricity. The diversion of water from the dam to the powerhouse results in a reach immediately downstream of the dam with lower than natural flows, termed the bypassed reach (also referred to as the diversion reach in Canada, dewatered reach in the USA, or depleted reach in the United Kingdom). Diverted water is then returned back to the river channel after passing through the powerhouse. RoR hydropower operations thus result in unique forms of flow regulation when compared to reservoir-storage hydropower dams or RoR dams built for purposes other than hydropower (e.g., water diverted for irrigation or municipal uses), which are consequently likely to influence river ecosystems in different ways.

The high-gradient rivers where most RoR hydropower projects are located are also often the well-oxygenated, clear, and cold river habitat favoured by many anadromous and resident salmonids (subfamilies Salmoninae) (Shaw 2004; Wohl 2006). Salmonid fishes exhibit a wide range of life history strategies, some of which are more likely than others to be sensitive to the effects of RoR hydropower (Table 2). Overall, low-head dams have the potential to impede the completion of salmonids life cycles through two primary mechanisms: blocking movement and migration among important habitats, or by chronic exposure to reduced or more variable flows within the footprint of RoR hydropower. For example, anadromous salmon species with life histories requiring long-distance freshwater migrations through high order streams, like steelhead (*Onchorhynchus mykiss*) and Atlantic (*Salmo salar*) salmon, may be especially vulnerable to encountering barriers from dams along their long migrating journey. Salmonids with resident life histories like rainbow (*O. mykiss*) and brook trout (*Salvelinus fontinalis*) that spend the entirety of their lives in freshwater and do not undergo extensive freshwater migrations, are more likely to be vulnerable to the effects of chronic exposure to RoR hydropower. Salmonids like adfluvial and fluvial Bull Trout (*S. confluents*) that both undergo extensive freshwater migrations and spend large portions of their lives in higher order streams are likely to be among the most vulnerable salmonids to barriers to migration and chronic exposure to RoR hydropower. In contrast, the short residence time in freshwater and shorter freshwater migrations of pink (*O. gorbuscha*) and chum (O. *keta*) salmon make them potentially the least vulnerable to impacts from RoR hydropower (Table 2). Other species like Chinook salmon (*O. tshawytscha*) tend to spawn in larger systems less likely to be impacted by RoR low-head dams. Overall, the overlap between RoR hydropower operations and salmonid habitats only provides a basis for possible negative consequences to salmonid fishes. Our review of pathways below highlights the many knowledge gaps remaining about the relative vulnerability of salmonids to flow diversion by RoR hydropower.

Changes to natural hydrographs due to RoR hydropower operations are expected to vary by reach (upstream, downstream, and bypassed) in rivers influenced by RoR hydropower. The creation of headponds inundates riparian areas and fundamentally interrupts the NFR in reaches immediately upstream of low-head dams by reducing flow variability, velocity, and turbulence, and increasing the deposition of fine sediment (Csiki and Rhoads 2010; Butler and Wahl 2011). Such changes in physical habitats can lead to impacts on riverine ecosystems by reducing water quality and altering the abundance, richness, and composition of periphyton, invertebrate, and fish assemblages (Santucci et al. 2005; Mueller et al. 2011; Anderson et al. 2014). In contrast, the flow regime in reaches downstream of RoR powerhouses is expected to be the most similar to the NFR since water diverted for power generation is returned to rivers after passing through turbines (Poff and Hart 2002; Kibler and Tullos 2013; Senay et al. 2016). Nonetheless, the return of water at the tailrace may have a hydraulic impact on benthic macroinvertebrate composition (Anderson et al. 2015) or fish as a result of dissolved gas super-saturation (Weitkamp and Katz 1980). RoR hydropower operations are expected to cause the greatest changes to the NFR in bypassed reaches, where a proportion of flow is removed for power production. The amount of flow removed can vary widely depending on national, regional, or local regulations (e.g. up to 100% in some systems in China, Kibler and Tullos 2013, or the Czech Republic, Kubečka et al. 1997) or the time of year. The degree of flow alteration in bypassed reaches can be especially pronounced during seasonal periods of low to moderate natural flows, when the amount of water diverted by RoR hydropower operations translates into the highest proportion of flow removed from the channels. For example, up to 97% of the natural flow was diverted for RoR hydropower during fall, winter, early spring, and late summer months in some snow-dominated watersheds of western Canada or during dry fall, mid-summer, and winter months in rainfall-runoff dominated mountainous areas of China (Figure 3). Diverting the highest proportion of flow during periods of low flow results in large changes to the frequency, duration, timing, and magnitude of low flows in bypassed reaches compared to natural conditions (Ovidio et al. 2008; Kibler and Tullos 2013). In contrast, during seasonal periods of high natural flows (and episodic high flow events), bypassed reaches downstream of RoR hydropower dams more closely match the NFR because headponds have limited water storage capacity (Poff and Hart 2002) and withdrawals for power production are proportionally smaller. For example, the proportion of flow removed during late spring and early summer months only equals 6-30% of discharge during high flows in the snow-dominated watersheds of Northwestern Canada or rainfall-runoff dominated mountainous areas of China (Figure 3). Seasonal alterations to the NFR by RoR hydropower operations, in addition to the physical barrier presented by low-head dams, in turn affect physical and geomorphic characteristics of rivers that are important for salmonid fishes.

A large amount of literature documents changes in water quality, habitat quantity, and geomorphology in rivers downstream of reservoir-storage hydropower systems (reviewed by Poff and Zimmerman 2010). Though evidence in the peer-reviewed literature specific to RoR hydropower is more limited (n = 31), it suggests water quality, habitat quantity, and geomorphology can also be affected by RoR hydropower operations (Kubečka et al. 1997; Baker et al. 2011; Nislow and Armstrong 2012; Bilotta et al. 2016). Changes to NFR following diversion of flow can affect water quality mainly through changes to temperature regimes, pH, and dissolved oxygen (Valero 2012). Changes to NFR also alter channel hydraulic, sediment transport, and geomorphology downstream of low-head dams. Such changes to water quality and physical habitat in turn diminish habitat quality, quantity, and diversity for fishes (Baker et al. 2011; Fuller et al. 2016). The diversion of flow for RoR hydropower, and subsequent changes to water quality and physical habitats in bypassed reaches, therefore constitutes the first pathway of effect by which RoR hydropower has the potential to influence salmonids. We further consider two additional pathways of effect based on other characteristics of RoR hydropower: the presence of low-head dams (Pathway 2), and anthropogenic flow fluctuations due to the diversion of water (Pathway 3). The three pathways of effect are described below, where we draw upon the empirical evidence from the peer-review literature specific to RoR hydropower to support hypothesized mechanisms of impact for salmonid fishes.

Pathway 1: Reduction of flow in the bypassed reach

The effects of flow diversion on water quality and habitat quantity in bypassed reaches were reported in 24 studies specifically focussed on RoR hydropower (Figure 2), although only 10 directly report consequences for salmonids (Table 1). Consequences for fish ranged from shifts in species assemblages and age composition, to declines in biomass and density. For example, in the bypassed reaches of 20 out of 23 RoR hydropower systems surveyed in the Czech Republic, water diversion by RoR hydropower dams was found to cause a shift in fish assemblages from large- to small-bodied species, as well as a decline in individual weight and biomass (Kubečka et al. 1997). Those systems that diverted more than half the average annual discharge saw decreases in fish biomass of over 60% (Kubečka et al. 1997). Similarly, low flows generated by RoR hydropower were associated with a decrease in adult trout densities in 7 out of 11 bypassed reaches studied in France (Sabaton et al. 2008), as well as declines of 42-53% in the biomass of brown trout and shifts in size and age composition from adults to juveniles over four years in a bypassed reach in Belgium (Ovidio et al. 2008). The operation of RoR hydropower plants also lead to small decreases in species richness in several rivers in the UK (Bilotta et al. 2016). Below we outline the main mechanisms by which declines in flow may lead to declines in salmonid biomass, density, and changes in size structure in bypassed reaches of rivers regulated by RoR hydropower.

The diversion of flow for the production of electricity has led to documented changes to water quality parameters including dissolved oxygen, pH, conductivity, invertebrate communities, and temperature regimes in bypassed reaches of rivers regulated by RoR hydropower. In general, changes to water quality parameters were small, and frequently studies offered opposite conclusions as to the direction and magnitude of effects, especially for water temperature and macroinvertebrates communities. For example, Valero (2012) recorded short-term increases in pH as well as declines in dissolved oxygen and conductivity in the bypassed reach of a RoR hydropower project in Spain. However, slightly lower average pH and variable conductivity were noted in bypassed reaches in China (Zhou et al. 2009; Wu et al. 2010a; Wu et al. 2012). Empirical evidence of the effects of flow reduction on water temperature in bypassed reaches is also mixed. The factors influencing stream temperatures are a complex mix of external drivers and internal stream dynamics (Poole and Berman 2001), and reducing flow in a river reach has the potential to lead to warmer and more variable stream temperature regimes. Studies conducted in bypassed reaches of rivers with RoR hydropower dams report slight increases in water temperature in Spain (Valero 2012), USA (McManamay et al. 2015), and China (Fu et al. 2008; Zhou et al. 2008; Zhou et al. 2009; Wu et al. 2010a; Wu et al. 2012), but no significant differences between bypassed and upstream reaches in Portugal (Jesus et al. 2004). Low flows during dry and hot seasons, however, triggered markedly warmer temperatures in bypassed reaches (~1-3C) compared to upstream reaches in Costa Rica (Anderson et al. 2006) and the Czech Republic (Kubečka et al. 1997), and compared to water temperature immediately downstream in China (~5-6C, Wu et al. 2010b). Finally, primary producers like diatoms were adversely affected in bypassed reaches in China (Wu et al. 2010b; Wu et al. 2012), while one study points out that significant differences in algal community composition between upstream and bypassed sites appeared only after two years of operation (Wu et al. 2009). In addition, macroinvertebrates and zooplankton were also affected, with for example decreases in species richness and abundance of benthic macroinvertebrates of up to 38% and 54%, respectively, in Sweden (Englund and Malmqvist 1996), decreases in biomass, density and richness of macroinvertebrates in Portugal (Jesus et al. 2004) and China (Fu et al. 2008), and decreases in density of zooplankton during low flow months in China (Zhou et al. 2008). Conversely, other studies in bypassed reaches of RoR hydropower systems documented increases in benthic diatom richness, likely due to a relaxation of predation pressure from macroinvertebrates and creation of habitat more favorable to algal growth at lower flows (Wu et al. 2010b). In other cases, no conclusive evidence of effects, positive or negative, on macroinvertebrate biomass or density have been observed in bypassed reaches (Kubečka et al. 1997; Sabaton et al. 2008). Despite such empirical evidence of changes to water quality parameters in bypassed reaches of RoR hydropower, neither the factors influencing these changes nor consequences for fish have been clearly identified in the studies reviewed. For example, of all the studies reporting on changes to water temperatures, pH or conductivity, only three (Anderson et al. 2006; Kubečka et al. 1997; Valero 2012) report on the size of the rivers (small to medium), the length of bypassed reaches (0.05 to 4 km), or the amount of flow diverted (59-100%) (Table 1). Details about designs and river characteristics are equally sparse in the studies reporting changes to invertebrates assemblages (Table 1). Such limited details about ecological context and RoR hydropower design on rivers where studies were conducted limit the opportunity to suggest why some studies would note increases in water quality parameters while others do not. We can nonetheless hypothesize that changes to water quality, temperature, and invertebrates are likely to affect fish habitat and food supply.

