Quantifying Salmon-Derived Nutrient Loads from the Mortality of Hatchery-Origin Juvenile Chinook Salmon in the Snake River Basin

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NOTE

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Abstract

Hatchery supplementation of anadromous salmon is extensive across the Pacific Northwest region with millions of juvenile salmon stocked annually. The influence of hatchery-origin fish as prey items in recipient ecosystems has been explored, but influences of these fish on broader stream nutrient dynamics has not been well-studied. Salmon-derived nutrients (SDN) associated with the mortality of adult anadromous salmon provide key subsidies to freshwater habitats. While a number of studies have estimated current and historic SDN loading from returning wild salmon, SDN contributions from the mortality of hatchery-origin juveniles (many of which die in the stream prior to emigration) remains largely unknown. We conducted a mass balance analysis of SDN input and export via hatchery activities (stocking and broodstock collection) in the Snake River watershed. Using Chinook salmon *Oncorhynchus tshawytscha* as a model species, we accounted for yearly SDN input (via hatchery-origin juvenile fish mortality) and export (via broodstock collections and presmolt growth) over 6 years (2002–2007) in the portion of the Snake River upstream from Lower Granite Dam accessible to anadromous fish. In the year with highest smolt mortality (2003), hatchery-origin smolt mortality provided a net input of SDN equivalent to approximately 8,100 returning adults. In the year with lowest smolt mortality (2004), hatchery activities collectively yielded a net loss of nutrients. Although the mass of SDN from hatchery-origin smolts may be presented in adult equivalencies, functional influences of SDN from hatchery smolt mortality are likely to differ. Salmon-derived nutrients from hatcheries enter food webs through largely piscivorous pathways whereas SDN from adult carcasses enter food webs through multiple pathways at multiple trophic levels. The SDN from hatchery-origin smolts probably influence different components of the food web more than do adult carcasses and have the potential to more directly affect predator populations.

Nutrient availability can influence fundamental characteristics and functions of an ecosystem. In many stream environments, anadromous salmonids accumulate up to 90% of their adult body weight in the ocean and return to spawn and die in their natal streams where they can add a substantial amount of nutrients to otherwise nutrient-poor headwaters. The subsidies that these salmon-derived nutrients (SDN) provide to recipient streams can increase growth and biomass of periphyton, invertebrates, resident fish, juvenile anadromous fish, and riparian vegetation (Cederholm et al. 1999; Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Given its potential to boost stream productivity, a number of studies have worked to quantify SDN input from returning adult salmon and to determine how declines in salmon stocks are likely to influence associated stream ecosystems (Lyle and Elliott 1998; Jonsson and Jonsson 2003; Nislow et al. 2004; Scheuerell et al. 2005; Verspoor et al. 2010). In the U.S. Pacific Northwest, nutrient flux estimates have focused almost exclusively on wild salmon populations (Cederholm et al. 1999; Scheuerell et al. 2005; Moore et al. 2007), leaving the effects of SDN contributions from hatcheries largely unexplored.

