NRC Research Press

PERSPECTIVE

Bidirectional connectivity in rivers and implications for watershed stability and management[1]

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Abstract: River networks are connected in both upstream and downstream directions on large spatial scales by movement of water, materials, and animals. Here I examine the implications of these linkages for the stability, productivity, and management of watersheds and their migratory fishes. I use simple simulations of watershed alteration to illustrate that degradation can erode the productivity and stability of both upstream and downstream fisheries. Through analysis of an existing global dataset on rivers, I found that larger rivers tend to be more fragmented than smaller rivers. I offer three challenges and opportunities for the future management of watersheds. First, given that human impacts can spread up and down rivers, there is a need to align the scales of impact assessments with the natural scale of river systems. Second, free-flowing rivers naturally dampen variability; thus, the conservation of connectivity, habitat, and biodiversity represents a key opportunity to sustain the processes that confer stability. Third, watersheds represent natural units of social–ecological systems; watershed governance would facilitate reciprocal feedbacks between people and ecosystems and enable more social–ecological resilience.

Résumé : Les réseaux hydrographiques sont connectés tant vers l'amont que vers l'aval à de grandes échelles spatiales par le déplacement de l'eau, de matières et d'animaux. J'examine les conséquences de ces liens sur la stabilité, la productivité et la gestion des bassins versants et de leurs poissons migrateurs. J'emploie des simulations simples de l'altération des bassins versants pour illustrer le fait que la dégradation peut éroder la productivité et la stabilité des ressources halieutiques tant vers l'amont que vers l'aval. En analysant un ensemble existant de données planétaires sur les rivières, j'ai constaté que les grandes rivières ont tendance à être plus fragmentées que les rivières plus petites. Je propose trois défis et occasions à saisir pour la gestion future des bassins versants. D'abord, étant donné que les impacts humains peuvent se propager vers l'amont et l'aval des rivières, il est nécessaire que l'échelle d'évaluation des impacts coïncide avec l'échelle naturelle du réseau hydrographique. Deuxièmement, les rivières au libre cours atténuent naturellement la variabilité, de sorte que la conservation de la connectivité, des habitats et de la biodiversité représente une occasion clé pour soutenir des processus qui confèrent de la stabilité. Troisièmement, les bassins versants constituent des unités naturelles de systèmes socioécologiques; la gouvernance des bassins versants faciliterait des rétroactions réciproques entre les humains et les écosystèmes et permettrait une plus grande résilience socio-écologique. [Traduit par la Rédaction]

Introduction

Given our economic and cultural reliance on river systems and the services they provide (Postel et al. 1996), the degradation of freshwater habitats is increasingly a genuine threat to the supply of key ecosystem services such as clean water, energy generation, and food production (Dudgeon et al. 2006; Milly et al. 2008; Vörösmarty et al. 2010). Fish represent a key example of a natural resource that is supported by river systems. Fisheries provide important economic and cultural resources globally as well as in Canada; many of these fisheries target migratory fishes such as anadromous salmon (Lapointe et al. 2014). Recreational fisheries contributed a total of $8.3 billion to the economy of Canada in 2010 through buying supplies, equipment, and costs of fishing trips (Fisheries and Oceans Canada 2012). There were an estimated 3.29 million people in Canada who participated in recreational fishing in 2010, fishing for an annual cumulative total of 40 million days (angler-days), and catching approximately 190 million fish in that year (Fisheries and Oceans Canada 2012). Furthermore, fisheries are a critical part of First Nations economies — salmon fisheries in British Columbia have existed for at least 5000 years (Harris 2001; Ames 2003; Lepofsky et al. 2005). While some commercial salmon fisheries are likely among the most sustainable commercial fisheries in the world (e.g., Bristol Bay, Alaska, sockeye salmon (*Oncorhynchus nerka*); Hilborn et al. 2003), other salmon populations are imperiled or have been extirpated (Gustafson et al. 2007). The state of freshwater biodiversity and ecosystems continues to erode because of a variety of cumulative human activities (Schindler 2001; Dudgeon et al. 2006; Strayer and Dudgeon 2010; Vörösmarty et al. 2010). Given these increasing pressures upon river systems and the goods and services they produce, there is an ever-growing need for science to inform management of river systems. These challenges apply globally, as well as within specific regions such as western Canada, which is the focus of this perspective.

In this manuscript, I posit that bidirectional linkages in river networks influence their dynamics, conservation, and management. I focus on upstream–downstream (longitudinal) linkages. First, I discuss scales of connectivity in river systems and the consequences of this connectivity. Second, I use simulations to explore how scenarios of watershed alterations impact the stability and productivity of upstream and downstream fisheries. Third, I analyze the extent of flow modification and fragmentation of

Received 22 October 2014. Accepted 1 February 2015.

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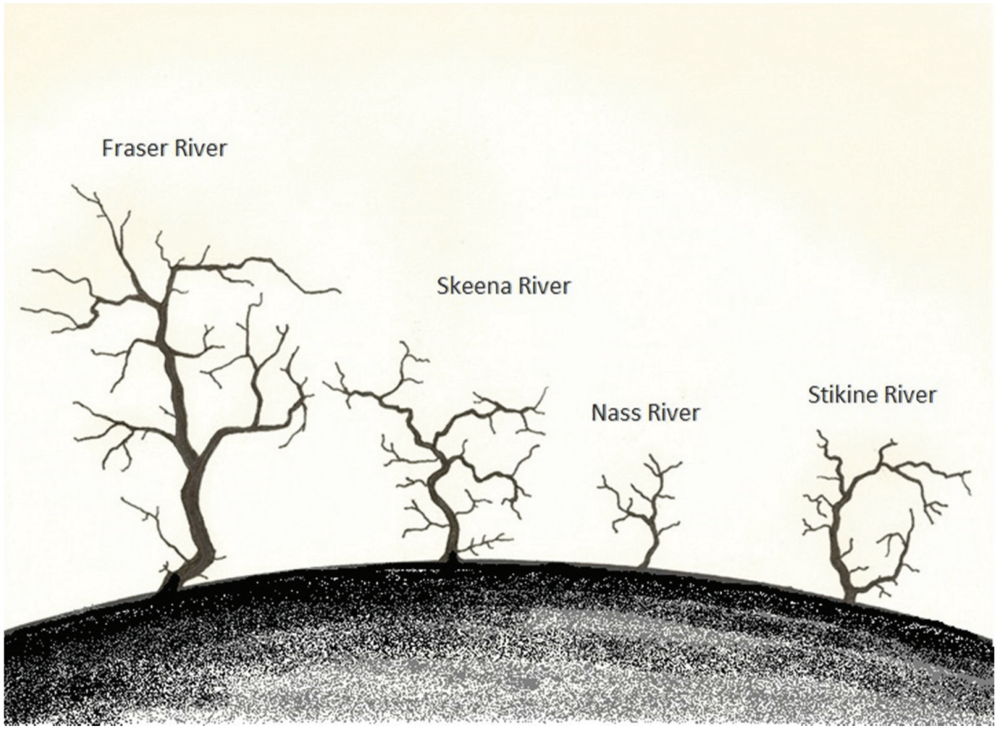
[1]This paper is derived from the J.C. Stevenson Lecture presented at the Canadian Conference for Fisheries Research meeting in Yellowknife, Northwest Territories, January 2014.

