

Salmon-mediated nutrient flux in selected streams of the Columbia River basin, USA

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Abstract: Salmon provide an important resource subsidy and linkage between marine and land-based ecosystems. This flow of energy and nutrients is not unidirectional (i.e., upstream only); in addition to passive nutrient export via stream flow, juvenile emigrants actively export nutrients from freshwater environments. In some cases, nutrient export can exceed import. We evaluated nutrient fluxes in streams across central Idaho, USA, using Chinook salmon (*Oncorhynchus tshawytscha*) adult escapement and juvenile production data from 1998 to 2008. We found in the majority of stream-years evaluated, adults imported more nutrients than progeny exported; however, in 3% of the years, juveniles exported more nutrients than their parents imported. On average, juvenile emigrants exported $22\% \pm 3\%$ of the nitrogen and $30\% \pm 4\%$ of the phosphorus their parents imported. This relationship was density-dependent and nonlinear; during periods of low adult abundance, juveniles were larger and exported up to 194% and 268% of parental nitrogen and phosphorus inputs, respectively. We highlight minimum escapement thresholds that appear to (i) maintain consistently positive net nutrient flux and (ii) reduce the average proportional rate of export across study streams. Our results suggest a state shift occurs when adult spawner abundance falls below a threshold to a point where the probability of juvenile nutrient exports exceeding adult imports becomes increasingly likely.

Résumé : Les saumons assurent un transfert des ressources et un lien importants entre les écosystèmes marins et terrestres. Ce flux d'énergie et de nutriments n'est pas unidirectionnel (c.-à-d. uniquement vers l'amont); en plus de l'exportation passive de nutriments assurée par l'écoulement de l'eau, les émigrants juvéniles exportent activement des nutriments hors des milieux d'eau douce. Dans certains cas, l'exportation de nutriments peut surpasser leur importation. Nous avons évalué les flux de nutriments dans des cours d'eau du centre de l'Idaho (États-Unis) à partir de données sur l'échappement d'adultes et la production de juvéniles de saumon quinnat (*Oncorhynchus tshawytscha*) recueillies de 1998 à 2008. Nous avons constaté, pour la majorité des années-cours d'eau évaluées, que les adultes importaient plus de nutriments que leur descendance en exportait. Cela dit, pour 3 % des années, les juvéniles exportaient plus de nutriments que leurs parents en importaient. En moyenne, les émigrants juvéniles exportaient l'équivalent de $22\% \pm 3\%$ de l'azote et $30\% \pm 4\%$ du phosphore importés par leurs parents. Cette relation dépendait de la densité et était non linéaire; durant les périodes de faible abondance d'adultes, les juvéniles étaient plus grands et exportaient jusqu'à 194 % et 268 % des apports parentaux d'azote et de phosphore, respectivement. Nous mettons en lumière des seuils d'échappement minimums qui semblent (i) maintenir un flux net de nutriments uniformément positif et (ii) réduire le taux d'exportation proportionnel moyen dans les cours d'eau étudiés. Nos résultats suggèrent qu'un changement d'état se produit quand l'abondance des géniteurs adultes tombe sous un seuil au-delà duquel la probabilité que les exportations de nutriments par les juvéniles dépassent les importations par les adultes est de plus en plus grande. [Traduit par la Rédaction]

Introduction

Migratory salmonids are important vectors of energy (carbon (C)) and nutrients (nitrogen (N), phosphorus (P), potassium (K), and calcium (Ca)) between marine and freshwater ecosystems (Lyle and Elliot 1998; Cederholm et al. 1999; Gende et al. 2004). For example, salmon drive nutrient fluxes across habitat boundaries and influence community and food web structure in both aquatic and terrestrial ecosystems (Willson et al. 1998; Gende et al. 2002; Moore et al. 2007; Wipfli and Baxter 2010). Spawning salmon contribute an estimated 5%–95% of the N and P loading in salmon-bearing catchments (Gresh et al. 2000), and even small input of C and nutrients from salmon may be important to the maintenance of trophic productivity in recipient habitats (Larkin and Slaney 1997). This seasonal resource subsidy affects food web productiv-

ity and influences a diverse array of flora and fauna in ecosystems across the North Pacific (Polis et al. 1997; Naiman et al. 2002).

The Columbia River basin in western North America was historically one of the world's largest producers of wild anadromous salmonids, with large amounts (e.g., an estimated 2.3 to 3.1 million kg of N and 0.3 to 0.4 million kg of P) of marine-derived nutrients (MDN) annually delivered by Pacific salmon (*Oncorhynchus* spp.) to inland landscapes; however, contemporary populations have declined following periods of intense commercial harvest, hydrosystem development, hatchery production, habitat loss, and food web alterations (Gresh et al. 2000; Naiman et al. 2012). It is now estimated that only 6%–7% of historical MDN are currently delivered to the Pacific Northwest by anadromous fishes (Gresh et al. 2000). The departure from historical conditions (i.e., salmon populations reduced >90%) represents a cultural, economic, aesthetic, and eco-

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logical loss (Gresh et al. 2000; Naiman et al. 2002). In the Snake River basin, where further declines in salmon and steelhead populations coincided with the development and operation of the Federal Columbia River Power System, numerous Endangered Species Act listings have mobilized human efforts to address the multitude of factors limiting recovery (Petrosky and Schaller 2010). A lack of MDN in headwater aquatic ecosystems of the Snake River basin was identified as a potential mechanism that lowers stream-rearing carrying capacities for juvenile salmonids, even at population sizes far below historical levels (Achord et al. 2003). The recovery of these at-risk stocks may depend upon rebuilding MDN levels to support adequate ecosystem function and salmon population productivity (Adkison 2010).

The role of allochthonous organic matter and MDN in aquatic and terrestrial systems has been the focus of extensive scientific investigation and represents a complex interaction among biomass and nutrient processes, biotic and abiotic interactions, trophic pathways, and food web dynamics (Rex and Petticrew 2008; Mulholland and Webster 2010; Tank et al. 2010). In a conceptual model of energy and nutrient flow to stream fishes, Wipfli and Baxter (2010) highlight multiple pathways and effects — autochthonous production of benthic invertebrates, tributary subsidies, terrestrial subsidies, and allochthonous marine subsidies — all playing vital roles in driving productivity and trophic processes in fish-bearing food webs. Each component is proposed to be relative, integrated, and influenced by factors such as timing, the spatial and ecological context of habitat within riverine networks, as well as the nutritional quality and quantity of respective food resource components. Salmon are a high-quality, seasonal food and a nutrient resource important in aquatic and terrestrial food webs, and a lack of marine subsidies in the Snake River basin could have major consequences for the productivity of recipient ecosystems across the landscape (Wipfli and Baxter 2010).