An analysis of SDN budgets that includes hatchery activities must consider a number of additional pathways above and beyond those included in an analysis of wild fish alone (Figure 1). For example, in managed systems, returning adult fish are collected for broodstocks to produce juvenile fish that are out-planted 1 to 2 years later. These broodstock collections represent a loss of SDN from streams, but mortality of the out-planted juveniles prior to their migration to the ocean represents a novel input of SDN to the streams in which fish are stocked. These management-associated inputs and losses of SDN in streams have not been quantified in Pacific Northwest ecosystems. The relationship between inputs via hatchery fish mortality and export via broodstock collections establish the
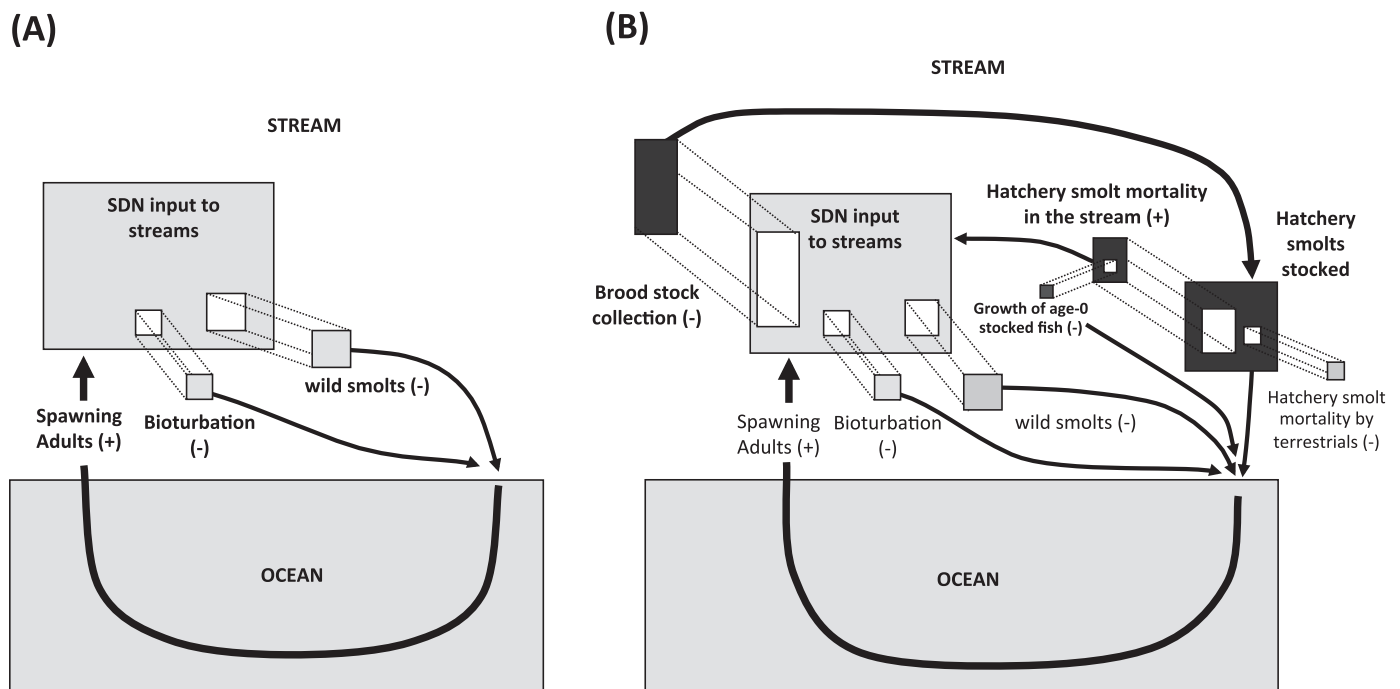
(A)

(B)

FIGURE 1. Conceptual model for transport of salmon-derived nutrients (SDN) in (**A**) natural and (**B**) managed stream systems. The aspects of this process addressed in the current mass balance analysis are represented by the darkly shaded boxes. Transport of SDN in the managed system assumes that age-1 hatchery smolts emigrate shortly after stocking and that only age-0 fish have time to add biomass within the system prior to emigration.

potential for a net loss or a net gain of SDN as a result of hatchery activities. In this study we focus on quantifying nutrient fluxes of nitrogen (N) and phosphorus (P) associated with broodstock collections and hatchery smolt mortality from a mass balance perspective. We do not address the food web effects of stocking, which have been well reviewed in earlier papers (Eby et al. 2006; Kostow 2009; Gozlan et al. 2010; Ellis et al. 2011).

Stocking has become a common fisheries management tool to enhance the recovery of endangered species and to create fishable populations in small streams, large rivers, and lakes. Nutrient input from stocking is generally assumed to be negligible; however, studies that have tested this assumption by quantifying and evaluating these inputs are rare (Nislow et al. 2004). In the present study, we evaluate potential nutrient input or loss associated with stocking in the Snake River basin, a system with high stocking effort and hatchery-origin smolt mortality rates that regularly exceed 40%.

METHODS

We evaluated SDN loading and loss associated with removal and stocking of Chinook salmon *Oncorhynchus tshawytscha* in the portions of the Snake River upstream of Lower Granite Dam that are accessible to anadromous fish, which encompass parts of Idaho, Oregon, and Washington. This tributary to the Columbia River contains numerous anadromous fish populations, many of which are supplemented by hatcheries. The main stem of the Snake River and many of its larger tributaries are a highly

