Impact of American Shad in the Columbia River

Final Report

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Executive Summary

This report from the U.S. Geological Survey (USGS) to the Bonneville Power Administration (BPA), presents on results of studies on the Impact of American Shad in the Columbia River (Project Number 2007-275-00). This final report summarizes work conducted between May 1, 2007 and December 31, 2010. The report is organized into five chapters with a general study background preceding the first chapter. The chapters address various work elements outlined in the statements of work for the contract period as summarized below.

Chapter 1 provides information on the diet of juvenile and adult American shad that were captured during 2007 and 2008. We examined the stomach contents of 436 American shad captured in 2007 and 1,272 captured in 2008. The diet of age-0 American shad varied spatially and temporally, but was comprised primarily of crustaceans and insects. Prey diversity of age-0 American shad, as assessed by the Shannon Diversity Index, increased with decreasing distance to the estuary. Pre- and partial-spawn adult American shad primarily consumed *Corophium* spp. throughout the Columbia River; however, post-spawn adults primarily consumed gastropods upstream of McNary Dam.

Chapter 2 describes growth characteristics of age-0 American shad based on otolith analysis. The objective was to determine time of hatch and size at age of age-0 fish. This information will enable better quantification of prey consumption with a bioenergetics model. Fish used in the development of a growth model ranged in age from 6 to 66 days and a polynomial regression model with ln transformed total length and age values provided the best fit for growth.

Chapter 3 describes parameterization of a Wisconsin bioenergetics model for age-0 American shad using published physiological data on American shad and closely related alosine species. The model can be used as a tool to explore various hypotheses about how age-0 American shad directly and indirectly affect Columbia River salmon through ecological interactions in lower Columbia River food webs. We demonstrate the utility of bioenergetics models to address management questions by using the American shad bioenergetics model to explore prey consumption by age-0 American shad. In addition, we use a fall Chinook salmon bioenergetics model to explore the growth potential of juvenile fall Chinook salmon predating on age-0 American shad in the lower Columbia River.

Chapter 4 presents findings from two ancillary investigations completed during the contract period; assessment of the levels of thiaminase activity in juvenile and adult American shad and characterization of some life history traits, including the age and interoparity of adult fish. Thiaminase activity of Columbia River American shad was typically higher than that reported for alewives from 10 stocks in the Great Lakes, suggesting that additional studies should be conducted to determine if predators of American shad exhibit thiamine deficiency. We found differences in age, size, and spawning frequency between male and female American shad. Most spawning males were age 4 (range 3-6) and most females were age 5 (range 4-7). Overall, males had a higher rate of iteroparity than females, and females were larger than males of the same age.

Chapter 5 verifies the existence of a "freshwater" type life history variant of juvenile American shad in the Columbia River by examination of length frequencies and otolith analysis. Our results show that some juvenile American shad remain in freshwater for 1-2 years. Even if this life history variant is relatively rare within the American shad population, the sheer abundance of American shad produced in the Columbia River basin could result in appreciable numbers, potentially with significant ecological impact. We also show that migratory patterns among Columbia River juvenile and adult American shad are variable and more complicated than previously thought.

In addition to these chapters, we also published a paper, not reproduced here, that describes the prevalence of *Ichthyophonus*, a Mesomycetozoean parasite of wild marine fishes, in Columbia River American shad. The results raise questions regarding the risk for sympatric salmonids and the role of *Ichthyophonus* as a population-limiting factor affecting American shad in the Columbia River. The citation for that paper is:

Hershberger, P. K., B. K. van der Leeuw, J. L. Gregg, C. A. Grady, K. M. Lujan, S. K. Gutenberger, M. K. Purcell, J. C. Woodson, J. R. Winton, and M. J. Parsley. 2010. Amplification and transport of an endemic fish disease by an introduced species. Biological Invasions 12:3665-3675.

Study Background

American shad *Alosa sapidissima* is an anadromous fish native to the Atlantic coast of North America. In 1871, American shad were transported across the United States by railroad and introduced into the Sacramento River, California (Green 1874). The transcontinental introduction was successful, and within a few years American shad began colonizing other Pacific coast river systems. By 1885, American shad were well established in the lower Columbia River (Smith 1896); however, high seasonal flows and natural barriers limited upstream migration of adults (Petersen et al. 2003). Although hydroelectric development of the lower Columbia River began in 1938 and inundated natural barriers to adult American shad migration (Petersen et al. 2003), it wasn't until fish ladders at the dams were modified in the 1970s to improve adult salmon passage that the number of adult American shad passing Bonneville Dam increased dramatically (Monk et al. 1989). From 1938–1957 an average of 16,700 adults passed Bonneville Dam each year (Quinn and Adams 1996). In the past decade, on average over 3 million adults pass Bonneville Dam annually and more than 5.4 million adults passed Bonneville Dam in 2004. However, the counts of adult American shad at Bonneville Dam began a precipitous decline in 2004 that continued through the conclusion of this study. Hydroelectric development of the Columbia River has warmed water temperatures, reduced flow, and shifted the annual thermograph as a result of impoundment (Ebel et al. 1989; Quinn and Adams 1996; Quinn et al. 1997). These changes have created favorable environmental conditions for upriver migration and spawning of adult American shad, as well as optimal growth and survival conditions for larval and juvenile stages (Petersen et al. 2003). Today, American shad are a highly successful introduced species in the Columbia River basin, with some adults migrating upstream as far as Rock Island Dam on the Columbia River and upstream of Lower Granite Dam on the Snake River.

Non-native fishes frequently impact native fish at multiple scales from population-level impacts to modifying food webs and altering ecosystem function (Rosenzweig 2001; Simon and Townsend 2003). Non-native species typically compete with native species for food and space in aquatic food webs, facilitate the spread and virulence of diseases, and alter habitat (Mack et al. 2000; Simberloff et al. 2005; Strauss et al. 2006; Rahel and Olden 2008).

The abundance of American shad in the Columbia River raises concerns about their impact on native salmonids. Although the spawning migration of American shad overlaps spatially and temporally with that of Spring Chinook salmon, the most consequential ecological impacts of American shad may be linked to the large number of young produced each year in lower Columbia River impoundments and the estuary. Hydroacoustic and trawling surveys conducted during late summer and fall suggest that juvenile American shad can be extremely abundant at certain times and locations in the lower 500 km of the Columbia River. For example, hydroacoustic transects across John Day Reservoir during night hours, along with trawls to verify species composition, have shown juvenile American shad distributed from shore to shore and throughout the water column (Petersen et al. 2003). The great abundance of young American shad in the lower Columbia River is suspected to have direct and indirect impacts on anadromous salmonids.

American shad may influence the aquatic community structure of the Columbia River through numerous trophic interactions: age-0 American shad provide food for juvenile fall Chinook salmon, while juvenile American shad may compete with juvenile fall Chinook salmon and other small native fishes for prey. The large numbers of American shad present in the river may alter or deplete zooplankton populations that sustain rearing salmon while contributing to the growth and population size of large predatory fishes that feed on juvenile salmon. Other fishes, such as the native prickly sculpin, may benefit from abundant and energy-rich American shad prey as well.

Several conditions exist that suggest important species interactions are occurring between age-0 fall Chinook salmon and American shad. Large numbers of American shad hatch and rear in lower mainstem reservoirs of the Columbia River overlapping temporally and spatially with age-0 fall Chinook salmon. Diet studies on age-0 fall Chinook confirm that they feed on age-0 American shad. In addition, there appears to be considerable dietary overlap between age-0 fall Chinook salmon and American shad, and the juvenile fish of both species gradually move downstream and into the estuary as they grow. The co-occurrence of emigrating fall Chinook salmon with abundant numbers of larval American shad in large mainstem reservoirs, the similar emigration timing of these species, as well as the extended rearing period of juvenile American shad and fall Chinook salmon in the Columbia River estuary suggests that inter-specific interactions are occurring.

The overarching objectives of this project were to collect temporally and spatially explicit data on the diet of juvenile and adult American shad, develop a bioenergetics model for American shad to provide decision support, compile existing data on American shad and fall Chinook salmon to populate bioenergetics models that can be used to test various hypotheses about interactions between salmonids and American shad, and to conduct empirical investigations to gain insight into several areas of study where American shad may have impact in the Columbia River. Over the past four years, the project has collected and analyzed detailed temporal and spatial data on the diet of American shad, investigated the role of American shad as vectors of disease, analyzed the growth of age-0 American shad and developed a bioenergetics

model for the species. These topics are described in detail in the following chapters. In addition, project personnel collaborated extensively with other researchers to investigate important and sometimes unique aspects of American shad, including disease, thiaminase activity, and general life history. The findings from this work contribute to a better understanding of American shad in the Columbia River, their impact on salmon restoration efforts, and provide direction for additional research.

Acknowledgments

The following individuals contributed greatly to the various aspects of this project. Dr. James Petersen was the lead proposal and project proponent and unfortunately passed away just as this project began. Bjorn van der leeuw, Jessica Fischer, Paolo Lazatin, Joe Mullen, Eric (Pete) Kofoot and Joe Warren (USGS) all assisted with various tasks including field sampling, laboratory processing, data entry, and summarization. Bobby Begay (Columbia River Intertribal Fish Commission) and Steve Lee (University of Idaho) provided assistance in capturing shad from the adult fish facility at Bonneville Dam. Dean Ballinger, Bruce Mills, Greg Kovalchuk and John Barton (Pacific States Marine Fisheries Commission) provided assistance with collecting juvenile shad at the smolt monitoring facility at Bonneville Dam. We extend our thanks to the many other people who provided assistance over the course of this effort. Most of these individuals are recognized on title pages or in acknowledgments of various chapters in this report. Cost share for portions of this work were provided by the USGS's Western Fisheries Research Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Chapter 1
Diet of Juvenile and Adult American Shad in the Columbia River

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Abstract

The diet of juvenile and adult American shad *Alosa sapidissima* captured from various locations in the Columbia River was investigated during 2007 and 2008. Collection efforts in 2007 were restricted to fish collected from existing adult and juvenile fish collection facilities located at Bonneville Dam and to adult shad captured by angling downstream from Bonneville Dam. In 2008, we used gillnets, electrofishing, beach seining, or cast nets to collect juvenile and adult shad from the saline estuary near Astoria (approximately river km 24) to just upstream from McNary Dam (approximately river km 472). We examined the stomach contents of 436 American shad captured in 2007 and 1,272 captured in 2008. Fish caught within the river were much more likely to contain food items than fish removed from fish collection facilities.

The diet of age-0 American shad varied spatially and temporally, but was comprised primarily of crustaceans and insects. Prey diversity of age-0 American shad, as assessed by the Shannon Diversity Index, increased with decreasing distance to the estuary. Pre- and partial-spawn adult American shad primarily consumed *Corophium* spp. throughout the Columbia River; however, post-spawn adults primarily consumed gastropods upstream of McNary Dam.

Introduction

The great abundance of non-native juvenile and adult American shad *Alosa sapidissima*, in the Columbia River has raised concerns about the potential for competition for food with juvenile salmon. Juvenile salmon and American shad are planktivorous fish in the Columbia River, with salmon eating largely cladocerans (Rondorf et al. 1990) and shad reportedly eating primarily cyclopoid copepods (Petersen et al. 2003; Haskell et al. 2006). The timing of larval and juvenile American shad migrating past McNary Dam coincides closely with the migration of juvenile endangered fall Chinook salmon from the Snake River. Haskell et al. (2006) suggested diet overlap between juvenile fall Chinook salmon and juvenile shad and changes in the plankton community in John Day Reservoir. They concluded that the high densities of larval and juvenile shad in John Day Reservoir in summer are removing cladocerans that otherwise are an important diet item of subyearling fall Chinook salmon (Rondorf et al. 1990).

Although adult American shad are generally thought to stop feeding during their upriver spawning migration, Walter and Olney (2003) found that they continue to feed in estuarine and lower reaches of the York River during their upstream migration and while returning to the ocean after spawning (Walter and Olney 2003). If large numbers of adults are entering the Columbia River and feeding during May through July, they could directly compete with outmigrating juvenile salmonids. Little is known about the feeding habits of adult American shad in the Columbia River but an investigation conducted more than 40 years ago revealed that the stomachs of two spent female American shad captured in the Bonneville Dam forebay contained the remains of 16 and 9 juvenile salmon (Wendler 1967). The author raised the concern that a potentially adverse predator-prey relationship would exist if American shad populations increased. History has shown that counts of adult American shad at Bonneville Dam did indeed increase from the levels seen in the late 1960's (Figure 1).

Knowledge of the spatial and temporal components of American shad diet in the Columbia River is needed to better assess the interaction between these fish and native salmonids. Our goal in this study was to increase knowledge on the diet of juvenile and adult American shad by expanding the spatial and temporal extent of past work. Our specific objectives were to describe the spatial and temporal variability in the diet of juvenile American shad during their downstream migration and describe the diet of pre-, partial-, and post-spawn American shad.

Methods

Field collections of American shad began in 2007, the first year of funding for this project, and were restricted to sampling efforts that could be conducted while we pursued an Endangered Species Act Section 10 scientific research permit that would enable the use of standard fish sampling gears. Thus, in 2007 the diet analysis was restricted to fish collected from adult and juvenile fish collection facilities located at Bonneville Dam and to adult shad captured by angling downstream from Bonneville Dam. The information derived from sampling in 2007 served to inform sampling design and analysis for 2008. In 2008, after obtaining a Section 10 scientific research permit, we used gillnets, electrofishing, beach seining, and cast nets to collect juvenile and adult shad from additional areas on the mainstem of the Columbia River (Figure 2).

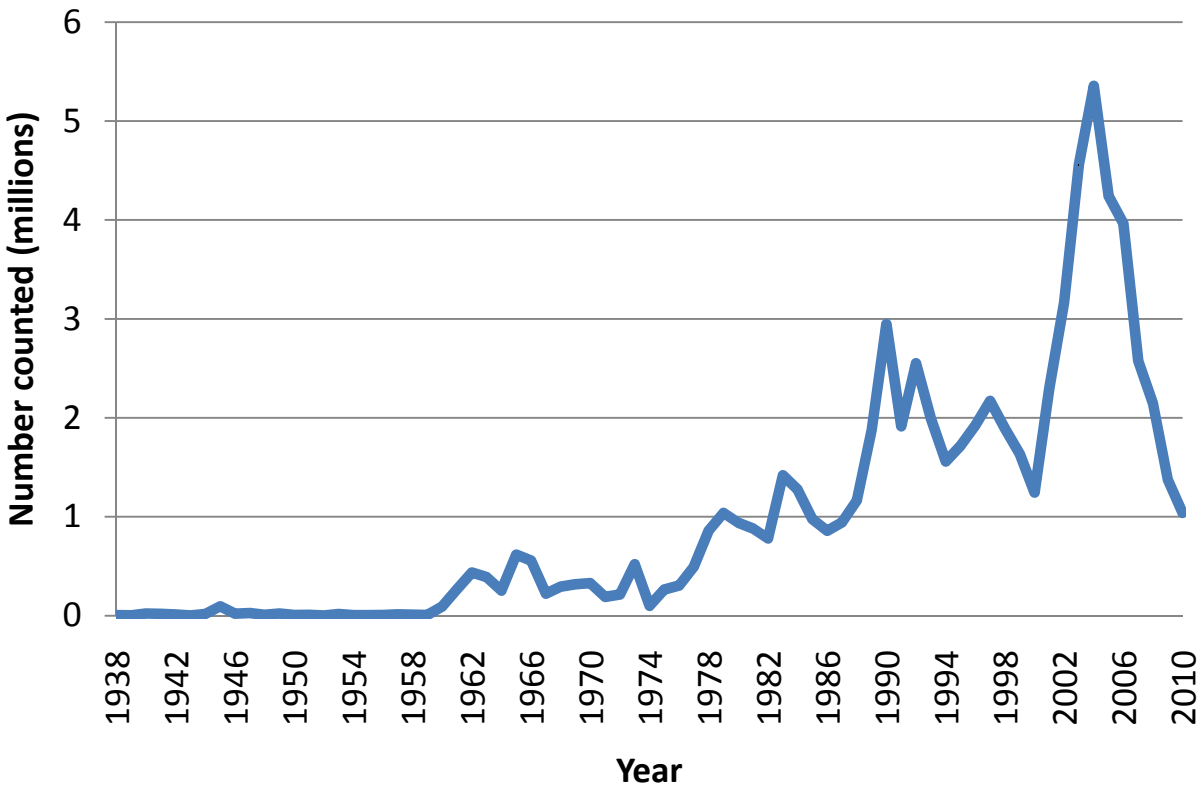

Figure 1. Numbers of adult American shad counted passing upstream through Bonneville Dam fishways from 1938 - 2010. Counts were obtained from the Columbia River DART (Data Access in Real Time) website (http://www.cbr.washington.edu/dart/).

Fish collection

In 2007, juvenile American shad were collected for diet analysis from the Bonneville Dam juvenile fish collection facility at two week intervals beginning August 13 and extending through October. Fish were measured for fork length (FL) to the nearest 0.1 mm with digital calipers and weighed to the nearest 0.01 g. Whole fish were placed into a labeled vial with 10% neutral buffered formalin and transported to the laboratory. After seven days the fish were rinsed with water and transferred to 70% ethanol for long-term storage prior to diet analysis.

Adult American shad were collected by angling with lures typically used by recreational fishers. Angling occurred during June downstream of Bonneville Dam between Ives and Pierce islands near river km 229. Adult American shad were also captured by dip netting during July from the Bonneville Dam juvenile and adult fish collection facilities. Fish were dispatched with a blow to the head, then measured for FL to the nearest mm and weighed to the nearest g with a Pesola or Homs scientific hanging scale. The stomach was dissected and spawning condition verified by examination of the gonads. Fish in pre-spawning condition had full gonads and post-spawn fish showed depleted gonads. Partially-spawned fish exhibited shrunken but not depleted gonads. The gonads of partially spawned males appeared wrinkled and often had reddish

margins. The stomachs were individually labeled and preserved in neutral buffered formalin for a minimum of seven days then rinsed in water and transferred to 70% ethanol for long-term storage.

In 2008, juvenile American shad were collected for diet analysis at five in-river locations every two weeks beginning August 6 and extending through mid-November. In-river sampling locations were at Skamokawa, WA (river km 56), Cathlamet, WA (river km 64), Crims Island (river km 89), and immediately downstream of Bonneville (river km 227 - 230), John Day (river km 336 - 340), and McNary (river km 465 - 468) dams. Fish were collected with a 20.73 m long x 1.52 m tall beach seine with a mesh size of 4.7 mm. The beach seine was pulled for 2-3 minutes in a downstream direction perpendicular to shore. Juvenile American shad captured in the beach seine were immediately removed, measured for FL with digital calipers and weighed on a digital scale (0.01 g). Whole American shad were placed individually into sample bags, placed on dry ice, and transported to the laboratory where they were placed in a -80°C freezer until analysis.

Adult American shad were collected by boat electrofishing and gillnetting in 2008. Boat electrofishing was conducted downstream of Bonneville (river km 227 - 230), and near John Day (river km 344 - 348) and McNary (river km 467 - 470) dams. Fish were collected from the saline portion of the lower Columbia River estuary (river km 24 - 40) by gillnetting. Gillnets were made of 13.65 cm or 13.97 cm monofilament mesh with a 4.54-kg breaking strength. Each gillnet had a maximum length of 457.2 m and a maximum depth of 4.27 – 4.88 m. Gillnets were drifted for no more than 45 minutes at a time.

Adult American shad were measured for FL to the nearest mm and weighed to the nearest g. Spawning condition was determined by examination of the gonads as described above. The stomachs were dissected from fish, placed in individual sample bags, immediately frozen on dry ice, and then transferred into a -80°C freezer at the laboratory for storage.

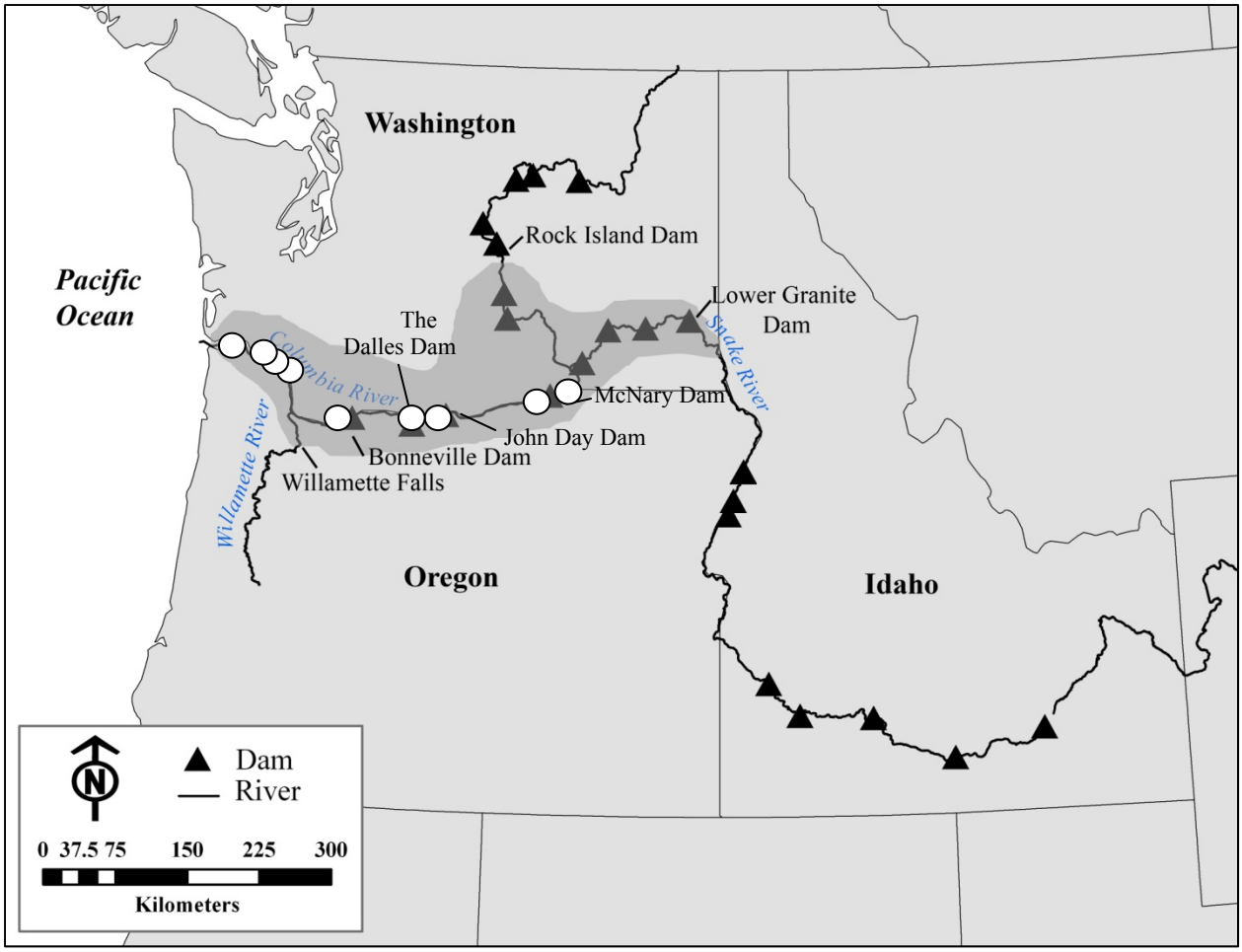

Figure 2. Map showing American shad distribution in the Columbia River basin (darker shaded area). Open circles indicate general areas where juvenile and adult American shad were captured for diet analysis in 2008. Capture locations in 2007 included only the Bonneville Dam tailrace and the juvenile and adult fish collection facilities located at Bonneville Dam.

Diet characterization

In 2007, prey in the stomach contents from juvenile and adult shad were identified and enumerated. The stomachs from preserved juvenile fish were removed from the fish by cutting below the esophagus and above the intestine. For all samples, fat, tissue, and blood were pulled and rinsed from around the stomach. The stomach was blotted dry and a stomach weight was taken (0.00001 g) on a digital analytical balance. The stomach contents were then removed using micro-dissecting tools and by gently rinsing with water. If the stomach contained food, the empty stomach was blotted dry, weighed (0.00001 g), and then discarded. The difference in weights provided the total weight of stomach contents. Empty stomachs and stomachs with non-food items were noted.

In 2008, fish were randomly selected from among the various sites and sampling dates to reduce investigator bias in the analysis of diet samples. Individual fish were thawed slightly

before being weighed to the nearest 0.01 g on a digital scale. The fish was then dissected under a stereomicroscope and the stomach removed by cutting below the esophagus and above the intestine. Fat, tissue, and blood were pulled and rinsed from around the stomach. The stomach was blotted dry and a stomach weight was taken (0.00001 g) on a digital analytical balance. The stomach contents were then removed using micro-dissecting tools and by gently rinsing with water. The stomach was then blotted dry, weighed (0.00001 g), and discarded. The difference in weights provided the total weight of stomach contents. Empty stomachs and stomachs with non-food items were noted.

The prey of juvenile American shad captured in 2008 were analyzed by enumeration, weight, and occurrence. Each of these analytical methods provides unique insight into the diet; the enumeration of prey provides information on the feeding behavior of fish (MacDonald and Green 1983), the expression of diet by weight gives an estimate of the nutritional importance of each prey category in the diet, and measures of prey occurrence indicate population-wide food habits (Cailliet 1977).

Prey enumeration

Prey were enumerated from a minimum of ten stomach samples randomly selected from each sample date and location. Prey items were identified and whole prey were counted. Partially digested organisms were enumerated by counting characteristic body parts (e.g., *Daphnia* sp. anal spines). Samples that contained >800 individual prey items were enumerated by suspending the stomach contents in a known volume of water. The solution was slurried and split in half volumetrically using a pipette. Additional splits were performed until the sub-sample contained 50-100 individual prey items. Prey items in a sub-sample were counted and an estimate of the number of each prey type in the whole sample was made by multiplying the sub-sample count by the dilution factor. Samples suspended in water were allowed to settle in a test tube or were centrifuged to decant the water before prey items were preserved by prey category (Table 1) in vials containing 70% ethanol. Preserved samples were used to determine the ash-free dry weights of prey.

Frequency of Occurrence

After all prey from at least ten juvenile American shad were enumerated from each sampling location and date, the remaining fish stomachs were analyzed to determine the frequency of occurrence of each prey type. Individual prey items were not counted, however all contents were examined in order to identify each unique organism present within a sample. Samples were preserved as described above.

Percent by Weight of the Diet

The contents from individual juvenile American shad stomachs were processed to determine the dry and ash-free dry weight (AFDW) of each prey category (Table 1) that had been isolated during sorting as described above. The AFDW is the dry weight of the digestible portion of the prey that provides energy to the fish. We obtained the dry weight of individual prey categories within each stomach by emptying individual vials of sorted prey and rinsing the vial with deionized water into a Buchner funnel assembly fitted with a previously-weighed pre-ashed glass fiber filter. The liquids were drawn off using a vacuum hand pump. The filter containing the prey was then placed in an aluminum weigh pan and dried in a 60°C gravity oven for 24 hr. Filtered samples plus weigh pans were removed from the oven, allowed to cool for 10 minutes, and

weighed (0.00001 g) with a digital analytical balance. Filtered samples were returned to the drying oven for an additional 4 hr then reweighed. This drying process was repeated until a sample weight was within 5% of its previous weight. This represented the final dry weight. The samples were then ashed in a muffle furnace at 500°C for 1 hr to burn off the organic component of the diet. Ashed samples were allowed to cool for 10 minutes, and weighed (0.00001 g). The weight of the pre-ashed glass filters were subtracted from the ash weight of the prey category. The ash weight of the prey category was subtracted from the dry weight of a sample to give the AFDW of each prey category isolated from a stomach sample.

Table 1. Definitions of the six prey categories into which the stomach contents of juvenile American shad were grouped for the calculation of % ash-free dry weight of the prey.

Category	Contents included
Insecta	All insects, Collembola, and arachnids (whole and parts)
Crustacea	All crustaceans (whole and parts)
Mollusca	Clams and snails
Fish	Fish parts excluding loose scales
Misc/Unidentified	Unidentifiable or unknown
Non-Food	Nematodes, inorganic material, plant material, fish scales, bryozoan statoblasts

The diet of adult shad was characterized only by enumeration. Prey items were identified to the lowest possible taxonomic level and whole prey items were counted. Partially-digested prey that was difficult to identify were enumerated by counting characteristic body parts (e.g., *Daphnia* spp. anal spines). After identification and enumeration the stomach contents were discarded.

Data analysis

Indices of prey diversity were used to evaluate spatial and temporal differences in the prey of juvenile American shad. We used the Shannon Diversity Index to measure seasonal prey diversity by location in age-0 American shad. This widely-used index represents the frequency of occurrence of each taxonomic group and takes into account the number of species present and the abundance of each species. The Shannon Diversity Index (H') is maximized when taxonomic groups are present in equal numbers or unique species are present. The Shannon Diversity Index was calculated using counts of individual prey items in the diet as follows:

$$H' = -\sum p_i \ Log_{10} p_i$$

where p_i = the proportion of prey items in an individual taxonomic group. We excluded non-countable categories such as insect parts and unidentified organisms from this analysis.

We calculated the index of relative importance (IRI) to estimate the relative importance of prey consumed by juvenile American shad. We calculated the index as described by Pinkas et al. (1971) using weight rather than volume:

$$IRI = (W + N) \cdot O$$

where W = percent ash-free dry weight, N = percent number, and O = percent frequency of occurrence. To make the IRI results comparable between prey categories, IRI indices for all prey categories were converted to a percent of the sum of the available IRI values as follows:

$$\%\, IRI_i = 100 \cdot IRI_i \Big/ \sum_{i=1}^{n} IRI_i$$

where n is the total number of prey categories.

Results

2007

We examined the stomach contents of 436 American shad captured in 2007. We encountered a larger sized juvenile American shad, evident in a length frequency plot (Figure 3, see also Chapter 5) that resides in freshwater for 1-2 years. Given the unexpected yet relatively common presence of this life history form in our collections, we investigated their diet separately from age-0 and adult shad.

We examined the stomachs of 219 age-0, 56 freshwater-type juvenile, and 161 adult American shad in 2007 (Table 2). Most (55.7%) age-0 shad had some food in their guts. *Corophium* spp. were present in 34.7% of the guts followed by dipterans (13.7%), copepods (11.4%), gammerid amphipods (8.2%), mollusks (5.0%), and chironomid larvae (4.1%). Other food categories were found in less than 2% of the stomachs. Copepods were the most numerous items consumed (mean 38.44; range 0-605) followed by *Corophium* spp. (mean 4.76; range 0-42) and Diptera (mean 2.03; range 0-11).

The stomachs of freshwater-type juvenile shad examined in 2007 were mostly empty (Table 2). *Corophium* spp. were observed in the guts of four fish (3 contained 1 *Corophium* spp. each, 1 contained 6). Mollusks and insect parts were also observed in the guts of some fish.

Adult shad examined in 2007 only occasionally had food in their stomachs. Food was observed in the guts of 8 of 63 (12.7%) pre-spawn condition females and 6 of 38 (15.8%) males.

However, most food was unidentifiable digested material. Two females had consumed mollusks (clams); one of these also contained insect parts. One male had consumed two *Corophium* spp. and a chironomid, one had consumed a fish egg, and one had consumed a mollusk. Food was observed in only 3 of 46 (6.5%) post-spawn condition females and 1 of 14 (7.7%) males. One post-spawn condition female gut contained 2 copepods; the other 2 contained unidentifiable remains. The one post-spawn male gut contained a single chironomid. Other items noted in the guts of adult shad included conifer needles and woody debris.

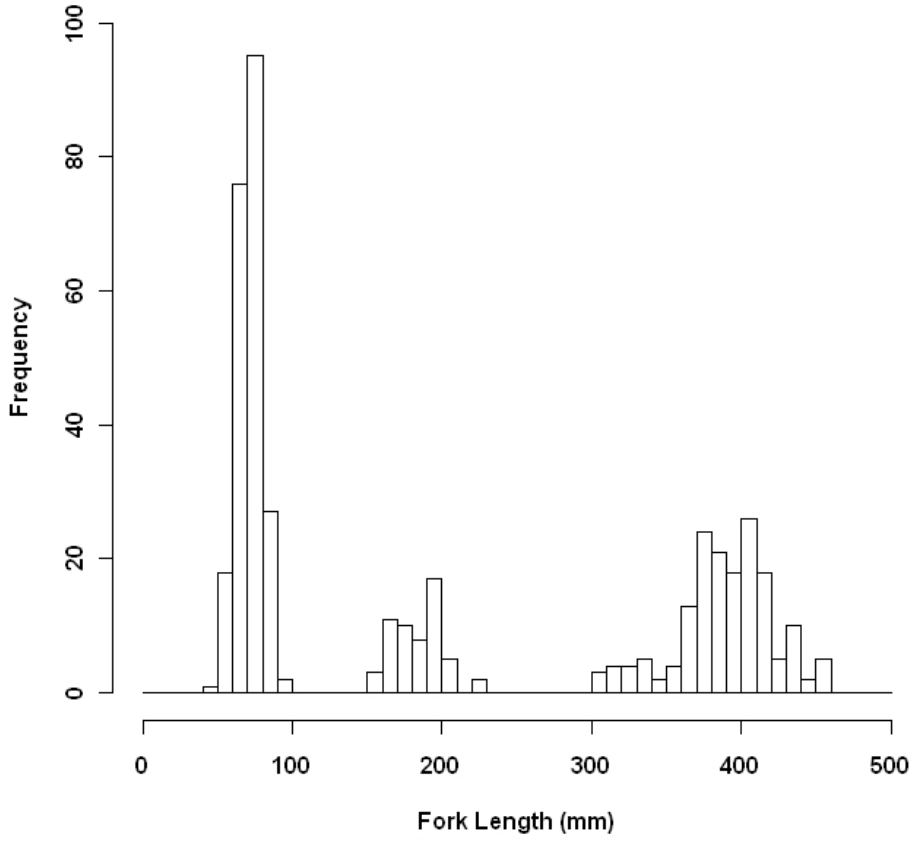

Figure 3. Length frequency histogram of American shad used in diet analysis in 2007. Adult fish (shown in the figure as fish >300 mm FL) were captured by angling downstream from Bonneville Dam. All other juvenile fish were obtained from the Bonneville Dam juvenile fish collection facility.

