Snake River Fall Chinook Salmon Life History Investigations

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1/1/2012 - 12/31/2012

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1. Executive Summary

a. Fish Population RM&E

This annual report describes the data collected and analyses conducted during calendar years 2012-2013 by staff of project 20023200. The USGS contributed only to the predation research and reservoir invertebrate work described in this report and the presentation of their results is consistent with USGS policy guidelines. The USGS is not responsible for the content provided by other contributing authors. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

The main goal of this project is to better understand juvenile Snake River fall Chinook salmon life history diversity and the factors that influence it. This is called for in RPA 55.4 "Investigate key characteristics of Snake River fall Chinook salmon early life history." We

investigated the importance of estuary entry and rearing to various Snake River fall Chinook salmon life histories. Otoliths were used to examine differences in estuary use between subyearlings and yearlings, and to determine natal habitats, rearing habitats, and overwintering habitat for returning adults. Estuary growth was best explained by estuary residence time and natal location.

b. Predation and Invasive Species Management RM&E

We investigated the extent of smallmouth bass predation on juvenile fall Chinook salmon in Lower Granite Reservoir as called for in the Fish and Wildlife Program, "The federal action agencies should work cooperatively with NOAA Fisheries, states, tribes, and the Council to review, evaluate, develop, and implement strategies to reduce non-native piscivorous predation on salmon and steelhead, especially by smallmouth bass, channel catfish, and walleye" (Page 52). Smallmouth bass stomach contents were collected and analyzed for the presence of juvenile salmon. Smallmouth bass abundance was estimated with mark-recapture techniques, and salmon consumption by bass was expanded based on bass abundance to determine the annual loss of juvenile fall Chinook salmon for the study period and area. The estimated loss of juvenile fall Chinook salmon to predation in Lower Granite Reservoir exceeded 109,000 fish in 2012. This information could be used to adaptively formulate better hatchery release strategies to reduce the effects of predation. Obtaining better estimates of smallmouth bass abundance and distribution in future years would reduce the uncertainty of estimates. This study will be completed by 2017.

We also examined the effects of various field temperature scenarios resulting from summer flow augmentation on juvenile fall Chinook salmon susceptibility to smallmouth bass predation in laboratory trials. Predation susceptibility of juvenile salmon acclimated at cool temperatures (10°C) was highest when exposed to predators at 24°C. These results indicate that predation susceptibility may be higher when a relatively large temperature difference exists between the Clearwater and Snake rivers; that is, when cool water flow augmentation occurs in summer.

Finally, we examined the role of different invasive invertebrates in lower Snake River reservoir food webs that are food, or competitors for food, for juvenile fall Chinook salmon. The Siberian prawn, a relatively new invader, is relatively abundant but its role on the food web is largely unexplored. Prawns are successfully reproducing and their diet is 81% Neomysis (an invasive opossum shrimp) which is heavily used at times by juvenile salmon for food. Neomysis has become very abundant in lower Snake River reservoirs in recent years and may be a profitable food item for many fish species.

2. Introduction

For each Fish and Wildlife Program Strategy briefly discuss how your project informs/supports the program sub strategies and associated management questions. The content may be reorganized into any format of your choosing.

a. Predation and Invasive Species Management RM&E

F&W Program Strategy: Evaluate the effects of the northern pikeminnow removal program and investigate strategies to reduce non-indigenous piscivorous (e.g., walleye, smallmouth bass) predation on salmonids.

F&W Program Management Question: What are the distributions, population sizes, and productivity; and what are the impacts and consumption rates of major piscivorous, avian, and marine mammal predators within the Columbia River Basin?

Predation

Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile salmonids *Oncorhynchus* spp. in the Pacific Northwest. The only evaluation of predation on subyearling Snake River fall Chinook salmon in the upper portion of Lower Granite Reservoir was conducted by Naughton et al. (2004). However, this study in the Snake River was conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook salmon (NMFS 1992). During this time, fall Chinook salmon abundance was at an historic low and may explain why consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima rivers where abundance was higher (Tabor et al. 1993; Fritts and Pearsons 2004). We speculate that predation on subyearlings by smallmouth bass in the Snake River may have increased in recent years for several reasons. Since their ESA listing, recovery measures implemented for Snake River fall Chinook salmon have resulted in a large increase in the juvenile population (Connor et al. 2013). For example, the annual subyearling passage index for fall Chinook salmon at Lower Granite Dam, the first dam encountered during downstream migration, was 18,533 in 1996 when the Naughton study was conducted but was 749,074 in 2013 (DART 2014). Both Zimmerman (1999) and Naughton et al. (2004) showed that fish can comprise a large portion of smallmouth bass diets. Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a large portion of smallmouth bass diets. Here we report on findings from work conducted in 2012. Our objective was to describe the seasonal variation in smallmouth bass diets and consumption of subyearlings during their rearing and outmigration period in Lower Granite Reservoir. This work is important to understand the effect of predation on juvenile salmon now that many of the populations are healthier than they were after ESA listing.

Previous research conducted by this project documented high mortality of hatchery-reared juvenile fall Chinook salmon emigrating from the Clearwater River at the confluence of the Snake and Clearwater rivers. Although the cause for this was unknown, we speculated that fish traveling through the large temperature differentials that exist in this area may make them more susceptible to predation if they were compromised by total dissolved gas exposure or thermal stress. We conducted controlled laboratory experiments to test these hypotheses. This information is important to understand the potential negative effects of summer flow augmentation on juvenile salmon originating from the Clearwater River.

F&W Program Strategy: Develop guidelines and procedures for monitoring for presence and prevalence of aquatic invasive species.

F&W Program Management Question: What guidelines and procedures are recommended for monitoring for presence and prevalence of aquatic invasive species?

Status and Trends

One non-native invertebrate that has recently become very abundant in Lower Snake River reservoirs is the estuarine opossum shrimp, *Neomysis mercedis*. Subyearlings prey heavily on this relatively large (~15 mm, total length) species when both are present in shallow water habitats during the spring (Tiffan and Connor 2012; Tiffan et al. 2014). Siberian prawns *Exopalaemon modestus* have also recently invaded lower Snake River reservoirs and have increased exponentially in abundance (Haskell et al. 2006). The role these species have on juvenile salmon feeding ecology and the food web remain largely unexplored, but warrants monitoring to better understand their ecology and effects on juvenile salmon.

b. Fish Population RM&E

F&W Program Strategy: Assess the status and trend of spatial distribution of fish populations.

F&W Program Management Question: What are the status and trend of spatial distribution of fish populations?

Status and Trend Monitoring

The goal of this research is to achieve a better understanding of the migratory patterns of reservoir-type fall Chinook. To do this, we will conduct micro-chemical and micro-structural analyses of their otoliths, sampled from both juveniles and adults. The geochemical analysis of fish otoliths (inner ear balance organs) allows for the reconstruction of important migrational behaviors because the tissue preserves a record of chemical experience of individual fish. By analyzing these chemical signatures, it is possible to identify the location and duration of juvenile Chinook residences during rearing in their natal site, downstream migration from their rearing areas, through the hydrosystem, through the estuary, and into the ocean. In addition, the width of daily increments is related to fish growth, and growth trajectories can be back-calculated from daily growth increments. Combining these approaches, we can use the otoliths of returning adult Fall Chinook to quantify seasonal and spatially explicit patterns of growth.

This work will determine the importance of different natal, rearing, and overwintering locations to life history pathways for Snake River fall Chinook salmon. This is significant because different life history strategies may result in different productivities, such as SARs, from different river systems. To aid in the sustainability of this population we must understand the relationship between life history pathway and natal origin and rearing location, and how each pathway contributes to the reproductive population.

F&W Program Strategy: Assess the status and trend of diversity of natural and hatchery origin fish populations.

F&W Program Management Question: What are the status and trend of diversity of natural and hatchery origin fish populations?

Uncertainty Research

Similar to that described above, it is not certain whether hatchery-origin fish are equally as productive or have the same fitness as natural-origin fish. Through the use of otolith microchemistry this project can quantify the origin and rearing location of unmarked returning adults, and thereby identify areas that are productive in terms of abundance and diversity of life history pathways.

