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The effect of seasonal fish migration on energy budgets in two coastal Michigan streams

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DEDICATION

This thesis is dedicated to my mother, Mary J. Dean, my grandmother, Wanda L. Hop, my grandfather, Duane L. Hop, my sister, Kaitlin E. Dean, and my brother, Jon D. Dean. Thank you for all your support and love as I completed this academic journey.

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ABSTRACT

Migratory fish are known to seasonally enter coastal stream systems but the magnitude of the effects these migrations have on stream energy budgets is not fully understood. The Laurentian Great Lakes have several introduced and native adfluvial fish, where only a few studies have investigated the impacts of their migration on energy budgets in Michigan coastal streams. We quantified the contribution of energy from Chinook salmon (*Oncorhynchus tshawytscha*) muscle and eggs, steelhead (*Oncorhynchus mykiss*) eggs, and larval white suckers (*Catostomus commersonii*) to coastal stream energy budgets. Energy densities and energy delivered to streams were estimated using bomb calorimetry and annual return data from the Little Manistee River Weir and other recent studies. In addition, we compared the energy contribution of these adfluvial fish tissues and aquatic insects to resident stream fish diets in two rivers in western Michigan. Specifically, we examined the energy contribution of Chinook eggs to steelhead parr diets in Bigelow Creek, MI and the contribution of energy by larval white suckers to brown trout (*Salmo trutta*) and non-migratory rainbow trout (*Oncorhynchus mykiss*) diets in the Big Manistee River, MI. Our measured energy density values differed markedly from values typically used in the literature, and indicate that some invertebrate groups (Trichoptera) have energy densities that do not significantly differ from salmon eggs which are typically perceived to be energy dense. Our results suggest that steelhead parr in Bigelow Creek consume more energy during the fall when salmon eggs are present. In contrast, large numbers of drifting larval white suckers in the Big Manistee River does not result in an increase in energy intake for trout during spring, but may satisfy base energy needs. Our results suggest that adfluvial fish are an important component of energy transfer between systems and contribute substantial energy to coastal stream energy budgets in Michigan.

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ABBREVIATIONS

Calorie (physics) – cal

Coarse particulate organic matter – CPOM

Dry weight – dw

Fine particulate organic matter - FPOM

Gram - g

Little Manistee River Weir – LMRW

Michigan Department of Natural Resources – MDNR

Salmon derived energy - SDE

Salmon marine-derived nutrients – SDN

Stable isotope analysis - SIA

Wet weight - ww

CHAPTER 1

INTRODUCTION

The absorption, storage, and transfer of energy, particularly light energy, within ecosystems has been a significant focus of ecological research for more than 60 years (Allan and Castillo 2007). Light energy is stored as chemical energy by plants through photosynthesis (Lindeman 1942). Plants will use much of this energy for respiration and basic metabolic function. When plants have energy in excess, plants will use it for growth, increasing plant biomass (Odum 1968) or will store the energy for future use. The sum of this energy in the form of organic biomass provides energy that drives biological communities in a particular ecosystem.

Energy locked away in plant biomass is distributed within the ecosystem by the action of consumer organisms. Heterotrophic organisms, or those that cannot capture light energy, consume plant biomass and use stored energy for their own respiration and production (Lindeman 1942). A hierarchy (i.e. trophic levels) forms when consumers unable to use energy provided by plant biomass consume those who can. Consumer physiological processes and transfer between successive trophic levels tend to convert this consumed energy into an unusable form (Lindeman 1942). Ultimately, all energy inputted is equivalently outputted, or “lost” as heat, where the heat energy is not recyclable, hence an open system. Thus, solar inputs are absolutely necessary to drive the ecosystem.

A majority of studies investigating energy flow within ecosystems have focused on aquatic ecosystems in comparison to terrestrial ecosystems, with much of the early work conducted in freshwater ecosystems (Benke et al. 1988). Energy transfer within an aquatic ecosystem, specifically streams, begins with the production of photosynthetic organisms (i.e.

algae) attached to the stream bed. This is termed an “autochthonous” source of energy, and is typically important for third order streams and greater (Minshall 1978, Anderson and Sedell 1979). Energy from algal biomass is typically used by macroinvertebrate and herbivorous fish communities. Algae are particularly important for aquatic insect larvae, such as midges, which in turn are important for the production of higher consumers, typically carnivorous fish (Winterbourn and Townsend 1991). Detritus, or dead plant and animals, are processed by the fungal and microbial communities.

The transfer of energy is not limited to the activities of organisms within a single ecosystem itself, especially in stream ecosystems. Terrestrial inputs, particularly leaf litter from plants in the riparian zone, have been considered a significant source of energy for most streams and acts as an energy linkage between terrestrial and stream ecosystems (Cummins 1974, Wallace et al. 1997). Because this energy input originates from outside the stream, it is termed an “allochthonous” source. Leaf litter entering a stream typically is more significant in the headwaters, where shading by vegetation is heavy (Vannote et al. 1980). The energy from this coarse particulate organic matter (CPOM) can be used by a range of macroinvertebrates, ranging from amphipods to stoneflies (Anderson and Sedell 1979). CPOM is processed, or shredded, as these macroinvertebrate feed, making the CPOM available to filter feeding macroinvertebrate communities as fine particulate organic matter (FPOM) (Winterbourn and Townsend 1991). Higher trophic levels, such as carnivorous fishes, indirectly depend on these litter inputs because they increase production of a majority of their macroinvertebrate prey. Additionally, higher trophic levels may directly benefit from terrestrial inputs, such as terrestrial insects that fall into the stream and are consumed (Nakano and Murakami 2001).

Energy distribution in streams and rivers is usually considered to be an upstream to downstream movement (Vannote et al. 1980). There are cases, however, where downstream to upstream energy distribution is possible, most notably caused by the migration of animals. Aquatic insects have been found to migrate downstream to upstream during mating flights (Pringle 1997). Many species of fish also migrate downstream to upstream, primarily for reproduction purposes, refuge, or in search of food (Flecker et al. 2010). Fish migrations are often a large scale event such as the case of Pacific salmon (*Oncorhynchus* spp.), with fish often travelling over 1,000 km with runs in the millions (Gende et al. 2002). Because of this, migrating fish have the potential to connect ecosystems separated by great distances and barriers; fish migration can connect oceans to freshwater bodies or vice versa (anadromy and catadromy, respectively), and freshwater bodies to other freshwater bodies (potadromy). However, the importance of migrating fish as an energy source for streams is not as well understood or as widely known as autochthonous and allochthonous energy sources. This is largely because the importance of landscape energy flow has only been recently recognized in the literature, where migrating fish are a major mechanism (Flecker et al. 2010).

The earliest data on fish migration focused more on nutrient dynamics rather than energy, particularly on their role as natural fertilizers in oligotrophic streams (Juday et al. 1932, Schindler et al. 2003). Anadromous Pacific salmon have received the most attention in this respect. Pacific salmon spend a majority of their adult life in the ocean, accumulating mass and nutrients that are later transported to freshwater streams when they spawn (Schindler et al. 2003). Phosphorus and nitrogen from decomposing salmon carcasses enriches aquatic and terrestrial plants and increases their production (Ben-David et al. 1998, Bilby et al. 1996). Macroinvertebrate communities are indirectly affected by these nutrients as well when feeding on autochthonous production, which has been found to increase macroinvertebrate production and subsequently, production of resident stream fish (Chaloner et al. 2004; Claeson et al. 2006). Potadromous (characins, catostomids) and other anadromous (clupeids, Atlantic salmon) fishes have been found to provide nutrients, but there is substantially less evidence (Flecker et al. 2010).

Migratory fish have recently been identified as potentially important energy sources to streams, especially when the migration purpose is to spawn (Flecker et al. 2010). Again, Pacific salmon have been the major focus. Because salmon are generally semelparous and runs are large, there is a significant amount of energy deposited in the stream as carcasses and eggs. This energy is distributed in the stream through direct consumption and decomposition of tissues (Gende et al. 2002). Large mammals, fish, and macroinvertebrates directly consume the eggs and/or flesh of carcasses, which has been linked to increased survival, densities, and growth of consumers (Gende et al. 2002). Microbial and fungal communities utilize energy from carcasses and nonviable eggs, but it is not clear how these communities transfer this energy to other segments of the ecosystem (Gende et al. 2002). There is less information on other anadromous species, but there have been few studies documenting potadromous characin and catostomid carcasses and eggs as useful energy sources in some streams (Flecker et al. 2010).