The magnitude of changes to water quality parameters noted in peer-reviewed literature specific to RoR hydropower are generally small in magnitude, and so their effects on salmonids remains unclear. Of all water quality parameters discussed above, alterations to temperature have the highest likelihood of significantly impacting cold-water species like salmonids (McManamay et al. 2015) since even small changes to water temperature regimes (e.g. 0.6°C) have the potential to directly affect metabolism and growth of poikilotherm fishes like salmonids (Beakes et al.

2014). In general, higher temperatures increase metabolic rates and potential for growth up to the thermal optimum, beyond which increases in water temperature are physiologically detrimental to fish and can lead to death (Brett 1995). Below the thermal optimum, increases in growth with temperature are only possible when food or other resources are not limiting (Bryant 2009; Taylor and Walters 2010). If food consumption decreases while water temperatures increase, fish experience higher metabolic costs that may lead to slower growth and later maturation (e.g., Van Poorten and McAdam 2010), or declines in total biomass (Beakes et al. 2014). The most important characteristic of RoR hydropower for temperature regimes in bypassed reaches may be the seasonality of flow diversion, and its consequence for water temperature, and ultimately, salmonids. For example, diverting proportionally more flow during periods of naturally low flows may accelerate the timing and increase the magnitude of warming in bypassed reaches of RoR hydropower systems during spring and summer. These periods of accentuated low flow in spring and summer also correspond to important times for spawning, incubating or rearing salmonids (Table 2). As found by studies conducted in reservoir-storage systems and in unregulated rivers, increased temperatures coinciding with low flows have the potential to change the timing of spawning migrations and interspecific interactions (e.g., Freeman et al. 2001; Bendall et al. 2012; Malcolm et al. 2012), reduce survival of smolts before and during migrations (Nislow and Armstrong 2012), and make fish more vulnerable to pathogens (Crozier et al. 2008; Mantua et al. 2010). Additionally, these extended periods of low flow can reduce water quality, limit movement of nutrients and sediment, and increase competition and predation (Lake 2000; Bradford and Heinonen 2008; Walters and Post 2011). In contrast, during winter months, reduced flows may decrease water temperature and increase the occurrence of frazil ice (i.e. ice anchored to the stream bottom) and freeze-thaw cycles, potentially leading to mortality of salmonid eggs by reducing oxygen concentrations, and of fry by damaging gill tissues (Bradford 1994; Bradford and Heinonen 2008). Though the consequences of low flows and changes to water temperature regimes observed in reservoir-storage systems and unregulated rivers may also manifest in bypassed reaches of rivers regulated by RoR hydropower, the magnitude of the differences in temperature experienced in bypassed reaches following flow diversion is poorly documented and so should be established more clearly and rigorously by future research and monitoring. As the River Continuum (Vannote et al. 1980) and Serial Discontinuity concepts (Ward and Stanford 1983) predict, natural gradients in abiotic parameters like temperature exist from headwaters to mouths of river systems. Control-impact comparisons between upstream and bypassed reaches can thus potentially confound water quality changes due to diversion of flow with the natural longitudinal changes through watershed networks. Comparisons to conditions before diversion of flow, or in reaches of similar order and network position, are thus needed to rigorously quantify the magnitude of changes to water temperature and other water quality parameters after flow diversion, and understand their consequences for metabolism, growth, and population dynamics of salmonids.

The second mechanism by which a reduction in flow from RoR hydropower operations could impact fish is through a reduction in habitat quantity and diversity (Anderson et al. 2006; Baker et al. 2011; Mueller et al. 2011). Overall, the literature demonstrates that the diversion of flow in streams reduces the depth and velocity of water in bypassed reaches, which generally lead to a decline in habitat quantity and quality, and in turn, a decline in fish biomass and density. For example, declines in the number of habitats due to reductions in flow was linked to a shift towards small-bodied fish species observed in several rivers regulated by RoR hydropower in the Czech Republic, in part because of increases in predation on larger-bodied fish species (Kubečka et al. 1997). Declines in European grayling (*Thymallus thymallus*) biomass of 76% and declines in proportions of adults in the population were associated with reductions in preferred deep and fast water habitats (Ovidio et al. 2008), a pattern also observed with reductions of rainbow and brown trout abundances in a bypassed reach in Chile (Habit et al. 2007). Lower densities of brown trout were found when greater amounts of water were diverted from bypassed reaches in a long-term study (Gouraud et al. 2008). Most of these systems appear to be in rather small, headwater rivers, with long bypassed reaches that diverted a high proportion of water during most of the year (Table 1). However, reduced flows in bypassed reaches were found to temper some negative effects of natural flooding events by reducing the mortality of emerging rainbow and brown trout fry in similar rivers in France (Capra et al. 2003; Gouraud et al. 2008). The potential for negative impacts of natural high spring or summer discharges on trout fry is further supported by studies on the influence of hydrological and biotic processes on the population dynamics of brown trout in France (Cattanéo et al. 2002), and on steelhead population dynamics in snowmelt-driven rivers of western Canada (Smith 2000). Anthropogenically-created lower flows can also reduce the metabolic costs of foraging and maintaining position for fish, thus increasing the amount of energy available for growth, as has been shown in reaches downstream of large reservoir-storage hydropower (Cleary et al. 2012). However, other research conducted in reservoir-storage systems supports the idea that reduced habitat availability due to lower flows downstream of reservoir-storage dams result in short-term increases in fish densities, subsequently leading to increases in competition among and within salmonid life stages, and increased susceptibility to disease (Bradford 1994; Nislow and Armstrong 2012). Geomorphically, lower flows can also reduce the frequency, diversity, and quantity of microhabitats including gravel bars, side channels, and pools which are important for salmonid spawning, overwintering and rearing, as well as for refugia during extreme flow events like floods or droughts (Sedell et al. 1990; Bonneau and Scarnecchia 1998; Walters and Post 2008).

In many countries and jurisdictions, mitigation measures for RoR hydropower operation, such as requiring minimum instream flows, are mandated to minimize the potential impacts of reduced flows on fish and fish habitat in RoR hydropower systems (e.g., France, Gouraud et al. 2008; Portugal, Santos et al. 2006; Sweden, Renöfält et al. 2010; for more information, see review by Anderson et al. 2014). In some cases, river systems with a highly modified NFR, but observing the required minimum flows (3-12% of natural flow) in reaches downstream of reservoir-storage and low-head dams, were able to maintain highly productive trout and invertebrate populations (Jowett and Biggs 2006). Unfortunately, only half of the empirical papers on effects of RoR hydropower that we reviewed mentioned the presence or absence of mitigation measures (n=16), and none of them discussed their results in light of the mitigation measures used, which prevents us from drawing stronger inferences about their effectiveness. Ultimately, the consequences of flow reductions in bypassed reaches downstream of RoR dams are likely to be highly dependent on the systems in which they occur. Bypassed reaches in fast flow, flashy systems may benefit from a decline in discharge and velocity because it would increase the amount of habitat available to fish during medium to high flows. On the other hand, the opposite may be true for lower gradient, more meandering rivers where a reduction in flow may limit the amount of habitat available to fish.

Pathway 2: The presence of low-head dams

A total of 13 peer-reviewed papers reported on the consequences of low-head dams in the context of RoR hydropower, ranging from fish entrainment in intake structures, to barriers to migration and habitat fragmentation, and effects on geomorphology and sediment transport (Figure 2, Table 1). Despite the limited peer-reviewed literature dedicated specifically to RoR hydropower, the potential for fish entrainment in infrastructures generating RoR hydropower is clear. Similar to reservoir-storage hydropower systems (Skalski et al. 2002), the intake structures of RoR hydropower projects may entrain fish in the penstock or turbines, leading to injury and mortality (Kubečka et al. 1997). Mortality rates following entrainment in intake structures of RoR hydropower dams increase with fish size (Kubečka et al. 1997), hydraulic head, the number of blades, and varies by turbine type (on average, 100% in Pelton turbines, 5-90% in Francis turbines, and 5-20% in Kaplan turbines; (Larinier 2008). Turbine mortality is inversely related to RoR hydropower plant size, because smaller capacity plants often contain small turbines that rotate faster than those in larger plants (Larinier 2008). The magnitude and seasonality of flow diversion by RoR hydropower may also affect fish entrainment in RoR hydropower intake structures. For example, fry in reaches upstream of RoR hydropower intakes may be at higher risk of entrainment during periods of naturally high flows that often coincide with when fry emerge (Table 2). Research conducted in reaches immediately downstream of reservoir-storage dams has documented increased mortality from predation due to disorientation or loss of equilibrium following entrainment (Čada 2001; Barnthouse 2013). The potential for similar sub-lethal effects of entrainment through the intake structures specific to RoR hydropower warrant investigation, especially given their long penstocks which may increase negative consequences of entrainment for fish compared to reservoir-storage systems. Finally, entrainment of invertebrates through RoR hydropower intake structures is also likely and may be accentuated at low flows, given empirical evidence noted from RoR dams built to supply water for municipal uses where up to 100% of drifting shrimp larvae were entrained at low flows (Benstead et al. 1999). Overall, the potential for fish entrainment through RoR hydropower structures is substantial and additional investigations specific to RoR operations are warranted.