Location details: For each F&W Program Strategy above, insert maps, aerial photos, or pictures of where your work was conducted. Below are links to existing project or contract map options created in cbfish.org or insert your own.

Project Map:

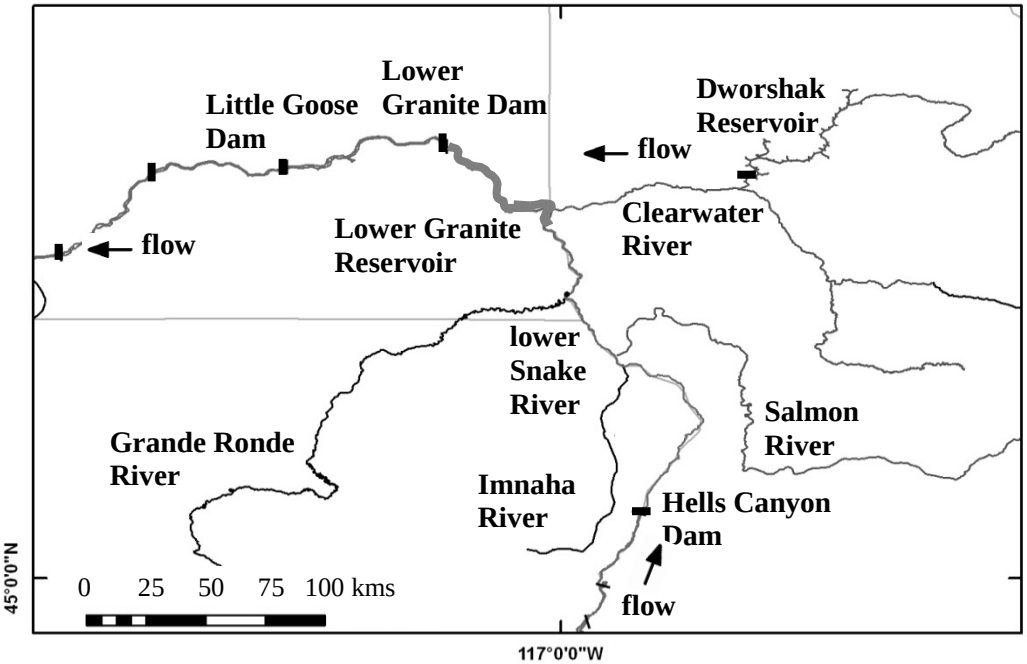

Figure 1. The Snake River basin including the Lower Granite Reservoir, the Snake River, the lower Clearwater River, and other tributary reaches where fall Chinook salmon spawn and produce natural offspring. All juveniles from those reaches must pass Lower Granite Dam.

Contract Map(s):

http://www.cbfish.org/Contract.mvc/Map/46273 REL 40

http://www.cbfish.org/Contract.mvc/Map/56575

http://www.cbfish.org/Contract.mvc/Map/56574

http://www.cbfish.org/Contract.mvc/Map/56065 REL 2

3. Methods: Protocols, Study Designs, and Study Area

Protocol Title: Abundance (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/267

Protocol Title: Collect predator diets (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/269

Protocol Title: Describe predator diets (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/271

Protocol Title: Estimate abundance (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/270

Protocol Title: Fish classification (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/324

Protocol Title: Lab Predation Rate (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/274

Protocol Title: Lab predaton trial (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/273

Protocol Title: Otolith analysis (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/321

Protocol Title: Otolith collection (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/318

Protocol Title: otolith growth analysis (2002-032-00) v1.0

Protocol Link: http://www.monitoringmethods.org/Protocol/Details/325

Additional information regarding fish classification and water sample analysis can be found in Hegg et al. (2013).

4. Results

a. Predation and Invasive Species Management RM&E

Field Predation

In 2012, we collected 329 smallmouth bass by angling and 366 bass by electrofishing in three reaches of Lower Granite Reservoir. We estimated a total of 4,348 bass (95% CI: 399-10,238) in the Snake River transition zone (i.e., confluence with Clearwater River upstream to Asotin, WA), followed by 8,188 bass (95% CI: 1,295-25,328) in the confluence reach (i.e., confluence with Clearwater River downstream to Port of Wilma), and 498 bass (95% CI: 143-1,736) in the Clearwater River transition zone (i.e., mouth upstream to Potlatch Mill) in 2012.

Smallmouth bass primarily consumed insects, crayfish, salmonids, and nonsalmonid fishes. At times salmonids comprised the majority of the diet by weight in all three reaches (Figure 2). Based on the size of ingested Chinook salmon, it is likely that most were fall Chinook salmon. Estimated mean size of Chinook salmon consumed in the Snake River transition zone was 73 mm (SD = 16.6 mm, N = 34, range = 43-121 mm) which was similar to the mean size of 72 mm (SD = 11.1 mm, N = 37, range = 48-93 mm) for ingested Chinook salmon in the Confluence reach. A total of 32 PIT tags were found in smallmouth bass stomachs. Most of the tagged fish were initially released at Big Canyon Creek on the Clearwater River and at Couse Creek on the Snake River. Most of the PIT-tagged fish from the Clearwater River were consumed in the Clearwater River Transition Zone (CRTZ) reach whereas most of the tagged fish released in the Snake River were consumed in the Snake River Transition Zone (SRTZ) reach. A total of 7 smallmouth bass had multiple PIT tags in their stomachs which ranged from 2 to 5 tags (Table 7). Smallmouth bass that consumed PIT-tagged Chinook salmon ranged in size from 175 to 318 mm TL.

Total loss of salmonids to smallmouth bass predation within our study area in 2012 was estimated to be 109,887 individuals (95% CI = 15,285-311,127). Coincident to the abundance estimates, the highest total consumption occurred in the Confluence (CON) reach (62,894 salmonids) followed by the SRTZ reach (41,753 salmonids), but the highest consumption rates (salmonids/bass/day) occurred in the CRTZ followed by the SRTZ. Total salmonid loss in the CRTZ reach was estimated at 5,240 fish, however data should be interpreted with caution as sample sizes were very low (only 17 samples examined). Consumption was first observed in the SRTZ during the week of 14 May and was last documented in the CON reach during the week of 6 August.

A complete reporting of 2012 field predation results can be found in Appendix B, Chapter One.

