NUTRIENT CYCLING BY LARGE CONSUMERS AT INDIVIDUAL, POPULATION, AND ECOSYSTEM LEVELS

By

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Abstract

Organisms modulate nutrient cycles by transforming, storing, and transporting nutrients. While the impact of microorganisms and autotrophs on local and global biogeochemical cycles is well studied, our understanding of the nutrient cycling role of macro-consumers is in its infancy. In the following thesis, I explore aspects of the role of aquatic vertebrates in ecosystem nutrient cycling. Recent studies demonstrate substantial intraspecific variability in body element composition arising from environmental conditions and ontogeny. First, I test whether body element concentration varies among life stages and populations of Atlantic salmon (*Salmo salar*) from three Newfoundland rivers. I demonstrate that most intraspecific variability is explained by life stage and inter-stage variability in element concentrations can be attributed to the energy and nutrient requirements of reproduction and migration. Second, using long-term population monitoring data, I test whether ontogenetic differences in body phosphorus (P) concentration influence the role of Atlantic salmon as net sources or sinks of freshwater P. I find that incorporating inter-stage variability in body composition into nutrient flux models qualitatively changes our assessment of these populations as P sources or sinks relative to assuming ontogenetic homogeneity of body P concentration. Third, I develop a framework to describe the stoichiometric traits of vertebrate populations and use the framework to evaluate ontogenetic variability in body stoichiometry and total nutrient storage in brook trout (*Salvelinus fontinalis*) populations and partition nutrients released by migrating Atlantic salmon between eggs and excretion. Finally, life history strategy

may influence interspecific variation in the ecosystem effects of migratory animals. I derive a two ecosystem model to investigate the ecosystem effects of migratory top consumers as subsidies. I formalized the hypothesis that iteroparous migratory animals should have stronger top-down effects on their biotic resource stocks than semelparous migratory animals, and that the response of ecosystem fluxes depends on the efficiency of consumer-mediated nutrient recycling. Overall, my findings suggest that interactions between ontogenetic development and life history strategy shape the nutrient cycling role of vertebrates. Connecting population structure and dynamics to nutrient cycles in this way may be a new path for 21st century ecological research and wildlife management.

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This research would not have been possible without the help of researchers at Department of Fisheries and Oceans Canada, especially J. Brian Dempson and Martha Robertson. Our discussions greatly influenced my work by making me think about the diversity of life history strategies in diadromous fish communities, the structure of population monitoring data and its associated constraints, and how population monitoring data can be applied to ecosystem ecology.

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Preface

This is a manuscript-based thesis. In the Introduction and Overview, I connect the themes of the subsequent chapters with broad strokes and list the topics I hope those chapter advance. In the Conclusion, I summarize the primary findings of the chapters and integrate them into a more general statement about how this research can be extended to meet the challenges of 21st century fish and wildlife management. The following manuscripts are included as chapters in my thesis:

(1) Whole body element composition of Atlantic salmon *Salmo salar* influenced by migration direction and life stage in three distinct populations.

(2) Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes.

(3) Length-nutrient content relationships for linking individuals and populations to ecosystem nutrient cycles.

(4) Ecosystem effects of top consumers with migratory and complex life cycles.

The first chapter is in press at the *Journal of Fish Biology*. The second chapter is published in *Ecosphere*. The third chapter is in preparation for *Ecology Letters*. The fourth chapter is under review at *The American Naturalist*.

Chapter 1: Introduction and Overview

"*One is constantly reminded of the infinite lavishness and fertility of Nature – inexhaustible abundance amid what seems enormous waste. And yet when we look into any of her operations that lie within reach of our minds, we learn that no particle of her material is wasted or worn out.*

-John Muir (1838-1914)

Nutrients are essential for life. In rarity they constrain and in excess they overwhelm. The transformation of nutrient between abiotic and biotic forms, termed nutrient cycling, is constantly underway at every level of biological organization from the cell to the biosphere. While biological energy transformations ultimately express the interaction of life with the sun, nutrient cycling ultimately expresses the interaction of life with the earth. For these reasons, the conservation or manipulation of nutrient cycles at intermediate and higher levels of organization (i.e., individual, population, community, ecosystem, biosphere) is important for maintaining and improving human well-being both locally and globally. As human impacts have expanded from local to global, we need to further embrace John Muir's poetic statement

Nutrient cycling has historically been the domain of biogeochemists who focus on the role of microorganisms and humans in transforming nutrients (Schlesinger 1997). Indeed, the major global fluxes of nitrogen (N) are dominated by microbial and human mediated nitrogen fixation and microbial denitrification while global carbon fluxes are

dominated by net primary production, fossil fuel combustion, and microbial respiration. Yet, ecologists have demonstrated that animals influence nutrient dynamics at local and regional scales in direct and indirect ways (reviewed by Vanni 2002). Animals directly modulate nutrient cycling by acquiring, transforming, storing, transporting, and recycling nutrients. They indirectly modulate nutrient cycling by influencing prey behavior and inducing trophic cascades (Schmitz et al. 2010). In this thesis, I tackle the direct effects of large aquatic animals on ecosystem level nutrient cycles. I begin with a review of animal mediated nutrient cycling at the individual and population level and show that understanding intraspecific variation in nutrient cycling may be associated with individual ontogeny while interspecific variation at the population level may be associated with life history strategy.

1.1. ANIMAL-MEDIATED NUTRIENT CYCLING AT THE INDIVIDUAL LEVEL

Understanding the roles of individuals in nutrient cycling begins with the concept of balanced growth because nutrient dynamics obey mass balance (DeAngelis 1992; Sterner and Elser 2002; Loreau 2010). The balanced growth equation separates nutrients consumed by an individual (C) between assimilation (A) and egestion (Eg). Assimilated nutrients are used for somatic growth (G) or reproduction (Rp), or are otherwise excreted (Ex) such that

(Eq 1.1) $C = A + Eg = G + Rp + Ex + Eg.$

At short temporal scales, this equation partitions individual consumption between three different pathways in an ecosystem nutrient cycle. Egested nutrients are available to

microbial decomposers, excreted nutrients are available to primary producers and heterotrophic microbes, and nutrients in growth and reproduction are available to predators. In the long term, egested nutrients can be re-mineralized and become available to primary producers while growth and reproduction becomes available to decomposers following the death of the individual, the failure of its gametes to produce embryos, or the death of its offspring.

In ecological stoichiometric theory, consumer body element composition is considered one major determinant of the partitioning of different nutrients between recycling (Ex+Eg) and production (G) pathways, and the consumer's resource element composition is the other (Sterner and Elser 2002). If consumers exhibit non-strict homeostasis of body element composition, meaning that the element ratio X:Y of growth varies with the X:Y of the resource because production efficiencies (C/G) for single nutrients are constant, then the elemental ratio of recycled nutrients is linearly associated with the elemental ratio of the resource consumed (Sterner and George 2000). However, the assumption of constant production efficiencies for single nutrients is invalid for most larger animals because these animals are thought to adjust production efficiency to maintain body element homeostasis (i.e., strict homeostasis; Sterner and Elser 2002). Thus, the element ratios of recycled nutrients may be better approximated by the elemental imbalance between the individual's body and its resource (Cross et al. 2003).

Strict homeostasis of vertebrate body element composition is a common simplifying assumption in bioenergetic (Kraft 1992; Schindler & Eby 1997) and theoretical models (Leroux et al. 2012) concerned with animal mediated nutrient cycling.

These models are important to our understanding of nutrient excretion by vertebrates because direct measurements of the composition and rates of nutrient excretion by individuals of many species in many ecosystems are unavailable (but see Vanni et al. 2002; Sereda and Hudson 2011; Allgeier et al. 2015; Tiegs et al. 2016; Showalter et al. 2016; Vanni and McIntyre 2016). The central part that body composition measurements play in bioenergetic models in particular caused rapid growth in the number of studies quantifying interspecific variability in vertebrate body element composition, especially in freshwater fishes (Hendrixson et al. 2007; Vanni et al. 2002; McIntyre and Flecker 2010). These efforts concluded that body element composition is largely taxon specific. Likewise, variation in individual animal excretion rates and stoichiometry are well explained by taxonomic identity, trophic guild, temperature, and body size (Allgeier et al. 2015; Vanni and McIntyre 2016) and poorly explained by body composition, at least at low levels of resolution. The difficulty for ecological stoichiometry to predict nutrient excretion rates using body composition may arise from (1) rates and ratios being measurements on different scales with different distributions**,** (2) inaccurate accounting of consumption rates when combining data from many disparate species (Vanni and McIntyre 2016) or (3) a poor understanding of intraspecific variability in both vertebrate body composition and the composition of their resources.

Recent work shows substantial variability in body element composition within taxa resulting from habitat type (Vrede et al. 2011; Tuckett et al. 2016), predation pressure (El-Sabaawi et al. 2012), and ontogeny (Pilati and Vanni 2007; Boros et al. 2015; Tiegs et al. 2016; Showalter et al. 2016). For example, Boros et al. (2015) found

that %C, %N, and %P differed by life stage among individual fathead minnows (*Pimephales promelas*) and sheepshead minnows (*Cyprinodon variegatus*) sampled as embryonic, post-embryonic, larval, juvenile, and adult life stages experiencing a single diet shift occurring at the juvenile stage. Similarly, total body N and P content expressed as number of moles and molar N:P of wood frogs peaked at intermediate larval life stages corresponding to the completion of bone ossification (Tiegs et al. 2016). Ontogenetic changes in body element composition coincide to changes in mass-specific excretion rates (Tiegs et al. 2016; Showalter et al. 2016) and shifts in diet composition (Pilati and Vanni 2007) suggesting that ontogenetic stage is important to consider when evaluating the nutrient cycling effects of individuals within populations.

1.2. ANIMAL MEDIATED NUTRIENT CYCLING AT THE POPULATION LEVEL

A single individual of most species in most ecosystems will not have measureable direct effects on ecological processes at the ecosystem level, but the aggregative effects of all individuals within a population or community may (Allen and Giloolly 2009). Indeed, when the nutrient content of all individuals within a vertebrate population are summed, vertebrate populations and communities can represent substantial pools of nutrients in aquatic ecosystems, particularly phosphorus (Kitchell et al. 1979; Milanovich et al. 2015).

The magnitude and pathway by which nutrients move into and out of this pool determines the population's or community's effect on ecosystem nutrient dynamics. For example, vertebrate community excretion in Rio Las Marias, Venezuela can provide 146% of algal P demand suggesting that vertebrate communities played an important role

in supporting primary production (Vanni et al. 2002) and the spatial distribution of fish among habitats creates hotspots of nutrient transformation rates (McIntyre et al. 2008). In contrast, Sereda and Hudson (2008) estimated that, although fish represented 54% and 55% of total epilimnetic P in two Ontario Lakes, nutrient excretion by fish only accounted for a maximum of 36% of epilimnetic phytoplankton regeneration. The high turnover time of nutrients in fish biomass relative to the turnover time of nutrients in phytoplankton biomass suggests that fish nutrient release should have a smaller effect on phytoplankton productivity than the release of nutrients by the phytoplankton themselves (Sereda and Hudson 2008). Yet, both of these examples examine only part of vertebrate nutrient releases (i.e., excretion) at short temporal scales by summing excretion rates by individuals according to body size (Sereda and Hudson 2008). While vertebrates may or may not contribute to primary productivity through excretion, how vertebrates interact with nutrient cycles at longer temporal scales requires accounting for population dynamics and the constraints on recycling of non-excretion releases (i.e., mortality and emigration; Vanni et al. 2013).

At longer timescales, nutrients stored in biomass by aquatic vertebrates are released from the population upon the deaths of individuals, where those nutrients may or may not be recycled into the food web through decomposition and remineralization. As such, the long-term net effect on ecosystem nutrient availability depends not only on population abundance and excretion rates, but also on mortality and remineralization rates. Thus, at longer timescales, the net flux of nutrients (F_{net}) between animal biomass and the rest of the ecosystem can be expressed as

(Eq 1.2) $F_{net} = \delta O - I$,

where I is the total input of nutrients into a population through consumption by all individuals, O is the output of nutrient from the population measured as the sum of excretion, egestion, and mortality, and δ is the rate at which outputs are recycled back into a biologically available form. A more precise formulation would include variable recycling rates for each output from the population.

1.3. ANIMALS AS NUTRIENT SUBSIDIES

Subsidies are inputs of individuals, material, or energy to an ecosystem from another ecosystem that increase the productivity of the recipient (Polis et al. 1997) and can play an important role in ecosystem regulation (Loreau and Holt 2004). Subsidies occur as consumer and resource fluxes (Allen and Wesner 2016); consumer fluxes include inputs of individuals at upper trophic levels and act as a top down force on lower trophic levels (i.e., depress *in situ* prey; McCoy et al. 2009), whereas resource subsidies include inputs to lower trophic levels (i.e., detritus, abiotic nutrients, and prey) and act as a bottom up force on food webs (Marczak et al. 2007; Holgerson et al. 2016). Empirical studies often focus on direct effects of resource fluxes on the recipient trophic level (Marczak et al. 2007; but, see Sato and Watanabe 2014). Meanwhile, recent theoretical studies on subsidies have taken a meta-ecosystem perspective (Loreau et al. 2003) and examined the effects of reciprocal consumer and resource fluxes between ecosystems on various ecological processes including trophic cascades (Leroux and Loreau 2012), food web stability (McCann et al. 2005), and nutrient co-limitation (Marleau et al. 2015). Animals

can simultaneously act as both consumer and resource subsidies depending on their behavior and life history, thus impacting food webs and nutrient cycling across ecosystems.

Animal movement is often nutrient translocation and is recognized as a way vertebrates directly contribute to the vertical distribution of nutrients in the food web (i.e., biomass pyramids) and the rates of cycling (Vanni 2002). Inputs of nutrients by animals immigrating or migrating to an ecosystem or habitat represent a subsidy with associated effects on the productivity and structure of the recipient ecosystem (Polis et al. 1997). For example, detritivorous gizzard shad (*Dorosoma cepedianum*) sequester P in the benthic zone of lakes and release P in the pelagic zone resulting in a gradual increase in pelagic P when without gizzard shad-mediated P translocation, pelagic P would decline (Vanni 2002). Roe deer move nutrients from fertilized cropland to forest patches across Europe (Abbas et al. 2012) and geese supply up to 40% of nitrogen and 75% of phosphorus in their wetland roosts by transporting nutrients from farm fields (Post et al. 1998). Migratory animals transport nutrients across ecosystem boundaries and, in some extreme cases inputs via migratory animals can support biota at regional scales (e.g., Pacific salmon; Schindler et al. 2003). Yet, the effects of migratory animals on food webs and nutrient cycles are sometimes inconsistent, depending on the behavior of the animals (e.g., nest digging by sockeye salmon decreases benthic mancroinvertebrate biomass and gross primary productivity; Moore et al. 2007; Holtgrieve et al. 2011). Meanwhile, bi-directional flows of migratory animals and the simultaneous delivery of consumer and resource subsidies may yield non-intuitive results. My thesis is concerned with how

organismal characteristics, primarily life history strategy and body composition, influence ecosystem nutrient cycles.

1.4. THESIS OVERVIEW

My thesis combines empirical studies, synthesis of large datasets, and mathematical modelling to address the role of life cycle and ontogeny in shaping the role of animals in nutrient cycling.

In Chapter 2, I test whether variation in body element composition of a migratory animal, the Atlantic salmon (*Salmo salar* L.), is explained by life stage and/or river of capture.

In Chapter 3, I explore the effect of differences in body composition among life stages on the role of populations as sources or sinks of nutrients in natal ecosystems.

In Chapter 4, I present an alternative method for incorporating animals into nutrient cycles using relationships between length and total body nutrient content. With further development and testing, these relationships may serve to bridge a gap between ecological stoichiometry, population ecology and traditional ecosystem ecology.

In Chapter 5, I derive and analyse a model to explore how trophic structure and ecosystem fluxes respond to variation in life history characteristics of top consumers with migratory life cycles.

In Chapter 6, I summarize my findings and briefly discuss why two current conceptual frameworks for connecting organisms to ecosystem structure and function may not be ideal for informing fish and wildlife management policy. Merging population and

ecosystem ecology probably requires returning to investigating intraspecific trait variability and understanding its impacts within and across ecosystems.

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Co-authorship Statement

This thesis is the result of my independent research. The breakdown of contributions by each author is as follows:

Chapter 2: Whole body element composition of Atlantic salmon *Salmo salar* influenced by migration direction and life stage in three distinct populations.

I developed the research, processed the samples with the help of volunteers, analyzed the data, and wrote the manuscript. S. Leroux contributed to question development, sample processing, data analysis, and writing. M. Robertson and J. B. Dempson collected the samples and made suggestions on the chapter.

Chapter 3: Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes.

I developed the research, processed the samples with the help of volunteers, analyzed the data, and wrote the chapter. S. Leroux contributed to the design of the research, data analysis, and writing. M. Robertson provided the population time series data for Campbellton River and Western Arm Brook. J. B. Dempson provided the population time series data for Conne River and made suggestions on the chapter.

Chapter 4: Length-nutrient content relationships as a tool for understanding the role of large consumers in ecosystem nutrient cycles.

I designed the research, derived the models, executed the brook trout sample collection, processed the samples with the help of undergraduate technicians, analyzed the data, and wrote the manuscript. S. Leroux contributed to the conceptual development, the logistics and collection of brook trout data, and writing. B. Palm-Flawd and C. Purchase collected and processed the Atlantic salmon egg samples.

Chapter 5: Ecosystem effects of top consumers with migratory and complex life cycles

I designed the research, derived and analyzed the model, and wrote the manuscript. S. Leroux contributed to the research design, the derivation and interpretation of the results, and writing.

Chapter 2: Whole body element composition of Atlantic salmon (*Salmo salar*) influenced by migration direction and life stage in three distinct populations

A version of this chapter can be found in the Journal of Fish Biology:

Ebel, J. D., S. J. Leroux, M. J. Robertson, and J. B. Dempson. 2016. Whole body element composition of Atlantic salmon *Salmo salar* influenced by migration direction and life stage in three distinct populations. Journal of Fish Biology 89:2365-2374. doi:10.1111/jfb13123

2.1. ABSTRACT

Body element content was measured for three life stages of wild Atlantic salmon *Salmo salar* from three distinct Newfoundland populations as individuals crossed between freshwater and marine ecosystems. Life stage explained most of the variation in observed body element concentration whereas river of capture explained very little variation. Element composition of downstream migrating post-spawn adults (i.e., kelts) and juvenile smolts were similar, and the composition of these two life stages strongly differed from adults migrating upstream to spawn. Low variation within life stages and across populations suggests that *S. salar* may exert rheostatic control of their body element composition. Additionally, observed differences in trace element concentration between adults and other life stages were probably driven by the high carbon concentration in adults because abundant elements, such as carbon, can strongly influence the observed

concentrations of less abundant elements. Thus, understanding variation among individuals in trace elements composition requires the measurement of more abundant elements. Changes in element concentration with ontogeny have important consequences for the role of fishes in ecosystem nutrient cycling and should receive further attention.

2.2. INTRODUCTION

Fish populations can control aquatic nutrient cycling because they can be substantial pools of elements within aquatic ecosystems (Vanni 2002) and transport elements between ecosystems (Moore and Schindler 2004; Twining et al. 2013). In theory, a fish's role in within-ecosystem nutrient cycling is determined by the elemental composition of its body relative to the composition of its food, which influences fish growth and excretion rates (Sterner and George 2000). Stoichiometric models of fish growth and nutrient cycling typically assume homeostatic regulation of body element composition within taxonomic groups (Sterner et al. 1992), and this assumption led to investigations evaluating interspecific variability in fish body element composition (Hendrixson et al. 2007; Dantas and Attayde 2007). Additional work has shown that substantial intraspecific variability among populations can arise through differences in habitat (Vrede et al. 2011; El-Sabaawi et al. 2012), and within populations through developmental shifts such as the shift from larval to juvenile stages (Pilati and Vanni 2007). For example, % carbon (C) decreased and % phosphorus (P) increased when gizzard shad *Dorosoma cepedianum* Lesueur 1818 reached ca. 30mm in length (Pilati and Vanni 2007). Meanwhile, Boros et al. (2015) found that % nitrogen (N) decreased, %C increased, and %P oscillated along a trajectory from embryonic and adult stages in fathead minnows *Pimephales promelas*

Rafinesque 1820 and sheepshead minnows *Cyprinodon variegatus* Lacepede 1803. Similarly, the shift from juvenile to the mature adult stage may also result in a change in body element composition, as may the release of elements during reproduction that marks the shift from pre-spawn to post-spawn adult (see Chapter 3).

Many fishes use different habitats at different stages of their life cycles, and at a population level, these migrations can represent substantial movements of elements (Vanni et al. 2013). Anadromous and catadromous fishes in particular transport nutrients between marine and freshwater ecosystems when juveniles migrate to the ocean and adults return to freshwater to overwinter or spawn (Moore and Schindler 2004; Chapter 3). Because different life stages move nutrients in different directions and certain life stages of a species can dominate fish community biomass in some ecosystems, quantifying ontogenetic shifts in fish element composition is important for determining how anadromous fishes modulate within ecosystem nutrient cycling and across ecosystem nutrient transport (Chapter 3). To date, few published studies present body element composition measurements of all migratory stages of a wild anadromous species that can capture potential interpopulation variability, inform nutrient cycling and transport models (Shearer et al. 1994; Talbot et al. 1986), and shed light on how body element composition changes during migration and reproduction (Chapter 3). The aim of this study was to determine the body element composition of three wild Atlantic salmon *Salmo salar* L. 1758 life stages, and evaluate differences with respect to variations in individual size, habitat use, and morphology that follow ontogeny.

2.3. MATERIALS AND METHODS

Whole body element content was quantified for adult *S. salar* returning to freshwater to spawn, as well as downstream migrating kelts (i.e., downstream migrating post-spawn adults), and smolts from three river systems in Newfoundland, Canada: Campbellton River (49° 17' N, 54° 56' W), Conne River (47° 55' N, 55° 41' W), and Western Arm Brook (51° 11' N, 56° 46' W). The three rivers drain different geographic regions of the island and the populations are genetically distinct (Bradbury et al. 2014). A more detailed description of study rivers can be found in Chapter 3.

At least four individuals of each life stage from each river were collected as they passed the monitoring facility located at the mouth of each river (Table A.2.1). Samples were homogenized as described in Chapter 3 before chemical analysis of carbon (C) and nitrogen (N), phosphorus (P), sulfur (S), potassium (K), magnesium (Mg), sodium (Na), and iron (Fe). Approximately 5 g of each wet sample was placed in a clean scintillation vial and refrozen at -20º C before shipping on dry ice to the Agriculture and Food Laboratory at University of Guelph where it was freeze dried to obtain dry mass and then analyzed for P, Ca, S, K, Mg, Na, and Fe on a VARIAN VISTRA-Pro simultaneous ICP-OES (www.varianinc.com) using test methods SNL-019,047 with a bovine liver standard (NIST 1577c). All samples exceeded detection limits by at least an order of magnitude (Table A.2.2). An additional 10-20 g of each sample was further prepared for C and N (C/N) analysis. C/N samples were dried at 50º C until a constant mass was obtained (ca. 5 d), and then ground to a fine powder with a mortar and pestle. Powdered sample was stored in a sealed vial for up to two months. Then, the vials were opened and placed in a

desiccator for one week prior to transferring 1 mg of dried sample into 7x7mm ultralight tin capsules and analyzed for C and N concentration with a Carlo Erba NA 1500 Series II Elemental Analyser (www.thermo.com) at the Stable Isotope Lab Facility at Memorial University of Newfoundland.

General linear models (GLM) were used to test whether life stages differed in terms of elemental composition by including body element concentration on a dry mass basis as the dependent variable. Life stage, river of origin, and the interaction of life stage with river of origin were used as explanatory factors. Akaike's Information Criterion corrected for small sample sizes (AIC_C) in the "AICcmodavg" R package (Mazerolle 2015) was used to determine the most parsimonious model to explain variation in *S. salar* body element composition. Explanatory factors included the interaction of life stage and river because of an *a priori* hypothesis that differences in environmental conditions and genetic make-up among populations (Bradbury et al. 2014) may lead to inter-population variability in the magnitude of differences in elemental composition among life stages. Model fits were compared by evaluating the percent of deviance explained, which is defined as the reduction in deviance caused by adding parameters to the intercept model, and expressed as $DevianceExplained = (D_{null} - D_{fitted}) * D_{null}^{-1}$, where D is the deviance extracted from the GLM summary. To evaluate differences in element concentration between pairs of life stages (i.e., adult vs. kelt, adult vs. smolt, kelt vs. smolt), effect sizes were calculated as the percent difference between measured concentrations in each life stage (e.g., $([C]_{adult} - [C]_{smolt}) * [C]_{adult}^{-1}$) and qualitatively assessed. To test for autocorrelation between elements, which may indicate

whether one element is driving observed concentrations of other elements, correlations between the most abundant elements in *S. salar* bodies were examined (i.e., C, N, P, Ca). All analyses were performed in R v.3.1.1 (R Core Team 2014).

2.4. RESULTS

A model with life stage was the most parsimonious model for most elements (Akaike weights 0.74 to 1.00) and explained most of the variation in body element concentration (Table 2.1; Figure 2.1). C and Na were the only elements where the best model included the interaction of life stage with river as the explanatory factor. Despite small sample sizes, life stage explained over 80% of deviance from the intercept model for C, N, P, Ca, Mg, and Na, and 40-70% of deviance from the intercept model for Fe, K, and S (Table 2.1). Models that included the interaction of life stage and river of origin better fit the data for all elements, but the increase in deviance explained was less than 10% and including the interaction term came at the cost of additional parameters.

Carbon concentration was 20-25% higher in adults than it was in either kelts or smolts (Figure 2.2a,b), but all other elements had higher concentrations in kelts and smolts than in adults (Figure 2.2c). The strongest percent difference in element concentrations between adults and other life stages occurred for Ca, followed by Fe, Na, and P (Figure 2.2a,b). Kelts and smolts, however, had very similar element concentrations for all elements except for Mg (Figure 2.2c). Across life stages, %N was negatively correlated with %C (Fig. 3a; Pearson's r = -0.76), as was %P (Figure 2.3b; Pearson's r = -0.93). Meanwhile, %N was positively correlated with %P (Figure 2.3c;

Pearson's $r = 0.77$) and %P was positively correlated with %Ca (Figure 2.3d; Pearson's $r = 0.99$). Elemental composition on a dry mass basis is preferred for use in stoichiometric models, but % element on a wet mass basis is required for application in nutrient transport models. As such, % element by wet mass is provided in Table A.2.3 and the differences between adults and other life stages for element concentrations on a wet mass basis are qualitatively similar to concentrations on a dry mass basis presented in Figure 2.1.

2.5. DISCUSSION

Salmo salar in this study spanned the range of C, N, and P concentrations observed in freshwater fishes. Mean adult element concentrations slightly exceeded the maximum of %C, was the extreme low end of %P, and near the mean %N observed in 95 freshwater species (McIntyre and Flecker 2010). Adult element concentrations in this study were similar to N and P values published for sockeye salmon *Oncorhynchus nerka* Walbaum 1792 (Donaldson 1967 as cited in Moore and Schindler 2004) and artificially reared *S. salar* (Talbot et al. 1986; Shearer et al. 1994). Kelt P concentration in this study was higher than presented for spawned adults prior to overwintering (Shearer et al. 1994), and similar to P concentration of wild kelts measured by Talbot et al. (1986). N, Ca, and Na concentration of kelts in Talbot et al. (1986) was also similar to concentrations in the present study. Smolts in the present study had lower concentrations of N, P, Ca, Na, and K than parr sampled by Talbot et al. (1986). Neither Talbot et al. (1986) or Shearer et al. (1994) measured C concentration. The results of this study run contrary to C, N, and P values presented for wild *S. salar* from the River Tweed, UK published by Lyle & Elliott (1998), although their values have been used by multiple nutrient transport and cycling

studies (e.g., Jonsson and Jonsson 2003a; Samways and Cunjak 2015), which may be problematic (Ebel et al. 2015). Specifically, adult *S. salar* in this study had 40% and 12% higher C and N concentration by wet mass, respectively, and 21% lower P concentration than shown by Lyle and Elliott (1998). This difference is probably due to the timing of fish collection relative to freshwater entry; however, Lyle and Elliot (1998) do not state when or where their samples were collected.