Fig. 1. Rivers as trees on Earth. This visual portrays several major rivers from western Canada, if they were tipped up on end, like trees, on Earth. The proportional heights of the rivers are approximately accurate to each other and to the relative size and curvature of the earth. For instance, the Fraser River is 1375 km long and the Earth's radius is 6378 km; thus, the Fraser River is portrayed as being 21% of the Earth's radius. For reference, all rivers would reach well into space, which begins at 100 km above the Earth's surface. The Nass, Stikine, and Skeena rivers are classified as having "pristine" flow regimes (Nilsson et al. 2005), while the Fraser River has no dams on its main stem but does have dams on major tributaries. River branching structures are drawn to approximate the real river network structure of each river system.



Canadian and global rivers to reveal that larger rivers are also more likely to have disrupted connectivity. Last, I overview key opportunities and challenges for watershed science and management, identifying mismatches among policy, application, and the natural scales of river systems. I focus on fisheries and salmon as key intersections of river ecosystems and natural resource management and use large British Columbian rivers as illustrative examples. However, many of the concepts examined in this manuscript apply to other processes and components of rivers, as well as other regions of Canada and the world. This paper illustrates how the bidirectional connectivity of large free-flowing rivers can confer stability to rivers and fisheries, yet also means that anthropogenic impacts can spread upstream and downstream river systems and suggests that there are opportunities to better incorporate these linkages into current watershed management approaches.

Scales of connection in river networks

Connectivity is one of the fundamental properties of rivers, yet this connectivity poses challenges for science and management. Gravity moves water and the materials it carries downstream from headwaters towards the ocean. Migratory fishes such as anadromous salmon can connect downstream habitats and upstream habitats. These bidirectional linkages make river networks one interconnected unit. However, the potentially enormous scale of connections in free-flowing river systems challenges our ability to quantify, perceive, and conceptualize these linkages. Indeed, scale is one of the foremost challenges in ecology (Levin 1992; Schneider 1994).

Metaphors can allow people to apply understanding from one system to another system to gain potentially useful insights. To help conceptualize the vast connections and network structures that are occurring in rivers, I offer a metaphor: *rivers as trees* (Fig. 1).

A river network, like a tree, has dendritic branching form and is connected by flows of water and movements of migratory fishes. Instead of sap moving water and nutrients throughout the branching network from trunk to leaves and back, salmon and other migratory fishes swim upstream and downstream, and water carries its properties and materials downstream through river networks, from headwaters to the ocean. What happens to the trunk of the tree will affect the branches. What happens in the branches can influence the trunk. Free-flowing rivers are, in essence, a large tree-like network. But instead of being 10s of metres tall, they can be 100s of kilometres long.

In considering several of the vast river systems in western Canada, they represent truly enormous "trees" that, if tipped on end, would extend past the atmosphere (Fig. 1). For instance, the length of the Fraser, Skeena, Stikine, and Nass rivers are 1375, 570, 539, and 380 km, respectively. These distances are substantial on a global scale; the radius of the Earth is approximately 6378 km, and the boundary between the atmosphere and space is around 100 km above the Earth's surface. These vast spatial networks are the scale at which connections potentially operate in these and other rivers.

The similarities between trees and river networks have been appreciated for many years (Horton 1945; Leopold 1971; Rodríguez-Iturbe and Rinaldo 2001). Branching structures such as those found in trees, rivers, and veins are efficient structures for the distribution of fluids (Leopold 1971; Horsfield 1990; Rodríguez-Iturbe and Rinaldo 2001) and naturally emerge through the evolution of both landscapes and organisms. These dendritic networks represent the potential paths of bidirectional connections for the biotic and abiotic components of river ecosystems (Campbell Grant et al. 2007). Of course, like any simplifying metaphor, considering rivers as trees does not capture some dimensions and properties of river systems. For example, while anadromous salmon provide a net movement of materials upstream (Moore and Schindler 2004), the majority of riverine flux is downstream driven by water flow; in contrast, trees predominantly bring water up from their roots. Furthermore, the tree metaphor does not capture river properties such as their connections to riparian habitats (Gregory et al. 1991; Baxter et al. 2005), dynamic habitat and channel structure (Stanford et al. 2005), and expansion and contraction with flow regimes (Bayley 1995). Perhaps rivers could be envisioned as blurry and pulsing trees that are swaying through geologic time, but this image admittedly sounds a bit psychedelic.

Consequences of connectivity

There is a rich history and a rejuvenated appreciation of the importance of whole-system perspectives on river systems (Hynes 1975; Vannote et al. 1980; Fausch et al. 2002; Wiens 2002; Stanford et al. 2005; McCluney et al. 2014). From a physical science perspective, transport of water and sediments leads to generalizable longitudinal patterns of sediment distribution within a drainage basin (Church 2002). One of the classic paradigms of stream ecology, the river continuum concept (Vannote et al. 1980), outlined how carbon flow and community structure predictably change from headwaters to outlets in rivers. Moving beyond the linear perspective of rivers, Benda et al. (2004) described how tributaries can deposit sediments and create areas of physical heterogeneity of sediments in the main river channel. These tributary junctions represent hotspots of both physical, chemical, and biological variability (Kiffney et al. 2006). Similarly, there is increasing appreciation of the importance of both upstream and downstream connections in the dynamics of rivers and their biota (Ward 1989; Gomi et al. 2002). The network structure and connectivity of rivers strongly influences the persistence and diversity of lotic metapopulations and metacommunities (Fagan 2002; Lowe et al. 2006; Muneepeerakul et al. 2008; Carrara et al. 2012; Mari et al. 2014; Yeakel et al. 2014). Indeed, whole-system approaches to river science that consider the connectivity and dendritic structure of river systems can provide insights into the dynamics of these important ecosystems (Fausch et al. 2002; Wiens 2002; McCluney et al. 2014; Moore et al. 2015).

