

Impacts of adfluvial spawners on ecology of Great Lakes tributaries

by

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ILM

Dad

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## ABSTRACT

Impacts of adfluvial spawners on ecology of Great Lakes tributaries

by

Lori Nicole Ivan

Co-Chairs: Edward S. Rutherford and J. David Allan

Anadromous fishes are known to increase productivity and biomass of biota in oligotrophic streams of the Pacific Northwest by depositing energy-rich eggs and nutrient-rich carcasses during spawning migrations. In more eutrophic Great Lakes tributaries, impacts of fish spawning migrations on stream ecosystems and fish production are poorly known but potentially significant, as several native adfluvial species are more abundant and fecund than introduced Pacific salmonids.

I conducted field surveys, manipulations, and simulation modeling to study the impacts of adfluvial fish spawners on Great Lakes tributaries. I used egg mats and egg incubators to determine density and survival of walleye (*Sander vitreus*) eggs in the Muskegon River, Michigan. I conducted field experiments to determine the impacts of semelparous Chinook salmon (*Oncorhynchus tshawytscha*) and iteroparous steelhead (*O. mykiss*) spawners on the ecology and productivity of two Muskegon River tributaries. I sampled stream biota and water chemistry before and after introductions of salmonid carcasses and eggs in a treatment stream, and compared results with samples collected

from a stream with natural salmonid runs. I also developed a cohort-based ecological model to determine the impacts of salmon carcass decomposition and salmon eggs on YOY steelhead growth and survival under varying nutrient regimes.

I estimated walleye spawn 2-4 billion eggs annually in the Muskegon River. Walleye egg survival was lower in uncovered traps than in covered incubators, and survival was higher in warmer years, suggesting predation and cold-water temperatures are important sources of egg mortality that affect walleye recruitment in the Muskegon River. Field experiments showed little impact of spawning salmonids on stream chemistry and macroinvertebrate biomass. In the natural stream, density of adult trout increased during spawning in all seasons. Resident trout that consumed salmonid eggs increased their energy intake. Model output revealed growth and survival of YOY steelhead increased by consuming salmonid eggs but not by effects of salmon carcass decomposition on stream nutrients and steelhead prey. Impacts were greatest in lower nutrient regimes. Results indicate adfluvial spawners may impact growth and survival of Great Lakes resident fishes by providing energy rich eggs as food sources in low nutrient streams.



# **Chapter 1**

## **Introduction**

Fish play an important role in nutrient and energy fluxes in aquatic ecosystems. In lakes, fish influence nutrient cycling primarily through excretion (Vanni 2002). For example in Lake Michigan, excretion by alewives was found to be an important mechanism in phosphorus cycling, with cycling rates comparable to that of zooplankton (Kraft 1993). Excretion by fishes also is an important mechanism in the transfer of nutrients from one habitat to another. Schindler and Eby (1997) argued that benthivorous fishes can affect nutrient cycling in lakes by consuming benthic invertebrates and excreting nutrients elsewhere. In addition to excretion, fishes can affect nutrient recycling through selectively foraging on zooplankton (Vanni and Layne 1997).

The role of fishes in stream nutrient and energy fluxes is less well understood. While a few studies show that fish excretion can be a significant component in nutrient recycling, the role of fish excretion in nutrient cycling in rivers needs further research (Vanni 2002). The importance of salmonids as nutrient and energy transporters is well documented in nutrient-poor systems in the Pacific Northwest (Gende et al. 2004; Johnston et al. 2004; Wipfli et al. 1998, 2003, 2004). Most Pacific salmon are semelparous and, as a result, die after spawning. Salmonids can affect nutrient chemistry and energy fluxes in stream ecosystems through the decomposition of carcasses left behind after spawning and the consumption of eggs deposited by spawners by resident

fishes and macroinvertebrates. Studies in the Pacific Northwest have shown that anadromous fish migrations may increase nutrient levels, primary productivity, biofilm biomass, invertebrate biomass, and fish growth and production concurrent with spawning events.

Decomposing salmon increase background nutrient levels and primary productivity in oligotrophic streams in the Pacific Northwest (Johnston et al. 2004; Wipfli et al. 2004). Nutrients leached from decomposing carcasses can be assimilated by primary producers. A variety of studies from subalpine streams (Richey et al. 1975), Lake Superior tributaries (Fisher Wold and Hershey 1999, Schuldt and Hershey 1995), and streams in the Pacific Northwest (Wipfli et al. 1999) indicate that primary production, periphyton biomass, and overall nutrient concentrations increase after salmon spawning migrations. In Sashin Creek, Alaska, greater than 90% of the nitrogen in benthic algae came from salmon carcasses (Kline et al. 1990). While a substantial amount of transported nutrients and energy is lost to the riparian edge or is quickly transported downstream (Gende et al. 2004), Johnston et al. (2004) and Wipfli et al. (2004) showed that chlorophyll a and periphyton levels increased in rivers with spawning salmonids up to several months following spawning runs.

Spawning migrations of Pacific salmon in the Pacific Northwest can increase biofilm (a growth of algae, fungi, and bacteria along the stream bottom) biomass, thereby providing a food source for stream macroinvertebrates. Increases in biofilm biomass have been observed on salmon carcasses as well as at sites downstream from carcasses via incorporation of organic nutrients into food webs by microbes living on stream substrates (Bilby et al. 1996; Durbin et al. 1979; Fisher Wold and Hershey 1999). In

some studies, the rapid uptake and sequestration of nutrients by the biofilm has limited the impact of spawning salmonids on primary productivity (Minshall et al. 1991).

Biofilm growth is responsible for the breakdown of carcasses and release of nutrients to the water column, which can be used by microbes further downstream to assist in the breakdown of leaves, wood, and other organic matter also found in these systems. An increase in biofilm might increase the rate of decomposition of carcasses, litter and wood within the stream (Chaloner et al. 2002b; Wipfli et al. 1998; Schuldt and Hershey 1995) and increase the rate at which nutrients are cycled from carcasses to the stream ecosystem.

Many studies have shown an increase in the density and biomass of stream macroinvertebrates in response to salmon spawning (Chaloner et al. 2002a) and carcass addition experiments in the Pacific Northwest (Chaloner et al. 2002b; Wipfli et al. 1998). Macroinvertebrate growth and reproduction increase by grazing on biofilm biomass either on carcasses or in stream reaches downstream of carcasses, and/or increased grazing on primary producers.

Finally, spawning salmon may increase growth, survival, and density of resident fishes (including young salmonids) through two pathways within the stream. First, salmonid carcass decomposition is known to increase growth (Wipfli et al. 2003) and survival of salmonid parr in Alaska streams through enhanced productivity of their macroinvertebrate prey (Wipfli et al. 1998), which respond to increased productivity at lower trophic levels. Increased productivity at lower trophic levels results in a higher production of salmon recruits because the growth rate of juvenile salmon is positively correlated with overwinter survival and negatively correlated with stream residency

(Quinn 2005). Second, in addition to nutrient leaching contributing to ecosystem productivity, spawning fishes deposit eggs into streams, which serve as calorie-rich food sources for stream residents. Bilby et al. (1998, 2001) found greater densities and better condition of fish that consumed salmon eggs and carcass tissue at sites with spawning salmon runs compared to fish at sites without runs. Prolonged presence of isotopic ratios characteristic of spawning salmonids in stream fishes demonstrates that the impact of these additions can last for months (Bilby et al. 1996).

The importance of adfluvial spawners in more nutrient-rich rivers, such as those in the lower Great Lakes, is not as evident. Although the Great Lakes support large populations of adfluvial fishes, including several species of suckers (*Catostomidae*), walleye (*Sander vitreus*), and introduced runs of Pacific salmonids, the influence of their spawning migrations on Great Lakes tributaries is poorly understood owing to the paucity of studies across the range of background nutrient concentrations in the streams, and to the diversity of adfluvial spawners occurring in the Great Lakes that are not present in the Pacific Northwest. Most studies in the Great Lakes have been conducted on salmonids in streams with low nutrient levels. Fisher Wold and Hershey (1999) found increased biofilm biomass on wood during salmonid spawning runs in an oligotrophic Lake Superior tributary. Decomposing salmonids in a Lake Superior tributary were shown to increase total phosphorous (TP), soluble reactive phosphorous (SRP), and periphyton biomass in natural streams and during carcass addition experiments (Schuldt and Hershey 1995). Furthermore, Schuldt and Hershey (1995) observed uptake of nitrogen from Chinook salmon carcasses in mayflies and caddisflies in these systems using stable isotope analysis. Sarica et al. (2004) found increases in mercury and nutrients at sites in a

Lake Ontario stream with high salmonid spawner densities, as well as increases of up to 25-fold in mercury levels in aquatic and terrestrial invertebrates which feed on Chinook salmon carcasses. However, phosphorous additions by decomposing salmonid carcasses were minimal in other Lake Ontario streams (Rand et al. 1992) as phosphorous was not limiting to primary producers during spawning runs.

Studies in Great Lakes tributaries have largely ignored direct inputs of salmon carcasses and eggs into the food web, a critical component of studies in the Pacific Northwest (Bilby et al. 1998; Chaloner et al. 2002b). Furthermore, the effects of adfluvial spawning events on growth and survival of macroinvertebrates or fish are unknown in the Great Lakes. Many Great Lakes tributaries function as important fish nursery areas, and the potential of spawning adfluvial fishes to increase this production is great as the biomass and fecundities of native adfluvial spawners are much higher than those of introduced salmonids (Wiley, Rutherford and Ivan, unpublished data). Merna (1979) and Godby (2000) both found that age-0 steelhead and brown trout consumed high amounts of salmon eggs in Bigelow Creek during Chinook salmon spawning runs. Work by Sarica et al. (2004) and Schuldt and Hershey (1995) documented movement of material from adfluvial fishes into the invertebrate community, which could increase food availability for fishes through increases in invertebrate biomass.

It is important to determine how adfluvial spawners affect stream communities in more eutrophic systems (including the Great Lakes). These systems support large biomasses of adfluvial spawners which can influence stream communities directly through egg deposition (energy pathway) and indirectly through carcass decomposition (nutrient pathway). The relative importance of the direct and indirect pathways by which

adfluvial spawners can affect stream communities is likely to vary across different nutrient regimes. Only by understanding the role of adfluvial fishes in stream nutrient and energy fluxes can managers make informed decisions on issues relating to dam removal, fish passage, and escapement levels. Understanding the connections between the Great Lakes and their tributaries may allow for predictions of changes in food web dynamics concurrent with changes in stream nutrient levels and fish abundances.

In this dissertation, I report results of empirical surveys, experimental manipulations, and modeling studies to quantify the importance of introduced (Chinook salmon and steelhead) and native adfluvial spawning species (including walleye and suckers) on the ecology and productivity of Great Lakes tributaries. In Chapter 1, I report results of field surveys and *in situ* incubator experiments to determine the density, production, and survival rate of eggs deposited by walleye in the Muskegon River. The Muskegon River historically supported a large walleye population, but current populations are supported by stocking. Poor egg survival, while being detrimental to walleye populations, suggests that a large flux of energy and nutrients may be consumed by the stream community.

In Chapter 2, I describe a field experiment to determine the impact of Chinook salmon and steelhead spawners on a natural stream and a manipulated stream (where carcasses and eggs from spawning salmonids are added to the stream in which they do not regularly spawn). In each stream, I collected information on nutrient and chlorophyll *a* levels, biofilm accrual rates, macroinvertebrate biomass, and fish densities, growth rates, and diets before and after spawning. Chinook salmon, a semelparous species, contributes both carcasses and eggs to the ecosystem while steelhead, an iteroparous

species, only contributes eggs to stream ecosystems as their mortality rates in streams are low. The differences in life history between Chinook salmon and steelhead permit comparison of the relative importance of the two pathways to stream and fish productivity in the Great Lakes.

In Chapter 3, I developed an ecosystem-based simulation model to determine the relative importance of adfluvial carcass decomposition and egg deposition to resident fish growth and survival under varying nutrient and spawning regimes. The model tracks cohorts spawned by steelhead to the end of their first year of growth. The model allows comparisons of adfluvial spawner impacts on stream ecosystems of varying background nutrient levels, and between the indirect (nutrient) and direct (energy) pathways.

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additions on stream resident salmonids. Transactions of the American Fisheries Society. 133:1440-1454.

## Chapter 2

### Density, production and survival of walleye (*Sander vitreus*) eggs in the Muskegon River, Michigan

#### Abstract

Walleye (*Sander vitreus*) is an important sport fish in the Great Lakes that is experiencing low reproductive success after severe population declines in the 1950s. In the Muskegon River, Michigan, the second largest tributary to Lake Michigan, natural reproduction of walleyes remains low and is largely supplemented by stocking. To determine factors influencing walleye reproductive success in the Muskegon River, in 2003 and 2004 I estimated walleye egg survival using *in-situ* egg incubators covered with nitex screening, and in 2005 and 2006 I estimated density and survival of fertilized eggs caught on furnace filter traps in regions of varying substrate. I back-calculated egg production from egg densities and survival rates, and also from estimates of female spawner abundance, length-frequency distributions, and length-fecundity relationships. Density of walleye eggs was higher in 2006 than in 2005, and higher in regions of gravel/cobble substrates. Total egg production estimates ranged from 2 to 4 billion eggs. Egg survival was higher in egg incubators (26-48%) than on egg traps (1.5%), suggesting predation is likely an important source of walleye egg mortality in the Muskegon River. Cold water temperature due to the presence of a bottom-draw dam on the river is also a likely source of low egg survival. Together, these results indicate that extended developmental stage durations and high predation rates are likely sources of egg mortality in the Muskegon River. Despite low egg survival rates, an estimated 30 million to 1 billion eggs were estimated to hatch based on the range of survival estimates and previous estimates of spawning population size and fecundity estimates. The low natural reproduction of walleyes in the Muskegon River is likely due to a combination of low walleye egg

survival and possibly the failure of walleye larvae to reach their nursery grounds in Muskegon Lake.

## **Introduction**

Walleye (*Sander vitreus*) is an ecologically and economically important adfluvial fish species in the Great Lakes. The Muskegon River is the second largest tributary to Lake Michigan and historically supported a large population of walleye, with estimates in the mid-1950s as high as 140,100 adult spawners (O’Neal 1997). However, by the 1960s walleye populations dwindled throughout the Great Lakes and dropped to roughly 6,000 individuals in the Muskegon River. Overfishing, alewife (*Alosa pseudoharengus*) predation on larvae, sea lamprey (*Petromyzon marinus*) predation on adults, and alterations in spawning and nursery habitat and water quality all may have contributed to this decline.

In the past decade, walleye populations across the Great Lakes have recovered, largely due to supplemental stocking programs. The current population of 38,000 spawning walleye adults in the Muskegon River (Hanchin et al. 2007) is still well below historic levels and is maintained almost entirely through these stocking programs. Natural reproduction of walleyes in the Muskegon River remains low, despite evidence in other Great Lake tributaries of successful natural reproduction (e.g., Fielder et al. 1997). Recent studies on the Muskegon River revealed that approximately 10% of captured juveniles in the fall were naturally spawned fish (Jude and Hensler 2006).

Factors affecting low natural reproduction of walleyes in the Muskegon River likely occur sometime between spawning and the juvenile stage. Walleye adults migrate up the Muskegon River in late March, and spawn in early April over a 22-km stretch of

river below Croton Dam (Figure 2.1). Survival rates are high for walleye eggs collected for rearing in a hatchery, and juveniles stocked in Muskegon Lake survive well (O'Neal 1997). Walleyes are broadcast spawners, and release their eggs over river substrates (Colby et al. 1979). Spawning eggs may settle in unfavorable substrates where they may be buried by sand or mud (Johnson 1961). Although walleye eggs are resistant to fluctuating water temperatures (Schneider et al. 2004), colder water temperatures increase incubation times (Koenst and Smith 1976), thereby increasing the likelihood of predation or exposure to inhospitable environmental conditions (Roseman et al. 2006). In the Muskegon River, eggs incubate for three to four weeks, depending on temperature, and are exposed to predators and turbulent river flows that could result in abrasion of eggs or failure of eggs to settle on suitable habitat for development. Poor larval fish survival may result from variability in flow regimes, predation on larvae, or discharge of cold water from the reservoir behind Croton Dam. Dam operation on the river alters flow levels and the duration, timing, temperature, and movement of water that transports larvae from spawning grounds through a wetland complex to their nursery area in Muskegon Lake. Walleye larvae may experience high mortality rates as they drift downstream from spawning grounds or after entering Muskegon Lake (Day 1991) due to predation, or fail to reach nursery grounds due to alterations in flow regimes.

The objectives of this paper are: 1) to estimate density, survival, and production of walleye eggs in the Muskegon River, and 2) to determine the importance of habitat variables and predation risk to walleye egg survival.

## **Methods**

### Site Location

The Muskegon River drains an area of approximately 6,000 km<sup>2</sup> in western Lower Michigan (Figure 1a). The river supports a diverse array of fishes, including members of cold, cool, and warm thermal guilds. Croton Dam, located near Newaygo, MI, is the first dam on the Muskegon River upstream from Lake Michigan and blocks upstream migration of adfluvial fishes, including walleyes. The river substrate in much of the 75 km of river below Croton Dam is composed of sand and muck substrate and is therefore unlikely to be suitable spawning habitat for walleyes. As a result, walleyes spawn in a more localized area stretching for approximately 19 km downstream from Croton Dam (Figure 2.1b), with most spawning occurring roughly two km below the dam.

### Egg Density

Density of walleye eggs was estimated from catches of eggs on furnace filter mats deployed on the river bottom during the 2005 and 2006 spawning seasons. The furnace filter mats (egg mats) were constructed using 60-cm by 38-cm steel frames and air furnace filters as described in Manny et al. (2007). Furnace filters were wrapped around the steel frames and held in place with binder clips. Frames were connected using chain and held *in situ* with cinder blocks. Egg mats were placed *in situ* at 12 locations in 2005 and 2006 between Croton Dam and Thornapple boat launch, representing approximately 10 km of river where walleyes spawn in high numbers (Figure 2.1b). Egg mats were placed in relatively shallow, nearshore areas to allow frequent sampling. Johnson (1961) found walleyes spawn in relatively shallow areas ranging from 30-76 cm in depth, so

placement of incubators in this study should represent areas where walleyes spawn. Sites were grouped into upstream, mid, and downstream areas based on presumed preference for spawning by walleyes. A gang of three mats and a gang of two mats were placed at each site in 2005 and 2006, respectively for a total of 36 mats in 2005 and 24 mats in 2006.

Mats were checked every other week for the presence of eggs, alternating mats so that half of the mats were checked one week and half the next. Sub-samples of eggs collected from mats were placed in incubators and held at Michigan Department of Natural Resources (MDNR) Wolf Lake State Fish Hatchery in Mattawan, MI until hatch when larvae were preserved for identification. Owing to time and manpower constraints, two to three subsections of each egg mat were collected and preserved using methods described by Galat (1972). Eggs on each subsection were counted and the developmental stage of each egg determined (Martin and Drewry 1978) using a compound microscope. Eggs were categorized as: stage 1, pre-organogenesis, stage 3: late embryonic with developed eyes, and stage 2: intermediate between stage 1 and stage 3. Egg density estimates were calculated as the number of eggs within a developmental stage on a mat subsection, divided by the area of that subsection. I attempted to sample eggs in river substrates surrounding egg mats, but was unsuccessful owing to equipment failure. Therefore, the only estimates of egg density and survival of naturally spawned eggs were from mat samples.

Differences in egg density across sites were determined by analysis of variance (ANOVA). Egg density data were log-transformed to meet assumptions of normality. If

the data did not meet the equal variance assumption of ANOVA, a non-parametric comparison (Welch's test statistic) was used instead.

To identify variables that may explain variation in density of walleye eggs, habitat data were obtained from field surveys and hydraulic flow models. Flow, hydraulic depth, shear stress, and stream power were predicted at each site using a calibrated hydraulics model (HEC-RAS, Dr. Michael Wiley, University of Michigan, personal communication). Data on substrate composition and macroinvertebrate biomass were estimated from field surveys conducted in 2003-2004, and interpolated throughout the study area using GIS (Dr. Michael Wiley, University of Michigan, personal communication). Macroinvertebrates were divided into four size categories including small (< 5mm), medium (5-10 mm), large (11-30 mm), and extra-large (>30mm). Stepwise regression analyses were conducted to identify habitat and invertebrate variables that were significantly related to egg density.

### Egg Survival

Two methods were used to estimate survival of walleye eggs in the Muskegon River. First, in 2003 and 2004 fertilized eggs were placed *in situ* in covered incubator chambers to estimate survival relative to changes in water quality and flow among different habitat types. Second, in 2005 and 2006 survival was estimated from changes in density over time of naturally spawned eggs collected on egg mats (see above) placed in the spawning area below Croton Dam.

### *Egg Survival in Incubator Chambers*



Plexiglas egg incubators were constructed as described in Manny et al. (1989). Each chamber consisted of three Plexiglas pieces bolted together, with 50 holes drilled into each piece. Fertilized eggs were placed within the wells of the middle section, and covered with the top and bottom pieces containing nitex mesh screening (2-mm in 2003, 0.5-mm in 2004). This design was desirable as it did not inhibit water flow through the incubator and protected eggs from abrasion and predation.

Walleye eggs were obtained from MDNR personnel who collected eggs from adult spawners below Croton dam during peak spawning in late March or early April. Eggs were fertilized and allowed to water-harden before being placed into incubator wells. In 2003, incubators were placed at three locations along the river where walleye spawning occurs (Figure 2.1b). I placed incubators in three different substrate types based on substrate composition (gravel/cobble, gravel/sand, and sand) as these three substrate types have been previously shown to have significant impacts on walleye egg survival (Johnson 1961). Replicate (n=3) incubators were placed within each habitat type, for a total of 27 incubators placed *in situ*. To serve as controls, two additional incubators were placed *in situ* near Croton Dam, suspended in water off the river bottom, while another incubator was placed in a tank at the Wolf Lake Hatchery in Mattawan, MI. In 2003, due to high water levels, three incubators (one from each habitat type) were lost from two of the locations leading to an unbalanced design. Due to a need to collect incubators at the end of the study, incubators were placed in relatively shallow habitat near the edges of rivers. In 2004, incubators were only placed at one location in gravel, gravel/sand, and sandy substrate types, with two incubators left at the MDNR Wolf Lake State Fish Hatchery to serve as controls.

To estimate egg survival, incubators were left *in situ* until just prior to hatch, which was estimated based on accumulated thermal units (ATUs) calculated from a US Geological Survey stream temperature gage, and an egg development – temperature relationship by Koenst and Smith (1976). Incubators were removed just prior to hatch and egg status was recorded.

Differences in survival rates among sites and habitat types were tested using ANOVA. If assumptions of equal variance were not met, data were analyzed using the nonparametric Welch's test. In 2003, a nested ANOVA was performed to test for differences in survival across locations as well as among substrate types. In 2004, as egg incubators were deployed at only one location, survival data were analyzed using a one-way ANOVA. To detect a difference in egg survival between 2003 and 2004, an ANOVA was performed using only data collected from the location sampled in both years.

As with density estimates, egg survival was related to habitat variables and invertebrate biomass estimates obtained from HEC-RAS and GIS models. Stepwise regressions were conducted to determine if relationships existed between observed egg survival and habitat and invertebrate variables. All statistical tests were conducted using SPSS version 11.5.

### *Egg Survival on Egg Mats*

Survival of walleye eggs on egg mats was estimated from changes in egg density on mats over time. The fraction surviving to time  $t$  ( $S_{\text{egg}}$ ) on mats was calculated as

$$S_{\text{egg}} = e^{-Zt} \quad (1)$$

where  $Z$  is the instantaneous daily mortality rate and  $t$  equals the time in days over which mortality occurs. In 2005,  $Z$  was determined by regressing the  $\log_e$  (egg density) against time. In 2006, it was impossible to sample mats on multiple dates because of manpower shortages and high water levels, so survival was estimated as

$$S_{\text{egg}} = D_s * A / N_0 \quad (2)$$

where  $D_s$  is the egg density ( $\#/m^2$ ) at developmental stage,  $A$  is the area of habitat available for spawning ( $m^2$ ), and  $N_0$  is the initial number of eggs. Area was determined using a GIS map of habitat (Dr. Michael Wiley, University of Michigan, personal communication) for the portion of river included in this study, or approximately 10 km of river. The spawning area was assumed to include all habitats with a substrate composition of greater than 25 percent gravel. The initial number of eggs ( $N_0$ ) was calculated using the estimated numbers of walleye females in the spawning run (Hanchin et al. 2007), length-frequency data from previous studies of the Muskegon River (Hanchin et al. 2007), a length-based fecundity relationship from Eschmeyer (1948), and an assumed fertilization rate of 70%, a value within the range of fertility estimates of walleye spawning on reefs in Western Lake Erie (Roseman et al. 1996). See Appendix 1 for additional information on calculations.

#### *Comparison among years*

Egg survival estimates and number of larvae expected to hatch were qualitatively compared among years and methods. First, egg survival rate was standardized for all years for the period from spawning to just prior to hatch. Survival rates in 2003 and 2004 were estimated directly from changes in numbers of live eggs surviving in incubators from spawning to just prior to hatch. In 2005 and 2006, egg survival rates were calculated using equation 2. These survival estimates were used to calculate instantaneous daily mortality estimates ( $Z$ ). Egg development times (days) for both incubators and egg mats were calculated using a temperature-development time relationship reported by Rose et al. (1999), and known temperatures measured at Croton Dam by a USGS gage. Using equation 1 and the estimates of  $Z$  and  $t$ , a standardized survival rate was calculated for 2005-2006. To determine the number of walleye larvae expected to hatch in each year, the estimated number of fertilized walleye eggs ( $N_0$ ) was multiplied by the standardized egg survival rate.

### Egg Production

Two methods were used to calculate the initial number of eggs deposited. First, egg production was estimated from numbers of walleye spawners, their length frequency distributions, and relative fecundities. Second, egg production was back-calculated from stage-1 egg density in 2005 only ( $D_e$ ), the area of spawning ( $A$ ), the estimate of daily mortality rate ( $Z/d$ ) from stage-1 through stage-3, and the number of days from spawning to stage-1 ( $t_{sp}$ ) as

$$N_0 = D_e * A / (\exp^{-Z*t_{sp}}) \quad (3)$$

## Results

### Egg Density

Results from the egg mat study revealed strong, localized spawning of walleyes within the Muskegon River, with most walleyes spawning near Croton Dam (Table 2.1), an area with a high percentage of cobble/gravel. Furthermore, walleyes spawned over a relatively short period of time, with most spawning occurring in 1-2 weeks as evidenced by the small overlap of eggs of different developmental stages on mats (Table 2.1).

Egg densities varied among years, locations, and egg development stage. In 2005, stage-1 egg densities ranged from 0-124,000/m<sup>2</sup>, with an average of 24,000/m<sup>2</sup>. Average stage-2 egg density was 14,000/m<sup>2</sup>, while stage-3 egg density averaged 600/m<sup>2</sup>. In 2006, the average stage-3 density was approximately 10 times as great as in 2005, at 8000/m<sup>2</sup>. In 2005, walleye egg density (stage-1) was significantly greater at upstream sites, an area of high cobble/gravel substrates, than downstream sites (Figure 2.2,  $p < 0.001$ , Games-Howell's post hoc test  $p < 0.001$ ). However, there was no difference in stage-2 or stage-3 egg densities among locations ( $p > 0.05$ ). In 2006, there was no difference in stage-3 egg density among locations (Table 2.1,  $p > 0.5$ ).

Relationships between habitat characteristics and walleye egg density varied between years. In 2005, medium-sized invertebrate biomass (defined as individuals 5-10 mm in size) and discharge were positively correlated with density of stage-1 walleye eggs (Figure 2.3,  $p < 0.0001$ ), while no relationship was found between individual habitat or invertebrate variables and stage-2 or stage-3 egg densities. In 2006, there was no relationship between individual habitat or invertebrate variables and stage-3 egg density. Egg mats located upstream near Croton Dam were placed in substrates with a high

percentage of gravel, while egg mats located downstream (with the exception of egg mat 1) were placed in mostly sand substrates. Velocity and shear stress were greatest at upstream sites while stream power was greatest downstream (Table 2.2). Upstream sites also had the greatest invertebrate biomass in all size categories except small (Table 2.3).

### Egg Survival

#### *Incubator Studies*

Egg survival varied more between years than among substrate types. In 2003, there was no significant difference in egg survival among locations or habitat types ( $p \geq 0.20$ , Games'-Howell post hoc test for unequal variance). Egg survival in all incubators ranged from 2 to 42%, with an average of  $25\% \pm 11.2\%$ . Survival of eggs in egg incubators suspended off the river bottom below Croton Dam ( $S=31\%$ ) was similar to average egg survival in incubators on the river bottom, while egg survival in incubators at Wolf Lake State Fish Hatchery was higher ( $S=54\%$ ). In 2004, there was a significant difference in egg survival among substrate types (Figure 2.4,  $p=0.016$ ). Incubators placed in areas with sand substrates had higher survival than incubators in areas with larger substrate types.

Considering only data from locations sampled in both years, egg survival was higher in 2004 than in 2003 ( $p<0.001$ ), with values ranging from 14-72%, and an average of  $S = 50\% \pm 15.4$  in 2004. Average survival of eggs under controlled temperatures and flow conditions at Wolf Lake Hatchery in 2004 was 68%. The average temperature at Wolf Lake State Fish Hatchery was  $11^{\circ}\text{C}$ , several degrees higher than the average

temperatures (2003 ave. = 5.4 °C; 2004 ave. = 7.8 °C) experienced by walleye eggs in the Muskegon River (Table 2.4).

Relationships between habitat variables and egg survival varied among years. In 2003, hydraulic depth was negatively associated with egg survival (Figure 2.5,  $R^2 = 0.25$ ,  $p = 0.02$ ), but in 2004 and for combined data from 2003 and 2004, no significant relationships were identified between habitat or invertebrate variables and egg survival. The highest percent gravel was found at the two upstream sites (Table 2.5) where velocity, shear, and power were also high. Furthermore, invertebrate biomass was greatest in habitats with a high percentage of gravel (Table 2.6)

#### *Egg Mat Surveys*

Egg survival estimates in 2005 obtained using equation 1 and 2 were both low. Survival of eggs estimated from changes in egg density over time (Figure 2.6, equation 1) was  $S = 1.04\%$ , and instantaneous daily mortality rate was  $Z = 0.19$ . Egg survival estimates based on equation 2 using stage-2 egg densities were higher, and ranged from  $S = 4-6\%$ , depending on variability in assumed number of females. In 2006, due to a high flow event, I was able to sample egg mats only once. All eggs on mats had already developed to stage-3, therefore it was not possible to calculate survival using equation 1. Estimates of egg survival in 2006 based on equation 2 using stage-3 egg densities ranged from 2-3%. All subsequent comparisons of survival between the two years, and between incubator and mat studies, will be based on estimates using equation 2.

#### *Comparison among years*

Comparisons of survival among years and methods using standardized survival estimates indicated that eggs survived better in incubators than on egg mats (Table 2.4). While water temperatures were similar from 2004 to 2006, they were, on average, 1.5 to 2 °C colder in 2003 than in other years. The number of eggs surviving to hatch ranged from 30 million (2005-2006) to more than a billion larvae (2004) (Table 2.4) depending on the year's standardized survival.

### Egg Production

Estimates of walleye egg production in 2005 provided by both methods were similar, and were between 3.1 and 4.2 billion eggs. The estimate calculated from numbers of spawning females was  $3.1 \pm 0.6$  billion eggs, while the estimate back-calculated from density of stage-1 eggs in 2005 was 4.2 billion eggs.

### **Discussion**

Despite recent increases in natural walleye reproduction throughout the Great Lakes (e.g., Fielder 2007), the walleye population in the Muskegon River continues to have low natural recruitment. I estimated walleye egg survival and potential factors affecting walleye egg survival using two methods. Egg survival rates were variable depending on the method and year. However, the estimated number of walleyes expected to hatch was high owing to the high fecundity of spawning females. Together, these results suggest that low natural recruitment of walleyes compared to historic recruitment in the Muskegon River is likely a combination of low egg survival and the failure of larvae to reach their nursery grounds.



## Density

Walleye appear to spawn over a short period of time and within a confined area of the Muskegon River. From 2003-2006, walleye spawned over a one to two week time period in late March and early April as indicated by the relatively small overlap of different developmental stages of eggs on egg mats. Spawning occurred in a small, localized area of the Muskegon River just below Croton Dam. By spawning in such a small area of the Muskegon River and in a compressed time interval, walleyes may increase the likelihood of reproductive failure compared to a population which spawns over several weeks in a variety of habitats.

The highest densities of walleye eggs in this study were found in an area of hard substrate and high macroinvertebrate biomass below Croton Dam. The association of walleye eggs with hard substrates found in this study is consistent with results from other studies (Johnson 1961, Colby et al. 1979) and suggests walleye prefer hard substrates for spawning. A strong, positive relationship was observed between egg density and both medium-sized invertebrates and discharge in 2005 but not in 2006, possibly owing to the difference in egg development stages sampled in each year, and the loss of several mats during 2006 in the upstream section of river.

Higher densities of stage-3 walleye eggs were found in 2006 than 2005. The most likely reason for the observed differences in stage-3 egg densities between 2005 and 2006 has to do with mat sampling. In 2006, I only sampled mats once so mats were never disturbed during egg incubation. In 2005, I sampled multiple times, disturbing the mats and the eggs incubating on them. The repeated sampling of egg mats in 2005 likely

reduced the number of stage-3 eggs on mats for this year. As such, survival in 2005 was calculated from stage-2 egg densities. Another possible reason for the greater density of stage-3 eggs observed in 2006 has to do with the assumption of equal numbers of female spawners between 2005 and 2006. There is great variation in the number of spawners from year to year, making this assumption highly unlikely. If there is significant annual variation in either the number or size of spawners, my estimates of survival will be incorrect and this variation could explain the differences in the observed egg densities on mats in 2005 and 2006.

### Survival

Walleye egg survival rates in this study were lower than in other studies of walleye egg survival (Table 2.7). Egg survival on exposed mats averaged 1.5% in this study. Other studies found higher survival rates for walleye eggs in western Lake Erie (ave. S = 23%, range 7-43%; Roseman et al. 1996) and Lake Winnibegoshish (ave. S = 13%, range = 0.6-35%; Johnson 1961). Only when eggs were incubated on muck habitats were survival rates similar to this study. The survival of walleye eggs in the Muskegon River is therefore much lower than in other populations of walleye spawners.

The poor survival of walleye eggs in the Muskegon River may be attributed to cold water temperatures experienced by walleye eggs. Previous research on walleye egg survival suggests that the optimum temperature ranges for egg fertilization (6 to 12°C) and incubation (9 to 15°C) (Colby et al. 1979) are higher than temperatures experienced by walleye eggs in the Muskegon River. In all 4 years studied, walleye eggs began incubating at water temperatures below 5°C, and water temperatures during incubation

averaged less than 10°C, well below the optimal temperature for walleye egg survival. Furthermore, walleye eggs incubating in the Muskegon River rarely experienced a temperature increase of 1°C a day that has been shown to be important in other studies of walleye egg survival (Colby et al. 1979).