Table 2. Summary of American shad stomachs examined for diet analysis in 2007. Pre-spawn condition adult fish were captured by angling downstream from Bonneville Dam. All other fish were obtained from the Bonneville Dam juvenile fish collection facility.

Stage	Total number of stomachs examined	Number of stomachs with food	% of stomachs with food
Age-0	219	122	55.7
Freshwater-type juveniles	56	5	8.9
Adult males	52	7	13.5
Pre-spawn	38	6	15.8
Post-spawn	14	1	7.7
Adult Females	109	3	6.5
Pre-spawn	63	8	12.7
Post-spawn	46	3	6.5

2008

We obtained 1,272 American shad in 2008 by sampling several in-river sites and by collecting fish from juvenile and adult fish collection facilities (Table 3). Initial assessment of the fish for stomach contents revealed that fish caught within the river were much more likely to contain food items than fish removed from the juvenile and adult fish collection facilities. Therefore, we excluded from further analyses those fish taken from these facilities. Three freshwater-type juveniles (FL=115, 129 and149 mm) captured in early July were also excluded, resulting in an analysis of the diet of 1,121 juvenile and adult American shad (Figure 4).

Table 3. Summary of the numbers of American shad captured in 2008 for diet analysis by location of capture.

Location	Age-0	Adult
Astoria		53
Cathlamet	5	
Crims	105	
Skamokawa	30	
Downstream from Bonneville Dam	200	109
Bonneville Dam adult fish facility		37
Bonneville Dam juvenile fish facility	47	
The Dalles Reservoir	174	113
John Day Reservoir	200	102
John Day Dam juvenile fish facility	64	
McNary Dam forebay		30

In 2008, 825 age-0 American shad were collected from in-river locations and from the Bonneville and John Day Dam juvenile fish collection facilities from August through November.

However, we excluded from further analyses those fish captured from the juvenile fish collection facilities (n = 111) because of the high proportion of empty stomachs seen in 2007 and again in 2008; 28.1% of the age-0 American shad stomachs collected in 2008 from the Bonneville Dam juvenile fish collection facility were empty as were 42.5% of the stomachs collected at the John Day Dam juvenile fish collection facility. In contrast, there were no empty stomachs from in-river age-0 fish collected during the 2008 sampling period (Table 4), although four stomachs (<1.0%) contained only non-food items (nematodes and fish scales).

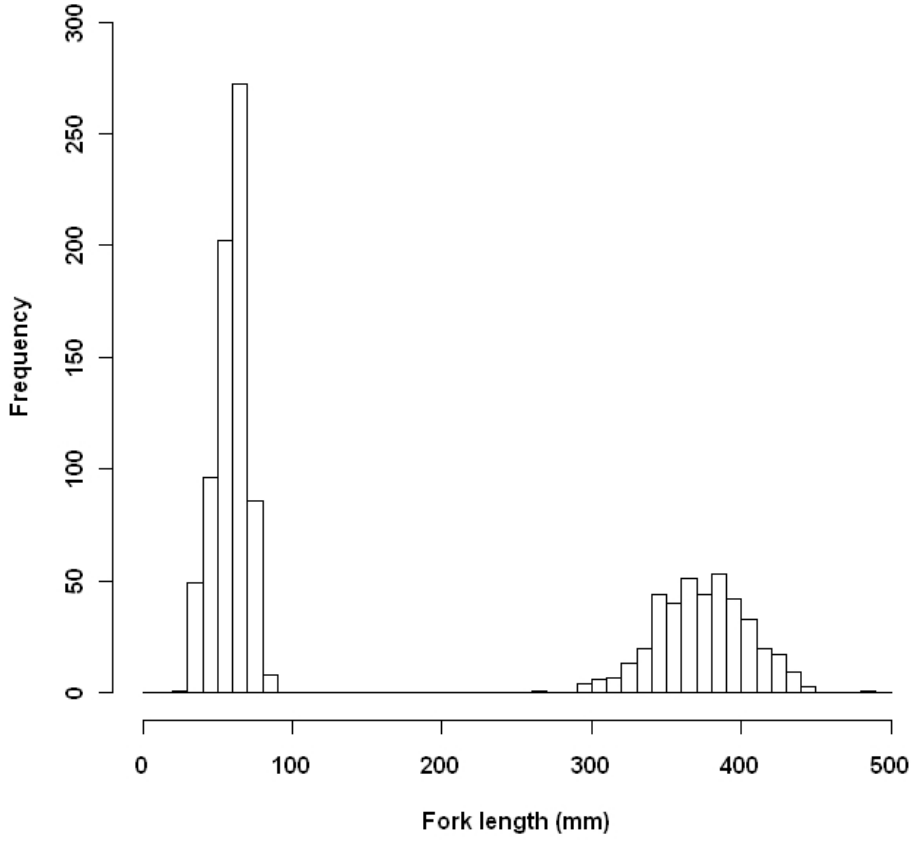

Figure 4. Length frequency histogram of 1,121 American shad captured from the Columbia River and used in diet analysis in 2008. Fish obtained from the adult and juvenile bypass facilities and freshwater-type juveniles were not used in diet analysis and are not represented in the histogram.

Age-0 diet

Percent Occurrence

Spatially and over the entire sampling period, crustaceans (primarily copepods and cladocerans) occurred most frequently in the stomach contents of age-0 American shad collected at reservoir sites (Table 4, Table 5). Insects occurred more frequently in fish collected from the two lower river freshwater estuary sites near Bonneville Dam and near Crims Island (Table 4).

Mollusks occurred infrequently in age-0 American shad stomachs at most locations, with higher frequencies observed at the sample site immediately downstream from Bonneville Dam and at Cathlamet, although the number of fish sampled at Cathlamet was quite small relative to numbers collected at the other locations (Table 4).

Temporally, crustaceans and insect prey categories occurred at nearly equal frequencies in the stomachs of age-0 American shad among months (Table 5). The higher occurrence of mollusks in November coincided with slightly lower occurrence frequencies of crustaceans and insects. Overall, August was the only month when crustaceans occurred more frequently than insects in the stomach contents of age-0 American shad.

Table 4. Percent frequency of occurrence by location for prey items in juvenile American shad collected in the Columbia River during 2008. Bold items represent all organisms of that prey category.

	John Day Reservoir n=200	The Dalles Reservoir n=174	Below Bonneville Dam n=200	Crims Island n=105	Cathlamet n=5	Skamokawa n=30	Overall n=714
Stomach Empty	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Insecta	**86.0**	**85.1**	**86.0**	**91.4**	**100.0**	**96.7**	**87.1**
Diptera	74.0	73.0	72.0	60.0	80.0	93.3	72.0
Diptera adult	8.5	11.5	13.5	13.3	--	--	10.9
Diptera pupae	53.5	52.3	52.0	20.0	80.0	90.0	49.6
Diptera larvae	41.0	49.4	29.0	39.0	80.0	80.0	41.3
Hemiptera adult	3.0	1.1	8.0	14.3	--	--	5.5
Hymenoptera adult	2.0	2.9	6.5	11.4	--	--	4.8
Tricoptera larvae	5.5	1.7	3.5	--	--	--	2.9
Ephemeroptera nymph	3.0	--	4.0	--	--	--	2.0
Plecoptera nymph	0.5	1.1	2.0	1.0	--	--	1.1
Odonota nymph	0.5	1.1	--	1.0	--	--	0.6
Coleoptera adult	0.5	0.6	1.0	1.9	--	--	0.8
Coleoptera larvae	2.5	0.6	0.5	--	20.0	3.3	1.3
Thysanoptera adult	1.0	--	--	--	--	--	0.3
Neuroptera adult	--	--	--	1.0	--	--	0.1
Unidentified insect	5.5	6.9	14.0	24.8	--	6.7	11.1
Crustacea	**96.0**	**86.8**	**74.0**	**72.4**	**100.0**	**100.0**	**84.3**
Copepoda	86.0	74.1	56.0	55.2	80.0	100.0	70.7
Calanoida	30.0	33.9	28.0	25.7	40.0	50.0	30.7
Cyclopoida	41.0	32.8	26.5	21.0	60.0	40.0	32.1
Arguloida	0.5	1.7	0.5	1.0	--	--	0.8
Amphipoda	28.0	25.9	28.5	14.3	60.0	20.0	25.5
Corophiidae	18.5	3.4	10.5	14.3	60.0	20.0	12.3
Corophium spp.	13.5	2.9	9.0	11.4	60.0	13.3	9.7
Corophium salmonis	2.5	--	1.0	3.8	--	3.3	1.7
Corophium spinicorne	3.5	0.6	1.5	--	--	3.3	1.7
Gammaridae	17.5	24.7	21.5	--	--	--	16.9
Isopoda	2.5	6.9	1.5	1.0	--	--	2.9
Neomysis mercedis	5.0	1.7	0.5	4.8	--	--	2.7
Ostracoda	31.5	55.2	6.5	6.7	40.0	--	25.4
Cladocera	33.5	29.3	9.5	35.2	60.0	100.0	29.0
Daphnidae	9.5	8.6	3.0	1.9	--	70.0	8.8
Bosminidae	12.5	10.9	5.5	28.6	60.0	23.3	13.3
Chydoridae	5.0	9.8	1.0	--	--	--	4.1
Sida crystallina	12.0	1.7	--	3.8	--	36.7	5.9
Leptidora kindtii	2.5	0.6	1.0	3.8	--	63.3	4.3
Molluska	**15.5**	**11.5**	**30.0**	**17.1**	**60.0**	**6.7**	**18.8**
Corbicula ssp	14.0	7.5	27.0	17.1	60.0	3.3	16.4
Gastropoda	3.0	4.0	10.0	--	--	3.3	4.8
Collembola	2.5	2.9	4.0	--	--	--	2.5
Hydracarina	17.0	12.6	6.5	4.8	--	--	10.4
Araneae	0.5	0.6	8.0	6.7	--	--	3.5
Oligocheta	--	1.1	--	--	--	--	0.3
Hirudinea	0.5	--	--	--	--	--	0.1
Turbellaria	--	--	0.5	--	--	--	0.1
Fish Parts	--	--	--	--	--	3.3	0.1
Unidentified items	--	1.7	3.0	1.9	--	3.3	1.7
Nematoda	15.5	21.8	33.0	8.6	--	--	20.2
Sand	4.0	5.7	3.5	13.3	--	6.7	5.7
Vegetation	3.5	3.4	2.0	4.8	--	--	3.1
Wood	0.5	0.6	--	16.2	--	--	2.7
Bryozoan statoblasts	41.0	0.6	0.5	1.9	--	--	12.0
Fish scales	20.5	23.0	31.5	4.8	--	--	20.9

Table 5. Percent frequency of occurrence by month for prey items in juvenile American shad collected in the Columbia River during 2008. Bold items represent all organisms of that prey category.

	August n=88	September n=245	October n=245	November n=136
Fork Length (mm), Mean (SD)	45.44 (8.95)	54.27 (10.03)	64.39 (5.46)	66.95 (6.30)
Stomach Empty	0.0	0.0	0.0	0.0
Insecta	**93.2**	**83.7**	**93.1**	**78.7**
Diptera	87.5	73.1	74.7	55.1
Diptera adult	2.3	6.9	18.4	10.3
Diptera pupae	77.3	44.9	55.1	30.1
Diptera larvae	60.2	50.2	30.2	33.1
Hemiptera adult	--	0.8	9.8	9.6
Hymenoptera adult	--	1.6	9.4	5.1
Tricoptera larvae	3.4	3.3	1.6	4.4
Ephemeroptera nymph	--	4.1	1.6	--
Plecoptera nymph	1.1	1.6	--	2.2
Odonota nymph	--	0.8	0.8	--
Coleoptera adult	--	0.4	0.8	2.2
Coleoptera larvae	5.7	0.8	0.4	0.7
Thysanoptera adult	--	0.4	0.4	--
Neuroptera adult	--	--	--	0.7
Unidentified insect	3.4	4.9	17.6	15.4
Crustacea	**98.9**	**82.4**	**85.3**	**76.5**
Copepoda	89.8	65.3	75.9	58.8
Calanoida	36.4	31.0	26.5	33.8
Cyclopoida	33.0	28.2	32.7	37.5
Arguloida	--	1.2	1.2	--
Amphipoda	25.0	19.6	19.6	47.1
Corophiidae	13.6	9.0	6.9	27.2
Corophium spp.	10.2	7.3	4.9	22.1
Corophium salmonis	1.1	0.8	1.6	3.7
Corophium spinicorne	2.3	1.6	0.4	3.7
Gammaridae	13.6	12.2	13.9	33.1
Isopoda	--	2.0	3.3	5.9
Neomysis mercedis	1.1	2.0	2.0	5.9
Ostracoda	3.4	24.5	35.9	22.1
Cladocera	54.5	16.7	27.3	37.5
Daphnidae	38.6	3.3	4.1	8.1
Bosminidae	12.5	6.5	17.1	19.1
Chydoridae	--	2.9	6.1	5.1
Sida crystallina	18.2	4.5	2.0	7.4
Leptidora kindtii	22.7	1.2	1.2	3.7
Molluska	**2.3**	**17.1**	**19.6**	**30.9**
Corbicula ssp	1.1	15.1	16.7	27.9
Gastropoda	1.1	4.1	6.9	4.4
Collembola	--	0.8	6.5	--
Hydracarina	1.1	10.6	14.7	8.1
Araneae	--	0.8	6.5	5.1
Oligocheta	--	--	0.4	0.7
Hirudinea	--	--	0.4	--
Turbellaria	--	0.4	--	--
Fish Parts	1.1	--	--	--
Unidentified items	4.5	1.2	1.2	1.5
Nematoda	22.7	24.5	16.3	17.6
Sand	3.4	7.8	4.5	5.9
Vegetation	--	3.3	4.5	2.2
Wood	--	3.3	2.4	3.7
Bryozoan statoblast	--	20.0	13.1	3.7
Fish scales	18.2	25.7	24.1	8.1

Percent number

We enumerated all prey items in a subsample of age-0 American shad stomachs (n = 316) to determine relative abundance. Prey items represented by the crustacean, insect, and mollusk prey categories were the most prevalent organisms (Table 6). By number, crustaceans, primarily copepods and *Bosmina longirostris*, made up more than 95% of the prey organisms found in juvenile American shad stomachs from all sampling locations except Cathlamet (Table 6). The Cathlamet location, which was sampled just once in August, had a higher percentage of insects than the other locations. Among the remaining sampling locations, the greatest relative abundance of insects was found in age-0 American shad sampled from The Dalles Reservoir, and the lowest relative abundance of ingested insects occurred at Crims Island. Mollusks, primarily *Corbicula fluminea*, made up no more than 1% of the organisms consumed by number at all locations. The relative abundance of crustacean, insect, and mollusk prey in the stomachs of age-0 American shad showed little variation by month (Table 7).

By number, copepods dominated the diet of age-0 American shad at all locations and during all months (Table 6, Table 7). The relative abundance of calanoid copepods was higher than that of cyclopoid copepods in the stomach contents of age-0 American shad from Skamokawa and Crims Island. The relative abundance of cyclopoid copepods increased each month from August to November. At Crims Island and Skamokawa, cladocerans had a high relative abundance compared to other locations. *Bosmina longirostris* was the most abundant cladoceran overall, but 68.8% of all cladocerans enumerated were *B. longirostris* from age-0 stomachs collected near Crims Island. The relative abundance of *Daphnia* spp. was highest in August with one-half of all *Daphnia* found occurring in fish collected from Skamokawa. Malacostracan crustaceans (e.g. *Corophium* spp.) were least abundant in the diet in the three lowermost estuary sampling locations and most abundant in the diet in the reservoirs. No gammarid amphipods were found in the stomach contents of age-0 American shad collected from the three lowermost estuary sampling locations, although they were the most abundant malacostracan in stomachs sampled from all other sites. Overall, the abundance of gammarid amphipods was higher than all other malacostracans combined. Malacostracans of all types were consumed in the greatest relative abundance during November. Dipterans outnumbered all other insects consumed at all locations and months. The relative abundance of adult insects in the stomachs of American shad increased with time (Table 7).

Table 6. Percent numerical composition by location for prey items in age-0 American shad collected in the Columbia River during 2008. Bold items represent all organisms of that prey category.

	John Day Reservoir	The Dalles Reservoir	Below Bonneville Dam	Crims Island	Cathlamet	Skamokawa	Overall
	n=79	n=71	n=103	n=49	n=4	n=10	n=316
Total number of prey	28078	17333	19199	27933	1603	4411	98557
Insect	**2.07**	**4.04**	**2.00**	**1.45**	**18.65**	**3.13**	**2.55**
Diptera	1.97	3.95	1.65	0.97	18.59	3.06	2.29
Diptera adult	0.06	0.20	0.23	0.15	--	--	0.14
Diptera pupae	0.74	1.54	0.98	0.09	16.97	1.65	1.05
Diptera larvae	0.75	0.91	0.37	0.34	1.62	1.41	0.63
Hemiptera adult	0.01	0.01	0.02	0.05	--	--	0.02
Hymenoptera adult	--	0.01	0.03	0.03	--	--	0.01
Tricoptera larvae	0.02	0.02	0.02	--	--	--	0.01
Ephemeroptera nymph	0.01	--	--	--	--	--	0.00
Plecoptera nymph	0.01	0.01	0.04	0.01	--	--	0.01
Coleoptera adult	0.01	0.01	0.01	0.00	--	--	0.01
Coleoptera larvae	--	0.01	--	--	0.06	--	0.00
Neuroptera adult	--	--	--	0.01	--	--	0.00
Unidentified insect	0.05	0.04	0.23	0.38	--	0.07	0.18
Crustacean	**97.68**	**95.67**	**96.92**	**98.36**	**81.10**	**96.85**	**97.06**
Copepoda	96.05	91.34	96.01	72.37	79.35	81.73	87.59
Calanoida	8.12	12.43	29.39	53.44	23.58	61.94	28.52
Cyclopoida	85.18	75.65	64.94	18.93	55.77	16.80	57.25
Arguloida	0.01	0.02	0.01	--	--	--	0.01
Amphipoda	0.32	0.47	0.32	0.05	0.31	--	0.25
Corophiidae	0.15	0.02	0.11	0.05	0.31	--	0.09
Corophium spp.	0.10	0.01	0.10	0.03	0.31	--	0.06
Corophium salmonis	0.01	--	0.01	0.02	--	--	0.01
Corophium spinicorne	0.04	0.01	0.01	--	--	--	0.01
Gammaridae	0.16	0.44	0.20	--	--	--	0.16
Isopoda	--	0.08	0.04	--	--	--	0.02
Neomysis mercedis	0.06	0.01	0.01	0.00	--	--	0.02
Ostracoda	0.42	1.06	0.11	0.02	0.25	--	0.34
Cladocera	0.82	2.69	0.43	25.91	1.19	15.12	8.83
Daphnidae	0.30	0.60	0.03	0.03	--	4.60	0.41
Bosminidae	0.26	1.26	0.30	21.44	1.19	0.09	6.45
Chydoridae	0.01	0.03	--	--	--	--	0.01
Sida crystallina	0.06	--	--	0.11	--	0.39	0.07
Leptidora kindtii	0.02	0.02	0.01	0.01	--	4.08	0.20
Mollusk	**0.10**	**0.14**	**0.97**	**0.16**	**0.25**	**0.02**	**0.29**
Corbicula ssp	0.10	0.13	0.89	0.16	0.25	--	0.27
Gastropoda	0.00	0.01	0.08	--	--	0.02	0.02
Collembola	0.01	0.04	0.03	--	--	--	0.02
Hydracarina	0.13	0.10	0.03	0.01	--	--	0.06
Araneae	--	--	0.06	0.02	--	--	0.02
Oligocheta	--	0.01	--	--	--	--	0.00

Table 7. Percent numerical composition by month for prey items in age-0 American shad collected in the Columbia River during 2008. Standard deviations of mean fish fork lengths are shown in parentheses. Bold items are summaries of all organisms of that prey category.

	August n=30	September n=105	October n=92	November n=89
Mean fish fork length (mm)	45.54 (8.06)	55.84 (10.11)	64.12 (5.67)	67.85 (5.97)
Total number of prey	7,378	39,231	29,511	22,437
Insecta	**3.81**	**2.03**	**3.05**	**2.36**
Diptera	3.73	1.98	2.83	1.67
Diptera adult	0.04	0.05	0.27	0.16
Diptera pupae	2.34	1.01	1.29	0.36
Diptera larvae	1.34	0.75	0.43	0.45
Hemiptera adult	--	0.01	0.03	0.06
Hymenoptera adult	--	0.01	0.02	0.02
Tricoptera larvae	0.01	0.01	0.02	0.02
Ephemeroptera nymph	--	0.01	--	--
Plecoptera nymph	0.03	0.02	--	0.02
Coleoptera adult	--	0.01	0.00	0.01
Coleoptera larvae	--	0.00	--	0.00
Neuroptera adult	--	--	--	0.01
Unidentified insect	0.04	0.01	0.15	0.54
Crustacea	**96.16**	**97.72**	**96.64**	**96.77**
Copepoda	85.35	94.16	79.70	87.22
Calanoida	53.52	47.77	11.68	8.80
Cyclopoida	28.87	44.96	65.78	76.84
Arguloida	--	0.01	0.01	--
Amphipoda	0.05	0.07	0.14	0.79
Corophiidae	0.01	0.02	0.04	0.29
Corophium spp.	0.01	0.02	0.03	0.21
Corophium salmonis	--	0.01	0.01	0.02
Corophium spinicorne	--	--	0.00	0.05
Gammaridae	0.04	0.05	0.10	0.49
Isopoda	--	0.02	0.00	0.05
Neomysis mercedis	--	0.00	0.00	0.09
Ostracoda	0.04	0.18	0.73	0.20
Cladocera	10.72	3.27	16.05	8.42
Daphnidae	3.77	0.04	0.33	0.08
Bosminidae	0.07	0.11	15.25	8.07
Chydoridae	--	0.00	0.02	0.00
Sida crystallina	0.28	0.02	0.00	0.16
Leptidora kindtii	2.44	0.01	0.01	0.04
Molluska	**0.01**	**0.20**	**0.12**	**0.78**
Corbicula ssp	--	0.16	0.12	0.78
Gastropoda	0.01	0.04	--	0.01
Collembola	--	0.00	0.05	--
Hydracarina	0.01	0.04	0.12	0.05
Araneae	--	--	0.03	0.03
Oligocheta	--	--	--	0.00

Percent Weight

The stomach contents from a subsample of age-0 American shad (n = 689) were processed to determine the ash-free dry weight of consumed prey. By weight, insects accounted for more than a third of the prey consumed by age-0 American shad at all locations except those from John Day Reservoir and Skamokawa (Table 8). The proportional weight of crustaceans was higher than that of insects during all months except October (Table 9). Mollusks contributed less than 2% to the weight of the stomach contents by location and by month. In many samples, there was also a considerable amount of unidentifiable digested material.

Table 8. Diet summary (% by weight) by location for age-0 American shad collected in the Columbia River during 2008. Empty stomachs were physically empty or contained material of no nutritional value. Mean total ash-free dry weight (AFDW) was calculated from the combined prey category AFDW of each fish. Standard deviations are in parentheses. Percent stomach contents are relative to AFDW of prey categories.

Location	Sample size	% Empty	Mean total prey AFDW (mg)	Composition by weight (%)			
				Crustacean	Insect	Mollusk	Other
John Day Reservoir	193	0.0	3.71 (2.90)	60.7	23.2	0.5	15.6
The Dalles Reservoir	167	3.0	4.51 (3.80)	42.4	44.5	0.1	13.0
Below Bonneville Dam	193	1.0	3.75 (2.04)	36.1	42.3	1.9	19.6
Crims Island	102	0.0	5.41 (3.96)	54.1	36.3	1.0	8.6
Cathlamet	5	0.0	6.32 (2.12)	49.5	50.5	0.0	0.0
Skamokawa	29	0.0	2.55 (1.35)	77.0	22.7	0.0	0.2
Overall	689	1.0	4.14 (3.14)	48.7	36.4	0.8	14.0

Shannon Diversity Index

The diversity of prey in the stomach contents of age-0 American shad generally increased with downstream progression of sample sites (Table 10). Overall, the stomach contents of age-0 American shad collected from John Day Reservoir were lowest in diversity of prey, and those from the estuary sites showed the highest diversity. Temporally, prey diversity was relatively high in John Day Reservoir in August but steadily declined during the fall months. In comparison, age-0 American shad collected from estuary locations showed a higher diversity of prey in their stomach contents across all months (Table 11).

Table 9. Diet (% by weight) for major prey categories by month for age-0 American shad collected in the Columbia River during 2008. Empty stomachs were physically empty or contained material of no nutritional value. Mean total ash-free dry weight (AFDW; mg) was calculated from the combined prey categories AFDW of each fish. Fork lengths (FL) are in mm. Standard deviations are in parentheses. Percent stomach contents are relative to AFDW of prey categories.

Month	Sample size	Mean FL	Empty (%)	Total prey AFDW	Composition by weight (%)			
					Crustacean	Insect	Mollusk	Other
August	86	45.57 (9.01)	0.0	2.58 (1.59)	64.0	29.1	0.0	6.8
September	234	54.13 (10.09)	2.1	3.37 (3.42)	58.1	21.6	1.1	19.3
October	236	64.44 (5.51)	0.4	5.16 (2.60)	38.5	47.1	0.3	14.0
November	133	66.84 (6.26)	0.8	4.66 (3.55)	51.6	36.7	1.8	9.9

Table 10. Diversity of prey items by location for age-0 American shad collected in the Columbia River during 2008.

Location	Shannon diversity index (H')
John Day Reservoir	0.224
The Dalles Reservoir	0.342
Below Bonneville Dam	0.357
Crims Island	0.464
Cathlamet	0.471
Skamokawa	0.439
Average	0.383

Table 11. Shannon diversity index (H') of prey items by month in age-0 American shad collected in the Columbia River during 2008. The freshwater estuary includes sampling locations downstream from Bonneville Dam, Crims Island, Cathlamet, and Skamokawa.

Month	John Day Reservoir			Freshwater estuary		
	n	Mean fork length (mm) (SD)	H'	n	Mean fork length (mm) (SD)	H'
August	10	40.07 (3.10)	0.401	20	48.27 (8.43)	0.441
September	23	56.59 (4.84)	0.241	59	59.37 (10.71)	0.339
October	35	63.17 (6.32)	0.228	35	64.18 (5.88)	0.486
November	11	65.62 (7.10)	0.151	52	69.22 (6.00)	0.574
Overall	79	58.67 (9.65)	0.224	166	62.13 (10.46)	0.505

Index of Relative Importance

A subsample of stomachs from age-0 American shad (n = 300) were used to calculate an index of relative prey importance (IRI). The calculated IRI for crustacean prey was considerably higher than that for insect and mollusk prey by location and month (Table 12, Table 13).

Table 12. Index of Relative Importance by location for prey categories in age-0 American shad collected in the Columbia River during 2008. Locations are ordered from upstream to downstream.

		Index of Relative Importance		
Location	Sample size	Crustacean	Insect	Mollusk
John Day Reservoir	77	88.4	11.5	0.0
The Dalles Reservoir	66	80.9	19.1	0.0
Below Bonneville Dam	98	76.9	22.2	0.9
Crims Island	46	74.3	25.5	0.2
Cathlamet	4	69.5	30.4	0.1
Skamokawa	9	80.3	19.7	0.0
Overall	300	80.9	18.9	0.2

Table 13. Index of Relative Importance by month for prey categories in age-0 American shad collected in the Columbia River during 2008.

				Index of Relative Importance		
Month	Sample size	Mean fork length (mm)	(SD)	Crustacean	Insect	Mollusk
August	29	45.74	(8.13)	83.9	16.1	0.0
September	98	55.71	(10.22)	85.9	14.0	0.1
October	87	64.15	(5.79)	78.6	21.4	0.0
November	86	67.72	(5.90)	77.0	22.1	0.8

Adult diet

The stomachs of 37% of adult American shad collected from Bonneville Dam adult fish facility in 2008 (n=37) contained prey whereas 74% of adult fish collected directly from the river by electrofishing or gillnetting (n=407) contained prey. Given the discrepancy, we excluded adult American shad that had been taken from the Bonneville adult fish facility from further analysis.

Corophium spp. were the most commonly occurring prey item (45.9% to 60.4%) in adult American shad at all locations except those captured from the McNary Dam forebay in October where they occurred in only 3% of stomachs sampled (Table 14). Gastropods were the most frequently occurring prey item (46.7%) in the diet of post-spawn adult fish captured in the McNary Dam forebay. Other prey also occurred, but with low frequency, in adult shad from all

locations. Adult shad collected from the estuary near Astoria frequently contained unidentifiable partially digested material. This material was present in large amounts and appeared to be from organisms not encountered in juvenile or adult shad collected anywhere else in the Columbia River during this study. Non food items including bits of wood and fish scales were seen in specimens from all locations.

Adult shad collected from the Columbia River downstream from Bonneville Dam and from The Dalles and John Day reservoirs usually contained fewer than 10 items per fish although individuals were captured that contained between 45 and 75 items (Table 15). The most numerous prey were corophid amphipods. One individual captured in the estuary contained over 200 *Corophium* spp., although most fish collected at that location contained little enumerable prey. Overall, the diet of post-spawn adult American shad contained more mollusks than the diet at other times of the spawning migration (Table 16, Table 17). The stomachs of most post-spawn fish were collected from the McNary Dam forebay on 17 October 2008 (n=30) and contained fewer than 10 prey items, however, four fish had consumed between 20 and 74 snails each and one had consumed over 1,000 copepods and 16 mysid shrimp.

Table 14. Percent frequency of occurrence by location of prey in the diet of adult American shad from the Columbia River during 2008. Bold items are summaries of all organisms of that prey category.

	Saline estuary near Astoria n=53	Downstream from Bonneville Dam n=109	The Dalles Reservoir n=113	Jobn Day Reservoir n=102	McNary Dam forebay n=30	Overall n=407
% empty stomachs	0.0	11.0	21.2	19.6	16.7	15.0
% empty of prey	22.6	40.4	38.1	34.3	43.3	36.1
Insecta	**11.3**	**11.9**	**8.9**	**14.7**	**0.0**	**10.8**
Diptera	3.8	6.4	0.9	2.9	0.0	3.2
Crustacea	**64.2**	**50.5**	**53.1**	**56.9**	**3.3**	**51.1**
Copepoda	15.1	0.9	0.0	0.0	3.3	2.5
Corophiidae	60.4	45.9	48.7	52.0	3.3	46.9
Gammaridae	5.7	12.8	15.9	16.7	3.3	13.0
Isopoda	0.0	0.0	7.1	0.0	0.0	2.0
Neomysis mercedis	3.8	0.0	1.8	3.9	3.3	2.2
Cladocera	1.9	0.9	0.0	2.0	0.0	1.0
Molluska	**5.7**	**2.8**	**2.7**	**2.0**	**50.0**	**6.4**
Corbicula spp.	5.7	1.8	0.9	1.0	6.7	2.2
Gastropoda	0.0	0.9	1.8	0.0	46.7	4.2
Other food items						
Collembola	0.0	0.0	0.0	0.0	6.7	0.5
Hydracarina	0.0	0.0	0.9	2.0	3.3	1.0
Fish parts	0.0	0.0	1.8	1.0	0.0	0.7
Unidentified fish eggs	11.3	2.8	8.0	4.9	0.0	5.7
Non food						
Sand	32.1	21.1	5.3	2.0	50.0	15.5
Vegetation	88.7	57.8	36.3	54.9	56.7	55.0
Wood	62.3	55.0	12.4	19.6	26.7	33.2
Bryozoa statoblasts	0.0	0.0	0.0	2.9	13.3	1.7
Fish scales	0.0	22.0	15.9	4.9	6.7	12.0
Unidentifiable digested material	54.7	13.8	7.1	15.7	26.7	18.7

Table 15. Percent numerical composition by location of prey in the diet of adult American shad from the Columbia River during 2008. Bold items are summaries of all organisms of that prey category.

