Assessment of Smolt Condition: Biological and Environmental Interactions

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Final Report
The impact of prey and predators
on juvenile salmonids

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Assessment of Smolt Condition: Biological and Environmental Interactions

Executive Summary

The Bonneville Power Administration (BPA) has funded the Assessment of Smolt Condition project since 1987. During that time the project changed frequently to meet the information needs of fish managers by conducting studies throughout the Columbia River basin. Past research has examined the influence of smolt physiological development and health on migration rate; differences in development and migration rates of smolts of hatchery or wild origins; and the impacts of hatchery practices on smolt development. The Smolt Assessment Project will not continue beyond 2004, and here we report on the final study of the project in which we used bioenergetics modeling to investigate predation on juvenile salmonids by northern pikeminnow, smallmouth bass, and walleye in the lower Columbia River reservoirs.

The first portion of the work reported here investigated the role of anadromous preyfish and water temperature in the growth and salmonid consumption of northern pikeminnow. This modeling will be combined with similar work completed as part of another BPA-funded project to identify large-scale northern pikeminnow predation patterns in the lower Snake and Columbia rivers. In attempting to understand the interactions driving smolt predation, our research identified three spatially separate northern pikeminnow predation patterns in the lower Columbia River basin. The biotic and abiotic factors contributing to these spatially distinct northern pikeminnow growth and predation patterns are: (1) release of large numbers of hatchery salmonids into the free-flowing Columbia River below Bonneville Dam, (2) rearing and emigration of large numbers of invasive American shad in the lower Columbia River reservoirs, and (3) low numbers of anadromous preyfish and warmer water temperatures in the lower Snake River reservoirs. Identification of these predation patterns provides management agencies with large-scale spatial information on the factors driving northern pikeminnow predation on juvenile salmonids in different areas of the lower Columbia River basin, and opportunities for development of innovative predation control measures.

The second portion of this study focused on the potential impact of larval and juvenile American shad, an invasive preyfish, on the growth and salmonid consumption of invasive predators in the lower Columbia River reservoirs. We estimated the late summer and fall diet of smallmouth bass and walleye, and used size-at-age data on smallmouth bass (Beamesderfer and Ward 1994) and walleye (Tinus and Beamesderfer 1994) collected in John Day Reservoir to run bioenergetics simulations under various prey and water temperature scenarios. Most significantly, our modeling on invasive aquatic predators suggests that a relatively small increase in the growth of smallmouth bass due to American shad preyfish in the late summer and fall diet could potentially result in a large increase in the proportion of juvenile salmonids consumed by this predator. Our results support earlier research and reinforces concern expressed by numerous authors that smallmouth bass predation may result in heavy losses of subyearling fall Chinook (Gray and Rondorf 1986; Curet 1993; Tabor et al. 1993; Poe et al. 1994; Zimmerman 1999; Duran et al. 2003; Petersen et al. 2004). Because of their smaller size and later migration period, wild fall Chinook from the Hanford Reach and Snake River may be more vulnerable to smallmouth bass predation than hatchery fish. Juvenile salmonids may also be vulnerable to smallmouth bass predation whenever foraging or flow patterns bring migrants near shorelines, or migrants are delayed in dam forebays, particularly later in the spring once water temperatures have warmed.

Bioenergetics modeling also suggests that the growth of walleye is enhanced by a late summer and fall diet of American shad. Unlike smallmouth bass, the increased walleye growth predicted with a fall diet that includes American shad produced only a modest rise in salmonid consumption. Bioenergetics simulations also suggest that warmer summer and fall water temperatures in the impounded lower Columbia River contribute substantially to the growth rates of smallmouth bass and walleye. The increased feeding rate of these introduced aquatic predators in response to warmer water temperatures during the summer months suggests these species may primarily impact subyearling fall chinook in the lower Columbia River.

Introduction

Emigrating juvenile salmon and steelhead face large numbers of aquatic predators as they move through the lower Snake and Columbia river migration corridors (Table 1 and 2). Three invasive species known to consume emigrating salmonids are smallmouth bass (Micropterus dolomieu), walleye (Stizostedion vitreum), and channel catfish (Ictalurus punctatus) (Gray and Rondorf 1986; Poe et al. 1991; Zimmerman 1999). The introductions of these predators into the Columbia River basin appear to be extremely successful; smallmouth bass and channel catfish are distributed in lower mainstem Columbia and Snake river reservoirs, smallmouth bass have also invaded free-flowing reaches, and walleye are established in the Columbia River reservoirs. Estimates of population densities, growth characteristics, and fecundity suggest that reservoir conditions in the lower Columbia River reservoirs are quite favorable for these introduced predators (Maule and Horton 1984, 1985; Poe et al. 1994; Zimmerman and Parker 1995).

Another invasive species, the anadromous American shad (Alosa sapidissima) may be a contributing factor in the success of these invasive predators. The American shad is native to the east coast of North American, and was introduced into the Sacramento River, California over a century ago (Petersen et al. 2003). Within a few years after the Sacramento River introduction, adult American shad spread north into other coastal tributaries and invaded the Columbia River (Petersen et al. 2003). Historically, the American shad population in the Columbia River was limited to the lowest portion of the river by the swift current and cascades of the Columbia River. Hydropower development of the lower Columbia River, beginning in 1938 with Bonneville Dam, continued to block upstream access to American shad until fish ladder modifications were completed in the 1970s (Petersen et al. 2003). These ladder modifications improved passage for adult salmonids, but also opened the impounded reservoirs of the lower Columbia River reservoirs to American shad invasion (Monk et al. 1989; Petersen et al. 2003). Large numbers of juvenile American shad now rear in and emigrate though the lower Columbia River and its reservoirs (Petersen et al. 2003). In recent years, the number of returning adult American shad has often outnumbered adult salmon and steelhead passing Bonneville Dam, and the largest American shad run ever recorded at Bonneville Dam was 4.7 million fish in 2003 (http://www.fpc.org).

The large number of juvenile American shad rearing and emigrating through the lower Columbia River reservoirs may be an important and largely unrecognized link to the predation mortality incurred by salmon and steelhead smolts. Juvenile American shad may influence the predator populations that prey on emigrating salmonids in several key ways. First, juvenile American shad are abundant in the reservoirs from mid-summer through fall, providing forage for predators at a time when juvenile salmonids are scarce. Second, juvenile American shad are also an energy-rich meal for predators, providing more calories/gram than most other prey available in the Columbia River. Third, because of hydroelectric impoundment, water temperatures in the lower Columbia River reservoirs remain warmer longer into the fall than under pre-impoundment conditions (Quinn and Adams 1996; Quinn et al. 1997; Sauter and Petersen, Report C in prep.). Warmer water temperatures increase the metabolic demand and fall foraging activities of aquatic piscivores. The combination of abundant juvenile American shad and warmer fall water temperatures provides aquatic predators with favorable fall growth conditions that did not exist 60 years ago.

Warmer fall water temperatures and abundant numbers of American shad in the lower Columbia River migration corridor may directly contribute to the population size, annual growth rate, and reproductive potential of aquatic predators preying on salmon and steelhead smolts.

Predation research on juvenile salmonids has primarily targeted a native predator, the northern pikeminnow (Ptychochelius oregonensis) for study and management, while the predation impact of invasive piscivores on emigrating smolts has received less attention. Much is known about the seasonal diet (Poe et al. 1991; Zimmerman 1999; Petersen and Sauter Report B, in preparation), behavior (Poe et al. 1994), density (Beamesderfer and Rieman 1991; Parker et al. 1995), growth rate (Vigg et al. 1990; Parker et al. 1995; Petersen Report A, in preparation), and fecundity (Knutsen and Ward 1997) of northern pikeminnow at various locations in the Columbia River basin.

Prior to the implementation of the northern pikeminnow management program, this native predator consumed an estimated 16.4 million juvenile salmonids annually in the impounded mainstem Snake and Columbia rivers (Beamesderfer et al.1996). An estimated 1.4 million juvenile salmonids were consumed each year in John Day Reservoir alone (Petersen 1994). Based on northern pikeminnow population and diet estimates from 1983 - 1986, and prey digestion rates, 78% of the juvenile salmonid losses in John Day Reservoir are due to northern pikeminnow predation and the remaining 22% is attributed to smallmouth bass and walleye (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991). Channel catfish are also a potentially important predator on juvenile salmonids in lower Snake and Columbia river reservoirs (Gray and Rondorf 1986; Zimmerman and Parker 1995) but were not included in salmonid loss estimates.

Recently, Sauter and Petersen (Report B, in preparation) used bioenergetics modeling to explain observed growth differences between northern pikeminnow collected from the free-flowing lower Columbia River compared to lower Snake River reservoirs. Bioenergetics simulations suggested that diet and annual temperature regime could explain the observed differences in predator growth between the two locations and a more complex pattern of northern pikeminnow predation dynamics in the Columbia River basin began to emerge (Petersen and Sauter, Report B, in preparation; Sauter and Petersen, Report C, in preparation). In the current paper, we expand on previous northern pikeminnow bioenergetics modeling to (1) model the influence of invasive American shad on northern pikeminnow growth and smolt consumption in the lower Columbia River reservoirs, (2) identify some of the spatial and temporal northern pikeminnow predation patterns in the lower Columbia River migration corridor, and (3) model the potential impact of invasive prey and predators on migrating juvenile salmonids.

Methods

Study Area

Previous bioenergetics modeling on northern pikeminnow sought to explain observed growth differences between populations in the lower Snake River reservoirs and the free-flowing Columbia River below Bonneville Dam (Petersen and Sauter, Report B in preparation). The current study examines the impact of invasive American shad on the growth and smolt consumption of northern pikeminnow and two invasive predators, smallmouth bass and walleye, in the lower Columbia River reservoirs (LCRR). Our study area extended from Bonneville Dam forebay to McNary Dam tailrace, and includes Bonneville, The Dalles, and John Day reservoirs.

Data compilation

We compiled data from a variety of published and unpublished sources to investigate hypotheses about predator growth and smolt consumption in the LCRR. No additional field effort was conducted to fulfill the data requirements.

Table 1. Common invasive aquatic predator and preyfish species found in the migration corridor of the lower Columbia River (Barfoot et al. 2002), their lifestage at that trophic level and migratory status.