Differences in average water temperature between 2003 and 2004 likely contributed to the variation in the observed survival rates in incubator chambers in those years. The average temperature was almost 2°C colder in 2003 than in 2004, and the average survival during 2003 was 26%, roughly half that experienced by eggs in 2004. In both years, egg survival in control incubators held at the Wolf Lake State Fish Hatchery (held at 11 °C) was higher than average survival in the Muskegon River where average temperatures were 3-4 °C colder.

Longer incubation times due to colder water temperatures are known to affect survival of walleye eggs. Johnson (1961) found time to hatch (a function of temperature) of walleye eggs was negatively correlated with survival. Likewise, Roseman et al. (1996) found wind scour and long incubation times (a function of slow warming rates) negatively affected survival of walleye eggs on offshore reefs in western Lake Erie. Smith and Koenst (1975) found walleye egg survival increased when temperatures increased 1°C a day starting at 5°C. Water temperatures were also found to be the single most important predictor of walleye year class strength in a regression analysis of Lake Erie walleye recruitment variability (Busch et al. 1975).

Longer incubation times can affect walleye egg survival by increasing predation risk, disease, or the risk of abrasion during high flow events. The nitex mesh covers on the incubators protected eggs from predation and abrasion or burial in sediments. The

difference in egg survival between 2003 and 2004 may have resulted from disease coincident with longer incubation times in 2003. While not quantified, I did observe high rates of fungal growth on dead eggs in incubators in 2003.

Temperatures in the Muskegon River may be lower than expected owing to the presence of Croton Dam. Water temperatures below the dam are colder than normal in the spring and the rate at which the water warms is slower than expected as Croton Dam is a bottom draw dam with a large reservoir that, in the spring, remains cold and homogeneous. The large reservoir behind Croton Dam makes water temperatures in the Muskegon River much colder than would be experienced by eggs in other rivers or in the Muskegon River before 1959, when a large flood eliminated a dam further downstream near Newaygo, Michigan.

Laboratory studies indicate that most egg mortality occurs early in walleye egg development (Latif et al. 1999; Heidinger et al. 1997). Latif et al. (1999) found 80% of all egg mortality occurred between 50-100 hours after fertilization when eggs were incubated at 10°C. Any environmental stress is likely to be most important early in egg development. In this study, cold water temperatures were likely one reason for the observed low egg survival. In 2003, survival was half that of survival in 2004. In addition to longer incubation times, lower water temperatures early in egg development could also be an important source of egg mortality. In 2003, average water temperatures were 3.6°C for the first 4 days of development while in 2004 the average was 5.3°C. Over the first 10 days of incubation, the average water temperatures in 2005 and 2006 were 3.2°C and 5.9°C respectively. Water temperatures in 2003 dipped down to 2.5°C several days after incubation of eggs began. It is possible that most of the mortality of

eggs observed in incubators occurred early in development and also likely that cold water temperatures contributed to the low survival in 2003.

Substrate composition also may have had significant effects on egg survival in some years. Previous studies indicate that walleye spawn on gravel/cobble substrates where egg survival is highest (Johnson 1961, Colby et al. 1979). Egg survival estimates from incubators were lower in habitats with cobble/gravel substrates than in habitats with sand substrates. However, incubators do not mimic what eggs experience on river bottoms as they omit predators and protect eggs from being swept downstream. In 2003 and 2004, incubators in some high flow environments (gravel/cobble sites) were subject to a great deal of turbulence and were seen to bounce on the bottom, while incubators in low flow environments (sand habitats) were unperturbed on bottom. This might explain why survival in 2004 was higher on sandy substrates. In contrast, annual flow differences of almost 30 cm/s between 2005 and 2006 had little effect on egg survival, as survival rates estimated from mat surveys were similar in those years.

A comparison of walleye egg survival between study methods suggested that predation was the most likely cause of lower egg survival in exposed mats compared to protected incubators. Although a comparison between study methods is problematic, because the methods used to estimate survival between egg incubators and egg mats were different and did not lend themselves to statistical comparisons, egg survival in incubators in both 2003 and 2004 was at least 25-fold greater than survival in mats in 2005 and 2006. In other studies, egg predation by fish has been reported as a major cause of poor egg survival. Roseman et al. (2006) found a myriad of fish predators consumed walleye eggs on reefs in western Lake Erie. Some of the same egg predators in Roseman

et al.'s (2006) study, including mottled sculpin (*Cottus bairdi*), white sucker (*Catostomus commersonii*), and johnny darter (*Etheostoma nigrum*), are very abundant on the walleye spawning grounds in the lower Muskegon River (David 2008). More recent analysis of fish diets from lower Muskegon River also has identified juvenile rainbow trout (*Oncorhynchus mykiss*) as a consumer of walleye and sucker eggs (Damon Krueger, University of Michigan, personal communication). While incubators may not have prevented all egg predation, they were more effective than egg mats at protecting eggs from predators.

Egg mats likely provided a better estimate of survival than egg incubators as they more closely simulated environmental conditions experienced by walleye eggs in the Muskegon River. I used two methods to estimate survival on egg mats. First, I estimated survival using changes in egg densities from one stage to another. Second, I used estimates of female spawners, assumed area for spawning, and length-frequency and length-fecundity relationships to estimate the number of spawned walleye eggs. I then calculated survival based on this assumed initial number of eggs and egg densities estimates from mats. When both methods were used in 2005, the method to estimate survival from changes in density over time gave a lower survival rate ( $S = 1.0\%$ ) than estimates from known numbers of adult spawners ( $S = 4-6\%$ ). However, when the survival rate based on equation 2 was standardized among methods and years using temperature information from the USGS gage at Croton Dam, and known information on the ATUs required for walleye egg development, the estimated walleye egg survival rate between the two methods was almost exactly the same (density  $S = 1.04\%$  and assumed initial number of eggs  $S = 1.4\%$ ), increasing my confidence in the 2005 survival estimates.

However, due to the number of assumptions required for estimating survival using equation 2, and the sensitivity of the survival estimate to these assumptions, in the future it would be better to quantify changes in density where possible to estimate survival.

Despite lower egg survival estimates on mats, the number of spawning females and their high fecundities were estimated to produce approximately 30 million walleye larvae. This production of larvae is similar to larval production estimates from the Maumee River, a tributary to Lake Erie (Mion et al. 1998). Recent attempts to capture walleye larvae during downstream migrations were unsuccessful (Jude and Hensler 2006). In 2003, these authors sampled 13 river stations weekly starting in early April. In 2004, they sampled 8 stations in the lower river and 20 stations in Muskegon Lake. The rivers sites were selected as previous research had documented higher abundances of walleye larvae at these sites (Day 1991). In 2003, no walleye larvae were collected. In 2004, densities of walleye larvae were collected at the mouth of Mosquito Creek, a tributary low on the Muskegon River, and were low (peak density = 143 larvae /1000 m<sup>3</sup>). The annual difference in larvae catches is consistent with the lower egg survival in 2003 compared to 2004. The low catches of walleye larvae catches in both years suggests that walleye hatching near Croton Dam do not survive the journey downstream to Muskegon Lake.

### Study Biases

It was hoped that incubators would provide information on the importance of egg predation to egg survival through comparison with egg mats, which can be used to estimate density of naturally spawned eggs as well as egg survival. During 2003

collections, however, some incubators contained small invertebrates that might have contributed to egg loss. For the most part, these invertebrate predators were members of Chironomidae and are unlikely to consume eggs. To avoid invertebrate predation in 2004, the nitex mesh size was decreased and incubators were retrieved shortly before hatch.

It is possible that the survival estimates from mats do not represent actual survival of walleye eggs in the Muskegon River. While mats offer habitat for macroinvertebrate predators and therefore decrease egg survival, it is also likely that the mats might offer better protection from effects of shear or from fish predators than would open substrate alone. Attempts were unsuccessful to sample egg densities using other methods such as vacuum pumps (Roseman et al. 1996) because of pump failure. If survival on mats is better than surrounding substrates, survival estimates in 2005 and 2006 will be artificially inflated. Furthermore, as previously stated, survival estimates in 2005 and 2006 are strongly dependent on the assumptions used in equation 2 (i.e. spawning population size, fecundity, spawning area). If the estimates of population size, fecundity, or spawning area are wrong, or vary between 2005 and 2006, the survival estimates on egg mats will be biased. Overestimating population size or fecundity translates into an underestimate of survival while overestimating the area available to spawners overestimates survival.

## **Conclusion**

Survival of walleye eggs in the Muskegon River is likely impacted by three factors. First, cold water temperatures extend egg incubation times and subsequently expose eggs to sources of mortality (predation, scouring, or disease) for long periods of



time. Second, most females spawn over a relatively short period of time in a small section of the river just below the dam, essentially “placing all their eggs in one basket”. As a result, episodic discharges from dam releases above the spawning grounds may lower survival through scour or decreased water temperatures and extend exposure of eggs to potential sources of mortality. Third, based on the estimates of survival from artificial surfaces and the subsequent estimate of larval fish production, it is likely that low levels of natural walleye reproduction in the Muskegon River are due not only to poor egg survival, but also to the failure of larval walleyes to reach their nursery habitat in Muskegon Lake, a journey of almost 75 km (Jude and Hensler 2006).

This study suggests that the presence of Croton Dam may impact natural recruitment of walleyes in the Muskegon River. The large reservoir behind the dam keeps water temperatures in the Muskegon River abnormally cold in the spring when walleyes spawn. Furthermore, the localized spawning of walleye over a relatively short period of time means that all eggs spawned are subject to the same environmental stressors. Likewise, the area of primary walleye spawning has high densities of invertebrate predators. Walleye egg survival in the Muskegon River will likely remain low without mitigation of water temperatures via changes in dam operations.

Table 2.1. Density of walleye eggs (No./m<sup>2</sup>) in 2005 and 2006 in the Muskegon River by developmental stage (1, 2, 3) and area of river (downstream, mid-stream, upstream) on sampling dates in 2005 and 2006.

Date	Downstream Egg Stage			Midstream Egg Stage			Upstream Egg Stage		
	1	2	3	1	2	3	1	2	3
4/12/2005	778			170			71907		
4/20/2005		128		1858	12751			23392	
4/28/2005			459			1743			2472
5/4/2005			0			33			284
4/20/2006			1464			11977			6531

Table 2.2. Habitat variables in areas of egg mat placement in 2005 and 2006. Substrate composition data are based on surveyed habitat in locations with egg mats, while discharge (Q, m<sup>3</sup>/s), velocity (m/s), depth (m), shear stress (N/m<sup>2</sup>), and stream power (N/ms) were based on modeled output from Hec-Ras models developed for the Muskegon River.

MAT	Cobble / Gravel	Silt / Sand	Q	Velocity	Depth	Shear	Power
1	40	50	96.64	0.05	0.86	1.06	0.06
2	5	95	96.56	0.63	2.67	10.22	6.74
3	5	95	96.56	0.63	2.67	10.22	6.74
4	60	40	96.53	na	na	na	na
5	65	30	96.33	0.05	0.84	0.51	0.03
6	65	30	96.32	0.05	1.01	1.22	0.08
7	65	30	96.27	0.03	0.37	0.41	0.01
8	65	30	96.26	0.11	1.85	4.19	0.55
9	65	35	94.52	0.16	0.69	2.93	0.58
10	60	40	94.48	0.13	0.46	2.36	0.41
11	90	5	94.48	0.64	1.47	8.64	5.61
12	90	5	94.48	0.64	1.47	8.64	5.61

Table 2.3. Invertebrate biomass (mg-dry/ m<sup>2</sup>) in areas of egg mat placement in 2005 and 2006 in the Muskegon River. Biomass variables are based on sampling of the Muskegon River during 2003-2004. Data were then extrapolated to the rest of the river. Habitat types are based on large substrate particles, a mix of substrate particle size, and small particles. Invertebrate categories were defined as small (< 5 mm), medium (5-10 mm), large (11-30 mm) and extra-large (> 30 mm).

MAT	Small	Medium	Large	X-Large
1	203	680	807	0
2	351	806	882	0
3	351	806	882	0
4	193	559	663	0
5	203	680	807	0
6	203	680	807	0
7	203	680	807	0
8	203	680	807	0
9	241	585	682	0
10	241	585	682	0
11	310	2909	7425	420809
12	310	2909	7425	420809

Table 2.4. Average daily temperature (Temp °C), average daily discharge (disch, cfs), incubation time (days), instantaneous daily mortality rate ( $Z\ d^{-1}$ ), percent survival (S), and estimated eggs to hatch (Eggs Hatched) in the Muskegon River during the four study years. Temperature and discharge are from USGS gage data at Croton Dam averaged during the time incubators and mats were in the river. Survival estimates for 2005-2006 are based on assumed numbers of females from Hanchin et al. (2007), lengths from the 2003 Muskegon River walleye egg take, a length-fecundity relationship from Eschmeyer (1948), an assumed fertility rate (Roseman et al. 1996), density of eggs collected by egg mats, and area of spawning habitat available. Values in parentheses are  $\pm$  s.d. of the mean.

Year	Temp (°C)	Ave Discharge (cfs)	Incubation Time (days)	Z ( $d^{-1}$ )	S (%)	Eggs Hatched
2003	5.4 (2.01)	1,917 (553.7)	27	0.05	26.3	5.86E+08
2004	7.8 (1.88)	2,782 (368.4)	23	0.03	48.2	1.07E+09
2005	7.6 (2.00)	3,022 (1362.3)	23	0.19	1.4	3.05E+07
2006	7.1 (2.32)	3,959 (1056.1)	24	0.17	1.6	3.54E+07

Table 2.5. Habitat variables in areas of incubator placement in 2003 and 2004. Substrate composition is based on surveyed habitat in locations with incubators, while discharge (Q, m<sup>3</sup>/s), velocity (m/s), depth (m), shear stress (N/m<sup>2</sup>), and stream power (N/ms) were based on modeled output from Hec-Ras models developed for the Muskegon River. Habitat types are based on substrate composition: large (cobble/gravel), mix (gravel/sand), and small (sand).

Habitat	Location	Cobble/ Gravel	Silt/ Sand	Q	Velocity	Depth	Shear	Power
Large	Croton	90	0	53.98	0.78	0.88	15.28	12.02
Mix	Croton	10	90	53.98	0.69	1.30	9.12	6.39
Small	Croton	0	100	53.99	0.06	0.22	0.61	0.04
Large	Thornapple	70	0	57.53	0.35	2.03	3.97	1.41
Mix	Thornapple	90	10	57.54	0.41	2.38	5.07	2.12
Small	Thornapple	0	100	57.54	0.12	1.37	1.26	0.15
Large	Newaygo	75	25	64.67	0.46	1.86	2.32	1.08
Mix	Newaygo	40	60	64.87	0.47	1.92	4.74	2.22
Small	Newaygo	20	80	64.86	0.06	0.48	0.89	0.05

Table 2.6. Invertebrate biomass (mg-dry / m<sup>2</sup>) in areas of incubator placement in 2003 and 2004. Biomass estimates are based on sampling of the Muskegon River during 2003-2004. Data were then extrapolated to the rest of the river. Habitat types are based on substrate composition: large (cobble/gravel), mix (gravel/sand), and Small (sand). Invertebrate categories were defined as small (< 5 mm), medium (5-10 mm), large (11-30 mm) and extra-large (> 30 mm).

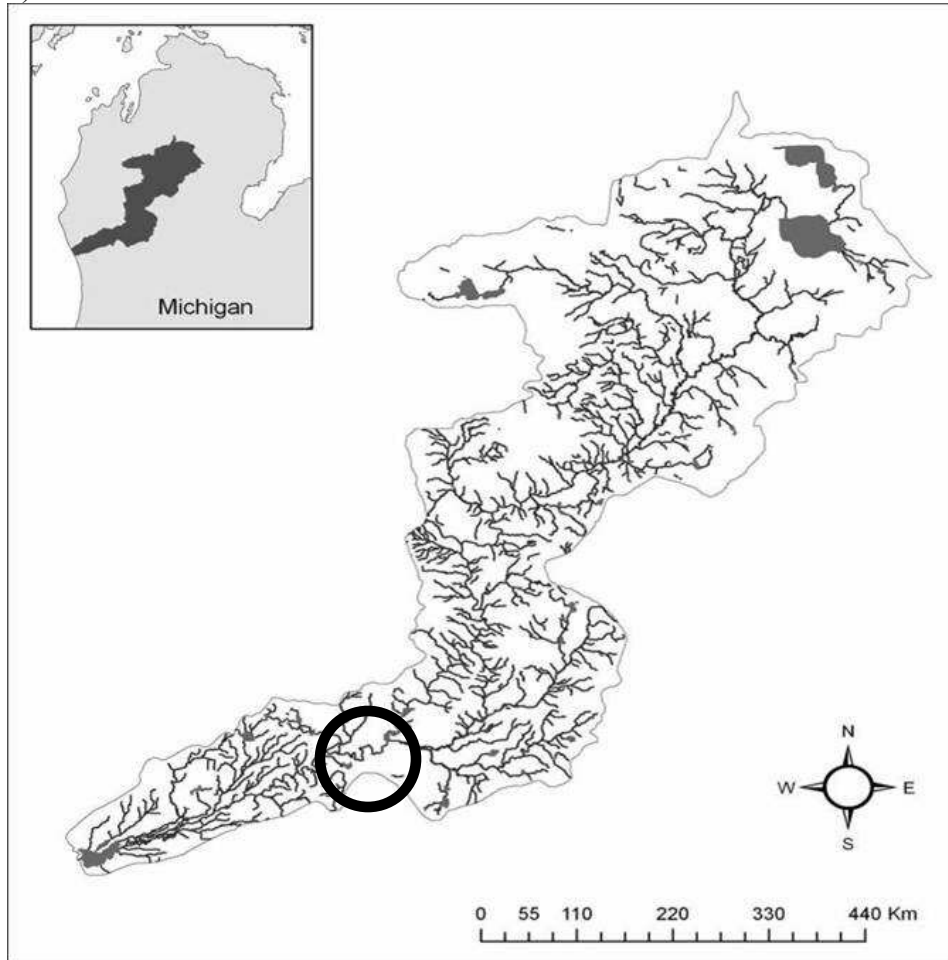
Habitat	Location	Small	Medium	Large	X-Large
Large	Croton	310	2909	7425	420809
Mix	Croton	310	2909	7425	420809
Small	Croton	296	696	782	0
Large	Thornapple	103	517	1699	15642
Mix	Thornapple	103	517	1699	15642
Small	Thornapple	176	346	411	0
Large	Newaygo	118	274	972	0
Mix	Newaygo	32	231	688	14902
Small	Newaygo	395	447	384	0

Table 2.7. Estimated walleye egg survival rates and incubation times on substrate composition types from western Lake Erie (Roseman et al. 1996) and Wisconsin (Johnson 1961).

Study	Location/Substrate	Year	% Survival	Incubation (days)
Roseman et al. 1996	Toussaint reef	1994	43	11
	Toussaint reef	1995	14	22
	Niagara reef	1994	30	11
	Niagara reef	1995	7	22
	Average	1994	37	11
	Average	1995	13	22
Johnson 1961	Muck	1956	0.6	20-24
	Muck	1957	4.5	12-14
	Muck	1958	3.6	16-21
	Muck	1959	1.2	16-18
	Firm Sand	1956	2.7	20-24
	Firm Sand	1957	9.9	12-14
	Gravel Added	1958	35.7	16-21
	Gravel Added	1959	25.9	12-18
	Gravel-rubble	1956	17.5	14-16
	Gravel-rubble	1957	17.9	12-16
	Gravel-rubble	1956	34.3	na
	Gravel-sand	1957	17.4	na
Gravel-Rubble	1958	5.2	18-21	
Firm Sand	1958	13.2	16-21	



a)



b)

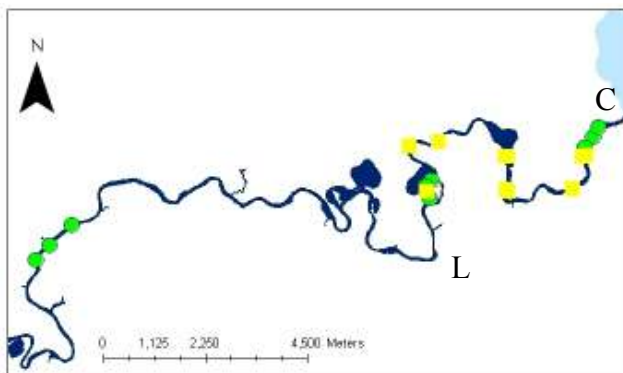


Figure 2.1. Map of the a) Muskegon River Watershed, Michigan and b) study location for walleye sampling. The circled area represents the 19 km of the Muskegon River sampled for walleye egg survival estimates. Green circles represent incubator locations in 2003 (in 2004, incubators were only placed at the middle section of river) while yellow squares show locations of egg mats in 2005 and 2006 (approximately 10 river miles). L and C are the locations of the Thornapple boat launch and Croton Dam, respectively.

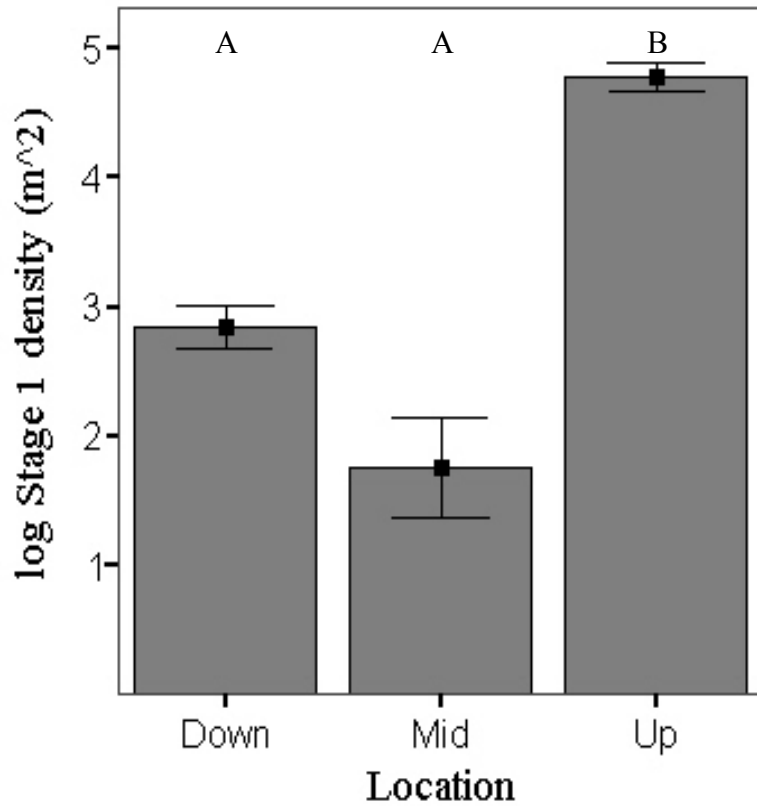


Figure 2.2. Mean density of stage-1 walleye eggs (No./m<sup>2</sup>)  $\pm$  s.e. at three locations in the Muskegon River ( $p < 0.0005$  for Welch's test assuming unequal variance) in 2005. Letters indicate significant differences between groupings based on Games-Howell's post hoc test ( $p < 0.0005$ ).

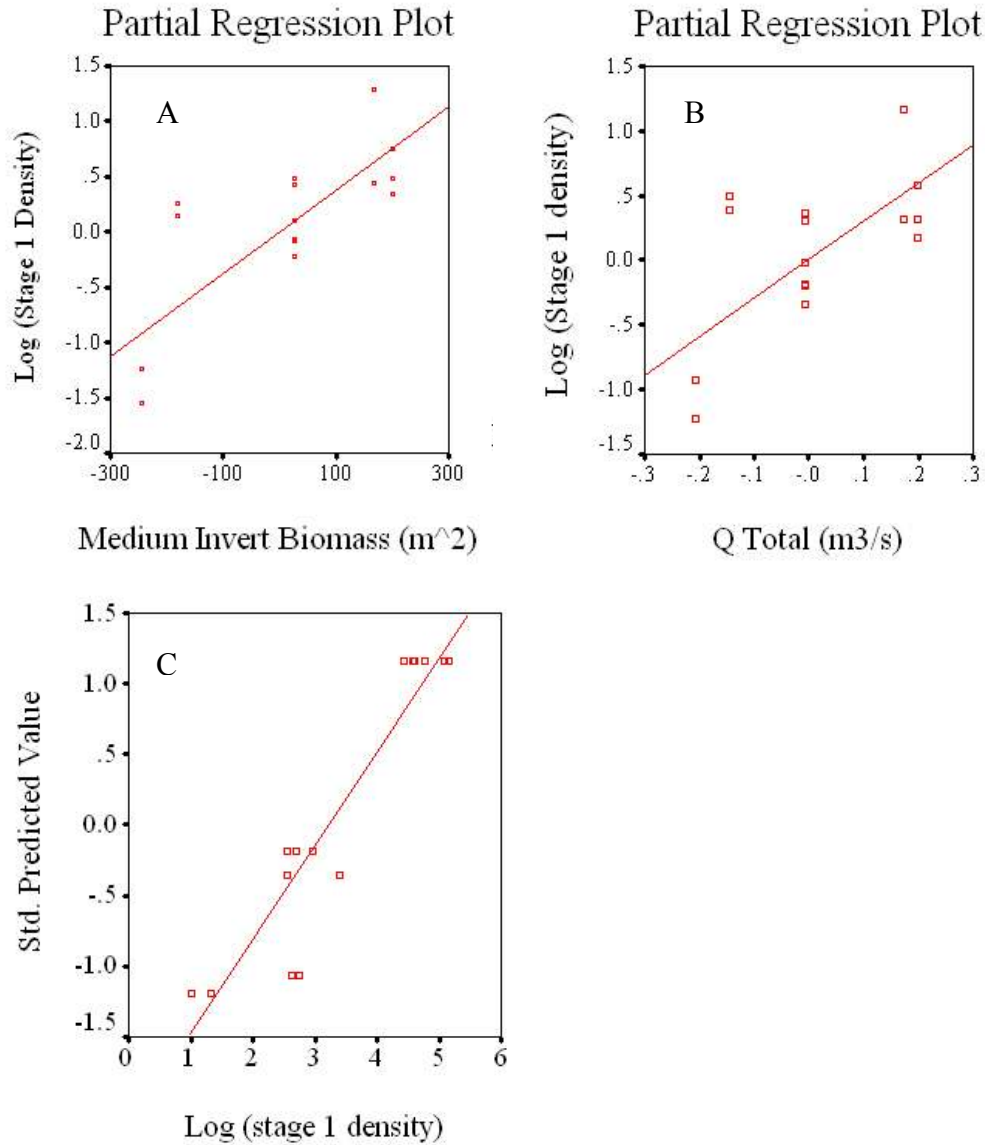


Figure 2.3. Residuals of regression of stage-1 walleye egg density in 2005 against a) medium-sized (5-10 mm) macroinvertebrate biomass ( $R^2 = 0.63$ ), b) discharge (Q total) ( $R^2 = 0.46$ ) and medium invertibrate biomass and discharge combined ( $R^2 = 0.88$ ,  $n = 16$ ). Please not differences in scale axes.

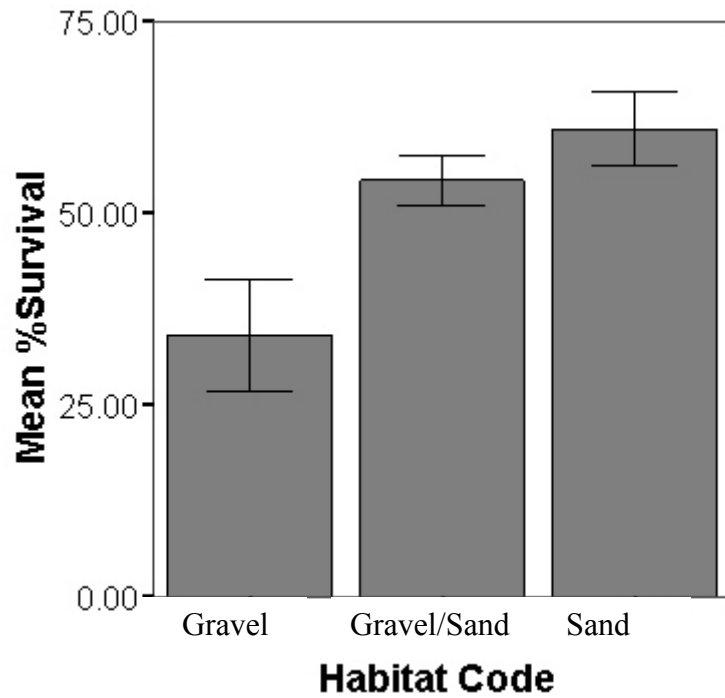


Figure 2.4. Percent survival of walleye eggs in incubators near the Thornapple boat launch site across habitat types in 2004 ( $p=0.016$ ). Error bars represent  $\pm$  S.E. Habitat was defined based on visual observations of substrate type.

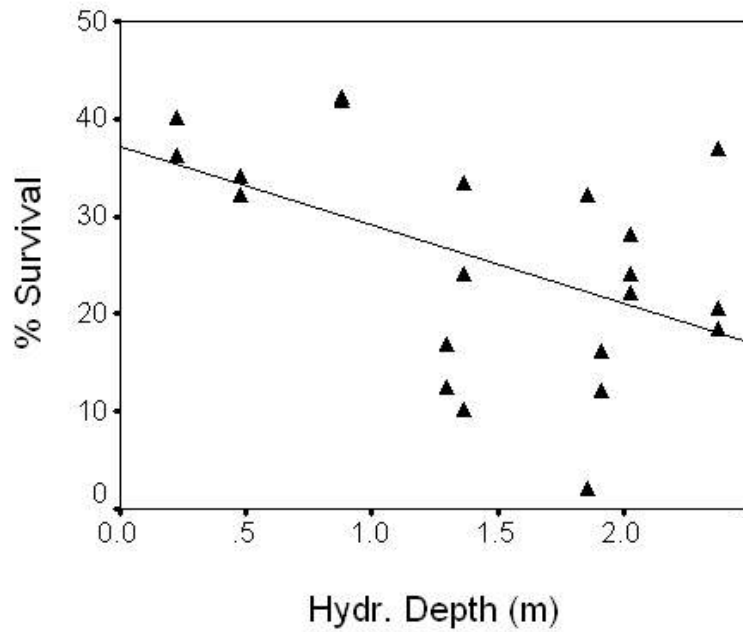


Figure 2.5. Regression of egg survival on hydraulic depth (m) for 2003 incubator study ( $p=0.023$ ,  $R^2=0.25$ ,  $n=21$ ). Habitat was defined based on visual observations of substrate type.

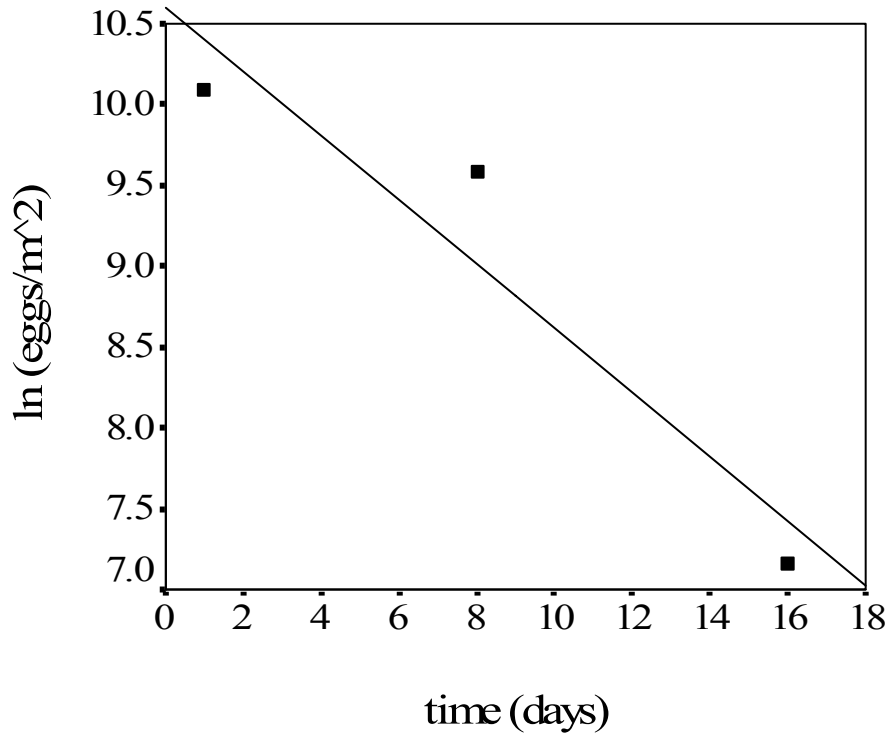


Figure 2.6. Regression of log densities of walleye eggs against time in 2005.  $y = -0.20x + 10.6$ ,  $R^2 = 0.90$ ,  $p=0.201$ . The estimated slope corresponds to a daily mortality rate of 18.1%.

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## Chapter 3

### Impacts of adfluvial spawners on water chemistry, biomass and productivity in two Great Lakes tributaries

#### Abstract

Anadromous and adfluvial fishes are known to increase nutrients, primary productivity, invertebrate biomass, and resident fish growth and survival in oligotrophic streams of the Pacific Northwest. In more eutrophic systems, the impacts of these spawners are poorly documented. I conducted field experiments to determine the impacts of a fall spawner (Chinook salmon, *Oncorhynchus tshawytscha*) and a spring spawner (steelhead, *O. mykiss*) on the ecology and productivity of two tributaries to the Muskegon River, Michigan. I used a before-after/treatment-control design to sample stream biota and water chemistry before and after introduction of salmon carcasses and eggs in a manipulated stream, where the density of carcasses and eggs could be controlled owing to the lack of natural salmonid spawning in the river. I used a similar approach to sample another tributary where salmon and steelhead spawn naturally. Impacts varied between the natural and manipulated systems, as well as between years and seasons. Adfluvial spawners had little effect on nutrient concentrations, chlorophyll a, biofilm accrual rates, or macroinvertebrate biomass in either stream, although impacts were greater in the manipulated stream where carcass densities in the fall were larger than in the natural stream. Density of adult brown trout (*Salmo trutta*) increased during peak spawning of Chinook salmon in fall and during steelhead spawning in spring in the natural system, but not after egg or carcass introductions in the manipulated system. Based on gut content analysis a large proportion of fish consumed eggs when available (up to 69%) and the energy consumed by these fish was almost entirely derived from eggs. Juvenile and adult trout that had salmon eggs in their stomachs had higher energy intake relative to fish without salmon eggs in their diets. Trout residing in reaches with salmonid spawning

activity did appear to increase in length but not weight. The results suggest that adfluvial spawners may impact eutrophic streams by providing calorie-rich food sources to stream resident fishes, while nutrient additions do little to stimulate production of lower trophic levels unless densities of spawners are high.

