

APPLIED ISSUES

Stream amphibians as metrics of critical biological thresholds in the Pacific Northwest, U.S.A.: a response to Kroll *et al.*

HARTWELL H. WELSH JR AND GARTH R. HODGSON

USDA Forest Service, Pacific Southwest Experiment Station, Redwood Sciences Laboratory, Arcata, CA, U.S.A.

SUMMARY

1. Kroll, Hayes & MacCracken (in press) Concerns regarding the use of amphibians as metrics of critical biological thresholds: a comment on Welsh and Hodgson 2008. *Freshwater Biology*, criticised our paper [Welsh & Hodgson (2008) Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest. *Freshwater Biology*, 53, 1470–1488] proposing the use of headwater stream amphibians as metrics of stream status in the Pacific Northwest (PNW). They argued that our analysis of previously published data reflected circular reasoning because we reached the same conclusions as the earlier studies. In fact, we conducted a meta-analysis to address new questions about the optimum values and thresholds (based on animal densities) for abiotic stream attributes that were found to be important to these amphibians in earlier studies. This is analogous to determining blood pressure thresholds or fat-to-weight ratios that facilitate predicting human health based on meta-analyses of earlier data from studies that found significant correlations between these variables and relative health.
2. Kroll *et al.* argued that we should not make inference to environmental conditions across the PNW from data collected in California. We collected data from northern California and southern Oregon, the southern extent of the PNW. We made inference to the Klamath-Siskiyou and North Coast bioregions, and argued that available research on these headwater species indicates that our results have the potential to be applied throughout the PNW with minimal regional adjustments.
3. Kroll *et al.* contended that we need reproductive success, survival estimates and density estimates, corrected for detection probabilities, to establish relationships between animal density and stream attributes. Reproductive success and survival estimates are important for demographic modelling and life tables, but they are not necessary to demonstrate meaningful relationships with abiotic conditions. Both corrected occupancy estimates and individual detection probabilities are unnecessary, and take multiple sampling efforts per site, or onerous mark release and re-capture studies, respectively, to determine accurately.
4. Kroll *et al.* questioned the use of stream amphibians as a surrogate for measuring physical parameters, such as water temperature, claiming that measuring the physical parameters directly is more efficient. Here they misinterpreted the main point of our paper: stream organisms are integrators of what happens in a catchment, and carefully selected species can serve as surrogates for the biotic community and the relative condition of the network environment.

Correspondence: Hartwell H. Welsh Jr, USDA Forest Service, Pacific Southwest Experiment Station, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521, U.S.A. E-mail: hwelsh@fs.fed.us

5. Kroll *et al.* claimed that we demonstrated weak inferences regarding ecosystem processes. We argue that by relating densities of stream amphibians with changes along abiotic environmental gradients that are commonly affected by anthropogenic activities, we are establishing biological links to gradients that represent important ecosystem processes and identifying biometrics that can be used to quantify the status (health) of these gradients.

Keywords: biometrics, lotic amphibians, stream health

Introduction

We recently proposed using three amphibians as metrics of critical biological thresholds in headwater streams of the Pacific Northwest (PNW) of North America (Welsh & Hodgson, 2008), an idea that has prompted concerns and criticism from timber industry biologists and a state Fish and Wildlife biologist (Kroll, Hayes & MacCracken, in press; see also Welsh, Pope & Wheeler, 2009). We welcome the opportunity to address their concerns here and to bring greater focus to the related issues of habitat alteration and fragmentation in the stream networks of the PNW. The interconnected tributaries and main stem channels of these river catchments represent complex ecological systems that can be advantageously viewed as dendritic networks (Grant, Lowe & Fagan, 2007). The interactions between and among the abiotic and biotic processes within them are poorly understood and often fragile (Montoya, Pimm & Solé, 2006), yet they provide vital habitats for early life stages of one of the most valuable natural resources of this region, the native salmonids (Groot & Margolis, 1991). These fishes, all now in drastic decline, once played a vital role carrying ocean-derived nutrients to the upland forest landscapes infused by these networks (e.g. Helfield & Naiman, 2001; Merz & Moyle, 2006; Holtgrieve, Schindler & Jewett, 2009). Until recently, they also played a large role in the economy of the PNW. We find both of these facts compelling reasons to develop and test biometrics that can be used to assess the condition (i.e. health) of these networks in terms of their ability to sustain native fauna that evolved in these clear, cold water systems. Kroll *et al.* (in press) agreed with our contention that the approach of using animal metrics is conceptually well established, but argued that it is poorly developed. We are puzzled then as to why they would challenge our proposal. We can not imagine a better way to

develop and improve the science in support of effective bio-monitoring (Tabor & Aguirre, 2004) than to quantitatively evaluate the relationships of those species with high potential, and to advocate for further testing to substantiate the evidence and refine the application (e.g. Niemi & McDonald, 2004; Nichols & Williams, 2006). Further, we can not imagine a more important objective than recovering the capabilities of these catchment networks to again support healthy populations of salmonids.

