

Do riparian zones qualify as critical habitat for endangered freshwater fishes?

John S. Richardson, Eric Taylor, Dolph Schluter, Mike Pearson, and Todd Hatfield

Abstract: Identification of critical habitat is a key step in conservation and recovery of endangered and threatened freshwater fish. Critical habitat under Canadian and US legislation may include habitat that is not directly used by listed fish, provided it is necessary for species conservation or recovery. Riparian habitat meets biological criteria for critical habitat because riparian zones are integral to aquatic ecosystem functions of importance to many fish species and other organisms. These functions include provision of shade for temperature-sensitive species, control of channel complexity and sediment inputs through bank stabilization, input of large wood and allochthonous energy sources, and filtering of nutrients and toxins from adjacent land. In response to decades of stream-riparian research, widespread implementation of regulations to protect riparian zones in most developed countries represent a de facto consensus that riparian buffers are essential for aquatic ecosystem health and the maintenance of populations of fish and other species. Consistent with widespread riparian regulations deemed necessary to protect not-at-risk species, riparian habitat adjacent to a body of water containing a listed freshwater species should be considered biologically critical unless the habitat requirements of individual taxa are demonstrated to be insensitive to the ecological functions associated with riparian habitat.

Résumé : L'identification de l'habitat critique est une étape essentielle dans la conservation et la récupération des poissons d'eau douce menacés et en voie de disparition. Dans les législations canadienne et américaine, l'habitat critique peut inclure des milieux qui ne sont pas directement utilisés par les poissons concernés, à la condition qu'ils soient nécessaires pour la conservation ou la récupération de ces espèces. Les habitats riverains possèdent les critères biologiques d'habitats critiques parce que les zones riveraines sont nécessaires pour assurer des fonctions de l'écosystème aquatique d'importance pour plusieurs espèces de poissons et pour d'autres organismes. Ces fonctions incluent la production d'ombre pour les espèces sensibles à la température, le contrôle de la complexité du chenal et des apports de sédiments par la stabilisation des rives, l'apport de sources d'énergie allochtones et de débris ligneux de grande taille et la filtration des nutriments et des toxines provenant des terres adjacentes. À la suite de décennies de recherche sur la relation entre les cours d'eau et la zone riveraine, la mise en application très commune dans la plupart des pays développés de règlements pour protéger les zones riveraines représente un consensus de facto reconnaissant que les zones tampons riveraines sont essentielles à la santé des écosystèmes aquatiques et le maintien des populations de poissons et d'autres espèces. En accord avec les règlements largement répandus sur les zones riveraines jugées nécessaires pour la protection des espèces non vulnérables, tout habitat riverain adjacent à un milieu aquatique contenant une espèce d'eau douce figurant sur la liste des espèces en péril devrait être considéré comme biologiquement critique, à moins qu'on démontre que les besoins d'habitat de ce taxon particulier sont insensibles aux fonctions écologiques associées à l'habitat riverain.

[Traduit par la Rédaction]

Introduction

Canada's new legislation to protect endangered species, the Species At Risk Act (SARA; Government of Canada 2002), has been in place since 2002. As with most nascent

environmental legislation designed to protect endangered species, there is confusion and controversy over aspects of both science and implementation. The most controversial steps are the listing process (Mooers et al. 2007; Hutchings and Festa-Bianchet 2009) and the identification of critical

Received 5 March 2010. Accepted 30 April 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 25 June 2010. J21700

J.S. Richardson.¹ Department of Forest Sciences, University of British Columbia, 3041-2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

E. Taylor and D. Schluter. Department of Zoology, University of British Columbia, 2204 Main Mall, Vancouver, BC V6T 1Z4, Canada.

M. Pearson. Pearson Ecological, 3150 271 Street, Aldergrove, BC V4W 3H7, Canada.

T. Hatfield. Solander Ecological Research, 1324 Franklin Terrace, Victoria, BC V8S 1C7, Canada.

¹Corresponding author (e-mail: john.richardson@ubc.ca).

habitat for a listed species (Rosenfeld and Hatfield 2006). The decision to list is obviously pivotal because it determines which species will be subject to legal protection (Mooers et al. 2007). Once listed, decisions regarding critical habitat are equally far-reaching, because they establish the extent, attributes, and location of protected habitat and strongly influence habitat management, socio-economic impacts (e.g., Jones et al. 2006), and compensation to affected parties (e.g., Takekawa and Beissinger 1989; Kautz and Cox 2001).

Because spatial location and attributes of critical habitat profoundly affect species' persistence and the potential for socio-economic impacts, definitions of critical habitat for a listed species need to be (i) technically sound (i.e., firmly based in science and the biology of the focal species, so that definitions will ensure species persistence) and (ii) consistent with the criteria for critical habitat set out in legislation. In the following discussion, we briefly consider whether riparian habitat meets technical and biological criteria for critical habitat as applied to freshwater fishes and other listed aquatic organisms in lakes and streams (where riparian habitat refers to the vegetated zone adjacent to a water body; for detailed definitions, see Gregory et al. 1991, Naiman et al. 2005, and Richardson et al. 2005). This issue is topical because it impacts dozens of species and thousands of kilometres of aquatic and riparian habitat, has widespread implications for the conservation and management of listed freshwater fishes throughout Canada and the US, and has the potential for significant socio-economic impacts in many jurisdictions (e.g., Jones et al. 2006; but for economic benefits of riparian restoration, see Theurer et al. 1985). We recognize that areas well beyond the riparian zone also exert strong controls on aquatic habitat of listed species through effects on hydrology, water quality, and geomorphology (Harding et al. 1998; Kreutzweiser et al. 2008), and that broader protection may be required to maintain desired ecosystem attributes in many situations (e.g., Saunders et al. 2002; Abell et al. 2007; Nel et al. 2009). However, in this paper, we consider only the relevance of the riparian zone for conservation of species at risk and argue that there is scientific consensus on the dependence of aquatic ecosystems on the integrity of their riparian areas. Our goal is not to duplicate existing reviews of riparian function (e.g., Pusey and Arthington 2003; Naiman et al. 2005; Richardson and Danehy 2007), but rather to evaluate the significance of the riparian zone to the conservation of endangered freshwater species, an important conservation issue that has received little attention in the primary literature.