Trophic Level	Common Name	Scientific Name	Life stage	Migratory status
Predator	Smallmouth bass	*Micropterus dolomieu*	juveniles and adults > 75 mm	resident
	Walleye	*Stizostedion vitreum*	adult	resident
	Channel catfish	*Ictalurus punctatus*	adult	resident
Potential Preyfish	American shad	*Alosa sapidissima*	juvenile	anadromous
	Common carp	*Cyprinus carpio*	juvenile	resident
	Bluegill	*Lepomis macrochirus*	juvenile	resident
	Pumpkinseed	*Lepomis gibbosus*	juvenile	resident
	Crappie	*Pomoxis* spp.	juvenile	resident
	Yellow perch	*Perca flavescens*	juvenile	resident
	Bullhead	*Ameiurus* spp.	juvenile	resident

Table 2. Common native predator and preyfish species of the lower Columbia River, their lifestage at that trophic level, and migratory status (Poe et al. 1991; Zimmerman 1999).

Trophic Level	Common Name	Scientific Name	Life Stage	Migratory status
Predator	Northern pikeminnow	*Ptychocheilus oregonensis*	Juveniles and adults >250 mm	resident
Potential preyfish	Chinook salmon	*Oncorhynchus tshawytscha*	parr and smolts	anadromous
	Steelhead	*Oncorhynchus mykiss*	parr and smolts	anadromous
	Peamouth	*Mylocheilus caurinus*	juveniles	resident
	Chiselmouth	*Acrocheilus alutaceus*	juveniles	resident
	Redside shiner	*Richardsonius balteatus*	juveniles/adults	resident
	Longnose dace	*Rhinichtys cataractae*	juveniles/adults	resident
	Largescale sucker	*Catostomus macrocheilus*	juveniles	resident
	Bridgelip sucker	*Catostomus columbianus*	juveniles	resident
	Sand roller	*Percopsis transmontana*	juveniles/adults	resident
	Sculpins	*Cottus.* spp.	juveniles/adults	resident
	Lamprey	*Petromyzontidae* spp.	juveniles	resident

Bioenergetics modeling

We used bioenergetics modeling to investigate the growth and smolt consumption of northern pikeminnow, smallmouth bass, and walleye under various diet and water temperature scenarios. Bioenergetics simulations were developed to test the hypothesis that the observed growth patterns of predators in the LCRR can be explained by the presence of American shad in predator diets and the annual water temperature regime of impoundments. The bioenergetics models were also used to estimate smolt consumption of predator populations in the LCRR under the current temperature regime and to predict smolt consumption by predators growing without juvenile American shad in their diets. Since changes in the availability of juvenile American shad in predator diets might also affect the overall availability of prey, we also predicted smolt consumption by predator populations growing without American shad in their diets and under reduced feeding opportunities. Although we consider channel catfish a potentially important predator on juvenile salmonids in LCRR, there were insufficient growth and diet data available on this species to develop simulations.

Bioenergetics modeling of northern pikeminnow, smallmouth bass, and walleye were run using the software of Hanson et al. (1997). For the northern pikeminnow simulations we used the physiological parameters developed by Petersen and Ward (1999). Physiological parameters for our smallmouth bass model were taken from Roell and Orth (1993), and walleye parameters were developed by Kitchell et al. (1977). Bioenergetics models are expanded versions of the general form of the bioenergetics balanced energy equation:

growth = consumption – (respiration + egestion + excretion).

See Hanson et al. (1997) or Petersen and Ward (1999) for full model development.

We compared the observed growth of each predator species under the current water temperature regime and diet that includes American shad (nominal model) with the predicted growth of predators under three scenarios: (1) current water temperature regime without American shad in predator diets, (2) historic water temperature regime and a diet that includes American shad, and (3) historic water temperature regime without juvenile American shad in the diet. We estimated salmonid consumption by predator populations based on cohort growth under the observed size-at-age and seasonal diet of predators and current water temperature regime (nominal model) as well as under "reduced growth" and "reduced growth and feeding" scenarios. The "reduced growth" simulation predicted salmonid consumption by predators growing under a diet without juvenile American shad, while the "reduced growth and feeding" simulation predicted salmonid consumption by predator populations growing without juvenile American shad in their diet and under reduced feeding opportunities. Input parameters for the bioenergetics models included the first and last day of the analysis, and the starting and final mass (g) or total consumption (p-value estimate) of predator cohorts. These input parameters are explained in more detail below.

Seasonal growth of predators

Our bioenergetics simulations allowed northern pikeminnow to grow from April 1 to November 30 (243 days), and smallmouth bass and walleye to grow from April 17 to November 30 (234 days) under the LCRR temperature regime. The growth period of predators was based on the 10-year average date that reservoir water temperatures dropped below 10˚ C in the fall

(www.cqs.washington.edu/dart/dart.html). We assumed the growth of predators is very low or negative when water temperature is below 10˚ C (± 0.5˚ C), but allowed the spring growth period of northern pikeminnow to begin 17 days earlier than that of invasive predators to coincide with the early spring smolt migration (Petersen and Ward, 1999). We assumed the native northern pikeminnow is better adapted to begin feeding at slightly lower water temperatures in the spring than invasive predators in the LCRR. Optimal temperatures for growth are higher for adult walleye (20˚ - 28˚C) and smallmouth bass (26˚ - 29˚C) than for northern pikeminnow (20.1˚ - 22.7˚C) (Armour 1993a and b; Petersen and Ward 1999).

We used northern pikeminnow size-at-age data from 1990 – 1992 to construct von Bertalanffy growth curves for fish collected from the LCRR (Petersen, Report A in preparation). These data were collected prior to the large-scale bounty removal of northern pikeminnow. Growth increments from the von Bertalanffy analyses were converted from fork length to mass (g) using the linear model developed by Parker et al. (1995). For the invasive predators, we used size-at-age data for smallmouth bass collected from the upper John Day Reservoir in 1982 – 1986 (Beamsderfer and Ward 1994) and walleye collected from John Day Reservoir fish in 1990 -1991 (Tinus and Beamsderfer 1994). Predator size-at-age data were used in the nominal bioenergetics models to estimate the feeding level (p-value) of predator cohorts.

Proportion of maximum consumption

The proportion of maximum consumption or "p-value" in the bioenergetics model represents an estimate of the average feeding rate for a cohort of fish during the simulation period. We fit a p-value to each predator cohort by inputting observed size-at-age data into the nominal bioenergetics models for each predator. Constant p-values for each predator species could not be used since p-values decline as fish increase in size.

Predator growth simulations

Using size-at-age growth increments and the corresponding nominal p-values, we interpolated p-values for five predator starting sizes (mass, g) (Table 3). The interpolated p-values were input into the bioenergetics model for each predator species along with the starting size of cohorts to predict predator growth under the current water temperature regime without American shad preyfish (simulation A), and under the historic water temperature regime with (simulation B) and without (simulation C) American shad preyfish (Table 4). The five starting sizes were chosen to predict growth across the size range of each predator population.

Smolt consumption simulations

Nominal p-values were used to estimate smolt consumption by predator populations under the nominal and reduced growth bioenergetics models. Under the nominal model, we predicted the smolt consumption of predators with observed (northern pikeminnow) or estimated (smallmouth bass and walleye) proportions of American shad in their diets with the nominal p-value fit to the observed starting and final size of predator cohorts. For the reduced growth model, an estimate of smolt consumption for predators growing without American shad in their diet was made by inputting the predicted starting size of predator cohorts with nominal p-values. Reduced growth and feeding simulations had the predicted starting size of predator cohorts growing under a diet without American shad input with reduced p-values. Reduced p-values were generated by fitting a p-value to the starting size of predator cohort growing under a diet without American shad in the

nominal bioenergetics model. In this case, the starting size was input as both the starting and final size in the nominal model. Because the difference in nominal p-values between predator cohorts is not constant, we generated reduced p-values using the nominal bioenergetics model rather than reducing p-values by a constant proportion, for example, 10%. By fitting reduced p-values to the starting sizes of cohorts growing under a diet without American shad in the nominal bioenergetics model of each predator, the reduced p-values reflect the same proportions between predator cohorts as the nominal p-values generated from observed size-at-age data on each predator species.

To estimate the cumulative annual smolt consumption of each predator species growing under a diet with and without American shad, we used the observed size-at-age frequency data reported for northern pikeminnow (1990, Columbia River Reservoirs, female fish only (Parker et al. 1995)), walleye (1990 – 1991, John Day Reservoir, both sexes (Tinus and Beamsderfer 1994)), and smallmouth bass (1990 – 1992, LCR basin, both sexes (Zimmerman and Parker 1995)) to establish the age structure of a 1000 fish population. The number of individual predators in each age class of the 1000 fish population was then multiplied by the estimated annual smolt consumption of an individual predator of age x (years) and summed across all cohorts that were potential predators (> 250 mm FL for northern pikeminnow; ≥ 200 mm FL for walleye (Poe et al. 1991); ≥ 75 mm FL for smallmouth bass (Beamsderfer and Ward 1994)) to get the cumulative annual smolt consumption for each predator species growing under a diet with and without American shad.

Table 3. Starting weights (g) of northern pikeminnow, smallmouth bass and walleye used in bioenergetics growth simulations.

Modeled start weights (g) for predator growth		
Northern pikeminnow	Smallmouth bass	Walleye
100	200	300
400	600	1000
750	1000	3000
1100	1200	4000
1400	1400	5000

Table 4. Five starting sizes of northern pikeminnow, the predicted final mass (g) of fish, and the "growth" p-values used to estimate final mass (g) under current water temperature and dietary conditions. "No-growth" p-values, used to estimate the smolt consumption of predators, are given here for comparison purposes only, since smolt consumption estimates were calculated across all predator cohorts rather than the five starting sizes.