In central Idaho, many stream autotrophic communities are nutrient-limited (Thomas et al. 2003; Sanderson et al. 2009), and their productivity may be enhanced by the upstream flux of MDN in the form of anadromous fishes. These inherently oligotrophic streams receive nutrient inputs from a variety of biotic (i.e., anadromous fishes, riparian vegetation, and instream biological N fixation) and abiotic (i.e., atmospheric, geologic, and groundwater) sources (Triska et al. 1984). Considering historical declines of salmon and steelhead across the landscape (Gresh et al. 2000), the importance of MDN delivered by anadromous fishes to streams in this region has received considerable attention. For example, naturally spawning Chinook salmon (*Oncorhynchus tshawytscha*) represent a seasonal resource subsidy and linkage between marine and land-based ecosystems (Gende et al. 2002; Naiman et al. 2002; Wipfli and Baxter 2010); however, this flow of energy and nutrients is not unidirectional (i.e., upstream only). In addition to passive nutrient export via stream flow, juvenile emigrants actively export nutrients from natal freshwater rearing habitats (Moore and Schindler 2004). In some cases, nutrient export by juveniles can exceed import by adults, with a profound influence on organic matter and nutrient budgets (Scheuerell et al. 2005; Moore et al. 2011) and potentially imposing a compensatory effect on salmon productivity in freshwater ecosystems.

Several studies have examined the role that Pacific salmon play in affecting large-scale nutrient fluxes in riverine environments, and the effects can vary as habitats become modified or populations decline. In Alaskan streams with robust sockeye salmon (*Oncorhynchus nerka*) populations, Moore and Schindler (2004) found that P import by adults far exceeded smolt export, which is the typical role of Pacific salmon in inland ecosystems as net nutrient importers. However, they hypothesized, and demonstrated analytically, that net P export was possible at low population sizes, depending upon the strength of density-dependent factors. In modeling an Idaho limnetic system, Gross et al. (1998) found that if the smolt-to-adult survival rate is less than the smolt-

to-adult mass ratio, then juvenile salmon become net exporters of nutrients. Evidence of net nutrient export was demonstrated in the Snake River basin by Scheuerell et al. (2005), who called it a “negative feedback loop”, and in coastal California streams by Moore et al. (2011), who referred to it as the “stripping” of nutrients out of freshwater systems. What is generally a net nutrient surplus may become a net nutrient deficit in modified habitats with chronically low escapement levels. These studies highlight four critical ecological uncertainties: (i) will patterns of net nutrient flux change as salmon populations decline; (ii) will density-dependent processes (i.e., compensation) at low population sizes facilitate the net export of nutrients from freshwater rearing habitats; (iii) will net nutrient export maintained over time lead to compensatory population dynamics (i.e., depensation) and increased risks of extinction; and (iv) how will the rapid loss of MDN affect freshwater ecosystems over time?

We evaluated the nutrient flow (N and P fluxes) from adult import and juvenile export in seven streams across central Idaho, USA, using spring–summer Chinook salmon adult escapement and juvenile life-stage-specific emigrant data from 1998 to 2008. We constructed salmon-derived nutrient budgets and examined relationships among net nutrient flux (import minus export) and juvenile Chinook salmon population life-history behavior, survival, and condition. We hypothesized that net nutrient flux would be influenced by density-dependent factors and that variable nutrient fluxes would be related to biological characteristics of juvenile Chinook salmon populations. These relationships were described and evaluated using scatterplot and nonparametric multidimensional scaling (NMS) ordination that illustrated patterns in juvenile condition across populations and identified associations to nutrient fluxes, adult and juvenile densities, juvenile life-history behavior, and juvenile survival. Finally, we demonstrate the use of change point and conditional probability analyses in conjunction with nutrient flux data to identify ecologically important adult escapement thresholds.

Materials and methods

Study area

Our study streams are located across a broad geographic area and represent a diverse array of aquatic and terrestrial habitats. We used data from seven sampling sites located in the headwater spawning habitat of the Salmon and Clearwater rivers of central Idaho (Fig. 1). The Salmon River subbasin drains approximately 36 217 km². Landforms vary from high-elevation mountain ranges to plateaus and canyons within the Rocky Mountain geographic province. Parent geology is dominated by granite and quartz diorite (NPCC 2004). The South Fork Salmon River and Secesh River study areas represent headwater sections of the South Fork Salmon River, Marsh Creek is a headwater stream of the Middle Fork Salmon River, the upper Salmon River study area is in the headwater portion of the Salmon River above Sawtooth Hatchery, and the Pahsimeroi River is a tributary to the Salmon River. The Clearwater subbasin drains approximately 24 980 km². The subbasin is characterized by regions of mountains, plateaus, and canyons within the Rocky Mountain geographic province. Parent geology is dominated by granite and schist (NPCC 2003). Crooked Fork Creek and Colt Killed Creek converge to form the Lochsa River, located in the east-central portion of the Clearwater subbasin. Typical of Intermountain West watersheds, precipitation in our study area is largely a result of winter snowfall, with high flows occurring during spring runoff and base flows occurring the rest of the year. Our study streams are located in the Western Forested Mountains (ecoregion II) Northern Rockies (ecoregion III) ecoregion and are generally characterized as oligotrophic (USEPA 2000). Detailed study stream and associated basin characteristics are described in Table 1 (USGS 2007).

Fig. 1. Map of Salmon River and Clearwater River subbasins, Idaho, USA, showing seven study streams where adult import and juvenile export of nitrogen and phosphorus by Chinook salmon was compiled to estimate nutrient fluxes over time.