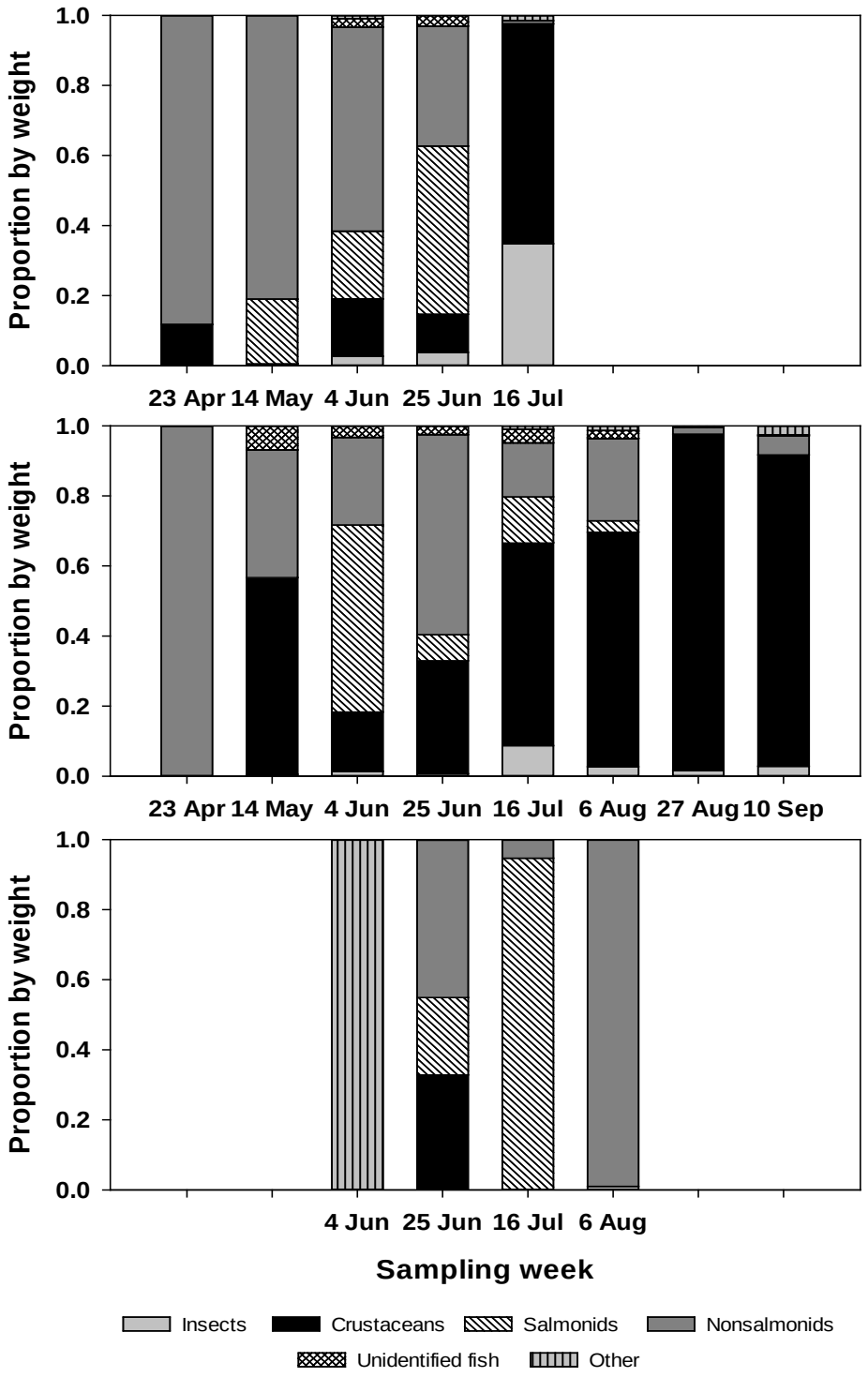

Figure 2. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Snake River Transition Zone reach (top panel), the Confluence reach (middle panel), and the Clearwater River Transition Zone reach (bottom panel) of Lower Granite Reservoir in 2012.

Lab Predation Study

To simulate field temperature conditions, we acclimated juvenile fall Chinook salmon to temperatures typical of the Clearwater River (10°C) and Snake River (17°C) and exposed them to predators at 17°C and 24°C. The only significant effect of temperature on predation susceptibility was found for fish acclimated at 10°C and exposed to smallmouth bass at 24°C, otherwise predations susceptibilities were similar. These results indicate that predation susceptibility may be higher when a relatively large temperature difference exists between the Clearwater and Snake rivers; that is, when cool water flow augmentation occurs in summer. However, it is also clear that juvenile salmon have a large capacity to endure short term temperatures changes that may not always increase their susceptibility to predation.

A complete reporting of 2012 field predation results can be found in Appendix B, Chapter Two.

Invasive Species Sampling

Siberian prawns are present throughout both Lower Granite and Little Goose reservoirs but their biomass was generally higher in Little Goose Reservoir. They are more abundant in deep water but juvenile prawns tend to occupy shallow water after they are produced in August and September. Prawns only live for a little more than one year. Prawns are predatory and their diet consists mainly of Neomysis (81%) and other invertebrates. Given their preference for deep habitats, it is unlikely that they are used by juvenile salmon for food, but may be used for other salmon predators such as walleye, smallmouth bass, and channel catfish.

Neomysis were also very abundant in both reservoirs and dominated the benthic invertebrate biomass. Their biomasses are relatively high compared to other mysid populations. Interestingly, Neomysis move into shallow habitats that juvenile fall Chinook salmon also use for rearing making them accessible as a profitable food source. It is not known at this time whether Neomysis consume primarily detritus or zooplankton, which juvenile salmon also use for food.

A complete reporting of 2012 field predation results can be found in Appendix B, Chapter Three.

b. Fish Population RM&E

Adult Otolith Sampling

Adult otolith collection is a yearly effort which has been ongoing since 2006. Otolith collection occurs at Lyons Ferry Hatchery each fall (Oct-Nov) during spawning. The sample is considered to be a representative, random sample of the population due to the subsampling

of fish for conducted as part of spawning at Lower Granite Dam. All un-marked, untagged fish which are presumed wild are dissected and their otoliths are collected. Subsequent scale analysis is used to determine hatchery/wild origin with more precision and a representative sample of known wild fish is then selected for analysis.

Currently analysis of adult otoliths is focused on the 977 adult otoliths sampled during the 2012 spawning season. Of these sampled fish, 76 have been determined to be of wild origin based on scale analysis. These samples have been sorted and preparation has begun, with analysis planned for the Summer and Fall of 2014.

The 2013 spawning season yielded 512 presumed wild fish. Subsampling and preparation of these otoliths is planned for Fall of 2014, with preparation and analysis to be completed during Fall of 2014 and Spring of 2015.

Juvenile Otolith Sampling

Sampling of juvenile fish is conducted on the spawning grounds each summer. Five locations are sampled, the Lower and Upper Snake River, Grande Ronde and the Upper and Lower Clearwater Rivers. A sample size of six is targeted from each location.

In 2013 six fish were sampled from each location except the Clearwater, from with 13 samples were taken from sampling mortalities. In 2014, six fish were sampled from each location in the Snake and Grande Ronde Rivers. Juvenile sampling is still ongoing in the Clearwater River for 2014.

Otolith Analysis and Fish Classification

Based on otolith analyses, we found no significant differences between subyearlings and yearlings in terms of age and size at estuary entry and exit, and estuary growth. On average, subyearlings and yearlings spent about 27 and 30 days in the estuary, respectively, and grew about 38 and 41 mm during that time. Strontium isotopic ratios from water samples taken at various locations were useful for determining river of origin (i.e., natal location), and juvenile rearing and overwintering locations of returning adults (Table 1). Most adults were estimated to have originated, reared, and overwintered in the lower Snake River, which was consistent with results from the analysis of adults collected in previous years (2006-2008). Relative to previous results we also observed a decrease in the proportion of adults that originated and reared in the Clearwater and Salmon Rivers, and an increase in adults that originated, reared and overwintered in the Upper Snake River (Figure 3).

We did not see a relationship between body size at estuary entry and exit, and estuary growth with natal origin, rearing, and overwintering location (Figure 4). Similarly, we did not see a relationship between age at estuary entry and exit, and estuary residence time with natal origin, rearing, and overwintering location (Figure 5).

Water Chemistry Sampling & Analysis

Water samples are collected seasonally to provide an ongoing archive of variation within the spawning reaches of the Snake and Clearwater Rivers. The results of this sampling are then used to classify otolith signatures to their location of origin. All samples are analyzed using isotope dilution on a Finnigan MAT 262 Multi-Collector Thermal Ionization Mass Spectrometer (TIMS) for $^{87}Sr/^{86}Sr$ ratio.

In January 2014, twenty-four water samples were analyzed from throughout the basin at the MIT Isotope and Geochronology lab in Cambridge, MA. These samples covered the 2011 and 2012 sampling seasons for each major spawning reach of the Snake and Clearwater Rivers. Discriminant analysis of these samples will follow in 2014.

