EFFECTS OF SALMON-DERIVED NITROGEN ON RIPARIAN FOREST GROWTH AND IMPLICATIONS FOR STREAM PRODUCTIVITY: COMMENT

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Helfield and Naiman (2001) examined the role that marine-derived nitrogen (MDN) plays in the growth of trees along streams in Alaska, and found that MDN and tree growth rates were significantly higher near streams with anadromous Pacific salmon (*Oncorhynchus* spp.) than streams without salmon. They suggested a positive feedback mechanism where salmon contribute nutrients to grow larger trees, and larger trees create better habitat conditions for spawning salmon. While it is clear that salmon contribute MDN to streamside vegetation, it cannot be concluded from this study that MDN causes trees to grow faster or larger. Their paper fails to support this conclusion for three reasons: (1) they did not consider other important environmental variables that control tree growth, including soil type and drainage, (2) sample sites were selectively chosen and possibly biased, and (3) statistical tests were applied over differing sample frames, giving a strong likelihood of Type I and Type II errors.

Pacific salmon play an important role in transporting MDN into freshwater stream systems. Isotopic analyses of streamside vegetation reveal that MDN contributes up to 25% of foliar nitrogen (N), depending on the size of the salmon run, the plant species being sampled, the distance from stream, and the number and activity pattern of fish-eating mammals (Kline et al. 1990, Bilby et al. 1996, Ben-David et al. 1998, Willson 1998, Hilderbrand et al. 1999). Helfield and Naiman's study (2001) returns similar findings and is not remarkable in that regard. However, what is notable is their finding that tree growth rates are significantly increased by MDN.

Helfield and Naiman (2001) assume, a priori, that nitrogen (N) availability is the primary factor limiting tree growth in their study area. Although soils in southeast Alaska are generally deficient in nitrogen (Harris and Farr 1974), this is just one of many factors that

contribute to site productivity and influence tree growth rates. Ben-David (1998), who also studied nitrogen enrichment by salmon in the Kadashan watershed, cautioned (p. 54): "The magnitude of such effects (on productivity), and their actual importance, however, remains uncertain. Understanding the limiting nature of nutrients on productivity and the relative contribution of salmon to those nutrient pools will be essential for management and restoration of riparian systems in the Pacific Northwest."

The author's own data, comparing basal area growth with foliar $\delta^{15}N$, reflects similar ambiguity. They examined the relationship between foliar $\delta^{15}N$ and tree growth rates (Helfield and Naiman 2001: Fig. 3), and found no relationship. This result is key, because it illustrates the tenuous linkage between nitrogen enhancement and tree growth in this specific context. They speculate that the lack of relationship may be due to the fact that trees growing in areas with spawning salmon receive nutrients above some threshold level where growth is no longer nutrient limited. If so, it is difficult to make the case that salmon are instrumental in making trees grow faster. The only conclusion that can be fairly drawn from the scatter of data points in Helfield and Naiman's Fig. 3 is that for the levels of MDN measured, there is no effect on growth rate in these trees.

Further evidence of the strength of the correlation between salmon and productive forests can be discerned from maps showing the location of salmon spawning streams and forest stands with large trees. In the Kadashan drainage, for example, some stands of large trees do occur in close proximity to salmon spawning streams; but they also occur in places where salmon are absent (Fig. 1). In addition, there are many kilometers of stream that have spawning salmon, but where the adjacent forest is not productive (Fig. 1). The exceptions are telling. While MDN may contribute to the rapid growth of trees, it is clear from the exceptions that other factors exert a significant, and perhaps overwhelming, influence on tree growth.