As the importance of migratory fish as energy sources to streams becomes more clearly defined, it is important to identify current gaps in knowledge. A majority of the literature has focused on Pacific salmon within their native ranges, while studies on other types of migrating fish within native or non-native ranges remains sparse (Flecker et al. 2010). Interestingly, the Laurentian Great Lakes region provides an opportunity to examine migratory fish not typically included in bioenergetics studies. The Great Lakes are home to several migratory fish including introduced salmonids such as the Pacific salmon and steelhead (*Oncorhynchus* spp.) and natives like the walleye (*Sander vitreus*), suckers (*Catostomus* spp.), and lake sturgeon (*Acipenser fulvescens*).

There have been a few studies that have examined the effects of different migratory fish on Great Lakes coastal streams. There is some information on how nutrients from migratory fish affect Great Lakes coastal streams but the effects tend to vary. Nutrients released from Chinook salmon (*Oncorhynchus tshawytscha*) into Lake Superior tributaries were found to stimulate productivity (Schuldt and Hershey 1995) but were found to have non-significant or negative effects on benthic communities in other Upper Peninsula tributaries (Collins et al. 2011). Iteroparous fish, such as the longnose sucker (*Catostomus catostomus*) and white sucker (*Catostomus commersonii*) were recently found to stimulate production in a few Lake Michigan tributaries due to increased nutrients but similar data for other species are lacking (Burtner 2009, Childress et al. 2014, Childress and McIntyre 2015). So far, there has been only one study that has investigated energy contributions to stream energy budgets from migratory fish, where Ivan et al. (2011) found Chinook and steelhead eggs were an important source of energy for brown trout (*Salmo trutta*) in two western Michigan tributaries.

Purpose

The purpose of this study was to further delineate the role of migratory fish as a source of energy to biological communities in streams in the Laurentian Great Lakes region. Specifically, we attempted to quantify the amount of energy delivered into Michigan coastal streams by migrating fish that have been widely studied elsewhere due to their significance (Pacific salmon, steelhead trout) and species that have not been widely studied (white sucker). Additionally, this study aimed to quantify the energy contribution of these introduced and native migratory fish to resident stream fish diet in two coastal streams in Michigan.

Scope

Previous literature on energy flow in stream ecosystems has focused on two energy sources: autochthonous production from aquatic plants and allochthonous material derived from the riparian zone (Minshall 1978, Naiman and Decamps 1997). Energy flow at a landscape-scale is a recent concept, where migratory animals can play a significant role as energy transporters between boundaries (Flecker et al. 2010). Migratory fish are one such example, travelling great distances that link bodies of water never thought possible (Flecker et al. 2010). These fish can act as energy subsidies, but most of the literature focuses on select species in certain areas that occur naturally (e.g. Pacific salmon in the Pacific Northwest). This study expands upon this literature by focusing on both natural and unnatural (introduced) migrants in a relatively understudied area (Laurentian Great Lakes region).

Assumptions

1. We assume that the sampled tissues in this study were not biased and were representative of the population.
2. We assume that there is little variation in energy density of organism tissues between years and streams in Michigan.
3. We assume that there is little variation in energy density of aquatic insect tissues across order and life stage in Michigan.
4. We assume the bomb calorimeter was accurate in its measurements.

5. We assume the weights (dry and wet) of organism tissues were unbiased and representative of typical organism tissues in the population.
6. We assume that sampling for tissues was random and unbiased.

Objectives

We aimed to quantify the contribution of migratory fish organic material (energy) available to coastal stream energy budgets and that are commonly consumed by resident stream fish using bomb calorimetry. Specifically, we aimed to: (1) measure the energy densities of larval white suckers, Chinook salmon female and male muscle, Chinook salmon eggs, and steelhead eggs, all of which are seasonally abundant in coastal streams, in addition to adult trichopterans and adult ephemeropterans; (2) calculate the total energy associated with migratory fish moving into two different coastal streams; and (3) compare energy densities of Chinook eggs, larval white suckers, and aquatic insects, and their relative contribution to resident fish energy intake.

Significance

There are a limited number of studies on the role of migratory fish as nutrient and energy subsidies in coastal streams of the Laurentian Great Lakes region, where energy subsidies have received less attention than nutrients (Schuldt and Hershey 1995, Burtner 2009, Collins et al. 2011, Ivan et al. 2011). Studies in the Pacific Northwest have found that energy subsidies can supplement multiple trophic levels, stimulating detrital, macroinvertebrate, and fish production (Schindler et al. 2003). This study will further delineate the role of migratory fish in subsidizing trophic levels in the context of Great Lakes streams. If there is evidence that migratory fish are important energy subsidies to Great Lakes stream ecosystems, then there needs to be discussion on how to properly manage Michigan's migratory fish populations to maintain stable energy dynamics.

There are several anthropogenic stressors that can negatively affect migrating fish, dams being one of the most detrimental (Freeman et al. 2003). Dams can reduce abundance of migratory fish and alter the movement of energy into streams (Freeman et al. 2003). Michigan has several dams that block fish passage, where stream ecosystems dependent on energy subsidies from migratory fish may suffer because of a dam blocking this energy delivery. In addition, Michigan has also executed dam removals; this allows migrants to move farther than previously, moving energy deposition further upstream. If migratory fish are important energy sources, stream ecosystems are at risk of energy losses if a dam is implemented or removed.

There also have been recent declines in returns of migratory fish to Michigan's coastal streams (MDNR). Introduced migrants (primarily salmonines), such as the Chinook, Coho, and steelhead have had depleted returns from tens of thousands in the 1970's to mere hundreds in 2015 (MDNR). The salmonine populations have begun to suffer because of dwindling food source abundance and energy (Jacobs et al. 2013). Native migrants are also feeling pressure; for example, management has implemented rehabilitation programs for lake sturgeon to prevent extirpation (Hayes and Caroffino 2012). Because the information on the importance of migratory fish energy to stream ecosystems is limited, it is not known what the impacts will be with these changing fish communities.

In conclusion, this study will add to the general literature on fish migration as an energy source. Additionally, this study will expand knowledge on the importance of migratory fish in

Great Lakes coastal stream energy budgets and provide information for future management decisions.

Definitions

Adfluvial – Fish that spawn in streams, where the young will migrate out to a lake system to mature and return to that stream for the next spawning event.

Energy density – amount of energy within an organism on a per unit basis, generally mass (grams)

CHAPTER II

MANUSCRIPT

The effect of seasonal fish migration on energy budgets in two coastal Michigan streams

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ABSTRACT

Migratory fish are known to seasonally enter coastal stream systems but the magnitude of the effects these migrations have on stream energy budgets is not fully understood. The Laurentian Great Lakes have several introduced and native adfluvial fish, where only a few studies have investigated the impacts of their migration on energy budgets in Michigan coastal streams. We quantified the contribution of energy from Chinook salmon (*Oncorhynchus tshawytscha*) muscle and eggs, steelhead (*Oncorhynchus mykiss*) eggs, and larval white suckers (*Catostomus commersonii*) to coastal stream energy budgets. Energy densities and energy delivered to streams were estimated using bomb calorimetry and annual return data from the Little Manistee River Weir and other recent studies. In addition, we compared the energy contribution of these adfluvial fish tissues and aquatic insects to resident stream fish diets in two rivers in western Michigan. Specifically, we examined the energy contribution of Chinook eggs to steelhead parr diets in Bigelow Creek, MI and the contribution of energy by larval white suckers to brown trout (*Salmo trutta*) and non-migratory rainbow trout (*Oncorhynchus mykiss*) diets in the Big Manistee River, MI. Our measured energy density values differed markedly from values typically used in the literature, and indicate that some invertebrate groups (Trichoptera) have energy densities that do not significantly differ from salmon eggs which are typically perceived to be energy dense. Our results suggest that steelhead parr in Bigelow Creek consume more energy during the fall when salmon eggs are present. In contrast, large numbers of drifting larval white suckers in the Big Manistee River does not result in an increase in energy intake for trout during spring, but may satisfy base energy needs. Our results suggest that adfluvial fish are an important component of energy transfer between systems and contribute substantial energy to coastal stream energy budgets in Michigan.