modified and extensively managed. We focus on Chinook salmon in this study because (1) they are an economically and ecologically important species that historically dominated much of the Snake River watershed but have experienced steady and significant population declines over the last century (Petrosky et al. 2001), and (2) the majority of salmon stocking in the portion of the Snake River accessible to anadromous fish is conducted with juvenile Chinook salmon (although there are considerable stocking efforts for other anadromous salmonids in the basin as well). Within the Snake River basin, Chinook salmon are separated into two Evolutionarily Significant Units (ESUs; distinct population segments of Chinook salmon that are treated separately under the U.S. Endangered Species Act). These two ESUs—the Snake River Spring–Summer (SRSS) Chinook salmon ESU (a stream-type lineage) and the Snake River Fall (SRF) Chinook salmon ESU(an ocean-type lineage)—are both listed as threatened under the Endangered Species Act, and are subject to separate but extensive hatchery supplementation. Many of the stocks currently used for these efforts are derived from and belong to the ESUs. Because we focus our annual estimate of SDN from hatchery activities on basin-wide potential for SDN loading, we do not distinguish between spring–summer versus fall Chinook salmon ESUs in the overall mass balance analysis. In our site-specific analysis of SDN input, we focused only on stocking of the spring–summer ESU. The majority of juvenile Chinook salmon stocked in the Snake River are from the spring–summer ESU, and stocking events for these fish tend to be the largest biomass additions.

We used data on juvenile fish passage collected at the uppermost passable dam on the Snake River, Lower Granite Dam (LGD), located at river kilometer 172 (river mile 107) of the Snake River in Garfield, Washington. Chinook salmon that spawn in the Snake River upstream from LGD pass a total of eight large hydroelectric dams, four on the main stem of the Columbia River and four on the lower main stem of the Snake River. These dams and associated passage facilities create passage bottlenecks, but they are also ideal points for counting fish (Scheuerell et al. 2005). A subset of the emigrating smolts that pass through each system are counted daily and this value is used to estimate total passage through each dam facility. There are 10 hatcheries and 31 stocking sites upstream of LGD; in recent years between 12.4 million and 15.5 million juvenile Chinook salmon have been out-planted annually. The majority of juveniles (74% to 87% by number and 91% to 97% by mass) are stocked as age-1 smolts.

Mass balance calculations.—We calculated the net annual flux of SDN to the Snake River associated with stocking juvenile salmon upstream of LGD using a mass balance approach. The annual hatchery-activity SDN flux was estimated from stocking mortality (input), broodstock collection (output), and the growth of age-0 hatchery fish (output) in each of six consecutive years (2002–2007) (Figure 1). We focused here on direct input and output processes associated with out-planting and broodstock collection in the reaches upstream of LGD (dark gray boxes in Figure 1b). We therefore did not include input via returning adults of hatchery origin in this analysis. Estimates of downstream passage of hatchery-origin smolts at LGD, stocking locations upstream of LGD, stocking levels at each stocking site, the mean mass of hatchery smolts each year, and smolt mortality were obtained from The Fish Passage Center (FPC) website (www.fpc.org/) (FPC 2007) or were calculated from data provided by the FPC. A complete census of hatchery broodstock collections that includes all sites in all years is not available for Snake River hatcheries upstream of LGD. Therefore, in order to estimate broodstock collection numbers, we used the number of hatchery smolts that were out-planted in a given year and back-calculated the number of adults that would be needed to produce this number of hatchery fish from collections 2 years prior. For this estimate we assumed that, on average, each mating pair produced approximately 3,200 smolts for release in the Snake River (one adult per 1,600 stocked smolts at the target 1:1 sex ratio used by most hatcheries) (Idaho Department of Fish and Game et al. 2008). The estimated mass of an individual adult Chinook salmon collected for broodstocks was taken from Scheuerell et al. (2005) for full-sized adults (5.5 kg). The proportion of adult and juvenile Chinook salmon that is P (adult, 0.0038; juvenile, 0.0043) and N (0.03 for adult and juvenile) were taken from Scheuerell et al. (2005), Moore et al. (2004), and Thomas et al. (2003).

We assumed relatively rapid emigration and therefore no significant biomass accumulation before passing LGD for fish stocked at age 1 (primarily SRSS smolts) within the Snake River system (Scheuerell et al. 2005). We did, however, account for growth of age-0 fish stocked upstream from LGD. The total mass of SDN lost from the system owing to growth and subsequent emigration of these hatchery-origin age-0 Chinook salmon from the SRF Chinook salmon ESU was calculated by multiplying mean accrued mass per fish in that year by the number of hatchery-origin age-0 individuals that passed LGD in the fall and the fraction of total juvenile Chinook biomass that is either N or P. We used age-0 summer survival estimates from FPC reports and initial stocking densities to estimate the number of age-0 hatchery-origin fish that migrated in the fall. We assumed a 41% increase in smolt biomass between stocking and out-migration based on data from Connor et al. (2008). Chinook salmon eggs are rarely out-planted so we did not include hatchery-origin eggs in this mass balance study as was done in Nislow et al. (2004).