	Saline estuary near Astoria n=53	Downstream from Bonneville Dam n=109	The Dalles Reservoir n=113	John Day Reservoir n=102	McNary Dam forebay n=30	Overall n=407
% containing prey	77.4	59.6	61.9	65.7	56.7	63.9
Total number of prey consumed	383	293	326	576	1216	2794
Maximum number of prey in an individual	202	46	56	73	1030	1030
Insecta	**0.8**	**3.8**	**0.3**	**0.9**	**0.0**	**0.7**
Diptera	0.5	2.4	0.3	0.7	0.0	0.5
Other	0.3	1.4	0.0	0.2	0.0	0.2
Crustacea	**94.8**	**90.1**	**70.3**	**89.4**	**83.8**	**85.5**
Copepoda	11.7	0.3	0.0	0.0	82.2	37.4
Corophiidae	78.1	85.7	52.8	82.8	0.2	43.0
Gammaridae	3.4	3.4	11.0	2.3	0.1	2.6
Isopoda	0.0	0.0	5.8	0.0	0.0	0.7
Neomysis mercedis	0.8	0.0	0.6	2.4	1.2	1.2
Cladocera	0.8	0.7	0.0	1.9	0.0	0.6
Molluska	**0.8**	**1.0**	**0.9**	**0.2**	**16.0**	**7.3**
Corbicula spp.	0.8	0.7	0.0	0.2	0.2	0.3
Gastropoda	0.0	0.3	0.9	0.0	15.8	7.0
Other food items						
Collembola	0.0	0.0	0.0	0.0	0.2	0.1
Hydracarina	0.0	0.0	0.3	0.3	0.1	0.1
Fish parts	0.0	0.0	2.5	0.0	0.0	0.3
Unidentified fish eggs	3.7	5.1	25.8	9.0	0.0	5.9

Table 16. Percent frequency of occurrence of prey in the diet of adult American shad in the Columbia River during 2008. Bold items are summaries of all organisms of that prey category.

		Adult spawning state					
		Pre-Spawn		Partial-Spawn		Post-Spawn	
	All	Male	Female	Male	Female	Male	Female
	n=407	n=189	n=116	n=56	n=7	n=29	n=10
% empty stomachs	15.0	14.8	10.3	23.2	14.3	10.3	40.0
% empty of prey	36.1	37.0	35.3	33.9	14.3	37.9	50.0
Insecta	**10.8**	**10.1**	**13.8**	**14.3**	**14.3**	**0.0**	**0.0**
Diptera	3.2	2.6	5.2	1.8	14.3	0.0	0.0
Crustacea	**51.1**	**55.6**	**52.6**	**53.6**	**71.4**	**10.3**	**40.0**
Copepoda	2.5	2.6	3.4	0.0	0.0	3.4	0.0
Corophiidae	46.9	51.3	46.6	51.8	71.4	10.3	30.0
Gammaridae	13.0	13.2	9.5	25.0	0.0	6.9	10.0
Isopoda	2.0	2.1	3.4	0.0	0.0	0.0	0.0
Neomysis mercedis	2.2	0.5	2.6	3.6	14.3	3.4	10.0
Cladocera	1.0	0.5	2.6	0.0	0.0	0.0	0.0
Molluska	**6.4**	**1.6**	**5.2**	**1.8**	**14.3**	**48.3**	**10.0**
Corbicula ssp	2.2	0.5	4.3	0.0	14.3	3.4	10.0
Gastropoda	4.2	1.1	0.9	0.0	0.0	44.8	10.0
Other food items							
Collembola	0.5	0.0	0.0	0.0	0.0	3.4	10.0
Hydracarina	1.0	0.5	0.9	0.0	14.3	3.4	0.0
Fish parts	0.7	0.5	0.0	3.6	0.0	0.0	0.0
Unidentified eggs	5.7	3.7	8.6	7.1	14.3	0.0	10.0
Non food							
Sand	15.5	12.2	21.6	0.0	0.0	48.3	10.0
Vegetation	55.0	49.2	64.7	51.8	42.9	62.1	60.0
Wood	33.2	29.1	44.0	26.8	28.6	31.0	30.0
Bryozoa statoblasts	1.7	0.0	0.0	1.8	14.3	10.3	20.0
Fish scales	12.0	13.2	18.1	1.8	0.0	3.4	10.0
Unidentifiable digested material	18.7	14.8	23.3	23.2	0.0	24.1	10.0

Table 17. Percent numerical composition of prey in the diet of adult American shad in the Columbia River. Bold items are summaries of all organisms of that prey category.

		Adult spawning state					
		Pre-spawn		Partial-spawn		Post-spawn	
	All	Male	Female	Male	Female	Male	Female
	n=407	n=189	n=116	n=56	n=7	n=29	n=10
% containing prey	63.9	63.0	64.7	66.1	85.7	62.1	50.0
Total prey consumed	2794	474	675	296	61	1217	71
Maximum number of prey in an individual	1030	46	202	73	20	1030	43
Insecta	**0.7**	**2.1**	**1.2**	**0.3**	**1.6**	**0.0**	**0.0**
Diptera	0.5	1.3	0.9	0.3	1.6	0.0	0.0
Other	0.2	0.8	0.3	0.0	0.0	0.0	0.0
Crustacea	**85.5**	**90.1**	**87.9**	**88.9**	**91.8**	**84.2**	**36.6**
Copepoda	37.4	2.5	5.0	0.0	0.0	82.2	0.0
Corophiidae	43.0	79.5	74.7	82.8	90.2	0.4	22.5
Gammaridae	2.6	5.7	3.7	5.4	0.0	0.4	0.0
Isopoda	0.7	1.7	1.6	0.0	0.0	0.0	0.0
Neomysis mercedis	1.2	0.2	0.7	0.7	1.6	1.2	14.1
Cladocera	0.6	0.4	2.1	0.0	0.0	0.0	0.0
Molluska	**7.3**	**0.6**	**0.9**	**0.0**	**1.6**	**15.6**	**5.6**
Corbicula sp	0.3	0.2	0.6	0.0	1.6	0.1	1.4
Gastropoda	7.0	0.4	0.3	0.0	0.0	15.5	4.2
Other food items							
Collembola	0.1	0.0	0.0	0.0	0.0	0.1	1.4
Hydracarina	0.1	0.2	0.1	0.0	1.6	0.1	0.0
Fish	0.3	0.0	0.0	2.7	0.0	0.0	0.0
Unidentified fish eggs	5.9	6.8	9.9	8.1	3.3	0.0	56.3

Discussion

The characterization of the diet of American shad in the Columbia River provided here increases knowledge of the spatial and temporal aspects of American shad diet from previous investigations. We showed that diet varies among areas and over time, and that fish captured from the river provide a better characterization of the diet than those easily obtained from fish passage facilities at dams. Additional research is still needed to further understand the effect that American shad have on Columbia River food webs and aquatic invertebrate and native fish populations (Independent Scientific Advisory Board 2011), as the physical and biotic environments comprising the home range of Columbia Basin American shad are constantly changing as a result of changes in operations of the hydropower system and as a result of changing climate.

Differences in diet between fish captured from the river and those removed from fish passage facilities are likely due to lack of feeding in fish passage facilities and differential digestion rates for various prey. We suspect that smaller bodied prey such as crustacean zooplankton are digested more quickly than the larger bodied organisms that were more prevalent in the diets of juvenile and adult American shad taken from fish passage facilities.

Previous studies of age-0 American shad feeding have shown diverse diets in East coast rivers, however insects often were the most important prey item (Walburg 1957; Massmann 1963; Grabe 1996; Ross et al. 1997) . Domermuth and Reed (1980) reported that chironomid pupae made up the greatest volume of stomach contents, although cladocerans were the most abundant and most strongly selected for prey item in a 30-km long, wide and slow flowing section of the Connecticut River. In a different section of the same river, Levesque and Reed (1972) found that crustacean zooplankton (cladocerans and copepods) and chironomid pupae and larvae were important prey. Our study showed that both crustacean and insect prey are important in the diet of age-0 American shad in the Columbia River. Organisms from both prey groups occurred in the majority of stomachs sampled. Although differences in frequency of occurrence were small between groups, numbers of crustaceans consumed greatly outnumbered insects consumed. Overall, in 2008, copepods were the most frequently occurring crustacean with cyclopoid and calanoid copepods occurring at similar frequencies. The larval and pupal stages of dipteran insects occurred more often than any other insect. Crustacean zooplankton were the most abundant prey with copepods and cladocerans making up more than 90% of the organisms identified during all months and at all sampling locations except for the freshwater estuary sampling site near Cathlamet. There, insects accounted for more than 18% of prey although the sample size was small (n=4). Numerically, insects were not abundant in the diet of age-0 American shad. However, when considered by weight, insects made up a considerable portion of the diet with some exceptions. At the John Day Reservoir and at the Skamokawa sampling locations insects made up less than a third of the diet by weight in age-0 fish captured. Crustaceans were also important and made up more than 50% of the diet by weight at John Day Reservoir, Crims Island, and Skamokawa sampling locations. The index of relative importance showed that crustaceans were the most important prey type with a maximum value of 88% in the John Day Reservoir. The relative importance of insects increased as age-0 fish moved downstream and approached the estuary. The diet of fish captured at the Skamokawa location, where fish were only sampled once in August, was an exception. An increase in Shannon's index of diversity corresponded with the increasing importance of insects, showing that age-0 American shad consume both insects and crustaceans during their downstream migration rather than ceasing to feed on zooplankton in favor of a diet of insects.

The zooplankton assemblage in the Columbia River is dynamic, with new species, primarily copepods, arriving by ballast water and previously introduced species and native species declining (Cordell et al. 2008). Past studies of the diet of age-0 American shad from the John Day Reservoir have shown that crustacean zooplankton (cyclopoid copepods and cladocerans) were the most important prey (Petersen et al. 2003; Haskell et al. 2006). Haskell et al. (2006) found seasonal variation in age-0 American shad diets that corresponded with seasonal variations in prey abundance of the cladocerans *Daphnia* spp. and *Bosmina longirostris*. In our study, the abundance of *Daphnia* spp. in the diets of age-0 American shad caught in John Day Reservoir peaked in August, similar to the findings of Haskell et al. (2006) for fish sampled in 1994. In 2008, however there was not a spike in *Bosmina* abundance in diets as was described by Haskell et al. (2006) in 1994 and 1995. Furthermore, cyclopoid copepods were the most abundant prey

item during all months of sampling in 2008, despite the August spike in *Daphnia* spp. consumption. In the Columbia River freshwater estuary, calanoid copepods and *Daphnia* spp. were the most important prey items for age-0 American shad during the fall of 1980 (Hammann 1980; McCabe et al. 1983). In our study, age-0 American shad were rarely captured in the area sampled during 1980. Skamokawa was sampled on just one day in August 2008 and calanoid copepods were the most abundant prey item. Two sampling attempts in September at Skamokawa did not capture American shad, so collection efforts were made near Cathlamet. The few fish captured from Cathlamet in September (n=4) showed cyclopoid copepods to be the most abundant prey item, but insects contributed just over 50% of the total weight of stomach contents. In the beginning of October sampling efforts at Cathlamet and near the John Day River just upstream from Tongue Point resulted in the capture of only one age-0 American shad from Cathlamet. This fish had consumed, by weight, mostly insects.

Our study found evidence that adult American shad in the Columbia River feed during their spawning migration. A majority of all adult shad sampled in 2008 contained prey although most of these individuals (80%) consumed fewer than 10 enumerable prey items. Previous research in East coast rivers (Walter and Olney 2003; Harris and McBride 2009) also found that feeding occurred during spawning runs, and that the intensity of feeding, measured by a stomach fullness index, decreased with distance from the ocean.

The benthic amphipod, *Corophium* spp., was consumed more often and in greater numbers than other prey in the Columbia River, although pre-spawn fish captured in the saline estuary contained large amounts of digested material from unidentified organisms. In contrast, pelagic crustaceans (copepods and mysid shrimp) were the dominant prey reported in adult American shad diets on the East coast. The consumption of benthic-oriented *Corophium* spp. improbably suggests benthic foraging by adult shad. Instead, it's likely that consumption occurred during vertical migrations known to occur among these benthic organisms [(Davis 1978; Wilson 1983) cited in (Muir and Emmett 1988)] or perhaps *Corophium* spp. were introduced to the water column as a result of American shad spawning behavior which has been reported to stir sand into the water column in shallow areas (Walburg and Nichols 1967). This may also explain the high occurrence of sand and wood in the stomachs of adult American shad.

Harris and McBride (2009) found American shad eggs in the stomachs of adult American shad sampled in Florida's St. Johns River. We found fish eggs in adult American shad stomachs sampled at all Columbia River locations from late-May to mid-July, however the eggs were not further identified.

The feeding intensity of adult American shad in freshwater increased after the completion of spawning in iteroparous populations of shad on the East coast (Walter and Olney 2003). Post-spawn fish from the Columbia River also fed, although there were a slightly higher percentage of individuals with empty stomachs compared to pre and partial-spawn fish. Most post-spawn fish (77%) reported here were collected in October from the McNary Dam forebay approximately three months after prior sampling of post-spawn adults. The diet of these individuals was considerably different than the diet of post spawn fish sampled earlier in the year and at other locations, as gastropods were more numerous in the diet of these fish. However, there was considerable variability in the diet of these fish as well; one individual had consumed over 1,000 copepods, 15 mysid shrimp, and several amphipods, snails and clams. In aggregate, these results

suggest that there are spatial and temporal influences on the diet of post-spawn adult American shad.

Wendler (1967) reported the presence of juvenile salmon (35mm – 42mm in length) in the stomachs of two spent females dip-netted from the Bonneville Dam forebay. One female contained 16 juvenile salmon and the other contained nine. No date or sample size was reported with this data and it was suggested that the hatchery release of salmon fry in the area of the sampling location could have resulted in a high concentration of salmon available as prey. We identified no salmon in the stomachs of adult American shad sampled during 2007 and 2008. Walter and Olney (2003) reported the infrequent occurrence of fish in adult shad diets. Similarly, only two individuals in our study contained evidence of unidentified fish as prey. The two fish were captured concurrently from The Dalles Reservoir in July; one was a pre-spawn male that contained 12 otoliths from unidentified fish in its stomach and one was a partially spawned male that contained 8 partially digested and unidentified larval fish in its stomach. Thus, it does not appear that juvenile salmon or other fish are a significant source of prey for adult American shad; however they may opportunistically feed on fish if availability is high.

Considering the yearly differences that can occur in zooplankton abundance coinciding with water temperature and flow differences (Haskell et al. 2006), it would be beneficial, in future research, to conduct zooplankton sampling concurrent with the capture of age-0 American shad. This would provide a more accurate description of feeding behavior using the prey availability information to determine a selectivity index.

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Chapter 2
Growth Characteristics and Otolith Analysis on Age-0 American Shad

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Introduction

Otolith microstructure analysis provides useful information on the growth history of fish (Campana and Jones 1992, Bang and Gronkjaer 2005). Microstructure analysis can be used to construct the size-at-age growth trajectory of fish, determine daily growth rates, and estimate hatch date and other ecologically important life history events (Campana and Jones 1992, Tonkin et al. 2008). This kind of information can be incorporated into bioenergetics modeling, providing necessary data for estimating prey consumption, and guiding the development of empirically-based modeling scenarios for hypothesis testing. For example, age-0 American shad co-occur with emigrating juvenile fall Chinook salmon originating from Hanford Reach and the Snake River in the lower Columbia River reservoirs during the summer and early fall. The diet of age-0 American shad appears to overlap with that of juvenile fall Chinook salmon (Chapter 1, this report), but juvenile fall Chinook salmon are also known to feed on age-0 American shad in the reservoirs (USGS unpublished data). Abundant, energy-dense age-0 American shad may provide juvenile fall Chinook salmon opportunities for rapid growth during the time period when large numbers of age-0 American shad are available. Otolith analysis of hatch dates and the growth curve of age-0 American shad could be used to identify when eggs, larvae, and juveniles of specific size classes are temporally available as food for fall Chinook salmon in the lower Columbia River reservoirs. This kind of temporally and spatially explicit life history information is important to include in bioenergetics modeling scenarios. Quantitative estimates of prey consumption could be used with spatially-explicit estimates of prey abundance to construct a quantitative assessment of the age-0 American shad impact on a reservoir food web.

Analysis of the age-0 American shad growth trajectory or individual growth records may show evidence of differential growth rates over time that may be linked to environmental conditions such as water temperature (Leach and Houde 1999, Meekan et al. 2003), size-selective mortality (Folkvord et al. 1997), developmental changes in metabolic rate (Bang and Gronkjaer 2005, Bochdansky et al. 2005), feeding ability (Schmitt and Holbrook 1984, Luecke

1986, Johnson and Dropkin 1995, Johnson and Dropkin 1996), and intra- and inter-specific competition (Crecco and Savoy 1987, Marchand and Boisclair 1998, Gadomski and Wagner 2009). For example, environmental conditions associated with John Day reservoir may eliminate or reduce the availability of many aquatic and terrestrial insect prey types (Rondorf et al. 1990). Many juvenile fishes, including age-0 American shad and juvenile fall Chinook salmon may be foraging on limited insect prey in John Day Reservoir (Gadomski and Wagner 2009). Because larger insect prey has higher energy densities than most zooplankton prey, and insect availability may be limited in John Day reservoir, the growth of American shad may be constrained once fish grow to a size where they could exploit larger, more energy-dense insect prey (Mayer and Wahl 1997).

Similarly, as age-0 American shad grow, they are able to forage on larger zooplankton with higher energy densities than smaller individuals of the same species, or other smaller-bodied zooplankton species (Schael et al. 1991, Mayer and Wahl 1997). Intra- and inter-specific demand for larger-bodied and higher energy zooplankton prey may reduce the availability of these prey items (Tabor et al. 1996). Constrained growth increments on the otolith microstructure of juvenile American shad or other planktivorous fish could help identify important interactions between fishes that may be linked to the year class strength of age-0 American shad and prey partitioning in John Day reservoir.

The objective of this study was to determine time of hatch and size-at-age of age-0 American shad in lower Columbia River reservoirs for use with the American shad and fall Chinook salmon bioenergetic models. Size-at-age data on age-0 American shad can be used to generate quantitative estimates of prey consumption with the American shad bioenergetics model. Otolith microstructure analysis was used to provide reference points on the temporal availability of early life stages and sizes of American shad in the reservoir (Limburg 1996a,b, Limburg et al. 1999). Additional analyses on the age-0 American shad growth trajectory in John Day reservoir may reveal differential growth patterns during the early life history of these fish that are linked to developmental differences between individual fish, transient environmental conditions, or food web constraints (Limburg 1996a).

Study area and fish sampling

Age-0 American shad (n = 620) were collected from late July through early September 2009 at Bonneville Dam and John Day Dam juvenile fish facilities (BONJFF and JDAJFF, respectively) and at in-river sampling sites downstream of McNary Dam (BMCN, river km 465 – 468) and near Crow Butte in John Day reservoir (river km 423). Early larvae were sampled primarily from BONJFF. At the in-river sites, larval and juvenile American shad were collected by beach seine. The seine was 20.73 m long, 1.52 m in height, and had a mesh size of 4.7 mm. We fished nearshore habitats to a depth of approximately 1.2 m. The seine was pulled in a downstream direction, perpendicular to shore with the current, and fished for 2 – 3 minutes per attempt. American shad captured in the seine were immediately removed from the seine, measured for FL and TL with digital calipers, and weighed on a digital scale (0.01). Whole fish were anesthetized with MS-222 and put into vials of 95% ethanol. Samples were transported to the Columbia River Research Laboratory and stored prior to delivery to the Western Fisheries Research Center for otolith analysis.

Early larvae were sampled primarily from BONJFF because these small fish were difficult to collect from in-river sites. Bi-weekly collections of age-0 American shad targeted fish between 10 and 100 mm total length (TL). These collections were divided into nine 10 mm size classes (Table 1). The TL, fork length (FL; mm), and weight (wt; g) of each fish were recorded at the time of sampling. Fish lengths were recorded to a tenth of a millimeter with a digital caliper. Otoliths were dissected from the fish to determine size-at-age and estimate hatch dates. Otolith microstructure analysis was conducted on a representative sub-sample of age-0 American shad from each size class. Fish were sub-sampled by grouping into length classes and then assigning a random number to each sample. We sorted the random numbers numerically and processed $\geq$ 30 samples per length class.

Otolith processing and analysis

Intact left otoliths were processed for microstructural analysis. Right otoliths were substituted when a left otolith was broken in a length class with fewer than 34 samples. Each otolith was embedded in epoxy resin, sulcus-side down and mounted on microscope slides using Crystalbond thermoplastic glue. Excess resin was removed with an Isomet saw. Each sample was ground on a lapping wheel with increasingly finer abrasive slurries to the point where the otolith nucleus (usually a single primordium) was at the surface. Each sample was flipped and ground on the second side until the increments in the analysis area were optimally visualized. Processed otoliths were photographed using a digital camera attached to a compound microscope and examined using ImagePro software by MediaCybernetics. A reference line was drawn from the rostrum through the single nucleus. A transect was then drawn from the reference line to the dorsal edge at an angle of 80° (±5°; Figure 1). Increments show up as alternating dark and light bands on the processed otolith. The increments were interpreted as one day's growth for the fish and marked along the otolith transect according to the methodology of Stevenson and Campana 1992. Under normal conditions, increments are formed daily beginning at hatch in American shad (Hendricks et al. 1990). Following hatch, there are a number of weak increments until onset of exogenous feeding when the increments become more distinct. The increments on each transect were marked, starting at the edge of the core, noting the hatch and first-feed "checks" (prominent marks on the otolith) just outside the core, and continuing to the outer edge of the otolith (Figure 2). The number (age in days since hatch) and distance between increments (increment width corresponding to daily growth) was estimated for each otolith. Each sample was marked and then reviewed by a single reader.

Data analysis

Hatch dates for age-0 American shad were estimated by subtracting the estimated age of a fish from the ordinal date of capture. We used the R statistical program to fit models to the data (R Development Core Team 2008). Growth modeling on age-0 American shad related the explanatory variable age to the response variable total length (TL). Linear and non-linear regressions were used to analyze the growth of age-0 American shad (Campana and Jones 1992). Growth data on age-0 American shad were fit to a simple linear regression:

$$TL = a + bAge,$$

where a is the intercept, and b the slope.

The data were also described using a polynomial regression of the form:

$$TL = a + b_1 Age + b_2 Age^{\wedge 2},$$

where a, b_1 , and b_2 are regression parameters.

A mechanistic model in the form of the non-linear Gompertz growth function (Gompertz 1825, Campana and Jones 1992) with the general equation:

$$TL = ae^{-be(-cAge)},$$

was used to explain the relationship between TL and age; a, b, and c are the parameters to be estimated.

The predicted values from natural log (ln) transformed regressions were back transformed to calculate Akaike's Information Criterion (AIC). Models were evaluated for excessive skew or kurtosis, and compared using AIC:

$$AIC = n \log(RSS/n) + 2K,$$

where *RSS* is the residual sum of squares and *K* is the number of parameters in the model. Delta-AIC (Δ-AIC) was calculated for each model as follows:

$$Delta\ AICi = \Delta i = AICi - minAIC,$$

where minAIC is the AIC value of the "best" model (i.e. the model with the lowest absolute AIC value; Mazerolle 2006). The best model was selected based on how well the model fit the data (r^2) and AIC and Δ-AIC values for the best and alternative models.

Results

Length and age data on age-0 American shad are summarized in Table 1. The smallest size class of American shad ranged from 10.0 – 19.9 mm TL and the largest class was from 90.0 – 99.9 mm TL (Table 1). Hatch dates ranged from 19 June to 29 July, 2009. Based on mean daily water temperatures from John Day Dam tailrace during this time period (www.cbr.washington.edu/dart; accessed 17 Dec 2010), adult American shad spawned at temperatures between 15.9 and 21.4 °C and larvae hatched at temperatures between 16.9 and 22.8 °C. At the time of collection, the youngest larva in the sample was 6 days old with a TL of 13.4 mm and the oldest fish was 66 days old with a TL of 96.1 mm.

A scatterplot of age versus TL indicated that the growth of age-0 American shad had a linear or slightly sigmoidal growth trajectory (Figure 3). Total length data were non-normally distributed (Shapiro-Wilk; $W = 0.9571$, $p < 0.0001$). Age was also non-normally distributed (Shapiro-Wilk; $W = 0.9723$, $p < 0.0001$). Natural log transformation was used to stabilize the heteroscedastic variances.

The descriptive polynomial regression model with ln transformed TL and age values (LM6) produced the best fit for age-0 American shad growth with an r^2 value of 1 ($p < 0.0001$). Least squares AIC identified LM6 as the "best" model (–601.99; Tables 3 and 4; Figure 4). A simple linear model with ln transformed TL and age (LM3) produced the next best fit (r^2 of 0.99; $p <$ 0.0001) and an AIC value of 229.57 (Tables 3 and 4). The delta-AIC value of LM3 (831.56) indicated this model had considerably less support than LM6. A Δ-AIC < 2 suggests good evidence for the alternative model. Models with Δ-AIC values between 3 and 7 are less likely,

and values > 10 indicates very poor evidence for the model (Burnham and Anderson 2002:70; Mazerolle 2006). By definition, the "best" model, in this case LM6, has a Δ-AIC of 0.

Discussion

In this study, we found that a polynomial regression model with ln transformed TL and age values described the growth of larval and juvenile age-0 American shad better than the non-linear Gompertz growth function with ln transformed TL. The Gompertz model was previously used to describe the growth of larval and juvenile American shad from the Connecticut River (Crecco et al. 1983).

Among the age-0 American shad that were aged, the size class of fish between 30.0 and 39.9 mm TL (n = 34) were of interest. Diet analysis on a small number of juvenile fall Chinook salmon (n = 13) collected from John Day Reservoir in 1996 indicated that these fish were feeding on this size class of American shad. In the summer of 2009, American shad within this size class were collected at JDAJFF and Crow Butte between 3 Aug and 20 Aug, 2009. Age estimates indicated these fish hatched between 4 July and 23 July. These fish ranged from 22 to 37 days old on the day they were collected.

Size-at-age data from the age-0 American shad growth trajectory can be used to make quantitative estimates of prey consumption by age-0 American shad when the bioenergetics model is validated (Chapter 3, this report). This type of quantitative consumption data is useful in the construction and analysis of complex reservoir food web interactions.

Use of otolith microstructure analysis to determine the hatch date, age, and the growth rate of age-0 American shad can provide valuable information for use in developing bioenergetics modeling scenarios to test various hypotheses about age-0 American shad and their interactions with other species. In this study, otolith ages were used to identify when and at what temperature age-0 American shad hatched in Columbia River reservoirs. From this information, we determined the approximate dates when specific size classes of age-0 American shad became available to juvenile fall Chinook salmon in lower Columbia River reservoirs.

Additional information can be extracted from the otoliths collected on age-0 American shad in 2009. The otoliths could provide information on estimates of individual metabolic rates (Gronkjaer and Schytte 1999; Bang and Gronkjaer 2005) and growth trajectories, daily growth rates, mortality rates, and hatching intervals to determine spawning intensity and duration. Determining the effect of environmental conditions on the differential mortality of early larvae might be particularly useful information. In the Connecticut River, adult recruitment was highly correlated with the year class strength of juvenile American shad four to six years earlier (Crecco et al. 1983). Crecco and Savoy (1984) determined that year class strength was established prior to the juvenile life stage in American shad, and that larval growth and survival were highly correlated with water temperature in the Connecticut River. The strong correlation between larval mortality and temperature suggests otolith techniques could be used as a tool to rapidly evaluate American shad recruitment (Crecco and Savoy 1985, 1987).

Similarly, otolith- derived growth information on American shad in the Columbia River could be used with bioenergetics modeling (Chapter 3, this report) to explore larval growth under various temperature and feeding conditions. A better understanding of American shad larval

mortality under different temperature, flow, and foraging conditions in Columbia River reservoirs could provide a basis for predicting in-season year class strength of juvenile American shad. Order of magnitude predictions on year class strength could be used with bioenergetics modeling to estimate the potential in-season ecological impacts of age-0 American shad on predatory fish populations, zooplankton dynamics, and nutrient input. One technical product of this bioenergetics modeling could be in-season guidance to management agencies on the level of control measures applied to predatory fish populations in the reservoirs, based on the predicted in-season mortality of larval American shad.

Most years, between 1 and 2.5 million adult American shad pass Bonneville Dam to spawn in the lower Columbia River reservoirs (www.FPC.org; accessed 11/2/2010); however, adult runs of $\geq$ 4 million fish were observed for years 2003 through 2006). The ability to predict future run sizes of adult American shad using larval mortality estimates appears to be feasible and could assist in the development of management strategies for this non-native species in the Columbia River.

The strong correlation between temperature, flow, and the early larval survival of American shad (Crecco and Savoy 1985, 1987) suggests that warmer water temperatures and lower flows due to impoundment have supported the survival of larval American shad in the Columbia River (Ebel et al. 1989, Quinn and Adams 1996, Petersen et al. 2003). In the Connecticut River, the growth rate and survival of early larval stages of American shad increased steadily as seasonal water temperatures rose from 15 to 20 °C (Crecco and Savoy 1985).

The spawning migration of American shad has also responded to changing thermal conditions in the Columbia River. Quinn and Adams (1996) found that the annual timing of adult American shad passage at Bonneville Dam is highly correlated with water temperature. As the thermal regime of the Columbia River has warmed in response to impoundment and climatic conditions (Ebel et al. 1989, Beamish et al. 1999), the American shad spawning migration has passed Bonneville Dam earlier in the spring (Quinn and Adams 1996). The spawning migration now occurs more than five weeks earlier than in the past (Quinn and Adams 1996). Warmer water temperatures are associated with the expansion of American shad in lower Columbia River reservoirs as well (ISAB 2011).

Because the spawning migration of adult fish and early survival of larval American shad are both strongly linked to water temperature, future reservoir warming due to climate change could alter the hatch timing, growth rates, and overall survival of age-0 American shad as well as their impact on salmonids and other native fishes in the Columbia River. Based on historic patterns, the timing of the American shad spawning migration at Bonneville Dam may continue to advance as the Columbia River thermal regime responds to climatic warming (Quinn and Adams 1996). Lower Columbia River water temperatures increased at a rate of 0.38 °C per decade or about 1.9 °C from years 1953 – 1998 (NRC 2004). Although some of this temperature increase occurred in response to dams, river impoundment, and water withdrawal in the Columbia River Basin, average air temperatures in the Pacific Northwest warmed 0.6 – 1.7 °C over the 20th century (Mote et al. 1999) suggesting that climate change was responsible for some of the warming observed in Columbia River water temperatures (NRC 2004). Air temperatures will continue to increase with a warming climate (ISAB 2011). Climate models project air temperature increases in the Pacific Northwest for 2045 of about 1 to about 4 °C for individual months (NRC 2004). Because the upper thermal tolerance of salmonids (~ 20 – 24 °C, Mohseni et al. 2003) is lower than that of American shad (Stier and Crance 1985), warmer water

temperatures in the lower Columbia River that adversely impact native salmonids will still be within the optimal temperature range for larval and juvenile American shad. Warmer spring water temperatures in the lower Columbia River will result in earlier emergence and faster growth of age-0 American shad. These temporal changes in the American shad life history in the Columbia River could result in important shifts in reservoir food webs that directly and indirectly affect native salmonids. Combining otolith microstructure analysis and bioenergetics modeling provides a flexible and rigorous platform for investigating how climate change could potentially affect interactions between American shad, predatory fishes, and native salmonids in the Columbia River.

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Table 1. Number (*N*) of age-0 American shad collected in 2009, mean total length (TL) of the full sample, number (*n*) of fish sub-sampled for aging, mean total length (TL; mm) of the sub-sample, median age and age range by size class. Standard deviations of the lengths are in parentheses.

Size class (mm)	*N*	Mean TL (mm): full sample	*n*	Mean TL (mm): sub sample	Median age (days)	Age range (days)
10-19	5	16.8 (2.8)	5	16.8 (2.8)	8	6-11
20-29	139	23.8 (2.3)	35	24.0 (2.3)	17	10-24
30-39	96	34.9 (2.6)	34	34.2 (2.6)	26	22-37
40-49	60	44.6 (2.6)	36	44.6 (2.6)	37	29-44
50-59	45	55.4 (2.8)	34	55.1 (2.8)	39	32-46
60-69	90	66.1 (2.9)	33	66.3 (2.7)	46	38-52
70-79	123	74.4 (2.8)	32	75.3 (2.7)	51	42-63
80-89	54	84.0 (2.7)	37	83.9 (2.7)	58	48-64
90-99	8	95.0 (2.4)	7	95.3 (2.3)	59	50-66
Total	620	52.1 (22.11)	253	55.1 (21.91)	40	6-66

Table 2. Mean, standard deviation (SD), and median (Med.) of the total lengths of age-0 American shad ($n = 253$) by collection date and location. BONJFF = Bonneville Dam juvenile fish facility, JDAJFF = John Day Dam juvenile fish facility, BMCN = below McNary Dam in John Day Reservoir (RM 289 – 291). Crow Butte is at river km 423 in John Day Reservoir. These data were used to model the growth of American shad in John Day reservoir.