Critical habitat under SARA is defined as "... the habitat that is necessary for the survival or recovery of a listed wildlife species, and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species" and may include "... spawning grounds and nursery, rearing, food supply, migration, and any other areas on which aquatic species depend directly or indirectly [our emphasis] in order to carry out their life processes ..." (Government of Canada 2002, s. 2(1)). (For the purpose of the following discussion, we interpret survival to represent long-term persistence of at least a minimum viable population and recovery to represent achievement of a population recovery target, which may equal or exceed the population

size required for survival or persistence.) It is noteworthy that the above definition explicitly allows for the identification of habitat as critical even when it is not directly used by a species. This is especially relevant to species in freshwater habitats, where water quality and physical habitat structure are strongly influenced by activities on land (Harding et al. 1998; Abell et al. 2007; Nel et al. 2009).

Critical habitat under the US Endangered Species Act (ESA) is also broadly defined as "... the specific areas within the geographical area occupied by the species ... on which are found those physical or biological features essential to the conservation of the species." and "... specific areas outside the geographical area occupied by the species if the agency determines that the area itself is essential for conservation" (Endangered Species Act of 1973; United States Congress 1973). This definition is also explicit in permitting areas that indirectly affect a species to be identified as critical, provided that a clear case can be made that it is "essential for conservation", i.e., it is not required that the habitat be directly occupied. It therefore follows that even though riparian habitat is not directly used by aquatic species, it meets the general technical criteria for critical habitat of aquatic species under both Canadian and US legislation, provided that a sound technical and biological case can be made that it is necessary habitat for species conservation and recovery. In contrast with Canadian legislation, US legislation explicitly allows the assessment of critical habitat to include consideration of socio-economic impacts. Regulators in the US have identified riparian areas as critical habitat for some species (e.g., Gila Chub; US Fish and Wildlife Service 2005) but not others (e.g., National Oceanic and Atmospheric Administration (NOAA) 2005, 2009), while clearly acknowledging that unoccupied upland terrestrial habitat qualifies as critical for aquatic species (e.g., NOAA 2000, 2005).

Does riparian habitat meet biological criteria for critical habitat of freshwater fishes?

We argue that an objective biological definition of critical habitat exists based on the habitat required for species persistence or to meet a recovery target (e.g., Rosenfeld and Hatfield 2006; Richardson and Thompson 2009). Based on the assumption of population limitation by habitat quantity and quality, Rosenfeld and Hatfield (2006) proposed simple screening criteria for evaluating whether habitat features were likely to be biologically critical to species persistence. These criteria include (i) habitat that is necessary to maintain ecosystem integrity and function or (ii) habitat that is disproportionately important (either among or within different habitat types) the singular or cumulative loss of which will result in significant population-level effects (for a recovered or recovering population) and (iii) the set or subset of habitats required for a species or population to persist (or achieve a recovery target). Note that candidate habitats do not have to meet all of these criteria to qualify as critical, and habitat that does not meet these criteria may be critical for reasons other than population limitation (see Rosenfeld and Hatfield 2006, their appendix A-5). Below we briefly consider whether the attributes of riparian habitat meet these

Table 1. Application of criteria for assessing whether aquatic critical habitat is sensitive to riparian function for selected aquatic taxa.

	Salmon– trout	Nooksack dace	Stickleback species pairs	White sturgeon	Deepwater sculpin
(1) Is in-stream critical habitat quality affected by riparian function?					
In-stream (or in-lake) habitat attribute					
Bank stability	Y	Y	—	—	—
Sedimentation	Y	Y	?	—	—
Terrestrial prey and organic matter input	Y	—	?	—	—
Aquatic prey production	Y	Y	—	—	—
Large wood and complex habitat	Y	—	—	—	—
(2) Is water quality affected by impaired riparian function in a way that could compromise species persistence?					
Water quality attribute					
Temperature	Y ^a	Y	—	—	—
Water clarity or turbidity	—	—	Y ^b	—	—

Note: Salmon–trout, generalized salmonids; Nooksack dace, *Rhinichthys* sp.; stickleback species pairs, *Gasterosteus* sp.; white sturgeon, *Acipenser transmontanus*; deepwater sculpin, *Myoxocephalus thompsonii*. Y indicates that a functional attribute is required for persistence of a species, a question mark (?) indicates uncertainty in requirement, and a dash (—) indicates that the function associated with the riparian zone may not be required for species' persistence.

^aIn streams where temperature is near an upper threshold.

^bDecreased water clarity could trigger hybridization through impaired mate recognition (see text).

criteria in the case of freshwater bodies containing listed species.