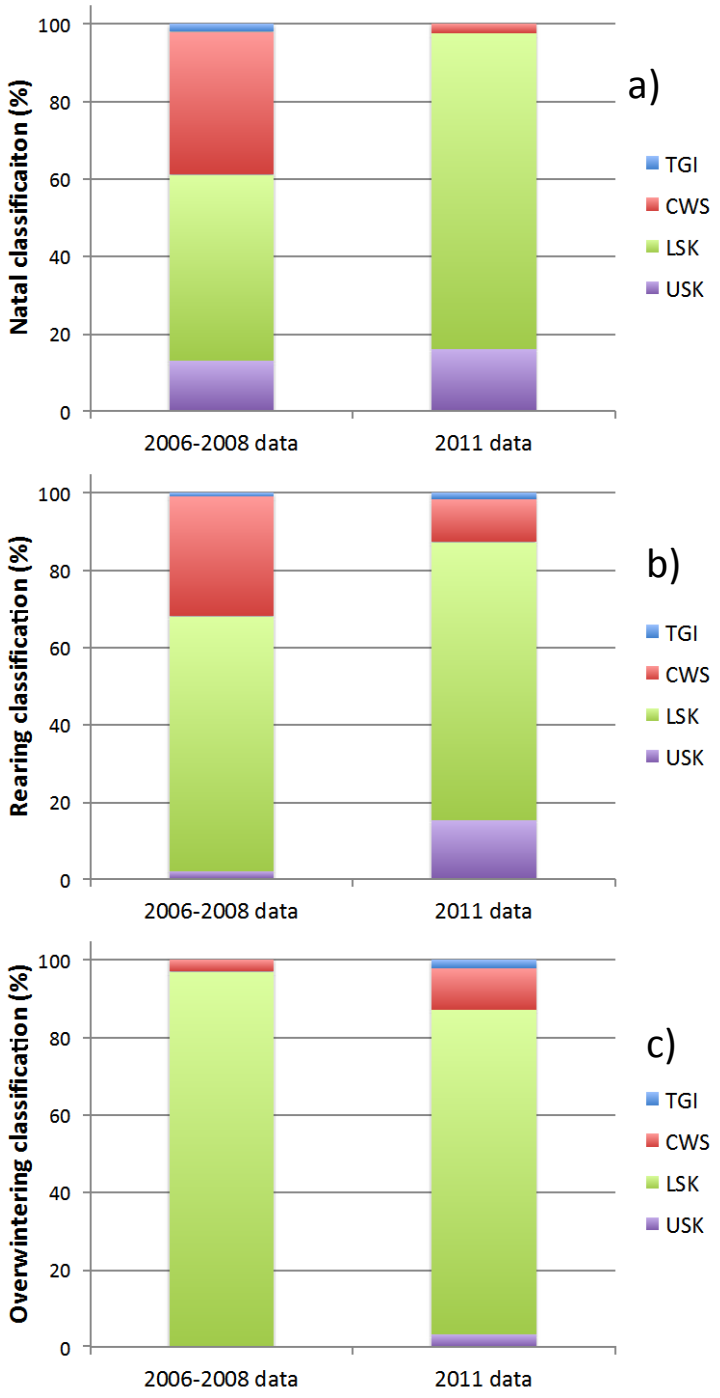

Figure 2: Comparison of fish classification (%) from Hegg et al. (2013) and this study (2006-2008 and 2011 collected adults, respectively) with regards to their a) natal, b) rearing, and c) overwinter location. Abbeviations: TGI (Tucannon, Grande Ronde, Imnaha), CWS (Clearwater), LSK (Lower Snake), USK (Upper Snake)

Table 1: Results of the classification of adults (based on otolith microchemistry signatures of Sr87/Sr86) to their natal, rearing, and overwintering location, and the classification of juveniles for which their rearing location was known.

River groupings (code)	Natal locations (%)	Sub-yearling	Yearling (%)	% Female	% Yearling female
Tucannon, Grande Ronde, Imnaha (TGI)	0 (0)	0	0	0	0
Clearwater, Salmon (CWS)	3 (2)	1	2 (66)	66	33
Lower Snake (LSK)	102 (82)	25	77 (76)	72	55
Upper Snake (USK)	20 (16)	6	14 (70)	65	45
Total sample size	125	32	93		
River groupings (code)	Rearing locations (%)	Sub-yearling	Yearling (%)	% Female	% Yearling female
Tucannon, Grande Ronde, Imnaha (TGI)	2 (2)	2	0	0	0
Clearwater, Salmon (CWS)	14 (11)	3	11 (79)	71	57
Lower Snake (LSK)	90 (72)	24	66 (73)	74	53
Upper Snake (USK)	19 (15)	3	16 (84)	63	58
Total sample size	125	32	93		
River groupings (code)	Overwintering locations (%)	Sub-yearling	Yearling (%)	% Female	% Yearling female
Tucannon, Grande Ronde, Imnaha (TGI)	2 (2)			50	
Clearwater, Salmon (CWS)	10 (11)			100	
Lower Snake (LSK)	78 (84)			68	
Upper Snake (USK)	3 (3)			100	
Total sample size	95				
River groupings (code)	Known rearing locations (%)	Rearing classification (%)	% correct classification		
Lower Snake (LSK)	19 (90)	18 (86)	100		
Upper Snake (USK)	2 (10)	3 (14)	95		

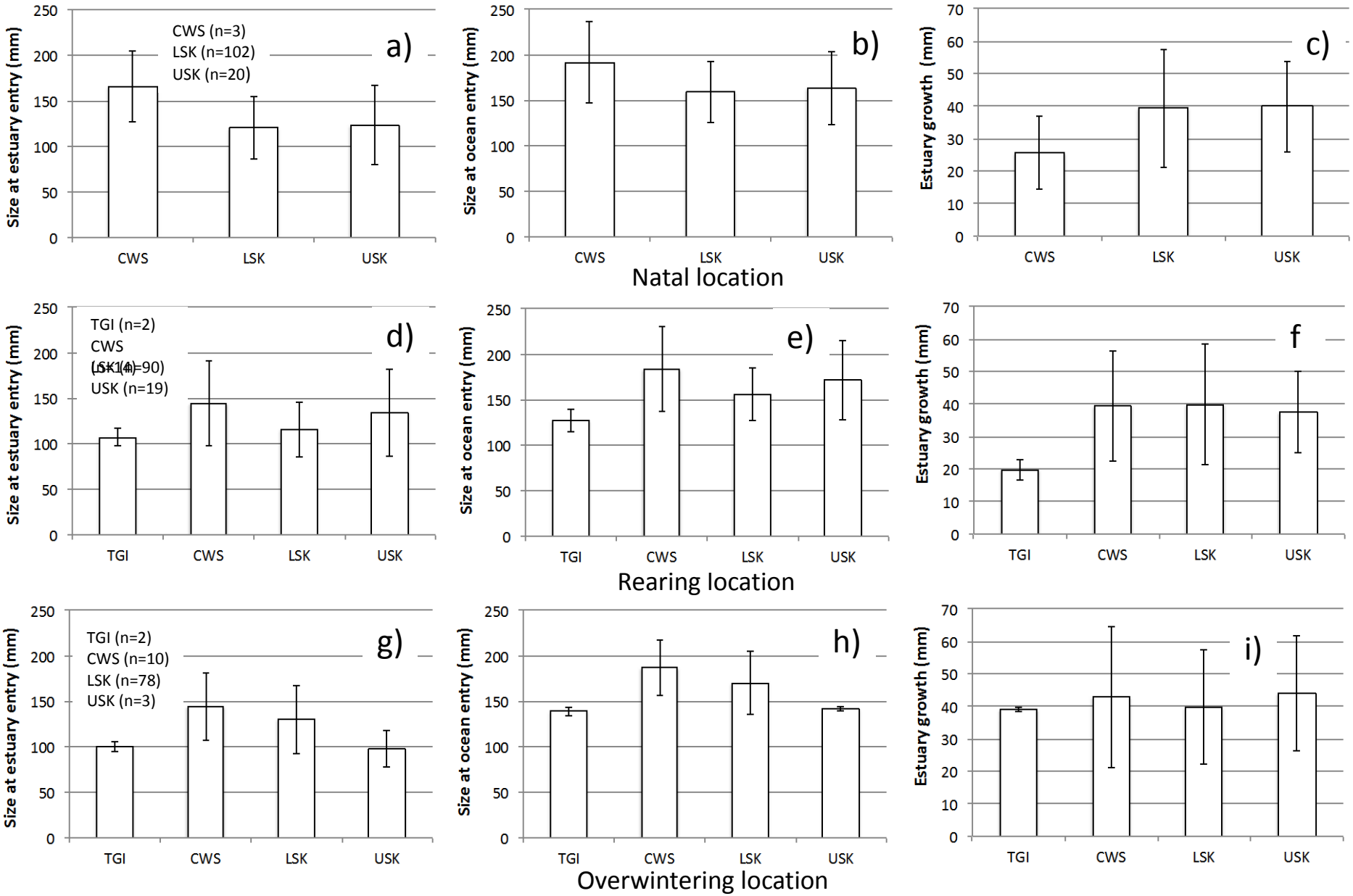

Figure 4 Otolith derived back-calculated estimates of Chinook salmon body size at estuary and ocean entry and estuary growth for individuals classified to their natal (a-c), rearing (d-f), and overwintering (g-i) locations. Classifications are based on otolith microchemistry (Sr87/Sr86). Sample sizes are indicated for each location and means (box) and standard deviations (whiskers) are depicted. See Figure 3 for location abbreviations.