Date	*N*	Location											
		BONJFF			JDAJFF			Crow Butte			BMCN		
		Mean	SD	Med.	Mean	SD	Med.	Mean	SD	Med.	Mean	SD	Med.
Jul 23	8										23.0	1.5	23.7
Jul 28	10										20.9	3.7	22.4
Aug 3	21				55.4	10.4	59.0						
Aug 5	16	23.1	3.2	22.8									
Aug 6	30				35.3	8.7	33.2						
Aug 6	4							32.9	2.4	32.5			
Aug 13	28				54.0	10.5	53.5						
Aug 17	27				62.6	14.4	58.7						
Aug 20	28							43.2	3.3	43.7			
Aug 31	23				81.1	9.1	80.2						
Sep 3	38				79.4	9.1	81.8						
Sep 10	20				75.8	6.1	75.5						

Table 318. Parameter estimates, standard error (*SE*), *t*-value, and probability of obtaining a greater *t*-value by chance for the linear regression model LM3 and the polynomial regression model LM6 on age-0 American shad.

Model	r^2	Parameter	Estimate	SE	*t*-value	$p > \|t\|$
LM3	0.99	*a*	1.8346	0.03328	55.12	<0.0001
		b	1.349522	0.0008038	1678.90	<0.0001
LM6	1.00	*a*	10.4018	0.02145541	484.8	<0.0001
		b	0.795014	0.015936	49.89	<0.0001

Table 4. Akaike's information criteria (AIC) and delta-AIC (Δ-AIC) were used to quantify the fit of linear, descriptive polynomial, and mechanistic non-linear regression growth models to age-0 American shad total length versus age data. Natural log (ln) transformation of the total length and age variables were used in some models; predicted values were back-transformed prior to applying AIC. Smaller AIC values indicate statistically better fits.

Model	Number of Parameters	AIC	Δ-AIC
Linear regression			
LM1: TL = a + bAge	2	1010.65	1612.64
LM2: LnTL = a + bAge	2	964.00	1565.99
LM3: LnTL = a+bLnAge	2	229.57	831.56
Polynomial regression			
$LM4: TL = a + b_1Age + b_2Age^2$	3		
$LM5: LnTL = a + b_1Age + b_2Age^2$	3	475.85	1077.84
$LM6: LnTL = a + b_1LnAge + b_2LnAge^2$	3	-601.99	0
Non-linear regression (Gompertz)			
$NLM1: TL = ae^{-be(-cAge)}$	3	1003.53	1605.06
$NLM2: LnTL = ae^{-be(-cAge)}$	3	581.26	1183.25

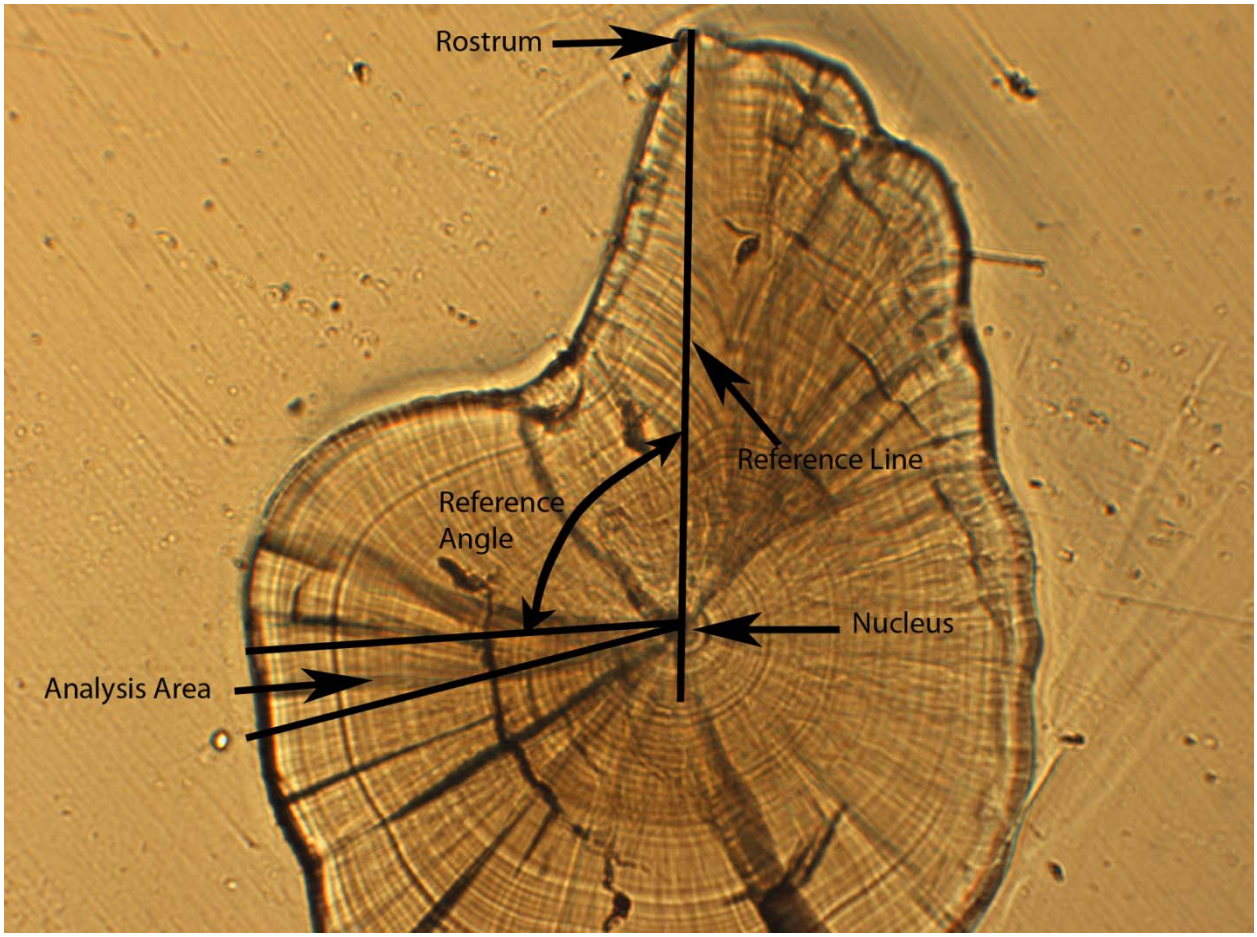

Figure 1. A juvenile American shad otolith with labeled microstructural elements.

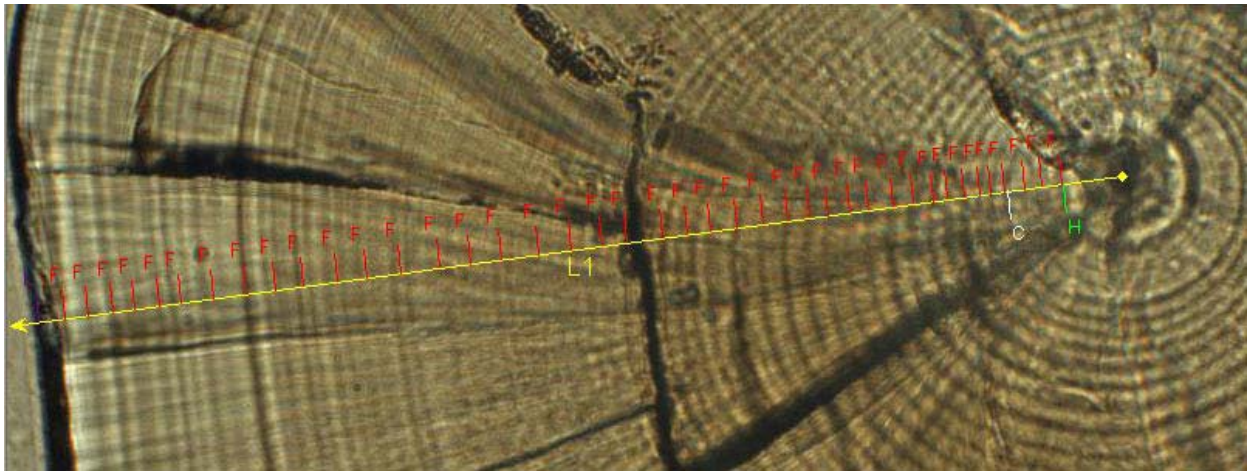

Figure 2. An age-0 American shad otolith with certain microstructural features marked: H=hatch check, C=first feed check, F=daily increments. This fish was captured August 3, 2009, giving a hatch date of June 23 and estimated spawning date of June 18.

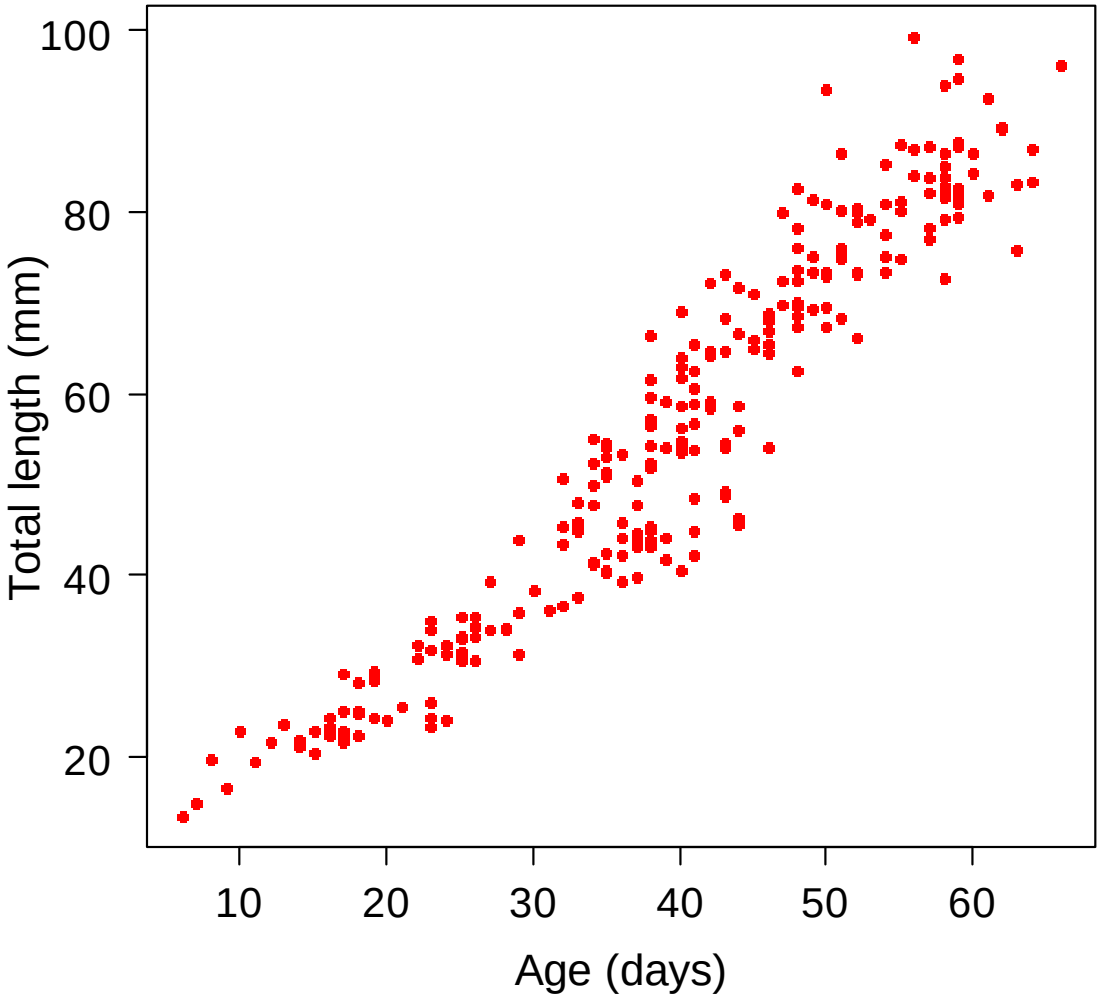

Figure 3. Scatterplot of age versus total length of age-0 American shad collected from lower Columbia River reservoir locations.

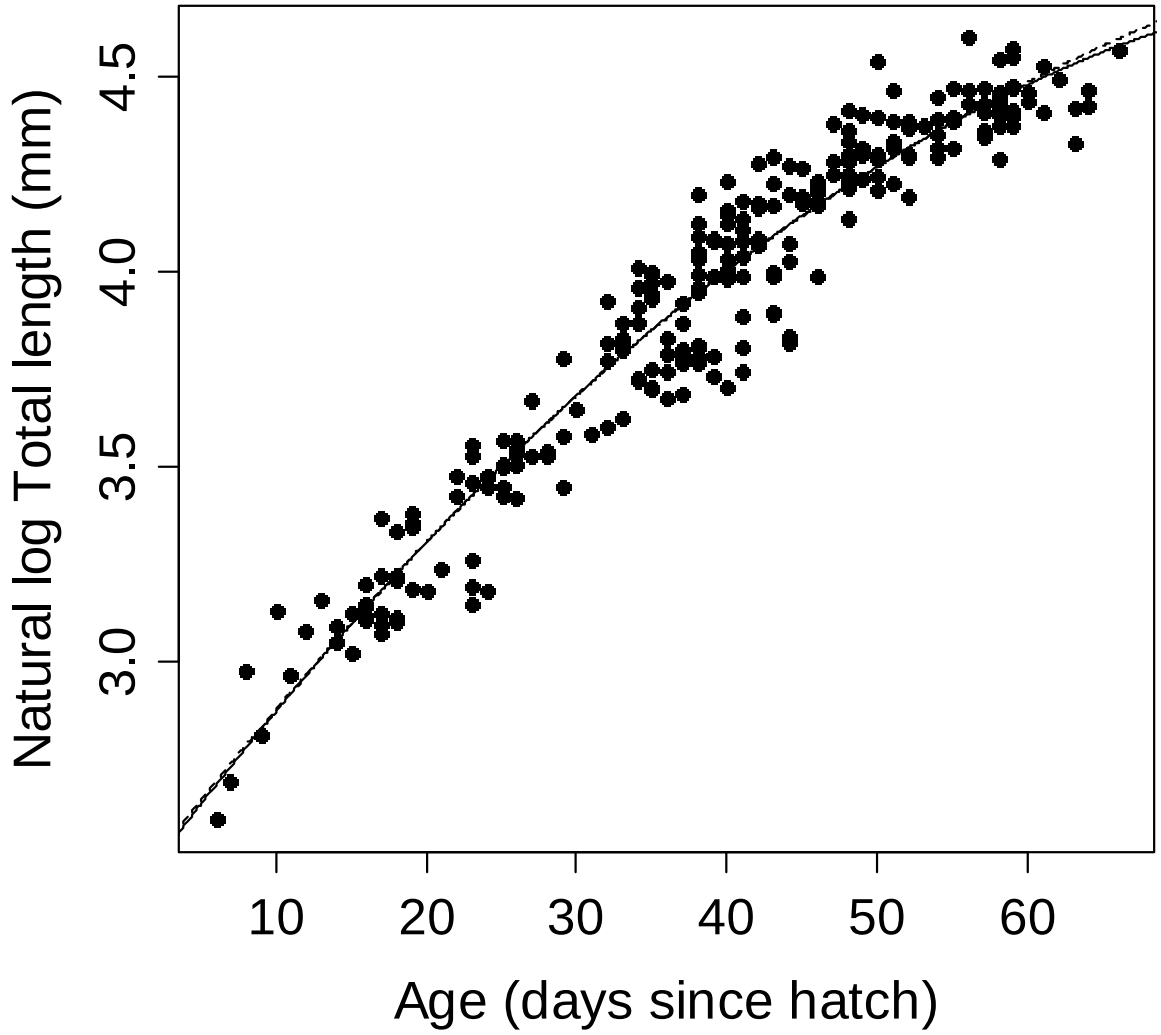

Figure 4. Non-linear Gompertz growth function (dotted line) and polynomial regression with quadratic term (solid line) fitted to the age versus ln transformed total length of age-0 American shad.

Chapter 3
Development of a Bioenergetics Model for age-0 American Shad

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Introduction

Bioenergetics modeling can be used as a tool to investigate the impact of non-native age-0 American shad (*Alosa sapidissima*) on reservoir and estuary food webs. The model can increase our understanding of how these fish influence lower trophic levels as well as predatory fish populations that feed on juvenile salmonids. Bioenergetics modeling can be used to investigate ecological processes, evaluate alternative research hypotheses, provide decision support, and quantitative prediction. Bioenergetics modeling has proven to be extremely useful in fisheries research (Ney et al. 1993,Chips and Wahl 2008, Petersen et al. 2008). If growth and diet parameters are known, the bioenergetics model can be used to quantify the relative amount of zooplankton or insects consumed by age-0 American shad. When linked with spatial and temporal information on fish abundance, model output can guide inferential hypothesis development to demonstrate where the greatest impacts of age-0 American shad might occur.

Bioenergetics modeling is particularly useful when research questions involve multiple species and trophic levels (e.g. plankton communities). Bioenergetics models are mass-balance equations where the energy acquired from food is partitioned between maintenance costs, waste products, and growth (Winberg 1956). Specifically, the Wisconsin bioenergetics model (Hanson et al. 1997) is widely used in fisheries science. Researchers have extensively tested, reviewed, and improved on this modeling approach for over 30 years (Petersen et al. 2008). Development of a bioenergetics model for any species requires three key components: 1) determine physiological parameters for the model through laboratory experiments or incorporate data from a closely related species, 2) corroboration of the model with growth and consumption estimates from independent research, and 3) error analysis of model parameters.

Wisconsin bioenergetics models have been parameterized for many of the salmonids and predatory fishes encountered in the lower Columbia River (Petersen and Ward 1999). The Wisconsin bioenergetics model has not been developed for American shad, however Limburg (1996) parameterized a simplified bioenergetics growth model for this species. A common application for the Wisconsin bioenergetics model is to estimate the consumption or growth of a fish population under different temperature and feeding scenarios (Ney 1993). One advantage of the bioenergetics approach is that consumption can be estimated without direct field

measurements of predation rate (prey·predator^{-1}· day^{-1}; Petersen and Ward 1999). Field estimates of fish consumption are time consuming and costly to determine, and estimates may show wide variance due to environmental and sampling variability. However, the consumption parameters used in a newly developed bioenergetics model must be verified with field and laboratory estimates of consumption (Ney 1993).

The objective of this research was to parameterize a Wisconsin bioenergetics model for age-0 American shad using published physiological data on American shad and closely related alosine species. The American shad bioenergetics model will be used as a tool to explore various hypotheses about how age-0 American shad directly and indirectly affect Columbia River salmon through ecological interactions in lower Columbia River food webs. One over-arching focus of the larger research project was to identify potential interactions between age-0 American shad and juvenile salmonids, addressing potential outcomes through bioenergetics modeling scenarios. This report contains two bioenergetics modeling applications to demonstrate how these models can be used to address management questions and direct research effort. The first modeling application uses the American shad bioenergetics model described in this report to explore prey consumption by age-0 American shad (Chapter 1, this report). Dietary data on age-0 American shad and previously published reports on the diet of juvenile fall Chinook salmon (Rondorf et al. 1990, USGS unpublished data) suggested there might be considerable dietary overlap between these species in the lower Columbia River. The U.S. Geological Survey (USGS) was interested in using the American shad bioenergetics model to explore hypotheses concerning dietary overlap between age-0 American shad and emigrating fall Chinook salmon. The second modeling application uses the fall Chinook salmon bioenergetics model (Koehler et al. 2006) to explore the growth potential of juvenile fall Chinook salmon predating on age-0 American shad in the lower Columbia River. This modeling was based dietary information on a small number of age-0 fall Chinook salmon (n = 13) collected in John Day Reservoir in 1994 - 1996 (unpublished USGS data). Analysis of this dietary data found that these salmonids were feeding primarily on age-0 American shad (> 75% by weight).

Model variables

External variables are input into parameterized bioenergetics models to create temporally and spatially unique model runs. External variables include the diet, growth, prey energy densities, and the thermal experience of fishes. These external variables are specific to the species under investigation and study area.

Temperature

Current and historic mean daily water temperature records from the mainstem Columbia River and its tributaries were accessed online at www.cbr.washington.edu/dart. Modeled predictions for stream temperature under various climate scenarios were accessed online at cses.washington.edu/cig. Temperature records are important external variables in bioenergetics modeling because the rates of physiological processes are temperature dependent (Ney 1993).

Diet

Temporal and spatially explicit dietary data on age-0 American shad (Chapter 1, this report) were collected bi-weekly at five in-river sampling locations from late July through mid-November, 2008. Diet sampling was conducted at Skamokawa (river km 56), Crims Island (river

km 89), and downstream of Bonneville (river km 227-230), John Day (river km 344 - 348), and McNary (river km 467 - 470) dams.

Energy densities

Age-0 American shad (n = 208) were collected bi-weekly for energy density determination (joules/g wet weight) at Bonneville (7 Sept - 31 Oct, 2001) and McNary (22 Aug – 5 Dec, 2001) dam juvenile fish facilities (USGS unpublished data;Table 1). Fish were stored at –70°C until the analyses were performed. Energy density was determined following the method of Hartman and Brandt (1995). Up to 15 juvenile American shad (range 2 – 15 fish) were analyzed for energy density from each weekly sample at each location.

Energy densities were subset by fish size and sample timing. Small American shad were classified as ≤ 110 mm at McNary (range 37 – 109 mm) and ≤ 130 mm at Bonneville (range 79 - 124 mm). Large fish were classified as > 110 mm (range 112 – 139 mm) and > 130 mm (range 143 – 187 mm) at McNary and Bonneville, respectively. Biweekly sampling periods were grouped as early (Aug 22 – Oct 15 at McNary; Sept 7 – 30 at Bonneville) and late (Oct 16 – Dec 5 at McNary; Oct 1 – 31 at Bonneville) periods (Table 1). Because age-0 American shad feed on lower trophic levels but are also prey for larger piscivorous fishes, the energy densities of age-0 American shad can be used in bioenergetics models for predatory fish as well as the American shad bioenergetics model.

Growth

The growth trajectory of age-0 American shad (Chapter 2, this report) was determined from the otoliths of fish collected at Bonneville and John Day Dam juvenile fish facilities (BONJFF and JDAJFF, respectively) and at in-river sampling sites downstream of McNary Dam (BMCN, river km 465 – 468) and near Crow Butte in John Day reservoir (river km 423) from late July through early September 2009.

Model development—internal parameters

The first step toward developing a Wisconsin-style bioenergetics model for American shad involved a thorough literature review of existing consumption and respiration estimates for these fish (Table 2). In addition to a literature review, I collaborated with fisheries researcher Dr. Karin Limburg at New York state university in Saracuse to obtain raw data on American shad physiology. This data was used to facilitate internal parameter selection for the bioenergetics model and support model validation. New models may incorporate existing parameters from a closely related species or combine parameters from a closely related species with published values. In some instances, using physiological parameters from a closely related species may be feasible when physiological parameters are not available on the species of interest (Petersen et al. 2008). The literature review was expanded to include pertinent physiological data on other alosines including alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*) as well as other members of the Clupeidae family including herring (*Clupea harengus*) and gizzard shad (*Dorosoma cepedianum*; Table 2).

Published values for American shad were compared to published parameter values for closely related fishes (Table 2). Published parameter estimates were applied to model equations to calculate and compare intermediate values of parameter components when a published parameter on American shad differed substantially from other estimates. Through this parameter selection process, many of the parameter estimates published in the Wisconsin bioenergetics model for alewife (Stewart and Binkowski 1986) were identified as possible values for an American shad model (Tables 3 and 4). For example, the swimming speed of age-0 American shad (Katz 1978) contributed to parameter values in the alewife model. Many of the published parameter values for various clupeid physiological rates were similar. This observation supported the use of the alewife parameter values in the American shad bioenergetics model. The physiological parameter values for juvenile alewife published by Stewart and Binkowski (1986) tended to lie in the mid-range of all published values investigated for clupeids.

Limburg's (1996) parameter estimates for the temperature algorithm $f(\theta)$ for consumption published by Thornton and Lessem (1978) were also included in the Wisconsin-style American shad bioenergetics model (Table 3). Other parameters used in the Limburg (1996) model could not be adapted to the Wisconsin model because multiple parameters were combined into a single value. A hybrid bioenergetics model was developed for American shad using parameter estimates from the Wisconsin alewife model (Stewart and Binkowski 1986) with the Thornton and Lessem (1978) temperature parameters for age-0 American shad determined by Limburg (1996; Tables 3 and 4).

Model corroboration

Statistical comparison of model predictions with observed laboratory and field measurements of growth and consumption are used to corroborate the accuracy of model parameters. Validating model output with empirical measurements is particularly important when a bioenergetics model will be used for quantitative food web assessments (Hansen et al. 1993, Ney 1993, Chipps and Wahl 2008). Bioenergetics applications which involve quantitative food web assessments estimates fish consumption of various prey species in grams of prey per grams of predator per day (g/g/d).

The American shad bioenergetics model predictions were evaluated against field and laboratory estimates of consumption and growth. Field estimates of consumption were determined for age-0 American shad collected in John Day reservoir of the Columbia River in 1994 and 1995 (USGS unpublished data). Evacuation rate and daily ration of age-0 American shad were estimated following the method of Eggers (1977, 1979).

During field trials, juvenile American shad were collected with a 12 m long monofilament mesh trawl with a 4.6 m^2 opening. Nine trials were conducted over 24-hour time periods from August to November each year. The trawl was towed upstream, parallel to shore for a period of 10 minutes covering a distance of about 2300 m. All fish were collected in the mainstem Columbia River from a five-kilometer stretch downstream of Arlington, OR (river km 382-387). Up to 15 fish were collected every four hours, with the initial fish collection time repeated to achieve seven fish collections within a 24-hour trial period. Captured fish were immediately frozen using liquid nitrogen and stored at -80 °C prior to examination of the stomach contents.

The weights of the stomach content of fish were determined in the laboratory. Thawed fish were measured to the nearest millimeter fork length and weighed to the nearest 0.0001 g. The

stomach contents of fish were removed with the aid of a dissecting microscope, placed in aluminum drying pans, and dried for 24 hours at 60°C in an oven. After removal of stomach contents, fish bodies were also dried and their weight recorded to the nearest 0.0001 g. These data were used to estimate daily mean ration (D; Eggers 1979):

$$D = F * R * 24 + (S_{24}-S_0),$$

where S is the weight of the stomach contents (Hayward et al 1991, and Tudor 2001), F is mean gut fullness of all fish during a trial and R is the evacuation rate during the trial. Daily ration was calculated in g dry/100 g wet fish/d for comparison to other studies (Boisclair and Leggett 1988). Evacuation rate (R) was calculated as the greatest exponential decrease in F (mean gut fullness) between two successive sample periods within a trial:

$$R = \ln F_{(t+1)} - \ln F_t / T,$$

where F is a ratio calculated from the grams stomach weight divided by the grams fish weight ($G_t/W_{t)}$,and T is the time period between two trials. The ratio F was calculated as g prey/g fish in terms of dry g/dry g, wet g/wet g, and dry g/100 wet g. Because the wet weight of stomach contents was not measured directly, the method of Rieman and Falter (1981) was used to convert dry weight to wet weight.

Laboratory estimates of consumption for age-0 American shad were derived from raw data collected by Limburg (1994). Limburg's study consisted of an initial period when all fish were held at ~ 22° C for 10 days, and five subsequent growth periods, when fish were divided into 18 experimental tanks. Experimental tanks were held at constant temperatures between 14 – 29 °C. Consumption estimates were calculated for one 13 day growth period. The number of fish in each tank ranged from 149 - 167 during this growth period. We estimated consumption (g/g/d) from Limburg's raw laboratory data using the mean weight of fish in each tank over the experimental period, the rations consumed per fish for each tank, and the number of days of the experiment.

Visual comparisons of model predictions were made with corresponding field and laboratory consumption estimates using scatter, line, regression, and box plots. Statistical analyses were used to evaluate how well observed field and laboratory consumption estimates matched predicted values generated by the bioenergetics model. Summary mean and standard deviation estimates were calculated for observed field and laboratory consumption and predicted consumption values. The Shapiro-Wilks normality test was applied to the observed data. Paired *t*-tests were used to detect significant differences between observed and predicted values.

Mean square error (*MSE*), mean absolute error (*MAE*), mean absolute percentage error (*MA%E*), and regression coefficients (r^2) were calculated to evaluate the simple linear regressions from observed and predicted values. The location of the regression lines with respect to regression coefficients for an intercept = 0 and slope = 1 (perfect fit) were determined with *t*-tests. *MSE* represents the variance around the perfect fit (Theil 1961). Statistical decomposition of the *MSE* (Theil 1961, Rice and Cochran 1984, Wahl and Stein 1991, Chipps and Wahl 2004)

was used to evaluate sources of error and the degree of systematic error in model predictions. Decomposition of the *MSE* is expressed as:

$$MSE = (1/n)\sum_{i=t}^{n}(P_i - A_i)^2$$
$$= (\bar{P} - \bar{A})^2 + (S_P - rS_A)^2 + (1 + r^2)S_A^2$$
$$= Z + S + R,$$

where n is the number of paired observations; P_i and A_i are the predicted and observed values, respectively; $\bar{P}$, $\bar{A}$, S_P, and S_A are the means and standard deviations of P_i and A_i, respectively; r is the correlation coefficient; Z is the error associated with the difference between the predicted and observed mean values; S is the slope error when the slope deviates from unity (slope = 1) and error component R is residual error. Mean (Z) and slope (S) error values indicate the level of systematic error and should be near 0, while residual (R) error should be near 1.

Bonferroni joint confidence intervals (*CI*) were used to assess bias by testing the null hypothesis that the regressions of observed on predicted values included intercepts of 0 and slopes of 1 (Neter et al. 1983, Chipps and Wahl 2004). We used the reliability index (RI) developed by Leggett and Williams (1981) to evaluate the acceptability of the model. This index is a number $k \geq 1$ determined from model predictions and the corresponding set of observations; the number k is calculated as follows:

$$k = \frac{1+\sqrt{\frac{1}{n}\sum_i^n [(1-\frac{A_i}{P_i})/(1+\frac{A_i}{P_i})]^2}}{1-\sqrt{\frac{1}{n}\sum_i^n [(1-\frac{A_i}{P_i})/(1+\frac{A_i}{P_i})]^2}},$$

where P_i represents model predictions and A_i represents observed estimates from the field and laboratory studies. Using the reliability index, model predictions are interpreted as agreeing within a factor of k of the observed values (Leggett and Williams 1981, Rice and Cochran 1984, Wahl and Stein 1991). Statistically, to agree within a factor of k, all observations would be expected to lie between 1/k times the predicted value and k times the predicted value 68% of the time (Leggett and Williams 1981, Rice and Cochran 1984, Wahl and Stein 1991).

Bioenergetic model simulations of observed laboratory and field measures

Empirical measurements of fish weight and the mean daily water temperature observed during the independent field study were used with dietary information collected on age-0 American shad (Chapter 2, this report) to construct model simulations of the daily consumption of age-0 American shad. Model simulations generated daily consumption predictions for comparison with the calculated estimates reported in the field study. Daily consumption (g/g/d) was predicted with the American shad bioenergetics model under the observed diet of age-0 American shad in John Day reservoir (Table 5) and the mean weight of fish and mean daily temperature for each field sampling date (Table 6). The mean values ($\pm$ SD) for predicted and observed field consumption (g/g/d) were 0.090 (0.020) and 0.077 (0.028), respectively (Table 7). The data were normally distributed. The paired *t*-test for observed field versus predicted values

indicated modeled predictions of consumption were not significantly different from observed values (*t*-test; $t = 1.70$; $df = 8$; $p = 0.1266$). Linear regression was used to generate a regression coefficient (r^2) between the observed field estimates (A) of age-0 American shad consumption and predictions (P) generated by the American shad bioenergetics model (Table 7; Figure 1). The result of the regression of field estimates of daily consumption on modeled predictions was: $P = -0.002433 + 0.88203 \cdot A$, ($r^2 = 0.389$; $F = 4.46$; $p = 0.0726$). The intercept was not significantly different from 0 (*t*-test; $t = -0.05$, $df = 1$, $p = 0.96$) and the slope was not significantly different from 1 (*t*-test; $t = 2.11$, $df = 1$, $p = 0.07$). The *t*-test of the intercept = 0 hypothesis indicated there was no consistent systematic deviation in the model predictions from the observed field estimates (Table 7). Furthermore, there was no significant difference in the slopes of the observed and predicted values, therefore the observed and predicted values are assumed to not differ in sensitivity. These conclusions are supported by the Bonferroni joint CI for the intercept and slope of the regression of field vs. modeled consumption because the 95% CI for intercept and slope include 0 and 1, respectively, as possible values (Table 8). Decomposition of the *MSE* for the field regression produced estimates of the mean, slope, and residual errors that indicated the errors were not systematic. The reliability index for the field versus predicted values was 1.0.

Similarly, daily consumption (g/g/d) estimates calculated from Limburg's (1994) laboratory experiments were compared with model predictions. The mean weight of fish, tank temperature, published energy density of the pelleted food used in the experiments (14925.3 J/g), and the experimental time period were used in the American shad bioenergetics model to generate model predictions (Figure 1). The regression equation describing the relationship between the observed (*A*) and predicted (*P*) estimates of daily consumption for age-0 American shad in the laboratory was: $P = -0.00555 + 0.89362 \cdot A$, ($n = 18$; $r^2 = 0.773$; $F = 54.46$; $p < 0.0001$; Figure 1). The mean ($\pm$ SD) daily consumption estimates (g/g/d) of modeled and observed laboratory estimates were 0.049 (0.011) and 0.039 (0.011), respectively (Table 7). The data were normally distributed. The paired *t*-test for observed versus predicted values indicated modeled predictions of consumption were significantly different from observed values (*t*-test; $t = -8.46$; $df = 17$; $p < 0.0001$; Table 7). The results for the *t*-test of the hypothesis intercept = 0 indicated there was no consistent systematic deviation in the model predictions from the observed laboratory estimates; however, there was a significant difference in the slopes of the observed and predicted values, indicating a systematic proportional bias between observed and predicted values. These conclusions are supported by the Bonferroni joint CI for the intercept and slope of the regression of laboratory versus modeled consumption because the 95% CI for intercept included 0 while the 95% CI for slope did not include 1 (Table 8). Decomposition of the *MSE* for the laboratory regression indicated that there was systematic bias in the regression due to the significant difference in the mean values of laboratory and model estimates; the slope error was relatively small (0.01) but the mean and residual errors were large (0.80 and 0.19, respectively). Mean error and slope error should have values close to 0 and residual error near 1 if errors are not systematic. The reliability index for the laboratory versus predicted values was 1.35 (Table 8).

