esa ECOSPHERE

Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes

J. D. Ebel,[1,]† S. J. Leroux,[1] M. J. Robertson,[2] and J. B. Dempson[2]

[1]*Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9 Canada*
[2]*Fisheries and Oceans Canada, Science Branch, St. John's, Newfoundland A1C 5X1 Canada*

Citation: Ebel, J. D., S. J. Leroux, M. J. Robertson, and J. B. Dempson. 2015. Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes. Ecosphere 6(8):136. http://dx.doi.org/10.1890/ES14-00516.1

Abstract. Nutrient transport across ecosystem boundaries by migratory animals can regulate trophic and biogeochemical dynamics of recipient ecosystems. The magnitude and direction of net nutrient flow between ecosystems is modulated by life history, abundance and biomass, individual behavior, and body element composition of migrating individuals. We tested common assumptions applied to nutrient transport models regarding homeostasis of species' body element composition across space and ontogenetic stage. We quantified whole body phosphorus (P) concentration of three life stages of wild Atlantic salmon (*Salmo salar* L.) from three distinct populations in Newfoundland, Canada, to evaluate the importance of river of origin and life stage as predictors of salmon %P. We found that life stage was a more important predictor of salmon %P than river of origin, and that %P of post-spawn adults migrating downstream to the ocean (i.e., kelts) was more similar to %P of juveniles migrating downstream to the ocean (i.e., smolts) than it was to %P of adults migrating upstream to spawn. We then compared nutrient flux for the three rivers over a 20-year period calculated with body composition values extracted from existing literature and our direct measurements to evaluate how assumptions regarding spatial and ontogenetic homogeneity in salmon %P influenced the observed P fluxes. We demonstrate that assuming equality of kelt %P and adult %P results in an overestimate of net nutrient flux to rivers by Atlantic salmon and the erroneous conclusion that Atlantic salmon populations are unconditional sources of nutrients to their natal watersheds. Instead, Newfoundland's salmon populations are conditional sinks of freshwater P, which is the opposite functional role of Pacific salmon. Our results highlight that a better understanding of intraspecific variation in body element composition of fishes is a prerequisite to determining their role in global biogeochemical cycling.

Key words: anadromous; balance; food web; function; life history; limitation; Newfoundland; nutrient; *Salmo salar*; source; sink; stoichiometry.

Received 18 December 2014; revised 27 February 2015; accepted 18 March 2015; **published** 7 August 2015. Corresponding Editor: W. Cross.

† **E-mail:** jde786@mun.ca

Introduction

Nutrient transport by organisms can be an important ecosystem process (Vanni 2002, Bauer and Hoye 2014), as flows of nutrients influence trophic dynamics and biogeochemical processes in recipient ecosystems (Seale 1980, Leroux and Loreau 2008, Childress et al. 2014). Pacific salmon are a classic example of a species long considered as an ecological and biogeochemical

force because they move nutrients between marine and freshwater ecosystems. Pacific salmon (*Oncorhynchus* spp.) assimilate nutrients in marine ecosystems and deposit those nutrients in freshwater ecosystems in the form of gametes, excretions, and carcasses. In turn, the nutrients support resident fish populations (e.g., Bentley et al. 2012), aquatic macroinvertebrates (e.g., Wipfli et al. 1999), terrestrial vegetation (e.g., Hocking and Reynolds 2011), and terrestrial predators (e.g., Holtgrieve et al. 2009).

The magnitude and direction of nutrients transported across ecosystem boundaries depends on population size, the behavior of individuals while inhabiting the different ecosystems, and their biochemical characteristics. Migrating Pacific salmon, which can number in the millions, commit their entire bodies to the spawning process and hence the watershed ecosystem as a consequence of their semelparous life history strategy. Annual nitrogen and phosphorus imports by adults can be substantial at the watershed scale (e.g., Gresh et al. 2000, Moore and Schindler 2004). In the last decade, numerous studies have concluded that semelparous Pacific salmon are net sources of nitrogen and phosphorus to their natal watersheds when populations are considered healthy (e.g., Moore and Schindler 2004, Scheuerell et al. 2005, Kohler et al. 2013). Anadromous Atlantic salmon (*Salmo salar* L.) are iteroparous and the majority of adults spawning in late autumn survive to overwinter in freshwater and return to the ocean as kelts (i.e., post-spawn adults). Juvenile Atlantic salmon spend 2–8 years feeding and growing in their natal watersheds prior to migration as smolts, which may also influence patterns in the magnitude and direction of nutrient transport across species. To date, however, nearly all iteroparous anadromous fishes have been found to be net nutrient sources to their rearing watersheds (see Lyle and Elliott 1998, Jonsson and Jonsson 2003*a* for Atlantic salmon, Moore et al. 2011 for steelhead trout, West et al. 2010 for alewives).

At the ecosystem level, the balance of adult import with smolt export, termed nutrient flux, determines the status of an anadromous fish population as a nutrient source or sink (Loreau et al. 2013). In a recent review of the concept of sources and sinks, Loreau et al. (2013) define a net source or sink as a subsystem that is a net importer or exporter of a specific entity to an ecosystem. As such, a salmon population is a source of nutrients to the freshwater ecosystem when the amount of nutrients imported from the ocean by adults exceeds the amount of nutrients exported by smolts during their migration to the ocean (i.e, annual flux > 0). A population is a sink of nutrients in the freshwater ecosystem when the reverse is true; when smolt export exceeds adult import (i.e., flux < 0). For iteroparous species, a basic model calculates nutrient flux as the difference between nutrients imported by spawning adults and nutrients exported by smolts and kelts migrating to the ocean (Moore et al. 2011). The model is expressed as

$$\text{Flux}_t = A_t M_{a,t} N_a - (S_t M_{s,t} N_s + k b_t A_t M_{a,t} N_k)$$

where A is the number of spawning adults, S is smolt count, M is fish mass, N is whole body nutrient concentration, k is the proportion of spawning adults that survive to exit the river as kelts (i.e., overwinter survival rate), and b is the proportion of imported adult body mass that exits the river as kelt body mass. Subscripts t, a, s, and k refer to year, adult, smolt, and kelt, respectively. This nutrient flux model is data intensive and long term datasets that include all parameters are rare, especially for iteroparous fishes, which require additional information about the kelt export pathway.

In this nutrient flux model, biomass flow is converted to nutrient flow by scaling biomass estimates by nutrient content of fishes on a wet weight basis, which makes nutrient content an important parameter in a nutrient flux model. Whole-body nutrient content, however, is rarely measured directly for the populations or species of interest. Atlantic salmon nutrient flux estimates have relied on body composition values measured over 30 years ago. Separate investigations quantified (Lyle and Elliott 1998, Jonsson and Jonsson 2003*a*) or modelled (Nislow et al. 2004) nutrient transport via Atlantic salmon using percent carbon, nitrogen and phosphorus (P) values from unpublished data collected in the late 1970s and mentioned in an article on brown trout (*Salmo trutta*) body composition (see Elliott 1976). Nutrient transport by Pacific salmon species, including one iteroparous species

(Moore et al. 2011), was quantified using whole body %P of sockeye salmon collected from Iliamna Lake, Alaska, USA, and published in a 1967 doctoral thesis (see Table 1).

By using the nutrient content values published in studies conducted in different ecosystems (Table 1), all previous salmonid-mediated nutrient flux studies implicitly assume that salmon elemental composition does not vary among species or within species across space. However, work on other fishes has documented significant intraspecific variation in %P arising from sex, ontogeny, size, physical habitat, feeding history, and geographic location (Hendrixson et al. 2007, McIntyre and Flecker 2010, El-Sabaawi et al. 2012). The magnitude of variation in %P within salmonid species in the wild is unknown. In addition, studies focused on iteroparous salmonids explicitly assume that kelts exiting the river have a wet weight nutrient content equal to that of incoming spawning adults (Lyle and Elliott 1998, Moore et al. 2011), but measurements of artificially reared Atlantic salmon show clear changes in %P during this portion of their life cycle (Shearer et al. 1994). Whether the two previously held assumptions regarding spatial variability and ontogenetic equivalency of %P are correct has not been explicitly tested, nor do we understand how our nutrient flux estimates respond when these assumptions are violated.

