September 24, 2019

Dr. D. Peters

Editor-in-Chief

Ecosphere

Dear Dr. Peters and Editorial Board Members,

Please find our attached manuscript entitled “Riparian soil nitrogen cycling and isotopic enrichment in response to a long-term salmon carcass manipulation experiment,” which we are submitting as an Article. This work has not been published previously or concurrently submitted for publication elsewhere. It was previously submitted to Ecology (ECY18-1346) and a transfer offer to Ecosphere was made. It has been revised to address reviewer comments.

The ecological community has long been fascinated by the role of salmon in supplying nutrients to inland terrestrial and aquatic ecosystems. Using nitrogen (N) stable isotope analysis, it has been established anadromous, semelparous fish species (salmon) contribute substantial amounts of nutrients to coastal ecosystems and their importance to animal consumers is widely recognized(Cederholm et al 1999). This has led to specific management actions in the Pacific Northwest to mitigate the loss of salmon nutrients. For example, in the Columbia River Basin where Pacific salmon populations have declined, legislation requiring compensatory mitigation has led to nutrient enhancement programs, on the foundation that habitats have lost critical nutrients from salmon and therefore augmentation is necessary to in order to maintain ecosystem function (Collins et al. 2015). There is also widespread belief that salmon nutrients enhance terrestrial primary productivity through nutrient fertilization and this, in-turn, enhances salmon populations (sensu, Helfield and Naiman 2001). In fact, the scientific basis for this belief is generally weak (reviewed in this manuscript) and recent work published in Ecology shows an equivocal response of riparian tree growth to an extremely large salmon nutrient manipulation (Quinn et al 2018).

In this manuscript, we measure the response of soil N pools, N transformation rates, and N stable isotope ratios to a 20-year salmon carcass manipulation. We assess whether expectations of increased vegetative growth in response to salmon subsidies are warranted given our observations of ecosystem nitrogen cycling and consider the implications of this finding.

Key findings in our paper are:

1. Salmon carcass manipulation did not increase plant-available nitrogen pools (NH4+ and NO3-) or inorganic nitrogen transformation rates, indicating a minimal effect of salmon on soil fertility over the long-term.
2. The isotopic signature of soil ammonium is highly enriched in 15N relative to the organic N sources indicating strong fractionations with soil N cycling. This demonstrates that previous estimates of percent marine derived nutrient contribution to terrestrial producers are overestimates, and should be carefully evaluated before using these estimates to generate management targets.
3. Landscape and site variability, including stand demography and/or water availability, are likely more important drivers of vegetative growth than salmon derived nitrogen for this system, and this should be considered when assessing the benefits of marine derived nitrogen in other systems.

We believe this work is well-suited for *Ecosphere* for the following reasons:

1. This work is the first large-scale experiment to examine soil responses to a salmon manipulation in detail. Given that soils have an essential mediating role in the transfer of salmon nutrients to plants, this has been a major gap in knowledge to date.
2. The manuscript provides additional insight into ecosystem response to the salmon manipulation conducted in Quinn et al. 2018 by measuring separate but complimentary ecological responses thus providing a more complete understanding of salmon contributions to the entirety of riparian ecosystems.
3. This study has direct relevance to management as there are numerous existing and planned programs for salmon nutrient replacement that are predicate on assumptions we call into question. While we examine a single ecosystem in Alaska, we believe these results are generalizable and broadly applicable in all salmon systems (Pacific, Atlantic, and Great Lakes) as chemical processes we measure are not unique.

This manuscript has been approved for submission by all authors and is not being considered for publication elsewhere. Please address correspondence to me at: University of Washington, School of Aquatic and Fishery Sciences, Seattle, WA 98195. Email: mfeddern@uw.edu; Phone: (603) 651-6802.

Please contact me with any questions.

Sincerely,

Megan Feddern

**References**

Cederholm, C.J., M.D. Kunze, T. Murota, and A. Sibatani. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* **24**: 6-15.

Collins, S.F., A.M. Marcarelli, C.V. Baxter and M.S. Wipfli. 2015. A critical assessment of the ecological assumptions underpinning compensatory mitigation of salmon-derived nutrients. *Environmental Management* **56**: 571-586.

Helfield, J. M. and R. J. Naiman. 2002. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* **82**: 2403-2409.

Quinn, T.P., J. Helfield, C.S. Austin, R. Hovel, and A.G. Bunn. 2018. A multidecade experiment shows that fertilization by salmon carcasses enhanced tree growth in the riparian zone. *Ecology* **99**: 2433-2441.