Kroll *et al.* (in press) accused us of arguing for the use of 'animal occurrence' (e.g. Kroll *et al.*, 2008) as a reliable indicator of network health, when in fact the response metrics we advocated were the presence and relative densities of three species. They further expressed the opinion that our arguments for the use of these stream-associated amphibians (SAA), the coastal tailed frog (*Ascaphus truei* Stejneger), the coastal (formerly Pacific) giant salamander (*Dicamptodon tenebrosus* Baird & Girard) and the southern torrent salamander (*Rhyacotriton variegatus* Stebbins & Lowe) as indicators of network health were faulty. They chose also to disparage our use of the terms ecosystem health and ecological integrity by labelling them as non-specific jargon, and claimed that we did not adequately define these terms. In fact, we defined evidence of a healthy ecosystem in PNW stream networks as consisting of tributary components with high ecological integrity (Westra *et al.*, 2000). Further, we noted specifically that ecological integrity in these networks is most often compromised by changes in three abiotic attributes, fine sediments, water temperature and large woody debris (LWD), each with high potential for perturbations from anthropogenic sources (e.g. Waters, 1995; Montgomery *et al.*, 2003; Welsh, Hodgson & Karraker, 2005). We noted, based on patterns observed across multiple studies over 23 years, that streams that appeared to be in the best condition (healthiest) had lower water temperatures,

lower fine sediment loads and 20–25% LWD cover and were consistently found in late-seral reference forests (see RCBI in Stoddard *et al.*, 2006). We also found that the streams with these conditions also had consistently higher densities of SAA. This suggested to us that the relative states of these attributes in low order reaches could be directly linked to densities of SAA and, as such, SAA could serve as biometrics for this critical suite of components that also influence downstream conditions for native salmonids (e.g. Freeman, Pringle & Jackson, 2007; Meyer *et al.*, 2007; Wipfli, Richardson & Naiman, 2007).

Kroll *et al.* (in press) noted three objectives for their comments; the first was to address four assumptions they deemed we failed to evaluate empirically in our paper (Welsh & Hodgson, 2008). Their second and third objectives were statements that monitoring should be linked with testable biological hypotheses, and also framed so that one can evaluate the effectiveness of specific management practices. We concur with both ideas and have no disagreement, but, given their mention, Kroll *et al.* (in press) implied that we did not give them adequate consideration. We address each issue below.

Responses to Kroll *et al.* about four assumptions

Assumption one: circular logic

Kroll *et al.* (in press) argued that our reasoning was circular because we relied on earlier datasets to establish our case, and, in their view, followed with logical and empirical assumptions that did not receive rigorous evaluation, and that produced preordained outcomes. We did use earlier datasets, those from a series of studies that revealed consistent species-specific patterns indicating similar relationships between SAA numbers and three abiotic attributes of interest. We also found these patterns to be consistent with results of others (see citations in Welsh & Hodgson, 2008). We followed the evidence of consistent patterns from multiple correlative studies linking SAA numbers with these three abiotic attributes and conducted new analyses with combined datasets to examine the nature of those patterns. Our primary objective (to quote our critics who appear to have missed this key aspect of our paper) was to "...better focus on the estimation of the size and variation of specific responses..." (Kroll *et al.*, in press:5). We find

nothing preordained about this approach, and find that we are not alone in the view that meta-analyses can be of great value (Arnqvist & Wooster, 1995).