Starting mass (g)	Final mass (g)	Proportion of maximum consumption (p-value) used in bioenergetics runs: nominal	reduced
100	219	0.313258	0.211887
400	543	0.241311	0.191006
750	876	0.211431	0.182709
1100	1197	0.194791	0.178005
1400	1466	0.184747	0.175179

Diet of Northern pikeminnow

Detailed seasonal data on the diet of predators is needed for a complete bioenergetics modeling effort. Northern pikeminnow gut contents collected for previous diet studies in the LCRR by boat electroshocking provided data on the spring and summer diet (Poe et al. 1991; Shively et al. 1991; Petersen et al. 1993; Zimmerman 1999). Many of these studies tended to concentrate sampling effort in tailrace and forebay boat restricted zones (BRZ) near dams where northern pikeminnow congregate to prey on large numbers of juvenile salmonids. We incorporated data that was collected outside the BRZ of the dams into the generalized diet constructed for bioenergetics modeling. The fall diet of northern pikeminnow was constructed from fish caught by anglers and collected by the northern pikeminnow management program (NPMP). Angler-caught northern pikeminnow were primarily collected from mid-reservoir locations, and did not include any BRZ fish (Sauter and Petersen; Report B, in preparation). Based on these data, we constructed a generalized seasonal profile of the northern pikeminnow diet with and without juvenile American shad for the LCRR. The diet of northern pikeminnow was divided into five categories of prey: salmonids, American shad (AMS), other fish, crustaceans, and miscellaneous. We constructed the summer and fall diet so that American shad supplemented and then replaced the juvenile salmonid portion of the diet in August. The miscellaneous category consisted of prey with relatively low caloric value such as mollusks, insects, and plant material. Changes in the proportion of juvenile salmonids and American shad in the northern pikeminnow diet shifts the proportions of crustaceans and miscellaneous prey during some time periods since diet proportions must total 100% to run the bioenergetics model.

For the fall diet simulations without American shad, we assumed that northern pikeminnow would increase their predation slightly on "other fish" (+5%) if juvenile American shad were not available. The observed and hypothesized northern pikeminnow diets are summarized in Table 5.

Table 5. Observed and hypothetical northern pikeminnow diets for the LCRR used in bioenergetics modeling. The observed seasonal diet of northern pikeminnow consisting of 25% American shad (AMS), and a hypothetical fall diet without American shad were modeled.

Time period	Prey category (%)				
	salmonids	AMS	other fish	crustaceans	miscellaneous
	Observed seasonal diet of northern pikeminnow with 25% American shad in the fall diet				
April/May	40	0	10	35	15
June/July	10	0	10	40	40
Aug 1 – 14	10	10	10	35	35
Aug 15 – 31	0	25	5	35	35
Sept/Oct	0	25	5	35	35
Nov/Dec	0	10	10	40	40
	Hypothetical seasonal diet of northern pikeminnow without American shad				
April/May	40	0	10	35	15
June/July	10	0	10	40	40
Aug 1 – 14	10	0	10	40	40
Aug 15 – 31	0	0	10	45	45
Sept/Oct	0	0	10	45	45
Nov/Dec	0	0	10	45	45
Proportion Indigestible[a]:	0.033	0.0165	0.0165	0.1	0.4

[a] Stewart et al. (1983) and Petersen and Ward (1999)

Sources: Petersen et al. 1990, 1991, & 1993; Poe et al. 1991; Shively et al. 1991; Zimmerman 1999; Sauter and Petersen Report B, in preparation.

Diet of Invasive predators

We based the fall diet of smallmouth bass and walleye on previous spring and summer diet studies on these species (*see* Poe et al. 1991; Shively et al. 1991; Zimmerman 1999). Juvenile salmonids are available to smallmouth bass and walleye from early April through much of August in LCRR. Crayfish are an important component of the smallmouth bass diet, while walleye feed almost entirely on preyfish (Poe et al. 1991; Shively et al. 1991; Zimmerman 1999). For our bioenergetics simulations, we assumed that the fall diet of these invasive predators was an extension of their spring and summer diets, and that juvenile American shad became important in the diet of these predators in early August. We constructed the late summer and fall diet of smallmouth bass (Table 4) so that the portion of juvenile salmonids in the diet was supplemented and then replaced by juvenile American shad. Changes in the proportion of juvenile salmonids, American shad, and other preyfish in predators' diets shifts the proportions of crustaceans and miscellaneous prey during some time periods since diet proportions must total 100% to run the bioenergetics model.

We constructed a more detailed preyfish diet for walleye than for smallmouth bass or northern pikeminnow since walleye are highly piscivorous and previous research suggests only a small proportion of their diet is non-fish prey (Poe et al. 1991; Zimmerman 1999). The walleye diet consists of five prey categories: salmonids, American shad (AMS), sculpin, other fish, and miscellaneous (Table 6).

Table 6. The observed seasonal diet of smallmouth bass in LCRR compiled from several sources. A hypothetical diet without American shad was also developed. These diets were used to estimate the growth and potential salmonid consumption of smallmouth bass in LCRR using a bioenergetics model.

	Prey category (%)				
Time period	salmonids	AMS	other fish	crustaceans	miscellaneous
	Estimate of current seasonal diet of smallmouth bass				
April/May	0	0	20	50	30
June	0	0	34	62	4
July	23	0	10	55	12
Aug 1 – 14	16	15	10	55	4
Aug 15 – 31	0	15	23	58	4
Sept/Oct	0	15	23	58	4
Nov/Dec	0	10	0	40	50
	Hypothetical seasonal diet without American shad preyfish				
April/May	0	0	20	50	30
June	0	0	34	62	4
July	23	0	10	55	12
Aug 1 – 14	16	0	10	62	12
Aug 15 – 31	0	0	26	62	12
Sept/Oct	0	0	26	62	12
Nov/Dec	0	0	10	40	50
Proportion Indigestible[a]:	0.033	0.0165	0.0165	0.1	0.4

[a] Stewart et al. (1983)

Sources: Poe et al. 1990; Shively et al. 1991; Tabor et al. 1994; Zimmerman 1999; Sauter, unpublished data.

Table 5. The observed seasonal diet of walleye in LCRR compiled from several sources. A hypothetical diet without American shad (AMS) was also developed. These diets were used to estimate the growth and potential salmonid consumption of walleye in LCRR using a bioenergetics model.

	Prey category (%)				
Time period	salmonids	AMS	sculpin	other fish	miscellaneous
	Estimate of current seasonal diet of walleye				
April/May	20	0	50	20	10
June	20	0	50	20	10
July	20	0	50	20	10
Aug 1 – 14	20	0	50	20	10
Aug 15 – 31	0	20	50	20	10
Sept/Oct	0	20	50	20	10
Nov/Dec	0	20	50	20	10
	Hypothetical seasonal diet without American shad preyfish				
April/May	20	0	50	20	10
June	20	0	50	20	10
July	20	0	50	20	10
Aug 1 – 14	20	0	50	20	10
Aug 15 – 31	0	0	50	30	20
Sept/Oct	0	0	50	30	20
Nov/Dec	0	0	50	20	10
Proportion Indigestible[a]:	0.033	0.011	0.011	0.011	0.4

[a] Stewart et al. (1983)
Sources: Poe et al. 1991; Zimmerman 1999

Caloric density of prey

The caloric densities of various prey items in predator diets are an integral part of the bioenergetics model. The energy densities of many prey items consumed by aquatic predators in LCRR appear in Table 6. Our model used a caloric density of 5.56 kJ/g for juvenile American shad (Sauter and Petersen; Report C, in preparation) and a value of 4.31 kJ/g for juvenile salmonids (Rondorf et al. 1985). For the "other fish" proportion of the northern pikeminnow and smallmouth bass diets, which included sculpin, we used an energy density of 5.4 kJ/g. Sculpin constitute about 50% of the walleye diet in the spring and summer so we listed this species as a separate prey category in the walleye diet along with salmonids, American shad (AMS), other fish, and miscellaneous (Table 6). Since we placed sculpin, a preyfish with a relatively high caloric density into a separate diet category in the walleye diet, we reduced the caloric density of the other fish category to 4.1 kJ/g, a value similar to that of salmonids (Table 7) and in the middle range of caloric densities listed for other preyfish (see Hanson 1997).

Table 6. The energy density (kJ/g) of common prey items of aquatic predators in the Columbia River basin.

Species	Energy density (kJ/g wet mass)	Source
Steelhead	4.61	Roby et al. (1998)
Chinook salmon	3.98	Roby et al. (1998)
Chinook salmon	4.31	Rondorf et al. (1985)
Coho salmon	5.04	Roby et al. (1998)
Sockeye salmon	5.07	Roby et al. (1998)
Sculpins	5.44	Rottiers and Tucker (1982); Brocksen et al. (1968)
American shad	5.67	Roby et al. (1998)
	5.56	Petersen and Sauter, Report D (in preparation)
Crayfish/crustaceans	4.51	Cummins and Wuycheck (1971)
Miscellaneous	2.62	Petersen and Ward (1999)

Water temperature

Water temperature and body mass regulate the basal metabolic rate, feeding rate, and digestion of fish, so temperature is an important component of bioenergetics modeling. We averaged 15 years of daily forebay scrollcase temperature records collected from 1980 – 1995 at John Day and Bonneville dams (www.cqs.washington.edu/dart/dart.html) to create an annual profile of LCRR water temperatures for our modeling. The historic temperature model for the unimpounded free-flowing LCR was provided by Yearsley (1999) (Figure 1).

Availability of anadromous preyfish

Rearing and emigrating anadromous preyfish are present in the LCRR from early April through November (http://www.fpc.org). The annual emigration of anadromous fishes begins with the spring emigration of hatchery and wild juvenile salmon and steelhead in April; by mid-June, subyearling fall Chinook salmon are rearing and emigrating through the reservoirs, and juvenile American shad become abundant in early August. The emigration of juvenile American shad continues through much of the fall in the LCRR (Figure 2).

Predator growth curves

Data on the size-at-age of northern pikeminnow, smallmouth bass, and walleye in LCRR were available from previous research (see Beamsderfer and Ward 1994; Tinus and Beamsderfer 1994; Petersen, Report A, in preparation). We compiled additional size-at-age data from predator populations at other locations in the Pacific Northwest and North America to compare the growth rates of aquatic predators in the LCRR with fish collected at other locations.