The low-head dams associated with RoR hydropower can act as barriers to upstream and downstream movements of fishes (Santucci et al. 2005; Habit et al. 2007; Santos et al. 2012) and fragment river networks (Vannote et al. 1980). Many RoR hydropower dams have fish passage structures to restore upstream, but not downstream, migrations, however their efficiency in passing fish is highly variable (Kubečka et al. 1997; Santos et al. 2012). For example, the presence of 15 consecutive RoR dams in a single river in the USA blocked upstream migrations of up to a third of local fish species, leading to species being present only in the upper or lower sections, but not in the central regions of the river where most of the dams were concentrated (Santucci et al. 2005). Another study in France found that only 16 out of 30 (53%) fish passage structures at RoR hydropower dams allowed migrating individuals to move upstream without delays (Larinier 2008), and a study in Portugal found that 8 out of 18 (44%) fish passage structures allowed fish passage between bypassed and upstream reaches (Santos et al. 2006). In contrast, downstream migrations are expected to be less affected since RoR dams are generally low-elevation and passable at high flows, provided that entrainment does not occur and passage over the dam is not traumatic for fish (Anderson et al. 2006; Boubée and Williams 2006; Larinier 2008). For example, neither the relative abundance, richness, nor diversity of fishes differed between upstream and bypassed reaches in 18 RoR hydropower systems studied in Portugal, despite the fact that 55% of the dams had unsuitable fish passage structures, suggesting that downstream migrations of migratory species at high flows might be occurring (Santos et al. 2006). Furthermore, indicators of community composition like species richness and fish abundance were not statistically different between control and impacted sites in several rivers regulated by RoR hydropower in the UK (Bilotta et al. 2016). However, large uncertainties remain regarding impacts of low-head dams on downstream fish movements that do not coincide seasonally with high flows. Nevertheless, the artificial disruption of longitudinal connectivity by

RoR dams is akin to terrestrial habitat fragmentation, and can affect the composition of fish assemblages by favoring more generalist species (e.g., Santucci et al. 2005; Anderson et al. 2006) or disfavoring small or benthic species unable to pass dams (Habit et al. 2007). RoR hydropower dams are often located in high gradient streams that tend to support relatively small salmonid populations, and habitat fragmentation as a result of impassable barriers may also increase the potential for genetic drift or reduce population viability. Small populations are generally at higher risk of adverse consequences from genetic drift, including inbreeding depression and increased vulnerability to environmental stress and stochasticity (Altukhow *et al.* 2000; Heggenes and Røed 2006; Lucas et al. 2009). Overall, the potential for habitat fragmentation due to the presence of low-head RoR dams represents a substantial threat to salmonid populations, which all undertake migrations between spawning, rearing and overwintering habitats.

Finally, RoR hydropower dams may act as discontinuities in the geomorphology of rivers, affecting the natural transport of sediment and organic matter in streams (Fuller et al. 2016), and in turn, the quality and quantity of fish habitat. Low-head RoR hydropower dams and the presence of headponds create conditions that are likely to interrupt the NFR and natural longitudinal connectivity of rivers, but the fact that low-head dams often become overtopped at high flows may compound the magnitude of the geomorphologic disruptions. Evidence suggests that RoR dams and headponds temporarily store sediments, and therefore alter the timing and size of sediment delivered to the bypassed and downstream reaches compared to NFR (Kibler and Tullos 2013; Fuller et al. 2016). RoR hydropower dams may also intercept different forms of organic matter including coarse woody debris. Coarse woody debris is a key component of fish habitat as it promotes the formation of pools, limits erosion, and provides cover and refugia (Sedell et al. 1990; Mossop and Bradford 2004). Comparisons between bypassed and upstream reaches of low-head RoR dams found higher levels of fine sediment and significantly slower water velocity in 13 bypassed reaches, as well as significant differences between upstream and bypassed reaches in 32 of 41 hydraulic variables (Baker et al. 2011). Based on their modelling results, Baker et al. (2011) also concluded that small, low-gradient streams with smaller-sized substrate were more susceptible to fine-sediment accumulation than large streams. However, RoR dams that are regularly overtopped at high flows are expected to experience fewer discontinuities in the morphological and sediment size distribution of stream channels (Kondolf 1997; Kibler and Tullos 2013; Csiki and Rhoads 2013). The proportion of flow diverted is also of importance for the transport of sediments. For example, (Morris 1992) found that the diversion of less than 2 m^3s^{-1} (< 8% of annual peak flood) of water for hydroelectricity production did not affect the transport of spawning size gravel in a salmonid stream, given the considerably higher discharge left in the bypassed reach. Beyond the uncertainties regarding how sediment transport is affected downstream of RoR hydropower dams, higher fine sediment deposition as well as coarsening of substrates are expected to generate negative effects for salmonids. For example, new research shows that grain-size coarsening downstream of powerhouses could degrade salmonid habitat in RoR hydropower systems, particularly in streams with naturally high sediment supply rates (Fuller et al. 2016). Based on literature from manipulative experiments, higher fine sediment embeddedness will often induce a shift in invertebrate assemblages from drifting to burrowing taxa, resulting in reduced food supply for resident salmonids, and higher feeding costs (Suttle et al. 2004). Higher embeddedness can also clog spawning gravel, reducing the survival of overwintering eggs and alevins (Kondolf 1997), and affect primary production by decreasing diatom richness and diversity (Wu et al. 2009). For example, experimental increases in deposited fine sediments in shallow riffles led to up to 90% lower rainbow trout survival attributed to the decline in overall riverine habitat complexity and increased predation (Harvey et al. 2009). We conclude that fish entrainment, habitat fragmentation, and alteration to geomorphology and sediment transport induced by the presence of low-head dams all have the potential to negatively affect salmonids. The fact that RoR hydropower dams may be overtopped at high flows has the potential to mediate the severity of some of these impacts, but the absence of published research makes such determinations impossible at present.

Pathway 3: Anthropogenic Flow Fluctuations

We found only one peer-reviewed paper (Almodóvar and Nicola 1999) that evaluated the potential for flow fluctuations downstream of RoR hydropower dams to impact fishes (Figure 2, Table 1). However, the operation of RoR hydropower dams has the potential to create anthropogenic variations in flow in both bypassed and downstream reaches of rivers where they operate. Rapid fluctuations in flow downstream of dams and powerhouses in RoR hydropower systems may occur as a result of intentional increases or decreases in the proportion of stream flow diverted to turbines to optimize electricity production, or because of emergency shutdowns or operational malfunctions that unexpectedly halts the diversion of water. Because headponds have no water storage capacity, changes in the amount of water diverted for RoR electricity generation are quickly propagated downstream as flow fluctuations in both the bypassed and downstream reaches. However, the potential effects of flow fluctuations on river ecosystems and salmonids differ in bypassed and downstream reach. As the amount of stream flow diverted to RoR turbines decreases, the amount of water rerouted to the bypassed reach increases rapidly, while flow released at the tailrace of the powerhouse is reduced. The reduction of flow at the tailrace causes a temporary decrease in flow in the downstream reach, lasting until the rerouted water travels through the bypassed reach and reaches the powerhouse. The drop in flow downstream of powerhouses depends on site-specific characteristics including channel confinement, substrate type, and bathymetry, as well as characteristics of the RoR hydropower facilities, including the length of the penstock and the presence of mitigating structures like turbine bypass valves (Hunter 1992 in Bell et al. 2008).

Rapid anthropogenic fluctuations of flow in bypassed and downstream reaches have the potential to create negative consequences for fish ranging from unintentional downstream displacement, to increased stress and mortality. We found only a single study from the peer-reviewed literature, which reported that fluctuations in flow downstream of a small RoR diversion dam in Spain (diverting 85 to 100% of the seasonal discharge) lead to an average change in stage of 30 cm over minutes (Almodóvar and Nicola 1999). These frequent fluctuations in flow caused declines of brown trout density (-50%) and biomass (-43%), displacement of 0+ trout, and no change to macroinvertebrates in the first year following flow diversion (Almodóvar and Nicola 1999). In reservoir-storage systems, rapid increases in flow have also been associated with the downstream displacement of juvenile trout, increased energetic costs for fry, and scouring of redds (Harby and Halleraker 2001; Nislow and Armstrong 2012). Conversely, rapid decreases in flow can lead to a decrease in stage in downstream reaches that can strand fish on rapidly dewatered channel margins, or trap fish in disconnected side channels and isolated pools. Data from an unregulated montane stream in the USA Pacific Northwest show that natural fluctuations in stage rarely exceeded 5 cm per hour (Hunter 1992 in Bell et al. 2008), while frequent declines in river stage of 80-90 cm over 10 minutes were reported downstream of a reservoir-storage dam in Norway (Hvidsten 1985). Fish stranding or isolation in side channels may in turn lead to negative effects on survival, biomass, density, or fitness, as reported in studies from reservoir-storage systems (Young et al. 2011; Nagrodski et al. 2012; Senay et al. 2016). Given the limited research that has specifically sought to understand the consequences of anthropogenic flow fluctuations in RoR hydropower systems, large uncertainties remain about how their effects differ from those documented downstream of reservoir-storage systems where most peer-reviewed research has occurred.

RoR hydropower operations produce artificial fluctuations in flow that are likely to pose risks to salmonids that differ from those posed by large dams and reservoir-storage systems. For example, periods of natural low flow are often when RoR hydropower operations divert the highest proportion of flow, or create frequent fluctuations from practices called ‘flow cycling’, by which water is temporarily stored in penstocks to generate power for short periods of time (Hunter 1992 in Bell et al. 2008). These periods often coincide with the presence of newly emerged salmonid fry. Salmonid fry are likely to be the most vulnerable life history stage to the negative effects of anthropogenic flow fluctuations as they have limited swimming capacities and inhabit low-velocity, shallow habitats that are highly susceptible to dewatering (Bell et al. 2008; Korman et al. 2011). Flow fluctuations during natural low flow periods may also reduce the availability of salmonid rearing habitats, as well as interfere with spawning of anadromous and resident salmonids downstream of powerhouses (Nagrodski et al. 2012). Besides their timing, the frequency and magnitude of anthropogenic flow fluctuations from RoR operations have the potential to generate impacts to salmonids. For example, even small, but repeated, flow fluctuations were found to decrease the feeding time, growth, and survival of fish (Young et al. 2011). In addition, small but frequent anthropogenic fluctuations in flow have also been found to reduce fish density and biomass when compared to infrequent but large fluctuations generated by storage-reservoir hydropower in Canada (Senay et al. 2016). These findings may be particularly relevant for RoR hydropower systems which can create more frequent pulses in flow compared to reservoir storage hydropower due to the lack of water storage in headponds, and wider magnitude fluctuations during low flow seasons. Overall, how seasonal low flow periods and anthropogenic flow fluctuations interact to influence salmonid survival and growth in bypassed and downstream reaches of rivers regulated by RoR hydropower remains largely unknown. However, the potential for fluctuating flows to perturb fish habitat, induce fry mortality, and increase stress and activity costs for salmonids suggest that anthropogenic flow fluctuations are likely to be important for salmonid populations.