Assumption two: the spatial applicability of our results

Kroll *et al.* (in press) expressed concern that we generalised from the relationships found with SAA in northwest California to the entire PNW. Biogeographers generally include northwest California as part of the great temperate rainforest belt in western North America, considering it a part of the PNW (e.g. Udvardy, 1975; Schoonmaker, von Hagen & Wolf, 1997). Bailey (1998) viewed northwest California as the southern portion of a humid temperate domain, although he sub-divided it into two eco-regions. More relevant to the application of our results is the fact that these SAA occur as far south as Mendocino and Sonoma Counties on the northern California coast, and inland in the states' coastal and Klamath Mountains. In addition, they range north through western Oregon and Washington (torrent salamanders) and into British Columbia, Canada (tailed frog and giant salamander) (Jones, Leonard & Olson, 2005). We agree with Kroll *et al.* (in press) that SAA abundances and responses to abiotic attributes can vary with latitude and longitude (e.g. Bury *et al.*, 1991), and with altitude (Welsh & Hodgson, 2008; fig. 8). However, the more pertinent question is what is the nature of these different responses? Do they vary in degree, such that regional adjustments can be quantified and applied, or do they vary in a way that responses are not predictable, thus rendering SAA unsuitable as biometrics? We would argue that extensive field and laboratory research on SAA across the PNW (see citations in Welsh & Lind, 1996, 2002; Bury, 2008) indicates predictable responses (with minor variations) to a wide range of attribute states including those used in Welsh & Hodgson (2008). Changes in many of these attribute states have also been linked with anthropogenic disturbances such as road building and timber harvesting (Sarr *et al.*, 2005; Kroll, 2009). Although we demonstrate our case with data from streams in the north coast and Klamath-Siskiyou bioregions of California, similarities in the realised niches of SAA across the PNW leaves little doubt of their value as metrics of attribute states regardless of some minor regional variations (e.g. Huff, Hubler & Borisenko, 2005). We found it interesting that this

issue was not a concern to Kroll *et al.* (2008) who generalised about factors affecting SAA distributions across all of western Oregon and Washington, applying them not just to this broad geographic region, but also across species within SAA genera (e.g. *Rhyacotriton* and *Dicamptodon*).

Assumption three: shared evolutionary histories and similar life requisites

Kroll *et al.* (in press) argued that since there is no evidence that anadromous fishes and SAA interacted historically and there is little research supporting our contention that SAA and downstream biota such as native salmonids share evolutionary histories, that any statements about their similar life requisites (e.g. relationship to cold water) is 'at best premature, and at worst inaccurate'. Although SAA are permanent residents in headwaters and salmonids only spend part of their lives in downstream reaches, they both have specific life history requirements that link them to the same cold water PNW streams in which they evolved. We are curious, regardless of available research, just how one supports the view that these two entities could avoid having shared evolutionary histories given their shared distributions in PNW stream networks. As to the notion of limited spatial overlap, while it appears to vary by SAA species, this idea is not accurate (e.g. Parker, 1993; Harvey, White & Nakamoto, 2009). We in fact found overlap between salmonids and giant salamanders in 19 of 22 (86%) and 16 of 21 (76%) of fish-bearing reaches in Mattole River and South Fork Trinity River tributaries, respectively, of northern California (H.H. Welsh & G.R. Hodgson, unpubl. data). Larval tailed frogs were found in five of 22 (22.7%) and four of 21 (19%) of fish-bearing tributaries, respectively, of the same river networks (H.H. Welsh & G.R. Hodgson, unpubl. data). We suspect the fact that limited overlap is the result of this question not being adequately investigated. The views expressed by our critics appears to be the result of not recognising that stream reaches and tributaries in these catchments are parts of entire and interacting network systems (Watts & Strogatz, 1998; Proulx, Promislow & Phillips, 2005; Grant *et al.*, 2007). The abiotic components and resident biota in these systems are inextricably interlinked by hydrologic connectivity (Freeman *et al.*, 2007). Contrary to their contention of little support for our argument,

there is in fact a substantial body of research establishing linkages and interactions throughout these networks (e.g. Gomi, Sidel & Richardson, 2002; Wipfli, 2005; Meyer *et al.*, 2007; Wipfli *et al.*, 2007). The inter-relatedness of sub-components within these networks is not only well established, but others before us have discussed its importance to the recovery and sustainability of native salmonids (e.g. Naiman & Latterell, 2005). We submit that the question of shared environmental requisites associated with the abiotic attributes of interest is similarly well-established and hardly in dispute (e.g. Welsh & Ollivier, 1998; Suttle *et al.*, 2004; Huff *et al.*, 2005). This is particularly true of the early life requisites of salmonid hatching, rearing and freshwater foraging (e.g. Naiman & Latterell, 2005; Harvey *et al.*, 2009).