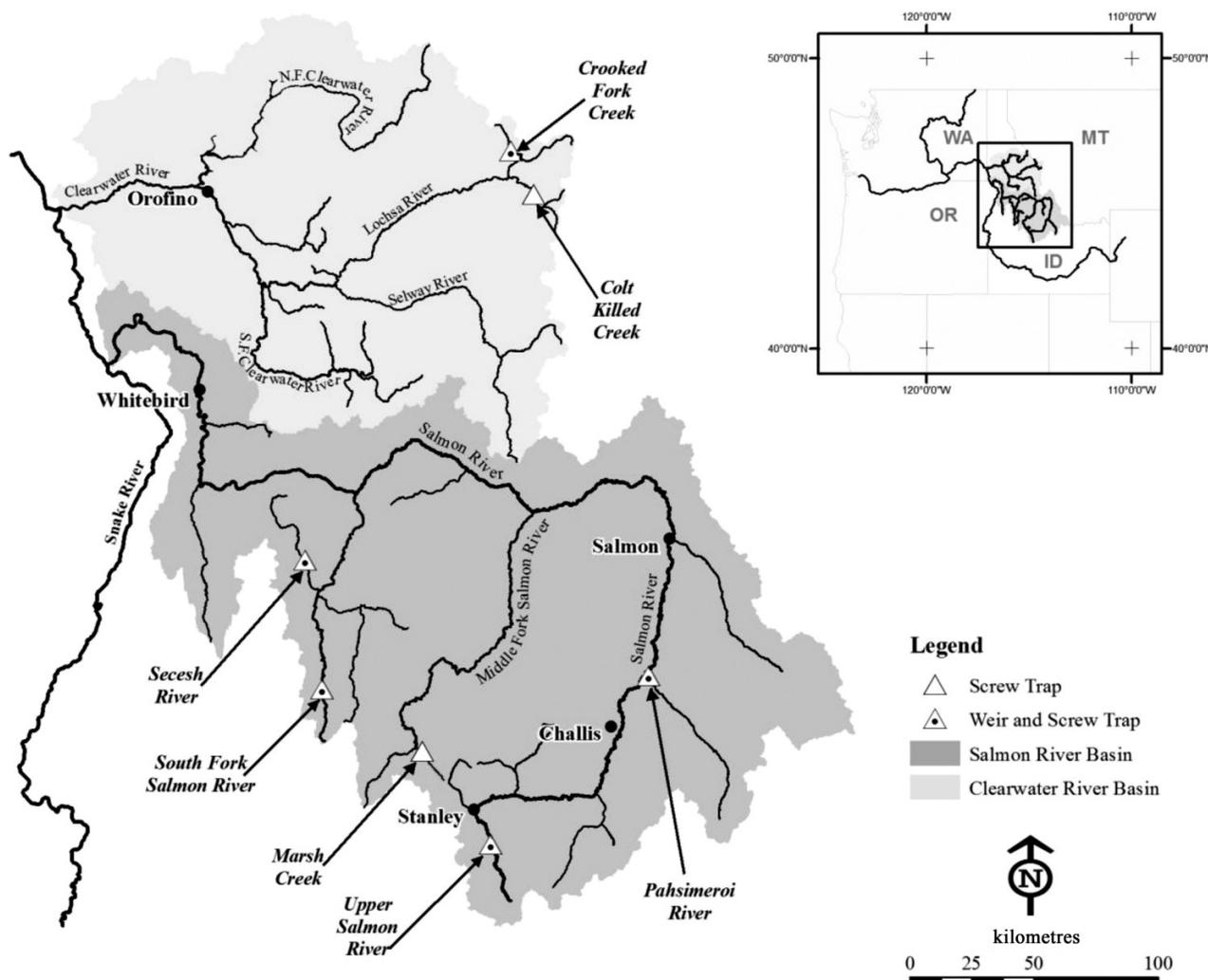


Table 1. Study stream drainage characteristics.

Stream	Size (km ²) ^a	Mean basin elevation (m)	Mean annual precipitation (cm)	Available spawning habitat (km) ^b
Upper Salmon River	769	2445	83	69
Pahsimeroi River	2149	2249	50	40
Marsh Creek	133	2222	67	20
South Fork Salmon River	237	2021	96	25
Secesh River	289	2085	109	48
Colt Killed Creek	640	1850	133	67
Crooked Fork Creek	435	1774	138	40

^aRepresents the upstream drainage basin area relative to the location of juvenile rotary screw traps and adult weirs.

^bRepresents the available spawning habitat above juvenile and adult monitoring sites.

Data collection and analyses

We created salmon-derived nutrient budgets using adult escapement (import) and brood year specific juvenile emigration (export) data from Salmon and Clearwater subbasin streams. To make direct comparisons with previous studies (Moore and Schindler 2004; Scheuerell et al. 2005; Moore et al. 2011), we used percent wet mass contents of 3.04% N and 0.38% P for adult Chinook salmon and 2.49% N and 0.43% P for juvenile Chinook salmon (Donaldson 1967; Larkin and Slaney 1997; Kline and Willette 2002). We acknowledge potential variation (spatial and temporal) in the proximal composition of N and P in Chinook salmon adult and

juvenile populations. Although we did not directly measure nutrient composition, we feel that the values used in our analyses accurately represent Chinook salmon N and P concentrations in general. We utilized a range of brood years (1998–2008) from seven streams and analyzed a total of 69 stream-years: 9 years from Colt Killed Creek, 11 years from Crooked Fork Creek, 11 years from Marsh Creek, 10 years from Secesh River, 6 years from South Fork Salmon River, 11 years from Upper Salmon River, and 11 years from Pahsimeroi River. Brood years without complete age- and size-specific adult escapement estimates paired with complete age- and size-specific juvenile production estimates (i.e., brood

Table 2. Study stream subbasin, data collection, and brood year information.

Stream	Subbasin	Adult escapement	Juvenile production	Brood years
Upper Salmon River	Salmon	Weir counts	Screw trap	1998–2008
Pahsimeroi River	Salmon	Weir counts	Screw trap	1998–2008
Marsh Creek	Salmon	Redd counts	Screw trap	1998–2008
South Fork Salmon River	Salmon	Weir counts	Screw trap	1999–2006 ^a
Secesh River	Salmon	Weir counts	Screw trap	1999–2008
Colt Killed Creek	Clearwater	Redd counts	Screw trap	1998–2008 ^b
Crooked Fork Creek	Clearwater	Weir counts	Screw trap	1998–2008

^aBrood years 2001 and 2003 not included in analyses.

^bBrood years 2005 and 2007 not included in analyses.

year specific juvenile production from parental spawners) were excluded from our analyses (Table 2). Our study stream locations largely represent areas with naturally spawning Chinook salmon populations, although limited hatchery supplementation efforts have occurred in certain study streams (Venditti et al. 2010). Estimates of adult escapement and juvenile production in our study streams, and associated biomass estimates used to derive nutrient budgets, are not confounded by hatchery production in downstream areas.

Adult escapement

Chinook salmon spawner escapement was determined by weir counts or numerically expanding standardized redd counts that encompassed all available spawning areas (Venditti et al. 2010; Hassemer 1993) (Table 2). A value of 2.54 fish-redd⁻¹ was used to expand the number of redds counted to estimate the number of spawning adults in areas where no weir data was available. We used this value because it is (i) based on collected data (Kucera and Faurot 2002) and (ii) a value within the range of those determined for multiple Idaho streams (Kucera and Faurot 2005; Tardy 2011; Denny and Kusnierz 2012). Length and age data from carcass recoveries and sampling at weirs was used to determine the mean length of spawners for three age-classes (age-3 to age-5). The mass (kg) of returning spawners was estimated via the mass-length (cm) relationship for spring Chinook salmon used by Haukenes and Moffitt (2002). The equation is $W = bL^x$, where b equals 5.9×10^{-6} , and x equals 3.1482.

Import of N and P by adult Chinook salmon

Following Moore and Schindler (2004), we calculated the gross import of nutrients n (N or P) by adult Chinook salmon produced from study streams st in brood year t as:

$$\text{Import}_{n,st,t} = \sum_{st,t} (\text{ESC}_{st,age,t} \cdot \text{AM}_{st,age,t} \cdot P_{n,st,adult})$$

where $\text{ESC}_{st,age,t}$ is the stream- and age-specific Chinook salmon escapement in brood year t , $\text{AM}_{st,age,t}$ is the adult average mass of stream- and age-specific spawners in brood year t , and $P_{n,st,adult}$ is the proportion of nutrients in stream spawners.

Juvenile emigration and survival

Emigrating juvenile Chinook salmon were collected by rotary screw traps (Table 2), and emigration estimates were derived by mark-recapture techniques. The abundance of four emigrant life-history types (fry, parr, presmolt, and smolt) was estimated with mark-recapture software developed by Steinhorst et al. (2004). Fry were age-0 Chinook salmon that passed the trap in the spring prior to 1 July and were marked with Bismarck Brown dye. Parr were age-0 fish that passed the trap between 1 July and 31 August. Presmolts were age-0 fish collected between 1 September and the end of the trapping season. Smolts were age-1 juveniles that passed the trap during their second spring. Parr, presmolts, and smolts were marked with passive integrated transponder (PIT)

tags and released upstream of the screw traps to provide recapture data. Emigrant length (mm FL) and mass (g) measurements were collected at rotary screw trap locations with the exception of fry. Because length and mass measurements for fry were not available in our study streams, we estimated average fry mass to be 1 g based on data collections from a representative stream (Shoshone Bannock Tribes, Yankee Fork Salmon River, unpublished data).