We identified two primary areas of uncertainty in this analysis associated with (1) collection efforts in hatchery broodstock traps and (2) the fate of excess and spawned out salmon carcasses from hatcheries. Some hatcheries collect additional fish at their traps above and beyond broodstock requirements in order to reduce interaction between wild and hatchery-origin adult fish. The number of fish collected in excess of broodstock needs is inconsistently reported. This represents an unaccounted-for removal of SDN from streams in our analysis. However, as the value of nutrient subsidies from salmon has been increasingly promoted, a growing number of hatcheries are making carcasses (both excess fish and "spawned-out individuals") available for nutrient addition back into the stream if they are pathogen free (Idaho Department of Fish and Game et al. 2008). Unfortunately, the number of carcasses returned to the stream is also unavailable in aggregate and inconsistently reported in individual reports. This represents an unaccounted-for addition back to the stream in these systems. In the absence of useable data for either excess adult removal or carcass additions back to the stream, we assume that these processes balanced out in our analysis with broodstock carcasses returned to the stream, thereby compensating for excess adult collection at broodstock traps.

Nutrients may also be lost from the system at stocking sites via bioturbation of sediments in the presence of a high density of fish (Moore et al. 2004, 2007; Holtgrieve and Schindler 2011). Juvenile fish do not engage in redd construction so their influence via bioturbation is likely to be lower than is it for adult fish; however, when stocked at high densities, bioturbation effects are clearly possible. For the purpose of this analysis, we did not consider export via bioturbation as its influence is highly dependent upon stream size, stream substrate conditions, and fish densities.

Because broodstock collections and the stocking of hatchery smolts occur at different times of year, an annual mass balance may not reflect realized nutrient inputs to the system via stocking. In addition, stocking itself is conducted across a range of stream sizes with varying degrees of potential dilution of

nutrients from hatchery-origin smolts. We therefore conducted an additional analysis that focused specifically on SDN input via stocking mortality across the 31 sites where spring–summer Chinook salmon smolts are stocked in spring. The majority of spring–summer Chinook salmon stocking effort in the Snake River occurs in the spring. For a representative year (2006), we estimated potential increases in stream nutrient concentrations for the duration of stocking, assuming 10% mortality at the input site over the duration of the stocking effort (equation 1).

$$\Delta[\text{nutrient}] = \frac{N_s \cdot m_s \cdot M_s \cdot P_s}{Q \cdot 86,000 \cdot d} \quad (1)$$

Where $\Delta[\text{nutrient}]$ represents the potential change in nutrient concentration due to hatchery-origin smolt mortality at a stocking site; N_s indicates the total number of smolts stocked at a given location; m_s indicates the mean mass of fish stocked; M_s indicates the hatchery smolt mortality rate (as a proportion) at the stocking site—we used a value of 0.1 in Figure 3; P_s indicates the proportion of stocked fish mass represented by the nutrient of interest (e.g., nitrogen or phosphorous at 0.03 and 0.0043, respectively); Q indicates discharge in cubic meters per second during stocking; 86,400 accounts for the number of seconds in a day and d indicates the number of days over which stocking occurred. Although total mortality estimates for Chinook salmon smolts between stocking and LGD was about 40% in 2006, we used a local mortality rate of 10% for this analysis because most hatchery smolt mortality in these systems occurs downstream from the initial stocking location (Muir et al. 2001; Smith et al. 2003). Stocking efforts lasted anywhere from 1 to 39 d, but most were quite short, with a median stocking duration of 2.5 d. We also estimated potential maximum nutrient concentration increases due to stocking separately for each of the 31 stocking sites using total nutrient input estimates (mass of nutrients), mean discharge at those sites during the month that stocking occurred, and the number of days over which stocking occurred (total volume of water). This calculation assumes all nutrients from dead fish become available in a biologically reactive inorganic form. This assumption provides an upper limit on potential nutrient availability associated with hatchery-origin SDN.

