

Utah State University

DigitalCommons@USU

---

All Graduate Theses and Dissertations

Graduate Studies

---

5-2014

## The Ecosystem Role of Fishes in Lotic Environments

Christopher C. Wheeler  
*Utah State University*

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Ecology and Evolutionary Biology Commons](#)

---

### Recommended Citation

Wheeler, Christopher C., "The Ecosystem Role of Fishes in Lotic Environments" (2014). *All Graduate Theses and Dissertations*. 3694.

<https://digitalcommons.usu.edu/etd/3694>

This Dissertation is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact [digitalcommons@usu.edu](mailto:digitalcommons@usu.edu).



THE ECOSYSTEM ROLE OF FISHES IN LOTIC ENVIRONMENTS

by

Christopher C. Wheeler

A dissertation submitted in partial fulfillment  
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

Approved:

---

Todd A. Crowl  
Major Professor

---

Scott W. Miller  
Major Professor

---

Michelle A. Baker  
Committee Member

---

Charles P. Hawkins  
Committee Member

---

Michael L. Scott  
Committee Member

---

Mark R. McLellan  
Vice President for Research and  
Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY  
Logan, Utah

2014

Copyright © Christopher C. Wheeler 2014

All Rights Reserved

## ABSTRACT

## The Ecosystem Role of Fishes in Lotic Environments

by

Christopher C. Wheeler, Doctor of Philosophy

Utah State University, 2014

Major Professors: Dr. Todd A. Crowl and Dr. Scott W. Miller  
Department: Watershed Sciences

Among stream organisms, fishes are especially likely to influence ecosystem properties as a result of their unique properties. The functional role played by many freshwater fishes remains unknown, however. Furthermore, fish effects are often context-dependent. Thus, identifying different factors that mediate fish effects is a critical step in understanding ecosystem dynamics and managing freshwater resources. To address these issues, I studied the ecosystem role of fishes in lotic environments. My specific research objectives included (1) quantifying migratory fish excretion and determining its importance to stream nutrient dynamics, (2) determining how two adfluvial salmonids affect different stream ecosystem properties, and (3) performing a meta-analysis of fish effects in lotic ecosystems.

Results indicated that migratory fish excretion can be a significant nutrient subsidy to recipient ecosystems. However, the excretion subsidy magnitude varied considerably across space and time, and was related to changes in both biotic and abiotic conditions. Excretion subsidies were large relative to tributary nutrient export and were capable of

meeting the majority of ecosystem nutrient demand during migrations. However, migrant fertilization impacts were relatively limited. In contrast, migrants had more substantial negative effects on periphyton chlorophyll-*a* due to spawning activity. In general, field results agreed with results from the meta-analysis. Fishes in streams tended to have positive effects on nutrient concentrations (ammonium and soluble reactive phosphorus) and periphyton chlorophyll-*a*. Strong differences in effect sizes existed among trophic guilds and taxonomic groups, whereas effect size variation among abiotic and methodological covariates was far less pronounced. The meta-analysis also revealed that effects of some fishes (e.g., stonerollers) can rival those of native Pacific salmon. Finally, the meta-analysis demonstrated that data extraction choices can influence final conclusions in meta-analyses.

Overall, my work demonstrates the important functional role of fishes in lotic environments by identifying ecosystem effects associated with adfluvial migrants, as well as factors that mediate effects. Additionally, my meta-analysis illustrated the capacity of fishes to affect ecosystem properties, suggesting more research should examine fish functional roles in streams. While fish effects in streams vary, the roles of these widespread organisms should be understood given their potential influence on ecosystem dynamics.

## PUBLIC ABSTRACT

## The Ecosystem Role of Fishes in Lotic Environments

Christopher C. Wheeler

It is important for humans to understand how ecosystems work because we depend on them for a variety of products and services. For example, rivers and streams provide fisheries, improved water quality, and recreational opportunities to many individuals. In rivers, interactions among fishes, other stream plants and animals, and the physical river environment can influence continued provision of these valuable services. However, the role played by many freshwater fishes in the provision of these services remains unknown. Additionally, it is important to identify different factors that affect the outcome of interactions involving riverine fishes. To address these issues, I evaluated how fishes influence different properties of rivers and streams, using a combined approach that summarized previous studies of fish effects on trophic structure and organic matter processing and incorporated field work in natural systems.

Overall, my work demonstrated that fishes can play important roles in rivers and streams. In particular, fish spawning migrations from lakes to streams can introduce nutrients to streams. Compared with other nutrient sources for streams, nutrients delivered by fish migrations can be substantial, and they may be used by other plants and animals in the stream to increase productivity. Beyond nutrient introduction, the physical disturbance of river sediments caused by the spawning activity of large migratory fishes can influence the availability of food resources for other stream animals. Additionally,

my summary of previous fish studies indicated the consistent influence of fishes on nutrient dynamics and other stream organisms. While the role of riverine fishes varies, natural resource managers and researchers should focus on understanding how these widespread organisms influence valuable ecosystem services derived from freshwater resources.

DEDICATION

For Sam and Jon.



## ACKNOWLEDGMENTS

Funding for this project was provided by the S. J. and Jessie E. Quinney Foundation, the Quinney College of Natural Resources, the Department of Watershed Sciences, the Utah State University Ecology Center, and the June Sucker Recovery Implementation Program. I am very grateful to all of the funding sources for the assistance they provided.

This project would not have been possible without help and support that I received from a large number of individuals. First, I would like to thank my entire committee for the guidance, suggestions, encouragement, and logistical support they provided.

Collectively, the group fostered my development as a scientist, and I would not have arrived at this point without their assistance. In particular, my two co-advisors, Todd Crawl and Scott Miller, provided me the opportunity and flexibility to pursue the exact questions in which I was most interested, and I am very grateful for their faith in me. Secondly, an overwhelming number of people provided invaluable support in the field or lab, often on short notice or at inconvenient times. Individuals from the Crawl, Miller, Baker, and Bug Labs all contributed to this project in one way or another, and I am very appreciative of their efforts. Additionally, I received considerable help from Phaedra Budy and Gary Thiede in the Fish Ecology Lab. Other faculty and staff who offered substantial input included Susan Durham, Beth Neilson, John Stevens, and Wayne Wurtsbaugh. Brian Bailey and Enid Kelley from the Watershed Sciences department office were always able to answer my questions in the most helpful and gracious way possible, and both of them provided invaluable support and assistance. Stephanie White, Marv Bennett, and Carol Bierschwale from the Ecology Center also generously provided

logistical support. I would like to acknowledge the help I received from individuals with the Utah Department of Wildlife Resources. Justin Robinson and Alan Ward at Strawberry Reservoir always made sure I had the information, resources, and access that I needed and there is no doubt that fieldwork was more focused and more enjoyable as a result.

I would like to thank the different authors who graciously provided raw data for me to include in the meta-analysis: Katie Bertrand, Evan Childress, Scott Collins, Graham Forrester, Chad Hargrave, Lori Ivan, Dave Janetski, Justin Murdock, A. J. Reisinger, Annika Walters, and Tim Wootton.

Finally, I would like to thank my incredible family. My wife and my daughters helped me maintain perspective throughout the process and always served as the most welcome and helpful type of distraction. I would not be the person I am today without them, and I will always be incredibly grateful for their love and the sacrifices they made in order for me to complete this project.

Christopher C. "Kit" Wheeler

# CONTENTS

x

	Page
ABSTRACT.....	iii
PUBLIC ABSTRACT .....	v
DEDICATION.....	vii
ACKNOWLEDGMENTS .....	viii
LIST OF TABLES.....	xi
LIST OF FIGURES .....	xiii
CHAPTER	
1. INTRODUCTION .....	1
2. MIGRATORY FISH EXCRETION AS A NUTRIENT SUBSIDY TO RECIPIENT STREAM ECOSYSTEMS.....	9
3. ECOSYSTEM RESPONSES TO ADFLUVIAL SALMONID MIGRATIONS IN TRIBUTARIES OF A CENTRAL UTAH RESERVOIR.....	47
4. A QUANTITATIVE SYNTHESIS OF FISH EFFECTS ON TEMPERATE STREAM ECOSYSTEM STRUCTURE AND FUNCTION.....	88
5. SUMMARY.....	127
APPENDIX.....	132
CURRICULUM VITAE.....	150

## LIST OF TABLES

Table	Page
2-1 Comparison of biological, physical, and chemical characteristics between Indian and Trout Creeks during migrant presence .....	39
2-2 ANCOVA results for nutrient (NH <sub>4</sub> -N and SRP) excretion rates and ratios .....	40
2-3 Pearson's correlation coefficients between average $E_d/T_d$ values (i.e., spawning means) and different independent variables capable of influencing the contribution of migrant excretion subsidies to nutrient cycling .....	41
3-1 Comparison of hydrogeomorphic characteristics between Indian and Trout Creeks.....	76
3-2 Two-way ANOVA results for periphyton biomass (as chlorophyll- <i>a</i> ; $\mu\text{g cm}^{-2}$ ) as a function of fish (present or absent) and particle size (four size classes).....	77
3-3 Repeated measures ANOVA results for dissolved nutrient concentrations as a function of migrants (treatment vs. control reaches) and time .....	78
3-4 Results and interpretation of two-way ANOVAs for nutrient-diffusing substrata (NDS) responses (chlorophyll- <i>a</i> ; $\mu\text{g cm}^{-2}$ ) during three different time periods in 2012.....	79
3-5 Repeated measures ANOVA results for food web stable isotope ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ) values as a function of migrants (treatment reaches vs. control reaches) and time .....	80
4-1 Response variables considered for meta-analysis of fish effects on temperate stream ecosystem structure and function .....	119
4-2 Covariates included as potential mediators of fish effects in temperate stream ecosystems.....	120
A-1 Strawberry River fish trap size distribution data from 2011 and 2012.....	142
A-2 Particle size distributions measured during 2012 .....	143
A-3 Benthic particle size quartiles in Strawberry Reservoir tributaries .....	144

		xii
A-4	Information from studies used in the meta-analysis of fish effects in temperate stream ecosystems.....	145

## LIST OF FIGURES

Figure	Page
2-1	Location of Strawberry Reservoir in Utah and specific study streams.....42
2-2	Size scaling of NH <sub>4</sub> -N (A) and SRP excretion rates (B), and excreted molar N:P ratios (C) for Bonneville cutthroat trout (BCT) and kokanee (KOK) in Strawberry Reservoir tributaries.....43
2-3	Comparison of daily estimates of migrant excretion load with tributary nutrient export (i.e., $E_d/T_d$ ) for 2011 migrations in Trout Creek (A), 2012 migrations in Trout Creek (B), 2011 migrations in Indian Creek (C), and 2012 migrations in Indian Creek (D).....44
2-4	Box plots of average $E_d/T_d$ values in Strawberry Reservoir tributaries.....45
2-5	Comparison of migrant excretion flux ( $E$ , open symbols) with areal uptake ( $U$ , closed symbols) of NH <sub>4</sub> -N (A) and SRP (B) in Indian and Trout Creeks .....46
3-1	Live migrant and carcass densities in Indian (A) and Trout (B) Creeks during 2012.....81
3-2	Benthic substrate chlorophyll- <i>a</i> biomass as a function of migrant presence and particle size.....82
3-3	Concentrations of NH <sub>4</sub> (A), NO <sub>3</sub> (B), and SRP (C) during 2012 in Trout Creek.....83
3-4	Concentrations of NH <sub>4</sub> (A), NO <sub>3</sub> (B), and SRP (C) during 2012 in Indian Creek.....84
3-5	Nutrient response ratios (NRR; $\ln$ [treatment/control]) of chlorophyll- <i>a</i> on nutrient diffusing substrates from separate time periods in Indian (A) and Trout (B) Creeks during 2012.....85
3-6	Stable isotope ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ) values for periphyton (A and C) and scraper invertebrates (Heptageniidae larvae; B and D) in Trout Creek during 2012.....86
3-7	Stable isotope ( $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ) values for periphyton (A and C) and scraper invertebrates (Elmidae larvae, <i>Optioservus</i> spp.; B and D) in Indian Creek during 2012.....87

4-1	Geographic locations of the studies used in the meta-analysis of fish effects in temperate lotic environments .....	121
4-2	Effect of fishes (mean effect sizes $\pm$ 95% confidence intervals) on temperate stream ecosystem structural and functional characteristics .....	122
4-3	Effect size estimates (mean effect size $\pm$ 95% confidence intervals) of different fish taxonomic groups in temperate stream ecosystems .....	123
4-4	Effect size estimates (mean $\pm$ 95% confidence intervals) of fishes in temperate stream ecosystems as a function of trophic guild .....	124
4-5	Influence of biomass on effect size estimates of fishes on temperate stream ecosystem structural and functional characteristics .....	125
4-6	Influence of time on effect size estimates of fishes on temperate stream ecosystem structural and functional characteristics .....	126
A-1	Comparison of snow water equivalent in the Strawberry Reservoir Valley during sample years (2011, 2012), relative to the 30-year median value between 1981 and 2010 .....	148
A-2	Effect size distributions for temperate stream ecosystem structural and functional characteristics .....	149

## CHAPTER 1

### INTRODUCTION

One of the fundamental objectives of ecology is to understand factors that influence ecosystem structure and function. Focusing on this objective entails asking basic science questions related to species interactions, relationships between biotic and abiotic ecosystem components, and fundamental ecosystem processes like primary production. Our collective knowledge of the factors governing ecosystem dynamics may help to sustain biodiversity and ensure continued provision of critical ecosystem services (Daily, 1997).

Animals have been shown to exert significant control over ecosystem structure and function (Naiman, 1988). Animal mediated-influence may occur through a variety of mechanisms, including consumer-resource interactions (e.g., Hairston, Smith & Slobodkin, 1960; Hrbacek *et al.*, 1961; Brooks & Dodson, 1965; McNaughton, 1985; Pastor *et al.*, 1988; Louda, Keeler & Holt, 1990), physical habitat modification (Laws, 1970; Thayer, 1979; Jones, Lawton & Shachak, 1994), and the introduction of nutrients, energy, and detritus to recipient habitats (e.g., Polis, Anderson & Holt, 1997; Nakano, Miyasaka & Kuhara, 1999; Naiman *et al.*, 2002). Direct and indirect effects associated with these mechanisms have the potential to change patterns of organismal distribution and abundance as well as biogeochemical cycling rates (Naiman, 1988).

In stream ecosystems, the notion that physical processes ultimately regulate community composition and ecosystem processes (e.g., nutrient cycling) has prevailed over time (Resh *et al.*, 1988; Vanni, 2010). While the influence of hydrology and



geomorphology cannot be discounted, more recent research has demonstrated that stream biota can also shape the distribution and abundance of organisms and resources. For example, beavers (Naiman, Melillo & Hobbie, 1986) and other vertebrates (e.g., Moore, 2006), amphibians (e.g., Whiles *et al.*, 2006), and a diverse array of invertebrates (e.g., Grimm, 1988a; Pringle *et al.*, 1993; Creed, 1994; Covich, Palmer & Crowl, 1999; Strayer *et al.*, 1999; Hall, Tank & Dybdahl, 2003; Atkinson *et al.*, 2013) have all been shown to influence stream ecosystem structure and function.

Over the past 35 years, the ecosystem effects of fishes in streams have been well documented. Through a variety of direct and indirect pathways (Matthews, 1998), fishes can alter algal biomass, structure, and composition (e.g., Power & Matthews, 1983; Power, 1984; Power, Matthews & Stewart, 1985; Power, Stewart & Matthews, 1988), invertebrate abundance, production, life history, and behavior (e.g., Flecker, 1992; Peckarsky & McIntosh, 1998; Hall, Taylor & Flecker, 2011), nutrient dynamics (e.g., Grimm, 1988b; McIntyre *et al.*, 2008; Ruegg *et al.*, 2011; Small *et al.*, 2011), stream metabolic properties (e.g., Taylor, Flecker & Hall, 2006; Holtgrieve & Schindler, 2011), and particulate dynamics (e.g., Flecker, 1996; Moore *et al.*, 2007).

Although fish effects on assemblage composition and material cycling can be substantial, they are not ubiquitous. Rather, fish effects are frequently context-dependent, varying over time and space in response to changes in biotic and abiotic conditions (Vanni, 2010; Gido *et al.*, 2010). Inter- or intraspecific biotic differences that mediate fish effects include variation in body size (e.g., Hall *et al.*, 2007), population density (e.g., Moore & Schindler, 2008), trophic guild (e.g., Schindler & Eby, 1997), body stoichiometry (e.g., Capps & Flecker, 2013), and reproductive traits (e.g.,

iteroparity vs. semelparity, timing). Similarly, abiotic factors like temperature (e.g., Kishi *et al.*, 2005), background nutrient concentrations (e.g., Flecker *et al.*, 2010), and hydrogeomorphic characteristics (e.g., Power, 1992; Flecker, 1997; Winemiller *et al.*, 2006; Power *et al.*, 2008) can alter the magnitude and direction of fish effects in streams.

Understanding and predicting fish effects in streams is important given escalating rates of human-induced community change in freshwaters and the valuable services provided by these ecosystems (Dudgeon, 2010). Consequently, I studied the ecosystem role of fishes in lotic environments, using a combined approach that summarized published studies of fish effects and incorporated field work focused on determining fish effects in natural systems. My specific research objectives included (1) quantifying population-level excretion of dissolved inorganic nutrients by migratory fishes and determining its importance to ecosystem nutrient dynamics, (2) determining how two adfluvial salmonids affect different stream ecosystem properties, and (3) performing a quantitative synthesis (i.e., meta-analysis) of fish effects in lotic ecosystems. A common theme linking all objectives was the context-dependency of fish effects, and I explicitly incorporated this perspective into my research, with the aim of identifying biotic and abiotic characteristics that most strongly mediated fish effects.

My field survey centered on adfluvial migrations of two introduced salmonids (Bonneville cutthroat trout and kokanee salmon) in Strawberry Reservoir, Utah. In one chapter, I used short-term (~ 30 minute) incubations of individuals from both species to determine excretion rates and ratios. I then combined these values with observed size distributions and migrant densities to estimate population-level excretion. I determined the relative importance of migrant-derived nutrients by comparing them with ecosystem

nutrient demand and tributary nutrient export. Additionally, I evaluated how the relative contribution of migrant excretion to nutrient cycling varied as a consequence of changing abiotic and biotic conditions (Chapter 2). I also determined effects of the migratory salmonids on a suite of stream ecosystem properties: periphyton biomass, dissolved nutrient concentrations, nutrient limitation, and food web dynamics. Here, I assessed how migrant effects differed between species and streams used for spawning (Chapter 3).

My meta-analysis (Chapter 4) consisted of a broad literature review to address the question of how fishes affect structural (dissolved nutrient concentrations, periphyton biomass and composition) and functional (leaf decomposition and net ecosystem metabolism) characteristics of stream ecosystems. Moreover, I examined how fish effect sizes varied as a function of different biotic, abiotic, and methodological factors. Finally, I compared how fish effect sizes differed between two different approaches for extracting data from published studies.

#### LITERATURE CITED

- Atkinson C.L., Vaughn C.C., Forshay K.J. & Cooper J.T. (2013) Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. *Ecology*, **94**, 1359-1369.
- Brooks J.L. & Dodson S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28-35.
- Capps K.A. & Flecker A.S. (2013) Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131520.
- Covich A.P., Palmer M.A. & Crowl T.A. (1999) The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. *BioScience*, **49**, 119-127.
- Creed R.P. (1994) Direct and indirect effects of crayfish grazing in a stream community. *Ecology*, **75**, 2091-2103.

- Daily G. (1997) *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington, DC.
- Dudgeon D. (2010) Prospects for sustaining freshwater biodiversity in the 21<sup>st</sup> century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability*, **2**, 422-430.
- Flecker A.S. (1992) Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. *Ecology*, **73**, 927-940.
- Flecker A.S. (1996) Ecosystem engineering by a dominant detritivore in a diverse tropical stream. *Ecology*, **77**, 1845-1854.
- Flecker A.S. (1997) Habitat modification by tropical fishes: environmental heterogeneity and the variability of interaction strength. *Journal of the North American Benthological Society*, **16**, 286-295.
- Flecker A.S., McIntyre P.B., Moore J.W., Anderson J.T., Taylor B.W. & Hall R.O. (2010) Migratory fishes as material and process subsidies in riverine ecosystems. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 559-592.
- Gido K.B., Bertrand K.N., Murdock J.N., Dodds W.K. & Whiles M.R. (2010) Disturbance-mediated effects of fishes on stream ecosystem processes: concepts and results from highly variable prairie streams. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 593-617.
- Grimm N.B. (1988a) Role of macroinvertebrates in nitrogen dynamics of a desert stream. *Ecology*, **69**, 1884-1893.
- Grimm N.B. (1988b) Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agosia chrysogaster* (Pisces: Cyprinidae). *Environmental Biology of Fishes*, **21**, 143-152.
- Hairton N.G., Smith F.E. & Slobodkin L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421-425.
- Hall R.O., Tank J.L. & Dybdahl M.F. (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and Environment*, **1**, 407-411.

- Hall R.O., Koch B.J., Marshall M.C., Taylor B.W. & Tronstad L.M. (2007) How body size mediates the role of animals in nutrient cycling in aquatic ecosystems. In: *Body Size: The Structure and Function of Aquatic Ecosystems*. (Eds A.G. Hildrew, D. Raffaelli & R. Edmonds-Brown). Cambridge University Press, New York, NY, 286-305.
- Hall R.O., Taylor B.W. & Flecker A.S. (2011) Detritivorous fish indirectly reduce insect secondary production in a tropical river. *Ecosphere*, **2**, doi: 10.1890/ES11-00042.1
- Holtgrieve G.W. & Schindler D.E. (2011) Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology*, **92**, 373-385.
- Hrbacek J., Dvorakova M., Korinek V. & Prochazkova L. (1961) Demonstration of the effect of fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton assemblage. *Verhandlungen des Internationalen Verein Limnologie*, **14**, 192-195.
- Jones C.G., Lawton J.H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373-386.
- Kishi D., Murakami M., Nakano S. & Maekawa K. (2005) Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*, **50**, 1315-1322.
- Laws R.M. (1970) Elephants as agents of habitat and landscape change in East Africa. *Oikos*, **21**, 1-15.
- Louda S.M., Keeler K.H. & Holt R.D. (1990) Herbivore influences on plant performance and competitive interactions. In: *Perspectives on Plant Competition*. (Eds J.B. Grace & D. Tilman). Academic Press, San Diego, CA, 413-444.
- Matthews W.J. (1998) *Patterns in Freshwater Fish Ecology*. Chapman & Hall, San Francisco, CA.
- McIntyre P.B., Flecker A.S., Vanni M.J., Hood J.M., Taylor B.W. & Thomas S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? *Ecology*, **89**, 2335-2346.
- McNaughton S.J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 259-294.
- Moore J.W. (2006) Animal ecosystem engineers in streams. *BioScience*, **56**, 237-246.

- Moore J.W., Schindler D.E., Carter J.L., Fox J., Griffiths J. & Holtgrieve G.W. (2007) Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. *Ecology*, **88**, 1278-1291.
- Moore J.W. & Schindler D.E. (2008) Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology*, **77**, 275-284.
- Naiman R.J., Melillo J.M. & Hobbie J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254-1269.
- Naiman R.J. (1988) Animal influences on ecosystem dynamics. *BioScience*, **38**, 750-752.
- Naiman R.J., Bilby R.E., Schindler D.E. & Helfield J.M. (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399-417.
- Nakano S., Miyasaka H. & Kuhara N. (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, **80**, 2435-2441.
- Pastor J., Naiman R.J., Dewey B. & McInnes P. (1988) Moose, microbes, and the boreal forest. *BioScience*, **38**, 770-777.
- Peckarsky B.L. & McIntosh A.R. (1998) Fitness and community consequences of avoiding multiple predators. *Oecologia*, **113**, 565-576.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289-316.
- Power M.E. (1984) Habitat quality and the distribution of algae-grazing catfish in a Panamanian stream. *Journal of Animal Ecology*, **53**, 357-374.
- Power M.E. (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology*, **73**, 1675-1688.
- Power M.E. & Matthews W.J. (1983) Algae-grazing minnows (*Campostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia*, **60**, 328-332.
- Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*, **66**, 1448-1456.
- Power M.E., Stewart A.J. & Matthews W.J. (1988) Grazer control of algae in an Ozark mountain stream: effects of short-term exclusion. *Ecology*, **69**, 1894-1898.

- Power M.E., Parker M.S. & Dietrich W.E. (2008) Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs*, **78**, 263-282.
- Pringle C.M., Blake G.A., Covich A.P., Buzby K.M. & Finley A. (1993) Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia*, **93**, 1-11.
- Resh V.H., Brown A.V., Covich A.P., Gurtz M.E., Li H.W., Minshall G.W. *et al.* (1988) The role of disturbance in stream ecology. *Journal of the North American Benthological Society*, **7**, 433-455.
- Ruegg J., Tiegs S.D., Chaloner D.T., Levi P.S., Tank J.L. & Lamberti G.A. (2011) Salmon subsidies alleviate nutrient limitation of benthic biofilms in southeast Alaska streams. *Canadian Journal of Fisheries & Aquatic Sciences*, **68**, 277-287.
- Schindler D.E. & Eby L.A. (1997) Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology*, **78**, 1816-1831.
- Small G.E., Pringle C.M., Pyron M. & Duff J.H. (2011) Role of the fish *Astyanax aeneus* (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. *Ecology*, **92**, 386-397.
- Strayer D.L., Caraco N.F., Cole J.J., Findlay S. & Pace M.L. (1999) Transformation of freshwater ecosystems by bivalves. *BioScience*, **49**, 19-27.
- Taylor B.W., Flecker A.S. & Hall R.O. (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*, **313**, 833-836.
- Thayer C.W. (1979) Biological bulldozers and the evolution of marine benthic communities. *Science*, **203**, 458-461.
- Vanni M.J. (2010) Preface: when and where do fish have strong effects on stream ecosystem processes? In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 531-538.
- Whiles M.R., Lips K.R., Pringle C.M., Kilham S.S., Bixby R.J., Brenes R. *et al.* (2006) The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology and the Environment*, **4**, 27-34.
- Winemiller K.O., Montoya J.V., Roelke D.L., Layman C.A. & Cotner J.B. (2006) Seasonally varying impact of detritivorous fishes on the benthic ecology of a tropical floodplain river. *Journal of the North American Benthological Society*, **25**, 250-262.

CHAPTER 2  
MIGRATORY FISH EXCRETION AS A NUTRIENT SUBSIDY  
TO RECIPIENT STREAM ECOSYSTEMS<sup>1</sup>

SUMMARY

1. There is compelling evidence that consumer excretion can be an important component of nutrient cycling in aquatic ecosystems. Uncertainty concerning the functional role of many freshwater organisms remains, including those with migratory life history strategies that may introduce nutrients to recipient systems. Although generalizations remain elusive, differing abiotic and biotic conditions mediate the relative contributions of excretion to nutrient cycling.
2. Given the paucity of information on the functional significance of potamodromous fishes, we quantified the magnitude, variability, and importance of fish excretion in the context of stream nutrient cycling. In 2011-12, we collected data from a central Utah reservoir used by two potamodromous fishes (Bonneville cutthroat trout – BCT, *Oncorhynchus clarkii utah*; kokanee salmon – KOK, *Oncorhynchus nerka*) with temporally separated spawning migrations. To quantify the contribution of two migratory freshwater fishes to tributary nutrient cycling, we extrapolated interspecific measurements of per-capita nitrogen (N) and phosphorus (P) excretion rates to the population level within the local environmental context of two tributaries.
3. We observed differences in excretion subsidies between species and tributaries. BCT excretion rates and ratios were significantly greater than those for KOK.

---

<sup>1</sup> Co-authored by Kit Wheeler, Scott W. Miller & Todd A. Crowl



Estimates of the ratio of population-level migrant excretion to tributary nutrient export were highly variable through time and between tributaries. Evidence suggested these estimates were influenced by spatiotemporal hydrologic variation and were positively related to ratios of migrant biomass to discharge. During migrations, estimates of daily migrant excretion loading comprised a maximum of 6-859% and 1-388% of tributary  $\text{NH}_4\text{-N}$  and SRP export, respectively.

4. Measurements of nutrient uptake suggested that migrant excretion could meet a substantial portion of ecosystem nutrient demand. Migrant excretion fluxes comprised 46-188% of ecosystem  $\text{NH}_4\text{-N}$  demand and varied between streams and species. In contrast, the proportion of SRP demand supplied by migrant excretion (35%) was invariant.
5. These results demonstrate an important functional role for potamodromous fishes as nutrient sources in recipient ecosystems. Furthermore, our data provide empirical support for predictions of when and where effects of fish-derived nutrients will be strongest, thereby advancing the understanding of context-dependent migratory fish effects in riverine ecosystems. Although widespread and common, we suggest that potamodromous fishes are overlooked but important organisms capable of substantially affecting stream nutrient cycling.

## INTRODUCTION

Nutrients that originate in one ecosystem and move across boundaries into different systems can have pronounced impacts on population, community, and ecosystem dynamics within recipient habitats (Polis, Anderson & Holt, 1997). Due to periodic or

seasonal migrations among ecosystems, animals can influence ecological processes by nutrient translocation. For example, animal-derived nutrients, commonly called subsidies, can have bottom-up effects in recipient habitats by reducing resource limitation of primary producers (Flecker *et al.*, 2010).

Although excretion is not the only mechanism by which animal nutrient subsidies are introduced to recipient systems (Flecker *et al.*, 2010), it is generally considered the most direct (Vanni, 2002). Due to its potential importance, the release of dissolved nutrients via consumer excretion has been the focus of numerous studies in aquatic ecosystems. For example, consumer-driven nutrient recycling can play a critical role in sustaining lake primary production (e.g., Schaus *et al.*, 1997) and phytoplankton community composition (e.g., Elser *et al.*, 1988). Similarly, excretion by stream invertebrates (e.g., Grimm, 1988a; Hall, Tank & Dybdahl, 2003) and vertebrates (e.g., McIntyre *et al.*, 2007; Small *et al.*, 2011) can alter ambient nutrient concentrations (e.g., Capps & Flecker, 2013a) and nutrient limitation of algae (e.g., Atkinson *et al.*, 2013).

Migratory fishes that spend all of their lifecycle in freshwater are common around the world yet remain understudied relative to diadromous fishes that use both marine and freshwater habitats (Flecker *et al.*, 2010). Potamodromous (confined to freshwaters) migrations can be associated with feeding, reproduction, or seeking refuge from unfavorable conditions, and may take place among a variety of freshwater habitats (e.g., main-stem rivers and tributaries, impoundments and inlets; Northcote, 1997). Regardless of the motivation or location, potamodromous fish migrations provide opportunities for significant nutrient subsidies to recipient systems (Flecker *et al.*, 2010), although very few studies have evaluated the role of these taxa as nutrient transporters (but see

Childress, Allan & McIntyre, 2014). In addition, whole-system scale excretion rates of freshwater fishes are rarely considered in studies of stream nutrient dynamics (but see Grimm, 1988b; McIntyre *et al.*, 2008; Tronstad, 2008; Small *et al.*, 2011; Wilson & Xenopoulos, 2011). Therefore, considerable uncertainty remains about the potential contribution of migratory freshwater fish excretion subsidies to lotic ecosystem nutrient cycling.

The ability to predict ecosystem responses to migratory fish effects (e.g., excretion, bioturbation, carcass decomposition) is frequently context dependent. Vanni (2010) and others (e.g., Moore, 2006) recognized the importance of hydrologic context and suggested fish effects should be greatest under relatively low flow conditions. Flecker *et al.* (2010) offered a series of predictions for when migratory freshwater fish subsidies should be maximized, namely when the ratio of migrant biomass to recipient ecosystem size is high, ambient nutrient concentrations are low, and system retention rates are high. However, empirical assessments of these predictions are uncommon (but see Janetski *et al.*, 2009 for a quantitative synthesis of Pacific salmon effects).

To test a subset of predictions regarding the influence of biotic and abiotic conditions on migratory freshwater fish effects, we quantified the magnitude and variability of potamodromous migrant excretion subsidies, as well as their importance to tributary nutrient cycling. We had three primary study objectives: (1) to examine differences in nitrogen (N) and phosphorus (P) excretion rates and ratios between two congeneric migratory freshwater fishes, (2) to describe the contribution of migrant excretion subsidies to tributary nutrient dynamics, and (3) to evaluate the influence of migrant

biomass, spatial, and temporal hydrologic variability on the relative importance of migrant excretion subsidies.

## METHODS

### *Study site*

Tributaries of Strawberry Reservoir, a large (surface area = 48 km<sup>2</sup>), high elevation (2316 m) impoundment in east-central Utah, were selected to describe the contribution of migratory freshwater fish excretion to recipient system nutrient dynamics (Fig. 2-1). Yearly precipitation in the Strawberry Valley is approximately 580 mm, with most falling as snow between November and March (Utah Department of Environmental Quality, 2007). As the most popular cold water sport fishery in Utah, the reservoir is stocked with multiple salmonids, including the adfluvial migrants Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) and kokanee salmon (KOK; *Oncorhynchus nerka*). These two adfluvial species have temporally separated spawning migrations. BCT migrate during the late spring and early summer, and constitute the overwhelming majority of migratory fish biomass in tributaries during this time (A. Ward & J. Robinson, Utah Division of Wildlife Resources, personal communication). In contrast, KOK migrate during the fall and are the only migratory fish present in tributaries. Salmonid spawning activity is most concentrated in two inlet streams, Indian Creek and Trout Creek (Orme, Knight & Beauchamp, 1995; Knight, 1997; Fig. 2-1). Indian Creek (watershed area = 40.0 km<sup>2</sup>) is a second-order, low gradient (slope = 0.01), meandering (sinuosity = 1.64) system, whereas Trout Creek (12.2 km<sup>2</sup>) is a first-order system with greater slope (0.03) and reduced sinuosity (1.18). Additionally, the larger watershed area of Indian Creek

creates more intra- and interannual hydrologic variation than is present in Trout Creek, where flows are comparatively constant (Table 2-1).

We collected data from reaches accessible to adfluvial migrants in both tributaries during 2011 and 2012. The extent of accessible habitat was delineated by the presence of non-passable, upstream beaver dams and was verified by migrant counts above the dams. Considerable hydrologic variability was observed between the two study years, with 2011 exceeding and 2012 below 30-year median snow water equivalent values (see Fig. A-1 in Appendix). In 2011, BCT data from the Indian Creek watershed were collected in Streeper Creek (8.2 km<sup>2</sup>), the primary tributary of Indian Creek, due to elevated and extended runoff conditions that prevented sampling in the main channel. Streeper Creek was not sampled during 2012 because low discharge prohibited BCT access, meaning that reaches sampled during 2012 were necessarily farther downstream. Although steeper (slope = 0.02), the planform (sinuosity = 1.58) and channel geometry (i.e., width, depth) of Streeper Creek are similar to Indian Creek. Hereafter we exclusively use Indian Creek to represent any sampling that occurred within the entire Indian Creek watershed (i.e., Indian Creek main channel or Streeper Creek), but acknowledge inferential restrictions exist because of our inability to sample the same area each year.

#### *Excretion rates and ratios*

We determined migrant N (as NH<sub>4</sub>) and P (as soluble reactive phosphorus [SRP]) excretion rates during spawning runs by incubating individual migrants. Individuals used for excretion incubations ( $n_{\text{BCT}} = 49$ ;  $n_{\text{KOK}} = 24$ ) were collected in 2011 using an electric fish trap at the confluence of the Strawberry River, a primary tributary of the reservoir.

We incubated individuals in closed containers filled with river water (30-60 L) for approximately 30 minutes (range = 21-40 minutes; Whiles *et al.*, 2009). Incubated individuals represented the entire range of migrant size variation (BCT = 375-650 mm total length [TL]; KOK = 296-553 mm TL). All incubations took place between 0900 and 1830 hours. Water temperature was measured in each container at the beginning and end of incubations to ensure temporal variation was minimal (maximum change was 1°C). Incubated fish were measured to the nearest mm (TL), and length-weight regressions (A. Ward & J. Robinson, unpubl. data) were used to estimate body mass. Water samples were collected immediately before and after each incubation and differences in N and P concentrations were used to calculate nutrient excretion rates and N:P ratios. All water samples were filtered through pre-combusted Whatman GF/F filters and frozen until analysis. Water samples were analyzed using colorimetry at the University of New Hampshire Water Quality Analysis Laboratory (Durham, NH). The phenate (EPA 350.1; Solorzano, 1969) and ascorbic acid (EPA 365.3; Murphy & Riley, 1962) methods were used to quantify NH<sub>4</sub>-N and SRP, respectively.

Previous studies of aquatic consumer excretion have attempted to control for microbial activity during incubations by filtering water used for incubations and using control incubations without consumers. We modified this procedure for two reasons. First, the large incubation volumes used in this study made pre-filtration logistically impractical. Second, the control incubations described above may fail to account for increased microbial activity in response to nutrients added via excretion. To account for these issues, control incubations using nutrient additions were also conducted on each sampling date. The same procedures were used for the control incubations as for the fish

incubations and microbial activity rates ( $A_{MIC}$ , mg NH<sub>4</sub>-N or SRP hr<sup>-1</sup>) were calculated as follows:

$$A_{MIC} = \frac{Add_{NUT} - (\Delta C_{NUT,CTRL} V_{INC,CTRL})}{T_{INC,CTRL}} \quad (1)$$

where  $Add_{NUT}$  is the mass of N (as NH<sub>4</sub>Cl) or P (as K<sub>2</sub>HPO<sub>4</sub>) added to simulate fish excretion in control incubations,  $\Delta C_{NUT,CTRL}$  is the measured change in nutrient concentration during control incubations,  $V_{INC,CTRL}$  is the control incubation volume, and  $T_{INC,CTRL}$  is the control incubation time. Excretion nutrient masses (i.e.,  $Add_{NUT}$ ) were estimated for an appropriate range of migrant body mass (150-3000 g wet weight) using models for non-detritivorous fishes (Table 2 in Sereda, Hudson & McLoughlin, 2008). Results from the control incubations and ordinary least squares regression were used to develop models for microbial activity rates ( $A_{MIC}$ ) as a function of migrant body mass. Adjusted per-capita excretion rates ( $E_{IND}$ , mg NH<sub>4</sub>-N or SRP hr<sup>-1</sup>) were then calculated as follows:

$$E_{IND} = \frac{\Delta C_{NUT,FISH} V_{INC,FISH}}{T_{INC,FISH}} + A_{MIC} \quad (2)$$

where  $\Delta C_{NUT,FISH}$  is the measured change in nutrient concentration during fish incubations,  $V_{INC,FISH}$  is the fish incubation volume, and  $T_{INC,FISH}$  is the fish incubation time. Our models indicated that  $A_{MIC}$  was positively related to body mass, suggesting stimulation of microbial nutrient uptake following excretion. Therefore, our excretion rate estimates generally increased as a result of our microbial activity estimates.

Although control incubations without fish and nutrients were not used, we feel confident attributing observed changes in dissolved nutrient concentrations to the incubated fish and microbes as a result of the relatively short incubation times. Additionally, other

excretion studies have attributed nutrient concentration changes observed during incubations to aquatic consumers in the absence of control incubations without consumers (e.g., Grimm, 1988a; Post & Walters, 2009; Benstead *et al.*, 2010).