Avenues for Future Research

As highlighted by our literature search, published empirical research on the impact of RoR hydropower on the ecology of river ecosystems (n=31 peer-reviewed studies) and salmonids specifically (n=10 peer-reviewed studies) is very limited. Despite this limited literature, we found that RoR hydropower operations alter NFR in unique ways by changing the timing, and increasing the magnitude, frequency, and duration of low flow periods in bypassed reaches downstream of RoR hydropower dams. Moreover, the low-head dams of RoR hydropower facilities create unique conditions upstream and downstream since they may be overtopped by water at high flows. Though in need of additional study, this phenomenon may allow for more flushing of sediment and downstream passage of fish compared to reservoir-storage dams, thus potentially reducing the potential for discontinuities in habitat and impacts on stream geomorphology. RoR hydropower dams also divert a considerable proportion (up to 97% of incoming flow, Figure 3) of water away from the natural river channel for the production of electricity. We found a clear pattern where the magnitude of flow diversion by RoR hydropower varies by season, and is proportionally higher when flows in rivers are naturally low. Moreover, flow fluctuations in bypassed and downstream reaches of RoR hydropower systems typically occur unexpectedly, and differ in timing, frequency, magnitude, and duration from those occurring downstream of reservoir-storage systems. All these pathways of effects from RoR hydropower have the potential to alter habitat quantity and quality, and to negatively affect salmonid survival, growth, and fitness. We reiterate the need to standardize data and report details on project designs and environmental characteristics of rivers where the studies are conducted to allow for more powerful quantitative comparisons between RoR hydropower schemes and studies in the future (Anderson et al. 2014, Bilotta et al. 2016). For example, very few papers reported ecological details like climactic zones (only 6 of the 31 empirical papers), location in watershed (n=9 out of the 31 empirical papers), or river size (only 17 of the 31 empirical papers reported mean annual discharge for example), which precluded us from explicitly categorizing the studies and the range of effects based on these criteria. Our review also highlights the lack of empirical knowledge about the effects of RoR hydropower on salmonid species other than brown trout, which were the focus of over 90% of the empirical papers on salmonids we reviewed. In addition to the specific knowledge gaps identified in our review of the literature in each section above, below we identify three areas where future research is most needed. We chose to highlight these three research priorities because we believe they represent uncertainties related to those processes with the greatest potential to affect resident and anadromous fish populations. Addressing these knowledge gaps will help reduce the currently large uncertainties surrounding impacts of RoR hydropower on river ecosystems and salmonids, and in turn reduce conflict between proponents and opponents of additional RoR hydropower energy development.

(1) *Effects of amplified, short- and long-term low flow periods.* The effects of natural and anthropogenically-induced high flows on salmonids have received more attention than the effects of low flows (Lake 2000; Jowett et al. 2005). With the exception of research on environmental

flows (e.g., Poff and Matthews 2013), most research has focused on large magnitude changes, particularly for large dams and reservoir-storage systems (Poff and Zimmerman 2010). Our literature review revealed that RoR hydropower operations artificially generate longer and more frequent periods of low flow compared to natural flow regimes. The semi-predictable seasonal low flows resulting from RoR hydropower operation also represent a unique opportunity to study how increases in the duration, frequency, and magnitude of low flow periods affect fish and river ecosystems in isolation of other factors (Niemi et al. 1990; Matthews and Marsh-Matthews 2003; Waples et al. 2009).

(2) *Effects of anthropogenic flow fluctuations*. Other reviews have highlighted important knowledge gaps about how the magnitude, frequency, and timing of anthropogenic flow fluctuations downstream of reservoir-storage hydropower systems affect the growth, survival, and reproductive success of fish (Young et al. 2011; Nagrodski et al. 2012). These knowledge gaps are also relevant to rivers regulated by RoR hydropower, although we argue the gaps are even larger. We found very little peer-reviewed literature that examined how RoR hydropower fluctuations in flow deviate from the NFR or how these deviations impact salmonids in the bypassed and downstream reaches (n=1). In addition to direct impacts, research is needed to quantify potential indirect impacts of anthropogenic flow fluctuations on salmonids, as deviations from NFR are expected to affect food availability for fish by altering the composition and biomass of invertebrate communities. Beyond individual-level consequences, there is also a need to understand how short-term and individual level impacts of flow fluctuations scale up to the population level. Individual mortality or reductions in reproductive potential due to fish stranding can translate into reductions in population growth rates if they occur frequently, but density-dependent growth and survival of salmonid fishes may partially or completely compensate for

early life-history mortality caused by RoR operations (Shuter 1990; Harby and Halleraker 2001). The consequences of anthropogenic flow fluctuations on individual fishes and populations need to be established in RoR hydropower systems before appropriate mitigation measures can be developed to compensate for potential losses.

(3) *Cumulative impacts of multiple RoR hydropower projects*. Multiple RoR hydropower projects may be developed within individual watersheds to achieve energy production targets. For example, 15 low-elevation dams exist over 160 km in a Illinois river, USA (Santucci et al. 2005), and over 260 RoR hydropower dams are currently under consideration in 28 of the 32 major river valleys in the Indian Himalayas (1 RoR hydropower dam per 32 km of river, Grumbine and Pandit 2013). Multiple RoR hydropower projects in the same watershed may interact in additive, synergistic, or antagonistic ways to affect river ecosystems (e.g. increasing turbidity and decreasing invertebrate quality, Santucci et al. 2005) and salmonid populations (e.g. to alter or delay upstream fish migrations, Larinier 2008; Lucas et al. 2009). Some studies suggest that landscape-scale impacts per unit of energy may be greater for RoR hydropower dams than for large hydropower dams (Bakken et al. 2012; Kibler and Tullos 2013), while others reach the opposite conclusion (Taylor 2010). However, these conclusions are limited because they have not explicitly considered whether impacts from multiple RoR dams accumulate in non-linear ways (Larinier 2008). In addition, the impacts of RoR hydropower to salmonid populations are likely to depend on the regional context in which individual RoR hydropower projects are built (Habit et al. 2007). Flow diversion by RoR hydropower in watersheds with existing impacts from forestry and other industries will likely have different, and possibly compounding, effects on salmonids in contrast to watersheds with largely intact upland and riparian forests (Reice et al. 1990; Bunn and Arthington 2002). The disparity between the regional spatial scale relevant to the

survival and persistence of most salmonid populations and the often reach-specific scale at which environmental impacts of individual RoR hydropower projects are typically assessed needs to be addressed.

The rapid adoption of RoR hydropower around the world presents both opportunities for increasing renewable energy production, and challenges in predicting impacts to salmonids and river ecosystems. The spatial and temporal scales of anthropogenic perturbations from RoR hydropower are likely to differ from the historical conditions under which salmonids evolved. These perturbations may alter life-history diversity, population size, and connectivity among sub-populations, weakening their ability to dampen variability in the dynamics of regional population complexes (i.e., the portfolio effect; Tilman et al. 1998; Yeakel et al. 2014) and leading to reduced population resilience in the face of additional environmental change (Waples et al. 2008; Waples et al. 2009; Moore et al. 2015). The inherent characteristics of RoR hydropower infrastructures and operations, such as small non-storage headponds, low-head dams, bypassed reaches with reduced flows, and anthropogenic flow fluctuations, uniquely alter NFR. The limited peer-reviewed literature we found specific to RoR hydropower strongly suggests that impacts to salmonids and other fishes are probable under certain conditions, which is supported by better studied impacts of other forms of flow regulation. However, we caution that the knowledge developed from other types of flow regulation may not be directly applicable to RoR hydropower (Senay et al. 2016). As such, research specific to how RoR hydropower operations alter the NFR and how these alterations impact fish populations and river ecosystems is needed to confirm the pathways and mechanisms we outline in this paper. A suite of small-scale studies examining individual-level impacts on salmonids as well as long-term and large scale experimental studies would be useful to identify effective mitigation and management strategies for river ecosystems where RoR hydropower dams have the potential to impact salmonids. These strategies may be as simple as protocols dictating the rate at which water levels may be diverted or fluctuate, or as complex as full-watershed analyses to determine how to best maintain connectivity of salmonid populations and manage cumulative impacts across multiple dams and river networks. As the global need for RoR hydropower increases, concerted efforts to study the impacts of RoR hydropower dams on salmonids is crucial to ensure that evidence-based decisions are made for sustainable management of salmonid populations, and the river ecosystems in which they occur.

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Literature cited

Abbasi, T., and Abbasi, S.A. 2011. Small hydro and the environmental implications of its extensive utilization. Renew. Sustain. Energy Rev. 15: 2134–2143. doi:10.1016/j.rser.2010.11.050.

Almodóvar, A., and Nicola, G.G. 1999. Effects of a small hydropower station upon brown trout *Salmo trutta L*. in the river Hoz Seca (Tagus Basin, Spain) one year after regulation. Regul. Rivers Res. Manag. 15: 477–484.

Altukhow, Y.P., Salmenkova, E.A., and Omelchenko, V.T. 2000. The theoretical principles of population genetics. *In* Salmonid Fishes: Population biology, genetics and management, English translation edited by J. Thorpe and G. Carvalho. Blackwell, United Kingdom. pp. 1–32.

Anderson, D., Moggridge, H., Shucksmith, J.D., and Warren, P.H. 2015. Quantifying the impact of water abstraction for low head “run of the river” hydropower on localized river channel hydraulics and benthic macroinvertebrates. River Res. Appl.: 1–12. doi:10.1002/rra.2992.

Anderson, D., Moggridge, H., Warren, P., and Shucksmith, J. 2014. The impacts of “run-of-river” hydropower on the physical and ecological condition of rivers. Water Environ. J. doi:10.1111/wej.12101.

Aroonrat, K., and Wongwises, S. 2015. Current status and potential of hydro energy in Thailand: a review. Renew. Sustain. Energy Rev. 46: 70–78. doi:10.1016/j.rser.2015.02.010.

Baker, D.W., Bledsoe, B.P., Albano, C.M., and Poff, N.L. 2011. Downstream effects of diversion dams on sediment and hydraulic conditions of Rocky Mountain streams. River Res. Appl. 27: 388–401. doi:10.1002/rra.1376.

Bakken, T.H., Sundt, H., Ruud, A., and Harby, A. 2012. Development of small versus large hydropower in Norway -- comparison of environmental impacts. Energy Procedia 20: 185–199. doi:10.1016/j.egypro.2012.03.019.

Barnthouse, L.W. 2013. Impacts of entrainment and impingement on fish populations: a review of the scientific evidence. Environ. Sci. Policy 31: 149–156. doi:10.1016/j.envsci.2013.03.001.

Beakes, M.P., Moore, J.W., Hayes, S.H., and Sogard, S.M. 2014. Wildfire and the effects of shifting stream temperature on salmonids. Ecosphere 5(5): 1–14. doi:10.1890/ES13-00325.1.

Bell, E., Kramer, S., Zajanc, D., and Aspittle, J. 2008. Salmonid fry stranding mortality associated with daily water level fluctuations in Trail Bridge Reservoir, Oregon. North Am. J. Fish. Manag. 28: 1515–1528. doi:10.1577/M07-026.1.

Bendall, B., Moore, A., Maxwell, D., Davidson, P., Edmonds, N., Archer, D., Solomon, D., Greest, V., Wyatt, R., and Broad, K. 2012. Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. Fish. Manag. Ecol. 19: 475–483. doi:10.1111/j.1365-2400.2011.00811.x.

Benstead, J.P., March, J.G., Pringle, C.M., and Scatena, F.N. 1999. Effects of a low-head dam and water abstraction on migratory tropical stream biota. Ecol. Appl. 9(2): 656–668.

Bilotta, G.S., Burnside, N.G., Gray, J.C., and Orr, H.G. 2016. The effects of run-of-river hydroelectric power schemes on fish community composition in temperate streams and rivers. Plos One: 1–15. doi:DOI:10.1371/journal.pone.0154271.

Bonneau, J.L., and Scarnecchia, D.L. 1998. Seasonal and diel changes in habitat use by juvenile bull trout (*Salvelinus confluentus*) and cutthroat trout (*Oncorhynchus clarki*) in a mountain stream. Can. J. Zool. 76: 783–790.