We investigated the interaction between whole salmon %P and the patterns and magnitude of P transport between the ocean and freshwater ecosystems. We chose to evaluate P dynamics because this element exhibits the highest intra- and interspecific variation in fishes (Sterner and George 2000, Vanni et al. 2002, El-Sabaawi et al. 2012) and is commonly considered to be the dominant limiting nutrient in freshwater ecosystems. First, we quantified whole body %P of three life stages of Atlantic salmon from three populations inhabiting rivers of insular Newfoundland, Canada, to assess whether ontogeny and population can explain intraspecific variation in wild Atlantic salmon %P. We expected adult %P to be equal to kelt %P as assumed previously (Lyle and Elliott 1998) and both stages to have lower %P than smolt as previously shown (Shearer et al. 1994). Second, we examined the sensitivity of flux estimates to (1) variation in %P among populations and (2) the assumption that %P of kelt and spawning adults are equal (see Lyle and Elliott 1998, Jonsson and Jonsson 2003*a*, Moore et al. 2011) to test the hypothesis that small differences between assumed and measured %P values compound to influence ecosystem flux estimates.

Materials and Methods

To accomplish our two objectives, we determined whole body %P of spawning adult, kelt, and smolt Atlantic salmon migrating to and from Campbellton River, Conne River, and Western Arm Brook (henceforth Campbellton, Conne, Western Arm) of insular Newfoundland (Fig. 1) and compiled time series data for Atlantic salmon from these three rivers (Appendix A: Table A1). Newfoundland presents a unique opportunity to examine nutrient flux from migratory Atlantic salmon because it is one of the last areas in North America with healthy wild populations of this species (Parrish et al. 1998) relative to other portions of its range.

Study system

Campbellton, Conne, and Western Arm are in three distinct geographic regions of Newfoundland (Fig. 1). Campbellton flows into Notre Dame Bay on the northeast coast of the island and is underlain by marine siliciclastic sedimentary rock and felsic volcanic rock; Conne into Bay d'Espoir on the south coast and is underlain by marine siliciclastic sedimentary rock; and Western Arm into the Straight of Belle Isle on the Great Northern Peninsula and is underlain by thin-bedded limestone, dolostone, and shales (Colman-Sadd et al. 2000; Fig. 1). Anadromous and resident forms of *Salmo salar* numerically dominate the fish communities in the three study rivers. Other freshwater fishes include brook trout (*Salvelinus fontinalis*), American eel (*Anguilla rostrata*), rainbow smelt (*Osmerus mordax*), and three-spined stickleback (*Gasterosteus aculeatus*). The occasional upstream migrating American shad (*Alosa sapidissima*) is found at the counting fence at Western Arm (Chadwick 1982), while alewife (*Alosa pseudoharengus*) periodically occurs at Conne (O'Connell and Dempson 1996).

Salmon populations on Campbellton, Conne, and Western Arm have been monitored by Fisheries and Oceans Canada since 1993, 1986,

Table 1. Whole body %P of migratory life stages of selected anadromous fishes extracted from the literature and used in fish mediated P flux studies. %P presented as percent of wet weight.

Species	Study	Population	%P			Used by:
			Adult (*n*)	Kelt (*n*)	Smolt (*n*)	
Salmo salar	Shearer et al. (1994)†	Artificial rearing	0.40 (5)	0.48 (5)	0.52 (5)	None
	Lyle and Elliott (1998)‡	River Tweed, UK	0.47 (5)	0.47 (0)	0.45 (9)	Lyle and Elliott (1998), Jonsson and Jonsson (2003)§
	Talbot et al. (1986)	Mixed	0.39 (4)	0.58 (2)	0.45 (8)	Jonsson and Jonsson (2003)§
	This study	Newfoundland, Canada	0.37 (14)	0.54 (15)	0.63 (20)	NA
Alosa pseudoharengus	Durbin et al. (1979), West et al. (2010)	Pausacaco Pond, Rhode Island, USA	0.42 (29)	0.45 (14)	0.58	West et al. (2010), Twining et al. (2013)
Oncorhynchus nerka	Donaldson (1967)	Lake Illiamna, Arkansas, USA	0.38	NA	0.43	Moore and Schindler (2004), Scheuerell et al. (2005), Moore et al. (2011), Kohler et al. (2013)
Oncorhynchus spp.	Larkin and Slaney (1997)#	British Columbia, Canada	0.36	NA	...	Larkin and Slaney (1997), Gresh et al. (2000)††, Thomas et al. (2003)‡‡

† Cultured fish. Adults sampled as maturing fish in July. Kelts sampled as post-spawn fish with gonads removed. Smolt sampled as 32 g parr in freshwater. Numbers extracted from figure using ImageJ.

‡ Adult and kelt %P assumed to be equal. Cited as Elliott (1976), which presents brown trout (*Salmo trutta*) proximate composition.

§ Cite Lyle and Elliott (1998) and Talbot et al. (1986) but the authors did not clarify the numbers used.

¶ Unpublished dissertation with restricted access. Numbers were extracted from Moore and Schindler (2004).

Based on personal communication, average of five species (*O. nerka, O. kisutch, O. gorbuscha, O. keta, O. tschawytshca*).

†† Used 0.35 %P but cite Larkin and Slaney (1997) who used 0.36 %P.

‡‡ Cite Donaldson (1967), but use number from Larkin and Slaney (1997).

and 1971, respectively. Adult salmon and smolts were enumerated at counting fences (Appendix A: Table A1). We refer the reader Appendix A for a brief description of enumeration protocols and to Downton et al. (2001), Dempson et al. (2004), and Chadwick (1982) for a detailed description of enumeration protocols on Campbellton, Conne, and Western Arm, respectively. Smolts typically migrate to the ocean at ages 2–5 (O'Connell and Ash 1993) and return to spawn after one winter at sea. All three populations were exploited in Newfoundland's coastal mixed-stock commercial fishery until a moratorium in 1992. Because of this drastic change in management, we chose to include only years after the commercial fishery moratorium in our study (i.e., 1993–2012).

Recreational fishing is allowed on Campbellton and 7–15% of small salmon (<63 cm) are retained by anglers (Downton et al. 2001). Conne supports a limited recreational harvest (DFO 2014), previously supported a First Nations subsistence fishery (Dempson et al. 2004), and the fjords near the mouth of the river have sheltered part of Newfoundland's expanding salmon and trout (*Oncorhynchus mykiss*) aquaculture industry since the mid-1980s. In Western Arm, recreational fishing was prohibited in 1988 (Mullins et al. 2001). Therefore, the Western Arm salmon population experienced zero legal removal of adult fish from the river above the counting fence during the years included in our study. Conne is included in the South Newfoundland population which was recently deemed threatened (COSEWIC 2010), while the other two populations are considered not at risk.

Quantifying whole body %P of adults, kelts, and smolts

To test whether nutrient content of salmon differed by life stage and/or population, we quantified whole body %P of at least four individuals of each life stage from each population (Appendix B: Table B1). Fish were collected at counting fences on the three study rivers by

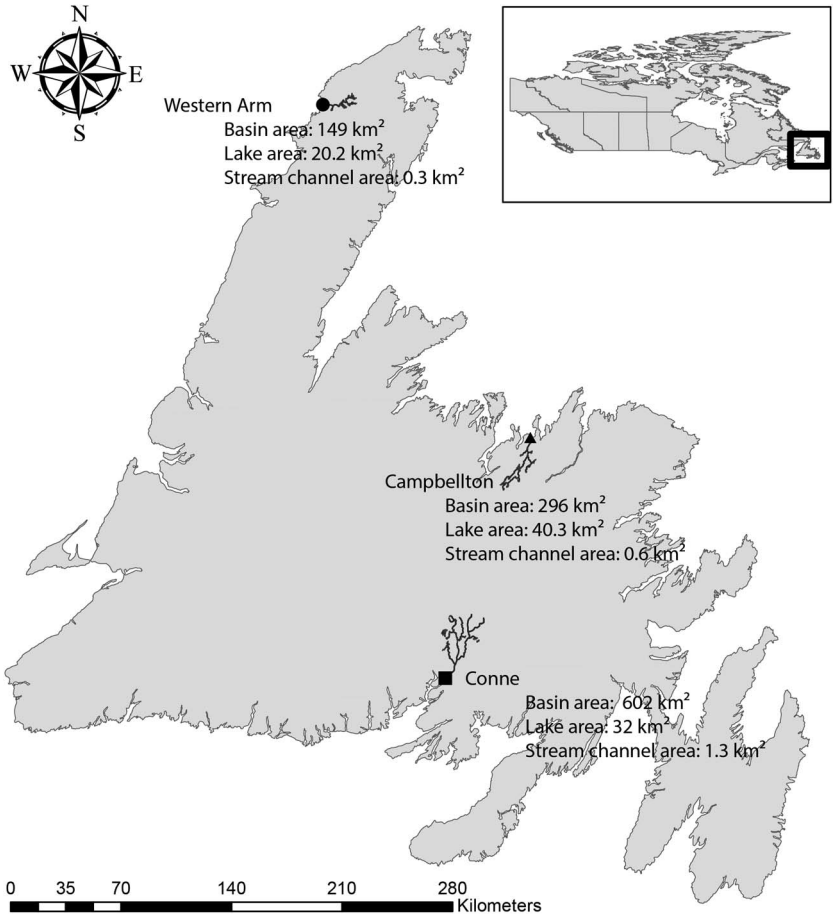

Fig. 1. Map of insular Newfoundland, Canada, (inset) showing three study watersheds where Atlantic salmon were collected for elemental analysis and, subsequently, salmon-mediated P flux was estimated.