To ensure interspecific comparisons reflected thermal conditions encountered by BCT and KOK, we standardized measured excretion rates to the average stream temperature across stream and year combinations ( $n = 4$  for each species; 10°C for BCT; 8°C for KOK) following Haefner (2005):

$$E_{IND,avg} = E_{IND,I} Q^{(avg-I)/10} \quad (3)$$

where  $E_{IND,avg}$  is the excretion rate at the average stream temperature during migrant presence,  $E_{IND,I}$  is the excretion rate at the respective incubation temperature  $I$ ,  $avg$  is the average stream temperature during migrant presence, and  $Q$  is 2.0, a temperature coefficient ( $Q_{10}$ ) for fish N and P excretion rates (Vanni, 2002; Johnson *et al.*, 2010).

#### *Migrant excretion load and tributary nutrient export*

We compared daily estimates of migrant excretion load ( $E_d$ ) with daily estimates of tributary nutrient export ( $T_d$ ; both quantities measured as g NH<sub>4</sub>-N or SRP d<sup>-1</sup>) during migrations in 2011 (May-November) and 2012 (April-November). Migrant excretion load was calculated as:

$$E_d = A_{M,d} \sum_{i=1}^n p_i EXC_i \quad (4)$$

where  $A_{M,d}$  is migrant abundance in the system on day  $d$ ,  $n$  is the number of body size bins (overall range = 251-700 mm TL; 50-mm bins),  $p_i$  is the proportion of migrants in the  $i^{\text{th}}$  size bin, and  $EXC_i$  is the excretion rate of an average-sized individual in the  $i^{\text{th}}$  size bin.



To estimate migrant abundance, we conducted regular streamside migrant counts (range = 1-16 days between counts). Counts were conducted by 1-2 observers during periods of maximum visibility (0900-1600) by walking upstream from the tributary mouth to the barrier impeding upstream movement. To minimize the possibility of double-counting, individual migrants were counted only after they retreated downstream of an observer or once an observer passed a known point of refuge (e.g., undercut bank). The number of observed migrants was assumed to represent  $A_{M,d}$  on a given measurement date and we used linear interpolation to produce a complete record of daily migrant counts. We used linear interpolation because the overwhelming majority of intervals between successive streamside counts (109 of 115) were less than estimated residence times for individuals ( $BCT_{\text{Indian}} = 10.5$  d;  $BCT_{\text{Trout}} = 7.5$  d;  $KOK_{\text{All}} = 14.1$  d; Knight, 1997; K. Wheeler, unpubl. data), reducing the potential of missing any migration pulses. We acknowledge, however, that migrant abundance estimates could be influenced by unaccounted for error sources, including detection probabilities and undetected migration pulses between successive streamside counts.

We used the migrant size distribution estimated from fishes collected at the Strawberry River electric fish trap in 2011 ( $n_{\text{BCT}} = 315$ ,  $n_{\text{KOK}} = 704$ ) and 2012 ( $n_{\text{BCT}} = 642$ ,  $n_{\text{KOK}} = 479$ ) to estimate the proportion of individuals in different size classes ( $p_i$ ), and assumed identical, temporally constant distributions for migrants in Indian and Trout Creeks (Orme *et al.*, 1995; Table A-1). We used length-weight regression models to estimate average body mass (wet weight) for each size class. We standardized measured excretion rates to average stream temperatures using equation 3, and developed

temperature-standardized size-dependent excretion rate models for each combination of species, stream, year, and nutrient.

We calculated  $T_d$  (daily tributary nutrient export) as the product of daily discharge and dissolved nutrient concentrations. Daily discharge values were obtained from a combination of manual discharge measurements (made just upstream of tributary mouths), installed stage-height recorders (TruTrack Ltd., Christchurch, NZ), and linear interpolation. To estimate dissolved nutrient concentrations, we collected duplicate water samples for dissolved nutrients upstream of tributary mouths every 1-3 weeks during spawning periods, and filtered samples in the field through pre-combusted Whatman GF/F filters. Filtered samples were stored in the dark and on ice until frozen, which at all times occurred within four hours of collection. Samples were subsequently analyzed for  $\text{NH}_4\text{-N}$  and SRP as described previously and we used linear interpolation to produce a complete record of daily concentrations. Because we did not collect stream water chemistry samples more frequently, our estimates of tributary nutrient export ( $T_d$ ) should be interpreted cautiously. Stream water chemistry samples were analyzed at the University of New Hampshire Water Quality Analysis Laboratory (2011 samples) and the Utah State University Aquatic Biogeochemistry Analytical Laboratory (2012 samples; Logan, UT).

As it compares the magnitude of migrant excretion subsidies to tributary nutrient export,  $E_d/T_d$  provides an indication of the relative contribution of migrant excretion to stream nutrient cycling (Tronstad, 2008). This ratio is conceptually similar to a measure of ambient nutrient pool turnover (McIntyre *et al.*, 2008). We opted to use  $E_d/T_d$  because our data were collected at relatively coarse spatial and temporal scales.

However,  $E_d/T_d$  and the measure of ambient nutrient pool turnover produce identical values (Appendix A-1).

### *Ecosystem nutrient demand*

To measure ecosystem  $\text{NH}_4\text{-N}$  and SRP demand, we modified the *in situ* microcosm approach described by Hoellein *et al.* (2009), which allowed us to partition demand among different benthic particle sizes. The influence of particle size on nutrient demand was examined because the effects of migrant redd excavation on periphyton biomass can vary as a function of substrate size (Holtgrieve *et al.*, 2010). We made measurements at a single time point during the BCT and KOK migrations in both study streams in 2012 and used particles from four different size classes that were delineated using quartiles associated with the *B*-axis of substrate particles (Table A-2). To ensure complete spatial coverage of each study reach where demand was measured, we haphazardly divided study reaches into six sub-units of approximately equal length and collected particles from randomly selected locations in each sub-unit. Particles  $> 9$  mm *B*-axis were collected by hand; smaller particles were collected by sliding a plastic spatula under an inverted specimen cup inserted into benthic substrates (Hoellein *et al.*, 2009). Particle collection procedures were identical for each subunit, stream, and species combination. Study reaches where demand measurements were made were subsections of accessible stream length.

We modified Hoellein *et al.*'s (2009) approach by placing collected particles in WhirlPak© bags (0.53 L) and filling each bag with nutrient-amended water. The number of particles added to bags was identical within each particle size class. Rather than

adding nutrients directly to the stream, two 15-L volumes were collected from each study stream. We added N (as  $\text{NH}_4\text{Cl}$ ) to one volume and P (as  $\text{KH}_2\text{PO}_4$ ) to the other to elevate ambient stream concentrations of the added nutrient by relatively small amounts ( $50 \mu\text{g L}^{-1}$ ). We chose to measure uptake of each nutrient separately because we were more interested in making inferences about how the stream reach removes nutrients from the water column than the capacity of the stream to recycle excreted nutrients. In that way, our measurements attempted to mimic stream spiraling studies that usually administer N and P separately (Stream Solute Workshop, 1990; Schade *et al.*, 2011). Across all combinations of stream, species, and nutrient, total particle area within each bag ranged between 20 and  $136 \text{ cm}^2$ , and was determined by summing exposed 2-D surface area for all particles within an individual bag. Surface areas were estimated from particle photos with ImageJ software (Rasband, ImageJ). Filled bags were incubated within a  $5\text{-m}^2$  area of the stream to maintain ambient temperature and light levels among all replicates. During the BCT migration, incubation times were between 2.0-3.7 hours, while KOK incubations ranged between 1.5-2.4 hours. Upon removal from the stream, we recorded the volume of nutrient-amended water added to each bag. Water samples ( $n = 3-4$ ) collected from each volume of nutrient-amended water represented initial dissolved nutrient concentrations. These initial samples were compared with final samples collected after incubation ( $n = 1$  from each replicate) to determine concentration changes during incubation. Water samples were collected and analyzed as described previously. We calculated nutrient uptake ( $U$ ;  $\mu\text{g NH}_4\text{-N}$  or  $\text{SRP m}^{-2} \text{ hr}^{-1}$ ), which is analogous to nutrient demand (Webster & Valett, 2006), as:

$$U = \frac{\Delta C_{NUT} V_{INC}}{A_{PART} T_{INC}} \quad (5)$$

where  $\Delta C_{NUT}$  is the measured change in nutrient concentration (i.e., initial – final),  $V_{INC}$  is the incubation volume,  $A_{PART}$  is the total particle area within a bag, and  $T_{INC}$  is the incubation time. In general, nutrient uptake was calculated as the average of all individual replicates because particle size did not have a strong effect on uptake (one-way ANOVA;  $P < 0.05$  for only one of eight possible stream, species, and nutrient permutations). For the one case where particle size did have an effect, we calculated  $U$  as the weighted average of the four size class means.

For comparison with nutrient uptake, migrant excretion flux ( $E$ ;  $\mu\text{g NH}_4\text{-N}$  or  $\text{SRP m}^{-2} \text{hr}^{-1}$ ) was calculated as:

$$D_M \sum_{i=1}^n EXC_i p_i \quad (6)$$

where  $D_M$  is migrant density (ind.  $\text{m}^{-2}$ ) and  $EXC_i$  and  $p_i$  are as defined in equation 4. We used the average of migrant counts made in the study reach where uptake measurements occurred as our estimate of migrant abundance. Because we collected uptake data during 2012, we used the 2012 size distribution data to determine  $p_i$ . Areas ( $\text{m}^2$ ) within uptake measurement study reaches were estimated by multiplying mean stream width by reach lengths (Trout Creek, 127 m; Indian Creek, 188 m).

### *Statistical analyses*

Because excretion rates and ratios generally scale allometrically with body mass, we modeled them after the equation  $E = aM^b$  where  $E$  is excretion rate or ratio,  $M$  is body mass,  $a$  is a scaling coefficient, and  $b$  is a scaling exponent (Hall *et al.*, 2007). Excretion rates, N:P ratios, and body size data were  $\log_{10}$ -transformed prior to analyses. To test for interspecific differences in nutrient excretion rates and ratios, we used temperature-

standardized excretion rates and ANCOVA with body size as a covariate, and calculated type III sums of squares to mitigate unequal sample sizes. In addition, we centered body size (i.e.,  $x_i - \bar{x}$ ) prior to the analysis in order to ensure that data in the treatment groups (i.e., species) were being compared over the same range of the covariate (Gotelli & Ellison, 2004). To test our prediction that hydrologic differences influenced average values of  $E_d/T_d$ , we used two-way ANOVA with year and stream as factors after grouping across nutrients and species. Additionally, we used Pearson's correlation coefficient to examine relationships between the relative contribution of migrant excretion subsidies (i.e.,  $E_d/T_d$  means during spawning periods) and potential drivers (biomass, discharge, and biomass/discharge). R 3.0.1 (R Development Core Team, 2013) was used for all analyses.

## RESULTS

Adfluvial migrants were present in Strawberry Reservoir tributaries for 7-10 weeks. The one exception was the 2011 BCT migration, which was longer (ca. 14 weeks) due to sustained runoff conditions (Table 2-1). Migrant biomass was generally higher for KOK than for BCT for any given stream and year combination, although values were largely within the same order of magnitude (Table 2-1). Indian Creek discharge was more temporally variable than Trout Creek. For example, peak discharge during BCT migrations was approximately six times higher than maximum discharge during KOK migrations in Indian Creek, whereas peak discharge during BCT migrations was, on average, only 1.4 times greater than peak discharge during KOK migrations in Trout Creek (Table 2-1). During spawning migrations, average ambient stream temperatures

were 1-3°C lower during KOK presence than during BCT presence, and interannual temperature variation was more pronounced in Indian Creek than in Trout Creek (Table 2-1). Ambient concentrations of NH<sub>4</sub>-N and SRP in both tributaries were typically lower than 20 and 8 µg L<sup>-1</sup>, respectively, although exceptions and variation did exist (Table 2-1).

#### *Excretion rates and ratios*

Excretion rates and ratios were greater for BCT than for KOK and were positively related to body size for both species in most instances (Fig. 2-1 A-B). Allometric scaling exponents for BCT were  $0.71 \pm 0.11$  (mean  $\pm$  SE) for NH<sub>4</sub>-N ( $P < 0.001$ ) and  $0.40 \pm 0.10$  for SRP ( $P < 0.001$ ), compared with  $0.96 \pm 0.10$  for NH<sub>4</sub>-N ( $P < 0.001$ ) and  $0.66 \pm 0.15$  for SRP ( $P < 0.001$ ) for KOK. Variation explained by body size was greater for NH<sub>4</sub>-N excretion rates than for SRP and greater for KOK than for BCT (Fig. 2-1 A-B). Body size did not have a significant effect on excreted N:P ratios for KOK (scaling exponent =  $0.25 \pm 0.25$ ,  $P = 0.27$ ). Although body size did have a positive effect on BCT N:P (scaling exponent =  $0.38 \pm 0.14$ ,  $P = 0.009$ ), the variation explained was less than that for BCT excretion rates (Fig. 2-1 C). While we found significant effects of species on all excretion responses, body size  $\times$  species interactions were not significant for excretion rates or ratios (all  $P > 0.12$ ; Table 2-2). These patterns indicate that scaling coefficients (i.e., y-axis intercepts), not scaling exponents (i.e., slopes), differed between BCT and KOK.

*Migrant excretion load and tributary nutrient export*

Calculated values of  $E_d/T_d$  varied over two orders of magnitude (Fig. 2-3). Considering all stream, year, and species combinations, the range of peak  $E_d/T_d$  values for  $\text{NH}_4\text{-N}$  was 6-859% ( $150 \pm 102\%$ ; mean  $\pm$  SE,  $n = 8$ ), while SRP peak values ranged between 1-388% ( $74 \pm 46\%$ ). When daily  $E_d/T_d$  values were averaged over each one of the studied spawning periods, the mean values, hereafter called spawning means, were lower though still substantial ( $\text{NH}_4\text{-N}$  range = 1-194%,  $37 \pm 23\%$ ; SRP range = 0-105%,  $23 \pm 13\%$ ). Across all periods of migrant presence ( $n = 1206$  observations), 66% of daily  $E_d/T_d$  values were less than 10%. However, higher  $E_d/T_d$  values did occur, as 23% of values were greater than 20%, 14% percent of values exceeded 50%, and 5% of values were more than 100% (Fig. 2-3).

Several trends were evident in  $E_d/T_d$  spawning means when compared between streams, years, species, and nutrients (Fig. 2-4). Migrant excretion represented a larger proportion of tributary nutrient export in Indian ( $52 \pm 24\%$ ; mean  $\pm$  SE) than in Trout Creek ( $7 \pm 2\%$ ). Similarly,  $E_d/T_d$  spawning means tended to be greater during the relatively dry 2012 ( $53 \pm 24\%$ ) than during the relatively wet 2011 spawning seasons ( $7 \pm 2\%$ ). Likewise, the proportion of tributary nutrient export met by migrant excretion was typically greater for KOK ( $45 \pm 24\%$ ) than for BCT ( $14 \pm 7\%$ ). Finally,  $E_d/T_d$  spawning means were usually greater for  $\text{NH}_4\text{-N}$  ( $37 \pm 23\%$ ) than for SRP ( $23 \pm 13\%$ ).

Using  $E_d/T_d$  spawning means as response variables, we found a significant stream  $\times$  year interaction ( $F_{1,12} = 6.02$ ,  $P = 0.030$ ) after grouping across nutrients and species. Pairwise comparisons indicated that 2012 Indian Creek  $E_d/T_d$  values were greater than



the other three possible combinations, which were not statistically different (Tukey's HSD;  $P \leq 0.05$ ).

There was a significant positive correlation between spawning means and the ratio of migrant biomass to discharge (Table 2-3). This was true regardless of whether peak or average biomass and discharge data were used and was not dependent on nutrient. Neither biomass nor discharge was significantly correlated with spawning means when considered in isolation, although the magnitude of correlation coefficients was consistently higher for discharge than for biomass (Table 2-3).

#### *Ecosystem nutrient demand*

We observed spatiotemporal and nutrient-specific variation in excretion fluxes ( $E$ ) and measurements of ecosystem nutrient demand ( $U$ ; Fig. 2-5). Average  $\text{NH}_4\text{-N}$  excretion fluxes varied approximately two-fold (range = 281-540  $\mu\text{g NH}_4\text{-N m}^{-2} \text{ hr}^{-1}$ ), while slightly more variation existed in average SRP flux (range = 35-95  $\mu\text{g SRP m}^{-2} \text{ hr}^{-1}$ ). However, patterns were different between streams. Average  $E$  was higher for BCT in Indian Creek, but higher for KOK in Trout Creek, regardless of nutrient (Fig. 2-5). Average values of  $U$  were higher for  $\text{NH}_4\text{-N}$  (range = 271-825  $\mu\text{g NH}_4\text{-N m}^{-2} \text{ hr}^{-1}$ ) than for SRP (range = 93-269  $\mu\text{g SRP m}^{-2} \text{ hr}^{-1}$ ), but spatiotemporal patterns differed between the two nutrients. Average  $\text{NH}_4\text{-N}$  uptake varied more between streams than over time (i.e., between species) and was higher in Indian Creek than in Trout Creek (Fig. 2-5 A). Spatial variation also existed in average SRP uptake, but the pattern was different due to relatively high temporal variation in Trout Creek  $U$  measurements. Average SRP uptake

values were higher in Indian Creek during the BCT migration, but were higher in Trout Creek during the KOK migration (Fig. 2-5 B).

Maximum and minimum values for  $E$  and  $U$  were not aligned, resulting in considerable variation in the proportion of nutrient demand met by migrant excretion flux (i.e.,  $E/U$  values), although patterns differed between nutrients. For  $\text{NH}_4\text{-N}$ , the range of  $E/U$  was 46-188% ( $99 \pm 31\%$ , mean  $\pm$  SE), and values were higher in Trout Creek than in Indian Creek, regardless of species (Fig. 2-5 A). Conversely,  $E/U$  was constant for SRP (range = 34-37%,  $36 \pm 1\%$ ) and showed minimal variation across streams or species (Fig. 2-5 B). For  $\text{NH}_4\text{-N}$  species-level differences, the proportion of nutrient demand being met by migrant excretion subsidies depended on system. Values of  $E/U$  were greater for BCT than KOK in Indian Creek, but greater for KOK than BCT in Trout Creek.

## DISCUSSION

Our results indicate that migratory fish excretion can be a significant nutrient subsidy to spawning tributaries. Observed differences in per-capita excretion rates, when scaled to population levels and combined with abiotic stream characteristics, indicated the extent of variation in the relative contribution of excretion subsidies to stream nutrient pools. Nevertheless, direct comparisons indicated that migrant excretion subsidies could meet a majority of ecosystem nutrient demand during spawning migrations, suggesting that migratory fish excretion subsidies can be an important component of nutrient cycling in tributaries. However, differences in biotic and abiotic conditions among systems are

likely to mediate the relative effect of migrant excretion subsidies on stream nutrient dynamics.

### *Excretion rates and ratios*

While previous studies have demonstrated a wide range of nutrient recycling rates and ratios among fishes (Schindler & Eby, 1997; Vanni *et al.*, 2002; McIntyre *et al.*, 2008), they often spanned broad taxonomic groups (i.e., families or orders). Here, we found significant differences in excretion rates and ratios for closely related species. Studies of taxonomically diverse fish assemblages indicate that individual species can have disproportionate effects on stream nutrient cycling as a result of different excretion rates (e.g., Small *et al.*, 2011) or ratios (e.g., Capps & Flecker, 2013b). Our results suggest that similar interspecific variation in nutrient recycling rates – and by extension contribution by individual species to whole-system nutrient cycling – can exist in communities with relatively low taxonomic diversity.

There are several possible explanations for interspecific variation in nutrient excretion rates and ratios. Because metabolic rates are temperature dependent, nutrient excretion rates are positively related to temperature (Vanni, 2002). Consequently, migrant BCT excretion rates should exceed migrant KOK excretion rates due to higher ambient stream temperatures during spring BCT migrations. Our data were consistent with this expected pattern and thus support the idea that differences in ambient stream temperature contribute to interspecific variation in excretion rates. However, factors such as diet and body nutrient content may also mediate differences in BCT and KOK excretion rates and ratios. In Strawberry Reservoir, reproductively mature BCT are carnivores, whereas

adult KOK are zooplanktivores (Ward, Robinson & Wilson, 2007). These two prey items have different nutrient ratios (Cross *et al.*, 2005), which can ultimately influence excretion ratios (Sterner & Elser, 2002). Furthermore, differences in BCT and KOK body nutrient content, should they exist, could also influence excretion rates and ratios. For example, Vanni *et al.* (2002) found a strong relationship between P excretion rate and body P content within a large group of tropical aquatic vertebrates.

#### *Migrant excretion load and tributary nutrient export*

Previous studies have documented excretion subsidies by fishes (McIntyre *et al.*, 2008; Bouletreau *et al.*, 2011; Capps & Flecker, 2013a) and other stream consumers including snails (Hall *et al.*, 2003; Moslemi *et al.*, 2012), salamanders (Keitzer & Goforth, 2013), mussels (Atkinson *et al.*, 2013), and shrimp (Benstead *et al.*, 2010). Our study, however, illustrates the potential magnitude of nutrient excretion subsidies by potamodromous fishes in spawning streams (see Tronstad, 2008 for a similar example). During our two-year study,  $E_d/T_d$  values at times exceeded 20% and peaked at more than 800%. While there are methodological caveats to consider, these results support our original prediction that migratory fish excretion can represent a substantial nutrient subsidy to recipient habitats. Furthermore, the high variability in daily  $E_d/T_d$  values (more than a hundredfold) agreed with our expectation that the relative contribution of migratory fish excretion to tributary nutrient cycling would fluctuate in response to changes in abiotic and biotic conditions.

Our findings specifically identify the key role of temporal and spatial hydrologic variation in mediating the contribution of migrant excretion to tributary nutrient cycling.

Our observations of maximum  $E_d/T_d$  in Indian Creek during a relatively dry year (Fig. 2-4 D) were consistent with previous work that identified maximum influence of consumer excretion during periods of reduced flow (McIntyre *et al.*, 2008; Benstead *et al.*, 2010; Capps & Flecker, 2013a; Keitzer & Goforth, 2013). Additionally, our finding that stream and year both significantly influenced  $E_d/T_d$  supports the notion that hydrology mediates consumer excretion subsidies, and indicates spatiotemporal variation in the likely contribution of migrant excretion subsidies to tributary nutrient cycling.

Our data indicate that the ratio of migrant biomass to system size, as measured by discharge, can mediate the contribution of migrant excretion to nutrient cycling. We found significant correlations between  $E_d/T_d$  spawning means and the ratio of migrant biomass to discharge, which provides empirical support for Flecker *et al.*'s (2010) hypothesis that migrant subsidies are most likely to be significant when biomass is high relative to system size (see Janetski *et al.*, 2009 also). Thus, while spatial (e.g., Benstead *et al.*, 2010) or temporal (e.g., Keitzer & Goforth, 2013) differences in biomass can mediate the relative importance of migrant excretion subsidies, we concur with others who suggested biomass to discharge ratios may be useful predictors of fish effects in riverine systems. We caution, however, that as with any natural experiment, our results are correlative and derived from relatively small sample sizes. Thus, it would be valuable for future studies to investigate causal relationships among a broader range of systems and through formal experimentation.

*Ecosystem nutrient demand*

BCT and KOK excretion subsidies met 34-188% of ecosystem nutrient demand, suggesting the critical contribution migratory fishes make to stream nutrient cycling during spawning migrations. Furthermore, our  $E/U$  values provide important context for calculated  $E_d/T_d$  values, which indicate the size of excretion subsidies relative to tributary nutrient export. While large at times for BCT and KOK in our study systems,  $E_d/T_d$  values do not provide an explicit measure of the significance of excretion subsidies to whole-system nutrient dynamics because they do not reflect nutrient demand. In contrast,  $E/U$  values indicate the relative importance of excretion subsidies, and the large ( $\geq 30\%$ ) values we observed reflect the significant role of migratory fish excretion in our study streams. In general, our results underscore the importance of ambient conditions when considering consumer excretion subsidies in an ecosystem context. Consumer excretion subsidies are only likely to be significant if they arrive at a time when or place where nutrient demand is high relative to supply.

Although limited in number, comparisons with previous fish studies that quantified  $E/U$  suggest excretion by migratory fishes like BCT and KOK may be especially important to nutrient cycling in recipient streams. For both species, our  $E/U$  values for  $\text{NH}_4\text{-N}$  and SRP are higher than or comparable with most published values for individual fish species (Grimm, 1988b; Tronstad, 2008; Small *et al.*, 2011; Capps and Flecker, 2013b) or fish assemblages (McIntyre *et al.*, 2008; Wilson & Xenopoulos, 2011). Large  $E/U$  values can result from either larger excretion fluxes or reduced nutrient demand, but the magnitude of our observed  $E/U$  values is likely related to the former. Average migrant biomass in our study streams (ca.  $22 \text{ g m}^{-2}$ ) was high relative to fish biomass in

most previous studies, and elevated biomass will increase excretion fluxes, all else being equal. Indeed, it was only those studies with higher fish biomass that reported higher or comparable  $E/U$  values: McIntyre *et al.* (2008; 44.2 g m<sup>-2</sup>); Small *et al.* (2011; 31 g m<sup>-2</sup>); Capps and Flecker (2013b; 240 g m<sup>-2</sup>). Additionally, individual fish in studies with the highest  $E/U$  values were generally smaller than migratory BCT and KOK in Strawberry Reservoir tributaries. Because mass-specific excretion rates are higher for smaller individuals than for larger individuals, differences in population size structure may amplify differences in  $E/U$  values (Hall *et al.*, 2007).

Our  $E/U$  values illustrate the important nutrient subsidy likely provided by migratory fish excretion in recipient streams, but there are caveats to consider when interpreting or generalizing our ecosystem demand results. While our approach for measuring demand allowed us to examine the effect of particle size on nutrient uptake rates, our use of no-flow microcosms and short-term nutrient additions may have biased our calculations of  $E/U$  by underestimating  $U$  and therefore inflating  $E/U$  values (Bott *et al.*, 1997; Mulholland *et al.*, 2002). However, Hoellein *et al.* (2009) reported consistently higher uptake rates using similar microcosms than using whole-stream enrichment methods that permit flow through study reaches. Thus, even if our results represent maximum migrant excretion contributions, they characterize the relative importance of nutrient subsidies delivered by migratory fishes.

## CONCLUSION

Our work demonstrates an important functional role for potamodromous fishes as nutrient subsidies in recipient ecosystems. Additionally, we take important steps towards

resolving the context dependency of fish effects in streams by providing empirical support for predictions of when and where effects of fish-derived nutrients are strongest. Given the prevalence of migratory life histories among fishes, as well as the ubiquity of lakes and reservoirs that contain such taxa, it is likely that other systems receive the same types of nutrient subsidies that are delivered by migratory salmonids in our study streams. In such cases, managers should be aware of the potential for introduced fishes to have impacts extending beyond single systems. While the net outcomes of fish migrations can be more complex than nutrient addition alone (e.g., Holtgrieve & Schindler, 2011), the consequences of migrations for primary and secondary production within recipient systems should be considered. Finally, we note that the work reported here relates to only one mechanism (i.e., excretion) by which migratory fishes can deliver nutrients and other materials to recipient ecosystems. Other mechanisms like carcass decomposition can also be important and should be considered when evaluating ecosystem-level effects of migratory fishes. While considerable variation exists in the magnitude of migratory fish nutrient subsidies, it should be a focus of natural resource managers and researchers to understand the ecosystem function of these widespread organisms, especially in light of accelerating anthropogenic activities that directly reduce migrant abundance (Allan *et al.*, 2005) and restrict or sever migratory pathways (Freeman *et al.*, 2003).

#### LITERATURE CITED

- Allan J.D., Abell R., Hogan Z., Revenga C., Taylor B.W., Welcomme R.L. *et al.* (2005) Overfishing of inland waters. *BioScience*, **55**, 1041-1051.
- Atkinson C.L., Vaughn C.C., Forshay K.J. & Cooper J.T. (2013) Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. *Ecology*, **94**, 1359-1369.



- Benstead J.P., Cross W.F., March J.G., McDowell W.H., Ramirez A. & Covich A.P. (2010) Biotic and abiotic controls on the ecosystem significance of consumer excretion in two contrasting tropical streams. *Freshwater Biology*, **55**, 2047-2061.
- Bott T.L., Brock J.T., Baattruppedersen A., Chambers P.A., Dodds W.K., Himbeault K.T. *et al.* (1997) An evaluation of techniques for measuring periphyton metabolism in chambers. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 715-725.
- Bouletreau S., Cucherousset J., Villeger S., Masson R. & Santoul F. (2011) Colossal aggregations of giant alien freshwater fish as a potential biogeochemical hotspot. *PLoS One*, **6**, e25732.
- Capps K.A. & Flecker A.S. (2013a) Invasive fishes generate biogeochemical hotspots in a nutrient-limited system. *PLoS One*, **8**, e54093.
- Capps K.A. & Flecker A.S. (2013b) Invasive aquarium fish transform ecosystem nutrient dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20131520.
- Childress E.S., Allan J.D. & McIntyre P.B. (2014) Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems*, **17**, 522-534.
- Cross W.F., Benstead J.P., Frost P.C. & Thomas S.A. (2005) Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshwater Biology*, **50**, 1895-1912.
- Elser J.J., Elser M.M., MacKay N.A. & Carpenter S.R. (1988) Zooplankton-mediated transitions between N- and P-limited algal growth. *Limnology & Oceanography*, **33**, 1-14.
- Flecker A.S., McIntyre P.B., Moore J.W., Anderson J.T., Taylor B.W. & Hall R.O. (2010) Migratory fishes as material and process subsidies in riverine ecosystems. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 559-592.
- Freeman M.C., Pringle C.M., Greathouse E.A. & Freeman B.J. (2003) Ecosystem-level consequences of migratory faunal depletion caused by dams. In: *Biodiversity, Status, and Conservation of the World's Shads*. (Eds K.E. Limburg & J.R. Waldman). American Fisheries Society, Symposium 35, Bethesda, MD, 255-266.
- Gotelli N.J. & Ellison A.M. (2004) *A Primer of Ecological Statistics*. Sinauer Associates, Inc. Sunderland, MA.

- Grimm N.B. (1988a) Role of macroinvertebrates in nitrogen dynamics of a desert stream. *Ecology*, **69**, 1884-1893.
- Grimm N.B. (1988b) Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agosia chrysogaster* (Pisces: Cyprinidae). *Environmental Biology of Fishes*, **21**, 143-152.
- Haefner J.W. (2005) *Modeling Biological Systems*. Springer, New York, NY.
- Hall R.O., Tank J.L. & Dybdahl M.F. (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Frontiers in Ecology and Environment*, **1**, 407-411.
- Hall R.O., Koch B.J., Marshall M.C., Taylor B.W. & Tronstad L.M. (2007) How body size mediates the role of animals in nutrient cycling in aquatic ecosystems. In: *Body Size: The Structure and Function of Aquatic Ecosystems*. (Eds A.G. Hildrew, D. Raffaelli & R. Edmonds-Brown). Cambridge University Press, New York, NY, 286-305.
- Hoellein T.J., Tank J.L., Rosi-Marshall E.J. & Entekin S.A. (2009) Temporal variation in substratum-specific rates of N uptake and metabolism and their contribution at the stream-reach scale. *Journal of the North American Benthological Society*, **28**, 305-318.
- Holtgrieve G.W., Schindler D.E., Gowell C.P., Ruff C.P. & Lisi P.J. (2010) Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology*, **55**, 2598-2611.
- Holtgrieve G.W. & Schindler D.E. (2011) Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology*, **92**, 373-385.
- Janetski D.J., Chaloner D.T., Tiegs S.D. & Lamberti G.A. (2009) Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**, 583-595.
- Johnson C.R., Luecke C., Whalen S.C. & Evans M.A. (2010) Direct and indirect effects of fish on pelagic nitrogen and phosphorus availability in oligotrophic Arctic Alaskan lakes. *Canadian Journal of Fisheries & Aquatic Sciences*, **67**, 1635-1648.
- Keitzer S.C. & Goforth R.R. (2013) Spatial and seasonal variation in the ecological significance of nutrient recycling by larval salamanders in Appalachian headwater streams. *Freshwater Science*, **32**, 1136-1147.

- Knight C.A. (1997) *Spawning attributes and early life-history strategies of adfluvial cutthroat trout in the Strawberry Basin, Utah*. MS Thesis, Utah State University, Logan.
- McIntyre P.B., Jones L.E., Flecker A.S. & Vanni M.J. (2007) Fish extinctions alter nutrient recycling rates in tropical freshwaters. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 4461-4466.
- McIntyre P.B., Flecker A.S., Vanni M.J., Hood J.M., Taylor B.W. & Thomas S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? *Ecology*, **89**, 2335-2346.
- Moore J.W. (2006) Animal ecosystem engineers in streams. *BioScience*, **56**, 237-246.
- Moslemi J.M., Snider S.B., MacNeill K., Gilliam J.F. & Flecker A.S. (2012) Impacts of an invasive snail (*Tarebia granifera*) on nutrient cycling in tropical streams: the role of riparian deforestation in Trinidad, West Indies. *PLoS One*, **7**, e38806.
- Mulholland P.J., Tank J.L., Webster J.R., Bowden W.B., Dodds W.K., Gregory S.V. *et al.* (2002) Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. *Journal of the North American Benthological Society*, **21**, 544-560.
- Murphy J. & Riley J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, **27**, 31-36.
- Northcote T.G. (1997) Potamodromy in Salmonidae: living and moving in the fast lane. *North American Journal of Fisheries Management*, **17**, 1029-1045.
- Orme, R.W., Knight, C.A. & Beauchamp, D.A. (1995) *Spawning and Recruitment of Strawberry Reservoir Salmonids*. Annual Report for Fiscal Year 1995. Utah Cooperative Fisheries and Wildlife Unit, Department of Fisheries and Wildlife, Utah State University, Logan. 89 p.
- Polis G.A., Anderson W.B. & Holt R.D. (1997) Towards an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289-316.
- Post D.M. & Walters A.W. (2009) Nutrient excretion rates of anadromous alewives during their spawning migration. *Transactions of the American Fisheries Society*, **138**, 264-268.
- R Development Core Team. (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland.  
Available at: <http://imagej.nih.gov/ij/>, 1997-2012.
- Schade J.D., MacNeill K., Thomas S.A., McNeely F.C., Welter J.R., Hood J. *et al.* (2011) The stoichiometry of nitrogen and phosphorus spiraling in heterotrophic and autotrophic streams. *Freshwater Biology*, **56**, 424-436.
- Schaus M.H., Vanni M.J., Wissing T.E., Bremigan M.T., Garvey J.A. & Stein R.A. (1997) Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology & Oceanography*, **42**, 1386-1397.
- Schindler D.E. & Eby L.A. (1997) Stoichiometry of fishes and their prey: implications for nutrient recycling. *Ecology*, **78**, 1816-1831.
- Sereda J.M., Hudson J.J. & McLoughlin P.D. (2008) General empirical models for predicting the release of nutrients by fish, with a comparison between detritivores and non-detritivores. *Freshwater Biology*, **53**, 2133-2144.
- Small G.E., Pringle C.M., Pyron M. & Duff J.H. (2011) Role of the fish *Astyanax aeneus* (Characidae) as a keystone nutrient recycler in low-nutrient Neotropical streams. *Ecology*, **92**, 386-397.
- Solorzano L. (1969) Determination of ammonia in natural waters by the phenylhypochlorite method. *Limnology & Oceanography*, **14**, 799-801.
- Sterner R.W. & Elser J.J. (2002) *Ecological Stoichiometry: the Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Stream Solute Workshop. (1990) Concepts and methods for assessing solute dynamics in stream ecosystems. *Journal of the North American Benthological Society*, **9**, 95-119.
- Tronstad L.M. (2008). *Ecosystem consequences of declining Yellowstone cutthroat trout in Yellowstone Lake and spawning streams*. Ph.D. dissertation. University of Wyoming, Laramie.
- Utah Department of Environmental Quality, Division of Water Quality. (2007) *Strawberry Reservoir Water Quality Study and TMDL*. Salt Lake City. 97 p.
- Vanni M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341-370.
- Vanni M.J. (2010) Preface: when and where do fish have strong effects on stream ecosystem processes? In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 531-538.

- Vanni M.J., Flecker A.S., Hood J.M. & Headworth J.L. (2002) Stoichiometry of nutrient recycling by vertebrates in a tropical stream: linking species identity and ecosystem processes. *Ecology Letters*, **5**, 285-293.
- Ward A., Robinson J. & Wilson R. (2007) *Strawberry Reservoir Salmonid Diet Study 2005*. Federal Aid Project Number F-41-R, Publication Number 07-07. Utah Department of Wildlife Resources, Division of Wildlife Resources, Salt Lake City. 36 p.
- Webster J.R. & Valett H.M. (2006) Solute dynamics. In: *Methods in Stream Ecology* (Eds R.H. Hauer & G.A. Lamberti), pp. 169-185. Academic Press, Amsterdam, The Netherlands.
- Whiles M.R., Huryh A.D., Taylor B.W. & Reeve J.D. (2009) Influence of handling stress and fasting on estimates of ammonium excretion by tadpoles and fish: recommendations for designing excretion experiments. *Limnology & Oceanography: Methods*, **7**, 1-7.
- Wilson H.F. & Xenopoulos M.A. (2011) Nutrient recycling by fish in streams along a gradient of agricultural land use. *Global Change Biology*, **17**, 130-139.

**Table 2-1** Comparison of biological, physical, and chemical characteristics between Indian and Trout Creeks during migrant presence. Differences in accessible habitat length reflect temporal variation in upstream migration boundaries. All 2011 BCT data from Indian Creek were collected in Streeper Creek (see methods). Where applicable, values are means and ranges.