Keywords: adfluvial migration, energy subsidy, calorimetry, bioenergetics, salmon, trout, sucker, eggs, muscle

INTRODUCTION

Energy, in the form of organic matter, that is available to stream communities is derived from either autochthonous or allochthonous sources (Benke et al. 1988). Autochthonous organic matter is produced by organisms within the stream, and may be the most usable energy source (Minshall 1978). Typically, allochthonous organic matter is derived from the terrestrial vegetation within the watershed. Generally, a large fraction of this organic matter is leaf litter (Naiman and Decamps 1997) and requires conditioning before it is available to various trophic levels due to the presence of cellulose and other structural components. Normally this organic matter travels from upstream to downstream passing through several invertebrate functional feeding groups (Vannote et al. 1980).

Alternatively, organic matter may be transported from downstream to upstream (Flecker et al. 2010) following several routes. For example, Pringle (1997) noted that aquatic insects will move upstream during mating flights. Not only does this migration repopulate upstream stream segments, it may redistribute energy along the stream corridor. Stream-bound fish also migrate upstream for reproduction, feeding, or refuge from harsh conditions (Flecker et al. 2010).

For rivers connected to lakes or marine ecosystems, seasonal migrations of fish, particularly during spawning, may represent an alternative source of organic material and alter nutrient availability (Lessard and Merritt 2006) and energy inputs (Gende et al. 2002, Ivan et al. 2011). Energy can be incorporated into stream energy budgets through direct consumption of organic matter (eggs or tissues) and/or may be available indirectly through detrital pathways

(Gende et al. 2002). Although the role of detrital pathways has not been examined in depth (Gende et al. 2002), organic matter consumed directly has been found to increase lipid content, density, biomass, and growth of resident stream fish and macroinvertebrates (Wipfli et al. 2003, Heintz et al. 2004, Rinella et al. 2012).

A majority of studies have focused on how Pacific salmon affect stream energy budgets within the Pacific Northwest (Janetski et al. 2009). There have been fewer studies conducted in freshwater systems, and most are restricted to lake energy dynamics, most notably in the Laurentian Great Lakes region (Pothoven et al. 2006, Paterson et al. 2009, Fahnenstiel et al. 2010). Recent data, however, have suggested that both introduced and native migratory (i.e. adfluvial) fish may modify coastal stream conditions within the Laurentian Great Lakes region (Collins et al. 2011, Ivan et al. 2011, Childress et al. 2014, Childress and McIntyre 2015). Burtner (2009) evaluated changes in stream metabolism before and after the sucker spawning run into a northern Michigan coastal stream and suggested an increase in stream metabolism may have been due to the addition of organic carbon associated with the run. Ivan et al. (2011) recorded an increase in resident brown trout densities and food consumption in coastal Michigan streams receiving salmon eggs. However, it is unclear how much energy is associated with seasonal migrations of adfluvial Great Lakes fish and if this energy does supplement stream fish energy intake.

The purpose of this study was to quantify the potential seasonal contribution of energy from Chinook salmon, steelhead, and white suckers to the energy budgets of two coastal Michigan streams. In addition, we assessed the contribution of these energy sources to resident stream fish diets. Specifically, we: (1) measured the energy densities of larval white suckers, Chinook salmon female and male muscle, Chinook salmon eggs, and steelhead eggs, all of which are seasonally abundant in coastal streams, in addition to adult Trichoptera and adult Ephemeroptera; (2) calculated the total energy associated with migratory fish moving into two different coastal streams; and (3) compared energy densities of Chinook eggs, larval white suckers, and aquatic insects, and their relative contribution to resident fish energy intake. We chose these tissues for comparisons because they have been found to be a major seasonal component of resident stream fish diets in two coastal Michigan streams.

METHODOLOGY

Study area and tissue collection

We selected two west Michigan coastal stream systems for this study; the Manistee/Little Manistee River system and the Muskegon River/Bigelow Creek system. Both connect with Lake Michigan through a drowned river mouth habitat and receive spring and fall migrations of adfluvial fish. Data from diet studies conducted on these two coastal river systems served as the basis for this study. The first was a diet study of trout that were resident during spring in the Manistee River, MI below Tippy Dam (Conte and Luttenton unpublished data). Tippy Dam forms the upstream boundary for adfluvial fish migration in the Manistee River. During late May, brown and rainbow trout primarily consumed adult Ephemeroptera, adult Trichoptera, and larval chironomids; by early to mid-June, >70% of both trout species were consuming larval white sucker exclusively, and in large numbers. The remaining trout continued to consume adult ephemeropterans, adult trichopterans, and larval chironomids (Conte and Luttenton unpublished data). The second study quantified diets of age 0+ steelhead parr in the Muskegon River and Bigelow Creek, a small cold water tributary (Luttenton et al. 2015). Croton Dam, a surface-draw hydroelectric-generating facility, is the limit for upstream migration on the Muskegon River. Parr diets were analyzed during summer and fall from 2011 to 2013. The fall sample period coincided with the Chinook salmon spawning run. Fall parr diets generally consisted of larval Trichoptera, larval Ephemeroptera, and salmon eggs. Previous studies have reported similar diets for parr in this system (Godby et al. 2007, Ivan et al. 2011).

To quantify caloric content of tissues of fall migrants, we obtained representative samples from various locations, based partly on season and logistics. Chinook salmon muscle tissue and eggs were obtained from the Michigan Department of Natural Resources (MDNR) egg collection facility on the Little Manistee River (referred to as the Little Manistee River Weir – LMRW). Chinook salmon muscle tissue was collected from 15 males and 14 females during egg-take operations during fall 2013. Muscle tissue energy was quantified because Chinook contribute energy as carcasses in addition to eggs because they are semelparous. Chinook eggs were collected from the same female individuals used for muscle tissue analysis.

Steelhead eggs were collected during egg-take operations at the LMRW during spring 2015. Approximately 80% of steelhead do not survive after spawning (P. Seelbach, personal communication), but there has been no data documenting if a majority of steelhead die in the river or lake so we did not include steelhead muscle in our analysis. Fish eggs and muscle tissue were transported on ice to the lab and frozen.

Newly emerged larval white suckers and adult trichopterans were collected from the Manistee River 2 km downstream from Tippy Dam during spring 2014 (M. Holtgren and S. Ogren, personal communication). Samples were collected using drift nets that were deployed after sunset. Following collection, the samples were frozen until processing. Subsequently, the samples were thawed and larval suckers and adult Trichoptera were removed for calorimetric analysis. Adult Trichoptera were also collected in early summer 2015 from the Muskegon River below Croton Dam using a D-net and insect net.

We used adult *Hexagenia limbata* as a representative Ephemeroptera during this study. We collected adult *H. limbata* during June 2015 from the upper Manistee River because we could collect large numbers of individuals in a relatively short period of time. The insects were caught at dusk using insect nets. Although adult *H. limbata* were not actually found in fish gut contents, we believe they provide a reasonable estimate of the energy density of ephemeropterans on a per gram dry weight basis (cal/g dw) (see sample analysis).

Sample analysis

Prior to calorimetric analysis, we determined the wet weight (ww) of individual tissues to the nearest 0.00001 g. Wet weights were determined for 100 individual steelhead eggs, Trichoptera, and *H. limbata*. Salmon muscle wet weight was based on the average of two filets taken from fish collected at the LMRW in 2015 (G. Parks, Andy's Tackle Box, personal communication). Male and female wet and dry weights were assumed to be approximately the same. We did not determine wet weights of larval white suckers due to difficulties obtaining stable measurements. An average wet weight of Chinook salmon eggs was estimated from the weight of 50 eggs weighed individually. Following wet weight measurements, each sample was placed in a drying oven for 48 hours at 50 degrees Celsius. The samples were then weighed to determine dry weight (dw) to the nearest 0.00001 g. Dry weight for salmon muscle was calculated using equation (1).

$$(1)\ M_w = (W_w/(W_w+D_w)$$

M_w is the percent moisture on a wet basis (75%, Peters et al. 2007), W_w is the wet weight, and D_w is the dry weight.