First, is riparian habitat necessary to maintain aquatic ecosystem integrity and function? A very large body of science has developed over the past five decades documenting the importance of riparian zones to the health of freshwater ecosystems (Forest Ecosystem Management Assessment Team (FEMAT) 1993; Pusey and Arthington 2003; Naiman et al. 2005). Riparian zones provide a variety of functions, ranging from prevention of excessive stream bank erosion (Hassan et al. 2005) to maintenance of channel structure (Murphy and Koski 1989; Montgomery et al. 1995; Sweeney et al. 2004), shading of streams (Kiffney et al. 2003; Pusey and Arthington 2003; Moore et al. 2005), filtration of nutrients and toxins from adjacent agricultural fields (e.g., Barling and Moore 1994; Martin et al. 1999; Gay et al. 2006), protection from livestock grazing (Armour et al. 1994), and provision of allochthonous energy subsidies and a supply of large wood from riparian trees (Murphy 1995; Allan et al. 2003; Richardson et al. 2010). Riparian processes affect habitat attributes of importance to lake-dwelling fish (e.g., Christensen et al. 1996; Pace et al. 2004; Roth et al. 2007), as well as fish in rivers and streams, although impacts of riparian processes on physical habitat structure may be more pronounced in streams. Removal or disturbance of riparian vegetation can also facilitate the invasion of terrestrial and aquatic alien species (Pusey and Arthington 2003), which is a major factor in the decline of aquatic species at risk (Dextrase and Mandrak 2006). Moreover, stream and riparian systems are strongly linked by cross-ecosystem subsidies of resources flowing in both directions (e.g., Sabo and Power 2002; Knight et al. 2005; Richardson et al. 2010) and other processes that make it impossible to consider each subsystem in isolation.

This evidence is summarized in many reviews of riparian function (e.g., Gregory et al. 1991; Pusey and Arthington 2003; Naiman et al. 2005), as well as numerous studies documenting the effects of riparian alteration on fish and inver-

tebrate community structure (e.g., Jones et al. 1999; Lorion and Kennedy 2009a, 2009b). Evidence for the negative effects of riparian forest removal on aquatic biota and ecosystems has been so overwhelming that most jurisdictions in the developed world have enacted legislation to protect riparian habitat (e.g., Blinn and Kilgore 2001; Lee et al. 2004; B.C. Ministry of the Environment 2005), with the primary goal of maintaining the health of aquatic ecosystems including populations of nonlisted biota, despite the significant costs of doing so (e.g., Jones et al. 2006). This legislation represents a de facto, multijurisdictional consensus on the importance of the riparian zone to aquatic species and reflects the strength of the science on which it is based. The only aspect up for debate is the exact width of buffer required for any particular water body or function (Kiffney et al. 2003; Marczak et al. 2010), which may depend on the ecology of the focal species.

Because the habitat requirements of species differ, consideration of riparian habitat as critical should depend on the effect that riparian habitat has on the quality of in-stream habitat for the species in question. It is possible that riparian habitat will be critical for some species but not for others. For example, riparian habitat may not be critical for a warm-water species that (i) is tolerant of siltation and turbid water, (ii) does not require clean gravel for egg incubation, and (iii) is only minimally dependent on allochthonous energy inputs. The humpback chub (*Gila cypha*; Minckley and Deacon 1991), a warm-water species adapted to the turbid waters of the Colorado River where riparian vegetation is naturally poorly developed, may be one example where riparian habitat is not an important component of critical habitat. However, fish species with habitat requirements that are unaffected by the functions associated with riparian vegetation are uncommon. It is much more common that riparian habitat plays a crucial general role in maintaining aquatic ecosystem function and health (Barling and Moore 1994; Murphy 1995; Pusey and Arthington 2003), as evidenced by the prescriptive nature of regulated riparian buf-

fers, i.e., fixed widths rather than taxon- and site-specific widths. As a result, the default assumption should be that riparian habitat is necessary for the maintenance of proper ecosystem function and therefore is biologically critical for water bodies containing listed species. Application of this assessment should be abandoned only when there is clear evidence to the contrary for any specific taxon. Given the widespread regulatory requirement for riparian buffers on fish-bearing streams that harbour nonlisted species, to consider riparian habitat as not critical for the persistence of listed species would implicitly afford listed species less protection than taxa that are deemed not at risk.

The second criterion for biological significance is whether riparian habitat is disproportionately important relative to other available habitats and whether its loss can result in significant population-level effects. One of the core principles of critical habitat protection is that some habitats may be extremely important for species persistence, whereas others may be lost or degraded with minimal population-level effects. In some cases, it may be necessary to protect all of the available habitat for a species to ensure persistence, for instance, the hot water *Physa* that exists in a single hot spring (Te and Clarke 1985) and stickleback species pairs with global distribution restricted to a single lake (Hatfield 2009). However, in cases where habitat limitation is less extreme or less sensitive to disturbance, it may not be necessary to protect an entire drainage basin, and species' persistence can be ensured by identifying and protecting the most functionally important habitats. While the general functional importance of riparian habitat is well established (e.g., Gregory et al. 1991; Naiman et al. 2005; Richardson and Danehy 2007), its significance relative to other habitats in a drainage basin can be understood by considering the population-level effects of removing a riparian buffer adjacent to a stream relative to the effects of removing an equivalent area of forest distant from the water body. Although some upland terrestrial habitats in a drainage basin may be disproportionately important to aquatic ecosystem function (i.e., areas that are critical for slope stability or groundwater recharge), it is clear that in most cases, removing an upland strip of forest will have a much smaller impact on aquatic ecosystem function than removing an equivalent area adjacent to a water body.

The disproportionate importance of the riparian zone relative to other terrestrial habitats suggests that riparian habitat also meets the third biological criterion for critical habitat: that riparian habitat is part of the subset of habitats required for a species or population to persist (or achieve a population recovery target). As noted earlier, there is a general consensus in the scientific literature that an intact riparian zone is required to maintain normal aquatic ecosystem function and healthy fish populations. This consensus is manifest in both the near-universal riparian protection regulations afforded to fish-bearing streams in developed countries and the consistent focus on riparian restoration to rehabilitate degraded aquatic ecosystems (e.g., Beechie and Bolton 1999; Bernhardt et al. 2005), including the active restoration of riparian zones to aid recovery of many listed aquatic species (e.g., Hyatt et al. 2004; Pearson et al. 2008). Ultimately, the most definitive test of the importance of riparian forest to species persistence is to remove it in a controlled experi-