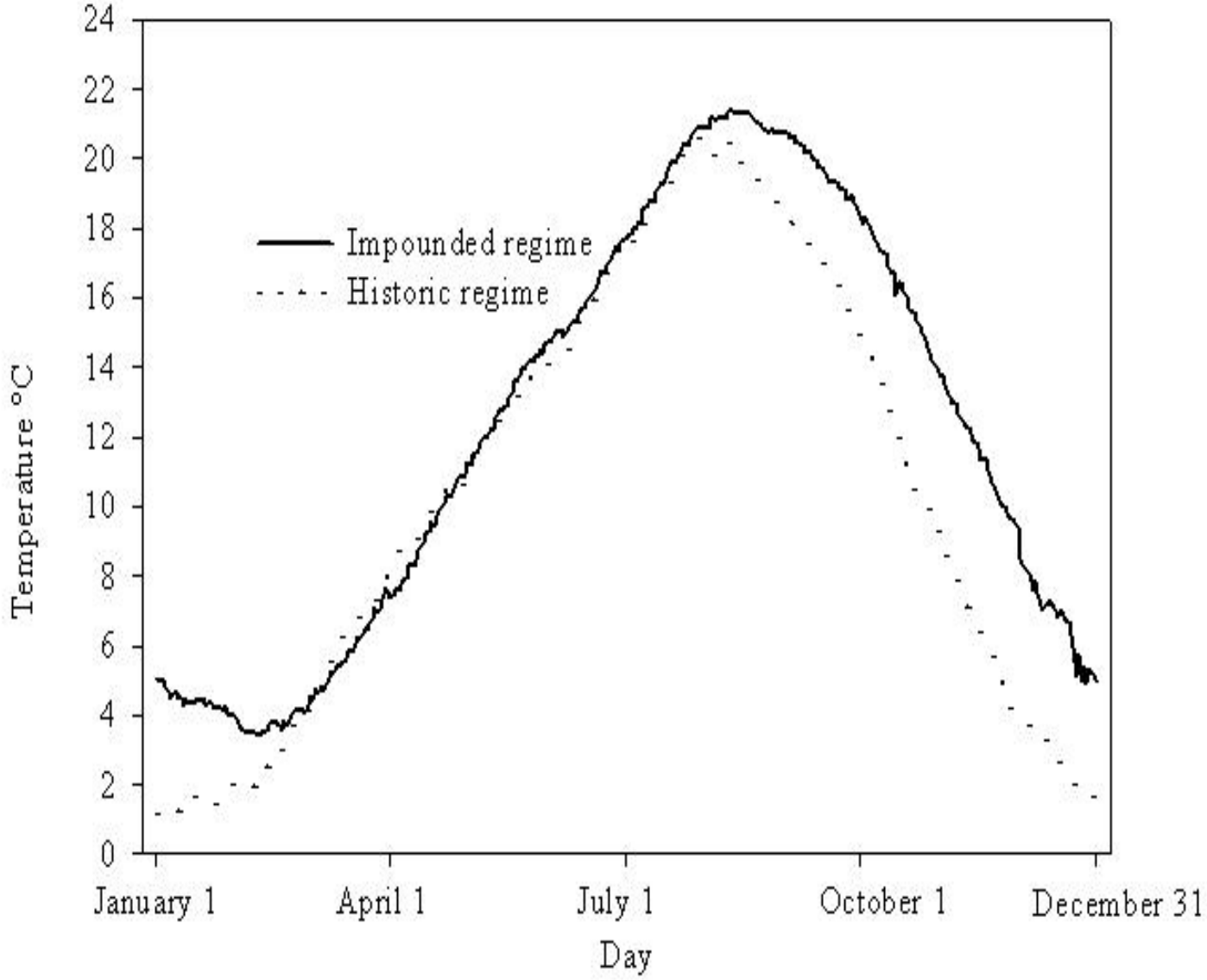

Figure 1. Impounded and historic water temperature profile of the LCRR showing (1) later peak summer water temperatures, (2) warmer peak summer water temperatures, and, (3) warmer fall and winter water temperatures.

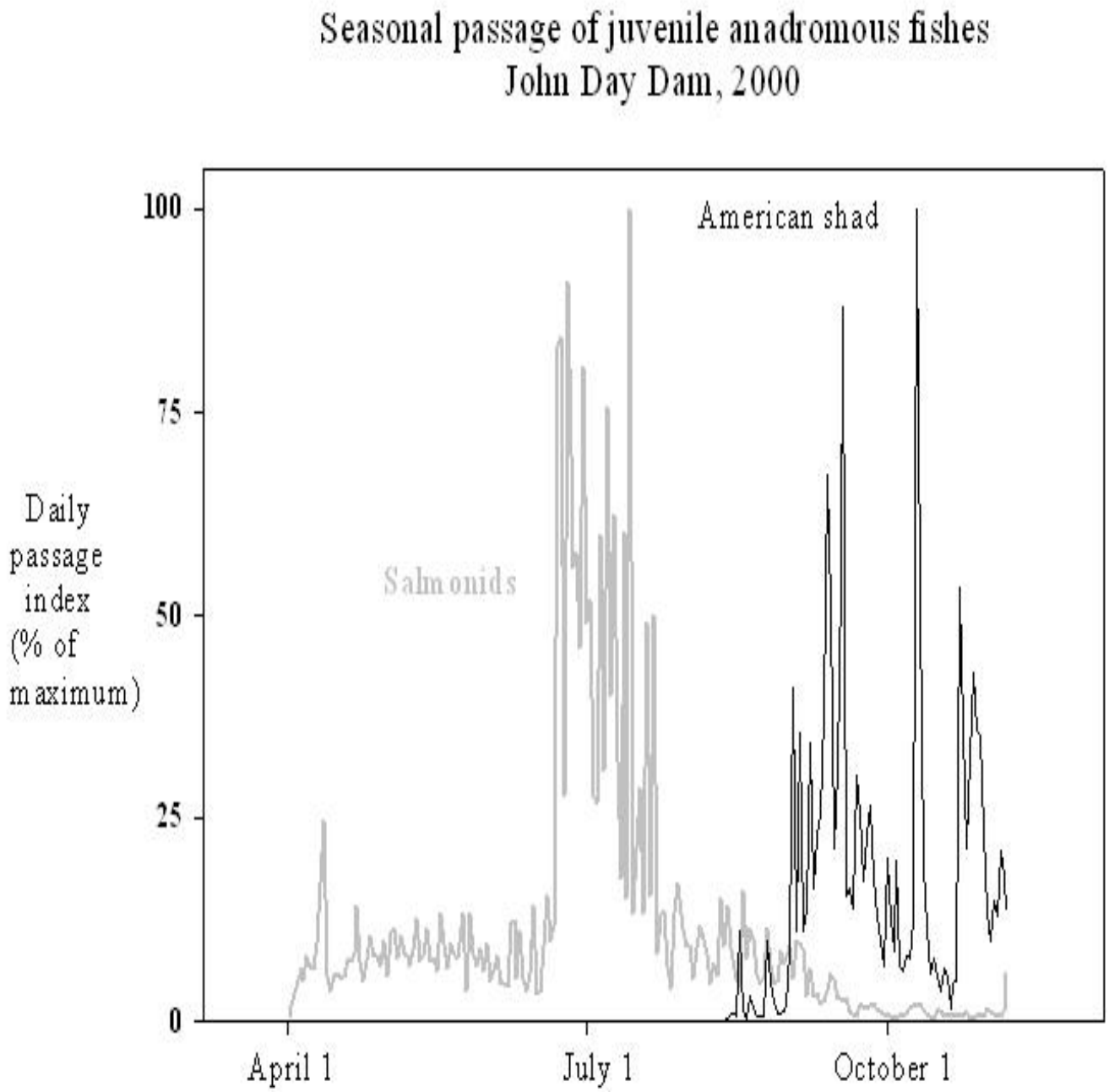

Figure 2. Seasonal passage of juvenile anadromous salmonids and American shad at John Day Dam in 2000. Passage counts were made at the John Day Dam fish collection facility and the index is relative to the maximum count for each species.

Results

Bioenergetics

For each predator species, we tested the hypothesis that a supplemental fall diet of juvenile American shad and reservoir water temperatures was equally important in producing the observed growth rates of aquatic predators in LCRR. Our bioenergetics simulations suggest that both the presence of American shad and higher water temperatures since impoundment are important to predator growth, but the growth contribution of these two factors varied by predator species.

The influence of American shad on smolt consumption varied by predator species in LCRR. A supplemental diet of American shad had a relatively small impact on northern pikeminnow (+6.8%) and walleye (+3.3%) smolt consumption, but produced a 16.0% increase in smallmouth bass consumption.

Northern pikeminnow

Simulations on northern pikeminnow suggest that while both American shad and impounded water temperatures are important growth factors for northern pikeminnow in LCRR, the observed diet of 25% American shad produced slightly greater annual increases in growth than water temperature alone (Table 9, simulation A). Comparison of the observed growth of northern pikeminnow under a fall diet of 25% American shad with the predicted growth of fish with no American shad in the fall diet and a fall diet of 25% American shad under historic water temperatures (simulation A versus B) suggest that American shad contribute as much as or more to the observed annual growth of northern pikeminnow than water temperature. In fact, the warmest annual water temperatures each year may slow northern pikeminnow growth in LCRR (Petersen and Ward 1999). Simulation C which combined historic water temperatures with no American shad preyfish predicted the slowest growth rates for northern pikeminnow. The presence of American shad in the fall diet of LCRR northern pikeminnow made a relatively small difference in the number of juvenile salmonids consumed by this predator (6.8%) (Table 10). Smolt consumption by northern pikeminnow declined markedly under the reduced growth and feeding simulation. Northern pikeminnow smolt consumption might potentially decline by 18.2% under reduced feeding opportunities that might exist if juvenile American shad were not present in the diet.

Smallmouth bass

We predicted the growth of smallmouth bass in LCRR under three growth scenarios: (A) the current reservoir temperature regime and no American shad in the fall diet, (B) the historic temperature regime with 16% American shad in the fall diet, and (C) the historic temperature regime with no American shad in the fall diet. Our bioenergetics modeling on smallmouth bass suggests that the warmer water temperatures of the impounded LCRR have a much greater affect on the growth of this invasive predator than the presence of American shad (Table 11); however, the growth difference produced by a fall diet of 16% American shad under the reservoir water temperature regime increased smallmouth bass consumption of juvenile salmonids by 16.0% (Table 12). Our modeling suggests a much larger reduction in smolt consumption by smallmouth bass might occur if American shad were removed from the diet and this condition affected feeding opportunities (43.4%). Increased annual growth due to the warmer reservoir water temperatures has the greatest effect on the smaller size classes of smallmouth bass, which make up the largest proportion of the population. These bioenergetics results should be considered preliminary, since there were no fall field data available on which to base the fall diet of smallmouth bass in LCRR.

Table 9. Bioenergetics modeling comparing nominal annual growth (mass, g) with predicted growth of northern pikeminnow under four simulations: (A) current water temperatures and no American shad (AMS), (B) historic water temperatures and current fall diet conditions (25% AMS), and (C) historic water temperatures and no AMS in the fall diet. The % change (% Δ) between the nominal and simulated growth is given for each scenario. To compare the current reservoir water temperature regime with historic conditions, see Figure 1. Temp = temperature.