Dry tissue was formed into pellets using a Parr Z 4027 Pellet Press. The pellets were weighed to the nearest 0.00001 g. Individual pellets of steelhead eggs (n=20), *H. limbata* (n=20), and trichopterans (n=20) were produced by combining a sufficient number of individuals to reach ~0.025 g. Wings and legs were not removed from the insects. We also produced pellets from muscle tissue for each male (n=15) and female (n=12) Chinook salmon. Individual pellets (n=12) were produced using eggs collected from individual females following the same procedure used for steelhead eggs. Sample sizes for Chinook female muscle and eggs were reduced because of outliers from semimicrobomb malfunction and more pellets could not be prepared due to limited tissue. The energy content of each pellet was determined using a 1425 Parr Semimicrobomb Calorimeter. The calorimeter was calibrated with benzoic acid (6,318 cal/g dw) before combustion of tissue pellets (percent recovery 99.9%).

To improve our estimates of aquatic insect energy density, we adjusted our estimates for non-digestible material by subtracting the energy density of chitin. However, we could not use exoskeletons from adult trichopterans or adult ephemeropterans because we could not collect a sufficient amount of chitin to create pellets. Thus, we estimated the energy density of chitin by combusting Coleoptera, Orthoptera, and Odonata exoskeletons because they were easily obtainable and could be obtained in large quantities for analysis. Exoskeletons were identified to family. A different family was used for each pellet; families include Scarabaedae, Carabidae, Lamypyridae, Gryallacridae, Acrididae, and Libellulidae. Average chitin energy density was 5,250 cal/g dw. Exoskeletons were removed from the coleopterans, orthopterans, and odonatans, then crushed with a mortar and pestle, formed into pellets (n=10) using the pellet press, and combusted in the calorimeter. We multiplied the average chitin energy density by the average weight of chitin of a whole insect. Average weight of the chitin was found by multiplying the average percent chitin of adult trichopterans and adult ephemeropterans by the average whole weight (Higgs et al. 1995, Cauchie 2002). We then subtracted the chitin caloric estimate from whole insect caloric estimates.

We estimated how much energy was consumed by resident stream fish using diet data and our measured caloric values for aquatic insects and migratory fish tissue. We assumed that energy density and content did not vary significantly between years for each tissue type, and that weights were similar for both adult and larval insects. We also assumed that the energy density of successive insect life stages is relatively similar on a cal/g dw basis as well. This is a typical assumption in bioenergetics literature (Moore et al. 2008), but we note a recent study suggested larval and adult stage energy densities tend to differ (Gray 2005). In addition, we assumed that energy density of *H. limbata* on a cal/g dw basis was representative of Ephemeroptera in general because of the similarity between our value and other reported values (Cummins and Wuycheck 1971, Hanson et al. 1997). Because *H. limbata* is one of the larger insects in Michigan streams, we used a smaller, more representative weight in our analyses. Trout tended to consume *Baetis* spp., which have an average wet weight of 0.000397 g, reducing our Ephemeroptera energy content estimate to 0.40 digestible calories for our analysis (M. Luttenton, unpublished data). Because we did not have weights for larval chironomids, we used energy densities and weights of chironomids reported by Nolte (1990, larval stage 0.0025 g dw) and Gray (2005, 6,108 cal/g dw) for our calculations of energy intake of Big Manistee River trout.

Statistical analyses

We used a Shapiro-Wilk test to determine if energy density data for each tissue type was normally distributed. Female Chinook salmon muscle and eggs were paired and analyzed using Pearson's correlation before further analyses to determine if they were correlated. Adult

Trichoptera were collected from two different locations in different years (Manistee River 2014, Muskegon River 2015). We compared adult Trichoptera energy content between year/site using a t-test to determine if the data could be pooled for subsequent analyses. We tested for differences in mean energy densities among tissues using one-way ANOVA and post-hoc Holm's test. Analyses were performed using R software version 3.2.3.

RESULTS

Energy density data for each tissue type was found to have a normal distribution. Trichoptera energy density data for the Manistee River and Muskegon River were pooled for analyses because the data were similar (t-test; $t(18)=-0.023$, $p=0.98$) and homoscedastic (Levene's test; $F(1,18)=0.18$, $p=0.68$). Pooled adult Trichoptera data were also normally distributed ($p=0.74$). The energy densities of Chinook female muscle and eggs were not correlated ($t(10)=-0.91$, $p=0.38$). Energy densities across tissue types were not homoscedastic (Levene's test; $F(6,112)=5.70$, $p<0.001$), so we applied a Welch's correction (McDonald 2009).

Energy densities of tissues ranged from 4,758 cal/g dw to 6,216 cal/g dw (Table 1), and varied significantly by tissue type (1-way ANOVA; $F(6,46)=78.55$, $p<0.001$). Adult trichopterans, Chinook eggs, and steelhead eggs were the most energy dense tissues at >6,200 cal/g dw (Table 1) and were not significantly different (Table 2). Chinook muscle energy density ranged from 4,759 cal/g dw to 5,092 cal/g dw with female energy density slightly lower than male muscle but there was no significant difference (Table 1, 2). Larval white sucker energy density (5,726 cal/g dw) was significantly higher than both male or female Chinook muscle and adult *H. limbata* (5,277 cal/g dw), but was lower than adult Trichoptera and salmonid eggs (Table 1, 2). Similarly, adult Trichoptera energy densities were significantly higher than the energy content of *H. limbata* (Table 1, 2). In contrast, the energy density of adult *H. limbata* was significantly higher than female Chinook muscle but was not significantly different in energy density compared to male Chinook muscle (Table 1, 2).

Obviously, the energy content of an intact organism is dependent on the size and weight of the organism. To calculate the energy content of an intact organism (e.g., whole salmon, single egg or insect) we multiplied the measured energy density of each tissue type by the actual weight of an individual item. Two salmon filets (female or male) contain an estimated 3.5 to 3.8×10^6 calories, the single largest amount of energy on a per item basis (Table 3). In comparison, a single larval sucker contains only 5 calories per individual (Table 3). Salmonid eggs have more energy per individual than either insect group; a single Chinook egg or steelhead egg contains 571 calories and 212 calories respectively (Table 3). Although eggs and adult Trichoptera had similar energy densities on a per gram dw basis (Table 1, 2), the energy content varied widely among individual items (1 egg or 1 adult Trichoptera) (Table 3). For example, a single steelhead egg contains 12 times more energy than a single adult Trichopteran (18 calories). Although adult *H. limbata* had a lower energy density per gram dw, a single *H. limbata* contains 100 calories, 5 times more energy than a single adult Trichopteran (Table 3).

DISCUSSION

Seasonal energy contribution to coastal streams

Seasonal spawning migrations of native and non-native fish appear to deliver substantial quantities of lake-derived energy to the Manistee River and Muskegon River systems. However, the total quantity of energy is primarily a function of two factors, one being the actual energy content of a particular tissue type and the second being related to the total number of individuals associated with a particular spawning event. For example, the cal/g dw of Chinook muscle is relatively low compared to salmon eggs, but an entire Chinook carcass constitutes a significant amount of biomass, and thus energy. In contrast, salmon eggs are more energy dense (cal/g dw) but energy per egg is relatively small. However, a female carrying 4,499 eggs (Sapak and Jonas 2015) transports nearly 1.10×10^6 calories in addition to the calories in muscle tissue.

Using 2013 Little Manistee River data (6,427 adults, LMRW fish count data, MDNR), an average of 4,671 eggs/female (S. Trapp, personal communication), and assuming half the population was female, we calculated that 2.33×10^{10} calories would have been imported as muscle tissue and 8.57×10^9 calories would have been imported as eggs to the Little Manistee River (~110 ha) in fall 2013. Fish counts at the Little Manistee River weir during fall salmon migrations historically have ranged from approximately 2,000 to 40,000 individuals providing an estimated 7.47×10^9 to 1.49×10^{11} calories from muscle, and egg deposition would constitute an additional 2.67×10^9 to 5.34×10^{10} calories during the fall spawning of Chinook salmon in the Little Manistee River and rivers of similar size. In smaller streams, such as Bigelow Creek (3.2 ha), fall Chinook salmon densities have been estimated at 800 adults/ha (Carl 1980). At this density, Chinook salmon carcasses would contribute 9.56×10^9 calories, and assuming females accounted for half the spawning individuals, eggs would represent an additional 3.48×10^9 calories in smaller streams in fall.