Counter to the initial expectation, there was evidence that kelts and smolts in this study had equivalent elemental composition, whereas adult *S. salar* sampled after feeding in marine habitats differed strongly from kelts and smolts. Thus, ontogenetic variation in body element composition observed in this study may result from differences in the energetic and material requirements of life stages as determined by the direction of migration and marked by recent feeding activity. The consistency in element concentration across populations and within life stages suggests that *S. salar* in these study rivers may exhibit programmed rheostasis, where an individual regulates its body composition around multiple set points defined by its life cycle (Mrosovsky 1990). Most examples of rheostatic control of body composition is related to changes in body fat content through periods of anorexia (Mrovosky 1990), which can be indirectly connected to the elemental changes between smolts and adults, and adults and kelts in this study because carbon is the dominant component of lipids. By including carbon, the results of the present study parallel previous work assessing inter-life stage variation in energy content of wild *S. salar* (Jonsson and Jonsson, 2003b; Dempson et al. 2004) and a shift towards increased lipid storage in young-of-the-year gulf menhaden *Brevoortia patronus*

Goode 1878 (Deegan 1986). Similarly, investigations examining differences in crude fat and energy levels were noted in Conne River parr rearing in fluvial versus lacustrine habitats with outgoing smolts characterized by lower values of each of these components (Dempson et al. 2004) as the smoltification process often results in reduced levels of lipids (Wedermeyer et al. 1980; McCormick et al. 1998). Strong differences in elemental composition among life stages moving in different directions with low spatial variation supports the hypothesis that there is a proximate basis for ontogenetic shifts involving migration (Thorpe 1986; Thorpe et al. 1998).

Carbon comprises a large portion of dry mass; adult dry mass was 51-58% C whereas kelt and smolt dry mass was 37-47 % C (Figure 2.1). Negative correlations of C with N (Figure 2.3a), and C with P (Figure 2.3b), when compared to the positive correlations of P with N (Figure 2.3c) and P with Ca (Figure 2.3d) suggest that the strong difference in %C among life stages is probably the driver of differences in the concentrations of other, less abundant elements. The interaction of river with life stage improved the fit of general linear models for C concentration suggesting that environmental differences among streams may act directly on C by influencing energy budgets (El-Sabaawi et al. 2012). Differences in C concentration within life stages, but among rivers, however, were not high enough to cause appreciable differences in the concentrations of most other elements. The interaction of life stage and river also provided a better fit for Na concentration, potentially resulting from spatial variation in progress towards shifting from hypo-osmotic to hyper-osmotic regulation (or *vice versa*) at the time when individuals were captured at counting fences (Potts et al. 1985).

In conclusion, life stage was revealed to be a primary driver of body element composition of wild *S. salar*. Different life stages appear to have distinct elemental signatures, and composition is also profoundly influenced by recent behaviour and environmental conditions (i.e., overwintering and subsequent downstream migration). To the authors' knowledge, this is the first study that measured both whole body macro-element (i.e., C and N) and trace element concentrations in *S. salar* at a set point in space and ontogeny (the freshwater-marine interface), which has explained some previously observed differences in trace element concentrations among life stages (Talbot et al. 1986; Shearer et al. 1994). Differences in trace element concentrations between adults and other life stages appear to be related to C storage levels, probably in the form of lipids. Kelts and smolts had similar element concentrations despite large differences in body size. More generally, differences between adults and other life stages show that timing of sampling relative to the reproductive phenology and behaviour of fishes can be an important determinant of observed elemental concentrations, which should be considered in nutrient recycling and transport models involving fishes.

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Table 2.1. Results of general linear models quantifying the importance of life stage and river of origin as predictors of *Salmo salar* body element concentration on a dry mass basis.

Element	Model	k	Log Likelihood	AICc	ΔAICc	Akaike weights	Deviance Explained
Carbon	Life stage X River	10	125.46	-224.63	0.00	1.00	94.58
	Life stage	4	106.20	-203.43	21.20	0.00	87.48
	Intercept	2	58.41	-112.56	112.08	0.00	0.00
	River	4	60.00	-111.01	113.61	0.00	6.66
Nitrogen	Life stage	4	172.83	-336.69	0.00	0.98	84.55
	Life stage X River	10	177.71	-329.13	7.55	0.02	87.51
	Intercept	2	129.87	-255.46	81.22	0.00	0.00
	River	4	130.72	-252.46	84.22	0.00	3.61
Phosphorus	Life stage	4	200.94	-392.91	0.00	0.77	86.42
	Life stage X River	10	208.38	-390.48	2.43	0.23	90.17

	Intercept	2	155.03	-305.77	87.14	0.00	0.00
	River	4	155.97	-302.97	89.94	0.00	4.04
Calcium	Life stage	4	164.61	-320.24	0.00	0.74	80.17
	Life stage X River	10	172.22	-318.15	2.08	0.26	85.76
	Intercept	2	127.39	-250.50	69.74	0.00	0.00
	River	4	128.64	-248.30	71.94	0.00	5.29
Sulfur	Life stage	4	280.10	-551.23	0.00	0.94	68.98
	Life stage X River	10	286.01	-545.73	5.49	0.06	76.00
	Intercept	2	253.18	-502.08	49.14	0.00	0.00
	River	4	253.54	-498.10	53.13	0.00	1.54
Potassium	Life stage	4	245.68	-482.39	0.00	1.00	67.91
	Life stage X River	10	246.84	-467.39	15.00	0.00	69.48
	Intercept	2	219.55	-434.81	47.58	0.00	0.00
	River	4	219.57	-430.17	52.23	0.00	0.11

Magnesium	Life stage	4	369.19	-729.40	0.00	1.00	90.17
	Life stage X River	10	372.22	-718.15	11.25	0.00	91.39
	Intercept	2	315.82	-627.36	102.03	0.00	0.00
	River	4	316.46	-623.94	105.46	0.00	2.73
Sodium	Life stage X River	10	292.42	-558.56	0.00	1.00	93.57
	Life stage	4	275.16	-541.34	17.22	0.00	86.37
	Intercept	2	229.31	-454.34	104.22	0.00	0.00
	River	4	230.11	-451.24	107.32	0.00	3.40
Iron	Life stage	4	405.13	-801.29	0.00	0.98	46.71
	Life stage X River	10	409.80	-793.31	7.97	0.02	56.50
	Intercept	2	390.66	-777.03	24.25	0.00	0.00
	River	4	391.28	-773.59	27.70	0.00	2.69

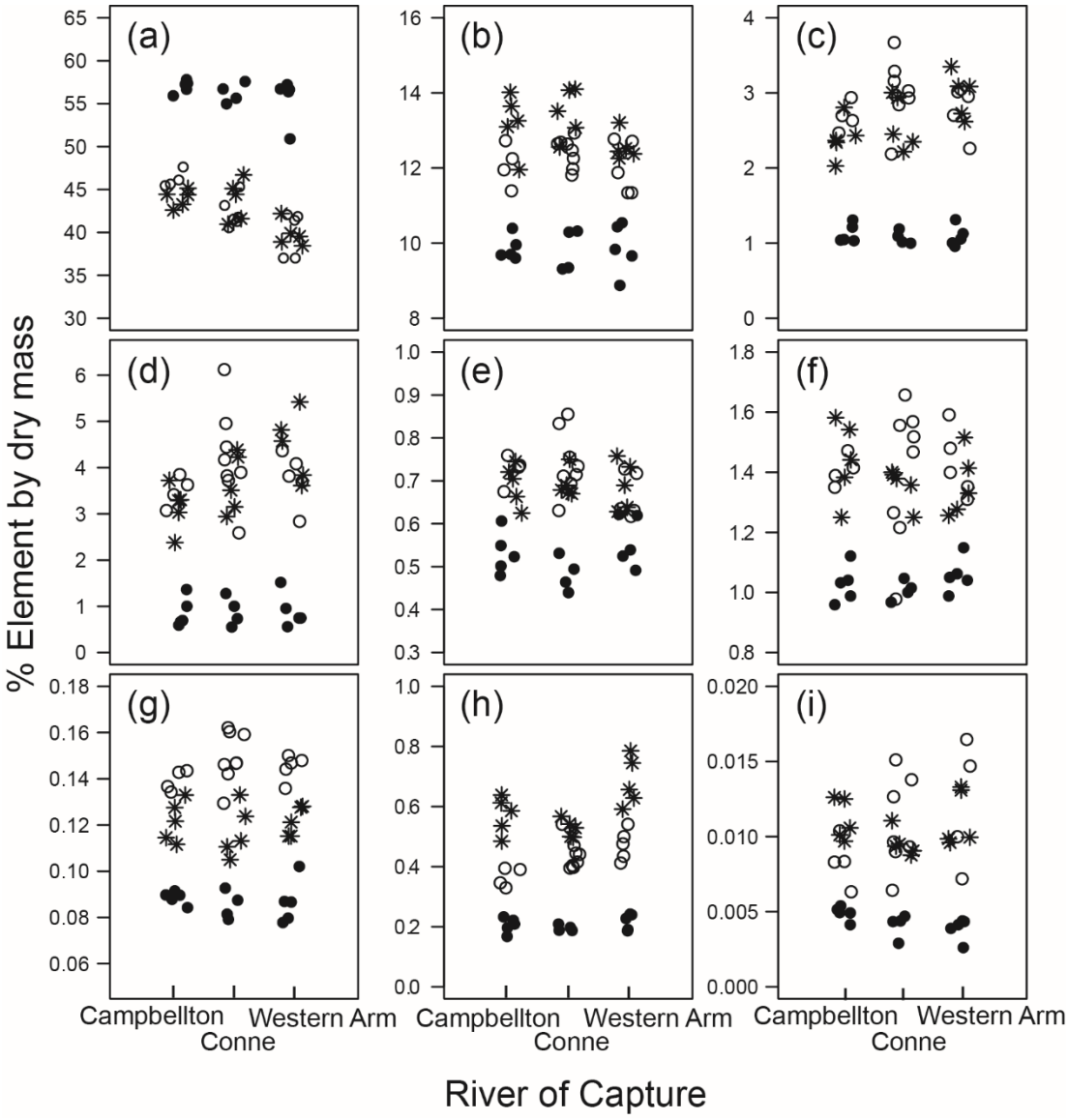

Figure 2.1. Whole body (a) carbon, (b) nitrogen, (c) phosphorus, (d) calcium, (e) sulfur, (f) potassium, (g) magnesium, (h) sodium, and (i) iron concentrations of adult (●), kelt (*), and smolt (○) *Salmo salar* captured at counting fences installed at three rivers located on the island of Newfoundland. Concentrations are presented as percent of dry mass.

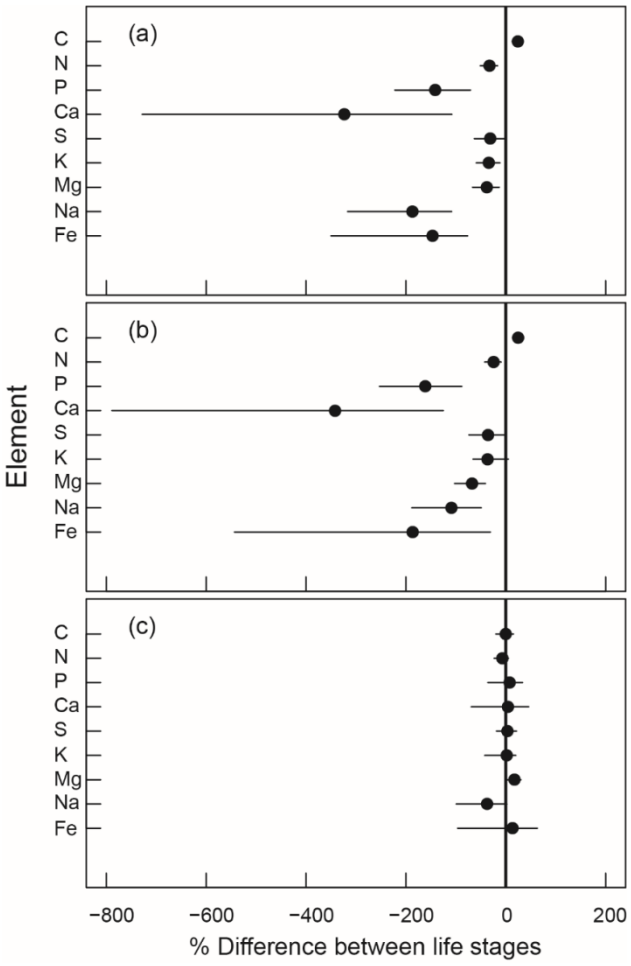

Figure 2.2. Percent difference in whole body element concentration between *Salmo salar* (a) adults and smolts, (b) adults and kelts, and (c) kelts and smolts collected from three watersheds in Newfoundland, Canada. Percent difference was calculated as (mean of life stage 1- mean of life stage 2) / mean of life stage 1. Confidence intervals were calculated by ranking the percent differences between all combinations of individuals of the life stages being compared and removing the upper and lower 2.5%.

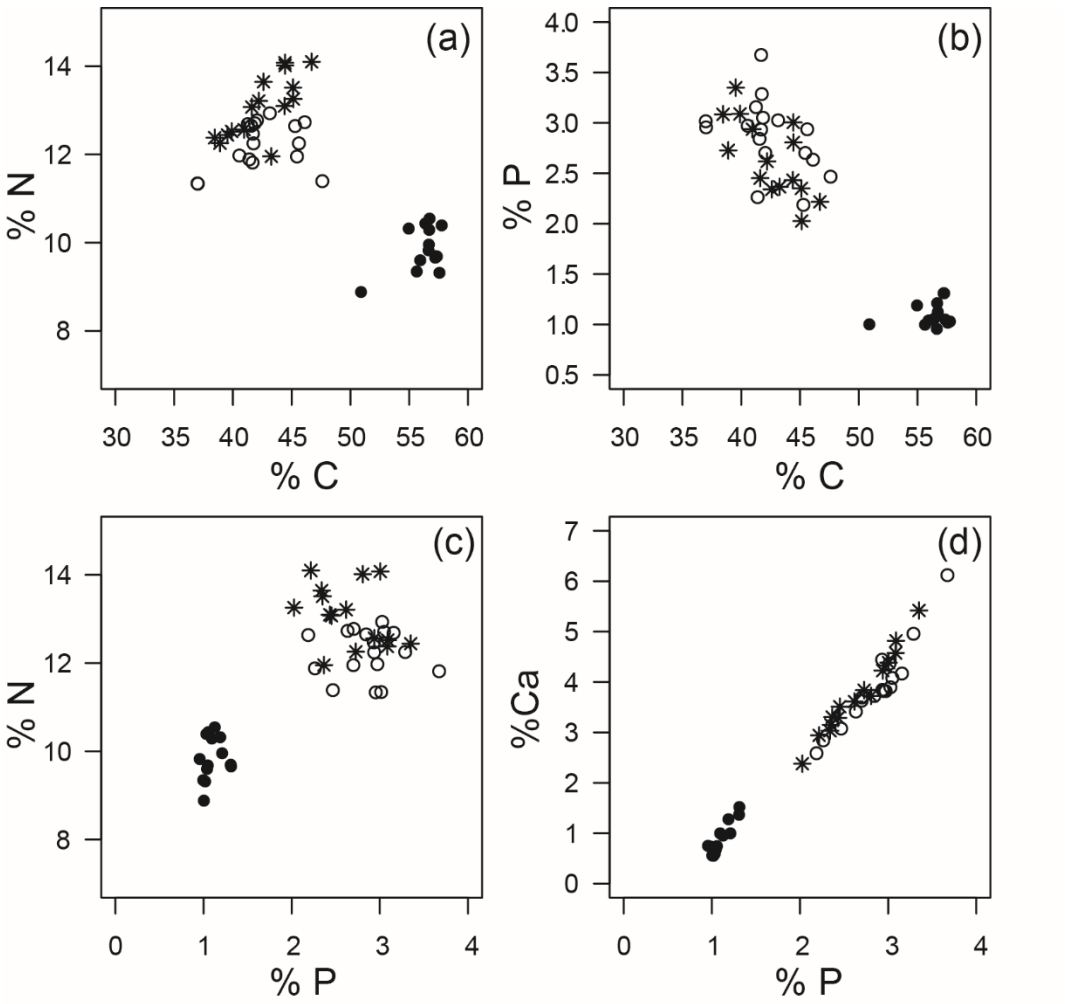

Figure 2.3. Correlations between (a) % C and %N, (b) %C and %P, (c) %P and %N, and (d) %P and %Ca of adult (●), kelt (*), and smolt (○) *Salmo salar*. Percent element is presented on a dry mass basis.

Chapter 3: Ontogenetic differences in Atlantic salmon phosphorus concentration and its implications for cross ecosystem fluxes

A version of this paper can be found in Ecosphere:

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3.1. 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 over-estimate 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 intra-specific variation in body element composition of fishes is a prerequisite to determining their role in global biogeochemical cycling.

3.2. 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 over-winter 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 among-species patterns in the magnitude and net direction of nutrient transport across ecosystems. 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; Moore et al. 2011; West et al. 2010).

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

$$Flux_t = A_t M_{a,t} N_a - \left(S_t M_{s,t} N_s + k b_t A_t M_{a,t} N_k \right)$$

where A is the number of spawning adults, S is smolt count, M is mean 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 2003a) 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 1970's 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 and published in a 1967 doctoral thesis (Table 3.1).

By using the nutrient content values published in studies conducted in different ecosystems (Table 3.1), 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 2003a; Moore et al. 2011) to test the hypothesis that small differences between assumed and measured %P values compound to influence ecosystem flux estimates.

3.3. 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 (Figure 3.1) and compiled time series data for Atlantic salmon from these three rivers (Table A.3.1). 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.

3.3.1. Study system

Campbellton, Conne, and Western Arm are in three distinct geographic regions of Newfoundland (Figure 3.1). 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; Figure 3.1). 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, and 1971, respectively. Adult salmon and smolts were enumerated at counting fences (Table A.3.1). 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 (< 63cm) 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".

3.3.2. 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 (Table A.3.2). Fish were collected at counting fences on the three study rivers by Fisheries and Oceans Canada personnel, placed in polyethylene bags and frozen before being transported to Memorial University of Newfoundland, St. John's, Newfoundland, 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 A.3.2.

We fit general linear models (GLM) with wet weight %P as the dependent variable and life stage, river of capture, and both life stage and river of capture 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

$$DevianceExplained = \left(D_{null} - D_{fitted}\right) / D_{null};$$

where D is the deviance extracted from the GLM summary.

3.3.3. 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 (< 63cm 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 (Table A.3.2). 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 (Table A.3.1). 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 1993-2012, thus we used weights and lengths of large salmon on Conne River measured from 1986-1992 (n = 6 salmon) 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 A.3.4).

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.3.1). 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.

3.3.4. 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 v.2.15.2 for all calculations and statistical analyses (R Core Team 2012).

3.4. RESULTS

3.4.1. 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 (Figure 3.2). Life stage was more important in explaining among-individual variation in whole-body P concentration than was river (Table 3.2).

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 3.2).

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 (Figure 3.2). 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).

3.4.2. Annual P flux using river-specific salmon P concentration

As expected, a logarithmic relationship existed between the lengths and weights of adults and kelts (Figure 3.3a). Weight at a given length for kelts was 55 to 65% of adult weight upon entering the river (Figure 3.3b). Parameter *b* applied to each year ranged from 0.56 to 0.59 for small salmon and 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; Figure 3.4). Median annual P flux was -0.45kg ± 4.07SD, -6.79kg ± 4.05SD, and -0.15 kg ± 1.71SD 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 (Table A.3.4).

3.4.3. 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 flux values that diverged significantly from our directly measured, river-specific values, but the elevations of regressions did not differ significantly between the pooled regional and the river-specific estimate (Figure 3.4). 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 A.3.4).

3.5. 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 (Figure 3.2a) and fell in the middle of the range of dry weight %P of freshwater fishes (1% to 6%P by dry mass; McIntyre and Flecker 2010; Figure 3.2b). 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 3.2). 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 2003a; 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 over-estimate actual Atlantic salmon-mediated P flux across the marine-freshwater ecosystem boundary (Figure 3.4), 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.

3.5.1. Whole body % phosphorus

Life stage explained 65% of variation in %P among individuals, whereas river explained under 2% (Table 3.2). 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 (Figure 3.2c). 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 (Figure A.3.1). 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 2003b) 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 2003b), 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 et al. (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 inter-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).

3.5.2. 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 twenty 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 1987-1992 (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 conditions 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 2003a; see Table 3.1). 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 A.3.4), 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.

3.6. REFERENCES

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Table 3.1. 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	Adult (n)	Kelt (n)	Smolt (n)	Used by:
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	0.37 (14)	0.54 (15)	0.63 (20)	NA
Alosa pseudoharengus	Durbin et al. (1979), West et al. (2010)	Pausacaco Pond, RI	0.42 (29)	0.45 (14)	0.58	West et al. (2010), Twining et al. (2013)

Oncorhynchus nerka	Donaldson (1967) ¶	Lake Illiamna, AK	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	0.36	NA	…	Larkin and Slaney (1997), Gresh et al. (2000) ††, Thomas et al. (2003) ‡‡

Notes:

† 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 Elliot (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)

Table 3.2. 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	AICc	Δ AIC_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

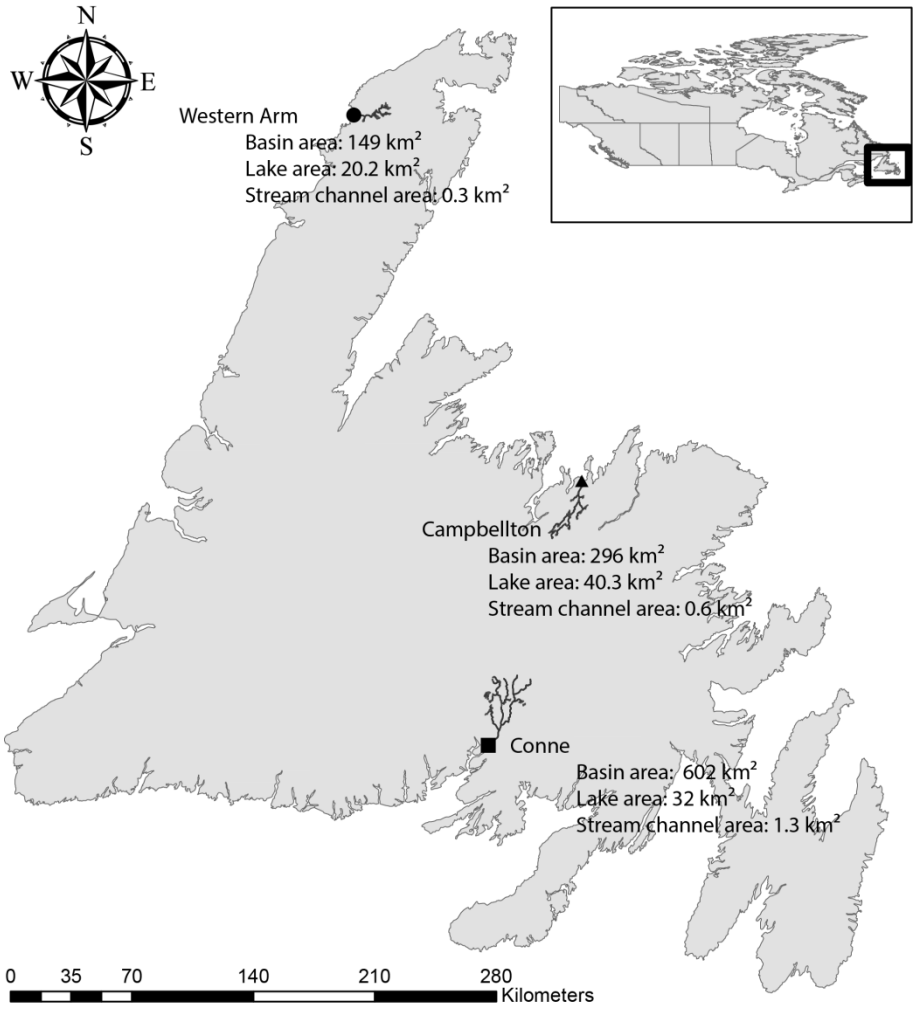

Figure 3.1. Map of insular Newfoundland, Canada (inset) showing three study watersheds where Atlantic salmon were collected for elemental analysis and, subsequently, salmon-mediated P flux was estimated.

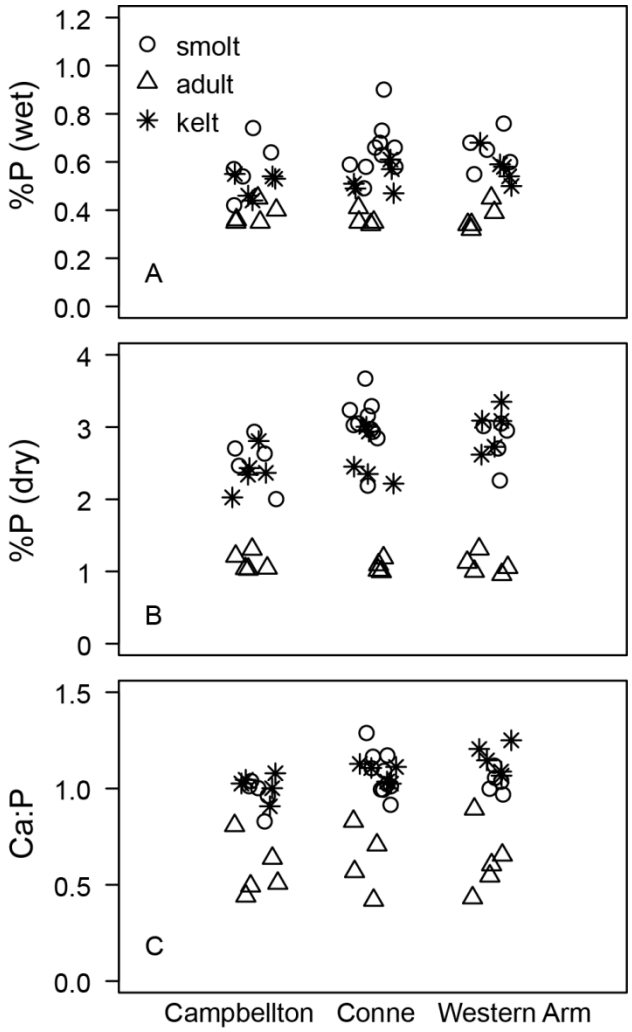

Figure 3.2. Whole body phosphorus concentration (panel A & B) and Ca:P (panel C) of Atlantic salmon adults (open triangle), kelts (asterisk), and smolts (open circle) captured in three insular Newfoundland rivers. Phosphorus concentration is presented on a wet mass basis (A) and dry mass basis (B). Mean wet weight %P for each river and life stage combination is provided in Appendix A.3.2.