		Northern pikeminnow simulations					
Nominal		A		B		C	
Current temps & 25% AMS		Current temps No AMS		Historic temps & 25% AMS		Historic temps & no AMS	
Starting mass (g)	Final mass (g)	size (g)	%Δ	size (g)	%Δ	size (g)	%Δ
100	219	186	-15.1	190	-13.2	167	-23.7
400	543	489	-9.9	508	-6.4	469	-13.6
750	876	806	-8.0	840	-4.1	789	-9.9
1100	1197	1114	-6.9	1161	-3.0	1100	-8.1
1400	1466	1373	-6.3	1431	-2.4	1363	-7.0

Table 11. The nominal annual growth and interpolated p-values for five starting sizes of smallmouth bass in LCRR. Simulations show the predicted final size of smallmouth bass under (A) current water temperatures (temp) and no American shad in the fall diet (No AMS), (B) historic water temperatures with 16% American shad in the fall diet, and (C) historic water temperatures with no American shad in the fall diet. The % change (% Δ) between the observed final size and simulation growth is given for each scenario. To compare the current water temperature regime with historic conditions, see Figure 1.

			Smallmouth bass simulations					
Nominal*			A		B		C	
Current temps & 16% AMS			Current temps & no AMS		Historic temps & 16% AMS		Historic temps & no AMS	
Start size (g)	Final size (g)	growth p-value		% Δ		% Δ		% Δ
200	467	0.29589	448	-4.1	381	-18.4	369	-21.0
600	846	0.21681	825	-2.5	757	-10.5	742	-12.3
1000	1247	0.19636	1222	-2.0	1144	-8.3	1127	-9.6
1200	1378	0.17304	1353	-1.8	1285	-6.7	1268	-8.0
1400	1503	0.15264	1481	-1.5	1421	-5.5	1405	-6.5

* No field data are currently available on the fall diet of smallmouth bass. Our current growth model relied on a reasonable estimate of the fall diet of smallmouth bass.

Table 10. Cumulative predicted smolt consumption and percent change in consumption by LCRR northern pikeminnow under the current fall diet of 25% American shad and under a hypothetical diet without American shad. Age 1 and 2 northern pikeminnow cohorts consume few juvenile salmonids (x), and were not included in this analysis. Pred = individual predator.

Predicted Northern pikeminnow smolt consumption Estimated average population size in John Day Reservoir = 85,000[a]									
		Reservoir diet with 25% American shad			Reservoir diet without American shad Growth effect			Reservoir diet without American shad Growth and reduced feeding effect	
Age	Population frequency per 1000 fish	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)
1	x	x	x	x	x			x	x
2	x	x	x	x	x			x	x
3	2	126	35.7	71.4	104	35.7	71.4	35.0	70
4	15	228	61.8	123.6	196	52.9	105.8	55.9	838
5	40	350	89.0	1424	309	78.7	1259.2	78.3	3132
6	140	481	114.8	4592	431	103.7	4148	100.0	14000
7	100	616	138.8	19432	559	126.9	17766	121.2	12120
8	115	748	160.2	16020	684	148.1	14810	140.8	16192
9	140	874	179.2	20608	804	166.7	19170.5	158.6	22204
10	115	991	195.8	27412	916	182.9	25606	174.7	20091
11	140	1098	210.1	24162	1019	197.1	22666.5	189.1	26474
12	90	1195	222.6	31164	1112	209.5	29330	201.7	18153
13	65	1281	233.2	20988	1195	219.9	19791	213.8	13897
14	30	1358	242.4	15756	1269	233.1	15151.5	223.4	6925.4
15	5	1425	250.2	7756.2	1334	240.6	7458.6	231.7	1390.2
16	3	1483	256.7	1540.2	1390	243.2	729.6	238.7	716.1
Total salmon (g) consumed per 1000 predators:				**191,049**			**178,064**		**156203**
% change:							**-6.8**		**-18.2**

[a] Rieman et al. 1991

Table 12. Predicted salmonid consumption (g) by smallmouth bass in LCRR per individual predator (pred) and cohort. The % change in salmonid consumption attributed to faster growth from American shad in the fall diet compared to a diet without American shad is also given.

Predicted Smallmouth bass smolt consumption Estimated average population size in John Day Reservoir = 35,000[a]									
		Reservoir diet with 16% American shad			Reservoir diet without American shad Growth effect			Reservoir diet without American shad Growth and reduced feeding effect	
Age	Population frequency per 1000 fish	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)
1	x	x	x	x	x	x	x	x	x
2	643	98	7.2	4629.6	91	6.1	3922.3	4.5	2894
3	214	294	20.1	4301.4	279	16.5	3531	10.1	2161
4	71	550	32.2	2286.2	530	26.9	1909.9	16.2	1150
5	24	787	38.3	919.2	766	32.4	777.6	21.4	514
6	24	1053	46.6	1118.4	1028	39.8	955.2	26.8	643
7	12	1245	47.0	564	1221	40.3	483.6	30.6	367
8	6	1392	47.6	285.6	1369	41.0	246	33.4	200
9	3	1500	43.4	130.2	1477	41.1	123.3	35.4	106
10	3	1530	51.1	153.3	1509	43.2	129.6	36.0	108
Total salmon (g) consumed per 1000 predators:				**14,388**			**12,078**		**8,143**
% change:							**-16.0**		**-43.4**

[a] Rieman et al. 1991

Walleye

Bioenergetics modeling on walleye suggests that American shad are the most important factor contributing to the annual growth rate of this predator, particularly as walleye increase in size. Our simulations suggest that the availability of American shad in the late summer and fall as well as current reservoir water temperatures during the fall contribute to the annual growth rate of walleye in LCRR (Table 13). The predicted impact of walleye growth due to a 20% American shad fall diet under the impounded water temperature regime increased the estimated smolt consumption of walleye by 3.3% (Table 14). A 6.2% decrease in smolt consumption by walleye was predicted without juvenile American shad in the diet and under reduced feeding opportunities. These bioenergetics results should be considered preliminary, since there were no fall field data available on which to base the fall diet of walleye in LCRR.

Table 13. The nominal annual growth and interpolated p-values for five starting sizes of walleye in LCRR. Simulations show the predicted final size of walleye under (A) current water temperatures (temp) and no American shad in the fall diet (No AMS), (B) historic water temperatures with 20% American shad in the fall diet, and (C) historic water temperatures with no American shad in the fall diet. The % change (% Δ) between the observed final size and simulation growth is given for each scenario. To compare the current water temperature regime with historic conditions, see Figure 1.

			Walleye simulations						
Nominal* Current temps & 20% AMS			A Current temps & no AMS		B Historic temps & 20% AMS		C Historic temps & no AMS		
Starting mass (g)	Final mass (g)	growth p-value		% Δ		% Δ		% Δ	
300	1574	0.49615	1417	-10.0	1365	-13.3	1248	-20.7	
1000	1885	0.37137	1748	-7.3	1761	-6.6	1655	-12.2	
3000	3621	0.32183	3428	-5.3	3515	-2.9	3361	-7.2	
4000	4443	0.31144	4225	-4.9	4345	-2.2	4170	-6.1	
5000	5391	0.31168	5140	-4.7	5286	-1.9	5084	-5.7	

* No field data are currently available on the fall diet of walleye. Our current growth model relied on a reasonable estimate of the fall diet of walleye.

Predator Growth Curves

Growth curves and a comparison of the size-at-age of 6 year-old predators for various locations suggest that growth conditions for northern pikeminnow (Figure 3, Table 15), smallmouth bass (Figure 4, Table 16), and walleye (Figure 5, Table 17) are quite favorable in LCRR. The average total length (TL, mm) of 6 year-old northern pikeminnow in LCRR (379 mm) is larger than the value reported for the lower Columbia River below Bonneville Dam (362 mm) or for other locations across the Pacific Northwest including Lake Washington, WA (359 mm) (Table 15). Although size-at-age information on smallmouth bass and walleye were only available for John Day Reservoir, data from these populations indicates 6 year-old predators are larger in this reservoir than at most other locations reported.

Table 14. Predicted salmonid consumption (g) by walleye in LCRR per individual predator (pred) and cohort. The % change in salmonid consumption attributed to faster growth from American shad in the fall diet compared to a diet without American shad is also given.

Predicted Walleye smolt consumption Estimated average population size in John Day Reservoir = 10,000[a]									
		Reservoir diet with 20% American shad			Reservoir diet without American shad Growth effect			Reservoir diet without American shad Growth and reduced feeding effect	
Age	Population frequency per 1000 fish	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	mass (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)	salmon consumed per pred (g)	salmon consumed per cohort (g)
1	102	182	9.6	979.2	149	9.6	979.2	0.5	51
2	72	925	135.4	9748.8	829	120.2	8654.4	37.6	3835
3	155	1794	289.9	44934.5	1661	269.5	41772.5	152.6	10987
4	251	2557	399.8	100350	2399	379.3	95204.3	270.6	41943
5	96	3201	481.4	46214.4	3023	460.6	44217.6	366.9	92092
6	140	3764	548.7	76818	3567	540.7	75698	444.6	42682
7	24	4214	598.9	14373.6	4005	591.7	14200.8	510.4	71456
8	45	4658	650.5	29272.5	4432	625.5	28147.5	562.1	13490
9	39	4978	682.7	26625.3	4745	673.9	26282.1	611.8	27531
10	79	5382	731.6	57796.4	5130	691.6	54636.4	647.7	25260
11	36	5498	733.2	26395.2	5253	747.2	26899.2	691.5	54628
12	45	5267	692.3	31153.5	5043	720.7	32431.5	705.1	25384
13	8	4195	529.5	4236	4040	513.3	4106.4	681.2	30654
Total salmon (g) consumed per 1000 predators:				**468,897**			**453,230**		**439,993**
% change:							**-3.3**		**-6.2**

[a] Rieman et al. 1991

Beamesderfer and Ward (1994) split their analysis of John Day Reservoir smallmouth bass size-at-age into upper and lower reservoir fish (Table 16). The average TL (mm) of 6 year-old upper reservoir fish (409 mm) was 11% larger than that of lower reservoir fish (364 mm). Smallmouth bass from upper John Day reservoir were also larger at age 6 than fish collected further upstream from a free-flowing section of the Columbia River at Hanford Reach, WA (380 mm) (Barfoot, unpublished data) and lower Snake River reservoirs (302 mm) but smaller than the reported size of 6 year-old smallmouth bass collected from 9 populations in California (462 mm) (Beamesderfer and North 1995).