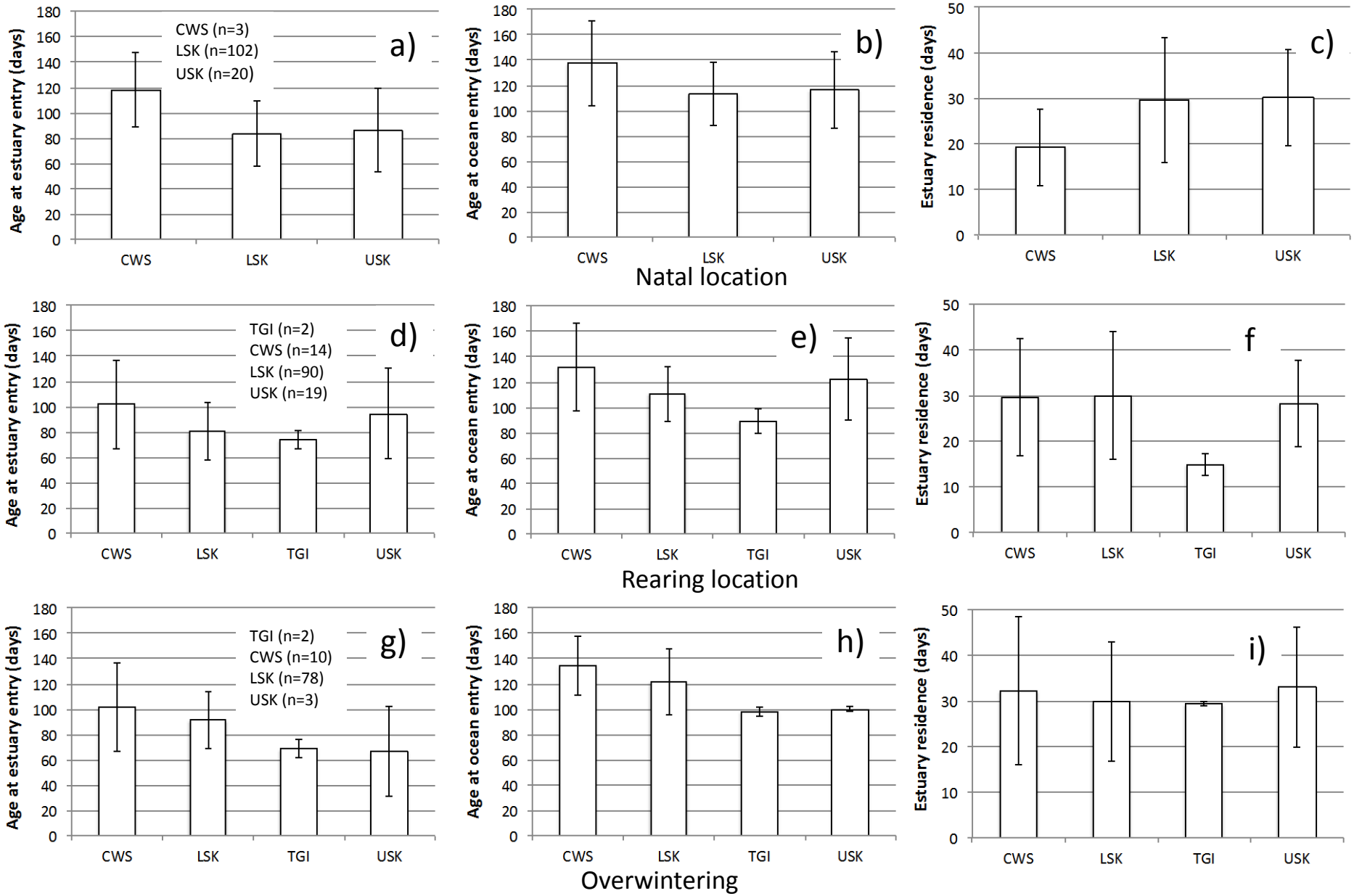

Figure 5. Otolith derived back-calculated estimates of Chinook salmon age (days) at estuary and ocean entry and estuary residence for individuals classified to their natal (a-c), rearing (d-f), and overwintering (g-i) locations. Classifications are based on otolith microchemistry (Sr87/Sr86). Sample sizes are indicated for each location and means (box) and standard deviations (whiskers) are depicted. See Figure 3 for location abbreviations.

5. Synthesis of Findings: Discussion/Conclusions

Lessons Learned: Explain how the results of this project benefit fish and wildlife. Address each applicable sub-strategy and management question(s), provided in the Introduction for higher-level or project/program level adaptive management. If studies are incomplete, discuss preliminary findings. (Refer to the RM&E Annual Technical Reporting guidance document for more information on content to include).

a. Predation and Invasive Species Management RM&E

Field Predation

Although this study is ongoing, we showed that smallmouth bass predation on subyearling fall Chinook salmon in the upper portion of Lower Granite Reservoir has increased substantially since the time the last predation study was conducted in the mid-1990s (Naughton et al. 2004). This is due to a number of factors. First, hatchery supplementation has directly increased the population via annual releases of juveniles and indirectly as a result of increased production from natural spawners (Connor et al. 2013). Second, consumption rates of juvenile salmon by smallmouth bass are generally higher today than they were in the 1990s. The latter may be a response to the greater abundance of the subyearling population. Consequently, the loss of subyearlings is much greater than in the 1990s when the population was at historically low levels following ESA listing. Our results provide managers with insight into the extent of predation on subyearlings by smallmouth bass in Lower Granite Reservoir.

Lab Predation Study

Exposure to large temperature differentials and subsequent exposure to predators have the potential to increase mortality of juvenile fall Chinook salmon. However, because fish can select suitable temperatures through behavioral thermoregulation as they transition through heterogeneous thermal environments, they may be able to reduce any associated predation risk. Habitat overlap with smallmouth bass during the summer when bass have higher feeding rates likely increases their mortality.

Invasive Species

The food web in the lower Snake River reservoirs has changed in the last 20 year and now includes invasive species that have become very abundant. Neomysis may channel energy stored in detritus to juvenile salmon when they are preyed upon. This would represent a trophic benefit to both juvenile salmon and resident fishes. However, Neomysis can also compete with fishes for zooplankton. Our current sampling will determine the extent to which this occurs. Whether Siberian prawns are having a negative, positive, or neutral effect on the food web and juvenile salmon is less clear. They may be having an indirect effect on juvenile salmon by serving as prey for their predators or consuming their prey (i.e., Neomysis). It would be prudent to monitor these invasive species at least on a quarterly basis.

b. Fish Population RM&E

We showed that the majority of returning adult fall Chinook originated, reared, and overwintered in lower Snake River, while relatively few fish originated and reared in upper Snake River and Clearwater and Salmon Rivers. Comparing these results to that of previous work (also from this project; Hegg et al. 2013) highlights temporal variability in natal origin, rearing and overwintering locations of fall Chinook salmon. Specifically, our results using adults collected in 2011 show that upper Snake River and Clearwater and Salmon Rivers were found to be more and less important as natal and rearing locations, respectively, when compared to the earlier results (Hegg et al. 2013) that used fish collected in 2006-2008. Furthermore, our work indicated that the yearling life history pathway comprised 74% of the adults we sampled in 2011 compared to 62% for those sampled in 2006-2008 (Hegg et al. 2013). Our results provide managers important information regarding the contribution of different life history pathways to the adult population, and the locations from which they originated and reared.

Understanding how when and for how long fish reside in different habitats (e.g. estuary) can help inform management actions, for example timing the release of hatchery fish so as to reduce the potential of density dependence. Further, knowing what factors influence growth and how much fish grow in different habitats is important since fish that attain larger body sizes are likely to have improved survival to adulthood. Our results investigating age and growth indicated fish reside in the estuary for a similar period of time and grow similar amounts regardless of life history pathway, natal origin, and rearing and overwintering location. When we investigated what factors explain variability in estuarine growth we found that estuary residence time and natal origin were most important. These results suggest that when fish originate from a particular area (e.g., Snake River), and have the opportunity to reside in the estuary for relatively longer periods of time (perhaps more than a month), they will attain a larger body size, which in turn could increase their chance of survival.