ment and to document the effects on population abundance and persistence. In most cases, the rarity of species at risk, ethical issues, financial and logistic constraints, and the necessity to act quickly to prevent extinction preclude this type of experiment. However, in many instances, the experiment has already taken place, albeit without controls, and it is clear that removal of riparian forest (along with a suite of other habitat impacts, e.g., Findlay et al. 2001; Kerr and Cihlar 2004) is typically associated with the decline or endangerment of many taxa (e.g., Williams et al. 1993; Pess et al. 2002; Pearson 2007). In general, evidence is strong that degradation or removal of riparian vegetation can contribute to population declines that put species at greater risk because of smaller population sizes (Caughley 1994) and lower intrinsic rates of population increase in degraded habitats (Rosenfeld and Hatfield 2006). This supports the general conclusion that riparian habitat is part of the subset of overall habitats required for species persistence. Population viability analysis (PVA) is another approach for assessing the effects of habitat change on extinction risk (Akçakaya 2000; Haight et al. 2002), but the precise effects of riparian loss on vital rates (e.g., survival, growth, and fecundity) are inadequately parameterized for most listed species. In the absence of this information, explicitly considering whether loss of riparian function would degrade aspects of critical in-stream habitat quality is a useful interim criterion for evaluating the importance of riparian habitat to any particular taxon (Table 1).

We now briefly consider application of this logic to selected taxa (Table 1). We consider as examples a generalized salmonid and four endangered fish taxa that occupy distinctly different habitats: Nooksack dace (*Rhinichthys* sp.), a small fluvial cyprinid; stickleback species pairs (*Gasterosteus* sp.), which are found in a limited number of small coastal lakes in British Columbia; white sturgeon (*Acipenser transmontanus*), a large-river species native to British Columbia and the US Pacific Northwest; and the deepwater sculpin (*Myoxocephalus thompsonii*), which is endemic to deep cold-water lakes (Scott and Crossman 1973).

Most in-stream habitat attributes of importance to salmonids are sensitive to loss of riparian function, ranging from the negative effects of sedimentation on gravel interstices used for egg incubation to loss of pool habitat created by large wood inputs (Table 1). The other end of the sensitivity continuum is bracketed by deepwater sculpin. Although the detailed habitat requirements of deepwater sculpin are poorly understood, as a profundal benthic invertivore found at depths greater than 20 m in large cold-water lakes (e.g., Great Bear and the Laurentian Great Lakes; Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2006), the ecology and persistence of deepwater sculpin should be relatively insensitive to riparian function. The three other listed species fall between these extremes of sensitivity (Table 1). Nooksack dace is a riffle-dwelling cyprinid with a limited distribution in southern British Columbia, where it is native to streams subject to a variety of habitat impacts associated with urbanization and agriculture. Because juvenile and adult Nooksack dace spawn and live in riffles, where they forage interstitially on benthic invertebrates, in-stream riffle habitat has been identified as biologically critical (Pearson 2007). Although there is no research

on sediment impacts specific to Nooksack dace, abundant research on ecologically similar benthic insectivores (e.g., Mebane 2001) has demonstrated severe negative effects of sediment inputs through infilling of coarse substrate interstices, leading to decreased invertebrate prey abundance (Wood and Armitage 1997; Thompson et al. 2001; Suttle et al. 2004) and decreased interstitial habitat for benthic fish (for a more detailed development of these arguments, see Pearson 2007). Although riparian functions associated with provision of shade and allochthonous inputs are likely also important to dace, control of bank erosion leading to excessive sediment inputs to riffle habitat is probably the most important function of riparian vegetation that qualifies it as critical terrestrial habitat for protecting critical in-stream riffle habitat for Nooksack dace. It may also be an asset to conservation of this species that riparian areas can reduce flux of other contaminants as well, including nutrients and pesticides.

Stickleback species pairs, in contrast, are lake-dwelling limnetic and benthic-feeding invertivores that have locally co-evolved to feed on contrasting pelagic and benthic resources. Reproductive isolation between these recently evolved species is somewhat fragile (Kraak et al. 2001; Taylor et al. 2006) and is maintained by assortative mating based on differences in body size, male colouration, and possibly nesting microhabitat. Recently evolved fish species are sensitive to hybridization due to habitat changes such as increased turbidity that can interfere with mate recognition, which has been associated with hybridization and collapse of cichlid species in Lake Victoria (Seehausen et al. 1997). Two of five listed stickleback species pairs in Canada have already become extinct, and similar concerns about the effects of habitat change on hybridization apply to the remaining pairs. In contrast with Nooksack dace, it is a concern for stickleback species pairs that alteration or degradation of riparian habitat leads to an increase in turbidity or other habitat change, elevating the rate of hybridization, which is the primary reason for recommending the riparian zone as biologically critical for stickleback species pairs (Hatfield 2009).

White sturgeon is the largest freshwater fish in North America. Adults occupy a range of deepwater mainstem habitats in large rivers; habitat use by young juveniles can include low-velocity habitats such as side channels, tributary confluences, backwaters and sloughs (Bennett et al. 2005) or deep, low-velocity mainstem habitats and lake habitat (RL&L Environmental Services Ltd. 2000; Neufeld and Spence 2002; Golder Associates Ltd. 2003). Although riparian vegetation and large wood of riparian origin may have considerable influence on the channel and floodplain structure of medium to large rivers (Latterell et al. 2006; Latterell and Naiman 2007; Naiman et al. 2010), at present, there is no clear evidence that modification of the riparian zone will degrade in-stream critical habitat attributes for the listed populations of white sturgeon or decrease their probability of persistence (Table 1); consequently, recovery teams in the USA and Canada did not identify riparian habitat as biologically critical (US Fish and Wildlife Service 1999; National Recovery Team for White Sturgeon 2009).