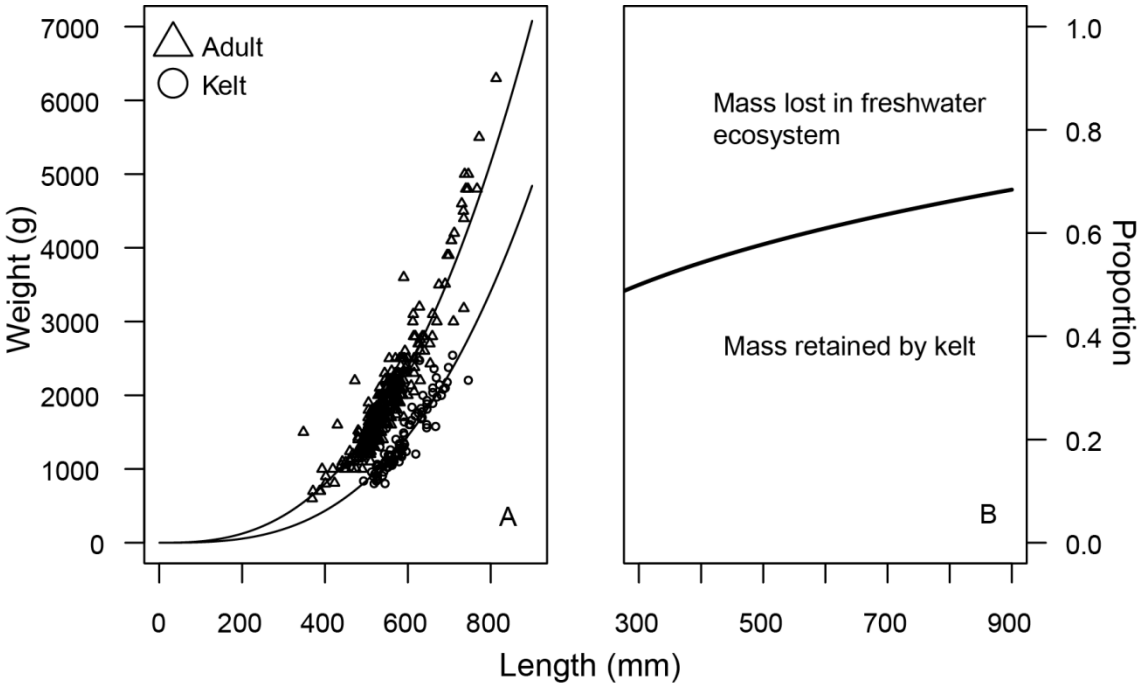

Figure 3.3. Length-weight relationships (panel A) for adults (n = 339, $y = 10^{-4.10+2.69\ (\log(X))}$, adjusted $R^2 = 0.86$) and kelts (n = 85, $y = 10^{-5.11 + 2.98\ (\log(X))}$, adjusted $R^2 = 0.82$) collected from Newfoundland rivers and used to estimate the proportion of adult mass that exits the river retained in kelts (panel B) in the nutrient flux model for a given length of adult (i.e., parameter *b*).

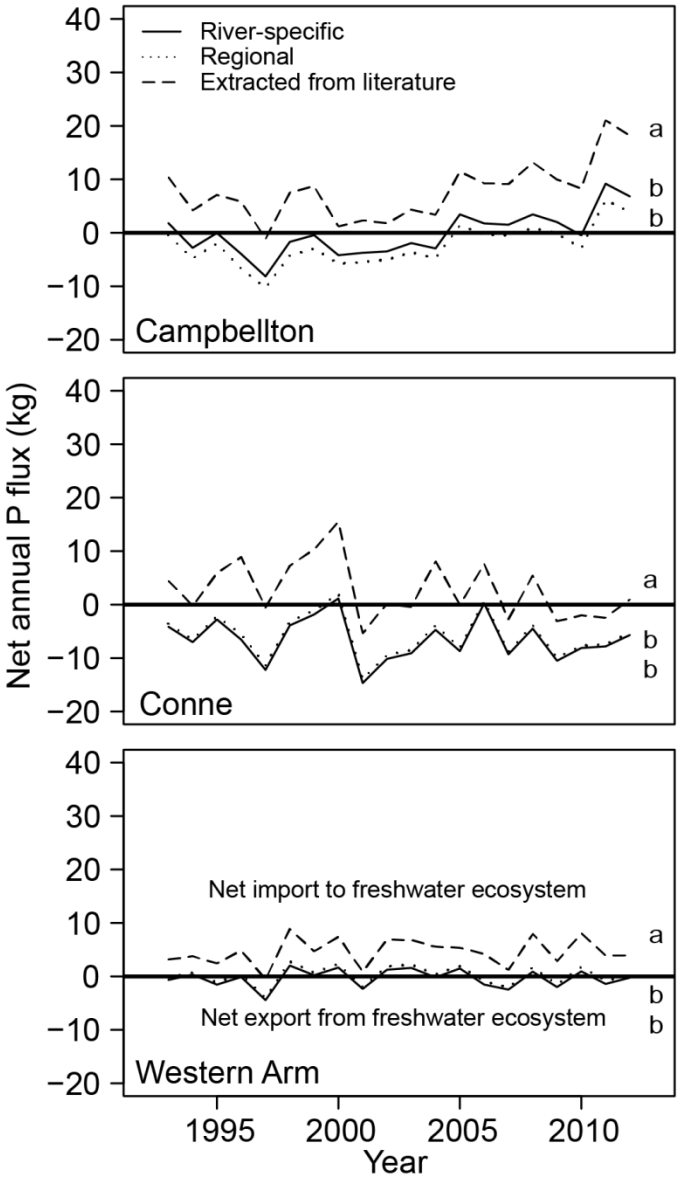
River-specific
Regional
Extracted from literature
Campbellton
Conne
Western Arm
Net import to freshwater ecosystem
Net export from freshwater ecosystem
a
b
b
Net annual P flux (kg)
Year
40
30
20
10
0
−10
−20
1995
2000
2005
2010

Figure 3.4. 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 Elliot (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.

Chapter 4: Length-nutrient content relationships as a tool for understanding the role of large consumers in ecosystem nutrient cycles.

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4.1. ABSTRACT

Managing vertebrate populations may at long temporal scales require a nutrient cycling perspective, which in turn requires an understanding how body nutrient composition changes with size and season, and a way to measure it for many species. We suggest that differences in scaling coefficients between body size and the contribution of various tissue types to total body mass indicate that the accrual rates of multiple elements change over an organism's ontogeny. These changes can be quantified using population level relationships between length metrics and total body nutrient content, which we term length-nutrient content relationships (LNCRs). When placed in the context of mass balance, LNCRs can be used to make quantitative predictions about how changes in population age and size structure influence the vertebrate consumers' functional role in terms of multiple elements. We illustrate two potential practical applications of LNCRs:

calculating nutrient standing stocks of brook trout and estimating nutrient investment in migration and reproduction by Atlantic salmon. The framework we develop here may help advance broad ecological theory by translating individuals into nutrients at the population level.

4.2. INTRODUCTION

Organisms are an important biogeochemical force. Macro-biota modulate nutrient cycles by storing nutrients in biomass (Kitchell et al. 1979), releasing nutrients via excretion (Vanni et al. 2002) and death (Boros et al. 2015*b*), and translocating nutrients within and across ecosystems (Moore and Schindler 2004). The strength of direct effects of biota on nutrient cycling is often taxon specific (Vanni et al. 2002) and are regulated by the elemental composition of individuals and the size and dynamics of populations (Kraft 1992; Vanni et al. 2013). Thus, our understanding of the role of biota in biogeochemical cycling hinges on linking individual and population level characteristics (i.e., body composition, ontogeny, behavior, and biomass) to within and across ecosystem patterns in nutrient distribution, flow strengths, and trophic production. Here we propose a novel method to connect individual and population level characteristics to the roles of vertebrates in ecosystem nutrient cycles.

Mass balance requirements constrain systems at all levels of biological organization (DeAngelis 1992; Sterner and Elser 2002; Loreau 2010). As such, mass budgets are key to connecting individuals to ecosystem processes. Mass balance at the individual level is expressed in the balanced growth equation, where nutrients consumed

by individuals (C) can either be assimilated (A) or egested (Eg). Assimilated nutrients can be used for biomass production (P), which includes somatic growth (G) and reproduction (Rp), or are otherwise excreted (Ex). A simple balanced growth equation (Loreau 2010) integrating these phenomenon takes the form

(Eq. 4.1) $C = A + Eg = G + Rp + Ex + Eg$

All of these individual level processes scale with body size (Peters 1983), and the combination of body size scaling with the balanced growth equation provides the foundation for determining the role of organisms in ecosystems.

Ecological stoichiometry has emerged as a powerful tool that uses principles of mass balance to determine element ratios in organisms and their resources to investigate aspects of ecosystem structure and function (Sterner and Elser 2002), such as the association of the elemental composition and rates of excretion with consumer and resource body composition. Ecological stoichiometry has predominantly addressed questions regarding small organisms (reviewed by Hessen et al. 2013) such as zooplankton (e.g., Elser and Urabe 1999) and macroinvertebrates (e.g., Cross et al. 2003; Frost et al. 2006), with a more limited body of empirical literature on the ecosystem roles of larger consumers, such as vertebrates (Schindler and Eby 1997; Vanni et al. 2002; McIntyre and Flecker 2010). Much work on vertebrate stoichiometry is concerned with linking biodiversity with ecosystem function by investigating interspecific variation in body composition (Hendrixson et al. 2007; McIntyre and Flecker 2010) and its consequences for total nutrient excretion (Vanni et al. 2002; Allgeier et al. 2015).

Recent work has revealed substantial intraspecific variation in vertebrate body composition (Boros et al. 2015a) and excretion, especially with respect to ontogeny (Boros et al. 2015a; Showalter et al. 2016). Intraspecific variability in body stoichiometry is also attributed to reproductive phenology (Chapter 2). Intraspecific variability in body composition among life stages, space, and time, which can be greater than interspecific variability, likely confounds results obtained by stoichiometric models that assume constant body composition with growth (e.g., Kraft 1992; Schindler and Eby 1997), and from the extrapolation of direct, one time measurements of nutrient excretion to the population level over long temporal scales (e.g., Sereda et al. 2008). The current discord between assumptions of vertebrate nutrient cycling models and the reality of intraspecific variability in body composition precludes the accurate incorporation of the nutrient cycling role of vertebrates into species and population specific fish and wildlife management policies.

The ability to move between demography and ecosystem processes in similar currencies is an important step towards unifying population and ecosystem ecology while incorporating ecosystem processes into fish and wildlife management. We develop a framework to describe the stoichiometric traits of populations of indeterminate vertebrates and use these descriptions to predict the role of large consumers in modulating ecosystem structure and function over multiple temporal scales. To achieve this goal we broadly examine what we know about changes in physical structure with growth through the tradition of allometry and link that knowledge to what we know about the elemental composition of vertebrates through the lens of stoichiometry. We suggest length-nutrient

content relationships; LNCRs) as a means to measure intraspecific variability in body composition, and then discuss how these relationships can be applied to estimate nutrient fluxes at the population level. We use two small datasets of salmonid body element composition to illustrate potential LNCR applications. We end with a discussion of future development and applications of LNCRS to theory and practice, as well as their limitations.

4.3. BODY SIZE SCALING OF BODY ELEMENT COMPOSITION

Body size relationships are some of the strongest relationships described (Peters 1983; Hatton et al. 2015). These relationships typically take the form $Y= aX^b$, where X is the size of an organism determined by a measurement of linear dimension (i.e., length or mass), Y is the characteristic we seek to predict, *a* is a constant, and *b* is a scaling coefficient. Traditional body size relationships, operationalized under the term allometry, describe the scaling of shape with size and its corresponding morphological and physiological consequences (Gould 1966). Allometry arose from questions about changes in organism form with size that result from differential growth rates among body parts (Huxley 1932) and was used to explore ontogenetic changes within taxa and phylogenetic relationships among taxa (Gould 1966). Relationships between length and mass remain a staple in fisheries and wildlife biology where they form the basis for body condition indices (Froese 2006; Peig and Green 2010).

In modern ecology, body size scaling is a framework for predicting physiological, behavioral, and ecological processes based on individual body size, usually body mass

(Peters 1983). In contrast to traditional allometry, body size scaling in modern ecology focuses on interspecific patterns because theoretical development of these relationships sought to predict general patterns to applicable to macroecology (Brown et al. 2004). Individual body mass is a good predictor of biomass production (Brown et al. 2004), net primary production (White et al. 2007), food web structure (Hatton et al. 2015) and stability (Otto et al. 2007), and individual excretion rates (Sereda et al. 2008; Allgeier et al. 2015). Intraspecific body size scaling is seldom studied in the context of ecological processes, but is the cornerstone of recent theoretical developments in population ecology (deRoos and Persson 2013).

Relationships between body size and body element composition remain poorly developed despite body composition being an important component of consumer-mediated nutrient recycling models (Sterner 1990; Kraft 1992; Eby and Schindler 1997). A relationship between body stoichiometry and body size at the macroecological level has been hypothesized (Elser et al. 1996) because of the differences in the relative contributions of different mechanical structures to total body mass along a gradient from prokaryotes to blue whales (Reiners 1986). These mechanical structures include organelles and biochemical components at the cellular level and tissues at the organismal level. Elser et al. (1996) hypothesized that prokaryote and metazoan invertebrate nitrogen (N) to phosphorus (P) ratio should increase with body mass because body P concentration is positively associated with specific growth rate (Elser et al. 2003) and specific growth rate declines with body mass (Peters 1983). The opposite trend is hypothesized for vertebrates because bone comprises an increasing percentage of total body mass with

increasing body size, and bone is P-rich relative to other tissue types (Elser et al. 1996; Vanni 1996). Exploration of interspecific body size-element composition relationships in vertebrates have focused on fish. Generally, associations of body mass with body stoichiometry and per cent body element composition are weak because body element composition depends heavily on taxonomic identity (Hendrixson et al. 2007; Allgeier et al. 2015).

Intraspecific scaling of body composition has not been adequately considered within the realm of ecological stoichiometry, maybe because the relative amount of an element (i.e., per cent) often forms weak or non-significant allometric relationships with body size (Sterner and George 2002; Tiegs et al. 2016). This is not surprising given that body size is also a weak predictor of relative measures of tissue and molecule types (Peig and Green 2009). In contrast, absolute measures of tissue and molecule contribution (i.e., mass) are strongly associated with body size in both determinate and indeterminate growers (Peig and Green 2009). For example, fat mass, protein mass, water mass, and ash mass are strongly correlated with body mass, snout-to-vent length and total body length in water snakes (Peig and Green 2009). Skeletal mass scales isometrically with snount-vent-length in lizards (Metzger and Herrel 2006) and scales positive allometrically with total body length in rattle snakes (Prange and Christman 1976). The evidence for strong associations between absolute measures of body composition and body size suggests that intraspecific scaling of total body nutrient content with length may be a natural extension of body size scaling relationships in ecology. This may aid the application of ecological stoichiometry to ecosystem-based vertebrate management because ecosystem functions of

individuals change with ontogeny (Showalter et al. 2016), body size is a good predictor of ontogeny (deRoos and Persson 2013), and vertebrate management has long occurred at the species or population level and harvest is body size selective.

4.4. LENGTH-NUTRIENT CONTENT RELATIONSHIPS (LNCRS)

We define length-nutrient content relationships (LNCRs) as the relationship between the absolute amount of nutrient in an indeterminate vertebrate and a longitudinal measurements (e.g., total body length, fork length, snout-to-vent length, standard length). LNCRs are an extension of body mass-length relationships as commonly used to compare and contrast vertebrates within and among taxa (Froese 2006; Peig and Green 2010). Within a growth class of many organisms, particularly fish, mass often increases exponentially with body length. Total body nutrient content should also follow this exponential increase because body mass (M) and total body nutrient content (N_x) are linearly related, being that N_x is the product of mass and the proportion of mass comprised of a given nutrient. Formally, LNCRs take the form

(Eq. 4.2) $N_x = aL^b$

Where a is the intercept of the regression of N_x with a length measurements (L) used as the independent variable, and b is the slope of the regression. In its most basic form, the model requires a length measurement (e.g., fork length, snout-vent-length, total length, standard length), the wet weight of an individual without stomach contents, and whole body nutrient concentration of individuals along the full length range of the population or cohort of interest.

4.4.1. Estimating Individual Level Nutrient Accrual

Estimating nutrient accrual within a population is important for understanding how a population directly impacts ecosystems at intermediate temporal scales because the net flow of nutrients in a population makes those nutrients unavailable to primary producers. Unfortunately, estimating nutrient accrual at the individual level, the aggregate of which is accrual at the population level, is impossible with the general equation for measuring growth rate (Bumpers et al. 2015)

(Eq. 4.3) $GR = \frac{\ln M_f - \ln M_i}{(t+1)-t}$

Where, GR is growth rate, M_i is the initial body mass, M_f is the final body mass, and *t* is the time between measurements because a researcher cannot measure body nutrient concentration on the same individual twice. Body nutrient content can only be measured following lethal sampling. This problem might easily be solved by assuming constant body nutrient concentration along a growth trajectory (Kraft 1992; Schindler and Eby 1997; Vanni et al. 2013); however, there is often differential growth rates among tissue types and tissue types differ in their nutrient composition, which can cause changes in body nutrient concentration with growth (Boros et al. 2015a). We suggest LNCRs may serve to circumvent this problem by generalizing changes in body element concentration at the population level in a way that permits the use of mass balance.

LNCRs provide a simple means of calculating nutrient accrual over any period defined by a change in length. Length-at-age is a common metric in population data of indeterminate growers, thus length can often be used as a surrogate for age (Vanni 1996).

Given that an individual of length L_1 at age *t* is expected to be L_2 at age *t*+1, then individual accrual of nutrient ($N_{x,accrued}$) over that period is

(Eq. 4.4) $N_{x,accrued} = a_x L_2^{b_x} - a_x L_1^{b_x}$

Then, nutrient accrual rate (NAR) is estimated as

(Eq. 4.5) $NAR = \frac{N_{x,accrued}}{(t+1)-t}$

This basic formulation can be applied when we expect that the relationship between length and nutrient content to be the same during both periods of interest (i.e., *t*, *t*+1).

This constraint on LNCR application is similar to the constraint on the use of length-weight relationships to calculate growth rates (Ricker 1975). Just as the coefficients of length-weight relationships can change seasonally according to a taxon's phenology, so may LNCRs. Therefore, with long lived taxa in many natural settings, a LNCR formed with samples collected at the beginning of a growing season can only infer nutrient accrued at the annual scale (e.g., age 1 to age 2). To estimate nutrient accrual at shorter time scales (i.e., over a growing season), the population must be sampled at the beginning and end of the period of interest to form two LNCRs with period specific coefficients. In this scenario, we can calculate nutrient accrual rate as

(Eq. 4.6) $NAR_{seasonal} = \frac{a_{x,t+1} L_{t+1}^{b_{x,t+1}} - a_{x,t} L_t^{b_{x,t+1}}}{(t+1)-t}$

Where $a_{x,t} L_t^{b_x}$ is the season specific LNCR and $(t+1) - t$ is the time difference between sample periods.

4.4.2. ACCRUAL OF MULTIPLE NUTRIENTS AT THE INDIVIDUAL LEVEL

Growth and reproduction require energy investment in somatic and gonadal tissue (deRoos and Persson 2013), but also require multiple nutrients (Sterner and Elser 2002). The differences in tissue growth over time suggest that different nutrients may be accrued at different rates in animals of different sizes and ages. This differential nutrient accrual ultimately leads to observed changes in body stoichiometry along ontogeny (Pilati and Vanni 2007, Boros et al. 2015a, Chapter 2). We can capture these changes in body stoichiometry using LNCRs constructed for different nutrients (N_x, N_y) on the same sample set by scaling N_x and N_y by their respective molar masses and dividing the molar quantities to produce molar X:Y. A simple exercise comparing the responses of dividing power relationships with different scaling coefficients (b) provides a set of conditions under which nutrients are accrued isometrically or allometrically relative to each other, the latter indicating that body stoichiometry changes with length. Body X:Y remains constant across body sizes when $b_x = b_y$, decreases with body size when $b_x < b_y$, and increase with body size when $b_x > b_y$ (Figure 4.1). Thus isometric growth in terms of multiple nutrients (i.e., accrual in constant proportions) occurs only when the scaling coefficients of LNCRs for each element are equal. When coefficients differ, the individuals exhibit changes in body stoichiometry with changes in body length.

4.4.3. NUTRIENT ACCRUAL AT THE POPULATION LEVEL

LNCRs are population level generalizations of the change in nutrient content in an individual's body through growth, which can be extended to place population dynamics

in the context of nutrient cycling at intermediate temporal scales. Populations are groups of individuals of the same species in a given area, and the dynamics of populations include not only changes in the number of individuals, but also changes in size structure occurring with sustained harvest and stochastic mortality events. Because different sized individuals may have different body stoichiometries and different nutrient accrual rates, the total net flux of nutrients into a population is highly dependent on its size structure. Here, we describe how LNCRs can be used to estimate the flow of nutrients between a population and its ecosystem by calculating the total mass of nutrients accrued in a population and explore how changes in size-specific loss rates affect whether a population is a source or sink of nutrients (Vanni et al. 2013).

Consider a population consisting of *k* cohorts or size classes. The total nutrient X mass within cohort *j* is the total nutrient content of an individual (Eq. 4.2) times the number of individuals (n_j) in the cohort expressed as

(Eq. 4.7) $N_{x,j} = n_j a_x L_j^{b_x}$

Then the total nutrient X mass contained in the populations (i.e., standing stock), an aspect of ecosystem structure, is the sum of nutrient mass in *k* cohorts at time *t*,

(Eq. 4.8) $N_{population,x,t} = \sum_{j=1}^{k} n_j a_x L_j^{b_x}$

The accrual of nutrients in a population is the difference between inputs and outputs of nutrients from a population and can be positive or negative depending on whether the population as a whole is gaining or losing nutrients, respectively. Input of nutrients to

population biomass (I_{pop}) is the maximum accrual of nutrients by a population assuming no mortality or dispersal losses calculated as

(Eq 4.9) $I_{pop} = \sum_{j=1}^{k} n_j\left(a_x L_{j+1}^{b_x} - a_x L_j^{b_x}\right)$.

If we assume nutrients are lost from cohorts at rate l_j only at the beginning of the period of interest (i.e., before growth within cohorts occurs) the outputs from the population (O_{pop}) is the sum of nutrient nutrient losses from *j* cohort calculated as

(Eq. 4.10) $O_{pop} = \sum_{j=1}^{k} l_j n_j a_x L_j^{b_x}$,

and nutrient accrual by the population is then

(Eq. 4.11) $Accrual = \sum_{j=1}^{k} n_j\left(a_x L_{j+1}^{b_x} - a_x L_j^{b_x}\right) - \sum_{j=1}^{k} l_j n_j a_x L_j^{b_x}$.

The net flux of nutrients between a population and the ecosystem it inhabits is an aspect of a population's functional role in its ecosystem and reflects whether a population is a net sink or source of ecosystem nutrients (Loreau et al. 2013). When more nutrients are sequestered in vertebrate biomass and made unavailable to primary producers than released in an available form the population is a net sink. When more nutrients are released from a population over time in a form available to primary producers than transformed into an unavailable form, the population is a net source. Ultimately, whether a population removes or supplies nutrients to primary producers depends on whether nutrients that are lost from the population are recycled through remineralization (Vanni et al. 2013). To determine whether a population is a net sink or source of nutrients, we split cohort specific loss rate l_j into losses occurring from mortality (m_j) and dispersal (d_j) rates

such that total loss rate is the sum of mortality and dispersal rates because mortality losses may be recycled within the ecosystem whereas nutrient losses through dispersal are permanent. From the standpoint of the ecosystem, gross input (I_{pop}) to the population is an output from the other subsystems. Inputs to the ecosystem from the population are the mortality fraction of population outputs (Eq. 4.10) further reduced by the efficiency with which mortality losses are recycled (i.e., recycling efficiency δ). As such, net flux between the population and the ecosystem is calculated as

(Eq. 4.12) $$F_x = \delta \sum_{j=1}^{k} m_j n_j a_x L_j^{b_x} - \sum_{j=1}^{k} n_j \left(a_x L_{j+1}^{b_x} - a_x L_j^{b_x} \right)$$

Where a population is a net sink of nutrients when population accrual exceeds recycled mortality losses (i.e., $F_x < 0$) and a net source when the reverse is true (i.e., $F_x > 0$). All parameters in Eq. 4.12 can be estimated using LNCRs to obtain individual accrual rates, population estimates to obtain abundances, and capture-mark-recapture models to estimate mortality and dispersal rates.

4.5. LNCR IN PRACTICE

4.5.1. ILLUSTRATION #1: EVALUATING ONTOGENETIC VARIABILITY IN BODY STOICHIOMETRY IN BROOK TROUT (SALVELINUS FONTINALIS) AND CALCULATING NUTRIENT STANDING STOCKS WITH SINGLE SEASON LNCRS.

With our first case study, we used one-sample period LNCRs for five populations of brook trout (*Salvelinus fontinalis*) to (i) illustrate a possible use of LNCRs by testing whether LNCRs vary within elements among populations and within populations among

elements and (ii) use LNCRs to estimate standing stock of multiple elements at the population level. We sampled brook trout in 50-m segments of five second and third order streams in Terra Nova National Park Newfoundland and Labrador, Canada from 15-17 June 2015; Charlottetown Brook, Cobblers Brook, Davey Ann's Brook, Spracklin Brook, and Yudle Pond Brook (Table A.4.1). We estimated population density with three pass depletion electrofishing using a Smithroot LR-24 backpack electrofisher and barrier nets located at the upstream and downstream edges of study segments. All captured individuals were measured for mass and fork length and at least 10 individuals from each population were lethally sampled for analysis of C, N, and P. We selected individuals for chemical analysis so that the overall sample contained individuals spanning the size gradient found in a given segment. Fish samples were placed on ice and then frozen at -20°C for up to two months before being prepared for chemical analysis. Please refer to Appendix A.4.1 for more information on sample processing and analysis.

We constructed LNCRs (i.e., Eq. 4.2) for each brook trout population by regressing natural log-transformed total body nutrient content of each individual (calculated as % nutrient on a wet mass basis by wet weight measured in the lab without stomach contents) against natural log transformed fork length of samples. Because the slopes and elevations of LNCRs for each element did not differ among populations (Figure 4.2; Table A.4.2.), we conclude that body element content of a given size fish does not vary among populations. As such, we pooled data from all streams within elements for further statistical analysis and calculations.

We were interested in whether body stoichiometry varied along a body size gradient of brook trout in study systems during late spring as indicated by differences in the slopes of LNCRs among elements. LNCR slopes (*b*) were 3.17, 3.09, and 2.94 for C, N, and P respectively (Figure 4.2); however, these differences were not statistically significant (Appendix A.4.2; Table A.4.4.). Therefore, we conclude that C:N, C:P, and N:P ratios do not vary with body length at the population level during the sampling period; a result possibly arising from considerable variability within elements among individuals and low within stream sample size.

Our second goal was to estimate the distribution of nutrients among cohorts and the total standing stock of nutrients held within the brook trout population using LNCRs. We estimated the storage of nutrients within cohorts for each brook trout population by multiplying the number of individuals in the cohort by the total body nutrient content from the LNCR (Eq. 7). Total nutrient standing stock of the population was calculated using Eq. 8. Estimated standing stocks of C, N, and P in brook trout populations in our study segments ranged from 66-301, 17-79, 3-15 $mg \cdot m^{-2}$, respectively (Table 4.1), which is similar to the vertebrate standing stocks in other small stream ecosystems (Milanovich et al. 2015). Uncertainty around the estimated stock (95% CI) reflects the uncertainty in the cohort size estimates (number of individuals; Table A.4.5) rather than the uncertainty in the LNCR for the given element. We feel that this is justified due to the high R^2 of LNCRs for these populations (Figure 4.2).

In this illustration, we found that brook trout body composition did not change with body length, thus estimating standing stock with LNCRs should yield similar results

to simply multiplying population biomass by nutrient concentration in this scenario. The lack of differences in body composition among sizes we observed may be the result of similar allocation of body element resources to growth during this sampling period. Future work should investigate whether this pattern holds throughout the year, particularly when larger, mature individuals begin allocating resources to gonadal tissue in early autumn.

4.5.2. Illustration #2: Estimating subsidies delivered by migrating Atlantic salmon (Salmo salar)

Migrating animals represent important nutrient subsidies to ecosystems they inhabit over their life cycles; however it is often difficult to quantify individual contributions to the total magnitude of subsidies when organisms are iteroparous and how individual contributions are partitioned among different trophic pathways. In our second illustration, we approximated the amount of nutrients released by female Atlantic salmon during migration, spawning, and overwintering using a two season LNCR (Eq. 4.6) constructed for pre-spawn mature adult Atlantic salmon (termed adults) migrating from the ocean to freshwater and post-spawn Atlantic salmon (termed kelts) migrating from freshwater to the ocean. Migrating and spawning adult Atlantic salmon do not feed in freshwater, typically lose 35-45% of their body mass during their freshwater spawning and overwintering period (Chapter 3), and do not change in fork length. As such, changes in body mass and composition can be attributed to losses occurring in the freshwater

ecosystem only, which is a measure of the magnitude of a subsidy delivered by an individual.