## **Introduction**

Fish cycle nutrients and spur primary productivity through a variety of mechanisms. In lakes, fish transport nutrients predominately through excretion (Vanni 2002). In rivers, fishes play a prominent role in transporting nutrients into streams during extensive spawning runs, as exemplified by spawning salmonids in the Pacific Northwest (Gende et al. 2002).

The understanding of fish as nutrient and energy transporters in streams derives largely from work on salmonids in the Pacific Northwest (Gende et al. 2004; Johnston et al. 2004; Wipfli et al. 1998, 2003, 2004), an area known for its nutrient-poor waters. Streams with spawning salmonids have higher levels of primary productivity, invertebrate biomass, fish biomass, and fish recruitment than streams without salmon runs (Wipfli et al. 2003; Bilby et al. 2001; Cederholm et al. 1999). Gende et al. (2004) quantified the amount of nutrients and energy transported by spawning salmonids into Pacific Northwest streams, and found that a substantial amount of transported material is lost to the riparian edge via terrestrial predators or is quickly transported downstream. Despite losses of imported material, Johnston et al. (2004) and Wipfli et al. (2004) showed an increase in chlorophyll *a* and periphyton levels in rivers with spawning salmonids up to several months following spawning runs. Increased production of lower trophic levels concurrent with spawning events can lead to increases in invertebrate biomass (Chaloner et al. 2002a; Chaloner et al. 2002b; Wipfli et al. 1998), which in turn

provide food for growing salmon in streams (Wipfli et al. 2003; Bilby et al. 1998; Bilby et al. 1996). Returning salmon not only produce the next generation of salmon, but also provide sources of food for these young fishes by depositing eggs and stimulating increases in macroinvertebrate biomass.

While the effects of spawning salmon are well documented in nutrient-poor streams of the Pacific Northwest, it is not clear what impacts these fish have in more eutrophic systems such as those found in the Great Lakes. Several studies in the Great Lakes and other more nutrient-rich systems show fish may affect nutrient concentrations (Schuldt and Hershey 1995), decomposition rates of leaf litter (Durbin et al. 1979) and wood (Fisher Wold and Hershey 1999), and nutrient cycling into the invertebrate community (Schuldt and Hershey 1995). However, Schuldt and Hershey (1995) studied the effects of salmon in two nutrient-poor streams in which the total phosphorus (TP) concentrations in reaches without salmon spawning were below 15 µg/l and ranged from 5.7-14.5 µg/l. Two studies conducted in more nutrient-rich waters found different results. Rand et al. (1992) found no impact of spawning Chinook salmon on lower trophic levels of a Lake Ontario tributary, while Sarica et al. (2004) found levels of mercury and nutrients increased after salmon runs in another Lake Ontario tributary. However, both of these authors only looked at impacts of spawning salmon on lower trophic levels. Additional work is required to determine the impact of these spawning fishes on fish communities in more eutrophic systems.

Tributaries to the Great Lakes receive spawning migrations from several adfluvial spawners. In the fall, Chinook salmon (*Oncorhynchus tshawytscha*) is the principal adfluvial species spawning in Great Lakes tributaries. Chinook salmon are semelparous,

and may impact stream communities during spawning events by depositing calorically-rich eggs and leaving behind carcasses after spawning, which release nutrients and increase productivity in more nutrient-poor systems. In the spring, native fish species, including walleye (*Sander vitreus*) and several sucker species (Catostomidae), as well as naturalized populations of steelhead (*O. mykiss*), are the principal spawners. Spring spawners are iteroparous and, unlike Chinook salmon, have low mortality rates during spawning runs. Therefore, the impact of spring spawners on stream communities likely occurs through egg deposition. Previous studies in the Great Lakes have been conducted solely on Chinook salmon, neglecting the potential impact of these other adfluvial spawners.

The objectives of this paper are to determine the relative impact of adfluvial spawners on stream ecosystems under natural and mimicked spawning conditions. Specifically, the impacts were determined of spawning Chinook salmon and steelhead on stream nutrient levels, primary productivity, biofilm biomass, invertebrate biomass, and resident fish density, diet and growth.

## **Methods**

To consider the ecological impacts of adfluvial fishes on all stream trophic levels, a before-after/treatment-control (BATC) design was used in two small streams. Bigelow Creek (hereafter referred to as the natural system), a tributary of the Muskegon River, is open to adfluvial spawning fishes and provided a natural setting for determining the impact of adfluvial fishes on stream communities. The Middle Branch River (hereafter referred to as the manipulated system), a tributary of the Muskegon River located above a

migration barrier, provided a more controlled reach where known numbers of carcasses and eggs of adfluvial spawners could be added.

Two 100-m long sampling reaches, one upstream and the other downstream, were established in both the manipulated and natural streams. In the manipulated system, only the downstream reach received egg and carcass addition treatments while the upstream reach served as a control. In the natural system, the upstream reach was accessible to spawning Chinook salmon and steelhead in all but one season of the study (fall 2005). However, only two spawning salmonids were captured at this reach during the study, so spawning density was likely low. As such, the upstream section of the natural system could not be used as a control but rather as an indication of impacts at low spawning levels.

Carcass and egg additions were made to the manipulated stream in both spring and fall. In the spring of 2006 and 2007, the impact of steelhead spawning on stream communities was mimicked through introductions of steelhead eggs (approximately 8000 grams obtained from spawning adults by hatchery personnel at the Little Manistee River Weir in Manistee, MI) into the downstream reach of the manipulated stream. It was not possible to obtain and add carcasses or eggs of native adfluvial species into the streams owing to agency concerns about spreading viral hemorrhagic septicemia (VHS) or bacterial kidney disease (BKD). In fall of 2005 and 2006, Chinook salmon carcasses and pre-treated eggs from the Little Manistee Weir were placed *in situ* in the downstream reach in the manipulated stream. Carcasses were added by staking them into the stream bed (Chaloner et al. 2002b) while eggs were placed into bowls held in place on the river bottom using rocks. Only Chinook salmon carcasses which tested negative for BKD

were placed into the study reach. In 2005, 47 Chinook salmon carcasses were added to the downstream reach, while in 2006, 36 carcasses were added. These numbers of carcasses and eggs were added to simulate the observed density of spawning Chinook salmon (800 spawners/ha) steelhead (100 spawners/ha) in Bigelow Creek (Carl 1980, Swank 2005), and in the nearby Pere Marquette River (Workman 2002). To determine the impact of spawning adfluvial fishes under natural conditions, the natural stream was sampled before and during salmonid spawning runs during fall 2005 and 2006, and spring 2006 and 2007.

Water column nutrients, chlorophyll a, biofilm, macroinvertebrate biomass, and fish density and diet were sampled at all reaches prior to treatment (or spawning) and at least twice afterwards. To better determine the impact of Chinook salmon and steelhead on growth of resident trout, pit tags were implanted into individual fish in the fall of 2006 and spring of 2007 to track their movement, growth, and diet composition.

### Nutrients

Replicate samples of water were collected at each reach to determine nutrient and chlorophyll a concentrations. Water bottles were rinsed several times before filling with stream water and were kept on ice in the dark until samples could be processed in the lab. All samples were processed within several hours of collection.

All nutrient concentrations were determined with an autoanalyzer as described in Davis and Simmons (1979). Samples (50 ml) of unfiltered water were digested in an autoclave using potassium persulfate for TP analysis. TP concentration was determined using the molybdate-ascorbic acid method based on the formation of phosphomolybdate

blue complex. Soluble reactive phosphorus (SRP), nitrate (NO<sub>3</sub>), and ammonia (NH<sub>4</sub>) were processed by filtering water through a 0.2 µm Nylon filter and stored frozen until analysis. Concentrations of SRP were determined using the same method as TP, while NO<sub>3</sub> was determined using the cadmium reduction method based on the azo dye reaction. Ammonia was determined by the phenate method based on the indophenol blue reaction. Nutrient concentrations were determined by comparing peak heights to known standards using regression.

Chlorophyll a was processed by filtering 100 ml of water through a GF/F filter and freezing (<0°C) the filter until concentrations could be analyzed using a fluorometer. Samples were digested with 90% acetone for 24 hours prior to concentration determination. Samples were then analyzed fluorometrically and concentrations determined based on known filtered amounts (Welschmeyer 1994).

### Biofilm

Biofilm accrual rates were measured based on growth on tiles placed *in situ*. Collected tiles were scraped clean and the contents frozen until analysis. All biofilm samples were filtered onto pre-dried and weighed filters, dried for 24 hours, and re-weighed to get total dry weight (mg) for all tiles. Tiles were lost in fall 2005. In spring 2006, tiles were simply placed *in situ* and left for 6 weeks and 9 weeks during spawning or manipulation. In fall 2006 and spring 2007, tiles were placed *in situ* before treatment/spawning, and again after treatment/spawning for four weeks each to observe the change in rate of accumulation before and after treatment.

## Macroinvertebrates

Macroinvertebrate biomass was determined using a 0.67-m<sup>2</sup> Hess sampler. At least 3 replicate samples were taken in each reach before and after each carcass or egg treatment. All invertebrates were preserved in ethanol for later identification in the lab. Macroinvertebrates were identified to family using Merritt and Cummings (1996), with lengths taken on at least 10 specimens from each sample. Dry weights were then calculated from known weight-length regressions from Smock (1980) and Benke et al. (1999). Biomass of macroinvertebrate families and orders were compared between treatment and control reaches. Trends in the scraper foraging guild were noted as this group was believed to be most sensitive to the presence of salmon carcasses (Lessard and Merritt 2006).

## Fish

Density, diet, and growth rate of fish were measured in all reaches. Fish density was estimated by a 2-pass depletion approach using a barge electrofisher. Individual fishes were identified to species and measured for length and weight. A subsample of fish less than 10 cm was sacrificed for diet estimation and preserved in ethanol. Larger adults were sampled for diets with gastric lavage. All diets were preserved in ethanol and contents identified in the lab. Macroinvertebrates in stomachs were identified to family while other diet items were identified and weighed (wet weight). To place all diet items in similar units, macroinvertebrates were converted from dry weight to wet weight using taxa-specific, dry weight-wet weight relationships (Ciancio et al. 2007, Hanson et al. 1997). Energy content of stomach samples was estimated based on known energy



densities for eggs (Gende et al. 2004) and macroinvertebrates (Dieterman et al. 2004, Hanson et al. 1997). In fall 2006 and spring 2007, pit tags were embedded in trout greater than 12 cm to determine growth rates and movements of individual fish between upstream and downstream reaches.

### Statistical Analyses

Nutrients, chlorophyll a, and macroinvertebrate biomass data were analyzed using a paired-sample design based on the average difference in concentration or biomass between treatment and control reaches in the manipulated system and upstream and downstream reaches in the natural system. The difference between averages was analyzed using a simple t-test, setting the initial difference (before treatment or spawning) as  $\mu_0$ . Differences in biofilm accrual rates among reaches and across time were analyzed using analysis of variance (ANOVA).

Caloric content of fish diets was compared between fish that consumed eggs and fish that ate invertebrates or fish. Energy consumed was compared after adjusting for fish length as a covariate. Differences in fish energy consumption among reaches and time were analyzed using ANOVA. Data were  $\log(\text{value}+1)$  transformed to meet assumptions of normality (Zar 1999). To determine the overall impact of spawning on the energy intake of trout in control (upstream) and treatment (downstream) reaches in both the natural and manipulated systems, an ANOVA was performed with reach, time, and reach-time interactions on total energy consumed for each reach-time combination.

Differences in growth rates of pit-tagged individual fish between treatment and control reaches were analyzed using a t-test. All data were log-transformed when

necessary to meet assumptions of normality and homoscedascity and analyzed using SPSS version 11.5. Differences were considered significant at the  $\alpha = 0.1$  level due to small sample sizes.

## **Results**

### Nutrients and Biofilm

There were no differences in water chemistry or chlorophyll a levels due to Chinook salmon spawning in the fall in the natural system (Figure 3.1, Table 3.1). In the manipulated system, the treatment reach had higher TP and NH<sub>4</sub> in fall 2005 and higher NH<sub>4</sub> in fall 2006 (Figure 3.1, Table 3.2). In spring, the treatment reach in the natural system had higher TP, NO<sub>3</sub> and chlorophyll a levels than the control after steelhead spawning (Figure 3.2, Table 3.3). There were no other differences between treatment and control reaches in other water chemistry parameters, chlorophyll a, or biofilm (Figures 3.3 and 3.4, Table 3.4) in any of the four seasons.

### Macroinvertebrates

In the natural system, there were no significant differences in invertebrate biomass related to a treatment effect in any season (Figures 3.5 and 3.6, Tables 3.1 and 3.3) for any invertebrate variables in either fall or spring. In the manipulated system, the treatment reach had significantly greater biomass of Trichoptera in the fall of 2005 and greater biomass of Diptera in the fall of 2006 (Figure 3.5, Table 3.2) compared to the control reach. There were no other significant increases in invertebrate biomass at the

treatment reach relative to the control reach in the manipulated system (Figure 3.6, Table 3.4).

### Fish

While I was unable to statically test for differences in density of adult trout due to infrequent sampling, there did appear to be a response of adult brown trout density to carcass additions in the natural stream. Trout density was higher during peak spawning in fall 2005 (October) and fall 2006 (November) (Figure 3.7). Trout density also increased in spring 2006 and, to a lesser degree, in spring 2007 (Figure 3.7) after steelhead spawning. In the manipulated stream, density of adult brown trout did not appear to respond to carcass or egg additions (Figure 3.7). In fact, trout density appeared to increase at the control reach relative to the treatment reach.

The proportion of resident trout consuming eggs was higher in fall than spring (Table 3.5) except in spring 2007, when there were similar numbers of resident trout in consuming eggs the treatment reach of the manipulated stream as in fall 2005 and 2006. Despite efforts to keep upstream/ control reaches free of salmonid eggs, eggs were found in diets of a few trout in these reaches. In the natural stream, the destruction of a barrier to migration after fall 2005 sampling was evidenced by the higher proportion of trout consuming eggs after fall 2005. In the spring, there were no stomach samples collected from resident trout in the natural stream; therefore, no comments can be made about the relative influence of spawning steelhead on stomach content analysis in this stream in the spring. However, in the manipulated stream, the proportion of fish consuming eggs was higher in spring 2007 than spring 2006. Up to 69% of fish in the reach with high

spawning densities had stomachs with eggs in their stomachs when grouping gut content samples collected on dates after egg introductions.

In fall and spring, individual trout that ate salmon eggs consumed more energy than trout that ate only invertebrates or fish in both the natural and manipulated systems based on instantaneous gut content analysis (Figures 3.8 and 3.9). Furthermore, more than 90% of the energy in stomachs of fish with eggs came from the eggs themselves (Table 3.6).

To determine the relative importance of spawned eggs to the overall energy intake of resident trout, I compared the total energy intake of all fish in the control versus treatment reaches. The relative impact of spawners on overall energy consumption by the resident trout population was variable. In fall 2005, fish at the downstream reach consumed more energy than fish at the upstream reach in the natural system (Figure 3.10a). After spawning, energy consumption decreased at the upstream reach but increased slightly at the downstream reach. In fall 2006, after salmon spawning occurred, energy consumption by fish in the upstream reach increased slightly, while fish in the downstream reach significantly increased their energy intake (Figure 3.10b). In the manipulated stream in fall 2005, fish at the control reach consumed less energy than at the treatment reach both before and after the introduction of salmon eggs and carcasses (Figure 3.10c). In fall 2006, fish at the treatment reach significantly increased their energy intake after carcass and egg introductions and consumed more energy than did fish at the upstream reach (Figure 3.10d).

Due to the low number of diets available for analysis in the natural system in the spring, it was not possible to analyze data from these reaches. During spring 2006 in the

manipulated system, there were no significant differences in energy consumed by trout before or after egg introduction, or between treatment and control reaches (Figure 3.11a). In contrast, during spring 2007 in the manipulated stream, total energy consumed by fish increased after egg introduction (Figure 3.11b).

More trout were pit tagged in the manipulated stream than in the natural stream (Table 3.7). Similar numbers of trout were tagged in the treatment and control reaches of the manipulated system while twice as many fish were tagged in the downstream (treatment) reach as compared to the upstream reach in the natural system. Tag recapture rates were similar between treatment and control reaches in both the natural and manipulated systems. However, there were more recaptures in the manipulated system than in the natural system. In both the natural and manipulated streams, there were no individuals recaptured outside of reaches where they were originally tagged.

Although adult trout that consumed eggs obtained more energy than fish that did not consume eggs, their growth in weight did not improve in either the natural or the manipulated system after eggs and carcasses were introduced (Figure 3.12c, d  $p > 0.1$ ). In fact, in the natural system, fish weight appeared to decrease at the downstream (treatment) reach relative to the upstream (control) reach. However, it did appear that fish growth in length increased in both streams at the downstream (treatment) reaches compared to the upstream (control) reaches (Figure 3.12a, b), although this increase was not statistically significant.

## **Discussion**

Spawning Chinook salmon or steelhead appeared to have little or no impact on water chemistry, primary productivity, biofilm accrual rates, or macroinvertebrate biomass in manipulated and natural streams, although impacts appeared to be greater as salmonid spawner density increased. The main effects of spawning adfluvial salmonids on the stream communities appeared to be on consumption and potential growth rates of resident fish. Resident trout that consumed salmonid eggs increased their total energy intake compared to those without eggs in their stomachs based on gut content analysis of fish sampled repeatedly after egg introductions. Comparisons of the upstream (control) to the downstream (treatment) reaches revealed that salmonid spawning significantly impacted the energy intake of resident trout in reaches with spawning activity. While energy consumption at the downstream (treatment) reach appeared to have a greater impact during Chinook salmon spawning in the fall, steelhead spawning had similar impacts in 2007 when the study sampling design better reflected energy intake by resident trout.

In this study, there was a variable response in stream nutrient chemistry or chlorophyll a concentrations to introductions of fall or spring salmonid spawners. The lack of response is likely attributable to higher background nutrient concentrations in Muskegon River tributaries compared to streams elsewhere. The natural and manipulated streams in this study had higher nutrient concentrations compared to streams studied in Lake Superior and the Pacific Northwest where salmon spawners have affected stream nutrient dynamics, although the difference between reaches without salmon in streams in these three regions were not as large as expected. Schuldt and Hershey (1995) studied two Lake Superior tributaries where TP concentrations ranged from 5.7-14.5  $\mu\text{g/l}$  in

reaches without salmon and 8.1-27.5  $\mu\text{g/l}$  in reaches with spawners. In the Pacific Northwest, average SRP concentrations were 2, 4, and 7.5  $\mu\text{g/l}$  when salmon were present and never greater than 2  $\mu\text{g/l}$  when salmon were not present (Chaloner et al. 2004). In contrast, TP concentrations in the control reach in the natural and manipulated streams averaged 18  $\mu\text{g/l}$ , and 16  $\mu\text{g/l}$ , respectively, while SRP concentrations in the natural and manipulated streams were 1.4  $\mu\text{g/l}$ , and 3.4 $\mu\text{g/l}$  respectively. SRP values in the manipulated stream are greater than those observed in the Pacific Northwest when salmon are not present. However, the natural stream in my study has similar SRP values to those in the Pacific Northwest, although daily values can be much greater than the average values observed by Chaloner et al. (2004). TP values for both the natural and manipulated streams are within ranges observed by Schuldt and Hershey (1995), although the average TP value from control reaches in both streams are slightly higher than in control reaches studied by Schuldt and Hershey (1995). While the background nutrient concentrations in reaches without salmonid spawning of streams in the Pacific Northwest, Lake Superior, and the lower Great Lakes are not as different as first expected, concentrations are generally higher in the natural and manipulated streams than the streams studied by either Chaloner et al (2004) or Schuldt and Hershey (1995).

Results of studies of adfluvial spawner impacts on more nutrient-rich tributaries to Lake Ontario were consistent with results of my study, and suggest adfluvial spawners have little effect on stream nutrient pathways in mesotrophic streams. Rand et al. (1992) found no increase in primary productivity during salmonid spawning runs in a Lake Ontario tributary. Increases in phosphorous concentrations resulting from decomposing carcasses were minimal in these tributaries. Although the phosphorous contribution from

salmon carcasses was small on an annual basis, daily total phosphorous released from carcasses accounted for up to 50 percent of the total phosphorous leaving the river system (Rand et al. 1992). Even so, phosphorous additions from carcasses still remained inconsequential to the total productivity of this stream.

In this study, nutrient addition resulting from carcass decomposition had a statistically greater positive effect on the manipulated system than on the natural system in the fall. It was thought that adfluvial spawners would be more likely to impact water chemistry in the natural system due to its lower observed background nutrient levels. While carcass densities added to the manipulated stream were designed to mimic spawner densities in natural streams, all carcasses were added on one day rather than over a longer time as observed during natural spawning runs in the natural stream. As a result, the densities in the manipulated stream were 3-4 times the densities of carcasses noted on any one day in the natural stream. Despite additions of high carcass numbers, phosphorus concentrations should not have increased by more than 1  $\mu\text{g/l}$  based on mass balance calculations. In this study, TP in the manipulated system increased up to 4  $\mu\text{g/l}$  after carcass addition, suggesting that carcass decomposition was not the sole source of nutrient addition to the downstream treatment reach.

The observed increases in nutrients at the treatment reaches might have been caused by random events occurring within the stream that were not controlled for by the experiment. Both the natural and manipulated streams are located within the Muskegon River watershed, and are therefore accessible to anglers, nutrient inputs from different land uses, and other factors that can alter stream chemistry in ways not associated with the experiment. Together, the decomposition of carcasses within the reach and other



sources of nutrients that affect only the downstream reach might have resulted in the greater impacts observed in the manipulated system. Furthermore, the lack of control over carcasses and timing of spawning in the natural system versus the manipulated system might also explain why effects were observed in the manipulated but not the natural system. Spawners had access to the upstream reach in the natural system in fall 2006, and while the density was low, it may have been great enough to impact nutrient levels, decreasing the differences between upstream and downstream reaches. That eggs were consumed by resident trout at upstream/control reaches suggests that the impact of spawning salmonids in these reaches lowered the difference in nutrient concentrations between upstream and downstream reaches.

Chinook salmon were hypothesized to have more of an impact on stream chemistry and primary productivity than the iteroparous, spring spawning steelhead, since salmon are semelparous and die after spawning in the fall. However, contrary to expectations, concentrations of TP, NO<sub>3</sub>, and chlorophyll a increased in the natural system in spring after steelhead spawning but not after introduction of salmon carcasses or eggs in fall 2005 or 2006. This nutrient increase may have been caused by excretion by adult trout, as a large increase was noted in the density of adult brown trout concurrent with the large nutrient increases in the natural system. No increase in nutrients or trout density was observed in the manipulated stream in spring, supporting the contention that increased fish density led to the increased nutrients measured at the treatment reach in the natural system.

In contrast to other studies in streams of varying nutrient concentrations, there was no discernable response in biofilm accrual rate to carcass decomposition or spawning

in this study. Fisher Wold and Hershey (199) found increased rates of wood decomposition and increased biofilm biomass on salmon carcasses in Lake Superior tributaries. Durbin et al. (1979) found alewife spawning led to increased litter respiration, decreased litter in tanks, and increased algal biomass. It is possible that the lack of response of biofilm accrual to salmon spawning in the current study was caused by macroinvertebrate grazing on tiles. Furthermore, both streams were relatively shaded. Biofilm growth would therefore also be light-limited, decreasing the likelihood of a response to increased nutrient concentrations.

Based on studies in the Pacific Northwest and Lake Superior, it was hypothesized that macroinvertebrate biomass, especially members of the Chironomidae family and the scraper trophic guild, would increase in response to salmon carcass introductions. However, in this study, macroinvertebrate biomass did not appear to increase in response to carcass or egg additions except after introductions of high carcass densities in the manipulated stream. Other researchers have noted variable responses by the stream invertebrate community to carcass introductions. Wipfli et al. (1998) observed an overall increase in total invertebrate biomass, while Chaloner et al. (2004) found higher biomass of chironomids but not mayflies, a finding similar to Lessard and Merritt (2006). In the Great Lakes, Schuldt and Hershey (1995) quantified nitrogen movement from decomposing salmonids into caddisflies and mayflies using stable isotopes, but did not measure changes in biomass.

The sampling design in this study may not have allowed detection of macroinvertebrate responses to salmon spawning and carcass addition. Invertebrates in river substrates were sampled using a Hess sampler; therefore, taxa colonizing wood or

carcasses were not sampled. Chaloner et al. (2002a) found 27 species of invertebrates associated with carcasses in a natural Alaskan stream and Chironomidae was the most abundant invertebrate taxon found. Likewise, Walter et al. (2006) found a positive impact of spawning salmon on the growth and density of a caddisfly (*Ecclisomyia conspersa*) in a Pacific Northwest stream, and a high number of these individuals were associated with the carcasses themselves. Invertebrate taxa such as Chironomidae act as a functional group known as shredders and are thought to be very important in carcass decomposition. Shredders increase the rate of nutrient release by breaking up the carcass tissue and exposing anoxic subsurface zones. It is likely that samples of invertebrates on carcasses would have resulted in an increase in chironomid biomass compared to samples in the benthos.

Low sample size also may have contributed to the inability to observe impacts of spawning events on the macroinvertebrate community. Despite this, in the manipulated reach, an increase was observed in overall biomass of Trichoptera and Diptera in the fall of 2005 and 2006, respectively. The large number of carcasses placed into the treated reach in the manipulated system serve as a food source for invertebrates and may have made it more likely to observe an impact of spawning Chinook salmon on the invertebrate community than in the natural system. It also is not surprising that an increase in macroinvertebrate biomass in the spring was not observed as only eggs were added at this time and, as evidenced by the quick removal of eggs by resident trout, few eggs would have been available for colonization by invertebrates.

Resident trout appeared to show a numerical response to salmon spawning in this study. Density of adult brown trout increased after Chinook salmon or steelhead

spawning in the natural system in fall 2005 and spring 2006. Others have noted increased densities of age-0 trout during spawning events (Bilby et al. 1998). Bilby et al. (1998) found density of resident trout increased during spawning runs, then slowly decreased after spawning. Increases in fish density during spawning suggest fish are traveling to reaches with spawners to obtain additional food resources such as salmon eggs and invertebrates.

The biggest impact of adfluvial fishes on the study streams appeared to be the change in diet and subsequent increase in energy consumption by resident trout during spawning events. In both the natural and manipulated systems, individual trout substantially increased their energy intake during spawning in both fall and spring based on instantaneous gut content analysis. Trout that consumed eggs obtained considerably more energy than trout that did not consume eggs. Variability among individuals in proportion of eggs consumed suggests individual fish vary in their preference for egg consumption, a result consistent with earlier studies of trout diets in Lake Michigan tributaries (Merna 1979). When trout consumed eggs, the bulk of the energy in their diets was a result of egg consumption.

Chinook salmon spawning also increased the overall energy intake of fish at downstream (treatment) reaches relative to fish at upstream (control) reaches. In the natural system, fish at the upstream reach maintained a higher energy intake in fall 2006 than in fall 2005 owing to the destruction of a barrier to salmon migrations after 2005, which allowed trout in the upstream reach to also have access to eggs. The proportion of fish with eggs in their diets in the upstream reach after fall 2005 in the natural stream indicates the importance of the barrier to blocking salmon migrations. However, results

show that Chinook salmon spawning increases the energy intake of all trout residing in reaches with spawning activity, suggesting that spawning activity is energetically important to the entire fish community, not just a few individuals. Steelhead spawning likely has an impact on the caloric intake of resident fish, but this impact may not be as great as impacts of Chinook salmon, probably due to lower densities of steelhead spawners compared to Chinook salmon spawners.

The discrepancy in effects of egg introductions on energy consumption by fish between spring 2006 and 2007 is likely an artifact of differences in the timing of sampling between the two years. In spring 2006, fish were sampled several days after egg placement and, while egg traps were empty, few fish had eggs in their stomachs. In contrast, in spring 2007, fish sampling was conducted 24 hours after eggs were introduced, and most fish had eggs in their stomachs, making these results more representative of the response of trout to steelhead spawning than results from the spring 2006 sampling. From this analysis, it can be inferred that eggs do not remain in trout stomachs for much longer than a few days. It would be necessary to sample trout diets almost every day during the spawning season or use stable isotopes to quantify the extent of egg consumption by the resident trout community.

Surprisingly, the increase in energy from salmon eggs consumed by fish in the presence of spawners did not influence fish weight, although there did appear to be a trend in both the manipulated and natural systems towards a greater increase in fish length at the treatment reach relative to the control reach. Unfortunately, due to the low recapture rate, it was not possible to determine if individuals that consumed eggs had greater increases in length or weight relative to those recaptured fishes that did not

consume eggs. Furthermore, low recapture rates also made an effect of egg consumption on fish growth difficult to determine.

The variability in egg consumption and growth among individual fishes has been noted by other researchers. Reichert et al. (2008) found that nitrogen stable isotopes of coho salmon parr were highly variable, suggesting incidence of parr feeding on salmon carcasses varied widely among individuals. Wipfli et al. (2003) found a positive impact of salmon spawning on growth of stream resident salmonids in Alaska, but the impact did not increase as the number of carcasses placed in channels increased, suggesting there is a limited benefit of carcass addition to stream resident salmonids. It is also important to note that the increased growth observed in studies like these, while variable, does not necessarily confer a survival advantage for these fishes (Lang et al. 2006).

## **Conclusion**

Despite the high nutrient concentrations and productivity of many streams in the Great Lakes, spawning fishes may still affect stream ecosystems through direct inputs into the food web. Eggs deposited by spawning salmonids are consumed by a high proportion of resident trout in systems where spawning occurs. The energy intake of fish consuming eggs increases relative to fishes that do not consume eggs, and the high proportion of trout consuming eggs means that the impact of spawning adfluvial fishes on trout energy consumption benefits the entire trout population. While fish length appeared to increase in reaches with spawning activity, future work is required to determine the overall importance of egg consumption on the growth and survival of those populations.

At high spawning densities, spawning adfluvial fishes can impact stream ecosystems by increasing background nutrient levels and macroinvertebrate biomass, even in more eutrophic streams such as those found in the lower Great Lakes. Background nutrients can also increase as a result of increased excretion rates by resident fish attracted to adfluvial fish spawning activity.

In addition to spawning salmon and steelhead, Great Lakes tributaries have other adfluvial spawners, including walleye and suckers, which may also contribute energy to the streams in which they spawn. While their eggs are not as energy rich or as large as those of salmonids, walleye and suckers spawn their eggs over open river substrates, thereby making them available to the entire stream community. Future work in the Great Lakes is required to determine the role of these native spawners on stream ecosystems and resident fish and juvenile trout growth in the Great Lakes.

Table 3.1. Average concentrations of nutrients, chlorophyll a and invertebrate biomass for the natural stream for fall 2005 and fall 2006 after salmonid spawning or carcass/egg introductions. Nutrients include total phosphorus (TP,  $\mu\text{g/l}$ ), soluble reactive phosphorus (SRP,  $\mu\text{g/l}$ ), ammonia ( $\text{NH}_4$ ,  $\mu\text{g/l}$ ), nitrate ( $\text{NO}_3$ ,  $\text{mg/l}$ ), and chlorophyll a (chl a,  $\mu\text{g/l}$ ). Invertebrate taxa are in units of  $\text{mg-dry/m}^2$  and scrapers represent the scraper trophic guild. In the natural system, the upstream reach had lower densities of spawners than the downstream reach, while in the manipulated system the upstream reach served as a control with no spawning salmon. Values in parentheses are  $\pm$  s.e. of the mean.

Variable	Natural			
	2005 Up	2005 Down	2006 Up	2006 Down
TP	15.78 (1.852)	15.54 (1.63)	20.84 (0.475)	15.64 (0.805)
SRP	0.79 (0.199)	1.36 (0.527)	1.23 (0.342)	1.52 (0.215)
$\text{NH}_4$	8.59 (5.642)	5.16 (1.80)	16.64 (1.634)	6.37 (3.929)
$\text{NO}_3$	0.95 (0.498)	1.26 (0.618)	0.2 (0.019)	0.2 (0.037)
Chl a	4.14 (0.945)	3.69 (1.634)	7.97 (4.078)	6.25 (3.356)
Diptera	0.92 (0.195)	3.43 (1.756)	0.57 (0.179)	1.49 (0.872)
Ephemeroptera	7.8 (0.591)	2.93 (2.833)	1.68 (0.000)	0.78 (0.023)
Trichoptera	3.6 (3.543)	2.44 (0.476)	3.59 (1.386)	2.21 (0.343)
Chironomids	0.07 (0.0118)	0.55 NA	0 (0.000)	0.77 NA
Scrapers	21.82 (30.361)	11.18 (8.051)	8.73 (4.918)	6.73 (3.965)



Table 3.2. Average concentrations of nutrients, chlorophyll a and invertebrate biomass for the manipulated streams for fall 2005 and fall 2006 after salmonid spawning or carcass/egg introductions. Nutrients include total phosphorus (TP,  $\mu\text{g/l}$ ), soluble reactive phosphorus (SRP,  $\mu\text{g/l}$ ), ammonia ( $\text{NH}_4$ ,  $\mu\text{g/l}$ ), nitrate ( $\text{NO}_3$ ,  $\text{mg/l}$ ), and chlorophyll a (chl a,  $\mu\text{g/l}$ ). Invertebrate taxa are in units of  $\text{mg-dry/m}^2$  and scrapers represent the scraper trophic guild. In the natural system, the upstream reach had lower densities of spawners than the downstream reach, while in the manipulated system the upstream reach served as a control with no spawning salmon. Values in parentheses are  $\pm$  s.e. of the mean.