Fisheries and Oceans Canada personnel, placed in polyethylene bags and frozen before being transported to Memorial University of Newfoundland, St. John's, Newfoundland, Canada, for initial processing. Whole fish were homogenized by wet grinding multiple times and refrozen for analysis for total phosphorus at the Agriculture and Food Laboratory at the University of Guelph on an VARIAN VISTRA-Pro simultaneous ICP-OES according to standard protocols. Further detail regarding fish sample preparation is provided Appendix B.

We fit general linear models (GLM) with wet weight %P as the dependent variable and life stage, population, and both life stage and population as explanatory variables. We used Akaike's information criterion corrected for small sample sizes (AIC_c) in the AICcmodavg R package to determine the weight of evidence in support of life stage and or river as important predictors of variation in salmon %P. We calculated effect size of life stage and river as the percent difference in mean whole-body P concentration among life stages and between rivers within life stages, respectively. We compared model fits according to the reduction in deviance caused by adding parameters to the null model, expressed as a percent of the deviance of the null model. Mathematically, it is expressed as

$$\text{Deviance explained} = (D_{null} - D_{fitted})/D_{null}$$

where D is the deviance extracted from the GLM summary.

Estimating phosphorus fluxes

We used population counts to estimate 60 river

years of P flux via Atlantic salmon with the basic P flux model modified for application to an iteroparous species by accounting for P export by kelts similar to that described in the introduction of this article (e.g., Moore et al. 2011). Newfoundland's adult salmon data, summarized in Appendix A, are split into two sets for a given year; one set for small salmon (<63 cm fork length; FL) and another set for large salmon (>63 cm FL). Large salmon in these rivers are typically repeat spawners. Therefore, we altered the basic P flux model to incorporate these two groups into calculations of adult import and kelt export as

$$Import_{adult,t} = A_{small,t}M_{small,t}N_a + A_{large,t}M_{large,t}N_k$$

$$Export_{kelt,t} = kb_{small}A_{small,t}M_{small,t}N_k + kb_{large,t}A_{large,t}M_{large,t}N_k$$

where, subscripts *small* and *large* refer to small salmon or large salmon data from which parameters (defined in the *Introduction*) were calculated as described below. Smolt export was calculated as described in the introduction.

Annual P import by spawning adults and export by smolts was calculated using spawning escapement, weights, and whole body %P of spawning adults and smolts (Appendix B: Table B2). Spawning escapement was calculated by adjusting actual counts of adults passing upstream through the counting fences for the number of individuals removed from the system by recreational anglers as determined from analysing data obtained from an angler license stub return system on Campbellton (plus an estimate for unreturned license stubs) and via reports from fishery guardians on Conne. Counts and spawner escapement on Western Arm were nearly identical during this period because recreational angling is prohibited in this system (Appendix A: Table A1). We compiled smolt weights measured annually for 100–300 individuals on each stream as they passed through counting fences. Adult weights and lengths for small adults were measured on all three study streams for nearly all of the study years. Large salmon measurements were available for almost all years on Western Arm and for five years on Campbellton. If the weights of smolt or adults were not measured on a river in a given year, we used the mean measured weight over the entire time series of the same size class and life stage for that river. Large salmon were not measured for weight at Conne from 1993 to 2012, thus we used weights and lengths of large salmon on Conne River measured from 1986 to 1992 ($n = 6$) and applied it to the whole time series.

Estimating P export by kelts was not as direct as estimating P import by adults or P export by smolts because complete counts of out-migrating kelts from Newfoundland rivers are rare. Overwinter survival on Campbellton for 1994–2012 was 0.57 (range: 0.31–0.76; M. Robertson, *unpublished data*) where outmigrating kelts are captured in the smolt counting fence. Kelts are rarely captured in counting fences on Conne and Western Arm because they presumably migrate before the smolt fences are installed in the spring. Although we can expect variability in overwinter survival among rivers and years, we applied this mean post-spawn survival rate to all three study rivers. To address the uncertainty in kelt survival, we compared P flux estimated with a mean, high, low and measured annual overwinter survival rates for Campbellton (see Appendix D).

Direct measurements of the mass of adults retained by kelts upon exiting the river (b) are also rare for Newfoundland rivers. We estimated parameter b in nutrient flux model by inserting annual mean lengths of adults into length-weight relationships for kelts measured in 2014 on Campbellton ($n = 75$) and Western Arm ($n = 10$) and adults measured on Campbellton ($n = 175$), Conne ($n = 64$), and Western Arm ($n = 100$). The proportion of adult mass retained by kelt (parameter b) for each year in the series was calculated as

$$b = 10^{\alpha_k + \beta_k \log_{10}(L_t)} / 10^{\alpha_a + \beta_a \log_{10}(L_t)}$$

where α and β are slopes and intercepts of the length-weight relationship for kelts (subscript k) and adults (subscript a), and L_t is the mean fork length of adults measured at the counting fence in year t. If mean length of either small or large adults was not available for a given year and river, we used the mean length over the entire time series for that river (Appendix A). Since our salmon count, weight, and length data was specific to either small or large salmon, we calculated separate b's for each group of fish using $L_{small,t}$ and $L_{large,t}$ to estimate total P exported by kelts.

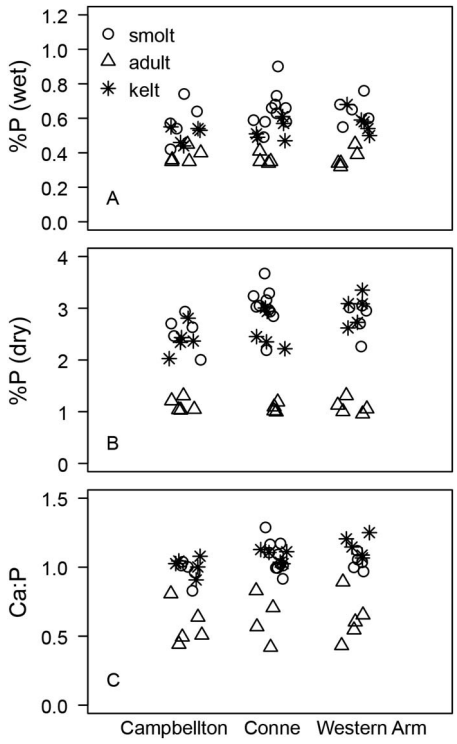

Fig. 2. Whole body phosphorus concentration (A and B) and Ca:P (C) of Atlantic salmon adults (open triangle), kelts (asterisk), and smolts (open circle) captured in three insular Newfoundland rivers. Phosphorus concentration is presented on a wet mass basis (A) and dry mass basis (B). Mean wet weight %P for each river and life stage combination is provided in Appendix B.