	Migration timing	Migrant biomass (g m <sup>-2</sup> )	Discharge (L s <sup>-1</sup> )	Ambient NH <sub>4</sub> -N (µg L <sup>-1</sup> )	Ambient SRP (µg L <sup>-1</sup> )	Maximum velocity (m s <sup>-1</sup> )	Average stream temperature (°C)	Accessible habitat length (m)
Indian Creek								
2011 BCT	05/26 - 08/31	6.0 (0.2-18.5)	364 (119-1123)	7.7 (2.5-31.7)	2.9 (1.0-7.4)	0.57 (0.41-0.96)	10	1883
2011 KOK	09/08 - 11/13	18.0 (0.1-55.7)	160 (112-202)	9.4 (2.5-20.7)	3.4 (1.6-6.5)	0.66 (0.59-0.73)	7	3315
2012 BCT	04/29 - 07/14	24.0 (0.1-57.1)	93 (55-235)	16.5 (15.1-18.1)	2.3 (1.8-2.8)	0.49 (0.20-0.83)	12	3315
2012 KOK	08/25 - 10/27	18.9 (0.0-75.6)	23 (11-40)	8.3 (4.3-11.9)	2.7 (2.5-3.1)	0.28 (0.26-0.30)	10	3615
Trout Creek								
2011 BCT	05/26 - 08/31	26.4 (0.5-84.6)	271 (169-371)	9.2 (2.5-28.2)	7.5 (3.7-15.0)	1.01 (0.63-1.21)	9	2446
2011 KOK	09/09 - 11/02	51.6 (0.2-120.1)	200 (184-215)	13.5 (2.5-23.0)	8.4 (4.0-13.8)	1.16 (1.10-1.22)	6	2446
2012 BCT	05/07 - 07/11	9.5 (0.2-33.6)	97 (86-103)	15.9 (13.8-17.7)	2.3 (1.8-2.6)	0.72 (0.58-0.90)	8	2446
2012 KOK	08/28 - 10/27	23.0 (0.1-54.0)	85 (72-97)	18.8 (10.0-25.8)	2.2 (1.4-3.8)	0.68 (0.59-0.74)	7	2298

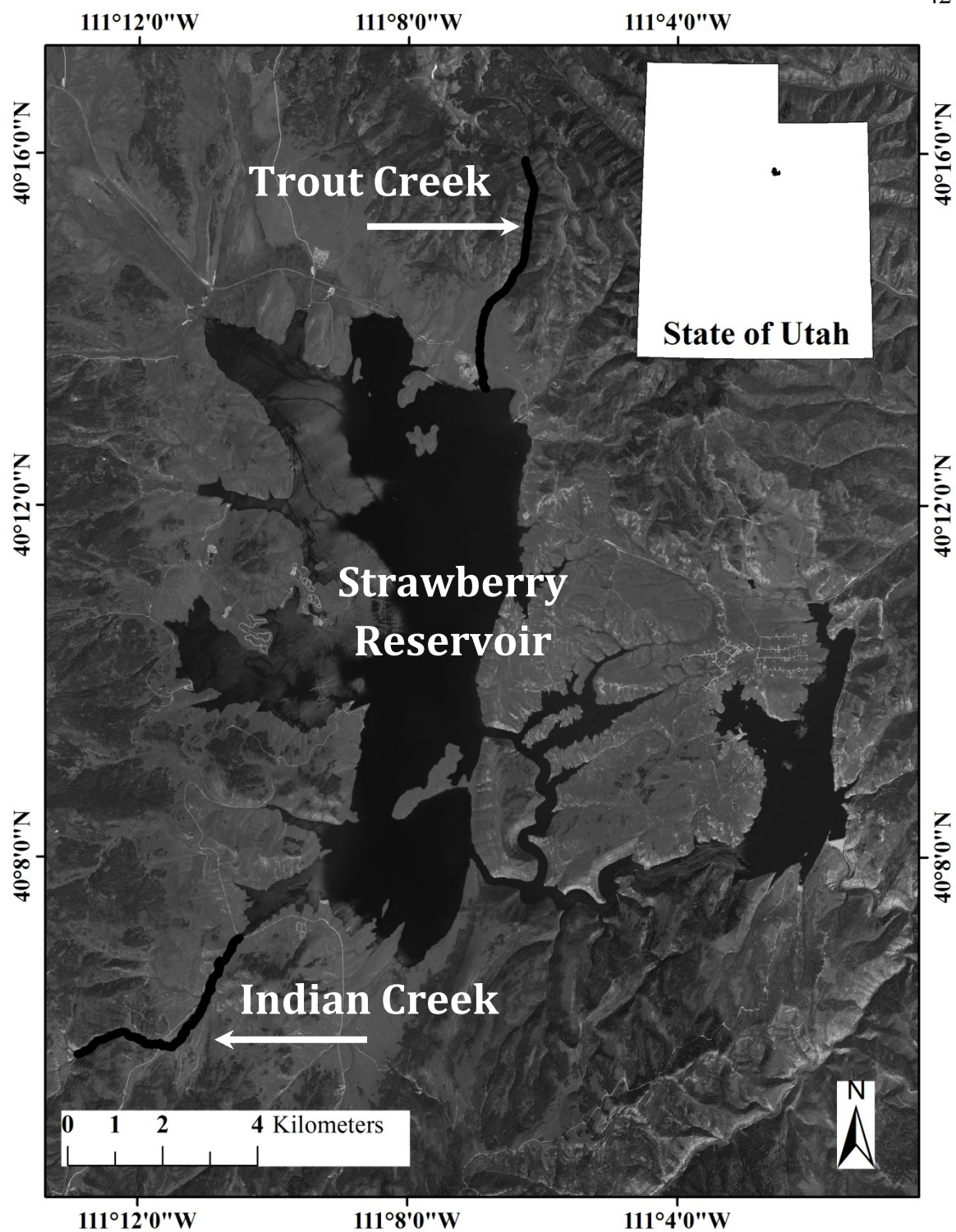
**Table 2-2** ANCOVA results for nutrient (NH<sub>4</sub>-N and SRP) excretion rates and ratios. Excretion rates, N:P ratios, and body size (i.e., wet mass) data were log<sub>10</sub>-transformed prior to analyses. To test for interspecific differences in nutrient excretion rates and ratio, we used temperature-standardized excretion rates and type III sum of squares as a result of unequal sample sizes. Due to interspecific body size differences, we centered body size (i.e.,  $x_i - \bar{x}$ ) prior to the analyses in order to ensure that data in the treatment groups (i.e., species) were being compared over the same covariate range.

factor	df	SS	<i>F</i>	<i>P</i>
NH <sub>4</sub> -N rate				
body size	1	0.72	49.73	< 0.001
species	1	1.66	115.47	< 0.001
body size × species	1	0.03	2.07	0.155
Residuals	67	0.97		
SRP rate				
body size	1	0.22	12.32	< 0.001
species	1	0.27	15.49	< 0.001
body size × species	1	0.04	2.43	0.124
Residuals	68	1.20		
NP ratio				
body size	1	0.20	6.63	0.012
species	1	0.92	30.19	< 0.001
body size × species	1	0.01	0.24	0.627
Residuals	68	2.07		

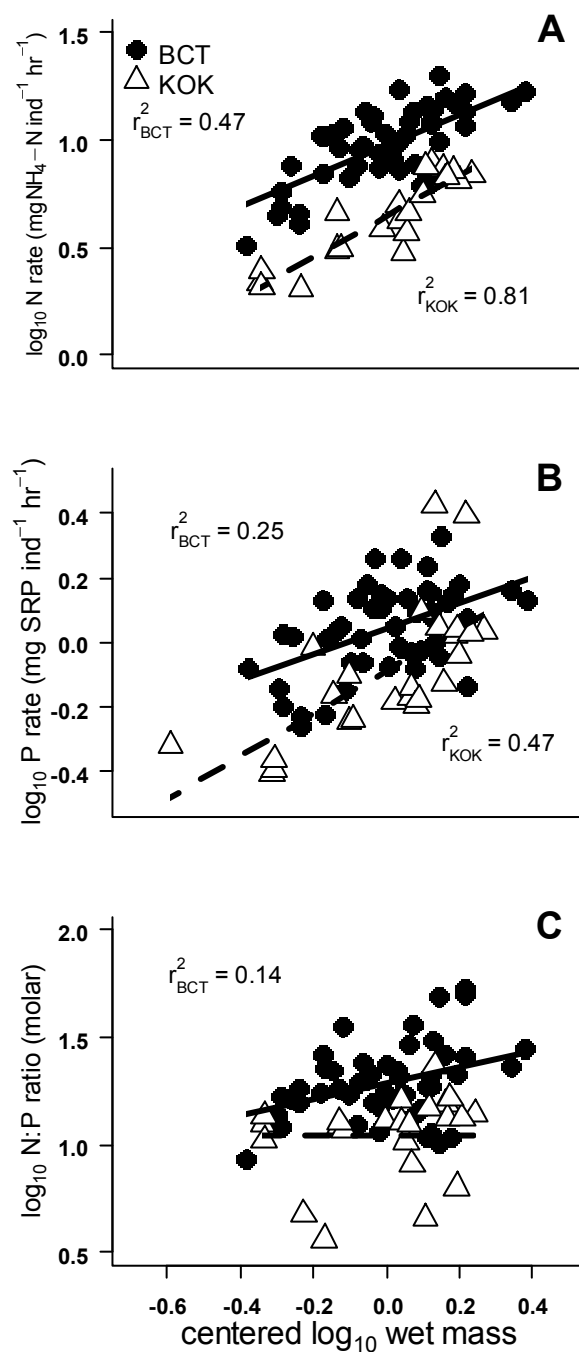
**Table 2-3** Pearson's correlation coefficients between average  $E_d/T_d$  values (i.e., spawning means) and different independent variables capable of influencing the contribution of migrant excretion subsidies to nutrient cycling. Statistically significant correlations are denoted by \* ( $P < 0.05$ ) and \*\* ( $P < 0.005$ ). BM, biomass; Q, discharge.

Response	Peak BM (g m <sup>-2</sup> )	Average BM (g m <sup>-2</sup> )	Peak Q (L s <sup>-1</sup> )	Average Q (L s <sup>-1</sup> )	Peak BM per Q (g m <sup>-2</sup> per L s <sup>-1</sup> )	Average BM per Q (g m <sup>-2</sup> per L s <sup>-1</sup> )
Average $E_d/T_d - N$	0.20	-0.06	-0.36	-0.57	0.93**	0.95**
Average $E_d/T_d - P$	0.14	-0.08	-0.37	-0.62	0.87*	0.92*

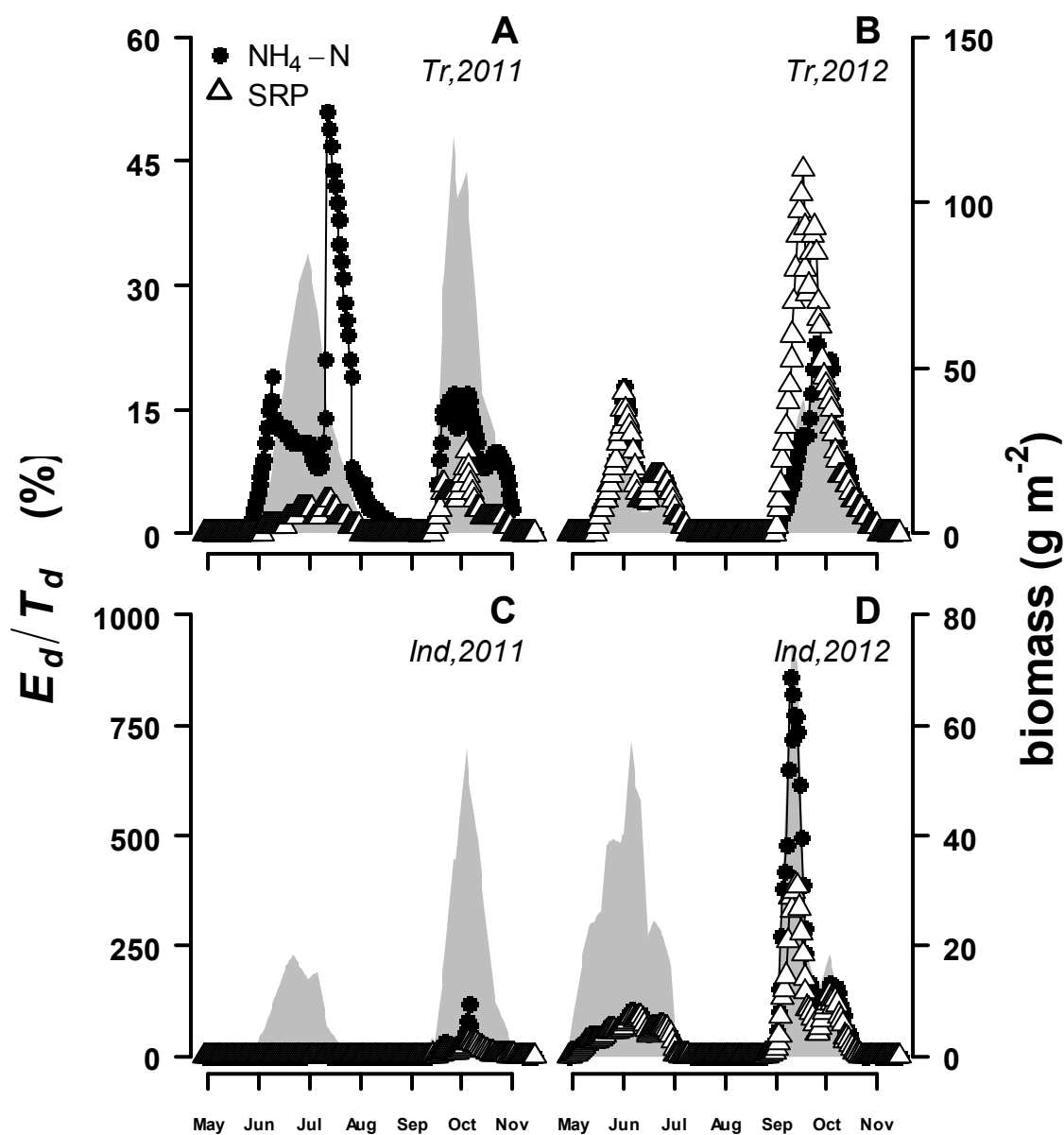




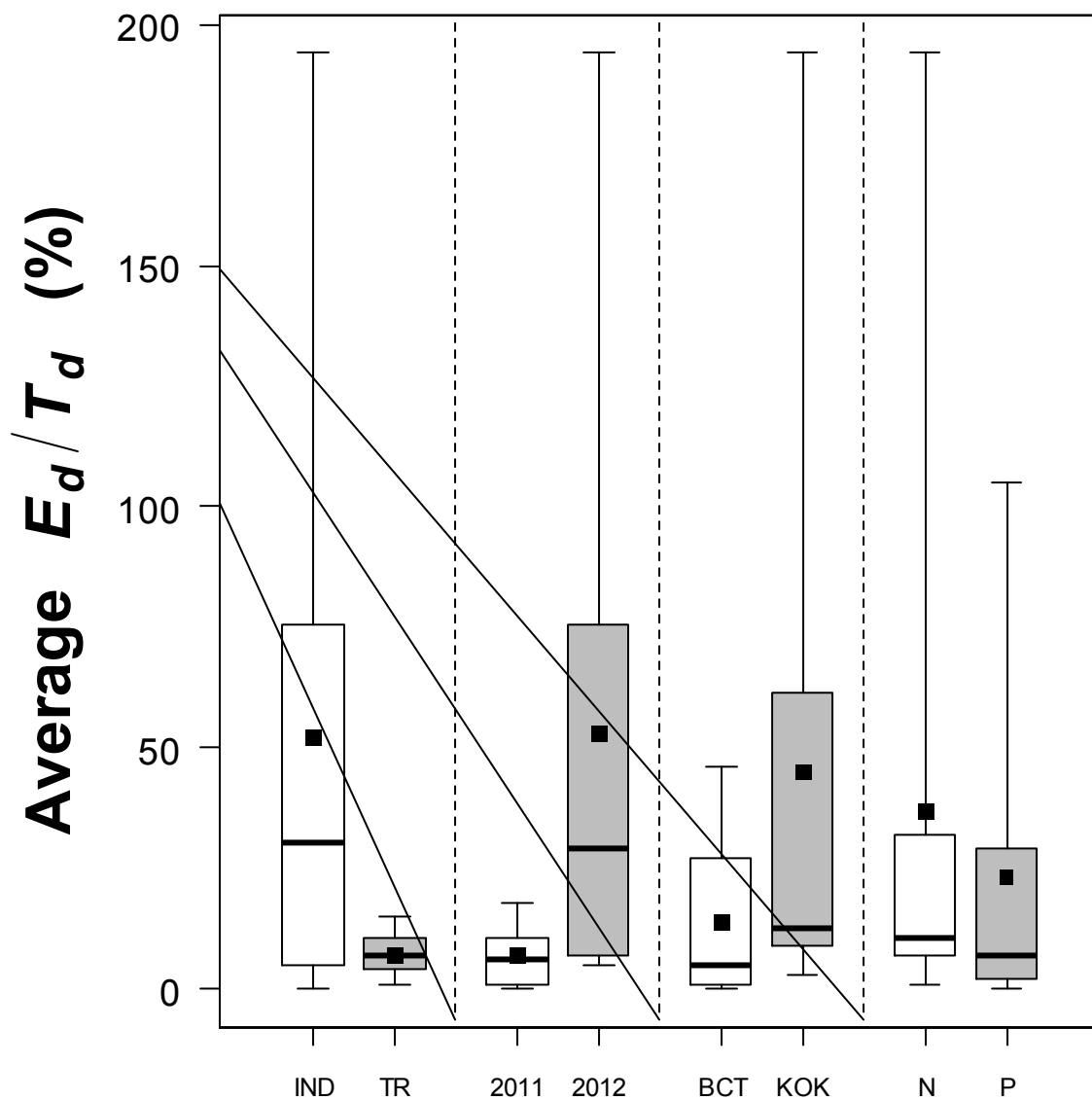
**Fig. 2-1** Location of Strawberry Reservoir in Utah and specific study streams. Tributary streams are thickened and darkened for emphasis.



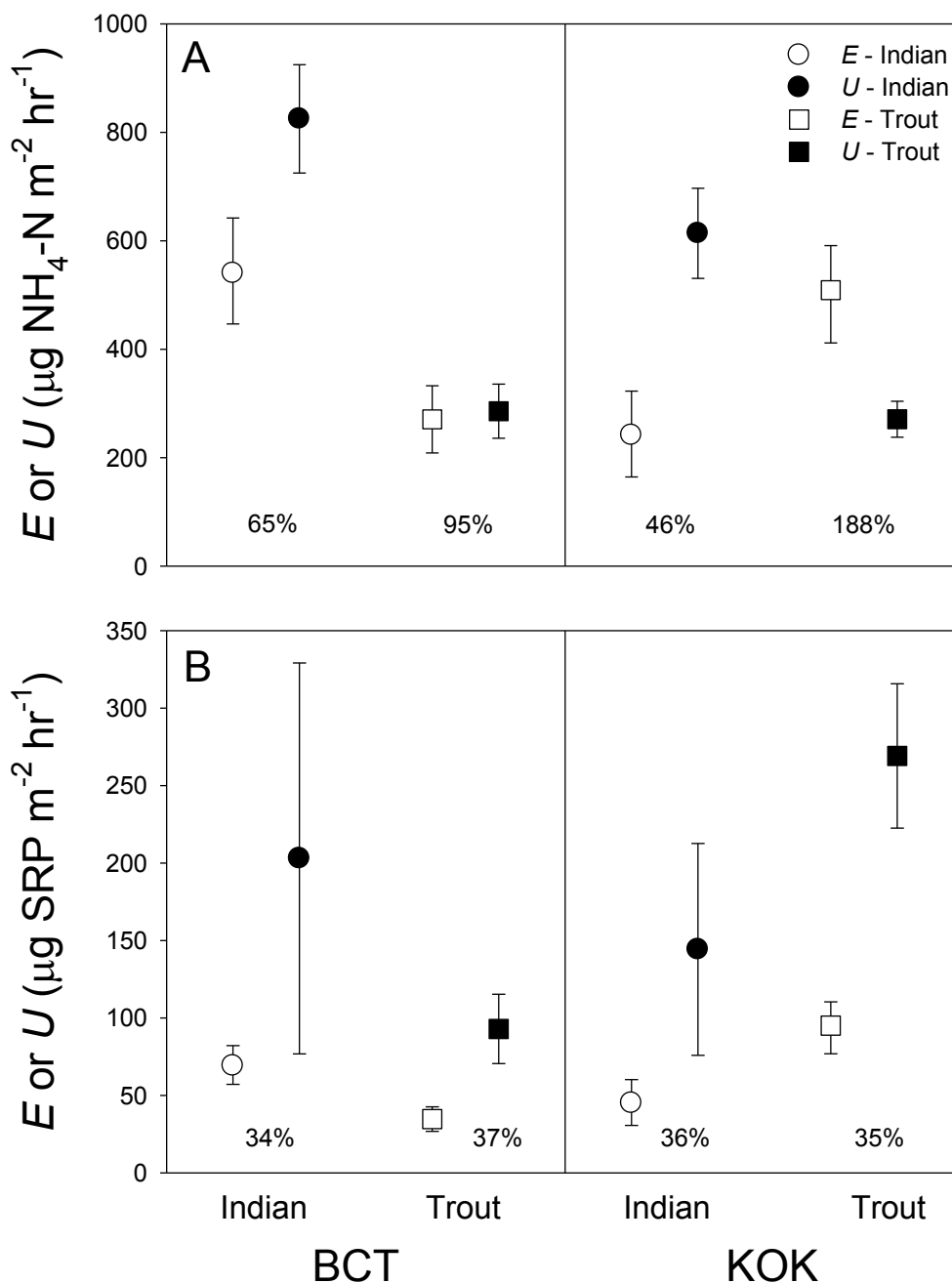
**Fig. 2-2** Size scaling of  $\text{NH}_4\text{-N}$  (A) and SRP excretion rates (B), and excreted molar N:P ratios (C) for Bonneville cutthroat trout (BCT) and kokanee (KOK) in Strawberry Reservoir tributaries. Note differences among y-axis scales. Solid (BCT) and dashed (KOK) lines reflect ordinary least squares regression for each species. Horizontal line for KOK N:P excretion ratios reflects non-significant effect ( $P = 0.27$ ) of body size and represents average value. Excretion rates were standardized to average temperatures across stream and year combinations ( $10^\circ\text{C}$  for BCT,  $8^\circ\text{C}$  for KOK).



**Fig. 2-3** Comparison of daily estimates of migrant excretion load with tributary nutrient export (i.e.,  $E_d/T_d$ ) for 2011 migrations in Trout Creek (A), 2012 migrations in Trout Creek (B), 2011 migrations in Indian Creek (C), and 2012 migrations in Indian Creek (D). The grey polygons in each graph depict temporal patterns in migrant biomass: BCT migrate during the spring, and KOK migrate during the fall. In each graph,  $E_d/T_d$  is plotted on the left vertical axis and migrant biomass is plotted on the right vertical axis. Note the differences in both y-axis scales between upper (Trout Creek) and lower (Indian Creek) panels. Elevated and extended runoff prevented assessment of the 2011 BCT migration in the Indian Creek main channel, so data were instead collected from a primary tributary (Streeper Creek; see methods).



**Fig. 2-4** Box plots of average  $E_d/T_d$  values in Strawberry Reservoir tributaries. Each set of two boxes, separated by vertical dashed lines, accounts only for the distinction represented on the x-axis immediately below the boxes (i.e., the data is grouped across all other potential sources of variation). For each box,  $n = 8$ . The top, bottom, and line through the middle of the box correspond to the 75<sup>th</sup>, 25<sup>th</sup>, and 50<sup>th</sup> percentile (median), respectively. The whiskers extend from minimum to maximum values. Solid squares represent arithmetic means.



**Fig. 2-5** Comparison of migrant excretion flux ( $E$ , open symbols) with areal uptake ( $U$ , closed symbols) of  $\text{NH}_4\text{-N}$  (A) and SRP (B) in Indian and Trout Creeks. Note differences in y-axis scales between graphs. All  $U$  measurements were made during 2012 spawning migrations of BCT and KOK. Percentages indicate values of  $E/U$  for specific combinations of stream, nutrient, and species. Variation around  $E$  is associated with migrant densities, while variation around  $U$  is associated with individual replicates. Values presented as mean  $\pm$  SE.

## CHAPTER 3

ECOSYSTEM RESPONSES TO ADFLUVIAL SALMONID MIGRATIONS IN  
TRIBUTARIES OF A CENTRAL UTAH RESERVOIR

## SUMMARY

1. Migratory freshwater fishes are capable of affecting the structure and function of riverine ecosystems, yet many of these taxa remain understudied. Globally, Pacific salmonids (*Oncorhynchus* spp.) are one of the most widely introduced migratory fishes, but studies of their ecological effects on lotic ecosystems are geographically limited. Consequently, abilities to generalize ecosystem-level effects related to non-native salmonids and identify factors that mediate such effects are limited.
2. In this study, I examined how two species of introduced migratory salmonids affected a suite of ecosystem properties (benthic chlorophyll-*a*, dissolved nutrient concentrations, autotrophic nutrient limitation, food web responses) in two tributaries of a central Utah reservoir. To do this, I used existing migration barriers and compared responses between stream reaches with (i.e., treatment) and without (i.e., control) migrants.
3. Despite relatively low densities, adfluvial migrants reduced benthic chlorophyll-*a* in treatment reaches, where concentrations were, on average, 25% lower (range = 97% decrease – 133% increase) than in control reaches. There were also isolated occurrences of elevated dissolved inorganic nitrogen concentrations, incorporation of migrant-derived nutrients into stream food webs, and alleviation

of nitrogen limitation in treatment reaches during periods of migration. However, these types of fertilization effects were generally weak, a result that reflects the importance of migrant densities and ambient nutrient dynamics.

4. My results were consistent with other studies of introduced salmon, illustrating the capacity of these fishes to influence stream ecosystem properties.

Additionally, the results highlight the influence of local biotic and abiotic conditions on the ecosystem effects of migratory freshwater fishes.

## INTRODUCTION

For some time, ecological researchers have recognized that relatively sedentary, resident organisms can influence community structure and ecosystem function (e.g., Paine, 1966; Brown & Heske, 1990; Bohlen *et al.*, 2004). More recently, these concepts have been expanded to include mobile ecosystem residents and how they may similarly affect ecosystem properties (e.g., McNaughton, 1985; Yang, 2004). The latter scenario applies to many freshwater fishes that use multiple habitats (e.g., lakes and streams) during their life cycles (Flecker *et al.*, 2010). Migratory freshwater fishes can alter ecosystem dynamics in both tropical (e.g., Winemiller & Jepsen, 1998; Taylor, Flecker & Hall, 2006) and temperate (e.g., Childress, Allan & McIntyre, 2014) riverine systems. Much uncertainty remains, however, about the functional role of many freshwater fishes, as well as the different factors that influence fish effects.

Although many freshwater fish species remain understudied, studies of anadromous Pacific salmon (*Oncorhynchus* spp.) illustrate many of the potential ecosystem effects of fishes. Principal among these effects is the fertilization of freshwater streams during

spawning (e.g., Gende *et al.*, 2002). Salmon-derived nutrients can increase water column dissolved nutrient concentrations (e.g., Johnston *et al.*, 2004; Levi *et al.*, 2011) and enhance abundance, biomass, production and growth of periphyton (e.g., Mitchell & Lamberti, 2005), invertebrates (e.g., Wipfli, Hudson & Caouette, 1998; Wipfli *et al.*, 1999), and resident fishes (e.g., Denton, Rich & Quinn, 2009; Rinella *et al.*, 2012). Additionally, nutrients provided by salmon spawning runs can alleviate autotrophic nutrient limitation (e.g., Ruegg *et al.*, 2011) and increase rates of ecosystem processes like nitrification (e.g., Levi *et al.*, 2013). More recent work has documented the substantial benthic disturbance that is also frequently associated with the spawning activity of these fishes. In the process of excavating large (1-17 m<sup>2</sup>; Groot & Margolis, 1991) spawning redds, anadromous salmon can decrease standing stocks of periphyton (e.g., Moore & Schindler, 2008; Tiegs *et al.*, 2009) and invertebrates (e.g., Minakawa & Gara, 1999; Peterson & Foote, 2000; Moore, Schindler & Scheuerell, 2004), increase particulate matter export (e.g., Moore *et al.*, 2007; Hassan *et al.*, 2008), and shift stream metabolism from net autotrophic to net heterotrophic states (e.g., Holtgrieve & Schindler, 2011).

An emerging objective of salmon researchers is to identify the biotic and abiotic conditions that ultimately determine the net ecosystem effects associated with these fishes. For example, the size of benthic substrates can mediate salmon effects; smaller particles are more easily disturbed by salmon and thus more likely associated with periphyton or invertebrate reductions, whereas larger particles less susceptible to disturbance are more likely associated with fertilization from salmon-derived nutrients (Janetski *et al.*, 2009; Holtgrieve *et al.*, 2010). Furthermore, it can be informative to



consider how other factors like land use patterns influence benthic substrates and thus indirectly mediate salmon effects in streams (e.g., Tiegs *et al.*, 2008). Changes in biotic conditions can also influence the direction or magnitude of the net ecosystem effects associated with anadromous salmon. Salmon runs vary over space and time (e.g., Ruegg *et al.*, 2012) and some recent studies concluded that spawner biomass (i.e., mass area<sup>-1</sup>) and species identity can both influence ecosystem responses to spawning migrations in aquatic (e.g., Janetski *et al.*, 2009) as well as terrestrial (e.g., Hocking & Reimchen, 2010) habitats. Regardless of whether net ecosystem effects of salmon migrations are controlled by biotic characteristics of the spawning run, abiotic conditions within streams or the surrounding watershed, or some combination of these factors, attempts to identify the most important regulating factors may well enhance predictive capabilities regarding salmonid ecosystem effects.

Given the extensive stocking of salmonids around the world (Crawford & Muir, 2008), the spatial extent over which their ecosystem effects are realized likely extends far beyond their native range. Despite such widespread introductions, studies examining effects of introduced salmonids have largely been limited to the Great Lakes region, where millions of Chinook (*O. tshawytscha*) and coho (*O. kisutch*) salmon have been stocked annually since the 1960s (Crawford, 2001). Results from these studies indicate non-native salmonids may have a range of effects (i.e., positive, negative, or neutral) on periphyton biomass (Rand *et al.*, 1992; Schuldt & Hershey, 1995; Ivan, 2009; Collins *et al.*, 2011; Janetski *et al.*, 2014), invertebrate densities (Denison & Meier, 1979; Ivan, Rutherford & Johengen, 2011; Janetski *et al.*, 2014), and dissolved nutrient concentrations (Rand *et al.*, 1992; Schuldt & Hershey, 1995; Sarica *et al.*, 2004; Collins

*et al.*, 2011; Ivan *et al.*, 2011; Janetski *et al.*, 2014). Studies of salmonids introduced to areas other than the Great Lakes region are rare and report contradictory ecosystem effects of carcass decomposition on periphyton biomass (Richey, Perkins & Goldman, 1975; Minshall, Hitchcock & Barnes, 1991). Likewise, studies of ecosystem responses other than dissolved nutrients and standing stocks of periphyton or invertebrates to introduced salmonids are very limited. Consequently, our ability to generalize ecosystem-level effects related to introduced salmonids and to identify factors mediating such effects would be enhanced by expanding both the geographic scope of similar studies and the suite of measured ecosystem responses.

In this study, I examined how two species of introduced migratory salmonids affected a suite of ecosystem properties (benthic chlorophyll-*a*, dissolved nutrient concentrations, autotrophic nutrient limitation, food web responses) in two tributaries of a central Utah reservoir. This approach allowed me to assess migrant ecosystem effects, and it also permitted an evaluation of the influence of different biotic (species) and abiotic (hydrogeomorphic) conditions on the effects. I predicted benthic algal responses to migrants would be mediated by particle size, with increased biomass more likely on larger particles and decreased biomass more likely on smaller particles. Given the potential for migratory salmonids to introduce nutrients to tributary ecosystems via excretion (Chapter 2) and carcass decomposition, I also predicted water column dissolved nutrient concentrations would increase in response to migrant presence. Furthermore, I expected migrant-derived nutrients would be assimilated by stream biota, with ensuing changes to the nutrient limiting primary production and energy flow within stream food webs. Finally, I predicted that evidence of the incorporation of migrant-derived nutrients

would be stronger (1) in the tributary with greater hydrogeomorphic retention and thus longer solute residence time and (2) with a semelparous species that migrates during reduced flow periods and exhibits population-wide post-spawning mortality.

## METHODS

### *Study area*

To address the ecosystem effects of introduced migratory salmonids, I collected data in 2012 from two different tributaries (Indian Creek and Trout Creek) of Strawberry Reservoir (40°8' N, 111°2' W), which is the most popular cold-water fishery in Utah. Two non-native salmonids use the tributaries for spawning and have temporally separated migrations. Bonneville cutthroat trout (BCT; *Oncorhynchus clarkii utah*) migrate during the spring following snowmelt peaks, whereas kokanee salmon (KOK; *Oncorhynchus nerka*) migrate during fall baseflow conditions (Sigler & Sigler, 1996; Chapter 2). The life histories of these fishes may result in counteracting influences on ecosystem properties. For example, both species excavate large (~ 1 m<sup>2</sup>; K.Wheeler, personal observation) redds relative to stream size (average wetted channel width: Indian = 3 m, Trout = 2 m), which may represent a significant benthic disturbance. These fishes may also introduce nutrients to the streams via excretion during migration (Chapter 2) and carcass decomposition, the latter of which is especially likely for semelparous KOK that die after spawning.

### *Study design*

To evaluate ecosystem responses to migrants, I established study reaches within each stream that differed only with respect to the presence of adfluvial migrants. Large beaver

dams in both streams served as the upstream extent of migrations for both species (K. Wheeler, unpubl. data), although the linear distance available to or used by migrants was not necessarily the same for both species. I took advantage of these naturally existing migration barriers to establish treatment (i.e., accessible to migrants) and control (i.e., inaccessible to migrants) reaches in each stream, and counted migrants in these designated reaches 1-2 times weekly during migrations. To minimize potential confounding effects of the beaver dams on measured ecosystem responses, study reaches in both streams were > 490 m from the barrier dam. Neither stream received appreciable tributary input between treatment and control reaches.

*Field methods: hydrogeomorphic differences between systems*

To characterize hydrogeomorphic differences between streams, I collected a suite of abiotic variables. I manually measured discharge just upstream from tributary mouths at irregular intervals depending on the hydrologic stage between April and November (interval range = 4-29 days; Indian Creek:  $n = 20$ ; Trout Creek:  $n = 21$ ). I measured wetted channel widths (Indian Creek:  $n = 89$ ; Trout Creek:  $n = 75$ ) in both channels during July, reasoning this time period represented average conditions between spring and fall flow extremes. To enable a more complete comparison of hydrogeomorphic conditions, estimates of depth, velocity, channel units (i.e., riffle, run, pool), and particulate retention were generated by sampling three representative 100-m reaches in each stream during baseflow. At each reach, depth and velocity were measured longitudinally along the thalweg at 5-meter intervals and the proportional length of different channel units was estimated visually. I followed procedures outlined by

Lamberti & Gregory (2006) to determine particulate retention rates. Abscised and air-dried *Ginkgo biloba* leaves ( $n = 500$ ; soaked overnight prior to release to ensure neutral buoyancy) were released at the upstream end of each reach, and the number of leaves collected at the downstream end was monitored for a specified period of time (30 and 60 minutes in Trout and Indian Creeks, respectively). At the conclusion of the collection period, an inventory of retained leaves was performed by counting the number of leaves within each five-meter interval of the reach. When  $\geq 25\%$  of the total number of located leaves was collected at the downstream end of reaches, I fit leaf retention data to a negative exponential decay model  $P_d = P_0 e^{-kd}$  where  $P_0$  is the number of particles released into the reach,  $P_d$  is the number of particles still in transport at some downstream distance  $d$  from the release point, and  $k$  is the particulate retention rate. In all other cases, I used the retention inventory (73-94% of released leaves were detected) to calculate a weighted average distance traveled by an individual leaf, and assumed  $k$  was the reciprocal of that distance.

*Field methods: ecosystem responses*

To determine the effects of BCT and KOK on periphyton, I measured benthic algal biomass (as chlorophyll-*a*) on substrates collected from two areas – one that was used by spawning migrants, and one that was not. Particles were collected at or near peak spawning activity for both species. During the BCT migration, I collected all particles from the treatment reach. I used particles from obvious spawning redds to serve as “treatment” samples and particles from undisturbed areas as “control” samples. In both cases, I selected particles haphazardly. To eliminate the possibility of misidentifying

spawning locations, I collected particles from random locations in treatment and control reaches during KOK sampling. I was interested in the effect of particle size on the periphyton response to migrants (Holtgrieve *et al.*, 2010), so I used pebble counts (Wolman, 1954) of 100-200 particles in each reach to identify four size quartiles based on the length of the *B*-axis (2<sup>nd</sup> longest side; see Table A-3 in Appendix). I collected three to eight particle “samples” from each of the four size classes during periphyton sampling, grouping multiple particles from the same size class to form composite samples in some cases. I categorized all particles < 9 mm as fines, and collected samples from this size class by sliding a plastic spatula under an inverted specimen cup inserted into benthic substrates (Hoellein *et al.*, 2009). I scrubbed the exposed surface area of collected particles, rinsed them with water, and recorded the total volume of the generated periphyton slurry. I then filtered a known slurry volume onto pre-ashed Whatman GF/F filters, wrapped filters in aluminum foil, and froze them. For fine particles, which could not be scrubbed individually, I added a known volume of water to sample containers, shook them vigorously for one minute, allowed settling for 90 seconds, and used a syringe to remove supernatant for filtration. In the lab, I extracted chlorophyll-*a* from samples for 24 h at 4°C in 95% ethanol following a 5-minute hot (78°C) water bath (Biggs & Kilroy, 2000), and analyzed samples fluorometrically (Aquafluor fluorometer, Turner Designs, Sunnyvale, CA). To express chlorophyll-*a* on an areal basis, I digitally photographed the exposed area of each particle and determined surface area using Image J software (Rasband, ImageJ), summing multiple particle surface areas when necessary.

I collected duplicate water samples from the downstream end of treatment and control reaches every 1-3 weeks between April and November (Indian Creek:  $n = 14$ ; Trout Creek:  $n = 15$ ) to evaluate temporal changes in dissolved nutrient concentrations. I filtered samples in the field through pre-ashed Whatman GF/F filters into acid-washed Nalgene bottles, stored them on ice in the dark, and froze them (within four hours) until analysis. Samples were analyzed spectrophotometrically for  $\text{NH}_4\text{-N}$ ,  $\text{NO}_3\text{-N}$ , and SRP (3020 Autoanalyzer, Astoria-Pacific Inc., Clackamas, OR) at the Utah State University Aquatic Biogeochemistry Lab (Logan, UT).

To determine if BCT or KOK altered autotrophic nutrient limitation, I used nutrient-diffusing substrates (NDS) following the protocols of Tank *et al.* (2006). NDS consisted of plastic cups filled with approximately 30 mL of agar amended with one of three treatments:  $\text{NH}_4\text{-N}$  (0.5 M  $\text{NH}_4\text{Cl}$ ),  $\text{PO}_4\text{-P}$  (0.5 M  $\text{KH}_2\text{PO}_4$ ), or  $\text{NH}_4 + \text{PO}_4$ , and a control with no nutrients added. I used  $\text{NH}_4$  and  $\text{PO}_4$  because they are the primary inorganic forms of nitrogen (N) and phosphorus (P) excreted by freshwater fishes (Wood, 1995; Vanni, 2002). For deployment, I attached NDS to plastic bars in random order, nailed bars into benthic substrates in a riffle area, and placed bars perpendicular to flow. To evaluate temporal changes in limitation, I deployed replicates ( $n = 5\text{-}7$ ) of each NDS treatment in treatment and control reaches of each stream at three different times: during BCT spawning, between BCT and KOK spawning, and during KOK spawning. Additional sampling events were not possible given the incubation time (18-22 days) for NDS, the temporal length of adfluvial migrations, and weather constraints that limited site access prior to BCT migrations. At the end of each incubation period, I placed discs in individual containers, put them on ice and froze them (within two hours) until analysis.

I measured chlorophyll-*a* on each disc following a 20-hour extraction in 95% ethanol at room temperature, and used a non-acidification method (Welschmeyer, 1994) for fluorometric analysis (10-AU fluorometer, Turner Designs, Sunnyvale, CA).