Variable	Manipulated			
	2005 Cont	2005 Treat	2006 Cont	2006 Treat
TP	10.84 (1.675)	11.25 (2.005)	18.84 (5.076)	22.81 (5.556)
SRP	3.31 (0.843)	3.31 (0.915)	4.03 (1.707)	3.77 (1.16)
$\text{NH}_4$	11.91 (2.460)	11.96 (2.256)	11.52 (0.523)	10.96 (0.802)
$\text{NO}_3$	0.88 (0.138)	0.91 (0.116)	0.81 (0.177)	0.81 (0.137)
Chl a	1.14 (0.361)	0.85 (0.060)	0.55 (0.000)	0.56 (0.137)
Diptera	0.97 (0.533)	0.81 (0.409)	0.39 (0.225)	0.61 (0.317)
Ephemeroptera	1.27 (0.714)	3.66 (4.707)	1.14 (1.004)	1.19 (0.455)
Trichoptera	1.3 (0.304)	1.17 (0.394)	1.07 (1.003)	1.65 (0.581)
Chironomids	0.37 (0.063)	0.44 (0.152)	0.23 (0.151)	0.53 (0.207)
Scrapers	18.04 (18.574)	12.88 (6.396)	7.71 (6.582)	8.23 (5.312)

Table 3.3. Average concentrations of nutrients, chlorophyll a and invertebrate biomass for the natural stream for spring 2006 and spring 2007 after salmonid spawning or carcass/egg introductions. Nutrients include total phosphorus (TP,  $\mu\text{g/l}$ ), soluble reactive phosphorus (SRP,  $\mu\text{g/l}$ ), ammonia ( $\text{NH}_4$ ,  $\mu\text{g/l}$ ), nitrate ( $\text{NO}_3$ ,  $\text{mg/l}$ ), chlorophyll a (chl a,  $\mu\text{g/l}$ ). Invertebrate taxa are in units of  $\text{mg-dry/m}^2$  and scrapers represent the scraper trophic guild. (chl a). In the natural system, the upstream reach had lower densities of spawners than the downstream reach, while in the manipulated system the upstream reach served as a control with no spawning salmon. Values in parentheses are  $\pm$  s.e. of the mean.

Variable	Natural			
	2006		2007	
	Up	Down	Up	Down
TP	16.94 (0.475)	21.25 (0.874)	14.63 (2.099)	17.51 (3.669)
SRP	1.12 (0.342)	0.77 (0.186)	2.86 (0.903)	2 (0.588)
$\text{NH}_4$	9.12 (1.633)	11.11 (1.552)	10.06 (0.335)	12.85 (1.490)
$\text{NO}_3$	0.1 (0.019)	0.122 (0.015)	0.1 (0.034)	0.12 (0.031)
Chl a	2.2 (0.185)	2.51 (0.218)	1.63 (0.145)	2.06 (0.172)
Diptera	4.36 (5.574)	3.67 (4.709)	0.14 NA	5.76 NA
Ephemeroptera	9.41 (9.416)	0.98 (0.489)	0.89 NA	0.38 NA
Trichoptera	7.79 (0.840)	1.18 (0.603)	3.06 NA	0.47 NA
Chironomids	0.20 (0.163)	0.28 (0.093)	0.14 NA	0.35 NA
Scrapers	31.92 (4.918)	6.7 (3.965)	1.71 NA	0.73 NA

Table 3.4. Average concentrations of nutrients, chlorophyll a and invertebrate biomass for the manipulated stream for spring 2006 and spring 2007 after salmonid spawning or carcass/egg introductions. Nutrients include total phosphorus (TP,  $\mu\text{g/l}$ ), soluble reactive phosphorus (SRP,  $\mu\text{g/l}$ ), ammonia ( $\text{NH}_4$ ,  $\mu\text{g/l}$ ), nitrate ( $\text{NO}_3$ ,  $\text{mg/l}$ ), chlorophyll a (chl a,  $\mu\text{g/l}$ ). Invertebrate taxa are in units of  $\text{mg-dry/m}^2$  and scrapers represent the scraper trophic guild. (chl a). In the natural system, the upstream reach had lower densities of spawners than the downstream reach, while in the manipulated system the upstream reach served as a control with no spawning salmon. Values in the parentheses are  $\pm$  s.e. of the mean.

Variable	Manipulated			
	Cont	2006 Treat	Cont	2007 Treat
TP	17.41 (1.093)	18.51 (1.639)	18.19 (1.731)	17.40 (1.821)
SRP	3.43 (1.736)	3.48 (1.918)	6.55 (0.090)	6.55 (0.362)
$\text{NH}_4$	13.53 (1.284)	14.20 (1.640)	18.2 (1.340)	17.78 (0.676)
$\text{NO}_3$	0.86 (0.086)	0.86 (0.753)	0.8 (0.136)	0.77 (0.116)
Chl a	2.01 (0.968)	1.89 (0.751)	1.64 (0.318)	1.5 (0.322)
Diptera	0.65 (0.394)	1.19 (1.017)	0.23 NA	0.11 NA
Ephemeroptera	1.26 (0.047)	1.4 (0.768)	1 NA	1.39 NA
Trichoptera	3.57 (3.230)	1.39 (0.452)	1.09 NA	3.7 NA
Chironomids	0.31 (0.138)	0.11 (0.018)	0.03 NA	0.08 NA
Scrapers	16.82 (12.812)	6.43 (1.561)	2.67 NA	28.23 NA

Table 3.5. Proportion of resident trout that consumed eggs after spawning in the natural and manipulated streams in fall 2005 and 2006 and spring 2006 and 2007. No diet data were available from the downstream reach in the natural stream in spring 2007.

Stream	Reach	Fall05	Fall06	Spring06	Spring07
Natural	Upstream	0.09	0.47	0.00	0.33
	Downstream	0.40	0.69	0.00	NA
Manipulated	Control	0.00	0.23	0.00	0.03
	Treatment	0.66	0.55	0.08	0.63

Table 3.6. Proportion of joules consumed by resident trout contributed by eggs in the natural and manipulated streams in fall 2005 and 2006 and spring 2006 and 2007. No diet data were available from the downstream reach in the natural stream in spring 2007.

Stream	Reach	Fall05	Fall06	Spring06	Spring07
Natural	Upstream	0.86	0.97	0.00	0.99
	Downstream	0.97	1.00	0.00	NA
Manipulated	Control	0.00	0.94	0.00	0.29
	Treatment	0.99	0.99	0.67	0.99

Table 3.7. Total number of tagged and recaptured adult trout in the manipulated and natural system by treatment and control reaches. ‘Rate’ is percent recapture rate, ‘Most Recap’ is the maximum number of recaptures of an individual, and ‘Most Days’ refers to the longest time between tagging and recapture of an individual fish. No fish were captured in a reach other than the one in which they were tagged.

Reach	Treatment	Total Tagged	Total Recap	Rate	Most Recap	Most Days
Manipulated	Control	42	11	26.19	4	264
	Treatment	45	10	22.22	5	248
	Control	15	4	26.67	4	264
Natural	Treatment	33	6	18.18	3	264

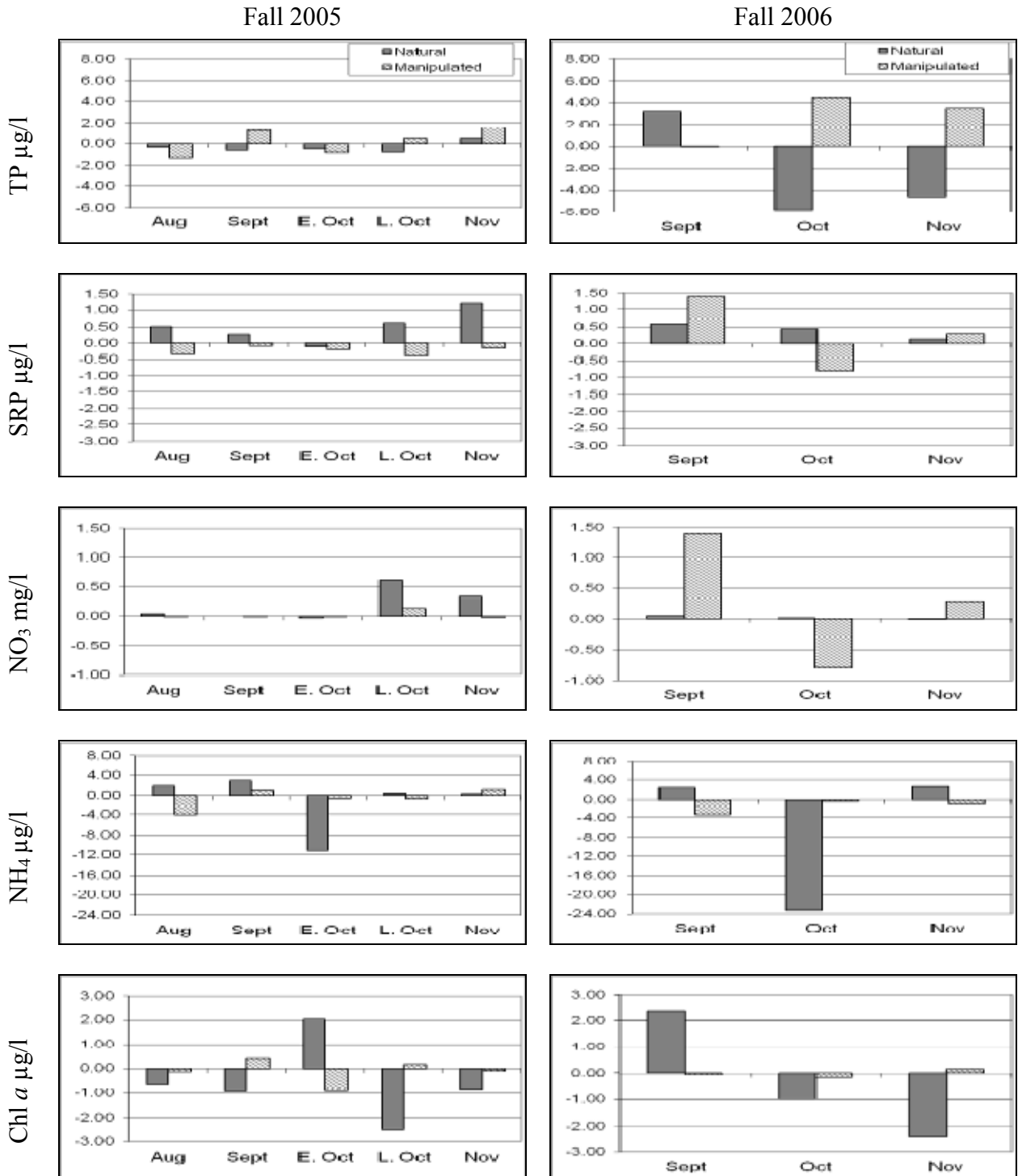


Figure 3.1. The average difference in concentration of TP (µg/l), SRP (µg/l), NO<sub>3</sub> (mg/l), NH<sub>4</sub> (µg/l) and chl a (µg/l) for fall 2005 and fall 2006. Differences were determined by averaging values from the control (upstream) reach and subtracting it from the average values for the treatment (downstream) reach. The natural system is shown in solid while the manipulated system is shown in stripes. All spawning occurs after September sampling.

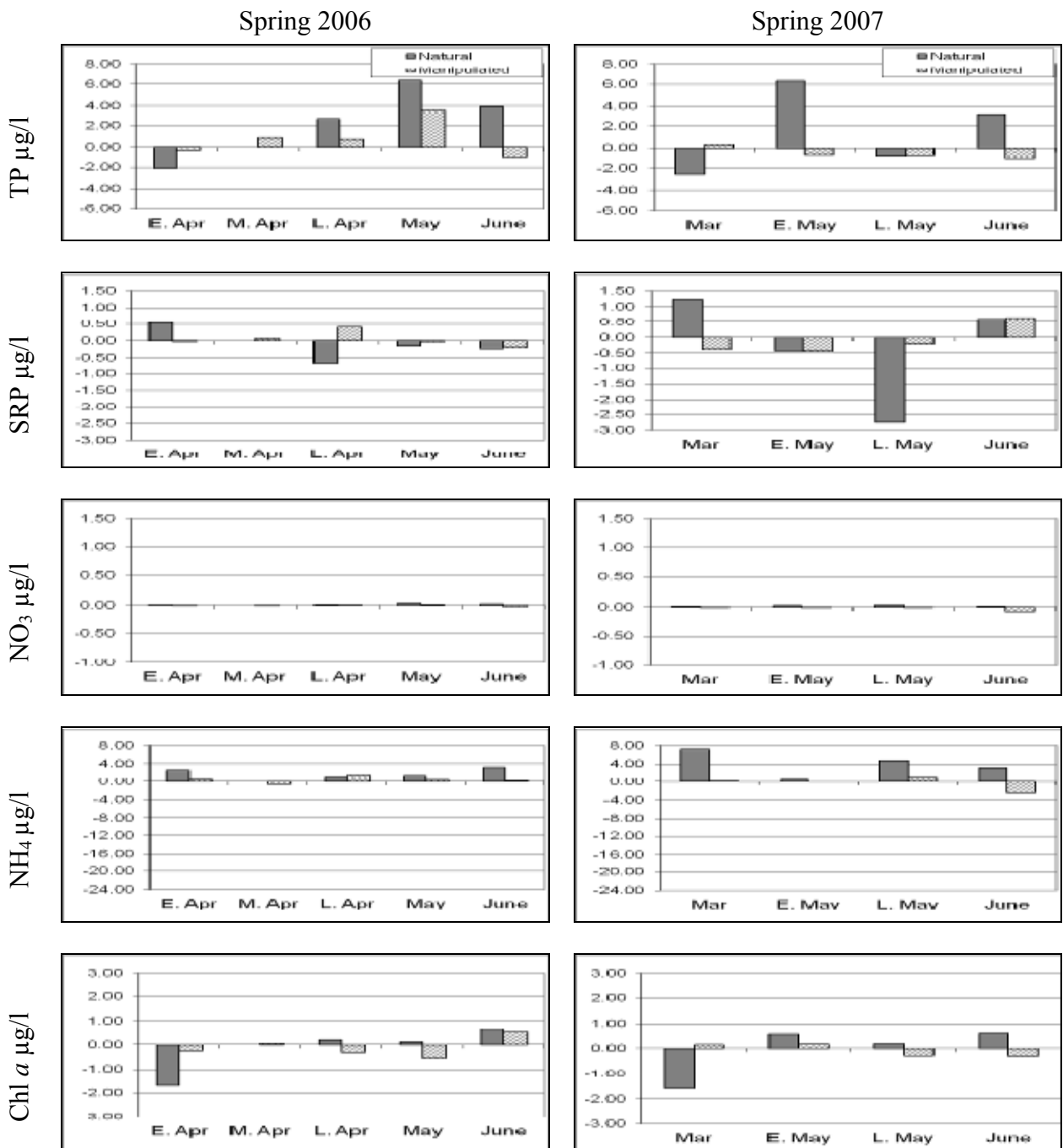
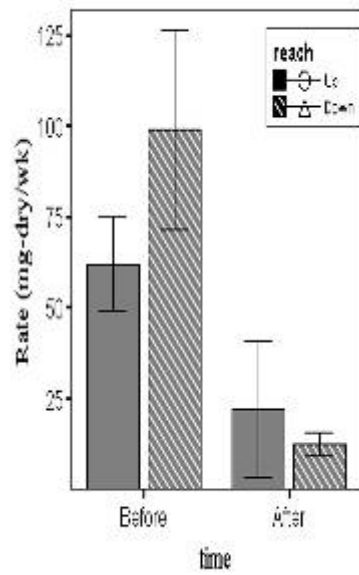
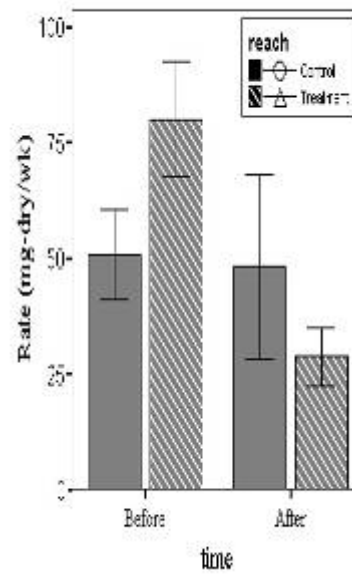


Figure 3.2. The average difference in concentration of TP ( $\mu\text{g/l}$ ), SRP ( $\mu\text{g/l}$ ),  $\text{NO}_3$  ( $\text{mg/l}$ ),  $\text{NH}_4$  ( $\mu\text{g/l}$ ) and chl a ( $\mu\text{g/l}$ ) for spring 2006 and spring 2007. Differences were determined by averaging values from the control (upstream) reach and subtracting it from the average values at the treatment (downstream) reach. The natural system is shown in solid while the manipulated system is shown in stripes. All spawning occurs after mid April in 2006 and March in 2007.



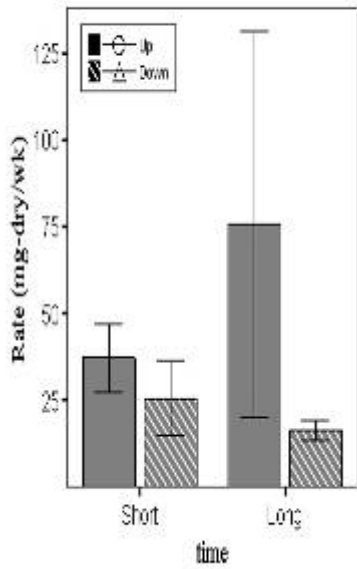


A

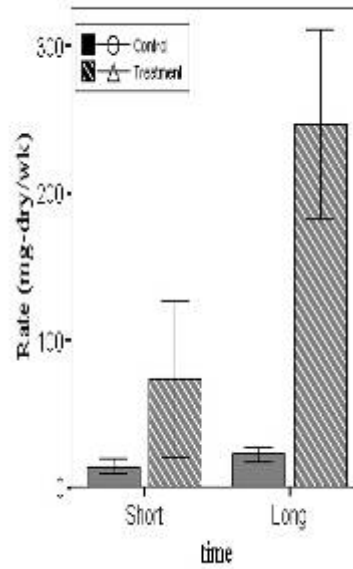


B

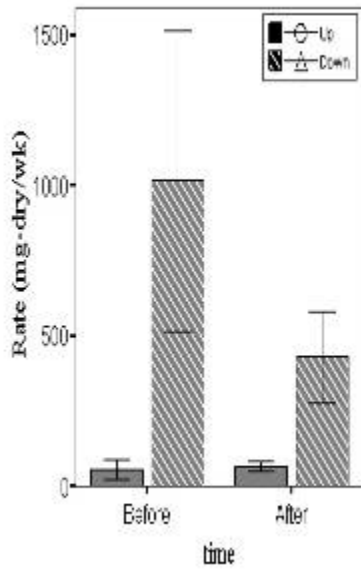
Figure 3.3. Average rate of biofilm accrual (mg dry/wk)  $\pm$  s.e. on tiles for A) the natural and B) the manipulated system for fall 2006 before and after spawning.



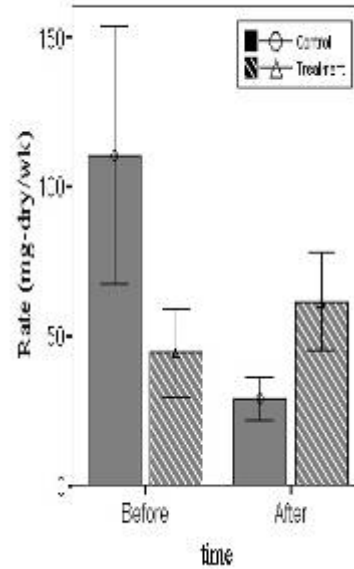
A.



C.



B.



D.

Figure 3.4. Mean biofilm accrual rates (mg dry/wk)  $\pm$  s.e. before and after either treatment with eggs or spawning of steelhead for A) natural-spring 2006, B) natural-spring 2007, C) manipulated-Spring 2006, and D) manipulated-spring 2007.

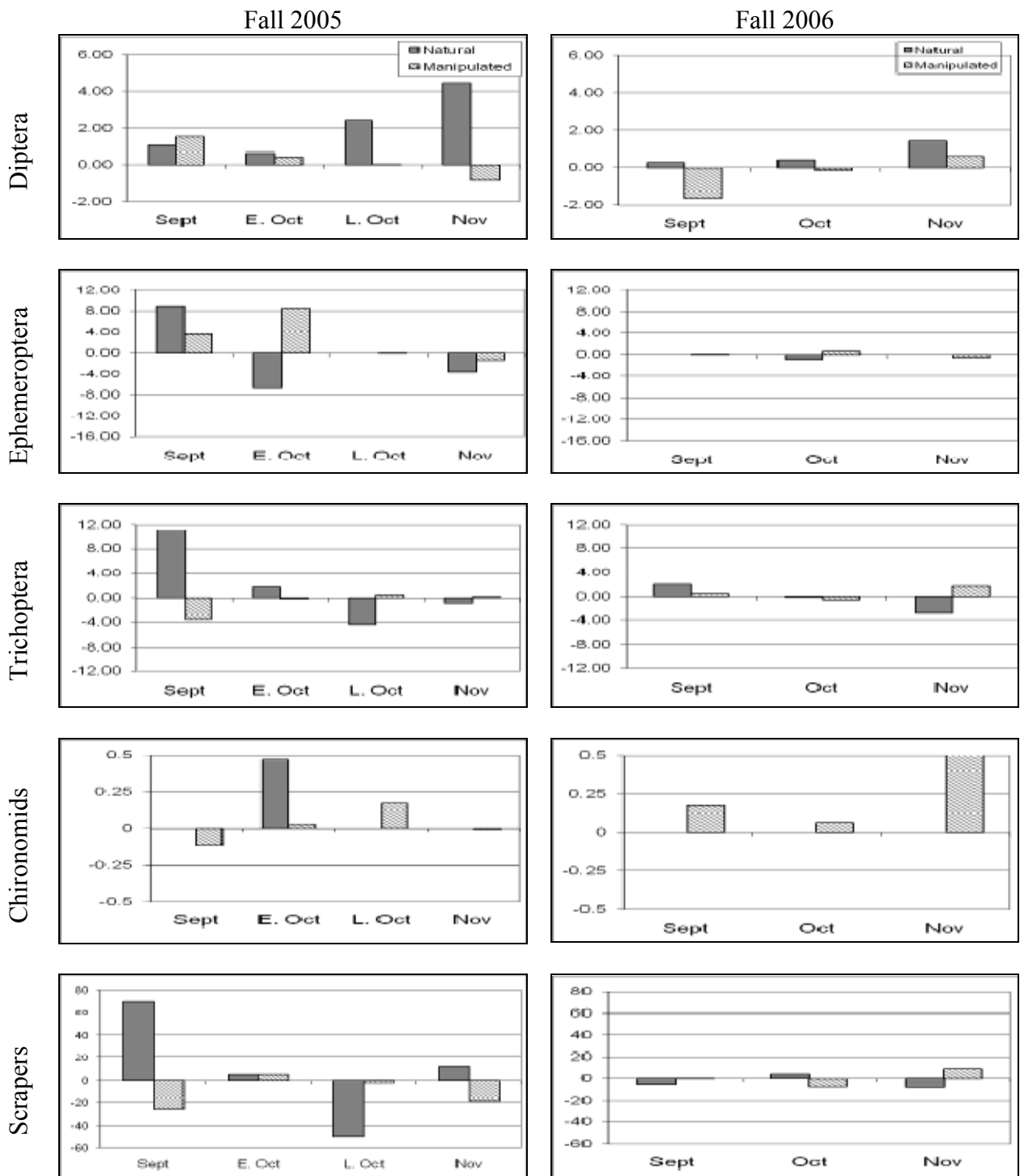


Figure 3.5. The average difference in dry weight ( $\text{mg}/\text{m}^2$ ) for Diptera, Ephemeroptera, Trichoptera, Chironomidae and scrapers for fall 2005 and 2006. Differences were determined by averaging the values from the control (upstream) reach and then subtracting from the average value at the treatment (downstream) reach. The natural and manipulated systems are shown in solid and stripes respectively. All spawning occurs after September.

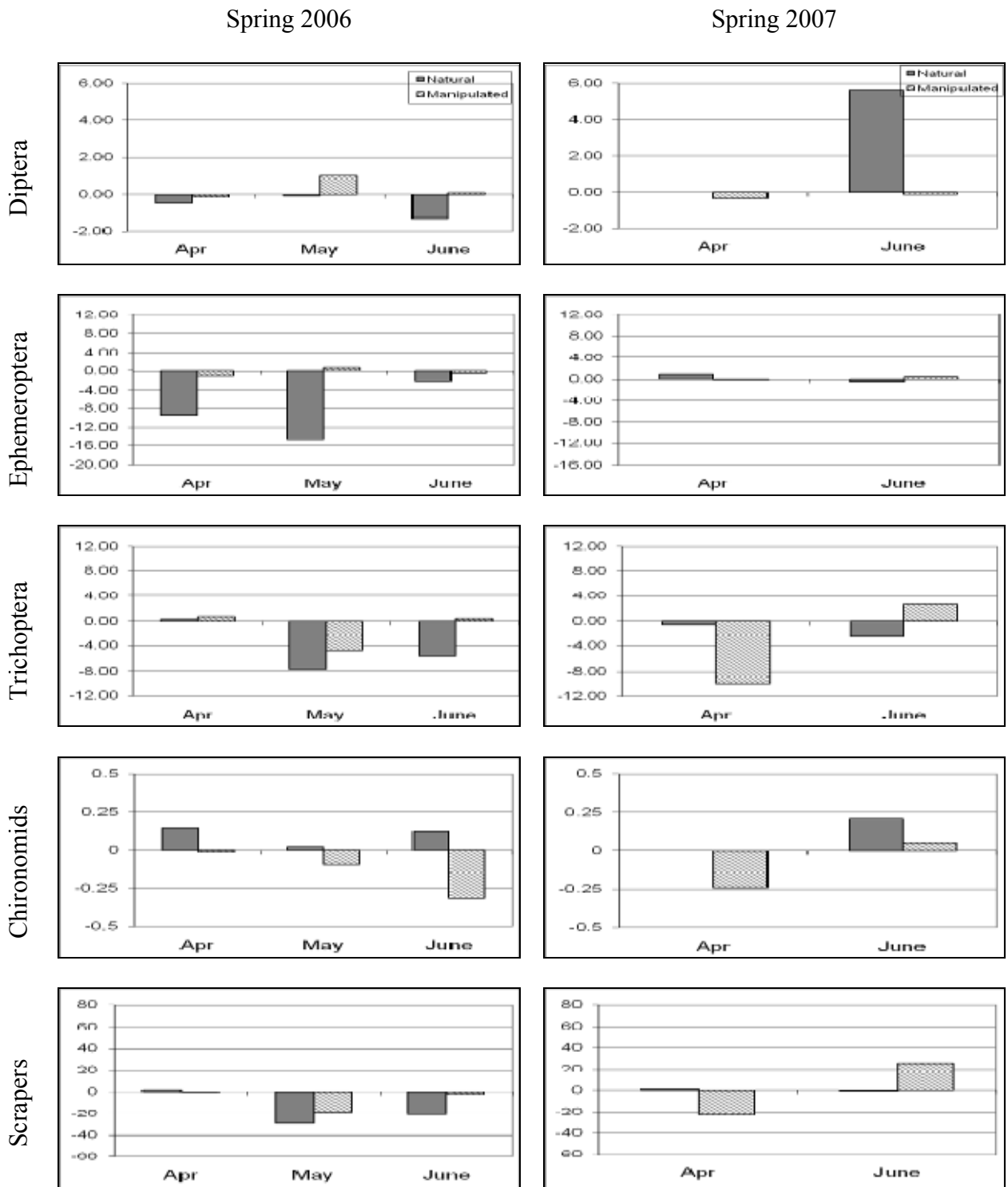


Figure 3.6. The average difference in dry weight ( $\text{mg}/\text{m}^2$ ) for Diptera, Ephemeroptera, Trichoptera, Chironomidae and scrapers for spring 2006 and 2007. Differences were determined by averaging values from the control (upstream) reach and subtracting from the average values at the treatment (downstream) reach. The natural and manipulated systems are shown in solid and stripes respectively. All spawning occurs after April.

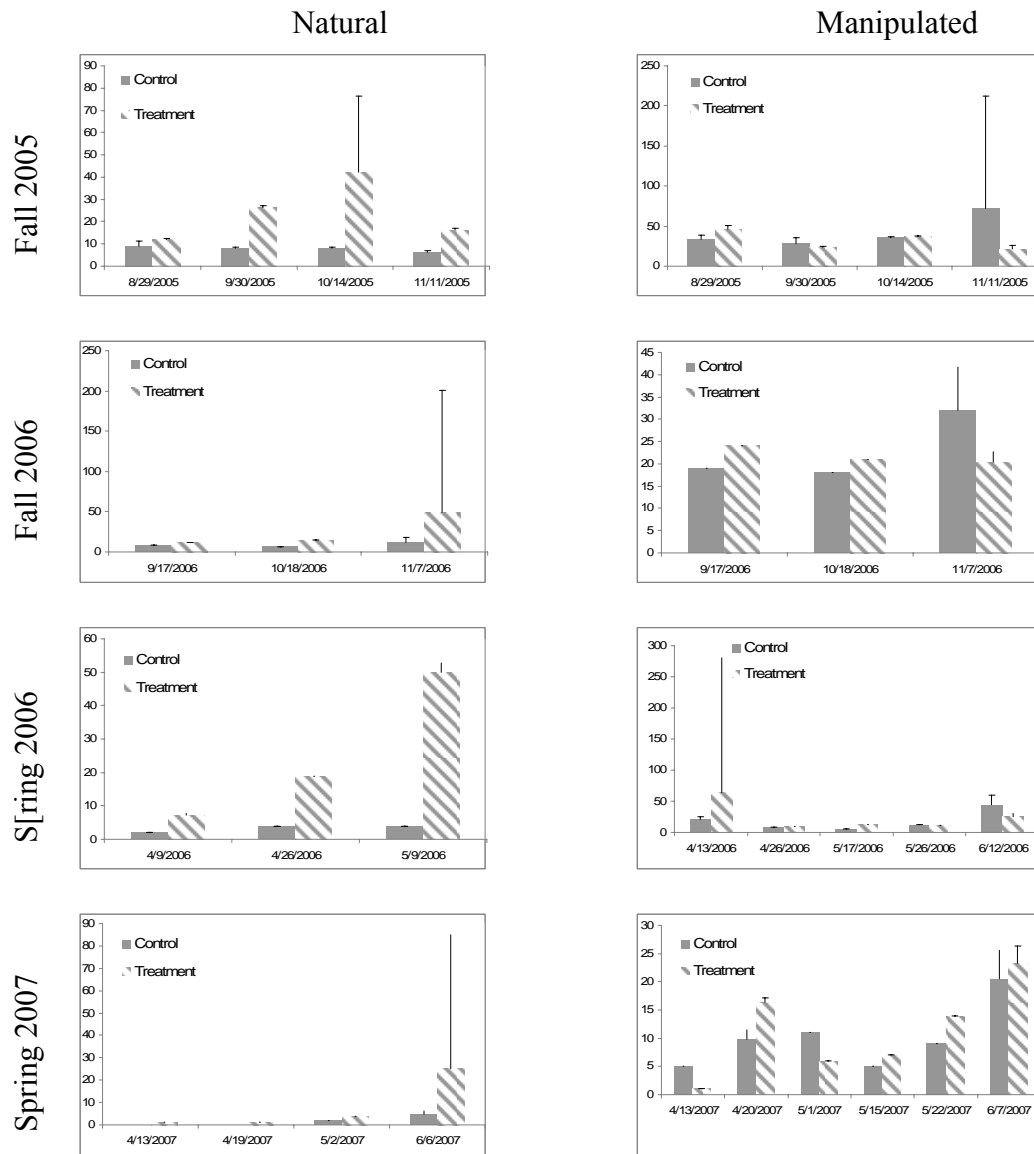


Figure 3.7. Mean density ( $\pm$ s.e.) of adult brown trout using two-pass depletion estimates for the natural and manipulated systems in fall 2005 and 2006 and spring 2006 and 2007. In fall, all spawning occurred after September while in spring all spawning occurred after April. Control reaches had low or no densities of spawners while treatment reaches had spawning activity (natural) or contained carcasses and eggs added *in situ*.

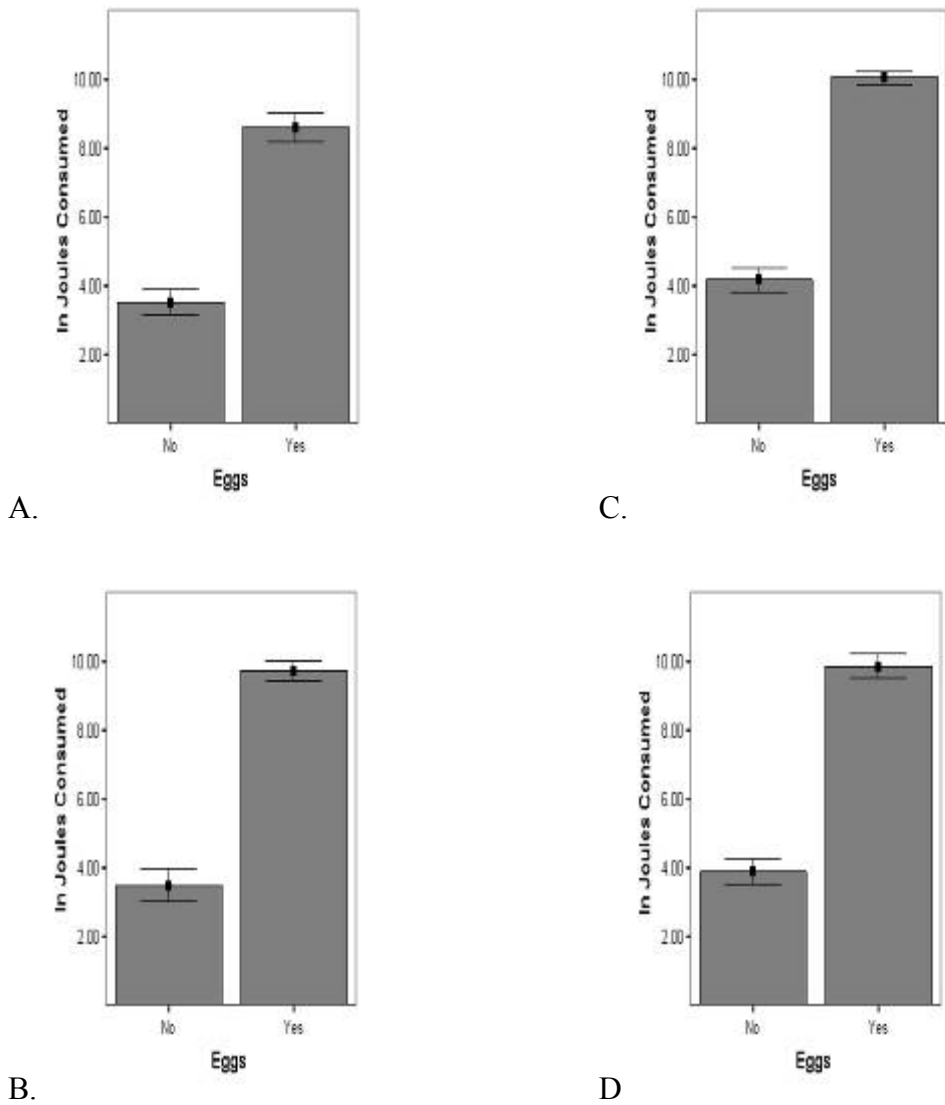
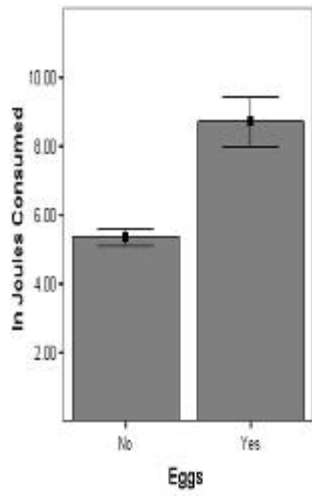
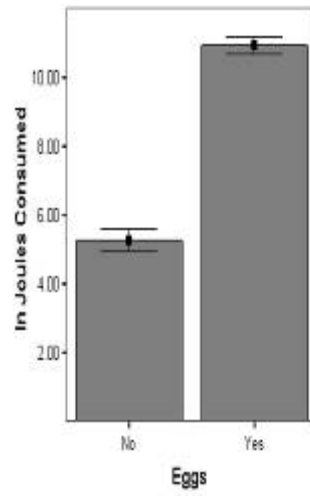


Figure 3.8. Mean total joules ( $\pm$ s.e.) consumed by resident trout with and without eggs in diets in A) Natural-Fall 2005, B) Natural- Fall 2006, C) Manipulated-Fall 2005 and D) Manipulated-Fall 2006.