Sensitivity of flux model to assumptions regarding salmon %P

To determine the sensitivity of P flux estimates to variation in whole body %P that may occur when applying nutrient content values obtained from distant systems or assuming kelt and adults %P are equivalent, we calculated P flux using three different sets of salmon %P values: (1) means of population specific %P as a percentage of wet mass, (2) a regional value calculated as the mean of %P (wet mass) of all individuals sampled from the three study rivers, and (3) %P values published in Lyle and Elliott (1998), which assumed that adult and kelt %P is equal. To determine whether the body composition values affected the characteristics of the P flux time series, we used simple linear regressions of P flux against time for flux estimates calculated using the three different %P values described above. We tested for homogeneity of regression coefficients and equality of elevations for k regressions as described by Zar (2010). When significant differences in either regression coefficients or elevation were found, we conducted multiple comparisons with Tukey HSD tests. We used R version 2.15.2 for all calculations and statistical analyses (R Development Core Team 2012).

Results

Whole-body P-content of three life stages of Atlantic salmon

Overall, differences in salmon %P among rivers but within life stages was not as strong as differences among life stages (Fig. 2). Life stage was more important in explaining among-individual variation in whole-body P concentration than was river (Table 2). Life stage explained 65% of variation in %P among individuals, whereas river only explained 1.6%. Although a model including both life stage and river provided a slightly better fit to the data than did the model including life stage as the sole predictor, it came at the cost of an additional parameter (Table 2).

We explored the magnitude of difference in whole-body %P between life stages on a wet mass basis because this is the metric most suitable for nutrient flux models. When individuals were pooled across rivers, adult P concentration was 45% lower than that of kelt; kelt P concentration was 18% lower than that of smolts; smolt P concentration was 70% higher than that of adults. Similar patterns held true within rivers (Fig. 2). The highest %P was observed in Conne smolt and was similar to smolts from Western Arm. The lowest %P occurred in Conne adults, but the difference in adult %P between the highest and lowest river was less than 0.02 %P. The ratio of calcium to P (Ca:P), an indicator of the amount of P contained within bone (Pilati and Vanni 2007), was higher in smolts (mean = 1.01) and kelts (mean = 1.10) than it was in adults (mean = 0.60).

Table 2. Results of general linear models of whole body P concentration of Atlantic salmon from three insular Newfoundland rivers with life stage and river of capture as explanatory variables.

Model	k	Log likelihood	AIC_c	ΔAIC_c	Akaike weights	Deviance explained
Life stage	3	55.34	−104.15	0	0.52	64.73
Life stage + river	4	56.45	−103.98	0.16	0.48	66.28
Intercept	2	29.81	−55.36	48.79	0	0.00
River	3	30.20	−53.89	50.29	0	1.56

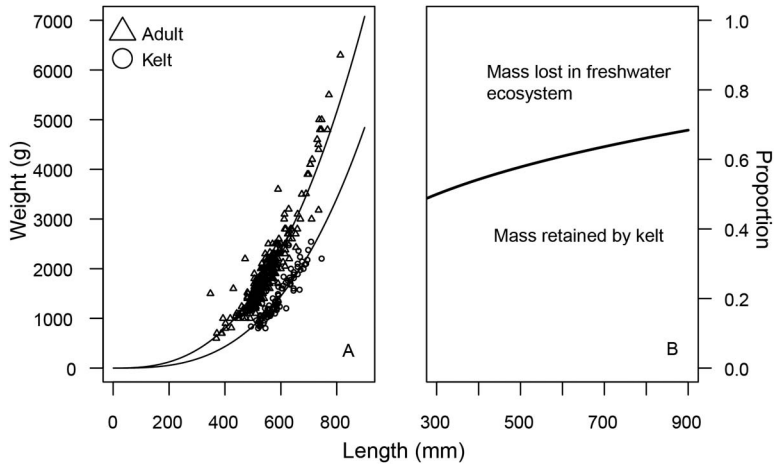

Fig. 3. Length-weight relationships (A) for adults ($n = 339$, $y = 10^{-4.10+2.69\ (\log(X))}$, adjusted $R^2 = 0.86$) and kelts ($n = 85$, $y = 10^{-5.11+2.98\ (\log(X))}$, adjusted $R^2 = 0.82$) collected from Newfoundland rivers and used to estimate the proportion of adult mass that exits the river retained in kelts (B) in the nutrient flux model for a given length of adult (i.e., parameter b).

Annual P flux using river-specific salmon P concentration

As expected, a logarithmic relationship existed between the lengths and weights of adults and kelts (Fig. 3A). Weight at a given length for kelts was 55–65% of adult weight upon entering the river (Fig. 3B). Parameter b applied to each year ranged from 0.56 to 0.59 for small salmon and from 0.62 to 0.65 for large salmon depending on the mean length of small and large adults for that year.

Using river-specific %P measurements, we estimated that Atlantic salmon exported more phosphorus as smolts and kelts than was imported by adults on the three study rivers (solid line; Fig. 4). Median annual P flux was −0.45 kg ± 4.07 SD, −6.79 kg ± 4.05 SD, and −0.15 kg ± 1.71 SD for Campbellton, Conne, and Western Arm, respectively. Campbellton was the only river to exhibit weak but statistically significant positive linear trend in P flux over the study period ($y = 0.439x - 4.801$, df = 18, $r^2 = 0.37$, $p = 0.003$). Salmon were net exporters of P in all streams; over the 20 year period, smolts exported 102% and 108% of P deposited by adults in Campbellton and Western Arm (i.e., deposit = net import). In contrast, smolts exported 188% of adult deposited P in Conne (Appendix C: Table C1).

Effect of body composition value source on P flux estimates

The source of %P for the different life stages (i.e., river specific, regional, or literature value) did not influence the slope of linear trend in flux over the study period but significantly affected the elevation of that trend (Campbellton, $F_{0.05(2),56} = 21.13$, $p < 0.001$; Conne, $F_{0.05(2),56} = 28.96$, $p < 0.001$; Western Arm $F_{0.05(2),56} = 15.18$, $p < 0.001$). Using multiple comparison tests, we found that %P values that assumed equal %P of adults and kelts (Lyle and Elliott 1998) yielded

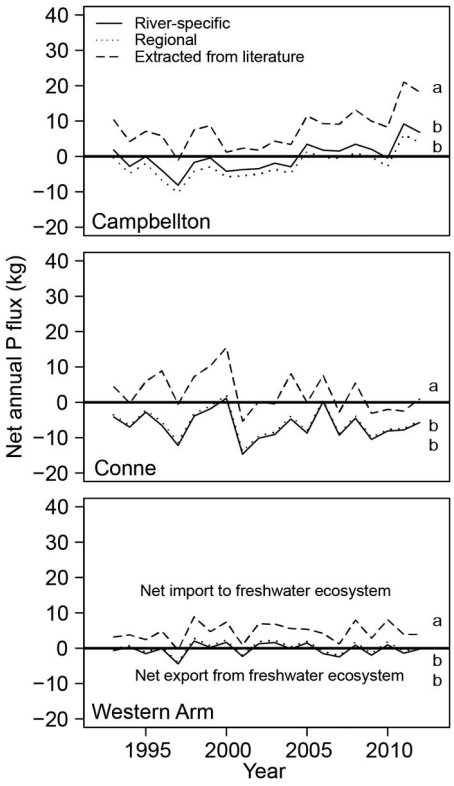

Fig. 4. Time series of net flow of phosphorus via Atlantic salmon from three Newfoundland rivers from 1993 and 2012 calculated using three different whole body phosphorus concentration values. The thick horizontal line denotes annual P flux = 0. Values above this line indicate that P is imported to the freshwater ecosystem, whereas values below indicate P is exported from the freshwater ecosystem. The different lines describe flux values estimated using river-specific, regional, and previously published salmon P concentration values. River-specific and regional P concentration values were obtained through direct measurement of fish from study rivers. The values extracted from the literature are described in Lyle and Elliott (1998). Significant differences between pairs of time series determine with Tukey HSD multiple comparison tests for differing elevations of linear regressions for flux against time ($p < 0.05$) are indicated with contrasting letters.

flux values that diverged significantly from our directly measured, river specific values, but the elevations of regressions did not differ significantly between the regional and the pooled estimate (Fig. 4). Median P flux estimated with body %P extracted from Lyle and Elliott (1998) was higher than those estimated with our directly measured %P in all three rivers. In contrast to river-specific %P, the assumption that adult and kelt nutrient content is equal led to the opposite pattern, where flux estimates were positive in all streams in nearly all years. As expected, low overwinter survival rates resulted in higher P flux than high overwinter survival rates, but P flux estimated with mean overwinter survival held constant over the entire time period did not differ from variable, directly measured overwinter survival on Campbellton (Appendix D).