Spring spawning migrations may constitute a similar upstream transfer of energy from downstream locations. During spring, steelhead may provide a smaller, but still significant amount of energy to selected coastal streams in comparison to Chinook. We acquired steelhead eggs for calorimetry during spring 2015; using 2015 Little Manistee River data (2,857 adults, LMRW fish count data, MDNR), an average of 3,805 eggs/female (S. Trapp, personal communication), and assuming half the population was female, approximately 1.15×10^9 calories would have been imported into the Little Manistee River in spring as steelhead eggs in 2015. Little Manistee Weir personnel have recorded steelhead migrations ranging from 1000 to 10,000 individuals. This would account for 4.02×10^8 to 4.24×10^9 calories every spring for similar size rivers receiving runs of these magnitudes. Note that this is an underestimation because the weir is not closed continuously during the steelhead migration which would allow some number of individuals to pass upstream without being counted. In small streams like Bigelow Creek with an estimated 100 steelhead adults/ha (Swank 2005) in spring, and assuming females accounted for half the spawning individuals, eggs would represent 1.29×10^8 calories in smaller streams.

In addition to steelhead, white suckers (and other Catostomidae) migrate into coastal streams and rivers to spawn in spring. Childress et al. (2014) estimate that approximately 100,000–1,000,000 White suckers enter large rivers and 100–10,000 enter small rivers annually for spawning. In the Big Manistee River, larval white suckers account for a significant portion of the drift during late May or early June (Conte and Luttenton, unpublished data). Assuming half the population is female, and that the average number of larvae per white sucker female is 35,000 (average 20,000-50,000 eggs/female, Galloway and Kevern 1976), we calculated that larval suckers would represent 9.39×10^9-9.39×10^{10} calories in the spring in larger rivers such as the Big Manistee River. In smaller streams, larval suckers would represent 9.39×10^6-9.39×10^8 calories.

Using our 2015 estimate from the Little Manistee for steelhead and combining energy estimates for white suckers (9.39×10^8 calories) during spring migrations, the Little Manistee River could realize a total of 1.07×10^9 calories from steelhead eggs and larval white suckers. During fall, a total of 3.19×10^{10} calories in the form of Chinook muscle and eggs could be transferred from downstream locations (using 2013 LMRW and MDNR data). The combined spring and fall energy transported into this coastal stream may be 3.29×10^{10} calories.

Estimates of annual energy transfer by adfluvial fishes to a particular coastal river will vary depending on a number of factors. As noted above, the number of fish migrating during any season will vary depending on spawning success during previous years and conditions in the adjoining lake ecosystem (Trudel et al. 2005). In addition, the energy content of a particular tissue may differ from year to year due to changes in the forage base leading up to a spawning event (Cummins and Wuycheck 1971). Similarly, the number of eggs/female will depend on forage as well. Regardless of this variation, the total energy transfer by adfluvial fish into coastal rivers is substantial on an annual basis.

Migratory fish supplementing stream resident fish diets

We acknowledge that only a fraction of the energy transferred by adfluvial fish is incorporated into the resident stream community. However, it is clear that tissues of adfluvial fish are consumed by resident fishes (Ivan et al. 2011). In that regard, the energy density of various prey items available to consumers has been a central tenant of food-web energy dynamics and bioenergetics modeling. We determined the energy content of six different tissue types that are available to stream fish on a seasonal basis and have been identified as a significant component of fish diets in previous studies; specifically fall diet studies of resident stream fish were conducted on Bigelow Creek (Merna 1986, Godby 2000, Godby et al. 2007, Ivan et al. 2011, Luttenton et al. 2015) and spring diet studies were carried out on the Big Manistee River (Conte and Luttenton, unpublished data).

Big Manistee River Brown and rainbow trout sampled from the Big Manistee River consumed a variety of prey items, but dominant prey items included larval white suckers, adult

Trichoptera, adult Ephemeroptera, and larval chironomids. (Conte and Luttenton, unpublished data). Analysis of rainbow and brown trout diets found that 100% of trout (21 fish sampled per species) primarily consumed these insects during late May (Table 4). By early June, 20% (3/18 fish sampled) of brown trout and 40% (7/16 fish sampled) of rainbow trout exclusively consumed larval suckers in early June (Table 4) while the remaining trout continued consuming insects (Table 4). The percentage of trout consuming larval suckers increased to 85% for brown trout (18/21 fish sampled) and 75% for rainbow trout (15/20 fish sampled) by early mid-June (Table 4) while the remaining trout continued consuming insects (Table 4).

Prior to larval sucker emergence (May 22), 100% of brown trout diet was composed of adult trichopterans, adult ephemeropterans, and larval chironomids (Table 4). Based on a diet of insects, we estimate that the trout consumed 504 calories during this time period. After larval suckers emerge, 20% of the brown trout sampled on June 12 began exclusively consuming larval suckers, representing an energy intake of 193 calories, while 80% remained consuming adult trichopterans, adult ephemeropterans, and larval chironomids, representing an energy intake of 161 calories (Table 4). By June 14, brown trout consuming larval suckers had an energy intake of 725 calories, while the remaining trout consumed 2,173 calories as adult trichopterans, adult ephemeropterans, and larval chironomids (Table 4).

Rainbow trout exhibited a pattern in their diets similar to brown trout prior to and after larval sucker emergence, but they consumed more individuals regardless of prey type (Table 4). On May 22, 100% of rainbow trout diets were composed of adult trichopterans, adult ephemeropterans, and larval chironomids (Table 4); trout consumed 973 calories as insects on this sample date. After larval sucker emergence, 40% of rainbow trout began exclusively consuming larval suckers, eating more individuals on June 12 than brown trout (Table 4). On

June 12, the rainbow trout consuming larval suckers consumed 1,014 calories, while the remaining 60% of rainbow trout consumed 281 calories in the form of aquatic insects (Table 4). By June 14, the number of larval suckers consumed for brown and rainbow trout diet were similar, where 75% of rainbow trout were consuming 789 calories worth of larval suckers while the 25% of rainbow trout consuming adult trichopterans, adult ephemeropterans, and larval chironomids consumed 1,255 calories worth of these insects (Table 4).

It appears that exclusive consumption of larval suckers provided more energy than insects prior to larval sucker emergence for both rainbow and brown trout. The 20% of brown trout consuming larval suckers acquired slightly more energy than the 80% consuming aquatic insects on June 12, but had to consume more individual prey items than those consuming just aquatic insects (Table 4). This may represent a transition in foraging as larval suckers become more numerous in the drift and brown trout begin taking advantage of the abundance of larval suckers in the drift. But, it appears that eating suckers requires trout to consume more individuals to meet energetic demands; a single adult Trichopteran (18 calories) and larval chironomid (15 calories) contains more energy than a single larval sucker (5 calories). Rainbow trout gained considerably more energy consuming larval suckers on June 12 when compared to rainbow trout consuming aquatic insects and brown trout consuming only larval suckers (Table 4). This could be attributed to rainbow trout's predisposition to aggressiveness or simply a greater energy need (Conte and Luttenton unpublished data).

On June 14, the relatively small percentage of brown and rainbow trout consuming aquatic insects (i.e. adult trichopterans and adult ephemeropterans) acquired more energy than fish eating only larval suckers (Table 4). Thus, it appears that the consumption of larval suckers by trout in the Big Manistee River may not be driven by energy. The large percentage of brown and rainbow trout that continue to forage on larval suckers may do so simply because of the large number of larvae present compared to the number of trichopterans and ephemeropterans.

Bigelow Creek Over three years, daily fall diets of steelhead parr in Bigelow creek were primarily composed of Chinook salmon eggs, larval trichopterans and larval ephemeropterans (Table 5), whereas chironomids, amphipods, and terrestrial insects would comprise a small remainder (<1%). In fall 2011, parr acquired less energy (38 calories) from consuming salmon eggs than from consuming larval trichopterans (62 calories), but more energy than larval ephemeropterans (8 calories). In fall 2012, parr obtained more energy from salmon eggs (156 calories) than larval trichopterans (47 calories) and larval ephemeropterans (8 calories). Parr in fall 2013 consumed more salmon eggs by weight than the two previous falls while the larval aquatic insect consumption remained similar to fall 2012. Parr in fall 2013 consumed 2,066 calories of salmon egg, 51 calories of larval trichopterans and 8 calories of larval ephemeropterans.