A



B

Figure 3.9. Mean total joules ( $\pm$ s.e.) consumed by resident trout with or without eggs in diets in the manipulated system in A) spring 2006 and B) spring 2007.

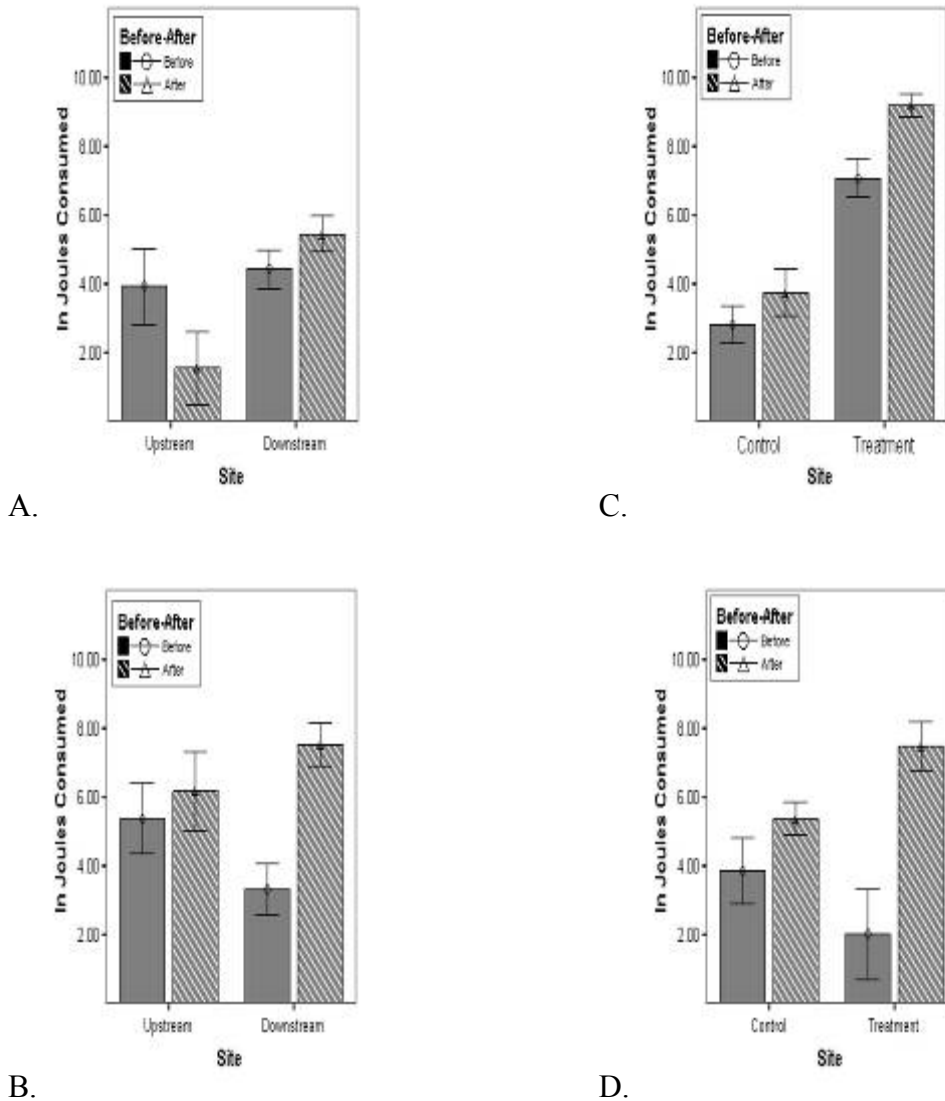
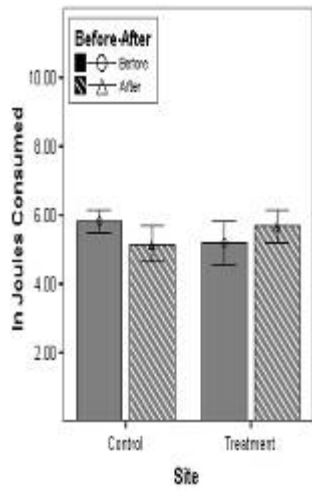
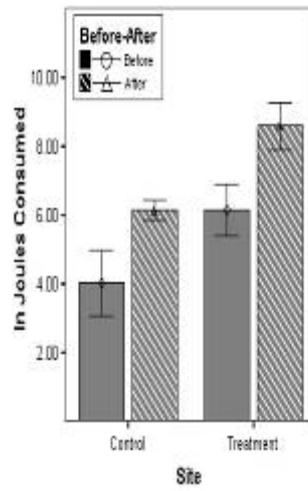


Figure 3.10. Mean total joules ( $\pm$  s.e.) consumed by resident trout in the upstream and downstream reaches before (solid) and after (slash) Chinook salmon spawning in A) Natural- Fall 2005, B) Natural- Fall 2006, C) Manipulated-Fall 2005 and D) Manipulated-Fall 2006. Mean joules consumed represents the average joules consumed by the fish community sampled at a reach.





A



B

Figure 3.11. Mean total joules ( $\pm$ s.e.) consumed by resident trout in the control and treatment reaches before (solid) and after (slash) egg introductions in the Manipulated system in a) spring 2006 and b) spring 2007. Mean joules consumed represents the average joules consumed by the fish community sampled at a reach.

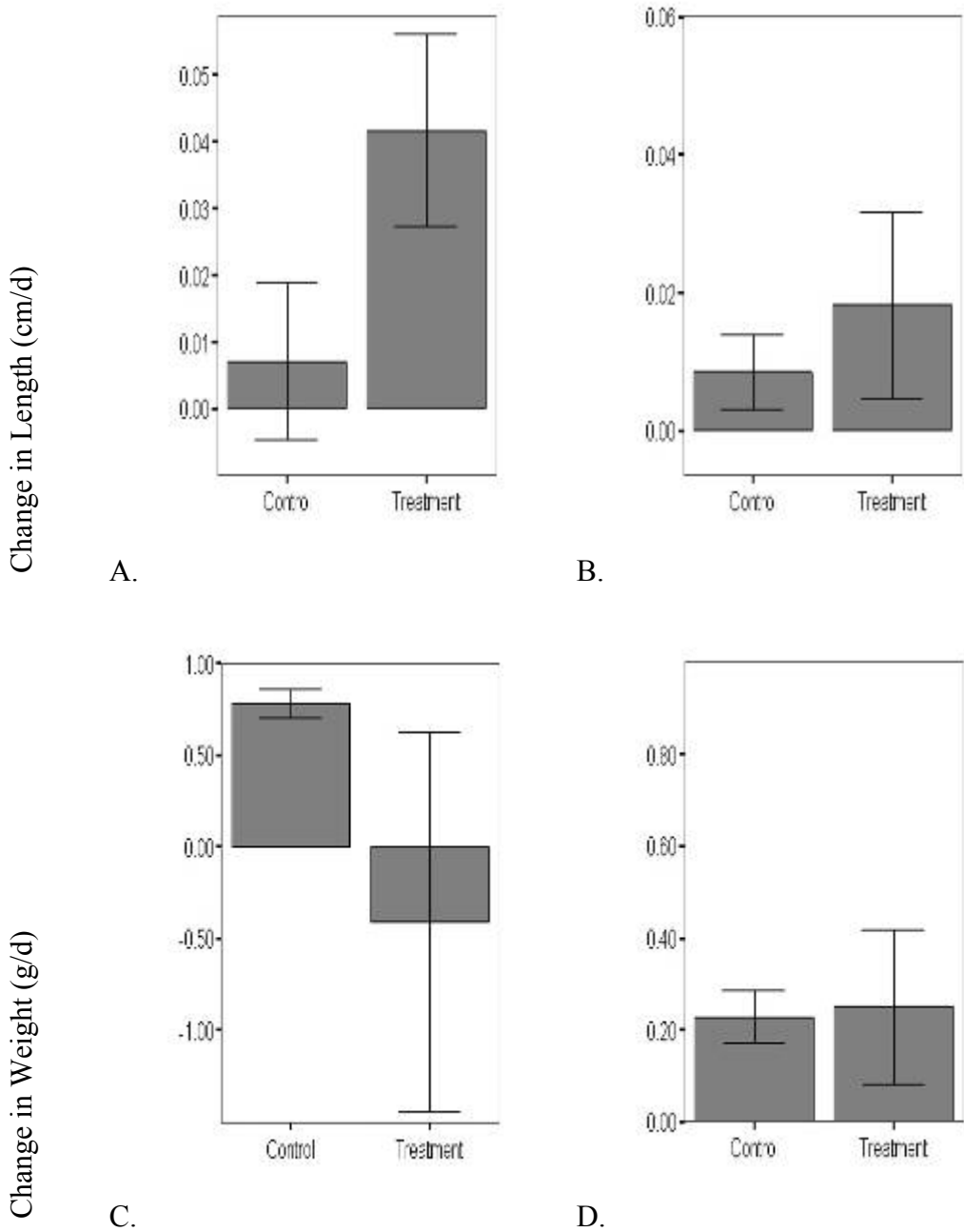


Figure 3.12. Mean change ( $\pm$  s.e.) in growth of adult pit-tagged trout over time in response to Chinook salmon spawning or carcass or egg introductions in the natural or manipulated systems. A) Change in length (cm) in the natural system; B) change in length in the manipulated system; C) change in weight (g) in the natural system; and D) change in weight in the manipulated system. Changes include all fish sampled from a reach over the entire sampling time period.

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## Chapter 4

### **Determining the Ecological Impacts of Adfluvial Fishes on a Small Great Lakes Tributary Using a Cohort-based Simulation Model**

#### **Abstract**

Spawning and subsequent mortality of anadromous fish are known to increase nutrients, primary productivity, invertebrate biomass, and resident fish growth and survival in oligotrophic streams in the Pacific Northwest. In more eutrophic streams, the impact of anadromous and adfluvial spawners is less clear or well understood. I used a cohort-based model to simulate the impact of Chinook salmon (*Oncorhynchus tshawytscha*) spawning on stream nutrient pools, macroinvertebrate production, and growth and survival of young-of-year (YOY) steelhead (*O. mykiss*). Density, growth, and survival of YOY steelhead were modeled from egg deposition, when daily cohorts were formed, through the end of the first year. YOY steelhead cohorts consumed macroinvertebrates, Chinook salmon eggs, or both, and grew via a bioenergetics subroutine. Simulations were run at baseline nutrient levels (nitrogen = 1900 g/d or 0.38 mg/l; phosphorus = 850 g/d or 16 µg/l) for a 1-ha stream, as well as half baseline and twice baseline loads for varying numbers (0, 800, and 2000) of Chinook salmon spawners. To determine the importance of Chinook salmon spawning and carcass decomposition on egg consumption, growth, and survival of YOY steelhead, the model was run for three additional scenarios for each nutrient level: introductions of salmon carcasses only; salmon eggs only; or allowing macroinvertebrates to grow directly from feeding on carcasses. Results indicated that YOY steelhead grew better as background nutrient levels increased. Presence of Chinook salmon increased YOY growth and, at low-nutrient levels, survival. Chinook salmon increased YOY steelhead growth more in low-nutrient model simulations relative to higher nutrient simulations. Consumption of eggs

affects growth and survival of YOY steelhead more than carcass decomposition, especially at low-nutrient levels.

## **Introduction**

The understanding of fish as nutrient and energy transporters derives largely from work on salmonids in the Pacific Northwest (Gende et al. 2002; Johnston et al. 2004; Schindler et al. 2003; Wipfli et al. 1998, 2003, 2004), an area known for its nutrient-poor waters. Streams with spawning salmonids have higher levels of primary productivity, invertebrate biomass, fish biomass, and fish recruitment (Wipfli et al. 2003; Bilby et al. 2001; Cederholm et al. 1999; Richey et al. 1979) than streams without spawning salmonids. Gende et al. (2004) were among the first to quantify the amount of nutrients and energy transported into natural streams by spawning salmonids in the Pacific Northwest, revealing that a substantial amount of transported material is lost to the riparian edge or is quickly transported downstream. Despite losses of imported material, Johnston et al. (2004) and Wipfli et al. (2004) showed an increase in chlorophyll a and periphyton levels in rivers with spawning salmonids up to several months following spawning runs. Increases in lower foodwebs concurrent with spawning events stimulate increases in invertebrate biomass (Chaloner et al. 2002a; Chaloner et al. 2002b; Wipfli et al. 1998), which in turn provides food for growing salmon in streams (Wipfli et al. 2003; Bilby et al. 1998; Bilby et al. 1996). Therefore, returning adult salmon not only produce the next generation of salmon, but also provide sources of food via increased macroinvertebrate biomass.

Spawning salmon in the Pacific Northwest provide eggs and carcasses for direct consumption and growth of resident and juvenile fishes (Bilby et al. 1998). Eggs are



energy rich (Gende et al. 2004) and provide an easy source of energy for fish. Eggs become available to stream fishes when they spill out of the redd during spawning and superimposition, when a female digs a redd over a previously dug redd. While superimposition can be a significant source of egg loss at high spawner densities (Fukushima et al. 1998), the importance of spillage is controversial as some authors believe it is significant, while others found it to be a low fraction of all eggs spawned (Healey 1991).

The impacts of spawning salmonids in the Pacific Northwest do not increase linearly with increased numbers of spawners. Rather, there is a plateau effect. This plateau effect, where in the rate of impacts level off as spawner density increases, has been observed in both lower trophic levels (Wipfli et al. 1999) and in the fish community (Wipfli et al. 2003). Therefore, the impact of spawning adfluvial fish on YOY growth depends greatly on the density of adfluvial spawners.

While the effects of spawning salmon on oligotrophic streams are well documented, it is unclear what impacts these fish have in more eutrophic systems, such as those found in the Great Lakes. Several studies in the Great Lakes show impacts of Chinook salmon spawners on nutrients, wood decomposition rates, and movement of nutrients into the invertebrate community. However, these studies were conducted in relatively low-nutrient waters (Fisher Wold and Hershey 1999; Schuldt and Hershey 1995). Two studies conducted in more nutrient-rich waters found different results. Rand et al. (1992) found no impact of spawning Chinook salmon on a tributary of Lake Ontario, while in another Lake Ontario tributary Sarica et al. (2004) found that high concentrations of mercury in spawning salmon were transferred to stream biota and

nutrient concentrations increased in the water column. However, both of these authors looked at impacts of spawning salmon on lower trophic levels. Additional work is required to determine the impact of these spawning fish on fish communities in more eutrophic systems.

There are two mechanisms by which adfluvial fishes can impact stream fish growth and survival. Chinook salmon can impact growth and survival of stream fish directly through consumption of salmon eggs and carcass tissue. Chinook salmon also may impact resident fish growth and survival indirectly via carcass decomposition. Carcass decomposition may lead to increased growth and survival of resident fish via increases in the productivity of lower trophic levels that ultimately increase the availability of macroinvertebrates for resident fish consumption. Furthermore, carcasses can be directly used by macroinvertebrates, which can then be eaten by fish. Conceptually, the direct pathway can be thought of as an energy pathway because resident fishes primarily feed directly on energy-rich eggs (Figure 4.1). Conversely, the indirect pathway can be thought of as a nutrient pathway, as the increased growth of macroinvertebrates consumed by fish is a net result of nutrient addition from carcass decomposition, although direct macroinvertebrate growth on carcasses also involves energy transfer.

The indirect pathway is thought to be important in the overall growth, survival, and productivity of salmonids in nutrient-poor streams of the Pacific Northwest. As a consequence, management agencies add salmon carcasses and carcass analogs to streams (Kohler et al. 2008) as a means of mitigating decreased productivity due to low adult salmon returns to streams. However, the energy pathway (i.e., egg consumption) is a

potentially important product of spawning migrations that increases growth of resident salmonids concurrent with spawning runs (Bilby et al. 1998).

I hypothesize that the nutrient pathway is likely to have little impact on more nutrient-rich stream communities in the Great Lakes, as their productivity usually is much greater than in oligotrophic streams. I also hypothesize that resident fish are likely to benefit more from the direct consumption of eggs spawned by adfluvial fishes than by indirect impacts of carcasses on lower trophic levels and resident fish prey. Egg consumption by resident fishes can result in increased fish growth, survival or both if mortality is size-selective. Fish survival can increase if additional prey from eggs decreases fish foraging time, and therefore predation risk.

The objectives of this paper are to determine the relative impact of spawning Chinook salmon on the growth and survival of YOY steelhead. More specifically, I developed a cohort-based model to simulate the importance of the energy pathway (egg consumption) and the nutrient pathway (carcass decomposition) on growth and survival of YOY steelhead under different background nutrient loadings. I hypothesized that 1) YOY steelhead will grow and survive better as background nutrient levels increase, 2) the impact of Chinook salmon on growth of YOY steelhead will be greatest in nutrient-poor systems, and 3) the relative importance of the two pathways to the production of YOY steelhead will shift from the nutrient pathway to the energy pathway as background nutrient loadings increase.

## **Methods**

### Site Description

The Muskegon River drains approximately 7,000 square kilometers and has a total length of 350 kilometers. Due to the presence of barriers on the river, however, only 80 river kilometers are available to the adfluvial fishes that spawn in the river. Bigelow Creek is the main cold-water tributary of the Muskegon River available to spawners. It is a ground-water-fed system with an average width of 6 meters and average flow of 0.7 m<sup>3</sup>/s (Godby 2000). Steelhead spawning runs are low in Bigelow Creek (approximately 100 spawners) (Dr. David Swank, NOAA National Marine Fisheries Service, Santa Cruz, CA, personal communication), while Chinook salmon spawn in greater numbers (approximately 800 spawners) (Carl 1980).

### Model Description

To understand the potential impact of adfluvial spawners on water nutrients, invertebrate biomass, and fish production in Great Lakes tributaries, I developed an ecosystem model in Visual Basic 2003 that tracks biomass of Chinook salmon and steelhead female spawners, Chinook salmon carcasses, eggs, macroinvertebrates, YOY steelhead, and concentration and loads of nutrients (nitrogen, phosphorous) in the water column. The model simulates effects of Chinook salmon spawning on YOY steelhead in Bigelow Creek, a tributary of the Muskegon River which flows to Lake Michigan. For information on the code structure, see Appendix 2.

### Steelhead Spawning

The initial number of YOY steelhead in the model is determined by size and number of adult female steelhead spawners. Adult steelhead enter Bigelow Creek to

spawn in the spring (Figure 4.1), and modeled steelhead spawn starting on Julian day 80 (March 21). A random function generates a variety of weights for each individual fish with an average weight of  $2.54 \text{ kg} \pm 0.5$ . The number of eggs spawned is based on a weight-fecundity relationship (Dr. David Swank, NOAA National Marine Fisheries Service, Santa Cruz, CA, personal communication),

$$S = 1260 * W^{14.1}, \quad (1)$$

where S is the fecundity of a female steelhead and W is the weight of the individual female (Table 4.1). Eggs are placed into an array of daily cohorts and hatch when accumulated thermal units (ATU), the number of degree days eggs have experienced since they were deposited into a redd, exceed  $310 \text{ }^\circ\text{C}$  (Kraus 1999). After hatch, egg cohorts become yolk-sac fry, experiencing a daily mortality rate of 2.25% estimated for steelhead parr in the Manistee and Muskegon Rivers (Godby et al. 2007, Tyler and Rutherford 2007). Yolk-sac fry emerge from gravel and commence feeding when the cohort ATU exceeds  $500 \text{ }^\circ\text{C}$  (Kraus 1999). At this time, they are classified as young-of-year (YOY) and are assigned an average length of 20 mm (Tyler and Rutherford 2007).

#### Chinook Salmon Spawning and Carcass Decomposition

Chinook salmon contribute energy and nutrients to streams through egg deposition (energy pathway) and the decomposition of carcasses (nutrient pathway). Chinook salmon spawning is modeled similarly to steelhead spawning but occurs over a 50-day period starting in mid-September. Length-weight relationships for Chinook salmon are based on studies of Chinook salmon in the Muskegon River ( $R^2 = 0.91$ ). The length-fecundity relationship used is

$$\text{Fecundity} = 0.00195 * \text{Length}^{2.234} \quad (2)$$

and is from studies of ocean-type Chinook salmon from the Pacific Northwest (Healy and Heard 1984). There is no length-fecundity relationship available for the Muskegon River.

Chinook salmon have a semelparous life history and thus experience 100 percent mortality following spawning. Carcass retention in the stream reach was assumed to be 75 percent because retention rates are likely greater in Bigelow Creek than in the Pacific Northwest owing to the lower numbers of terrestrial consumers and lower flow rates. This assumption also is supported by previous studies in Bigelow Creek that revealed that tagged carcasses were often seen over several weeks in the same locations (L. Ivan, unpublished data). The nutrient contribution of Chinook salmon varies depending on the number of fish spawning and the randomly assigned weight for each spawner because the phosphorus and nitrogen levels in each fish are assumed to be a constant proportion of body weight (Schindler and Eby 1997). Carcass decomposition releases bound nutrients to the environment and is determined by an exponential decay function

$$\text{ChDec} = \text{carc} * (1 - \exp(-K)), \quad (3)$$

where ChDec = g/m<sup>2</sup> of Chinook salmon carcass tissue lost, carc = g/m<sup>2</sup> of Chinook salmon carcasses available and K is the rate of decomposition (Parmentar and Lamerra 1999) (Table 4.1).

### Background Nutrient Levels

Average nitrogen and phosphorus loads (g/d) are parameters in the model determined using data from periodic sampling of Bigelow Creek. Simulations were run

at baseline nutrient levels, defined as the average nitrogen (1900 g/d) and phosphorus (850 g/d) loads for Bigelow Creek, as well as at low levels (half the nitrogen and phosphorus loads) and high levels (twice the nitrogen and phosphorus loads). Nutrient concentrations were allowed to vary inversely with daily flow. Therefore, at baseline simulations, loading values produced TP concentrations that averaged 16 µg/l while nitrogen concentrations averaged 0.38 mg/l. Concentrations increased with additions from carcass decomposition. Nutrient loads and water flow into and out of the stream reach were checked to ensure mass-balance. The amount of water flowing into the modeled stream reach was based on measured flows in Bigelow Creek. Pool volume of the modeled reach was determined by multiplying area by depth. Water depth (D) changes as

$$D = \exp^{-1.446} * D_a^{0.125} * f^{0.202} \quad (4)$$

where  $D_a$  is the drainage area of Bigelow Creek ( $m^2$ ) and  $f$  is the measured flow ( $m^3/s$ ) (Su-Ting Cheng, University of Michigan, personal communication) (Table 4.1).

Outflowing water was simulated as the difference between the current day's pool volume and the previous day's pool volume. Nutrient concentrations ( $g/m^3$ ) in the pool and in outflowing water were based on the total mass of nitrogen and phosphorus in grams divided by the volume of water.

### Foraging

Model YOY steelhead can forage on macroinvertebrates, eggs deposited by spawning Chinook salmon, or both. Foraging on both macroinvertebrates and eggs is based on a Holling's Type II functional response. As such,  $p$ , the proportion of

maximum consumption by YOY steelhead (see equation 7), increases as density increases of either eggs or macroinvertebrates, but this increase eventually levels off with further increases in prey density. The functional response of YOY to macroinvertebrates was calibrated to early growth of YOY steelhead in Bigelow Creek (Godby et al. 2007), while functional response to eggs was estimated to allow fish to grow to weights observed in Michigan streams at the end of the year. In the fall, YOY cohorts eat both macroinvertebrates and eggs based on diet percentages determined by Godby (2000). However, not all cohorts have access to eggs, especially at low egg densities. When eggs are present, a random function determines if a cohort is allowed to consume eggs each day that they are available; otherwise, YOY continue to consume macroinvertebrates. Randomly assigning prey types to cohorts causes greater variability in growth and survival of cohorts, which is observed in many studies as some individuals consume more eggs than others (Merna 1979, Godby et al. 2007,). If YOY steelhead can consume eggs, the proportion of eggs in the diet depends on the availability of eggs. When eggs are not available, or when a cohort is not randomly assigned to consume eggs, YOY steelhead feed on macroinvertebrates.

### Macroinvertebrate Growth

Invertebrate biomass grows via a logistic growth function as

$$M_{t+1} = M_t * (1 + r * (1 - (M_t/k))) - C, \quad (5)$$

where  $M_{t+1}$  is the biomass of macroinvertebrates ( $\text{g}/\text{m}^2$ ) at time  $t+1$ ,  $M_t$  is the biomass of macroinvertebrates ( $\text{g}/\text{m}^2$ ) at time  $t$ ,  $r$  is the intrinsic rate of increase,  $C$  is the consumption of macroinvertebrates ( $\text{g}/\text{m}^2$ ) by YOY steelhead, and  $k$  is the



macroinvertebrate carrying capacity ( $\text{g}/\text{m}^2$ ) (Table 4.1). Carrying capacity for macroinvertebrates is defined by biomass estimates from coldwater streams around Michigan (Riseng et al. 2004). Riseng et al. (2004) determined average nutrient concentrations and macroinvertebrate biomass for many coldwater streams in the Midwest. Average biomass of macroinvertebrates from Riseng et al. (2004) ranged from 1.5 to 152.7  $\text{g.wet}/\text{m}^2$ , with an average of 20.5  $\text{g.wet}/\text{m}^2$ . Maximum biomass from Bigelow Creek for the two most abundant taxa was 61.2  $\text{g.wet}/\text{m}^2$  (Godby 2000). By assuming carrying capacity was 2.5 times standing stocks of macroinvertebrates sampled across an array of background nutrient concentrations, the maximum value of macroinvertebrates is higher than observed for most streams (Huryn and Wallace 2000), but not outside the range reported in similar streams. I assumed that carrying capacity was 2.5 times the invertebrate standing stock determined by Riseng et al. (2004). To simulate the impact of macroinvertebrate growth during carcass decomposition, a scalar was used on the intrinsic rate of increase ( $r$ ). The intrinsic rate of increase therefore varies as a function of phosphorous, nitrogen, and water temperature (Dr. Michael Wiley, University of Michigan, personal communication) as

$$\text{sca} = (0.3188 * \log(\text{P}) + 0.119 * \text{T} + (474.17 * 10^{-6}) * \text{N} + 3.969) / \text{max} \quad (6)$$

$$r = r_w * \text{sca} \quad (7)$$

where sca is the relationship between macroinvertebrate biomass and water parameters, P is total phosphorus concentration ( $\mu\text{g}/\text{l}$ ), T is water temperature ( $^{\circ}\text{C}$ ), N is dissolved inorganic nitrogen concentration ( $\text{mg}/\text{l}$ ), max is the maximum observed invertebrate biomass ( $\text{g}/\text{m}^2$ ) predicted for Bigelow Creek based on the scalar relationship and the maximum nitrogen and phosphorus concentrations and temperature in the model, and  $r_w$

is the intrinsic rate of increase from Watanabe et al. (2005). Carcass decomposition releases phosphorous and nitrogen into the water column, increasing nutrient levels. The intrinsic rate of increase for macroinvertebrate biomass changes as nutrient levels change; it therefore changes with increased phosphorous and nitrogen from carcass decomposition. Temperatures used in the model were based on average daily temperatures measured using Hobos submersible data recorders placed *in situ* in Bigelow Creek in 2005. It was assumed that 20 percent of macroinvertebrate carrying capacity was unavailable for YOY steelhead consumption due to either limits in fish gape size or the fact that some macroinvertebrates would be buried in the sediment and therefore inaccessible to foraging steelhead. Furthermore, it was assumed that only 10 percent of the available macroinvertebrate biomass would be in the drift where most of the YOY steelhead forage (Tyler and Rutherford 2007).

### YOY Growth

A bioenergetics model simulated growth of YOY steelhead. The bioenergetics model is based on a mass balance equation that relates consumption to growth, respiration, and wastes as

$$C = G + R + F + U, \quad (8)$$

where C is consumption ( $\text{g g}^{-1} \text{d}^{-1}$ ), G is growth ( $\text{g g}^{-1} \text{d}^{-1}$ , both gonadal and somatic), R is respiration ( $\text{g g}^{-1} \text{d}^{-1}$ ), and F+U is waste loss ( $\text{g g}^{-1} \text{d}^{-1}$ ) (Brandt and Hartman 1993, Ney 1993). Typically, one solves for growth or consumption by knowing or estimating the other values. I solved for YOY steelhead growth. Realized consumption is expressed as a proportion 'p' of maximum consumption ( $C_{\text{max}}$ ) given fish weight and ambient

temperature. The proportion of maximum consumption was modeled based on a Holling's Type II functional response to prey density.

I used a series of bioenergetics equations from Hansen et al. (1997) as modified by Railsback and Rose (1999) to model YOY steelhead growth (Table 4.1). Based on these equations, consumption is modeled as

$$C = C_{\max} * p * f(T), \quad (9)$$

where  $C_{\max}$  is the maximum consumption ( $\text{g g}^{-1} \text{d}^{-1}$ ),  $p$  is the proportion of the maximum that is actually consumed, and  $f(T)$  is a function describing the temperature-dependence of consumption. Energy from respiration, egestion, and excretion must be subtracted from the total energy consumed in order to calculate growth. Respiration includes standard metabolism (respiration of an inactive, unfed fish), active metabolism, and specific dynamic action (the energy required to digest food). Standard metabolism is defined as

$$R = RA * W^{\text{RB}} * f(T), \quad (10)$$

where  $RA$  and  $RB$  are constants,  $W$  is the fish mass ( $\text{g}$ ), and  $f(T)$  is a function describing temperature-dependence of respiration. Energy lost due to specific dynamic action is defined as

$$S = SDA * (C - F), \quad (11)$$

where  $S$  is the proportion of assimilated energy lost to specific dynamic action,  $SDA$  is specific dynamic action, and  $F$  is the egestion rate ( $\text{g g}^{-1} \text{d}^{-1}$ ). Finally, active metabolism is defined as

$$ACT = 5.328 * W^{0.485} \quad (12)$$

Calculating respiration involves estimating grams of oxygen consumed by fishes and, as such, final values must be multiplied by an oxicalorific conversion factor. Specific dynamic action is dependent on both consumption and egestion. Waste loss is divided into egestion and excretion. Egestion is determined as

$$F = FA * T^{FB} * e^{(FG - p)} * C, \quad (13)$$

where FA, FB, and FG are constant coefficients and T is temperature ( $^{\circ}\text{C}$ ), and C is consumption. Excretion is modeled as

$$U = UA * T^{UB} * e^{(UG - p)} * (C - F), \quad (14)$$

where UA, UB and UG are constant coefficients similar to the egestion coefficients, C is consumption and F is egestion.

Daily growth of modeled YOY steelhead is based on consumption of both macroinvertebrates and eggs on a daily basis. The model tracks mean weight, mean length, and the number of individuals for each daily YOY steelhead cohort. Average weight of each cohort is multiplied by the number of surviving YOY within a cohort to get the total YOY biomass for each cohort.

### Survival of YOY

Survival of YOY steelhead is determined based on predation and starvation mortality. A YOY steelhead with a weight 50 percent below the expected weight based on length-weight regressions for a fish of its length is assumed to have starved (Tyler and Rutherford 2007). The model converts weight to length using a length-weight relationship for YOY steelhead as

$$L = 46.73 * W^{0.337} \quad (15)$$

where L is the length in mm and W is the weight in grams (Table 4.1). While fish are allowed to lose weight, they are not allowed to lose part of their skeletal structure; therefore they never decrease in length. Predation mortality on YOY steelhead is simulated as a size-based function

$$m = 0.02 + 3 / (L^{1.9}) \quad (16)$$

where m is instantaneous daily mortality rate of predation mortality and L is YOY steelhead length (Tyler and Rutherford 2007).

### Model Calibration and Simulations

The baseline simulation of the model was calibrated to data collected by Godby et al. (2007). Baseline conditions were defined as 50 spawning female steelhead and no Chinook salmon spawners assuming a 50:50 sex ratio. To determine the relative impact of background nutrient levels on growth of YOY steelhead, simulations were run at baseline and half (low) and twice (high) baseline nutrient loads. Additional simulations were run with 800 and 2000 Chinook salmon spawners (assuming a 50:50 sex ratio) to determine the importance of Chinook salmon spawning on growth and survival of YOY steelhead. These densities were selected to mimic densities of spawning Chinook salmon in Bigelow Creek (800/ha) (Carl 1979) and in the Pacific Northwest (2000/ha) (Chaloner et al. 2004), respectively. The two pathways by which salmon may impact stream communities, and as a result, growth and survival of YOY steelhead, are the nutrient and energy pathways. To determine the relative importance of these two pathways, I ran simulations at all three nutrient levels when carcasses only and eggs only were allowed into the system from 800 and 2000 spawning Chinook salmon. Finally,

macroinvertebrates can colonize carcasses directly, leading to an increase in macroinvertebrates, not from a bottom-up nutrient effect, but from a direct effect through macroinvertebrate consumption of the carcasses themselves (Chaloner et al. 2002b). Therefore, I ran a simulation whereby macroinvertebrates grew an additional 0.5% a day when carcasses were present. Egg consumption by model YOY steelhead was not allowed during these simulations because previous simulations showed egg consumption had a disproportionately large effect on steelhead growth compared to the indirect nutrient pathway from carcass decomposition.

For each simulation combination, five simulations were conducted to obtain an average estimate for weight, length, density, and biomass of an average YOY steelhead at the end of the model year. I used analysis of variance (ANOVA) to determine differences in overall average weight, length, density, and biomass of YOY steelhead among model simulations. Statistical differences were considered significant at the  $\alpha = 0.05$  level. Comparisons were made of YOY density, growth and survival among the three background nutrient levels when no Chinook salmon were present, and within a nutrient level for all simulations where Chinook salmon were present (either eggs only, carcasses only, both eggs and carcasses present, and direct macroinvertebrate growth from carcasses)

### Sensitivity Analysis

To determine the relative importance of parameters to model output, I ran several sensitivity analyses and varied each model parameter by 10% while holding the other parameters constant. I included several variables important to macroinvertebrate

populations, including carrying capacity, intrinsic rate of increase, the percentage of available macroinvertebrates for YOY steelhead consumption, and direct growth of macroinvertebrates from carcasses. Two survival parameters, including the daily mortality rate experienced by larvae and the survival of steelhead eggs from deposition to hatch, also were adjusted by 10%. Both carcass retention percentages and the decomposition parameter that determines decomposition rate were likewise adjusted. Finally, as egg availability was likely important in determining the relative importance of egg consumption to carcass decomposition to overall YOY growth, the percent eggs available to individual steelhead also was adjusted by 10%.