Maule and Horton (1985) and Tinus and Beamesderfer (1994) report similar mean total lengths (TL, mm) for 6 year-old walleye in John Day Reservoir, although sampling occurred 10 years apart. Age 6 walleye appear to be growing faster in John Day Reservoir than fish sampled from many other locations in North America (Table 17) based on published data.

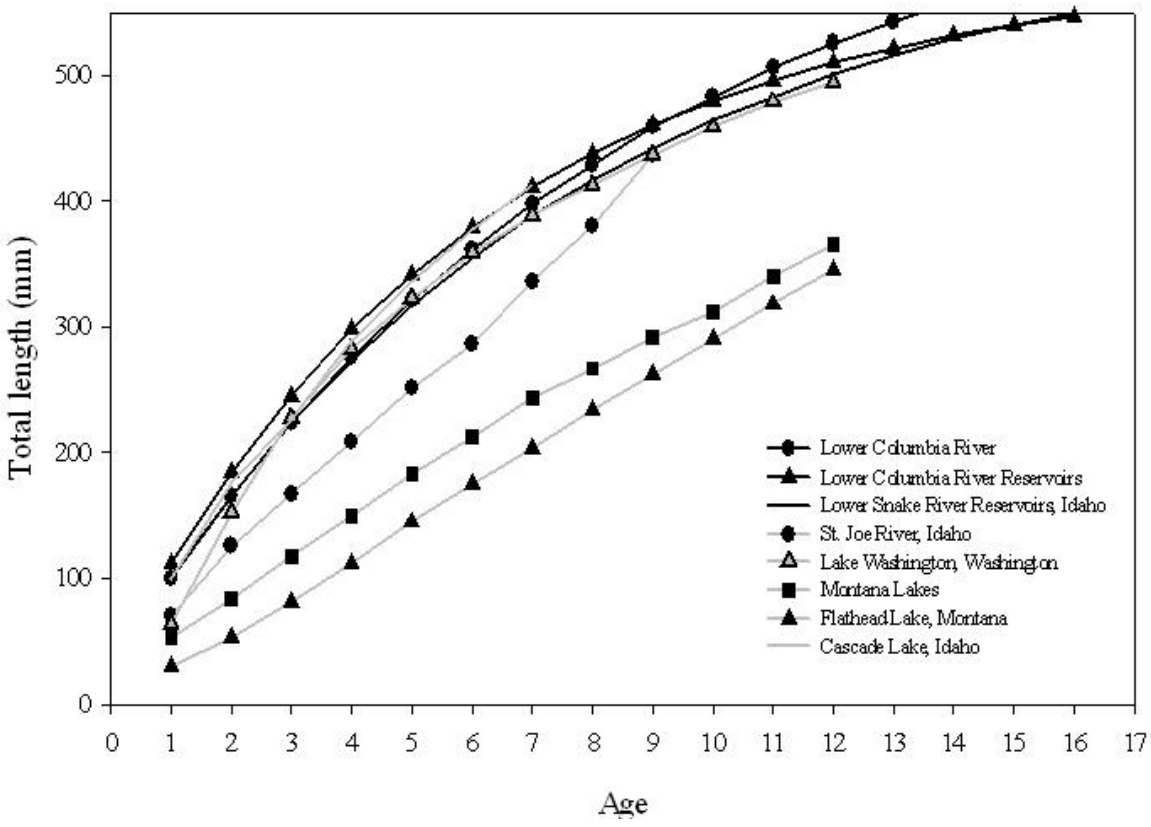

Figure 3. Growth curves for northern pikeminnow taken from various locations in the northwestern United States. "Lower Columbia River" refers to the free-flowing section downstream of Bonneville Dam. "Lower Columbia River reservoirs" refer to the impounded section of river between Bonneville and McNary dams. Sources: Petersen (Report A, in preparation), Olney 1975, Casey 1962. Original fork lengths (FL) were convert to total length (TL) using the relationship of FL to TL determined for Lake Washington northern pikeminnow by Olney 1975.

Table 15. Comparison of the size-at-age of 6 year-old northern pikeminnow reported for locations throughout the Pacific Northwest. Size-at-age is given as total length (TL, mm). Standard and fork length data was converted to TL using the equations of Olney (1975).

	Northern pikeminnow	
Location	Average TL (mm)	Reference
LCRR OR/WA	379	Petersen Report A, in preparation
Cascade Reservoir, ID	378	Casey 1962
Lower Columbia River, OR/WA	362	Petersen Report A, in preparation
Lake Washington, WA	359	Olney 1975
Lower Snake River Reservoirs, WA	355	Petersen Report A, in preparation
St. Joe River, ID	286	Reid 1971
Montana Lakes, MT	213	Peters 1964
Flathead Lake, MT	175	Rahrer 1963

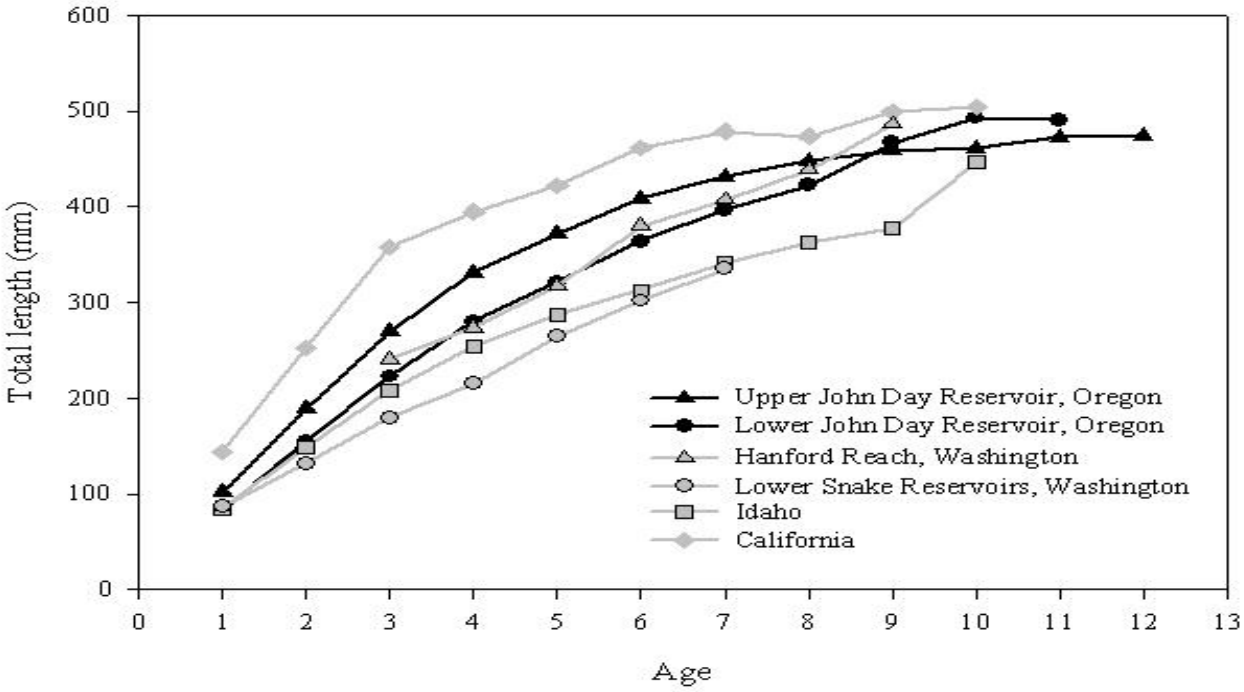

Figure 4. Growth curves for smallmouth bass taken from various locations in the United States. Fork lengths were converted to total length (x 1.04) as per Carlander 1977. Sources: Barfoot (unpublished data); Beamesderfer and Ward 1994; Petersen et al. 1999; Beamesderfer and North, 1995.

Table 16. Comparison of the size-at-age of 6 year-old smallmouth bass reported for locations throughout the western United States. Size-at-age is given as total length (TL, mm).

	Smallmouth bass	
Location	average TL (mm)	Reference
California	462	Beamesderfer and North 1995
Upper John Day Reservoir, OR/WA	409	Beamesderfer and Ward 1994
Lower John Day Reservoir, OR/WA	364	Beamesderfer and Ward 1994
Hanford Reach, WA	380	Barfoot, unpublished data
Lower Snake River Reservoirs, WA	302	Barfoot, unpublished data
Idaho	313	Beamesderfer and North 1995

Figure 5. Growth curves for walleye in upper and lower John Day Reservoir of the lower Columbia River, and for other locations in the United States. Much of this data was summarized by Maule and Horton 1985. Sources: Maule and Horton, 1995; Tinus and Beamesderfer 1994; Stroud 1949; Eschmeyer 1950; Hartman and Margraf 1992; Serns 1984; Kempinger and Carline 1977. Mass (g) of Western Lake Erie, Ohio walleye were converted to FL using the equation of Maule and Horton 1995; FL were converted to TL (x 1.06) as per Colby et al. 1979.

Table 17. Comparison of the size-at-age of 6 year-old walleye collected at locations throughout the western United States. Size-at-age is given as total length (TL, mm).

	Walleye	
Location	average TL (mm)	Reference
Upper John Day Reservoir 1980 - 1981	660	Maule and Horton 1985
John Day Reservoir 1990 - 1991	658	Tinus and Beamesderfer 1994
Norris Reservoir, TN	545	Stroud 1949
Escanaba Lake, WI	452	Kempinger and Carline 1977
Lake Gogebic, MI	445	Eschmeyer 1950
Western Lake Erie, OH	414	Hartman and Margraf 1992
Lac la Ronge, Canada	406	Rawson 1957

Discussion

In this study, we used bioenergetics modeling to look at two different aspects of aquatic predation on juvenile salmonids. The first portion of our work investigated the impact of juvenile American shad and the impounded water temperature regime on growth and salmonid consumption by northern pikeminnow in LCRR. The second portion of this study explored the impact of American shad and the impounded water temperature regime on the growth and salmonid consumption of two invasive predators in the reservoir system: smallmouth bass and walleye.

Northern pikeminnow predation

Our bioenergetics modeling suggests that important factors influencing the growth of northern pikeminnow in LCRR are the co-occurrence of large numbers of juvenile American shad and the warmer water temperatures of the impounded Columbia River during the fall. Petersen (Report A, in preparation) identified fish in the free-flowing Columbia River below Bonneville Dam as the fastest growing northern pikeminnow population in the lower Columbia River basin; other research reports that this location also has the greatest abundance of northern pikeminnow and the highest rate of northern pikeminnow predation on juvenile salmonids in the Columbia River system (Ward et al. 1995).