Discussion

We set out to (1) assess whether ontogenetic stage or river of origin were important predictors of salmon %P, and (2) to quantify Atlantic salmon mediated P flux for three Newfoundland rivers using salmon body P measurements of different resolutions (i.e., river specific, regional means, and existing literature values). Our results clearly depict differences in Atlantic salmon %P among life stages, and that these differences modulate the species' functional role in their natal freshwater ecosystems. The Atlantic salmon sampled in our study exhibited a wide range of %P, but most of the variation occurred among rather than within life stages. Smolt and kelt %P in this study differed on average by only 0.09%P by wet weight (Fig. 2A) and fell in the middle of the range of dry weight %P of freshwater fishes (1–6%P by dry mass; McIntyre and Flecker 2010; Fig. 2B). Adult wet weight %P, however, was on average 0.29% lower than smolt wet weight %P and fell at the extreme low end of the range for freshwater fishes. Ontogeny explained a larger portion wet weight %P variation among individual Atlantic salmon than was explained by population of origin (Table 2). By qualitatively assessing the effect size of life stage on wet weight %P, we reject the hypothesis that wet weight %P of adults entering the river to spawn is equal to the wet weight %P of post-spawn kelts exiting the river. Therefore, the assumption of equal wet weight %P in adults and kelts, which is used by several previous nutrient flux studies (Lyle and Elliott 1998, Jonsson and Jonsson 2003*a*, Moore et al. 2011), is likely invalid, at least for

populations examined in the current study. We show for three insular Newfoundland salmon rivers, this assumption caused us to overestimate actual Atlantic salmon-mediated P flux across the marine-freshwater ecosystem boundary (Fig. 4), such that our interpretation of the ecosystem function of these populations changed from considering these populations as P sources to concluding that they are P sinks or exhibit a balanced flow in the long term.

Whole body % phosphorus

Life stage explained 65% of variation in %P among individuals, whereas river explained under 2% (Table 2). The overwhelming evidence for life stage as a driver of intraspecific variation in %P is consistent with studies on gizzard shad (*Dorosoma cepedianum*; Pilati and Vanni 2007), Eurasian perch (*Perca fluviatilus*; Vrede et al. 2011), and artificially reared Atlantic salmon (Shearer et al. 1994) that show a change in %P on a dry mass basis with ontogeny. These studies attribute ontogenetic changes %P (dry weight) to the ossification of bones during growth as demonstrated by positive relationships between body size and %P in immature fishes. We observed the opposite pattern; %P wet weight declined from smolts to adults and increased from the adults to kelts. The pendulum-like shift in %P during the smolt-adult-kelt ontogeny shows that material allocated for reproduction and the time in the reproductive cycle can influence observed intraspecific variability in body nutrient composition.

Previous investigations of fish nutrient content attribute interspecific variability to skeletal structure (Sterner and George 2000, Hendrixson et al. 2007, McIntyre and Flecker 2010). Intraspecific variation in %P has been attributed to local environmental conditions that influence %C (i.e., predation; El-Sabaawi et al. 2012) and to ontogeny (Pilati and Vanni 2007). Pilati and Vanni (2007) measured individual %P along a size gradient that encompassed ontogenetic diet shifts and concluded that the %P of fish beyond a threshold size was stable. Yet, their study did not include adult fishes approaching or immediately following a reproductive event, at which time sequestered resources are allocated to gamete production rather than growth. We followed the approach of Pilati and Vanni (2007) by using Ca:P ratios to qualitatively assess whether differences in P content between life stages of Atlantic salmon in our study were associated with changes in contribution of bone to body mass (Fig. 2C). Ca:P of smolts and kelts was similar to gizzard shad juveniles and is approximately one-half the Ca:P of bone (fish bone, 2.14; Hendrixson et al. 2007). Adult Ca:P was one-quarter the Ca:P of bone suggesting that more P was stored in tissues other than bone when salmon return to freshwater than when they migrate to the ocean.

The increase in body %P between adult and kelt life stages suggests some form of dilution of body P by other elements in adult salmon. In our study, %C was approximately 100% higher in returning adults than it was in kelts and smolts (Appendix B: Fig. B1). The high %C of adults is likely associated with the storage of lipids during the ocean-feeding phase of the species' life cycle. The difference between %C in adults and kelts results from the allocation of energy to gonadal development (Jonsson and Jonsson 2003*b*) and the catabolism of free fatty acids during migration and periods of sustained swimming during non-feeding freshwater residence over the winter (Doucett et al. 1999). Thus, we speculate that the low %P observed in Atlantic salmon adults relative to smolts and kelts, is likely caused by the stoichiometric dilution of P by C. This finding highlights the need to measure not only energy content (see Jonsson and Jonsson 2003*b*), but also nutrient content of fishes along their entire life histories from larval to post-spawn stages, which is rarely done for wild fishes.

We were surprised that river explained only a small portion of variation in salmon %P because spatial differences in %P have been found in other fishes (Boros et al. 2012, El-Sabaawi et al. 2012). El-Sabaawi and colleagues (2012) found that the presence of limestone in watersheds had a greater influence on %P of Trinidadian guppies than did genetic lineage because limestone deposits have direct effects on the amount of P cycling in aquatic ecosystems and thus a different biogeochemical setting for juvenile growth. We expected similar watershed effects to emerge in our study because Western Arm is underlain by limestone and dolostone, whereas the other two study streams are underlain by siliciclastic rocks with low P content (Colman-Sadd et al. 2000).

The three salmon populations presumably rear under different biogeochemical conditions, are genetically distinct (Bradbury et al. 2014), and leave the freshwater ecosystem at different ages (O'Connell and Ash 1993), yet we found no appreciable differences in body %P. We conclude that environmental factors and fine scale genetic differences are not drivers of salmon %P at the resolution we examined in this study. Our sample size may not have been large enough to capture intra-population variation within life stages, particularly smolt. However, it is likely that evolutionary forces associated with resource allocation to reproduction are at play in these systems.

Body stoichiometry is a biochemical descriptor of an individual's traits and is subject to natural selection because biochemical characteristics of certain anatomical features provide fitness benefits (Kay et al. 2005). Similar to classic phenotypes such as behavior, and morphology, the elemental composition, acquisition, assimilation, allocation, and excretion by organisms can be considered an elemental phenotype (Jeyasingh et al. 2014). Indeed, the biochemical signature of evolution can be seen in the association of body stoichiometry with phylogeny (Hendrixson et al. 2007). The consistency in %P among the three study populations within life stages may relate to the interaction of proximate factors (i.e., physiological states) with genetic thresholds that some researchers have used to model variation in the timing of ontogenetic shifts in Atlantic salmon (Thorpe et al. 1998), such as the migration of juveniles to the ocean and adults to freshwater. The low coefficient of variation within life stages, the similarity in smolt %P among populations, and the convergence of %P at the smolt and kelt stages suggests that %P may be a conserved elemental phenotype related to migration timing: a classic phenotype (Jeyasingh et al. 2014). Kay et al. (2006) found similar stage-structure differences in body P-content in pavement ants (*Tetramorium caespitum*), which they attributed to the structural needs of the various stages from larvae to worker ants (Kay et al. 2006). Currently, the effect of body elemental composition on behavioral patterns and the reproductive success of fishes is unknown, but is important to understand (Kay et al. 2005).

Phosphorus flux

Atlantic salmon can be either sources or sinks of P in freshwater ecosystems. Sources and sinks can be conditional or unconditional (Loreau et al. 2013); the former meaning that whether a subsystem imports or exports an entity depends on conditions within the subsystem or ecosystem, and the latter meaning that a subsystem is an importer or exporter of an entity under all conditions. In the context of anadromous salmonids, spawning adults are an unconditional source of nutrients to freshwater ecosystems, whereas smolts are an unconditional sink. When considering a river's entire salmon population as the subsystem of interest, however, the balance of adult import with export by smolt determines whether a salmon population is source or sink of nutrients in freshwater ecosystems.