## **Results**

### Model Calibration

I adjusted values for the Holling's Type II functional response until growth of YOY steelhead in baseline simulations without Chinook salmon present was similar to steelhead growth measured in Bigelow Creek, MI (Godby et al. 2007) (Figure 4.2). In baseline simulations without spawners, modeled YOY steelhead grew slightly slower than observed by Godby et al. (2007) for the entire year. Growth of modeled steelhead with the addition of 800 Chinook salmon spawners to the baseline simulation better mimicked data from Godby et al. (2007) later in fall. This was expected because YOY steelhead in Godby et al.'s (2007) study consumed a high percentage of eggs. Simulated YOY densities fell within the confidence interval of expected densities found by Godby et al. (2007) for both simulations.

## Model Results

There was a significant difference in weight, length, density, and biomass of YOY steelhead (Table 4.2,  $p < 0.001$ ) among the three background nutrient levels. For low-nutrient simulations, YOY steelhead were smaller and had lower densities than in baseline simulations, while YOY steelhead were smaller and had lower densities under baseline conditions than in higher nutrient simulations.

The presence of Chinook salmon increased weight, length, and biomass of YOY steelhead over values predicted for baseline simulations without Chinook spawners (Table 4.3,  $p < 0.001$ ). YOY steelhead population density was unaffected by spawning Chinook salmon. In low-nutrient simulations, the presence of Chinook spawners increased YOY steelhead weight, length, and biomass (Table 4.4,  $p < 0.001$ ). YOY density increased in low-nutrient simulations only when Chinook salmon spawners or only eggs from spawners were added. YOY steelhead weight, length and biomass, but not population density, also increased with presence of Chinook spawners in high background nutrient simulations (Tables 4.5,  $p < 0.001$ ).

At all three nutrient levels, YOY steelhead weight and length were higher in simulations with 2000 Chinook salmon spawners than in simulations with 0 and 800 Chinook spawners (Tables 4.3-4.5). However, YOY steelhead density was relatively unaffected by spawning salmon in all nutrient simulations (Tables 4.3-4.5).

The impact of Chinook salmon spawners on modeled YOY steelhead occurred primarily through consumption of salmon eggs. Weights, lengths, and population density of YOY steelhead were similar in the zero Chinook salmon simulations and simulations with only carcasses from spawning Chinook salmon (Tables 4.3-4.5). Allowing



macroinvertebrates to grow directly off of carcass tissue increased YOY weight, length, and biomass in all nutrient simulations compared to values in simulations with zero Chinook salmon spawning (Tables 4.3-4.5).

Comparison of the relative impact of spawners at the three nutrient levels shows that spawners have the greatest impact at low nutrient levels. Spawning Chinook salmon produced the greatest percent increase in weight and length of YOY steelhead in the low-nutrient simulations (Figure 4.3). This pattern held true for both YOY density and biomass (Figure 4.4), although the impact was not as great for the observed population density.

For the baseline simulation, the greatest percent increase in YOY steelhead weight occurred with 2000 Chinook spawners (carcasses and eggs) and when only eggs were available from 2000 Chinook spawners (Figure 4.3). Allowing macroinvertebrates to grow directly off carcasses had the second largest impact on YOY growth. The third largest impact on YOY growth was from 800 Chinook spawners, and with only eggs available from 800 Chinook spawners.

In low-nutrient simulations, YOY steelhead growth was greatest in simulations with 2000 spawners (carcasses and eggs) and 2000 spawners (eggs only) (Figure 4.3). At low nutrient levels, YOY growth was greater in simulations with 800 Chinook salmon spawners, or the eggs from 800 Chinook salmon than in simulations where macroinvertebrates were allowed to grow directly off of carcasses.

At high nutrient levels, YOY steelhead growth was similar in simulations with adding 2000 salmon, adding the eggs only from 2000 salmon, or allowing macroinvertebrates to grow directly off of carcasses. The second most important impact

on YOY growth in high-nutrient regimes occurred in simulations with 800 Chinook salmon or the eggs from 800 Chinook salmon (Figure 4.3).

### Sensitivity Analysis

Results of the sensitivity analysis show that model predictions of YOY steelhead weight, length, and cohort biomass are most sensitive to variation in estimates of macroinvertebrate carrying capacity and the availability of macroinvertebrates to YOY steelhead consumption (Figures 4.5 and 4.6). In contrast, model predictions of YOY steelhead cohort density at the end of the model run were most sensitive to variation in the survival rate of eggs to hatch (Figure 4.6). Predicted weight of YOY steelhead at the end of the year was the most sensitive output variable to model parameters, followed by YOY steelhead length.

### **Discussion**

The model simulates the impact of an adfluvial spawner, Chinook salmon, on the growth and survival of YOY steelhead from hatch through the end of their first year. Comparisons of YOY steelhead growth and survival among low, baseline, and high nutrient simulations revealed that YOY grew and survived better at higher background nutrient levels when salmon are not present.

The impact of Chinook salmon spawning on modeled YOY steelhead growth was greatest in the low-nutrient simulations, as predicted. Compared to simulations at low-nutrient levels without spawners, weight of YOY steelhead doubled with the addition of 800 Chinook salmon and increased almost 5 times when 2000 Chinook salmon were

added. The large increase in weight of YOY fishes in these simulations resulted in a similar increase in YOY cohort biomass. The impacts of Chinook salmon spawners in baseline nutrient simulations were not as great as those observed in low-nutrient simulations, but YOY steelhead were still longer and heavier at the end of the growing year. While differences were significant, the increases in weight and length of YOY steelhead in the high-nutrient simulations were not as drastic as the baseline or low-nutrient simulations.

Predicted effects of Chinook salmon on density of YOY steelhead were generally limited and only occurred in the low-nutrient simulations. Relative to effects on YOY weight and biomass, the impact of spawners on population density was small in all nutrient simulations suggesting that, while YOY growth might benefit from adfluvial spawners, survival may not. One reason for the lack of a spawning effect on YOY population density is the low survival rate of individual steelhead early in the model season, which results in a relatively low population density when salmon enter the stream to spawn. Since YOY survival is dependent on length, the relative impact of salmon will be less if YOY steelhead are larger when Chinook salmon spawn. Although Bilby et al. (1998) noted an increase in juvenile trout density during salmonid spawning in the Pacific Northwest, this increase likely was a consequence of fish moving into stream reaches where spawners are present rather than an improvement in survival. The model does not allow for immigration of fishes into the stream reach.

Both the greater observed weight and abundance of YOY steelhead during Chinook salmon spawning in the model are consistent with other studies in the Pacific Northwest. Wipfli et al. (2003) observed increased body mass and fork length in age-0

coho salmon during pink salmon carcass addition experiments. Age-0 coho salmon also exhibited a doubling of growth following spawning of adult coho salmon in a Washington stream (Bilby et al. 1996), a result similar to YOY steelhead growth rates under conditions of low nutrient concentrations and high Chinook spawner density in the model.

Effects of adding additional Chinook salmon spawners on model YOY growth were expected to diminish at high salmon spawner densities as observed by researchers in the Pacific Northwest (Wipfli et al. 2003). However, no plateau effect of spawner density on YOY growth was observed in the baseline and high nutrient simulations. YOY growth in the high and baseline nutrient simulations experienced a greater increase in growth from zero Chinook salmon spawners to 2000 Chinook salmon spawners than expected if a plateau was reached. However, the low availability of eggs when 800 Chinook salmon spawners were present was not enough to increase growth of YOY steelhead due to the large numbers of YOY steelhead competing for relatively few eggs in the higher nutrient simulations. The addition of 2000 Chinook salmon spawners increased the relative cohort/egg ratio in the high and baseline nutrient simulations, resulting in a greater than expected impact of increased numbers of spawners in higher and baseline nutrient simulations.

Wipfli et al. (2003) observed an asymptotic relationship between density of Chinook salmon spawners and juvenile salmonid growth that was not replicated by my model simulations. These authors did not notice sharp decreases in increased growth of age-0 coho until spawner densities reached 1 carcass per  $m^2$  in a mesocosm experiment, well above the 0.2 carcass per  $m^2$  used in this model. The spawner densities required for

an asymptotic relationship observed in Wipfli et al.'s (2003) study were much higher than observed densities in Bigelow Creek, MI and greater than the observed spawner densities in the natural system studied by Wipfli et al. (2003, 0.54 spawners per m<sup>2</sup>).

Model simulations suggested that energy effects of salmon spawners on YOY size and density were greater than effects from nutrient additions. Egg consumption by YOY steelhead led to a large increase in growth in all nutrient regimes while carcass decomposition had little impact on YOY growth. Bilby et al. (1998) noted high consumption of eggs by both coho salmon and age-0 and age-1 steelhead, which likely were responsible for increased growth rates in the streams studied. In my model, YOY steelhead that consumed eggs had variable growth in all three nutrient simulations, as some cohorts had more access to eggs than others. However, the greatest increase in YOY steelhead growth occurred when YOY consumed salmon eggs in low-nutrient simulations.

The nutrient pathway was hypothesized to be more important to YOY growth in low-nutrient conditions than in high-nutrient conditions. However, carcass decomposition did not impact YOY growth and survival in the model simulations at any background nutrient level. Part of the relatively small impact of carcasses has to do with the loss of nutrients from the stream owing to flow. Most of the nutrients brought into the stream via spawners are quickly transported downstream. Rapid removal of nutrients downstream, or to the riparian edge, is consistent with findings of Johnston et al. (2004) and Gende et al. (2004). Both these researchers observed a rapid removal of nutrients leaking from carcasses placed in streams in the Pacific Northwest. A significant source of removal of nutrients is due to the removal of carcasses via consumption by terrestrial

birds and mammals (Cederholm et al. 1989, Gende et al. 2004). However, few carcasses were observed within a 3m width of the riparian edge during carcass surveys in 2005 in Bigelow Creek (L. Ivan, unpublished data). In a Lake Ontario stream, Sarica et al. (2004) noted a significant reduction in the impacts of spawning salmon on stream communities due to bear predation. It is likely that, at least in some streams, consumption by terrestrial predators in the Great Lakes may be less than observed in the Pacific Northwest.

Another reason for the lack of a response by YOY steelhead to carcass decomposition is the low responsiveness of the scalar used on the macroinvertebrate intrinsic rate of increase ( $r$ ) to changes in nutrient levels. Several researchers (Chaloner et al. 2004, Schuldt and Hershey 1995, Cleason et al. 2006) observed impacts of spawning salmon on water nutrient levels, and Reger and Kevern (1981) noted a positive increase in biomass of macroinvertebrates with increased water nutrients. The lack of a response by macroinvertebrates to nutrients was mitigated in model simulations when macroinvertebrates were allowed to grow directly off carcasses. Some macroinvertebrate taxa are known to colonize and consume carcasses in low-nutrient streams of the Pacific Northwest Chaloner et al. (2002b). Direct consumption by macroinvertebrates on salmon carcasses is likely a more important pathway for macroinvertebrate production and energy flow to fish in high-nutrient streams than the bottom-up nutrient pathway. However, Schuldt and Hershey (1995) observed little use of carcasses by macroinvertebrates in Lake Superior tributaries. Therefore, the relative importance of carcass decomposition versus carcass colonization and consumption by macroinvertebrates to macroinvertebrate growth remains unknown.

The greater response in growth of modeled YOY steelhead to egg consumption relative to carcasses decomposition suggests that the majority of the increase in weight of resident fishes observed in the Pacific Northwest is due to egg consumption and not the bottom-up effect of carcass decomposition as proposed by many Pacific Northwest researchers. However, carcass analogs, made from ground-up carcasses, can increase condition, production, and lipid concentrations in juvenile salmon (Wipfli et al. 2004). These authors also noted an increase in fish condition and production with carcass addition experiments. Together, these results suggest that juvenile salmon may feed directly on carcasses. While some large trout may consume carcasses, no carcass flesh was observed in stomachs of YOY steelhead in Bigelow Creek (L. Ivan, unpublished data), and Bilby et al. (1998) found that carcass flesh comprised only a small proportion of YOY steelhead diets in the Pacific Northwest. Furthermore, the growth of macroinvertebrates from feeding on carcasses is also an important energy pathway in streams in the Pacific Northwest. Model results show that allowing invertebrates to grow directly off carcasses increases weight and biomass of YOY steelhead in all nutrient simulations. In high-nutrient simulations, this pathway was as important as adding 2000 Chinook salmon spawners. However, the increase in YOY weight from this mechanism was greatest at low-nutrient levels.

### Model Limitations

There are several limitations with the model design which may have affected the results. YOY steelhead were assumed to feed on prey according to a Hollings Type II functional response. Parameter values were adjusted to make fish grow to a size

observed in Bigelow Creek (Godby et al. 2007). While it is reasonable to assume that fish may consume via a Type II functional response, the values used are parameterized to allow YOY steelhead to grow as expected and thus have no biological meaning.

Although my assumption is likely true that the carrying capacity of macroinvertebrates is dependent on background nutrient levels, the shape of that relationship is unknown. The weak and insignificant relationship between standing stock of macroinvertebrates and phosphorus concentrations from Riseng et al. (2004) was used to determine carrying capacity for different background nutrient levels. Conceptually, it makes sense that macroinvertebrate biomass would be lower at lower nutrient levels, as shown by Reger and Keven (1981). Indeed, many studies in the Pacific Northwest, as well as management practices in the region, include adding carcasses to bolster primary productivity. However, the carrying capacities for macroinvertebrates used in this study strongly impacted model results. The sensitivity analysis showed that the model was most sensitive to estimates of macroinvertebrate carrying capacity, as well as the availability of those invertebrates to YOY steelhead. These results indicate further studies are warranted to better understand nutrient effects on macroinvertebrate carrying capacity in lower Great Lakes tributaries.

The relationship between standing stock of macroinvertebrates in Michigan rivers (Michael Wiley, University of Michigan, unpublished data), temperature, and nutrient concentrations is another important aspect of the model that could explain the lack of response by the stream community to spawning salmon. The model was not as sensitive to perturbations of the macroinvertebrate intrinsic rate of increase, but raising the intrinsic rate of increase by 10% did result in a 5% increase in YOY steelhead weight.



Given the large range of intrinsic rate of increase estimates by Watanabe et al. (2005), better information is required on this relationship.

I assumed an additional 0.5% daily increase in macroinvertebrate biomass when carcasses were present to simulate known colonization of carcasses by macroinvertebrates. While not as sensitive to perturbations as carrying capacity, increasing growth of macroinvertebrates on carcasses by 10% resulted in a 5% increase in weight of YOY steelhead. It is difficult to determine if the observed increase in macroinvertebrates in studies in the Pacific Northwest is a result of increased productivity due to decomposition or due to direct colonization of carcasses owing to the unresponsiveness of  $r$  to changes in nitrogen and phosphorus. Field studies suggest that populations of chironomids will colonize and grow on salmon carcasses in Pacific Northwest streams (Lessard and Merritt 2006). Additionally, Schuldt and Hershey (1995) used stable isotopes to demonstrate macroinvertebrates feed and grow on salmon carcasses in Lake Superior.

Another critical assumption of the model is the availability of salmonid eggs to YOY steelhead. Determining the relative importance of carcass decomposition and egg consumption is highly dependent on how many eggs are available for YOY consumption. Superimposition increases the amount of eggs available to the stream community as the number of spawners increase (Fukushima et al. 1998, Healey 1991). Assuming 0.5% of eggs are made available to the stream community during daily spawning means that, at higher spawning densities, more eggs will be available for consumption by YOY steelhead. I therefore used a conservative estimate of egg availability for YOY steelhead consumption. Surprisingly, sensitivity analysis showed that YOY steelhead weight was

not sensitive to the availability of eggs. However, previous studies on Bigelow Creek, MI showed high levels of egg consumption by YOY steelhead (Godby 2000, Merna 1979), and the availability of salmon eggs to steelhead in the model is likely an underestimate. Therefore, the lack of sensitivity by YOY growth to egg availability might only reflect model assumptions of spawner density.

The assumed rate of carcass decomposition is an important component of the model due to the link between nutrient concentrations and macroinvertebrate growth, but the model did not appear to be very sensitive to this parameter. Soft tissue decomposes faster than hard tissue in rotting fish. Therefore, the rate of nutrient release from decomposition likely slows as decomposition progresses. As such, the rate of decomposition in the model is overestimated later in the decomposition process.

Egg survival to hatch and daily larval survival were also thought to be important parameters to model outcome. While weight of YOY steelhead at the end of the year did not appear to be sensitive to these two parameters, YOY density was most sensitive to egg survival to hatch. This is not unexpected as more eggs that hatch result in more individuals surviving to the end of the year.

Bioenergetics models also have several limitations that should be acknowledged. First, bioenergetics models require many parameters. Growth will be incorrectly predicted if parameters are incorrectly estimated. This imprecision is compounded as the equations used to estimate growth are nonlinear (Ney 1993). Bioenergetics models are especially vulnerable to estimates of the proportion of maximum consumption ( $p$ ) and energy density. As  $p$  in the model is dependent on prey density, fish growth is highly sensitive to small changes in macroinvertebrate or egg densities.

Second, bioenergetics models are dependent on activity costs. Many modelers use a constant activity function that has little experimental basis. Assuming an unvarying activity constant is probably invalid (Boisclair and Sirois 1993). However, activity values that vary through time require data that are difficult to obtain. As such, I used a constant activity multiplier assumed for other foraging models of young steelhead (Railsback and Rose 1999).

## **Conclusions**

Model results revealed that fish grow better in higher nutrient regimes owing to increased abundance of macroinvertebrates. Adding Chinook salmon, in general, increased weight and length of YOY steelhead and, in low nutrient regimes, YOY density. YOY steelhead in low-nutrient simulations increased weight and length more in the presence of Chinook salmon spawners than fish in baseline or high-nutrient simulations when salmon were added. Direct consumption of salmon eggs by YOY steelhead increased growth more than did stimulation of lower trophic levels through carcass decomposition and direct macroinvertebrate growth on carcasses, except in high-nutrient regimes when direct macroinvertebrate growth on carcasses was equally important as egg consumption.

The high observed consumption of salmon eggs by resident stream fishes in the wild suggests that eggs play a vital role in maintaining salmon stocks in the Pacific Northwest. However, fish eggs may not be as critical to growth and survival of resident fish in more eutrophic Great Lakes tributaries as in the oligotrophic streams of the Pacific Northwest. While growth did increase in baseline and high nutrient conditions, fish in

these systems are likely to experience lower mortality rates, especially over winter, due to higher YOY growth rates prior to salmon spawning. It is possible that high rates of egg consumption by fishes in higher nutrient regimes will have a negative impact on fish communities because of potentially high concentrations of contaminants in fish eggs (Merna 1979, Sarica et al. 2004). Future work is required to determine if benefits of egg consumption to young fish outweigh the possible negative impacts of contaminant transfer, especially in the more nutrient-rich streams of the Great Lakes.

Table 4.1. Values of parameters with sources used in the model grouped by parameter type. All biological data are in grams wet.

<b>Description</b>	<b>Value</b>	<b>Units</b>	<b>Source</b>
<b>Physical Parameters and Variables</b>			
Ave P Load-Base	1900	g/d	Ivan 2008, unpub
Ave N Load-Base	850	g/d	Ivan 2008, unpub
Area available to spawners	1	ha	Godby 2000
Initialize Depth	0.5	m	Ivan 2008, unpub.
drainage area	84.8	km <sup>2</sup>	SuTing, Pers Comm, 2008
Value needed for depth calc	0.125	unitless	SuTing, Pers Comm, 2008
Value needed for depth calc	0.202	unitless	SuTing, Pers Comm, 2008
<b>Macroinvertebrate Parameters and Variables</b>			
Carrying capacity- Low	53	g/m <sup>2</sup>	Riseng et al. 2004
Carrying capacity- Base	78	g/m <sup>2</sup>	Riseng et al. 2004
Carrying capacity- High	115	g/m <sup>2</sup>	Riseng et al. 2004
Intrinsic rate of increase	0.0075	1/y	Watanabe et al. 2005
Initial biomass of invertebrates	0.5 k	g/m <sup>2</sup>	Estimated
Available macroinvertebrates	10%	g/m <sup>2</sup>	Tyler and Rutherford 2007
Direct Growth	0.50%	unitless	Estimated
<b>Steelhead Hatch &amp; Larvae Parameters and Variables</b>			
Size at hatch	0.081	g	Tyler and Rutherford 2007
Length at hatch	20	mm	Tyler and Rutherford 2007
Daily mort of larvae	0.0225	unitless	Tyler and Rutherford 2007
Survival of eggs to hatch	0.293	unitless	Quinn 2005
ATU to hatch	310	C	Kraus 1999
ATU to emerge	500	C	Kraus 1999
<b>Steelhead Fecundity Parameters and Variables</b>			
Fecundity of steelhead	1260	unitless	D. Swank 2005, unpub.
Fecundity of steelhead	14.11	unitless	D. Swank 2005, unpub.
Ave. weight of spawner	2.56	kg	L. Ivan, 2004 unpub.
Std dev of spawner weight	0.5	kg	
<b>Decomposition Parameters and Variables</b>			
%N by weight	0.0253	Prop.	Schindler & Eby1997
%P by weight	0.005	Prop.	Schindler & Eby1997
Carcass Retention	75%	g/m <sup>2</sup>	Estimated
Decomposition parameter	0.061	unitless	Parmenter & Lamarra 1991
<b>YOY growth Parameters and Variables</b>			
Length functions	46.73	unitless	Tyler and Rutherford 2007
Length functions	0.337	unitless	Tyler and Rutherford 2007
Energy density of eggs	9250	J/g	Gende et al. 2004
Energy density of Invertebrates	3362.5	J/g	Dieterman et al. 2004
Percent diet	0.9	unitless	Godby 2000
% eggs available	0.5	unitless	Estimated

Table 4.1 continued.

<b>Description</b>	<b>Value</b>	<b>Units</b>	<b>Source</b>
<b>YOY growth Parameters and Variables</b>			
Length functions	46.73	unitless	Tyler and Rutherford 2007
Length functions	0.337	unitless	Tyler and Rutherford 2007
Energy density of Chinook	9250	J/g	Gende et al. 2004
Energy density of Invertebrates	3362.5	J/g	Dieterman et al. 2004
Percent diet	0.9	unitless	Godby 2000
% eggs available	0.5	unitless	Estimated
<b>Chinook Salmon Fecundity Parameters &amp; Variables</b>			
Mortality of spawners	1	unitless	Assumed
Fecundity parameters	828	mm	Ivan, 2008, unpub. Data
Fecundity parameters	0.5	unitless	Estimated
Length-fecundity relationship	0.00195	unitless	Healy and Heard 1984
Length-fecundity relationship	2.234	unitless	Healy and Heard 1984
Length-weight relationship	0.000006	unitless	Ivan, 2008, unpub. Data
Length-weight relationship	3.0555	unitless	Ivan, 2008, unpub. data
Weight of egg	0.15	g	Auer 1982
<b>Bioenergetics Parameters</b>			
CA	0.628	g/g/d	Hanson et al. 1997
CB	-0.3	unitless	Hanson et al. 1997
CQ	3.5	unitless	Railsback and Rose 1999
CTO	25	°C	Railsback and Rose 1999
CTM	22.5	°C	Railsback and Rose 1999
CTL	24.3	unitless	Railsback and Rose 1999
CK1	0.2	unitless	Railsback and Rose 1999
CK4	0.2	unitless	Railsback and Rose 1999
RA	0.013	gO <sub>2</sub> /d	Railsback and Rose 1999
RB	-0.217	unitless	Hanson et al. 1997
RQ	2.2	unitless	Railsback and Rose 1999
RTO	22	°C	Railsback and Rose 1999
RTM	26	°C	Railsback and Rose 1999
RTL	0	unitless	Railsback and Rose 1999
RK1	0	unitless	Railsback and Rose 1999
ACT	1.3	cm/s	Railsback and Rose 1999
SDA	0.172	unitless	Hanson et al. 1997
FA	0.212	unitless	Hanson et al. 1997
FB	-0.222	unitless	Hanson et al. 1997
FG	0.631	unitless	Hanson et al. 1997
UA	0.0314	unitless	Hanson et al. 1997
UB	0.58	unitless	Hanson et al. 1997
UG	-0.299	unitless	Hanson et al. 1997
Conv	13608	J/gO <sub>2</sub>	J. Breck, per. Comm. 2005

Table 4.2. Comparisons of average weight (g), average length (mm), average population density (#/m<sup>2</sup>), and biomass (g/m<sup>2</sup>) across three nutrient simulations: baseline, low (0.5X baseline), and high (2X baseline). Different letters show significant differences between simulations at p<0.0001.

Nutrient Level	Weight		Length		#/m <sup>2</sup>	Biomass		
	(g)	Sig.	(mm)	Sig.		(g/m <sup>2</sup> )	Sig.	
Base	8.45	A	95.84	A	0.0175	A	0.148	A
Low	2.35	B	62.98	B	0.0131	B	0.031	B
High	22.04	C	132.38	C	0.0195	C	0.43	C

Table 4.3. Model predictions of average weight (g), average length (mm), average population density (#/m<sup>2</sup>), and biomass (g/m<sup>2</sup>) of YOY steelhead under varying conditions of nutrient loadings and numbers of Chinook salmon spawners. Simulations include: baseline nutrients only (base), baseline nutrients + 800 (base+800) and 2000 Chinook salmon spawners (base+2000); baseline nutrients + eggs only from 800 Chinook salmon spawners (base+800e) and 2000 Chinook salmon spawners (base+2000e); baseline nutrients + carcasses only of 800 Chinook salmon spawners (base+800c) and 2000 Chinook salmon spawners (base+2000c); and baseline nutrients + direct consumption of macroinvertebrates only from 800 Chinook spawners (base+800d) and 2000 Chinook salmon spawners (base+2000d). Different letters show significant differences (Sig.) in results among simulations at p<0.0001.

Simulation	Weight (g)	Sig.	Length (mm)	Sig.	#/m <sup>2</sup>	Sig.	Biomass (g/m <sup>2</sup> )	Sig.
Base	8.45	A	95.84	A	0.0175	A	0.148	A
Base+800	10.93	CD	104.48	B	0.0169	A	0.184	B
Base+800e	10.80	C	104.12	B	0.0173	A	0.186	B
Base+800c	8.61	B	96.44	A	0.0169	A	0.146	A
Base+800d	11.44	C	105.97	B	0.0173	A	0.198	C
Base+2000	15.19	E	116.43	C	0.0173	A	0.260	D
Base+2000e	15.16	E	116.31	C	0.0172	A	0.259	D
Base+2000c	8.67	B	96.65	A	0.0171	A	0.145	A
Base+2000d	11.55	CD	106.31	B	0.0170	A	0.196	C



Table 4.4. Model predictions of average weight (g), average length (mm), average population density (#/m<sup>2</sup>), and biomass (g/m<sup>2</sup>) of YOY steelhead under conditions of low nutrient concentrations (0.5X baseline nutrients) and varying numbers of Chinook salmon spawners. Simulations include: low nutrients only (low), low nutrients + 800 (low+800) and 2000 Chinook salmon spawners (low+2000); low nutrients + eggs only from 800 Chinook salmon spawners (low+800e) and 2000 Chinook salmon spawners (low+2000e); low nutrients + carcasses only of 800 Chinook salmon spawners (low+800c) and 2000 Chinook salmon spawners (low+2000c); and low nutrients + direct consumption of macroinvertebrates only from 800 Chinook spawners (low+800d) and 2000 Chinook salmon spawners (low+2000d). Different letters show significant differences (Sig.) in results among simulations at p<0.0001.

Simulation	Weight		Length		#/m <sup>2</sup>	Biomass		
	(g)	Sig.	(mm)	Sig.		(g/m <sup>2</sup> )	Sig.	
Low	2.35	A	62.98	A	0.0131	ABC	0.031	A
Low+800	5.25	E	82.70	E	0.0137	BC	0.072	C
Low+800e	5.30	E	83.05	E	0.0135	BC	0.071	C
Low+800c	2.36	A	63.12	A	0.0133	AC	0.031	A
Low+800d	3.48	D	70.98	D	0.0131	AC	0.045	B
Low+2000	10.36	F	103.78	F	0.0139	BC	0.144	D
Low+2000e	10.59	F	104.85	F	0.0135	BC	0.143	D
Low+2000c	2.38	B	63.28	B	0.0128	ABC	0.030	A
Low+2000d	3.46	C	70.81	C	0.0133	ABC	0.046	B

Table 4.5. Model predictions of average weight (g), average length (mm), average population density (#/m<sup>2</sup>), and biomass (g/m<sup>2</sup>) of YOY steelhead under conditions of high nutrient concentrations (2X baseline nutrients) and varying numbers of Chinook salmon spawners. Simulations include: high nutrients only (high), high nutrients + 800 (high+800) and 2000 Chinook salmon spawners (high+2000); high nutrients + eggs only from 800 Chinook salmon spawners (high+800e) and 2000 Chinook salmon spawners (high+2000e); high nutrients + carcasses only of 800 Chinook salmon spawners (high+800c) and 2000 Chinook salmon spawners (high+2000c); and high nutrients + direct consumption of macroinvertebrates only from 800 Chinook spawners (high+800d) and 2000 Chinook salmon spawners (high+2000d). Different letters show significant differences (Sig.) in results among simulations at p<0.0001.

Simulation	Weight (g)	Sig.	Length (mm)	Sig.	#/m <sup>2</sup>	Sig.	Biomass (g/m <sup>2</sup> )	Sig.
High	22.04	A	132.38	A	0.0195	A	0.430	A
High+800	23.24	C	134.73	C	0.0199	A	0.462	B
High+800e	23.53	C	135.30	C	0.0194	A	0.456	B
High+800c	21.85	A	132.00	A	0.0199	A	0.434	A
High+800d	26.47	D	140.70	D	0.0194	A	0.512	C
High+2000	26.25	D	140.25	D	0.0197	A	0.516	C
High+2000e	26.84	D	141.28	D	0.0190	A	0.507	C
High+2000c	22.19	AB	132.68	AB	0.0193	A	0.429	A
High+2000d	26.63	D	140.99	D	0.0191	A	0.509	C

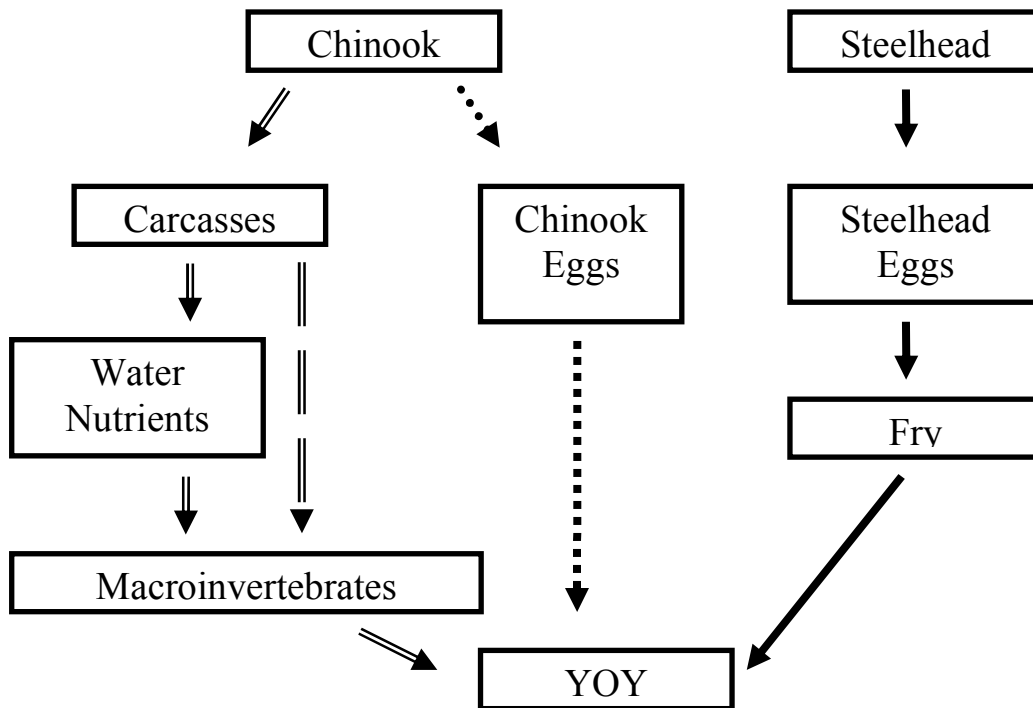


Figure 4.1. Flow diagram showing the movement of material from spawning adfluvial fish (Chinook salmon and steelhead) as followed in the model. Steelhead spawn in the spring, depositing eggs, which hatch into fry and ultimately YOY steelhead, whose growth and survival are tracked through the year via natal cohorts. Chinook salmon spawn in the fall and leave behind carcasses and eggs. Carcasses decompose, releasing nutrients into the water column, affecting the growth of the macroinvertebrate community. A small portion of the macroinvertebrate community is assumed to feed directly on the carcasses. Eggs spawned by Chinook salmon are available to the stream community and are therefore available for consumption by YOY steelhead. The developmental pathway is shown by solid arrows, the energy pathway by dotted arrows, the dashed lines show the direct link between carcasses and macroinvertebrates, and the nutrient pathway is shown by the double-lined arrow.