Comparison of the deviance measures *RMSE*, *MAE*, and *MA%E* between the field and laboratory regressions indicate greater accuracy for the laboratory versus predicted than for field versus predicted regressions (Table 7). Despite the large systematic errors identified in the laboratory corroboration, there was less variance between values and high correlation ($r^2 = 0.77$) between the observed and predicted values. The small number of observations in the field

corroboration resulted in high variance and a lower correlation between observed and predicted values (r^2 = 0.39; Table 7).

Visual comparison of the field and laboratory data with predicted values (Figures 1 and 2) suggests that the estimated consumption values from laboratory calculations were systematically low. Conversely, the validity of the field versus predicted consumption regression was compromised by the small number of field observations and large variance, although the deviation was not systematic.

Parameter sensitivity, error analysis, and sensitivity simulations

The importance of submodels (e.g. for consumption, respiration) within the bioenergetics model can be evaluated through sensitivity and error analysis (Kristiansen et al. 2007). Sensitivity and error analysis were performed on the physiological parameters of the American shad bioenergetics model to determine if small changes in parameter values resulted in large changes in model output. We did not assess changes in model output in response to uncertainty in external variables such as water temperature and diet, which can also be important (Bartell et al. 1986). Classical sensitivity analysis using the individual parameter perturbation method varies a single parameter ($\pm$10%), while other parameters remain unchanged from the nominal level (Table 9). This process is repeated until the effect of varying each physiological parameter has been evaluated. Sensitivity analysis indicated that two consumption parameter values, the intercept (CA) and slope (CB) of C_{max} on fish mass, changed by > 10 % in response to perturbation. To demonstrate how uncertainty in the value of an estimated parameter can affect modeled output, a modeling scenario was devised and simulations were run to estimate cumulative zooplankton consumption (g) by age-0 American shad under nominal and adjusted CA and CB parameter values (Table 10, Figure 3). Despite the usefulness of sensitivity analysis in identifying sensitive parameters in the bioenergetics model, the results of this linear methodology are potentially biased because some parameters may be represented by nonlinear functions, and modeled output may be sensitive to the variance of these parameters (Gardner et al. 1981, Bartell et al. 1986). Higher order effects resulting from covariance of model parameters are ignored in sensitivity analysis as well (Gardner et al. 1981, Bartell et al. 1986).

Because the possibility of larger errors arising from parameter covariance and/or non-linear relationships is not reliably considered in sensitivity analyses using single variable perturbations, error analysis was also performed on the American shad bioenergetic parameters (Bartell et al. 1986). The use of error analysis to test for model precision evaluates the entire model simultaneously by exploiting statistical variability because each parameter is considered a random variable (Gardner et al. 1981). Model precision is a function of parameter variability as are the values of external inputs such as temperature, fish size, and diet composition. Some effects of varying the external inputs for fish size and % C_{max} can be seen in Table 10. As fish size increased, the %Δ from nominal consumption tended to decrease for most levels of C_{max} when the CA parameter value was altered $\pm$ 10%, but %Δ from nominal consumption increased when the CB parameter was perturbed.

A modified Monte Carlo analysis with uniform latin hypercube sampling (Rose et al. 1991) was used to efficiently sample from the input distributions ($\pm$ 10% of nominal parameter value) of each internal parameter in the bioenergetics model. The advantage of the latin hypercube sampling approach is that each parameter is represented in a fully stratified manner (McKay et

al. 2000) and random samples are generated from all the ranges of possible values giving insight into the extremes of the probability distributions of the outputs (www.ccl.rugers.edu). Nominal values for each parameter were used in place of a mean value and varied by ± 10% to establish a 10% coefficient of variation (CV) range, although the "true" variability of each parameter is unknown (Letcher et al. 1996, Kristiansen et al. 2007). Uniform sampling with latin hypercube sampling was used rather than following a Gaussian normal distribution because most parameters were borrowed from alewife rather than experimentally determined for American shad. By sampling uniformly, variability was evaluated over a broader range of parameter uncertainty within 10% of the nominal parameter value; other authors have conducted error analyses using both normal and uniform distributions (Bartell et al. 1986, Megrey and Hinckley 2001, Kristiansen et al. 2007). The stratified sampling design of the latin hypercube approach assured that parameter values were not clustered, and that all regions in the random parameter space were sampled uniformly. Monte Carlo iterations were used to generate 200 physiological parameter sets within ± 10% of nominal parameter values for the American shad bioenergetics model. Estimates of the mean, standard deviation, coefficient of variation, and median values for each parameter were calculated from the 200 simulations for comparison with the nominal value of each parameter (Table 11).

Classic sensitivity analysis and previous error analysis on the alewife model by Bartell et al. (1986) suggested consumption parameters CA and CB had a large influence on model output. Changes in model output due to perturbation of CA and CB parameter values were evaluated using a bioenergetics simulation that predicted the consumption (g/g/d) of a 5-g American shad feeding at 20% maximum consumption and 21.1°C. This simulation was used to compare the consumption output of the nominal parameter values with that of 10 randomly selected parameter sets from the 200 Monte Carlo iterations. The percent change (%Δ) between nominal and each of the 10 parameter sets were calculated to compare differences in modeled output between the nominal and simulated parameter sets (Table 12). Submodel parameter values (G1, L1, G2, L2) and output parameters (KA, KB) for the Thornton and Lessem (1978) algorithm of the consumption equation were explicitly calculated to compare nominal submodel parameter and modeled output values with the 10 simulated parameter sets (Table 12).

Model applications

A potential application for a finalized American shad bioenergetics model is to estimate the feeding rate of these fish on various prey (e.g. zooplankton, insects) and to estimate quantitative consumption predictions (g/g/d) from growth data. To demonstrate this application, I compiled the fork lengths of age-0 American shad collected in 1994-1996 on successive sampling days in John Day Reservoir (river km 382 – 387; USGS unpublished data; Haskell et al. 2006). Because the weights of these fish were not available, I converted the fork lengths of these fish to weights (g) by running a length-weight regression on age-0 American shad size data collected at Bonneville and McNary dam juvenile fish facilities in 1999-2001 and 2007 (Fish Passage Center data, www.fpc.org). The resulting regression equation was applied to 1994-1996 fork length data to generate a weight estimate for each fish. The mean daily weights of age-0 American shad were used as growth estimates in the American shad bioenergetics model with mean daily scrollcase temperatures from John Day Dam to estimate the feeding rate of fish (expressed as % C_{max}) and predict total prey consumption (Table 13).

Bioenergetics models are also useful for hypothesis testing. To demonstrate this modeling capability, we estimated the growth of juvenile fall Chinook salmon in John Day reservoir in July under diets with and without American shad prey. The juvenile fall Chinook salmon bioenergetics model of Koehler et al. (2006) was used to run the diet simulations. Although this model was initially developed for adult Chinook salmon (Stewart and Ibarra 1991), the model was corroborated and parameter values were verified by Koehler et al (2006) for juvenile fall Chinook salmon. Unpublished USGS diet data on juvenile fall Chinook salmon suggests that these juvenile salmon feed on age-0 American shad. The diet of juvenile fall Chinook salmon (*n* = 13) collected from John Day Reservoir in 1996 consisted of >75% age-0 American shad by weight. Because of these findings, we designed bioenergetics simulations to estimate the growth of juvenile fall Chinook salmon in John Day Reservoir under a diet consisting of 15, 50, and 80% American shad (Table 14) at a relatively high feeding rate of 60% C_{max}. The growth of juvenile fall Chinook salmon was modeled using data from fall Chinook salmon sampled at the McNary Dam juvenile fish facility in early July 2008-2009 (Figure 4). These fish had a mean FL of 107 mm and an estimated weight of 13.5 g when they entered John Day reservoir and this data was used as the starting size of fish in two growth simulations. I ran the bioenergetics model over two 15-day time periods in July using the 10-yr average mean daily water temperatures from McNary Dam scrollcase . The 10-yr mean daily water temperatures modeled during period 1 were between 17.6 and 20.0 °C and mean daily water temperatures during the period 2 simulations were between 19.4 and 22.2 °C. Time periods used in these simulations were from July 1–15 (period 1; ordinal days 182–196) and July 16-30 (period 2; ordinal days 197-211).

In period 1, the bioenergetics model predicted that juvenile fall Chinook salmon in the 13.5 g size range would grow faster if American shad were part of the diet of these fish during the first half of July (Figure 4). The feeding level (60% C_{max}) modeled in the juvenile fall Chinook bioenergetics simulations was fairly high; under most conditions the simulated growth of fish under any diet regime with this level of food availability would be positive. However, during period 2 the 10-yr (2000-2009) mean daily water temperatures in John Day reservoir (ordinal days 197-211) were above the thermal tolerance of salmonids (> 20 °C; Cherry et al. 1977, Hokanson et al. 1977, Cech and Myrick 1999, Richter and Kolmes 2005). Because daily mean temperatures were generally above the thermal tolerance of salmonids, juvenile fall Chinook salmon in the 13.5 g size range lost weight during this time period under all diet scenarios.

There are at least two caveats to this modeling assessment on juvenile fall Chinook salmon in John Day reservoir. Although we modeled juvenile fall Chinook residence time in John Day reservoir for 15-day time periods, the residence time of these fish in the reservoir is variable, and influenced by flow conditions. Tiffan et al. (1996) reported that juvenile fall Chinook spent 1 to nearly 3 weeks in the reservoir and the earliest and latest fish moved through the reservoir more quickly than mid-season migrants. In 2008 and 2009, most juvenile fall Chinook passed John Day Dam from mid-June through July, with peak migrations from late June through mid-July (Fish Passage Center data; www.fpc.org). Dam passage data suggests that most juvenile fall Chinook emigrate through John Day reservoir before summer water temperatures increase above the thermal tolerance of salmonids. It is also possible that the mean daily temperatures used in the bioenergetics model did not capture the actual thermal experience of these fish. Although water temperatures in the lower Columbia River reservoirs are generally well mixed, cooler water may be available to fish at depth or from other cold water sources (e.g. springs, hyporheic flow, tributary streams). Juvenile fall Chinook salmon may be able to moderate the negative growth effects of water temperatures in John Day reservoir during the warmest period of the

summer through behavioral thermoregulation if sufficient cold water refugia were available (Ward and Stanford 1995, Poole and Berman 2001, Sauter et al. 2001).

Discussion

A bioenergetics model has been developed for age-0 American shad. Literature review indicated that there was little empirical data available specifically on juvenile American shad to parameterize the model and laboratory-derived parameter estimation was beyond the scope of this study. As a result, most parameter values for the bioenergetics model were borrowed from alewife, a closely related species. Although there is more work to be done to corroborate the model and verify parameter values for the American shad bioenergetics model, the work we have completed on the model to date and the general robustness of the bioenergetics modeling approach (Stewart and Binkowski 1986) suggests that the proposed physiological parameters of the model are satisfactory for hypothesis testing. Model error can be reduced by fitting the bioenergetics model to observed growth rather than consumption (Bartell et al. 1986) and increasing the number of growth observations during the time interval of interest (Stewart and Binkowski 1986).

Adult American shad are larger than alewife, and there are differences in the life histories of these fish that may be reflected in physiological performance. Physiological differences between alewife and American shad may be large enough that the use of alewife parameters in the American shad bioenergetics model yields inaccurate estimates of growth and consumption. The Wisconsin alewife bioenergetics model published by Stewart and Binkowski (1986) was developed from laboratory estimates of metabolism, swimming speed, and maximum consumption. Evaluation and synthesis of research results with other available information on alewife and related taxa led Stewart and Binkowski (1986) to conclude that the alewife model could be applied to any clupeid, given the observed growth and appropriate site-specific data on the species of interest. For example, Stewart and Binkowski (1986) found that the swimming speeds of alewife were similar to the volitional swimming speeds of age-0 American shad (Katz (1978).

Bartell et al. (1986) undertook an extensive sensitivity and error analysis on the alewife model presented by Stewart and Binkowski (1986). Classic sensitivity and error analyses were used to evaluate the predicted growth and consumption estimates of the Wisconsin alewife bioenergetics model. Bartell et al. (1986) concluded that the bioenergetics model provided realistic forecasts for alewife. Several researchers found that bioenergetics models do a better job of estimating consumption given growth measurements than for estimating final growth from consumption (Kitchell et al. 1977, Bajer et al. 2004); this was true for the alewife model (Bartell et al. 1986). Error analyses on the egestion (FA) and excretion (UA) parameters indicated the magnitude of errors on these parameters were dependent on consumption rates, the result is that these parameters have little effect on model output (Bartell et al. 1986, Ney 1993).

Laboratory validation of model performance requires measuring the food consumption of different size groups of juvenile American shad under several combinations of temperature and feeding. Model parameters proposed for juvenile American shad would be validated if empirically derived laboratory estimates of growth and consumption were accurately predicted by the model. Monte Carlo techniques could be employed to corroborate the model by

comparing observed growth of age-0 American shad in John Day reservoir (Chapter 2, this report) to model prediction with methodologies such as those used by Petersen and Paukert (2005). Brandt and Hartman (1993) suggested a tiered approach to corroborating new models with laboratory evaluation of growth and consumption predictions prior to undertaking field studies. Successful corroboration of the model generally requires that model output and independent laboratory or field data agree within 15% (Chipps and Wahl 2008).

Additional laboratory and field effort are needed to finalize the corroboration of the American shad bioenergetics model. This step must be completed before the model can be used to make quantitative predictions of consumption for age-0 American shad. We reported on field estimates versus modeled predictions of consumption and found predicted values showed little systematic error, but the correlation coefficient was low ($r = 0.62$). The low correlation coefficient may be primarily attributed to the small number of field samples collected ($n = 9$). A larger sample size will be needed to validate modeled consumption output with field estimates because of the large variance around the mean field estimate of consumption. The large variation associated with field estimates is not too surprising given the number of uncontrolled environmental variables that may be encountered during field studies. The bioenergetics model appeared to predict consumption reasonably well despite the small number of consumption estimates made in the field. Discrepancies between field estimates and model predictions were too large to finalize corroboration of the model.

The laboratory consumption estimates on modeled predictions failed to corroborate the bioenergetics model, although the correlation coefficient was good ($r = 0.88$). Laboratory consumption estimates on predicted values showed systematic error of the mean and slope. The slope of the regression was significantly different from 1, indicating mean laboratory estimates were significantly different from the predicted model values. Laboratory consumption estimates were calculated using raw data from a previous study by Limburg (1994). Assumptions were made about the data in order to calculate laboratory consumption estimates that may have been inaccurate, leading to the observed discrepancy between our laboratory estimates and the consistently larger modeled consumption predictions. It is also possible that laboratory results were biased. For example, fish may have fed below their maximum consumption rate due to stress (Barton and Schreck 1987) or the pelleted food used in the study (Petersen and Paukert 2005).

There is a broad array of computational techniques available today that can be applied to the statistical verification of model parameters. Monte Carlo simulations, optimization, multiple parameter sampling designs, and other techniques have been used by various authors to verify bioenergetics parameters (Rose et al. 1991, Letcher et al. 1996, Megrey and Hinckley 2001, Paakkonen et al. 2003, Petersen and Paukert 2005, Kristiansen et al. 2007, Tyler and Bolduc 2008). Additional corroboration and parameter verification of the age-0 American shad model should be completed before the model is used to predict quantitative consumption estimates for American shad. Assessment of model output in response to uncertainty in the values of external variables such as water temperature and diet can be important (Bartell et al. 1986) and should be considered as well.

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Table 1. Mean mass (g) and energy density (joules/gram) of small and large age-0 American shad collected at Bonneville and McNary juvenile fish collection facilities during early (1 Sept – 30 Sept at Bonneville; 22 Aug– 15 Oct at McNary) and late (1 Oct - 31 Oct at Bonneville; 16 Oct – 15 Dec at McNary) fall sample periods.

	Early			Late		
Location	N	Mean mass (g)	Mean joules/g	N	Mean mass (g)	Mean joules/g
McNary						
small (≤ 110 mm FL)	76	4.72	5084	42	6.01	4015
large (> 110 mm FL)	1	16.20	6866	13	21.62	6118
Bonneville						
small (≤ 130 mm FL)	45	7.84	5725	18	11.96	5262
large (> 130 mm FL)	12	55.57	5539	1	41.90	4044

Table 2. Physiological parameters considered in the development of a bioenergetics model for American shad. Published parameter values by author are followed by species, parameter set, and abbreviated parameters described in Tables 2 and 3. Consumption =C, respiration = R.

Author	Species	Parameter set—parameters
Burbidge 1974	*Alosa aestivalis* (Mitchill)	R—RQ
Klumb et al. (2003)	*Alosa pseudoharengus*	R—RA, RB, RQ, RTO, RK1, RK4, RK5
Lantry (1997)	*Dorosoma cepedianum*	R—RQ
Leonard et al. (1999)	*Alosa sapidissima*	R—RA, RQ
Limburg (1994)	*Alosa sapidissima*	C—CA , CB, CQ, CTO, CTM, CTL, CK1, CK4
		R—RA, RB, RQ, RTO
Limburg (1996)	*Alosa sapidissima*	C—CB, CQ, CTO, CK1
		R—RA, RB, RQ, RTO, SDA
Ross et al. (1992)	*Alosa sapidissima*	R—RA
Rudstam (1988)	*Clupea harengus*	C—CA, CB
Stewart and Binkowski (1986)	*Alosa pseudoharengus*	C—CA, CB, CQ, CTO, CTM, CTL, CK1, CK4
		R—RA, RB, RQ, RTO, RTL, RK1, RK4, ACT, BACT, SDA

Table 3. Consumption parameter set used in the Wisconsin bioenergetics model for age-0 American shad. Parameters were used in mathematical equations that expressed maximum feeding potential as a function of fish weight and temperature. Parameters in capital letters (e.g. CA, CB) refer to equations in the software of Hanson et al. (1997) for estimating consumption. Sources: 1—Stewart and Binkowski (1986); 2—Limburg (1994).

Parameter	Parameter description	Parameter value	Source
CA	intercept of C_{max} v. wt	0.8464	1
CB	slope of C_{max} v. wt	-0.3	1
CQ	temperature for CK1 (°C)	4.0	1
CTO	low optimum temperature (° C)	25.5	2
CTM	high optimum temperature (° C)	28.0	2
CTL	temperature for CK 4 (° C)	32.5	2
CK1	proportion of C_{max} at CQ	0.17	1
CK4	proportion of C_{max} at CTL	0.01	1

Table 4. Respiration parameter set used in the Wisconsin bioenergetics model for age-0 American shad. Parameter values were used in mathematical equations that express oxygen consumption and swimming speed as functions of fish weight and temperature. Parameters in capital letters (e.g. RA, RB) refer to equations in the software of Hanson et al. (1997) for estimating metabolism. Source: 1—Stewart and Binkowski (1986).

Parameter	Parameter description	Parameter value	Source
RA	intercept respiration v. wt	0.0037	1
RB	slope respiration v. wt	-0.215	1
RQ	respiration v. temperature	0.0548	1
RTO	slope respiration v. swim speed	0.03	1
RTL	cutoff temperature for respiration v. swim speed	9	1
RTM	set to zero	0	
RK1	intercept swim speed v. wt when temp > RTL	22.08	1
RK4	slope swim speed v. wt	-0.045	1
ACT	intercept swim speed v. wt when temp < RTL	5.78	1
BACT	slope swim speed v. wt when temp < RTL	0.149	1
SDA	Specific dynamic action	0.175	1

Table 5. Prey type and percentage of prey type by weight in the age-0 American shad diet in John Day reservoir from diet studies conducted in 2008 (Chapter 1, this report). The energy density of prey (joules/g) was taken from various sources. The percent by weight and energy density of each prey type were used in the American shad bioenergetics model to estimate and compare modeled consumption (g/g/d) with observed field estimates.

Prey type	% of diet	Energy density (joules/g)	Source
Crustacean	61.0	3,883	Storch (2005)
Insect	23.0	3,400	McMichael et al. (1997)
Mollusk	0.5	2,800	Beauchamp (2009)
Other	15.5	2,800	Beauchamp (2009)

Table 6. Date, mean daily water temperature (°C), and mean fish weight (g) of age-0 American shad collected in John Day Reservoir in 1994 and 1995 for field derived estimates of fish consumption (g/g/d; wet weight). Observed field estimates of consumption are given with predicted values generated by the American shad bioenergetics model. The difference (Predicted – Observed) between the observed and predicted values is given.

				Consumption (g/g/d; wet weight)		
Date	Temperature °C	Mean fish wt. (g)	N	Observed	Predicted	Difference
9/06/1994	20.7	3.39	94	0.09162	0.10189	0.01027
9/26/1994	19.8	7.27	94	0.10264	0.08024	-0.02239
10/17/1994	18.6	4.06	67	0.04966	0.08666	0.03699
11/17/1994	14.6	5.52	96	0.08031	0.06465	-0.01556
8/21/1995	19.3	1.24	92	0.10973	0.12035	0.01061
9/14/1995	20.4	2.36	95	0.10393	0.10916	0.00523
9/26/1995	18.8	2.70	102	0.05301	0.09671	0.04369
10/17/1995	15.4	2.99	82	0.07901	0.09336	0.01435
11/06/1995	11.1	3.76	76	0.02764	0.05848	0.03087

Table 7. Statistical verification measures for model predictions versus observed estimates of consumption from field studies (USGS unpublished data; Haskell et al. 2006) and a laboratory experiment by Limburg (1994). SD = standard deviation, O*i* = observed values, P*i* = predicted values, *b* = slope.

	Field	Laboratory
Number of observations	9	18
Mean P*i*	0.090	0.049
SD	0.020	0.011
Mean O*i*	0.077	0.039
SD	0.028	0.011
Shapiro-Wilks normality	0.92^{ns}	0.94^{ns}
Paired *t*-test O*i* = P*i*	1.70^{ns}	-8.46^{**}
Linear regression		
r^2	0.39	0.77
Intercept (*a*)	-0.002	-0.005
t-test *a* = 0	-0.05^{ns}	-0.91^{ns}
Slope (*b*)	0.882	0.894
t-test *b* = 1	2.11^{ns}	4.18^{*}
Mean square error (*MSE*)	0.00056	0.00003
Mean absolute error (*MAE*)	0.021	0.011
Mean absolute percentage error (*MA%E*)	39.33	31.56

^{ns} not significant; $^{*}P < 0.05$; $^{**}P < 0.0001$.

Table 8. Decomposition of Mean Square Error (*MSE*), Bonferroni joint confidence intervals for the intercepts (β_0) and slopes (β_1), and Reliability Index (RI) for field and laboratory values regressed on modeled consumption estimates.

	Decomposition of *MSE* Sources of Error			Bonferroni Joint Confidence Intervals		
Consumption	Mean	Slope	Residual	$\beta_0 \pm$ 95% CI	$\beta_1 \pm$ 95% CI	RI
Field	0.12	0.004	0.87	-0.0020 $\pm$ 0.0909	0.8820 $\pm$ 0.9875	1.00
Laboratory	0.80	0.01	0.19	-0.0055 $\pm$ 0.0151	0.8936 $\pm$ 0.2994	1.35

Table 9. Sensitivity of American shad bioenergetics model output to uncertainty in individual parameter values was investigated by systematically adjusting each nominal parameter value ± 10% and expressed as % change (% Δ, ± 10%) from nominal.

Parameters	Nominal value	(± 10 %)	% Δ (+ 10%)	% Δ (- 10%)	Rank
Consumption					
CA	0.8464	(0.7618 – 0.9310)	-14.68	13.7	1
CB	-0.3	(-0.27 - -0.33)	-11.09	9.57	2
CQ	4	(3.6 – 4.4)	0.15	-0.10	12
CTO	25.5	(22.95 – 28.05)	4.22	-3.34	3
CTM	28.0	(27.7 2 – 28.28)	0.00	0.10	13
CTL	32.5	(32.17 – 32.82)	0.05	0.00	14
CK1	0.17	(0.168 – 0.172)	-0.15	0.20	11
CK4	0.01	(0.0099 – 0.0101)	0.00	0.00	15
Respiration					
RA	0.00367	(0.00363 – 0.00371)	1.67	-1.67	5
RB	-0.2152	(-0.21305 - -0.21735)	-0.79	0.88	9
RQ	0.0548	(0.05425 – 0.05535)	2.11	-1.87	4
RTO	0.03	(0.0297 – 0.0303)	1.03	-0.93	7
RTL	9	(8.91 – 9.09)	0.00	0.00	15
RK1	22.08	(21.859 – 22.301)	1.03	-0.93	8
RK4	-0.045	(-0.04455 - -0.04545)	-0.10	0.15	12
ACT	5.78	(5.722 – 5.838)	0.00	0.001	15
BACT	0.149	(0.147 – 0.150)	0.00	0.05	14
SDA	0.175	(0.173 – 0.177)	1.03	-0.98	6
Egestion/Excretion					
FA	0.16	(0.158 – 0.162)	0.83	-0.79	10
UA	0.1	(0.099 – 0.101)	0.59	-0.54	11

Table 10. Classic sensitivity analysis on the proposed age-0 American shad bioenergetics parameters indicated the model was sensitive to ± 10% adjustments in CA and CB parameter values. The effect of ± 10% adjustments in the nominal value of the CA and CB parameters on cumulative zooplankton consumption (g) estimates is shown for three sizes of juvenile American shad at three levels of food availability (% C_{max}). Sensitivity was defined as a percent change (%Δ) from nominal consumption output of ≥ 5% and is given for each ± 10% perturbation of CA and CB by fish size and %C_{max}.

			Modeled cumulative zooplankton consumption (g) output			
			CA		CB	
Fish size	% C_{max}	Nominal zooplankton consumption (g)	-10 (%Δ)	+10 (%Δ)	-10 (%Δ)	+10 (%Δ)
2 g	0.3	4.2	3.6 (14.3)	4.8 (14.3)	4.3 (-2.4)	4.0 (4.8)
	0.5	8.9	7.5 (15.7)	10.4 (-16.8)	9.4 (-5.6)	8.4 (5.6)
	0.8	19.8	16.4 (17.2)	23.6 (-19.2)	21.7 (-9.6)	18.2 (8.1)
5 g	0.3	7.5	6.6 (12.0)	8.6 (-14.7)	8.1 (-8.0)	7.1 (5.3)
	0.5	15.3	13.1 (14.4)	17.6 (-15.0)	16.7 (-9.1)	14.0 (8.5)
	0.8	31.9	26.8 (16.0)	37.5 (-17.6)	36.1 (-13.2)	28.5 (10.7)
8 g	0.3	10.3	9.0 (12.6)	11.6 (-12.6)	11.2 (-8.7)	9.5 (7.8)
	0.5	20.4	17.6 (13.7)	23.3 (-14.2)	22.6 (-10.8)	18.4 (9.8)
	0.8	41.3	48.2 (-16.7)	35.0 (15.2)	47.3 (-14.5)	36.4 (11.9)

Table 11. The nominal value, mean, standard deviation (SD), coefficient of variation (CV), and median value of each physiological parameter used in the American shad bioenergetics model. Summary statistics were generated from 200 Monte Carlo simulations of the American shad bioenergetics model parameter set. A uniform Latin hypercube design randomly selected each parameter within ± 10% of the nominal value for each simulation.

Parameter	Nominal	Mean	SD	CV	Median
CA	0.8464	0.8443	0.051	5.99	0.8408
CB	-0.300	-0.300	0.018	-5.88	0.3009
CQ	4.00	3.971	0.240	6.04	3.9535
CTO	25.5	25.517	1.472	5.77	25.5183
CTM	28.0	27.910	1.540	5.52	27.9503
CTL	32.5	32.694	1.861	5.69	32.7960
CK1	0.17	0.171	0.00967	5.67	0.1716
CK4	0.01	0.010	0.00056	5.55	0.0101
RA	0.00367	0.003674	0.000214	5.83	0.0039
RB	-0.2152	-0.21569	0.012057	-5.59	0.21482
RQ	0.0548	0.05495	0.003075	5.60	0.05492
RTO	0.03	0.02992	0.001818	6.08	0.03001
RTL	9.0	8.98736	0.514547	5.72	9.01950
RK1	22.08	22.14391	1.261735	5.70	22.1159
RK4	-0.045	-0.04493	0.002586	-5.76	0.04487
ACT	5.78	5.77464	0.339226	5.87	5.74462
BACT	0.149	0.14913	0.008605	5.77	0.14980
SDA	0.175	0.17481	0.010466	5.99	0.17534
FA	0.16	0.16112	0.009121	5.66	0.16185
UA	0.1	0.09996	0.00586	5.86	0.10047
Energy density	5200	5201.9	295.99	5.69	5223.47

Table 12. Predicted consumption (g/g/d) was simulated for a 5-g American shad feeding at 20% maximum consumption and 21.1°C under the nominal and 10 simulated parameter sets. Percent change (%Δ) evaluates the difference in consumption output between the nominal parameter set and each of the simulated parameter sets. Submodel parameter values (G1, L1, G2, L2) and output parameters (KA, KB) for the Thornton and Lessem (1978) algorithm were calculated for comparison of nominal with 10 simulated parameter sets. Simulated parameter values were within ± 10% of the nominal parameter value.

	Thornton and Lessem submodel parameter values and output							
Simulation	G1	L1	Output KA	G2	L2	Output KB	Predicted consumption (g/g/d)	%Δ
Nominal	0.25476	77.982	0.94108	1.8864	2.19E + 09	1	0.09830	----
1	0.28577	125.053	0.96438	1.5895	1.59E + 08	0.999999	0.10073	2.48
2	0.27257	97.696	0.95094	2.6764	4.00E + 13	1	0.09933	-1.39
3	0.25185	80.563	0.93578	1.2428	51973227	0.999998	0.09774	-1.59
4	0.24914	71.071	0.93427	2.7465	4.77E + 13	1	0.09758	-0.16
5	0.23652	54.595	0.91982	3.1261	4.52E + 11	1	0.09608	-1.55
6	0.24195	64.100	0.92138	1.7474	2.97E + 08	1	0.09624	0.17
7	0.25497	71.064	0.93515	1.2175	10192670	0.999991	0.09768	1.49
8	0.27638	108.425	0.95190	0.9262	308360.9	0.999704	0.09940	1.76
9	0.24722	69.390	0.92989	1.3689	1.00E + 08	0.999999	0.09713	-2.28
10	0.23976	66.188	0.93021	16.5984	5.72E + 66	1	0.09716	0.03

Table 13. Estimated feeding level (% C_{max}) and total consumption (g/g/d) achieved by age-0 American shad in John Day reservoir on successive sampling dates in 1994-1996. Ordinal date is the numbered day of the year beginning with 1 on January 1. Predicted weight (wt.; g) was estimated from a length-weight regression applied to known fork lengths (FL) of fish passing McNary Dam (Fish Passage Center data, www.fpc.org).

Year Date	Ordinal day	FL (mm)	Predicted Wt (g)	% C_{max}	Total consumption (g/g/d)
1994					
Aug 8	220	33	24.6	-----	------
Aug 20	232	53	37.1	45.3	1.704
Sep 6	249	64	45.2	29.6	1.395
Sep 20	263	85	62.9	41.9	1.492
Oct 15	288	75	54.1	13.5	0.786
Oct 31	304	80	58.4	23.8	0.834
1995					
Aug 18	230	43	30.5	-----	------
Sep 6	249	52	36.5	25.9	1.391
Sep 9	252	55	38.6	31.6	0.327
Sep 23	266	58	40.7	22.5	0.870
Oct 15	288	69.5	49.6	27.4	1.461
Nov 1	304	71	50.8	20.5	0.654
1996					
Sep 12	255	53	37.1	-----	------
Oct 6	279	56.5	39.6	21.0	1.311
Oct 27	300	55	38.6	17.0	0.850

Table 14. Hypothetical diets of juvenile fall Chinook salmon in John Day reservoir were input into four bioenergetics modeling scenarios to estimate the growth of juvenile fall Chinook. General dietary information came from Rondorf et al. (1990).