RESULTS AND DISCUSSION

Broodstock collections and the out-planting of juvenile Chinook salmon collectively yielded a net input of nutrients to the portion of the Snake River upstream of LGD accessible to anadromous fish in 5 of the 6 years studied (Figure 2). Year-to-year variability in juvenile survival was the primary influence on whether these hatchery activities were a net source or a net sink for nutrients. In the 1 year that stocking activities did not yield a net nutrient input (2004), smolt survival was high owing to relatively high stream and main-stem flows (FPC 2007). The mass of nutrients removed via broodstock collections and in-stream

growth of age-0 fish together were thus greater than inputs associated with smolt mortality. Nutrient inputs during years with low smolt survival appear substantial on an annual basis, and P inputs can be equivalent to as many as 8,100 returning adults in a year. According to FPC estimates, between 38,000 and 110,000 returning adult Chinook salmon (wild and hatchery-origin combined) passed LGD annually from 2002 to 2007. On an annual basis, the maximum SDN loads from juvenile hatchery Chinook salmon could therefore represent a substantial increase in SDN upstream of LGD (increases of 7% to 21% above P loads provided by all adults in years with a net input of hatchery-origin SDN).

It is important to note, however, that while the mass of hatchery-origin SDN may be relatively large, the ecological effects of SDN input from hatchery smolts are unlikely to match SDN input from adult mortality on a 1:1 basis. Many of the key pathways for nutrient assimilation into the stream ecosystem differ between SDN from hatchery-origin juvenile Chinook salmon and SDN from returning adult Chinook salmon that spawn and die in the stream (including adults of hatchery origin or wild origin). Juvenile fish are often eaten whole by individual predators at or near the top trophic position in the stream (Muir et al. 2001; Kostow 2009; Monzyk et al. 2009). In contrast, adult carcasses generally support organisms at a broad range of trophic positions (Chaloner et al. 2002; Wipfli et al. 2010). In addition, most stocking occurs at a different time of year than spawning does, and the type of streams into which fish are stocked differ from those in which wild adult fish spawn.

Salmon carcasses can increase secondary production in streams both directly via consumption of the carcass itself (Bilby et al. 1998; Chaloner and Wipfli 2002; Claeson et al. 2006) and indirectly via release of biologically reactive inorganic nutrients, which promote primary production and subsequent increases in grazer biomass (Wipfli et al. 1998; Johnston et al. 2004; Cak et al. 2008). Inorganic nutrients released as carcasses decay support primary production. The carcass itself can also support stream macroinvertebrates and other detritvores that feed on the flesh (Bilby et al. 1998; Chaloner and Wipfli 2002; Janetski et al. 2009). If smolts and fry do die and leave carcasses in the stream, the carbon and nutrient subsidies from these fish are likely to enter the stream ecosystem in a manner similar to that of retained adult carcasses. However, given the smaller size of juvenile carcasses relative to adult carcasses, dead smolts and dead fry persist for a much shorter period of time in the stream leading to a shorter period of influence on the stream food web (Elliott 1997).