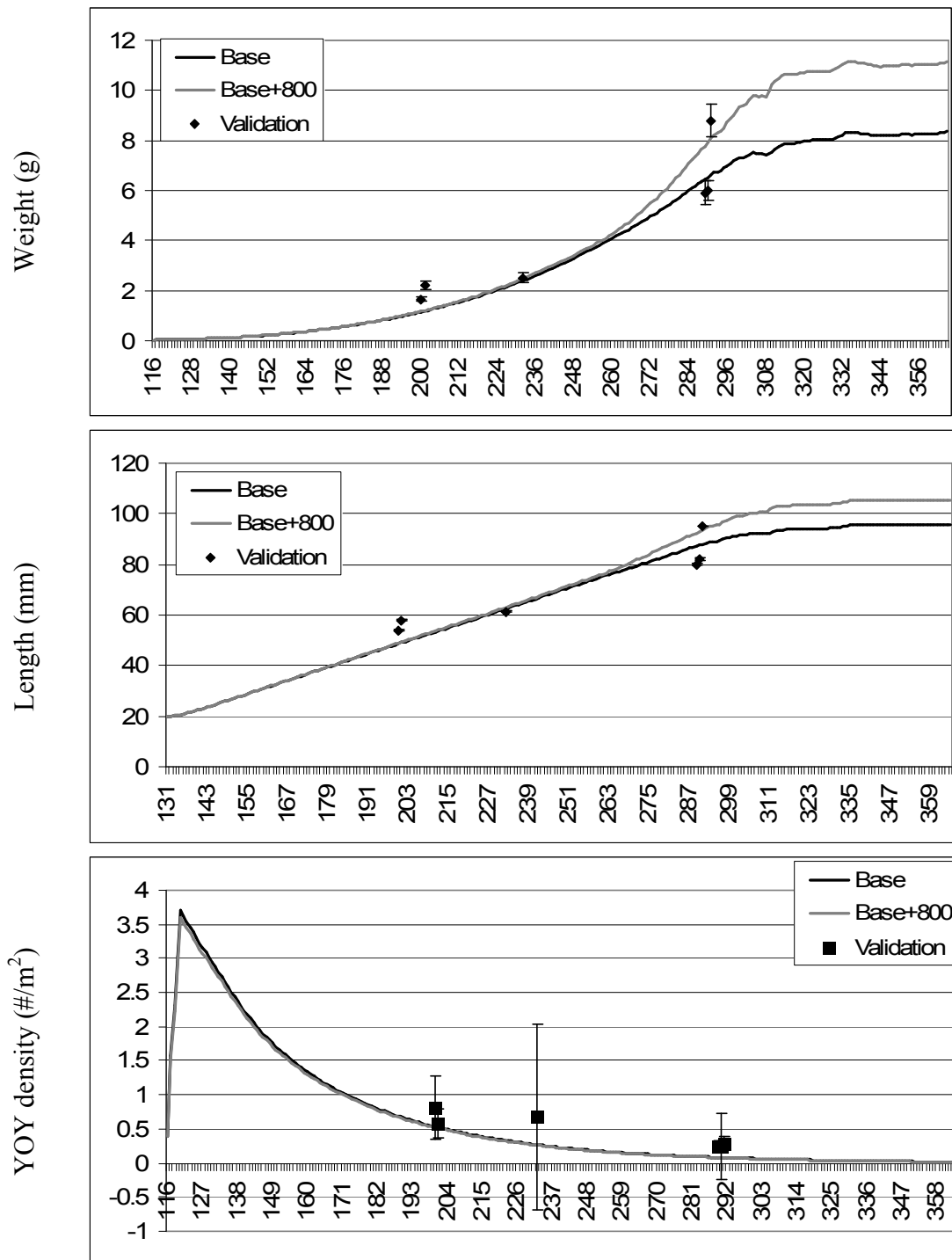


Figure 4.2. Comparison of model simulations of YOY steelhead dynamics under baseline nutrient concentrations with and without 800 salmon spawners with observed data (Godby et. al. 2007) on YOY steelhead weight (Top); length (Mid); and population density ( $\#/m^2$ ) (Bottom) over time. Average weight and length data include  $\pm$  s.e. while population density is shown with  $\pm$  95% C.I.

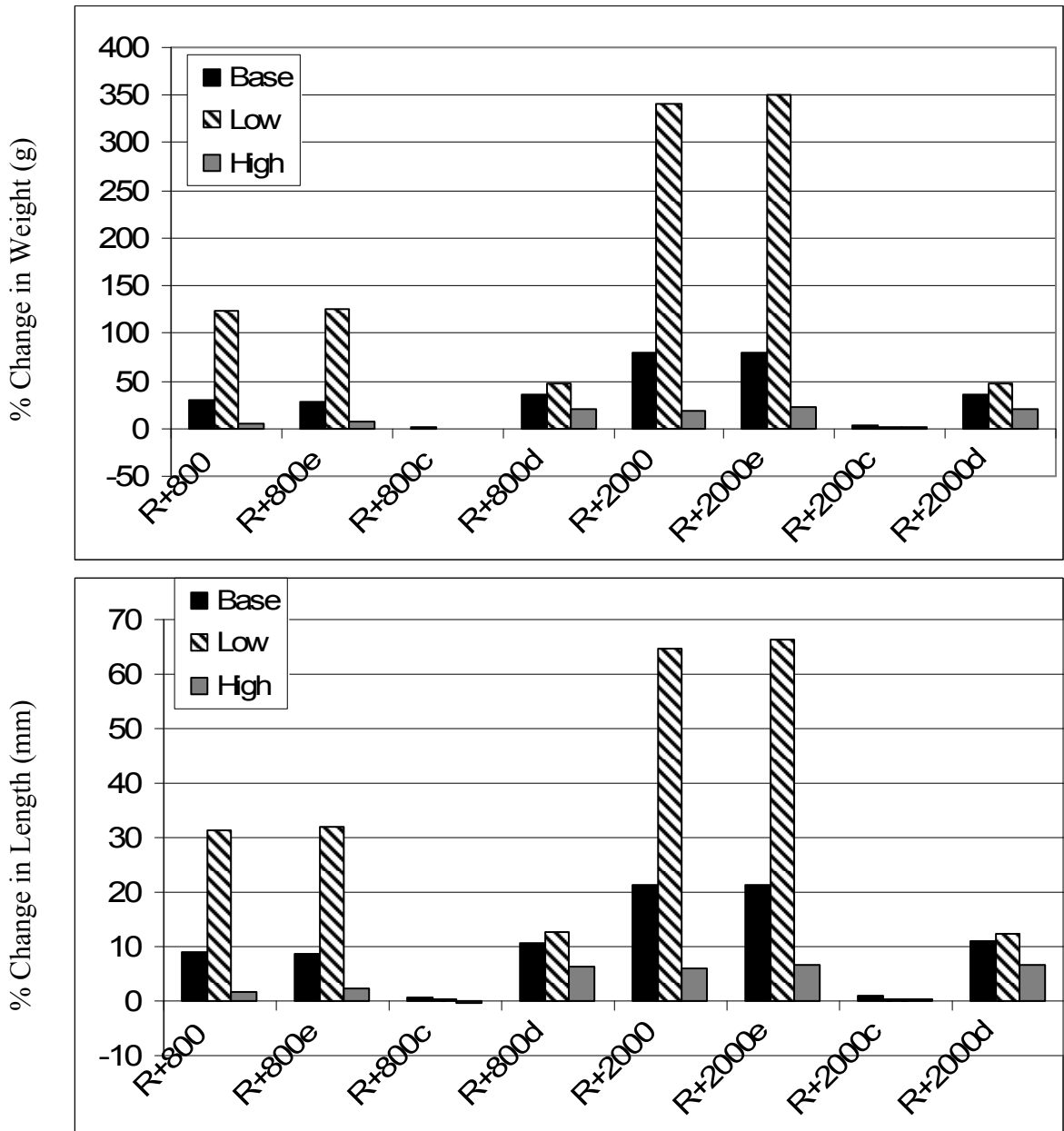


Figure 4.3. Percent change in weight and length of model YOY steelhead from no Chinook salmon spawning (R) under scenarios of varying nutrient conditions and numbers of salmon spawners. Scenarios include: 800 Chinook spawners (R+800), eggs of 800 Chinook spawners only (R+800e), carcasses of 800 Chinook spawners only (R+800c); 800 Chinook spawners with direct growth of macroinvertebrates on carcasses (R+800d), 2000 Chinook (R+2000), eggs of 2000 Chinook spawners only (R+2000e), carcasses only of 2000 Chinook spawners (R+2000c), and 2000 Chinook spawners with direct growth of macroinvertebrates on carcasses (R+2000d). Baseline are shown in solid black, low in hashed, and high in solid grey.

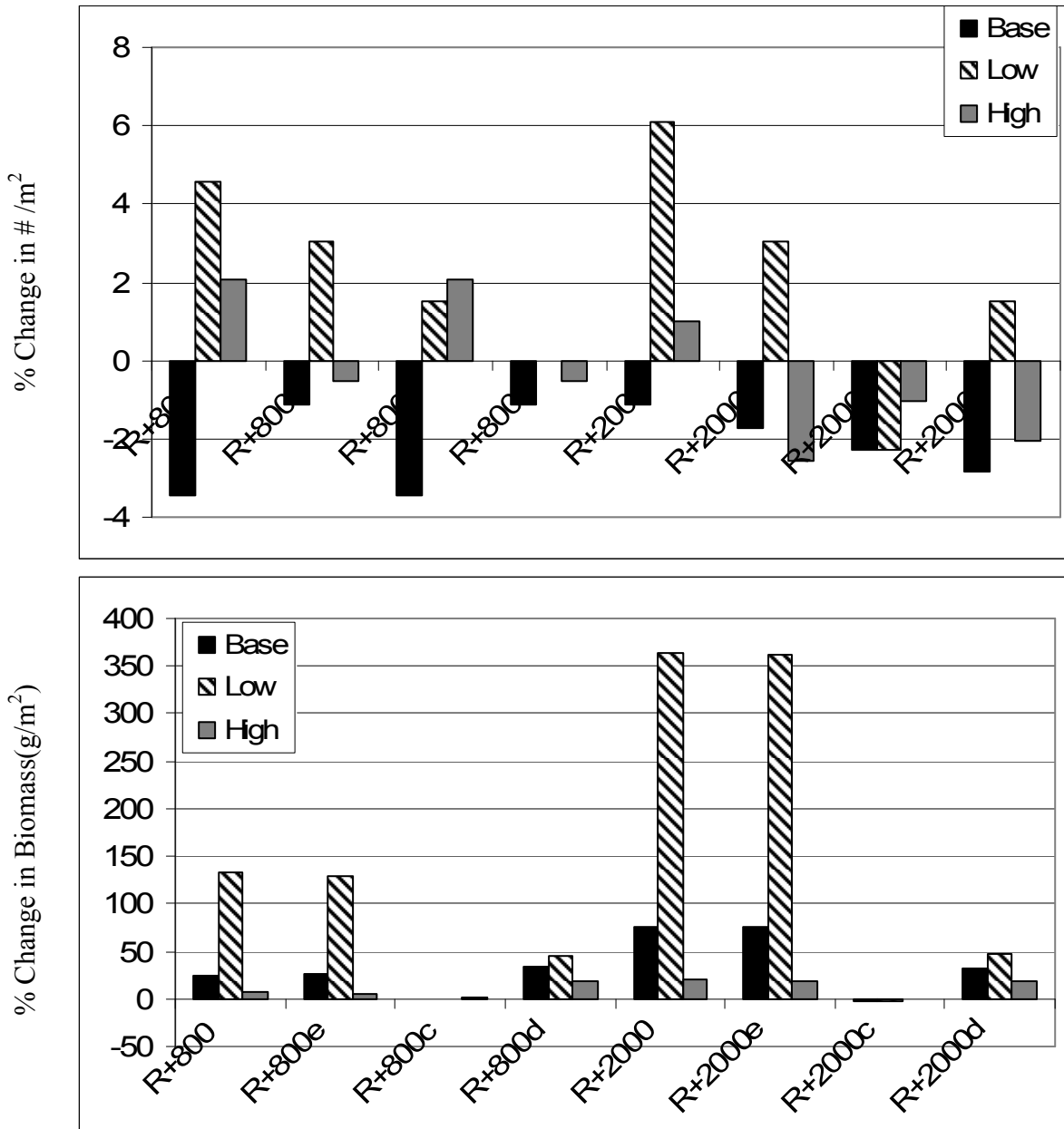


Figure 4.4. Percent change in density and biomass of model YOY steelhead from no Chinook salmon spawning (R) under scenarios of varying nutrient conditions and numbers of salmon spawners. Scenarios include: 800 Chinook spawners (R+800), eggs of 800 Chinook spawners only (R+800e), carcasses of 800 Chinook spawners only (R+800c); 800 Chinook spawners with direct growth of macroinvertebrates on carcasses (R+800d), 2000 Chinook (R+2000), eggs of 2000 Chinook spawners only (R+2000e), carcasses only of 2000 Chinook spawners (R+2000c), and 2000 Chinook spawners with direct growth of macroinvertebrates on carcasses (R+2000d). Baseline are shown in solid black, low in hashed, and high in solid grey.

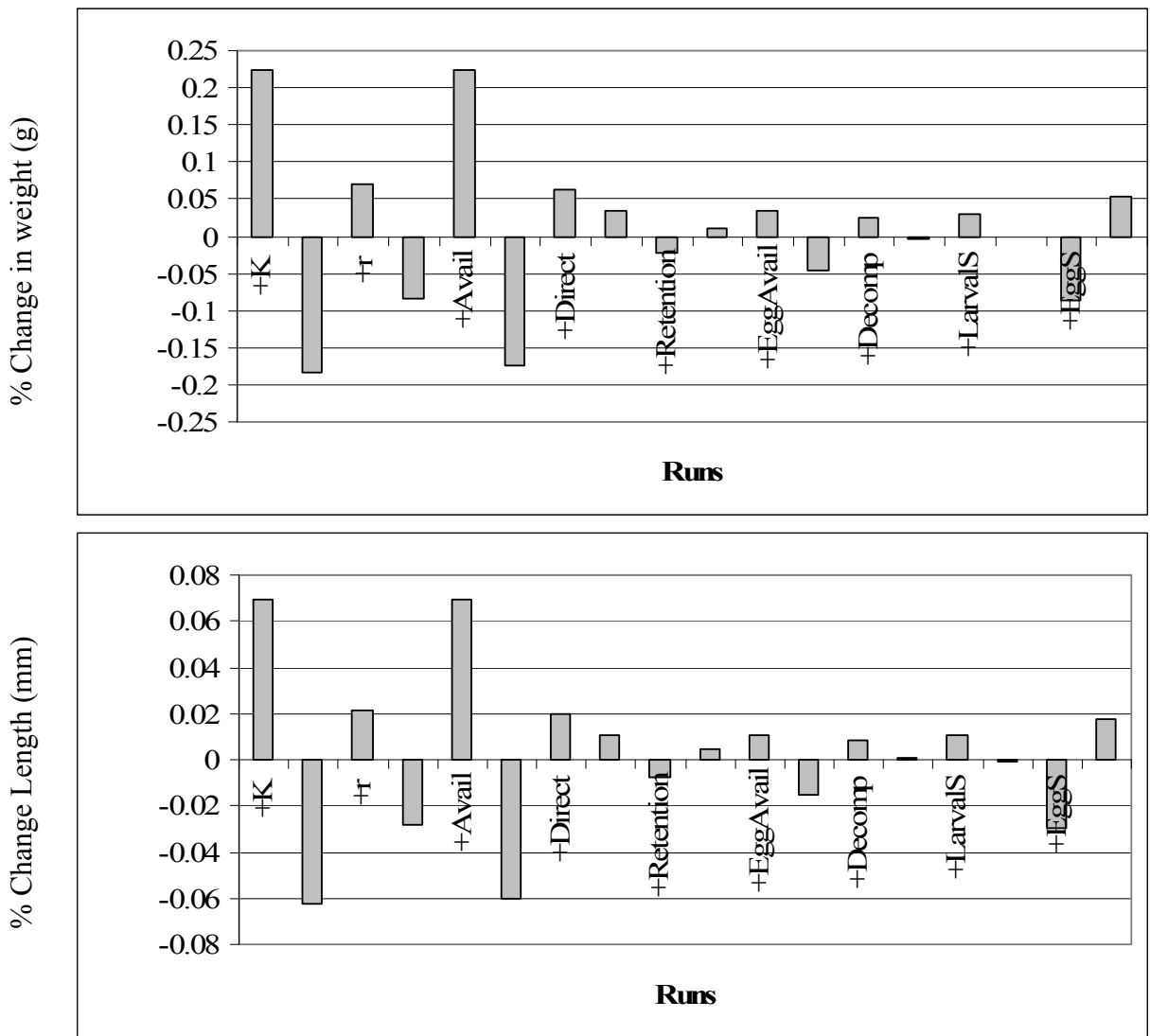


Figure 4.5. Sensitivity analysis of YOY steelhead weight and length to perturbations in model parameters. Histogram values represent percent change in weight and length of model YOY steelhead from model simulations under baseline conditions (intermediate nutrient concentrations, 800 Chinook salmon spawners) when each parameter is varied alone by  $\pm 10\%$  of the original parameter value used in the model. Parameter variables are macroinvertebrate carrying capacity (K), macroinvertebrate intrinsic rate of increase (r), % available macroinvertebrates (Avail), direct growth off of carcasses (Direct), carcass retention (retention), % eggs available (Egg Avail), decomposition rate (Decomp), daily larval survival (Larvals) and egg survival to hatch (EggS).

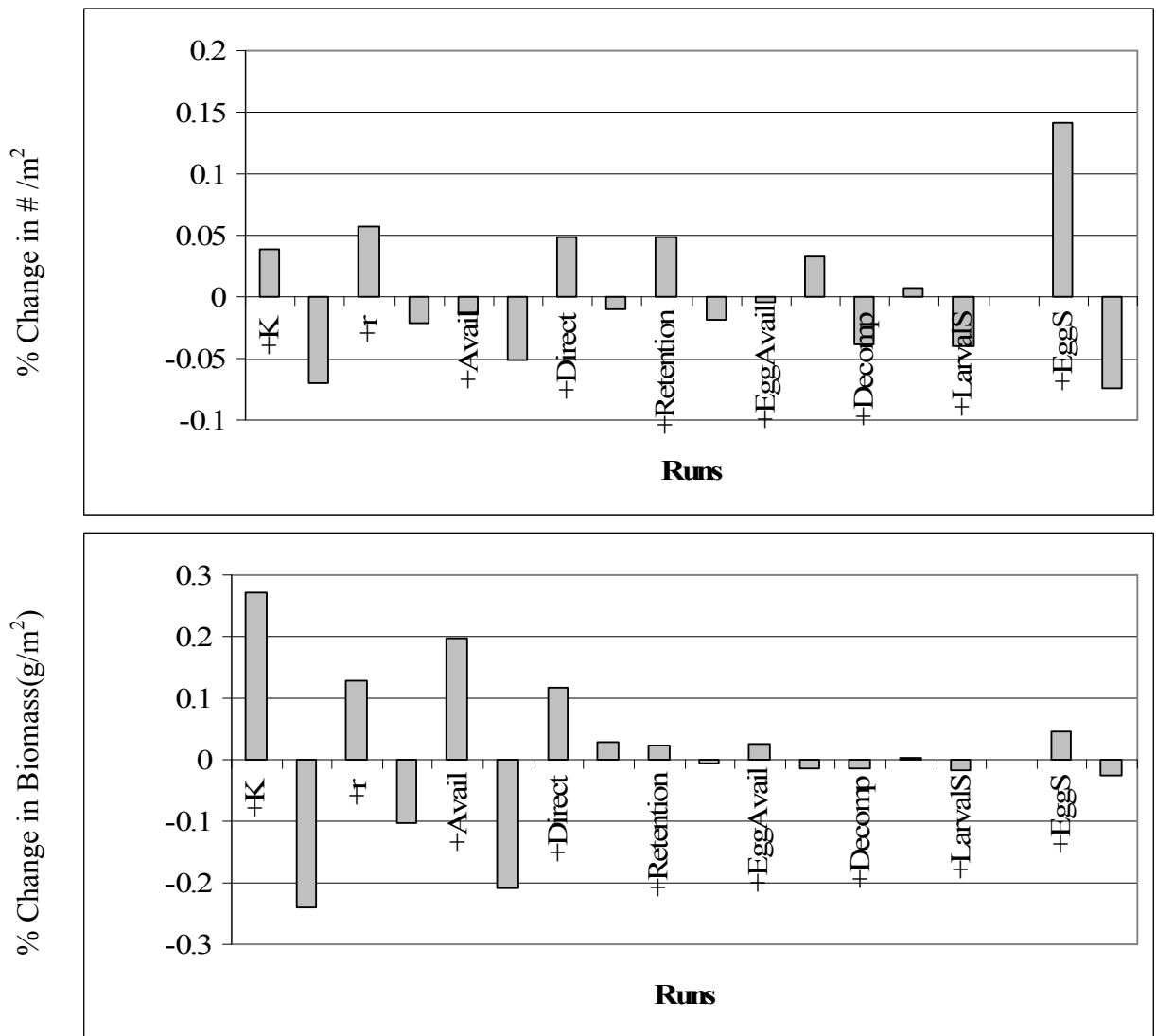


Figure 4.6. Sensitivity analysis of YOY steelhead cohort density and biomass to perturbations in model parameters. Histogram values represent percent change in density and biomass of model YOY steelhead from model simulations under baseline conditions (intermediate nutrient concentrations, 800 Chinook salmon spawners) when each parameter is varied alone by  $\pm 10\%$  of the original parameter value used in the model. Parameter variables are macroinvertebrate carrying capacity (K), macroinvertebrate intrinsic rate of increase (r), % available macroinvertebrates (Avail), direct growth off of carcasses (Direct), carcass retention (retention), % eggs available (Egg Avail), decomposition rate (Decomp), daily larval survival (LarvalS) and egg survival to hatch (EggS).



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## Conclusion

Anadromous and adfluvial fishes, such as Chinook salmon (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), walleye (*Sander vitreus*), and suckers (Catastomidae), play an important role in the transport and cycling of nutrients and energy between oceans or large lakes and the tributaries where they spawn. Migratory spawners transport nutrients and energy into streams in the forms of eggs and carcasses. Much is known about the impacts of spawning salmon in the Pacific Northwest. These fishes deposit eggs and leave behind carcasses that are critical to the growth and survival of resident fishes and juvenile salmonids. Nutrients from decomposing fishes increase water nutrient concentrations (Chaloner et al. 2004), primary productivity (Johnston et al. 2004; Wipfli et al. 2004), biofilm biomass (Bilby et al. 1996), decomposition rates of leaves and wood within streams (Chaloner et al. 2002b; Wipfli et al. 1998), and macroinvertebrate biomass (Chaloner et al. 2002a; Chaloner et al. 2002b). Increases in lower trophic levels result in increased food for young salmonids. Young salmonids in the Pacific Northwest can also consume energy-rich eggs deposited by spawning adults. Together, increases in macroinvertebrates and eggs can increase resident fish and juvenile salmonid growth (Wipfli et al. 2003) and possibly survival.

In more eutrophic systems, the impact of spawning adfluvial fishes on resident fishes likely occurs through egg deposition and not carcass decomposition. Unlike systems in the Pacific Northwest, tributaries in the Great Lakes receive spawning runs of introduced and naturalized Chinook salmon and steelhead, as well as native spawners

such as walleye and several sucker species. These native spawners dominate the biomass of spawning fishes in Great Lakes tributaries. In contrast to semelparous Pacific salmonids that have low fecundities (4-6,000 eggs/female) and bury their eggs in redds, iteroparous native adfluvial spawners are highly fecund (20-300,000 eggs/female) and broadcast their eggs over river substrates. Thus, while eggs from native spawners are not as energy rich as salmonid eggs, they are readily available to the stream community and are much more abundant.

I found that broadcast-spawning walleye in the Muskegon River, Michigan deposited eggs that experience a relatively high rate of mortality. The difference in survival rates of walleye eggs placed in covered incubators compared to eggs collected on exposed mats suggests that predation is an important source of mortality for walleye eggs. Furthermore, cold water temperatures in the Muskegon River increase incubation times of walleye eggs resulting in increased mortality of walleye eggs. Walleye spawn in a small section of the Muskegon River and over a relatively short time period in the spring. Therefore, adverse effects such as cold water temperatures or high-flow events that occur during a prolonged incubation period can impact the majority of eggs spawned. Larvae that do survive to hatch often fail to reach nursery grounds in Muskegon Lake. Poor egg survival, as well as failure of larvae to reach their rearing grounds, results in poor natural recruitment of walleye in the Muskegon River. Therefore, much of the energy walleye deposit as eggs in the Muskegon River remains there for the stream biota to consume.

Field surveys in Bigelow Creek (natural stream), a tributary of the Muskegon River where salmonids spawn naturally, revealed little impact of spawning steelhead or

Chinook salmon on stream nutrient concentrations or biota. Effects of spawning steelhead and Chinook salmon were more apparent in Middle Branch River (manipulated stream), another Muskegon River tributary where Chinook salmon carcasses and eggs were placed *in situ* to simulate spawning, and where densities of carcasses and eggs could be controlled. In the natural system in spring, nutrient concentrations increased in reaches with high steelhead spawning densities, likely a result of increased fish excretion rates caused by an increase in adult brown trout density when steelhead were present. The manipulated system had increased nutrient concentrations in reaches with added Chinook salmon carcasses and eggs compared to the control reach in the fall, although results were not consistent between years. Carcass density was greater in the manipulated system than in the natural system where spawning occurred over an extended period of time and, as a consequence, was the only stream where significant impacts of carcass introductions were observed. This may also explain why macroinvertebrate densities increased only in the manipulated system in response to carcass introductions. As such, adfluvial fishes can impact more eutrophic streams of the Great Lakes when spawner densities are high.

More than 50% of all trout in both the natural and manipulated streams consumed salmon eggs based on instantaneous gut content analysis. Fish that consumed eggs increased their energy intake compared to fish without eggs. The high consumption of salmonid eggs by trout living in streams where spawning occurs suggests that fishes in the Great Lakes tributaries are likely to benefit from deposition of eggs by spawning Chinook salmon and steelhead.

Finally, an ecosystem model was developed to determine impacts of spawning Chinook salmon on YOY steelhead among streams with different background nutrient levels, as well as determine the relative importance of the energy (egg deposition) and nutrient (carcass decomposition) pathways to growth and survival of young-of-year (YOY) steelhead. Model results show that YOY steelhead grow better in higher nutrient streams owing to the larger macroinvertebrate biomass available for consumption. Impacts of salmon carcass and egg introductions are greatest in low nutrient streams. Much of the increase in weight of model YOY steelhead at all background nutrient levels occurred through egg consumption. This result was surprising as most spawned eggs are deposited into redds and only become available to resident fishes during spillage or superimposition. The availability of spawned eggs to model YOY was therefore low. When macroinvertebrates were allowed to grow directly off carcasses in the model, the presence of carcasses increased YOY steelhead growth. More research is required to determine if the response of streams in the Pacific Northwest or Great Lakes to salmon spawning migrations occurs through a bottom-up nutrient pathway or via macroinvertebrate colonization of carcasses as suggested by the model.

Together, these results show that adfluvial fishes provide a large source of energy for the stream community in the form of spawned eggs. While the number of salmonid eggs available to the stream community is relatively small as most eggs are spawned directly into redds, the high energy content of these eggs makes them a vital source of energy for YOY steelhead heading into winter. This large input of energy is likely the reason for increased growth of juvenile salmonids in the Pacific Northwest.



In tributaries of the Great Lakes, adult Chinook salmon and steelhead are likely to impact juvenile salmonids and resident fishes in a manner similar to that of the Pacific Northwest. However, the presence of native adfluvial spawners in Great Lake tributaries, including walleye and several species of suckers, adds additional sources of energy in the form of broadcast spawned eggs. Low egg survival rates and the high fecundity of these species suggest a large energy source is added to streams during spring spawning runs. Previous sampling on the Muskegon River found walleye and sucker eggs in the diets of rainbow trout (Damon Krueger, University of Michigan, personal communication); other fishes common in the Muskegon River are known egg consumers. Future work is required to determine the importance of eggs from walleye and suckers as an energy source for stream fishes and juvenile salmonids in tributaries of the Great Lakes.

The overall impact of spawning adfluvial fishes in Great Lakes tributaries, while not as great as observed in oligotrophic streams of the Pacific Northwest, can be quite important and is highly dependent on background nutrient levels. Even in eutrophic streams, large densities of adfluvial spawners can increase nutrient concentrations and macroinvertebrate biomass due to carcass decomposition and colonization. The influence of spawning adfluvial fishes on YOY steelhead and other resident fishes is likely a result of the consumption of deposited eggs by these fishes. Native adfluvial spawners, owing to their high fecundity and broadcast-spawning behavior, contribute a large source of energy to the stream community. Removal of adfluvial spawners therefore would have detrimental effects on biota of oligotrophic Great Lakes tributaries, or in eutrophic tributaries where densities of spawners are high.

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Appendix 1. Calculations for walleye egg production and survival.

To calculate the total number of eggs produced by spawning walleye in the Muskegon River, I used previous estimates of population size (37,851 spawning fish), an estimate of the female portion of the spawning population (38%) and length-frequency data (Hanchin et al. 2007). Length-frequency data were used to estimate the number of spawning adults in each length category, and the percent of females in each category was assumed to be the average percent (38%) for the population. To determine the total number of eggs deposited by the entire population, I used size-related fecundity estimates from Eschmeyer (1948). Females less than 48.3 cm were assumed to have 91,897 eggs, females of length 58.4 cm were assumed to have a fecundity of 220,589 eggs, females less than 66 cm were assumed to have a fecundity of 264,373 eggs, and all females 66 cm or larger were assumed to have a fecundity of 366,244 eggs.

Table 1. Estimation of total egg production by walleye in the Muskegon River in 2003-2006.

cm	#/cm category	#Fish / Category for Population	#Female / Category	# eggs deposited by females
33	1	8	3	2.85E+05
35.6	7	57	22	2.00E+06
38.1	11	90	34	3.14E+06
40.6	35	286	109	9.98E+06
43.2	48	392	149	1.37E+07
45.7	46	376	143	1.31E+07
48.3	86	702	267	2.45E+07
50.8	272	2221	844	7.76E+07
53.3	512	4181	1589	1.46E+08
55.9	708	5782	2197	2.02E+08
58.4	616	5030	1912	4.22E+08
61	565	4614	1753	4.64E+08
63.5	511	4173	1586	4.19E+08
66	436	3561	1353	4.96E+08
68.6	308	2515	956	3.50E+08
71.1	243	1984	754	2.76E+08
73.7	146	1192	453	1.66E+08
76.2	69	564	214	7.84E+07
78.7	15	123	47	1.70E+07

To determine the survival of walleye eggs in the Muskegon River in 2005 and 2006 from egg mat studies, I estimated the amount of habitat available to spawning fishes in the reach of river where most spawning activity has been documented. Assuming that areas with greater than 25% gravel would be used by spawning adult walleye, I estimated from river habitat surveys by conducted by Dr. Michael Wiley, University of Michigan in 2003 and 2004 that 7,580 m<sup>2</sup> of river was available to spawning walleye. I used estimates from Hanchin et al. (2007) to obtain a mean number ( $\pm$  95% C.I.) of adult spawning females (assuming 38% were female) to provide a range in the number of spawning females (11,600, 14,383, and 17,159 females). The number of eggs produced by all females was calculated as described in Table 1. I assumed a fertilization rate of 70% (Roseman et al. 1996). I multiplied the average density of eggs on mats found during mat surveys in 2005 and 2006 by the area of river available to spawning walleye to estimate the total number of eggs in the area sampled. Based on the number of eggs deposited, and the total number of stage-2 and stage-3 eggs in 2005 and 2006 respectively, I was able to estimate survival as No. of Staged Eggs/ # Eggs fertilized.

Table 2. Estimation of walleye egg survival and production in 2005 and 2006.

Year	# Females	# Eggs Deposited	# Eggs fertilized	Ave Density (No./m <sup>2</sup> ) Staged Eggs	No. of Staged Eggs	Survival
2005	1.16E+04	2.57E+09	1.80E+09	1.45E+04	1.10E+08	0.06
2005	1.44E+04	3.18E+09	2.23E+09	1.45E+04	1.10E+08	0.05
2005	1.72E+04	3.79E+09	2.66E+09	1.45E+04	1.10E+08	0.04
2006	1.16E+04	2.57E+09	1.80E+09	7.64E+03	5.79E+07	0.03
2006	1.44E+04	3.18E+09	2.23E+09	7.64E+03	5.79E+07	0.03
2006	1.72E+04	3.79E+09	2.66E+09	7.64E+03	5.79E+07	0.02

Appendix 2. Visual Basic 2003 code for the cohort-based ecosystem model. All comments are denoted by '.