I used stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) to determine whether migrant-derived nutrients were incorporated into stream food webs. I focused my stable isotope analyses on periphyton and scraper invertebrates, reasoning that any fertilization effects associated with migrant presence would appear first in basal resources (i.e., periphyton) prior to consumption by herbivores (i.e., scrapers). I collected stable isotope samples of periphyton and scrapers from control and treatment reaches in both streams. To collect periphyton samples, I scraped substrates following established procedures (Steinman, Lamberti & Leavitt, 2006), and I collected invertebrates from nine randomly selected riffle habitats with a Surber sampler (mesh = 500  $\mu\text{m}$ ). Invertebrates were preserved in 70% ethanol in the field. I generated three replicate periphyton and scraper samples at each one of five different time points (before BCT spawning, during BCT spawning, between BCT and KOK migrations, during KOK spawning, after KOK spawning) to evaluate temporal variation in stream food webs. Individual periphyton replicates were generated by haphazardly collecting six substrate particles from each third of every sampling (treatment or control) reach. I scrubbed particles in the field, and pooled each slurry from six particles as a composite sample. Slurries were placed on ice and frozen within four hours until analysis. To prepare periphyton samples, I thawed slurries and homogenized them before withdrawing a subsample that was dried to constant mass at 60°C in a glass petri dish. I generated invertebrate replicates by identifying scrapers common to treatment and control reaches in each stream (Indian Creek: *Optioservus* spp.



[Elmidae] larvae; Trout Creek: Heptageniidae larvae), and drying three groups of multiple individuals to constant mass at 60°C. Dried periphyton and scraper samples were homogenized and weighed in tin capsules (Costech Analytical Technologies Inc., Valencia, CA), and shipped for natural abundance  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis at the University of California at Davis Stable Isotope Facility (PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer, Sercon Ltd., Cheshire, UK). Values are reported as the difference between stable isotope ratios of samples and international lab standards (Vienna Peedee Belemnite for  $\delta^{13}\text{C}$  and atmosphere  $\text{N}_2$  for  $\delta^{15}\text{N}$ ), and are referred to as delta ( $\delta$ ) values in units of per mil (‰).

### *Statistical analyses*

When possible, I used *t*-tests to examine hydrogeomorphic differences between streams. To evaluate the effects of migrants and particle size on periphyton biomass, I used two-way ANOVA with migrants (present or absent) and particle size as factors for each stream-species combination ( $n = 4$ ). When there was a significant interaction, I used *t*-tests to examine the effect of migrants on each one of the particle size quartiles, using a Bonferroni-adjusted  $\alpha$  value of 0.0125 (0.05/4). To evaluate temporal patterns in dissolved nutrients and stable isotope values, I used repeated measures ANOVA (rmANOVA) with time and migrants (i.e., treatment vs. control reaches) as factors. Separate analyses were performed for each stream-nutrient combination ( $n = 6$ ; e.g., Collins *et al.*, 2011) and each stream-biota-isotope combination ( $n = 8$ ). Significant migrant  $\times$  time interactions indicated divergent conditions between treatment and control reaches. I used two-way ANOVA to with the presence and absence of each nutrient (N

and P) as factors to determine which nutrient was limiting autotrophic growth (Tank *et al.*, 2006). Additionally, I calculated nutrient response ratios (NRR; Tank & Dodds, 2003) to compare the relative magnitude of the response of algal biomass to nutrient addition between locations (treatment vs. control) and among time periods. I used bootstrapping (1000 iterations) to generate mean NRR values and 95% confidence intervals for each NDS treatment-time-location combination ( $n = 18$ ) in each stream. I used  $\alpha = 0.10$  for all tests of statistical significance with dissolved nutrient concentrations due to low sample sizes and high expected variability. For all other response, I used  $\alpha = 0.05$ . R 3.0.1 (R Development Core Team, 2013) was used for all analyses.

## RESULTS

### *Hydrogeomorphic differences between streams*

The hydrogeomorphic environment differed significantly between Indian and Trout Creeks (Table 3-1). Mean discharge, velocity (maximum and average), % riffle habitat, and channel slope were all lower in Indian Creek than in Trout Creek (all  $P < 0.015$ ; Table 3-1). Conversely, average depth, wetted channel width, % pool and run habitat, sinuosity, and particulate retention were all higher in Indian Creek (all  $P < 0.045$ ; Table 3-1).

### *Migrant density patterns between streams*

While less pronounced than the hydrogeomorphic distinctions, migrant densities also differed between streams. Average live BCT ( $0.058 \pm 0.011$  ind  $m^{-2}$ ; mean  $\pm$  SE) and carcass ( $0.010 \pm 0.003$  ind  $m^{-2}$ ) densities were 1.5 and 14 times higher in Indian Creek, respectively, but mean densities of live KOK ( $0.111 \pm 0.020$  ind  $m^{-2}$ ) were 2.5 times

higher in Trout Creek (Fig. 3-1). Average KOK carcass densities ( $0.017 \text{ ind m}^{-2}$ ) were similar between streams.

#### *Ecosystem responses to adfluvial migrants*

Spawning activity of BCT and KOK tended to be associated with benthic disturbance, as mean periphyton chlorophyll-*a* values were lower ( $25 \pm 16\%$  decrease) on treatment substrates than on control substrates in 12 of 16 possible combinations. However, the magnitude of the response differed between systems and as a function of particle size (Fig. 3-2). While these data imply disturbance from spawning affects periphyton, the statistical results were not corroborative in all cases. Migrants did have significant (both  $P < 0.035$ ; Table 3-2) effects on chlorophyll-*a* biomass in Indian Creek, regardless of species. Additionally, there was a significant fish  $\times$  size interaction during BCT spawning in Trout Creek, with chlorophyll-*a* lower on treatment substrates than on control substrates for size C particles only ( $t = -4.20$ ,  $df = 4.8$ ,  $P = 0.009$ ; Fig. 3-2 B). However, neither fish nor particle size had significant effects on chlorophyll-*a* biomass in Trout Creek during the KOK migration (Fig. 3-2 D). Average periphyton responses during BCT migration were not significantly different from those during KOK migration ( $t = -1.70$ ,  $df = 14$ ,  $P = 0.110$ ).

BCT and KOK migrations had relatively moderate impacts on dissolved inorganic nitrogen (DIN) concentrations in only Trout Creek.  $\text{NH}_4$  and  $\text{NO}_3$  concentrations were both influenced by the interaction between migrants (i.e., treatment vs. control reaches) and time (Table 3-3), and these differences appeared closely related to changes in treatment reach concentrations. In particular, there was divergence in concentrations

between the treatment reach and the control reach at the onset of the KOK migration for  $\text{NH}_4$  (Fig. 3-3 A), as well as during the middle of the KOK migration for  $\text{NO}_3$  (Fig. 3-3 B). The only other significant migrant  $\times$  time interaction was for  $\text{NO}_3$  in Indian Creek (Table 3-3). However, this result was driven largely by temporal patterns of  $\text{NO}_3$  concentrations in the control reach, which exhibited substantially more temporal variation than those in the treatment reach (Fig. 3-4 B).

Neither BCT nor KOK consistently altered patterns of autotrophic nutrient limitation between creeks. Adfluvial migrants were only associated with alleviating nutrient limitation in Trout Creek, where the control reach was N-limited during the BCT migration in Trout Creek, but the treatment reach displayed no form of nutrient limitation (Table 3-4). During other time periods in Trout Creek, autotrophic responses were similar between treatment and control reaches (Table 3-4). NDS deployment in Indian Creek revealed consistent N limitation over time in the treatment reach, suggesting migrants did not alleviate autotrophic nutrient limitation (Table 3-4). In contrast, nutrient limitation in the Indian Creek control reach varied among time periods, with no single incident of strict N limitation.

Calculated NRR results were similar to the NDS results and indicated relatively little impact of adfluvial migrants on patterns of nutrient limitation or inhibition (Fig. 3-5). The one exception was associated with the Trout Creek BCT migration, where mean NRR values for the N treatments (+N, +N+P) were lower in treatment reaches than in control reaches, indicating potential alleviation of N limitation (Fig. 3-5 B). Generally speaking, mean NRR values did not exhibit much variation between control and treatment reaches, as evidenced by the frequency with which confidence intervals

overlapped. Likewise, patterns in NRR values were largely similar between control and treatment reaches among different NDS treatments during individual incubations.

Finally, temporal trajectories of NRR values were similar between control and treatment reaches, regardless of NDS treatment.

Isotopic signatures in Trout Creek provided the greatest support for the incorporation of migrant-derived nutrients into stream food webs. Mean values of periphyton and scraper (Heptageniidae larvae)  $\delta^{15}\text{N}$  both increased in the treatment reach compared to the control during sampling events coinciding with migrant presence, although the migrant  $\times$  time interaction was not significant for periphyton (Fig. 3-6 C-D; Table 3-5). Additionally, there was a significant migrant  $\times$  time interaction for scraper  $\delta^{13}\text{C}$ , which appeared to be driven by divergence between treatment and control reaches during the BCT migration (Fig. 3-6 B). KOK tissue values for  $\delta^{13}\text{C}$  were  $-31.3 \pm 0.7$  and  $14.5 \pm 0.1$  (mean  $\pm$  SE;  $n = 5$ ) for  $\delta^{15}\text{N}$  and, assuming relatively similar values for BCT tissue, it is likely that assimilation of migrant-derived nutrients would have enriched scraper  $\delta^{13}\text{C}$  as well as periphyton and invertebrate  $\delta^{15}\text{N}$ . Similar patterns were not observed in Indian Creek, where significant migrant  $\times$  time interactions, when present, were characterized by isotopic depletion in treatment reach samples (Fig. 3-7; Table 3-5).

## DISCUSSION

It is increasingly clear that ecosystem-level effects of fishes in streams are context-dependent (Vanni, 2010). Consequently, it is important to consider not only the magnitude and direction of fish effects, but also different abiotic and biotic factors that influence them (e.g., Janetski *et al.*, 2009). In this study, the most substantial effect of

migratory BCT and KOK in Strawberry Reservoir tributaries was associated with benthic disturbance that decreased periphyton chlorophyll-*a* concentrations. Beyond this effect, the strongest and most consistent result of fish migrations appeared to be DIN additions in Trout Creek, which was associated with the alleviation of autotrophic N limitation and elevated  $\delta^{15}\text{N}$  values in primary producers and consumers. These results suggest the potential for migratory fishes to influence characteristics of stream ecosystems, but observed responses were not necessarily consistent with my original predictions. Such deviation from expectations illustrates that ecosystem responses to introduced salmonids often depend upon biotic and abiotic characteristics associated with individual streams and fish taxa.

#### *Ecosystem responses to adfluvial salmonid migrations*

In general, periphyton biomass was lower on treatment particles than on control particles, suggesting that introduced salmonids disturb benthic substrates while spawning in Strawberry Reservoir tributaries. Additionally, results suggest the benthic disturbance is partially mediated by abiotic (i.e., substrate) characteristics of streams. This response is not surprising given the large size of the adfluvial migrants (Strawberry River 2012 fish trap size estimates [TL, mm/wet weight, g]: BCT = 488/872, KOK = 450/886; A. Ward & J. Robinson, unpubl. data), spawning behaviors that involve repeated contact with benthic sediments (Sigler & Sigler, 1996), and the relatively small substrate size classes observed in Trout and Indian Creeks (Table A-3). Holtgrieve *et al.* (2010) studied periphyton response to Pacific salmonids in Alaska and identified size thresholds for the disturbance of benthic particles (vulnerable: < 60 mm *B*-axis; invulnerable > 110 mm).

Comparing these thresholds with observed particle size distributions, 91 and 76% of benthic sediments were vulnerable in treatment reaches of Trout and Indian Creeks, respectively. However, at the time of spawning, anadromous Pacific salmon are frequently larger than Strawberry Reservoir BCT and KOK (Groot & Margolis, 1991). Therefore, the threshold of substrate vulnerability is likely lower than the 60-mm value determined by Holtgrieve *et al.* (2010), which may be biased toward larger particles. Consequently, it is reasonable to assume that benthic disturbance associated with Strawberry Reservoir salmonids would be strongest where the proportion of smaller substrates is greatest. Indeed, 35 and 50% of Indian Creek substrates were < 4 mm and < 20 mm (*B*-axis), respectively, whereas these size classes constituted 11 and 37% of Trout Creek substrates. These patterns of substrate vulnerability were largely consistent with statistical results. Adfluvial migrants had significant negative effects on chlorophyll-*a* biomass in Indian Creek, regardless of species. In contrast, disturbance effects of BCT in Trout Creek were limited to one particle size class, and KOK did not have significant effects on chlorophyll-*a* (Table 3-2).

Observed patterns of disturbance related to adfluvial migrants in Strawberry Reservoir tributaries were consistent with results of similar taxa in other systems. Studies of introduced salmonids in Great Lakes tributaries have reported similar or greater disturbance effects on periphyton biomass, with migrant density and biomass often playing key roles in the magnitude of observed effects (Collins *et al.*, 2011; Janetski *et al.*, 2014). The most common non-native salmonids in the Great Lakes are Chinook and coho, and individuals are considerably larger than Strawberry Reservoir BCT and KOK (Chinook = 4080 g; coho = 2260 g; Collins *et al.*, 2011). This size difference may

explain why observed disturbance effects were not even more pronounced in Indian and Trout Creeks.

In addition to disturbance effects, I observed isolated evidence of DIN additions associated with BCT and KOK migrations. The effects were generally weak, however, and likely reflected observed differences between migrant-derived nutrient fluxes and ecosystem nutrient demand. There were different nutrient trajectories between treatment and control reaches, particularly for  $\text{NH}_4$  and  $\text{NO}_3$  and Trout Creek (Fig. 3-4 B-C), but there was not strong, consistent evidence of elevated nutrient concentrations during migration periods. However, the relatively weak responses of water column dissolved nutrients to BCT and KOK largely reflect patterns reported in the literature for introduced salmonids. While some studies have reported increased nutrient concentrations in response to migrations (e.g., Richey *et al.*, 1975; Schuldt & Hershey, 1995; Collins *et al.*, 2011), others have failed to detect responses, often attributing the absence of responses to higher ambient dissolved nutrient concentrations (e.g., Sarica *et al.*, 2004; Ivan *et al.*, 2011; Janetski *et al.*, 2014). Furthermore, specific patterns of benthic nutrient demand will influence whether or not water column concentrations increase. My measurements of benthic nutrient uptake, which serves as a proxy for demand, indicated that it often exceeded nutrients supplied by migrant excretion during 2012, especially for SRP and in Indian Creek (Chapter 2). Thus, it is not surprising that the positive nutrient responses I observed during adfluvial migrations in Strawberry Reservoir tributaries were for  $\text{NH}_4$  and  $\text{NO}_3$  in Trout Creek, where excess DIN from migrant excretion or carcass decomposition may elevate water column concentrations after demand is saturated. The  $\text{NO}_3$  response may be explained by increased nitrification rates, a result that has been



observed in Pacific salmon streams in Alaska (Levi *et al.*, 2013). While we did not measure nitrification rates, observed temporal patterns of  $\text{NH}_4$  and  $\text{NO}_3$  in Trout Creek during KOK migration were consistent with this hypothesis – peaks in  $\text{NH}_4$  concentrations preceded those of  $\text{NO}_3$ , suggesting the possibility of  $\text{NH}_4$  conversion to  $\text{NO}_3$  via nitrification.

Beyond changes in DIN concentrations, migrant-derived nutrients appeared to have isolated effects on autotrophic nutrient limitation and energy flow within stream food webs. However, the inconsistency of significant migrant effects suggests nutrients delivered by BCT and KOK migrations did not produce strong responses in these stream characteristics during 2012. In Trout Creek, BCT appeared to alleviate  $\text{NH}_4$  limitation present in the upstream control reach (Table 3-4), and lower mean NRR values for the nitrogen NDS treatments (+N, +N+P) in the treatment reach relative to the control reach (Fig. 3-5 B) supported this pattern. The potential for BCT to alleviate  $\text{NH}_4$  limitation was suggested by migrant nutrient supply and benthic demand data collected in Trout Creek.  $\text{NH}_4$  excreted by BCT was capable of meeting 95% of benthic  $\text{NH}_4$  demand (Chapter 2), which indicates the likelihood that migrant-derived  $\text{NH}_4$  (from excretion and carcass decomposition) can alleviate existing  $\text{NH}_4$  limitation. In contrast, migrant  $\text{NH}_4$  excretion only met 46-65% of benthic  $\text{NH}_4$  demand in Indian Creek (Chapter 2), suggesting they were not capable of altering  $\text{NH}_4$  limitation that persisted throughout 2012. The relatively small effects of BCT and KOK on patterns of nutrient limitation are consistent with Rand *et al.* (1992) and Janetski *et al.* (2014), neither of which found consistent alteration of nutrient limitation by introduced salmonids in Great Lakes tributaries. However, they contrast with another study that showed substantial salmon effects on

temporal patterns of nutrient limitation (Ruegg *et al.*, 2011). These contradictory results suggest that the effect of salmonids on nutrient limitation is variable and likely dependent on interactions between migrant-derived nutrient fluxes and background nutrient concentrations.

The incorporation of migrant-derived nutrients into stream food webs was limited to Trout Creek, where patterns of isotopic enrichment in scrapers were evident during migrations. Enrichment patterns were not evident in periphyton, however, which suggests that Trout Creek scrapers (Heptageniid mayflies) used other food resources. Janetski *et al.* (2009) also reported moderately stronger isotopic enrichment in invertebrates than in periphyton, although enrichment effects of the focal taxa (Pacific salmon) were positive for both organisms. Similar to this study, Schuldt & Hershey (1995) and Fisher Wold & Hershey (1999) reported  $\delta^{15}\text{N}$  enrichment of stream biota (grazing mayflies, periphyton) in Lake Superior tributaries where introduced Chinook salmon spawn. However, studies that examine isotopic responses of stream biota to migratory fishes other than anadromous Pacific salmon are rare (but see Walters, Barnes & Post, 2009 and Childress *et al.*, 2014 for other examples reporting incorporation of migrant-derived N).

### *The role of context*

I found moderate support for the prediction that that nutrients delivered by semelparous KOK that migrate during reduced flow periods and exhibit population-wide post-spawning mortality would have stronger ecosystem effects. For example, migrant  $\times$  time interactions for  $\text{NH}_4$  and  $\text{NO}_3$  concentrations in Trout Creek appeared to be more

strongly related to the KOK migration (Fig. 3-3 A-B). Likewise, differences in Trout Creek scraper  $\delta^{15}\text{N}$  between treatment and control reaches were more pronounced during the KOK migration than during the BCT migration (Fig. 3-6 D). However, Trout Creek scraper  $\delta^{13}\text{C}$  values diverged between treatment and control reaches during the BCT migration (Fig. 3-6 B), and BCT appeared to alleviate  $\text{NH}_4$  limitation in Trout Creek (Table 3-4).

In addition to variation between species, I expected to find more evidence for the incorporation of migrant-derived nutrients in Indian Creek because of greater hydrogeomorphic retentiveness than Trout Creek (Table 3-1). However, all available lines of evidence (nutrient concentrations, autotrophic nutrient limitation, stable isotopes) suggested that effects of migrant-derived nutrients were stronger or more likely in Trout Creek. Consequently, it appears that measures of hydrogeomorphic retention are not good predictors of adfluvial salmonid effects, at least in the Strawberry Reservoir tributaries I sampled. Alternatively, the measures I used to quantify hydrogeomorphic retention did not accurately reflect that characteristic in these streams.

Beyond hydrogeomorphic differences between streams and variation in species reproductive strategies and timing, there are other factors capable of mediating ecosystem responses to migratory fishes. Density can be an important regulator of migrant effects (e.g., Moore & Schindler, 2008; Janetski *et al.*, 2014), but there were not striking differences in migrant densities between species or streams (Fig. 3-1). Background nutrient concentrations have also been suggested as an important regulator of fish effects (Flecker *et al.*, 2010), and work in Great Lakes tributaries has frequently attributed relatively moderate effects of introduced salmonids to dissolved nutrient concentrations

that are much higher than streams within the native range of Pacific salmonids (e.g., Janetski *et al.*, 2014). During 2012, ambient concentrations of  $\text{NH}_4$  and SRP were relatively low in Indian ( $\text{NH}_4 \sim 12 \mu\text{g L}^{-1}$ ; SRP  $\sim 2.5 \mu\text{g L}^{-1}$ ) and Trout ( $\text{NH}_4 \sim 17 \mu\text{g L}^{-1}$ ; SRP  $\sim 2.3 \mu\text{g L}^{-1}$ ) Creeks, however, so background nutrient levels, in isolation, may not be good predictors of salmonid effects in all systems. Rather, it may be more informative to consider the magnitude of migrant-derived nutrient fluxes relative to nutrient demand in recipient habitats. Finally, interannual variation in discharge and migrant density could influence migratory fish effects. In particular, migrant biomass:discharge ratios may be good predictors of effect magnitudes, at least for effects related to nutrients (e.g., water column concentrations, isotopic enrichment; Janetski *et al.*, 2009). However, such ratios were higher during 2012, a relatively dry year, in Strawberry Reservoir tributaries than during 2011, which was a relatively wet year (Chapter 2). Consequently, ecosystem-level effects related to BCT and KOK in Indian and Trout Creeks may be limited by migrant densities and biomass that are relatively low compared with native salmon streams in the Pacific Northwest and Great Lakes tributaries.

## CONCLUSION

Results from this study suggest that benthic substrate disturbance associated with introduced migratory salmonids can be substantial in areas outside of the Great Lakes region. Additionally, adfluvial migrations may provide nutrients that produce changes in ambient concentrations, nutrient limitation, or energy flow through stream food webs. However, the magnitude of such nutrient-related effects likely depends on the relative size of migrant-derived nutrient fluxes and may be smaller than that associated with

benthic disturbance. Similar to work done with non-native salmonids in other systems, fish effects were not consistent among and within the responses I measured. Such inconsistency illustrates that ecosystem responses to introduced salmonids often depend upon biotic and abiotic characteristics associated with individual streams and fish taxa. Generalizations regarding fish effects on stream ecosystem properties remain elusive, but studies that identify or confirm the important role of mediators like reproductive characteristics of species, hydrogeomorphic features of streams, and migrant densities can help researchers and managers anticipate and understand consequences associated with introduced salmonids.

#### LITERATURE CITED

- Biggs B.J.F. & Kilroy C. (2000) Stream Periphyton Monitoring Manual. National Institute of Water and Atmospheric Research, Christchurch, NZ.
- Bohlen P.J., Scheu S., Hale C.M., McLean M.A., Migge S., Groffman P.M. *et al.* (2004) Non-native invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment*, **2**, 427-435.
- Brown J.H. & Heske E.J. (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**, 1705-1707.
- Childress E.S., Allan J.D. & McIntyre P.B. (2014) Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems*, **17**, 522-534.
- Collins S.F., Moerke A.H., Chaloner D.T., Janetski D.J. & Lamberti G.A. (2011) Response of dissolved nutrients and periphyton to spawning Pacific salmon in three northern Michigan streams. *Journal of the North American Benthological Society*, **30**, 831-839.
- Crawford S.S. (2001) *Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects*. Canadian Special Publication of Fisheries and Aquatic Sciences, 132, Bethesda, MD.
- Crawford S.S. & Muir A.M. (2008) Global introductions of salmon and trout in the genus *Oncorhynchus*: 1870-2007. *Reviews in Fish Biology and Fisheries*, **18**, 313-344.

- Denison D.L. & Meier P.G. (1979) Effects of salmon spawning activity on macroinvertebrates in a small Michigan stream. *Great Lakes Entomologist*, **12**, 57-61.
- Denton K.P., Rich H.B. Jr. & Quinn T.P. (2009) Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. *Transactions of the American Fisheries Society*, **138**, 1207-1219.
- Fisher Wold A.K. & Hershey A.E. (1999) Effects of salmon carcass decomposition on biofilm growth and wood decomposition. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 767-773.
- Flecker A.S., McIntyre P.B., Moore J.W., Anderson J.T., Taylor B.W. & Hall R.O. (2010) Migratory fishes as material and process subsidies in riverine ecosystems. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 559-592.
- Gende S.M., Edwards R.T., Willson M.F. & Wipfli M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917-928.
- Groot C. & Margolis L. (1991) *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC.
- Hassan M.A., Gottesfeld A.S., Montgomery D.R., Tunnicliffe J.F., Clarke G.K.C., Wynn G. *et al.* (2008) Salmon-driven bed load transport and bed morphology in mountain streams. *Geophysical Research Letters*, **35**, L04405.
- Hocking M.D. & Reimchen T.E. (2010) Salmon species, density and watershed size predict magnitude of marine enrichment in riparian food webs. *Oikos*, **118**, 1307-1318.
- Hoellein T.J., Tank J.L., Rosi-Marshall E.J. & Entekin S.A. (2009) Temporal variation in substratum-specific rates of N uptake and metabolism and their contribution at the stream-reach scale. *Journal of the North American Benthological Society*, **28**, 305-318.
- Holtgrieve G.W., Schindler D.E., Gowell C.P., Ruff C.P. & Lisi P.J. (2010) Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology*, **55**, 2598-2611.
- Holtgrieve G.W. & Schindler D.E. (2011) Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology*, **92**, 373-385.

- Ivan L.N. (2009) *Impacts of adfluvial spawners on ecology of Great Lakes tributaries*. Ph.D. dissertation. University of Michigan, Ann Arbor.
- Ivan L.N., Rutherford E.S. & Johengen T.H. (2011) Impacts of adfluvial fish on the ecology of two Great Lakes tributaries. *Transactions of the American Fisheries Society*, **140**, 1670-1682.
- Janetski D.J., Chaloner D.T., Tiegs S.D. & Lamberti G.A. (2009) Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**, 583-595.
- Janetski D.J., Chaloner D.T., Moerke A.H., Levi P.S. & Lamberti G.A. (2014) Novel environmental conditions alter subsidy and engineering effects by introduced Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 502-513.
- Johnston N.T., MacIsaac E.A., Tschaplinski P.J. & Hall K.J. (2004) Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **61**, 383-403.
- Lamberti G.A. & Gregory S.V. (2006) CPOM transport, retention, and measurement In: *Methods in Stream Ecology*. (Eds F.R. Hauer & G.A. Lamberti). Academic Press, San Francisco, CA, 273-289.
- Levi P.S., Tank J.L., Tiegs S.D., Ruegg J., Chaloner D.T. & Lamberti G.A. (2011) Does timber harvest influence the dynamics of marine-derived nutrients in Southeast Alaska streams? *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 1316-1329.
- Levi P.S., Tank J.L., Tiegs S.D., Chaloner D.T. & Lamberti G.A. (2013) Biogeochemical transformation of a nutrient subsidy: salmon, streams, and nitrification. *Biogeochemistry*, **113**, 643-655.
- McNaughton S.J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 259-294.
- Minakawa N. & Gara R.I. (1999) Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *Journal of Freshwater Ecology*, **14**, 327-335.
- Minshall G.W., Hitchcock E. & Barnes J.R. (1991) Decomposition of rainbow trout (*Oncorhynchus mykiss*) carcasses in a forest stream ecosystem inhabited only by nonanadromous fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 191-195.

- Mitchell N.L. & Lamberti G.A. (2005) Responses in dissolved nutrients and epilithon abundance to spawning salmon in southeast Alaska streams. *Limnology and Oceanography*, **50**, 217-227.
- Moore J.W., Schindler D.E. & Scheuerell M.D. (2004) Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia*, **139**, 298-308.
- Moore J.W., Schindler D.E., Carter J.L., Fox J., Griffiths J. & Holtgrieve G.W. (2007) Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. *Ecology*, **88**, 1278-1291.
- Moore J.W. & Schindler D.E. (2008) Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology*, **77**, 275-284.
- Paine R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65-75.
- Peterson D.P. & Foote C.J. (2000) Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. *Transactions of the American Fisheries Society*, **129**, 924-934.
- R Development Core Team. (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rand P.S., Hall C.A.S., McDowell W.H., Ringler N.H. & Kennen J.G. (1992) Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2377-2385.
- Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland. Available at: <http://imagej.nih.gov/ij/>, 1997-2012.
- Richey J.E., Perkins M.A. & Goldman C.R. (1975) Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. *Journal of the Fisheries Research Board of Canada*, **32**, 817-820.
- Rinella D.J., Wipfli M.S., Stricker C.A., Heintz R.A. & Rinella M.J. (2012) Pacific salmon (*Oncorhynchus* spp.) runs and consumer fitness: growth and energy storage in stream-dwelling salmonids increase with salmon spawner density. *Canadian Journal of Fisheries and Aquatic Sciences*, **69**, 73-84.
- Ruegg J., Tiegs S.D., Chaloner D.T., Levi P.S., Tank J.L. & Lamberti G.A. (2011) Salmon subsidies alleviate nutrient limitation of benthic biofilms in southeast Alaska streams. *Canadian Journal of Fisheries & Aquatic Sciences*, **68**, 277-287.



- Ruegg J., Chaloner D.T., Levi P.S., Tank J.L., Tiegs S.D. & Lamberti G.A. (2012) Environmental variability and the ecological effects of spawning Pacific salmon on stream biofilm. *Freshwater Biology*, **57**, 129-142.
- Sarica J., Amyot M., Hare L., Doyon M-R. & Stanfield L.W. (2004) Salmon-derived mercury and nutrients in a Lake Ontario spawning stream. *Limnology and Oceanography*, **49**, 891-899.
- Schuldt J.A. & Hershey A.E. (1995) Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society*, **14**, 259-268.
- Sigler W.F. & Sigler J.W. (1996) *Fishes of Utah*. University of Utah Press, Salt Lake City.
- Steinman A.D., Lamberti G.A. & Leavitt P.R. (2006) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology*. (Eds F.R. Hauer & G.A. Lamberti). Academic Press, San Francisco, CA, 357-379.
- Tank J.L. & Dodds W.K. (2003) Responses of heterotrophic and autotrophic biofilms to nutrients in ten streams. *Freshwater Biology*, **48**, 1031-1049.
- Tank J.L., Bernot M.J. & Rosi-Marshall E.J. (2006) Nitrogen limitation and uptake. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp.213-238. Academic Press, San Francisco, CA.
- Taylor B.W., Flecker A.S. & Hall R.O. (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*, **313**, 833-836.
- Tiegs S.D., Chaloner D.T., Levi P.S., Ruegg J., Tank J.L. & Lamberti G.A. (2008) Timber harvest transforms ecological roles of salmon in southeast Alaska rain forest streams. *Ecological Applications*, **18**, 4-11.
- Tiegs S.D., Campbell E.Y., Levi P.S., Ruegg J., Benbow M.E., Chaloner D.T. *et al.* (2009) Separating physical disturbance and nutrient enrichment caused by Pacific salmon in stream ecosystems. *Freshwater Biology*, **54**, 1864-1875.
- Vanni M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341-370.
- Vanni M.J. (2010) Preface: when and where do fish have strong effects on stream ecosystem processes? In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 531-538.

- Walters A.W., Barnes R.T. & Post D.M. (2009) Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 439-448.
- Welschmeyer N.A. 1994. Fluorometric analysis of chlorophyll-*a* in the presence of chlorophyll-*b* and pheopigments. *Limnology and Oceanography*, **39**, 1985-1992.
- Wipfli M.S., Hudson J.P. & Caouette J.P. (1998) Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1503-1511.
- Wipfli M.S., Hudson J.P., Chaloner D.T. & Caouette J.P. (1999) Influence of salmon spawner densities on stream productivity in Southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1600-1611.
- Winemiller K.O. & Jepsen D.B. (1998) Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, **53**, 267-296.
- Wolman M.G. (1954) A method of sampling coarse riverbed material. *Transactions of the American Geophysical Union*, **35**, 951-956.
- Wood C.M. (1995) Excretion. In: *Physiological Ecology of Pacific Salmon* (Eds C. Groot, L. Margolis & W.C. Clarke), pp. 379-438. University of British Columbia Press, Vancouver, BC.
- Yang L.H. (2004) Periodical cicadas as resource pulses in North American forests. *Science*, **306**, 1565-1567.

**Table 3-1** Comparison of hydrogeomorphic characteristics between Indian and Trout Creeks. In cases where multiple measurements were made, data are presented as means (SE). Statistically significant ( $\alpha = 0.05$ ) differences between streams are underlined. Q, discharge;  $U_{MAX}$ , maximum velocity; U, velocity; WCW, wetted channel width;  $k$ , particulate retention.

	Q ( $m^3 s^{-1}$ )	$U_{MAX}$ ( $m s^{-1}$ )	U ( $m s^{-1}$ )	Depth (m)	WCW (m)	Pool %	Riffle %	Run %	$k$ ( $m^{-1}$ )	Slope	Sinuosity
Indian Creek	0.065 (0.012)	0.36 (0.03)	0.15 (0.04)	0.24 (0.03)	3.01 (0.09)	15 (2)	34 (8)	51 (6)	0.0192 (0.0026)	0.01	1.64
Trout Creek	0.094 (0.003)	0.69 (0.03)	0.69 (0.04)	0.14 (0.01)	1.97 (0.07)	0 (0)	95 (2)	5 (2)	0.0062 (0.0021)	0.03	1.18
<i>t</i>	-2.60	-7.57	-9.48	2.94	9.10	6.38	-7.29	6.79	3.93	---	---
df	39	39	4	4	162	4	4	4	4	---	---
<i>P</i>	<u>0.013</u>	< <u>0.001</u>	< <u>0.001</u>	<u>0.042</u>	< <u>0.001</u>	<u>0.003</u>	<u>0.002</u>	<u>0.002</u>	<u>0.017</u>	---	---

**Table 3-2** Two-way ANOVA results for periphyton biomass (as chlorophyll-*a*;  $\mu\text{g cm}^{-2}$ ) as a function of fish (present or absent) and particle size (four size classes). Statistically significant ( $\alpha = 0.05$ ) effects are underlined.

		Indian Creek, BCT				Indian Creek, KOK			
factor	df	SS	<i>F</i>	<i>P</i>	df	SS	<i>F</i>	<i>P</i>	
Fish	1	14.802	4.978	<u>0.032</u>	1	19.556	6.660	<u>0.014</u>	
Size	3	6.361	0.713	0.550	3	21.335	2.422	0.082	
Fish $\times$ size	3	13.805	1.548	0.218	3	15.338	1.741	0.176	
Residuals	38	112.983			36	105.718			
		Trout Creek, BCT				Trout Creek, KOK			
factor	df	SS	<i>F</i>	<i>P</i>	df	SS	<i>F</i>	<i>P</i>	
Fish	1	0.023	0.011	0.919	1	0.965	1.653	0.207	
Size	3	64.865	9.766	< <u>0.001</u>	3	2.849	1.626	0.200	
Fish $\times$ size	3	31.332	4.717	<u>0.009</u>	3	3.371	1.924	0.143	
Residuals	27	59.778			36	21.022			

**Table 3-3** Repeated measures ANOVA results for dissolved nutrient concentrations as a function of migrants (treatment vs. control reaches) and time. Statistically significant ( $\alpha = 0.10$ ) effects are underlined.

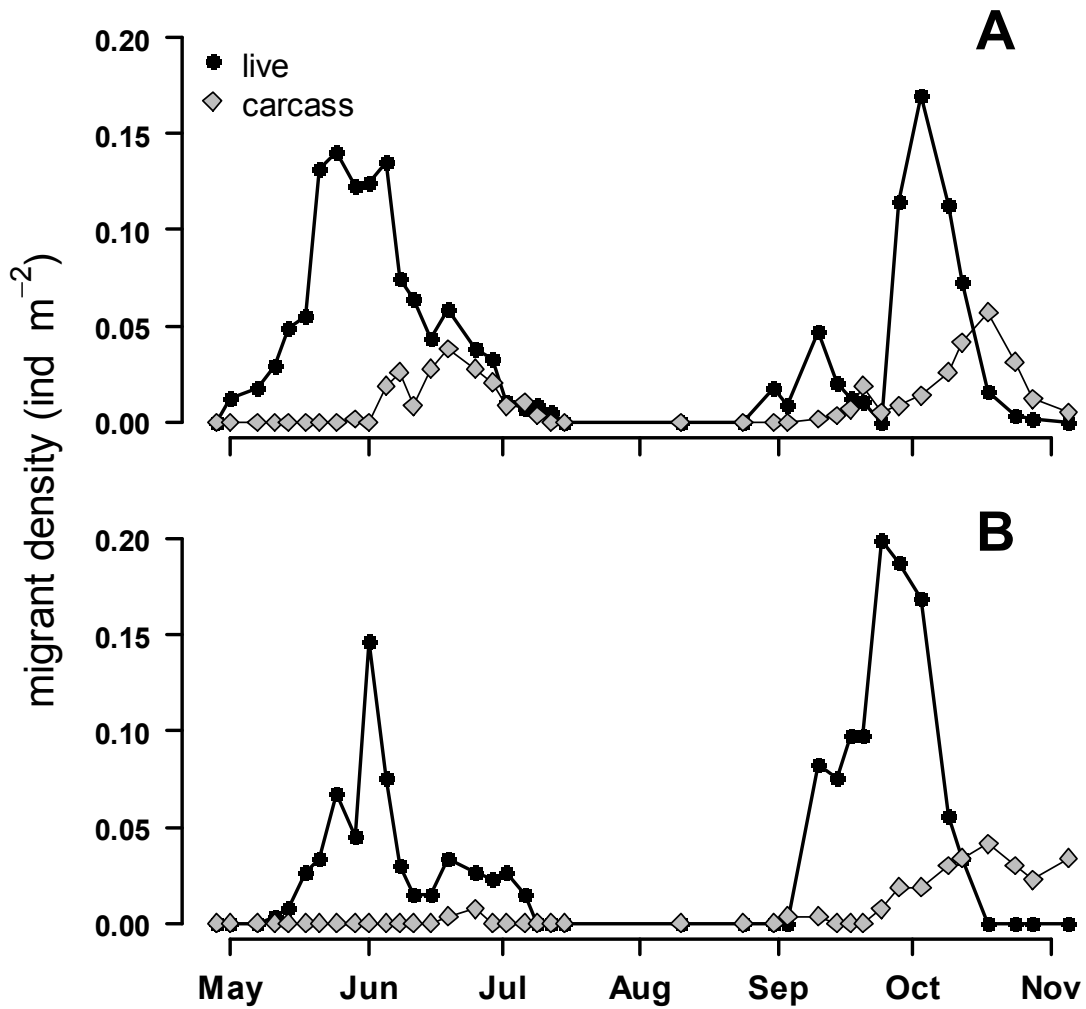
Indian Cr	Source	NH <sub>4</sub> ( $\mu\text{g L}^{-1}$ )				NO <sub>3</sub> ( $\mu\text{g L}^{-1}$ )				SRP ( $\mu\text{g L}^{-1}$ )			
		df	SS	F	P	df	SS	F	P	df	SS	F	P
<i>Between subjects</i>													
	Migrants	1	0.64	0.66	0.503	1	6601	1124	< <u>0.001</u>	1	6.11	7.27	0.114
	Residuals	2	1.96			2	12			2	1.68		
<i>Within subjects</i>													
	Time	13	739.80	4.68	< <u>0.001</u>	13	12158	152	< <u>0.001</u>	13	26.81	1.76	0.106
	Migrants $\times$ time	13	102.30	0.65	0.793	13	2336	29	< <u>0.001</u>	13	16.97	1.12	0.390
	Residuals	26	316.30			26	160			26	30.42		
<i>Trout Cr</i>													
<i>Between subjects</i>													
	Migrants	1	608.70	71.74	<u>0.014</u>	1	144492	21198	< <u>0.001</u>	1	7.00	20.43	<u>0.046</u>
	Residuals	2	17.00			2	14			2	0.69		
<i>Within subjects</i>													
	Time	14	621.40	5.76	< <u>0.001</u>	14	13798	24	< <u>0.001</u>	14	43.20	11.31	< <u>0.001</u>
	Migrants $\times$ time	14	313.40	2.91	<u>0.008</u>	14	6429	11	< <u>0.001</u>	14	2.96	0.78	0.685
	Residuals	28	215.80			28	1127			28	7.64		

**Table 3-4** Results and interpretation of two-way ANOVAs for nutrient-diffusing substrata (NDS) responses (chlorophyll-*a*;  $\mu\text{g cm}^{-2}$ ) during three different time periods in 2012. NDS were deployed in two reaches (T = treatment; C = control) of each stream during each time period. NDS treatments were nitrogen (N as  $\text{NH}_4$ ), phosphorus (P as  $\text{PO}_4$ ), nitrogen and phosphorus together (N+P), and the status of each stream-time combination is indicated as nutrient-limited (<sup>L</sup>), nutrient-inhibited (<sup>I</sup>), or neither (none). Limitation types are N, primary N and secondary P (1°N,2°P), and co-limitation by N and P (co), and were assigned following Tank & Dodds (2003). Inhibition types are N\* (inhibition by N in the absence of P) and co\* (inhibition by N and P in isolation). Interpretation of inhibition results was based on inspection of chlorophyll-*a* data. Statistically significant effects ( $\alpha = 0.05$ ) are underlined.