Juvenile survival to Lower Granite Dam (the first dam encountered by emigrating salmon) was estimated with PIT tags using a Cormack–Jolly–Seber model implemented by SURPH (Survival Under Proportional Hazards; available from <http://www.cbr.washington.edu/paramest/surph/>) software (Lady et al. 2010). For detailed descriptions of juvenile emigration methods, refer to Copeland and Venditti (2009) and Venditti et al. (2010).

Export of N and P by juvenile Chinook salmon

We calculated the gross export of nutrients n (N or P) by juvenile Chinook salmon produced from study streams st in brood year t as

$$\text{Export}_{n,st,t} = \sum_{st,t} (\text{JUV}_{st,age,t} \cdot \text{JM}_{st,age,t} \cdot P_{n,st,juvenile})$$

where $\text{JUV}_{st,age,t}$ is the stream- and age-specific number of juvenile emigrants for a given brood year t , $\text{JM}_{st,age,t}$ is the average mass of stream- and age-specific juveniles in brood year t , and $P_{n,st,juvenile}$ is the proportion of nutrients in stream-emigrating juveniles.

Salmon-derived nutrient flux budgets: import and export relationships

We used the results from calculations described above to investigate the mass balance, or net nutrient flux, by stream and brood year, for our dataset. Brood years when adult import of N and P by mass exceeded the juvenile export of N and P by mass represent a net gain of MDN, while brood years where juvenile export exceeded import represent a net loss of stream nutrients. Finally, we derived the proportion of nutrients exported by juvenile Chinook salmon relative to the amount imported by brood year spawners. Following Scheuerell et al. (2005), we fit a Beverton–Holt stock–recruit relationship to N and P imported by adults (stock) and the percentage of nutrients imported that juveniles exported (recruits) by brood year as

$$\text{Proportional nutrient export} = \text{Export}_{n,by\ juvenile} / \text{Import}_n$$

where the export of nutrients n (N or P) by brood year by juvenile Chinook salmon is a nonlinear function of the nutrients imported by parental spawners.

Escapement and proportional nutrient export: thresholds and conditional probabilities

We identified potential thresholds (i.e., change points) in the relationship between the amount of N or P imported by spawners and the percent exported by brood year juveniles with scatterplots and

tree regression using R statistical software (<http://www.r-project.org/>) and the GUI CADStat module (http://www.epa.gov/caddis/da_software_cadstat.html). This analysis uses the deviance reduction method (King and Richardson 2003; Qian et al. 2003) and a variation of the regression tree methods of Breiman et al. (1984) to determine change points in a dataset. We then used conditional probability analysis to evaluate a range of N and P imports and the associated likelihood that the proportion of nutrients exported would remain below thresholds identified in our change point analysis. Conditional probability analysis is available in CADStat. We used scripts developed by Hollister et al. (2008) and applied alpha values of 0.05 and 1000 bootstraps to develop confidence intervals in all conditional probability analyses. See Yuan et al. (2010) for further explanation of these analyses.

Ordination of juvenile Chinook salmon length and mass characteristics and relationships to salmon-derived net nutrient flux and environmental variables

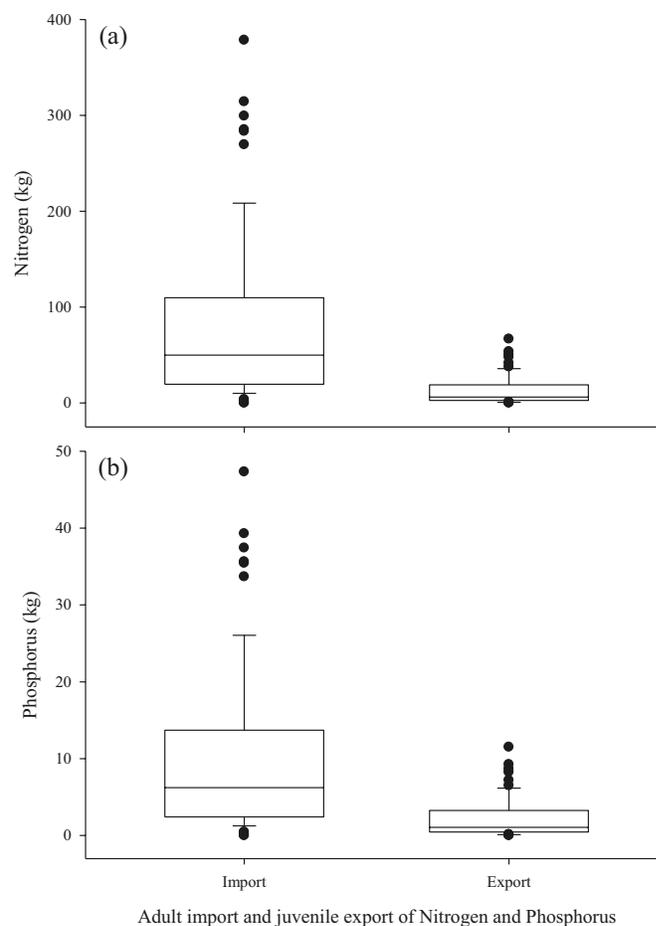
Multivariate analyses such as NMS commonly are used to illustrate patterns of community structure and are useful for inferring structure–environment relationships (Cao et al. 2002). NMS illustrates community patterns with an iterative process that searches for an ordination of samples that best represents a similarity matrix (Clarke 1993). NMS is also an appropriate ordination method for ecological data and provides an effective way to represent relationships graphically (McCune and Mefford 2011). We used NMS to explore spatial relationships (i.e., potential gradients) in ordination scores representing patterns of response covariation from a life-stage-specific juvenile Chinook salmon length and mass dataset. The dataset was compiled from biological measurements collected from rotary screw trap operations over multiple life-history stages. We performed a relativization to adjust our variables to standard deviates (mean = 0 and variance = 1). As such, each NMS ordination score consists of relative stream- and brood year specific measures and integrates: mean parr length and mass; mean presmolt length and mass; and mean smolt length and mass. The resulting ordination was used to represent relationships between life-stage-specific juvenile Chinook salmon length and mass characteristics among study streams. In addition to characterizing juvenile Chinook salmon populations by size, we correlated ordination scores to variables from our salmon-derived nutrient budgets as well as factors associated with density-dependent growth (e.g., escapement measures), productivity (e.g., juvenile emigrants per spawner), life-history patterns (e.g., proportion of parr, presmolt, and smolt emigrants by brood year), and survival. We show these variables as vectors correlated with our ordination scores. We generated NMS ordination and joint plots with PC-ORD software (McCune and Mefford 2011).

Results

Across study streams and periods, the average annual adult MDN import in individual study streams was 81 ± 10 kg of N (mean \pm 1 standard error) and 10 ± 1 kg of P. Correspondingly, juvenile Chinook salmon exported an average of 13 ± 2 kg of N and 2 ± 0.3 kg of P out of natal rearing habitats (Fig. 2; Table 3). We found a significant positive relationship between the amount of nutrients (N and P) imported by spawners and the amount of those same nutrients exported by juvenile progeny (Pearson's correlation (PC), $N = 69$, $r = 0.745$, $P < 0.001$; Fig. 3).