If marine-derived nitrogen is not creating this growth response, what other factor(s) might be responsible for more rapid tree growth on one site vs. another? Most previous work in southeast Alaska has found the best tree-growing sites to be associated with well-drained soils (Stephens et al. 1969, Harris and Farr 1974, Bormann et al. 1995, Robinson 1999). Harris and Farr (1974:14) noted: "Soil drainage is important in governing species distribution and vigor. Stream sides, gentle slopes, uplifted beaches, and well-drained valley bottoms offer the best growing conditions." Floodplain forests, in particular, tend to have a high percentage of relatively large Sitka spruce (*Picea sitchensis*) (Harris and Farr 1974, Hanley and Hoel 1996). The high productivity on these sites is strongly influenced by fluvial
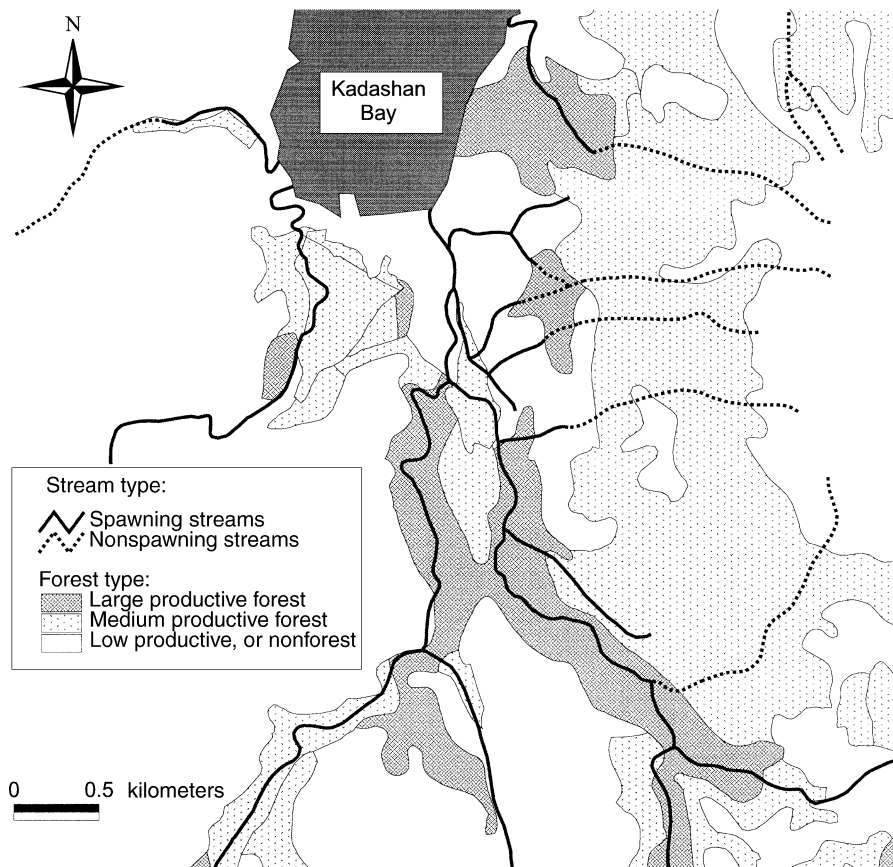
FIG. 1. The Kadashan drainage, Chichagof Island, southeast Alaska, showing forest stands of low, medium, and high productivity as well as well as spawning and nonspawning stream reaches. Data are from the USDA Forest Service, Region 10, Geographic Information System (GIS) database, Juneau, Alaska, USA.

processes, including the frequency, intensity, and extent of flooding (Harris and Farr 1974, McKee et al. 1982, Alaback and Sidle 1986, Hanley and Hoel 1996). Logically, one would expect a correlation between MDN and alluvial deposits because both originate in streams, and diminish with distance away. Given the lack of a relationship between growth rates and foliar MDN (Helfield and Naiman 2001: Fig. 3), and the imperfect spatial correspondence between the spawning status of a stream and associated forest productivity (Fig. 1), we cannot conclude rapid tree growth is primarily a function of MDN. Tree growth rates in the floodplain appear most strongly linked to patterns of alluvial deposition.

Nonrandomized sampling

Both productive and unproductive forest stands can be found along stream reaches that have spawning salmon. To avoid bias, the sites for selection must either be selected randomly, or systematically. For example, Hocking and Reimchen (2002) examined the contribution of salmon-derived nitrogen to terrestrial invertebrates by sampling systematically above and below waterfalls, which act as barriers to salmon migration. But Helfield and Naiman (2001) used no systematic criteria for selecting sites. They purport to have controlled for ecological and physical differences (Helfield and Naiman 2001, Table 1), yet the sites still differed in obvious ways. For example, the salmon spawning sites were located in spruce-dominated forest, presumably in the lower floodplain of the watershed. The nonspawning (reference) site was located adjacent to a series of ''smaller tributaries'' above the upstream extent of spawning in the watershed. The proportion of Sitka spruce and red alder (*Alnus rubra*) was 2.6 times higher on the spawning than the reference site. The selected spawning site had trees that were widely spaced and large in diameter. Alternative spawning sites with smaller trees were not selected. If differences in tree species composition and stand structure are evident when sites are selected for comparison, bias can easily intrude. Random or systematic sampling is the only way to avoid this possibility.

Type I and Type II errors

Helfield and Naiman (2001) reported no significant differences in selected physical and ecological characteristics on the spawning and reference sites they compared (Helfield and Naiman 2001: Table 1). However, this conclusion is based on statistical tests having just two degrees of freedom, which virtually assures Type II error (Eberhardt and Thomas 1991). With so few replicates, statistical power is extremely low, and the test will not be able to detect a difference when differences exist. A more informative approach would be to estimate the difference in means (i.e., effect size) between two areas for variables of interest, along with confidence intervals on the differences (Johnson 1999). For example, it is informative that Sitka spruce composition differed by 260% between types, yet the test had insufficient power to detect this difference. Additional replicates in the study would be the only way to improve the precision of these estimates.