We used a two season LNCR formulation to estimate total amount of nutrients released during migration, spawning and overwintering and whether elements were released in different amounts relative to the body nutrient content of the incoming adult. As described in Eq. 4.6, we regressed log-transformed total body nutrient content of samples of each life stage (adults and kelts) using data from 13 adults and 14 kelts collected from three streams on the island of Newfoundland, Canada. Individuals crossed the freshwater-marine boundary in April-May 2014 and July-August 2014, respectively (see Appendix A.4.4. for detailed methods). As expected, we found lower C, N, and P content in kelts than in adults of a given length (Figure 4.3). By applying mass balance to individuals at freshwater entry and exit (i.e., Eq. 4.6), we estimate Atlantic salmon that survive spawning and overwintering release 135-415 g C, 19-55 g N, and 0.5-3.3 g P per individual over the 8-9 months they reside in freshwater. By placing these losses (i.e., adult N_x – kelt N_x) relative to the initial body nutrient content upon freshwater entry (i.e., adult N_x), we estimate that female Atlantic salmon release 70-80%, 50-65%, and 16-30% of their initial body C, N, and P during their entire freshwater migration, respectively (Figure 4.4 ; Total released). For comparison, Jonsson et al. (1997) estimated that Atlantic salmon in a Norwegian river expended 60-70% of body energy reserves during upstream migration and spawning. Similarly, Hendry and Berg (1999) estimated that sockeye salmon (*Oncorhynchus nerka*) expended 65-75% of body energy reserves between freshwater entry and death. Both studies used relationships between fish length and the

sum of somatic and gonadal energy content (Jonsson et al. 1997; Hendry and Berg 1999) similar to the LNCRs we describe. Thus, our estimates of total nutrient release obtained using a two season LNCR (Eq. 4.6) offer a complementary method for evaluating the costs of migration and reproduction using similar principles, but in a way that can place salmon in the context of ecosystem nutrient cycling (Reiners 1986) while simultaneously quantifying an important metric for evolutionary biology, investment in reproduction, in terms of nutrients.

To quantify the effects of anadromous fish mediated subsidies, it is important to distinguish between nutrients released in the form of eggs and nutrients released as excretions and respiration (see Eq. 1) because the two releases can support different parts of the aquatic food web. Eggs are available to higher trophic levels and decomposers (e.g., Bentley et al. 2012), whereas excretions are available to autotrophs and microbes (Tiegs et al. 2011). To partition the proportion of nutrient released during the migration and spawning between eggs and excretions, we constructed an additional LNCR for the nutrient content of salmon eggs (Figure 4.3) by collecting eggs from mature female Atlantic salmon captured at a fish holding facility on the Exploits River, Newfoundland Canada (see Appendix A.4.4 for detailed sample collection and processing methods). By regressing log-transformed total egg nutrient content against female fork length, we estimate that female Atlantic salmon between 45 and 63 cm fork length release 30-95 g C, 6- 19g N, and 0.6 – 1.8 g P per female as eggs (Figure 4.3). By examining the magnitude of egg release relative to body nutrient content upon freshwater entry (i.e., $N_{x,\ eggs}$ / $N_{x,\ adults}$), we estimated individuals invest 15-18%, 18-21%, and 15-19% of total body C, N,

and P content upon freshwater entry in eggs (Figure 4.4; lower line, light yellow shading) with the remainder of losses being attributable to excretion and respiration for C and excretion for N and P.

4.6. PERSPECTIVES

We develop a tool to link large consumers and ecosystem nutrient cycles using measurements of total body nutrient content in conjunction with common population level measurements such as body length, age, and population size. We envision that LNCRs may serve a number of uses in both basic and applied ecology because they rely on the principle of mass balance that underlies both the metabolic theory of ecology (Brown et al. 2004) and ecological stoichiometry (Sterner and Elser 2002). Allen and Gillooly (2009) outline four theoretical principles for predicting nutrient and energy fluxes at the ecosystem level using sub-cellular structure and kinetics in order to merge and extend both theoretical frameworks. With a basic LNCR (Eq. 4.2), we acknowledge Principle II – biomass is comprised of metabolic and structural pools with distinct allometries and element compositions (Allen and Gillooly 2009) – when we explicitly connect total body element content to total body length. As we extend the use of LNCRs to the population level (Eq. 4.8-4.12), we acknowledge Principle IV – the storage, flux, and turnover of energy and materials in biological communities and ecosystems can be estimated by summing across individuals in that community – when we sum the nutrient contents of individuals within ecosystems at multiple points in time.

We add two points to Allen and Gillooly's (2009) synthesis to further assist in the application of ecological stoichiometry to populations: (i) elemental composition of an individual can vary in predictable ways over the course of its life due to changes in the proportional representation of structural components with implications for predicting nutrient fluxes at the individual level and (ii) populations consist of individuals at different stages of development, which influence the rates and composition of nutrient fluxes at the population level. LNCRs begin to address both points because these relationships implicitly incorporate variation in body element composition that follow ontogeny and phenology in a manner that permits the use of mass balance at seasonal and annual scales. Ontogeny is implicit in the basic LNCR because we assume ontogeny changes along a size gradient, which we applied to the population level in Illustration #1. In a two season LNCR we explicitly incorporate ontogeny and phenology, which we used to estimate fluxes out of individual Atlantic salmon in Illustration #2. Standing stocks and fluxes are key aspects of ecosystem theory (DeAngelis 1992, Loreau 2010). LNCRs may increase the precision of estimates of stocks and fluxes for indeterminate vertebrates, such as many fish, reptiles, and amphibians, especially at longer temporal scales. Similar methods have been used to great effect for terrestrial plants (Kerkhoff and Enquist 2006).

LNCRs may shed light on feedbacks between ecology and evolution, a major focus of modern ecology in these times of rapid environmental change (Post and Palkovacs 2009). Kay et al. (2005) developed a stoichiometric framework for macroevolutionary biology by describing how the genetic determinants of body composition are shaped by abiotic (e.g., growing season length, temperature, and UV

radiation) and biotic (e.g., competition, predation, sexual interactions) factors. More recently, Jeyasingh et al. (2014) called for shifting attention towards intraspecific variation in elemental composition to address connections between ecology and evolution by merging ecological stoichiometry with population genetics. LNCRs may facilitate this effort because a LNCR is a stoichiometric characteristic of a population that emerges from selective forces acting on individual body composition, which is considered an elemental phenotype (Jeyasingh et al. 2014). Then, phenotypic variation in a population at any one time is reflected in the residual variance of the regression. Consistent, unidirectional shifts in LNCR coefficients at evolutionarily relevant temporal scales suggest ecologically important changes in organismal structure that can be traced directly to gene frequencies in a population and feed back on ecosystem processes such as nutrient standing stocks and population level accrual rates.

Animal populations and communities have the strongest impacts on nutrient cycling at ecosystem and regional scales (Schmitz et al. 2013). At short temporal scales, the spatial distribution of fish can create areas of high nutrient availability (McIntyre et al. 2008) with consequences for ecosystem productivity (Allgeier et al. 2014) and anadromous fish modulate primary and secondary production in their natal ecosystems by transporting nutrients between marine and freshwater ecosystems (Levi et al. 2013). At longer temporal scales, animals existing in stable populations are hypothesized to be long-term nutrient sinks at the whole ecosystem level (Sereda et al. 2008), but only when nutrient contained in their bodies are not re-mineralized because nutrient are transformed into a recalcitrant form and stored in sediments (Vanni et al. 2013; Boros et al. 2015b) or

populations are harvested. These examples suggest that fish, wildlife, and ecosystem managers can implement policies that have direct effects on nutrient cycles by influencing animal storage pools, but these policies require refinement of our understanding of how nutrients are distributed within populations and among populations across space.

Over-exploitation of fish stocks is pervasive with well-studied consequences for the abundance of organisms at lower trophic levels arising from consumptive effects (Frank et al. 2005). Recently, some ecologists have shifted their focus to the effects of animal harvesting on ecosystem productivity via non-consumptive effects. Layman et al. (2011) found that gray snapper (*Lutjanus griseus)* excretion rates at the population level were 400 to 500% higher in unfished sites than fished sites in the Bahamas and connected this difference in nutrient availability to primary production. Similarly, Allgeier et al. (2016) found mixed models including fishing pressure as a categorical variable (i.e., fished or unfished) best explained aspects of nutrient storage and recycling at the level of reef fish communities in the Caribbean.

Our understanding of the effects of harvest on nutrient cycles at larger spatial and temporal scales is more limited, but evidence suggests that commercial and recreational harvest can influence nutrient cycles by changing short term fluxes, but also may change the total amount of nutrients in an ecosystem. Maranger et al. (2008) estimated that the proportion of N fertilizer runoff removed from coastal ecosystems via commercial fisheries declined from 60% to 20% between 1960 and 2000. Likewise, Hjerne and Hansson (2002) estimated that herring, sprat, and cod fisheries removed approximately 2% and 18% of anthropogenic N and P load moving to the open ocean from the Baltic

Sea, respectively. Thus, commercial harvest may alter long term nutrient dynamics with consequences for ecosystem productivity, especially in ecosystems with low exogenous inputs. The opposite may also be true; harvest may serve as a tool to mitigate the effects of anthropogenic nutrient loading by removing excess nutrients from ecosystems in a form that is edible for humans. Indeed, managers have a long history of removing fish to control algal blooms in eutrophic lakes (Hansson et al. 1998, Schaus et al. 2010). Given the magnitude of global fish harvests, the diversity of species exploited, the size-specific nature of current fish harvest regulations, and potential local scale effects, we believe that LNCRs may help us manage fish populations for both food production and conserving or manipulating nutrient cycles at ecosystem, regional, and global scales by refining estimates of harvest related nutrient removal by accounting for interspecific, ontogenetic, and phenological variability in fish body composition.

There are a number of paths for the future development of LNCRs as a tool for bridging ecosystem and population ecology. First, LNCRs require further testing using datasets with larger sample sizes. In Illustration #1, our within-population sample size was low and inter-individual variability in body composition may have masked true differences among populations. In Illustration #2, the confidence intervals on our estimates of proportion of body nutrient released are wide, which we attribute to the small sample sizes within life stage and the diversity of populations represented in the dataset. Large uncertainty in estimates obtained by dividing predictions, as we executed in Illustration #2, are expected because of the propagation of errors associated with merging independent measurements. We illustrate how LNCRs differ along a species phenology

using pre-spawn and post-spawn Atlantic salmon, but anadromous salmon are an extreme example due to their complex, migratory life cycle. Changes may be more subtle or extreme for non-migratory species if LNCRs are analyzed for pre-and post-spawn periods.

The specificity of LNCR coefficients to a population and time period needs to be known. Is a relationship applicable season after season so that LNCRs can be used in long term studies? If the coefficients change from year to year − why? Coefficients may change during years of high food availability, low temperature, species invasion, *et cetera*, where the difference between LNCR slopes can potentially be used as a nutrient explicit expression of body condition (Peig and Green 2010) at the population level. If LNCR coefficients depend on the timing of sampling relative to reproductive phenology (Illustration #2), then changes in LNCR coefficients over years may suggest shifts in the timing of reproduction.

There is a disconnect between population and ecosystem ecology in both theory and practice arising from a difference in the units of analysis; ecosystem ecologists use atoms and energy, whereas population ecologists use biomass and individuals. With further development, LNCRs may serve to translate individuals into nutrient masses using a standardized measurement with applications in basic macroecology, evolutionary ecology, and the management of population and ecosystems.

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Table 4.1. Carbon, nitrogen, and phosphorus standing stock ($mg \cdot m^{-2}$; lower 95%CI, upper 95%CI) in brook trout populations inhabiting five streams in Terra Nova National Park in June 2015. Confidence intervals were obtained using the 95% confidence intervals from the cohort size estimates from three pass depletion methods (see Appendix A.4.1).

Element	Stream	Age 0+	Age 1+	Age 2+	Age 3+	Total
Carbon	Charlottetown	0.4 (0.3, 0.5)	4.4 (0, 8.8)	44.8 (0.8, 88.9)	14.2 (14.2, 14.2)	63.8 (15.2, 112.3)
	Cobblers	0.3 (0.2, 0.4)	16.1 (15.5, 16.7)	116.6 (115.2, 118.1)	25.9 (25.9, 25.9)	158.9 (156.8, 161.0)
	Davey Ann's	0	10.9 (5.7, 16.1)	131.9 (131.9, 131.9)	0	142.8 (137.6, 147.9)
	Spracklin	28.3 (24.8, 31.7)	42.3 (34.4,50.1)	55.7 (38.5, 72.9)	174.4 (93.9, 255.9)	301.1 (191.7, 410.6)
	Yudle	3.2 (2.2, 2.2)	6.1 (6.1, 6.1)	151.1 (135.9, 166.3)	131.5 (70.6, 192.3)	291.9 (214.8, 369.0)
Nitrogen	Charlottetown	0.1 (0.1, 0.1)	1.2 (0, 2.4)	11.8 (0.2, 23.3)	3.6 (3.6, 3.6)	16.7 (3.9, 29.4)
	Cobblers	0.1 (0.1, 0.1)	4.4 (4.2, 4.5)	30.6 (30.2, 31.0)	6.6 (6.6, 6.6)	41.7 (41.1, 42.2)
	Davey Ann's	0	3.0 (1.6, 4.4)	34.6 (34.6, 34.6)	0	37.6 (36.2, 39.0)
	Spracklin	8.2 (7.2, 9.1)	11.7 (9.5, 13.8)	14.7 (10.2, 19.3)	44.4 (23.8, 64.9)	78.9 (50.7, 107.2)
	Yudle	0.9 (0.6, 1.2)	1.6 (1.6, 1.6)	40.2 (36.1, 44.2)	33.7 (18.1, 49.3)	76.4 (56.5, 96.4)
Phosphorus	Charlottetown	0.02 (0.02, 0.03)	0.24 (0, 0.47)	2.24 (0.04, 4.45)	0.67 (0.67, 0.67)	3.2 (0.7, 5.6)
	Cobblers	0.02 (0.01, 0.03)	0.89 (0.86, 0.93)	5.85 (5.78, 5.92)	1.21 (1.21, 1.21)	8.0 (7.9, 8.1)

Davey Ann's	0	0.61 (0.32, 0.90)	6.63 (6.63, 6.63)	0	7.2 (7.0, 7.5)
Spracklin	1.85 (1.63, 2.08)	2.44 (1.99, 2.90)	2.86 (1.98, 3.74)	7.99 (4.29, 11.70)	15.2 (9.9, 20.4)
Yudle	0.21 (0.14, 0.27)	0.33 (0.33, 0.33)	7.88 (7.09, 8.67)	6.18 (3.32, 9.04)	14.6 (10.9, 18.3)

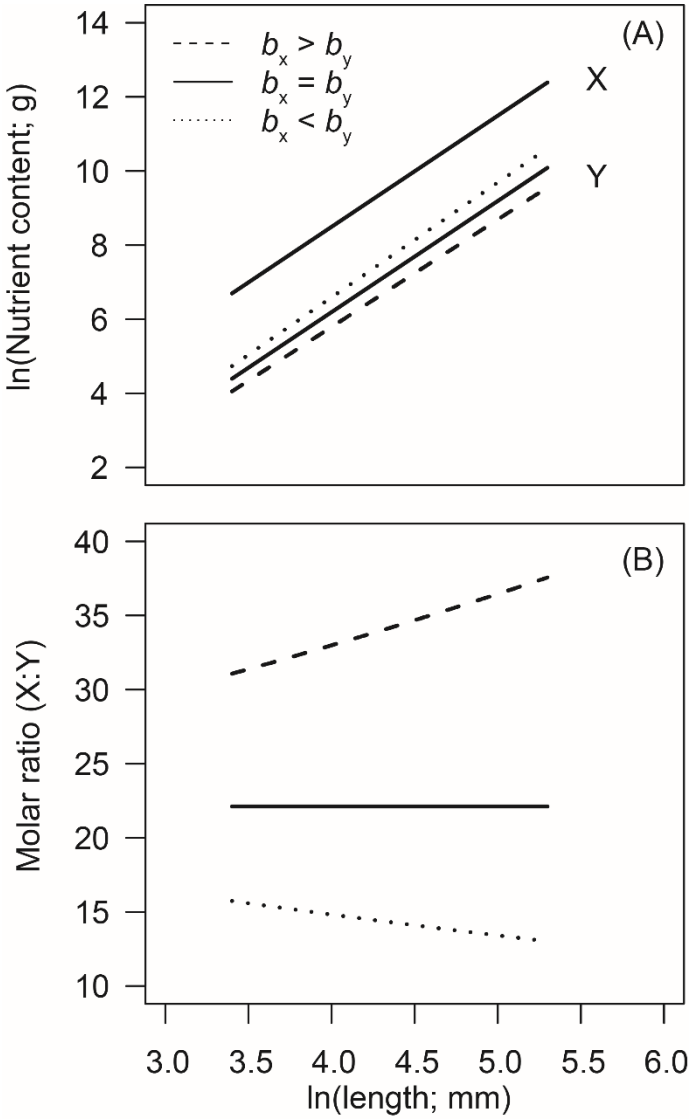
(A)
$b_x > b_y$
$b_x = b_y$
$b_x < b_y$
X
Y
ln(Nutrient content; g)
14
12
10
8
6
4
2
(B)
Molar ratio (X:Y)
40
35
30
25
20
15
10
3.0
3.5
4.0
4.5
5.0
5.5
6.0
ln(length; mm)

Figure 4.1. Simulation of how differences among LNCR coefficients for multiple elements correspond to changes in body stoichiometry with increasing body length. Panel (A) depicts LNCRs for nutrient X (upper line) and Y (lower lines) when $a_x = 0.03$, $a_y = 0.003$, $b_y = 3$ (solid upper line), $b_x=3$ (solid lower line), $b_x = 2.9$ (dashed lower line), and $b_x = 3.1$ (dotted lower line). Panel (B) depicts the body ratio assuming that nutrient X is nitrogen and nutrient Y is phosphorus when $b_x = b_y$ (solid line), $b_x > b_y$ (dashed line), and $b_x < b_y$ (dotted line).

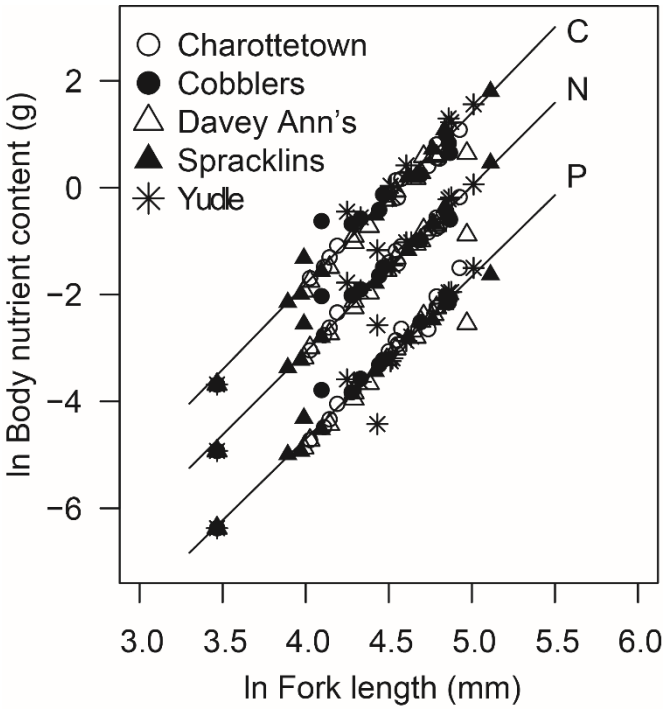

Figure 4.2. Length nutrient content relationships of C ($\ln(N_C) = -14.45 + 3.17\ln(fl)$, $R^2 = 0.95$, n=62), N ($\ln(N_N) = -15.42 + 3.09\ln(fl)$, $R^2 = 0.95$, n=62), and P ($\ln(N_P) = -16.39 + 2.94\ln(fl)$, $R^2 = 0.95$, n=62) for five brook trout populations in Terra Nova National Park, NL. Different symbols denote different populations.

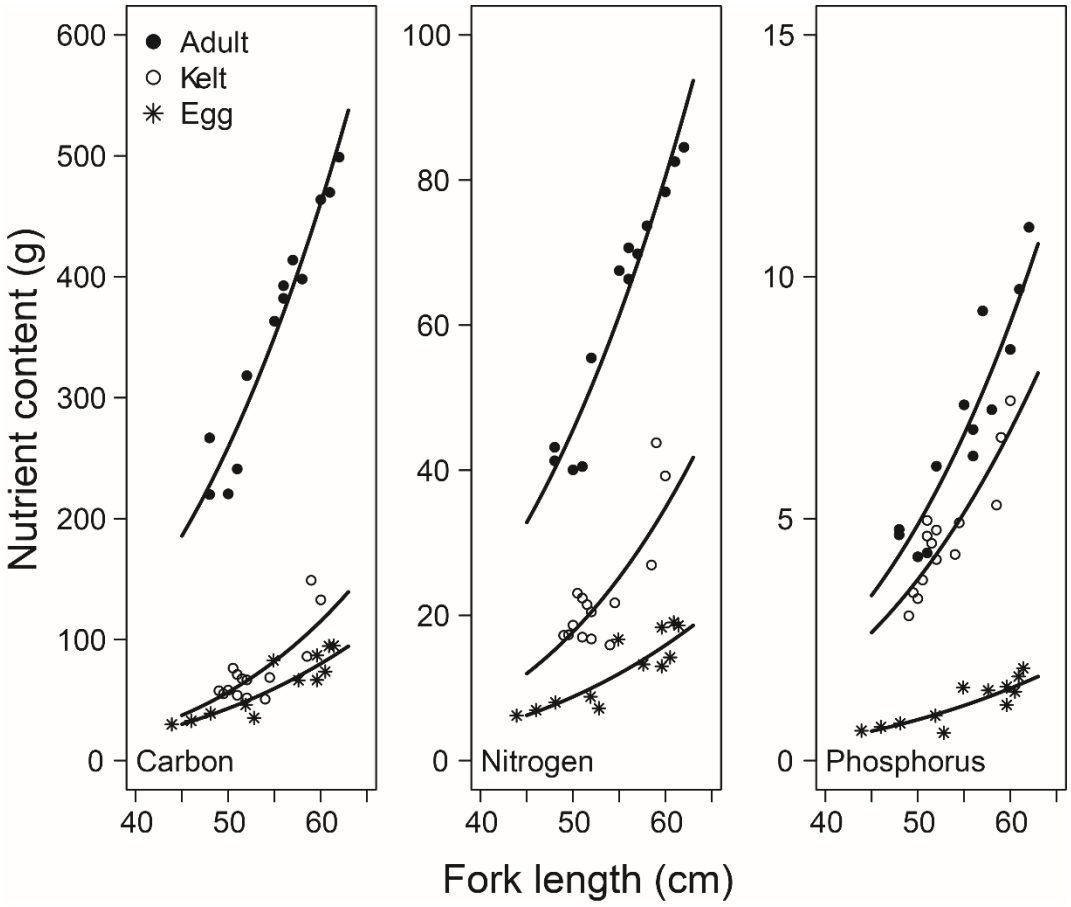
Adult
Kelt
Egg
Nutrient content (g)
Carbon
Nitrogen
Phosphorus
Fork length (cm)
600
500
400
300
200
100
0
100
80
60
40
20
0
15
10
5
0
40
50
60

Figure 4.3. Length nutrient content relationships (LNCRs) of carbon (left), nitrogen (middle), and phosphorus (right) for Atlantic salmon adult body content (solid circles; n=13) and kelt body content (open circles; n=14) sampled in July-August 2013 and April-May 2014, respectively, from Campbellton River, Conne River**,** and Western Arm Brook, Newfoundland and Labrador Canada. Asterisks represent the nutrient content of eggs non-lethally retrieved from mature female Atlantic salmon captured in the Exploits River, Newfoundland and Labrador in November 2014 (n=12). Solid lines indicate predictions from ordinary least squares regression of natural log-transformed nutrient content against natural log-transformed fork length for adults ($N_C = e^{-6.79+3.15*\ln(fl)}$, R^2=0.91; $N_N = e^{-8.37+3.11*\ln(fl)}$, R^2=0.92; $N_P = e^{-11.68 + 3.39*\ln(fl)}$, R^2=0.85), kelts ($N_C = e^{-11.24+3.91*\ln(fl)}$, R^2=0.63; $N_N = e^{-11.63+3.71*\ln(fl)}$, R^2=0.65; $N_P = e^{-11.557 + 3.29*\ln(fl)}$, R^2=0.78), and eggs ($N_C = e^{-9.54+3.40*\ln(fl)}$, R^2=0.83; $N_N = e^{-10.55+3.25*\ln(fl)}$, R^2=0.81; $N_P = e^{-12.37 + 3.11*\ln(fl)}$, R^2=0.74).

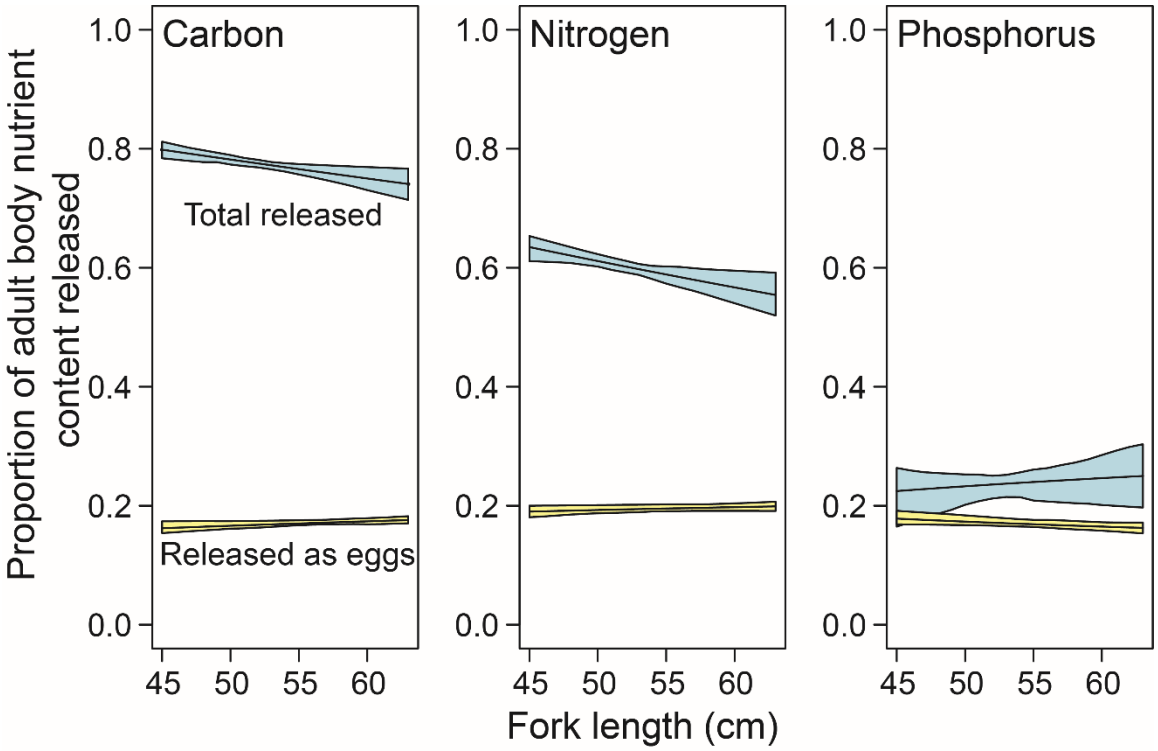

Figure 4.4. The proportion of adult body nutrient content released by anadromous Atlantic salmon during upstream migration, spawning, and downstream migration (upper line; light blue shading) and the proportion of adult body nutrient content released as eggs (lower line; light yellow shading). Shaded areas represent the 90% confidence intervals of our estimates of proportion of body nutrient content released and was determined by randomly removing one datum from each dataset (i.e., adults, kelts, and eggs) 100 times, re-calculating the proportions, and removing the upper and lower 5% of the proportion estimates.

Chapter 5: Ecosystem effects of top consumers with complex and migratory life cycles

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5.1. ABSTRACT

Migratory consumers with complex life cycles, in which individuals experience ontogenetic habitat and diet shifts, couple the dynamics of ecosystems through interdependent, bi-directional flows of individuals and material; a special type of subsidy not yet incorporated into ecosystem theory. We derived a meta-ecosystem model consisting of natal and adult ecosystems connected by flows of migrating top consumers and evaluated how changes in the relative magnitude and form of subsidies (i.e., consumer or resources fluxes) that occur within and among migratory taxa regulate trophic structure and ecosystem fluxes. We demonstrate that increasing migration rates always decreases resource stocks, but can sometimes increase resource production in the recipient ecosystem. In the donor ecosystem, increasing migration rates always increases resource stock, but can sometimes decrease resource production. The direct incorporation of adult-borne subsidies into juvenile consumers can increase natal ecosystem fluxes, but only when juvenile losses through mortality and excretion are recycled efficiently. Our analyses revealed that ecosystem fluxes are more useful metrics for understanding

variation in the ecosystem effects of migratory consumers because production responds to both top-down and bottom-up forces. With human activity exerting extreme pressure on migratory consumers, we need to connect these organisms' characteristics to their ecosystem effects.