Assumption four: the absence of SAA and relationships to stream processes

We do not dispute the fact that SAA distributions are not continuous across their geographic ranges (Jones *et al.*, 2005). Nor do we disagree that high genetic divergences suggest different and distinct biogeographic histories among these lineages (for citations of genetic studies see Kroll *et al.*, in press). We acknowledge that historical factors have had a profound influence on the distributions of SAA. On the other hand, contrary to the assertion of our critics, we did not argue that SAA absence can only be the result of 'unhealthy headwater processes'. Kroll *et al.* (in press) take our quote out of context when they make this claim. The quote, in a section entitled 'Headwater amphibians and current timber practices' (Welsh & Hodgson, 2008:1482), is part of a discussion about commercial forests in California where SAA are known to occur, but exist in depressed numbers or are locally absent in many harvested areas (see details in Welsh, Roelofs & Frissell, 2000). Here, as in much of the commercial timberlands to the west of the Cascades crest in the PNW, a region where these species are also known to be historically well distributed throughout most forested areas, it is reasonable to assume that anthropogenic activities are at least partly responsible for their low numbers compared with populations in streams on nearby un-logged old-growth reference stands. We do state in this same section that "...it may take further investigation to discern the actual mechanism(s)..." responsible for

the reduced numbers of SAA (Welsh & Hodgson, 2008:1483). However, given the differences in occurrence and densities on commercial timberlands compared with nearby un-logged reference areas, the mechanism responsible is likely to have an anthropogenic origin (e.g. Ashton, Marks & Welsh, 2006).

Additional concerns

Status of our knowledge on stream amphibian ecology

Kroll *et al.* (in press) contended that the ecology of these species is so poorly known that they should not be used in the manner we propose. This, they argue, is because SAA responses to changes in particular attributes cannot be confidently interpreted and could be caused by a number of other things. We strongly disagree with the notion that SAA ecology is poorly known (e.g. see species accounts in Lannoo, 2005). Although we may lack a complete knowledge of every aspect of SAA ecology, this is certainly not the case with the relationships of SAA and the three abiotic attributes that are the subjects of our paper (see Welsh & Lind, 1996, 2002; Bury, 2008; and citations therein). We agree that a multitude of environmental factors and their interactions can potentially influence the presence and relative abundance of SAA. Similarly, differential responses to multiple factors can influence births, deaths, emigration and immigration. However, the very point of our paper is that even with the unknown influences of other factors, we can establish distinct relationships between SAA numbers and the conditions of three important stream attributes. Furthermore, all of these attributes have well-established links to anthropogenic disturbances (e.g. Waters, 1995; Montgomery *et al.*, 2003; Welsh *et al.*, 2005) and the related status of SAA (e.g. Corn, Bury & Hyde, 2003). We do not argue these are the only factors that can influence SAA numbers, but we see no reason that other factors cannot be discerned and monitored simultaneously (see below).

Detection and occupancy

The recent emphasis in the literature on modelling site occupancy (e.g. MacKenzie *et al.*, 2002; Kroll, 2009; Kroll *et al.*, in press) reminds us of the similar embrace of information theory, often to the exclusion of other useful analytical approaches (Stephens *et al.*, 2005).

We would argue here as well that embracing this single approach may not be the right fit for every situation. We suggest that workers ask themselves if highly accurate site occupancy estimates are really needed to address their research questions and thus worth the extra effort and expense required. Many studies were designed before the advent of occupancy models and do not meet the assumptions of these mathematical models; many relied instead on protocols designed to maximise detectability (i.e. minimise false-negatives). These studies have provided many valuable results.

We agree it is desirable to determine and correct for detection probability when using abundance or density estimates, but find that this issue has little relevance to our paper (Welsh & Hodgson, 2008). For many questions, ascertaining individual detection probabilities is unnecessary, especially if individual differences are unrelated to the variable of interest or the direction of the bias is known and can be taken into consideration. Kroll *et al.* (in press) express concern that individual detection probabilities for amphibians may vary because of environmental characteristics. However, any bias in our studies would lead to conservative estimates of the beneficial effects of two of the three attributes of interest (low fine sediments and >LWD cover) because detections would be more difficult in the more pristine stream environments where unsedimented coarse substrata and more LWD would provide greater amounts of cover for animals to hide, making them harder to detect. We did not address individual detection probabilities in our realised niche analysis (Welsh & Hodgson, 2008; figs 1 & 2), because we did not view this as an issue of concern based on our highly effective sampling protocols. These protocols were designed to minimise false-negative detections by intensively sampling for animal density data in stream reaches large enough to support multiple individuals, and at appropriate times and places where SAA are most likely to occur when present. Considering detection probabilities might have slightly narrowed the niche width for fine sediments in this analysis, but otherwise would have no effects of consequence. The level of effort needed to accurately determine individual detection probabilities for all species and sites surveyed would be prohibitive. Mark and re-capture approaches or the successive removal sampling from closed reaches required to