Upstream and downstream impacts of anthropogenic activities

The bidirectional connectivity of river systems also means that human impacts in one part of the watershed could impact other parts of the watershed (Pringle 1997; Stanford and Ward 2001; Meyer et al. 2007; McCluney et al. 2014). Most obviously, upstream anthropogenic land use activities can impact downstream habitats (Meyer et al. 2007). For instance, chemical spills will be propagated downstream by water flows, such as a catastrophic spill of contaminants from a timber yard in the Thames River that spread from the spill site downstream 80 km to the estuary, exterminating most of the downstream fish and invertebrates (Dowson et al. 1996). A controversial Canadian example is the emerging evidence that oil sands development leads to downstream contamination in the water of the Athabasca River from cadmium, copper, lead, mercury, nickel, silver, and zinc (Kelly et al. 2010) and is potentially associated with contamination of fish and elevated cancer rates of people living downstream (Schindler 2010).

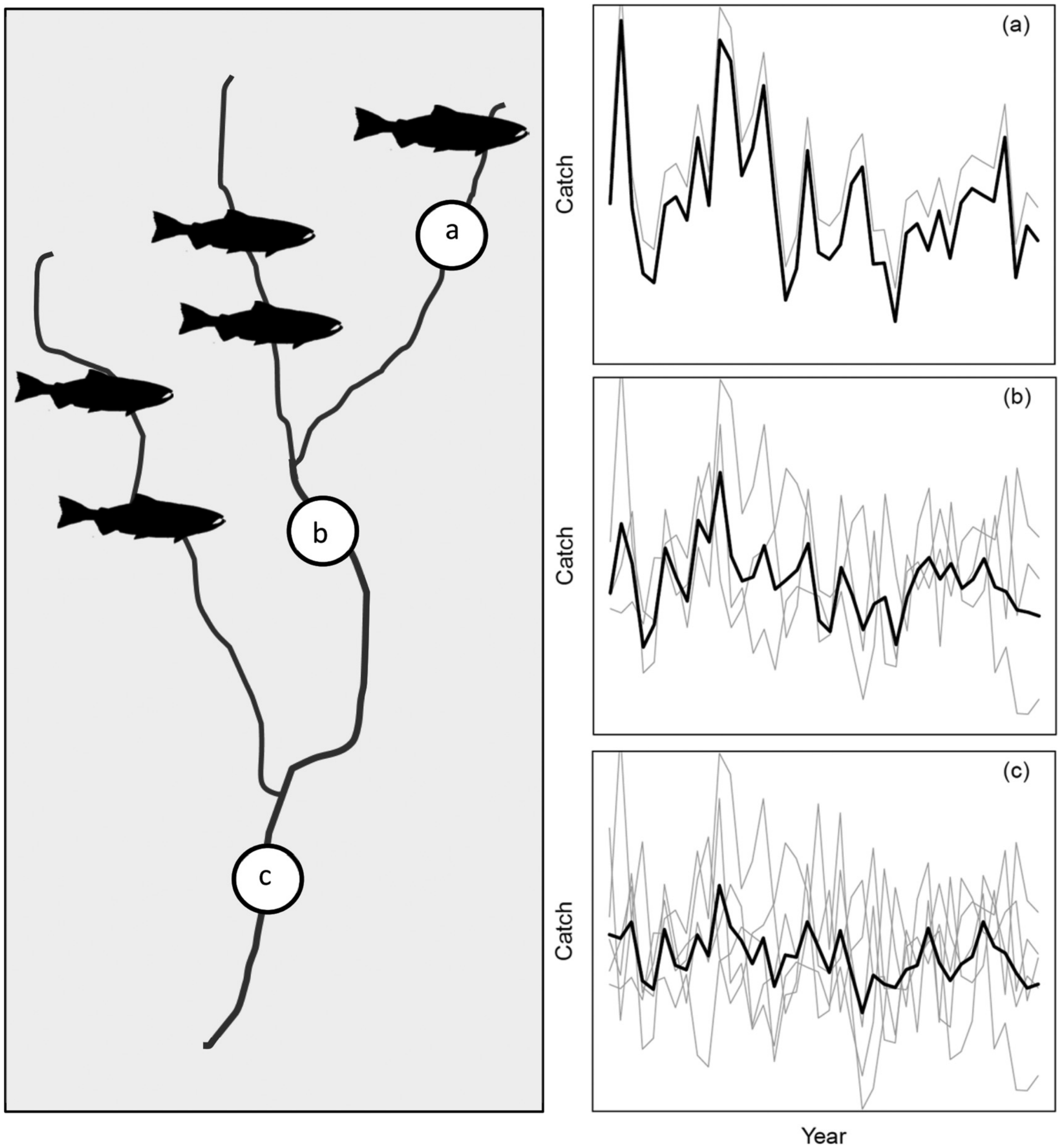
Downstream human activities can also impact upstream habitats and populations. For instance, dams that block animal migrations will impact upstream habitats (Pringle 1997; Greathouse et al. 2006). In the United States, salmon have been extirpated from much of the upstream habitat of their historic range because of the construction of impassable dams, extirpating an estimated 29% of historical populations (Gustafson et al. 2007). Furthermore, for species that depend on downstream habitats for different parts of their life history, degradation of downstream habitat could have impacts that reach far upstream. For example, estuary degradation has decreased Chinook salmon survival by threefold (Magnusson and Hilborn 2003) and potentially impacted stream communities and ecosystems as well as fisheries as far upstream as salmon spawn. While salmon provide an archetype of the importance of riverine connectivity, there are many other migratory riverine species that have received less attention. For instance, potamodromous species migrate between freshwater habitats, ranging from bull trout (*Salvelinus confluentus*) that move in and out of lakes and can make spawning migrations that are greater than 100 km (Dunham and Rieman 1999) to northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*) that migrate in and out of lakes (Chapman et al. 2012). Thus, owing to the bidirectional connectivity in rivers with migratory animals, human impacts can spread both upstream and downstream.