There is a general consensus that Pacific salmon populations are unconditional sources of nutrients to their natal streams (Moore and Schindler 2004, Scheuerell et al. 2005) or should be (Moore et al. 2011, Kohler et al. 2013). In our study on Atlantic salmon over a 20-year period, flow of P into freshwater via adult salmon and the flow of P back to the ocean via smolts was almost perfectly efficient in Campbellton and Western Arm, meaning that adult salmon deposited nearly the same amount of P that was exported by smolts. Meanwhile, the Conne salmon population is a P sink in 90% of years included in our study and the median P flux is much more negative than the other populations. Median annual P flux on Conne is the most negative estimate we have found for an anadromous fish population. Atlantic salmon adult returns to Conne declined 80% between 1987 and 1992 (Dempson et al. 2004) and has continued to decline (Robertson et al. 2013) coincident with increases in salmonid aquaculture production in the region and is included in the South Newfoundland population that was designated as threatened under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) guidelines (COSEWIC 2010). We conclude that healthy Atlantic salmon populations in this study shift between sources and sinks of P at the annual scale and are balanced at longer temporal scales. It appears that Atlantic salmon populations experiencing a long term decline potentially due to adverse marine condi-

tions may be unconditional P sinks.

Anadromous salmonids exhibit a wide range of phenotypes (e.g., semelparity/iteroparity, spawning density, duration of parr stage) in an equally wide range of freshwater habitats, from small oligotrophic mountain streams to coastal rivers and lakes. Amongst the diversity of spawning and rearing strategies, one consequence of life history is common to all anadromous salmonids: they move nutrients between the ocean and freshwater. The ubiquity of this ecosystem function makes flux a useful metric for comparing and understanding the interplay of salmon with their natal ecosystems among species and regions. Yet, the utility of such comparisons is predicated on the accuracy of flux estimates. In our study, the differences between adult and kelt %P has important implications for obtaining ecosystem flux via iteroparous species. The use of %P values from Lyle and Elliott (1998) leads us to a different conclusion about the ecosystem role of Atlantic salmon than our own direct measures of Atlantic salmon %P. By assuming that %P of adults and kelts are equal, we would erroneously conclude that Atlantic salmon are consistently net importers of P to all three Newfoundland streams, whereas by accounting for differences between kelts and adults we conclude the opposite; that stable or growing Atlantic salmon populations are balanced and declining populations are sinks. Therefore, our results call into question the strength of the net P import by salmon populations to the River Tweed (Lyle and Elliott 1998) and the River Imsa (Jonsson and Jonsson's 2003*a*; see Table 1). This problem may be more pronounced in flux estimates for iteroparous fishes than it is for semelparous fishes due to the addition of post-spawn export by kelts; a value that depends on estimates of post-spawn survival rate (see Appendix D), proportion of mass lost during spawning and residence, and kelt nutrient composition.

Nutrient mass models of migratory animals and the patterns that emerge may shine light upon the evolution of different life history strategies within and among species, as well as provide new insights into the temporal dynamics of populations in the context of their ecosystem. Nutrient inputs by anadromous fishes can play a defining role in short-term ecosystem processes including fish production (e.g., Bentley et al. 2012). Underlying the short-term ecological processes associated with nutrient inputs are the long term trends in nutrient deposition and extraction. We highlight the need for information regarding the elemental composition of migratory animals where possible to understand ontogenetic and spatial patterns because it allows populations to be placed accurately in the context of long term biogeochemical cycling. Additionally, our results contradict the common notion that naturally functioning anadromous fish populations are ubiquitously net sources of all nutrients to freshwater ecosystems, raising questions about what factors determine the magnitude and direction of animal-mediated flows of specific nutrients.

Acknowledgments

We would like to thank the researchers, technicians, and other employees of Department of Fisheries and Oceans Canada who collected data on the three study systems for the past 20 years. Their efforts are essential to the understanding and conservation of Atlantic salmon. A. L. Tanner made our study system map. Numerous volunteers assisted with salmon sample processing. A. E. Kohler, B. M. Elledge, the Leroux Lab, the Hurford lab, and two anonymous reviewers provided helpful comments on this manuscript. We would also like to acknowledge NSERC Discovery Grant, Research and Development Corporation of NL Ignite R&D Grant, and Memorial University of Newfoundland for funding.

Literature Cited

Bauer, S., and B. J. Hoye. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 344:61–79.

Bentley, K. T., D. E. Schindler, J. B. Armstrong, R. Zhang, C. P. Ruff, and P. J. Lisi. 2012. Foraging and growth responses of stream-dwelling fishes to inter-annual variation in a pulsed resource subsidy. Ecosphere 3:113.

Boros, G., J. Jyvasjarvi, P. Takacs, A. Mozsar, I. Tatrai, M. Sondergaard, and R. I. Jones. 2012. Between-lake variation in the elemental composition of roach (*Rutilus rutilus* L.). Aquatic Ecology 46:385–394.

Bradbury, I. R., L. C. Hamilton, M. J. Robertson, C. E. Bourgeois, A. Mansour, and J. B. Dempson. 2014. Landscape structure and climatic variation determine Atlantic salmon genetic connectivity in the Northwest Atlantic. Canadian Journal of Fisheries

and Aquatic Sciences 71:246–258.

Chadwick, E. M. P. 1982. Dynamics of an Atlantic salmon stock (*Salmo salar* L.) in a small Newfoundland River. Dissertation. Memorial University of Newfoundland, St. John's, Newfoundland, Canada.

Childress, E. S., J. D. Allan, and P. B. McIntyre. 2014. Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. Ecosystems 17:522–534.

Colman-Sadd, S. P., J. P. Hayes, and I. Knight. 2000. Geology of the island of Newfoundland (digital version of Map 90-01 with minor revisions). Map 2000-30, scale 1:1000000. Newfoundland Department of Mines and Energy, Geological Survey, Newfoundland, Canada.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada]. 2010. COSEWIC assessment and status report on the Atlantic Salmon *Salmo salar* (Nunavik population, Labrador population, Northeast Newfoundland population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada. www.sararegistry.gc.ca/status/status_e.cfm

Dempson, J. B., G. Furey, and M. Bloom. 2004. Status of Atlantic salmon, *Salmo salar*, in Conne River, SFA 11, Newfoundland, 2003. Canadian Science Advisory Secretariat Research Document 2004/057. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Dempson, J. B., and D. E. Stansbury. 1991. Using partial counting fences and a two sample stratified design for mark-recapture estimation of an Atlantic salmon smolt population. North American Journal of Fisheries Management 11:27–37.

DFO [Department of Fisheries and Oceans]. 2014. Newfoundland and Labrador angler's guide 2014-2015. DFO/2014-1920. Fisheries and Oceans Canada, Ottawa, Ontario, Canada.

Donaldson, J. R. 1967. The phosphorus budget of Iliamna Lake, Alaska, as related to the cyclic abundance of sockeye salmon. Dissertation. University of Washington, Seattle, Washington, USA.

Doucett, R. R., R. K. Booth, G. Power, and R. S. McKinley. 1999. Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights from stable isotope analysis. Canadian Journal of Fisheries and Aquatic Sciences 56:2172–2180.

Downton, P. R., D. G. Reddin, and R. W. Johnson. 2001. Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2000. Research Document 2001/031. Canadian Science Advisory Secretariat, Ottawa, Ontario, Canada.

Durbin, A. G., S. W. Nixon, and C. A. Oviatt. 1979. Effects of spawning migration of the Alewife, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology 60:8–17.

Elliott, J. M. 1976. Body composition of brown trout (*Salmo trutta* L.) in relation to temperature and ration size. Journal of Animal Ecology 45:273–289.

El-Sabaawi, R. W., E. Zandona, T. J. Kohler, M. C. Marshall, J. M. Moslemi, J. Travis, and A. S. A.S. Flecker. 2012. Widespread intraspecific organismal stoichiometry among populations of the Trinidadian guppy. Functional Ecology 26:666–676.

Gresh, T., J. Lichatowich, and P. Schoonmaker. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries 25:15–21.

Hendrixson, H. A., R. W. Sterner, and A. D. Kay. 2007. Elemental stoichiometry of freshwater fishes in relation to phylogeny, allometry, and ecology. Journal of Fish Biology 70:121–140.

Hocking, M. D., and J. D. Reynolds. 2011. Impacts of salmon on riparian plant diversity. Science 331:1609–1612.

Holtgrieve, G. W., D. E. Schindler, and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 24:1125–1135.

Jeyasingh, P. D., R. D. Cothran, and M. Tobler. 2014. Testing the ecological consequences of evolutionary change using elements. Ecology and Evolution 4:528–538.