Prey category (%)				
American shad	Cladocerans	Terrestrial insects	Diptera	Other
		Scenario 1 – no American shad		
0	58	20	17	5
		Scenario 2 – 15% American shad		
15	48	15	5	15
		Scenario 3 – 50% American shad		
50	20	15	10	5
		Scenario 4 – 80% American shad		
80	0	10	5	5

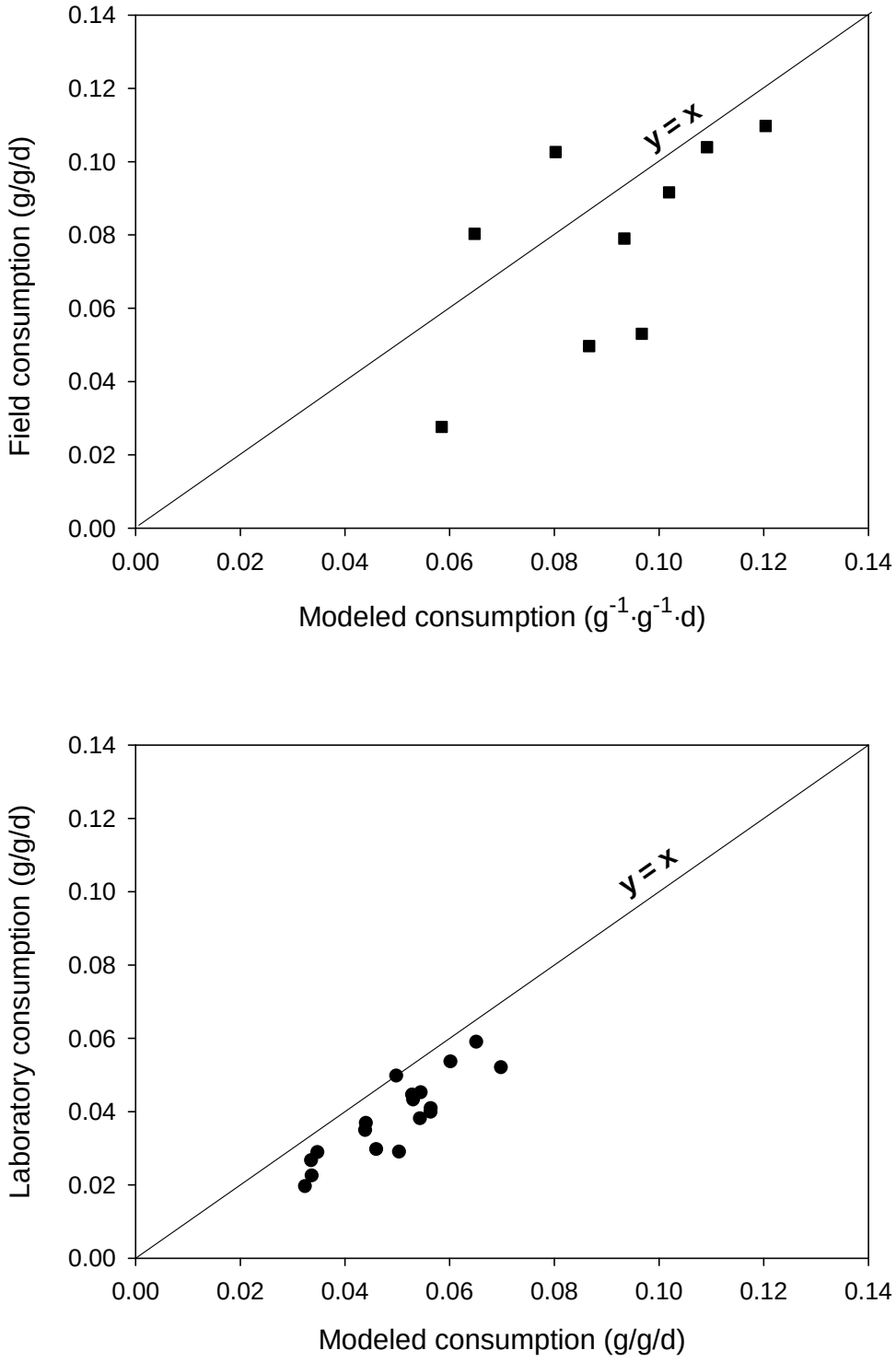

Figure 1. Comparison of field and laboratory estimates of consumption versus values predicted by the age-0 American shad bioenergetics model.

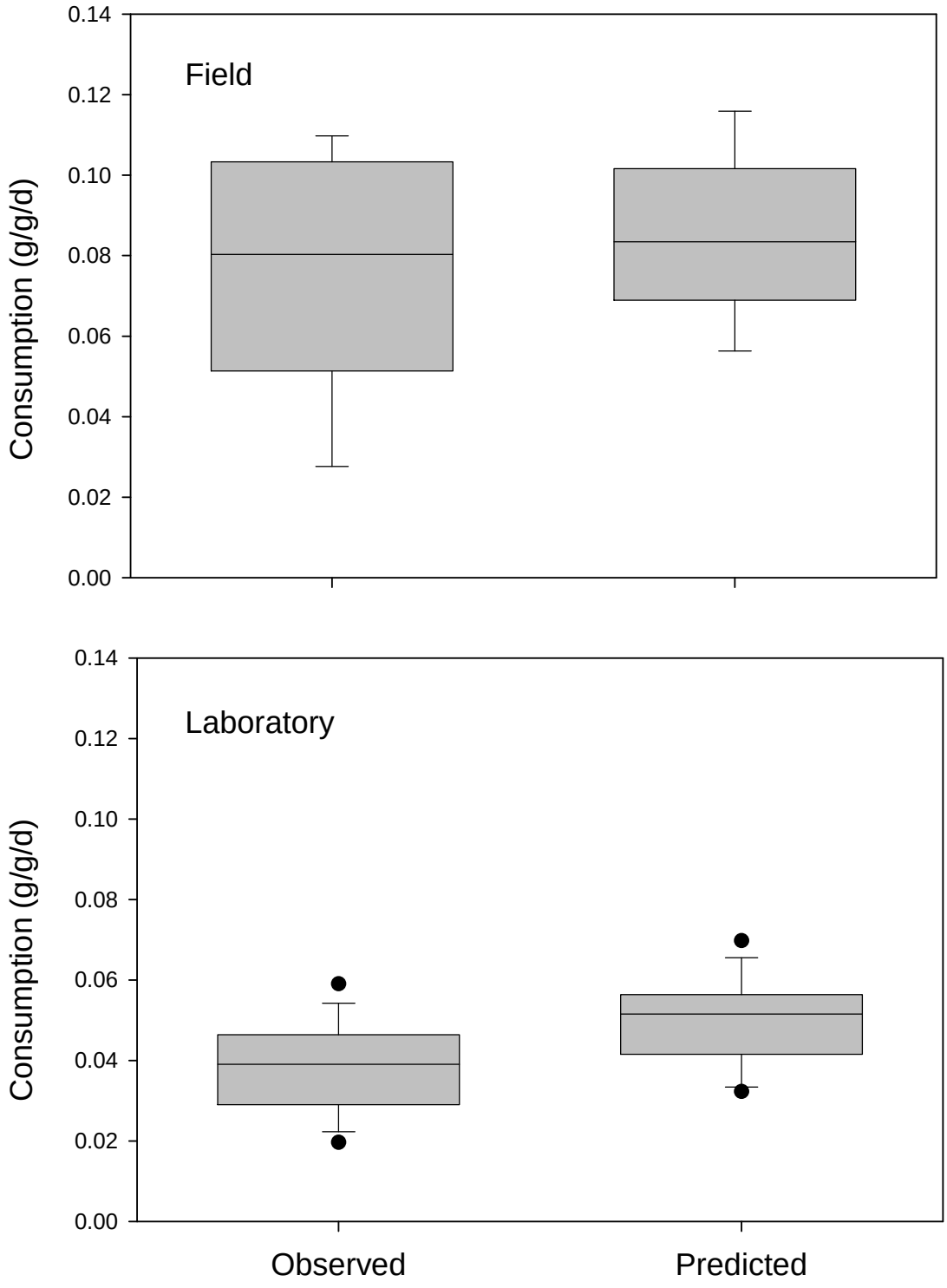

Figure 2. Box plots of field and laboratory estimates of consumption compared to predicted values generated with the age-0 American shad bioenergetics model.

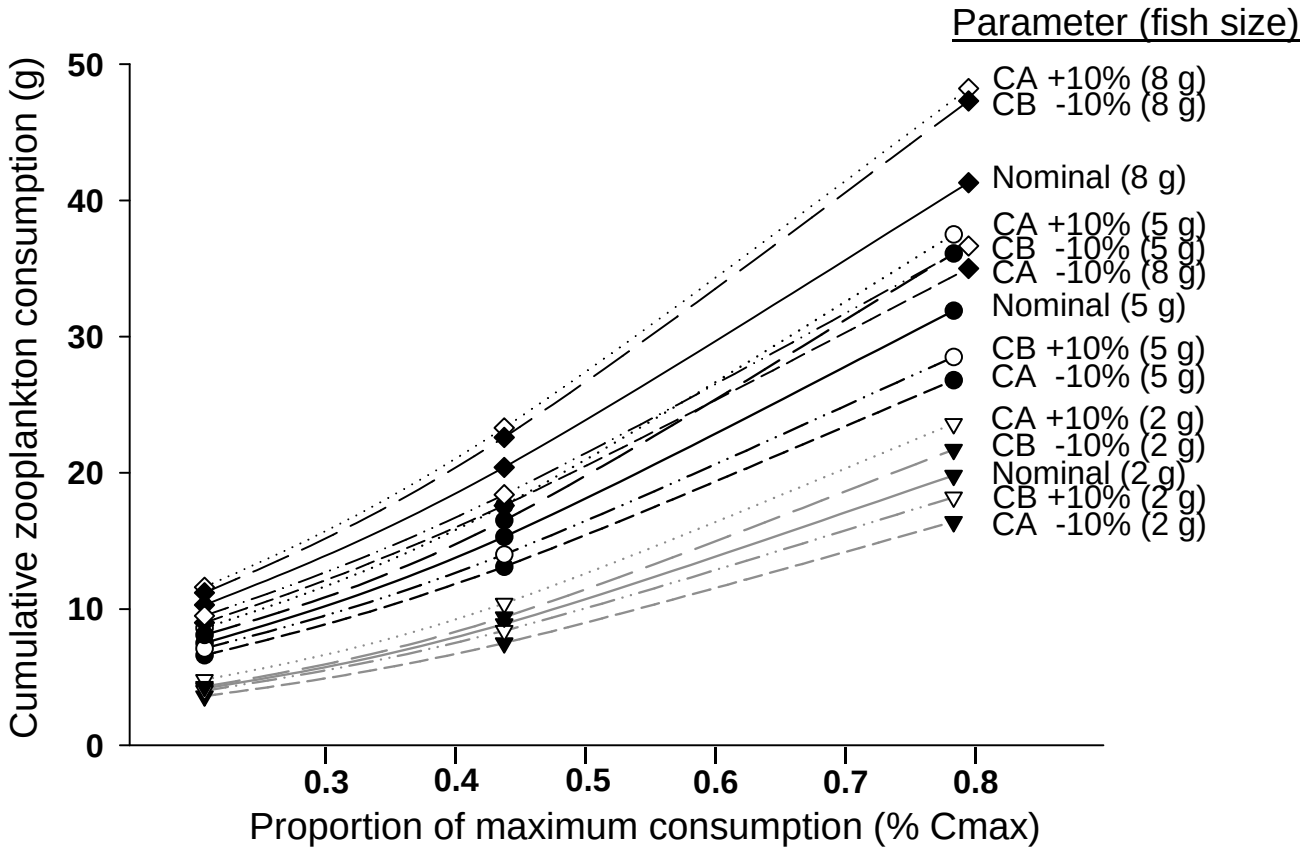

Figure 3. Classic sensitivity analysis on the intercept (CA) and slope (CB) parameters for consumption in the American shad bioenergetics model. CA and CB parameters were borrowed from the alewife bioenergetics model (Stewart and Binkowski 1986).

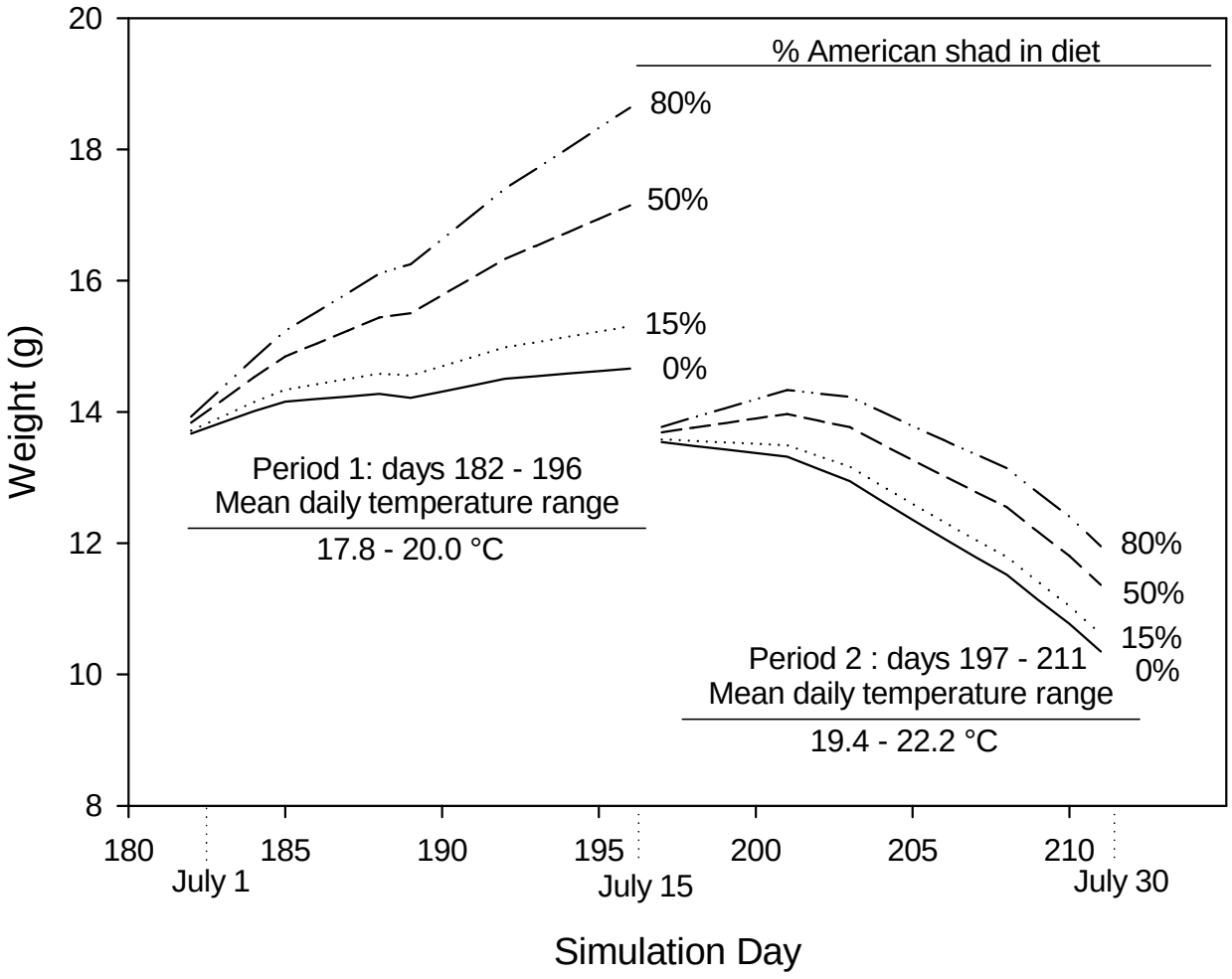

Figure 4. Bioenergetic simulations for juvenile fall Chinook salmon (Koehler et al. 2006). Proportions of juvenile American shad in the diet of fall Chinook were varied from 0, 15%, 50%, and 80% in the model under a $\%C_{max}$ of 60% (a measure of food availability) and observed 10-yr average scrollcase water temperatures at McNary Dam.

Chapter 4
Thiaminase Activity and Life History Investigations in American Shad in the Columbia River

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Abstract

American shad *Alosa sapidissima* fry were successfully transplanted from the Atlantic to the Pacific coast in 1871 and have subsequently proliferated. The Columbia River population is in the millions, yet few investigations have been conducted to better understand their life history, population dynamics, or potential impacts on other species. In 2007 and 2008 we captured American shad from the Columbia River to assess levels of thiaminase activity and to characterize some aspects of American shad life history. Thiaminase levels in age-0 and adult fish were high and ranged from 4,113-20,874 pmol/g/min. Ages of spawning American shad ranged from 3-7 years and iteroparity was approximately 33-36% in the spawning population. Males were typically younger and smaller and had a higher degree of iteroparity than females.

Introduction

American shad *Alosa sapidissima*, an anadromous species native to the east coast of the United States, has long been a highly valued commercial and sport fish. The California Fish Commission paid biologist Seth Green to transport American shad fry across the country in milk cans by rail in 1871 (Green 1874). Since then, they have expanded their range from Todos Santos Bay, Mexico to Cook Inlet, Alaska and Kamchatka Penninsula, Russia (Moyle 2002). Initially, the Columbia River population remained at low levels, but increased after dam construction improved spawning and rearing conditions (Petersen et al. 2003). Their spawning range in the Columbia River Basin now includes the mainstem river to Rock Island Dam, the Snake River beyond Lower Granite Dam, and the Willamette River, with limited passage beyond Willamette Falls (Figure 1; based on data obtained from www.fpc.org and Doug Cramer, PGE, pers. comm. 2011). American shad enter many Columbia River tributaries (John Day River,

Clatsop and Deschutes counties, Umatilla River, County) but we are unaware of any reports of spawning in these tributaries.

The number of adult American shad passing Bonneville Dam peaked at over 5.2 million fish in 2004, but has since declined, down to just over one million in 2010. A large number of American shad spawn in the Columbia River downstream from Bonneville dam, so the number of adults entering the Columbia River each year to spawn is actually much higher than the counts at Bonneville Dam (Petersen et al. 2003). Their numbers have increased such that in 29 of the past 33 years, American shad outnumber all species of Pacific salmon combined migrating past Bonneville Dam (Figure 2).

The introduction of non-native fish often has consequences beyond competition for food or space. With American shad, areas of concern include the amplification and transport of disease organisms, specifically *Ichthyophonus*, with possible effects on native fish populations (Hershberger et al. 2010) and the parasitic nematode *Anisakis simplex*, which may present an emerging risk to wildlife and some human consumers of American shad (Shields et al. 2002). The consumption of American shad could have additional effects on the fish that prey on them, such as white sturgeon *Acipenser transmontanus*, northern pikeminnow *Ptychocheilus oregonensis* and walleye *Sander vitreus* (Petersen et al. 1994; Rinchard et al.). Salmonines in the Great Lakes that consume large quantities of alewife develop a deficiency in thiamine and this deficiency may be responsible for causing early mortality syndrome and subsequent poor recruitment (Brown et al. 2005). Laboratory experiments have demonstrated unequivocally the ability of dietary thiaminase to induce low thiamine levels (Honeyfield et al. 2005). Since American shad and alewives are congeners, American shad are suspected to have high thiaminase activity.

Despite the fact that American shad are well-established and numerous in the Columbia River, only a few investigations have been conducted to better understand their life history, population dynamics, or potential impacts to other species (Harvey and Kareiva 2005; Petersen et al. 2003; Quinn and Adams 1996; Sanderson et al. 2009). In their native range, American shad spawn in freshwater, with fry rearing in rivers for several months before migrating to the ocean in their first year. Age at first maturity ranges from three to six, with some iteroparous individuals living to age eleven (Cating 1953). The tendency toward greater degree of iteroparity or repeat-spawning increases at higher latitudes, ranging from 0 (i.e. semelparity) to 73% (Leggett and Carscadden 1978). The range of ages reported for spawning Columbia River American shad is from two to six (n=25) and the rate of iteroparity is 32% (Petersen et al. 2003).

In 2007, the Bonneville Power Administration provided funding to the U.S. Geological Survey's Western Fisheries Research Center, Columbia River Research Laboratory to conduct studies on various aspects of the impact of American shad in the Columbia River. The main focus of the project was to investigate the diet of American shad (Chapter 1) and on the development and collaboration of bioenergetics models that could be used in further investigations (Chapter 3). Here, we report findings from several ancillary tasks completed during the course of the larger investigation, including assessments of the thiaminase activity of adult and age-0 American shad and characterization of some life history traits, including the age and iteroparity of adult fish.

Methods

Thiaminase activity

Age-0 fish were dipnetted from the Bonneville Dam (Figure 1) juvenile fish bypass system between August and October, 2007 and sorted by fork length (FL) into one of three length groups (< 60 mm FL, 60-79 mm FL, and > 80 mm FL). Adult fish were obtained by angling approximately 2-4 km downstream from Bonneville Dam in June, 2007. Individual fish were wrapped in aluminum foil, flash frozen on dry ice for transportation, and then stored in a -80 C freezer prior to analysis. Thiaminase activity was assessed by USGS staff at the Columbia Environmental Research Center, Columbia, Missouri, following the methods of Zajicek et al. (2005). We then compared thiaminase activity in relation to size of age-0 shad using regression analysis and gender of adult fish with a *t*-test for differences in means.

Life history

Adult shad were captured during their spawning migration in 2008 by one of three ways; gillnetting (April-May; mesh size 13.65 – 15.89 cm) in the Columbia River Estuary (CRE) between Tongue Point and Harrington Point (river km 29-39), angling (June-July) downstream from Bonneville Dam (BBON, river km 227-230), and dip netting (June-July) from the Bonneville Dam adult fish facility (BDAFF, river km 233). The fish were measured for length, weighed, and scales were collected. Gender was determined by examination of the gonads. Otoliths were taken from a subsample of fish (BBON and BDAFF only) representing three time periods in the spawning run: early (June 12-20), middle (June 21-30) and late (July 1-10).

Scales from individual fish were soaked in 10% potassium hydroxide solution for one minute, teased apart with a probe, rubbed to remove mucus, rinsed in deionized water, and examined for quality. A scale was considered to be of good quality if it had the usual scale structures (freshwater mark, striae, transverse grooves and annuli) present from the focus to the edge of the scale (Cating 1953). Three good quality scales were mounted between two slides, then examined under a dissecting scope with transmitted light to identify spawning marks, which are the scars left on the scale from previous spawning migrations (Judy 1961). Otoliths (left and right sagitta) were extracted from thawed heads, cleaned in deionized water and the age determined using reflected lighting to distinguish annuli.

We trained and evaluated age-reader competence using digital images of otoliths from marked, known-age fish (Hendricks et al. 1991; McBride et al. 2005). The Columbia River shad otoliths were aged twice by an individual reader. The samples were then sent to an independent reader for validation. Their ageing results were compared with our ages and differences were reconciled, resulting in a final age determination. It is important to note that we considered the otolith edge as the last annulus when determining fish age, based on the collection dates (William Duffy, NOAA, pers. comm. 2010).

A subsample (n=50 of 163) of otoliths were aged (BDAFF and BBON only): early (n=10), middle (n=30), and late (n=10), with near equal numbers of males and females selected within each time period. Descriptive statistics, chi-square tests and length frequency analysis were calculated using Excel 2007 (Microsoft, Redmond, Washington). The significance level used for all analyses was 0.05.

Results

Thiaminase activity in individual Columbia River American shad ranged from 4,113-20,874 pmol/g/min (Figure 3). Thiaminase activity in adult female American shad was lower than that found in males (Table 1). The difference was statistically significant (*t*-test, df=4, p=0.002) but the sample size was small. Thiaminase activity in age-0 fish was variable and means for three size classes (Table 2) were higher than mean thiaminase activity in adult female fish (Table 1; Figure 3). Regression analysis revealed a significant positive relation ($p < 0.0001$) between fork length and thiaminase activity in age-0 fish (Figure 4).

A total of 2,144,756 American shad passed Bonneville Dam in 2008 with a peak of 917,871 shad counted the week of June 16th (Figure 5). Gillnetting in the lower, brackish waters of the Columbia River (river km 29-39) resulted in catches of American shad that were skewed towards larger, predominantly female fish (Table 3). Fish collected by angling (BBON) were predominantly male during all run periods, but the male-to-female ratio decreased over time. Fish sampled at the adult fish facility (BDAFF), also showed a high male-to-female ratio early in the run, which decreased to nearly equal in the middle and late stages of the run. Males were smaller and more likely to be repeat spawners than females (Table 3; Figure 6).

Of the subsample of fish aged, the youngest males were age 3 whereas the youngest females were age 4. Most males were age 4 (mean=4.5 years; range 3-6; SD 0.8124) and most females were age 5 (mean=5.1 years; range 4-7; SD 0.7409) (Table 4). Overall, males had a higher rate of iteroparity than females (Figure 7). Females were generally larger than males of the same age (Figure 8).

Discussion

Thiaminase activity of juvenile and adult Columbia River American shad was typically higher (4,113-20,874 pmol/g/min; Figure 3) than that reported for alewives from 10 stocks in the Great Lakes (range 1,650 – 7,281 pmol/g/min; Fitzsimons et al. 2005) where early mortality syndrome in salmon is of great concern and alewives are a primary prey of the salmon (Brown et al. 2005). While thiaminase activity in Columbia River American shad was high, there are several factors that can mediate the effects of consumption of prey with high thiaminase activity including lipid composition of the prey and variability in the predator diet (Fitzsimons et al. 2005; Honeyfield et al. 2005). The results reported here suggest that additional investigations should be conducted to determine if Columbia River predators of American shad including white sturgeon, salmon, and other native and non-native piscivores exhibit thiamine deficiency. The sample sizes in this pilot study were small but the information presented here can be used to derive sample size estimates for planning future studies.

Describing the life history of a population of fish is a challenging endeavor, especially for a large population like the Columbia River American shad. First, sampling effort must be sufficient to statistically represent the population. Second, the sampling method must be unbiased or adjusted for bias, so that size, sex and age are all accurately represented. Third, the sampling must temporally and spatially represent the population. The data presented in this report are a first step toward this goal. One-hundred-eighty-eight adults were sampled by three different methods, at three locations, distributed throughout the spawning season. The sample size was small compared to the more than 2 million fish that passed Bonneville dam in 2008. The

biases associated with each sampling method need to be considered when interpreting life history data, and indeed our results reflect some of those biases. Gillnets are known to be size-selective for American shad (Gibson and Daborn 1995) and our catches reflect that larger fish, typically females, were captured by this gear. For instance, the male-to-female ratio from gillnet-caught fish (0.14:1 CRE) was substantially different from the ratio derived from fish caught further upstream near Bonneville Dam (mean =1.81:1 BBON and BDAFF combined). It is unlikely that the high percentage of females in the CRE sample could have been due to females entering the river mouth earlier than males, since males typically enter first (Glebe and Leggett 1981), but more likely due to the gillnet selecting for larger individuals. Indeed, the size of mesh in the gillnet we were permitted to fish was the size mandated for use in Columbia River commercial shad fisheries that target mature females for their roe. Gillnet selectivity was further substantiated by the smaller mean size of the male and female fish captured upriver (Table 3).

The sex ratio of the fish captured by angling downstream from Bonneville dam heavily favored males (2.64:1), while the ratio of males to females from the Adult Fish Facility was more evenly distributed (1.18:1), suggesting that angling may select for males. There was a decrease in the male-to-female ratio over the spawning season from both capture methods at Bonneville Dam (Table 3), especially notable in the BDAFF samples (2.29:1 down to 0.88:1).

Comparisons of life history characteristics between Table 3 and Table 4 show differences in age, size and spawning frequency for each gender, consistent with those seen in their native range (Limburg et al. 2003). However, some differences may be influenced by biases in sampling methodologies and how the subsample of fish used for age characterization was derived. For example, the repeat spawning rate was widely variable among sampling locations and run timing. In the full sample, the overall repeat spawn rate was 33%; 18.8% for females and 41.7% for males. The subsample repeat spawning rate was 36%; 25% for females and 46% for males. The sex ratio in the subsample was purposely chosen to be near 1:1 to summarize the life history characteristics of each sex, but sex ratio influences repeat spawning rate. The BDAFF sample representing the middle portion of the run seems to be under-represented and shows no male repeat spawners. The quantification of life history characteristics is subject to interpretation based on how accurately the sample reflects the entire population, which emphasizes the need for representative sampling. We encourage caution in the application of these results to population modeling and suggest that further studies be done to better characterize spawning runs of American shad in the Columbia River.

Acknowledgments

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Citations

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Table 1. Thiaminase activity in adult American shad collected in the Columbia River, June 2007. Inspection of the gonads showed that these fish were in pre-spawn condition. Standard deviations of the means are in parentheses.

Gender	Number of fish sampled	Composite type	Mean fork length (mm)	Mean weight (g)	Mean thiaminase specific activity (pmol/g/min)*
Female	3	Whole fish	382 (32.2)	770 (234.3)	8,792 (1,655.4)
Male	3	Whole fish	351 (33.5)	687 (150.4)	18,816 (1,841.8)

*Gender mean thiaminase activities are significantly different (*t*-test, df=4, $p \leq 0.05$)

Table 2. Thiaminase activity in three size classes of age-0 American shad collected in the Columbia River, 2007. Standard deviations of the means are in parentheses.

Size class	Number of fish sampled	Collection dates	Mean fork length (mm)	Mean weight (g)	Mean thiaminase specific activity (pmol/g/min)
< 60 mm TL	18	Aug - Sep	56 (2.6)	1.64 (0.25)	9,088 (3,402)
60 – 79 mm TL	20	Aug - Oct	70 (5.9)	3.34 (0.85)	14,061 (3,685)
> 80 mm TL	20	Aug - Oct	88 (5.1)	6.6 (1.21)	14,427 (3,818)
All age-0	58	Aug - Oct	71 (14.0)	3.9 (2.24)	12,644 (4,319)

Table 3. Characterization of the spawning run of American shad in the Columbia River during 2008 showing the influence of capture method and timing on catch composition. CRE=Columbia River Estuary gillnetting, BBON=Below Bonneville Dam angling, BDAFF=Bonneville Dam Adult Fish Facility dip netting, FL=fork length, M=male, F=female. Repeat spawners had one or more spawning check on their scales. Standard deviations are in parentheses. * indicates a significant difference from the expected ratio of 1:1, based on chi-square testing ($p \geq 0.05$, df=1).

				Females				Males			
Location	Run timing	n	Sex ratio M:F	n	Mean FL (mm)	Mean weight (g)	Proportion of repeat spawners	n	Mean FL (mm)	Mean weight (g)	Proportion of repeat spawners
CRE	River Entry	25	0.14:1*	22	414.9 (23.1)	1180.5 (179.3)	0.14	3	384.0 (52.9)	946.7 (432.9)	1.00
BBON	Early	33	3.13:1*	8	402.1 (10.6)	988.8 (134.5)	0.25	25	360.6 (30.8)	645.0 (172.7)	0.36
	Middle	43	2.58:1*	12	371.8 (48.7)	700.6 (246.5)	0.25	31	374.7 (26.7)	655.9 (124.1)	0.48
	Late	15	2.00:1	5	401.1 (18.7)	894.2 (170.2)	0.20	10	361.2 (27.3)	610.0 (148.6)	0.60
	Total	91	2.64:1*	25	395.6 (27.1)	885.7 (198.5)	0.24	66	363.0 (28.6)	630.2 (154.0)	0.46
BDAFF	Early	23	2.29:1*	7	399.7 (22.6)	934.4 (146)	0.14	16	358.8 (27.3)	612.8 (133.4)	0.44
	Middle	17	0.89:1	9	398.3 (27.8)	957.3 (175.2)	0.22	8	347.4 (26.4)	552.4 (142.5)	0.00
	Late	32	0.88:1	17	403.1 (24.4)	1034.9 (227.2)	0.18	15	312.3 (40.7)	396.5 (147.4)	0.33
	Total	72	1.18:1	33	399.9 (25.2)	973.6 (183.8)	0.18	39	344.9 (34.1)	545.2 (158.5)	0.31
All sample methods and sites combined		188	1.35:1*	80	402.7 (26.1)	1003 (218.4)	0.19	108	357.1 (32.5)	608.3 (178.3)	0.42

Table 4. Life history characteristics by age from a subsample (n=50) of male and female American shad captured at or near Bonneville Dam (BBON and BDAFF only) in 2008. Mean FL=mean fork length, Mean Wt=mean weight. Standard deviations are in parentheses.

Age	3	4	5	6	7	Overall
			Males			
Number	2	12	9	3	0	26
Mean FL (mm)	265.0 (11.3)	339.3 (18.5)	375.4 (20.1)	393.7 (17.6)		352.4 (37.4)
Mean Wt (g)	222.8 (20.0)	504.6 (82.7)	690.3 (122.66)	740.3 (96.0)		574.4 (170.1)
Proportion Repeat[1]	0.00	0.33	0.56	1.00		0.46
			Females			
Number	0	4	14	5	1	24
Mean FL (mm)		367.3 (49.0)	393.6 (20.3)	411.2 (14.9)	447.0 (0)	395.1 (29.9)
Mean Wt (g)		681.5 (301.2)	891.7 (180.9)	1005.6 (111.6)	1233.3 (0)	894.6 (219.3)
Proportion Repeat[1]		0.00	0.21	0.40	1.00	0.25
			Combined			
Number	2	16	23	8	1	50
Mean FL (mm)	265.0 (11.3)	346.3 (29.8)	386.5 (21.7)	404.6 (17.3)	447.0 (0)	372.9 (40.0)
Mean Wt (g)	222.8 (20.0)	548.8 (171.5)	812.9 (186.9)	906.1 (169.1)	1233.3 (0)	728.1 (251.9)
Proportion Repeat[1]	0.00	0.25	0.35	0.63	1.00	0.36[2]

[1]Proportion of individuals within an age class that are repeat spawners

[2]Overall repeat spawn rate is dependent on the sex ratio of the subsample, which may not be representative of the general population. See Discussion.