On the other hand, when Helfield and Naiman (2001) compare tree growth rates on spawning vs. reference sites ($N = 2$, paired comparisons), their statistical test has 48 degrees of freedom (Helfield and Naiman 2001: Fig. 2). To achieve this, Helfield and Naiman (2001) must assume their subplots are independent samples, even though they are strongly correlated spatially. The higher sample size gives the test more power, and yields a finding of significant difference. Basing a statistical significance test on pseudo-replicates results in testing a hypothesis other than the one indicated (Hurlburt 1984, Eberhardt and Thomas 1991). The hypothesis tested is whether the means differ between the two sites, not whether growth is affected by the presence of salmon. The sites differ in many ways in addition to the presence of salmon and it is impossible to disentangle the many factors without true replication.

The interface between terrestrial and marine ecosystems generally, and fish and riparian vegetation specifically, is an area of rapidly expanding ecological research in Alaska and the Pacific Northwest (Ben-David et al. 1998, Willson et al. 1998, Wipfli et al. 1998, Hilderbrand et al. 1999, Hocking and Reimchen 2002). In contributing to this field of research, Helfield and Naiman (2001) raise an interesting hypothesis about the effects of salmon on tree growth. However, by a combination of errors in design and analysis, they reach conclusions that are potentially incorrect and misleading. It would be unfortunate for future work on this important area of research to be limited, or redirected, on this basis.

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EFFECTS OF SALMON-DERIVED NITROGEN ON RIPARIAN FOREST GROWTH AND IMPLICATIONS FOR STREAM PRODUCTIVITY: REPLY

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Kirchhoff's (2003) criticisms of Helfield and Naiman (2001) focus mainly on our experimental design and apparent disregard of potentially confounding variables affecting forest growth. This is a timely comment on a topic with potentially important implications for forest and fisheries management. Kirchhoff (2003) raises some valid and important concerns, but these are not sufficient grounds to reject the findings of the original study.

Kirchhoff (2003) rightly points out the need to consider factors other than nitrogen (N) limitation which may influence tree growth. Nutrient limitation is complex and likely varies temporally as well as spatially within the study area. Some soils may shift seasonally between N and phosphorus (P) limitation, and cations may be limiting at certain times of the year at sites influenced by heavy rainfall. Nonetheless, studies of N fertilization in the region (e.g., Harris and Farr 1974, 1979) suggest that the assumption of N limitation, on a broad scale, is valid. Moreover, salmon tissues also contain P and other nutrients, which are delivered to spawning streams and adjacent riparian areas through many of the same mechanisms and pathways as marine-derived N (Mathisen et al. 1988, Larkin and Slaney 1997). Salmon-borne N might therefore serve as a surrogate for other marine-derived nutrients affecting riparian productivity. Unfortunately, tracing the movement of other marine-derived nutrients is a technical challenge that remains to be overcome.

Kirchhoff (2003) cites the lack of a linear relationship between foliar $\delta^{15}N$ and tree growth rates (Helfield and Naiman 2001: Fig. 3) as evidence that marine N enhancement has no effect on tree growth. This analysis fails to recognize that, in addition to marine N inputs, foliar $\delta^{15}N$ may be influenced by several other factors. Since individual samples may be influenced by fractionation due to microbial N processing in soils or preferential uptake of ^{14}N where N is abundant (e.g., at spawning sites), we would not expect to see a direct correlation between foliar $\delta^{15}N$ and N content. Nonetheless, the data do indicate that, on average, foliar $\delta^{15}N$ and basal area growth are both increased at spawning sites relative to reference sites. This, combined with the fact that foliar N content was also increased at spawning sites relative to reference sites (Helfield and Naiman 2001: Table 2), suggests that marine N inputs do contribute to enhanced growth. If trees at spawning sites receive nutrients above some threshold level at which growth is no longer nutrient limited, it stands to reason that those nutrients have an effect on growth. If those nutrients are derived in large part from spawning salmon, it is not so difficult to make the case that salmon play a role in making trees grow faster.