In summary, we conclude that consistent with existing science and widespread riparian regulations, riparian habitat should be considered biologically critical for most species of freshwater fish, unless the habitat requirements of individual

species indicate insensitivity to the ecological functions associated with riparian zones. The appropriate width of riparian buffer may be species- and site-specific and is best evaluated based on the biology of individual species using locally developed science or generic riparian regulations that are appropriate to the mature riparian plant community associated with a particular region, site, and water body. Although we have focused on the critical role of riparian habitat in this paper, we note that protecting the riparian zone may not in itself be sufficient to maintain stream ecosystem integrity (Roth et al. 1996; Roy et al. 2006; Kreutzweiser et al. 2008) or species at risk (Wenger et al. 2008) if development throughout a watershed (e.g., agriculture or urbanization) significantly alters hydrology or water quality. When a watershed is subject to extensive land use that may degrade in-stream habitat quality, sensitive aquatic species will persist only through careful management of development activities, and in some circumstances, larger areas of the drainage basin beyond the riparian zone may warrant consideration as biologically critical.

Finally, we suggest that scientists tasked with defining the biological attributes and spatial distribution of critical habitat for a particular species (in the biological rather than legal sense) should not base their assessments on whether habitat is protected by existing legislation or management options. While the suite of existing management tools and options available for habitat protection is an important consideration for implementing species recovery, it is irrelevant to the biological identification of critical habitat, which should be based on scientific principles and the biology of the species. Existing protection of riparian habitat through municipal, provincial, state, or federal legislation does not make riparian habitat any less biologically critical, although existing protection may minimize the socio-economic impacts of legal critical habitat designation and implementation.

References

- Abell, R., Allan, J.D., and Lehner, B. 2007. Unlocking the potential of protected areas for freshwaters. *Biol. Conserv.* **134**(1): 48–63. doi:10.1016/j.biocon.2006.08.017.
- Akçakaya, H.R. 2000. Viability analyses with habitat-based metapopulation models. *Popul. Ecol.* **42**(1): 45–53. doi:10.1007/s101440050008.
- Allan, J.D., Wipfli, M.S., Caouette, J.P., Prussian, A., and Rodgers, J. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Can. J. Fish. Aquat. Sci.* **60**(3): 309–320. doi:10.1139/f03-019.
- Armour, C., Duff, D., and Elmore, W. 1994. The effects of livestock grazing on riparian and stream ecosystems. *Fisheries*, **19**(9): 9–12. doi:10.1577/1548-8446(1994)019<0009:TEOLGO>2.0.CO;2.
- Barling, R.D., and Moore, I.D. 1994. Role of buffer strips in management of waterway pollution: a review. *Environ. Manage.* **18**(4): 543–558. doi:10.1007/BF02400858.
- B.C. Ministry of the Environment. 2005. Riparian area regulation: assessment methods. British Columbia Ministry of Environment, Queens Printer, Victoria, British Columbia. Available from www.env.gov.bc.ca/habitat/fish_protection_act/riparian/documents/assessment_methods.pdf.
- Beechie, T., and Bolton, S. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. *Fisheries*, **24**(4): 6–15. doi:10.1577/1548-8446(1999)024<0006:AATRSH>2.0.CO;2.