5.2. INTRODUCTION

Ecosystems are connected by flows of material and organisms, forming complex webs of interactions among ecosystems (Baxter et al. 2005; Marczak et al. 2007; Soininen et al. 2015). These flows are often referred to as subsidies. Subsidies are flows of material from one ecosystem that increase the productivity of a recipient in another ecosystem (Polis et al. 1997). Many empirical studies document strong effects of subsidies on food webs because subsidies can increase resource availability (Polis and Strong 1996; Nakano et al. 1999) or increase predator density (Knight et al. 2005) depending on subsidy type, quantity, quality, duration, and timing. Current theory concerning the role of subsidies in ecosystem dynamics focuses on the effects of sustained or pulsed subsidies on trophic dynamics (Takimoto et al. 2002; Leroux and Loreau 2008; Holt 2008; Takimoto et al. 2009), the reciprocal, but independent flows between ecosystems on trophic stocks (Leroux and Loreau 2012), independent nutrient flows among ecosystems on community stability and resilience (Gravel et al. 2010a; Marleau et al. 2010) and nutrient co-limitation (Marleau et al. 2015), and flows of consumers across habitats on food web stability (Huxel and McCann 1998; McCann et al. 2005). This theory, and most of the empirical work that inspired it, consider cross ecosystem fluxes to be passive and independent; it has not acknowledged that for many well studied subsidies, those borne

by migratory animals (but see Schreiber and Rudolf 2008; McCoy et al. 2009), the response of the donor ecosystem and the recipient ecosystem are inextricably linked by the naturally selected characteristics of the migrating taxa.

Organisms with migratory and complex life cycles, in which individuals transition in ecological niche and space during their lives (reviewed by Werner and Gilliam 1984), connect spatially distinct ecosystems through the consumption of local resources and subsequent transport of material and individuals across boundaries during their life cycles. These organisms include several large taxonomic groups including amphibians, homometabolous insects, diadromous fishes, *et cetera*. In these taxa, individuals move into and out of the ecosystem for different purposes and different portions of the material transported into an ecosystem act as consumer and resource subsidies, which are opposing forces on trophic structure. As such, migratory consumers are a special, yet common case of subsidies.

As a consumer subsidy, migrants contribute to the consumer population by producing offspring, re-establishing residency, or providing allochthonous prey, which is hypothesized to decrease autochthonous prey (McCoy et al. 2009; Blaustien et al. 2014; Collins et al. 2016). For example, adult amphibians deposit eggs in ponds and the resulting larvae tend to have top-down effects on their natal resources (Seale 1980; Nery and Schemera 2016). As a resource subsidy, material moves to lower trophic levels through migrating consumer excretion and mortality and is hypothesized to stimulate upper trophic levels by increasing primary production (Schindler et al. 2003). For example, anadromous fishes hatch and rear in freshwater ecosystems and migrate to

marine ecosystems to grow substantially in size before returning to freshwater to spawn. The material accrued during marine feeding phase of their life cycle is deposited in freshwater ecosystems as gametes, excretions, and carcasses, which constitutes a substantial material subsidy (Moore and Schindler 2004) which is hypothesized to stimulate both aquatic and terrestrial production (Schindler et al. 2003). Additionally, the material contained in different life stages migrate in different directions and represents a drain of material in the donor ecosystem and a subsidy to the other ecosystem (e.g., Chapter 3). At the same time, individual consumers leaving an ecosystem may relieve predation pressure on lower trophic levels in one ecosystem and increase it in the other ecosystem (McCoy et al. 2009). All of these processes have potential consequences for biomass distributions and ecosystem fluxes in both ecosystems that are difficult to measure. Ecosystem theory (e.g., Loreau and Holt 2004; Leroux and Loreau 2008) has not yet considered migratory complex life cycles and population models (Schrieber and Rudolf 2008; McCoy et al. 2009) have not incorporated feedbacks through material recycling.

Connecting subsidies to the ecosystem effects and population dynamics of organisms with complex and migratory life cycles requires a meta-ecosystem perspective (Loreau et al. 2003). A meta-ecosystem is a network of ecosystems connected by material or energy flows. Embedded within the connected ecosystems are communities comprised of trophic compartments, or trophic levels, which may respond to inputs or outputs of material to the local ecosystem. Furthermore, global mass balance constraints, where inputs must equal outputs to the entire network, explicitly acknowledge that material

flowing into one ecosystem necessarily comes from another. Recent meta-ecosystem theory predicts that the dispersal ability of organisms, community structure, and relative fertility of the connected ecosystems influence whether one ecosystem is a source or sink of material for other ecosystems (Gravel et al. 2010b; Marleau et al. 2014). Complex life cycles are a special case within a meta-ecosystem framework, where flows between ecosystems are actively transported by higher trophic levels and coupled through reproduction. Interdependent bi-directional flows have not yet been explored within meta-ecosystem theory, but this is important to understand given that migratory and complex life cycles are common across the animal kingdom and exhibit significant variation in life history characteristics among taxa, there is substantial evidence that these taxa have strong ecosystem effects (Janestski et al. 2009; Bauer and Hoye 2014), and migratory taxa face extreme anthropogenic pressure (Wilcove and Wilkelski 2008).

In this article, we merge principles from population and ecosystem models to explore how variation in the characteristics of migratory consumers with complex life cycles influence the ecosystems they inhabit over their life cycles. We derive a meta-ecosystem model to generate predictions about the responses of trophic structure and ecosystem functions to migrating top consumers. We use our abstract model consisting of two ecosystems coupled by reciprocal and active flows of a migrating consumer with a complex life cycle to address the following questions: (i) How does trophic structure at local and meta-ecosystem scales respond to changes in migration rates and partitioning of a subsidy between consumer and resource fluxes? (ii) Do subsidies from migratory consumers increase ecosystem fluxes (i.e., production and material cycling)?

5.3. MODEL DESCRIPTION

We derive a meta-ecosystem model comprised of two ecosystems each containing one basal abiotic compartment (N_i) and two biotic compartments; a resource (R_i) and a top consumer (C_i), where subscript *i* denotes the natal ecosystem (*i*=1) or the adult ecosystem (*i*=2) (Figure 5.1; Table 5.1; Table A.5.1). Each compartment describes a stock of mass and follows mass balance constraints at equilibrium. Each ecosystem receives constant inputs to basal compartment (N_i) at rate I_i and mass-dependent outputs at rate E_i. R_i represents a compartment of highly interconnected primary producer and herbivore species that behaves similarly to a food chain community module (Holt 1996). The meta-ecosystem is coupled via a consumer with a complex life cycle. Specifically, the consumer has a juvenile life stage (i.e., C_1) residing and feeding on biotic resources (i.e., R_1) in the natal ecosystem and an adult life stage (i.e., C_2) residing and feeding on biotic resources (i.e., R_2) in the adult ecosystem. Stock *k* uptakes stock *j* at a rate described by $f_{j,k}(k, j)$, where *j* denotes the resource and *k* denotes the consumer in each feeding interaction. Similar to other ecosystem and meta-ecosystem models (DeAngelis 1992; Gravel et al. 2010a; Gravel et al. 2010b; Leroux and Loreau 2010), we assume that uptake is described by linear functions, where uptake depends on the stock of both *j* and *k* and obeys the law of mass action. Specifically, recipient control trophic interactions are defined as, $f_{j,k}(k, j) = a_{j,k}kj$, where $a_{j,k}$ is the consumer *k* attack rate on resource *j*. Uptake is assimilated by a compartment with efficiency ε_i. Mass is lost from the consumer compartments (C_1, C_2) through mortality and excretion at rate m_i and recycles to the basal abiotic compartment (N_i) with efficiency δ_w where subscript *w* indicates the recycling

source (i.e., 1, 2, *r* for recycling of juvenile losses, recycling of adult losses, and recycling of abiotic subsidy, respectively). Because we are primarily interested in the effects of coupled subsidies on trophic structure and ecosystem fluxes, we assume no losses from R_i.

Natal and adult ecosystems are connected by active flows of mass via the consumers' migrations, and each flow represents a mass subsidy to the receiving ecosystem. We derived the model to generally describe migrations associated with complex life cycles. Therefore, reproduction can only occur in one ecosystem, which has implications for how the subsidy is distributed among trophic compartments. Specifically, the juvenile consumer (C_1) migrates at rate α from the natal ecosystem to the adult ecosystem and is entirely assimilated by the adult compartment (C_2). The reciprocal mass flow of adults migrating to the natal ecosystem occurs at rate β, but is assimilated by the juvenile consumer with subsidy conversion efficiency *r*. This subsidy conversion efficiency (*r*) describes the portion of the adult subsidy mass consisting of (i) gametes that form embryos that hatch into feeding offspring, (ii) adult subsidy mass (i.e., carcasses and gametes) that are ingested by juvenile consumers (Kiernan et al. 2010; Collins et al. 2016), and (iii) the temporary or permanent re-establishment of residency by returning adults (Bond et al. 2015), all of which directly contribute to stock and production of the juvenile compartment. The remainder of the mass transported into the natal ecosystem by adult consumers (i.e., 1-*r*) represents excretions and decomposed carcass materials, which are absorbed by abiotic compartment N_1 at efficiency δ_r. In this way, we divide the material transported by adult consumers during its migration to the natal ecosystem into

two trophic pathways. Doing this allows us to investigate direct and indirect effects of subsidies in ecosystems (Allen and Wesner 2016).

2.4. MODEL ANALYSIS

We were interested in how the characteristics of migratory consumers modulate their direct (top-down) and indirect (bottom-up) effects on trophic structure and ecosystem fluxes. We focus our equilibrium analyses on three parameters that generalize differences among taxa in the characteristics that determine the magnitude of a subsidy relative to the size of the consumer population (i.e., juvenile migration rate α, and adult migration rate β) and efficiency with which the subsidy to the natal ecosystem is incorporated into juvenile consumer mass (subsidy conversion efficiency r). A description of how different taxa can be mapped onto these parameters is contained in Figure 5.2. Because we are interested in variation in the above three parameters, we simplified our model by assuming all attack rates ($a_{j,k}$) and assimilation efficiency (ε_j) are equal.

Changes to the magnitude of subsidies can induce trophic cascades. The trophic cascade concept traditionally refers to changes in the distribution of biomass among trophic levels within an ecosystem that occur with changes in ecosystem fertility (i.e., nutrient supply) or changes in the presence and abundance of predators (Carpenter et al. 1985; Pace et al. 1999). Broadly, there are two ways in which migratory consumers may regulate biomass distribution; indirectly or directly. Indirect regulation occurs when subsidies from migratory consumers increase production at lower trophic levels, which has subsequent positive effects on stocks of all higher trophic levels. Direct regulation

occurs when subsidies from migratory consumers increase production of a higher trophic level, which has subsequent positive effects on stocks of non-adjacent trophic levels below it (Carpenter et al. 1985). To test the first part of question (i), whether increasing the magnitude of a subsidy has direct or indirect control of equilibrium stocks in the recipient and donor ecosystems, we qualitatively assessed the direction of the partial derivatives (i.e., positive or negative) of the equilibrium stocks with respect to adult migration rate (β) and juvenile migration rate (α). We tested the second part of question (i), that the way in which migratory consumers regulate meta-ecosystem biomass distribution is determined by life history strategy (i.e., subsidy partitioning) in a similar way; we qualitatively assessed the direction of the partial derivatives (i.e., positive or negative) of the equilibrium stocks with respect to the subsidy conversion efficiency (r).

Subsidies may influence ecosystem fluxes differently than they influence stocks (Loreau 2010). We focused on two types of fluxes; production (Φ_j; Table A.5.2) and within ecosystem recycling flux (RF_i; Table A.5.2). Production describes the mass flux into trophic compartments. Within ecosystem recycling flux describes the flow of material from upper trophic levels to the basal nutrient pool. To test the first part of question (ii), that increasing the magnitude of the subsidy has a positive effect on production by all trophic levels by increasing recycling flux in the recipient ecosystem and decreasing production in the donor ecosystem by removing material, we qualitatively assessed the direction of the partial derivatives of consumer and biotic resource production (Table A.5.2) at equilibrium with respect to juvenile migration rate (α) and adult migration rate (β). Finally, we tested the second part of question (ii) that taxa that

more efficiently transfer material to juvenile consumers have negative effects on natal ecosystem fluxes because they contribute less material to the abiotic resource pool (N_1), by qualitatively assessing the direction of the partial derivatives of production and recycling flux with respect to the subsidy conversion efficiency (*r*).

5.5. EQUILIBRIA

Our model has four equilibria, but only one where all compartments exist. We focus our analysis on this equilibrium because we are interested in deciphering how flows influence the full meta-ecosystem. The other equilibria are presented in Appendix A.5.2.

The equilibrium representing migratory animals that exhibit co-occurring ontogenetic habitat and diet shifts (i.e., all compartments exist) consists of the following equilibrium stocks;

$$\mathrm{N}_1^* = \frac{\varepsilon(I_1(\beta+\mu_2)+I_2\beta\rho)}{\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1}$$

$$\mathrm{R}_1^* = \frac{I_2\beta\big(r(\mu_1-m_1)+(r-\rho)(m_1+\alpha)\big)-I_1\big(\mu_2(m_1+\alpha)+\beta(m_1+\alpha-r\alpha)\big)}{a\varepsilon(-I_1(\beta+\mu_2)-I_2\beta\rho)}$$

$$\mathrm{C}_1^* = \varepsilon\mathrm{N}_1^*$$

$$\mathrm{N}_2^* = \frac{\varepsilon\left(I_1\alpha + I_2(\alpha + \mu_1)\right)}{\alpha\beta(1-\rho) + \mu_2(\alpha + \mu_1) + \beta\mu_1}$$

$$\mathrm{R}_2^* = \frac{-\left(I_1\alpha\varepsilon(E_2 - m_2\delta_2\varepsilon) + I_2\left(-m_2(\mu_1 + \alpha) - \beta\left(\mu_1 - \alpha(1-\rho)\right)\right)\right)}{a\varepsilon\left(I_1\alpha + I_2(\mu_1 + \alpha)\right)}$$

$$\mathrm{C}_2^* = \varepsilon\mathrm{N}_2^*$$

Where;

$$\mu_1 = E_1\varepsilon + m_1(1 - \delta_1\varepsilon^2)$$

$$\mu_2 = E_2\varepsilon + m_2(1 - \delta_2\varepsilon^2)$$

$$\rho = r - \delta_r\varepsilon^2(-1 + r)$$

In this equilibrium, compartment stocks and ecosystem fluxes depend on input and loss rates in both ecosystems demonstrating that migratory top consumers couple the dynamics of abiotic and biotic resources in the ecosystems they inhabit over their life cycle (Schrieber and Rudolf 2008; McCoy et al. 2009; Sun and de Roos 2015). By examining the equations for equilibrium stocks, we see that changes in the rate of consumer mortality losses are recycled back to the consumers (i.e., μ_1 and μ_2), the amount of the adult consumer subsidy is taken up by compartments in the natal ecosystem (i.e.,

ρ), and changes in basal inputs to one ecosystem (i.e., I_1 and I_2) feeds back on compartment stocks in the other ecosystem.

5.6. MIGRATORY CONSUMER EFFECTS ON TROPHIC STRUCTURE

Migratory consumers are, as described earlier, a special case of subsidies where the subsidy is not completely donor-controlled and the subsidy is received by multiple trophic levels within an ecosystem. Overall, our model showed that changes in the characteristics of migratory consumers occurring among and within communities and taxa have consistent effects on ecosystem stocks. Our analytical results demonstrate that increasing each of the three parameters (juvenile migration rate (α), adult migration rate (β), and subsidy conversion efficiency (r)) decreases biotic resource stocks in at least one ecosystem (Figure 5.3 a, b, c), which agrees with previous models showing direct regulation of ecosystem stocks through predation (Schrieber and Rudolf 2008; McCoy et al. 2009). Additionally, increasing α, β and r induces directional responses (i.e., positive or negative) of trophic stocks that are consistent across all combinations of feasible parameter described by our mathematical analysis (Table A.5.3, A.5.4, A.5.5).

The adult migration rate (β) determines the magnitude of the subsidy relative to adult consumer stock that flows to the natal ecosystem. In the natal ecosystem, juvenile consumer and abiotic resource stocks increase with increasing adult migration rate and biotic resource stock decreases (Figure 5.3b; Table A.5.4). In the adult ecosystem, biotic resource stock increases with increasing adult migration rate, while adult consumer and abiotic resource stocks decrease (Figure 5.3b). In our model, increasing the juvenile

migration rate induced a similar pattern of responses as increasing the adult migration rate, but in the opposite direction (Figure 5.3a; Table A.5.3). In the juvenile ecosystem, biotic resources stock increases while juvenile consumer and abiotic resource stocks decrease with increasing juvenile migration rate. In the adult ecosystem, adult consumer and abiotic resource stocks increase with increasing juvenile migration rate, and biotic resource stock decreases (Figure 5.3a).

Increasing adult migration rate causes a top-down trophic cascade in the juvenile ecosystem and increasing juvenile migration rate causes a top-down trophic cascade in the adult ecosystem. By stepping back to observe the meta-ecosystem, we found a "horseshoe cascade" under both scenarios (Figure 5.3a, b) marked by opposite directional responses of analogous trophic compartments; a decrease in juvenile biotic resource stock accompanies an increase in adult consumer resource stock. The addition of trophic levels below our migratory consumer by dividing our biotic resource compartments into primary producers and herbivores would change the directional response of the abiotic resource pool, but the response of the migratory consumers and their adjacent resource will remain the same as our current model. Thus a migratory consumer would have a positive effect on primary producers by both controlling herbivores and recycling material (Leroux and Loreau 2010).

Increasing the subsidy conversion efficiency (r) causes a top down trophic cascade in both ecosystems (Figure 5.3c; Table A.5.5) as opposed to the horseshoe cascade caused by changing the juvenile or adult migration rates. Consumer and abiotic resources in both ecosystems increase with increasing subsidy conversion efficiency, and

biotic resources in both ecosystems decrease. As the subsidy conversion efficiency approaches 1, the model more closely resembles a single population of consumers that feeds on two resources with independent carrying capacities (Holt 1977; McCann et al. 2005) or a piscivore that feeds in both pelagic and littoral habitats (Vadeboncoeur et al. 2005).

We explore the interactive effect of adult migration rate, juvenile migration rate, and subsidy conversion efficiency with a numerical simulation of our model (Figure 5.4) using a haphazard selection of parameters because the directional responses of compartment stocks should be the same under all combinations of feasible parameters (Tables A.5.3, A.5.4, A.5.5). We conducted a local stability analysis of our feasible equilibrium to confirm the stability of the results of our numerical simulations. Increasing the subsidy conversion efficiency had a stronger effect on stocks in the natal ecosystem than the adult ecosystem, and this property is robust to changes in the ratios of basal inputs and outputs between ecosystems. Furthermore, the larger change in juvenile ecosystem stocks over the gradient of subsidy conversion efficiency when adult migration rate is high versus when adult migration rate is low indicates that the subsidy conversion efficiency and adult migration rate act synergistically to enhance or depress juvenile ecosystem stocks (Figure 5.4). Increasing juvenile migration rate decreases top down pressure exerted on juvenile biotic resources and shifts that pressure to the adult ecosystem, resulting in a decrease in biotic resource stocks (Figure 5.4).

5.7. MIGRATORY CONSUMER EFFECTS ON ECOSYSTEM FLUXES

Ecosystem fluxes do not always respond in the same direction as their corresponding stocks (Figures 5.3 d, e, f; Tables A.5.6, A.5.7, A.5.8). In the natal ecosystem, recycling flux always increase with increasing adult migration rate (β; Figure 5.3e; Table A.5.7), but the direction of this response to increases in juvenile migration rate (α; Figure 3d; Table A.5.4) and subsidy conversion efficiency (*r;* Figure 5.3f; Table A.5.8) depend on parameter values. In contrast, adult ecosystem recycling flux always decreases with increasing adult migration rate, but, like in the natal ecosystem, the direction of the response depends on parameter values (Figure 5.3e; Table A.5.7). Thus, increasing adult migration rate increases recycling flux in the natal ecosystem by extracting it from adult ecosystem; an example of the physical constraints imposed on ecosystems by the law of mass conservation (Loreau et al. 2003; Loreau and Holt 2004).

The parameter dependent response of natal ecosystem recycling flux (i.e., the amount of material cycling from consumers to the abiotic resource compartment) to increasing juvenile migration rate highlights the importance of feedbacks between adult and juvenile stocks and the differences in the way material is recycled in the two ecosystems. We would expect natal ecosystem recycling flux to decrease with increasing juvenile migration rate similar to the decrease in adult ecosystem recycling flux associated with increasing adult migration rate. The two migration-based flows are functionally analogous because both flows are mass dependent; however, increasing the juvenile migration rate can result in an increase in natal ecosystem recycling flux under some conditions (Table A.5.6). The mass of migrating juveniles (i.e., αC_1^*) is completely

incorporated into adults consumer stock. Increased adult consumer stock leads to higher adult ecosystem recycling flux because adult recycling flux is mass dependent (i.e., m_2C_2*) and represents the sole contributor to adult ecosystem recycling flux. The increase in adult ecosystem recycling flux does not necessarily extract that mass from the natal ecosystem abiotic resource pool because the increase in adult stocks increases the reciprocal flow of mass back to juvenile via adult migration. Specifically, increasing juvenile migration rate has a positive effect on recycling flux in the natal ecosystem when recycling rate of adult losses back into the adult compartment (i.e. $m_2\delta_2\varepsilon^2$) is higher than the basal loss rate from the adult ecosystem (Table A.5.6).

Recycling efficiencies in the natal ecosystem (i.e., δ_1 and δ_r) play an important role in determining the direction of juvenile's biotic resource production response with increases in subsidy conversion efficiency (Figure 5.5; Table A.5.8). The subsidy conversion efficiency determines the portion of the adult borne subsidy that is directly incorporated into juvenile consumers, and its converse (i.e., 1-r) determines the amount of the subsidy that flows to the abiotic resource compartment in natal ecosystem (Figure 5.1). Increasing the subsidy conversion efficiency serves to shunt subsidy mass to the abiotic resource pool indirectly through juvenile mortality. This pathway increases natal ecosystem recycling flux by increasing juvenile stock when subsidy recycling efficiency (i.e., δ_r) is lower than the juvenile mortality recycling efficiency (i.e., δ_1). In turn, the increased recycling flux increases abiotic resource stock which, increases biotic resource production through mass action (Figure 5.5).

We expound on the influence of migration rates on biotic resource production in the natal ecosystem because it is of interest to practitioners managing declining migratory populations (Larkin and Slaney 1997; Moore et al. 2011; Kohler et al. 2013). To examine the disparity between the consistent response of natal ecosystem biotic resource (R_1) stock and variable response of biotic resource production to increases in juvenile and adult migration rates (α and β), we consider a special case of our model; when the subsidy conversion efficiency is one (i.e., $r = 1$). In this special case, there is no direct contribution of the adult borne subsidy to the juvenile abiotic resource pool, which is rare in nature, but occurs when humans stock fishes in aquatic ecosystems.

Biotic resource production in the natal ecosystem (Φ_{R1}) increases with increasing adult migration rate when $\partial \Phi_{R1}/\partial\beta$ (Table A.5.7) is positive, which requires that

$$E_1 < m_1\delta_1\varepsilon - \frac{\delta_r\varepsilon(m_1+\alpha)(r-1)}{r},$$

and natal ecosystem biotic production increases with increasing juvenile migration rate (α) when $\partial \Phi_{R1}/\partial\alpha$ (Table A.5.6) is positive, which requires that

$$E_2 < m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon} + \frac{\beta(-1+r)\left(1-m_1\varepsilon(\delta_1-\delta_r)\right)}{1-m_1\delta_1\varepsilon}.$$

When adults are perfectly efficient at converting migratory adult mass into juvenile mass (i.e. r =1), the above conditions for $\partial \Phi_{R1}/\partial\beta$ and $\partial \Phi_{R1}/\partial\alpha$ to be positive reduce to

$$E_1 < m_1\delta_1\varepsilon$$

and

$E_2 < m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon}$.

These simplified conditions highlight how the nutrient cycling aspects of life history strategy influence ecosystem properties. First, when there is no direct contribution of the subsidy to the natal ecosystem abiotic resource pool, biotic resource production (Φ_{R1}) increases with increasing migration rate, or subsidy magnitude, only when the efficiency with which juvenile losses through mortality and excretion are recycled through the abiotic resource pool to biotic resource pool ($m_1\delta_1\varepsilon$) is greater than the natal ecosystem basal export rate (E_1). Therefore, the few migratory adult consumers whose subsidy conversion efficiency approaches one because they (i) spend very little time reproducing in the natal ecosystem and produce live larvae (e.g., fire salamanders; Caspers et al. 2015) or (ii) entirely re-establish residency following the return to the natal ecosystem (e.g., *Salvelinus* spp.; Bond et al. 2015) can only increase mass flow in their natal ecosystem with higher adult migration rates if juvenile mortality and excretion rates are high and those losses are recycled efficiently, or if basal export rates are very low. As *r* decreases, the positive response of Φ_{R1} can be maintained at higher basal loss rates or lower juvenile loss recycling efficiencies.

Second, increasing the juvenile migration rate will always decrease juvenile biotic resource production when $r = 1$ (i.e., $\partial\Phi_{R1}/\partial\alpha < 0$; Table A.5.6) despite increasing juvenile biotic resource stock (i.e., $\partial R_1/\partial\alpha > 0$; Table A.5.3) because the adult ecosystem basal loss rate (E_2) is constrained above zero (see feasibility condition in *Equilibria*), but $m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon}$ will always be negative. Higher juvenile migration rates lead to increased

biotic resource stocks in the natal ecosystem, but those higher stocks have lower production because more mass is leaving the natal ecosystem than being returned via adults and subsequently recycled. This provides a theoretical foundation for the idea that the "enhancement" of migratory salmonids by artificial supplementation to compensate for caused by high adult mortality rates will slow the flow of material in food webs and, consequently, decrease ecosystem productivity (Eby et al. 2006).

5.8. DISCUSSION

Previous empirical studies considered organisms with complex life cycles to represent a resource subsidy (Schindler et al. 2003) or a consumer subsidy (Knight et al. 2005) to the natal ecosystem or the adult ecosystem. We have a rich set of theory for how migratory consumers act as consumer subsidies (McCann et al. 2005; Schreiber and Rudolf 2008; McCoy et al. 2009), and how ecosystems respond to resource subsidies (Loreau and Holt 2004). Yet, migratory consumers simultaneously act as both consumer and abiotic resource subsidies in multiple ecosystems. In this article, we extend theory on the interaction of consumers with the ecosystems they inhabit. We derived a meta-ecosystem model to explicitly account for the role of migratory consumers as both consumer and resource subsidies in natal ecosystems by partitioning adult borne material into two pathways, a direct contribution to juvenile consumers and an indirect contribution through the abiotic resource pool. Specifically, our model predicts that increasing juvenile and adult migration rates depresses biotic resource stocks in the recipient ecosystems by increasing predation pressure while increasing biotic resource stock in the donor ecosystems. Both of these are local scale effects that emerge from meta-ecosystem

properties mediated by the characteristics of consumer taxa. Increasing the efficiency with which adults convert material directly into juvenile consumers depresses resource stocks in both ecosystems simultaneously. Despite the negative association of adult migration rate (β) and subsidy conversion efficiency (r) with biotic resource stocks in the natal ecosystem, increasing these two characteristics of migratory consumers can increase biotic resource production when juvenile losses are recycled more efficiently than the subsidy to the abiotic resource pool. By explicitly incorporating material recycling into a theoretical model of complex life cycles, we show previously unexplored indirect effects of ontogenetic habitat and diet shifts on material flow through lower trophic levels, and connect them to variation in the characteristics of migratory taxa.