Estimates of net nutrient flux were highly variable through time; N and P net flux was 69 ± 9 kg and 8 ± 1 kg, respectively. Anadromous Chinook salmon adults imported more nutrients than their brood year progeny (i.e., emigrating juvenile fry, parr, presmolt, and smolt) exported in 97% of the stream-years represented in our dataset. In 3% of our evaluations, juvenile Chinook salmon exported more nutrients than their parents imported (Fig. 4; Table 3).

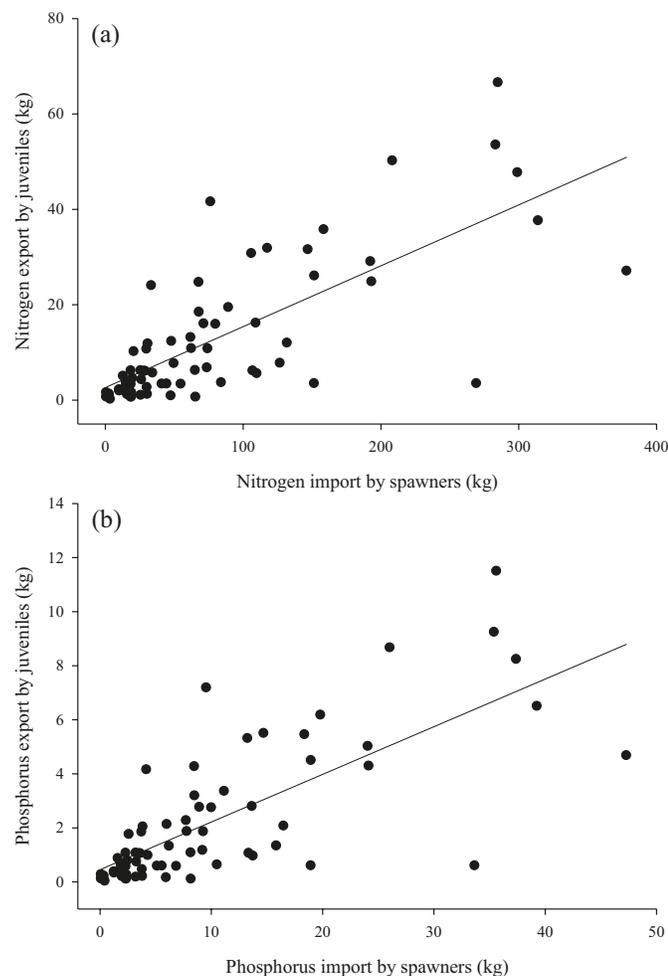
Fig. 2. Nitrogen (a) and phosphorus (b) import by adult Chinook salmon and the corresponding export of those same nutrients by brood year juvenile emigrants in Salmon River and Clearwater River subbasin streams. Box plots show the 10th, 25th, 50th, 75th, and 90th percentiles, as well as individual data points outside the 10th and 90th percentiles.



The proportion of nutrients exported by juvenile Chinook salmon relative to parental imports varied across streams and through time. On average, juvenile emigrants exported $22\% \pm 3\%$ of the N (range = 0%–194%) and $30\% \pm 4\%$ (range = 0%–268%) of the P their parents imported from the ocean. We found evidence of density-dependent factors influencing this nonlinear relationship (Figs. 5a, 5b). Visual inspection of the data identified change point regions for both N and P, and tree regression analysis estimated the actual change points for both. The first change point in the N dataset was identified at 84 kg, corresponding to a percent export of 31%. This percent export was used in our conditional probability analysis and indicated that when at least 84 kg of N are imported, there is a probability of ~ 0.75 (range 0.58–0.88) that percent export will remain below 31% (Fig. 5c). The mean percentage of N exported by juveniles when adults returned < 84 kg of N to spawning grounds was 26%, while the mean percentage of N exported by juveniles when adults returned > 84 kg of N was 14%. Nitrogen import of 84 kg corresponds with ~ 501 Chinook salmon spawners (5.5 kg average mass) or an average of ~ 14 (range = 7–25) Chinook salmon adults per kilometre of available stream spawning habitat (Fig. 5c). Tree regression identified the first change point in the P dataset at 11 kg, corresponding to a percent export of 43% (Fig. 5b). This percent export was used in our conditional probability analysis and indicates that when at least 11 kg of P are imported, there is a probability of ~ 0.75 (range 0.58–0.88) that

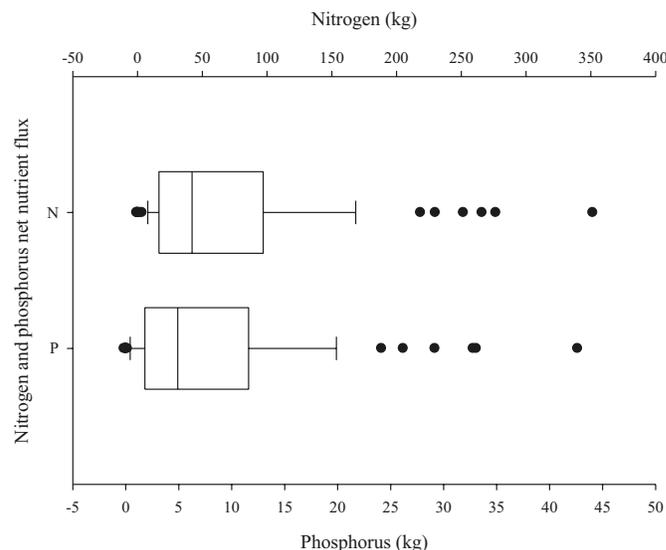
Table 3. Study stream nutrient (N and P) import, export, and net nutrient flux summary statistics.

Statistic	N_Import (kg)	N_Export (kg)	Net N_flux (kg)	P_Import (kg)	P_Export (kg)	Net P_flux (kg)
No. of observations	69	69	69	69	69	69
Minimum	0.00	0.00	-0.76	0.00	0.00	-0.17
Maximum	378.48	66.56	351.42	47.31	11.50	42.64
First quartile	19.80	2.71	17.66	2.48	0.47	1.82
Median	49.81	6.16	42.15	6.23	1.06	4.90
Third quartile	109.33	18.44	93.18	13.67	3.18	10.88
Mean	81.40	12.94	68.46	10.17	2.23	7.94
Standard error	10.42	1.80	9.16	1.30	0.31	1.09

Fig. 3. The relationship between nitrogen (a) and phosphorus (b) imported by adult Chinook salmon and those same nutrients exported by brood year juvenile emigrants in Salmon River and Clearwater River subbasin streams.

percent export will remain below 43% (Fig. 5d). The mean percentage of P exported by juveniles when adults returned <11 kg of P to spawning grounds was 35%, while the mean percentage of P exported by juveniles when adults returned >11 kg of P was 20%. P import of 11 kg corresponds with ~501 Chinook salmon spawners (5.5 kg average mass) or an average of ~14 (range = 7–25) Chinook salmon adults per kilometre of available stream spawning habitat (Fig. 5d).