- Bennett, W.R., Edmondson, G., Lane, E.D., and Morgan, J. 2005. Juvenile white sturgeon (*Acipenser transmontanus*) habitat and distribution in the Lower Fraser River, downstream of Hope, BC, Canada. *J. Appl. Ichthyology*, **21**(5): 375–380. doi:10.1111/j.1439-0426.2005.00659.x.
- Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'donnell, T.K., Pagano, L., Powell, B., and Sudduth, E. 2005. Ecology. Synthesizing U.S. river restoration efforts. *Science* (Washington, D.C.), **308**(5722): 636–637. doi:10.1126/science.1109769. PMID:15860611.
- Blinn, C.R., and Kilgore, M.A. 2001. Riparian management practices: a summary of state guidelines. *J. For.* **99**: 11–17.
- Caughley, G. 1994. Directions in conservation biology. *J. Anim. Ecol.* **63**(2): 215–224. doi:10.2307/5542.
- Christensen, D.L., Herwig, B.R., Schindler, D.E., and Carpenter, S.R. 1996. Impacts of lakeshore residential development on coarse woody debris in north temperate lakes. *Ecol. Appl.* **6**(4): 1143–1149. doi:10.2307/2269598.
- Committee on the Status of Endangered Wildlife in Canada. 2006. COSEWIC assessment and update status report on the deepwater sculpin *Myoxocephalus thompsonii* (western and Great Lakes – western St. Lawrence populations) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario. Available from www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_deepwater_sculpin_e.pdf.
- Dextrase, A.J., and Mandrak, N.E. 2006. Impact of alien invasive species on freshwater fauna at risk in Canada. *Biol. Invasions*, **8**(1): 13–24. doi:10.1007/s10530-005-0232-2.
- Findlay, C.S., Lenton, J., and Zheng, L. 2001. Land-use correlates of anuran community richness and composition in southeastern Ontario wetlands. *Ecoscience*, **8**: 336–343.
- Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team: USDA Forest Service, USDC National Oceanic and Atmospheric Administration National Marine Fisheries Service, USDI Bureau of Land Management, USDI Fish and Wildlife Service, USDI National Park Service and EPA. US Government Printing Office No. 1993-793-071. Available from www.blm.gov/or/plans/nwfpnepa/FEMAT-1993/1993_%20FEMAT-ExecSum.pdf.
- Gay, P., Vellidis, G., and Delfino, J.J. 2006. The attenuation of atrazine and its major degradation products in a restored riparian buffer. *Trans. Am. Soc. Agric. Biol. Eng.* **49**: 1323–1339.
- Golder Associates Ltd. 2003. Upper Columbia River juvenile white sturgeon monitoring, phase I investigations, fall 2002. Report prepared for BC Hydro, Castlegar, B.C. Available from a100.gov.bc.ca/pub/acat/public/viewReport.do?reportId=7105.
- Government of Canada. 2002. Species At Risk Act. 2002. R.S.C., c. 29. s 2 (1).
- Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. *Bioscience*, **41**(8): 540–551. doi:10.2307/1311607.
- Haight, R.G., Cypher, B., Kelly, P.A., Phillips, S., Possingham, H.P., Ralls, K., Starfield, A.M., White, P.J., and Williams, D. 2002. Optimizing habitat protection using demographic models of population viability. *Conserv. Biol.* **16**(5): 1386–1397. doi:10.1046/j.1523-1739.2002.99510.x.
- Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., and Jones, E.B.D., 3rd. 1998. Stream biodiversity: the ghost of land use past. *Proc. Natl. Acad. Sci. U.S.A.* **95**(25): 14843–14847. doi:10.1073/pnas.95.25.14843. PMID:9843977.
- Hassan, M.A., Church, M., Lisle, T.E., Brardinoni, F., Benda, L., and Grant, G.E. 2005. Sediment transport and channel morphology of small, forested streams. *J. Am. Water Resour. Assoc.* **41**: 853–876.
- Hatfield, T. 2009. Identification of critical habitat for sympatric stickleback species pairs and the Misty Lake parapatric stickleback species pair. DFO Can. Sci. Advis. Sec. Res. Doc. No. 2009/056. Available from www.dfo-mpo.gc.ca/CSAS/Csas/Publications/ResDocs-DocRech/2009/2009_056_e.pdf.
- Hutchings, J.A., and Festa-Bianchet, M. 2009. Canadian species at risk (2006–2008), with particular emphasis on fishes. *Environ. Rev.* **17**: 53–65. doi:10.1139/A09-003.
- Hyatt, T.L., Waldo, T.Z., and Beechie, T.J. 2004. A watershed scale assessment of riparian forests, with implications for restoration. *Restor. Ecol.* **12**(2): 175–183. doi:10.1111/j.1061-2971.2004.00364.x.
- Jones, E.B.D., Helfman, G.S., Harper, J.O., and Bolstad, P.V. 1999. Effects of riparian forest removal on fish assemblages in Southern Appalachian streams. *Conserv. Biol.* **13**(6): 1454–1465. doi:10.1046/j.1523-1739.1999.98172.x.
- Jones, K.L., Poole, G.C., and Meyer, J.L., Bumback, W., and Kramer, E.A. 2006. Quantifying expected ecological response to natural resource legislation: a case study of riparian buffers, aquatic habitat, and trout populations. *Ecol. Soc.* **11**(2): 15 (online). Available from www.ecologyandsociety.org/vol11/iss2/art15/.
- Kautz, R.S., and Cox, J.A. 2001. Strategic habitats for biodiversity conservation in Florida. *Conserv. Biol.* **15**: 55–77.
- Kerr, J.T., and Cihlar, J. 2004. Patterns and causes of species endangerment in Canada. *Ecol. Appl.* **14**(3): 743–753. doi:10.1890/02-5117.
- Kiffney, P.M., Richardson, J.S., and Bull, J.P. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. *J. Appl. Ecol.* **40**(6): 1060–1076. doi:10.1111/j.1365-2664.2003.00855.x.
- Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A., and Holt, R.D. 2005. Trophic cascades across ecosystems. *Nature* (London), **437**(7060): 880–883. doi:10.1038/nature03962. PMID:16208370.
- Kraak, S.B.M., Mundwiler, B., and Hart, P.J.B. 2001. Increased number of hybrids between benthic and limnetic three-spined sticklebacks in Enos Lake, Canada: the collapse of a species pair? *J. Fish Biol.* **58**(5): 1458–1464. doi:10.1111/j.1095-8649.2001.tb02300.x.
- Kreutzweiser, D.P., Good, K.P., Capell, S.S., and Holmes, S.B. 2008. Leaf-litter decomposition and macroinvertebrate communities in boreal forest streams linked to upland logging disturbance. *J. N. Am. Benthol. Soc.* **27**(1): 1–15. doi:10.1899/07-034R.1.
- Latterell, J.J., and Naiman, R.J. 2007. Sources and dynamics of large logs in a temperate floodplain river. *Ecol. Appl.* **17**(4): 1127–1141. doi:10.1890/06-0963. PMID:17555223.
- Latterell, J.J., Bechtold, J.S., O'Keefe, T.C., Van Pelt, R., and Naiman, R.J. 2006. Dynamic patch mosaics and channel movement in an unconfined river valley of the Olympic Mountains. *Freshwat. Biol.* **51**: 523–544. doi:10.1111/j.1365-2427.2006.01513.x.
- Lee, P., Smyth, C., and Boutin, S. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. *J. Environ. Manage.* **70**(2): 165–180. doi:10.1016/j.jenvman.2003.11.009. PMID:15160742.
- Lorion, C.M., and Kennedy, B.P. 2009a. Riparian forest buffers mitigate the effects of deforestation on fish assemblages in tro-