Jonsson, B., and N. Jonsson. 2003*a*. Migratory Atlantic salmon as vectors for the transfer of energy and nutrients between freshwater and marine environments. Freshwater Biology 48:21–27.

Jonsson, N., and B. Jonsson. 2003*b*. Energy allocation among developmental stages, age groups, and types of Atlantic salmon (*Salmo salar*) spawners. Canadian Journal of Fisheries and Aquatic Sciences 60:506–516.

Kay, A. D., I. W. Ashton, E. Gorokhova, A. J. Kerkhoff, A. Liess, and E. Litchman. 2005. Toward a stoichiometric framework for evolutionary biology. Oikos 109:6–17.

Kay, A. D., S. Rostampour, and R. W. Sterner. 2006. Ant stoichiometry: elemental homeostasis in stage structured colonies. Functional Ecology 20:1037–

1044.

Kohler, A. E., P. C. Kusnierz, T. Copeland, D. A. Venditti, L. Denny, J. Gable, and M. S. Wipfli. 2013. Salmon-mediated nutrient flux in selected streams of the Columbia River basin, USA. Canadian Journal of Fisheries and Aquatic Sciences 70:502–512.

Larkin, G. A., and P. A. Slaney. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22:16–24.

Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147–1156.

Loreau, M., T. Daufresne, A. Gonzalez, D. Gravel, F. Guichard, S. J. Leroux, N. Loeuille, F. Massol, and N. Mouquet. 2013. Unifying sources and sinks in ecology and Earth sciences. Biological Reviews 88:365–379.

Lyle, A. A., and J. M. Elliott. 1998. Migratory salmonids as vectors of carbon, nitrogen and phosphorus between marine and freshwater environments in north-east England. Science of the Total Environment 210:457–468.

McIntyre, P. S., and A. S. Flecker. 2010. Ecological stoichiometry as an integrative framework in stream fish ecology. American Fisheries Society Symposium 73:539–558.

Moore, J. W., S. A. Hayes, W. Duffy, S. Gallagher, C. J. Michel, and D. Wright. 2011. Nutrient fluxes and the recent collapse of coastal California salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 68:1161–1170.

Moore, J. W., and D. E. Schindler. 2004. Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 61:1582–1589.

Mullins, C. C., D. Caines, and S. L. Lowe. 2001. Status of Atlantic salmon (*Salmo salar* L.) stocks of Lomond River, Torrent River, and Western Arm Brook, Newfoundland, 2000. Research document 2001/039. Canadian Science Advisory Secretariat, Ottawa, Ontario, Canada.

Nislow, K., J. Armstrong, and S. McKelvey. 2004. Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography. Canadian Journal of Fisheries and Aquatic Sciences 61:2401–2410.

O'Connell, M. F., and E. G. M. Ash. 1993. Smolt size in relation to age at first maturity of Atlantic salmon (*Salmo salar*): the role of lacustrine habitat. Journal of Fish Biology 42:551–569.

O'Connell, M. F., and J. B. Dempson. 1996. Spatial and temporal distributions of salmonids in two ponds in Newfoundland, Canada. Journal of Fish Biology 48:738–757.

Parrish, D. L., R. J. Behnke, S. R. Gephard, S. D. McCormich, and G. H. Reeves. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Sciences 55:281–287.

Pilati, A., and M. J. Vanni. 2007. Ontogeny, diet shifts, and nutrient stoichiometry in fish. Oikos 116:1663–1674.

R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Robertson, M. J., L. K. Weir, and J. B. Dempson. 2013. Population viability analysis for the South Newfoundland Atlantic salmon (*Salmo salar*) designatable unit. DFO Canadian Science Advisory Secretariat Research Document 2013/090. Department of Fisheries and Oceans, Ottawa, Ontario, Canada.

Scheuerell, M. D., P. S. Levin, R. W. Zabel, J. G. Williams, and B. L. Sanderson. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). Canadian Journal of Fisheries and Aquatic Sciences 62:961–964.

Schwarz, C. J., and J. B. Dempson. 1994. Mark-recapture estimation of a salmon smolt population. Biometrics 50:98–108.

Seale, D. B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–1550.

Shearer, K. D., T. Asgard, G. Andorsdottir, and G. H. Aas. 1994. Whole body elemental and proximate composition of Atlantic salmon (*Salmo salar*) during the life cycle. Journal of Fish Biology 44:785–797.

Sterner, R. W., and N. B. George. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. Ecology 81:127–140.

Talbot, C., T. Preston, and B. W. East. 1986. Body-composition of Atlantic salmon (*Salmo salar* L) studied by neutron-activation analysis. Comparative Biochemistry and Physiology A: Physiology 85:445–450.

Thomas, S. A., T. V. Royer, G. W. Minshall, and E. Snyder. 2003. Assessing the historic contribution of marine-derived nutrients to Idaho streams. American Fisheries Society Symposium 34:41–55.

Thorpe, J. E., M. Mangel, N. B. Metcalfe, and F. A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12:581–599.

Twining, C. W., D. C. West, and D. M. Post. 2013. Historical changes in nutrient inputs from humans and anadromous fishes in New England's coastal watersheds. Limnology and Oceanography 58:1286–1300.

Vanni, M. J. 2002. Nutrient cycling by animals in

freshwater ecosystems. Annual Review of Ecology and Systematics 33:341–370.

Vanni, M. J., A. S. Flecker, J. M. Hood, and J. L. Headworth. 2002. Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. Ecology Letters 5:285–293.

Vrede, T., S. Drakare, P. Eklov, A. Hein, A. Liess, J. Olsson, J. Persson, M. Quevedo, H. R. Stabo, and R. Svanback. 2011. Ecological stoichiometry of Eurasian perch: intraspecific variation due to size, habitat and diet. Oikos 120:886–896.

West, D. C., A. W. Walters, S. Gephard, and D. M. Post. 2010. Nutrient loading by an anadromous alewife (*Alosa pseudoharengus*): contemporary patterns and predictions for restoration efforts. Canadian Journal of Fisheries and Aquatic Sciences 67:1211–1220.

Wipfli, M. S., J. P. Hudson, D. T. Chaloner, and J. R. Caouette. 1999. Influence of salmon spawner densities on stream productivity in Southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:1600–1611.

Zar, J. H. 2010. Biostatistical analysis. Fifth edition. Pearson Prentice Hall, Upper Saddle River, New Jersey, USA.

Supplemental Material

Appendix A

Atlantic salmon population characteristics

Table A1. Annual count, number of spawning individuals, mass, and length of smolt, small salmon (<63 cm), and large salmon (>63 cm) passing through counting fences installed above the head of the tide on three Newfoundland rivers from 1993 to 2012. Adults on Campbellton and Conne were enumerated by video camera systems installed at openings, person monitors located at openings during the day, and with adult traps. The Western Arm counting facility consisted of an adult trap checked daily. Smolts were counted at fences spanning the entire stream on Campbellton and Western Arm. Department of Fisheries and Oceans, in partnership with the Conne River Indian Band, operate two partial river smolt counting fences on Conne (Dempson and Stansbury 1991) and estimate the full smolt run using a mark-recapture estimator described by Schwarz and Dempson (1994).

Life stage	River	Count	Spawners	Mass (kg)	Length (cm)
Small adult	Campbellton	3043 ± 869	2586 ± 857	1.73 ± 0.44 [470]	53.6 ± 4.1 [470]
	Conne	2435 ± 1010	2305 ± 976	1.54 ± 0.31 [748]	51.9 ± 2.6 [748]
	Western Arm	1185 ± 380	1163 ± 376	1.99 ± 0.38 [1493]	55.0 ± 2.8 [1493]
Large adult	Campbellton	332 ± 160	335 ± 162	3.59 ± 0.67 [41]	68.6 ± 3.8 [41]
	Conne	135 ± 68	136 ± 66	2.97 ± 0.39 [6]	65.8 ± 2.59 [6]
	Western Arm	49 ± 34	47 ± 32	4.50 ± 1.07 [253]	72.7 ± 4.6 [253]
Smolt	Campbellton	40146 ± 8632	NA	0.05 ± 0.002 [20]	17.44 ± 0.48 [20]
	Conne	67209 ± 15745	NA	0.03 ± 0.002 [20]	14.86 ± 0.24 [20]
	Western Arm	15756 ± 3797	NA	0.05 ± 0.002 [20]	17.71 ± 0.71 [20]

Notes: Mean smolt weight and length is a pooled annual mean rather than of all smolt over the entire period. Values are given as mean ± SD, with number of fish in square brackets, except for smolt, where [20] refers to number of years rather than number of individuals.