A nonlinear relationship between the number of juvenile Chinook salmon produced by brood year and smolt size (g) provides clear evidence of density-dependent growth; smaller smolts were associated with larger brood year production (Fig. 6). Correspond-

Fig. 4. Net nutrient flux (import minus export) in Salmon River and Clearwater River subbasin streams. Box plots show the 10th, 25th, 50th, 75th, and 90th percentiles, as well as individual data points outside the 10th and 90th percentiles.

ingly, NMS ordination revealed a gradient of juvenile emigrant sizes across study streams and brood years. We found significant ($\alpha = 0.10$) correlations between NMS axis 1 scores and variables represented by joint plot vectors, including the following: net nutrient flux (N and P) measures (PC, $N = 69$, $r = -0.331$, $P = 0.006$; Fig. 7); the number of Chinook salmon redds per kilometre of available stream spawning habitat (PC, $N = 69$, $r = -0.343$, $P = 0.004$; Fig. 7); the number of juvenile emigrants per spawner (PC, $N = 69$, $r = -0.216$, $P = 0.077$; Fig. 7); juvenile survival (PC, $N = 69$, $r = 0.374$, $P = 0.002$; Fig. 7); the proportion of brood year juveniles that emigrated as parr (PC, $N = 69$, $r = -0.543$, $P < 0.001$; Fig. 7); the proportion of brood year juveniles that emigrated as presmolt (PC, $N = 69$, $r = 0.249$, $P = 0.046$; Fig. 7); and the proportion of brood year juveniles that emigrated as smolt (PC, $N = 69$, $r = 0.228$, $P = 0.067$; Fig. 7). We found no significant correlations to NMS axis 2 scores (Fig. 7). The percentage of variance represented by NMS ordination axes 1 and 2, calculated as the percentage of the variation in the reduced matrix relative to the original data matrix, was >99% and <1%, respectively.

Discussion

Evidence in the literature suggests that MDN imports by salmon spawners generally far exceed exports by juveniles, especially in streams containing functional habitat and abundant salmon runs (Moore and Schindler 2004). In more modified habitats, declining returns directly affect gross nutrient budgets in both freshwater and associated terrestrial ecosystems. In some circumstances, low spawner abundance coupled with density-dependent factors will

Fig. 5. The relationship between nitrogen (a) and phosphorus (b) imported from adult spawners and the proportional export of those same nutrients by brood year juvenile emigrants. Panels (c) and (d) are equivalent conditional probability plots showing the relationship between the number of adult spawner equivalents and the probability of N and P export <31% and <43%, respectively. The dotted vertical lines represent N import of 84 kg and P import of 11 kg.

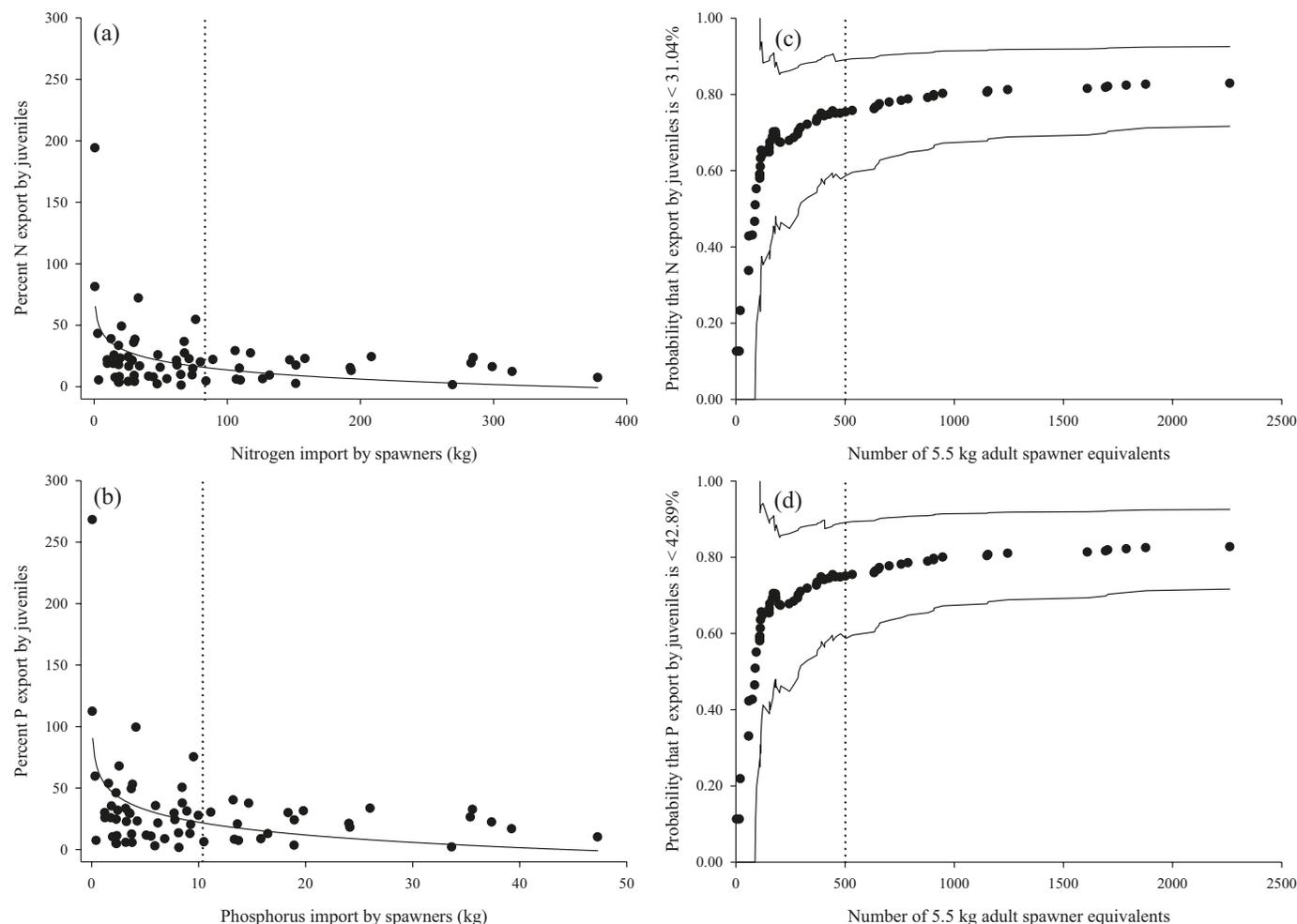
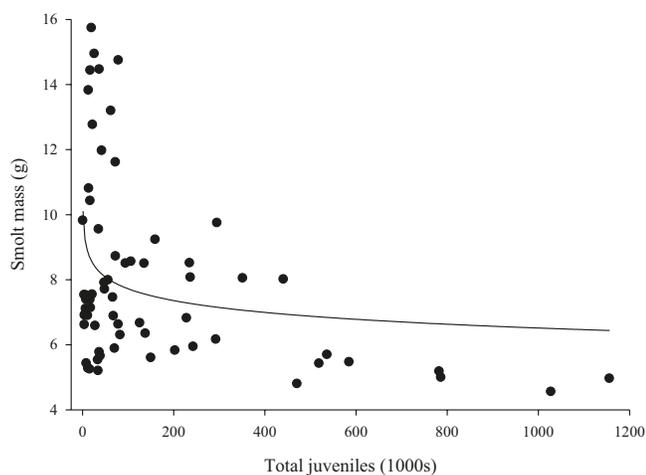


Fig. 6. The relationship between brood year juvenile production and smolt emigrant mass in grams.