- pical headwater streams. *Ecol. Appl.* **19**(2): 468–479. doi:10.1890/08-0050.1. PMID:19323203.
- Lorion, C.M., and Kennedy, B.P. 2009b. Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. *Freshw. Biol.* **54**(1): 165–180. doi:10.1111/j.1365-2427.2008.02092.x.
- Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Wood, S.L.R., and Richardson, J.S. 2010. Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. *Ecol. Appl.* **20**(1): 126–134. doi:10.1890/08-2064.1. PMID:20349835.
- Martin, T.L., Kaushik, N.K., Trevors, J.T., and Whiteley, H.R. 1999. Review: denitrification in temperate climate riparian zones. *Water Air Soil Pollut.* **111**(1/4): 171–186. doi:10.1023/A:1005015400607.
- Mebane, C.A. 2001. Testing bioassessment metrics: macroinvertebrate, sculpin, and salmonid responses to stream habitat, sediment, and metals. *Environ. Monit. Assess.* **67**(3): 293–322. doi:10.1023/A:1006306013724. PMID:11334445.
- Minckley, W.L., and Deacon, J.E. (Editors). 1991. *Battle against extinction: native fish management in the American west*. University of Arizona Press, Tucson, Arizona.
- Montgomery, D.R., Buffington, J.M., Smith, R.D., Schmidt, K.M., and Pess, G.R. 1995. Pool spacing in forest channels. *Water Resour. Res.* **31**(4): 1097–1105. doi:10.1029/94WR03285.
- Mooers, A.O., Prugh, L.R., Festa-Bianchet, M., and Hutchings, J.A. 2007. Biases in legal listing under Canadian endangered species legislation. *Conserv. Biol.* **21**(3): 572–575. doi:10.1111/j.1523-1739.2007.00689.x. PMID:17531035.
- Moore, R.D., Spittlehouse, D.L., and Story, A. 2005. Riparian microclimate and stream temperature response to forest harvesting — a review. *J. Am. Water Resour. Assoc.* **41**: 813–834.
- Murphy, M.L. 1995. Forestry impacts on freshwater habitat of anadromous salmonids in the Pacific Northwest and Alaska — requirements for protection and restoration. NOAA Coastal Ocean Program Decision Analysis Series No. 7. NOAA Coastal Ocean Office, Silver Spring, Maryland. Available from /www.cop.noaa.gov/pubs/das/das7.pdf.
- Murphy, M.L., and Koski, K.V. 1989. Input and depletion of woody debris in Alaska streams and implications for streamside management. *N. Am. J. Fish. Manage.* **9**(4): 427–436. doi:10.1577/1548-8675(1989)009<0427:IAADOWD>2.3.CO;2.
- Naiman, R.J., Décamps, H., and McClain, M.E. 2005. *Riparia: ecology, conservation, and management of streamside communities*. Elsevier Academic Press, San Diego, California.
- Naiman, R.J., Bechtold, J.S., Beechie, T.J., Latterell, J.J., and Van Pelt, R. 2010. A process-based view of floodplain forest patterns in coastal river valleys of the Pacific Northwest. *Ecosystems* (N.Y., Print), **13**(1): 1–31. doi:10.1007/s10021-009-9298-5.
- National Oceanic and Atmospheric Administration. 2000. Designated critical habitat: critical habitat for 19 evolutionarily significant units of salmon and steelhead in Washington, Oregon, Idaho, and California. *Fed. Regist.* **65**(32): 7764–7787.
- National Oceanic and Atmospheric Administration. 2005. Endangered and threatened species; designation of critical habitat for 12 evolutionarily significant units of west coast salmon and steelhead in Washington, Oregon, and Idaho; final rule. *Fed. Regist.* **70**(170): 52629–52858.
- National Oceanic and Atmospheric Administration. 2009. Endangered and threatened species; designation of critical habitat for Atlantic salmon (*Salmo salar*) Gulf of Maine distinct population segment; final rule. *Fed. Regist.* **74**(117): 29299–29341.
- National Recovery Team for White Sturgeon. 2009. Recovery strategy for white sturgeon (*Acipenser transmontanus*) in Canada [proposed]. Species at Risk Act Recovery Strategy Series, Fisheries and Oceans Canada, Ottawa, Ontario.
- Nel, J.L., Reyers, B., Roux, D.J., and Cowling, R.M. 2009. Expanding protected areas beyond their terrestrial comfort zone: identifying spatial options for river conservation. *Biol. Conserv.* **142**(8): 1605–1616. doi:10.1016/j.biocon.2009.02.031.
- Neufeld, M., and Spence, C. 2002. Kootenay River white sturgeon studies in British Columbia, 2001. Report prepared for Ministry of Environment, Lands and Parks, Nelson, British Columbia. Available from a100.gov.bc.ca/pub/acat/public/viewReport.do?reportId=176.
- Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van De Bogert, M.C., Bade, D.L., Kritzberg, E.S., and Bastviken, D. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* (London), **427**(6971): 240–243. doi:10.1038/nature02227. PMID:14724637.
- Pearson, M. 2007. An assessment of potential critical habitat for Nooksack dace (*Rhinichthys cataractae* ssp.) and salish sucker (*Catostomus* sp.). DFO Can. Sci. Advis. Sec. Res. Doc. No. 2007/058. Available from www.dfo-mpo.gc.ca/csas/Csas/DocREC/2007/RES2007_058_e.pdf.
- Pearson, M.P., Hatfield, T., McPhail, J.D., Richardson, J.S., Rosenfeld, J.S., Schreier, H., Schluter, D., Snee, D.J., Stejpcovic, M., Taylor, E.B., and Wood, P.M. 2008. Recovery strategy for Nooksack dace (*Rhinichthys cataractae*) in Canada. Species at Risk Act Recovery Strategy Series, Fisheries and Oceans Canada, Vancouver, British Columbia. Available from www.sararegistry.gc.ca/virtual_sara/files/plans/rs_nooksack_dace_0608_e.pdf.
- Pess, G.R., Montgomery, D.R., Steel, E.A., Bilby, R.E., Feist, B.E., and Greenberg, H.M. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash., U.S.A. *Can. J. Fish. Aquat. Sci.* **59**(4): 613–623. doi:10.1139/f02-035.
- Pusey, B.J., and Arthington, A.H. 2003. Importance of the riparian zone to the conservation and management of freshwater fish: a review. *Mar. Freshw. Res.* **54**(1): 1–16. doi:10.1071/MF02041.
- Richardson, J.S., and Danehy, R.J. 2007. A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. *For. Sci.* **53**: 131–147.
- Richardson, J.S., and Thompson, R.M. 2009. Setting conservation targets for freshwater ecosystems in forested catchments. In *Setting conservation targets for managed forest landscapes*. Edited by M.-A. Villard and B.-G. Jonsson. Cambridge University Press, Cambridge, UK. pp. 244–263.
- Richardson, J.S., Naiman, R.J., Swanson, F.J., and Hibbs, D.E. 2005. Riparian communities associated with Pacific Northwest headwater streams: assemblages, processes, and uniqueness. *J. Am. Water Resour. Assoc.* **41**: 935–947.
- Richardson, J.S., Zhang, Y., and Marczak, L.B. 2010. Resource subsidies across the land–freshwater interface and responses in recipient communities. *River Res. Appl.* **26**: 55–66.
- RL&L Environmental Services Ltd. 2000. Fraser River white sturgeon monitoring program — comprehensive report (1995 to 1999). Final report prepared for BC Fisheries. RL&L Environmental Services Ltd. Report No. 815F. Available from a100.gov.bc.ca/pub/acat/public/viewReport.do?reportId=6917.
- Rosenfeld, J.S., and Hatfield, T. 2006. Information needs for assessing critical habitat of freshwater fish. *Can. J. Fish. Aquat. Sci.* **63**(3): 683–698. doi:10.1139/f05-242.
- Roth, B.M., Kaplan, I.C., Sass, G.G., Johnson, P.T., Marburg, A.E., Yannarell, A.C., Havlicek, T.D., Willis, T.V., Turner, M.G., and Carpenter, S.R. 2007. Linking terrestrial and aquatic ecosystems: the role of woody habitat in lake food webs. *Ecol. Model.* **203**(3-4): 439–452. doi:10.1016/j.ecolmodel.2006.12.005.