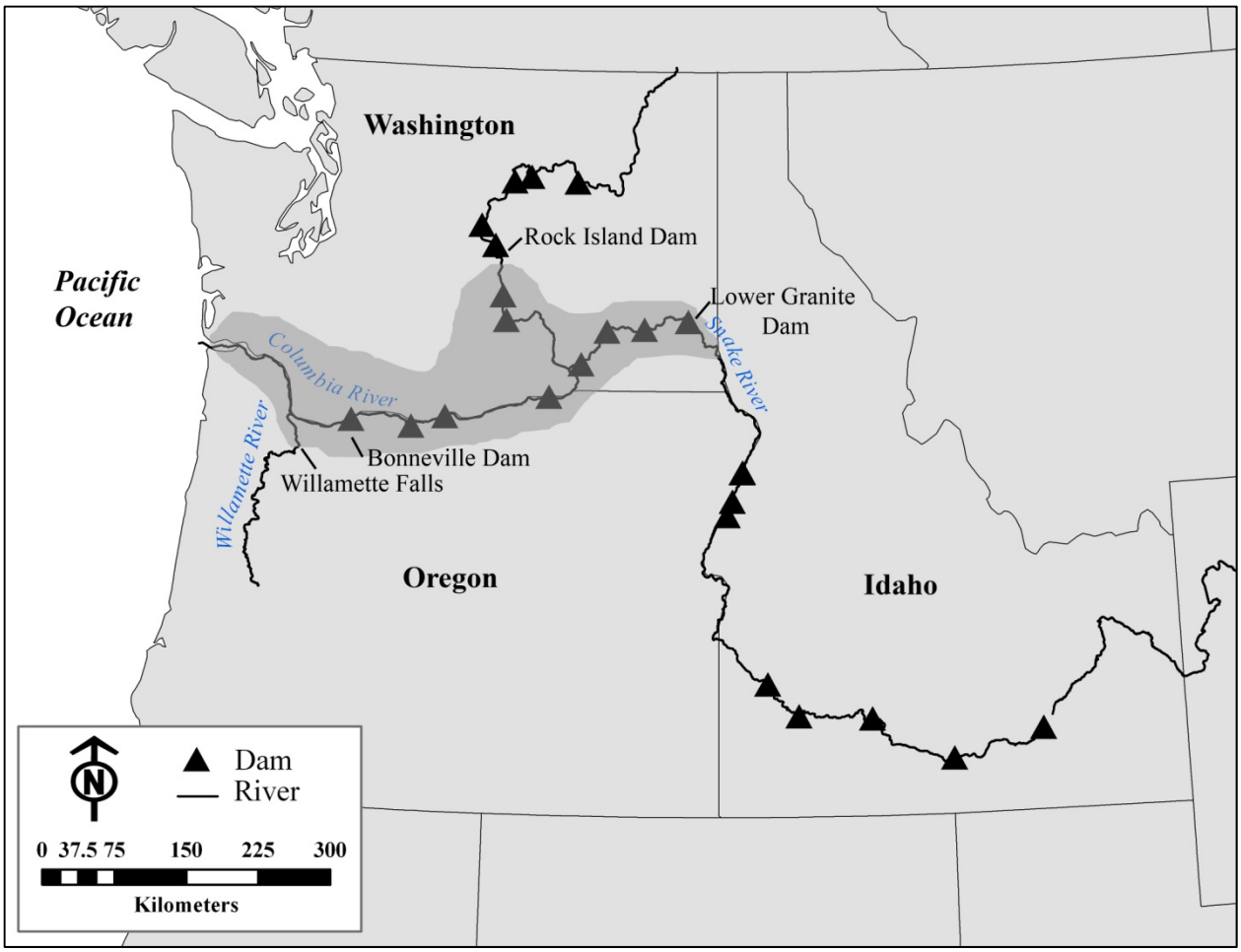

Figure 5. Map of the Columbia River Basin showing the locations of dams (black triangles) and the general distribution of American shad (grey shaded area).

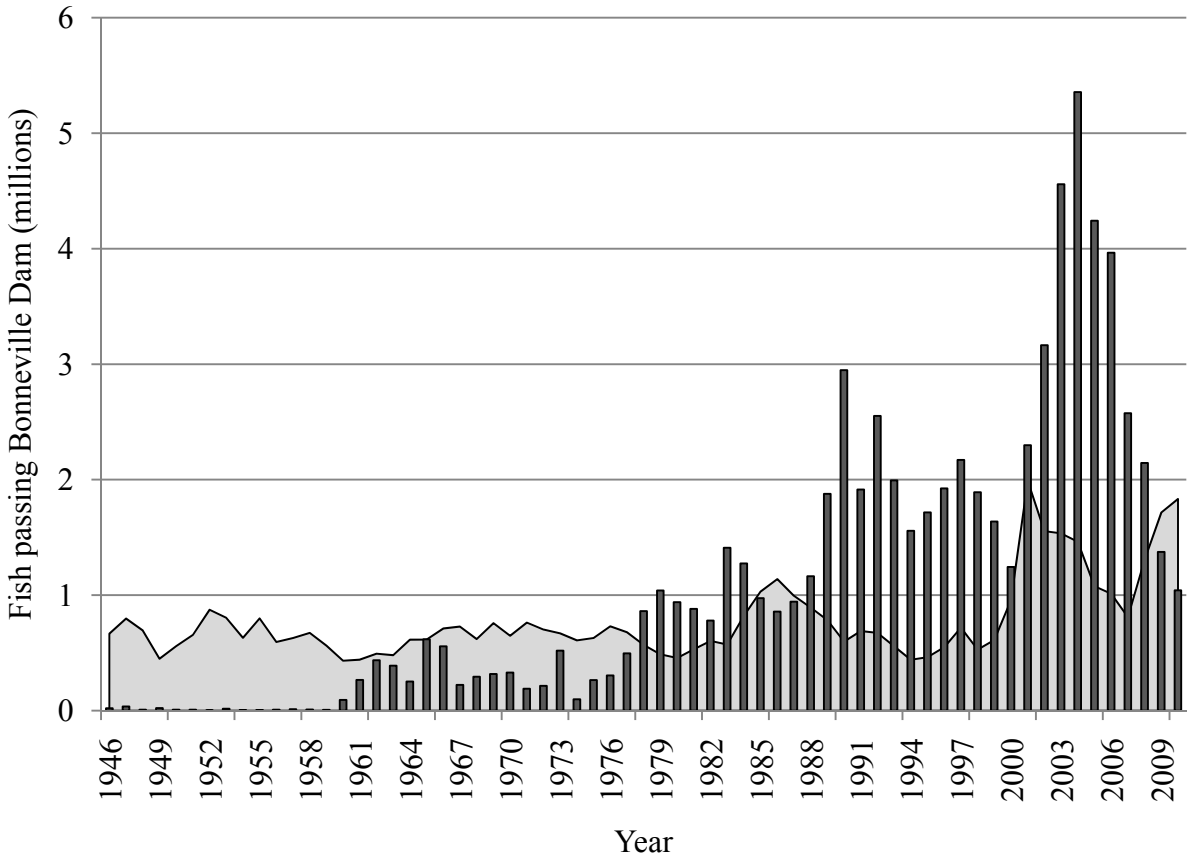

Figure 6. Number of adult American shad (dark bars) and Pacific salmon (all species combined, including steelhead; grey shaded area) counted passing upstream at Bonneville Dam since 1946. Data were obtained from www.cbr.washington.edu/dart/.

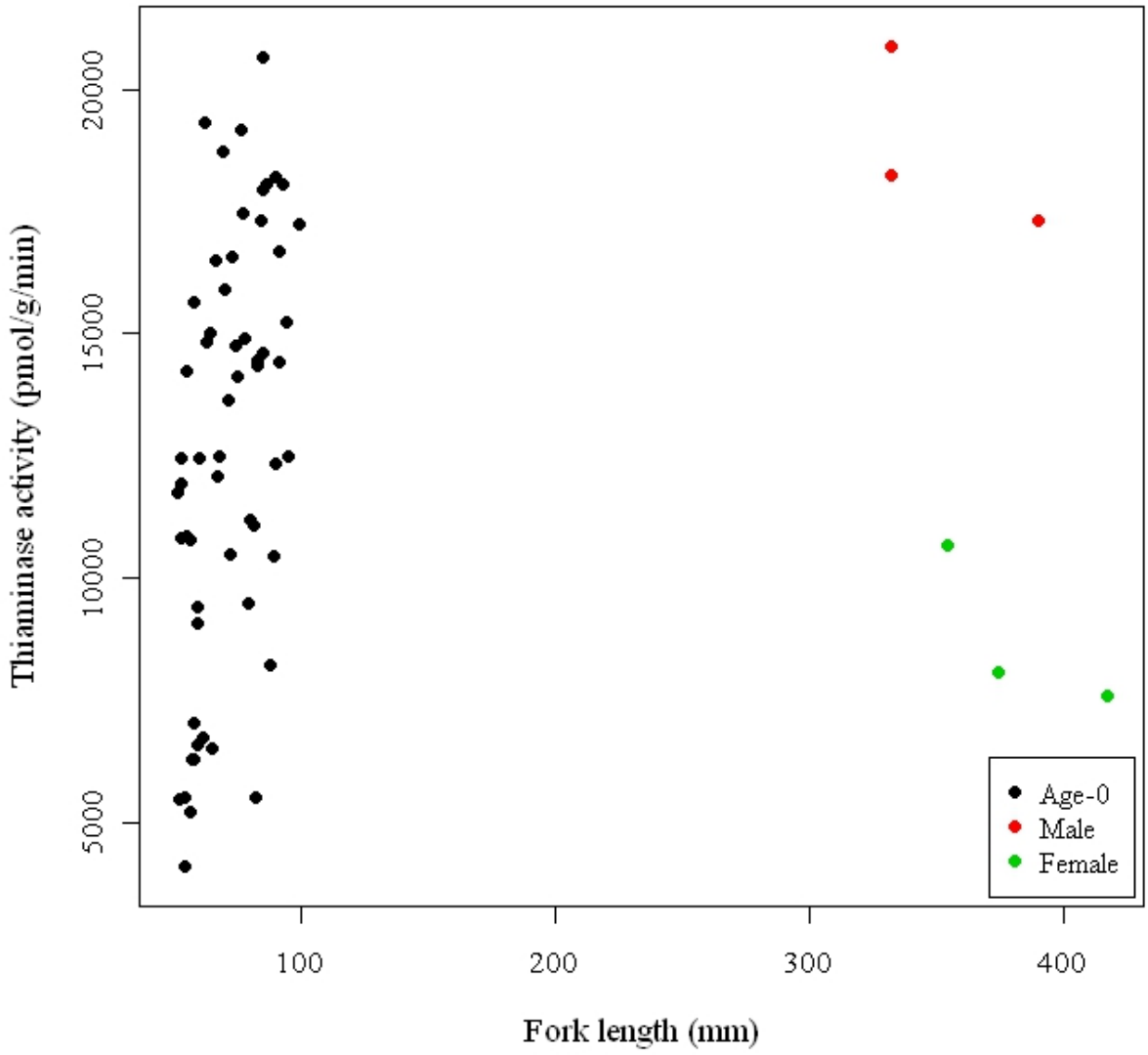

Figure 3. Thiaminase activity in 58 age-0 and 6 adult American shad collected from the Columbia River near Bonneville Dam in 2007.

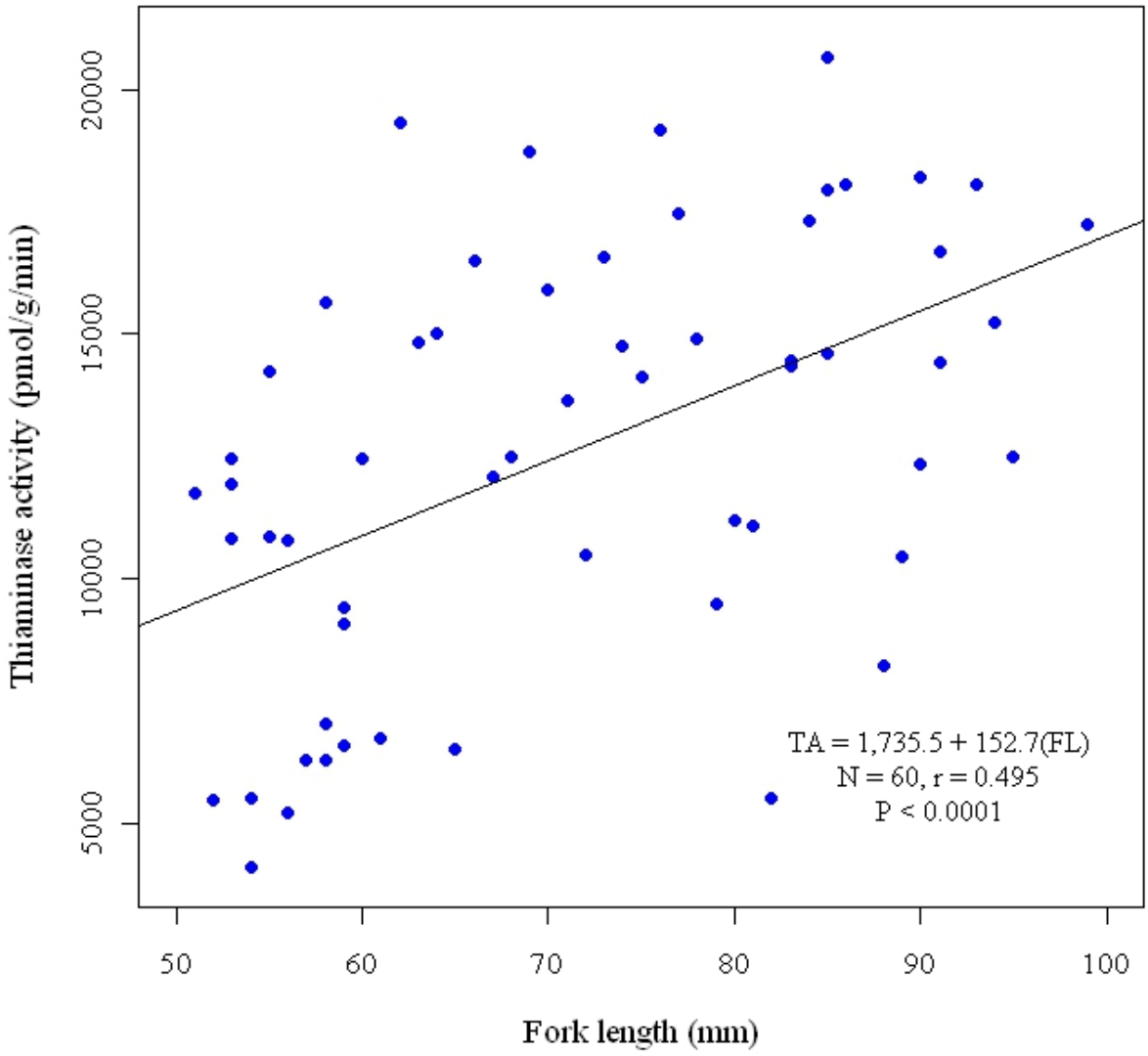

Figure 4. Thiaminase activity (TA) as a function of fork length (FL) in age-0 American shad from the Columbia River. The fish were collected from the Bonneville Dam juvenile fish facility during 2007.

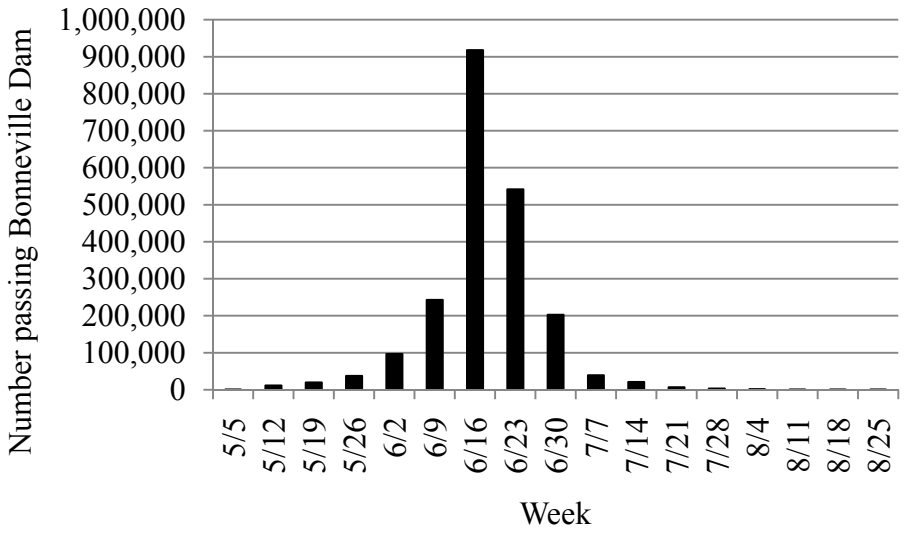

Figure 5. Weekly counts of adult American shad passing upstream at Bonneville Dam in 2008.

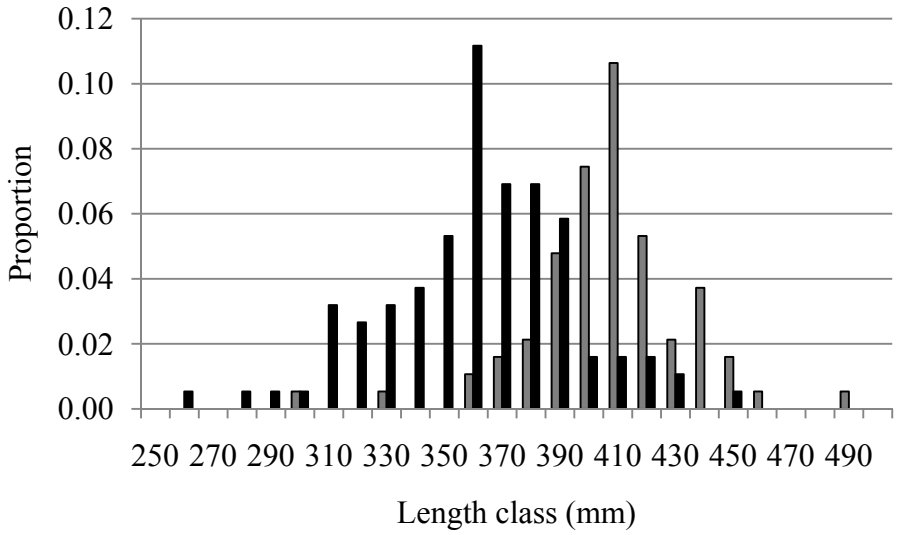

Figure 6. Length frequency of adult American shad sampled in 2008 (n = 188). Grey bars represent females, black bars represent males.

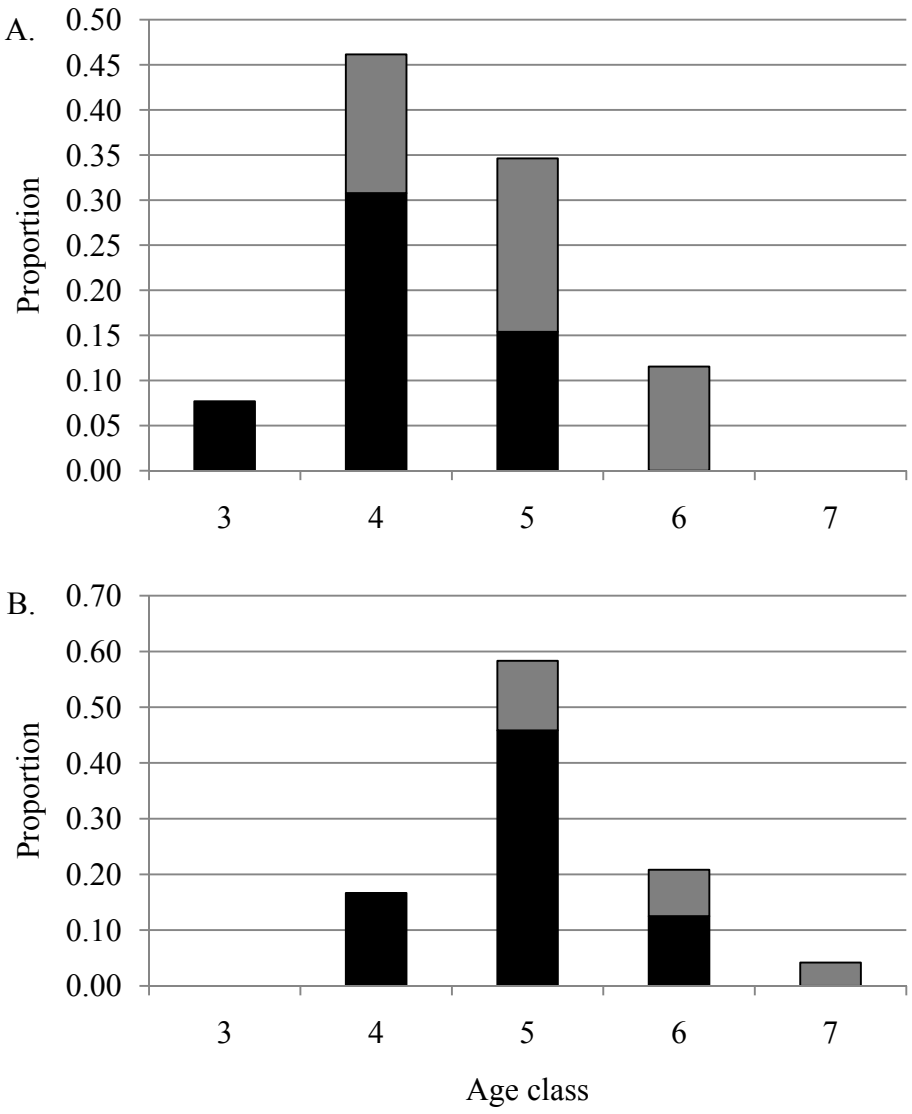

Figure 7. Age frequency distribution of male (A) and female (B) American shad showing the percent of fish that were first-time spawners (black bars) versus those that had spawned at least once (grey bars). The distributions were derived from a subsample (n = 50) of all the adult fish collected near Bonneville Dam in 2008.

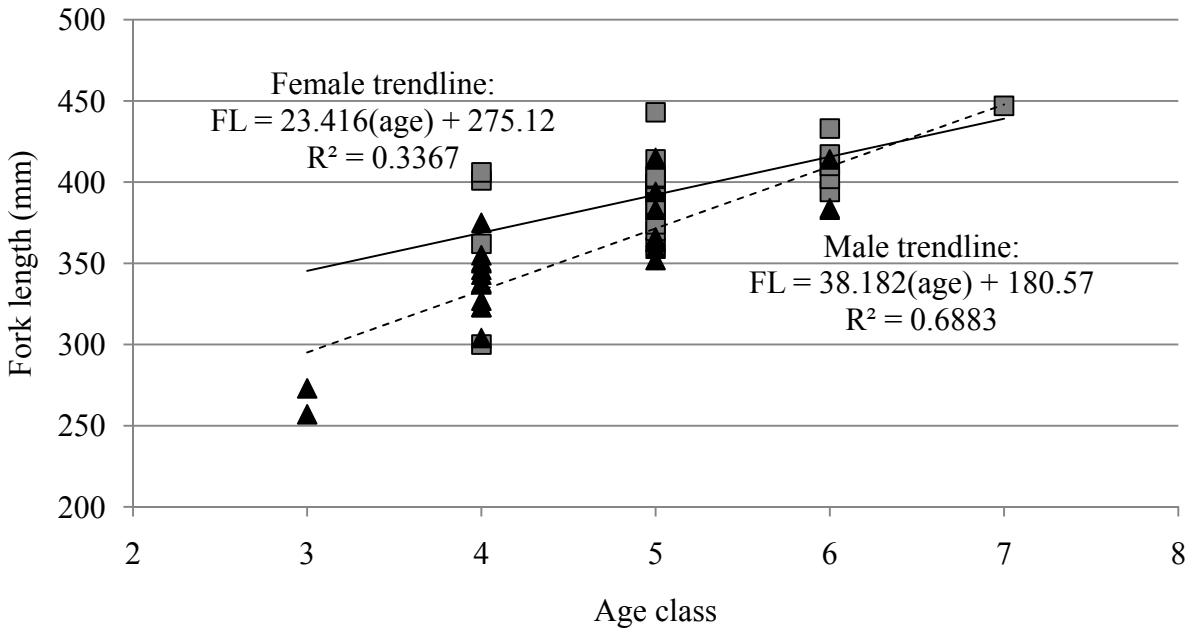

Figure 8. The relationship between fork length (FL) and age for male (black triangles, dotted line) and female (grey squares, solid line) American shad captured near Bonneville Dam in 2008 (n = 50).

Chapter 5
Verification of a 'freshwater-type' life history variant of juvenile American shad in the Columbia River

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Abstract

American shad are native to the Atlantic coast of North America and were successfully introduced to the Pacific coast in the 1870s. They are now more abundant in the Columbia River than are its native salmon. As in their native range, Columbia River American shad are anadromous and have been assumed to solely exhibit an 'ocean-type' life history, characterized by a short period of juvenile rearing in freshwater, followed by seaward migration and saltwater entry before age-1, with sexually mature individuals returning to freshwater to spawn beginning at age-3. During October 2007, emigrating juvenile American shad were captured in the juvenile fish monitoring facility at Bonneville Dam (river kilometer 235) on the Columbia River. Their length frequencies revealed the presence of two modes; the lower mode averaged 77 mm fork length (FL) and the upper mode averaged 184 mm FL. A subsample of fish from each mode was aged using otoliths. Otoliths from the lower mode (n=10) had no annuli, indicating that they were all age-0, while otoliths from the upper mode (n=25) had one or two annuli, indicating that they were either age-1 or age-2, respectively. Spawning adults collected in June 2007 averaged 393 mm FL (range 305-460 mm; n=21) and were estimated to range in age from 3-6. Elemental analyses of juvenile and adult otoliths provide evidence for deviations from the typical migration pattern expected for this species, including extensive freshwater rearing of up to two years. This evidence shows that a 'freshwater-type' of juvenile American shad exists as year-round or

transient residents in the Columbia River basin. The ecological role of this life history variant within the fish community is unknown.

Introduction

American shad (*Alosa sapidissima* Wilson 1811) are anadromous and native to the Atlantic coast of North America, where it has long been a highly valued commercial and sport fish. In 1871, biologist Seth Green was commissioned by the California Fish Commission to transport American shad fry across the country by rail for stocking into the Sacramento River (Green 1874). The effort was successful and American shad have expanded their range from southern California to southeast Alaska. In the Columbia River, the American shad population has expanded rapidly since dam construction, peaking at over 5.2 million in 2004, and is now more abundant than all species of salmon combined (www.fpc.org). Their spawning range within the Columbia River Basin includes the main stem to Rock Island Dam, the Snake River beyond Lower Granite Dam, and the Willamette River, with limited passage beyond Willamette Falls (Figure 1).

American shad on the Atlantic coast migrate to their home spawning ground between November and July, depending on latitude, and spawn at temperatures between 14 and 21°C (Leggett and Carscadden 1978; Facey and Van Den Avyle 1986). In the Columbia River, the spawning migration runs from May through July, with juveniles being abundant in main stem Columbia River reservoirs from late June through September, and then forming schools and emigrating to the ocean from August through December (Petersen et al. 2003). Trawl catches in John Day Reservoir show peak juvenile shad abundance in August, with some juveniles still present in November (Haskell et al. 2006). Laboratory experiments have shown that age-0 American shad cannot survive in freshwater past December (Zydlewski and McMcCormick 1997). However, it has been suggested that juveniles in some northern populations may remain in rivers and estuaries throughout their first winter (Facey and Van Den Avyle 1986) and documented that one landlocked population exists in Millerton Lake, CA (Moyle 1976), proving that, though anadromous, shad can adapt to freshwater rearing. There is evidence of emigration at a larger size in some juvenile American shad from Chesapeake Bay (Hoffman et al. 2008). Anomalous migrations between fresh and saltwater have also been shown through the analysis of American shad otoliths (Limburg 1995; Limburg 1998; Limburg et al. 2003).

Fish otoliths are a useful tool for reconstructing the life history of individual fish by providing such information as age, growth and migration history. Otoliths grow incrementally, generally accreting a layer of calcium carbonate and a protein matrix each day, producing a permanent record of the corresponding fish growth and environmental chemistry. Otolith microstructure analysis can provide useful information on fish age, growth and life history events through analysis of the pattern of layers, or increments (Jones 1992). Chemical analysis of otoliths (otolith microchemistry) can be used to trace the environmental history of fish (Secor et al. 1995; Elsdon et al. 2008). For example, strontium-to-calcium ratios (Sr/Ca) have been used to document diadromous migrations (Secor and Rooker 2000) and strontium isotopic ratios have been used to distinguish source populations and movements within watersheds (Kennedy et al. 2002).

During the past decade or so, biologists and others have noted the presence of a midsize Alosine in the Columbia River. Shields et al. (2007) suggested that these fish may indicate the

introduction of a different non-native Clupeid species, however, subsequent genetic analysis confirmed that these were American shad (D. Hasselman, oral communication, February 10, 2011). During our investigations we also noted the common occurrence of these midsize fish in our catches. We suspected that the midsize fish may represent a life history variant exhibiting extensive freshwater rearing in the Columbia River Basin. We termed this life history variant 'freshwater-type' and the age-0 emigrants 'ocean-type'. Our goal was to verify the presence of these 'freshwater-type' of juvenile American shad in the Columbia River through the examination of otoliths. Our specific objectives were: 1) to collect and age otoliths from three different size classes of American shad, 2) examine otolith microstructure for growth and pattern differences, and 3) sample the chemical composition of 'freshwater-type' juvenile and adult otoliths as indicators of their environmental history.

Methods

Fish Collection, Size and Age

For otolith ageing and analysis, we collected fish from three size classes. Fish from the smaller size classes (small and midsize) were obtained periodically during October 2007 from the juvenile bypass system, which diverts emigrating anadromous fish from the forebay at Bonneville Dam (river kilometer 235)(Figure 1) around the turbine intakes to improve their survival. The smallest size class of fish caught in the juvenile fish monitoring facility was subsampled due to the large numbers that pass through the facility and the midsize fish were all sampled since they were relatively rare (Figure 2). A small number from each group were placed on ice, then transported to the laboratory and frozen (-20°C). The fish were thawed and the pair of sagittal otoliths (the largest of three otolith pairs within teleost fishes) was extracted from 10 suspected age-0 fish and from 25 midsize juveniles. Fish from the largest size class were collected by three methods: (1) angling with artificial lures by boat 2-4 kilometers (km) downstream from Bonneville Dam, in the vicinity of Ives Island, June 2007, (2) gill net in the Columbia River estuary, April-May 2008, and (3) trawl off the west coast of Vancouver Island (WE Ricker Trawl Survey, Pacific Biological Station, Fisheries and Oceans Canada), May 2009. The otoliths from the Columbia River angling were extracted in the field and placed in scale envelopes (n=21), while otoliths from the Columbia River estuary and Vancouver Island were extracted in the lab from frozen heads (n=5 each). The Columbia River estuary and Vancouver Island samples were used to establish the Sr/Ca ratios for fresh and saltwater, since they were known to have experienced both environments, for comparison with the Sr/Ca ratios from the midsize fish collected in the juvenile fish monitoring facility. Gonads were examined from midsize juveniles to assess sexual maturity and from adults to determine maturity and sex.

Prior to ageing, the otoliths were cleaned in deionized water, air dried and measured to the nearest 0.1 mm with digital calipers and weighed to the nearest 0.00001 g. For ageing, the otoliths from each fish were then immersed in deionized water and examined with a dissecting microscope using fiber optic lighting from the side to distinguish annuli, which are darker continuous bands between the core and edge of the otolith, formed from tightly spaced banding associated with slow growth during winter. For juveniles, the ages were recorded as annuli counts, since they were caught in October, prior to the next winter growth season. The adult ages, however, were calculated as the annuli count plus one. The otolith edge is treated as an annulus since the new spring growth has not yet become distinguishable from the annulus, based

on otoliths from known aged American shad (M. Hendricks and W. Duffy, electronic communication, May 2009).

Length frequency analysis and descriptive statistics were used to summarize the data. Analysis of variance was performed using Excel 2007 (Microsoft, Redmond, Washington) to test for differences between age groups, using a significance level of 0.05.

Otolith Microstructure

Otoliths (generally the left otolith, unless broken) from all three size classes were processed for microstructural analysis by embedding them in epoxy resin, ventral-side down, and mounting them on microscope slides using Crystalbond thermoplastic glue. Excess resin was removed with an Isomet saw. Each sample was ground on a lapping wheel with increasingly finer abrasive slurries to expose the nucleus from which the otolith developed. Each sample was flipped and ground on the second side until the increments in the chosen area for analysis were optimally visualized. Each processed otolith was photographed using a digital camera attached to a compound microscope and examined using ImagePro software. A reference line was drawn from the tip (or rostrum) through the nucleus (Figure 3). A radial transect was then drawn from the nucleus to the dorsal edge at an angle between 80° and 90° from the reference line. This area for analysis was chosen as most consistently readable after visual comparison among samples and analysis using an alternate angle (10-20°) in an area closer to the post-rostrum, opposite the tip. Marks were placed at each increment, which were defined by alternating dark and light bands assumed to correspond to 24-hour growth periods (Stevenson and Campana 1992). Marks were also placed at prominent structures and where pattern changes indicated developmental or environmental shifts (Figure 6). The ImagePro software calculated the number of marks and distance between marks for each otolith.