Rivers as Nature's portfolios

The bidirectional connectivity and dendritic structure of free-flowing rivers with migratory fishes likely drives emergent properties of stability and resistance (McCluney et al. 2014; Moore et al. 2015). While some dimensions of river variability are key to maintaining key processes and productivity, such as annual floods (Bayley 1995), other aspects of river variability are associated with impaired supply of good and services, such as volatile fisheries catches. Because of their integration of asynchronous dynamics, rivers should act as a natural portfolio, resulting in more stable (less variable) downstream processes (Moore et al. 2015). Recently, this was termed the "watershed stability hypothesis" (Moore et al. 2015). All things being equal, there should be higher stability in more downstream locations of bigger river systems that integrate more diversity. The mathematics that underpins portfolio theory suggests that the dampening of fluctuations will depend on the richness that is integrated (number of units of biodiversity) as well as their asynchrony or response diversity (Doak et al. 1998; Yeakel et al. 2014; Anderson et al. 2015). The more asynchronous the diversity, the more aggregates will stabilize dynamics. Portfolio theory suggests that this stabilization should apply to both random variability as well as specific perturbations, thereby providing resistance and resilience to both known and unknown perturbations (Doak et al. 1998; Elmqvist et al. 2003; Anderson et al. 2015). Furthermore, in river systems, stability will depend on the strength of downstream and upstream connections and the relevant spatial scale for the process or ecosystem service in question. Thus, if local processes govern dynamics more so than upstream processes, then portfolio stabilization will contract to the corresponding spatial scale (Yeakel et al. 2014). Thus, free-flowing river systems may dampen variability and increase predictability of a variety of processes that occur in river systems (Moore et al. 2015).

First Nations fisheries for anadromous salmon in large watersheds provide an important system to illustrate and explore the predictions from the watershed stability hypothesis (Nesbitt 2014; Fig. 2). Migratory salmon return to numerous locations within a watershed to spawn, and because of their local adaptations, different life histories, and spatially heterogeneous environmental forcing, they can have asynchronous population dynamics (Mueter et al. 2002; Hilborn et al. 2003; Rogers and Schindler 2008; Moore et al. 2014). Fisheries that aggregate across these asynchronous dynamics can be more stable through time (Schindler et al. 2010; Nesbitt 2014; Moore et al. 2015). If we consider First Nations fisheries that occur in different locations within the Fraser River watershed, fisheries that are located high in the watershed have a relatively simple portfolio while fisheries at the base of the watershed draw from a highly diversified portfolio (Fig. 2). Following the predictions, food fisheries in the lower Fraser River that integrated greater salmon biodiversity have had more stable catches through time than upriver First Nations fisheries that integrated less diversity (Nesbitt 2014; Moore et al. 2015).

Fig. 2. Predicted fisheries stability in a river network, according to the watershed stability hypothesis. The left panel portrays a diagram of a hypothetical river network with salmon populations and fisheries that harvest different nested levels of salmon biodiversity. Fisheries are labeled with a letter according to the panels on the right. The right panels show the predicted catch of the upstream (*a*), intermediate (*b*), and downstream (*c*) fisheries. The thick black line is the predicted catch of the fishery, and the thin grey lines are the relative returns of the different salmon populations. The dynamics of the salmon populations show one representative set of iterations for the stochastic density-dependent model described in the text.



River network disassembly: simulations of fisheries and watershed alteration

The stability that can naturally arise from river structure and connectivity may be sensitive to degradation (Fagan 2002; McCluney et al. 2014). First of all, human activities that fragment river networks alter the patterns of connectivity that underpin stability (Yeakel et al. 2014). In fact, the dendritic structure of river networks may be particularly vulnerable to fragmentation; fragmentation of dendritic networks leads to smaller average fragment size than comparable linear systems (Fagan 2002). Furthermore, general conceptual and mathematical theory indicates that the stability of river networks could be impacted by upstream or downstream human alteration of specific habitats, their variability, and patterns of connectivity (McCluney et al. 2014; Yeakel et al. 2014). Given these unique properties of river networks, one potentially promising research frontier is the use of mathematical models of metapopulations in river networks to evaluate the system-wide consequences of different scenarios of anthropogenic activities (Mari et al. 2014; Yeakel et al. 2014; Anderson et al. 2015).

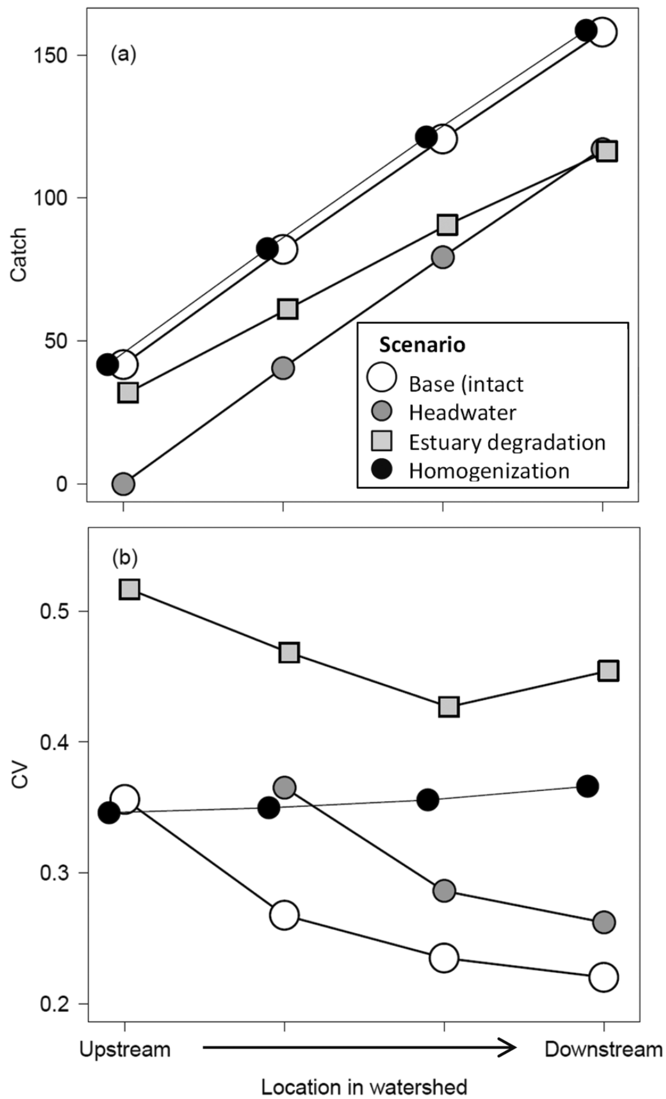
To illustrate and examine the potential upstream and downstream impacts of degradation, I used simple simulations of salmon fisheries within river networks. These simulations explored the stability of First Nations fisheries for anadromous salmon in a hypothetical watershed illustrated in Fig. 2. The results of these simulations illustrate how potential impacts of habitat alteration may alter the stability and productivity of First Nations fisheries. In this simulation, there are four salmon populations in the four headwater tributaries of the river network and four fisheries locations ranging from near the ocean, thereby targeting all populations, to an upstream fishery that targets one population. Thus, from upstream to downstream, the four fisheries integrate one, two, three, or four salmon populations. Salmon populations were simulated with a density-dependent population growth, nonoverlapping generations, and variability that had both shared as well as independent components. Specifically, populations followed a Beverton–Holt relationship:

$$R_{i(t+1)} = (a_i k_i S_{i(t)}) \big/ (k_i + a_i S_{i(t)}) + \varepsilon_{i(t)} \tag{1}$$

where i represents a population, t is a generation time, S is the number of spawning salmon, R is the number of returns, a_i is the productivity of the population ($a_i = 7$ unless otherwise noted), and k_i is related to the density dependence of the system ($k_i = 500$ unless otherwise noted). ε_i is the error and is defined by $\varepsilon_i = r_t + q_{i(t)}$, the sum of the shared (r_t) and independent ($q_{i(t)}$) error. These errors were normally distributed errors with standard deviations of 10 and 150, respectively, unless otherwise specified (see "homogenization" scenario). These error parameters lead to mean correlation coefficients among the harvested populations of approximately 0.22. Spawners in the next generation were equal to the recruits minus the fishery catch. Each fishery harvested 10% of the fish that swam by their location (Peterman 1980) with no allocation uncertainty. Simulations were run for 20 years, and there were 500 iterations. The median catch and the median coefficient of variation (CV) of annual catch were calculated for each fishery in each scenario. While the specific values of the results are of less importance, the relative patterns and changes in these patterns with scenarios of degradation are revealing. I examined four different scenarios, one base scenario and then three other scenarios of watershed degradation:

1. Base (intact watershed). This is the base scenario where there are four fisheries that integrate between one and four salmon populations, with the integrated diversity a function of location in the watershed.
2. Headwater extirpation. This scenario consists of setting the returning abundance to the uppermost salmon population to zero. This would represent the catastrophic extermination of a headwater population, such as due to the construction of a nonpassable dam or extreme habitat degradation (Gustafson et al. 2007).
3. Estuary degradation. Estuary habitat degradation was modeled to decrease both the habitat productivity and capacity. The initial ocean entry period is increasingly recognized as a critical period in the salmon life history (Parker 1968; Welch et al. 2009; Duffy and Beauchamp 2011), and estuary degradation is associated with decreased salmon marine survival rates (Magnusson and Hilborn 2003; Meador 2014). Given that all salmon populations move through the estuary, a_i and k_i were reduced by 20% for all populations, which represent conservative decreases in population productivity given previous studies on estuaries and salmon survival (Magnusson and Hilborn 2003; Meador 2014).
4. Homogenization. Salmon population dynamics were homogenized in this scenario, decreasing the response diversity within the watershed. Homogenization of salmon population dynamics has been observed in heavily altered salmon watersheds (Moore et al. 2010; Carlson and Satterthwaite 2011; Griffiths et al. 2014), potentially driven by erosion of population diversity through hatchery propagation (Pearse et al. 2010), anthropogenic homogenization of habitats, or a shift from local to shared environmental forcing. These changes were modeled by specifying the standard deviation of the error from independent (q) and shared (r) sources to be 10 and 150, respectively. These parameters were set to decrease the asynchrony among populations; correlation coefficients among populations were approximately 0.99.

Fig. 3. Scenarios of loss of salmon habitat capacity and fisheries catches, examined through density-dependent stochastic population models. Data portray median values across simulation runs of annual catches (*a*) and the coefficient of variation (CV) of catches (*b*). A lower CV indicates lower variation and higher stability of fishery catches. Catch and catch stability are portrayed as a function of watershed location. Simulations examined four scenarios: a base scenario with intact salmon populations, headwater extirpation scenario where the headwater salmon population was extirpated, estuary degradation scenario where loss of estuary habitat has decreased the productivity and carrying capacity of all salmon populations, and a homogenization scenario where the dynamics of salmon populations within the watershed were synchronized. More information about these simulations can be found in the text.



Model results

Simulations revealed that fisheries integrating more salmon populations were associated with higher average catches as well as more stable catches (Fig. 3; scenario intact watershed). The result that more downstream fisheries had higher catches (Fig. 3*a*) was obvious and is due to the model design, where each fishery harvests 10% of fish that swim by. Perhaps more importantly, downstream fisheries that integrate greater biodiversity also had more stable catches (Fig. 3*b*). Specifically, the CV in the headwater fishery was higher (CV = 0.36), while the CV in the most downstream fishery was lower (CV = 0.22), representing a 1/3 decrease in variability due to the portfolio effect. These results mesh with empirical observations that First Nations fisheries lower in watersheds have more stable catches (Nesbitt 2014; Moore et al. 2015).

The effects of extirpation in a headwater salmon population decreased catches and eroded catch stability down through the simulated river system (Fig. 3; scenario headwater extirpation). The proportional decrease in average annual fishery catch relative to the base case was directly related to the fishery location in the watershed, as the most upstream fishery completely lost their catch, while the most downstream fishery had a 25% decrease in average annual catch. Extirpation of the headwater population also increased fishery variability throughout the watershed. The CV of all fisheries increased as the diversity of their portfolio was reduced; downstream fisheries were more buffered from this loss, as they had greater initial diversity.

Degradation of estuary habitat decreased catches and increased volatility throughout the watershed (Fig. 3; scenario estuary degradation). The proportional change in fishery catches relative to the base scenario remained relatively constant across all catches. Intriguingly, fisheries all became more variable with degraded estuary habitat owing to shifts in the relative importance of density dependence, external variability, and fisheries. It should be noted that this increase is somewhat sensitive to model parameters (data not shown). This scenario suggests that estuary degradation can spread up through watersheds, potentially increasing volatility and decreasing catch.