More importantly, while some juvenile hatchery-origin fish die shortly after stocking and do indeed occur as carcasses in the stream, most of the mortality for stocked smolts occurs as a result of predation with direct consumption of an entire fish and no remaining carcass (Muir et al. 2001; Monzyk et al. 2009), a fundamentally different route than that of nutrients from adult carcasses. This substantial input from hatchery smolts for piscivorous predators can have cascading effects on the stream
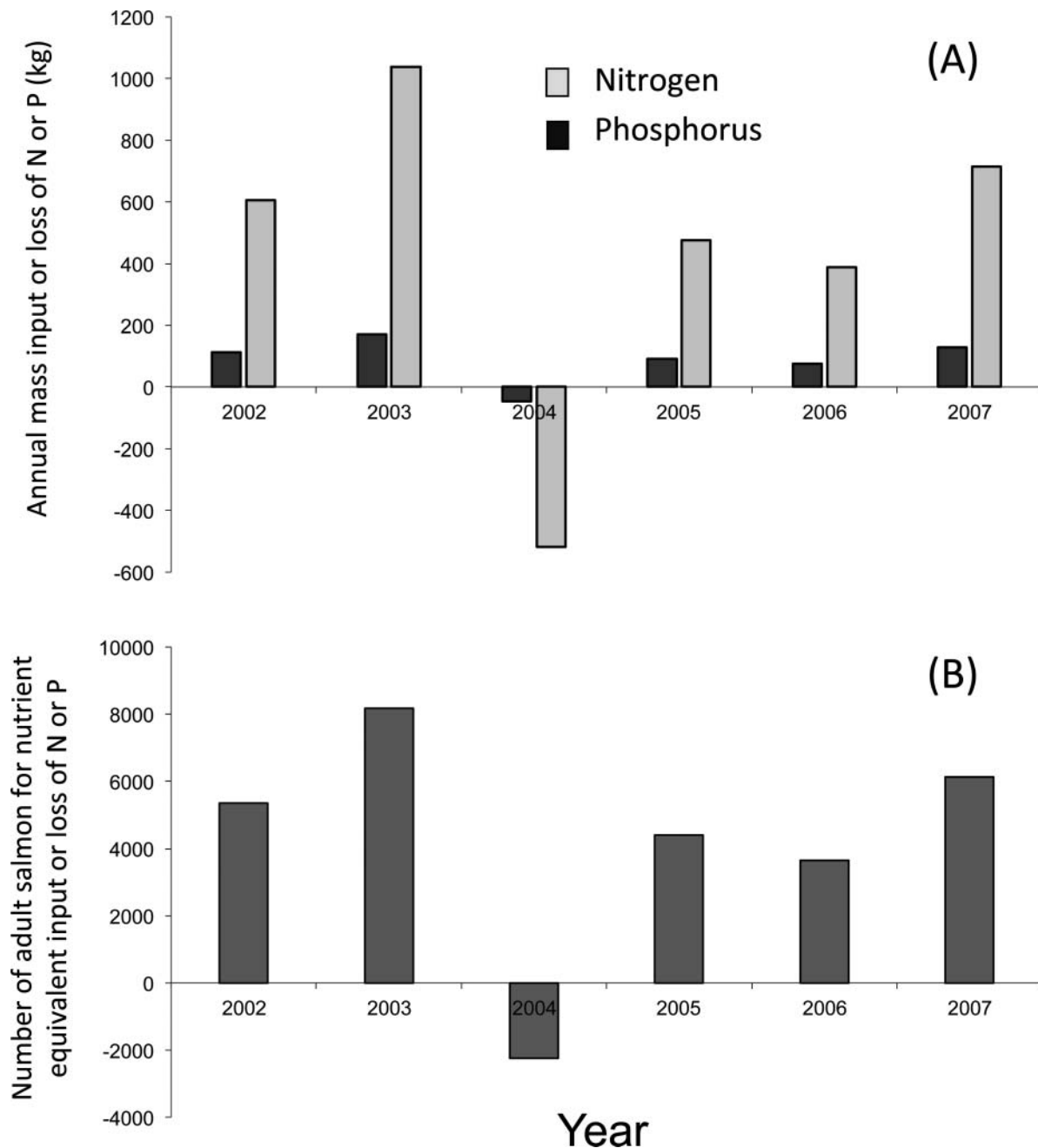
FIGURE 2. Panel A indicates the annual input and output of nitrogen (N) and phosphorus (P) via mortality of Chinook salmon smolts stocked upstream from Lower Granite Dam and panel B indicates the equivalent number of adult salmon for each year's addition and loss of nutrients (assuming adults are 0.38% P and have a mean mass of 5.5 kg, per Scheuerell et al. 2005).

food web (Kostow 2009). This includes bottom-up support of increased predator populations, which increases predation risk for native smolts (Eby et al. 2006; Kostow 2009; Gozlan et al. 2010; Ellis et al. 2011). Predation upon hatchery-origin juvenile Chinook salmon also has the potential to indirectly affect nutrient dynamics via predator excretion. Not all of the nutrients from a given prey item are assimilated. Some of the nutrients are excreted as highly available forms of inorganic nutrients,