make these determinations would be onerous, expensive to conduct, and certainly not worth the time and effort. This, rather than inadequate study designs, is the likely reason that studies cited by Kroll *et al.* (in press) did not incorporate individual detection probabilities in their analyses (see also Kroll, 2009). The fact that the majority of these studies had similar results showing negative impacts of forestry operations on SAA suggests that their conclusions are accurate regardless of having detection probabilities less than one. We admit these studies could have all shared a consistent bias; however, for this to be the case with so many studies is highly improbable.

We also differ with the opinion that detection is always an issue when estimating site occupancy and believe that this notion too needs some perspective. We used occupancy data in our generalised additive models analysis (Welsh & Hodgson, 2008), and admit that the potential exists for some slight variation in our models because of false-negatives. However, we would argue that any uncertainty in our occupancy estimates would be slight, conservatively biased and of little consequence given the effectiveness of our sampling protocols and our large sample sizes. We do, however, acknowledge a poor choice of words when we used 'detection probabilities' and 'detection rates' when what we meant was 'proportion of sites occupied' and 'occupancy rates', respectively (Welsh & Hodgson, 2008:1482).

We believe our combined analyses demonstrated the value of collecting density or relative abundance rather than just site occupancy data (e.g. Kroll *et al.*, 2008) when addressing questions about the relationships of SAA to environmental gradients. Site occupancy data alone are insufficient to determine the suitability of environmental conditions because finding an animal at a site does not demonstrate habitat suitability. Given that it is animal numbers *per se* that most strongly affects persistence and extinction probabilities of amphibian populations, it is more informative to seek evidence of abundance rather than occurrence (Schmidt, 2008).

Fluctuations in SAA populations: management activities or non-demonic intrusions

Kroll *et al.* (in press) claimed that when we proposed the use of SAA for monitoring stream health we ignored factors other than anthropogenic disturbances

that can influence population sizes (e.g. predators, disease, climate change, etc.; see citations in their paper). We did not adequately address this point in our paper and thank our critics for pointing that out. For brevity we refer to these factors collectively as 'non-demonic intrusions' [a term we borrowed from Oksanen (2004) who used it in an analogous context]. We are well aware of the potential for non-management-related factors to influence SAA numbers. We also agree that amphibian numbers can fluctuate in undisturbed conditions. However, these potential non-demonic intrusions comprise readily testable hypotheses that can, with well-designed studies, be either identified and incorporated as co-variables, or logically ruled out as causative agents. We would further note that habitat change is acknowledged as the single greatest factor in worldwide amphibian declines, with most declines traced to anthropogenic causes (Gardner, Barlow & Peres, 2007). Given current knowledge of amphibian ecology, we would recommend that monitoring programmes using SAA be designed so that multiple hypotheses can be simultaneously evaluated. There are many analytical tools available that can address multiple effects, interactive processes and synergisms, all of which can be identified and evaluated simultaneously with management activities (e.g. Hilborn & Mangel, 1997; Burnham & Anderson, 2002; Hobbs, 2009; and cites therein).

Headwater effects on downstream processes

Kroll *et al.* (in press:11) claimed that we argued "...that headwater habitats are the principal regulator of downstream populations of anadromous fishes..." ignoring the significant variation in population sizes that can come from factors such as ocean conditions, growth rates, survival, etc. (for a complete list and citations see Kroll *et al.*, in press). This claim is disingenuous as we made no such supposition, nor do we believe it to be true. What we did say was that headwater streams "...have a strong influence on downstream conditions and fish-bearing habitats..." (Welsh & Hodgson, 2008:1471). Our argument for the importance of headwater conditions for salmonids is based on their influence on downstream states, particularly spawning gravels and their relative status (see Gomi *et al.*, 2002; MacDonald & Coe, 2007; Richardson & Danehy, 2007). The status of these gravels, and associated water conditions, directly

influence egg hatching success and juvenile survival (Bisson *et al.*, 1992; Frissell, 1993; Suttle *et al.*, 2004). The absence of annual cohorts issuing forth from cold, clean, highly oxygenated gravels and growing to successfully out-migrate, will determine whether most of the factors invoked by Kroll *et al.* (in press) ever even come into play.