	BCT migration				Between migrations				KOK migration			
	N	P	N+P	Status	N	P	N+P	Status	N	P	N+P	Status
Indian Cr, C	< <u>0.001</u>	<u>0.004</u>	<u>0.008</u>	co <sup>L</sup>	< <u>0.001</u>	0.084	<u>0.039</u>	1°N,2°P <sup>L</sup>	0.329	0.447	0.410	none
Indian Cr, T	<u>0.031</u>	0.914	0.056	N <sup>L</sup>	< <u>0.001</u>	0.867	0.457	N <sup>L</sup>	<u>0.039</u>	0.209	0.089	N <sup>L</sup>
Trout Cr, C	<u>0.008</u>	0.729	0.884	N <sup>L</sup>	<u>0.021</u>	< <u>0.001</u>	< <u>0.001</u>	N* <sup>I</sup>	0.978	0.797	<u>0.008</u>	co* <sup>I</sup>
Trout Cr, T	0.214	0.487	0.564	none	0.072	<u>0.007</u>	< <u>0.001</u>	N* <sup>I</sup>	0.052	<u>0.001</u>	0.080	N* <sup>I</sup>

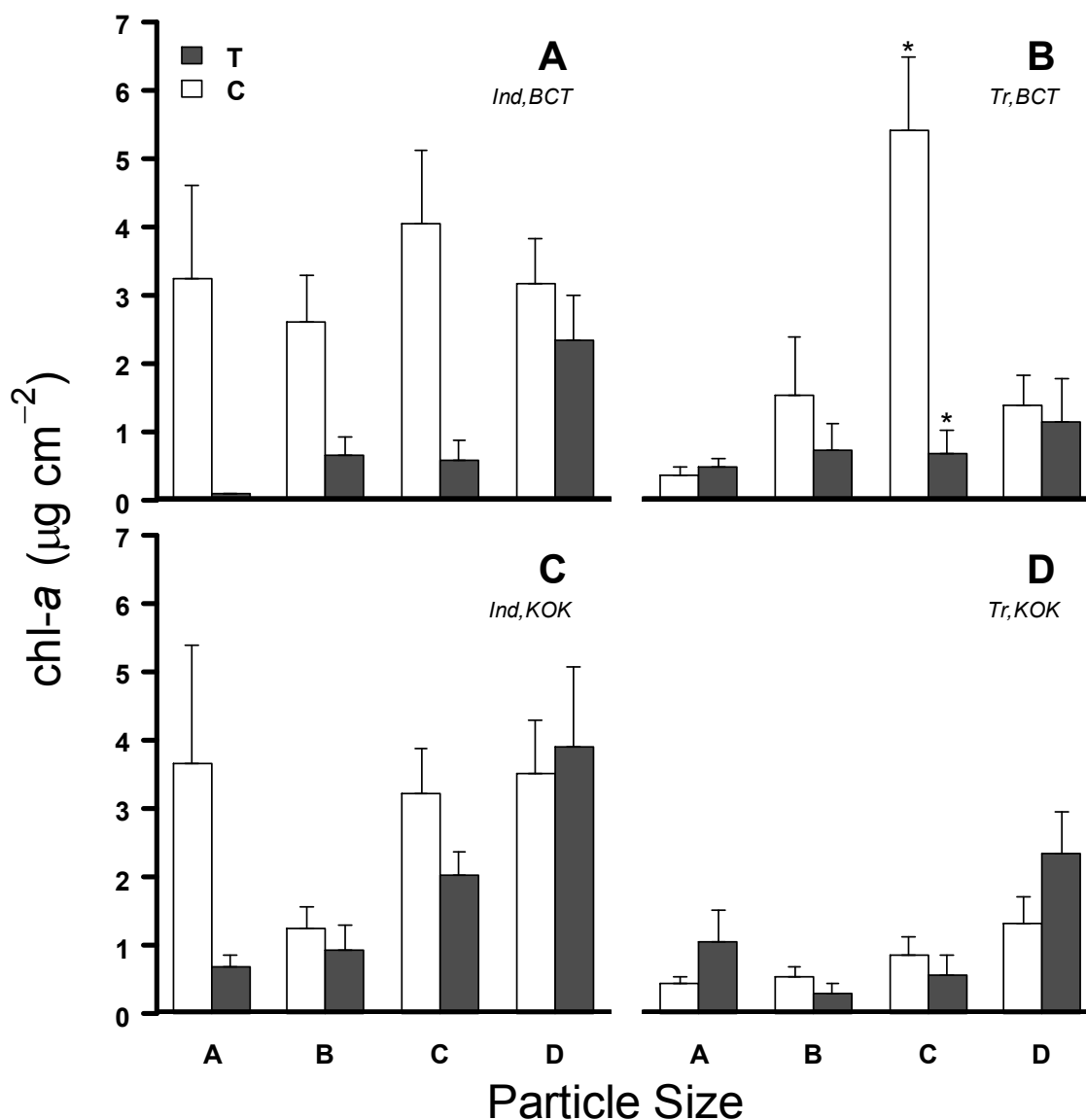
**Table 3-5** Repeated measures ANOVA results for food web stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) values as a function of migrants (treatment reaches vs. control reaches) and time. Statistically significant ( $\alpha = 0.05$ ) effects are underlined.

Indian Cr	Source	Periphyton $\delta^{13}\text{C}$				Periphyton $\delta^{15}\text{N}$				Scraper $\delta^{13}\text{C}$				Scraper $\delta^{15}\text{N}$			
		df	SS	<i>F</i>	<i>P</i>	df	SS	<i>F</i>	<i>P</i>	df	SS	<i>F</i>	<i>P</i>	df	SS	<i>F</i>	<i>P</i>
<i>Between subjects</i>																	
	Migrants	1	19.88	2.46	0.192	1	8.34	9.83	<u>0.035</u>	1	29.62	181.20	< <u>0.001</u>	1	0.20	1.23	0.330
	Residuals	4	32.35			4	3.40			4	0.65			4	0.65		
<i>Within subjects</i>																	
	Time	4	210.30	11.82	< <u>0.001</u>	4	84.80	29.08	< <u>0.001</u>	4	8.39	7.78	<u>0.001</u>	4	13.32	9.20	< <u>0.001</u>
	Migrants $\times$ time	4	36.69	2.06	0.134	4	2.38	0.82	0.533	4	7.67	7.12	<u>0.002</u>	4	4.41	3.05	<u>0.048</u>
	Residuals	16	71.20			16	11.67			16	4.31			16	5.80		
<i>Trout Cr</i>																	
<i>Between subjects</i>																	
	Migrants	1	147.45	41.43	<u>0.003</u>	1	5.69	5.11	0.087	1	200.88	513.50	< <u>0.001</u>	1	1.80	3.18	0.149
	Residuals	4	14.24			4	4.46			4	1.56			4	2.27		
<i>Within subjects</i>																	
	Time	4	136.64	14.92	< <u>0.001</u>	4	3.72	1.66	0.208	4	4.41	9.21	< <u>0.001</u>	4	7.87	7.91	<u>0.001</u>
	Migrants $\times$ time	4	14.89	1.63	0.216	4	4.87	2.17	0.118	4	13.61	28.42	< <u>0.001</u>	4	17.76	17.84	< <u>0.001</u>
	Residuals	16	36.64			16	8.96			16	1.92			16	3.98		

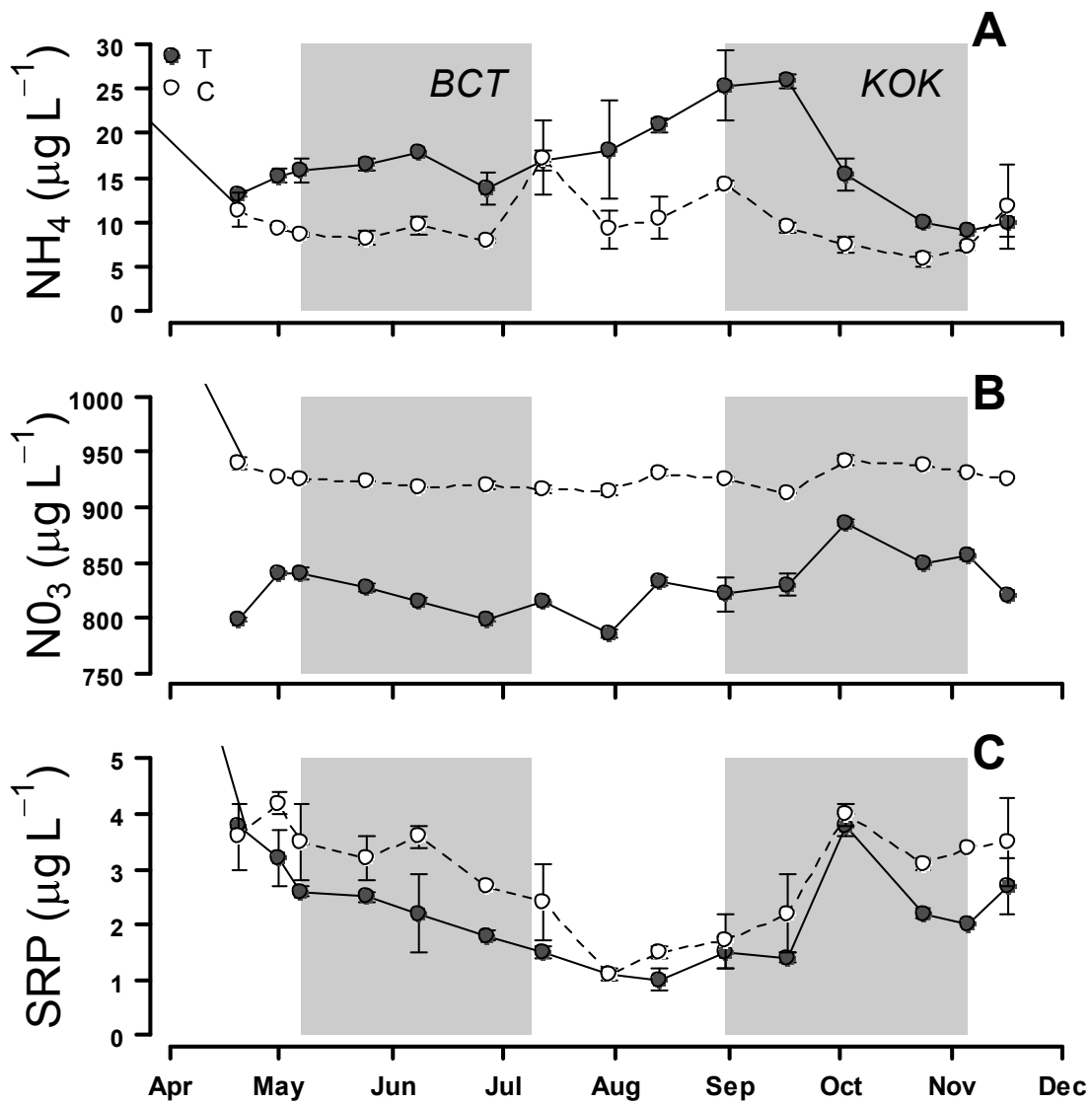


**Fig. 3-1** Live migrant and carcass densities in Indian (A) and Trout (B) Creeks during 2012. Spring migrants are Bonneville cutthroat trout (BCT; *O. clarkii utah*) and fall migrants are kokanee salmon (KOK; *O. nerka*). Densities are based on streamside migrant counts and reflect areas associated with designated treatment reaches in each stream.

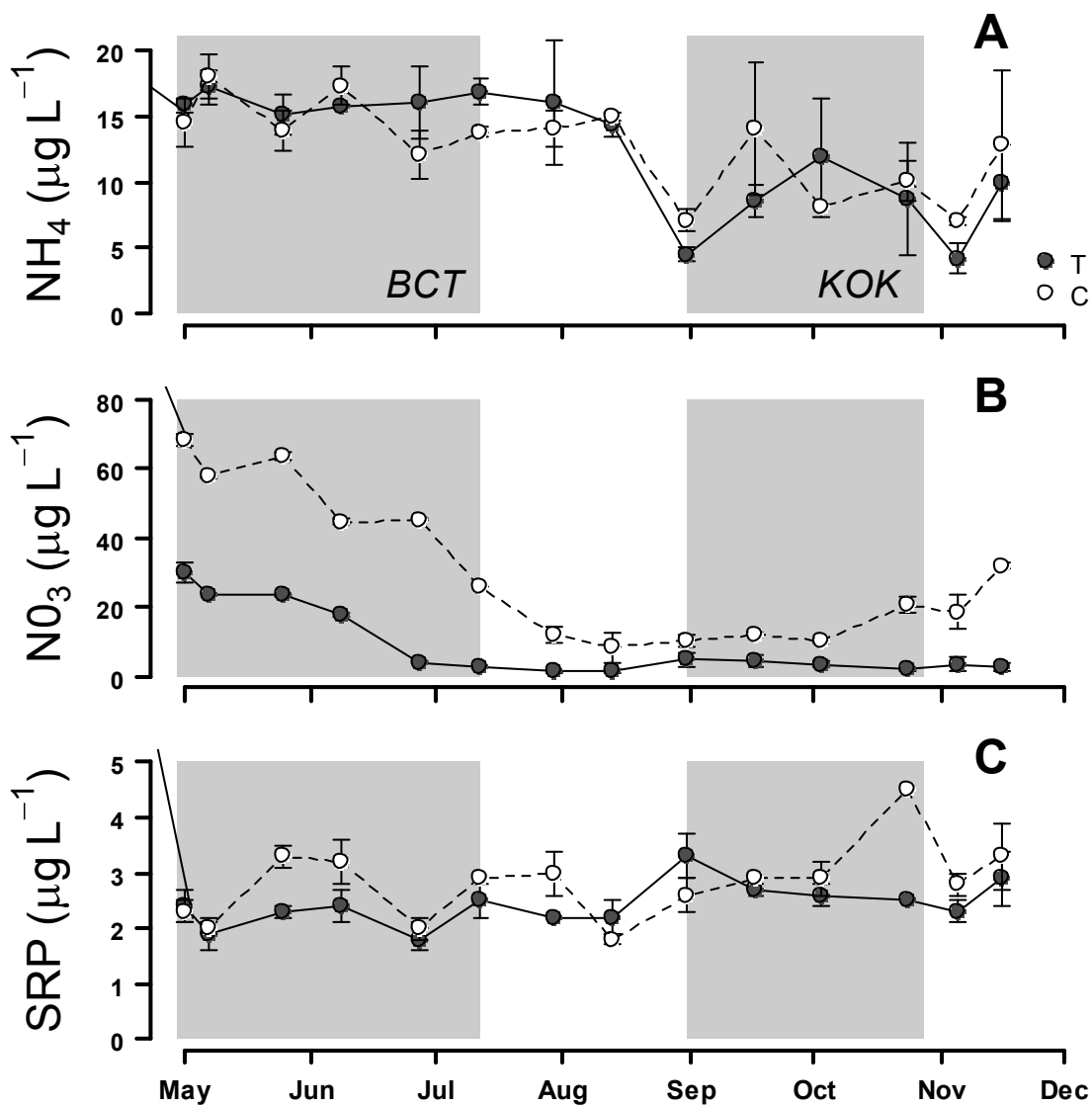




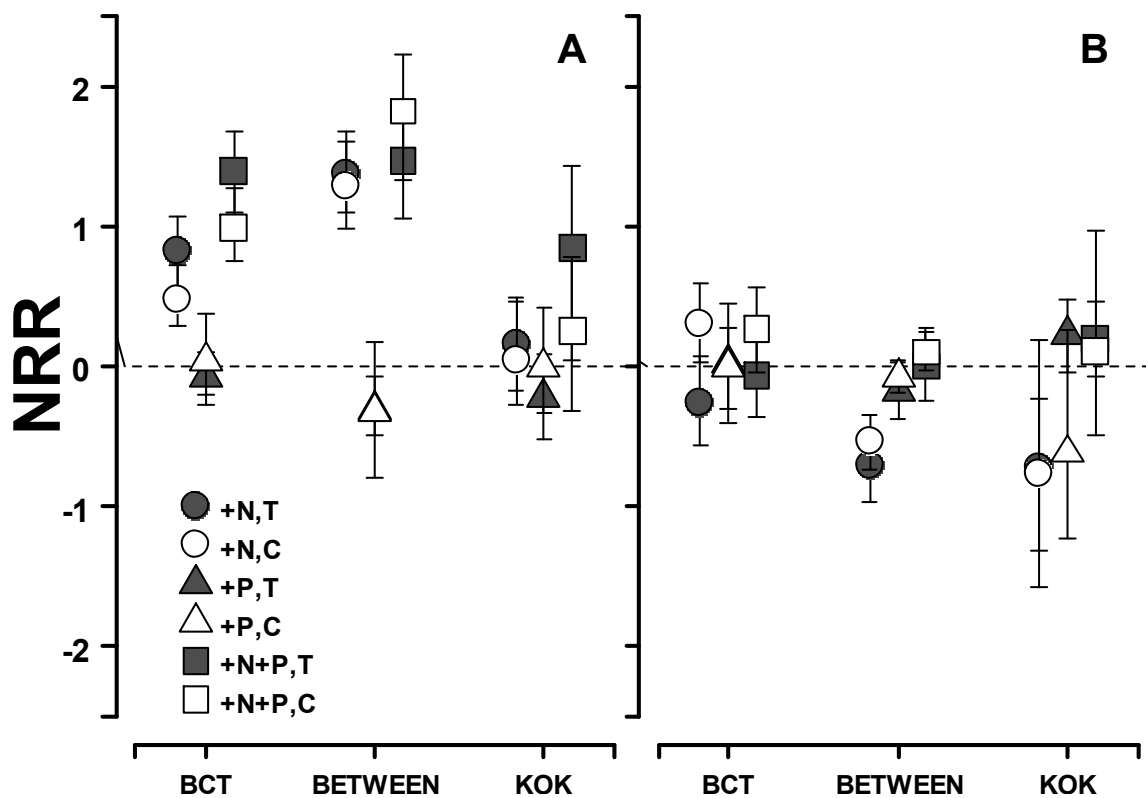
**Fig. 3-2** Benthic substrate chlorophyll-*a* biomass as a function of migrant presence and particle size. Substrates were sampled during periods at or near peak migrant densities for BCT in Indian (A) and Trout (B) Creeks, as well as for KOK in Indian (C) and Trout (D) Creeks. Migrants were present and active in areas where treatment (T) particles were collected and absent or inactive in locations where control (C) particles were collected. Particle size classes were delineated using quartiles associated with *B*-axis diameter, and denote increasing size from A to D. Statistically significant ( $\alpha = 0.05$ ) differences between T and C particles associated with post-hoc testing of significant fish  $\times$  particle size interactions are denoted with \*. Bars represent mean values + 1 SE.



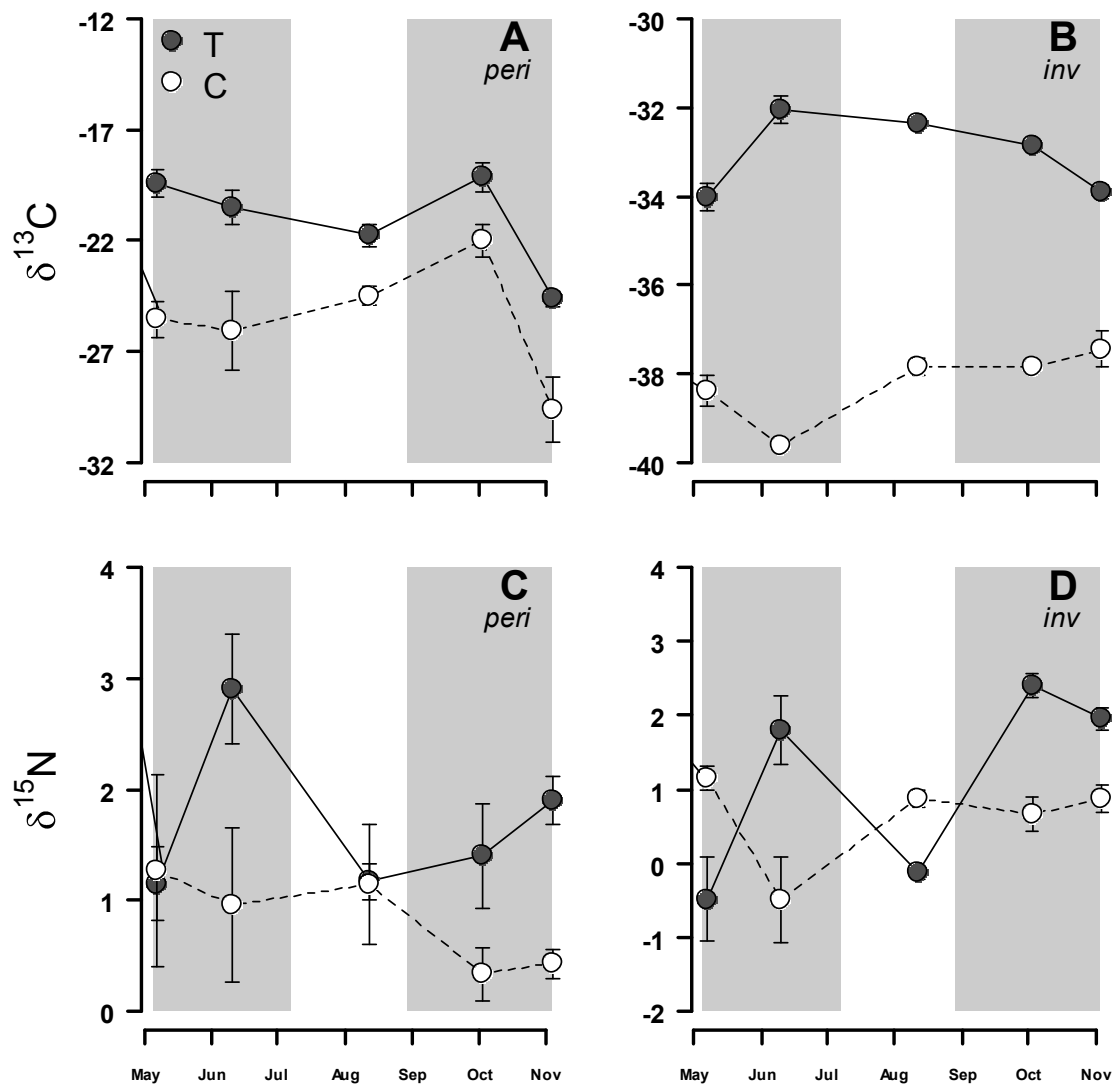
**Fig. 3-3** Concentrations of NH<sub>4</sub> (A), NO<sub>3</sub> (B), and SRP (C) during 2012 in Trout Creek. Samples were collected at the downstream ends of treatment (T) and control (C) reaches. Shaded areas indicate periods of migrant presence (spring = BCT; fall = KOK). Values are presented as means  $\pm$  1 SE ( $n = 2$ ).



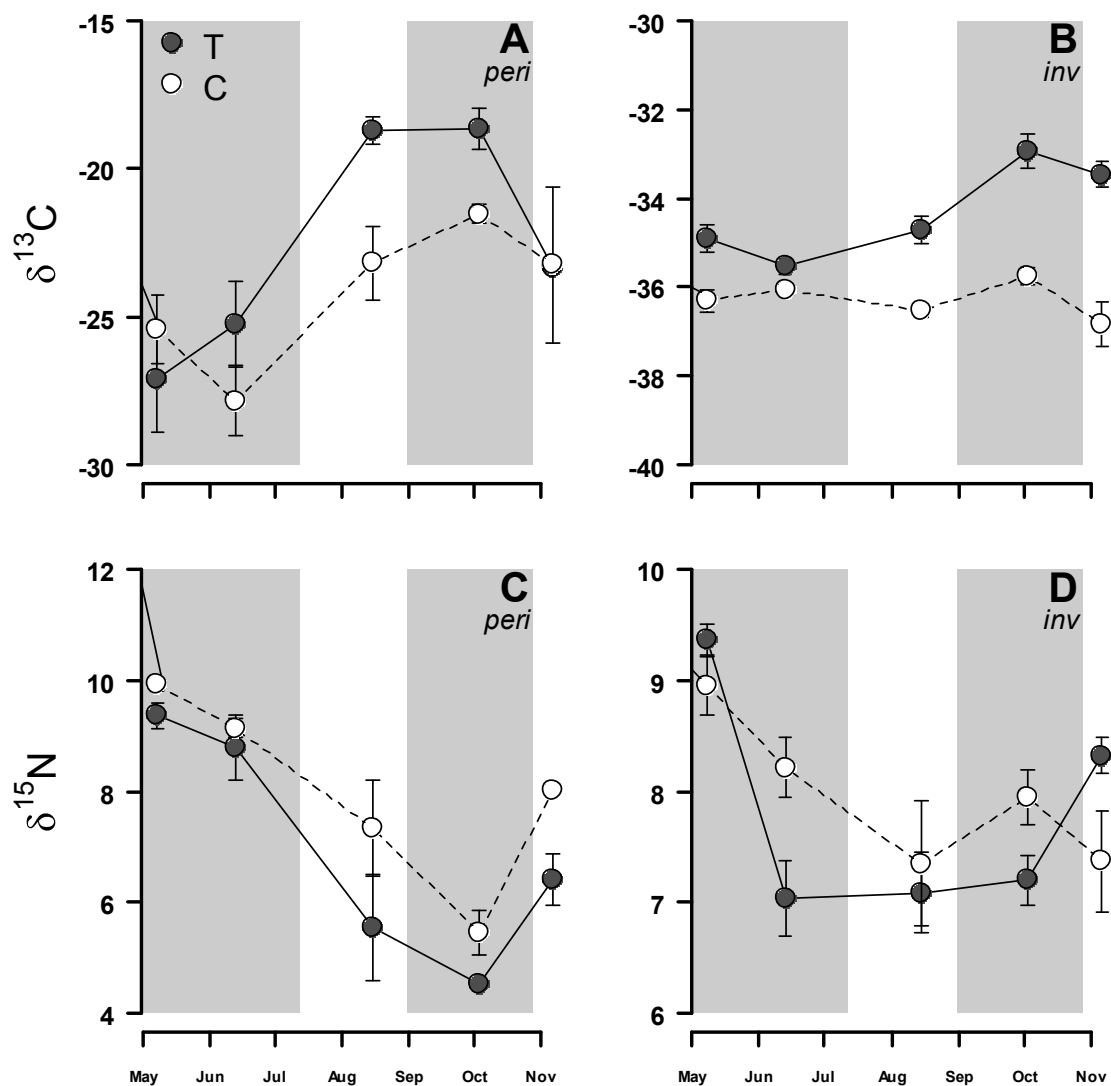
**Fig. 3-4** Concentrations of NH<sub>4</sub> (A), NO<sub>3</sub> (B), and SRP (C) during 2012 in Indian Creek. Samples were collected at the downstream ends of treatment (T) and control (C) reaches. Shaded areas indicate periods of migrant presence (spring = BCT; fall = KOK). Values are presented as means  $\pm$  1 SE ( $n = 2$ ).



**Fig. 3-5** Nutrient response ratios (NRR;  $\ln$  [treatment/ control]) of chlorophyll-*a* on nutrient diffusing substrates from separate time periods in Indian (A) and Trout (B) Creeks during 2012. Shown are bootstrapped means and 95% confidence intervals for each nutrient treatment (+N, +P, and +N+P) in two reaches (T = treatment; C = control) of each stream. BCT = during BCT migration, BETWEEN = time between BCT and KOK migrations, KOK = during KOK migration.



**Fig. 3-6** Stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) values for periphyton (A and C) and scraper invertebrates (Heptageniidae larvae; B and D) in Trout Creek during 2012. Shaded areas indicate periods of migrant presence (spring = BCT; fall = KOK). Values are presented as means  $\pm$  1 SE ( $n = 3$ ).



**Fig. 3-7** Stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) values for periphyton (A and C) and scraper invertebrates (Elmidae larvae, *Optioservus* spp.; B and D) in Indian Creek during 2012. Shaded areas indicate periods of migrant presence (spring = BCT; fall = KOK). Values are presented as means  $\pm$  1 SE ( $n = 3$ ).

## CHAPTER 4

A QUANTITATIVE SYNTHESIS OF FISH EFFECTS ON TEMPERATE STREAM  
ECOSYSTEM STRUCTURE AND FUNCTION

## SUMMARY

1. A number of individual studies have demonstrated the ability of fishes to affect stream ecosystem structure and function. However, a general consensus of the magnitude and direction of fish effects has not emerged. Furthermore, changing biotic and abiotic conditions in streams make it difficult to predict when and where fish effects will be strongest.
2. I conducted a quantitative synthesis (meta-analysis) of fish effects on structural (dissolved nutrient concentrations, periphyton biomass and composition) and functional (leaf decomposition and net ecosystem metabolism) characteristics of temperate stream ecosystems. In the analysis, I examined how fish effect sizes, or the magnitude of observed differences between the presence and absence of fishes, varied as a function of different biotic, abiotic, and methodological factors. Additionally, I compared how effect sizes differed between a frequently used but restrictive data extraction approach and a less restrictive data extraction approach that accounts for non-independence among observations.
3. Across 62 species included in the analysis, fishes had consistent positive effects on  $\text{NH}_4$ , soluble reactive phosphorus, and chlorophyll-*a*. The magnitude and direction of effect sizes differed among trophic guilds and taxonomic groups, whereas no significant differences were observed for abiotic and methodological

covariates. In some cases, the magnitude of effect sizes were comparable with native Pacific salmon, a taxa long regarded for having significant effects on the structure and function of freshwater habitats. The different data extraction approaches generally produced consistent results, but the restricted approach that limits the potential to extract multiple observations from a single study decreased the variance of effect size estimates, thereby raising the potential to identify significant effect sizes.

4. As one of the most conspicuous components of temperate stream ecosystems, fishes are likely to influence ecosystem structure and function given their trophic interactions, influence on nutrient dynamics, interactions with the benthic environment, and movement patterns. My results provide empirical support for this general idea and indicate the potential of a range of fishes – from small-bodied herbivores to large migratory species – to have substantial ecosystem-level effects in streams.

## INTRODUCTION

The role of abiotic factors (e.g., hydrology, temperature, light) in controlling stream ecosystem structure and function has long been recognized (Allan & Castillo, 2007). Over the past 30 years, stream ecologists have realized that lotic ecosystem dynamics may also be influenced by species interactions with other organisms and the physical environment (Vanni, 2010). Biotic control of stream ecosystem structure and function has been demonstrated for a wide range of taxa (e.g., Naiman, Melillo & Hobbie, 1986;



Strayer *et al.*, 1999; Crowl *et al.*, 2001), although questions remain about the ubiquity and magnitude of animal-mediated regulation of lotic ecosystem dynamics.

Among lotic organisms, fishes are especially likely to exert control over stream ecosystem structure and function given the variety of trophic interactions among them and other stream organisms, their influence on nutrient availability via sequestration and recycling, interactions with the benthic environment, and their relatively high mobility (Matthews, 1998; Vanni, 2002; Moore, 2006; Hall *et al.*, 2007; Vanni, 2010). In a classic example of fish effects in streams, Power, Matthews & Stewart (1985) found that piscivorous bass influenced the distribution of herbivorous prey fish among and within pools, an effect that subsequently controlled algal standing crops. Individual fish can also simultaneously exert top-down and bottom-up controls on primary production. For example, Knoll *et al.* (2009) experimentally separated direct (i.e., consumption) and indirect (i.e., nutrient recycling via excretion) effects of grazing catfishes on periphyton and demonstrated that these fishes affect algal biomass through both pathways. Beyond effects related to trophic interactions and nutrient cycling, bioturbation associated with feeding and spawning behaviors of some fishes significantly disturbs benthic habitats (Moore, 2006 and references therein). Finally, fish migrations between habitats present opportunities for nutrient introduction to recipient habitats via excretion (Chapter 2) or carcass decomposition (Cederholm *et al.*, 1999; Flecker *et al.*, 2010), as well as benthic disturbances related to spawning or feeding activity (Moore, Schindler & Scheuerell, 2004; Moore *et al.*, 2007).

While multiple case studies have demonstrated fish effects on stream ecosystem structure and function, these effects in streams are frequently context dependent (Gido *et*

*al.*, 2010; Vanni, 2010). For example, Power, Parker & Dietrich (2008) demonstrated that the occurrence of scouring winter floods regulated the extent of top-down control by fishes in a Northern California stream during summer baseflow conditions. In the absence of winter floods, predator-resistant grazers were not suppressed and thus top predators juvenile steelhead (*Oncorhynchus mykiss*) and roach (*Lavinia (Hesperoleucas) symmetricus*) had little or no influence on algal standing crops. Similarly, Gido *et al.* (2010) reported that the direction or magnitude of grazer (*Phoxinus erythrogaster*) or water-column minnow (*Cyprinella lutrensis*) effects on prairie stream structure and function were not consistent among experiments differing in terms of biotic, abiotic, and methodological characteristics. The lack of consistency makes it difficult to predict when and where fish effects in streams are likely to be largest (Gido *et al.*, 2010; Vanni, 2010), an uncertainty that is problematic given the considerable interest in links between freshwater biodiversity and ecosystem functioning (Dudgeon *et al.*, 2006; Vaughn, 2010). Thus, it is imperative to understand not only the functional roles of lotic fishes, but also the biotic and abiotic factors that modify such roles.

Given the number of existing case studies, a quantitative literature synthesis (i.e., meta-analysis) can be used to understand the ecosystem role of fishes in streams and the associated context dependency of fish effects. Science is often communicated through multiple independent studies that are linked by a common theme, and the ability to draw general conclusions or identify knowledge gaps from such a body of work in large part shapes advances in the field (Gurevitch & Hedges, 2001). Meta-analytic approaches have become increasingly popular in ecology due to their ability to quantitatively synthesize published studies and generate conclusions regarding the magnitude and

direction of effects related to a treatment or treatments of interest (Arnqvist & Wooster, 1995). Moreover, they may be used to identify important drivers of variation in effect size.

Here, I used meta-analysis to address the question of how fishes affect structural (dissolved nutrient concentrations, periphyton biomass and composition) and functional characteristics (leaf decomposition and net ecosystem metabolism) of stream ecosystems. In an effort to understand variation associated with fish effects in streams, I examined how effect sizes varied as a function of different biotic, abiotic, and methodological (i.e., those controlled by investigators) covariates. To put measured fish effects in context, I compared effects from this study with those from a similar study focused on native Pacific salmon (Janetski *et al.*, 2009), a taxa renowned for their ecological effects on stream ecosystems (Naiman *et al.*, 2002; Schindler *et al.*, 2003). Finally, I compared how effect sizes differed between two contrasting approaches for extracting data from published studies.

## METHODS

### *Data collection*

I searched the Institute of Scientific Information (ISI; Thomson Reuters) Web of Science online database and identified peer-reviewed papers published through June 2013 that quantified the effects of fishes on stream ecosystems. I also included studies referenced within articles obtained from this search or within relevant books (Matthews, 1998; Helfman *et al.*, 2009). Search terms included keyword combinations: (1) ‘fish\* or consumer\* or predat\* or graz\* or detrit\* or alg\* or herbiv\* or omnivor\* or carnivore\*’

and (2) ‘effect\* or impact\* or response\* or interaction\* or structur\* or propert\* or function\* or dynamic\* or direct or indirect or nutrient\* or invertebrate\* or alg\* or periphyton or producti\* or resource’ and (3) ‘ecosystem\* or freshwater\* or river\* or stream\* or creek\* or benth\* or aquatic’ in the article. The search returned a large (> 90,000) number of papers, so I screened results by first reviewing titles and then by reviewing abstracts. In addition to studies identified by this search, I also considered peer-reviewed articles published online between July and December 2013. Cumulatively, the literature search produced 76 viable papers, and I included data from two dissertations, bringing the total number of data sources to 78 (see Appendix A-2).

I used several criteria to identify studies appropriate for my analysis. First, I restricted my focus to studies conducted at temperate latitudes (23.5-66.5° N/S) due to the volume of fish-related studies done in this region. Within this geographic range, I did not consider studies of adult anadromous Pacific salmon conducted within their native ranges because these fishes were the subject of a previous meta-analysis (i.e., Janetski *et al.*, 2009). These criteria did, however, allow me to include studies of juvenile (i.e., freshwater) Pacific salmon in any temperate location, as well as studies of introduced adult Pacific salmon outside their native range (e.g., the Great Lakes). I included papers that focused on single species (e.g., Bertrand & Gido, 2007), fish assemblages (e.g., Effenberger *et al.*, 2011), or the addition or removal of a single species from a fish assemblage (e.g., Baxter *et al.*, 2004). Given my interest in examining stream ecosystem responses to fishes, I restricted my focus to studies conducted in flowing waters, regardless of whether study systems were experimental or natural. Finally, included

studies measured differences in one or more structural or functional characteristics (Table 4-1).

#### *Data extraction*

I extracted means, standard deviations, and sample sizes for control and treatment groups for each independent observation within a given study. When necessary, I used the data-extraction software WebPlotDigitizer v2.5 (<http://arohatgi.info/WebPlotDigitizer/>) to extract data presented in figures. In some instances, I obtained raw data from authors. If appropriate data could not be extracted or studies were not replicated, they were omitted. I defined treatment groups as those units (e.g., stream reaches, artificial channels, in-stream mesocosms) containing fish, whereas control groups lacked fish in either space or time. I considered multiple observations to be independent within a single study when they differed by one or more of my covariates of interest (Gurevitch & Hedges, 1999, 2001; Table 4-2). For example, I extracted six independent observations from a study conducted by Cheever & Simon (2009) over three seasons with two different fish species.