The coupling of ecosystem compartments in our model is consistent with previous models of consumer-connected ecosystems (McCann et al. 2005; Schreiber and Rudolf 2008; McCoy et al. 2009); however, we arrive at this conclusion under different assumptions. Schreiber and Rudolf (2008) explicitly examined the dynamics of two ecosystems connected by a consumer with a complex life cycle in a stage-structured consumer-resource model. In particular, they were interested in how resource productivity and consumer mortality rates in the two ecosystems affected the distribution of consumers between juvenile and adult habitats. These authors showed that consumer populations can exist in alternative stable states driven by the juvenile resource productivity relative to adult resource productivity, which was executed by changing resource carrying capacity under the assumption that resources experience logistic growth. In our model, we did not make assumptions about resource carrying capacity because density dependence of biotic

resources arises from parameters governing biotic resource (R_i) and abiotic resource (N_i) interactions and basal flows into and out of the abiotic resource compartment (DeAngelis 1992; Loreau 2010). Without an explicit assumption about the carrying capacity of the consumer's resource, we were able to address both the effects of a migratory consumer on trophic structure and ecosystem fluxes with the same model thereby merging food web and ecosystem ecology (Loreau 2010).

Increasing juvenile consumer production by increasing either the adult migration rate or the subsidy conversion efficiency has a negative effect on juvenile resource stock. This entails that increasing the adult migration rate and/or increasing the conversion efficiency of adult mass to juvenile mass (r) has a qualitatively similar effect on the adjacent lower trophic level, in this case R_1, as increasing the juvenile consumers resource attack rate (i.e., $a_{j,k}$) in a simple model of a tri-trophic system with no spatial flows (Leroux and Loreau 2015). Top down control of resources by taxa with efficient conversion has been shown both empirically (Knight et al. 2005) and theoretically (McCoy et al. 2009) in adult ecosystems and empirically in natal ecosystems (Blaustein et al. 2014). Top-down control of resources by migratory consumers with increasing migration borne subsidy rates is also common in nature. For example, Post et al. (2008) observed stronger top-down regulation of zooplankton biomass and increased chlorophyll *a* concentrations in lakes inhabited by anadromous alewife (*Alosa pseudoharengus*) populations compared to landlocked populations of the same species (Post et al. 2008) despite the increase in allochthonous material available to the base of the food web (West et al. 2010). Similar to our model predictions, the contribution of a subsidy directly to the

juvenile population outweighs the bottom-up effects on resource stocks that occur through the recycling of adult alewife excretions and carcass decomposition (Post et al. 2008).

Many studies on natural runs of Pacific salmon observe decreasing resource stocks with increasing adult salmon biomass (Moore et al. 2007) and researchers attribute this decline to nest digging activities in high density populations, which dislodges macroinvertebrates and sediments from stream substrates and decreases local stocks (Moore et al. 2007; Janetski et al. 2009). Although, our model predicts a decline at this trophic level, our model is not applicable to disturbance-driven biotic resource decline that these studies commonly observe. Our model does not treat adult digging behavior within spawning habitats, but focuses on where juveniles of these species rear; sockeye juveniles typically feed in lakes and pink salmon juveniles typically feed in estuaries, not often near the substrates from which they emerged and were initially disturbed by adults. For example, Juday et al. (1932) state the "rich crop of plankton produced by [three lakes in AK] is due, at least in part, to the fertilizing substances contributed to their waters by the decomposing carcasses of the salmon." While there no doubt this is true, the authors were unable to measure the longer term effects of increasing the adult subsidy, which is the scale of inference from our model. Following the "fertilizing substances" that increase plankton stock are the planktivorous offspring of the sockeye that consume it. This presents an opportunity to incorporate adult habitat engineering into a three ecosystem model, where adult mass may increase nutrient inputs to downstream rearing ecosystems through adult spawning disturbance.

Ecosystem models show that the responses of stock and production to changes in ecosystem conditions can be disconnected (de Mazancourt and Loreau 2000). In single ecosystem models without recycling, production always responds positively to increased input to basal nutrient compartments regardless of the addition of trophic levels because production is less affected by top-down forces than is biomass (Loreau 2010). Our model yielded parameter dependent responses of biotic resource production and within-ecosystem nutrient cycling in both ecosystems. Increasing juvenile migration rate (α) can increase natal ecosystem production despite increasing the movement of material out of the ecosystem, but only when consumer losses in the adult ecosystem are recycled efficiently, which allows the material to return to the natal ecosystem. The role of recycling efficiencies in modulating the response of production was common in our model (Tables A.5.6, A.5.7, A.5.8) and highlights the importance of non-consumptive mechanisms that may affect production more than biomass (Leroux and Loreau 2010; Schmitz et al. 2010; Leroux and Schmitz 2015). In this specific scenario, the non-consumptive mechanism occurs in a spatially distinct ecosystem than the production it influences. Because the directional response of production is sensitive to both bottom-up and top-down forces, we suggest that production is a better metric than stocks for evaluating the ecosystem effects of migratory consumers.

The characteristics of migratory consumers with complex life cycles vary considerably within and among taxa (Werner and Gilliam 1984). We have shown that variation in the combination of characteristics modulates the consumers' effects on local and meta-ecosystems, which has been suggested by some empirical studies (Chapter 3;

Childress et al. 2016). As such, future empirical studies on the ecosystem effects of migratory consumers may benefit from exploring differences in characteristics among populations within taxa, and among taxa within ecosystems, and to quantify these differences in metrics consistent with ecosystem processes (i.e., nutrients and energy).

Migration rates and subsidy conversion efficiency are empirically tractable parameters. Migration rates, measured as a proportion of total consumer mass in a given population that migrates to the other ecosystem, likely differ within taxa across time and space. Migration rates at the population level are a function of the probability that an individual migrates, and the age and size at which it migrates, if it does. For example, age at seaward migration of juvenile Atlantic salmon (*Salmo salar* L) decreases with increasing growth opportunities at the individual level, which are mediated by temperature and photoperiod (Metcalfe and Thorpe 1990). This variation can be accounted for in our model by changing the juvenile migration rate (α); juvenile migration rate increases with increasing growth opportunity. Given similar ecosystem characteristics, we predict that increases in juvenile population size in more northerly populations should have a stronger effect on prey resource stocks than more southerly populations. Similar predictions can be made for long-term shifts in the sea-age composition of spawning Atlantic salmon with changes in climate that influences adult migration rates (Otero et al. 2012).

Subsidy conversion efficiency (r) is essentially a population level measure of the uptake of the adult borne subsidy by juvenile consumers. It is the aggregation of individual adult traits (i.e., fecundity and egg size), adult behavior (i.e., feeding or not

feeding in the natal ecosystem), juvenile behavior (i.e., propensity for cannibalism; Rudolf 2007) and population level metrics (i.e., post-reproduction survival rate, adult sex ratio, and survival of offspring from fertilization to first feeding). Given similar ecosystem characteristics, we predict that semelparous species have a stronger positive effect on production than iteroparous species, unless the recycling of juvenile losses is high and efficient.

The predictions of our model apply to long term dynamics rarely captured in empirical studies. Yet, long term dynamics have consequences for the biogeochemical role of migratory consumers because subsidies occur in the conceptual realm of sources and sinks (Loreau et al. 2013). Material originates at a source, is delivered to another ecosystem as a subsidy, and is absorbed by a sink. A complex life cycle may result in a population being both a source and sink of ecosystem material, as the different portions of the population absorb material from one ecosystem and deliver it to another. Adults are unconditional sources of material to the natal ecosystem, whereas juveniles are unconditional sinks (Loreau et al. 2013). Because adults and juveniles populations are linked, the balance of the inputs and outputs determines whether a population deposits or extracts material from the natal ecosystem over time. When inputs to an ecosystem via reproducing individuals exceed outputs via non-reproducing individuals, the consumer is a net source to natal ecosystem. When the reverse is true, outputs exceed inputs, the consumer is a net sink (Loreau et al. 2013). Differences in migration characteristics have a strong effect on net flux, making net material flux a possible integrator of both ecosystem and consumer characteristics that can be measured using common population

monitoring data (e.g., Chapter 3). For example, semelparous sockeye salmon (*Oncorhynchus nerka*) have a low subsidy conversion efficiency (*r*) because in addition to gametes that produce offspring, sockeye also deposit their carcasses in the freshwater ecosystem. Sockeye salmon are typically unconditional net sources of material to their natal ecosystems (Moore and Schindler 2004). Atlantic salmon can survive spawning and have higher subsidy conversion efficiencies (*r*) than sockeye salmon (Figure 5.2). Atlantic salmon are conditional material sinks to their natal watersheds (Chapter 3). Underlying these net fluxes are the dynamics of the food webs and the recycling efficiencies (Vanni et al. 2013) that are described in our model.

Although we focus on migratory top-consumers, future theoretical work should explore how stocks and ecosystem fluxes will respond under different food web configurations, such as when juvenile migratory consumers are prey for resident predators, which is common in many ecosystems (e.g., Bentley et al. 2012) and relevant for predicting how the ecosystem effects of migratory consumers may change following invasion by resident predators (e.g., Sepulveda et al. 2013). Also, the active flows included in our model can be incorporated into more complex spatial networks that include both active and passive flows (see Marleau et al. 2014), thus providing a more expansive understanding of how migratory taxa interact with all of the food webs and ecosystems they pass through during their life cycle (Mouquet et al. 2005; Naimen et al. 2012). Understanding how different combinations of migrators' characteristics influence the stability of food webs (McCann et al. 2005) and the structure of a consumer population (i.e., juvenile dominated or adult dominated; Schrieber and Rudolf 2008)

under different ecosystems conditions may yield information on why a certain migratory taxa, or combinations of migratory taxa, exist in stable populations and communities in some ecosystems, but not in others. Finally, we model material flows in a single currency framework; however, juvenile migration flow and adult migration flow can have different stoichiometric ratios due to differences in body composition (Chapter 2) and elements may be differentially allocated among the different recycling pathways. Incorporating stoichiometric constraints into our model may clarify other important factors determining the consumptive and non-consumptive effects of migratory consumers (Leroux and Schmitz 2015).

Human activity has had a disproportionately strong effect on top consumers (Estes et al. 2011), and especially migratory top consumers (Wilcove and Wikelski 2008). It is imperative we have a holistic understanding of how human activities indirectly affect ecosystem structure and function by changing the characteristics of migratory taxa. Understanding and managing migratory consumers requires that we think across ecosystems when we study food webs because material is not wasted nor worn out, but rather ebbs and flows.

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Table 5.1. Model of ecosystem coupled by a migrating top consumer with variable and parameter definitions. Parameter constraints are provided in Table A.5.1.

Model equations
$\frac{dN_1}{dt} = I_1 - E_1N_1 - aR_1N_1 + \delta_1 m_1 C_1 + \delta_r(1-r)\beta C_2$
$\frac{dR_1}{dt} = \varepsilon a R_1 N_1 - a C_1 R_1$
$\frac{dC_1}{dt} = \varepsilon a C_1 R_1 + r\beta C_2 - \alpha C_1 - m_1 C_1$
$\frac{dN_2}{dt} = I_2 - E_2N_2 - aR_2N_2 + \delta_2 m_2 C_2$
$\frac{dR_1}{dt} = \varepsilon a R_2 N_2 - a C_2 R_2$
$\frac{dC_2}{dt} = \varepsilon a C_2 R_2 + \alpha C_1 - \beta C_2 - m_1 C_1$

Notes

†Variables: N_i, abiotic stock; R_i, resource stock; C_i, consumer stock.

‡Parameters: I_i, constant input to N_i; E_i loss rate from N_i; ε, Production efficiency; a, resource utilization rate; m_j, consumer loss rate; δ_r, recycling efficiency; β, mass flow rate from ecosystem 2 to ecosystem 1; α, mass flow rate from ecosystem 1 to ecosystem 2 ; r, subsidy conversion efficiency;

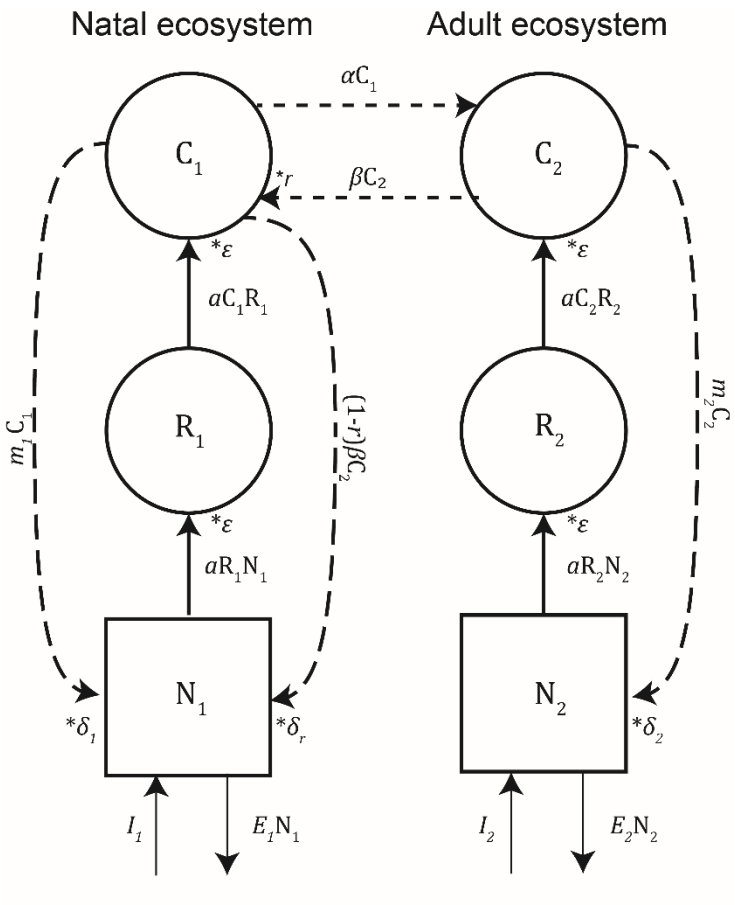

Figure 5.1**.** Conceptual diagram of two ecosystems linked by reciprocal flows of a migratory top consumer. Squares represent abiotic compartments and circles represent biotic compartments where N_i, R_i, and C_i denote inorganic nutrient, resources, and consumers, respectively. Thin lines represent basal inputs and losses; solid lines represent consumptive relationships; long dash lines represent nutrient recycling from biotic to abiotic compartments; short dash lines represent mass flows via consumer migration.

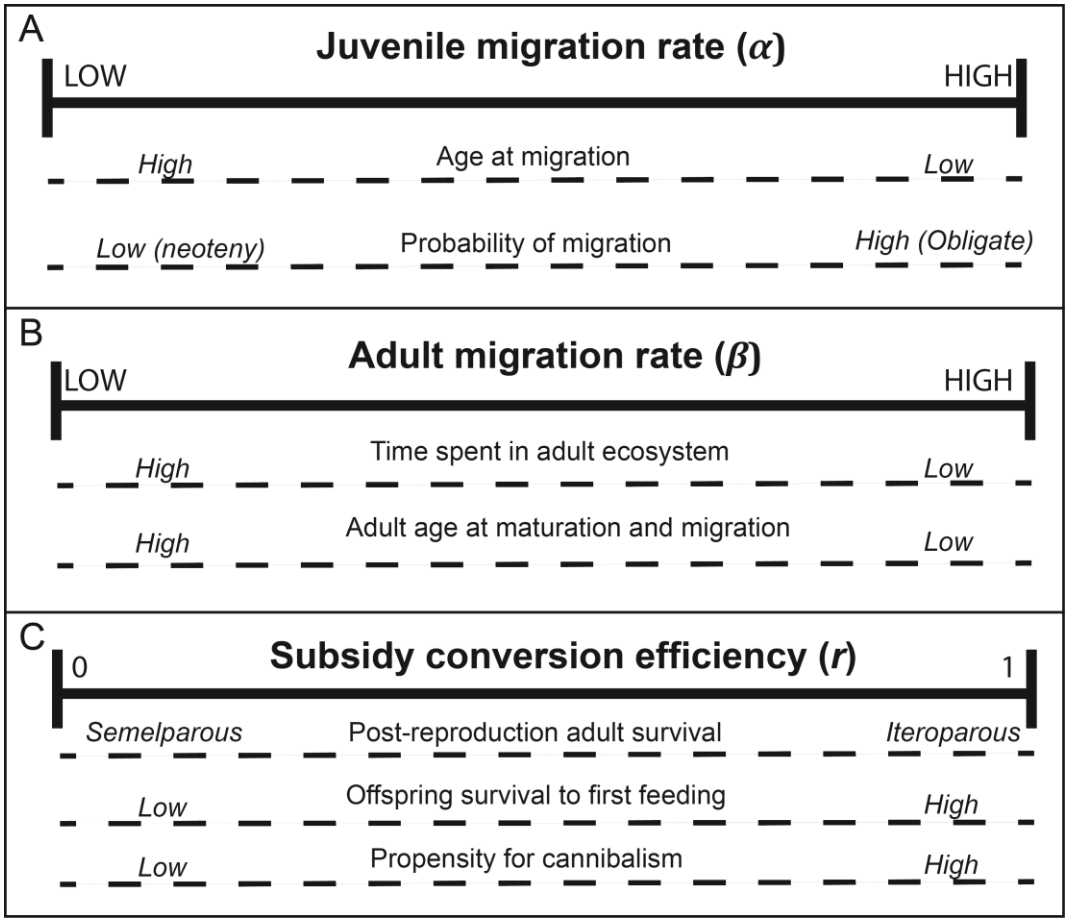
A
Juvenile migration rate (α)
LOW
HIGH
High
Age at migration
Low
Low (neoteny)
Probability of migration
High (Obligate)
B
Adult migration rate (β)
LOW
HIGH
High
Time spent in adult ecosystem
Low
High
Adult age at maturation and migration
Low
C
0
Subsidy conversion efficiency (r)
1
Semelparous
Post-reproduction adult survival
Iteroparous
Low
Offspring survival to first feeding
High
Low
Propensity for cannibalism
High

Figure 5.2. A conceptual diagram for mapping migration rates and subsidy conversion efficiency studied in the model on to the characteristics of migratory taxa with complex life cycles. Juvenile migration rate describes the proportion of the consumer compartment in the natal ecosystem that migrates to the adult ecosystem, and is negatively associated with the average age at migration from the natal ecosystem to the adult ecosystem and incorporates a gradient of partial migration (i.e., Tachniki and Koizumi 2016). For example, many anadromous charr species (*Salvelinus spp.*) have lower juvenile migration rates than Chinook salmon (*Oncorhynchus tshawytscha*) because charr populations tend to be partially migratory (e.g., Rikardsen et al. 2004), whereas Chinook rarely mature in their natal ecosystem and migrate to marine ecosystems in the first or second year of life (Healey 1991). Adult migration rate describes the proportion of the consumer compartment in the adult ecosystem that migrates to the juvenile ecosystem, and is negatively associated with age at maturation and time spent in the adult ecosystem. For example, anadromous charr species have higher adult migration rates than Chinook salmon because charr return to the natal ecosystem annually following a brief migration to the estuarine and marine ecosystems (e.g., Constonguay et al. 1982, Quinn et al. 2016), whereas Chinook salmon may spend more than five years in marine ecosystems before returning to the natal ecosystem (Healey 1991). Subsidy conversion efficiency describes the efficiency with which migrating adult consumer mass is converted into juvenile consumer mass that is actively feeding in the natal ecosystem, and is a function of post-reproduction adult survival rate, offspring survival rate to first feeding, and the propensity for cannibalism (i.e., consumption of adult flesh or gametes by juveniles). For example, charr species have a

higher subsidy conversion efficiency than Chinook salmon because charr are iteroparous with high post-reproduction survival rates, and exhibit facultative anadromy (Bond et al. 2015), whereas Chinook salmon are semelparous and most of the subsidy is deposited as carcasses in the natal ecosystem rather than deposited as embryos that survive to first feeding.

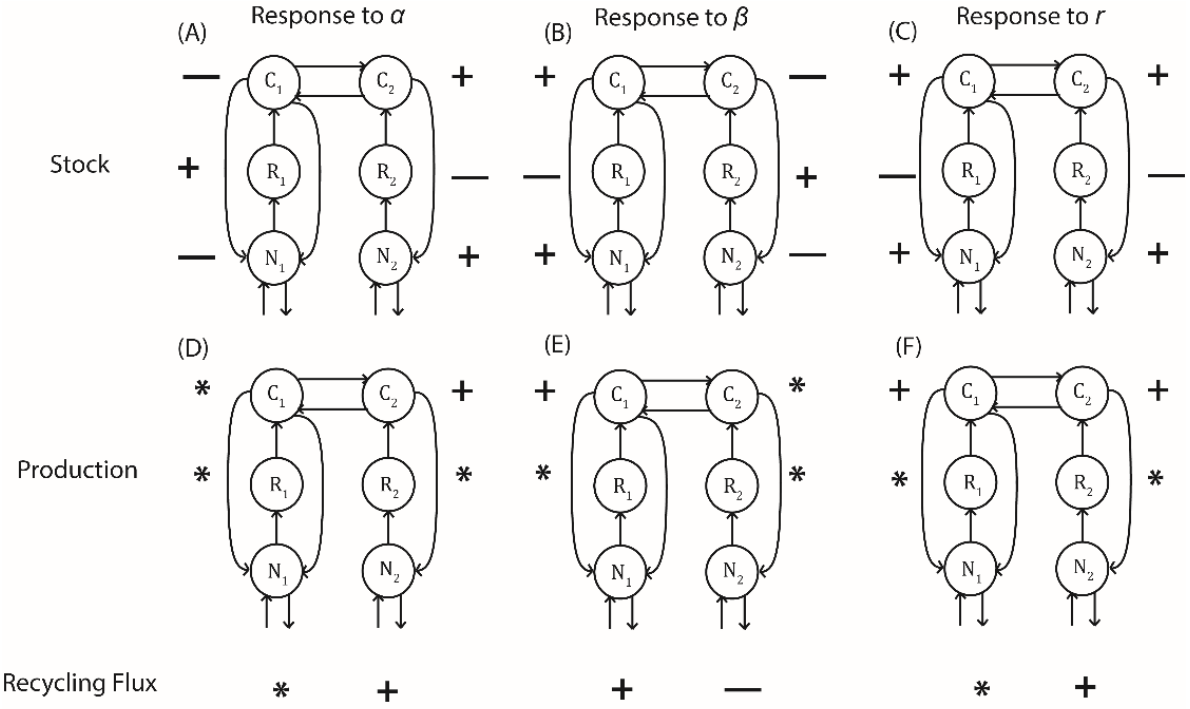
Response to α
Response to β
Response to r
(A)
(B)
(C)
(D)
(E)
(F)
Stock
Production
Recycling Flux
C1
C2
R1
R2
N1
N2

Figure 5.3. Qualitative assessment of analytical solutions for the response of equilibrium stocks (panels A, B, C) and ecosystem fluxes (panels D, E, F) to increasing juvenile migration rate (α; left column), adult migration rate (β; middle column), and subsidy conversion efficiency (r; right column). The sign to the immediate left or right of a compartment indicates whether the stock, production or recycling flux responds positively (+), negatively (-), or if the response could be either positive or negative depending on the full parameter set (*) to increases in the parameter noted at the top of each column. Note that there is no directional sign associated with abiotic resource production (Φ_{Ni}). Within ecosystem recycling flux (i.e., RF_i) and abiotic resource production (Φ_{Ni}) have the same partial derivatives because recycling flux and abiotic resource production are identical functions except the latter includes a constant and independent basal nutrient supply rate (I_i), which shifts abiotic resource production to a higher magnitude than recycling flux, but does not change the direction or shape of the response. Analytical solutions and conditions for positive responses to changes in migrations rates and subsidy conversion efficiency are found in Appendix A.5.3.

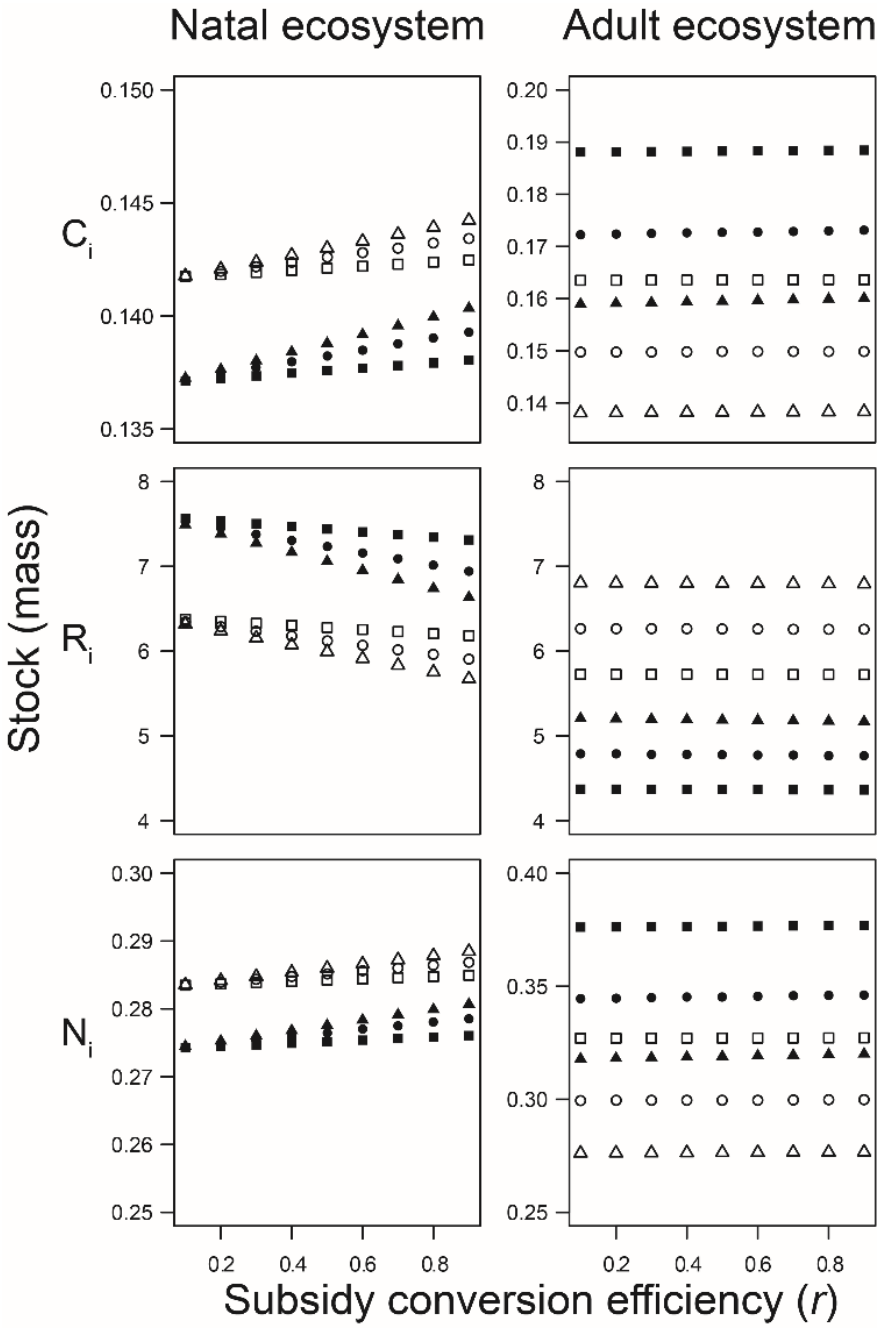
Natal ecosystem
Adult ecosystem
Stock (mass)
C_i
R_i
N_i
0.150
0.145
0.140
0.135
0.20
0.19
0.18
0.17
0.16
0.15
0.14
8
7
6
5
4
0.30
0.29
0.28
0.27
0.26
0.25
0.40
0.35
0.30
0.25
0.2
0.4
0.6
0.8
Subsidy conversion efficiency (*r*)

Figure 5.4. Numerical simulations for the response of equilibrium stocks in two ecosystems coupled by mass flows via a migratory top consumer to increases in the subsidy conversion efficiency, r, when adult migration rate (β) is low (β= 0.2; squares), moderate (β = 0.5; circles), and high (β = 0.8; triangles) under two juvenile migration rates, α = 0.2 (open shapes) and α = 0.8 (filled shapes). Other parameter values are I_1 = 10, I_2 = 1, E_1 = 30, E_2 = 0.5, a = 1, ε = 0.5, $m_1 = m_2 = 3$, $\delta_1 = \delta_2 = \delta_r = 0.2$. The equilibrium is locally stable (i.e., leading eigenvalues of the Jacobian matrix are negative) for the given parameter sets. See Appendix A.5.4 for equilibrium production for all trophic stocks associated with these parameter values.