Between fall 2011 and 2013, salmon eggs accounted for the increase in weight of food ingested by parr; the consumption of larval aquatic insects remained consistent while salmon eggs increased across all years. Weight of sampled parr were similar in fall 2012 and 2013 (8 g ww), but parr were heavier in fall 2011 (10 g ww). Specific daily consumption (g/g/day ww) was also similar in fall 2012 and 2013 (0.070 g/g/day) but was higher in fall 2011 (0.11 g/g/day). Thus, the increase in egg consumption may not be for maintaining larger body mass. The increase in egg consumption could be attributed to stronger Chinook salmon returns.

Parr appear to take advantage of salmon eggs when they are available, benefiting from the high caloric density and weight of the eggs; a single Chinook salmon egg with 571 calories contains 32 times more energy than a single larval Trichopteran (18 calories) and 1,428 times more than a single larval Ephemeropteran (0.40 calories). This additional energy may be stored for over-wintering or used for growth (Heintz et al. 2004, Ivan et al. 2011).

Bioenergetic Considerations

Early estimates of energy content of prey items were primarily determined using a Phillipson bomb or from proximate analysis and standard equivalents (Cummins and Wuycheck 1971, Brett 1995). Several issues have been identified with the accuracy of these methods (T. Trier, personal communication). Given the variability in analytical history and tissue energy density (Trudel et al. 2005), we felt that it was important to establish calorie estimates for the organisms that are part of resident trout diets and were used in this study.

We compared our energy density values to values that are commonly cited in the literature, where a 500-1,000 cal/g difference is considered significant (Cummins and Wuycheck 1971). A majority of bioenergetics literature cite energy densities from Cummins and Wuycheck (1971), Brett (1995), and Hanson et al. (1997). Literature values for salmonid eggs are ~3,000 cal/g dw less than our values of salmonid eggs (Table 6). In contrast, our values for female and male Chinook muscle are substantially lower (~1,500 cal/g dw) than the literature (Table 6). The value for larval fish energy density in the literature is similar to our value for larval suckers. Similarly, our value for adult *H. limbata* energy density compares closely to those in the literature (Table 6). Our value for adult trichopterans is ~1,200 cal/g greater than the literature (Table 6).

From these comparisons, it is clear that values either varied widely from the literature's (Chinook muscle, eggs, adult Trichoptera) or were similar (larval fish, adult Ephemeroptera). Variation in energy density values between studies may be due to species, ontogeny, seasons, regions, and methodology (Trudel et al. 2005), each of which can exacerbate potential error if values are used generically. Our data provides a few good examples of the potential. Our Chinook muscle was collected during the spawning run, while the value in the literature is not known; the high energy density suggests that the salmon was likely not spawning. Additionally, our adult Trichopteran energy density is surprising similar to the energy density of salmonid eggs; the common tenet is that salmonid eggs are at least three times more energy dense than invertebrates (Schindler et al. 2003). Using literature values to complete our calculations would have resulted in a significant underestimate of the contribution of insects to fish energy consumption, as well as an underestimate of egg and overestimate of muscle energy contribution to coastal stream energy budgets.

Conclusions

Our study quantified the energy imported to Michigan coastal streams by adfluvial fish in Michigan. Our study also provided evidence that salmon eggs provide additional energy while suckers do not provide additional energy for resident stream fish diets in two Michigan coastal streams. In addition, we highlighted potential issues when borrowing energy density parameters from the literature. We suggest direct calorimetric measurement when possible; while there is some monetary and manpower expenditure associated with this method, we believe it is worthwhile since it minimizes variation and error.

We acknowledge this study only examined diets of three stream fish species and included a limited number of adfluvial fish, representing a fraction of energy dynamics associated with seasonal fish migrations. There are other introduced and native adfluvials that could provide energy subsidies and there are other trophic pathways that may use this energy. For example, studies in the Pacific Northwest suggest macroinvertebrates, fungal, and microbial communities are affected by adfluvial energy (Gende et al. 2002). We suggest future research to consider these alternative adfluvials and pathways when examining stream energy budgets.

AUTHOR CONTRIBUTIONS

Emily M. Dean and Mark R. Luttenton participated in study design, data collection, analysis and data interpretation. Emily M. Dean drafted the manuscript, while Mark R. Luttenton revised the manuscript.

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TABLES

Table 1. Mean energy density by tissue type. Standard error was only calculated for calories per gram dry weight.

Tissue Type	N	Average energy density	
		cal/g dw	cal/g ww
Trichoptera	20	6,216 ± 52	3,149
Steelhead eggs	20	6,211 ± 40	3,009
Chinook eggs	12	6,209 ± 32	2,550
Larval white sucker	20	5,726 ±78	-
Hexagenia limbata	20	5,277 ± 40	1,051
Chinook male muscle	15	5,092 ± 97	1,697
Chinook female muscle	12	4,759 ± 159	1,586

Table 2. Results of the Holm's post-hoc test comparing tissue energy densities.

	Trichoptera	Chinook eggs	Chinook female muscle	Chinook male muscle	*Hexagenia limbata*	Steelhead eggs
Chinook eggs	1.00	-	-	-	-	-
Chinook female muscle	< 0.001	< 0.001	-	-	-	-
Chinook male muscle	< 0.001	< 0.001	0.075	-	-	-
Hexagenia limbata	< 0.001	< 0.001	< 0.001	0.20	-	-
Steelhead eggs	1.00	1.00	< 0.001	< 0.001	< 0.001	-
Larval white suckers	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

Table 3. Mean energy density, dry weight, wet weight, and digestible calories per tissue type. Aquatic insects were corrected for chitin. Standard error was only calculated for calories per gram dry weight.

Tissue Type	N	Average dw (g)	Average ww (g)	Average dw of chitin (g)	Energy per individual (whole) (cal)	Energy of chitin (cal)	Energy per individual (digestible) (cal)
Chinook male muscle	15	755.67	2,267.96	-	-	-	3,874,930
Chinook female muscle	12	755.67	2,267.96	-	-	-	3,596,079
Chinook eggs	12	0.092	0.22	-	-	-	571
Steelhead eggs	20	0.034	0.071	-	-	-	212
Hexagenia limbata	20	0.020	0.099	0.00089	104.49	4.70	100
Trichoptera	20	0.0031	0.0061	0.00019	19.27	1.18	18
Larval white suckers	20	0.00094	-	-	-	-	5

Table 4. Average number of individual prey items consumed by brown and rainbow trout on May 22, June 12, and June 14, 2007 in the Big Manistee River. Larval white suckers emerged after May 22. After sucker emergence, brown trout and rainbow trout were found to feed on either larval white suckers or aquatic insects exclusively.

Species	Prey item	Sampling date		
		May 22	June 12	June 14
Brown trout	Trichoptera	13	8^{a}	100^{a}
	Ephemeroptera	1	6^{a}	71^{a}
	Chironomids	18	1^{a}	23^{a}
	Total invertebrates	67	18^{a}	218^{a}
	Larval white suckers	0	36^{b}	135^{b}
Rainbow trout	Trichoptera	34	13^{c}	52^{c}
	Ephemeroptera	3	6^{c}	47^{c}
	Chironomids	24	3^{c}	20^{c}
	Total invertebrates	64	29^{c}	153^{c}
	Larval white suckers	0	189^{d}	147^{d}

Table 5. Average daily consumption of prey items (grams wet weight) by age 0+ steelhead parr in Bigelow Creek over three fall years.

Species	Prey item	Sampling date		
		Fall 2011	Fall 2012	Fall 2013
Steelhead parr	Total food ingested	0.045	0.083	0.83
	Trichoptera	0.021	0.016	0.017
	Ephemeroptera	0.010	0.010	0.01
	Salmon eggs	0.015	0.061	0.81

Table 6. Mean energy densities (in calories per gram dry weight) typically used in the literature compared to our directly measured values.