Boubée, J.A.T., and Williams, E.K. 2006. Downstream passage of silver eels at a small hydroelectric facility. Fish. Manag. Ecol. 13: 165–176.

Bradford, M.J., and Heinonen, J.S. 2008. Low flows, instream flow needs and fish ecology in small streams. Can. Water Resour. J. 33(2): 165–180.

Brett, J.R. 1995. Energetics. *In* Physiological Ecology of Pacific Salmon, Groot, C., L. Margolis, and W.C. Clarke. in cooperation with the Government of Canada, Department of Fisheries and Oceans, UBC Press, Vancouver. pp. 3–68.

Bryant, M.D. 2009. Global climate change and potential effects on Pacific salmonids in freshwater ecosystems of southeast Alaska. Clim. Change 95: 169–193. doi:10.1007/s10584-008-9530-x.

Bunn, S.E., and Arthington, A.H. 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manage. 30(4): 492–507. doi:10.1007/s00267-002-2737-0.

Butler, S.E., and Wahl, D.H. 2011. Distribution, movements and habitat use of channel catfish in a river with multiple low-head dams. River Res. Appl. 27: 1182–1191. doi:10.1002/rra.1416.

Čada, G.F. 2001. The development of advanced hydroelectric turbines to improve fish passage survival. Fisheries 26(9): 14–23. doi:10.1577/1548-8446(2001)026<0014:TDOAHT>2.0.CO;2.

Capra, H., Sabaton, C., Gouraud, V., Souchon, Y., and Lim, P. 2003. A population dynamics model and habitat simulation as a tool to predict brown trout demography in natural and bypassed stream reaches. River Res. Appl. 19: 551–568.

Cattanéo, F., Lamouroux, N., Breil, P., and Capra, H. 2002. The influence of hydrological and biotic processess on brown trout (*Salmo trutta*) population dynamics. Can. J. Fish. Aquat. Sci. 59(1): 12–22. doi:10.1139/F01-186.

Chiyembekezo, S.K. 2013. Energy situation, potential and application status of small-scale hydropower systems in Malawi. Renew. Sustain. Energy Rev. 26: 1–19. doi:10.1016/j.rser.2013.05.034.

COSEWIC 2006. COSEWIC assessment and update status report on the westslope cutthroat trout *Oncorhynchus clarkii lewisi* (British Columbia and Alberta population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.vii+67 pp. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_oncorhynchus_clarkii_lewisi_e.pdf

COSEWIC. 2010. COSEWIC assessment and status report on the Dolly Varden *Salvelinus malma malma* (Western Arctic populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. x + 65 pp. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_dolly_varden_0911_eng.pdf

COSEWIC. 2012. COSEWIC assessment and status report on the Bull Trout *Salvelinus confluentus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. iv + 103 pp. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_omble_tete_plat_bull_trout_1113_e.pdf

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G., and Huey, R.B. 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evol. Appl. 1: 252–270. doi:10.1111/j.1752-4571.2008.00033.x.

Csiki, S.J.C., and Rhoads, B.L. 2010. Hydraulic and geomorphological effects of run-of-river dams. Prog. Phys. Geogr. 34(6): 755–780. doi:10.1177/0309133310369435.

Csiki, S.J.C., and Rhoads, B.L. 2013. Influence of four run-of-river dams on channel morphology and sediment characteristics in Illinois, U.S.A. Geomorphology. doi:10.1016/j.geomorph.2013.10.009.

Cyr, J.-F., Landry, M., and Gagnon, Y. 2011. Methodology for the large-scale assessment of small hydroelectric potential: application to the province of New Brunswick (Canada). Renew. Eergy 36: 2940–2950. doi:10.1016/j.renene.2011.04.003.

Englund, G., and Malmqvist, B. 1996. Effects of flow regulation, habitat area and isolation on the macroinvertebrates fauna of rapids in north Swedish rivers. Regul. Rivers Res. Manag. 12: 433–445.

Freeman, M.C., Bowen, Z.H., Bovee, K.D., and Irwin, E.R. 2001. Flow and habitat effects on juvenile fish abundance in natural and altered flow regimes. Ecol. Appl. 13(1): 179–190.

Fu, X., Tao, T., Wanxiang, J., Fengping, L., Naicheng, W., Shuchan, Z., and Qinghua, C. 2008. Impacts of small hydropower plants on macroinvertebrate communities. Acta Ecol. Sin. 28(1): 45–52.

Fuller, T.K., Venditti, J.G., Nelson, P.A., and Palen, W.J. 2016. Modeling grain size adjustments in the downstream reach following run-of-river development. Water Resour. Res. 52. doi:doi:10.1002/2015WR017992.

Gouraud, V., Capra, H., Sabaton, C., Tissot, L., Lim, P., Vandewalle, F., Fahrner, G., and Souchon, Y. 2008. Long-term simulations of the dynamics of trout populations on river reaches bypassed by hydroelectric installations - analysis of the impact of different hydrological scenarios. River Res. Appl. 24: 1185–1205. doi:10.1002/rra.1129.

Groot, C., and Margolis, L (Editors). 1991. Pacific Salmon Life Histories. UBC Press, Vancouver, Canada, ISBN 0-7748-0359-2. 550 pp.

Grumbine, R.E., and Pandit, M.K. 2013. Threats from India's Himalaya dams. Science 339: 36–37.

Habit, E., Belk, M.C., and Parra, O. 2007. Response of the riverine fish community to the construction and operation of a diversion hydropower plant in central Chile. Aquat. Conserv. Mar. Freshw. Ecosyst. 17: 37–49. doi:10.1002/aqc.774.

Harby, A., and Halleraker, J.H. 2001. Ecological impacts of hydropeaking in rivers. Hydropower Dams (4): 132–135.

Harvey, B.C., White, J.L., and Nakamoto, R.J. 2009. The effect of deposited fine sediment on summer survival and growth of rainbow trout in riffles of a small stream. North Am. J. Fish. Manag. 29(2): 434–440. doi:10.1577/M08-074.1.

Heggenes, J., and Røed, K.H. 2006. Do dams increase genetic diversity in brown trout (*Salmo trutta*)? Microgeographic differentiation in a fragmented river. Ecol. Freshw. Fish 15: 366–375. doi:10.1111/j.1600-0633.2006.00146.x.

Hvidsten, N.A. 1985. Mortality of pre-smolt Atlantic salmon, *Salmo salar* L., and brown trout, *Salmo trutta* L., caused by fluctuating water levels in the regulated River Nidelva, central Norway. J. Fish Biol. 27: 711–718.

Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J., Postel, S.L., and Running, S.W. 2001. Water in a changing world. Ecol. Appl. 11(4): 1027–1045.

Jesus, T., Formigo, N., Santos, P., and Tavares, G.R. 2004. Impact evaluation of the Vila Viçosa small hydroelectric power plant (Portugal) on the water quality and on the dynamics of the benthic macroinvertebrate communities of the Ardena river. Limnetica 23(3–4): 241–256.

Jowett, I.G., and Biggs, B.J.F. 2006. Flow regime requirements and the biological effectiveness of habitat-based minimum flow assessments for six rivers. Int. J. River Basin Manag. 4(3): 179–189.

Jowett, I.G., Richardson, J., and Bonnett, M.L. 2005. Relationship between flow regime and fish abundances in a gravel-bed river, New Zealand. J. Fish Biol. 66: 1419–1436. doi:10.1111/j.1095-8649.2005.00693.x.

Kibler, K.M. 2011. Development and decommissioning of small dams: analysis of impact and context. PhD dissertation, Water Resources Engineering, Oregon State University, Corvalis, Oregon, United States of America.

Kibler, K.M., and Tullos, D.D. 2013. Cumulative biophysical impact of small and large hydropower development in Nu River, China. Water Resour. Res. 49: 3104–3118. doi:10.1002/wrcr.20243.

Kondolf, G.M. 1997. Hungry water: effects of dams and gravel mining on river channels. Environ. Manage. 21(4): 533–551.

Korman, J., Walters, C.J., Martell, S.J.D., Pine III, W.E., and Dutterer, A. 2011. Effects of flow fluctuations on habitat use and survival of age-0 rainbow trout (*Oncorhunchus mykiss*) in a large, regulated river. Can. J. Fish. Aquat. Sci. 68: 1097–1109. doi:10.1139/F2011-045.

Kubečka, J., Matěna, J., and Hartvich, P. 1997. Adverse ecological effects of small hydropower stations in the Czech Republic: 1. bypass plants. Regul. Rivers Res. Manag. 13: 101–113.

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. J. North Am. Benthol. Soc. 19(4): 573–592.

Larinier, M. 2008. Fish passage experience at small-scale hydro-electric power plants in France. Hydrobiologia 609: 97–108. doi:10.1007/s10750-008-9398-9.

Lucas, M.C., Bubb, D.H., Jang, M., Ha, K., and Masters, J.E.G. 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. Freshw. Biol. 54: 621–634. doi:10.1111/j.1365-2427.2008.02136.x.

Malcolm, I.A., Gibbins, C.N., Soulsby, C., Tetzlaff, D., and Moir, H.J. 2012. The influence of hydrology and hydraulics on salmonids between spawning and emergence: implications for the management of flows in regulated rivers. Fish. Manag. Ecol. 19: 464–474. doi:10.1111/j.1365-2400.2011.00836.x.

Mantua, N., Tohver, I., and Hamlet, A. 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Clim. Change 10(102): 187–223. doi:10.1007/s10584-010-9845-2.

Matthews, W.J., and Marsh-Matthews, E. 2003. Effects of droughts on fish across axes of space, time and ecological complexity. Freshw. Biol. 48: 1232–1253.

McManamay, R.A., Peoples, B.K., Orth, D.J., Dolloff, C.A., and Matthews, D.C. 2015. Isolating causal pathways between flow and fish in the regulated river hierarchy. Can. J. Fish. Aquat. Sci. 72: 1731–1748. doi:10.1139/cjfas-2015-0227.

McPhail, J.D. 2007. The freshwater fishes of British Columbia. The University of Alberta Press, Edmonton, Alberta, Canada. ISBN 978-0-88864-467-1, 620 pp.

Moore, J.W., Beakes, M.P., Nesbitt, H.K., Yeakel, J.D., Patterson, D.A., Thompson, L.A., Phillis, C.C., Braun, D.C., Favaro, C., Scott, D., Carr-Harris, C., and Atlas, W.I. 2015. Emergent stability in a large, free-flowing watershed. Ecology 96(2): 340–347.

Morris, S.E. 1992. Geomorphic assessment of the effects of flow diversion on anadromous fish spawning habitat: Newhalem Creek, Washington. Prof. Geogr. 44(4): 444–452.

Mueller, M., Pander, J., and Geist, J. 2011. The effects of weirs on structural stream habitat and biological communities. J. Appl. Ecol. 48: 1450–1461. doi:10.1111/j.1365-2664.2011.02035.x.