Growth Analysis

Growth analysis of known origin juvenile fish and of the juvenile portion of otoliths will be done to determine the spatial and temporal differences in growth between spawning areas in the basin. This information will allow us to tie juvenile migratory behavior to the effect of local growth conditions.

Analyzing otolith microstructure is a two-step process consisting of otolith preparation and observation (Campana and Neilson 1985). The left sagittal otoliths are embedded into an epoxy resin. Otoliths are cut and then polished to their central plane, where the otolith core and daily growth increments are most visible. Otoliths are then visualized under and light microscope, daily growth rings are counted and the width of these rings are measured.

This information is used to reconstruct growth trajectories covering the time period from natal rearing area to estuary residence for adults that demonstrated overwintering. Because growth exhibits seasonal patterns driven by temperature, this will enhance our ability to associate locations along otolith transects to times in the season. This will also allow us to assess how juvenile performance, as measured by growth, varies across habitats.

Our work is currently focused on improving our ability to reconstruct detailed early growth trajectories. Optical microscope results have not provided the unbroken growth trajectories at small fish sizes are needed, especially from adult otoliths. To this end we are working to improve the method using scanning electron microscope (SEM) imaging of otoliths. After polishing, otoliths are prepared for SEM analysis by etching the surface with light acid, which preferentially erodes the rings containing a lower amount of protein matrix (Secor et al. 1991). This provides a topographical surface which can be imaged using SEM, capturing rings which are not visible on a polished otolith. We expect to finalize a robust growth analysis technique during summer of 2014 and provide the first complete growth analysis under the next contract period.

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Appendix A: Use of Data & Products

Appendix B: Detailed Results

CHAPTER ONE

Smallmouth Bass Predation on Juvenile Fall Chinook Salmon in Lower Granite Reservoir on the Snake River

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INTRODUCTION

Predation by nonnative fishes is one factor that has been implicated in the decline of juvenile salmonids in the Pacific Northwest. Impoundment of much of the Snake and Columbia rivers has altered food webs and created habitat favorable for species such as smallmouth bass *Micropterus dolomieu*. Smallmouth bass are common throughout the Columbia River basin and have become the most abundant predator in lower Snake River reservoirs (Zimmerman and Parker 1995). This is a concern for Snake River fall Chinook salmon *Oncorhynchus tshawytscha* subyearlings that may be particularly vulnerable because of their relatively small size and because their main-stem rearing habitats often overlap or are in close proximity to habitats used by smallmouth bass (Curet 1993; Tabor et al. 1993).

Concern over juvenile salmon predation spawned a number of large-scale studies to quantify its effect in the late 1980s, 1990s, and early 2000s (Poe et al. 1991; Rieman et al. 1991; Vigg et al. 1991; Fritts and Pearsons 2004; Naughton et al. 2004). Smallmouth bass predation represented 9% of all salmon consumed by predatory fishes in John Day Reservoir, Columbia River, from 1983 through 1986 (Rieman et al. 1991). In transitional habitat between the Hanford Reach of the Columbia River and McNary Reservoir, juvenile salmon (presumably subyearlings) were found in 65% of smallmouth bass (>200 mm) stomachs and composed 59% of the diet by weight (Tabor et al. 1993). Within Lower Granite Reservoir on the Snake River, Anglea (1997) reported that subyearlings made up 7% of smallmouth bass diets, and Naughton et al. (2004) showed that monthly consumption (based on weight) ranged from 5% in the upper reaches of the reservoir to 11% in the forebay. However, these studies in the Snake River were conducted soon after Endangered Species Act (ESA) listing of Snake River fall Chinook salmon (NMFS 1992). During this time, fall Chinook salmon abundance was at an historic low which may explain why consumption rates were relatively low compared to those from studies conducted in the Columbia and Yakima rivers where abundance was higher (Tabor et al. 1993; Fritts and Pearsons 2004).

We speculate that predation on subyearlings by smallmouth bass in the Snake River may have increased in recent years for several reasons. Since their ESA listing, recovery measures implemented for Snake River fall Chinook salmon have resulted in a large increase in the juvenile population (Connor et al. 2013). In Lower Granite Reservoir, both Zimmerman (1999) and Naughton et al. (2004) showed that fish can comprise a large portion of smallmouth bass diets. Considering that subyearlings probably now make up a larger portion of the forage fish population, it is plausible they should make up a large portion of smallmouth diets. Second, migrating subyearlings delay downstream movement in the transition zones of the Clearwater River and Snake River for varying lengths of time (Tiffan et al. 2010) which increases their exposure and vulnerability to predators. Spatial overlap in locations of smallmouth bass and subyearlings that died during migration provides support for this (Tiffan et al. 2010). Finally, the

later outmigration of subyearlings from the Clearwater River results in their presence in Lower Granite Reservoir during the warmest summer months when predation rates of smallmouth bass should be highest. We initiated a study in 2012 to re-examine smallmouth predation on subyearlings in Lower Granite Reservoir. Our objectives were to 1) describe the seasonal variation in smallmouth bass diets during the subyearling rearing and outmigration period, and 2) estimate the abundance of smallmouth and quantify their consumption of subyearlings.

STUDY AREA

We conducted our study from April to September, 2012 in the upper portion of Lower Granite Reservoir on the Snake River (Figure 1). We chose this portion of the reservoir because subyearling rearing is common there and it is also an area where some fish delay their seaward migration, potentially increasing their vulnerability to predation (Tiffan et al. 2010; Tiffan and Connor 2012). We divided the study area into three reaches. The first included the Snake River from its confluence with the Clearwater River (river kilometer [rkm] 224) to Asotin, Washington (rkm 234). We refer to this reach as the Snake River transition zone (SRTZ) because the river transitions from free-flowing at Asotin to being impounded at the confluence. The SRTZ reach is analogous to the Snake River Arm reach in Naughton et al. (2004). The second reach included the Clearwater River from its mouth (rkm 0) to the Clearwater Paper Mill (rkm 4.6). We refer to this reach as the Clearwater River transition zone (CRTZ) because the river transitions from free-flowing at the mill to being impounded at its mouth. The CRTZ reach is analogous to the Clearwater River Arm reach in Naughton et al. (2004). The third reach included the Snake River from the Port of Wilma (rkm 217) upstream to the confluence of the Snake and Clearwater rivers (rkm 224). We refer to this reach as the confluence (CON).

The duration of sampling in each reach varied and coincided with the presence of subyearlings. Subyearlings disperse into the SRTZ reach from upstream spawning areas and hatchery release sites and are present in this reach from April through late June (Connor et al. 2002). By July, water temperatures exceed 20°C and subyearlings have emigrated from this reach. Because of later emergence, subyearlings produced in the Clearwater River are present in the CRTZ reach from late May through early September (Tiffan et al. 2010). Summer releases of cool water from Dworshak Reservoir maintain water temperatures in this reach around 12°C. Subyearlings originating from the Snake and Clearwater rivers are present in the CON reach from April through early September (Tiffan et al. 2010; Tiffan and Connor 2012).