Homogenization of salmon population dynamics led to no substantial changes in average annual catches but the loss of fishery stability (Fig. 3; scenario homogenization). Specifically, the CV of fisheries in this homogenization scenario was consistent across watershed locations and equal to the variability of the most upstream fishery. This represents an increase in CV (decreased stability) in the downstream fisheries relative to the base scenario. With the homogenization of salmon population dynamics, no longer does portfolio diversity and watershed location confer stability. The magnitude of this result is dependent on the relative magnitude of shared versus independent error. As asynchrony decreases with the erosion of the response diversity in population portfolios, portfolios will become more volatile (Markowitz 1952; Doak et al. 1998; Moore et al. 2010; Yeakel et al. 2014; Griffiths et al. 2014).

Collectively these simulations reveal that habitat degradation can spread both upstream and downstream, eroding the productivity and stability of fisheries. These simulations undoubtedly represent simplifications of real systems; for instance, simulations did not include temporal autocorrelation in error, salmon populations were set to have the same productivity and density-dependent parameters, and fisheries catches were allocated simplistically. Thus, these scenarios represent predicted patterns, but will be governed by the realities of the natural history, fisheries, and policies of any system. For example, in large watersheds such as in the Skeena River or Fraser River, First Nations fisheries may integrate several salmon species and dozens of salmon populations, leading to even stronger portfolio stabilization of downstream fisheries. Regardless, these simulations provide a framework for conceptualizing how anthropogenic degradation of watersheds can compromise upstream and downstream fishery productivity and stability.

Status of free-flowing rivers in Canada and the world

Human activities such as dam-building can sever the connectivity that underpins the resistance and stability of river systems. One of the major global alterations of river systems is the construction of dams (Nilsson et al. 2005). Dams provide benefits to society by storing water for consumption and agriculture and producing energy, but obstruct the movement of fish, water, and materials such as sediment (Pringle 1997; Nilsson et al. 2005). I examined the status of large rivers in Canada and globally using a previously compiled assessment of the anthropogenic fragmentation status of large rivers from across the world (Nilsson et al. 2005). I aimed to quantify the overall probability of fragmentation of rivers and whether this was a function of river size.

Globally, most large rivers have major dams on them (Nilsson et al. 2005). Specifically, 152 out of 245 (62%) large rivers outside of Canada are characterized as fragmented. In contrast, Canadian large rivers have lower probabilities of fragmentation; 20 out of 45 (44%) of large river systems are characterized as fragmented. Overall, Canada contains 13% of the world's large unfragmented rivers, a major component of these globally rare systems.

For both Canada and the entire world, larger rivers are more likely to be fragmented by large dams (Fig. 4). Specifically, for non-Canadian rivers, watershed size tended to be associated with an increase in the likelihood of fragmentation (logistic regression coefficient ± SE = 0.253 ± 0.134, P = .059). This pattern was stronger in Canadian rivers, where larger rivers were significantly more likely to be fragmented (logistic regression coefficient ± SE = 1.584 ± 0.58, P = 0.007). The Skeena River was the largest river in Canada classified as free-flowing. There are only 19 other rivers in the world that are larger than the Skeena River that are similarly unfragmented. Because these analyses are based on fragmentation and connectivity in terms of barriers of water flows and flow regimes, it is likely that similar patterns apply for the fragmentation of migratory fish movements in river systems. It is perhaps not surprising that larger rivers are more likely to be fragmented — with more watershed area there are likely more geographic opportunities to dam. Regardless, these data provide additional motivation for understanding the processes and dynamics of the remaining free-flowing rivers, as each remaining large free-flowing river is globally important.

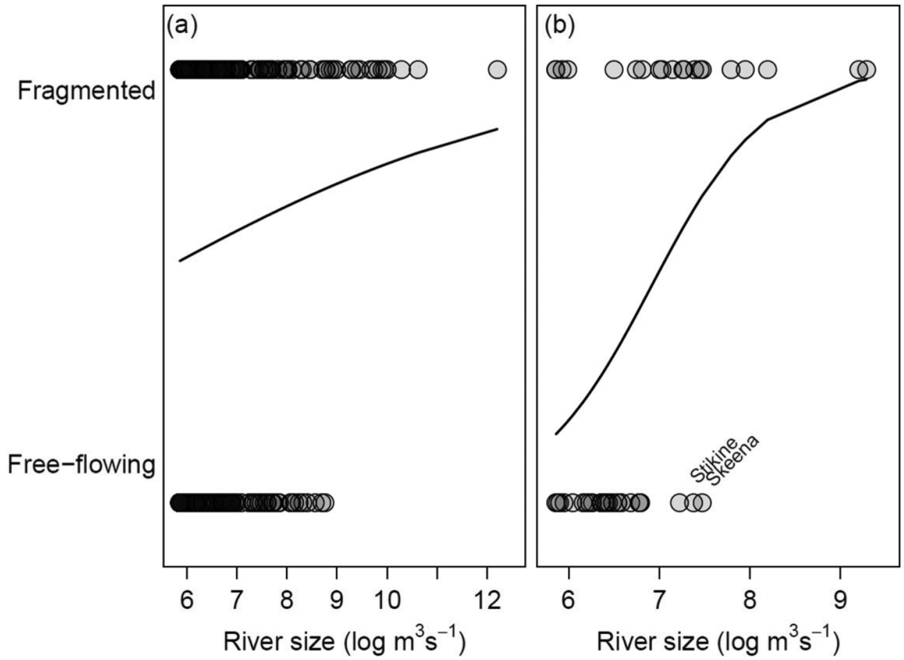
Weakened watershed protection

Watershed protection is governed by a complicated policy, regulation, and implementation landscape that is rapidly changing. Canada's environmental legislation that protects aquatic habitats and fish has recently been revised, decreasing the scope of environmental protection of river systems (Favaro et al. 2012; Hutchings and Post 2013). Large projects can require federal or provincial environmental assessments; in 2012, environmental assessment was considerably expedited, with decreased period for public comment (Gibson 2012). Furthermore, consideration of multiple potential large projects that are reviewed for environmental assessments, or cumulative effects assessments, have been deemed as being "impotent" in Canada (Duinker and Greig 2006), only pursued if the environmental assessment deems that there will be a substantial net negative effect. The Fisheries Act can also protect fish and fisheries from activities that occur in or near aquatic habitats, but this Act was recently "gutted" (Hutchings and Post 2013). In addition, authorization of these projects can hinge on habitat compensation, yet audits of habitat compensation projects in Canada revealed that the majority of projects fail to achieve "no net loss" of productive fish habitat (Harper and Quigley 2005; Quigley and Harper 2006). Lastly, incremental changes from land uses such as forestry and urbanization have contributed substantially to watershed alteration (Slaney et al. 1996), and these land uses are governed by different regulations. It is increasingly argued that Canada is not protecting its biodiversity and aquatic resources (Favaro et al. 2012; Hutchings and Post 2013; Palen et al. 2014). Canada currently lacks an effective policy framework to consider the cumulative alteration of interconnected habitats (Palen et al. 2014).