APPENDIX B

Salmon sample processing methods

Sample processing protocols differed slightly between mature fish, including kelts, and smolts due to differences in fish size (Appendix B: Table B1). We recorded fork length after mature fish had thawed for ~12 hours. Adults and kelts were filleted, the fillets were skinned, gut contents removed from the entrails, and the fillets plus the carcass were cut into pieces. We then weighed the cut pieces before grinding each fish through a 300 watt electric meat grinder (Cuisinart) three times; twice through a 7 mm diameter plate and once through a 3 mm plate. We removed the flank skin for the sake of efficiency and our sanity because initial attempts to grind test samples that included flank skin consistently clogged the grinder. We further homogenized approximately one quarter of ground fish sample with 10–15 one- to three-second bursts in a Magic Bullet food processor until the ground fish was a fine paste before taking 10–20 g subsamples for chemical analysis. Each sample was thoroughly mixed between grindings and all equipment was rinsed between samples.

The small size of smolts precluded the use of our grinder for smolt sample processing. Instead, thawed smolts were measured for fork length and round weight before their gut contents were removed. We placed whole smolts into the Magic Bullet food processor and chopped them into small pieces. Upon removing smolt from the food processor, we spent a maximum of 30 seconds picking out largest pieces of skin and scraped the attached tissue back into the sample. Each sample was then chopped into finer pieces with

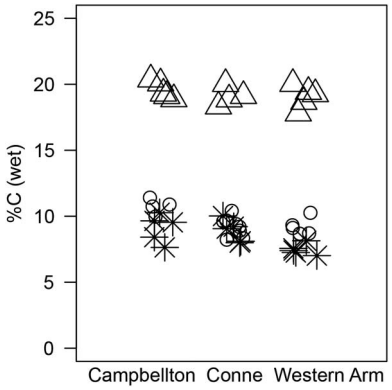

Fig. B1. Whole body carbon concentration on a wet mass basis of Atlantic salmon adults (open triangle), kelts (asterisk), and smolts (open circle) captured in three insular Newfoundland rivers. %C was measured on separate subsamples of the same fish as described in the main text. %C analysis was conducted on a Carlo Erba NA1500 Series II Elemental Analyser at the Stable Isotope Lab facility at Memorial University of Newfoundland according to standard methods (J. D. Ebel, *unpublished data*).

Table B2. %P on a wet weight basis of adults, kelts, and smolts collected in three Newfoundland Rivers in 2013.

River	Adult	Kelt	Smolt
Campbellton	0.38 ± 0.04	0.50 ± 0.05	0.58 ± 0.12
Conne	0.36 ± 0.03	0.53 ± 0.06	0.65 ± 0.11
Western Arm	0.37 ± 0.05	0.58 ± 0.07	0.65 ± 0.08

Note: Values are given as mean ± SD.

Table B1. Collection date, length, weight, and number of fish collected from three rivers on insular Newfoundland for quantification of whole-body phosphorus content.

River	Life stage	Collection date	*n*	Fork length (cm)	Weight(g)
Campbellton	Adult	30 Jul–03 Aug 2013	5	59.4 ± 2.4	2316.7 ± 240
	Kelt	May 2013	5	57.8 ± 7.7	1331.4 ± 586
	Smolt	May 2013	5	16.1 ± 1.9	42.7 ± 11.4
Conne	Adult	14–28 Jun 2013	4	49.48 ± 1.4	1238.8 ± 63.2
	Kelt	30–23 May 2013	5	50.5 ± 1.3	730.0 ± 76.3
	Smolt	30 Apr–06 May 2013	14	14.1 ± 1.4	26.6 ± 6.9
Western Arm	Adult	13–22 Jul 2013	5	55.6 ± 2.3	1968.1 ± 137.4
	Kelt	21–22 May 2013	5	54.0 ± 2.9	826.9 ± 151.9
	Smolt	30 May 2013	5	21.0 ± 3.0	54.4 ± 6.7

Note: Values are given as mean ± SD.

a knife and placed again into the food processor for 10–15 one- to three-second bursts before we stored a 10 g subsample for analysis. Following initial processing, all samples were refrozen and shipped to the Agriculture and Food Laboratory at the University of Guelph for analysis, where they were freeze dried, further homogenized, dry matter determined, and macro-element analysis conducted using test methods SNL-019,047.

Appendix C

Long term P flux via Atlantic salmon in three Newfoundland Rivers

Table C1. Total P flux for three Newfoundland salmon populations summed over a 20-year period (1993–2012). Efficiency was calculated as smolt export divided by net import.

River	Gross import (kg)	Net import (kg)	Smolt export (kg)	% efficiency
Campbellton	412	228	232	102
Conne	290	149	279	188
Western Arm	186	87	94	108

Appendix D

Sensitivity of P flux model estimates to changes in overwinter survival (parameter k)

We analyzed the sensitivity of the nutrient flux model to changes in parameter k in the same manner as we assessed the sensitivity of the model to assumptions regarding nutrient content (i.e., parameter N). We recalculated P flux over the 20-year study period for Campbellton using four sets of values for overwinter survival: the mean of annual survival rates measured on Campbellton between 1994 and 2012 (M. Robertson, *unpublished data*) held constant over the study period (i.e., same as main text), a high survival rate calculated as mean annual survival + 1 SD and held constant, a low survival rate calculated as mean annual survival rate − 1 SD and held constant, and the actual annual survival rates, which were variable over the study period.

Table D1. Results of a test for differences in elevation of k regressions conducted on time series produced by substituting four sets of values for the overwinter survival parameter in the nutrient flux model described in the main text. Significant differences found between pairs of regressions are indicated by contrasting capital letters in the superscripts.

Regression	Σx^2	Σxy	Σy^2	Residual SS	Residual DF
High survival^{A}	665	252.85	231.18	135.04	18
Low survival^{B}	665	331.84	421.20	255.61	18
Actual survival^{A,B}	665	435.83	476.00	190.37	18
Mean survival^{A,B}	665	291.93	315.60	187.44	18
Pooled regression				768.46	72
Common regression	2660	1312.46	1443.99	796.42	75
Total regression	9275	1060.69	1637.73	1516.43	78

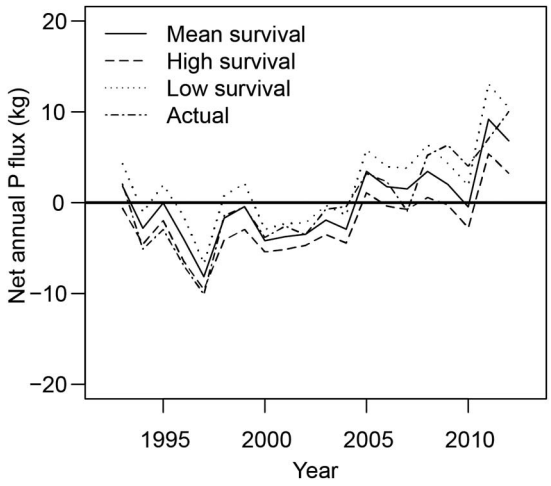

Fig. D1. Sensitivity of Atlantic salmon mediated P flux estimates to changes in overwinter survival rate (i.e., parameter k in nutrient flux model) on Campbellton River, Newfoundland, Canada. The solid line is estimated using mean overwinter survival rate measured from 1994 to 2012 and is the same as in the main text. High (long dash) and low (dotted) survival rates were determined as mean plus or minus one standard deviation (i.e., $k = 0.70$ and 0.43). We also included P flux estimated with directly quantified survival rates (actual; dash dot) and missing years (1993 and 1998) were replaced by the mean of the time series.

Because overwinter survival was not quantified in 1993 and 1998, we replaced these years with the mean of all annual survival estimates. We tested for differences in the elevations of k regressions (Zar 2010) and conducted multiple comparisons with Tukey HSD tests.

We found significant differences between the elevations of series produced with mean, high, low, and actual survival rates (Appendix D: Fig. D2; $F_{.05(2),75} = 22.60$, $p < 0.001$). Using multiple comparison tests, we found statistically significant differences ($p < 0.05$) only when we compared P flux time series estimated with high and low survival rates (Appendix D: Table D1).