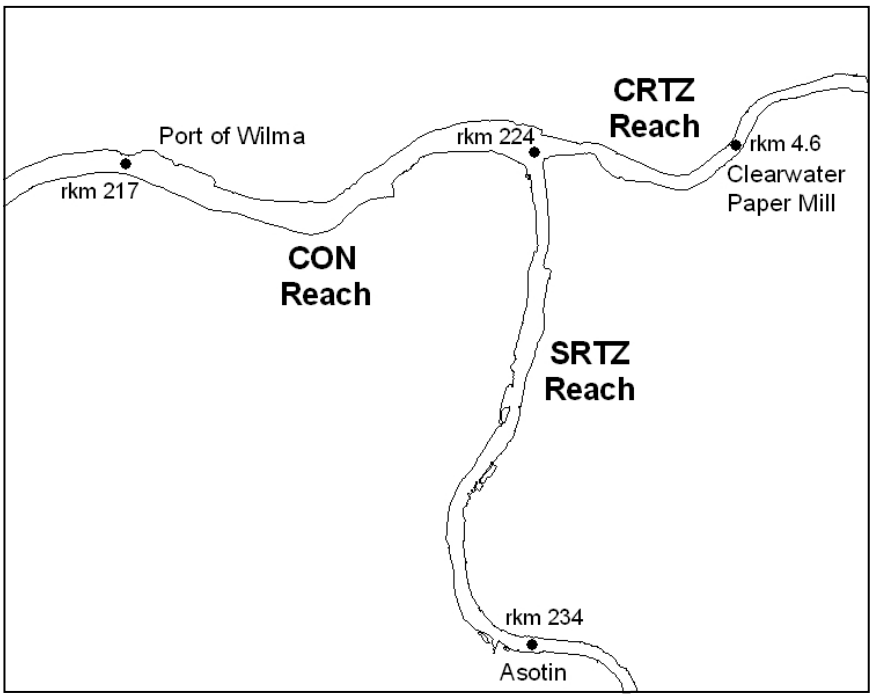

Figure 1. Map of the three study reaches of Lower Granite Reservoir that were sampled for smallmouth bass diet and consumption in 2012.

METHODS

Smallmouth bass collections

We collected smallmouth bass in each reach using angling or boat electrofishing. We initially used angling to minimize encounters with ESA-listed salmonids but later switched to electrofishing to increase catch of smallmouth bass following a period of poor angling success in the spring. ESA permit restrictions forced us to use angling again once water temperatures exceeded 18°C.

We divided each reach into 0.1-km sites that served as the basis for sampling. When we angled, we randomly selected 24-48 sites without replacement to sample within a given reach and week. These sites were typically sampled over a 2-4 d period. Angling was conducted tri-weekly from 23 April to 10 September by 2-5 people fishing out of 1-2 boats. Each site was fished during daytime by the crew of one boat for 20-30 min. Boats either remained stationary during sampling or drifted (no more than 100 m) along the shoreline when river velocities were high. The number of anglers and time angled were recorded for each site.

Nighttime electrofishing was conducted in the SRTZ and CON reaches on 4 June and 25 June and in the CRTZ reach tri-weekly from 4 June to 6 August. The cooler temperatures in the Clearwater River enabled us to expend more electrofishing effort in that river. The starting point of sampling transects were randomly selected from the pool of 0.1-km sites. The shorelines of transects were sampled in a downstream direction from transect starting points. Distances varied from 75 to 1540 m depending on river flow, shoreline habitat breaks, and obstructions. The time and distance sampled was recorded for each transect. Electrofishing output was 400 V DC with 60 pulses per second at 2-4amps. Smallmouth bass were collected by two dipnetters.

All captured smallmouth bass were placed in an aerated live well supplied with recirculating water and held no longer than 45-60 minutes for electrofishing events and 25-35 minutes for angling events before being processed and released. All fish greater than 150 mm total length (TL) were weighed, measured, and then tagged with a unique Floy tag.

At each sampling site, we collected stomach contents from up to 30 smallmouth bass using a modified non-lethal lavage (Seaburg 1957). The lavage instrument consisted of a ¼” diameter tube connected to a common garden spray nozzle that supplied filtered river water via a wash-down pump installed on the boat. Stomach contents were collected in a 425µm sieve and preserved in 90% ethanol.

Smallmouth bass abundance

We calculated catch-per-unit-effort (CPUE) for both angling and electrofishing to compare the efficiency of each method. CPUE for each reach and sampling week was calculated as the total number of smallmouth bass collected divided by the total sampling time (min).

Due to the relatively small number of tagged smallmouth bass recaptured in 2012, we used mark-recapture data collected during electrofishing in 2013 to estimate the abundance of fish >150 mm in the CON and SRTZ reaches. To test the assumption of similar abundances between years, we compared electrofishing CPUEs using analysis of variance (ANOVA). We used sampling occasions as a blocking variable, sampling reaches as treatments, and catch (fish/min) during electrofishing as the dependent variable. Electrofishing CPUEs within the SRTZ and CON were not significantly different between 2012 and 2013 (P= 0.284, F= 1.19, df= 1); therefore we assumed absolute abundances were also similar. To calculate absolute abundance, we divided each reach into two habitat types, riprap and non-riprap, and randomly selected two transect starting points per habitat type in each reach for a total of 8 transects (500-710 m). To minimize interference with other ongoing studies, we sampled riprap habitat on three occasions in 2013 (31 May, 4 June, and 25 June) and non-riprap habitat on two occasions (28 May and 30 May) in both reaches. All captured smallmouth bass >150 mm were tagged with a unique Floy tag and all recaptured fish were recorded. All fish were released in the center of transects and data for each reach were pooled by habitat type. We assumed no loss of tags during our study.

We used an open population mark-recapture model in program MARK (White and Burnham 1999) to estimate abundance of smallmouth bass in riprap habitat ($\widehat{N}_{riprap}$) for each reach (r) because we had multiple sampling occasions and the timespan between sampling occasions was 2 weeks. The POPAN parameterization of the Jolly-Seber model (Schwarz and Arnason 1996) was used to derive estimates of population abundance for each sampling occasion. A fully time-dependent model and models with constant survival and catchability (p) were fit and AIC was used to determine the best overall model. Due to confounding constraints on the first and last sampling occasion, the abundance estimate from the second sampling occasion was used. We estimated abundance ($\widehat{N}_{non-riprap}$) in the non-riprap habitat for each reach using a closed population model since we only had two sampling occasions and the duration between occasions was short (2 days). We calculated the Chapman estimator of the Petersen index (Seber 1982):

$$\widehat{N}_{non-riprap} = \frac{(n_1+1)(n_2+1)}{(R+1)} - 1 \,, \qquad (1)$$

where n_1 = number of bass caught and marked in the first sampling period, n_2 = number of bass caught in the second sampling period, and R = the number of recaptured bass in the second sampling period. We calculated variances of the estimates and calculated 95% confidence intervals (CI) using a normal approximation (Seber 1982). The abundance estimates (and CIs) for each habitat type per reach were then divided by the number of meters sampled (MS_h) to determine the number of fish per meter of shoreline. These estimates were then extrapolated to the number of total meters of shoreline habitat in each reach and summed to derive a total population estimate for each reach ($\widehat{N}_r$).

No mark-recapture sampling was conducted in the CRTZ reach because catch was very low. We derived an estimate of abundance from electrofishing catch data using the catch equation of Gulland (1983):

$$\text{fish/m} = q_r\left(\widehat{N}_{rh}/MS_{r,riprap}\right) \qquad (2)$$

where, q is catchability, r is reach, and MS_{riprap} is the total meters of shoreline sampled. We only considered riprap habitat because 88% of the shorelines of the CRTZ reach is lined with riprap. We assumed that q was constant and that the mean q from riprap sites in both reaches (SRTZ and CON) represented the q for the CRTZ reach. The constant catchability assumption was supported by the results from the model analysis (reported below), where the model with constant catchability (p) had the lowest AIC for both reaches. We solved for q for the SRTZ and CON reaches using the abundance estimates ($\widehat{N}_{CON,riprap}$ and $\widehat{N}_{SRTZ,riprap}$; with associated CIs) and the mean fish/m from electrofishing data collected from all transects within the reach for the time period sampled during the mark-recapture abundance estimates. We then calculated the mean q from both reaches and resolved equation 2 for $\widehat{N}_{CRTZ}$ using mean electrofishing fish/m data from the CRTZ.

Diet analysis

Smallmouth bass diet items were identified to the lowest practical taxon in the laboratory, and were placed into four groups: insects, crustaceans, fish, and other. All diet items were then enumerated, blotted for 30 s, and weighed (± 0.001 g). All insects were identified to Order and unidentifiable insect parts were not enumerated, but were weighed together as a group. Crustaceans were identified to order, and where possible to genus and species. All other prey that could not be assigned to a group were classified as “other” and often consisted of vegetation, rocks, and worms. Ingested fish were identified to lowest possible taxon (usually species) using diagnostic bones (i.e., dentary, cleithrum, opercle; Parrish 2006). Fish remains were soaked in warm water to soften muscle tissue which was then scraped from the bones. Bones were measured with an ocular micrometer mounted in a dissecting scope. We back-calculated fork length at ingestion for individual salmonid and other prey fish consumed using species-specific

bone-length regressions from the literature (Hansel et al. 1988) or to standard length (SL) with regressions developed by this study (Table 1). We used additional regressions to calculate FL from SL, nape to tail lengths, or dorsal standard lengths when necessary (Vigg et al. 1991; Parrish et al. 2006).