Monitoring and measuring habitat features

Kroll *et al.* (in press) point out the wide variation in responses we found for SAA and the three abiotic attributes of interest. Here they interpret our results to suit their arguments, focusing on our minimum and maximum values, and ignoring the fact that the majority of the data fell within relatively narrow ranges (i.e. the realised niches; see Welsh & Hodgson, 2008; figs 1 & 2). Their solution to this supposed problem of high variation is to measure the abiotic variables themselves (Kroll *et al.*, in press:12); and they offer numerous methods toward this end. However, measuring these abiotic attributes does not address the more relevant issue: establishing a comprehensive and reliable measure of headwater condition as it relates to its ecological function as habitat for native fauna. We think Karr (2006:10) captures this issue best when he states that, "A carefully formulated programme of biological monitoring is more cost-effective because organisms are the integrators of all that is happening in a watershed".

Headwater stream management in the Pacific Northwest

We believe that invoking 'an unknown level of uncertainty' (Kroll *et al.*, in press) in no way detracts from the relationships we have quantified (Welsh & Hodgson, 2008). It does mean that one needs to apply common sense, logic and parsimony, along with knowledge of species' biology when interpreting relationships in a monitoring framework. Furthermore, one should never discount the possible influences of unforeseen factors. These are and always will be the tenets of good science, but not reasons to reject the obvious value and usefulness of well-established relationships. Science has developed good tools to analyse multiple variables and complex interactions (see above) so that patterns and relationships can be discerned within a framework of variable uncertainty

and identifiable confidence levels. Establishing such inferences within an acceptable confidence level facilitates making sound decisions in an adaptive management framework (Walters, 1986) such that resource extraction industries can improve operations to reduce impacts to biodiversity and ecological services on the lands they manage.

Acknowledgments

The authors thank Karen Pope, Bret Harvey, Clara Wheeler and Blake Hossack for reviewing earlier drafts and making useful comments and edits that improved this manuscript.

References

- Arnqvist G. & Wooster D. (1995) Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution*, **10**, 236–240.
- Ashton D.T., Marks S.B. & Welsh H.H. Jr (2006) Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. *Forest Ecology and Management*, **221**, 183–193.
- Bailey R.G. (1998) *Ecoregions of North America (Map)*, Miscellaneous Publication 1548. U.S.D.A. Forest Service, Washington D.C.
- Bisson P.A., Quinn T.P., Reeves G.H. & Gregory S.V. (1992) Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest river systems. In: *Watershed Management: Balancing Sustainability and Environmental Change* (Ed. R. Naiman), pp. 189–232. Springer-Verlag, New York.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Bury R.B. (2008) Low temperature tolerances of stream amphibians in the Pacific Northwest: implications for riparian and forest management. *Journal of Applied Herpetology*, **5**, 63–74.
- Bury R.B., Corn P.S., Aubry K.B., Gilbert F.F. & Jones L.L.C. (1991) Aquatic amphibian communities in Oregon and Washington. In: *Wildlife and Vegetation of Unmanaged Douglas-fir Forests, PNW GTR-285* (Eds L.F. Ruggiero, K.B. Aubry, A.B. Carey & M.H. Huff), pp. 353–362. U.S.D.A. Forest Service, Pacific Northwest Research Station, Portland, OR.
- Corn P.S., Bury R.B. & Hyde E.J. (2003) Conservation of North American stream amphibians. In: *Amphibian Conservation* (Ed. R.D. Semlitsch), pp. 24–36. Smithsonian Press, Washington D.C.