Implications for watershed management

The bidirectional connectivity of river systems has several implications and opportunities for management (McCluney et al.

Fig. 4. Size and fragmentation of global (*a*) and Canadian (*b*) rivers. Data were extracted from the supplemental materials of (Nilsson et al. 2005) and then analyzed. I classified river systems as being "Canadian" if the majority of the system occurred within the country. Rivers were classified as free-flowing if they were assigned a "pristine" flow regime and as being fragmented if they were assessed as being "severely" or "moderately" regulated by dams according to (Nilsson et al. 2005). Classification was based on the proportion of the main channel that was left without dams and the number of dams in major tributaries (Nilsson et al. 2005). Curves show the best-fit logistic regression with river size (mean annual discharge, on a $\log_e$ scale) as the predictor variability and the fragmentation status as the response variable. The "Skeena" and "Stikine" rivers are labeled, following their reference in Fig. 1. Note that the two panels have different *x*-axis scales.



2014). Building off the ideas outlined in this manuscript and previous insights from holistic perspectives on watershed science and management (Fausch et al. 2002; Gomi et al. 2002; Schindler et al. 2008; Lertzman and Mackinnon 2014; McCluney et al. 2014; Moore et al. 2015), below I offer several observations regarding the nature of river systems. For each observation, I discuss a corresponding challenge for the policy and management of these systems and the opportunity to more effectively consider the connected nature of rivers.

1. Align scales of connection and impact assessment

Observation: Degradation of watersheds will spread up and down river networks

The bidirectional connectivity of river networks means that anthropogenic impacts can spread up and down river networks. Somewhat paradoxically, the same connectivity that buffers downstream systems means that the human impacts will have larger zones of influence (Pringle 1997). Degradation can spread upstream and downstream. For example, a chemical spill can disperse downstream to kill biota. Furthermore, by changing the diversity integrated by the river, human impacts can also erode the downstream or upstream stability of river systems. For example, headwater or estuary habitat degradation can erode both the productivity and the stability of fisheries throughout the watershed (Fig. 3). Thus, the connectivity of free-flowing river networks means that anthropogenic impacts can be dispersed widely. Given the enormous spatial scales of connectivity that can operate in river systems (Fig. 1), the vastness of potential consequences poses a fundamental challenge for the proper accounting of impacts.

Opportunity and challenge: Matching scales of assessments to scales of potential impacts in river systems

Given the multiple and potentially expansive scales of connections that occur in river systems, there is a need to broaden the scales of specific environmental assessments (Therivel and Ross 2007; Seitz et al. 2011). Canadian legislation mandates conservation of fish, fish habitat, and fisheries. While the Minister can grant exceptions, according to the Fisheries Act, "*No person shall carry on any work, undertaking or activity that results in serious harm to fish that are part of a commercial, recreational, or Aboriginal fisheries, or to fish that support such a fishery.*" Section 35 of the Constitution Act protects the rights of First Nations people to fish for food, social, and ceremonial purposes. Thus, from a simplistic perspective, it appears that potential projects that will degrade the habitats that sustain the stability and productivity of fish and fisheries, even if those fisheries are a 1000 km away from the development and connected to the proposed alteration of habitat by the migrations of fishes, challenge the Fisheries Act and the Canadian Constitution. However, environmental assessments for large projects in Canada may focus primarily on local impacts. For example, the environmental assessment application of a recently proposed pipeline defined the zone of downstream influence as 100 m upstream and 300 m downstream of the project and the regional assessment area as extending at least 1 km downstream (Prince Rupert Gas Transmission 2013). This contrasts with the known potential downstream impacts of chemical spills (e.g., >80 km downstream; Dowson et al. 1996). Thus, cumulative effects frameworks are challenged to consider multiple impacts that could be linked over vast spatial scales. Cumulative effects analyses should be aligned to the proper spatial and temporal scale of the ecologically and culturally relevant processes (Therivel and Ross 2007). A watershed scale is the intuitive scale for environmental assessments and cumulative effects assessments (Zedler 2003), especially for salmon-bearing watersheds. Indeed, recently there have been several watershed-level cumulative effects efforts across Canada, but it is uncertain whether these frameworks will be incorporated into decision-making and policy (Dubé et al. 2013).

2. Conserve natural resilience of free-flowing rivers

Observation: Free-flowing rivers provide a natural defense system against variability and environmental perturbations

Emerging research suggests that the diversity integrated by rivers naturally dampens fluctuations and buffers against localized change for a variety of critical processes, ranging from fisheries catches to water flows (Moore et al. 2015). Specifically, downstream locations in rivers have dampened variability compared with upstream habitats (e.g., flood in a small catchment or salmon population crash) through statistical averaging of their upstream portfolio. This portfolio effect should also dampen the response to known perturbations such as local climate change, thereby contributing to resilience. On the other hand, rivers will not absorb variation that is shared throughout a watershed (Moore et al. 2015), such as the seasonal pattern of precipitation and snowmelt, thereby preserving the large-scale flood-pulse that maintains riverine productivity (Bayley 1995). While there is uncertainty in regards to the ubiquity of this dampening, these findings indicate that free-flowing rivers may provide a natural defense system against perturbations. This stabilization, from flows to fisheries, likely represents an ecosystem service that provides enormous economic benefits to humankind. There is growing appreciation for the ability of various earth systems to absorb perturbations and that human activities can undermine these natural defense systems (Arkema et al. 2013).