Otolith Microchemistry

A subsample of otoliths from the larger size classes (n=10 midsize juveniles, n=5 large size individuals from the mouth of the Columbia River and n=5 large size individuals from Vancouver Island) were analyzed for strontium (Sr) and calcium (Ca) at the US Geological Survey, Electron Microprobe Laboratory in Menlo Park, CA, following established protocols (Zimmerman and Nielsen 2003; Zimmerman 2005). Elemental analysis was conducted with a JEOL 8900 Electron Microprobe, using a 15-kV, 50-nA, 10-µm-diameter beam. Strontiantite and calcite were used as standards for Sr and Ca, respectively. Each element was analyzed simultaneously and a counting time of 40 s was used to maximize precision. For each otolith, points were sampled along a transect from the nucleus to the edge of the otolith, with a spacing of 14 to 25 µm between sampling points. No statistical analyses were conducted due to the nature of this type of data, but interpretations of migration history were made based on visual inspection of graphs of the Sr/Ca values by distance from the nucleus for each otolith. Each otolith was then categorized into a life history pattern based on visual observation of the graph compared to expected values for fresh (low) and salt (high) water from the literature and the marine-caught samples. The life history patterns were summarized in a table and representative examples are shown.

Results

Age and Size

The length frequency of juvenile shad obtained from the juvenile fish monitoring facility revealed a bimodal distribution; fish in the lower mode (small size class) had a mean of 76.86 mm fork length (FL) (SD = 5.93; range 65-98 mm; n = 88) while the fish in the upper mode (midsize class) had a mean of 184.91 mm FL (SD=16.25; range 152-223 mm; n = 56) (Figure 4). Examination of the otoliths from a subsample of fish from each mode revealed that none of the fish in the lower mode had an annulus (age-0), however, all the fish in the upper mode had either one or two annuli (age-1 and age-2) (Figure 5). Table 1 summarizes the mean size at age for each size class. The mean fork length of age-1 fish was larger than the mean fork length of age-2 fish, but not significantly so (P>0.1295). Fish from the midsize class were sexually immature, whereas fish from the large size class were sexually mature (adult) and their estimated ages ranged from 3 to 6 years.

Microstructural Analysis

A possible saltwater entry check prior to the first annulus was identified on otoliths from the large size class (adults) (Figure 6). Mean increment width corresponding to freshwater growth (from the nucleus to the saltwater entry check) for the adults (n=6) was compared to first-year mean increment width (from the nucleus to the first annulus) for the midsize fish (n=10) and no significant differences were found (midsize class = 4.90 µm; large size class = 5.07 µm; P>0.68).

Microchemical Analysis

Strontium-to-calcium ratios (Sr/Ca) ranged from low values of 0.0005 to 0.0010 up to high values of 0.0020-0.0025. These values are consistent with published American shad otolith Sr/Ca ratios associated with fresh (low range) and salt (high range) water (Limburg 1995). Some fish exhibited expected patterns in their Sr/Ca ratios, that is, low ratios in freshwater and high in saltwater, but there was a high degree of variability in the results (Figure 7). The Sr/Ca patterns observed in these few fish suggest three American shad life history types; the expected 'ocean-type' with juveniles outmigrating at age-0, 'freshwater-type' with juveniles outmigrating at age-1 or age-2, and 'highly-variable' suggesting movements between fresh and saline environments throughout their life (Table 2).

Discussion

The upper mode of juvenile shad (midsize) caught in the Bonneville Dam juvenile fish monitoring facility during October 2007 were determined to be one and two year old fish. We termed these fish 'freshwater-type' juveniles and consider them an alternate life history variant of the typical 'ocean-type' life history. We expected to see a single annulus on these fish; however, some fish had two annuli, suggesting a multi-year freshwater residency. Some of the age-1 fish were larger than the age-2 fish. This could be from difficulty in ageing the fish (the first annulus is sometimes difficult to identify in adult American shad otoliths, M. Hendricks, electronic communication, May 2009) or from extreme growth in certain individuals. Columbia River American shad have been shown to have elevated growth rates and tolerance to a wide range of temperatures and salinities, when compared to fish from the Delaware River (Rottiers et al. 1992). American shad originating from the Snake River could have different growth patterns

than shad from the main stem Columbia River due to environmental or genetic differences and could have contributed to the high variation in length at age among 'freshwater-type' juveniles (Oliveira et al. 2002). Future research could help discriminate the source population of the 'freshwater-type' juveniles through otolith stable isotope analysis, based on the distinct geochemical signatures of these watersheds (Walther and Thorrold 2008), genetic analysis, or tagging studies.

We theorize that the development of a freshwater-type variant in the Columbia River may have resulted from delayed outmigration by age-0 fish. River morphology, fish passage conditions and slow-current habitats may extend the duration of downstream migration in some age-0 American shad. For example, juveniles with a long migration (i.e., Snake River fish) or those caught up in the slow currents of reservoirs and backwatered habitats adjacent to the river may not reach the estuary during the fall and remain in freshwater over the winter, as in the case of Snake River fall Chinook salmon (*Oncorhynchus tshawytscha*) (Connor et al. 2005). Spawning timing and growth rate differences may influence the relative contribution of migratory or resident life history population contingents. In white perch (*Morone americana*), early spawning, slow growing fish contribute more to the migratory contingent whereas late spawning, fast growing fish contribute more to the resident contingent (Kerr and Secor 2010). However, there was no significant difference in first-year growth rate between 'freshwater-type' juveniles and migratory adults as determined from mean increment width, suggesting that growth rate may not be a determining factor for remaining in freshwater. Our sample size for microstructural analysis was small due to the scope of the work and budget. Using a larger sample size of individuals representing different life history variants and life-stages within the same brood year to eliminate year to year variation in environmental conditions could provide a more robust analysis in the future.

The microchemistry results revealed three life history patterns relating to migration. The expected pattern of Sr/Ca ratios for 'ocean-type' adults would initially be low, corresponding to freshwater rearing (with a possible high level at the core due to maternal marine influence), and then rising, corresponding to migration and marine rearing; there could be periodic low levels toward the otolith edge corresponding to multiple spawning migrations (Figure 7 panels IIA and IIIA). The expected pattern of Sr/Ca ratios for 'freshwater-type' individuals would be consistently low (with a possible high level at the core due to maternal marine influence), corresponding to freshwater rearing for one or two years until capture, for juveniles, or with subsequent elevation due to migration and marine rearing, in the case of adults. Figure 7 IIIC shows a marine-caught fish of unknown origin with Sr/Ca ratios that may represent a 'freshwater-type' juvenile that spent two years in freshwater before migrating to the ocean, which suggests that these juveniles can have extended freshwater rearing and still maintain their ability to migrate and adapt to saltwater. The Sr/Ca ratios from all the Columbia River 'freshwater-type' juveniles were mainly low, consistent with freshwater rearing, but also showed anomalous peaks (Figure 7 panels IA-IC). This could indicate that the midsize fish had migrated to saltwater and then returned to freshwater, as has been shown with precocious yearling 'minijack' Chinook salmon from the Umatilla River (Zimmerman et al. 2003). If some fish migrate and rear in highly productive estuarine and marine habitats and then return as midsize fish to less productive fresh water, this would give them a growth advantage over resident 'freshwater-type' fish, and could explain why some age-1 fish were larger than age-2 fish. However, the Sr/Ca ratio peaks in the large age-1 fish (Figure 7 IB) were similar to other Columbia River 'freshwater-type' juveniles and none were sexually mature. Limburg (1998)

caught yearling American shad with elevated Sr/Ca ratios 97-208 km upstream of the mouth of the Hudson River estuary and hypothesized that younger ocean-phase fish may follow the adults into freshwater on their spawning migration. However, that stretch of the Hudson is tidally influenced and has no dams. It may not be possible for Columbia River juvenile shad to enter saltwater and then return upstream over 140 km to pass above Bonneville Dam via a fishway. Long distance upstream migrations of Chinook salmon 'minijacks' similar in size to the midsize shad have been documented in the Columbia River, with one fish traveling 600 km through 4 dams in 21 days (Beckman and Larsen 2005). If American shad are capable of such migrations, it could be documented by separately counting midsize upstream migrating shad in the fish ladders. The anomalous peaks in the Sr/Ca ratio of Columbia River 'freshwater-type' fish may also be explained by an altered uptake of strontium produced during stressful events (Kalish 1992), possibly including dam passage, or from residence within a localized freshwater source of strontium, as seen seasonally in some Idaho streams (Bacon et al. 2004). Several individuals showed a 'highly-variable' pattern (Figure 7 panels IIB, IIC, and IIIB), which was possibly the result of extended estuarine residence or movements among river, estuary and ocean environments (Limburg 1998; Hoffman et al. 2008).

Our results show that a 'freshwater-type' variant of juvenile American shad, which emigrate at a larger size and age than the typical 'ocean-type' shad, are residing in the Columbia River. Even if this life history variant is relatively rare within the American shad population, the sheer abundance of American shad produced in the Columbia River basin could result in appreciable numbers, potentially with significant ecological impact. We also show that migratory patterns among juveniles and adults are variable and more complicated than previously thought. Future research should include: (1) population size estimation and impact assessment of the 'freshwater-type' life history variant of American shad on the Columbia River ecosystem, especially impacts on salmonids, (2) investigation of the source populations of the 'freshwater-type' juveniles through genetic or otolith isotope analysis, and (3) identification of the source of the anomalous strontium peaks, again through otolith isotope or trace element analysis, to determine if the Columbia River 'freshwater-type' juveniles are transient or year-round residents. The presence of the 'freshwater-type' juveniles in the Columbia River and the unusual Sr/Ca transects suggest that American shad are capable of life history and migratory variability and flexibility, which may have aided in their adaptation and success on the Pacific coast of the U.S.

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Table 1. Characteristics of a subsample of American shad captured at Bonneville Dam during 2007. Gender of juvenile fish was not determined. Standard deviations for lengths are shown in parentheses. There was no statistically significant difference between age-1 and age-2 lengths (P>0.1295).

Size class	Sex	Age	No. aged	Mean FL (mm)
Small				
		0	10	70.7 (3.7)
Midsize				
		1	10	185.7 (24.6)
		2	15	174.7 (9.49)
		Midsize total	25	179.1 (17.6)
Large				
	Female	4	5	381.2 (21.3)
		5	5	420.2 (26.3)
		6	2	455.0 (7.1)
		Female total	12	409.8 (34.8)
	Male	3	1	319.0 (NA)
		4	3	351.0 (1.0)
		5	1	366.0 (NA)
		6	4	398.0 (12.7)
		Male Total	9	370.0 (30.2)
		Large Total	21	392.7 (38.0)

Table 2. Summary of the number of each life history pattern identified within each size class by microchemical analysis (n=10 per size class).

Life history pattern	Midsize	Large
'ocean-type'		3
'freshwater-type'	10[1]	1
'highly variable'		6

[1] Each of these 'freshwater-type' patterns had anomalous strontium peaks.

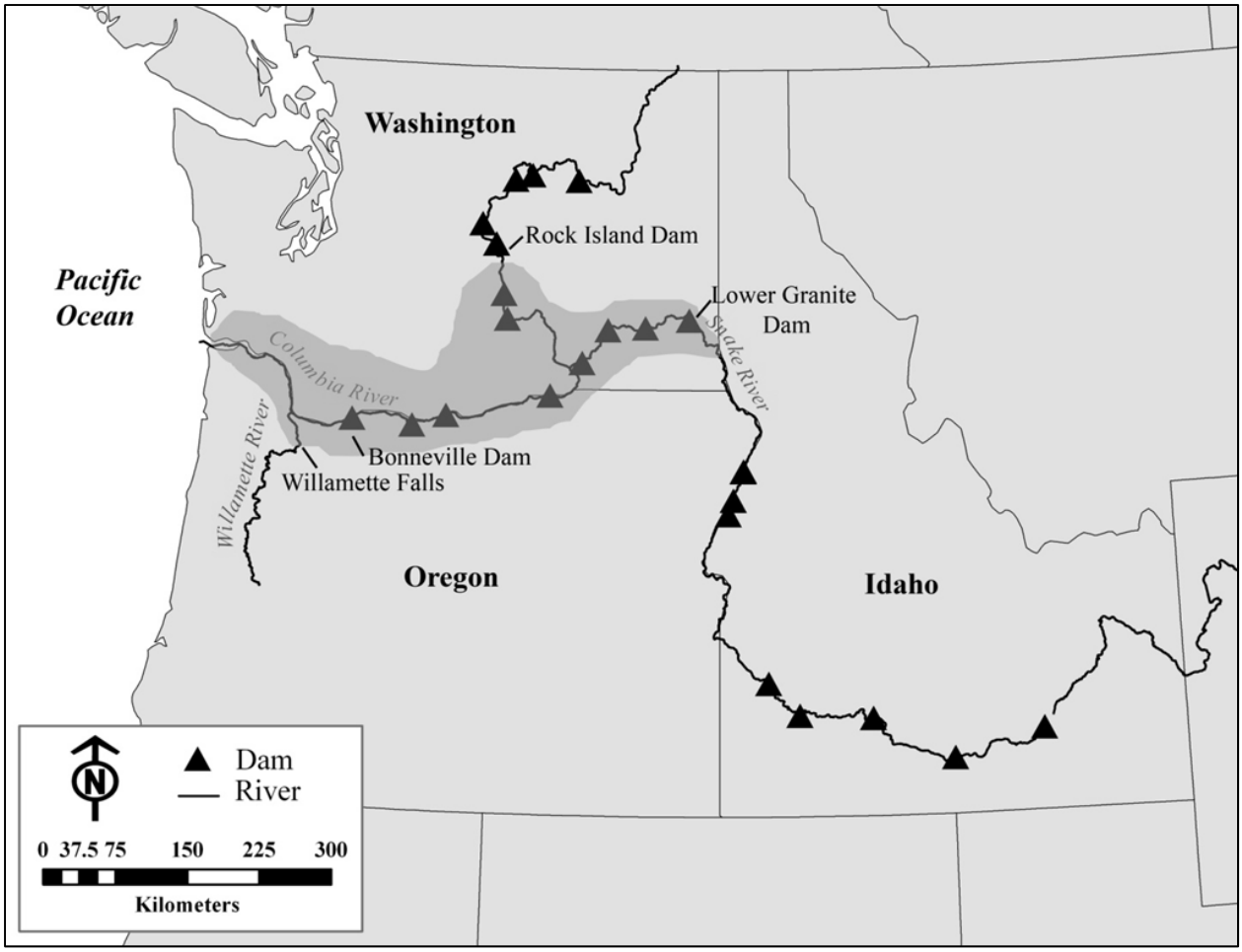

Figure 1. Distribution of American shad in the Columbia River Basin (grey shaded area).

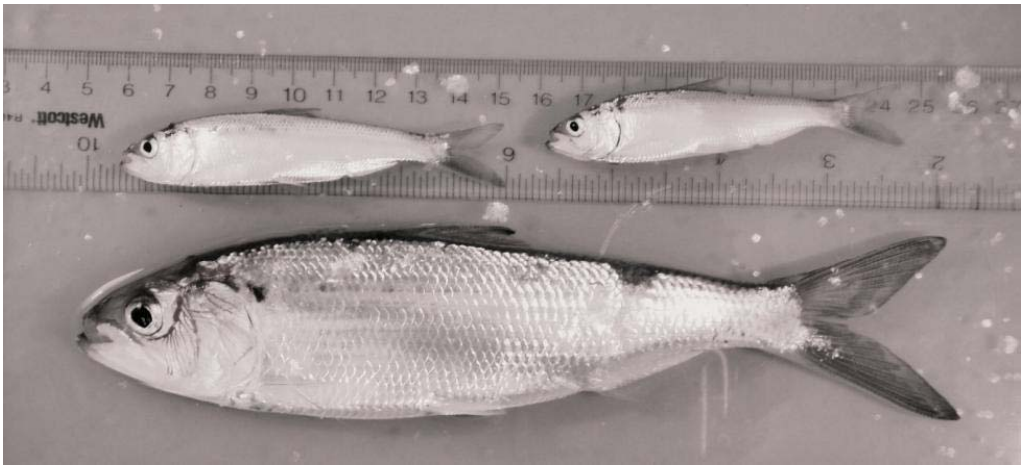

Figure 2. Examples of small size class (upper two fish, approximately 78-88 mm FL) and midsize class (lower fish, approximately 189 mm FL) juvenile American shad frequently encountered in the Columbia River, collected October 2007 at the Bonneville Dam juvenile fish monitoring facility.

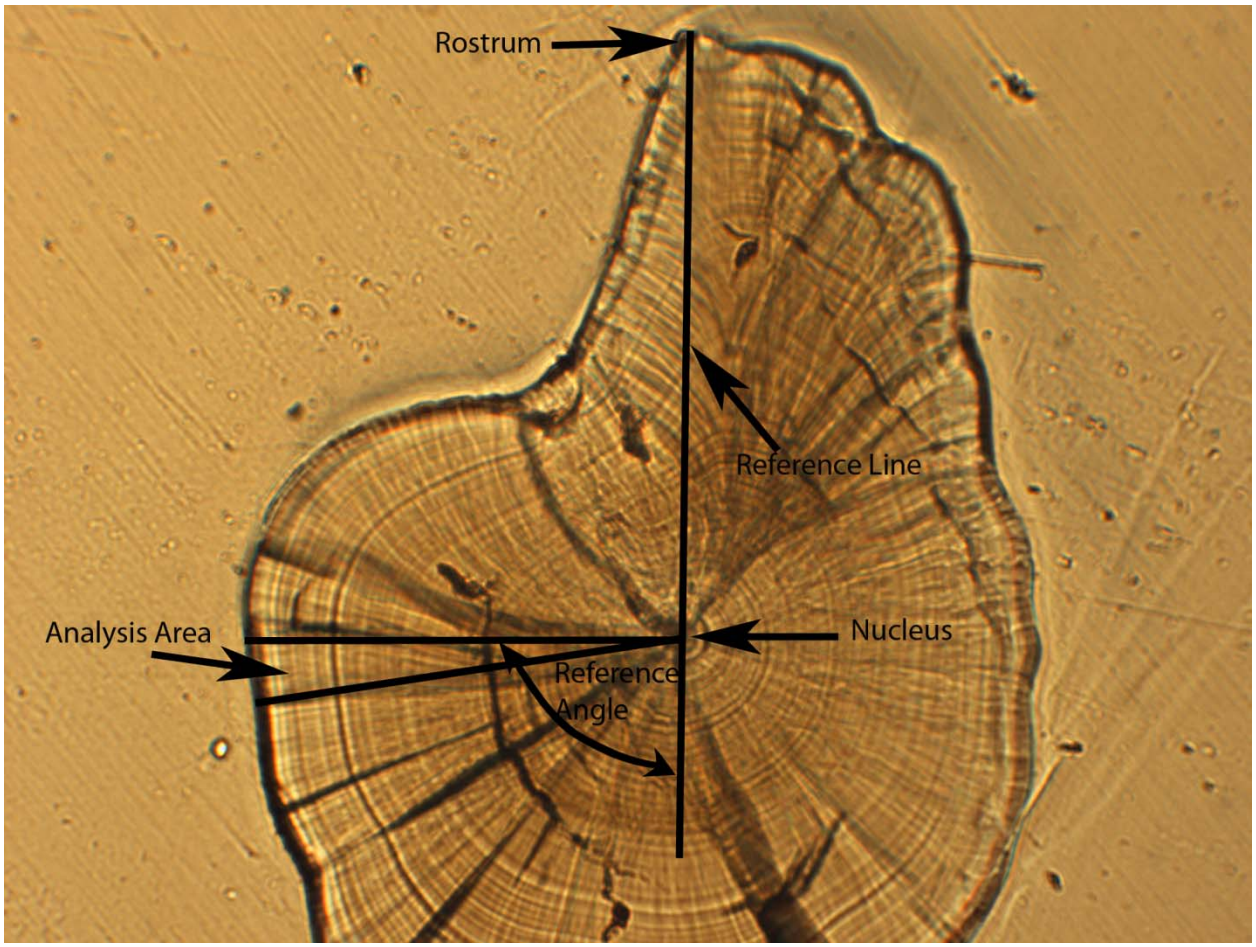

Figure 3. Image of an otolith from a 55-mm FL pre-migratory age-0 juvenile American shad. Features pertinent to microstructural analysis are noted.

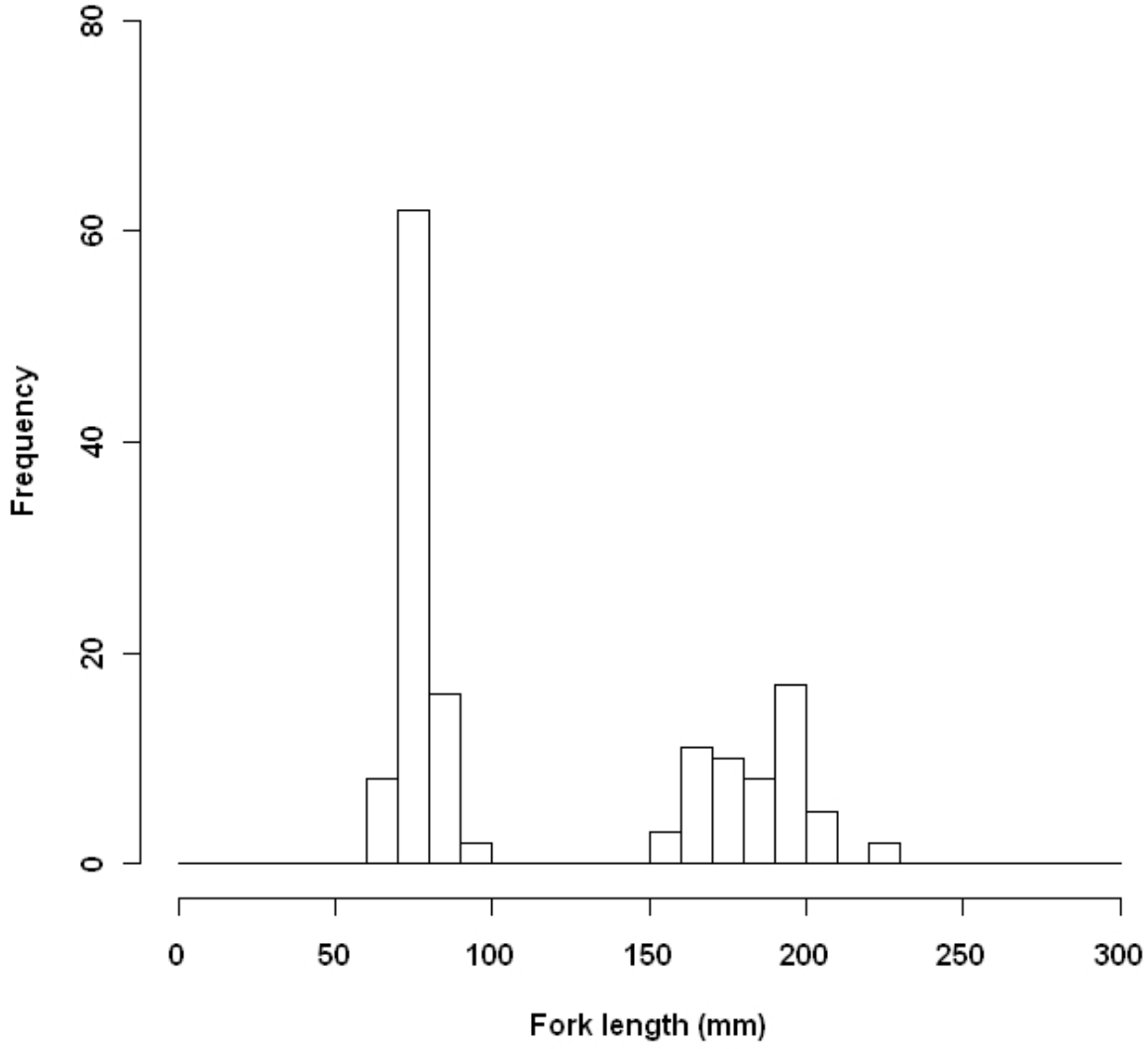

Figure 4. Length frequency of 144 juvenile American shad obtained from the juvenile fish monitoring facility at Bonneville Dam in October 2007 showing the two size classes present.

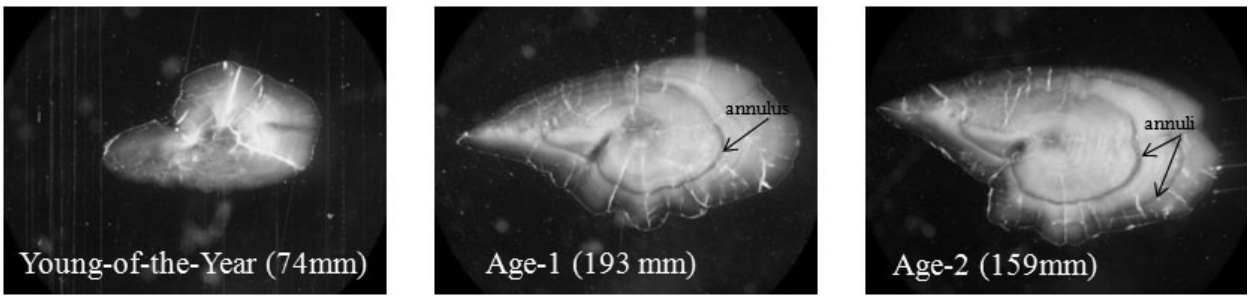

Figure 5. Representative otoliths from three American shad showing zero, one and two annuli. The fish were obtained from the juvenile fish collection facility at Bonneville Dam during October, 2007.

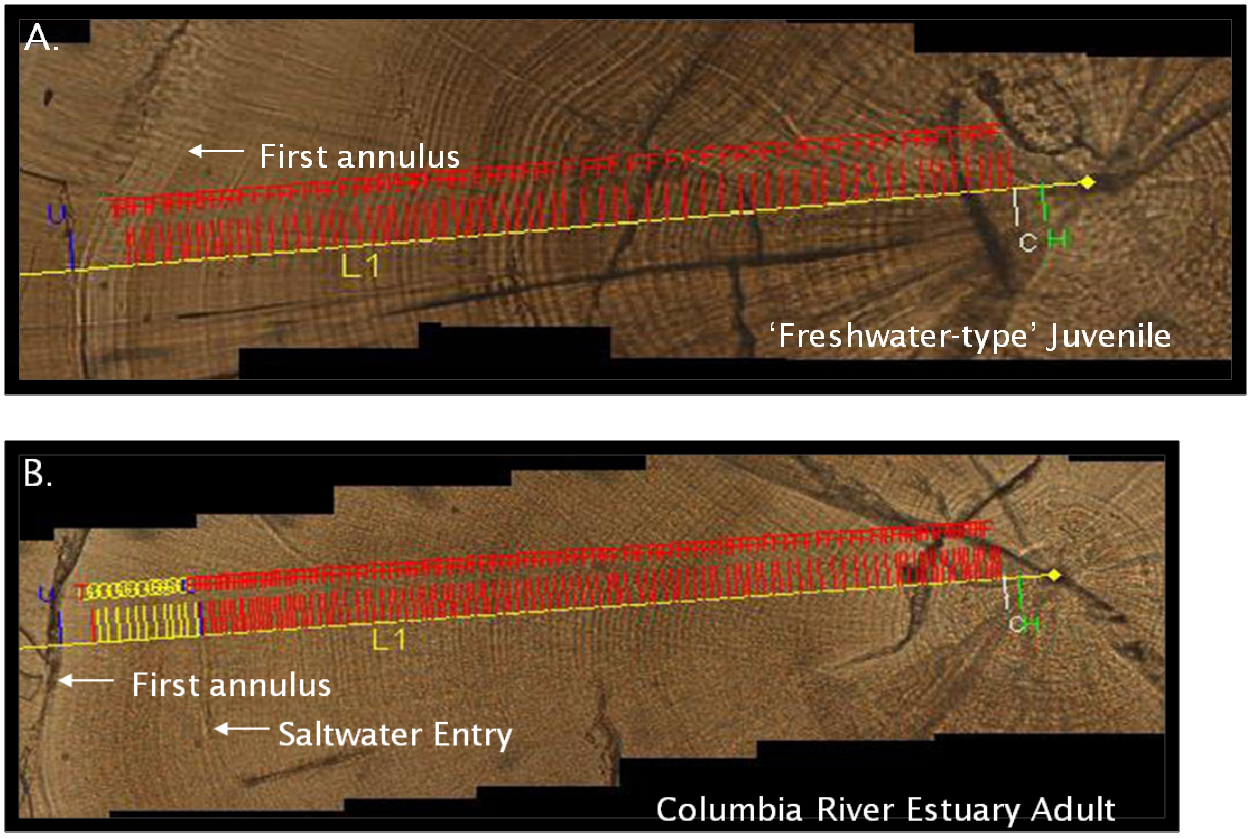

Figure 6. Images of an otolith from a 'freshwater-type' juvenile (A) and migrating adult (B) with marked transects across the first-year of growth representing the freshwater portion of their residence in the Columbia River.

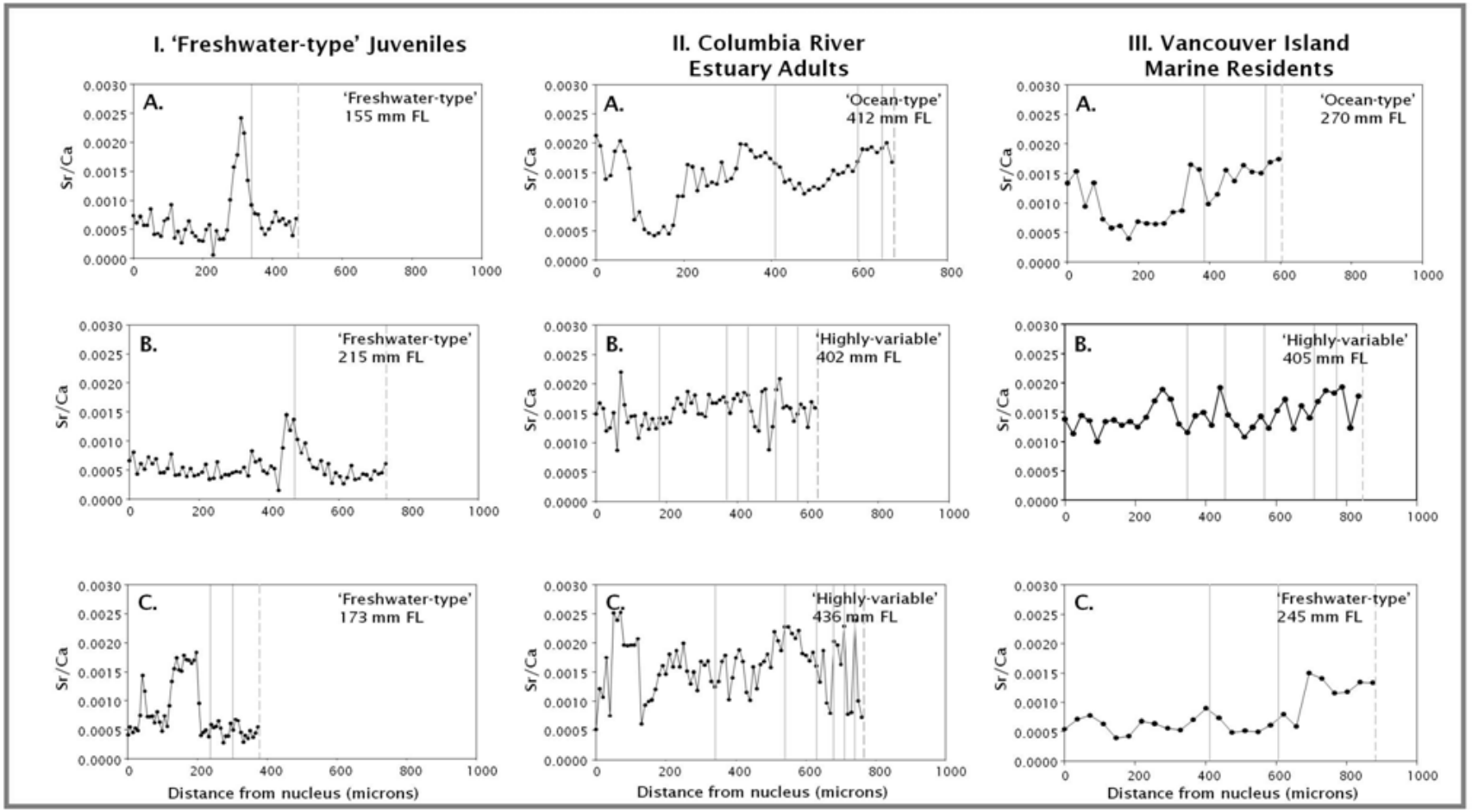

Figure 7. Ratios of strontium to calcium (Sr/Ca) from American shad otoliths from Columbia River 'freshwater-type' juveniles (I), Columbia River estuary adults (II), and Vancouver Island marine residents (III); three examples are given for each (panels A., B., and C). The natal river of marine resident fish captured off Vancouver Island, British Columbia is unknown. Solid grey lines indicate annuli; dashed grey lines indicate the otolith edge.