- Roth, N.E., Allan, J.D., and Erickson, D.L. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landsc. Ecol.* **11**(3): 141–156. doi:10.1007/BF02447513.
- Roy, A.H., Freeman, M.C., Freeman, B.J., Wenger, S.J., Ensign, W.E., and Meyer, J.L. 2006. Importance of riparian forests in urban catchments contingent on sediment and hydrologic regimes. *Environ. Manage.* **37**(4): 523–539. doi:10.1007/s00267-005-0029-1. PMID:16465563.
- Sabo, J.L., and Power, M.E. 2002. River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*, **83**: 1860–1869.
- Saunders, D.L., Meeuwig, J.J., and Vincent, A.C.J. 2002. Freshwater protected areas: strategies for conservation. *Conserv. Biol.* **16**(1): 30–41. doi:10.1046/j.1523-1739.2002.99562.x.
- Scott, W.B., and Crossman, E.J. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin No. 184.
- Seehausen, O., van Alphen, J.J.M., and Witte, F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science (Washington, D.C.)*, **277**(5333): 1808–1811. doi:10.1126/science.277.5333.1808.
- 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. doi:10.1890/03-5190.
- Sweeney, B.W., Bott, T.L., Jackson, J.K., Kaplan, L.A., Newbold, J.D., Standley, L.J., Hession, W.C., and Horwitz, R.J. 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proc. Natl. Acad. Sci. U.S.A.* **101**(39): 14132–14137. doi:10.1073/pnas.0405895101. PMID:15381768.
- Takekawa, J.E., and Beissinger, S.R. 1989. Cyclic drought, dispersal, and the conservation of the snail kite in Florida: lessons in critical habitat. *Conserv. Biol.* **3**(3): 302–311. doi:10.1111/j.1523-1739.1989.tb00090.x.
- Taylor, E.B., Boughman, J.W., Groenenboom, M., Sniatynski, M., Schluter, D., and Gow, J.L. 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Mol. Ecol.* **15**(2): 343–355. doi:10.1111/j.1365-294X.2005.02794.x. PMID:16448405.
- Te, G.A., and Clarke, A.H. 1985. *Physella (Physella) wrighti* (Gastropoda: Physidae), a new species of tadpole snail from Liard Hot Springs, British Columbia. *Can. Field Nat.* **99**: 295–299.
- Theurer, F.D., Lines, I., and Nelson, T. 1985. Interaction between riparian vegetation, water temperature, and salmonid habitat in Tucannon River. *Water Resour. Bull.* **21**: 53–64.
- Thompson, A.R., Petty, J.T., and Grossman, G.D. 2001. Multiscale effects of resource patchiness on foraging behaviour and habitat use by longnose dace, *Rhinichthys cataractae*. *Freshw. Biol.* **46**(2): 145–160. doi:10.1046/j.1365-2427.2001.00654.x.
- United States Congress. 1973. Endangered Species Act of 1973. Pub. L. 93–205, 81 Stat. 844, Dec. 28, 1973.
- US Fish and Wildlife Service. 1999. Recovery plan for the Kootenai River population of the white sturgeon (*Acipenser transmontanus*). US Fish and Wildlife Service, Portland, Oregon. Available from www.fws.gov/ecos/ajax/docs/recovery_plan/990930b.pdf.
- US Fish and Wildlife Service. 2005. Endangered and threatened wildlife and plants; listing gila chub as endangered with critical habitat. *Fed. Regist.* **70**(211): 66663–66721.
- Wenger, S.J., Peterson, J.T., Freeman, M.C., Freeman, B.J., and Homans, D.D. 2008. Stream fish occurrence in response to impervious cover, historic land use, and hydrogeomorphic factors. *Can. J. Fish. Aquat. Sci.* **65**(7): 1250–1264. doi:10.1139/F08-046.
- Williams, J.D., Warren, M.L., Jr., Cummins, K.S., Harris, J.L., and Neves, R.J. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, **18**(9): 6–22. doi:10.1577/1548-8446(1993)018<0006:CSOFMO>2.0.CO;2.
- Wood, P.J., and Armitage, P.D. 1997. Biological effects of fine sediment in the lotic environment. *Environ. Manage.* **21**(2): 203–217. doi:10.1007/s002679900019. PMID:9008071.