For each independent observation in a study, data were extracted for as many as ten covariates and seven dependent variables (Tables 4-1 & 4-2). When possible, I used two of the original dependent variables to calculate an eighth dependent variable (periphyton photosynthetic index,  $PPI = \text{chlorophyll-}a / \text{ash-free dry mass [AFDM]}$ ). Individual studies generally contained far less than the maximum of 18 possible variables. When fish biomass was not reported explicitly in a study, I attempted to use appropriate areas (e.g., study reach, experimental unit), fish abundance and per-capita mass to calculate it

(biomass = abundance  $\times$  per-capita mass / area). When necessary, I used FishBase (Froese & Pauly, 2013) or data from other included studies to determine per-capita mass. I recorded the taxonomy (family and species) of individual species, and also consolidated data for two taxonomic groups of interest: stream resident salmonids (“resident salmon” hereafter; i.e., brown, brook, cutthroat, and rainbow trout, Dolly Varden, Masu salmon, and juvenile anadromous salmon) and non-native migratory salmonids (“non-native salmon” hereafter; i.e., adfluvial adult *Oncorhynchus* spp. outside their native range). When provided, I used diet analyses given in each paper to assign species to trophic guilds. If such analyses were not included, I assigned trophic guilds based on diet information available through FishBase (Froese & Pauly, 2013). I assigned individual species to the omnivore guild when both invertebrates and algae made up at least 20% (by volume) of their diet. Additionally, I used the omnivore guild for assemblages with multiple species occupying different trophic guilds (e.g., Schneck, Schwarzbald & Melo, 2013). One trophic guild (“none”) included non-feeding migratory fishes (Araujo, Ozorio & Antunes, 2013). One season category (“multiple”) included data collected over a period spanning more than one season. I classified experimental designs as natural (e.g., reaches upstream and downstream of a fish barrier, comparisons of fish and fishless streams), artificial (strictly limited to artificial stream channels), or combination (e.g., fish enclosure/exclosure cages in natural streams). When possible, I distinguished observations based on whether or not protection from possible fish grazing existed (“protected” or “unprotected”). One nutrients category (“enriched”) reflected concentrations artificially elevated above ambient levels. Finally, I interpreted time as

the number of days since fish were introduced to study units, and only included day 0 data if it was clear that associated sampling was done following fish introductions.

### *Data analysis*

For my effect size metric, I used the log response ratio ( $L$ ), which is defined as the logarithm base  $e$  ( $\log_e$  or  $\ln$ ) of the treatment group mean ( $X_{TRMT}$ ) divided by the control group mean ( $X_{CTRL}$ ):  $L = \log_e (X_{TRMT}/X_{CTRL})$  (Cooper, Walde & Peckarsky, 1990; Hedges, Gurevitch & Curtis, 1999). Values of  $L > 0$  indicate a positive effect of the treatment (i.e., fish) on the response variable, whereas negative values of  $L$  indicate a negative effect. Additionally, the larger the absolute value of  $L$  is, the larger the magnitude of the treatment effect. I chose to use  $L$  as the effect size estimate for two reasons. First, it indicates ecological significance because it measures the proportional response generated by the treatment (Hedges *et al.*, 1999). Second, one of my goals was to compare my results with Janetski *et al.* (2009), who also used  $L$  to characterize ecosystem impacts associated with anadromous Pacific salmon.

The use of  $L$  is problematic when values of group means are  $\leq 0$ , as can happen for net ecosystem metabolism (NEM), where negative values indicate net energy loss from a stream ecosystem (Bott, 2006). Thus, I used Hedges'  $d$  to estimate fish effects on NEM. Hedges'  $d$  is defined as the difference between treatment and control group means divided by the pooled standard deviation:  $d = [(X_{TRMT} - X_{CTRL})/s_p] \times J$  (Hedges & Olkin, 1985), where  $s_p$  is the pooled standard deviation and  $J$  is an adjustment for bias due to small sample size (see Gurevitch & Hedges, 2001 for formulas).

Ecological meta-analyses frequently restrict data extraction when multiple observations are reported in an individual study. For example, previous analyses of time series data have used data from the final sampling date (e.g., Shurin *et al.*, 2002; Borer *et al.*, 2005; Marczak, Thompson & Richardson, 2007; Gruner *et al.*, 2008), dates of maximum difference between control and group means (e.g., Janetski *et al.*, 2009; Poore *et al.*, 2012), or computed grand means using individual sampling event means (e.g., Feminella & Hawkins, 1995). Such restrictions are often argued from ecological perspectives (e.g., a desire to measure maximum effect) and minimize the risk of non-independence among observations taken from a single study. However, they also reduce the size of the dataset, potentially obscuring important nuances (e.g., temporal variability) associated with treatment effects.

Due to this potential concern, I compared a typical restricted approach (restricted approach) with an alternative method that provided greater extraction flexibility by explicitly accounting for multiple forms of dependence among individual observations (dependence approach). The dependence approach accounted for sampling and hierarchical dependence among individual observations using a hierarchical Bayes linear model (see Stevens & Taylor, 2009 for computational details and Kulmatiski *et al.*, 2008 for an ecological application). Sampling dependence occurs when multiple treatment groups are compared with a single control group (e.g., Katano *et al.*, 2003) and hierarchical dependence occurs when multiple effect sizes are calculated for an individual study (e.g., calculate effect sizes for each sampling event in time-series data). Such dependence is problematic if not accounted for because either type can violate the



assumption of independence among observations, thereby inflating the significance levels of statistical tests and underestimating confidence intervals (Gurevitch & Hedges, 2001).

In contrast to the dependence approach, the restricted approach limited extraction to observations that varied by one or more of the designated categorical covariates subject to strict control by authors (e.g., Bolnick & Preisser, 2005; Marczak *et al.*, 2007). Most notably, this approach eliminated the possibility of using multiple observations from a single study that varied only with respect to (1) time since fish introductions or (2) density of a single species. When considering multiple observations from a single study with the restricted approach, I selected the single observation with maximum difference between control and treatment means because I wanted to compare my results with those of Janetski *et al.* (2009). On average, the restricted approach thinned original data sets (i.e., those used in the dependence approach) by  $43 \pm 13\%$  (mean  $\pm$  SD,  $n = 8$ ), although there was variation among responses (range = 25-71% reduction; Table 4-1).

Regardless of the data extraction approach used, I calculated mean effect size estimates in a hierarchical manner (after Gurevitch *et al.*, 1992; Marczak *et al.*, 2007), weighting individual effect sizes according to the error and sample size reported in each study (Gurevitch & Hedges, 2001). First, I determined overall mean effect sizes for each individual response, and then I calculated mean effect sizes for each category of different categorical covariate (Gurevitch & Hedges, 2001). I estimated 95% confidence intervals for mean effect sizes as means  $\pm$  2 SE, and interpreted confidence intervals that did not overlap zero as statistically significant effect sizes (Gurevitch *et al.*, 1992). I used weighted least-squares regression to test for relationships between effect size and (1) time, and (2) fish biomass (Rosenberg, Adams & Gurevitch, 2000), and I performed

regressions for both data extraction approaches. All analyses were done with the ‘metahdep’ package (Stevens & Nicholas, 2013) in R 3.0.1 (R Development Core Team 2013).

## RESULTS

Overall, 59 study locations were represented in the dataset, 25% of which were associated with multiple data sources. By far, the greatest number of study locations and observations came from North America, although data from South America, Europe, Asia, and Oceania were also included (Fig. 4-1). The analysis included 62 species, 66% of which were represented by a single data source, and 21 families. Cyprinidae ( $n=18$  species) and Salmonidae ( $n=9$  species) were the most frequently studied families, and the most commonly studied species came from these two families – central stonerollers (*Campostoma anomalum*,  $n=10$ ) and brown trout (*Salmo trutta*,  $n=13$ ). The number of observations taken from an individual data source ranged widely (1-69) and depended on the data extraction approach (Table A-4). Additionally, there was considerable variation among responses with respect to the total number of observations (Table 4-1). An examination of effect size distributions for response variables did not imply significant problems associated with publication bias, as estimates clustered near zero and tailed off in both directions, regardless of which data extraction approach was used and which response was considered (Fig. A-2).

### *Overall effect size estimates*

The broad group of fishes considered in the analysis had relatively small effects on temperate stream ecosystem structure and function (Fig 4-2). Overall mean effect size

estimates were positive for  $\text{NH}_4$ , SRP, and chlorophyll-*a*, and in some cases these estimates were significantly different from zero. In contrast, the effect of fishes on  $\text{NO}_3$ , AFDM, PPI, leaf decomposition, and NEM was not significantly different from zero.

*Overall fish effect sizes: comparison of data extraction approaches*

The different data extraction approaches had subtle effects on overall effect size estimates: the restricted approach tended to decrease or have minimal effects on the variance around mean effect size estimates. Consequently, there were more responses with statistically significant effect sizes using the restricted approach ( $n = 3$ ) than using the dependence approach ( $n = 1$ ; Fig. 4-2). With the exception of NEM, the two data extraction approaches produced consistent (i.e., both positive or negative) estimates of mean effect size for the different responses (Fig. 4-2). Additionally, for the analyzed data there was not a consistent bias introduced by either approach, evidenced by the fact that values of the ratio of mean  $L$  between the two approaches ( $L_{\text{RESTRICTED}}:L_{\text{DEPENDENCE}}$ ) were between 0.05 and 1.51 (mean  $\pm$  SE =  $0.84 \pm 0.18$ ,  $n = 8$ ).

*Overall fish effect sizes: comparisons with native Pacific salmon*

The direction of fish effects was generally similar between native Pacific salmon and fishes included in this study, but salmon effect sizes were much larger, especially for dissolved nutrient concentrations (Fig. 4-2). The ratio of mean  $L$  between the Janetski *et al.* (2009) results and my results ranged from 2.83-13.60 ( $6.31 \pm 1.97$ ,  $n = 5$ ). The one response that did exhibit differences in the directionality of fish effects was AFDM. Native Pacific salmon increased AFDM, whereas mean effect sizes for AFDM were not statistically different from zero in this study (Fig. 4-2).

*Effect size variability: the role of covariates*

Among the covariates considered, fish effect sizes exhibited the greatest variability among biotic variables. Distinctions among taxonomic groups revealed clear differences in effect sizes among non-native salmon, resident salmon, and stonerollers (Fig. 4-3). Similar to overall fish effects (i.e., Fig. 4-2), non-native salmon had positive mean effect sizes on  $\text{NH}_4$  and SRP that were statistically different from zero (restricted approach). Likewise, non-native salmon had minimal effects on  $\text{NO}_3$ . However, this group of fishes had strong negative effects on chlorophyll-*a* (Fig. 4-3 A), which contrasts with the positive overall fish effect as well as effects of native Pacific Salmon. Comparisons with the Janetski *et al.* (2009) results indicated the magnitude of non-native salmon effects on chlorophyll-*a* was 46% larger than Pacific salmon in their native streams (Fig. 4-3 A). In contrast, differences between the dissolved nutrient effects of non-native salmon and native Pacific salmon were the same as those observed in the overall dataset (i.e., Pacific salmon had much greater positive effects; Fig. 4-2).

Comparisons of effect sizes between resident salmon and stonerollers indicated substantial effects of these taxonomic groups, both of which impacted periphyton biomass, but in different directions. Resident salmon increased both chlorophyll-*a* and AFDM, whereas stonerollers decreased AFDM and did not affect chlorophyll-*a* (Fig. 4-3 B-C). The extent to which resident salmon increased AFDM ( $L = 0.94 \pm 0.31$ ; restricted approach) was 21% greater than their effect on chlorophyll-*a* but 14% less than the magnitude of stoneroller effects on AFDM. In terms of effects on ecosystem processes, resident salmon had minimal effects on leaf decomposition, which was similar to the

overall fish effect. In contrast, stonerollers had relatively strong effects on one aspect of ecosystem function, generally decreasing NEM.

The magnitude and direction of effect sizes also differed among trophic guilds, particularly for periphyton biomass and NEM. Non-feeding migratory fishes (trophic guild = “none”) decreased both chlorophyll-*a* and AFDM and herbivorous fishes had negative effects on AFDM. In contrast, invertivorous fishes increased both measures of periphyton biomass (Fig. 4-4 D-E). Herbivorous fishes, which included stonerollers, decreased NEM (restricted approach; Fig. 4-4 H). In general, omnivorous fishes had positive effects on chlorophyll-*a* and strong positive effects on NEM, although the NEM effect sizes were associated with very small sample sizes (Fig. 4-4 H).

Although one would intuitively expect the magnitude of fish effects to increase with fish biomass, I found no evidence for this relationship. Fish biomass ( $\text{g m}^{-2}$ ) was inversely related to only  $\text{NO}_3$ , chlorophyll-*a*, and PPI *L*, indicating that effect sizes actually decrease with biomass (Fig. 4-5). In each case, regression lines crossed the threshold of  $L = 0$  (i.e., fish have no effect), suggesting the directionality of fish effects may depend on biomass. For the most part, there was agreement between results produced by the two data extraction approaches for these three relationships, although the statistical weight of evidence (i.e., *P* values) differed between the dependence and restricted approaches. Overall, the amount of variation explained by biomass was relatively low ( $R^2 = 0.06\text{-}0.29$ ; Fig. 4-5).

In contrast to the distinctions associated with biotic covariates, variation in effect sizes among abiotic and methodological covariates was far less pronounced. In some cases, comparisons between or among covariate levels were uninformative due to low

sample sizes. For example, only three of the chlorophyll-*a* observations (1%; dependence approach) were associated with studies that protected substrates from potential fish grazing. Moreover, any effects presumably associated with these covariates were confounded with taxonomic groups or trophic guilds. For example, study design appeared to be an important influence on chlorophyll-*a* (restricted approach): in natural experiments, the mean effect of fishes was not different from zero ( $L = -0.27 \pm 0.23$ ,  $n = 30$ ), whereas mean effect sizes were positive for strictly experimental ( $L = 0.52 \pm 0.17$ ,  $n = 55$ ) and combination ( $L = 0.37 \pm 0.18$ ,  $n = 50$ ) approaches. However, 63% of the natural experiment observations were associated with non-native salmon, a taxonomic group that negatively affects chlorophyll-*a* (Fig. 4-3 A) and that was completely absent from strictly experimental and combination observations. Likewise, a striking difference between chlorophyll-*a* effects measured on artificial ( $L = 0.51 \pm 0.15$ ,  $n = 74$ ) vs. natural ( $L = 0.03 \pm 0.16$ ,  $n = 61$ ; restricted approach for all data) tiles was largely related to trophic guilds. 44% of natural substrate observations were associated with trophic guilds that had negative or equivocal effects on chlorophyll-*a* (non-feeding migrants and herbivores; Fig. 4-4 D), whereas 85% of artificial substrate observations were associated with guilds that had positive effects on chlorophyll-*a* (invertivores and omnivores; Fig. 4-4 D).

Effect sizes did not demonstrate strong temporal patterns (Fig. 4-6). Much like effects related to fish biomass, effect sizes were significantly related to time for a subset of the responses.  $\text{NH}_4$  (positive),  $\text{NO}_3$  (negative), and leaf decomposition (negative) were all related to time, but these relationships were only significant when the restricted data

extraction approach was used. Additionally, time explained very little of the observed variation in effect sizes ( $R^2 = 0.16-0.19$ ; Fig. 4-6).

## DISCUSSION

My analysis represents the most comprehensive quantitative synthesis of fish effects in streams to date, taking into account a wide variety of species, community, and ecosystem responses, as well as potential covariates. As such, it is a valuable contribution to a literature increasingly populated by similar syntheses of biotic control in lotic ecosystems (e.g., Feminella & Hawkins, 1995; Englund, Sarnelle & Cooper, 1999; Hillebrand, 2002; Janetski *et al.*, 2009). Across all 62 species included in the study, I observed consistent positive effects of fishes on dissolved nutrient concentrations ( $\text{NH}_4$  and SRP) and periphyton biomass (as chlorophyll-*a*). Additionally, I found that variation in these and other ecosystem responses, where effects were more muted, was better explained by biotic variables (trophic guild, taxonomic groups) than by abiotic and methodological covariates. Finally, my analysis illustrated potential consequences associated with different meta-analysis data extraction approaches, demonstrating that analytical choices can influence final conclusions in meta-analyses.

### *Overall effect sizes*

The relatively low *L* values I observed are not surprising considering the wide variety of fishes included in the analysis. In some cases, included fishes had contrasting effects on one or more of the response variables, therefore lowering the likelihood of observing consistent directionality in effect size estimates. For example, resident salmon and stonerollers both affected periphyton AFDM, but the directions of their effects were

opposite (Fig. 4-3 B-C). Despite the potential for offsetting interactions like these, there were some responses that illustrated consistently positive effects of fishes. Fishes in streams tended to increase both  $\text{NH}_4$  and SRP, which can likely be attributed to the recycling of nutrients via excretion (Vanni, 2002). The tendency of fishes to excrete inorganic nitrogen as  $\text{NH}_4$  may also help to explain why there was not also a positive effect of fishes on  $\text{NO}_3$  concentrations (Vanni, 2002). In addition to these positive effects on dissolved nutrients, fishes tended to elevate algal biomass (i.e., chlorophyll-*a*). This result indicates that positive fish effects on algal biomass, whether by trophic cascades in streams (Power, 1990a; Strong, 1992; Shurin *et al.*, 2002) or fertilization via nutrient delivery (e.g., Knoll *et al.*, 2009), were stronger or more common in this dataset than negative fish effects commonly associated with grazing.

Overall effect size estimates for structural responses tended to be greater or have smaller variance than average effects on functional responses, calling into question the importance of fishes on temperate stream ecosystem processes. Relatively small effect sizes could be associated with measurements of stream ecosystem processes in the presence of a relatively low number of species, none of which substantially affect the response of interest. Such a situation would tend to produce effect size estimates of low magnitude and variance, as seen for leaf decomposition (Fig. 4-2). However, the leaf decomposition observations ( $n = 43$ ; dependence approach) encompassed 16 different species, suggesting that the fishes included in this dataset are unlikely to substantially affect leaf decomposition rates in temperate streams. However, detritivorous fishes were absent from the dataset, which limits the generality of the decomposition results.

Alternatively, some individual species, taxonomic groups, or functional groups may have



substantial effects on ecosystem processes that are obscured when effect sizes are calculated for a larger group (e.g., the overall effect size estimates). This scenario likely applies to the NEM data, where significant negative effects related to stonerollers (Fig. 4-3 C) were masked by contrasting effects of other species.

*Comparisons with native Pacific salmon and the influence of taxonomic and trophic distinctions*

There are several possible reasons why dissolved nutrient effect sizes for the overall dataset and non-native salmon were both substantially lower than those reported for native Pacific salmon. All else being equal, fish nutrient effects should be strongest during periods of relatively low flow when discharge-related transport and dilution of fish-derived nutrients are minimized (Peterson *et al.*, 2001). The fact that 83% of the observations used to determine dissolved nutrient effect sizes were from baseflow or drought conditions suggests that the much stronger nutrient effects associated with native Pacific salmon are related to unique characteristics of these fishes and the freshwater systems where they spawn. Anadromous salmonids can affect dissolved nutrient concentrations by three mechanisms – excretion, gamete release, and carcass decomposition, elevating the potential for large nutrient effect sizes (Gende *et al.*, 2002). In contrast, lower nutrient effect sizes would be expected for species that do not experience synchronous mortality (e.g., after spawning). In this study, both the overall (70%) and non-native salmon (89%) datasets had considerable numbers of observations associated with salmonid species that do experience similarly high rates of post-spawning mortality. Thus, it is likely that factors other than carcass decomposition were driving the

differences in nutrient effect sizes between native Pacific salmon and other fishes (i.e., overall dataset and non-native salmon).

Two characteristics of native anadromous salmon migrations that are more likely to be different from those in the dataset used for this analysis are migrant biomass and background nutrient levels. Janetski *et al.* (2014) reported an average salmon biomass of nearly 1000 g m<sup>-2</sup> in native streams, which is approximately three times higher than average biomass in the cumulative (307 ± 46 g m<sup>-2</sup>; *n* = 126) and non-native salmon (332 ± 55 g m<sup>-2</sup>; *n* = 99) datasets. Likewise, ambient nutrient concentrations in native salmon streams are frequently very low compared with many regions where Pacific salmon have been introduced (Ivan, Rutherford & Johengen, 2011; Janetski *et al.*, 2014). Thus, it is less likely that non-native salmon will produce large relative increases in water column nutrient concentrations.

Although nutrient effects were relatively low for fishes in this study, other results revealed that specific groups of fishes can have effects on periphyton biomass (chlorophyll-*a* or AFDM) that are similar in magnitude to native Pacific salmon. For example, non-native salmon generally reduced chlorophyll-*a* through disturbance associated with their spawning activity, and these effects were stronger (i.e., larger absolute value of *L*) than those associated with Pacific salmon (Fig. 4-3 A). Effects of resident salmon on chlorophyll-*a* and AFDM were similar in direction and magnitude to those for native Pacific salmon, but the mechanism underlying the effect may be different. Benthic invertebrates frequently constitute a significant portion of resident salmon diets (Behnke, 1992). Thus, this group of fishes is more likely than migrating native Pacific salmon to decrease grazing invertebrate abundance or activity, increasing

algal biomass through a trophic cascade (e.g., McIntosh & Townsend, 1996), evidenced by the similarity of periphyton effects between resident salmon (Fig. 4-3 B) and invertivorous fishes (Fig. 4-4 D-E). In contrast, positive effects of native Pacific salmon on periphyton are more likely associated with bottom-up fertilization mechanisms related to the release of marine-derived nutrients (Gende *et al.*, 2002). Additionally, both groups of fishes may enhance periphyton biomass by recycling dissolved nutrients via excretion (Vanni, 2002).

Like non-native and resident salmon, stonerollers exhibited the capacity to have substantial effects on stream structure and function. Although stonerollers did not affect chlorophyll-*a*, they consistently lowered AFDM. Additionally, the magnitude of their effect on AFDM was, on average, greater than values for native Pacific salmon (Janetski *et al.*, 2009). In addition to negative effects on AFDM, stonerollers and the more general group of herbivorous fishes both decreased NEM (Figs. 4-3 & 4-4), an effect on ecosystem function that has also been reported for anadromous salmon (Holtgrieve & Schindler, 2011). By reducing AFDM but not chlorophyll-*a*, herbivorous fishes like stonerollers can increase the proportion of algal biomass in the periphyton (e.g., Taylor, Back & King, 2012), making reductions in primary production less likely. Therefore, the observed NEM decreases associated with stonerollers and grazing fishes are more likely linked with increased heterotrophic activity (i.e., ecosystem respiration) than reduced primary production. If true, this contrasts theoretical predictions that grazing fishes would only moderately influence stream heterotrophs, which are found primarily in subsurface regions not directly accessed by these fishes (Gido *et al.*, 2010).

### *The influence of biomass and time*

Fish biomass and time both had significant effects on effect size for a subset of responses, but neither covariate explained a substantial proportion of the observed variation in effect size (Figs. 4-5 & 4-6). Nevertheless, observed relationships between periphyton responses (chlorophyll-*a* and PPI) and fish biomass suggest that fishes may have positive effects on periphyton at low biomass and negative effects at higher biomass (Fig. 4-5 D,F). Although this relationship is counterintuitive, precedents do exist. For example, the net effect of native Loricariid catfishes on algal standing crops shifted from depletion at high biomass to enhancement at low biomass due to the removal of growth-inhibiting sediment by the fishes (Power, 1990b). Whether such biomass-mediated shifts in the directionality of fish effects are limited to interactions between grazing fishes and periphyton remains unknown, however. Variation in fish effects has also been observed over time in individual studies of grazing fishes (e.g., Taylor *et al.*, 2012), but the amount of variation in the overall dataset prevented detection of consistent relationships between effect sizes and time.

### *Methodological considerations in meta-analysis*

The use of multiple data extraction approaches permitted an evaluation of the influence of data selection criteria on effect size estimates and overall conclusions drawn from my analysis. While such considerations are not novel (e.g., Englund *et al.*, 1999; Meissner & Muotka, 2006), the dependence approach employed here allowed for a more complete extraction of data than frequently occurs in ecological meta-analyses. The most important contrast between the two data extraction approaches was that the restricted

approach, which is typically used in ecology, tended to produce lower variance around mean effect size estimates, thereby leading to different conclusions about fish effects in streams. However, this effect of the restricted approach on the variance around mean effect size estimates is likely to be a function of the data used in an analysis. For my analysis, the application of the restricted data extraction approach largely eliminated observations from individual studies that were collected at different times and fish biomass levels. This approach generally reduced sample variance, implying there was considerable variation in effect sizes that was associated with these two covariates in my dataset, which is not necessarily going to be true in all ecological scenarios. More generally, restricted data extraction approaches sometimes select the most extreme effect sizes (e.g., the time point of maximum difference between treatment and control groups; Janetski *et al.*, 2009), which can produce a bias toward finding significant treatment effects. This approach could reduce variation if extreme effects are consistently positive or negative, but could also increase variation if the directionality of effects is inconsistent.

My use of different data extraction approaches also enabled identification of the most robust patterns associated with fish ecosystem effects in temperate streams. For example, both the restricted and dependence approach indicated that fishes have positive effects on  $\text{NH}_4$ , whereas there is some evidence, but less certainty, regarding similar fish effects on SRP and chlorophyll-*a* (Fig. 4-2). It was not especially surprising that the different data extraction approaches led to different conclusions in some cases, but the widespread use of restrictive data extraction approaches in ecological meta-analyses does raise questions regarding methodological choices. For analyses specifically targeted to detect the

extremities of treatment effects, the use of restrictive data extraction approaches that select maximum effects is entirely appropriate. In contrast, methods that allow for more complete data extraction (i.e., dependence approach) may be better suited to address the generality of treatment effects and are likely applicable to a wide range of ecological questions. However, more comparisons of data extraction approaches are needed before final conclusions can be reached.

#### *Limitations and recommendations for future work*

The process of constructing the dataset for this analysis revealed several important limitations associated with the current understanding of fish effects in streams. The number of species included in the analysis (62) is the largest of any quantitative synthesis of fish effects in streams, but is still minuscule relative to the total number of fish species worldwide (> 30,000; Froese & Pauly, 2013). Although many fish species are not found in streams, it is clear that the functional role of a great number of lotic fishes have not been studied at this point, and that many studies have been focused on species of economic importance (i.e., the Salmonidae family). There is also a strong geographical bias among the selected studies (Fig. 4-1), a common phenomenon in the ecological literature (e.g., Pysek *et al.*, 2008), despite a designated focus on temperate streams. Collectively, these taxonomic and geographical biases result in relatively low diversity among study systems in the dataset. Additionally, most of the included studies were carried out in small natural or artificial streams (i.e., relatively low discharge, wetted width, etc.). While working in small systems is tractable, a predominant focus on those types of systems necessarily limits the ability to understand dynamics in larger systems

(Tank *et al.*, 2008). Without question, expanding the taxonomic and geographic extent of stream fish studies would extend inferential capability regarding fish effects, as would working in a broader group of study systems.

Database construction also revealed that our understanding of fish effects would be more complete if quantitative information about potential biotic and abiotic covariates was included in studies more frequently. For example, I was limited to a categorical classification of discharge because so few studies reported numerical measures.

Likewise, using reported biomass levels would be far more preferable than having to rely on estimates. Very few papers provided background nutrient concentrations, which may be substantial influences on the extent to which fish-derived nutrients are important to ecosystem nutrient dynamics (Flecker *et al.*, 2010). Benthic disturbance associated with fish activity appears to be largely regulated by particle size distributions (e.g., Holtgrieve *et al.*, 2010), but most papers included in my meta-analysis reported only qualitative information regarding substrates, which prevented me from testing the influence of substrate size. By including as much information as possible about these and other factors capable of mediating fish effects, our ability to understand and predict fish effects in streams would be strengthened.

## CONCLUSION

Fishes are one of the most conspicuous components of temperate stream ecosystems and are likely to influence community structure and ecosystem function given their trophic interactions, influence on nutrient dynamics, interactions with the benthic environment, and movement patterns. My analysis identified several consistent effects of

a diverse array of fishes in temperate streams. Furthermore, it illustrated the potential for individual species or taxonomic groups to have effects similar in magnitude to anadromous Pacific salmon, which have long been regarded as the archetypal illustration of fish effects in freshwater habitats. Consequently, it will likely be profitable to expand research efforts aimed at understanding functional roles of fishes in streams, with important implications for biodiversity-ecosystem functioning and continued provision of valuable ecosystem services.

#### LITERATURE CITED

- Allan J.D. & Castillo M.M. (2007). *Stream Ecology: Structure and Function of Running Waters*. 2<sup>nd</sup> edn., Springer, Dordrecht, The Netherlands.
- Araujo M.J., Ozorio R.O. & Antunes C. (2013) Energetic aspects of spawning migrations and their implications for the management of southern European diadromous fish populations. *Limnetica*, **32**, 303-320.
- Arnqvist G. & Wooster D. (1995) Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology and Evolution*, **10**, 236-240.
- Baxter C.V., Fausch K.D., Murakami M. & Chapman P.L. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85**, 2656-2663.
- Behnke R.J. (1992) *Native Trout of western North America*. American Fisheries Society Monograph 6. American Fisheries Society, Bethesda, MD.
- Bertrand K.N. & Gido K.B. (2007) Effects of the herbivorous minnow, southern redbelly dace (*Phoxinus erythrogaster*), on stream productivity and ecosystem structure. *Oecologia*, **151**, 69-81.
- Bolnick D.I. & Preisser E.L. (2005) Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology*, **86**, 2771-2779.
- Borer E.T., Seabloom E.W., Shurin J.B., Anderson K.E., Blanchette C.A., Broitman B. *et al.* (2005) What determines the strength of a trophic cascade? *Ecology*, **86**, 528-537.



- Bott T.L. (2006) Primary productivity and community respiration. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp.663-690. Academic Press, San Francisco, CA.
- Cederholm C.J., Kunze M.D., Murota T. & Sibatani A. (1999) Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries*, **24**, 6-15.
- Cheever B.M. & Simon K.S. (2009) Seasonal influence of brook trout and mottled sculpin on lower trophic levels in an Appalachian stream. *Freshwater Biology*, **54**, 524-535.
- Cooper S.D., Walde, S.J. & Peckarsky B.L. (1990) Prey exchange rates and the impact of predators on prey populations in streams. *Ecology*, **71**, 1503-1514.
- Crowl T.A., McDowell W.H., Covich A.P. & Johnson S.L. (2001) Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology*, **82**, 775-783.
- Dudgeon D., Arthington A.H., Gessner M.O., Kawabata Z-I., Knowler D.J., Leveque C. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163-182.
- Effenberger M., Diehl S., Gerth M. & Matthaei C.D. (2011) Patchy bed disturbance and fish predation independently influence the distribution of stream invertebrates and algae. *Journal of Animal Ecology*, **80**, 603-614.
- Englund G., Sarnelle O. & Cooper S.D. (1999) The importance of data-selection criteria: meta-analyses of stream predation experiments. *Ecology*, **80**, 1132-1141.
- Feminella J.W. & Hawkins C.P. (1995) Interactions between stream herbivores and periphyton: a quantitative analysis of past experiments. *Journal of the North American Benthological Society*, **14**, 465-509.
- Flecker A.S., McIntyre P.B., Moore J.W., Anderson J.T., Taylor B.W. & Hall R.O. (2010) Migratory fishes as material and process subsidies in riverine ecosystems. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 559-592.
- Froese R. & Pauly D. Editors. (2013) FishBase. Available: [www.fishbase.org](http://www.fishbase.org) (December 2013).
- Gende S.M., Edwards R.T., Willson M.F. & Wipfli M.S. (2002) Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*, **52**, 917-928.

- Gido K.B., Bertrand K.N., Murdock J.N., Dodds W.K. & Whiles M.R. (2010) Disturbance-mediated effects of fishes on stream ecosystem processes: concepts and results from highly variable prairie streams. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 593-617
- Gruner D.S., Smith J.E., Seabloom E.W., Sandin S.A., Ngai J.T., Hillebrand H. *et al.* (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters*, **11**, 740-755.
- Gurevitch J., Morrow L.L., Wallace A. & Walsh J.S. (1992) A meta-analysis of competition in field experiments. *American Naturalist*, **140**, 539-572.
- Gurevitch J. & Hedges L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142-1149.
- Gurevitch J. & Hedges L.V. (2001) Meta-analysis: combining the results of independent experiments. In: *Design and Analysis of Ecological Experiments* (Eds S.M. Scheiner & J. Gurevitch), pp. 347-369. Oxford University Press, New York, NY.
- Hall R.O., Koch B.J., Marshall M.C., Taylor B.W. & Tronstad L.M. (2007) How body size mediates the role of animals in nutrient cycling in aquatic ecosystems. In: *Body Size: The Structure and Function of Aquatic Ecosystems*. (Eds A.G. Hildrew, D. Raffaelli & R. Edmonds-Brown). Cambridge University Press, New York, NY, 286-305.
- Hedges L.V., Gurevitch J. & Curtis P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150-1156.
- Helfman G., Collette B.B., Facey D.E. & Bowen B.W. (2009) *The Diversity of Fishes: Biology, Evolution, and Ecology*. Wiley, Hoboken, NJ.
- Hillebrand H. (2002) Top-down versus bottom-up control of autotrophic biomass – a meta-analysis on experiments with periphyton. *Journal of the North American Benthological Society*, **21**, 349-369.
- Holtgrieve G.W., Schindler D.E., Gowell C.P., Ruff C.P. & Lisi P.J. (2010) Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology*, **55**, 2598-2611.
- Holtgrieve G.W. & Schindler D.E. (2011) Marine-derived nutrients, bioturbation, and ecosystem metabolism: reconsidering the role of salmon in streams. *Ecology*, **92**, 373-385.

- Ivan L.N., Rutherford E.S. & Johengen T.H. (2011) Impacts of adfluvial fish on the ecology of two Great Lakes tributaries. *Transactions of the American Fisheries Society*, **140**, 1670-1682.
- Janetski D.J., Chaloner D.T., Tiegs S.D. & Lamberti G.A. (2009) Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**, 583-595.
- Janetski D.J., Chaloner D.T., Moerke A.H., Levi P.S. & Lamberti G.A. (2014) Novel environmental conditions alter subsidy and engineering effects by introduced Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 502-513.
- Katano O., Aonuma Y., Nakamura T. & Yamamoto S. (2003) Indirect contramensalism through trophic cascades between two omnivorous fishes. *Ecology*, **84**, 1311-1323.
- Knoll L.B., McIntyre P.B., Vanni M.J. & Flecker A.S. (2009) Feedbacks of consumer nutrient recycling on producer biomass and stoichiometry: separating direct and indirect effects. *Oikos*, **118**, 1732-1742.
- Kulmatiski A., Beard K.H., Stevens J.R. & Cobbold S.M. (2008) Plant-soil feedbacks: a meta-analytical review. *Ecology Letters*, **11**, 980-992.
- Marczak L.B., Thompson R.M. & Richardson J.S. (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology*, **88**, 140-148.
- Matthews W.J. (1998) *Patterns in Freshwater Fish Ecology*. Chapman & Hall, San Francisco, CA.
- McIntosh A.R. & Townsend C.R. (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior? *Oecologia*, **108**, 174-181.
- Meissner K. & Muotka T. (2006) The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology*, **75**, 421-433.
- Moore J.W. (2006) Animal ecosystem engineers in streams. *BioScience*, **56**, 237-246.
- Moore J.W., Schindler D.E. & Scheuerell M.D. (2004) Disturbance of freshwater habitats by anadromous salmon in Alaska. *Oecologia*, **139**, 298-308.
- Moore J.W., Schindler D.E., Carter J.L., Fox J., Griffiths J. & Holtgrieve G.W. (2007) Biotic control of stream fluxes: spawning salmon drive nutrient and matter export. *Ecology*, **88**, 1278-1291.

- Naiman R.J., Melillo J.M. & Hobbie J.E. (1986) Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254-1269.
- Naiman R.J., Bilby R.E., Schindler D.E. & Helfield J.M. (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399-417.
- Peterson B.J., Wollheim W.M., Mulholland P.J., Webster J.R., Meyer J.L., Tank J.L. *et al.* (2001) Control of nitrogen export from watersheds by headwater streams. *Science*, **292**, 86-90.
- Poore A.G.B., Campbell A.H., Coleman R.A., Edgar G.J., Jormalainen V., Reynolds P.L. *et al.* (2012) Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, **15**, 912-922.
- Power M.E. (1990a) Effects of fish in river food webs. *Science*, **250**, 811-814.
- Power M.E. (1990b) Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology*, **71**, 897-904.
- Power M.E., Matthews W.J. & Stewart A.J. (1985) Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. *Ecology*, **66**, 1448-1456.
- Power M.E., Parker M.S. & Dietrich W.E. (2008) Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. *Ecological Monographs*, **78**, 263-282.
- Pysek P., Richardson D.M., Pergl J., Jarosik V., Sixtova Z. & Weber E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution*, **23**, 237-244.
- R Development Core Team. (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rosenberg M.S., Adams D.C. & Gurevitch J. (2000) MetaWin statistical software for meta-analysis version 2. Sinauer, Sunderland.
- Schindler D.E., Scheuerell M.D., Moore J.W., Gende S.M., Francis T.B. & Palen W.J. (2003) Pacific salmon and the ecology of coastal ecosystems. *Frontiers in Ecology and the Environment*, **1**, 31-37.
- Schneck F., Schwarzbald A. & Melo A.S. (2013) Substrate roughness, fish grazers, and mesohabitat type interact to determine algal biomass and sediment accrual in a high-altitude subtropical stream. *Hydrobiologia*, **711**, 165-173.

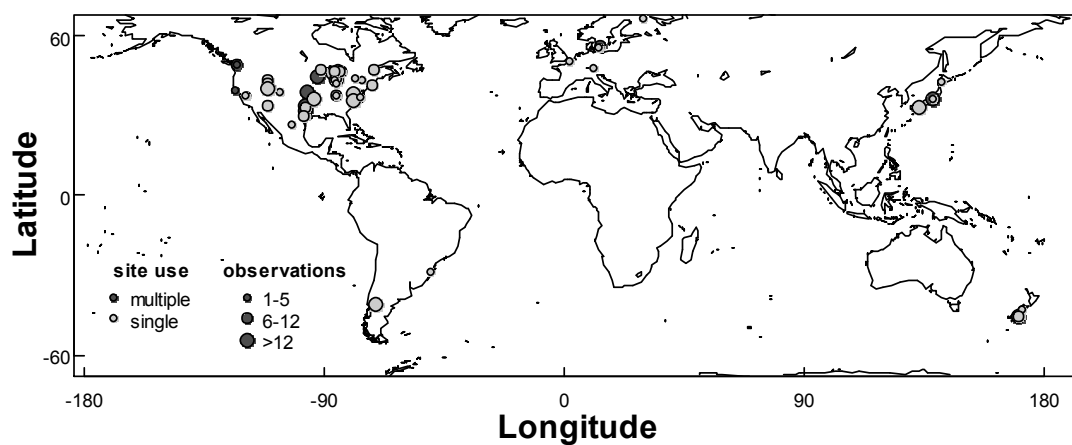
- Shurin J.B., Borer E.T., Seabloom E.W., Anderson K., Blanchette C.A., Broitman B. *et al.* (2002) A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters*, **5**, 785-791.
- Stevens J.R. & Taylor A.M. (2009) Hierarchical dependence in meta-analysis. *Journal of Educational and Behavioral Statistics*, **34**, 46-73.
- Stevens J.R. & Nicholas G. (2013) "metahdep: Hierarchical Dependence in Meta-Analysis", R package version 1.18.0.
- Strayer D.L., Caraco N.F., Cole J.J., Findlay S. & Pace M.L. (1999) Transformation of freshwater ecosystems by bivalves. *BioScience*, **49**, 19-27.
- Strong D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology*, **73**, 747-754.
- Tank J.L., Rosi-Marshall E.J., Baker M.A. & Hall R.O. (2008) Are rivers just big streams? A pulse method to quantify nitrogen demand in a large river. *Ecology*, **89**, 2935-2945.
- Taylor J.M., Back J.A. & King R.S. (2012) Grazing minnows increase benthic autotrophy and enhance the response of periphyton elemental composition to experimental phosphorus additions. *Freshwater Science*, **31**, 451-462.
- Vanni M.J. (2002) Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341-370.
- Vanni M.J. (2010) Preface: when and where do fish have strong effects on stream ecosystem processes? In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 531-538.
- Vaughn C.C. (2010) Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. *BioScience*, **60**, 25-35.