which can then promote primary production (Vanni 2002). The consumption of a larger number of hatchery-origin juveniles therefore has the potential to lead to elevated rates of inorganic nutrient availability. These excreted nutrients are likely to be released in low amounts though, and they are likely to be accessed and incorporated into the ecosystem in different times and places than are adult carcasses, which function as small localized point sources for inorganic nutrients.
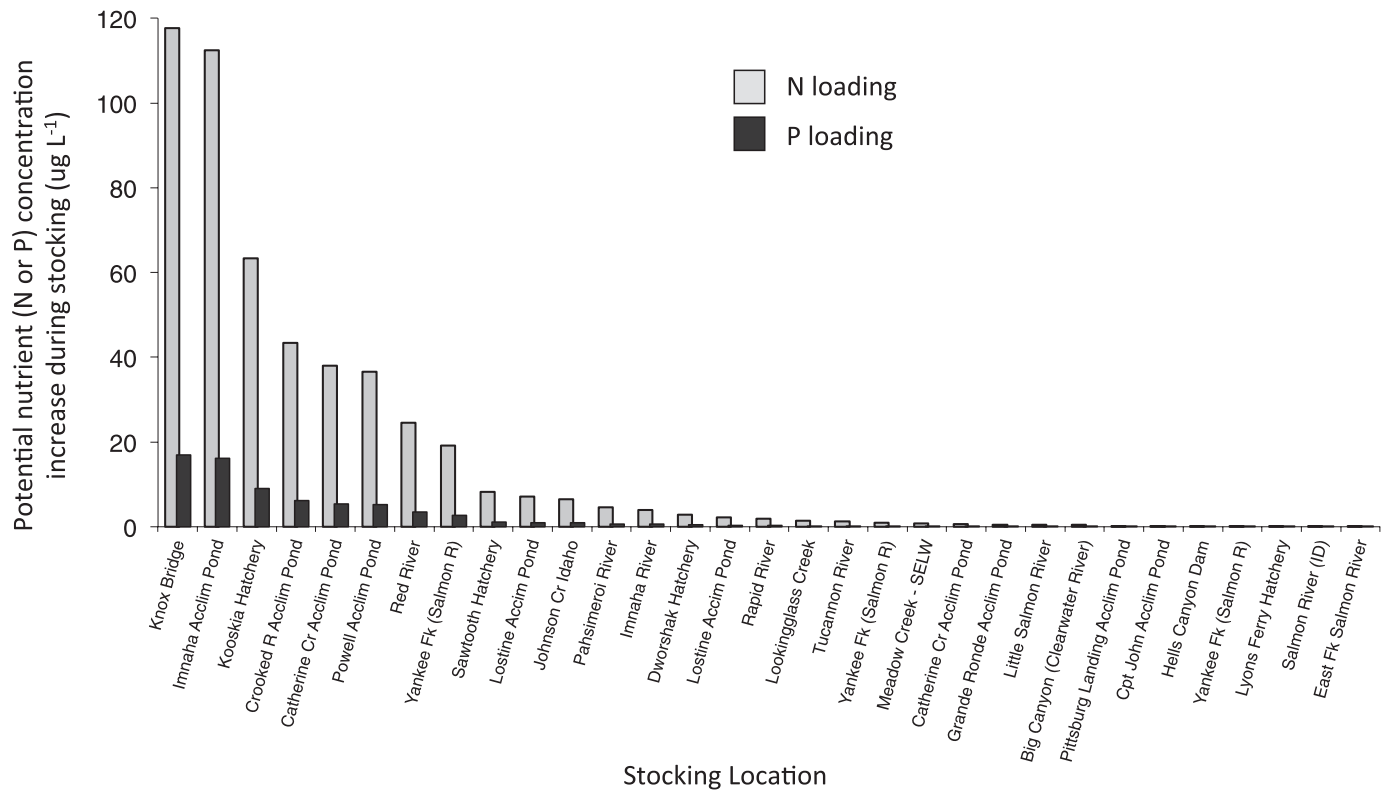
FIGURE 3.   Potential increases in stream nutrient concentration at each of 31 stocking sites in the portion of the Snake River accessible to anadromous fish upstream of Lower Granite Dam assuming 10% mortality of spring–summer hatchery-origin Chinook salmon smolts at each stocking site. Estimates of potential elevated nitrogen (N) concentrations are illustrated by the lightly shaded bars and estimates of potential elevated phosphorus (P) concentrations are illustrated by the solid bars.

Most juvenile Chinook salmon stocking occurs in mid to late spring, particularly for hatchery fish in the spring–summer ESU. This is also a time period when primary production in forested streams is generally highest—stream temperatures are increasing but leaf-out has not yet occurred (Roberts et al. 2007). Our analysis of site-by-site nutrient concentration changes represents maximum potential increases in nutrient availability at a time when elevated nutrients have the greatest potential to make a difference; however, these potential increases in concentration assume that all nutrients from dead hatchery fish are immediately available. We found a wide range in the potential increase in stream nutrient concentrations during the stocking period from a high of 117.7 µg/L of N and 16.9 µg/L of P to a low of less than 0.001 µg/L of N and less than 0.0001 µg/L of P (mean P and N of 2.3 and 16.1 µg/L, respectively, and median of 1.9 and 0.27 µg/L, respectively; Figure 3). For the majority of sites, nutrient inputs in spring 2006 led to potential inputs of less than 10 µg/L of N and 2 µg/L of P. In an assessment of periphyton biomass and chlorophyll *a* in salmon streams of the Fraser River system, British Columbia, Verspoor et al. (2010) found that net primary production was significantly and positively related to prespawning soluble reactive phosphorous concentrations that ranged from less than 1 µg/L