Our comparison of multiple growth curves from various northern pikeminnow populations indicates that LCRR fish grow faster than fish below Bonneville Dam for the first 9 years of life. Furthermore, the growth of northern pikeminnow below Bonneville Dam and in the LCRR exceeds that of other Pacific Northwest locations (Petersen Report A, in preparation). However, the growth rates observed in northern pikeminnow at these lower Columbia River locations apparently results from different foraging opportunities. Previous bioenergetics modeling by Sauter and Petersen (Report D, in preparation) suggests that the high growth rate observed in northern pikeminnow below Bonneville Dam may be driven by large numbers of hatchery salmonids released into the lower Columbia River each spring and the presence of juvenile American shad in the fall. Sauter and Petersen (Report D, in preparation) estimated that juvenile salmonids historically represented about 35% of the northern pikeminnow diet below Bonneville Dam in the spring and summer compared to > 60% today. Their modeling predicted that under the historic proportion of juvenile salmonids (35%), the average mass (g) of 6 year-old northern pikeminnow would decrease by 8.6%, from 416 g to 380 g. By reducing the proportion of juvenile salmonids in the northern pikeminnow diet to 35% and eliminating American shad preyfish from the system, the model predicted the growth of 6 year-old northern pikeminnow below Bonneville Dam could be reduced by 17% from 416 g to 345 g (Sauter and Petersen, Report D, in preparation). Since 65% of the approximately 200 million anadromous hatchery salmon and steelhead produced in the Columbia River basin each year are released into the lower 175 miles of the Columbia River (Artificial Production Review and Evaluation (APRE), Draft 2003), it is not surprising that hatchery fish contribute substantially to northern pikeminnow growth below Bonneville Dam.

Anadromous preyfish are an important part of the northern pikeminnow diet in the LCRR as well. Hatchery salmonids make up ~ 40% of the spring diet and large numbers of juvenile American shad contribute to the late summer and fall diet of northern pikeminnow in these reservoirs. The abundance of juvenile American shad during the late summer and fall may be

particularly important to northern pikeminnow growth since the impounded water temperature regime has extended the annual growth period of aquatic predators later into the fall. The abundance of emigrating hatchery salmonids and introduced American shad, as well as favorable fall water temperatures all have a positive growth affect on northern pikeminnow in the LCRR.

Although the presence of juvenile American shad increases the annual growth of northern pikeminnow in LCRR, this growth produced only slightly greater smolt consumption (6.8%) than simulations predicting smolt consumption under a fall diet without American shad. However, our simulations suggest that if a diet without American shad also resulted in reduced feeding opportunities for northern pikeminnow, the decrease in smolt consumption by this predator might be considerably larger (18.2%). The relatively small increase in northern pikeminnow smolt consumption produced by the current fall diet rich in American shad suggests no single dietary component exerts a dominant effect on northern pikeminnow growth in LCRR. Northern pikeminnow are omnivorous, and known to switch prey throughout the growing season (Poe et al. 1991; Zimmerman 1999); they also respond quickly to the feeding opportunities presented by high densities of anadromous preyfish (Collis et al. 1995; Shively et al. 1996) but search out a variety of abundant high-quality prey when anadromous preyfishes are temporally or spatially scarce (Poe et al. 1991; Petersen and DeAngelis 1992; Zimmerman 1999). Prickly sculpin (Cottus asper) and crayfish are both important components of the northern pikeminnow diet in the LCRR, and are energetically comparable to anadromous preyfish (Poe et al. 1991; Zimmerman 1999; Sauter and Petersen, Report C, in preparation).

Invasive Predators

The second portion of our study dealt with the impact of juvenile American shad on populations of invasive predators. Bioenergetic modeling on smallmouth bass and walleye suggests that the impounded water temperature regime is the most critical factor supporting the growth rates of these invasive predators in LCRR. Because there is less information available on the late summer and fall diets of these invasive predators, the impact of juvenile American shad on the growth and salmonid consumption of smallmouth bass and walleye is less certain. For our bioenergetics modeling we assumed that the well documented proportion of juvenile salmonids (primarily subyearling fall Chinook) in the diet of the predators during the summer (Poe et al. 1991; Shively et al. 1991; Zimmerman 1999) provided a good indication of the proportion of American shad in predator diets during the late summer and fall. Since juvenile salmonids and American shad temporally overlap in late summer, we structured predator diets for our simulations so that juvenile American shad became available to predators in early August and replaced the proportion of juvenile salmonids in predator diets by mid-August. The overall abundance of juvenile American shad and subyearling fall Chinook passing John Day Dam is similar in August, with the number of juvenile American shad increasing as subyearling fall Chinook decline during the month. Finally, the shoreline feeding behavior of subyearling fall Chinook (Mains and Smith 1956; Dauble et al. 1989; Poe et al. 1994) and larval and juvenile American shad (Miller 1993; Limburg 1996; Petersen et al. 2003) supports the use of similar dietary proportions for these two anadromous prey species in invasive predator diets.

Although there are varying degrees of uncertainty about the late summer and fall diet proportions of invasive aquatic predators in LCRR, previous researchers have found evidence that these predators encounter and consume larval and juvenile American shad (Zimmerman 1999; Petersen et al. 2003) and emigrating salmonids (Poe et al. 1991; Shively et al. 1991; Vigg et al. 1991; Zimmerman 1999). Overall, our modeling attributes 26.1% of the salmonid consumption in

LCRR to faster growth rates of northern pikeminnow, smallmouth bass and walleye foraging on juvenile American shad. Our simulations suggest that greater reductions in smolt consumption by predators might occur if the elimination of American shad from the reservoirs reduces the feeding opportunities of predators as well as their growth. The partitioning of food resources between northern pikeminnow, smallmouth bass, and walleye in LCRR, although unknown, may be quite dynamic. Substantial reductions in the availability of American shad may reduce the growth of predator populations and result in significant dietary shifts if competition for preyfish between predators increased.

Smallmouth bass

The inshore feeding pattern and use of mainstem shoreline, sloughs, and backwater habitats by juvenile American shad (Miller 1993; Limburg 1996; Petersen et al. 2003) provides good evidence for the spatial and temporal habitat overlap of American shad preyfish and smallmouth bass in LCRR. Smallmouth bass are recognized as an important predator on juvenile American shad on the east coast of North America where American shad are a native species (Johnson and Dropkin 1992; Johnson and Ringler 1995).

Bioenergetics simulations suggest that while a late summer and fall diet of American shad produces a minor increase in smallmouth bass growth, the indirect result of this growth in terms of the proportion of salmonids consumed by smallmouth bass is potentially quite large. Tabor et al. (1993) and other authors suggested that smallmouth bass consume large numbers of salmonid prey whenever the preferred habitat of smallmouth bass overlaps with subyearling fall Chinook rearing (Gray and Rondorf 1986; Curet 1993; Poe et al. 1994; Zimmerman 1999) and the abundance of juvenile salmonids is high (Warner 1972; Pflug and Pauley 1984). In fact, Tabor et al. (1993) found that the smallmouth bass diet consisted of 59% (by weight) subyearling fall Chinook in the upper portion of McNary Reservoir during the late spring and early summer. Research on LCRR smallmouth bass populations provides further evidence that the impact of this invasive predator on subyearling fall Chinook could be quite high and indirectly linked to the abundance of juvenile American shad. A study in John Day Reservoir by Vigg et al. (1991) noted that the mean daily preyfish ration of smallmouth bass is about twice that of other aquatic predators. This same study described the reservoir diet of smallmouth bass $\geq$ 200 mm as 82% fish. Smallmouth bass as small as 75 mm have been observed with salmonid prey in their stomach contents (Beamsderfer and Ward 1994); these small bass will probably consume larval, and juvenile American shad as well. And, although small individuals consume less prey than larger predators, 1 and 2 year old smallmouth bass make up a substantial proportion of the population in the LCRR (Zimmerman and Parker 1995) and may contribute significantly to salmonid losses.

Our bioenergetics work on smallmouth bass suggests this predator may contribute to the poor survival observed in subyearling fall Chinook migrating through the reservoir system in July and August (Conner et al. 1998; Muir et al. 1998; Connor et al. 2001; Smith et al. 2003; Tiffan et al. 2003). Vigg et al. (1991) report that smallmouth bass consumption of juvenile salmonids peaks in July and remains high through August, while consumption is declining during August in northern pikeminnow, walleye, and channel catfish. Although the reduced survival of late migrating subyearling fall Chinook through the reservoir system may be due directly to stress associated with high water temperatures (Coutant 1999; Mesa 2002), indirect effects of exposure to high water temperatures include increased predation mortality (Vigg and Burley 1991; Marine and Cech 2004), higher incidence of disease (Fryer and Pilcher 1974), and substantial increases in passage mortality at hydropower facilities (Muir et al. 1998; Perry et al. 2003).

As part of a study on turbine passage mortality of subyearling fall Chinook, Perry et al. (2003) released radio-tagged fish into McNary Dam tailrace and estimated their survival through the upper portion of John Day Reservoir. Upper John Day Reservoir has relatively high shoreline habitat complexity, including islands, mainstem shorelines, shallow marshes, backwaters, and sloughs that extend 46 km downstream of McNary Dam tailrace to Crow Butte. Large numbers of smallmouth bass use the extensive backwater areas (Beamsderfer and Ward 1994), and juvenile salmonids and American shad are also attracted to the varied shoreline habitat of this reach (Barfoot et al. 2002). Radio-tagged subyearling fall Chinook suffered 33.6% mortality migrating through upper John Day Reservoir (Perry, personal communication). Some of the loss reported for these subyearling fall Chinook was probably due directly to stress from tagging and high water temperatures (near 23.5˚ C), but predation, particularly by smallmouth bass, may also be an important factor contributing to this high mortality.