Murchie, K.J., Hair, K.P.E., Pullen, C.E., Redpath, T.D., Stephens, H.R., and Cooke, S.J. 2008. Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. River Res. Appl. 24: 197–217. doi:10.1002/rra.1058.

Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., and Cooke, S.J. 2012. Fish stranding in freshwater systems: sources, consequences, and mitigation. J. Environ. Manage. 103: 133–141. doi:10.1016/j.jenvman.2012.03.007.

Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5: 399–417. doi:10.1007/s10021-001-0083-3.

Niemi, G.J., DeVore, P., Detenbeck, N., Taylor, D., Lima, A., Pastor, J., Yount, J.D., and Naiman, R.J. 1990. Overview of case studies on recovery of aquatic systems from disturbance. Environ. Manage. 14(5): 571–587.

Nilsson, C., Reidy, C.A., Dynesius, M., and Revenga, C. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308: 405–408. doi:10.1126/science.1107887.

Nislow, K.H., and Armstrong, J.D. 2012. Towards a life-history-based management framework for the effects of flow on juvenile salmonids in streams and rivers. Fish. Manag. Ecol. 19: 451–463. doi:10.1111/j.1365-2400.2011.00810.x.

Ovidio, M., Capra, H., and Philippart, J.-C. 2008. Regulated discharge produces substantial demographic changes on four typical fish species of a small salmonid stream. Hydrobiologia 609: 59–70. doi:10.1007/s10750-008-9399-8.

Pittock, J., and Hartmann, J. 2011. Taking a second look: climate change, periodic relicensing and improved management of dams. Mar. Freshw. Res. 62: 312–320. doi:10.1071/MF09302.

Poff, N.L., Allan, D.J., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime. BioScience 47(11): 769–784.

Poff, N.L., and Hart, D.D. 2002. How dams vary and why it matters for the emerging science of dam removal. BioScience 52(8): 659–668. doi:10.1641/0006-3568(2002)052[0659:HDVAWI]2.0.CO;2.

Poff, N.L., and Matthews, J.H. 2013. Environmental flows in the Anthropocence: past progress and future prospects. Curr. Opin. Environ. Sustain. 5: 667–675. doi:10.1016/j.cosust.2013.11.006.

Poff, N.L., and Ward, J.V. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environ. Manage. 14(5): 629–645.

Poff, N.L., and Zimmerman, J.K.H. 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshw. Biol. 55: 194–205. doi:10.1111/j.1365-2427.2009.02272.x.

Poole, G.C., and Berman, C.H. 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environ. Manage. 27(6): 787–802. doi:10.1007/s002670010188.

van Poorten, B.T., and McAdam, S.O. 2010. Estimating differences in growth and metabolism in two spatially segregated groups of Columbia River white sturgeon using a field-based bioenergetics model. Open Fish Sci. J. 3: 132–141.

Postel, S., Daily, G.C., and Ehrlich, P.R. 1996. Human appropriation of renewable fresh water. Science 271(5250): 785–788.

Reice, S.R., Wissmar, R.C., and Naiman, R.J. 1990. Disturbance regimes, resilience, and recovery of animal communities and habitats in lotic ecosystems. Environ. Manage. 14(5): 647–659.

Renöfält, B.M., Jansson, R., and Nilsson, C. 2010. Effects of hydropower generation and opportunities for environmental flow management in Swedish riverine ecosystems. Freshw. Biol. 55: 49–67. doi:10.1111/j.1365-2427.2009.02241.x.

Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Hiram, W.L., Minshall, G.W., Reice, S.I., L., A.L., Bruce, J.B., and Wissmar, R.C. 1988. The role of disturbance in stream ecology. J. North Am. Benthol. Soc. 7(4): 433–455.

Robson, A., Cowx, I.G., and Harvey, J.P. 2011. Impact of run-of-river hydro-schemes upon fish populations. Scotland & Northern Ireland Forum for Environmental Research (SNIFFER).

http://www.sniffer.org.uk/files/1113/4071/0278/WFD114_Lit20review_FINAL_AUG2011.pdf

Rosenberg, D.M., Berkes, F., Bodaly, R.A., Hecky, R.E., Kelly, C.A., and Rudd, J.W.N. 1997. Large-scale impacts of hydroelectric development. Env. Rev 5: 27–54.

Sabaton, C., Souchon, Y., Capra, H., Gouraud, V., Lascaux, J.-M., and Tissot, L. 2008. Long-term brown trout populations responses to flow manipulation. River Res. Appl. 24: 476–505. doi:DOI: 10.1002/rra.1130.

Santos, J.M., Ferreira, M.T., Pinheiro, A.N., and Bochechas, J.H. 2006. Effects of small hydropower plants on fish assemblages in medium-sized streams in central and northern Portugal. Aquat. Conserv. Mar. Freshw. Ecosyst. 16: 373–388. doi:10.1002/aqc.735.

Santos, J.M., Silva, A., Katopodis, C., Pinheiro, P., Pinheiro, A., Bochechas, J., and Ferreira, M.T. 2012. Ecohydraulics of pool-type fishways: Getting past the barriers. Ecol. Eng. 48: 38–50. doi:10.1016/j.ecoleng.2011.03.006.

Sedell, J.R., Reeves, G.H., Hauer, F.R., Stanford, J.A., and Hawkins, C.P. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environ. Manage. 14(5): 711–724.

Senay, C., Taranu, Z.E., Bourque, G., MacNaughton, C.J., Lanthier, G., Harvey-Lavoie, S., and Boisclair, D. 2016. Effects of river scale flow regimes and local scale habitat properties on fish community attributes. Aquat. Sci. doi:10.1007/s00027-016-0476-1.

Shaw, T.L. 2004. The implications of modern hydro-electric power schemes for fisheries. Water Environ. J. 18(4): 207–209.

Shuter, B.J. 1990. Population-level indicators of stress. Am. Fish. Soc. 8: 145–166.

Skalski, J.R., Mathur, D., and Heisey, P.G. 2002. Effects of turbine operating efficiency on smolt passage survival. North Am. J. Fish. Manag. 22(4): 1193–1200. doi:10.1577/1548-8675(2002)022<1193:EOTOEO>2.0.CO;2.

Smith, B.D. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for snowmelt-driven watersheds of British Columbia in relation to freshwater discharge. Can. J. Fish. Aquat. Sci. 57(2): 285–297.

Smith, S.D., Wellington, A.B., Nachlinger, J.L., and Fox, C.A. 1991. Functional responses of riparian vegetation to streamflow diversion in the Eastern Sierra Nevada. Ecol. Appl. 1(1): 89–97.

Sopinka, A., van Kooten, G.C., and Wong, L. 2013. Reconciling self-sufficiency and renewable energy targets in a hydro dominated system: the view from British Columbia. Energy Policy 61: 223–229. doi:10.1016/j.enpol.2013.05.068.

Spänhoff, B. 2014. Current status and future prospects of hydropower in Saxony (Germany) compare to trends in Germany, the European Union, and the world. Renew. Sustain. Energy Rev. 30: 518–525. doi:10.1016/j.rser.2013.10.035.

Strayer, D.L., and Dudgeon, D. 2010. Freshwater biodiversity conservation: recent progress and future challenges. J. North Am. Benthol. Soc. 29(1): 344–358. doi:10.1899/08-171.1.

Suttle, K.B., Power, M.E., Levine, J.M., and McNeely, C. 2004. How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. Ecol. Appl. 14(4): 969–974.

Taylor, L.A. 2010. A comparison of the aquatic impacts of large hydro and small hydro projects. Master of Resource Management, School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia, Canada.

Tilman, D., Lehman, C.L., and Bristow, C.E. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? Am. Nat. 151(3): 277–282.

Valero, E. 2012. Characterization of the water quality status on a stretch of River Lérez around a small hydroelectric power station. Water 4: 815–834. doi:10.3390/w4040815.

Vörösmarty, C.J., and Sahagian, D. 2000. Anthropogenic disturbance of the terrestrial water cycle. BioScience 50(9): 753–765.

Walters, A.W., and Post, D.M. 2008. An experimental disturbance alters fish size structure but not food chain length in streams. Ecology 89(12): 3261–3267.

Walters, A.W., and Post, D.M. 2011. How low can you go? Impacts of a low-flow disturbance on aquatic insect communities. Ecol. Appl. 21(1): 163–174.

Waples, R.S., Pess, G.R., and Beechie, T. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evol. Appl. 1: 189–206. doi:10.1111/j.1752-4571.2008.00023.x.

Ward, J.V., and Stanford, J.A. 1983. The serial discontinuity concept in lotic ecosystems. *In* Dynamics of lotic ecosystems, T.D. Fontain and S.M. Bartell. Ann Arbor Science, Ann Arbor, Michigan. pp. 29–42.

Weitkamp, D.E., and Katz, M. 1980. A review of dissolved gas supersaturation literature. Trans. Am. Fish. Soc. 109(6): 659–702.

Weltman-Fahs, M., and Taylor, J.M. 2013. Hydraulic fracturing and brook trout habitat in the Marcellus Shale region: potential impacts and research needs. Fisheries 38(1): 4–15. doi:10.1080/03632415.2013.750112.

Wohl, E. 2006. Human impacts to mountain streams. Geomorphology 79: 217–248. doi:10.1016/j.geomorph.2006.06.020.

Wu, N., Tang, T., Zhou, S., Jia, X., Li, F., Liu, R., and Cai, Q. 2009. Changes in benthic algal communities following construction of a run-of-river dam. J. North Am. Benthol. Soc. 28(1): 69–79. doi:10.1899/08-047.1.

Yeakel, J.D., Moore, J.W., Guimaraes Jr., P.R., and de Aguiar, M.A.M. 2014. Synchronisation and stability in river metapopulation networks. Ecol. Lett. 17: 273–283. doi:10.1111/ele.12228.

Young, P.S., Cech, J.J. jr, and Thompson, L.C. 2011. Hydropower-related pulsed-flow impacts on stream fishes: a brief review, conceptual model, knowledge gaps, and research needs. Revies Fish Biol. Fish. 21: 713–731. doi:10.1007/s11160-011-9211-0.

Zhou, S., Tang, T., Wu, N., Fu, X., and Cai, Q. 2008. Impacts of a small dam on riverine zooplankton. Intern. Rev Hydrobiol 93(3): 297–311. doi:10.1002/iroh.200711038.

Zhou, S., Tang, T., Wu, N., Fu, X., Jiang, W., Li, F., and Cai, Q. 2009. Impacts of cascaded small hydropower plants on microzooplankton in Xiangxi River, China. Acta Ecol. Sin. 29: 62–68. doi:10.1016/j.chnaes.2009.04.008.

Table 1. Empirical peer-reviewed papers studying RoR hydropower impacts on river ecosystems and salmonids. [a]= brown trout, [b]= European grayling, [c]= trout, [d]= rainbow trout, [e]= Atlantic salmon, [f]= high-head scheme, [g]= low-head scheme; **= dams were in cascade; MAD= mean annual discharge.