to greater than 3 µg/L. Although streams in the Snake River ecosystem differ from those in the Fraser River, this result suggests that elevating stream P concentrations by ≥ 2 µg/L could affect in-stream primary production under the right conditions. The duration of any increase may be limited though. Estimates of potential maximum increases in nutrient concentration are calculated only over the stocking period and concentrations will probably return to prestocking levels relatively soon after stocking ends. In the absence of measurements of stream primary production, we cannot address this effect directly in the current study. Whether SDN from hatchery-origin fish influences primary production or any other aspect of the stream ecosystem over short or long time periods will depend upon the abundance of live fish, the number and persistence of carcasses, and ultimately, the chemical and physical conditions in the recipient stream (Ambrose et al. 2004; Mitchell and Lamberti 2005; Chaloner et al. 2007).

The age-0 fish stocked in this system are from the SRF Chinook salmon ESU, and typically out-migrate as subyearlings after a period of growth in the stream. This subset of stocking activity yielded a net loss of nutrients in all 6 years evaluated. Because the fish are stocked at a smaller size, the nutrient input associated with their mortality is much lower than it

is for age-1 individuals. In addition, the within-system growth and subsequent migration of age-0 fish from streams contributed substantially to annual nutrient losses associated with stocking activities for this ESU. In age-0 fish, which gain substantial biomass in the stream before they emigrate, the P and N that they accumulated is removed from the system rather than recycled within the system as would occur with a resident fish. This supports work by Nislow et al. (2004) suggesting that the age and stage of development at which stocking occurs can strongly influence the SDN nutrient budget. The mortality rates evaluated in this study do not account for terrestrial predation. Avian and other land-based predators remove fish and their nutrients from the system and therefore from the input portion of the basic mass balance analysis used here (Collis et al. 2001). We do not have a measure of terrestrial predator mortality at these sites so the SDN input associated with the simple smolt mortality is probably an overestimate in the current analysis.

While SDN from wild adult salmon has been well studied, SDN from hatchery-origin smolts has not. Overall, we demonstrated in this study that the impact of SDN from stocking juvenile Chinook salmon varied with age and stage of released fish, year-specific smolt survival rates, and local conditions. In most years hatchery activities lead to a net input of nutrients and the variability in SDN fluxes is driven primarily by the survival of hatchery-origin spring–summer smolts. When smolt survival was low there was a net influx of SDN to streams as a result of hatchery activities. When smolt survival was high, SDN removal via broodstock collections and in-stream growth of fall Chinook salmon juveniles exceeded total SDN inputs via in-stream mortality of hatchery-origin juveniles. This resulted in a net loss of SDN from the system via hatchery activities. In addition, the total mass and duration of a stocking event relative to stream discharge strongly influences maximum potential nutrient increases, and few sites will experience potential concentration increases larger than 10 µg/L of N and 2 µg/L of P for the duration of stocking.

There is indication that differences in nutrient flux due to stocking activities vary between the two ESUs examined, in association with their life history. Snake River Fall Chinook salmon—ocean-type fish that begin out-migration earlier in their life cycle—experience substantial growth as they move downstream. In addition, these smaller juveniles provide fewer nutrients when they die. As a result, the full range of stocking activities, including mortality of hatchery juveniles, nutrient loss associated with in-stream growth of hatchery-origin juveniles, and broodstock collection associated with this ESU alone consistently yielded a net loss of SDN.

In addition to input or export values, the pathway by which hatchery-origin SDN enters the stream food web is a key consideration in this or any mass balance analysis. The influence of hatchery-origin SDN on the broader stream ecosystem is dependent upon a number of local factors including the nature of hatchery smolt mortality at a stocking site, predator population size and density, food web dynamics, fish activ-

ity, stream geomorphology, background nutrient concentrations, and riparian and upland land use (Ambrose et al. 2004; Janetski et al. 2009; Harvey and Wilzbach 2010; Verspoor et al. 2010; Holtgrieve and Schindler 2011). A whole ecosystem approach will be needed as we move beyond this initial mass balance analysis to a broad assessment of the fate and influence of SDN from hatchery-origin fish.

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