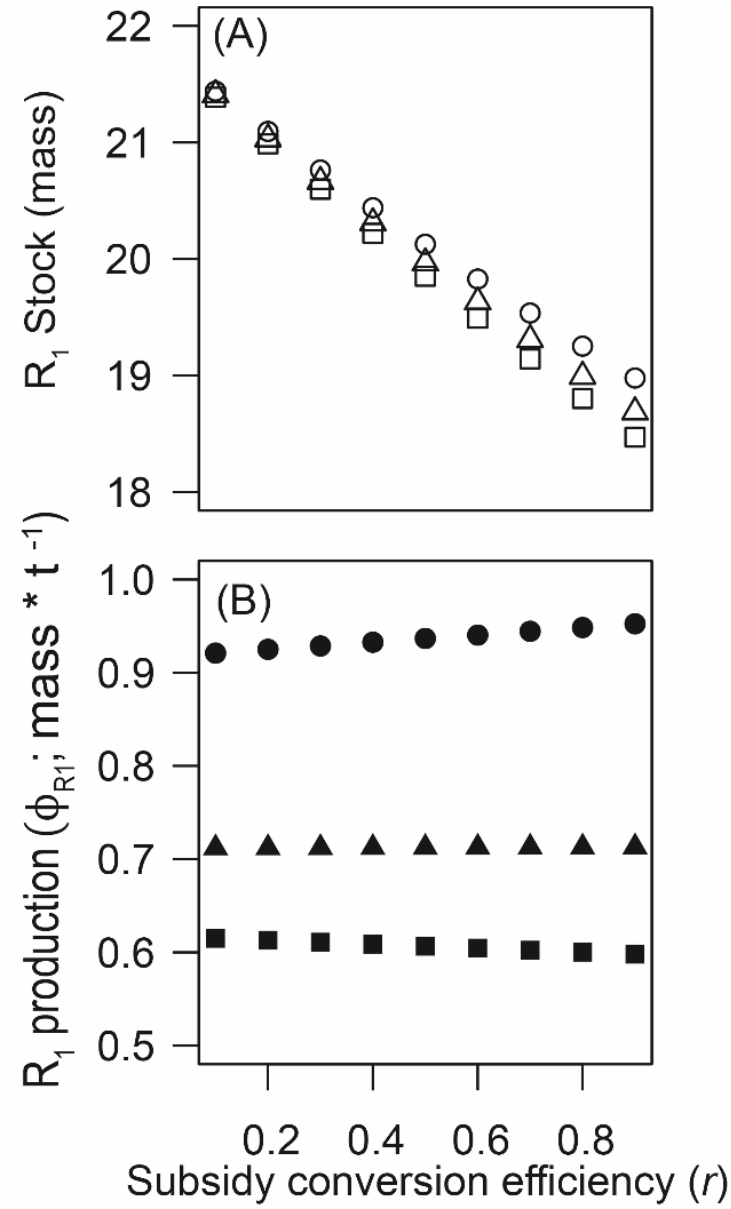
(A)
(B)
R_1 Stock (mass)
R_1 production (ϕ_{R1}; mass * t^{-1})
22
21
20
19
18
1.0
0.9
0.8
0.7
0.6
0.5
0.2
0.4
0.6
0.8
Subsidy conversion efficiency (*r*)

Figure 5.5. Response of natal ecosystem biotic resource stock and production to increasing subsidy conversion efficiency. Response of natal ecosystem biotic resource stock (panel A) and production (panel B) to increasing subsidy conversion efficiency (r; x-axis). Squares depict stocks and production when the subsidy is recycled more efficiently than juvenile losses ($\delta_r > \delta_1$; $\delta_r = 0.9$, $\delta_1 = 0.2$). Triangles depict stock and production the subsidy and juvenile losses are recycled with the same efficiency ($\delta_r = \delta_1 = 0.5$). Circles depict when the subsidy is recycled less efficiently than juvenile losses ($\delta_r < \delta_1$; $\delta_r = 0.2$, $\delta_1 = 0.9$). Other parameters used in this simulation were as follows: $I_1 = 1$, $E_1 = 0.01$, $I_2 = E_2 = 1$, $a = 1$, $\varepsilon = 0.5$, $\delta_2 = 0.3$, $m_1 = 10$, $m_2 = 3$, $\alpha = 0.9$, $\beta = 0.8$. The equilibrium is locally stable (i.e., leading eigenvalues of the Jacobian matrix are negative) for the given parameter sets.

Chapter 6: Conclusion

Large animals play important roles in ecosystems by storing, transporting, and releasing nutrients at times and places modulated by their life cycle. Most research on vertebrate-mediated nutrient recycling focuses on excretion as the predominant way that organisms interact with ecosystem nutrient cycling (Vanni 2002, Allgeier et al. 2015), but recent syntheses point out important long-term processes by which populations control nutrient availability by acting as net sources or sinks through births and deaths at the population level (Vanni et al. 2013). In this thesis, I use analysis of novel empirical data, synthesis of long-term data, and mathematical modelling to investigate various aspects of the role of aquatic vertebrates in ecosystem nutrient cycles. I found that:

(i) Atlantic salmon body element composition is mostly explained by life stage, and individuals do not have constant element compositions throughout their lives. Adults have higher concentrations of carbon and lower concentrations of nitrogen, phosphorus, and calcium than post-spawn adults and migrating juveniles. The difference in carbon probably influences the observed concentration of other elements because it is the most abundant element by dry mass. The consistency in element concentrations among individuals within life stages but across space suggests that Atlantic salmon exhibit rheostatic control of body element composition.

(ii) Differences in body element concentrations among life stages strongly influence the output of nutrient cycling models. In particular, I found that classifications of

Atlantic salmon populations as sources or sinks of nutrients made by previous studies that assumedequal body P concentration of upstream-migrating adults and downstream migrating post-spawn adults may be invalid. By accounting for ontogenetic variability in body element composition, I classified three Atlantic salmon populations as conditional P sinks to their natal ecosystems rather than unconditional P sources, which would have occurred by assuming that body element composition is constant over the life of an individual.

(iii) Body size relationships are some of the strongest in biology; however, interspecific scaling of body nutrient concentration with body mass has traditionally yielded poor results. I propose length-nutrient content relationships as a means for scaling from individual to population level nutrient fluxes. By using an absolute amount of nutrient as the dependent variable, LNCRs can be used to estimate ecosystem structures (e.g., body stoichiometry and standing stock of nutrients in a population) and functions (e.g., element release rates, nutrient accrual) when used in combination with common population monitoring data (e.g., abundance and individual lengths) and knowledge regarding species' phenology. It has potential applications in fish and wildlife management by linking population and ecosystem concepts.

(iv) Life history strategy is an important determinant of the ecosystem-level effects of subsidies borne by migratory consumers with complex life cycles. Iteroparous consumers should have stronger top-down effects on food webs than semelparous consumers in both ecosystems they inhabit over their life cycles. Meanwhile, the efficiency with which *in situ* consumer mortality is recycled to the base of the

natal food web relative to the recycling efficiency of subsidy material (e.g., adult carcasses and excretions) determines the directional response of biotic resource production to changing life history strategies.

Understanding the reciprocal interactions between population dynamics and ecosystem processes should be a major goal of ecological research as it applies directly to fish and wildlife management. Theoretical frameworks like ecological stoichiometry (Sterner and Elser 2002) and the metabolic theory of ecology (Brown et al. 2004) that have recently been applied to large consumer nutrient recycling (Allgeier et al. 2015, Vanni and McIntyre 2016) may be important advances for basic ecological understanding, but neither framework encompasses both ecosystem structure and function at management relevant extents (i.e., habitat and landscape).

Ecological stoichiometry utilizes ratios of elements as a means to connect multiple levels of organization (Sterner and Elser 2002). Defined as the patterns in proportions of elements in the reactants and products of chemical reactions, stoichiometry provides means of quantifying ecosystem structure, or the pattern or organization of compartments including connections between those compartments (Odum 1994). The elemental ratios of organisms' bodies, their resources, and released material (i.e., excretion, egestion, and reproduction) are aspects of ecosystem structure because they describe composition of compartments and connections in terms of the relative amounts of multiple elements. Ecosystem functions are flows through system structures and the transformations of material that accompany that flow (Odum 1994). A compartment's functional attributes include production, turnover time, residence time, and efficiency. Integrated over time,

these attributes determine a compartment's functional role as a source or sink of material within the overall system. Ecological stoichiometry cannot directly predict ecosystem functions because ratios are not rates and without actual quantities we can only infer how functional roles of organisms change over time, but cannot quantify how important these changes may be at an ecosystem level. Meanwhile, metabolic theory of ecology focuses predominantly on metabolism, an ecosystem function, and can only predict ecosystem structure (e.g., total population biomass; Brown et al. 2004) at macroecological levels which are not the focus of most wildlife management. I question whether we can predict fish biomass in a set of streams using the negative ¼ power scaling rule for relationships between population biomass and individual body size in a way that is accurate enough to inform management. This arises because the metabolic theory of ecology does not account for material requirements of organismal growth and reproduction, nor incorporate any information on ontogeny.

While many ecologists look for macroecological patterns in relationships between ecosystem structure and function, the taxonomic specificity of diets, body composition, and life history may preclude direct application to fish and wildlife management, at least for nutrients. My conclusions suggest that merging population and ecosystem ecology requires a return to examining intraspecific variability in species' traits which has recently been re-embraced by community ecology (Violle et al. 2012). Theoretical population models do not incorporate nutrient cycling by consumers as a possible determinant of resource availability (e.g., Schreiber and Rudolf 2008), whereas theoretical ecosystem models do not often test for the effects of trait variability (e.g., Leroux and Loreau 2010).

With the realization that vertebrates are important for ecosystem nutrient cycles and with ever decreasing wild vertebrate populations corresponding to the ever increasing level of human activity, the time to merge population and ecosystem ecology is now, but unfortunately occurs one small step at a time.

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A.2. Appendices for Chapter 2: Whole body element composition of Atlantic salmon *Salmo salar* influences by migration direction and life stage in three distinct populations.

A.2.1. Characteristics of sampled individuals, specifics of chemical analyses, and body element composition on a wet mass basis.

Table A.2.1 Characteristics of *Salmo salar* collected from three rivers on insular Newfoundland for quantification of whole-body nutrient concentration.

River	Life Stage	% Female	Collection Date	n	Fork length ± 1 SD (cm)	Weight ± 1 SD (g)
Campbellton	Adult	100	30 Jul – 03 Aug 2013	5	59.4 ± 2.4	2316.7 ± 240
	Kelt	100	01-10 May 2013	5	57.8 ± 7.7	1331.4 ± 586
	Smolt	NA	01-10 May 2013	4	16.1 ± 1.9	42.7 ± 11.4
Conne	Adult	50	14-28 Jun 2013	4	49.48 ± 1.4	1238.8 ± 63.2

	Kelt	80	23-30 May 2013	5	50.5 ± 1.3	730.0 ± 76.3
	Smolt	NA	30 Apr – 06 May 2013	8	14.1 ± 1.4	26.6 ± 6.9
Western Arm	Adult	60	13-22 Jul 2013	5	55.6 ± 2.3	1968.1 ± 137.4
	Kelt	100	21-22 May 2013	5	54.0 ± 2.9	826.9 ± 151.9
	Smolt	NA	30 May 2013	5	21.0 ± 3.0	54.4 ± 6.7

Table A.2.2. Extraction efficiency, reference levels, and detection limits for ICP-OES analysis of P, Ca, S, K, Mg, Na, and Fe completed at the Agriculture and Food Laboratory at University of Guelph.

Element	% recovery (based on NIST reference level)	NIST 1577c bovine liver reference levels (ppm)	Method detection limits (ppm)
P	96%	11750±270	17
Ca	109%	131±10	7
S	84%	7490±340	8
K	101%	10230±640	37
Mg	105%	620±42	15
Na	102%	2033±64	20
Fe	102%	197.94±0.65	2

Table A.2.3. Mean percent element composition presented on a wet mass basis for three migrating life stages of *Salmo salar* captured from three Newfoundland Rivers. Values presented are means that include all sampled fish of the given life stage.

Element	Adult ± 1SD	Kelt ± 1SD	Smolt ± 1SD
Dry Mass	33.76 ± 0.86	20.36 ± 1.37	22.48± 1.75
No. samples	14	15	17
Carbon	19.23 ± 0.72	8.49 ± 1.06	9.58± 0.92
Nitrogen	3.37 ± 0.15	2.60± 0.26	2.76± 0.12
Phosphorus	0.37 ± 0.04	0.54± 0.06	0.65± 0.10
Calcium	0.30 ± 0.11	0.76 ± 0.14	0.88± 0.21
Sulfur	0.18 ± 0.02	0.14 ± 0.01	0.16± 0.01
Potassium	0.35 ± 0.02	0.28 ± 0.03	0.32± 0.03
Magnesium	0.03 ± 0.002	0.02 ± 0.002	0.03± 0.003
Sodium	0.07 ± 0.01	0.12 ± 0.01	0.10± 0.01
Iron	0.001 ± 0.0003	0.002 ± 0.0004	0.003± 0.001

A.3. Appendices for Chapter 3: Ontogenetic differences in whole body phosphorus content and its implications for cross ecosystem fluxes.

A.3.1. Characteristics of study populations

Table A.3.1. Mean annual count, number of spawning individuals, mass, and length of smolt, small salmon (<63cm), and large salmon (> 63cm) passing through counting fences installed above the head of the tide on three Newfoundland rivers from 1993-2012. 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 (mean ± 1SD)	Spawners (mean ± 1SD)	Mass (kg; mean ± 1SD) [no. of fish]	Length (cm; mean ± 1SD) [no. of fish]
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. [20] refers to number of years, rather than number of individuals as presented for adults.

A.3.2. Sample processing methods and characteristics of sampled individuals

Sample processing protocols differed slightly between mature fish, including kelts, and smolts due to differences in fish size (Table A.3.2). We recorded fork length after mature fish had thawed for ca. 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 7mm diameter plate and once through a 3mm 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 ca. 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 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.

Table A.3.2. 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	Mean fork length ± 1 SD (cm)	Weight ± 1 SD (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

Table A.3.3. Mean %P on a wet weight basis of adults, kelts, and smolts collected in three Newfoundland Rivers in 2013.

River	Adult (%P ± 1SD)	Kelt (%P ± 1SD)	Smolt (%P ± 1SD)
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

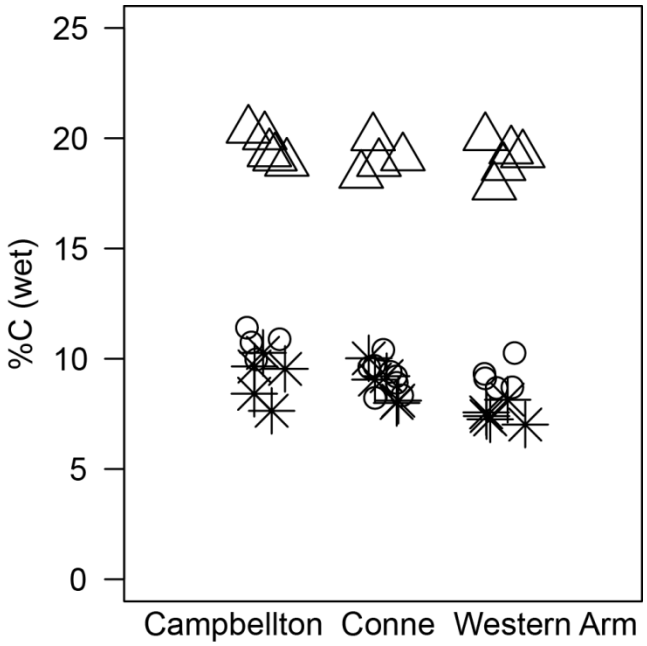

Figure A.3.1. Whole body carbon concentration on a wet mass basis of Atlantic salmon adults (open triangle), kelts (asterisk), and smolts (open circle) captured in three insular Newfoundland rivers. %C was measured on separate subsamples of the same fish as described in the main text. %C analysis was 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.

A.3.3. Long term P flux via Atlantic salmon in three Newfoundland Rivers

Table A.3.4 Total P flux for three Newfoundland salmon populations summed over a twenty 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

A.3.4. 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 4 sets of values for overwinter survival; the mean of annual survival rates measured on Campbellton between 1994-2012 (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 + 1SD 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. 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 (Figure A.3.2; $F_{.05(2),75} = 22.60$, $p < 0.001$). 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 (Table A.3.5).

Table A.3.5. 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

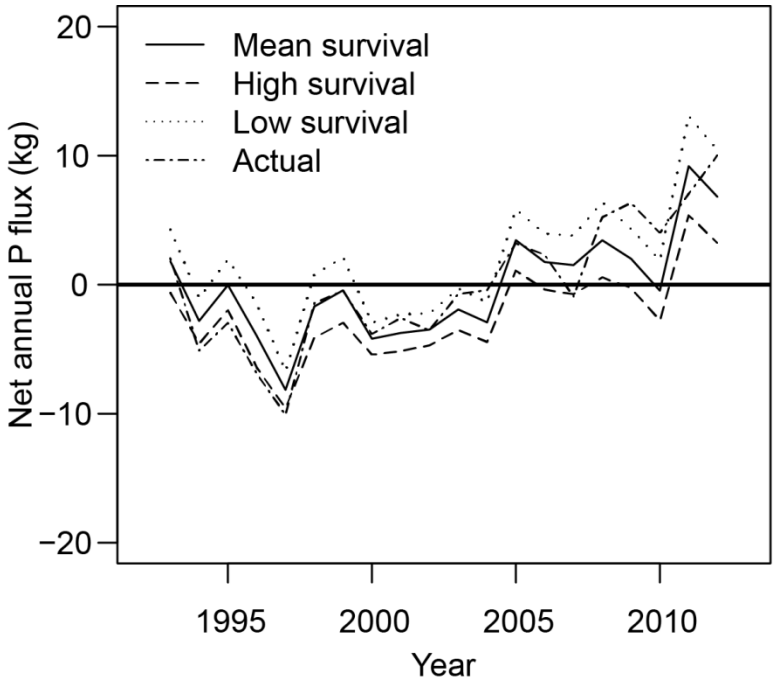

Figure A.3.2. Sensitivity of Atlantic salmon mediated P flux estimates to changes in overwinter survival rate (i.e., parameter k in nutrient flux model) on Campbellton River, NL. The solid line is estimated using mean overwinter survival rate measured from 1994-2012 and is the same as in the main text. 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.

A.4. Appendices for Chapter 4: Length-nutrient content relationships as a tool for understanding the role of large consumers in ecosystem nutrient cycles.

A.4.1. Additional information regarding Illustration 1 in the main text including brook trout sample processing and chemical analysis methods, the characteristics of study segments, the number brook trout individuals sampled from each stream, and the sample sizes.

Brook trout sample processing and analysis.

Brook trout samples were partially thawed, the stomach contents removed, and each fish was measured for fork length and wet mass. Samples were then dried at 60°C for ca. 7 days and dried samples were allowed to cool in a dessicator before being re-weighed and sealed in clean 60mL scintillation vials. For chemical analysis, we pooled all individuals weighing less than 0.25g dry weight (wet mass range 0.1-1.1 g; fork length range; 27-46mm) into one sample regardless of stream of capture because individual fish were too small to analyze for all three elements (i.e., C, N, and P) and in some streams we did not capture enough of these small individuals to constitute an adequate sample weight for analysis. Dried samples were shipped to the Agriculture and Food Laboratory at the University of Guelph where samples were ground in 5mL polyethylene vials with stainless steel grinding balls in a SPEX Sample Prep 2010 Geno/Grinder for three minutes at 1000 rpm. Some samples were further ground with a mortar and pestle.

Subsamples taken for %C and %N were analyzed on an Elementar Vario Macro Cube. Subsamples taken for %P analysis were digested with nitric acid in a CEM Marsxpress microwave digester and analyzed on a Varian Vista Pro ICP-OES.

Table A.4.1. Characteristics of segments sampled in five streams in Terra Nova National Park, Newfoundland and Labrador.

Stream	Coordinates	Discharge ($m^3 \cdot s^{-1}$)	Channel area sampled (m^2)	No. fish sampled	No. samples included in LNCR†
Charlottetown Brook	48° 26’40.06”N 54° 1’17.54”W	1.16	237	12	10
Cobblers Brook	48° 25’11.77”N 54° 8’11.46”W	0.24	151	15	14
Davey Ann's Brook	48° 36’50.81”N 53° 58’2.20”W	0.14	108	14	15
Spracklin Brook	48° 29’17.78”N 54° 1’18.93”W	0.1	94	26	16
Yudle Pond Brook	48° 26’9.62”N 54° 1’49.55”W	0.18	85	12	11

Notes

†Fish under weighing less than 0.25g dry weight (wet mass range 0.1-1.1 g; fork length range; 27-46mm) into one sample regardless of stream of capture because individual fish were too small to analyze for all three elements (i.e., C, N, and P) and in some streams we did not capture enough of these small individuals to constitute an adequate sample weight for analysis. For example, zero small fish were captured in Davey Ann’s Brook, however

we still included the young of the year body content in the LNCR analyses for consistency under the assumption that individuals of this size may still have been present in the sampled segment.

A.4.2. Results of ANCOVAs used to test for differences in the slopes and intercepts of LNCRs among populations within elements and among elements when individuals from all five populations were pooled.

To evaluate whether nutrient content of fish of a given length differed among populations, we used an ANCOVA and type II sum of squares with ln-transformed fork length as the independent variable and stream of capture as our categorical variable in the 'car' package in R (Fox and Weisberg 2011) to test whether the slopes and intercepts of LNCRs for each element (i.e., C, N, or P) differed. The slopes and intercepts of the LNCRs for each element did not differ among populations (Tables A.4.2, A.4.3) suggesting that either the forces acting on the amount of a given nutrient in brook trout bodies were the same in all five streams, or that the amount of C, N, or P in brook trout bodies are endogenously controlled. However, sample sizes within streams were low (Table A.4.1), which may have limited our ability to detect differences in LNCR coefficients among populations.

To evaluate ontogenetic variation in body element content, we tested for differences in the slopes among LNCRs for each element, we used an ANCOVA with type II sum of squares with ln-transformed body element content as our dependent variable, fork length as a continuous independent variable and element (C, N, P) as our categorical independent variable using the full dataset where individuals from each stream were pooled.

References

Fox, J. and S. Weisberg. 2011. An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage. URL: http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Table A.4.2. ANCOVA results for tests of differences in slopes of regressions of natural log-transformed total body carbon, nitrogen, and phosphorus against natural log transformed fork length (mm) among five populations of brook trout in Terra Nova National Park in June 2015. Slopes of the LNCR differ among streams if the interaction term, ln(fl)*stream, is statistically significant.

Element	Source	SS	df	F	*p*
Carbon	ln(fl)	103.21	1	1753.69	< 0.001
	Stream	0.397	4	1.688	0.17
	ln(fl) *Stream	0.198	4	0.8413	0.51
	Residuals	2.94	50		
Nitrogen	ln(fl)	97.41	1	1673.81	<0.001
	Stream	0.2	4	0.88	0.48
	ln(fl)*Stream	0.13	4	0.54	0.71
	Residuals	2.91	50		
Phosphorus	ln(fl)	93.2	1	1707.78	<0.001
	Stream	0.32	4	1.48	0.22
	ln(fl)*Stream	0.19	4	0.87	0.49
	Residuals	2.73	50		

Table A.4.3. ANCOVA results for tests of differences in intercepts of regressions of natural log-transformed total body carbon, nitrogen, and phosphorus against natural log transformed fork length (mm) among five populations of brook trout in Terra Nova National Park in June 2015. Intercepts of the LNCRs differ among streams if the categorical variable, stream, is a statistically significant source of variation.

Element	Source	SS	df	F	*p*
Carbon	ln(fl)	103.21	1	1774.56	<0.001
	Stream	0.4	4	1.71	0.17
	Residuals	3.14	54		
Nitrogen	ln(fl)	97.41	1	1732.8	<0.001
	Stream	0.2	4	0.91	0.47
	Residuals	3.04	54		
Phosphorus	ln(fl)	93.2	1	1724.75	<0.001
	Stream	0.32	4	1.49	0.22
	Residuals	2.92	54		

Table A.4.4. ANCOVA results for tests of differences in the slopes of LNCRs for different elements analyzed with all populations pooled. Slopes of LNCRs differ among elements if the interaction term, ln(fl)*Element, is a statistically significant source of variation.

Source	SS	df	F	*p*
ln(fl)	219.04	1	3622.48	<0.001
Element	268.08	2	2220.56	<0.001
log(fl)*Element	0.201	2	1.17	0.193
Residuals	10.88	180		

A.4.3. Method for classifying brook trout captured during sampling to different age classes.

Determining length-at-age

We did not directly quantify the age of brook trout in our study. To estimate length at age, we used length and age data of non-anadromous brook trout collected via electrofishing by Parks Canada in nearby, similarly sized streams (i.e, Terra Nova Brook, Wings Brook, and Minchins Pond Brook) in August 1981 (M. Langdon *unpublished data*). Age data for these populations was determined by examining annuli on the brook trout's otoliths (M. Langdon, *personal communication*). Age-at-length for June 2015 samples was estimated by assuming that change in length was constant over time (i.e., proportional change in length from age 1 to age 2 is equal to the proportional change in length of an age 1 individual from June to August), such that

$fl_{a,June} = fl_{a,August} - x \cdot fl_{a,August}$; where, fl is fork length (mm), subscript *a* is age class, and x is proportional change in fork length of over an age increment calculated as

$x = \frac{fl_{a+1,August} - fl_{a,August}}{fl_{a,August}}$. We quantified uncertainty around the mean age at length by using the same procedure but using the upper and lower 95% confidence interval (i.e., ±2SD) of August age at lengths to determine the upper and lower 95% confidence intervals.

We were interested in calculating the amount of C, N, and P stored in our five study populations at the time of sampling (i.e., standing stock) and the maximum potential nutrient accrual for each of our five populations. Both of these goals require that

we estimate the number of individuals per cohort. We estimated the number of individuals per cohort using the Zippin method of *k*-pass removal in the FSA package (Ogle 2016). This method assumes that the population is closed and that the capture probability of individuals and constant within and across sampling passes. We assigned captured individuals to age classes (cohorts) by subsetting our dataset into groups where individuals smaller than lower 95% CI fork length of age 1 individuals were assigned age 0+ cohort, individuals with fork lengths between the lower 95% CI fork length of age 1+ and the lower 95% CI fork length of age 2+ were assigned to the age 1+ cohort, individuals with fork lengths between the lower 95% CI fork length of age 2+ and mean fork length of age 3+ were assigned to the age 2+ cohort, and individuals smaller than the mean estimated fork length of age3+ fish were assigned to the age 3+ cohort..