Opportunity and challenge: Managing for watershed resilience

Management of natural resources is being increasingly challenged by ongoing global change and increasing climate variability (Milly et al. 2008). While enormous investment goes into engineering infrastructure to try to cope with variability (e.g., dams, levees, water-treatment facilities), conserving the natural systems that confer stability represents an opportunity for proactive management (Schindler et al. 2008; Bisson et al. 2009; Healey 2009; Lapointe et al. 2014). For salmon and the fisheries targeting them in particular, practices that degrade resilience include allowing extirpation of small populations, reducing life history and genetic diversity, and degradation of habitat (Healey 2009). Practices that facilitate resilience include protecting small populations, maintaining habitat, diversified fisheries, and managing for community resilience (Healey 2009). Indeed, policies that protect habitats and fish populations will preserve the existing portfolios of salmon biodiversity that enable stability and resilience (Ruckelshaus et al. 2002; Schindler et al. 2008, 2010; Healey 2009; Moore et al. 2010; Lapointe et al. 2014; Anderson et al. 2015). While there have been frameworks developed to achieve these goals (i.e., Wild Salmon Policy; Fisheries and Oceans Canada 2005), these frameworks arguably lack strong implementation or accountability. There remains a disconnect between these suggested principles and policies, and the management of salmon watersheds in practice. Habitat degradation continues, incidental overfishing of less-productive stocks is a continued challenge, and hatchery propagation remains a widespread and arguably failing prescription for supporting fisheries (Meffe 1992; Slaney et al. 1996). As a result, many salmon populations are threatened or extirpated, especially towards the southern part of their range (Gustafson et al. 2007), and many fisheries have correspondingly impaired resilience (Augerot and Smith 2010; Griffiths et al. 2014).

Managing for resilience also entails moving beyond static management goals to also incorporate more dynamic perspectives on natural resources. River systems and their salmon are naturally variable (Bayley 1995; Rogers et al. 2013), responding differently to perturbations, and this response diversity is what underpins their stability and resilience (Elmqvist et al. 2003; Schindler et al. 2008, 2010; Moore et al. 2015; Anderson et al. 2015). For example, north-facing catchments may respond differently to climate warming than south-facing catchments, and some salmon life histories may thrive with climate warming while others may struggle. Management and policies have the opportunity to set benchmarks and objectives that incorporate dynamics and response diversity. For instance, it has recently been argued that watershed restoration should move from static goals and approaches towards process-based approaches (e.g., instead of bank-armoring to restrict river erosion, restoration could reduce sediment supply by reestablishing riparian vegetation; Beechie et al. 2010). Alternatively, salmon management strategies such as setting harvest levels could be designed to be robust to natural fluctuations in abundance (Schindler et al. 2008), and recovery strategies for salmon metapopulations can incorporate aspects of their diversity (McElhany et al. 2000).

3. Watershed governance for social–ecological resilience

Observation: Watersheds represent natural social–ecological units

Given the connectivity of watersheds and river networks, human decisions within watersheds can impact the whole ecological unit. Watershed dynamics also influence the people and cultures that inhabit them, such as through the supply of water, energy, or fish. Thus, there are reciprocal feedbacks from the watershed to people, and it follows that watersheds represent a natural social–ecological unit (Yaffee 1999; Parkes et al. 2010).

Opportunity and challenge: Watershed governance and conservation

Watershed governance would enable the integration of human and natural components of watersheds (Parkes et al. 2010). Specifically, watershed governance would link decision-makers with citizens at the watershed scale, with decisions being informed by the state of its natural resources. Given the connectivity that defines a watershed, watersheds represent an obvious scale at which to align the scale of management with the scales of processes that are being managed. Despite these potential benefits, local watershed governance is still relatively rare (Blomquist and Schlager 2005).

Building resilience into management frameworks is a key challenge (Gunderson and Holling 2002; Elmqvist et al. 2003; Olsson et al. 2004). Characteristics of resilient management systems include responsiveness to ecological dynamics and flexibility in the management process (Olsson et al. 2004). Different management practices can either enhance or degrade the resilience of fisheries and salmon populations (Healey 2009; Augerot and Smith 2010). Insight can perhaps be gained into more resilient management systems by looking at historical salmon watershed management systems. Prior to European colonization, the many coastal aboriginal groups (i.e., First Nations) had well-established fisheries management systems, operating on a local scale (Harris 2001) and fostering tighter feedbacks between natural resources and management decisions. These fisheries and the cultures they supported operated for thousands of years, persisting through periods of major climate shifts (Lepofsky et al. 2005). Today, salmon fisheries management has shifted toward centralized management systems, with a single government department in charge of management decisions across Canada (Harris 2001). This shift in management systems from local to centralized likely has led to a decrease in the resilience of the salmon management system, making it less responsive to the local socioeconomic conditions (Healey 2009). There is an opportunity to learn from the past and to move towards watershed governance, such as the example of co-management of salmon resources in the Skeena River watershed by First Nations and Fisheries and Oceans Canada (Gottesfeld et al. 2009).

The large river systems of British Columbia represent key examples of systems that still have substantial connectivity, intact habitats, and diverse salmon populations. Many river systems to the south have lost much of their salmon biodiversity and riverine connectivity (Gustafson et al. 2007), and their portfolios of salmon biodiversity perform more poorly (Griffiths et al. 2014). As such, these more degraded river systems necessitate enormous economic inputs and engineering and management interventions (e.g., hatchery propagation) with arguably mixed results (Meffe 1992; Lichatowich 1999). The scientific appreciation of the resilience of large river systems comes at a critical time. First, given climate variability and change, resilience in social–ecological systems is increasingly important. Second, there are pressures from extractive industries that could alter the biodiversity, habitat integrity, and connectivity that underpins the underappreciated stability and resilience of large river systems. There is an opportunity to more fully consider the potential upstream and downstream impacts of potential land use activities, enabling a more balanced consideration of short-term resource extraction and long-term socioecological resilience. While resource extraction is often driven by perceived economic benefits, it is important to remember that healthy salmon populations sustain economies and have done so for thousands of years. Management systems that incorporate and account for the connectedness and diversity of vast tree-like river networks represent a critical advance to manage for resilient and productive ecosystems in the face of ongoing environmental change.

Acknowledgements

I thank the editorial board of the Canadian Journal of Fisheries and Aquatic Sciences for the honour and opportunity to present this paper for the J.C. Stevenson Lecture Award at the Canadian Conference for Fisheries Research meeting in Yellowknife, Northwest Territories, in January 2014. This paper especially benefitted from insights and assistance from two anonymous reviewers, Allen Gottesfeld, Dave Peacock, Justin Yeakel, Holly Nesbitt, Rolf Vinebrooke, Samantha Wilson, and Will Atlas.

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