Other research suggests smallmouth bass predation may not be limited to natural shoreline areas. A study by Duran et al. (2003) investigated the movements of radio-tagged northern pikeminnow and smallmouth bass in The Dalles Dam tailrace, an area with rocky shorelines, numerous bedrock islands, and backwater areas associated with the structural configuration of the dam. Although the predators that ingested radio-tagged juvenile salmonids could not be differentiated by species, Duran et al. (2003) found that the proportion of tagged juvenile salmonids ingested by northern pikeminnow and smallmouth bass increased between spring (2%) and summer (7%). Both predator species preferred bedrock substrate and shallow, low velocity water near structure. Despite their preference for the bedrock islands, artificial backwaters, and shoreline habitat, radio-tagged smallmouth bass were occasionally located further off-shore in the sluiceway zone where large numbers of juvenile salmonids concentrated. The study by Duran et al. (2003) suggests that juvenile salmonids are vulnerable to smallmouth bass predation whenever natural or artificial structures and flow patterns take migrating fish near shoreline areas.

Walleye

Bioenergetics modeling to assess the contribution of juvenile American shad towards the growth and salmonid consumption of walleye in LCRR produced results opposite from that of smallmouth bass. Our results suggest that juvenile American shad may be particularly important in explaining the high growth rate of walleye observed in LCRR, but this growth did not result in a large increase in salmonid consumption. Walleye are highly piscivorous in LCRR (Zimmerman 1999); nearly all of the prey (by weight) consumed by walleye in John Day Reservoir are fish (Poe et al. 1991). Zimmerman (1999) reported similar diet results for walleye at reservoir locations throughout the lower Columbia River basin. Like smallmouth bass, walleye show an exponential increase in the proportion of preyfish consumed between April and July (Vigg et al. 1991), and juvenile salmonids as well as American shad have been observed in the walleye diet (Gray et al. 1984; Maule and Horton 1984; Poe et al. 1988).

Our bioenergetics simulations suggest that juvenile American shad enhance walleye growth, but the proportion of salmonid consumption attributed to this growth was less for walleye (3.3%) than for either smallmouth bass (16.0%) or northern pikeminnow (6.8%). Based on the data available to us on population size, and our assumptions on the proportion of juvenile American shad in the walleye diet, the impact of American shad preyfish on walleye consumption of juvenile salmonids appears to be low in the LCRR (Beamsderfer and Rieman 1991; Zimmerman and Parker 1995).

Impact of juvenile American shad

Our bioenergetics modeling suggests that invasive American shad contribute to the growth of native and invasive aquatic predators in the LCRR, and that this growth increases the consumption of juvenile salmonids by northern pikeminnow, smallmouth bass, and walleye. The abundance of American shad in the late summer/fall diet of predators probably indirectly increases predator consumption of juvenile salmonids by increasing the growth and size of predator populations.

In this study, bioenergetics simulations predicted reduced growth and lower salmonid consumption by northern pikeminnow, smallmouth bass, and walleye in model runs without juvenile American shad in predator diets. Increased predator growth due to American shad may be the result of the high caloric density of juvenile American shad compared to alternative prey types, and/or increased foraging efficiency on shoaling juvenile American shad. We kept the feeding rate of predator cohorts constant in are growth models whether juvenile American shad were present or not. This approach assumes that predator cohorts consume similar proportions but less energetically profitable prey when American shad preyfish are not available. This assumption may or may not be correct. In bioenergetics modeling of northern pikeminnow growth in the lower Snake River, where there are relatively low numbers of anadromous preyfish, Sauter and Petersen (Report C, in preparation) used higher p-value estimates in simulations with large numbers of anadromous preyfish in the northern pikeminnow diet, arguing that the density of migrating preyfish fundamentally affects northern pikeminnow feeding behavior and growth. Many predators, including northern pikeminnow, appear to adjust their foraging behavior in response to changing prey density (Krebs and Kacelnik 1984; Lucas 1990; Petersen and DeAngelis 1992). Predators may feed rapidly and consume a larger ration of food when prey density is high (Tyler and Dunn 1976; Grove et al. 1978; Jobling 1982; Miglavs and Jobling 1989; Petersen and DeAngelis 1992), and this functional response may result in spatial differences in the size, density, and aggregation of northern pikeminnow (Petersen 2001).

Alternatively, the feeding rate of predators might be expected to decrease if highly aggregated American shad preyfish were not available to predators, in which case the difference between predator growth and salmonid consumption with and without juvenile American shad in the fall diet would increase. It is unlikely that the feeding rate of predators would rise in response to a diet without juvenile American shad because predators would have to increase their foraging activity on less aggregated, and perhaps less energy-rich prey, and intra- and inter-specific competition for preyfish might increase between predators. Our modeling assumption that the feeding rate of predator cohorts remains constant whether juvenile American shad are present or not, gives the most conservative estimate of differences in predator growth and salmonid consumption between the two fall diet conditions. When considering the smolt consumption of predators without American shad in their diets, we included bioenergetics runs that modeled reduced feeding opportunities and growth in our estimates. Under these conditions, predicted smolt consumption by predators decreased dramatically. However, some authors have suggested that large numbers of anadromous preyfish do not affect the feeding behavior of smallmouth bass and walleye (Poe et al. 1991).

Juvenile American shad may be a particularly easy source of food for aquatic predators near lower Columbia River dams, where emigrating fish suffer high stress-related mortality from delayed migration, confinement in fish passage facilities, dam passage, high water temperatures, and reduced predator avoidance (Shrimpton et al. 2001). Freshly dead preyfish offer as much energy to predators as live fish (Gadomski and Hall-Griswold 1992), and this non-evasive prey is

easily captured and may settle in areas of lower water velocity preferred by northern pikeminnow (Faler et al. 1988; Duran et al. 2003) and smallmouth bass (Sechnick et al. 1986; Todd and Rabeni 1989; Duran et al. 2003). Many predators use prey movement as a feeding cue (Ware 1973; Howick and O'Brien 1983; Irvine and Northcote 1983; Luczkovich 1988); however, northern pikeminnow preferentially fed on dead juvenile salmonids in laboratory experiments (Gadomski and Hall-Griswold 1992), and showed significant selection for dead juvenile salmonids in Bonneville Dam tailrace as well (Petersen et al. 1994). Petersen et al. (1994) also reports a very high proportion of American shad in the diet of northern pikeminnow during one year of the study at Bonneville Dam. Differences in the proportion of American shad in the northern pikeminnow diet at Bonneville Dam between years is probably linked to the abundance and timing of the American shad emigration which was much greater during the 1990 study period than in 1991 (Petersen et al. 1994). Although the response of smallmouth bass, and walleye to dead preyfish has not been investigated, the prevalence of injured and dead juvenile American shad near dam sites may contribute to the growth and increased salmonid consumption of invasive predators.

Conclusions

Northern pikeminnow, smallmouth bass, and walleye all display high growth rates in the LCRR. Petersen et al. (2003) suggests that faster growing predator populations may produce more offspring and consume a greater proportion of juvenile salmonids than slower growing populations. Identifying the prey species and environmental conditions that contribute to the growth of predators is important in planning and implementing strategies to reduce the impact of these predators on juvenile salmonids. Although northern pikeminnow predation has received the most attention, invasive predators are also known to consume large numbers of juvenile salmonids in LCRR (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Tabor et al. 1993; Zimmerman 1999). Previous studies also found indications that juvenile American shad might contribute to the growth of these predators (Gray et al. 1984; Maule and Horton 1984; Poe et al. 1988; Poe et al. 1991; Johnson and Ringler 1995; Johnson and Dropkin 1992). In this study, we identified juvenile American shad, an invasive preyfish, as an important prey species contributing to the growth of northern pikeminnow in LCRR. Bioenergetics modeling suggests that American shad are also a potentially important prey species contributing to the growth and salmonid consumption of invasive predators, particularly smallmouth bass, but better information on the feeding behavior and seasonal diets of these predators is needed.

The role of American shad in the growth and salmonid consumption of aquatic predators in LCRR is not surprising given the timing of the American shad emigration. The late summer and fall emigration of juvenile American shad provides an abundant source of anadromous preyfish for predators at a time when there are few juvenile salmonids available. The abundance of juvenile American shad and the warmer fall water temperatures of the LCRR creates opportunities for feeding and growth of predator populations that otherwise would not exist. If dam passage is associated with high levels of stress-related mortality in juvenile American shad as the laboratory research by Shrimpton et al. (2001) suggests, American shad may be a particularly easy source of high-quality food for aquatic predators. Research on the dam passage mortality of juvenile American shad, and the feeding responses of smallmouth bass and walleye to dead preyfish would offer important insights on predation issues near dams.

Smallmouth bass may be especially important when considering subyearling fall Chinook survival (Perry et al. 2003) for the following reasons: (1) smallmouth bass maintain a higher maximum daily ration later in the summer than the other aquatic predators (Vigg et al. 1991), (2)

there appears to be more extensive temporal and spatial overlap between the preferred habitat of smallmouth bass and the rearing habitat of subyearling fall Chinook and larval and juvenile American shad than with the other aquatic predators (Gray and Rondorf 1986; Petersen et al. 2003), (3) although our bioenergetics modeling suggests that larval and juvenile American shad have a limited effect on smallmouth bass growth, this growth translated into a substantial amount (16.0%) of salmonid consumption, (4) smallmouth bass are the second most abundant predator in John Day Reservoir and are most abundant in the impounded areas of the lower Columbia River (Beamsderfer and Rieman 1991; Zimmerman and Parker 1995), and (5) although northern pikeminnow are more abundant than smallmouth bass in the reservoir system, the peak summer water temperatures observed in the reservoirs (~22 ^{o} C) may reduce the feeding rate of northern pikeminnow during this period while increasing the feeding rate of smallmouth bass (Petersen and Ward 1999).

Because water temperatures remain cool in LCRR throughout much of the spring smolt migration, we concluded that northern pikeminnow are the most important source of predation mortality on juvenile salmonids. The growth and predation potential of smallmouth bass, walleye, and channel catfish is constrained by water temperatures during much of the spring emigration. For this reason, invasive predators in the LCRR may be a greater threat to subyearling fall Chinook than to other salmonids. The earliest portion of the subyearling fall Chinook emigration begins to move into the lower Columbia reservoirs in mid-June. This portion of the emigration is primarily hatchery fish released from Priest Rapids hatchery (Tiffan et al. 2003). Later migrants are primarily wild fish from the Hanford Reach and Snake River. The nearshore feeding and migration pattern, smaller size, and slower migration of wild subyearling fall Chinook (Haskell et al. 2001; Tiffan et al. 2003) combined with warmer late spring and summer water temperatures in the reservoirs probably make this salmonid species more vulnerable than spring migrants to invasive predator species. However, juvenile salmonids are susceptible to invasive predators whenever flow patterns take emigrants along shorelines or into structurally complex habitat and lower velocity waters.

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