Imports System.Math

Module mdlPFBC

\*\*\*\*\*

'This module contains all of the number crunching for the PFBC model

'Version 3 calculates all pools at end, consolidates;

'All inputs are in one file (including flow, temp, nutrients) for  
'entire year

'Units for pools changed to g/m<sup>2</sup> for biotic data and g/m<sup>3</sup> for water

'chemistry data

'Version 4 attempts to put in monte carlo simulations and follow cohorts  
'rather than individuals

'Version 5 is the modifications suggested by Yi-Chung that should have been done in

Version 4

'Version 6 creates a code that will mass balance the water and nutrients

\*\*\*\*\*

'input/output files

Public input\_folder As String

Public output\_folder As String

Public output\_file As String

'pools

Private chinook As Single 'pool for spawning chinook in g/m<sup>2</sup>

Private steelhead As Single 'pool for spawning steelhead in g/m<sup>2</sup>

Private macro As Single 'pool for macroinvertebrates in g/m<sup>2</sup>

Private Cheggs As Single 'pool for eggs from chinook salmon into the redd in g/m<sup>2</sup>

Private eggs(100) As Single '#/m<sup>2</sup> of eggs steelhead in system

Private eggbiomass(100) As Single 'g/m<sup>2</sup> of eggs steelhead in system

Private chincarc As Single 'pool for chinook carcasses in g/m<sup>2</sup>

Private Npool(400), Ppool(400) As Single 'pool of N and P in water column in g/m<sup>3</sup>

Private cheggsavailable As Single 'pool of chinook eggs available to YOY g/m<sup>2</sup>

Private biomass(100) As Single 'holds value of biomass of YOY for each cohort in  
g/m<sup>2</sup>

Private Weight(100) As Single 'weight of YOY for each daily cohort in g

Private cohort(100) As Single 'holds the number of eggs deposited each day by  
spawners in #/m<sup>2</sup>

Private YOYLength(100) As Single 'ave length (mm) of each cohort of YOY

'input file variables for 1 year

Public day As Int16

Public temperature(400) As Single 'holds value of temperature input file in degrees C

Public flowIn(400) As Single 'holds value of flow in cms

Public NconAve As Single 'holds average load value of nitrogen concentration in mg/l

Public PconAve As Single 'holds average load value of phosphorous concentration in mg/l

'fluxes

Private NCDe As Single 'flux of N from chinook to water column  $g/m^2/d$

Private PCDe As Single 'flux from chinook to water column  $g/m^2/d$

Private GramGrowth(100) As Single 'flux from invert and eggs to YOY  $g/m^2/d$

Private macroloss As Single 'loss of macros to fish in  $g/m^2/d$

Private eggloss As Single 'loss of eggs to fish in  $g/m^2/d$

'Z (mort) from Godby et al. 2007 averages .011 for Jul-Oct or Aug-Oct and 0.012 for Oct-Mar

Private StDec As Single ' decomposition steelhead carcasses  $g/m^2/d$

Private ChDec As Single 'decomposition of chinook carcasses in  $g/m^2/d$

Private EggsChSpawn As Single 'total weight of eggs from Chinook in  $g/m^2/d$

Private Carcflux As Single 'total carcass weight in  $g/m^2/d$

Private YOYhatch(100) As Single '#/m<sup>2</sup>/d off steelhead eggs to larvae

Private eggslarvaelost As Single ' $g/m^2/d$  of eggs lost to larvae

Private yoyloss(100) As Single '#/m<sup>2</sup>/d of YOY dying of natural causes

Private eggStGram As Single ' $g/m^2/d$  of eggs spawned by steelhead

Private ChinSpawn As Single ' $g/m^2/d$  of adult Chinook spawners entering system

Private yoylarvaeloss(100) As Single '#/m<sup>2</sup>/d of larvae die during yolksac development

Private macrolsostotal As Single 'adds up all the invertebrates consumed in  $g/m^2$

Private egglosstotal As Single

Private macroavailable As Single ' $g/m^2$  of macro community available to the YOY for consumption

Private macrorefuge As Single 'limits the amount of macros the YOY can consume

Private Nload(400) As Single ' value of nitrogen in the system in mg/d

Private Pload(400) As Single ' value of phosphorus in the system in mg/d

Private NconPool(400) As Single ' conc of N in the pool  $g/m^3$

Private Pconpool(400) As Single ' conc of P in the pool  $g/m^3$

Private NloadRemoved(400) As Single ' value of nitrogen removed from the system in mg/d

Private PloadRemoved(400) As Single ' value of phosphorus removed from the system in mg/d

Private PoolVol(400) As Single 'storage of the reach in  $m^3$

Private DepthChange(400) As Single 'tracks the change in depth in m

Private OldPoolVol As Single 'holds the previous day's pool vol to be used in the vol change calc

'check on massbalance of nutrients and water

Private MassNLoadCheck As Single 'checks to verify that nitrogen in the system is mass balanced

Private MassPLoadCheck As Single 'checks to verify that phosphorus in the system is mass balanced

'values need for model

Private mortSt As Single 'percent of spawners that die

Private steelmort As Single 'number of steelhead mortis, used for calculating remaining steelhead adults

Private steelweight As Single 'g of adult to spawn on one day

Private NitroFish(400) As Single 'converts NCDe from  $g/m^2$  to  $g/m^3$

Private PhosFish(400) As Single 'converts PCDe from  $g/m^2$  to  $g/m^3$

Private eggshavail As Single

Private r As Single 'value for intrinsic rate of increase for macro pop

Private iday As Short 'indices for daily and monthly loops

Private imonte As Short 'loop for multiple model runs

Private p As Single 'proportion of food entering bioenergetics equations

Private Nfish, Pfish, Cfish As Single 'N, P, and Cal in a typical fish as a percent of body weight (g)

Private Kdecom 'decomposition rate of carcasses

Private WeggS As Single 'average weight of a steelhead egg in g

Private macrogrowth As Single 'growth rate of the macroinvertebrates

Private PED As Single 'energy density of prey in joules/g

Public area As Short 'area of river in  $m^2$

Public depth(400) As Single 'in m

Private Growth As Single 'Growth in j/d

Private FED As Single 'steelhead energy density j/g

Private Consump As Single 'consumption in g/d

Private textmonth As String 'holds the value of the number of days in a month

Private Nwater As Single 'initial values of N in the water column in  $g/m^2$  but final values are multiplied by area and so are in g

Private Pwater As Single 'initial values of P in the water column in  $g/m^2$  but final values are multiplied by area and so are in g

Public spawnday As Int16 'Yi-Chung: holds the number of days for spawning

Private ATU(100) As Single 'holds the number of degree days for each cohort

Private icohort As Int16 'holds the value for the cohort to cycle through for loop

Private eggstoredd As Single

Private Lcheck(100) As Single 'holds value of length of YOY in mm which is only used if  $weight(today) > weight(previous)$

Private VolChange(400) As Single 'holds value of the storage change for the reach in question in  $m^3$

Private FlowOut(400) As Single 'hold value of the amount of water removed from the reach in  $m^3$

Private masswatercheck(400) As Single 'checks to determine if the water is mass balanced; should be zero

Private Nout(400) As Single 'concentration of the outflowing water N in  $ug/l$

Private Pout(400) As Single 'concentration of the outflowing water P in  $ug/l$

```

'Public variables from form
Public ParaName(100) As String 'parameter names from bioenergetics input file
Public ParaValue(100) As Single 'parameter values from bioenergetics input file
Public Stpop As Single 'number of female steelhead spawners
Public Chpop As Single 'number of female chinook spawners
Public PrintMoFlag As Boolean ' if true then print monthly
Public PrintDayFlag As Boolean 'if true then print daily

'variables within the input file of bioenergetics
Private CA As Single 'intercept of the allometric growth function
Private CB As Single 'slope of the allometric growth function
Private CTL, CTM, CK4, CK1, CQ, CTO As Single 'parameters relating growth to
temperature
Private RA As Single 'intercept of the allometric mass function (g/g/d)
Private RB As Single 'slope of mass function
Private RQ, RTO, RTM, RTL, RK1 As Single 'parameters relating respiration to
temperature
Private ACT, SDA As Single 'parameters relating to and specific dynamic action
Private FA, FB, FG As Single 'parameters relating to egestion
Private UA, UB, UG As Single 'parameters relating to excretion

Private stpopstart As Single 'holds the user inputed stpop start value
Private chpopstart As Single 'holds the user inputed stpop start value
Private areastart As Single 'holds the user inputed area start value
Private ChPopDay As Single 'number of chinook spawning on one day

Private NpoolPrevious As Single ' holds the prevoius day's Npool
Private PpoolPrevious As Single ' holds the previous day's Ppool
Private NloadAve As Single 'average Nitrogen load parameter for N pool
Private PloadAve As Single 'average phosphorus load parameter for P pool
Dim k As Single 'holds value of carrying capacity of invertis in g/m^2

'from my data for BCC ave is .664g/m^2 and max was 14.94 g/m^2: May not be
representative of what is really available
Private a, b As Single 'params needed for holling's type II response
Private cegg, degg As Single 'params for hollings type II for eggs
Private check As Single ' checks on the availability of eggs being high enough
Private dayconsump(100) As Single ' dummy variable that holds if the cohort
consumed eggs or not; 1 means cannot eat eggs the next day

```

```
Public Sub MonteCarlo()
```

```
*****
```

```
output_file = output_folder & "\model_output.txt"
```



```

'open output file
FileOpen(3, output_file, OpenMode.Output)
StpopStart = Stpop
ChpopStart = Chpop
areaStart = area
For imonte = 1 To 1

    'resetting all pools to zero before the start of the next monte run
    Stpop = stpopstart
    Chpop = chpopstart
    areastart = area
    Cheggs = 0
    cheggsavailable = 0
    chinook = 0
    chincarc = 0
    System.Array.Clear(Npool, 0, Npool.Length)
    System.Array.Clear(Ppool, 0, Ppool.Length)
    System.Array.Clear(NconPool, 0, NconPool.Length)
    System.Array.Clear(Pconpool, 0, Pconpool.Length)
    System.Array.Clear(PoolVol, 0, PoolVol.Length)
    System.Array.Clear(depth, 0, depth.Length)
    System.Array.Clear(NitroFish, 0, NitroFish.Length)
    System.Array.Clear(PhosFish, 0, PhosFish.Length)
    System.Array.Clear(DepthChange, 0, DepthChange.Length)
    System.Array.Clear(VolChange, 0, VolChange.Length)
    System.Array.Clear(cohort, 0, cohort.Length)
    System.Array.Clear(Weight, 0, Weight.Length)
    System.Array.Clear(eggs, 0, eggs.Length)
    System.Array.Clear(eggbiomass, 0, eggbiomass.Length)
    System.Array.Clear(biomass, 0, biomass.Length)
    System.Array.Clear(YOYhatch, 0, YOYhatch.Length)
    System.Array.Clear(yoylarvaeLoss, 0, yoylarvaeLoss.Length)
    System.Array.Clear(yoyloss, 0, yoyloss.Length)
    System.Array.Clear(GramGrowth, 0, GramGrowth.Length)
    System.Array.Clear(ATU, 0, ATU.Length)
    System.Array.Clear(YOYLength, 0, YOYLength.Length)
    System.Array.Clear(Nload, 0, Nload.Length)
    System.Array.Clear(Pload, 0, Pload.Length)
    System.Array.Clear(FlowOut, 0, FlowOut.Length)
    System.Array.Clear(Nout, 0, Nout.Length)
    System.Array.Clear(Pout, 0, Pout.Length)
    System.Array.Clear(masswatercheck, 0, masswatercheck.Length)

    ' Call RunInitial()
    Call PFBCCalcsMain()
Next

```

```

MsgBox("PFBC is finished. Congratulations.")
FileClose(3)
End Sub
Private Sub PFBCCalcsMain()
*****
'This subroutine does all the main calculations
*****
'Call Initial () 'initializes the variables for each run simulation
'monte carlo simulation
'For imonte = 1 To 100

For iday = 80 To 365
  If iday = 80 Then
    Call RunInitial()
  End If

  Call DayInitial()
  If (Stpop > 0) Then
    spawnDay = spawnDay + 1 'YiChung- updates spawnDay to determine the
number of days fish spawn over
    Call SteelheadSpawners()
  End If

  If (iday >= 260) And (Chpop > 0) Then

    Call ChinookSpawners()
  End If

  Call decomposition()
  Call Waternutrients()

'this goes away when the cohort loop is over
Dim x As Int16 'the number of temperature units required for a steelhead egg to
hatch
Dim y As Int16 'the number of temperature units required for a larvae to begin
feeding
x = 310 'degree days in C needed to hatch from Fritz Kraus Special Pub #99-2 in
AK
y = 500 'degree days in C needed to emerge from gravel: same source as x

For icohort = 1 To spawnDay

  If (ATU(icohort) >= x) And (cohort(icohort) = 0) Then
    Call Hatch()
  End If
  If (ATU(icohort) >= x) And (ATU(icohort) < y) Then

```

```

    Call YolkSac()
  End If
  If (ATU(icohort) >= y) Then
    Call Trophics()
    Call Bioenergetics()
    Call Popgrowth()
  End If
  Call Pools()
  Call PrintOut()
Next 'YC
Call MacroPop()
Next

```

End Sub

Private Sub RunInitial()

```

*****

```

```

'This subroutine initializes all variables and parameters for each model run

```

```

*****

```

```

chinook = 0 'in g/^2m
steelhead = 0 'in g/m^2
ChPopDay = Chpop / 50
Cheggs = 0 'g/m^2
chincarc = 0 'in g/m^2
NloadAve = 1900 'g/d
PloadAve = 850 'g/d
k = 78 ' 53 low, 78, 115 g/m^2
macro = 0.5 * k ' g/m^2
PconAve = PloadAve / (flowIn(iday) * 86400)
NconAve = NloadAve / (flowIn(iday) * 86400)
spawnday = 0 ' Yi-Chung

```

```

'Depth calcs

```

```

b = 1.1 'slope at origin macros
a = 0.125 'max macros
cegg = 100 'slope at origin egg
degg = 1 'max egg
Dim c As Short 'constant for the depth equation
Dim d As Short 'constant for the depth equation
Dim drainage As Short 'drainage area of bigelow creek km^2
c = 0.125
d = 0.202
drainage = 84.8 'km^2

```

'area definetly changes as a function of depth but assumed it is constant in this model run

'outflow is adjusted to make the water massbalance

```

    depth(iday) = Exp(-1.446) * Math.Pow(drainage, c) * Math.Pow(flowIn(iday), d)
'depth in m
    OldPoolVol = area * depth(iday) 'in m^3
    Npool(iday) = NconAve * OldPoolVol
    Ppool(iday) = PconAve * OldPoolVol
    NpoolPrevious = NconAve * OldPoolVol
    PpoolPrevious = PconAve * OldPoolVol
    *****
'Initialize bioenergetic input
    CA = ParaValue(1)
    CB = ParaValue(2)
    CQ = ParaValue(3)
    CTO = ParaValue(4)
    CTM = ParaValue(5)
    CTL = ParaValue(6)
    CK1 = ParaValue(7)
    CK4 = ParaValue(8)
    RA = ParaValue(9)
    RB = ParaValue(10)
    RQ = ParaValue(11)
    RTO = ParaValue(12)
    RTM = ParaValue(13)
    RTL = ParaValue(14)
    RK1 = ParaValue(15)
    ACT = ParaValue(16)
    SDA = ParaValue(17)
    FA = ParaValue(18)
    FB = ParaValue(19)
    FG = ParaValue(20)
    UA = ParaValue(21)
    UB = ParaValue(22)
    UG = ParaValue(23)

    *****
'initialize nutrient and weight values in fish

    Nfish = 0.0253 'percent of body weight
    Pfish = 0.005 'percent of body weight

End Sub
Private Sub DayInitial()
    *****
'initilize all fluxes to zero
'all fluxes are in g/m^2/d except for nutrients which are g/m^3/d

```

```

*****
ChDec = 0 'g/m^2/d
StDec = 0 'g/m^2/d
NCDe = 0 'g/m^2/d
PCDe = 0 'g/m^2/d
GramGrowth(icohort) = 0 'g/m^2/d
eggStGram = 0 'g/m^2/d
eggslarraelost = 0 'g/m^2/d
eggloss = 0 'g/m^2/d
eggstoredd = 0
ChinSpawn = 0 'g/m^2/d
Carcflux = 0 'g/m^2/d
macrogrowth = 0 'g/m^2/d
macroloss = 0 'g/m^2/d
yoyloss(icohort) = 0 '#/m^2/d
YOYhatch(icohort) = 0 '#/m^2/d
yoylarraeloss(icohort) = 0 '#/m^2/d
NitroFish(icohort) = 0 'g/m^3/d
PhosFish(icohort) = 0 'g/m^3/d
steelweight = 0 'g/m^2/d
steelmort = 0 'g/m^2/d
EggsChSpawn = 0 'g/m^2/d
eggshavail = 0 'g/m^2/d
macrolosstotal = 0 'g/m^2/d loss of inverts due to consumption by all cohorts
egglosstotal = 0 'g/m^2/d
End Sub
Private Sub SteelheadSpawners()
*****
    'This subroutine brings in steelhead to spawn and a proportion of these die and
decompose in the river
*****
    Dim StFec As Single 'approximates the eggs/females
    Dim a, b As Single ' parameters needed for fecundity regression

*****
    'calculating the average fecundity /female
    a = 1260
    b = 14.1

    'variables for random lengths for steelhead
    Dim Fweight(Stpop) As Single 'array with the number of fish
    Dim MFweight, SDFweight As Single 'fish weight and mean and standard deviation
    Dim ifish As Int16 'fish loop counter
    Dim v1, v2, vw As Single 'variables required for normal distribution algorithm
    Dim GasDev As Single ' variable to hold for the normal distribution
    Dim StPopDay As Single 'number of females spawners on one day

```

Dim totstegg As Single 'holds number of eggs for one day for all female spawners on that day

totstegg = 0 'resets totstegg to zero before next group of spawners enters

MFweight = 2.56 'mean weight in kg

SDFweight = 0.5

StPopDay = 5 'number of female spawners on one day; until get the random number generator working, will be

'set at 5

Randomize()

'For loop to randomly assign weight and fecundity to all female steelhead in the system

For ifish = 1 To StPopDay

'start of the algorithm to convert uniform distribution to normal

vw = 1

Do Until vw < 1

v1 = 2 \* Rnd() - 1

v2 = 2 \* Rnd() - 1

vw = v1 ^ 2 + v2 ^ 2

Loop

GasDev = v1 \* Sqrt(-2 \* Log(vw) / vw)

'end of the algorithm to convert uniform to normal dist

'the next line converts to the mean and stdev I want

Fweight(ifish) = MFweight + (SDFweight \* GasDev)

StFec = a \* Fweight(ifish) + b 'average number of eggs per female

totstegg = totstegg + StFec 'total number of eggs spawned by all females spawning on one day

Next

eggs(spawnday) = totstegg / area 'YC: populates cohort matrix with eggs from stfec #/m<sup>2</sup>

Stpop = Stpop - StPopDay 'lose spawners each day till none left, and the spawning is over

End Sub

Private Sub ChinookSpawners()

\*\*\*\*\*

'This subroutine brings in chinook to spawn and a proportion of these die and decompose in the river

\*\*\*\*\*

```

Dim Chfec As Single 'approximates the eggs/females
Dim WeggC As Single 'average weight of a chinook egg in g
Dim TotEggCh As Single 'number of eggs for entire pop
Dim Chweight(5000) As Single 'average weight of spawning female in kg

Dim mortch As Int16 'mortality rate of Chinook salmon
Dim totweight As Single 'holds value for weight of all fish spawned on one day
*****
'calculating the average number of eggs per female

'Chweight = 4.5 'kg

WeggC = 0.15 'g
mortch = 1

TotEggCh = 0
totweight = 0 'resets totstegg to zero before next group of spawners enters
Dim MFlength As Single
Dim sdflength As Single
Dim Flength(Chpop) As Single
MFlength = 828 'mean weight in cm
sdflength = 50
Dim a, b, c, d As Single ' a and b are params for length-weight regression from
Muskegon 2004 data
'c and d are from Damon for length-fecundity estimates
a = 0.000006
b = 3.0555
c = 0.00195
d = 2.234
'number of chinook spawning on one day

Dim V1, V2, Vw As Single
Dim GasDev As Single
Dim ifish As Int16
For ifish = 1 To ChPopDay
  Randomize()
  Vw = 1
  Do Until Vw < 1
    V1 = 2 * Rnd() - 1
    V2 = 2 * Rnd() - 1
    Vw = V1 ^ 2 + V2 ^ 2
  Loop
  GasDev = V1 * Sqrt(-2 * Log(Vw) / Vw)
  Flength(ifish) = MFlength + (sdflength * GasDev)
  Chweight(ifish) = a * Flength(ifish) ^ b
  Chfec = c * Flength(ifish) ^ d 'average number of eggs per female

```

```

    totweight = totweight + Chweight(ifish)
    TotEggCh = TotEggCh + Chfec 'total number of eggs spawned by all females
    spawning on one day
    Next
    EggsChSpawn = (TotEggCh * WeggC) / area 'total weight of eggs in g/m^2/d
    eggstoredd = 0.995 * EggsChSpawn
    eggshavail = 0.005 * EggsChSpawn
    ChinSpawn = totweight / area 'g/m^2/d of adult Chinook spawners
    Carcflux = ChinSpawn * mortch * 2 * 0.75 'g/m^2/d of chinook carcasses assumes
50:50 sex ratio
    'and 25% retention
    Chpop = Chpop - ChPopDay

End Sub
Private Sub Trophics()
    *****
    'This subroutine allows YOY to eat with a Holling's type II functional response
    *****
    ,
    'PED = 3363.72 'joules/g based on average diet of YOY in Bigelow Creek (Godby et
al 2007) and values
    'from Dieterman et al. 2004 and Gende et al.
    macrorefuge = 0.2 * k
    macroavailable = 0.1 * Max(0, (macro - macrorefuge)) 'g macro available for YOY
community Tyler and Rutherford
    check = 0
    Dim x As Single 'random number for eating eggs

    If (iday >= 260) And (cheggsavailable > 0) And (dayconsump(icohort) = 0) Then
        x = Rnd()
        If x < 0.3 Then
            PED = 9250 * 0.9 + 0.1 * 3362.5
            p = ((cegg * cheggsavailable) / (1 + degg * cegg * cheggsavailable)) * 0.9 + ((a
* macroavailable) / (1 + b * a * macroavailable)) * 0.1
            p = Min(1, p)
            If p < 0.1 Then
                PED = 3362.5
                p = ((a * macroavailable) / (1 + b * a * macroavailable))
                check = 1
            End If
        Else
            PED = 3362.5
            p = ((a * macroavailable) / (1 + b * a * macroavailable))
            check = 1
        End If
    End If

```



```

Else

    'joules/g based on average diet of YOY in Bigelow Creek (Godby et al 2007) and
values
    'from Dieterman et al. 2004 and Gende et al.

    PED = 3362.72
    p = ((a * macroavailable) / (1 + b * a * macroavailable))
    p = Min(1, p)

End If

End Sub

Private Sub Bioenergetics()
    *****
    ' Grows the average YOY steelhead on a daily timestep
    *****

    *****

    'consumption equations
    Dim Cmax As Single ' value for maximum consumption
    Dim G2, G1, L1, L2, KA, KB As Single ' holding variables to make consumption
equations easier
    Dim fT As Single 'consumption as a function of temperature
    Dim HoldWeight As Single 'holds value of weight for each cohort so that operations
are still allowed
    HoldWeight = Weight(icohort)
    Dim Econsump 'prey consumed in j/d

    Cmax = CA * HoldWeight ^ (CB) 'Determine maximum consumption g/d
    G2 = (1 / (CTL - CTM)) * Log((0.98 * (1 - CK4)) / (CK4 * 0.02))
    L2 = Exp(G2 * (CTL - temperature(iday)))
    KB = (CK4 * L2) / ((1 + CK4 * (L2 - 1)))
    G1 = (1 / (CTO - CQ)) * Log((0.98 * (1 - CK1)) / (CK1 * 0.02))
    L1 = Exp(G1 * (temperature(iday) - CQ))
    KA = (CK1 * L1) / (1 + CK1 * (L1 - 1))
    fT = KA * KB

    Dim percentdiet As Single
    percentdiet = 0.9
    Consump = Cmax * p * fT * HoldWeight 'g/d
    If (iday >= 260) And (cheggsavailable > 0) And (check = 0) And
(dayconsump(icohort) = 0) Then
        eggloss = Consump * cohort(icohort) * percentdiet
        macroloss = Consump * cohort(icohort) * (1 - percentdiet)
        While (eggloss + egglosstotal >= cheggsavailable) And (percentdiet > 0)

```

```

percentdiet = percentdiet - 0.1
p = (((cegg * cheggsavailable) / (1 + degg * cegg * cheggsavailable)) *
percentdiet) + (((a * macroavailable) / (1 + b * a * macroavailable) * (1 - percentdiet))))
p = Min(1, p)
PED = 9250 * percentdiet + (3362.5 * (1 - percentdiet))
Consump = Cmax * p * fT * HoldWeight
macroloss = Consump * (1 - percentdiet) * cohort(icohort)
eggloss = Consump * percentdiet * cohort(icohort)
End While
dayconsump(icohort) = 1

```

```

If p <= 0.1 Then
  PED = 3362.5
  p = (a * macroavailable) / (1 + b * a * macroavailable)
  macroloss = Consump * cohort(icohort)
  eggloss = 0
  dayconsump(icohort) = 0
End If
Else
  macroloss = Consump * cohort(icohort)
  dayconsump(icohort) = 0
End If

```

```
Econsump = Consump * PED 'j/d
```

```
*****
```

```
'respiration equations
```

```
Dim Y, Z, X, V As Single 'holding variables to make respiration equations easier to handle
```

```
Dim Activity As Single 'activity value for fish in cm/s
```

```
Dim fTresp As Single 'respiration as a function of temperature
```

```
Dim Resp As Single 'respiration in g/g/d
```

```
Dim S As Single 'portion of assimilated energy lost to SDA
```

```
Dim Conv As Single = 13608 'oxicalorific conversion factor J/gO2 from Dr. Jim
```

```
Breck
```

```
Y = Log(RQ) * (RTM - RTO + 2)
```

```
Z = Log(RQ) * (RTM - RTO)
```

```
X = (Z ^ 2 * (1 + (1 + 40 / Y) ^ 0.5) ^ 2) / 400
```

```
V = (RTM - temperature(iday)) / (RTM - RTO)
```

```
Activity = 5.328 * HoldWeight ^ 0.485 'from Rand et al. 1993
```

```
fTresp = V ^ X * Exp(X * (1 - V))
```

```
Resp = RA * HoldWeight ^ (RB) * fTresp * Conv * ACT * HoldWeight 'j/d
```

```
*****
```

```
'waste losses
Dim eges, excr ' hold values for egestion and excretion in g/d
```

```
eges = FA * temperature(iday) ^ FB * Exp(FG * p) * Econsump 'g/d
excr = UA * temperature(iday) ^ UB * Exp(UG * p) * (Econsump - eges) 'g/d
```

```
S = SDA * (Econsump - eges) 'g/d
```

```
'If (temperature(iday) <= 4) Then
'Resp = 0.7 * Resp
'End If
```

```
*****
```

```
'Growth of YOY steelhead is therefore equal to the following
```

```
Growth = Econsump - Resp - excr - eges - S 'j/d
```

```
End Sub
```

```
Private Sub PrintOut()
```

```
*****
```

```
'This subroutine prints results to an ASCII text file at the end of the year
```

```
*****
```

```
If (iday = 80 And imonte = 1) Then
```

```
'print header
PrintLine(3, "Daily output file for the PFBC model")
PrintLine(3)
PrintLine(3, "Pools are in g/m^2; fluxes are in g/m^2/d")
PrintLine(3)
```

```
PrintLine(3, " Run, Day, cohort no., double time, YOY weight, YOYcohort,
YOYbiomass, YOYLength, macros,p,cheogs, Nitrogen, Phosphorous, Npool, Ppool")
```

```
End If
```

```
'doubling time of inverts for exponential growth is .693/r
```

```
PrintLine(3, _
Format(imonte, "###"), _
",", Format(iday, "###"), _
",", Format(icohort, "###"), _
",", Format(0.693 / r, "##.#####;\0.00\"), _
",", Format(Weight(icohort), "##.#####;\0.00\"), _
",", Format(cohort(icohort), "##.#####;\0.00\"), _
",", Format(biomass(icohort), "##.#####;\0.00\"), _
",", Format(YOYLength(icohort), "##.#####;\0.00\"), _
",", Format(macro, "#.###"), _
",", Format(p, "#.#####"), _
",", Format(cheogsavailable, "#.#####"), _
```

```

",", Format(NconPool(iday), "#.#####"), _
",", Format(Pconpool(iday), "#.#####"), _
",", Format(Npool(iday), "#.#####"), _
",", Format(Ppool(iday), "#.#####")

```

End Sub

Private Sub Waternutrients()

```

*****

```

```

'converts input file nutrient data into grams

```

```

*****

```

```

'constants are from Su-Ting from the Muskegon River Hydraulic Geometry data for
the entire

```

```

'Muskegon watershed; for flow data from cms

```

```

Dim a As Short 'constant for the depth equation

```

```

Dim b As Short 'constant for the depth equation

```

```

Dim drainage As Short 'drainage area of bigelow creek km^2

```

```

a = 0.125

```

```

b = 0.202

```

```

drainage = 84.8 'km^2

```

```

'area definetly changes as a function of depth but assumed it is constant in this
model run

```

```

'outflow is adjusted to make the water massbalance

```

```

Nload(iday) = NloadAve

```

```

Pload(iday) = PloadAve

```

```

depth(iday) = Exp(-1.446) * Math.Pow(drainage, a) * Math.Pow(flowIn(iday), b)

```

```

'depth in m

```

```

PoolVol(iday) = area * depth(iday) 'pool volume for the day in m^3

```

```

VolChange(iday) = PoolVol(iday) - OldPoolVol 'volume of water lost or gained
from previous day

```

```

DepthChange(iday) = VolChange(iday) / area 'New Depth m

```

```

FlowOut(iday) = (flowIn(iday) * 86400 - VolChange(iday)) / 86400 'outflow of
water in m^3/s

```

```

NconPool(iday) = (NpoolPrevious + Nload(iday) + NitroFish(iday)) / (OldPoolVol
+ flowIn(iday) * 86400) 'g/m^3 in the pool

```

```

Pconpool(iday) = (PpoolPrevious + Pload(iday) + PhosFish(iday)) / (OldPoolVol +
flowIn(iday) * 86400) 'g/m^3 in the pool

```

```

Nout(iday) = FlowOut(iday) * 86400 * NconPool(iday) 'g/d N

```

```

Pout(iday) = FlowOut(iday) * 86400 * Pconpool(iday) 'g/d P

```

End Sub

Private Sub Hatch()

```

*****

```

```

'hatches the steelhead into YOY steelhead
*****
Dim esurv As Single 'mortality rate of steelhead eggs

esurv = 0.2637 'from Quinn
YOYhatch(icohort) = eggs(icohort) * esurv * 0.8 'total number of steelhead
larvae/m^2/d; 0.8 represents some
'not entering the redd

End Sub
Private Sub decomposition()
*****
'decomposing carcasses add to nutrient levels
*****

Kdecom = 0.061 'Parmenter and Lamarra 1991

If (chincarc > 0) Then
  ChDec = chincarc * (1 - Exp(-Kdecom)) 'g/m^2/d
  NCDe = ChDec * Nfish 'g/m^2/d
  PCDe = ChDec * Pfish 'g/m^2/d
End If

NitroFish(iday) = NCDe * area 'g/d; converting NCDe from g/m^2 to g/d
PhosFish(iday) = PCDe * area 'g/d; converting PCDe from g/m^2 to g/d

End Sub
Private Sub MacroPop()
*****
'This subroutine allows macroinverts to grow
'Eventually this subroutine will involve the mircobiota but,
'for now, microbiota are commented out
*****

Dim scalar As Single 'adjusts the r value based on phos, nitro and temp levels from
Mike Wiley
r = 0.0075 'max value from watanabe et al. 2005
Dim obsmax As Single
obsmax = 7 'as calcaulted from baseline nutrient estimates for Bigelow Creek @
Croton in gdw

scalar = 0.3188 * Log(Pconpool(iday) * 1000) 'convert load from g/m^3 to ug/l
scalar = scalar + 0.119 * temperature(iday)
scalar = scalar + (474.17 * 10 ^ -6) * (NconPool(iday)) 'Npool in g/m^3 = mg/l
scalar = scalar + 3.96969
scalar = scalar / obsmax

```

```

r = r * scalar
macrogrowth = macro * (1 + r * (1 - (macro / k)))
macro = macrogrowth - macrolosstotal
If chincarc > 0 Then
    macro = macro + 0.005 * macro ' only on for direct growth
End If
macroavailable = 0.1 * macro 'g macro available for YOY community Tyler and
Rutherford
cheggsavailable = cheggsavailable + eggshavail - egglosstotal
cheggsavailable = Max(0, cheggsavailable)
End Sub
Private Sub Popgrowth()
    Dim mort 'mortality of fish due to predation
    Dim holdW As Single 'holds the value of weight for a single cohort
    Dim ExpW As Single 'holds the value of the expected weight for a cohort
    Dim a, b As Single 'parameters required for the length-weight regression from Tyler
and Rutherford (2007)

    a = 46.73
    b = 0.337
    holdW = Weight(icohort)
    Lcheck(icohort) = a * holdW ^ b

    If Lcheck(icohort) < YOYLength(icohort) Then
        Lcheck(icohort) = YOYLength(icohort)
    Else
        Lcheck(icohort) = Lcheck(icohort)
    End If

    mort = 0.02 + 3 / (Lcheck(icohort)) ^ 1.9 'mortality rate from Tyler and Rutherford
2007
    ExpW = 10 ^ (Log((Lcheck(icohort) / a)) / Log(10) / b)
    If Weight(icohort) < 0.5 * ExpW Then
        yoyloss(icohort) = cohort(icohort)
    Else
        yoyloss(icohort) = cohort(icohort) * (1 - Exp(-mort))
    End If

    If (Weight(icohort) <= 20) Then
        FED = (4.18 + 0.0025 * Weight(icohort)) * 1000 'from Trudel et al. 2005
    Else
        FED = 5763 + 0.986 * Weight(icohort) 'j/g Rand et al. 1993
    End If

    GramGrowth(icohort) = Growth / FED 'g d-1 of one individual

```

```

End Sub
Private Sub Pools()
    Dim steggweight(icohort) As Single 'ave weight (g) of steelhead eggs from Little
Manistee Weir
    If icohort = 1 Then
        r = r
        steelhead = steelhead + steelweight * 2 - steelmort 'g m-2 of adults remaining
after spawning
        Cheggs = Cheggs + eggstoredd 'g/m^2 of Chinook eggs

        chinook = chinook + ChinSpawn 'g/m^2
        chincarc = chincarc + Carcflux - ChDec 'g/m^2
        'cheggsavailable = cheggsavailable + eggshavail
        Npool(iday) = NpoolPrevious + Nload(iday) + NitroFish(iday) - Nout(iday) 'g
        Ppool(iday) = PpoolPrevious + Pload(iday) + PhosFish(iday) - Pout(iday) 'g

        MassNLoadCheck = NpoolPrevious + Nload(iday) + NitroFish(iday) - Nout(iday)
- Npool(iday)
        MassPLoadCheck = PpoolPrevious + Pload(iday) + PhosFish(iday) - Pout(iday) -
Ppool(iday)
        masswatercheck(iday) = flowIn(iday) - VolChange(iday) - FlowOut(iday)
        PoolVol(iday) = PoolVol(iday) + VolChange(iday) ' pool volume in m^3
        depth(iday) = depth(iday) + DepthChange(iday) 'depth in m
        NitroFish(icohort) = 0
        PhosFish(icohort) = 0
        DepthChange(iday) = 0
        VolChange(iday) = 0
        OldPoolVol = PoolVol(iday)
        NpoolPrevious = Npool(iday)
        PpoolPrevious = Ppool(iday)
    End If
    cohort(icohort) = cohort(icohort) - yoyloss(icohort) + YOYhatch(icohort) -
yoylarvaeloss(icohort) 'YC #/m^2
    Weight(icohort) = Weight(icohort) + GramGrowth(icohort) 'YC ave weight in a
daily cohort in g

    'YOY can lose weight but not length
    If Lcheck(icohort) < YOYLength(icohort) Then
        YOYLength(icohort) = YOYLength(icohort) 'length of each cohort in mm
    Else
        YOYLength(icohort) = Lcheck(icohort)
    End If

    eggs(icohort) = eggs(icohort) - YOYhatch(icohort) '#/m^2 of eggs for each cohort
    eggbiomass(icohort) = eggs(icohort) * steggweight(icohort) 'g/m^2 of eggs for each
cohort

```

```

biomass(icohort) = cohort(icohort) * Weight(icohort) 'g/m^2 of YOY steelhead
macrolosstotal = macrolosstotal + macroloss
egglosstotal = egglosstotal + eggloss
macroloss = 0
eggloss = 0
YOYhatch(icohort) = 0
yoylarvaeloss(icohort) = 0
yoyloss(icohort) = 0
GramGrowth(icohort) = 0
ATU(icohort) = ATU(icohort) + temperature(iday) 'increments populated ATU
matrix to determine emergence
End Sub
Private Sub YolkSac()
'mortality of YOYpop during yolk sac development
Dim dailymort As Single 'the daily mortality of alevins from Tyler and Rutherford
2007
dailymort = 0.02225
yoylarvaeloss(icohort) = cohort(icohort) * dailymort '#/m^2/d of larvae die
Weight(icohort) = 0.081 'in g/fish based on Tyler and Rutherford (2007) where ave
YOYLength(icohort) = 20 'Larval steelhead emerges at 20mm and the equation
L=aW^b, where a=46.73 and b=0.337
End Sub

End Module

```