Prey Item	Cummins and Wuycheck 1971	Hanson et al. 1997	Brett 1995	Our study
Trichoptera	4,999	-	-	6,216
Steelhead eggs	3,598	-	-	6,211
Chinook eggs	3,598	-	-	6,209
Larval white suckers	-	5,802	-	5,726
Ephemeroptera	5,469	5,695	-	5,277
Chinook muscle	-	-	6,453[a]	4,925

Notes:

a: value derived from Higgs et al. (1995) from Brett (1995).

CHAPTER III

EXTENDED REVIEW OF LITERATURE

Bioenergetics has been considered an important concept in aquatic systems since Lindeman's (1942) investigation of energy transfer between trophic levels in Cedar Bog Lake (Benke et al. 1988). The term "bioenergetics" involves energy in relation to biological aspects of the stream such as production and feeding of organisms. Types of energy input into streams include autochthonous (i.e. within the stream) and allochthonous (i.e. outside the stream) sources; these sources have been extensively studied for their contribution towards freshwater stream energy (Benke et al. 1988). Autochthonous energy sources can be algae or organism fecal matter within a stream that provides energy to consumers (Minshall 1978). Allochthonous energy sources can be insects falling into the stream or leaf litter from riparian vegetation (Baxter et al. 2004). An additional energy source to a freshwater stream can come from migrating fish that enter streams to spawn (Bilby et al. 1996, Flecker et al. 2010, Ivan et al. 2011).

Migration is the movement of organisms from one location to another, usually at an expected time. Fish migrate for several reasons, such as feeding, reproduction, or refuge from harsh temperatures (Flecker et al. 2010). Migration can be defined as either diadromous, or the movement between saltwater and freshwater, or potadromous, that involves movement between freshwaters only (Flecker et al. 2010). Diadromous migration can be broken down into three major categories, but the most commonly studied of the three is anadromous. Pacific salmon are the model species of anadromous behavior. Many studies have focused on Pacific salmon, particularly in the Pacific Northwest, and the effect of their migration on recipient streams (Janetski et al. 2009).

Pacific salmon spend a majority of their lives growing in the ocean before returning to their natal freshwater streams for spawning. Salmon individuals at spawning grounds can reach up to the millions (Gende et al. 2002). After spawning, the salmon will die (i.e. semelparous species), and contribute nutrients to freshwater streams and energy as organic material (i.e. eggs, carcass). Considering the magnitude of salmon individuals at spawning, the amount of nutrients and energy contributed is massive.

Earliest data on fish migration has focused more on nutrients than energy, starting with Juday's et al. (1932) limnological study of Karluk Lake in Alaska. Juday et al. (1932) found that spawning sockeye salmon affected both lake and stream chemistry by depositing on average 2 million kg of organic matter and 5,000 kg of the important nutrient, phosphorus. Recent studies have quantified salmon marine-derived nutrients (SDN) and found that these nutrients have a generally positive effect on streams and the surrounding terrestrial ecosystem, and that SDN can supplement the stream for long periods of time (Naiman et al. 2002, Rinella et al. 2013). The dispersal of nutrients from salmon can take a few pathways: direct consumption of carcass or egg, consumption of organisms enriched with SDN, and recycling by processes such as excretion, leaching, and decomposition of carcass (Gende et al. 2002). Stable isotope analysis (SIA) is generally used to track nutrients through trophic levels or identify organisms enriched with SDN (Mantel et al. 2004). Salmon have heavy carbon and nitrogen isotopes, which makes SIA a useful candidate when investigating nutrient dispersal in streams from salmon spawners (Bilby et al. 1996).

Primarily, epilithic biofilm, terrestrial vegetation, and other primary producers are directly affected by recycling of SDN from decomposing carcass (Ben-David et al. 1998, Wipfli et al. 1999, Helfield and Naiman 2001, Johnston et al. 2004, Mitchell and Lamberti 2005, Claeson et al. 2006, Cak et al. 2008, Tiegs et al. 2009, Tiegs et al. 2011). Epilithic biofilm or standing stock tend to be enriched with carbon and nitrogen following salmon runs, resulting in increased growth rates and biomass (Cak et al. 2008, Kohler et al. 2008, Tiegs et al. 2009, Tiegs et al. 2011). However, epilithic response to SDN can be highly variable depending on salmon density and stream environment (Johnston et al. 2004). Terrestrial vegetation experience enrichment in nitrogen, meaning salmon could be natural fertilizers (Bilby et al. 1996, Helfield and Naiman 2001, Rüegg et al. 2011), but Ben-David et al. (1998) suggested that is largely dependent on if the vegetation has limited access to nitrogen.

SDN distribution to macroinvertebrates is usually through macroinvertebrates consuming primary producers that were supplemented by SDN (Bilby et al. 1996, Cederholm et al. 1999). Macroinvertebrates can be enriched by SDN indirectly by feeding on primary producers and microbes supplemented by SDN (Gende et al. 2002, Marcarelli et al. 2014). Several macroinvertebrate functional groups can be enriched by carbon and nitrogen, such as scrapers consuming SDN enriched biofilm and collectors and shredders consuming SDN enriched fine and coarse particulate matter, stimulating secondary production (Chaloner and Wipfli 2002, Claeson et al. 2006, Kohler et al. 2008). but this tends to be variable amongst taxa (Claeson et al. 2006). Generally, secondary production is stimulated in response to SDN in some mayfly species, but chironomids respond the most to SDN (Chaloner et al. 2004, Monaghan and Milner 2008; Lessard et al. 2009). Chironomids are hypothesized to be successful in terms of production because they respond well to SDN, but there is also the possibility that salmon spawners reduce competitors (i.e. disturbance), allowing chironomids to survive. Chironomids are a very important energy source for predators, such as juvenile salmonids (Chaloner et al. 2004). Assuming that chironomid (and possibly other macroinvertebrates) secondary production is a response to SDN, then SDN indirectly affects fish in addition to macroinvertebrates (Bilby et al. 1996).

It is difficult to differentiate if fish enriched with SDN from salmon were supplemented indirectly by consuming macroinvertebrates enriched by SDN (e.g. salmonids consuming chironomids), or by directly consuming carcass or egg from salmon; this is because SIA can only measure isotopic signatures but not reveal the mode of transport. Regardless, resident stream fish can be enriched with SDN when exposed to a salmon run. For example, Bilby et al. (1996) observed that several adult salmonids (i.e. Coho, steelhead, cutthroat trout) had increased carbon and nitrogen isotopes when salmon spawners moved into their habitat. It is important to note that the amount of nutrients incorporated into stream resident fish is dependent on spawner biomass (Rinella et al. 2012).

In addition to nutrients, salmon provide energy to the stream with organic material derived from eggs and carcass after spawning and death, respectively. Some studies have found that macroinvertebrates have increased growth rates in response to salmon spawners. The general consensus is that the incorporation of energy into macroinvertebrates is dependent on feeding ecology or species (Chaloner and Wipfli 2002). For example, Chaloner and Wipfli (2002) observed salmon flesh in microcosms and natural runs increased growth rates of shredder and collector functional groups only. Another example is Minkawa et al.'s (2002) observation that salmon meat was nutritionally important for some specific species of caddisfly *Asynarchus pacificus* and *Ecclisomyia conspersa*, but *E. conspersa* growth rate responded significantly greater than *A. pacificus* to salmon tissue. Consumption of salmon tissue can increase lipid content of some macroinvertebrates such as chironomids and stoneflies, which assists in overwintering (Heintz et al. 2010). Larger body size and fatness of macroinvertebrates in combination with increased secondary production (e.g. chironomids) from nutrients and energy creates a favorable prey environment for resident stream fish.

Resident stream fish can also consume energy directly by eating eggs or carcass flesh rather than indirectly by eating supplemented prey. Consumption of salmon carcasses and eggs can increase the lipid content of juvenile fish; this energy can be allocated into storage or enhance growth of juveniles (Heintz et al. 2004, Heintz et al. 2010). Densities, biomass, and growth rates of some resident stream fish such as brown trout, dolly varden, and sculpin increase in streams with the influx of salmon spawners, where diets are composed mostly of salmon eggs, an energy rich source (Ivan et al. 2011, Rinella et al. 2012, Koshino et al. 2013, Swain et al. 2014). Moreover, fish consuming tissue and eggs can maintain their body mass overwinter, indicating SDE acts as an important subsidy for overwintering, such as the case with cutthroat trout and dolly varden exposed to Pink salmon carcass treatments (Wipfli et al. 2003). Increased body mass from SDE implies the ability for fish to have higher chances of reproductive success and survival (Wipfli et al. 2003, Wipfli et al. 2004).