**Table 4-1** Response variables considered for meta-analysis of fish effects on temperate stream ecosystem structure and function. The total number of data sources used for each response is provided (# Sources), as are the number of observations for each data extraction approach (dep = dependence approach; rest = restricted approach). SRP, soluble reactive phosphorus; Chl-*a*, periphyton chlorophyll-*a*; AFDM, periphyton ash-free dry mass; PPI, periphyton photosynthetic index (= Chl-*a*/AFDM); % Loss, leaf decomposition (as % leaf pack mass lost); NEM, stream net ecosystem metabolism.

Response	units	# Sources	# Obs (dep)	# Obs (rest)
<i>Structural</i>				
NH <sub>4</sub>	μg L <sup>-1</sup>	9	46	26
NO <sub>3</sub>	μg L <sup>-1</sup>	12	49	29
SRP	μg L <sup>-1</sup>	8	43	25
Chl- <i>a</i>	μg cm <sup>-2</sup>	55	260	135
AFDM	mg cm <sup>-2</sup>	25	91	59
PPI	μg mg <sup>-1</sup>	14	52	39
<i>Functional</i>				
% Loss	%	15	43	28
NEM	g O <sub>2</sub> m <sup>-2</sup> hr <sup>-1</sup>	11	65	20

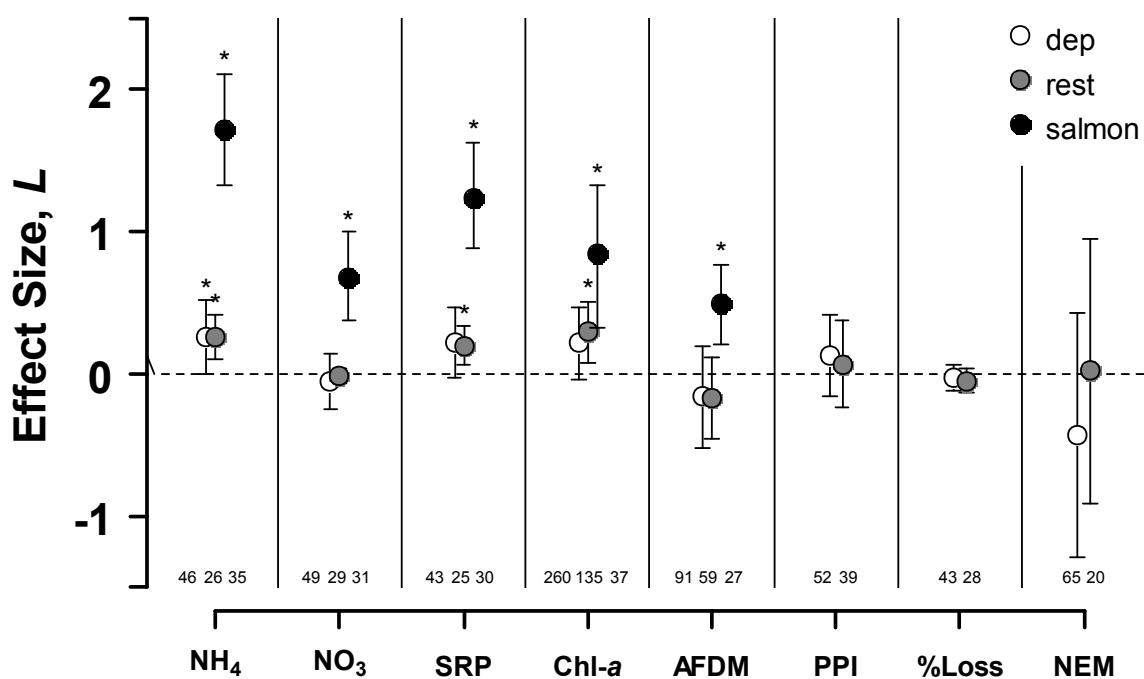
**Table 4-2** Covariates included as potential mediators of fish effects in temperate stream ecosystems. Some covariates were not applicable to one or more response variables.

Category	units or categories				
<i>Biotic</i>					
Biomass	(g m <sup>-2</sup> )				
Taxonomy	species	group			
Trophic guild	none	invertivore	herbivore	omnivore	
<i>Abiotic</i>					
Season	spring	summer	fall	multiple	
Hydrology	baseflow	drought	flood		
<i>Methodological</i>					
Design	natural	artificial	combination		
Grazing	protected	unprotected			
Nutrients	ambient	enriched			
Substrate	natural	artificial			
Time	(d)				

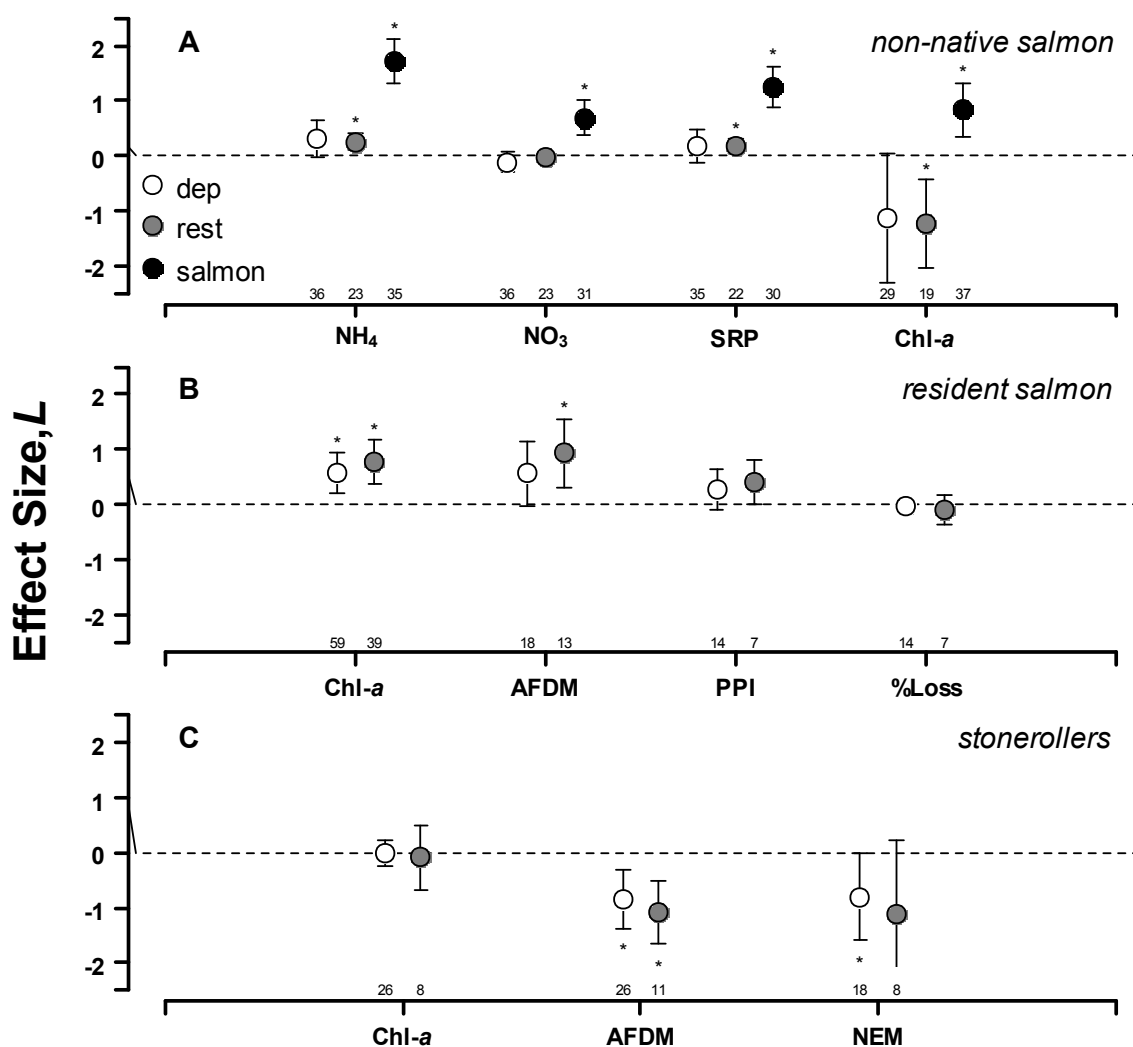


**Fig. 4-1** Geographic locations of the studies used in the meta-analysis of fish effects in temperate lotic environments. Some sites were included in more than one study (site use = multiple), whereas others were used only once (site use = single). The size of each circle is proportional to the number of observations included from a particular location.

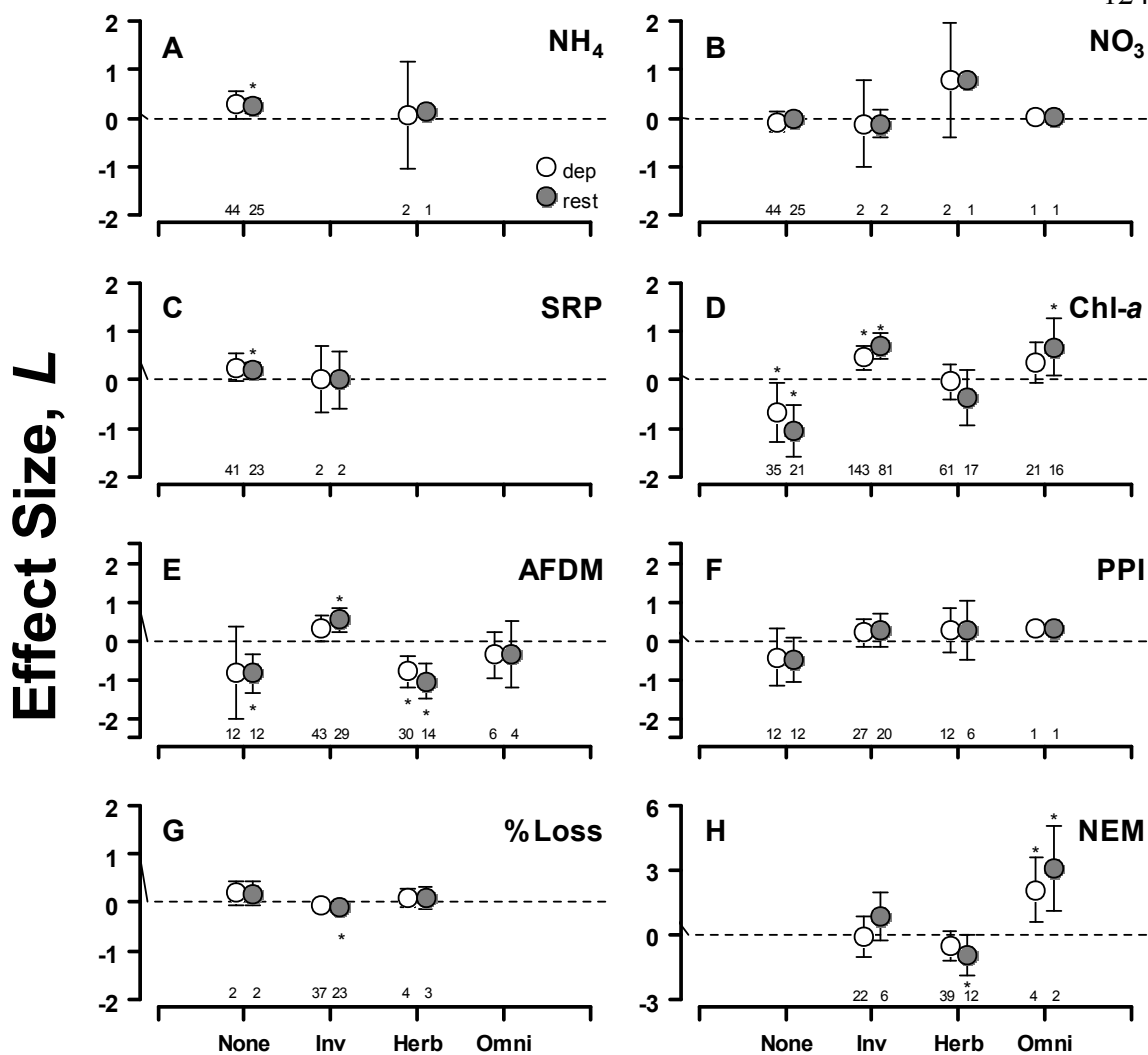




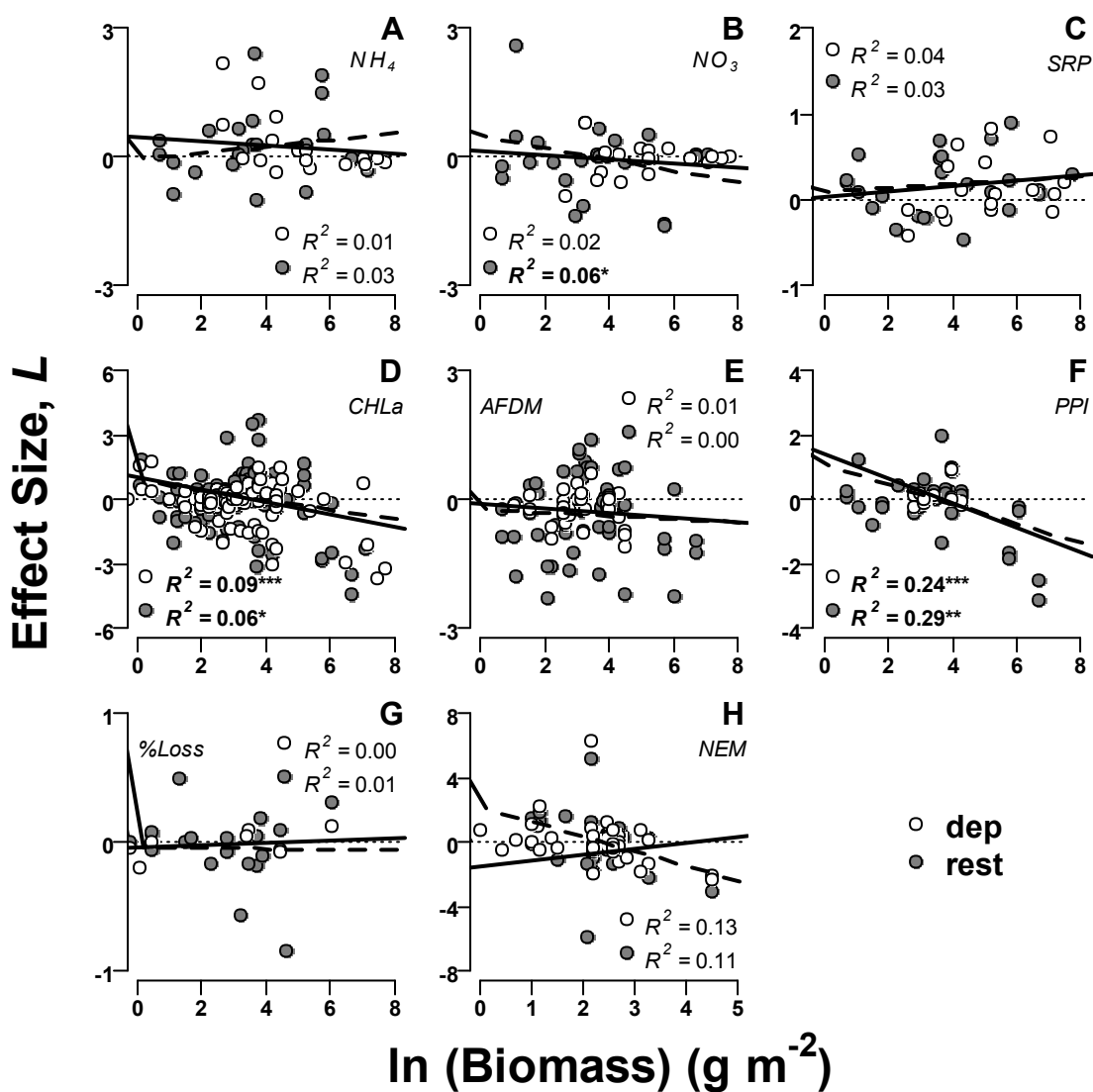
**Fig. 4-2** Effect of fishes (mean effect sizes  $\pm$  95% confidence intervals) on temperate stream ecosystem structural and functional characteristics. Response variables include dissolved nutrient concentrations (NH<sub>4</sub>, NO<sub>3</sub>, and soluble reactive phosphorus [SRP]), periphyton characteristics (chlorophyll-*a*, ash free dry mass [AFDM], and periphyton photosynthetic index [PPI; see methods]), leaf decomposition (as mass loss [%Loss]), and stream net ecosystem metabolism (NEM). The data extraction approaches used in this study are dependence (dep) and restricted (rest), and values are compared with data for native Pacific salmon (salmon; Janetski *et al.* [2009]). Effect size estimates significantly different from zero ( $\alpha = 0.05$ ) are denoted with \*, and sample sizes used to generate effect size estimates are shown along the x-axis for each response.



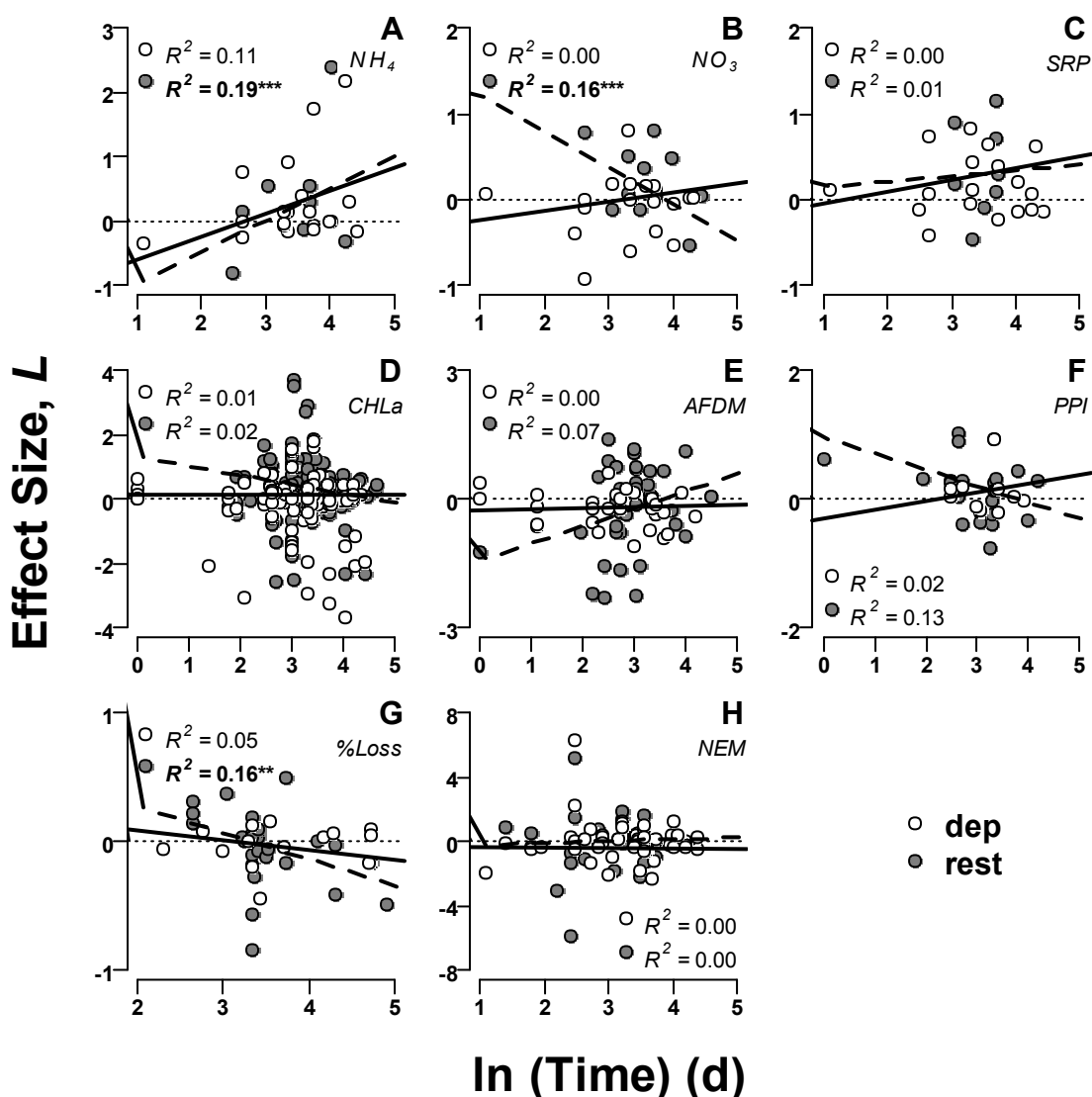
**Fig. 4-3** Effect size estimates (mean effect size  $\pm$  95% confidence intervals) of different fish taxonomic groups in temperate stream ecosystems. Non-native salmon are introduced Pacific salmon, resident salmon are stream-dwelling trout, char, and salmon (see methods), and stonerollers are *Campostoma* spp. Data extraction approaches used for this study are dependence (dep) and restricted (rest), and values for non-native salmon are compared with native Pacific salmon (salmon; Janetski *et al.* [2009]). Effect size estimates significantly different from zero ( $\alpha = 0.05$ ) are denoted with \*, and sample sizes used to generate effect size estimates are shown along the x-axis for each response.



**Fig. 4-4** Effect size estimates (mean  $\pm$  95% confidence intervals) of fishes in temperate stream ecosystems as a function of trophic guild. Trophic guilds are non-feeding (None), invertivorous (Inv), herbivorous (Herb), and omnivorous (Omni), and the data extraction approaches are dependence (dep) and restricted (rest). Note difference between NEM y-axis scale and all others. Effect size estimates significantly different from zero ( $\alpha = 0.05$ ) are denoted with \*, and sample sizes used to generate effect size estimates are shown along the x-axis of each panel.



**Fig. 4-5** Influence of biomass on effect size estimates of fishes on temperate stream ecosystem structural and functional characteristics. Note differences among y-axis scales. Regression lines are drawn for datasets produced by dependence (dep; filled and open circles; solid lines) and restricted (rest; filled circles only; dashed lines) approaches. Statistically significant ( $\alpha = 0.05$ ) regression slope estimates are denoted with bold text (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). SRP, soluble reactive phosphorus; CHLa, benthic chlorophyll-*a*; AFDM, ash-free dry mass; PPI, periphyton photosynthetic index; %Loss, leaf decomposition; NEM, net ecosystem metabolism.



**Fig. 4-6** Influence of time on effect size estimates of fishes on temperate stream ecosystem structural and functional characteristics. Note differences among y-axis scales. Regression lines are drawn for datasets produced by dependence (dep; filled and open circles; solid lines) and restricted (rest; filled circles only; dashed lines) approaches. Statistically significant ( $\alpha = 0.05$ ) regression slope estimates are denoted with bold text (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). SRP, soluble reactive phosphorus; CHLa, benthic chlorophyll-*a*; AFDM, ash-free dry mass; PPI, periphyton photosynthetic index; %Loss, leaf decomposition; NEM, net ecosystem metabolism.

## CHAPTER 5

## SUMMARY

My work demonstrates the potential of fishes to substantially affect stream ecosystem structure and function. In my survey of Strawberry Reservoir tributaries, I found that migratory fish excretion can represent a significant nutrient subsidy to spawning streams (Chapter 2). However, the magnitude of the subsidy was extremely variable across space and time. My data indicated variation was related to changes in both migrant densities and abiotic conditions such as discharge and background nutrient levels. Migrant excretion subsidies were large relative to nutrient export and were capable of meeting the majority of ecosystem nutrient demand during spawning migrations. However, migrant excretion subsidies usually failed to completely meet ecosystem nutrient demand. Consequently, fertilization impacts related to adfluvial migrants were relatively limited (Chapter 3). In contrast, there were benthic disturbance effects associated with Strawberry Reservoir migrants, a likely result of particle size distributions in spawning tributaries. Generally speaking, results from my field-based work agreed with patterns generated by my quantitative synthesis of fish effects in lotic ecosystems (Chapter 4). For example, the reductions in periphyton chlorophyll-*a* (i.e., benthic disturbance) observed in Strawberry Reservoir tributaries were consistent with effects of non-native salmon in other studies. Among the group of covariates I examined, specific taxonomic groups or trophic guilds proved to be the best differentiators of fish effects on stream ecosystem structure and function, as abiotic and methodological covariates did not provide much resolution. Overall, fishes in streams tended to have consistent positive

effects on  $\text{NH}_4$  and SRP, which represent primary inorganic nutrient forms excreted by fishes, as well as periphyton chlorophyll-*a*. My meta-analysis also revealed that the ecosystem-level effects of some fishes (e.g., stonerollers) are as large as those associated with native Pacific salmon. Given the acknowledged impacts associated with salmon migrations, this result suggests that more effort should be devoted to delineating the functional roles of freshwater fishes.

In addition to demonstrating fish effects in lotic ecosystems, my research also illustrated the influence of local biotic and abiotic conditions in regulating the type and magnitude of fish effects. While generalizations regarding fish effects in lotic systems are elusive (Gido *et al.*, 2010; Vanni, 2010), my field-based results provided empirical support for hypothetical predictions that ecosystem-level impacts of fishes should be largest when migrant biomass is high relative to system size (Flecker *et al.*, 2010). Like Janetski *et al.* (2009), I found positive relationships between ratios of migrant biomass and discharge and the magnitude of migrant excretion subsidies. However, the realized effects of fishes may depend on other conditions as well. For example, my results indicated the magnitude of migrant excretion subsidies was largest in Indian Creek during 2012, yet fertilization effects were limited to Trout Creek as a result of differences between migrant excretion fluxes and ecosystem nutrient demand. Flecker *et al.* (2010) also suggested that fish fertilization effects should be larger in systems with greater retentive capacity, all else being equal. My results, however, did not support this hypothesis, as fertilization effects of Strawberry Reservoir adfluvial migrants were higher in a stream with relatively low retentiveness. It is possible that my retention measurements may not have accurately reflected solute transport through spawning

streams. One important aspect of retentiveness that I did not address was groundwater-surface water exchange, and a higher degree of exchange would translate to increased retentive capacity (e.g., Morrice *et al.*, 1997). Thus, groundwater-surface water exchange may have been more pronounced in Trout Creek than in Indian Creek, driving the isolated occurrences of migrant fertilization impacts in a system that appeared to have reduced retention.

While a suite of abiotic and biotic conditions interacted to determine the net ecosystem effects of adfluvial migrants in Strawberry Reservoir tributaries, my meta-analysis did not suggest a strong predictive role for characteristics like migrant biomass and hydrologic context. However, I extracted much of these data on relatively coarse levels given how results were frequently presented in published studies. For example, I was limited to a categorical classification of discharge because so few studies reported quantitative measures. Additionally, there were very few papers that provided background nutrient concentrations, thus I was only able to contrast ambient and enriched nutrient conditions that did not reflect differences between nutrient supply and demand under ambient conditions. Benthic disturbance associated with fishes appears to be largely regulated by particle size distributions (e.g., Holtgrieve *et al.*, 2010), but most papers included in my meta-analysis reported only qualitative information regarding substrates, which prevented me from testing the influence of substrate size. These factors, as well as others, are all capable of influencing the type and magnitude of fish effects. Thus, our understanding of fish effects would be more complete if quantitative information about possible controls was included in studies whenever possible.



Although limited in some regards, my meta-analysis did identify the importance of functional distinctions for predicting fish effects. Classifications based on trophic guilds produced clear and consistent differences, as did distinctions between taxonomic groups (e.g., non-native salmon vs. resident salmon vs. stonerollers). While native Pacific salmon are generally regarded as the leading example of fish effects in freshwater habitats, my analysis revealed that other fishes are capable of exerting similarly strong control over stream structure and function. Additionally, fishes that do have strong effects are not necessarily the largest and most mobile species. Stonerollers and other herbivorous fishes are often relatively small, yet their functional distinctiveness among fishes as grazers likely increases their capacity to substantially affect ecosystem properties (Flecker *et al.*, 2010). Consequently, a wider diversity of fishes should be studied to develop a better understanding of fish effects in streams.

In conclusion, I found that fishes are likely to influence stream ecosystem structure and function as a result of their trophic interactions, influence on nutrient dynamics, interactions with the benthic environment, and movement patterns. Rather than being governed by a single biotic or abiotic factor, the direction and magnitude of fish effects are more likely to depend on relative values that reflect interactions among different factors. Streams are dynamic ecosystems, so local conditions and thus fish effects are likely to exhibit considerable variation over both space and time. Nevertheless, it should be a focus of natural resource managers and researchers to understand the ecosystem role of fishes in streams due to their potential influence on properties that affect continued provision of freshwater ecosystem services.

## LITERATURE CITED

- Flecker A.S., McIntyre P.B., Moore J.W., Anderson J.T., Taylor B.W. & Hall R.O. (2010) Migratory fishes as material and process subsidies in riverine ecosystems. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 559-592.
- Gido K.B., Bertrand K.N., Murdock J.N., Dodds W.K. & Whiles M.R. (2010) Disturbance-mediated effects of fishes on stream ecosystem processes: concepts and results from highly variable prairie streams. In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 593-617
- Holtgrieve G.W., Schindler D.E., Gowell C.P., Ruff C.P. & Lisi P.J. (2010) Stream geomorphology regulates the effects on periphyton of ecosystem engineering and nutrient enrichment by Pacific salmon. *Freshwater Biology*, **55**, 2598-2611.
- Janetski D.J., Chaloner D.T., Tiegs S.D. & Lamberti G.A. (2009) Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia*, **159**, 583-595.
- Morrice J.A., Valett H.M., Dahm C.N. & Campana M.E. (1997) Alluvial characteristics, groundwater-surface water exchange and hydrological retention in headwater streams. *Hydrological Processes*, **11**, 253-267.
- Vanni M.J. (2010) Preface: when and where do fish have strong effects on stream ecosystem processes? In: *Community Ecology of Stream Fishes: Concepts, Approaches, and Techniques*. (Eds K.B. Gido & D.A. Jackson). American Fisheries Society, Symposium 73, Bethesda, MD, 531-538.

APPENDIX

**Appendix A-1.** Mathematical comparison of metrics that indicate the relative size of consumer excretion subsidies,  $E_d/T_d$  and  $E_V/C_{amb}$ .

As defined by McIntyre *et al.* (2008), volumetric nutrient excretion rates ( $E_V$ , mg L<sup>-1</sup>), are calculated using the following expression:

$$E_V = \frac{E \times A \times T}{V} \quad (\text{A1})$$

where  $E$  is the areal nutrient excretion rate (mg m<sup>-2</sup> hr<sup>-1</sup>),  $A$  is substrate area (m<sup>2</sup>),  $T$  is travel time (hr), and  $V$  is volume (m<sup>3</sup>). Taking the expression we used for  $E$  (see *Ecosystem nutrient demand* methods, Chapter 2) and the expressions for  $A$ ,  $T$ , and  $V$  from McIntyre *et al.* (2008), equation A1 can be expanded:

$$E_V = \frac{(D_M \sum_{i=1}^n p_i EXC_i) \times (L \times W) \times (\frac{L}{U})}{(L \times A_{CS})} \quad (\text{A2})$$

where  $D_M$  is migrant density (ind m<sup>-2</sup>),  $p_i$  is the proportion of individuals in the  $i^{th}$  size bin,  $EXC_i$  is the per-capita nutrient excretion rate of an average sized individual from the  $i^{th}$  size bin (mg ind<sup>-1</sup> hr<sup>-1</sup>),  $L$  is reach length (m),  $W$  is reach width (m),  $U$  is reach velocity (m s<sup>-1</sup>), and  $A_{CS}$  is reach cross-sectional area (depth × width; m<sup>2</sup>).

If both sides of equation A2 are divided by ambient nutrient concentrations ( $C_{amb}$ ; mg L<sup>-1</sup>), and  $D_M$  is rewritten as migrant abundance ( $A_M$ ; ind) divided by substrate area (i.e.,  $L \times W$ ; m<sup>2</sup>), equation A2 can be rewritten:

$$E_V/C_{amb} = \frac{(A_M \sum_{i=1}^n p_i EXC_i) \times (L \times W) \times (L)}{(L \times A_{CS})(U)(C_{amb})} \quad (\text{A3})$$

Additional simplification of equation A3, coupled with the incorporation of the continuity equation from fluvial geomorphology ( $Q = U \times A_{CS}$ ), produces the following expression:

$$E_V/C_{amb} = \frac{A_M \sum_{i=1}^n p_i EXC_i}{Q C_{amb}} \quad (\text{A4})$$

As defined in the methods (see *Migrant excretion load and tributary export*, Chapter 2), the ratio comparing daily migrant excretion load ( $E_d$ ) to tributary nutrient export ( $T_d$ ) is:

$$E_d/T_d = \frac{A_{M,d} \sum_{i=1}^n p_i EXC_i}{QC_{amb,d}} \quad (A5)$$

Thus, these two different metrics used to assess the relative size of consumer excretion subsidies, expressed in equations A4 and A5, are mathematically equivalent provided the same time interval (e.g., day) is used.

#### LITERATURE CITED

McIntyre P.B., Flecker A.S., Vanni M.J., Hood J.M., Taylor B.W. & Thomas S.A. (2008) Fish distributions and nutrient cycling in streams: can fish create biogeochemical hotspots? *Ecology*, **89**, 2335-2346.

**Appendix A-2.** Full citations for all studies used in the meta-analysis of fish effects in temperate stream ecosystems.

- Abe S-I., Uchida K., Nagumo T., Ioriya T. & Tanaka J. (2001) Effects of a grazing fish, *Plecoglossus altivelis* (Osmeridae) on the taxonomic composition of freshwater benthic algal assemblages. *Archiv Fur Hydrobiologie*, **150**, 581-595.
- Baxter C.V., Fausch K.D., Murakami M. & Chapman P.L. (2004) Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. *Ecology*, **85**, 2656-2663.
- Bechara J.A., Moreau G. & Planas D. (1992) Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2093-2103.
- Benjamin J.R., Lepori F., Baxter C.V. & Fausch K.D. (2013) Can replacement of native by non-native trout alter stream-riparian food webs? *Freshwater Biology*, **58**, 1694-1709.
- Bertrand K.N. & Gido K.B. (2007) Effects of the herbivorous minnow, southern redbelly dace (*Phoxinus erythrogaster*), on stream productivity and ecosystem structure. *Oecologia*, **151**, 69-81.
- Bertrand K.N., Gido K.B., Dodds W.K., Murdock J.N. & Whiles M.R. (2009) Disturbance frequency and functional identity mediate ecosystem processes in prairie streams. *Oikos*, **118**, 917-933.
- Bondar C.A. & Richardson J.S. (2013) Stage-specific interactions between dominant consumers within a small stream ecosystem: direct and indirect consequences. *Freshwater Science*, **32**, 183-192.
- Bouwes N. (1999) *The impacts of native and nonnative fish on stream communities*. Ph.D. Dissertation. Utah State University, Logan.
- Buria L., Albarino R., Villanueva V.D., Modenutti B. & Balseiro E. (2010) Does predation by the introduced rainbow trout cascade down to detritus and algae in a forested small stream in Patagonia? *Hydrobiologia*, **651**, 161-172.
- Cheever B.M. & Simon K.S. (2009) Seasonal influence of brook trout and mottled sculpin on lower trophic levels in an Appalachian stream. *Freshwater Biology*, **54**, 524-535.
- Childress E.S., Allan J.D. & McIntyre P.B. (2014) Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems*, **17**, 522-534.

- Collins S.F., Moerke A.H., Chaloner D.T., Janetski D.J. & Lamberti G.A. (2011) Response of dissolved nutrients and periphyton to spawning Pacific salmon in three northern Michigan streams. *Journal of the North American Benthological Society*, **30**, 831-839.
- Dahl J. (1998a) Effects of a benthivorous and a drift-feeding fish on a benthic stream assemblage. *Oecologia*, **116**, 426-432.
- Dahl J. (1998b) The impact of vertebrate and invertebrate predators on a stream benthic community. *Oecologia*, **117**, 217-226.
- Dahl J. & Greenberg L. (1999) Effects of prey dispersal on predator-prey interactions in streams. *Freshwater Biology*, **41**, 771-780.
- Diehl S., Cooper S.D., Kratz K.W., Nisbet R.M., Roll S.K., Wiseman S.W. *et al.* (2000) Effects of multiple, predator-induced behaviors on short-term producer-grazer dynamics in open systems. *American Naturalist*, **156**, 293-313.
- Dinger E.C., Hendrickson D.A., Winsborough B.M. & Marks J.C. (2006) Role of fish in structuring invertebrates on stromatolites in Cuatro Ciénegas, Mexico. *Hydrobiologia*, **563**, 407-420.
- Effenberger M., Diehl S., Gerth M. & Matthaei C.D. (2011) Patchy bed disturbance and fish predation independently influence the distribution of stream invertebrates and algae. *Journal of Animal Ecology*, **80**, 603-614.
- Flecker A.S. & Townsend C.R. (1994) Community-wide consequences of trout introduction in New Zealand streams. *Ecological Applications*, **4**, 798-807.
- Forrester G.E., Dudley T.L. & Grimm N.B. (1999) Trophic interactions in open systems: effects of predators and nutrients on stream food chains. *Limnology and Oceanography*, **44**, 1187-1197.
- Gelwick F.P. & Matthews W.J. (1992) Effects of an algivorous minnow on temperate stream ecosystem properties. *Ecology*, **73**, 1630-1645.
- Gelwick F.P., Stock M.S. & Matthews W.J. (1997) Effects of fish, water depth, and predation risk on patch dynamics in a north-temperate river ecosystem. *Oikos*, **80**, 382-398.
- Gido K.B. & Matthews W.J. (2001) Ecosystem effects of water column minnows in experimental streams. *Oecologia*, **126**, 247-253.
- Greenberg L., Dahl J. & Bergman E. (2005) Indirect behavioral effects of a piscivore on trophic interactions in stream enclosures. *Archiv Fur Hydrobiologie*, **164**, 39-51.