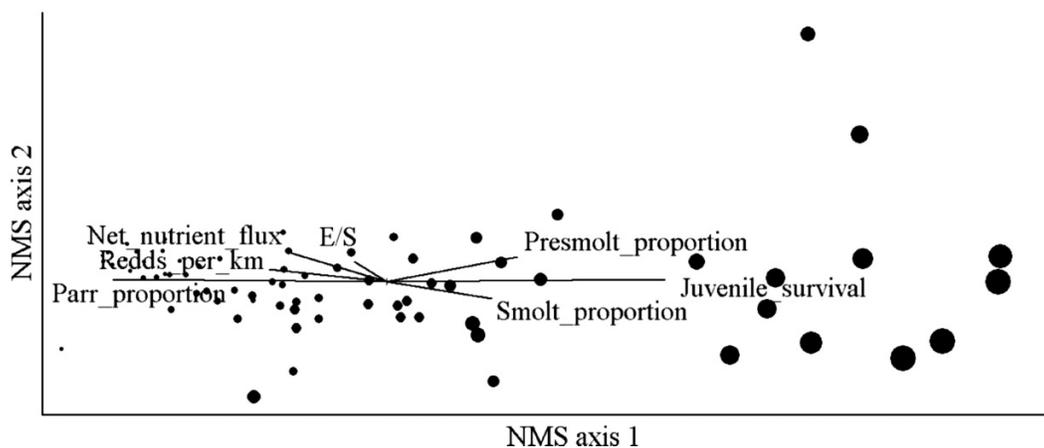


produce a net nutrient export by brood year juveniles (Moore et al. 2011; Gross et al. 1998). Net nutrient export, if sustained over time, may represent a reversal of past productivity patterns that were dominated by net nutrient import.

Our study streams are greater than 1000 km from the Pacific Ocean and are upstream of eight federal hydroelectric dams on the Columbia and Snake rivers. This geographic setting provides a unique opportunity to evaluate nutrient fluxes by Chinook salmon in headwater streams above highly modified habitats. We demonstrated that although net nutrient flux by Chinook salmon was generally positive, in some years juvenile salmon exported more nutrients than their parents imported. These results are similar to those of Moore et al. (2011) from modified habitats in northern California streams and suggest that the reversal of the “conveyor belt” of nutrients largely occurs under the context of low spawner abundances. Our results suggest that a state shift occurs when adult spawner abundance falls below a threshold to a point where the probability of juvenile nutrient exports exceeding adult imports becomes increasingly likely.

A model of adult Chinook salmon MDN import showed that net nutrient flux was density-dependent such that a greater proportion of the adult import was exported as spawner abundance declined. This relationship has important implications for the management of salmon populations and the stream systems in which they reside. In our evaluation, spawner abundance fluctuated up to three orders of magnitude during the study period, enabling a powerful analysis. Proportionally, nutrient export in our systems was higher than those found in other systems. In sockeye salmon streams of Bristol Bay, Alaska, Moore and Schindler (2004)

Fig. 7. Nonparametric multidimensional scaling (NMS) ordination of Chinook salmon parr, presmolt, and smolt emigrant life-stage length and mass characteristics across study streams and brood years. The size of ordination points scales with the mass (g) of smolt emigrants for each stream and brood year. Vector lines show biological and environmental variables that are significantly correlated to NMS axis 1; the angle and length of the line represent the direction and strength of the relationship, respectively. NMS summary: solution = two-dimensional; distance measure = Euclidean; iterations = 76; final stress = 2.178; and final instability < 0.001. Net_nutrient_flux is adult import minus juvenile export of N and P; Redds_per_km is the number of adult Chinook salmon redds per kilometre of available stream spawning habitat; E/S is the number of juvenile emigrants per adult spawner; parr_, presmolt_, and smolt_proportion are the proportion of juveniles that emigrated at respective life-history stages; and juvenile_survival is the survival rate to Lower Granite Dam.



found that N export by smolts averaged 12% (range = 0.7%–41.8%), and P export by smolts averaged 16% (range = 1.0%–64.7%). In contrast, our observed mean export values were 22% of N (range = 0%–194%) and 30% of P (range = 0%–268%), nearly double those of Moore and Schindler (2004). Our mean proportional export estimates for N and P were also higher than those from modified habitats in the Snake River basin (Scheuerell et al. 2005) and northern California streams (Moore et al. 2011).

The relationship between MDN import and proportional export described above was nonlinear, similar to observations of Scheuerell et al. (2005) and Moore et al. (2011). As suggested by Moore et al. (2011), this pattern appears to be driven by density-dependent processes whereby juvenile emigrants are larger and disproportionately more abundant at low spawner densities. Our results partially support this hypothesis; while larger juvenile emigrants were indeed associated with lower spawner densities, the number of emigrants per spawner was not disproportionately larger at lower spawner densities. Our NMS ordination illustrated a gradient of juvenile emigrant sizes across study streams and years that allowed exploratory analysis and interpretation of factors associated with the observed pattern. The size-at-age of juvenile Chinook salmon appeared to be influenced by density-dependent factors (Grant and Imre 2005) and was related to nutrient flux patterns at the population scale. Positive net nutrient flux (N and P) was related to populations with higher spawning densities, smaller juveniles, and larger proportions of the juvenile cohort that left natal reaches as subyearling parr. Larger juvenile emigrants, associated with lower spawner densities, spent more time in natal rearing habitats and exhibited relatively higher survival rates. This finding highlights potential compensatory mechanisms acting at the population scale. Similarly, differences in juvenile condition (i.e., length and mass at specific life stages) have been shown to be related to variable life-history trajectories (Beckman et al. 1998), aquatic system productivity (Wood 1995), and survival (Zabel and Achord 2004; Griswold et al. 2011).

As described by Anders and Ashley (2007) in “The clear-water paradox of aquatic ecosystem restoration”, nutrient losses from inherently oligotrophic systems, such as those found in central Idaho, may facilitate reduced biological productivity and become incapable of supporting historical fish production yields. To better understand the ecological context of MDN fluxes in freshwater

habitats, we examined scenarios that produced variable juvenile nutrient export outcomes relative to adult imports. For both N and P, we were able to determine thresholds in the import and proportional export relationship that correspond with escapement levels similar to those described for viable salmon populations by the Interior Columbia Basin Technical Recovery Team (ICTRT). On one side of our threshold, juvenile export of parental MDN was disproportionate, highly variable, and at times represented a net nutrient loss. On the other side of our threshold, juvenile export as a percentage of parental imports was lower, much less variable, and did not result in net nutrient export. From this information we determined the conditional probability of a given MDN import mass, and the equivalent number of spawners, necessary to maintain a “net gain” nutrient flux state. We estimated the minimum population-scale escapement necessary to (i) maintain a consistently positive net flux of MDN and (ii) reduce the average proportional rate of export across our study streams. As the amount of nutrients imported as adults increased, so did the likelihood that populations returned more nutrients to natal spawning and rearing habitats than their juvenile progeny exported.

This analysis represents an empirical method that evaluates salmon-derived import–export dynamics and is germane to natural resource managers seeking to incorporate the importance of MDN in management decisions. Incorporating salmon-derived nutrient flux considerations into management could help identify and test trophic productivity interactions that potentially influence restoration success. We propose that analyses such as presented here could be used to derive more “ecologically defensible” escapement targets (Peery et al. 2003) that seek to avoid high levels of proportional export and reduce the risk of net nutrient loss conditions from occurring over time. For example, managers could derive escapement targets that increase the probability that natal spawning and rearing habitats receive more nutrient inputs from parental spawners than associated losses from emigrant progeny. In this context, populations above highly modified habitats that exceeded threshold targets would more likely act as net importers of energy and nutrients. Furthermore, the associated losses (i.e., proportional export) of energy and nutrients by juvenile progeny would likely diminish. Taken together, these conditions would more closely mimic those found in ecosystems with

high-quality habitat and healthy salmon populations (Moore and Schindler 2004).