Potadromous salmon have received less attention than their anadromous counterparts, especially in the Laurentian Great Lakes region. Pacific salmon were introduced in the late 1960’s for sport and commercial fishing, retaining their migratory behavior. There have been a limited number of studies examining how Pacific salmon energy and nutrients affect stream energy budgets in Michigan coastal streams. Schuldt and Hershey (1995) found salmon carcass were an important nutrient source in oligotrophic tributaries of Superior, while Ivan et al. (2011) concluded that more nutrient rich areas will be relatively unaffected by salmon-derived nutrients. Ivan et al. (2011) also documented that Pacific salmon could be a strong contender as an energy source in lower peninsula streams, where eggs increased brown trout density and energy content.

Hildebrand (1971) and Collins et al. (2011) documented negative and positive effects from Pacific salmon; spawning tends to disturb benthic communities but can increase the availability of prey to the drift.

There is less information on migratory fish other than Pacific salmon in their natal ranges, and even more so in the Great Lakes region (Flecker et al. 2010). The Great Lakes is home to several other migrants, from introduced to native. Introduced migrants, other than Pacific salmon, include the steelhead. There has been one study that has documented steelhead as a potential energy source, where stream resident brown trout consumed steelhead eggs in spring (Ivan et al. 2011). Native migrants, such as suckers, have not been studied from an energy perspective but rather from a nutrient perspective. Longnose and white suckers have been found to stimulate productivity in some oligotrophic Great Lakes coastal streams (Burtner 2009, Childress et al. 2014, Childress and McIntyre 2015).

Because there are a limited number of studies on migratory fish as energy subsidies in the Great lakes region, it is not clear what the importance of these fish is to stream production or energy budgets. This is particularly alarming with the volatility of Great Lakes stream and lake communities. Dams have been implemented or removed altering fish passage, and there have been declines of migratory fish returns for both introduced and natives. These events can potentially disrupt the energy and nutrient contribution from migratory fish to stream communities. There needs to be more information on the effects of migrants on stream energy budgets to predict the potential impacts from recent events.

EXTENDED METHODOLOGY

Tissue Collection

Chinook eggs, Chinook muscle, and steelhead eggs were obtained from the Little Manistee River Weir in September 2013 and May 2015. Trichoptera and larval white suckers were collected with D-nets placed 3km downstream from Tippy Dam in June 2014. Additional trichoptera were captured from Muskegon River at the Pine street river access with bug nets in June 2015. *Hexagenia limbata* were collected with bug nets in July 2015 with bug nets near CCC Bridge Campground. All tissues were frozen and sent to the lab for analysis.

Tissue Weights

Tissues were thawed after removed from the freezer. Tissues were weighed to the nearest 0.00001 grams using a Mettler XS Excellence scale. Initial wet weights were recorded for each tissue to get an average wet weight for each (Chinook egg n = 50, steelhead egg n=100, trichoptera = 100, *H. limbata* = 100). Larval white suckers could not be weighed because of evaporation variability. Tissues were placed on pre-weighed tinfoil, weighed, then placed in a drying oven at 50 degrees Centigrade for 48 hours, except for Chinook eggs, which were placed in microcentrifuge tubes. Pre-weighed tin foil or tube were subtracted from the tissue to get an individual tissue wet weight. When removed from the oven, each tissue including the tinfoil or tube were weighed to get an average dry weight. Pre-weighed tin foil or tubes were subtracted from the tissue to get an individual tissue dry weight. Chinook female and male muscle wet weight was based on the average of two filets taken from fish collected at the LMRW in 2015 (G. Parks, Andy's Tackle Box, personal communication). Dry weight for salmon muscle was calculated using equation (1).

1. (1) $M_w = (W_w/(W_w+D_w)$

M_w is the percent moisture on a wet basis (75%, Peters et al. 2007), W_w is the wet weight, and D_w is the dry weight.

Pellet Creation

After tissues were weighed, each tissue was combined until ~0.025g was achieved. Then, the tissue was placed in the crucible of a Parr Pellet Press model Z 4027. A lever was pressed downward, where a hammer pressed the tissue into a compact pellet. This process was repeated to make a total of 20 pellets for each tissue, except for Chinook egg, Chinook male muscle, and Chinook female muscle, which were 15, 15, and 14 pellets made respectively.

Semimicrobomb Model

A 1425 Parr Semimicrobomb Calorimeter was used for finding energy density, or the heat of combustion (cal/g) of tissue. An attached 1672 Parr Thermometer was connected to a semimicrobomb for computing precise temperature measurements. Instructions on proper bomb use were followed from the Parr 1425 Semimicrobomb Calorimeter Operating Instruction Manual. Below is a synopsis of that process.

I. *Standardization of the semimicrobomb*

Benzoic acid tablets (6318 cal/g) were used to calculate the energy equivalent, W. A series of tests were run till a consistent W value was obtained. W was calculated as:

$$W = ((m)*6{,}318)+ f)/T$$

Where m = mass of the sample in grams, f = correction of fuse in calories, and T = temperature rise, given by the thermometer. Sample weight “m” is described in “II.” Fuse correction “f” is described in “i.” The value “W”, “m”, and “f” were used in the true heat of combustion calculation (ii) of the organism samples.

II. *Sample Pellet and Fuse Weight Before Bombing*

After pellets were created, each individual pellet was weighed to the nearest 0.00001 grams and recorded ("m"). A 10 cm piece of wire (1,400 cal/g) was cut, weighed, and recorded. Protocol proceeded as indicated in the operating manual.

III. *Calculating the Heat of Combustion*

The purpose of the thermometer was for calculation of gross heat of combustion, but calculations were also done by hand to ensure accurate calculation. Below is listed the calculations that were performed to obtain the "true" gross heat of combustion.

i. *Fuse Correction*

After the bomb was run, fuse wire was removed with tweezers, weighed and recorded. 1,400 (cal/g) was the heat of combustion of the wire. The fuse correction "f" was calculated as:

$$f = (\text{Wire weight beginning} - \text{Wire weight end}) * 1{,}400$$

ii. True Heat of Combustion

True heat of combustion was calculated as:

$$((W*T)-f)/m$$

Where W is the standard value from the benzoic acid trials, T from the temperature rise, f as fuse correction and m for mass of sample. The true heat of combustion is expressed in calories per gram (cal/g).

IV. *Calculating Energy Density*

The average of the dry weights (dw) were multiplied by the averaged values of the true heat of combustion. This gave an average energy content for tissue entering a stream. The calculations were performed as:

Average dw of larval sucker (g) * (average larval sucker cal/g dw)

Average dw of trichoptera (g) * (average trichoptera cal/g dw)

Average dw of ephemeroptera (g) * (average ephemeroptera cal/g dw)

Average dw of Chinook salmon egg (g) * (average Chinook salmon egg cal/g dw)

Average dw of female Chinook salmon muscle (g) * (Average female Chinook salmon muscle cal/g dw)

Average dw of male Chinook salmon muscle (g) * (Average male Chinook salmon muscle cal/g dw)

Average dw of steelhead egg (g) * (Average steelhead egg cal/g dw)

Statistical Analyses

Shapiro-Wilk normality were run on the energy density (n = 20 larval white sucker, n = 20 Trichoptera, n = 20 *H. limbata*, n = 12 Chinook salmon egg, n = 12 Chinook female muscle, n = 15 Chinook male muscle, n = 20 steelhead eggs). Data were normal for all energy densities. Trichoptera were collected in two different years and locations. We tested for differences between years and location with a t-test. Because there was no significant difference, we pooled trichoptera data together for the one-way ANOVA. Chinook eggs were taken from mothers whose muscle was also taken. Thus, the energy densities of the eggs and female muscle were analyzed with Pearson's correlation to find if both tissue energy densities can be used in the one-way ANOVA. Energy densities were tested for homoscedasticity with Levene's test to meet the assumptions of the one-way ANOVA. A Welch's correction (McDonald 2009) was applied due to lack of homoscedasticity. After the one-way ANOVA, multiple comparison Holm was run as a post-hoc.

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