- Freeman M.C., Pringle C.M. & Jackson C.R. (2007) Hydrologic connectivity and the contribution of stream headwaters to ecological integrity at regional scales. *Journal of the American Water Resources Association*, **43**, 5–14.
- Frissell C.A. (1993) Topology of extinction and endangerment of native fishes in the Pacific Northwest and California (U.S.A.). *Conservation Biology*, **7**, 342–353.
- Gardner T.A., Barlow J. & Peres C.A. (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166–179.
- Gomi T., Sidel R.C. & Richardson J.S. (2002) Understanding processes and downstream linkages of headwater systems. *BioScience*, **52**, 905–916.
- Grant E.H.C., Lowe W.H. & Fagan W.F. (2007) Living in the branches: population and ecological processes in dendritic networks. *Ecology Letters*, **10**, 165–175.
- Groot C. & Margolis L. (Eds) (1991) *Pacific Salmon Life Histories*. University of British Columbia Press, British Columbia.
- Harvey B.C., White J.L. & Nakamoto R.J. (2009) The effect of deposited fine sediment on summer survival and growth of rainbow trout in riffles of a small stream. *North American Journal of Fisheries Management*, **29**, 434–440.
- Helfield J.M. & Naiman R.J. (2001) The effects of salmon-driven nitrogen on riparian forest growth and implications for stream productivity. *Ecology*, **82**, 2403–2409.
- Hilborn R. & Mangel M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, NJ.
- Hobbs N.T. (2009) Forum: new tools for insight from ecological models and data. *Ecological Applications*, **19**, 551–598.
- Holtgrieve G.W., Schindler D.E. & Jewett P.K. (2009) Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecological Research*. doi:10.1007/s11284-009-0591-8.
- Huff D.D., Hubler S.L. & Borisenko A.N. (2005) Using field data to estimate the realized thermal niche of aquatic vertebrates. *Journal of Fisheries Management*, **25**, 346–360.
- Jones L.L.C., Leonard W.P. & Olson D.H. (Eds) (2005) *Amphibians of the Pacific Northwest*. Seattle Audubon Society, Seattle, WA.
- Karr J.R. (2006) Seven foundations of biological monitoring and assessment. *Biologia Ambientale*, **20**, 7–18.
- Kroll A.J. (2009) Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, U.S.A: a review. *Forest Ecology and Management*, **257**, 1188–1199.
- Kroll A.J., Risenhoover K., McBride T., Beach E., Kernohan B.J., Light J. & Bach J. (2008) Factors influencing stream occupancy and detection probability parameters of stream-associated amphibians in commercial forests of Oregon and Washington, USA. *Forest Ecology and Management*, **255**, 3726–3735.
- Kroll A.J., Hayes M.P. & MacCracken J.G. (in press) Concerns regarding the use of amphibians as metrics of critical biological thresholds: a comment on Welsh and Hodgson 2008. *Freshwater Biology*.
- Lannoo M. (2005) *Amphibian Declines: The Conservation Status of United States Species*. University of California Press, Berkeley, CA.
- MacDonald L.H. & Coe D. (2007) Influence of headwater streams on downstream reaches in forested areas. *Forest Sciences*, **53**, 148–168.
- MacKenzie D.I., Nichols J.D., Lachman G.B., Droege S., Royle J.A. & Langtimm C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- Merz J.E. & Moyle P.B. (2006) Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of central California. *Ecological Applications*, **16**, 999–1009.
- Meyer J.L., Strayer D.L., Wallace J.B., Eggert S.L., Helfman G.S. & Leonard N.E. (2007) The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association*, **43**, 86–103.
- Montgomery D.R., Collins B.D., Abbe T.B. & Buffington J.M. (2003) Geomorphic effects of wood in rivers. In: *The Ecology and Management of Wood in World Rivers, AFS Symposium 37* (Eds S.V. Gregory, K.L. Boyer & A. Gurnell), pp. 21–47. American Fisheries Society, Bethesda, MD.
- Montoya J.M., Pimm S.L. & Solé R.V. (2006) Ecological networks and their fragility. *Nature*, **442**, 259–264.
- Naiman R.J. & Latterell J.J. (2005) Principles for linking fish habitat to fisheries management and conservation. *Journal of Fish Biology*, **67**(Suppl. B), 166–185.
- Nichols J.D. & Williams B.K. (2006) Monitoring for conservation. *Trends in Ecology and Evolution*, **21**, 668–673.
- Niemi G.J. & McDonald M.E. (2004) Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 89–111.
- Oksanen L. (2004) The devil lies in details: reply to Stuart Hurlburt. *Oikos*, **104**, 598–605.