Kirchhoff's map (2003: Fig. 1) actually shows a disproportionate occurrence of large trees in close proximity to salmon spawning streams. Approximately 22.5 km of spawning streams are pictured, of which 34% (7.6 km) flows through areas of large productive forest and 66% (14.9 km) flows through areas of medium or low production. In contrast, approximately 10.5 km of non-spawning streams are pictured, of which only 9% (1 km) flows through areas of large productive forest, with 91% (9.6 km) flowing through areas of medium or low production. These calculations might even underestimate the effects of salmon. Of the 14.9 km of spawning stream adjacent to areas of medium or low forest production, a substantial proportion occurs either in tidally influenced, grassy areas adjacent to Kadashan Bay, or in areas of coho (*Oncorhynchus kisutch*) spawning habitat above the upstream extent of pink (*O. gorbuscha*) and chum (*O. keta*) spawning. Since coho spawn later in the growing season and in lower densities than do pink or chum, we would expect the timing and magnitude of marine nutrient inputs to be very different in these upstream areas.

Kirchhoff (2003) raises an important point regarding soil drainage and fluvial processes. Our study (Helfield and Naiman 2001) was weakened by a lack of data describing soil characteristics at study sites. More information regarding patterns of fluvial processes and soil drainage, as well as N pools and kinetics, would help to support the assertion that observed increases in tree growth were due to marine nutrients rather than other environmental factors. The fact that a relatively

small proportion of nonspawning stream length is adjacent to productive forest (Kirchhoff 2003: Fig. 1) suggests that alluvial deposition is not the primary factor affecting growth. Nonetheless, it should be recognized that such observational data cannot account for all potentially confounding variables.

Kirchhoff's (2003) point about nonrandomized sampling is also well taken. It should be recognized, however, that a paired design with samples collected above and below waterfalls would not avoid all bias. Waterfalls typically entail abrupt changes in elevation, channel morphology and fluvial dynamics, which may entail systematic differences in soil characteristics and patterns of riparian growth and species composition (Bartz 2002). In evaluating differences in site characteristics, it may be difficult to separate cause from effect: Spawning sites were dominated by Sitka spruce (*Picea sitchensis*), while western hemlock (*Tsuga heterophylla*) was dominant at reference sites (Helfield and Naiman 2001: Table 1). Studies of forest fertilization in coastal northwest forests have demonstrated that western hemlock does not respond as strongly or as consistently to nutrient inputs as does Sitka spruce (Chappell et al. 1992, Bix 1993). Spruce might therefore enjoy a competitive advantage over hemlock at sites with consistent inputs of salmon-derived N, possibly resulting in increased spruce abundance at spawning sites. Similarly, the fact that trees at spawning sites were larger in diameter than their counterparts at reference sites could be interpreted as a consequence of enhanced growth at spawning sites rather than a bias in site selection. Despite the greater stem density at reference sites, total annual growth per unit forest area was substantially increased at spawning sites relative to reference sites (Helfield and Naiman 2001: Fig. 4).

Kirchhoff (2003) rightly points out that additional replicates would help disentangle potentially confounding variables. Unfortunately, it is difficult to control for all possible factors affecting forest growth, particularly in a mensurative study spanning relatively large spatial scales. Hurlbert (1984) and subsequent authors (e.g., Hawkins 1986, Hargrove and Pickering 1992, Heffner et al. 1996) recognize that true replication is not possible in certain situations, and that unreplicated or pseudoreplicated studies may nonetheless support ecological inferences. To dismiss all unreplicated or pseudoreplicated studies as scientifically invalid would impede progress in landscape ecology (Hargrove and Pickering 1992). A balance must therefore be struck between Type I and Type II error.

If the hypothesis being tested is whether the means differ between sites (Helfield and Naiman 2001: Fig. 2), the data demonstrate that the mean basal area increment of Sitka spruce is significantly increased at sites with spawning salmon relative to sites without salmon. Kirchhoff's map (2003: Fig. 1) confirms that trees in areas adjacent to spawning streams have disproportionately enhanced growth rates. The fact that foliar N content and $\delta^{15}N$ values were similarly increased at spawning sites (Helfield and Naiman 2001: Table 2, Fig. 1) suggests that marine-derived nutrients contribute to these observed differences in growth. Kirchhoff (2003) presents some important caveats, but provides no evidence that these results are in fact driven by any other mechanism or bias. The weight of evidence supports the inference that salmon-derived N enhances riparian growth. The fact that subsequent studies have also reported connections between salmon-derived nutrients and riparian productivity (e.g., Drake et al. 2002, Reimchen et al., *in press*) adds further weight to this inference.

No one would claim that salmon are the sole factor affecting the productivity of riparian forests. Multiple factors affect forest growth, and their relative importance varies temporally and spatially within any given system. We identified salmon-derived nutrients as one such factor in coastal temperate ecosystems (Helfield and Naiman 2001). Although these findings are largely inferential, they provide a basis for the development of testable hypotheses and more targeted investigations to assert causality and identify the specific mechanisms at work. Kirchhoff (2003) raises some valid criticisms which can only help to guide further research in this area, but these should not be interpreted as grounds for dismissal of the evidence at hand.

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