The most common escapement goal calculations are stock-recruit models that are based on return per spawner production patterns (Hilborn and Walters 1992). Recently there has been emphasis on incorporating MDN and nutrient fluxes into salmon management as the importance of their influence on recipient ecosystem function has been recognized (Michael 1998; Scheuerell et al. 2005; Bernard and Clark 2009). We illustrate an empirical method that could be used to guide management objectives that seek to (i) maintain higher levels of nutrient retention and (ii) reduce the risk of net nutrient losses from occurring over time. In this case, a minimum of at least 500 fish in each of the study stream populations, or the average of ~14 (range = 7–25) Chinook salmon adults per kilometre of available stream spawning habitat, provided sufficient nutrient import to consistently exceed nutrient export and maintain a positive net nutrient flux. This finding also lends support to the minimum adult abundance thresholds developed by the ICTRT for use in determining viability of Endangered Species Act-listed Chinook salmon populations (ICTRT 2007).

Previous researchers uncovered (Moore and Schindler 2004; Scheuerell et al. 2005; Moore et al. 2011), and we confirmed empirically, an ecological mechanism that may stabilize salmon populations at a lower level where they remain vulnerable to stochastic catastrophes and loss of genetic variability. The ICTRT defined minimum viable population size thresholds based on demographic modeling with a criterion of a 5% probability of extinction over a 100-year period, but set a floor of 500 based on genetic concerns. Effects of demographic stochasticity increase exponentially as population size declines, although the effects of environmental stochasticity and random catastrophes can be ameliorated by a sufficiently positive population growth rate (Lande 1993). Density-dependent effects are evident on smolt production by spring-summer Chinook salmon in the Snake River basin (Copeland et al. 2005; Scheuerell et al. 2005), which includes our study populations. Density-dependent compensation theoretically allows populations to be resilient to stressors such as human exploitation (Rose et al. 2001); however, stabilizing mechanisms may trap a reduced population in a lower productivity state (Peterman 1987), which results in depensatory population dynamics (Liermann and Hilborn 2001) and increased risks of extinction.

An alternative method to establish escapement thresholds was proposed by Bilby et al. (2001) in western Washington streams where a saturation level of MDN (i.e., N stable isotope values) was identified at a density of 120 coho salmon (*Oncorhynchus kisutch*) carcasses per stream kilometre. This represents approximately 228 kg·km⁻¹ (from Peery et al. 2003) and can be compared with our study streams assuming that the functional relationship between coho biomass densities and MDN saturation levels is similar for Chinook salmon in our study area. In comparison, our study streams averaged 78 kg (range = 7–214 kg) of salmon biomass per kilometre of available stream spawning habitat, well below what Bilby et al. (2001) identified as a potential saturation level using stable isotope analyses, and even further below that recorded from natural and experimental streams in Alaska (Wipfli et al. 1999; Rinella et al. 2012). If this saturation level was applied as a recovery goal, as suggested by Peery et al. (2003), our individual study streams would need an average annual return of 1749 Chinook salmon spawners (5.5 kg average mass), or the equivalent average of ~47 (range = 25–87) Chinook salmon adults per kilometre of available stream spawning habitat. If returns met these goals, our data suggest that salmon would consistently act as net importers of MDN. On the other hand, if declines in salmon-derived energy and nutrient subsidies are sustained (e.g., in a net nutrient export condition), then alternative approaches such as interim nutrient supplementation may be warranted (Wipfli et al. 1999).

There is great interest in addressing nutrient limitations as a means of better managing salmon populations (Stockner 2003 and papers therein). Common options include managing salmon escapements (Peery et al. 2003) or adding exogenous nutrient subsidies (Kohler et al. 2012) to achieve elevated freshwater productivity, but such programs should be guided by knowledge of how nutrients move through, and interact with, stream ecosystems. It is important to note that gross nutrient budgets derived from adult escapement and juvenile production estimates do not address a myriad of complex nutrient dynamic processes. Furthermore, anadromous fishes are not the only source of organic matter and (or) nutrients in aquatic ecosystems; other sources include atmospheric, upstream catchment, terrestrial, and groundwater inputs. Nitrogen fixation and denitrification by stream microbes are also important N sources and sinks, respectively (Triska et al. 1984; Marcarelli et al. 2008). Regardless of alternative sources, salmon represent a high-quality, seasonal resource subsidy (Wipfli and Baxter 2010) that not only affect structural components of stream ecosystems, but also functional attributes (e.g., whole-stream metabolism; Levi et al. 2013). As Moore et al. (2011) point out, the ecological consequences of salmon-derived nutrient fluxes will likely be driven by nonlinear dynamics and complex direct and indirect pathways, all modulated by the environmental context (Janetski et al. 2009).

What remains unclear is how aquatic ecosystems will respond to the loss or decline of an important MDN subsidy over time (Wipfli and Baxter 2010). Declines in the abundance of Pacific salmon represent a form of disruption to a previously existing resource subsidy, with potentially dramatic effects upon the structure and function of recipient aquatic and terrestrial ecosystems (Naiman et al. 2002). Will stream biofilm communities respond to diminished MDN inputs through changes in community composition and function? How do changes in MDN subsidies alter internal nutrient fluxes, nutrient uptake rates, and transformations like nitrification, denitrification, and nitrogen fixation? These important questions are beyond the scope of this paper. However, understanding the basic components of salmon-derived nutrient budgets in oligotrophic headwater streams is an important research topic germane to the management and recovery of Pacific salmon in general. In a subset of our study streams, salmon-derived subsidies contributed ~15% (2%–33%) and ~7% (1%–13%) of the N and P, respectively, to seasonal nutrient budgets (A.E. Kohler and P.C. Kusnierz, unpublished data). These subsidies come at the end of the summer growing season and provide fish a timely energy and nutrient source prior to overwintering (Wipfli and Baxter 2010).

Pacific salmon depend upon habitat that supports diverse food webs and naturally functioning biogeochemical cycles. Reciprocally, the carrying capacity and stock productivity of these habitats is influenced by MDN and organic matter subsidies delivered by salmon (Adkison 2010; Schindler et al. 2003). As management strategies begin to recognize the ecological roles of salmon by incorporating “ecologically defensible” escapement goals (Gresh et al. 2000; Peery et al. 2003), predicting how changes in salmon abundance affect ecosystem processes, stream food webs, and the recovery of endangered species will become more tractable (Adkison 2010; Bernard and Clark 2009). We highlight minimum escapement thresholds that appear to (i) maintain consistently positive net nutrient flux and (ii) reduce the average proportional rate of export across study streams. Our results suggest a state shift occurs when adult spawner abundance falls below a threshold to a point where the probability of juvenile nutrient exports exceeding adult imports becomes increasingly likely. The present evaluation helps managers and natural resource specialists better understand the dynamics of salmon-derived nutrient fluxes in headwater streams above highly modified habitats.

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