References

Ogle, D. H. 2016. FSA: Fisheries Stock Analysis. R-package version 0.8.6

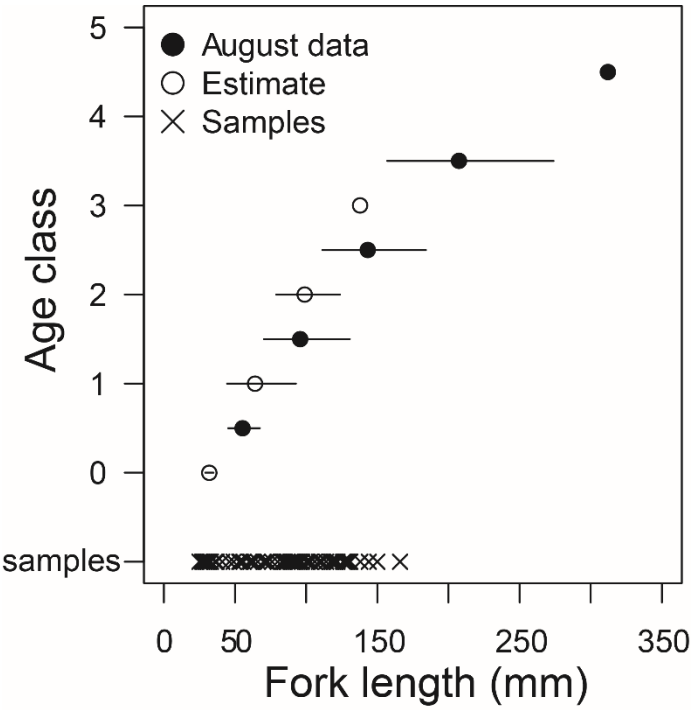
August data
Estimate
Samples
Age class
5
4
3
2
1
0
samples
0
50
150
250
350
Fork length (mm)

Figure A.4.1. Length of individuals of a given age class. Solid circles represent the mean age-at-length (± 2sd) of *Salvelinus fontinalis* collected from Minchins Pond Brook, Terra Nova Brook, and Wings Brook in August 1981 (n=140). This age-at-length data was used to back-calculate the expected age-at-length of fish sampled from five nearby, similarly sized streams in Terra Nova National Park in June 2015 (open circles). Age-at-length for June 2015 samples was estimated by assuming that change in length was constant over time, such that

$fl_{a,June} = fl_{a,August} - x \cdot fl_{a,August}$; where, fl is fork length (mm), subscript *a* is age class, and x is proportional change in fork length of over an age increment calculated as

$x = \frac{fl_{a+1,August} - fl_{a,August}}{fl_{a,August}}$. Actual length measurements of *S. fontinalis* sampled in 2015 (X) fall within the predicted range of lengths for age classes 0+ to 3+.

Table A.4.5. Number of individuals from each assigned age class in study segments (lower 95%CI, upper 95% CI) estimated from three-pass depletion sampling using the Zippen method (Ogle 2016).

Stream	0+	1+	2+	3+
Charlottetown	81 (71.2, 90.8)	20 (16.3, 23.7)	5 (3.5, 6.5)	3 (1.6, 4.4)
Cobblers	3 (2.5, 3.5)	2 (0, 4.0)	7 (0.1, 13.9)	1 (1, 1)
Davey Ann’s	2 (1.2, 6.8)	7 (6.8, 7.2)	12 (11.8, 12.1)	1 (1, 1)
Spracklins	0	4 (2.1, 5.9)	10 (10, 10)	0
Yudle	6 (4.0, 8.0)	1 (1, 1)	15 (13.5, 16.5)	3 (1.6, 4.4)

A.4.4. Additional details of our sampling collection, processing and analysis for Illustration #2: Partitioning individual losses between eggs and excretions in migrating Atlantic salmon (*Salmo salar*).

Adult and kelt sampling.

Individuals were sampled when they passed through counting facilities located near the freshwater/ marine boundary at the mouth of each river. Sampled adults fork length ranged from 48 - 62 mm and wet mass ranged from 1165-2450 g. Sampled kelt fork length ranged from 49 – 60 mm and wet mass ranged from 640 – 1300 g. We homogenized individuals and analyzed the resultant subsampled for C, N, P concentration according to methods described in Chapter 2. Data including wet weights, fork lengths, and body element concentrations are found in Ebel et al. (2016); however we removed a 70 cm kelt from our analysis because it was anomalously longer than any of the adults we sampled from the same streams. Characteristics of the watersheds and the sizes of populations sampled are provided in Chapter 3.

Egg sampling

We collected salmon eggs from individuals captured at the Grand Falls fish ladder on the Exploits River in 2014. Individuals selected for research and re-introduction purposes were held by the Environment Resources Management Association in large flow-through tanks adjacent to the river from initial capture in July – September until individuals reached full maturity in late October and early November 2014. Eggs were non-lethally retrieved from 12 females (fork length range 46-61 cm, body mass range 755-2342 g, egg

mass range 142-442 g) by standard protocols and probably represent just under 100% eggs present in each female. Females were released after eggs were retrieved. Eggs were transported in coolers to the Memorial University of Newfoundland, where they were separated from ovarian fluid with a strainer, weighed, subsampled, placed in a drying oven for 48-72 hours, measured for dry mass, and stored in a dessicator for five months prior to chemical analyses of C, N, and P. Dried samples were ground with a mortar and pestle. A portion of ground material was analyzed for C and N on a Carlo Erba NA1500 Series II Elemental Analyser at the Stable Isotope Lab facility at the Memorial University of Newfoundland and another portion of ground material was dissolved in nitric acid and hydrogen peroxide and analyzed for P concentration with a Perkin Elmer ELAN DRCII ICP-MS at the Inductively Coupled Plasma Spectrometry (ICPMS) Facility at the Memorial University of Newfoundland.

References

Ebel, J.; Leroux, S; Robertson, M.; Dempson, J. B. (2016): Whole body element composition of Atlantic salmon (Salmo salar L.). figshare. https://dx.doi.org/10.6084/m9.figshare.2056785.v1 Retrieved: Mar 16, 2016 (GMT)

A.5. Appendices for Chapter 5: Ecosystem effects of top consumers with migratory and complex life cycles

A.5.1. Parameter constraints and equations describing ecosystem fluxes

This appendix contains the parameter constraints (Table A.5.1) and the equations used to determine the response of production and within ecosystem nutrient recycling (Table A.5.2) for the model described in the main text.

Table A.5.1. Parameter definitions and constraints.

Parameter	Description	Constraints
I_i	Constant input to N_i	$I_i > 0$
E_i	Basal loss rate from N_i	$E_i > 0$
ε_i	Assimilation efficiency	$0 < \varepsilon_i < 1$
$a_{j,k}$	Attack rate	$a_{j,k} > 0$
m_i	Consumer loss rate	$m_i > 0$
δ_r	Recycling efficiency	$0 < \delta_i < 1$
β	Adult migration rate	$0 < \beta$
α	Juvenile migration rate	$0 < \alpha$
r	Subsidy conversion efficiency	$0 < r < 1$

Table A.5.2. Equations for evaluating production and within-ecosystem nutrient cycling flux.

Natal Ecosystem		Adult Ecosystem	
Function	Equation	Function	Equation
Φ_{R1}	$\varepsilon a R_1^* N_1^*$	Φ_{R2}	$\varepsilon a R_2^* N_2^*$
Φ_{C1}	$\varepsilon a C_1^* R_1^* + r\beta C_2^*$	Φ_{C2}	$\varepsilon a C_2^* R_2^* + \alpha C_1^*$
RF_1	$\delta_1 m_1 C_1^* + \delta_r (1-r)\beta C_2^*$	RF_2	$\delta_2 m_2 C_2^*$

A.5.2. All Equilibria

This appendix contains all four equilibria to the meta-ecosystem model included in the main text. Our model has four equilibria: (1) where only abiotic resource compartments are present, (2) where all compartments are present except for natal ecosystem biotic resources (i.e., R_1), (3) where all compartments are present except for adult ecosystem biotic resources (i.e., R_2), and (4) where all compartments are present in both ecosystems. We do not analyze Equilibrium 1 where;

$$N_1^* = \frac{I_1}{E_1}$$

$$N_2^* = \frac{I_2}{E_2}$$

because biota do not exist in the either ecosystem, and the ecosystems are not coupled by mass flows. Equilibria 2 and 3 are qualitatively similar, as one consumer life stage does not obtain resources in their respective ecosystem. Both of these equilibria are represented by life cycles of consumer taxa in nature. Equilibrium 2 describes the system at equilibrium when the juvenile life stage does not feed in the natal ecosystem. At equilibrium, these stocks are;

$$N_1^* = \frac{-\left(I_1\left(-\mu_2(m_1+\alpha)-\beta(m_1+\alpha-r\alpha)+I_2\beta\varepsilon^2\left(-m_1\delta_1 r+\delta_r(-1+r)(m_1+\alpha)\right)\right)\right)}{E_1\left(\mu_2(m_1+\alpha)+\beta(m_1+\alpha-r\alpha)\right)}$$

$$R_1^* = 0$$

$$C_1^* = \frac{I_2 r\beta\varepsilon^2}{\mu_2(m_1+\alpha)+\beta(m_1+\alpha-r\alpha)}$$

$$N_2^* = \frac{I_2\varepsilon(m_1+\alpha)}{\mu_2(m_1+\alpha)+\beta(m_1+\alpha-r\alpha)}$$

$$R_2^* = \frac{m_1(m_2+\beta)+\alpha(m_2+\beta-r\beta)}{a\varepsilon(m_1+\alpha)}$$

$$C_2^* = \frac{I_2\varepsilon^2(m_1+\alpha)}{\mu_2(m_1+\alpha)+\beta(m_1+\alpha-r\alpha)}$$

Equilibrium 2 can represent a number of diadromous fishes that have larval stages that migrate out of their natal ecosystem to the adult ecosystem soon after hatching and before first feeding (e.g., longnose sucker; Childress et al. 2015).

Equilibrium 3 describes the system at equilibrium when the adult life stage does not feed in the adult ecosystem. At equilibrium, these stocks are;

$$N_1^* = \frac{-I_1\varepsilon(m_2+\beta)}{-m_2(\alpha-\mu_1)-\beta\big(\mu_1-\alpha(1-\rho)\big)}$$

$$R_1^* = \frac{m_1(m_2+\beta)+\alpha\big(m_2+\beta(1-r)\big)}{a\varepsilon(m_2+\beta)}$$

$$C_1^* = \frac{-I_1\varepsilon^2(m_2+\beta)}{-m_2(\alpha+\mu_1)-\beta\big(\mu_1+\alpha(1-\rho)\big)}$$

$$N_2^* = \frac{-I_1\alpha m_2\delta_2\varepsilon^2 - I_2\Big(m_2(\mu_1+\alpha)+\beta\big(\mu_1+\alpha(1-\rho)\big)\Big)}{-E_2\Big(m_2(\mu_1+\alpha)+\beta\big(\mu_1+\alpha(1-\rho)\big)\Big)}$$

$$R_2^* = 0$$

$$C_2^* = \frac{I_1 \alpha \varepsilon^2}{m_2(\mu_1 + \alpha) + \beta\big(\mu_1 + \alpha(1-\rho)\big)}$$

Equilibrium 3 is exemplified by mayflies (Order Ephemeroptera), which feed as larvae in aquatic ecosystems before migrating and metamorphosing into adults in terrestrial ecosystems. Adult mayflies do not have mouthparts and do not feed in terrestrial ecosystems. Equilibria 2 and 3 always produce non-zero values for existing compartment stocks under the initial parameter constraints (table A.5.1).

Consumers represented by Equilibrium 2 and 3 experience ontogenetic habitat shifts, but do not experience ontogenetic diet shifts. In these scenarios, basal input rates, basal loss rates, and recycling efficiencies in only one ecosystem drive the consumers' dynamics. In the non-feeding ecosystem (i.e., the ecosystem without an existing biotic resource compartment), the migratory consumer acts as a subsidy to the abiotic resource compartment only. In Equilibria 2 and 3, the increase in abiotic resource in the non-feeding ecosystem can support other food webs in a bottom-up fashion that are not directly connected to the consumer. These forms of subsidy are commonly examined empirically (Baxter et al. 2005, Allen and Wesner 2016, Childress et al. 2016).

Equilibrium 4 describes a system where all compartments exist and is included in the main text. At equilibrium, these stocks are;

$$N_1^* = \frac{\varepsilon(I_1(\beta + \mu_2) + I_2\beta\rho)}{\alpha\beta(1-\rho) + \mu_2(\alpha + \mu_1) + \beta\mu_1}$$

$$R_1^* = \frac{I_2\beta\big(r(\mu_1 - m_1) + (r-\rho)(m_1+\alpha)\big) - I_1\big(\mu_2(m_1+\alpha) + \beta(m_1+\alpha-r\alpha)\big)}{a\varepsilon(-I_1(\beta+\mu_2) - I_2\beta\rho)}$$

$$C_1^* = \varepsilon N_1^*$$

$$N_2^* = \frac{\varepsilon\big(I_1\alpha + I_2(\alpha+\mu_1)\big)}{\alpha\beta(1-\rho) + \mu_2(\alpha+\mu_1) + \beta\mu_1}$$

$$R_2^* = \frac{-\Big(I_1\alpha\varepsilon(E_2 - m_2\delta_2\varepsilon) + I_2\left(-m_2(\mu_1+\alpha) - \beta\big(\mu_1 - \alpha(1-\rho)\big)\right)\Big)}{a\varepsilon\big(I_1\alpha + I_2(\mu_1+\alpha)\big)}$$

$$C_2^* = \varepsilon N_2^*$$

Where;

$$\mu_1 = E_1\varepsilon + m_1(1-\delta_1\varepsilon^2)$$

$$\mu_2 = E_2\varepsilon + m_2(1-\delta_2\varepsilon^2)$$

$$\rho = r - \delta_r\varepsilon^2(-1+r)$$

Unlike Equilibria 2 and 3, which produce non-zero stocks under all combinations of parameters, Equilibrium 4 only produces positive non-zero biotic resource stocks (i.e., R_1 and R_2) under a range of parameters defined by the inequality

$$\frac{m_2\delta_2\varepsilon}{m_1+\alpha} + \frac{I_2\beta(\rho-r)}{I_1\varepsilon} + \frac{I_2\beta r(\mu_1 - m_1) - \beta(m_1-\alpha-r\alpha)}{I_1\varepsilon(m_1+\alpha)} - \frac{m_2}{\varepsilon} < E_2$$

$$< m_2\delta_2\varepsilon + I_2\beta\left(\frac{E_1(1+m_2)}{I_1\alpha} + \frac{1-\rho+m_2}{I_1\varepsilon} + \frac{m_1(1+m_2)(1-\delta_1\varepsilon^2)}{I_1\alpha\varepsilon}\right)$$

Where the juvenile's biotic resource stock is zero or negative when ecosystem 2 basal loss rate (i.e., E_2) is lower than the left hand side of the in equality and the adult's biotic resource stock is zero or negative when ecosystem 2 basal loss rate is higher than the right-hand side of the inequality.

References

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Appendix A.5.3. Analytical solutions and qualitative evaluation of stocks and production presented in Ecosystem effects of consumers with migratory and complex life cycles.

In this appendix, we provide the analytical solutions and qualitative assessment of the directional response of equilibrium stocks, production, and within-ecosystem recycling flux to increases in the parameters for juvenile migration rate (α), adult migration rate (β), and subsidy conversion efficiency (r).

Table A5.3. Analytical solutions and qualitative evaluation of the response of equilibrium stock to increases in juvenile migration rate (α).

	$\partial_{stock^*}/\partial_{\alpha}$	Qualitative effect
N_1^*	$\frac{-\varepsilon\left(\mu_2+\beta(1-\rho)\right)\left(I_1\beta\rho+I_1(\beta+\mu_2)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative
R_1^*	$\frac{I_2\beta\delta_r\varepsilon^2(-1+r)+I_1(\beta(-1+r)-\mu_2)}{a\varepsilon(-I_1(\mu_2+\beta)-I_2\beta\rho)}$	Positive
C_1^*	$\frac{-\left(\varepsilon^2\left(\mu_2+\beta(1-\rho)\right)(I_1(\mu_2+\beta)+I_2\beta\rho)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative
N_2^*	$\frac{\varepsilon(-\mu_1)(-I_1(\mu_2+\beta)-I_2\beta\rho)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
R_2^*	$\frac{-\left(I_2(-\mu_1)(-I_1(\mu_2+\beta)-I_2\beta\rho)\right)}{a\varepsilon\left(I_1\alpha+I_2(\mu_1+\alpha)\right)}$	Negative
C_2^*	$\frac{\varepsilon(-\mu_1)(-I_1(\mu_2+\beta)-I_2\beta\rho)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive

Table A5.4. Analytical solutions and qualitative evaluation of the response of equilibrium stock to increases in adult migration rate (β).

	$\partial_{stock^*}/\partial_\beta$	Qualitative effect
N_1^*	$\frac{\varepsilon(-\rho)(-\mu_2)\left(I_1\alpha + I_2(\alpha+\mu_1)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
R_1^*	$\frac{-I_1 r\mu_2\left(I_1\alpha + I_2(\alpha+\mu_1)\right)}{a\varepsilon(I_1(\beta+\mu_2)+I_2\beta\rho)^2}$	Negative
C_1^*	$\frac{\varepsilon^2(-\rho)(-\mu_2)\left(I_1\alpha - I_2\mu_2(\alpha+\mu_1)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
N_2^*	$\frac{-\varepsilon\left(I_1\alpha + I_2(\alpha+\mu_1)\right)\left(\mu_1+\alpha(1-\rho)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative
R_2^*	$\frac{I_2\left(\mu_1+\alpha(1-\rho)\right)}{a\varepsilon\left(I_1\alpha + I_2(\alpha+\mu_1)\right)}$	Positive
C_2^*	$\frac{-\varepsilon^2\left(I_1\alpha + I_2(\alpha+\mu_1)\right)\left(\mu_1+\alpha(1-\rho)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative

Table A.5.5. Analytical solutions and qualitative evaluation of the response of equilibrium stock to increases in subsidy conversion efficiency (*r*).

	$\partial_{stock^*}/\partial_r$	Qualitative effect
N_1^*	$\frac{-\left(\beta\varepsilon(\mu_2+\beta)(-1+\delta_r\varepsilon^2)\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
R_1^*	$\frac{\beta\left(-I_1\alpha-I_2(\mu_1+\alpha)\right)\left(I_2\beta\delta_r\varepsilon^2+I_1(\mu_2+\beta)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative
C_1^*	$\frac{-\left(\beta\varepsilon^2(\mu_2+\beta)(-1+\delta_r\varepsilon^2)\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
N_2^*	$\frac{-\left(\alpha\beta\varepsilon(-1+\delta_r\varepsilon^2)\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
R_2^*	$\frac{I_2\alpha\beta(-1+\delta_r\varepsilon^2)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative
C_2^*	$\frac{-\left(\alpha\beta\varepsilon(-1+\delta_r\varepsilon^2)\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive

Table A.5.6. Analytical solutions and qualitative evaluation of equilibrium ecosystem fluxes to increases in juvenile migration rate (α).

	$\partial_{Production^*}/\partial_\alpha$	Qualitative effect
Φ_{R1}^*	$\frac{\varepsilon^2(-I_1(\mu_2+\beta)-I_2\beta\rho)\left(E_1\left(\beta(-1+r)\left(1-m_1\varepsilon(\delta_1-\delta_r)\right)-\mu_2(1-m_1\delta_1\varepsilon)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 < m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon} + \frac{\beta(-1+r)\left(1-m_1\varepsilon(\delta_1-\delta_r)\right)}{1-m_1\delta_1\varepsilon}$
Φ_{C1}^*	$\frac{-\left(\varepsilon^2(-I_1(\mu_2+\beta)-I_2\beta\rho)\left(m_1\beta\rho+(\mu_2+\beta)(E_1\varepsilon-m_1\delta_1\varepsilon^2)\right)\right)}{A^2}$	Positive* when $E_2 > m_2\delta_2\varepsilon - \frac{m_2+\beta}{\varepsilon} - \frac{m_1\beta\rho}{\varepsilon^2(E_1-m_1\delta_1\varepsilon)}$
Φ_{R2}^*	$\frac{\varepsilon^2(-\mu_1)(E_2-m_2\delta_2\varepsilon)(I_1(\mu_2+\beta)+I_2\beta\rho)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 < m_2\delta_2\varepsilon$
Φ_{C2}^*	$\frac{-\mu_1\varepsilon^2(m_2+\beta)(-I_1(\mu_2+\beta)-I_2\beta\rho)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive

RF_1^*	$\frac{-\left(\varepsilon^2(-I_1(\mu_2+\beta)-I_2\beta\rho)\left(m_1(\beta(-1+r)(\delta_1-\delta_r)-\delta_1\mu_2)-E_1\beta\delta_r\varepsilon(-1+r)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 < m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon} + \frac{\beta(-1+r)(m_1(\delta_1-\delta_r)-E_1\varepsilon\delta_r)}{m_1\delta_1\varepsilon}$
RF_2^*	$\frac{m_2\delta_2\varepsilon^2(-\mu_1)(-I_1(\mu_2+\beta)-I_2\beta\rho)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive

Table A.5.7. Analytical solutions and qualitative evaluation of the response of equilibrium ecosystem fluxes to increases in adult migration rate (β).

	$\partial_{Production^*}/\partial_\beta$	Qualitative effect
Φ_{R1}^*	$\frac{-\mu_2\varepsilon^2\left(-E_1 r+\varepsilon\left(m_1 r\delta_1-\delta_r(-1+r)(\alpha+m_1)\right)\left(-I_1\alpha-I_2(\alpha+\mu_1)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive if $E_1 < m_1\delta_1\varepsilon - \frac{\delta_r\varepsilon(m_1+\alpha)(r-1)}{r}$
Φ_{C1}^*	$\frac{-\left((-\mu_2)(-\rho)\varepsilon^2(\alpha+m_1)\left(-I_1\alpha-I_2(\alpha+\mu_2)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
Φ_{R2}^*	$\frac{\varepsilon^2(-E_2+m_2\delta_2\varepsilon)\left(-I_1\alpha-I_2(\alpha+\mu_1)\right)\left(\mu_1+\alpha(1-\rho)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when, $E_2 > m_2\delta_2\varepsilon$
Φ_{C2}^*	$\frac{-\left(\varepsilon^2\left(-I_1\alpha-I_2(\alpha+\mu_1)\right)\left(m_2\alpha\rho+\varepsilon(E_2-m_2\delta_2\varepsilon)(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 > m_2\delta_2\varepsilon - \frac{\alpha\rho m_2}{\varepsilon(\mu_1+\alpha)}$

RF_1^*	$\frac{-\mu_2\varepsilon^2\left(\left(-m_1\left(r\left(\delta_{Cj}-\delta_r\right)+\delta_r\right)+\delta_r(-1+r)(\alpha+\varepsilon E_1)\right)\left(I_1\alpha+I_2(\alpha+\mu_1)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
RF_2^*	$\frac{-m_2\delta_2\varepsilon^2\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\left(\mu_1+\alpha(1-\rho)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Negative

Table A.5.8. Analytical solutions and qualitative evaluation of the response of equilibrium ecosystem fluxes to increases in subsidy conversion efficiency (r).

	$\partial_{Production^*}/\partial_r$	Qualitative effect
Φ_{R1}^*	$\frac{\beta\varepsilon^2\left(-I_1\alpha - I_2(\mu_1+\alpha)\right)\left(E_1(\mu_2+\beta)+\varepsilon\left(\alpha\delta_r\mu_2 - m_1(\delta_1-\delta_r)(\mu_2+\beta)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 > m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon} + \frac{\beta(m_1(\delta_1-\delta_r)+E_1)}{\varepsilon(m_1(\delta_1-\delta_r)-E_1-\alpha\delta_r\varepsilon)}$
Φ_{C1}^*	$\frac{\beta\varepsilon^2(m_1+\alpha)(\mu_2+\beta)(-1+\delta_r\varepsilon^2)\left(-I_1\alpha - I_2(\mu_1+\alpha)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
Φ_{R2}^*	$\frac{-\left(\alpha\beta\varepsilon^2(-E_2+m_2\delta_2\varepsilon)(-1+\delta_2\varepsilon^2)\left(I_1\alpha + I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 < m_2\delta_2\varepsilon$
Φ_{C2}^*	$\frac{-\left(\alpha\beta\varepsilon^2(m_2+\beta)(-1+\delta_r\varepsilon^2)\left(I_1\alpha + I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive
RF_1^*	$\frac{\beta\varepsilon^2\left(-I_1\alpha - I_2(\mu_1+\alpha)\right)\left((\mu_2+\beta)\left(\delta_r E_1\varepsilon - m_1(\delta_1-\delta_r)\right)+\alpha\delta_r\mu_2\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive when $E_2 > m_2\delta_2\varepsilon - \frac{m_2}{\varepsilon} + \frac{\beta\left(\delta_r E_1\varepsilon - m_1(\delta_1-\delta_r)\right)}{\varepsilon\left(m_1(\delta_1-\delta_r)-\delta_r(E_1\varepsilon+\alpha)\right)}$

RF_2^*	$\frac{-\left(\alpha\beta m_2\delta_2\varepsilon^2(-1+\delta_r\varepsilon^2)\left(I_1\alpha+I_2(\mu_1+\alpha)\right)\right)}{(\alpha\beta(1-\rho)+\mu_2(\alpha+\mu_1)+\beta\mu_1)^2}$	Positive

A.5.4. Numerical simulations of equilibrium production to complement Figure 5.4 in Ecosystem effects of top consumers with migratory and complex life cycles.

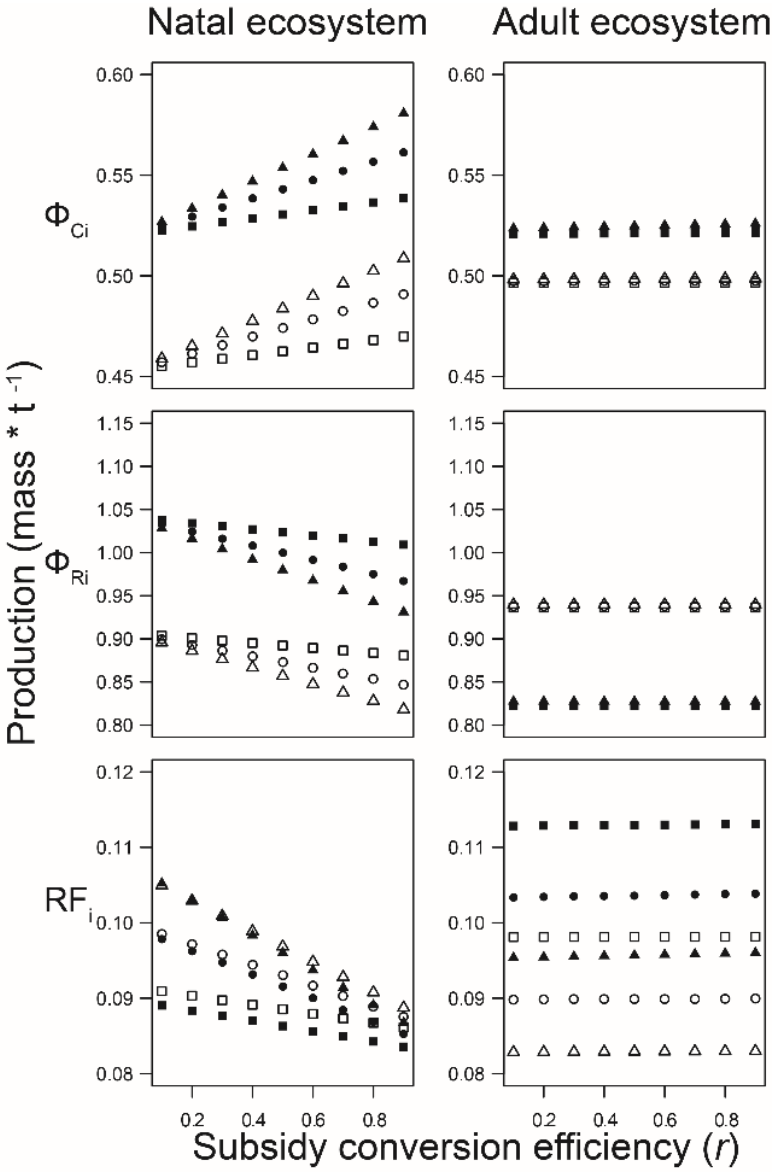

Figure A.5.1. Response of equilibrium production (Φi) and within-ecosystem recycling flux (RFi) in natal and adult ecosystems connected by bidirectional flows of a migratory consumer to increases in the subsidy conversion efficiency, r, when adult migration rate (β) is low (β= 0.2; squares), moderate (β = 0.5; circles), and high (β = 0.8; triangles) under two juvenile migration rates, α =0.2 (open shapes) and α=0.8 (filled shapes). Other parameter values are the same parameters used in the simulation of equilibrium stocks show in Figure 5.4 of the main text and are as follows: $I_1 = 10$, $I_2 = 1$, $E_1 = 30$, $E_2 = 0.5$, $a = 1$, $\varepsilon = 0.5$, $m_1 = m_2 = 3$, $\delta_1 = \delta_2 = \delta_r = 0.2$. The equilibrium is locally stable (i.e., leading eigenvalues of the Jacobian matrix are negative) for the given parameter sets.