Papers	Taxa/ characteristics	Mechanism(s) addressed	Type of dam(s)	Number of dams	Height of dam(m)	Length of bypassed reach (km)	MAD (cms)	Flow diverted
Pathway 1: Flow diversion								
Bilotta et al. 2016	Fish[a,e]	Reduction in habitat quantity and quality	hydropower[f,g] (54 kW)	23	11	0.22	---	---
Capra et al. 2003	Fish[a]	Reduction in habitat quantity and quality	Hydropower[f]	1	---	---	2.4	max of 4.4 cms
Gouraud et al. 2008	Fish[a]	Reduction in habitat quantity and quality	Hydropower[f]	3	7.1	4.5	8.55	--
McManamay et al. 2015	Fish	Changes to water quality	Hydropower and others	22**	--	--	--	--
Ovidio et al. 2008	Fish[a,b]	Reduction in habitat quantity and	Hydropower[f] (900 MW)	1	--	1.2	1.78	--

		quality						
Sabaton et al. 2008	Fish[a]	Changes to water quality	Hydropower[f]	7 (on 5 streams)	--	4.7	32.3	--
Mueller et al. 2011	Periphyton, aquatic macrophytes, macroinvertebrates and fish	Changes to water quality, reduction in habitat quantity and diversity	Hydropower	5	2.6	--	5.7	--
Anderson et al. 2015	Benthic macroinvertebrates	Changes to water quality	Hydropower[f] (30 kW)	1	3	~ 0.1	1.17	1.05 cms
Englund and Malmqvist 1996	Macroinvertebrates	Changes to water quality	Hydropower and others	51	--	--	10	86-99.8% reduction
Fu et al. 2008	Macroinvertebrates	Changes to water quality	Hydropower[f]	5**	--	--	--	--
Jesus et al. 2004	Macroinvertebrates	Changes to water quality	Hydropower[f]	1	--	--	0.93	90% in rainy season, 92% in drought season
Wu et al 2010a	Benthic diatoms	Changes to water quality	Hydropower[f]	23**	--	--	--	--
Wu et al 2010b	Benthic algal community	Changes to water quality	Hydropower[f]	1		~ 5	--	--
Wu et al. 2012	Benthic diatoms	Changes to water quality	Hydropower[f]	23**	--	--	--	--
Zhou et al. 2008	Zooplankton	Changes to water quality	Hydropower[f]	1	--	--	--	--
Zhou et al. 2009	Zooplankton	Changes to water quality	Hydropower[f]	6**	--	--	--	--

Valero 2012	Water quality	Changes to water quality	Hydropower[f] (11.8 MW)	1	11.05	3.4	14.4	59% of water flow
Pathway 1: Flow diversion and Pathway 2: Presence of low-head dams								
Anderson et al. 2006	Fish	Changes to water quality, reduction in habitat quantity and diversity, barrier to migration	Hydropower[f] (18 MW)	2	< 10	3	4.75	90-95% of MAD
Habit et al. 2007	Fish[a,d]	Reduction in habitat quantity and quality, barrier to migration	Hydropower[f] (130 MW)	2	--	14	25.8	up to 90% of MAD
Jowett and Biggs 2006	Fish[c]	mitigation measures	Hydropower and others	1	--	--	450	96.5-97.3%
Santos et al. 2006	Fish[a]	Reduction in habitat quantity and quality, barrier to migration	Hydropower[f] (3.97 MW)	18	5.8	--	--	--
Kubecka et al. 1997	Benthic and fish communities[a,b,c]	Changes to water quality, reduction in habitat quantity and diversity, fish	Hydropower[f] (< 10 MW)	23	all but one < 2	0.89	1.185	up to 100% of discharge

		entrainment, and barrier to migration						
Wu et al. 2009	Benthic algal community	Changes to water quality, discontinuities in geomorphology	Hydropower[f]	1	1.5	> 3	--	--
Pathway 1: Flow Diversion and Pathway 3: Flow fluctuations								
Almodovar and Nicola 1999	Fish[a]	Changes to water quality, flow fluctuations	Hydropower (0.7 MW)	--	--	--	0.40 (summer) to 2 (winter)	--
Pathway 2: Presence of low-head dams								
Boubée and Williams 2006	Fish	entrainment	Hydropower[f] (4.5 MW)	1	3.5	--	--	--
Larinier 2008	Fish	entrainment and barrier to migration	Hydropower[f, g] (< 10 MW)	(several schemes)	--	--	varied	--
Santos et al. 2012	Fish	Barrier to migration	Hydropower (< 10 MW)	37	--	--	--	--
Santucci et al. 2005	Fish, macroinvertebrates	Barrier to migration	Hydropower and other uses	15**	0.85	NA	662	--
Fuller et al. 2016	Geomorphology	discontinuities in geomorphology and sediment transport	Hydropower[f]	1	--	1	1.6	--

Kibler and Tullos 2013	Geomorphology	discontinuities in geomorphology and sediment transport	Hydropower[f] (19 MW)	31	8.8	6.8	3.1	up to 100%
Morris 1992	Spawning gravels	discontinuities in geomorphology and sediment transport	Hydropower[f] (2.3 MW)	1	--	~ 6	--	2

Table 2. Relative vulnerability of salmonid species to potential impacts from RoR hydropower, based on chronic exposure and the potential for dams to create barrier for migrations. Information on life history, spawning season and length of freshwater residency come from the references indicated by footnotes.

Common name	**Scientific name**	**Life history**	**Spawning season**	**Typical length of freshwater residency**[a]	**Relative vulnerability**	
					Barrier to migration[b]	**Chronic exposure**[c]
rainbow trout[d,e]	*Oncorhynchus mykiss*	Resident	Spring	life	High	Very high
steelhead[d,e]	*Oncorhynchus mykiss*	Anadromous	Spring	1-3 years	Very high	High
brown trout[d,e]	*Salmo trutta*	Resident	Late fall	life	High	Very high
sea-run brown trout[d,e]	*Salmo trutta*	Anadromous	Late fall	1-3 years	Very high	High
cutthroat trout[f]	*Oncorhynchus clarki spp.*	Resident	Late winter, spring	life	High	Very high
sea-run cutthroat trout[f]	*Oncorhynchus clarki spp.*	Anadromous	Late winter, spring	2-3 years	Very high	High
		Stream resident	Summer, fall	life	High	Very high
bull trout[g]	*Salvelinus confluentus*	Fluvial/adfluvial migrant	Summer, fall	life	Very High	Very high
		Anadromous	Summer, fall	2-3 years	Very High	High
Dolly Varden[h]	*Salvelinus malma malma*	Resident	Fall	life	High	Very High
		Anadromous	Fall	2-4 years	Very High	High
atlantic salmon[e]	*Salmo salar*	Anadromous	Fall	2-3 years	Very High	High
kokanee[d]	*Oncorhynchus nerka*	Resident	Fall	life	Moderate	Low
sockeye	*Oncorhynchus*	Anadromous	Fall	1-2 years	High	Low

salmon[d]	*nerka*					
masu salmon[d]	*Oncorhynchus masou*	Resident	Fall	life	High	Very High
		Anadromous	Fall	1-3 years	Very High	High
coho salmon[d]	*Oncorhynchus kisutch*	Anadromous	Fall	1-2 years	Very High	High
Chinook salmon[d]	*Oncorhynchus tshawytscha*	Anadromous	Fall	1-2 years	Moderate	Moderate
pink salmon[d]	*Oncorhynchus gorbuscha*	Anadromous	Fall	Days-weeks	Low	Low
chum salmon[d]	*Oncorhynchus keta*	Anadromous	Fall	Days-weeks	Low	Low

[a] Defined as time in freshwater post emergence from gravel

[b] Based on extent of freshwater migration and size of river systems spawning and rearing typically occurs in

[c] Based on portion of life cycle spent in freshwater and size of river systems spawning and rearing typically occurs in

[d] Groot and Margolis 1995

[e] McPail 2007

[f] COSEWIC 2007

[g] COSEWIC 2006

[h] COSEWIC 2010

Figure captions

Figure 1: Three main pathways of effects of RoR hydropower on salmonids and their associated main mechanisms of impacts. The number of empirical peer-reviewed papers identified in this review is shown in boxes between the pathways of effect (1-3) and their primary mechanisms.

Figure 2: Generalized schematic of a run-of-river hydropower facility. A low-elevation dam impounds the river and reroutes water downstream through a penstock, to turn turbines in the powerhouse and produce electricity. The diversion of water leaves a reach of the river with reduced flows (bypassed reach), but all water is returned to the downstream reach of the river via the tailrace. The headpond has little water storage capacity and so does not act as a reservoir. Powerlines are part of the transmission corridor that connects the facility to a centralized power grid.

Figure 3: Modeled natural upstream flows (black line) and flows passing through the bypassed reaches (dashed line) during an average runoff year below a low-head RoR hydropower dam in a) western Canada (high-head scheme in snowmelt-dominated Bull River, natural flow averaged from 2010-2013, diverted flow modelled with a hypothetical turbine flow of 9.9 cms; www.bchydro.com), and b) Yunnan Province, China (rain-dominated Gutan River, Lushui County, adapted from Kibler and Tullos 2013). Flow alterations in the bypassed reaches are most pronounced during naturally low to moderate flows, when RoR hydropower operations divert the greatest proportion of flow from the channel. The Bull River

has a minimum flow requirement that varies between 0.25 and 2.0 cms, depending on the season.