- Parker M.S. (1993) Predation by Pacific giant salamander larvae on juvenile steelhead trout. *Northwestern Naturalist*, **74**, 77–81.
- Proulx S.R., Promislow D.E.L. & Phillips P.C. (2005) Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, **20**, 345–353.
- Richardson J.S. & Danehy R.J. (2007) A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. *Forest Science*, **53**, 131–147.
- Sarr D.A., Odion D.C., Hibbs D.E., Weikel J., Gresswell R.E., Bury R.B., Czarnomski N.M., Pabst R.J., Shatford J. & Moldenk A.R. (2005) *Riparian Zone Forest Management and the Protection of Biodiversity: A Problem Analysis*, Tech. Bulletin 908. National Council for Air and Stream Improvement, Research Triangle Park, NC.
- Schmidt B.R. (2008) Steps toward better amphibian conservation. *Animal Conservation*, **11**, 469–471.
- Schoonmaker P.K., von Hagen B. & Wolf E.C. (Eds) (1997) *The Rainforests of Home: Profile of a North American Bioregion*. Island Press, Washington D.C.
- Stephens P.A., Buskirk S.W., Hayward G.D. & Martinez del Rio C. (2005) Information theory and hypothesis testing: a call for pluralism. *Journal of Animal Ecology*, **42**, 4–12.
- Stoddard J.L., Larsen D.P., Hawkins C.P., Johnson R.K. & Norris R.H. (2006) Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications*, **16**, 1267–1276.
- Suttle K.B., Power M.E., Levine J.M. & McNeely C. (2004) How fine sediment in riverbeds impairs growth and survival of juvenile salmonids. *Ecological Applications*, **14**, 969–974.
- Tabor G.M. & Aguirre A.A. (2004) Ecosystem health and sentinel species: adding an ecological element to the proverbial “canary in the mineshaft”. *EcoHealth*, **1**, 226–228.
- Udvardy M.D.F. (1975) *A Classification of the Biogeographical Provinces of the World*, IUCN Occasional Paper No. 18. International Union for the Conservation of Nature, Morges.
- Walters C. (1986) *Adaptive Management of Renewable Resources*. MacMillan Co., New York.
- Waters T.E. (1995) *Sediment in Streams: Sources, Biological Effects, and Control*. American Fisheries Society, Bethesda, MD.
- Watts D.J. & Strogatz S.H. (1998) Collective dynamics of ‘small-world’ networks. *Nature*, **393**, 440–442.
- Welsh H.H. Jr & Hodgson G.R. (2008) Amphibians as metrics of critical biological thresholds in forested headwater streams of the Pacific Northwest. *Freshwater Biology*, **53**, 1470–1488.
- Welsh H.H. Jr & Lind A.J. (1996) Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern California. *Journal of Herpetology*, **30**, 385–398.
- Welsh H.H. Jr & Lind A.J. (2002) Multi-scale habitat relationships of stream amphibians in the Klamath-Siskiyou Region of California and Oregon. *Journal of Wildlife Management*, **66**, 581–602.
- Welsh H.H. Jr & Ollivier L.M. (1998) Stream amphibians as indicators of ecosystem stress: a case study from California’s redwoods. *Ecological Applications*, **8**, 118–1132.
- Welsh H.H. Jr, Roelofs T.D. & Frissell C.A. (2000) Aquatic ecosystems of the redwood region. In: *The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods* (Ed. R. Noss), pp. 165–199. Island Press, Washington D.C.
- Welsh H.H. Jr, Hodgson G.R. & Karraker N.E. (2005) Influences of the vegetation mosaic on riparian and stream environments in a mixed forest-grassland landscape in “Mediterranean” northwestern California. *Ecography*, **28**, 537–551.
- Welsh H.H. Jr, Pope K.L. & Wheeler C.A. (2009) How reliable are amphibian population metrics? A response to Kroll *et al.* *Biological Conservation*, doi:10.1016/j.biocon.2009.05.032.
- Westra L., Miller P., Karr J.R., Rees W.E. & Ulanowicz R.E. (2000) Ecological integrity and the aims of the global integrity project. In: *Ecological Integrity: Integrating Environment, Conservation, and Health* (Eds D. Pimentel, L. Westra & R.F. Noss), pp. 19–41. Island Press, Washington D.C.
- Wipfli M.S. (2005) Trophic linkages between headwater forests and downstream fish habitats: implications for forest and fish management. *Landscape and Urban Planning*, **72**, 205–213.
- Wipfli M.S., Richardson J.S. & Naiman R.J. (2007) Ecological linkages between headwaters and downstream ecosystems: transport of organic matter, invertebrates, and wood down headwater channels. *Journal of the American Water Resources Association*, **43**, 72–85.

(Manuscript accepted 15 June 2009)