- Greig H.S. & McIntosh A.R. (2006) Indirect effects of predatory trout on organic matter processing in detritus-based stream food webs. *Oikos*, **112**, 31-40.
- Hargrave C.W. (2006) A test of three alternative pathways for consumer regulation of primary productivity. *Oecologia*, **149**, 123-132.
- Hargrave C.W., Ramirez R., Brooks M., Eggleton M.A., Sutherland K., Deaton R. *et al.* (2006) Indirect food web interactions increase growth of an algivorous stream fish. *Freshwater Biology*, **51**, 1901-1910.
- Herbst D.B., Silldorff E.L. & Cooper S.D. (2009) The influence of introduced trout on the benthic communities of paired headwater streams in the Sierra Nevada of California. *Freshwater Biology*, **54**, 1324-1342.
- Herrmann P.B., Townsend C.R. & Matthaei C.D. (2012) Individual and combined effects of fish predation and bed disturbance on stream benthic communities: a streamside channel experiment. *Freshwater Biology*, **57**, 2487-2503.
- Holomuzki J.R. & Stevenson R.J. (1992) Role of predatory fish in community dynamics of an ephemeral stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2322-2330.
- Inoue M. & Miyayoshi M. (2006) Fish foraging effects on benthic assemblages along a warm-temperate stream: differences among drift feeders, benthic predators and grazers. *Oikos*, **114**, 95-107.
- Ivan L.N., Rutherford E.S. & Johengen T.H. (2011) Impacts of adfluvial fish on the ecology of two Great Lakes tributaries. *Transactions of the American Fisheries Society*, **140**, 1670-1682.
- Janetski D.J., Chaloner D.T., Moerke A.H., Levi P.S. & Lamberti G.A. (2014) Novel environmental conditions alter subsidy and engineering effects by introduced Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 502-513.
- Katano O. (2007) Effects of experimental duration and density of Japanese dace *Tribolodon hakonensis* on the strength of trophic cascades on benthic algae. *Oecologia*, **154**, 195-205.
- Katano O. (2011) Effects of individual differences in foraging of pale chub on algal biomass through trophic cascades. *Environmental Biology of Fishes*, **92**, 101-112.
- Katano O. (2013) The trophic cascade from fish to benthic algae: manipulation of habitat heterogeneity and disturbance in experimental flow-through pools. *Fisheries Science*, **79**, 221-230.



- Katano O., Aonuma Y., Nakamura T. & Yamamoto S. (2003) Indirect contramensalism through trophic cascades between two omnivorous fishes. *Ecology*, **84**, 1311-1323.
- Katano O., Nakamura T. & Yamamoto S. (2006) Intraguild indirect effects through trophic cascades between stream-dwelling fishes. *Journal of Animal Ecology*, **75**, 167-175.
- Katano O., Natsumeda T. & Suguro N. (2013) Diurnal bottom feeding of predator fish strengthens trophic cascades to benthic algae in experimental flow-through pools. *Ecological Research*, **28**, 907-918.
- Kiffney P.M. (2008) Response of lotic producer and consumer trophic levels to gradients of resource supply and predation pressure. *Oikos*, **117**, 1428-1440.
- Kishi D., Murakami M., Nakano S. & Maekawa K. (2005) Water temperature determines strength of top-down control in a stream food web. *Freshwater Biology*, **50**, 1315-1322.
- Konishi M., Nakano S. & Iwata T. (2001) Trophic cascading effects of predatory fish on leaf litter processing in a Japanese stream. *Ecological Research*, **16**, 415-422.
- Ludlam J.P. & Magoulick D.D. (2010) Effects of consumer identity and disturbance on stream mesocosms structure and function. *Fundamental and Applied Limnology*, **177**, 143-149.
- Marks J.C., Power M.E. & Parker M.S. (2000) Flood disturbance, algal productivity, and interannual variation in food chain length. *Oikos*, **90**, 20-27.
- McCormick P.V. (1990) Direct and indirect effects of consumers on benthic algae in isolated pools of an ephemeral stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2057-2065.
- McIntosh A.R. & Townsend C.R. (1996) Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behavior? *Oecologia*, **108**, 174-181.
- McIntosh A.R., Peckarsky B.L. & Taylor B.W. (2004) Predator-induced resource heterogeneity in a stream food web. *Ecology*, **85**, 2279-2290.
- Meissner K. & Muotka T. (2006) The role of trout in stream food webs: integrating evidence from field surveys and experiments. *Journal of Animal Ecology*, **75**, 421-433.

- Murdock J.N., Gido K.B., Dodds W.K., Bertrand K.N. & Whiles M.R. (2010) Consumer return chronology alters recovery trajectory of stream ecosystem structure and function following drought. *Ecology*, **91**, 1048-1062.
- Nakano S., Miyasaka H. & Kuhara N. (1999) Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, **80**, 2435-2441.
- Nilsson E., Olsson K., Persson A., Nystrom P., Svensson G. & Nilsson U. (2008) Effects of stream predator richness on the prey community and ecosystem attributes. *Oecologia*, **157**, 641-651.
- Nystrom P. & McIntosh A.R. (2003) Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia*, **136**, 279-288.
- Nystrom P., McIntosh A.R. & Winterbourn M.J. (2003) Top-down and bottom-up processes in grassland and forested streams. *Oecologia*, **136**, 596-608.
- Power M.E. & Matthews W.J. (1983) Algae-grazing minnows (*Camptostoma anomalum*), piscivorous bass (*Micropterus* spp.), and the distribution of attached algae in a small prairie-margin stream. *Oecologia*, **60**, 328-332.
- Rand P.S., Hall C.A.S., McDowell W.H., Ringler N.H. & Kennen J.G. (1992) Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2377-2385.
- Reice S.R. (1991) Effects of detritus loading and fish predation on leafpack breakdown and benthic macroinvertebrates in a woodland stream. *Journal of the North American Benthological Society*, **10**, 42-56.
- Reisinger A.J., Presuma D.L., Gido K.B. & Dodds W.K. (2011) Direct and indirect effects of central stoneroller (*Camptostoma anomalum*) on mesocosm recovery following a flood: can macroconsumers affect denitrification? *Journal of the North American Benthological Society*, **30**, 840-852.
- Rosenfeld J.S. (1997) The influence of upstream predation on the expression of fish effects in downstream patches. *Freshwater Biology*, **37**, 535-543.
- Rosenfeld J.S. (2000a) Effects of fish predation in erosional and depositional habitats in a temperate stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1369-1379.
- Rosenfeld J.S. (2000b) Contrasting effects of fish predation in a fishless and fish-bearing stream. *Archiv Fur Hydrobiologie*, **147**, 129-142.

- Ruetz C.R. III, Newman R.M. & Vondracek B. (2002) Top-down control in a detritus-based food web: fish, shredders, and leaf breakdown. *Oecologia*, **132**, 307-315.
- Ruetz C.R. III, Vondracek B. & Newman R.M. (2004) Weak top-down control of grazers and periphyton by slimy sculpins in a coldwater stream. *Journal of the North American Benthological Society*, **23**, 271-286.
- Ruetz C.R. III, Breen M.J. & Vanhantsma D.L. (2006) Habitat structure and fish predation: effects on invertebrate colonization and breakdown of stream leaf packs. *Freshwater Biology*, **51**, 797-806.
- Sarica J., Amyot M., Hare L., Doyon M-R. & Stanfield L.W. (2004) Salmon-derived mercury and nutrients in a Lake Ontario spawning stream. *Limnology and Oceanography*, **49**, 891-899.
- Schneck F., Schwarzbald A. & Melo A.S. (2013) Substrate roughness, fish grazers, and mesohabitat type interact to determine algal biomass and sediment accrual in a high-altitude subtropical stream. *Hydrobiologia*, **711**, 165-173.
- Schuldt J.A. & Hershey A.E. (1995) Effect of salmon carcass decomposition on Lake Superior tributary streams. *Journal of the North American Benthological Society*, **14**, 259-268.
- Scott S.E., Pray C.L., Nowlin W.H. & Zhang Y. (2012) Effects of native and invasive species on stream ecosystem functioning. *Aquatic Sciences*, **74**, 793-808.
- Stelzer R.S. & Lamberti G.A. (1999) Independent and interactive effects of crayfish and darters on a stream benthic community. *Journal of the North American Benthological Society*, **18**, 524-532.
- Stewart A.J. (1987) Responses of stream algae to grazing minnows and nutrients: a field test for interactions. *Oecologia*, **72**, 1-7.
- Taylor J.M., Back J.A. & King R.S. (2012a) Grazing minnows increase benthic autotrophy and enhance the response of periphyton elemental composition to experimental phosphorus additions. *Freshwater Science*, **31**, 451-462.
- Taylor J.M., Back J.A., Valenti T.W. & King R.S. (2012b) Fish-mediated nutrient cycling and benthic microbial processes: can consumers influence stream nutrient cycling at multiple spatial scales? *Freshwater Science*, **31**, 928-944.
- Vaughn C.C., Gelwick F.P. & Matthews W.J. (1993) Effects of algivorous minnows on production of grazing stream invertebrates. *Oikos*, **66**, 119-128.

- Wach E. & Chambers R.M. (2007) Top-down effect of fish predation in Virginia headwater streams. *Northeastern Naturalist*, **14**, 461-470.
- Walters A.W., Barnes R.T. & Post D.M. (2009) Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences*, **66**, 439-448.
- Wheeler K. (2014) *The ecosystem role of fishes in lotic environments*. Ph.D. Dissertation. Utah State University, Logan.
- Woodward G., Papanoniou G., Edwards F. & Lauridsen R.B. (2008) Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. *Oikos*, **117**, 683-692.
- Wootton J.T. & Power M.E. (1993) Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Sciences of the United States of America*, **90**, 1384-1387.
- Zhang Y., Richardson J.S. & Negishi J.N. (2004) Detritus processing, ecosystem engineering and benthic diversity: a test of predator-omnivore interference. *Journal of Animal Ecology*, **73**, 756-766.

**Table A-1** Strawberry River fish trap size distribution data from 2011 and 2012. TL is total length,  $wt_i$  is the wet mass of an average sized individual from the  $i^{\text{th}}$  size bin, and  $p_i$  is the proportion of the migrant population within the  $i^{\text{th}}$  size bin during a given year.

TL (mm)	$wt_i$ (g)	BCT		$wt_i$ (g)	KOK	
		$p_{i,2011}$	$p_{i,2012}$		$p_{i,2011}$	$p_{i,2012}$
251-300	212	0.0000	0.0047	200	0.0057	0.0021
301-350	320	0.0032	0.0343	321	0.0568	0.0188
351-400	456	0.0190	0.0234	548	0.3153	0.1879
401-450	623	0.1111	0.1433	775	0.2315	0.3737
451-500	821	0.4762	0.4143	1002	0.2202	0.2088
501-550	1053	0.3111	0.2741	1229	0.1477	0.1754
551-600	1321	0.0635	0.0717	1456	0.0213	0.0292
601-650	1626	0.0159	0.0202	1683	0.0014	0.0042
651-700	1969	0.0000	0.0140		0.0000	0.0000

**Table A-2** Particle size distributions measured during 2012. Particle size ranges for each quartile were determined by pebble counts of 100-200 particles from the specific study reach where nutrient uptake measurements were made.

Percentile range	<i>B</i> -axis range (mm)	
	Indian Creek	Trout Creek
0-25	< 4 - 9	< 4 - 14
26-50	10 - 19	15 - 24
51-75	20 - 54	25 - 40
76-100	> 54	> 40

**Table A-3** Benthic particle size quartiles in Strawberry Reservoir tributaries. Measurements of 100-200 particles were made in two reaches (T = treatment, accessible to migrants; C = control, inaccessible to migrants) of each stream. Particles < 9 mm *B*-axis were classified as fines (f), and categories listed with each quartile (A-D) correspond with Figure 3-2.

Percentile range	<i>B</i> -axis range (mm)			
	Indian, T	Indian, C	Trout, T	Trout, C
0-25 (A)	f	f	f - 14	f - 14
26-50 (B)	10 - 19	10 - 17	15 - 24	15 - 27
51-75 (C)	20 - 54	18 - 58	25 - 40	28 - 56
76-100 (D)	> 54	> 58	> 40	> 56

**Table A-4** Information from studies used in the meta-analysis of fish effects in temperate stream ecosystems. Listed with each study are the responses for which data were extracted, the number of observations used in each extraction approach (dep = dependence; rest = restricted), and whether sampling dependence existed. Note that hierarchical dependence existed in any study with Obs (dep) > 1.

Study	Response(s)	Obs (dep)	Obs (rest)	Samp.
Abe et al. 2001	Chl- <i>a</i>	5	1	No
Baxter et al. 2004	Chl- <i>a</i>	1	1	No
Bechara et al. 1992	Chl- <i>a</i> , AFDM, PPI	10	4	No
Benjamin et al. 2013	Chl- <i>a</i>	6	2	Yes
Bertrand & Gido 2007	Chl- <i>a</i> , NEM	6	2	Yes
Bertrand et al. 2009	Chl- <i>a</i> , NEM	58	8	No
Bondar & Richardson 2013	% Loss	2	2	Yes
Bouwes 1999	Chl- <i>a</i>	12	6	Yes
Buria et al. 2010	Chl- <i>a</i> , AFDM, PPI, % Loss	17	13	No
Cheever & Simon 2009	Chl- <i>a</i> , AFDM, PPI	18	18	Yes
Childress et al. 2014	NH <sub>4</sub> , NO <sub>3</sub> , SRP, Chl- <i>a</i>	23	4	No
Collins et al. 2011	NH <sub>4</sub> , NO <sub>3</sub> , SRP, Chl- <i>a</i>	44	8	No
Dahl 1998a	Chl- <i>a</i>	4	2	Yes
Dahl 1998b	Chl- <i>a</i>	2	1	No
Dahl & Greenberg 1999	Chl- <i>a</i>	2	1	No
Diehl et al. 2000	Chl- <i>a</i>	2	1	Yes
Dinger et al. 2006	AFDM	2	2	No
Effenberger et al. 2011	Chl- <i>a</i>	2	2	No
Flecker & Townsend 1994	Chl- <i>a</i> , AFDM, PPI	12	6	Yes
Forrester et al. 1999	Chl- <i>a</i>	6	2	No
Gelwick & Matthews 1992	AFDM, NEM	6	2	No
Gelwick et al. 1997	AFDM, NEM	7	2	No
Gido & Matthews 2001	NEM	7	1	Yes
Greenberg et al. 2005	Chl- <i>a</i>	2	1	No
Greig & McIntosh 2006	% Loss	2	1	No
Hargrave 2006	NEM	12	6	Yes
Hargrave et al. 2006	Chl- <i>a</i>	8	2	Yes
Herbst et al. 2009	Chl- <i>a</i>	1	1	No
Hermann et al. 2012	Chl- <i>a</i> , % Loss	16	8	Yes
Holomuzki & Stevenson 1992	NO <sub>3</sub> , SRP, Chl- <i>a</i> , AFDM, PPI, % Loss	8	7	No

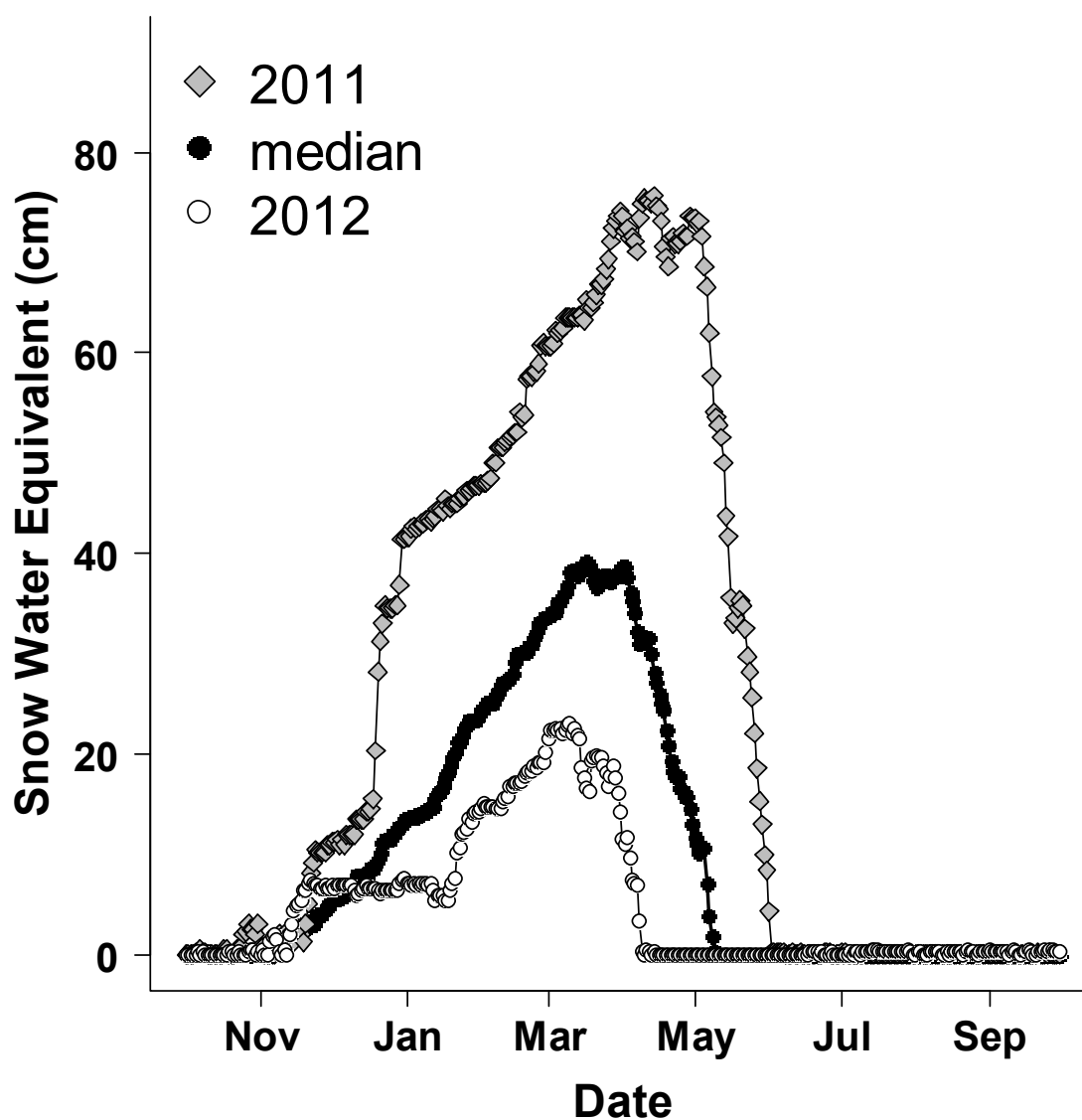


Table A-4 Continued.

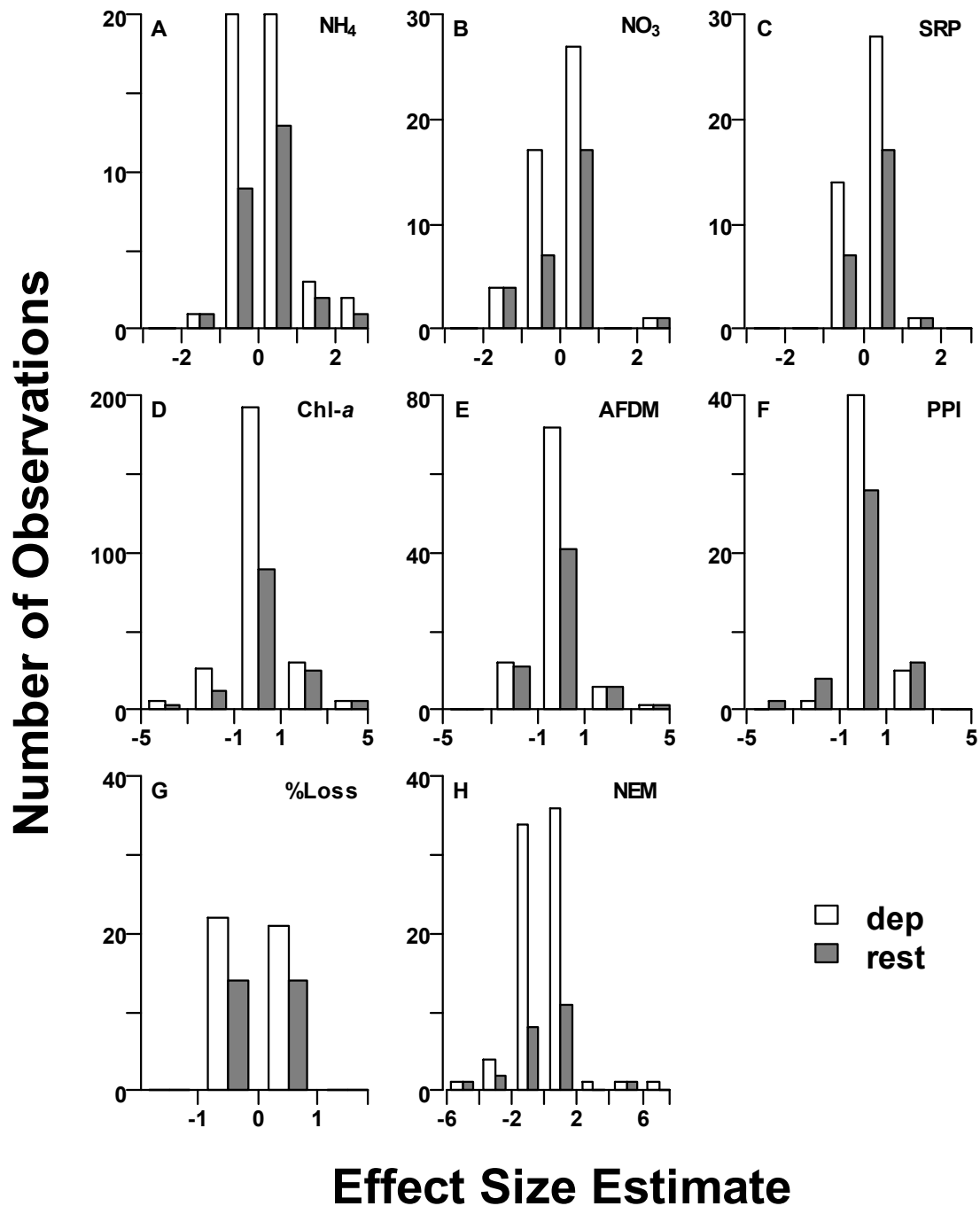
Study	Response(s)	Obs (dep)	Obs (rest)	Samp.
Inoue & Miyayoshi 2006	AFDM	13	5	No
Ivan et al. 2011	NH <sub>4</sub> , NO <sub>3</sub> , SRP	21	12	No
Janetski et al. 2014	NH <sub>4</sub> , NO <sub>3</sub> , SRP, Chl- <i>a</i> , AFDM, PPI	69	69	No
Katano 2007	Chl- <i>a</i>	10	4	Yes
Katano 2011	Chl- <i>a</i>	2	2	Yes
Katano 2013	Chl- <i>a</i>	2	2	No
Katano et al. 2003	Chl- <i>a</i> , NO <sub>3</sub>	15	6	Yes
Katano et al. 2006	Chl- <i>a</i>	7	7	Yes
Katano et al. 2013	Chl- <i>a</i>	9	9	Yes
Kiffney 2008	Chl- <i>a</i>	1	1	No
Kishi et al. 2005	Chl- <i>a</i>	2	2	No
Konishi et al. 2001	% Loss	1	1	No
Ludlam & Magoulick 2010	Chl- <i>a</i> , AFDM, PPI, % Loss, NEM	16	10	No
Marks et al. 2000	AFDM	2	2	No
McCormick 1990	NO <sub>3</sub> , SRP, AFDM	4	4	No
McIntosh & Townsend 1996	Chl- <i>a</i> , AFDM, PPI	6	6	Yes
McIntosh et al. 2004	Chl- <i>a</i>	2	2	No
Meissner & Muotka 2006	Chl- <i>a</i> , AFDM, PPI	3	3	No
Murdock et al. 2010	Chl- <i>a</i> , NEM	18	4	No
Nakano et al. 1999	AFDM	1	1	No
Nilsson et al. 2008	Chl- <i>a</i>	3	3	Yes
Nystrom & McIntosh 2003	Chl- <i>a</i>	4	4	Yes
Nystrom et al. 2003	Chl- <i>a</i>	1	1	No
Power & Matthews 1983	AFDM	1	1	No
Rand et al. 1992	Chl- <i>a</i>	2	2	No
Reice 1991	% Loss	13	8	No
Reisinger et al. 2011	NH <sub>4</sub> , NO <sub>3</sub> , Chl- <i>a</i> , NEM	8	4	No
Rosenfeld 1997	Chl- <i>a</i>	2	2	No
Rosenfeld 2000a	Chl- <i>a</i>	1	1	No
Rosenfeld 2000b	Chl- <i>a</i>	2	2	No
Ruetz et al. 2002	% Loss	3	1	No
Ruetz et al. 2004	Chl- <i>a</i> , AFDM, PPI	17	6	No
Ruetz et al. 2006	% Loss	1	1	No
Sarica et al. 2004	NH <sub>4</sub> , NO <sub>3</sub>	2	2	No

**Table A-4** Continued.

Study	Response(s)	Obs (dep)	Obs (rest)	Samp.
Schneck et al. 2013	Chl- <i>a</i> , AFDM, PPI	3	3	No
Schuldt & Hershey 1995	NH <sub>4</sub> , NO <sub>3</sub> , SRP, Chl- <i>a</i>	8	4	No
Scott et al. 2012	Chl- <i>a</i> , AFDM, PPI, % Loss	8	7	No
Stelzer & Lamberti 1999	Chl- <i>a</i> , AFDM, PPI	5	3	No
Stewart 1987	AFDM, NEM	4	4	No
Taylor et al. 2012a	Chl- <i>a</i> , AFDM, PPI	18	6	No
Taylor et al. 2012b	Chl- <i>a</i>	8	2	No
Vaughn et al. 1993	AFDM, NEM	12	4	No
Wach & Chambers 2007	% Loss	1	1	No
Walters et al. 2009	NH <sub>4</sub> , NO <sub>3</sub> , Chl- <i>a</i> , % Loss	7	5	No
Wheeler 2014	NH <sub>4</sub> , NO <sub>3</sub> , SRP, Chl- <i>a</i>	14	14	No
Woodward et al. 2008	Chl- <i>a</i> , % Loss	2	2	No
Wootton & Power 1993	AFDM	2	1	No
Zhang et al. 2004	% Loss	3	1	No



**Fig. A-1** Comparison of snow water equivalent in the Strawberry Reservoir Valley during sample years (2011, 2012), relative to the 30-year median value between 1981 and 2010. Data were obtained from Snotel station DSTU-1 (Daniels-Strawberry) and are available through the Colorado Basin River Forecast Center associated with the National Oceanic and Atmospheric Administration ([www.cbrfc.noaa.gov](http://www.cbrfc.noaa.gov)).



**Fig. A-2** Effect size distributions for temperate stream ecosystem structural and functional characteristics. Negative effect sizes suggest that fishes decrease the response relative to control units without fishes, whereas positive effect sizes suggest positive fish effects. Data extraction approaches used for this study are dependence (dep) and restricted (rest). Note differences among y-axis scales.

## CURRICULUM VITAE

**Christopher (Kit) C. Wheeler**

Biology Department  
 Georgia Southern University  
 PO Box 8042  
 Statesboro, GA 30460-8042

email: kitwheeler@gmail.com  
 cell: (334) 328-1823  
 office: (912) 478-4734

**EDUCATION****Ph.D. in Ecology (2014)**

Utah State University, Watershed Sciences Department and Ecology Center  
 Dissertation co-advisors: T.A. Crowl and S.W. Miller  
 Dissertation Title: The Ecosystem Role of Fishes in Lotic Environments

**M.S. in Sport Management (2005)**

Georgia Southern University, College of Health and Human Sciences

**M.Eng. in Environmental Engineering (1999)**

University of California, Berkeley, Department of Civil and Environmental Engineering  
 Thesis advisor: A.J. Horne (emeritus)

**B.C.E. with high honor in Civil Engineering (1997)**

Georgia Institute of Technology, School of Civil and Environmental Engineering

**RESEARCH & RELATED POSITIONS**

- 2014-present Regular Limited-Term Instructor, Biology Department, Georgia Southern Univ.
- 2008-2014 Graduate Research Assistant, Watershed Sciences Department, Utah State Univ.
- 2008 Lab Technician, Biology Department, Georgia Southern Univ.
- 2006-2007 Instructor, Department of Hospitality, Tourism, and Family & Consumer Sciences, Georgia Southern Univ.
- 2000-2004 Research Technician, J.W. Jones Ecological Research Center, Newton, GA
- 1997-1999 Graduate Research Assistant, Department of Civil and Environmental Engineering, Univ. of California, Berkeley
- 1996-1997 Student Research Assistant, Daniel Environmental Engineering Lab, School of Civil and Environmental Engineering, Georgia Institute of Technology

**PUBLICATIONS**

Opsahl, S.P., S.E. Chapal, D.W. Hicks and **K. Wheeler**, 2007. Evaluation of ground-water and surface-water exchanges using streamflow difference analyses. *Journal of the American Water Resources Association*, 43(5), 1132-1141.

**Wheeler, K.** and J. Nauright, **2006**. A global perspective on the environmental impact of golf. *Sport in Society*, 9(3), 427-443.

Opsahl, S.P., S.E. Chapal, and **K. Wheeler**, **2005**. Using stream gage data to quantify surface water/groundwater exchanges between the Upper Floridan aquifer and the lower Flint River, Georgia USA, 1989-2004. Pages 764-768 in K.J. Hatcher (ed.) *Proceedings of the 2005 Georgia Water Resources Conference*. University of Georgia, Institute of Ecology, Athens, GA.

**Wheeler, K.** and S.P. Opsahl, **2003**. Hydrologic controls on water chemistry and microbial activity in a small coastal plain stream. Pages 610-613 in K.J. Hatcher (ed.) *Proceedings of the 2003 Georgia Water Resources Conference*. University of Georgia, Institute of Ecology, Athens, GA.

Opsahl, S.P., **K. Wheeler**, R.A. Lane and J.C. Jenkins, **2003**. Effects of the Upper Floridan aquifer on water chemistry and oxygen metabolism in the lower Flint River during drought. Pages 614-618 in K.J. Hatcher (ed.) *Proceedings of the 2003 Georgia Water Resources Conference*. University of Georgia, Institute of Ecology, Athens, GA.

#### **MANUSCRIPTS IN REVIEW OR PREPARATION**

**Wheeler, K.**, S.W. Miller, and T.A. Crowl. Migratory fish excretion as nutrient subsidies to recipient ecosystems: magnitude, variability, and importance to whole-system nutrient cycling. Submitted to *Freshwater Biology*.

Wurtsbaugh W.A., N. Heredia, B.G. Laub, C. Meredith, H. Mohn, S.E. Null, D. Pluth, B.B. Roper, W.C. Saunders, D. Stevens, R.H. Walker and **K. Wheeler**. Approaches for studying fish production: do river and lake researchers have different perspectives? Submitted to *Canadian Journal of Fisheries & Aquatic Sciences*.

**Wheeler, K.**, S.W. Miller, and T.A. Crowl. Ecosystem structural and functional responses to adfluvial salmonid migrations in tributaries of a central Utah reservoir. In prep, target *Ecosystems*.

**Wheeler K.**, S.W. Miller, J.R. Stevens, and T.A. Crowl. A quantitative synthesis of fish effects on temperate stream ecosystem structure and function. In prep, target *Oecologia*.

#### **RESEARCH AWARDS & FELLOWSHIPS**

2014	Utah State Univ., Office of Graduate Studies and Research, Ph.D. Completion Fellowship
2013	Utah State Univ., Office of Student Involvement and Leadership, Graduate Enhancement Award
2012-2013	Utah State Univ., Office of Graduate Studies and Research, Graduate Research and Project Grant
2012-2013	Utah State Univ., Ecology Center assistantship
2012	Western Division American Fisheries Society student travel grant
2009-2013	Utah State Univ., Ecology Center graduate research support awards
2008-2012	Utah State Univ., College of Natural Resources Quinney Doctoral Fellowship

**RESEARCH EXPERIENCE**

- 2008-2014 Graduate Research Assistant, Watershed Sciences Department, Utah State Univ.
- Designed and implemented study of the ecosystem role played by migratory fishes in tributary streams, including proposal writing and funding acquisition, various field work (excretion measurements, spawner counts, nutrient limitation, water chemistry, discharge, aquatic invertebrates, backpack electrofishing, and other aspects of stream structure and function), hiring, training, and supervising field and lab technicians, data compilation and analysis, budget management, and presentation of results at international and regional professional meetings
  - Generated quantitative synthesis focused on the effects of fishes in lotic systems
  - Contributed to project focused on state shifts in reservoir ecology, including various field work (temperature/dissolved oxygen profiles, zooplankton, crayfish, chlorophyll-*a*, water chemistry, turbidity), data compilation and analysis, and presentation of results at stakeholder meetings
  - Contributed to project focused on protection and restoration of federally endangered fish (June sucker), including field work (non-native fish removal, fish community monitoring, documentation of tributary use during spawning) and review of species recovery plan
  - Contributed to project focused on various aspects of neotropical stream ecology, including field work (preliminary sampling of riparian zone-stream connections, long-term monitoring of freshwater shrimp dynamics)
- 2000-2004 Research Technician, J.W. Jones Ecological Research Center, Newton, GA
- Worked on projects including the evaluation of ground and surface water exchanges in the lower Flint River basin, water quality and nutrient dynamics in the lower Flint River, and the relationships among microbiological processes, water chemistry, and flow dynamics in palustrine wetlands
  - Planned, developed, and implemented standard operating procedures for field and lab activities
  - Supervised and coordinated activities of research assistants
  - Developed and managed data storage approaches
  - Involved in data compilation and analysis, preparation of written papers for publication and presentation of results at regional and international professional conferences and educational events
  - Participated in a variety of public relations activities designed to increase environmental awareness and public understanding of Center activities

- 1997-1999 Graduate Research Assistant, Department of Civil and Environmental Engineering, Univ. of California, Berkeley
- Worked on thesis project investigating link between algal blooms and onset of taste and odor problems in local reservoir
  - Assisted Ph.D. students involved in other projects (nutrient release from anoxic benthic sediments, watershed nitrogen cycling)
- 1996-1997 Student Research Assistant, Daniel Environmental Engineering Lab, School of Civil and Environmental Engineering, Georgia Institute of Technology
- Worked with graduate students researching phytoremediation of contaminated soils and groundwaters

### **TEACHING EXPERIENCE**

- 2013-2014 Instructor, Watershed Sciences Department, Utah State Univ.
- Fall 2013: NR/BIO 2220 *General Ecology*
- 2012-2013 Teaching assistant, Watershed Sciences Department, Utah State Univ.
- Fall 2012: NR/BIO 2220 *General Ecology*
- 2006-2007 Instructor, Recreation & Tourism Management Program, Georgia Southern Univ.
- Fall 2006: RECR 3236 *Planning Recreation Areas & Facilities*; RECR 3335 *Dynamics of Tourism*; RECR 4536 *Research and Evaluation*
  - Spring 2007: RECR 1530 *Foundations of Recreation and Leisure*; RECR 3236 *Planning Recreation Areas & Facilities*; RECR 3430 *Conference and Event Planning*
  - Collaborated with various local agencies and organizations in an effort to provide information and learning opportunities to students (Statesboro-Bulloch County Parks & Recreation Department; Keep Bulloch Beautiful; Georgia Southern Botanical Garden; Statesboro Convention & Visitors Bureau; Georgia Southern Athletic Department; Averitt Arts Center; Savannah Waterfront Association)

### **PRESENTATIONS**

Migratory fishes exhibit multi-functionality in riverine ecosystems – oral; Joint Aquatic Sciences Meeting, Portland, OR (2014)

Approaches for studying fish production: do river and lake researchers have different perspectives? – poster; Joint Aquatic Sciences Meeting, Portland, OR (2014)

Biotic influences on stream dynamics: a quantitative synthesis of fish impacts in lotic ecosystems – oral; Society for Freshwater Science, Jacksonville, FL (2013)

Nutrient transport by migratory fishes: excretion by adfluvial salmonids in a tributary of Strawberry Reservoir – oral; Society for Freshwater Science, Louisville, KY (2012)



Nutrient transport by fishes: potential impacts of migratory native fishes on stream ecosystem function – oral; Western Division of American Fisheries Society, Jackson, WY (2012)

Excretion by adfluvial fishes: interspecific variation and potential impacts – oral; American Fisheries Society, Seattle, WA (2011)

The role of migratory species in linking stream and lake ecosystems: nutrient translocation by adfluvial spawners – poster; <sup>1</sup>North American Benthological Society/American Society of Limnology & Oceanography, Santa Fe, NM, and <sup>2</sup>Western Division of American Fisheries Society, Salt Lake City, UT (2010)

Analysis of historical trends in groundwater discharge to the lower Flint River – poster; Lower Flint River Basin Research Conference, Albany, GA (2004)

Hydrologic controls on water chemistry and microbial activity in a small coastal plain stream – oral; Georgia Water Resources Conference, Athens, GA (2003)

Chickasawhatchee Swamp: Providing valuable ecological services in the lower Flint River basin – poster; Lower Flint River Basin Research Conference, Albany, GA (2002)

Investigating the relationships between source water chemistry and microbial activity in a small coastal plain stream – poster; American Society of Limnology & Oceanography Conference, Victoria, British Columbia (2002)

### **SERVICE ACTIVITIES & OUTREACH**

- |           |   |
|-----------|---|
| 2014      | reviewer for <i>Freshwater Biology</i>  |
| 2013      | graduate student representative, USGS Utah Cooperative Fish & Wildlife Research Unit search committee |
| 2013      | volunteer, iUTAH Summer Institute (component of ongoing Utah EPSCoR project)                          |
| 2012-2013 | Vice President, Utah State Univ. student chapter, American Fisheries Society                          |
| 2011-2013 | member, Utah State Univ. student chapter, American Fisheries Society                                  |
| 2011-2013 | Department representative, College of Natural Resources Graduate Student Council                      |
| 2010-2011 | co-chair, Utah State Univ. Ecology Center seminar series committee                                    |
| 2010      | volunteer, Utah State Univ. Extension Natural Resources Field Days                                    |
| 2009-2010 | member, Utah State Univ. Ecology Center seminar series committee                                      |

### **PROFESSIONAL DEVELOPMENT WORKSHOPS**

- |      |  |
|------|--|
| 2012 | Bayesian Modeling for Ecologists (M. Hooten, Colorado State Univ.) |
| 2011 | Stream Metabolism Estimation (R.O. Hall Jr., Univ. of Wyoming)     |

### **PROFESSIONAL MEMBERSHIPS**

- American Fisheries Society
- Society for Conservation Biology
- Society for Freshwater Science (formerly North American Benthological Society)

**REFERENCES**

Michelle Baker  
Professor, Biology Department  
Utah State Univ., Logan, UT  
michelle.baker@usu.edu  
Tel. 435-797-7131

Todd Crowl  
Professor, Biology Department / Director, Southeast Environmental Research Center  
Florida International Univ., Miami, FL  
facrowl@gmail.com / tcrowl@fiu.edu  
Tel. 305-348-3095

Scott Miller  
Director, BLM National Aquatic Monitoring Center / Assistant Professor, Watershed  
Sciences Department  
Utah State Univ., Logan, UT  
scott.miller@usu.edu  
Tel. 435-797-2612

Steve Opsahl  
Hydrologist, USGS Texas Water Science Center  
US Geological Survey, San Antonio, TX  
sopsahl@usgs.gov  
Tel. 210-691-9247