Figure 1

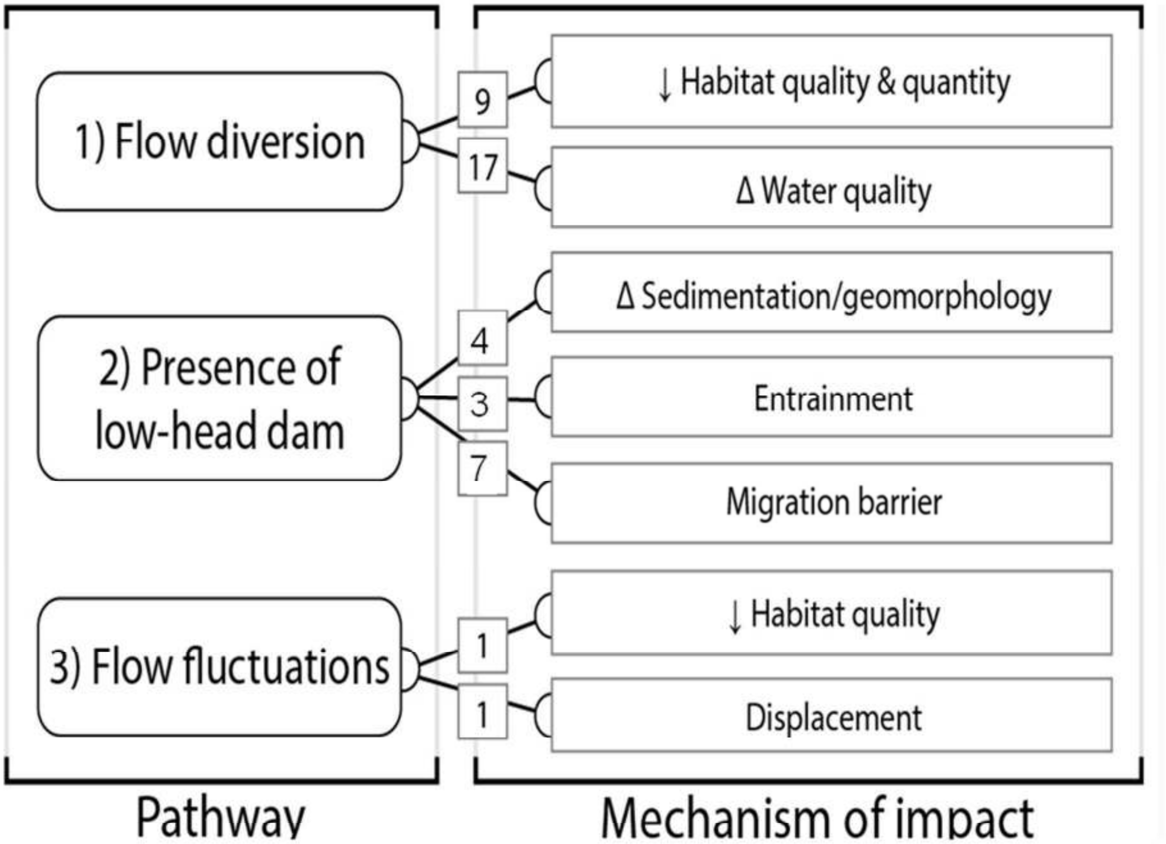

1) Flow diversion
2) Presence of low-head dam
3) Flow fluctuations
9
17
4
3
7
1
1
↓ Habitat quality & quantity
Δ Water quality
Δ Sedimentation/geomorphology
Entrainment
Migration barrier
↓ Habitat quality
Displacement
Pathway
Mechanism of impact

Figure 2

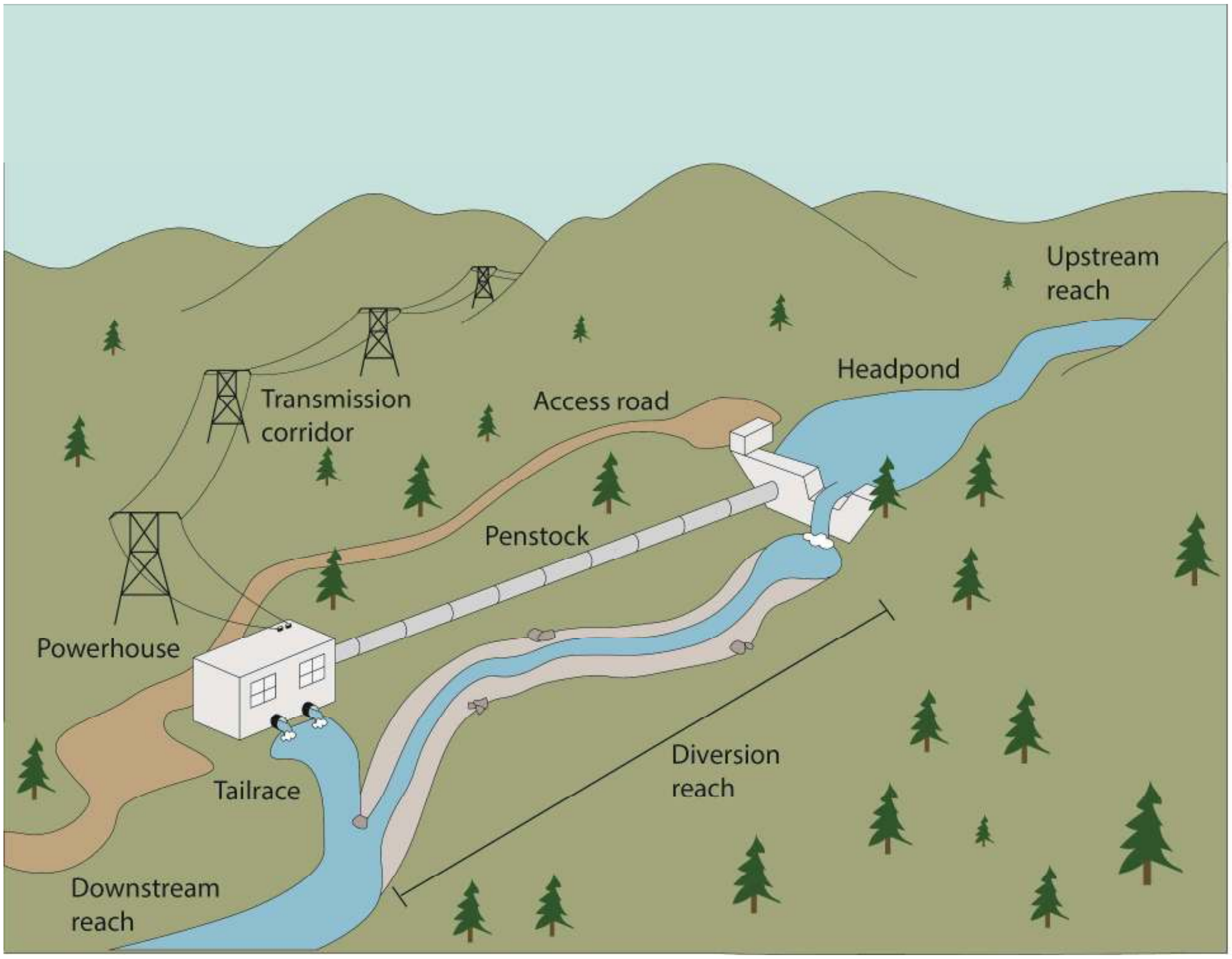
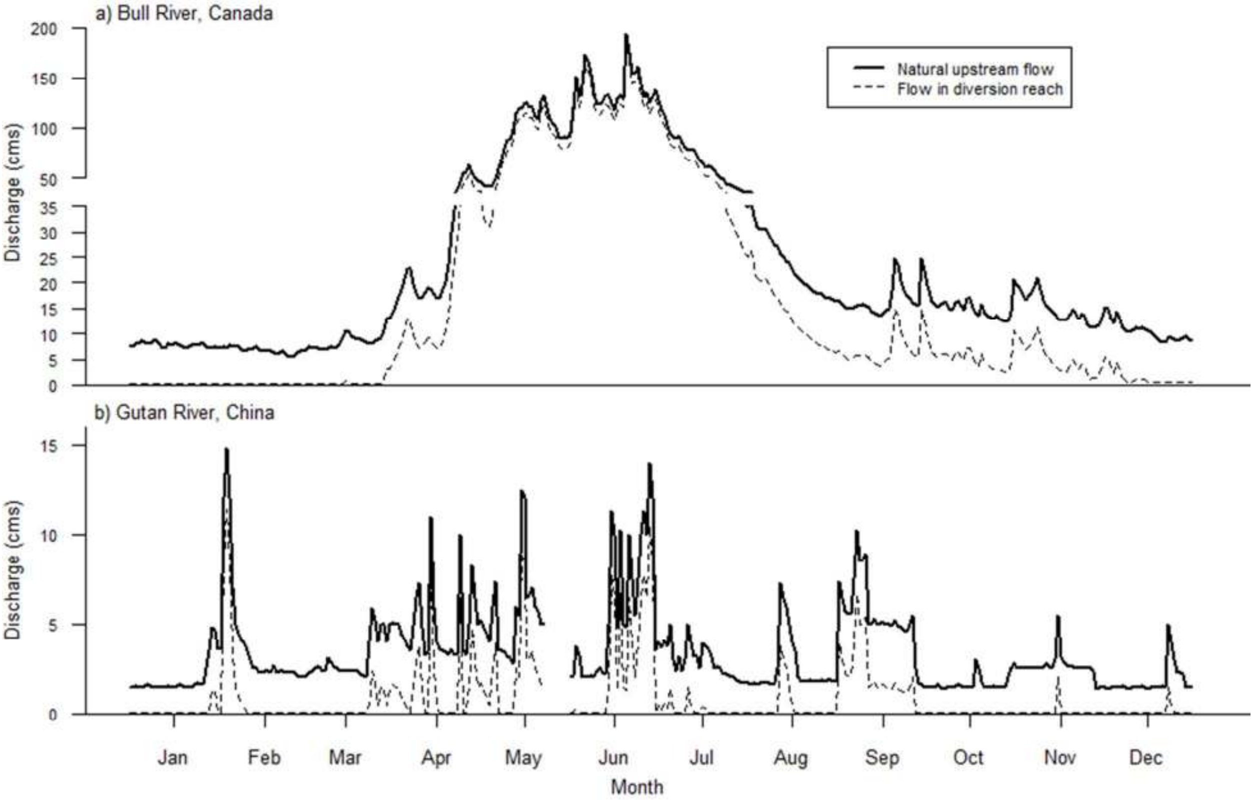

Upstream reach
Headpond
Transmission corridor
Access road
Penstock
Powerhouse
Diversion reach
Tailrace
Downstream reach

Figure 3


a) Bull River, Canada
Natural upstream flow
Flow in diversion reach
Discharge (cms)
200
150
100
50
35
30
25
20
15
10
5
0
b) Gutan River, China
Discharge (cms)
15
10
5
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Appendix 1. Non-empirical peer-reviewed papers on RoR hydropower.

Papers	Category	Country
Abbasi and Abbasi 2001	Global and historical perspective on emergence of ROR hydropower, general review of potential effects on ecosystem, cumulative impacts	India
Anderson et al. 2014	Review of ROR hydropower impacts on river ecosystems	UK, Europe
Aroonrat and Wongwises 2015	Geography, economy and politics of RoR hydropower	Thailand
Bakken et al. 2012	Comparison of small to large hydropower, cumulative impacts	Norway
Chiyembekezo 2013	Geography, economy and politics of RoR hydropower	Malawi
Cyr et al. 2001	Geography, economy and politics of RoR hydropower	Canada
Grumbine and Pumdit 2013	Geography, economy and politics of RoR hydropower	India
Jaccard et al. 2001	Geography, economy and politics of RoR hydropower	Canada
Kibler 2011	Comparison of small to large hydropower, cumulative impacts	China
Kotchen et al. 2006	Cost benefit analysis of hydropower dam relicensing	USA
Poff and Hart 2002	Classification of small dams and review of science of dam removal	USA
Renofalt et al. 2010	Effects of hydropower and environmental flow management on river ecosystems, cumulative impacts	Sweden
Shaw 2004	Implications of modern hydro-electric plants for fisheries and natural hydrographs	
Sopinka et al. 2013	Geography, economy and politics of RoR hydropower	Canada
Spänhoff 2014	Geography, economy and politics of RoR hydropower	Germany and Europe
Wang et al. 2010	Geography, economy and politics of RoR hydropower	China