Fish remains that did not contain diagnostic bones were classified as "unidentified" and were weighed. When a sample only contained unidentifiable fish parts along with a diagnostic bone, we associated all weight to the species identified. We calculated the maximum relative length of prey fish consumed by smallmouth bass (prey fish FL/bass TL * 100) to determine size of prey vulnerability.

Lavage efficiency

We determined our lavage efficiency by comparing the amount of food obtained by stomach lavage with that remaining in the stomach after lavage. About 5 fish per sampling week in the CON reach were first lavaged then euthanized so their entire digestive tract could be removed. The stomach was then cut open and rinsed with alcohol into a 425µm mesh sieve. Any remaining food was stored in a separate container and preserved with 90% ethanol. Later, percent lavage efficiency was calculated by dividing the wet weight of lavaged food by the total amount of food obtained (lavaged + stomach dissection) and multiplying by 100.

Consumption

Preliminary analyses of two different size classes of smallmouth bass (150-250 mm, >250 mm) did not show any differences in diet or consumption, therefore we pooled all fish for final analyses. We estimated the daily consumption of juvenile salmonids and other prey fish by smallmouth bass (≥150 mm) in each reach. First, we calculated the weight at ingestion (*WI*) of each fish species consumed using their predicted or actual fork length measurement and regressions from Vigg et al. (1991). Next, we calculated meal weight (*MW*) using an equation similar to Vigg et al. (1991) for individual bass that had prey fish in their stomach where the digested weight was within 90% of *WI* (WI_{90}):

$$MW = \sum_{i=1}^{n} WI_{90} + D \ , \qquad (3)$$

where $n =$ the number of prey fish in the stomach contents of an individual bass (that were <90% digested) and *D* is the digested weight of all other prey items (mainly insects and crustaceans) in the sample. We also included all digested weights of prey fish that were not within 90% of original weight in the calculation of *D* because meal weight has an impact on evacuation rates (Rogers and Burley 1991). We used 90% digestion (after Rogers and Burley

Table 1. Linear regressions for predicting various measures of fish length based on measurements of diagnostic bones. Regression model take the form of $y=a+bx$, where y is the fish length (mm) to be estimated, a is the intercept, b is the slope, and x is the measure of the diagnostic bone (mm).

Fish length measure	*N*	*a*	*b*	r^2
		Cleithrum		
Fork length	31	1.983	7.347	0.96
Standard length	114	-0.408	6.984	0.95
		Dentary		
Fork length	30	14.823	7.819	0.83
Standard length	96	13.291	7.499	0.80
		Opercle		
Fork length	12	9.844	10.888	0.89
Standard length	29	10.485	9.884	0.80

1991) because indigestible parts could remain in the gut of fish for long periods of time. We calculated the evacuation time (h) to 90% digestion (ET_{90}) for each bass using a model developed for smallmouth bass by Rogers and Burley (1991) and re-solved by Fritts and Pearsons (2004):

$$ET_{90} = (24.542)(MW^{0.29}e^{-0.15T}W^{-0.23})(24), \tag{4}$$

where T is temperature (°C; measured at time of sample collection) and W is bass weight (g; also taken at time of sample collection). The consumption rate (C; the number of salmonids per bass per day) was then calculated following Ward et al. (1995):

$$C = n_{90}(24/ET_{90}), \tag{5}$$

where n_{90} is the number of salmonids within 90% digestion found in individual bass. The mean C per reach per sampling occasion (CM) was calculated and inputted into the Fritts and Pearsons (2004) equation to estimate the daily number of salmonids consumed (SC) within each reach (r) for each sampling occasion (o):

$$SC_{ro} = \widehat{N}_r \cdot BS \cdot \ CM_{ro}, \tag{6}$$

where BS is the number of bass stomachs (per reach per sampling occasion) that contained at least one salmonid within 90% digestion divided by the total number of stomachs examined (per reach per sampling occasion), including bass that had empty stomachs. The abundance estimates for each reach from 2013 ($\widehat{N}_r$) were used because no estimates were made in 2012. We also calculated 95% CIs for SC_{ro} by multiplying the 95% CIs of each corresponding abundance estimate by SC_{ro}. Finally, the total loss of salmonids (S_{tot}) per reach in 2012 was calculated as:

$$S_{tot} = \sum_{i=1}^{n} SC_{ro} \times I\ , \tag{7}$$

where I is the interval between sampling occasions (i.e., 21 d in 2012). We also calculated consumption rates (salmonids/bass/day) similar to other studies so we could compare results. We obtained this by dividing SC_{ro} by the abundance estimates for each reach and sampling occasion.

RESULTS

Abundance

Relative abundance.—We sampled a total of 207 randomly selected sites, of which 185 were angled and 22 were sampled with electrofishing (Table 2). A total of 3,869 minutes were

Table 2. Seasonal catch-per-unit-effort of smallmouth bass collected by angling and boat electrofishing in three reaches of Lower Granite Reservoir in 2012.

Week beginning	Method	Number of sites	Effort (minutes)	Number captured	Number per site	Number per minute
			Snake River Transition Zone			
23 Apr	Angling	17	357	2	0.12	0.01
14 May	Angling	11	220	12	1.09	0.05
4 Jun	Angling	14	268	10	0.71	0.04
	Electrofishing	5	48	55	11.00	1.14
25 Jun	Electrofishing	2	56	67	33.50	1.19
16 Jul	Angling	17	340	27	1.59	0.08
All	Angling	59	1,185	51	0.86	0.04
	Electrofishing	7	105	122	17.43	1.17
			Confluence			
23 Apr	Angling	15	327	1	0.07	0
14 May	Angling	12	246	7	0.58	0.03
4 Jun	Angling	8	160	16	2.00	0.10
	Electrofishing	4	62	67	16.75	1.08
25 Jun	Electrofishing	3	136	160	53.33	1.17
16 Jul	Angling	63	195	27	4.50	0.14
6 Aug	Angling	11	233	48	4.36	0.21
27 Aug	Angling	33	684	121	3.67	0.18
10 Sep	Angling	19	393	58	3.05	0.15
All	Angling	104	2,238	278	2.67	0.12
	Electrofishing	7	198	227	32.43	1.15
			Clearwater River Transition Zone			
23 Apr	Angling	13	266	0	0	0
14 May	Angling	9	180	0	0	0
4 Jun	Electrofishing	2	36	3	1.50	0.08
25 Jun	Electrofishing	2	76	9	4.50	0.12
16 Jul	Electrofishing	2	56	3	1.50	0.05
6 Aug	Electrofishing	2	62	2	1.00	0.03
All	Angling	22	446	0	0	0
	Electrofishing	8	230	17	0.57	0.07

expended angling to collect 329 bass and 533 minutes were expended electrofishing to collect 366 bass. The grand mean CPUE was 1.15 smallmouth bass/min of electrofishing and 0.1 fish/min of angling in the SRTZ and CON reaches (Table 2). CPUEs were greater using electrofishing than angling in all reaches and sampling weeks. The week of 4 June was the only week in which both sampling methods were used in both the SRTZ and CON reaches. Few smallmouth bass were collected by angling during the first three sampling occasions in the SRTZ and CON reaches. During the summer, angling catch rates increased dramatically in the CON reach but remained lower than electrofishing catch rates in June. Only 17 smallmouth bass were collected in the CRTZ in 2012 (Table 2).

Absolute abundance.—The open population models with constant catchability fit the riprap mark-recapture data best (lowest AIC) for both reaches. The highest estimated density of bass (≥150 mm) was in the CON riprap habitat (0.78 bass/m) and the lowest density was in the SRTZ riprap (0.21 fish/m). The closed Chapman model also estimated higher bass densities for non-riprap habitats in the CON reach (0.36 fish/m) compared to the SRTZ reach (0.21 fish/m). The total abundance estimate for smallmouth bass for the CON reach was 8,188 (95% CI = 1,295-25,328) and 4,348 (95% CI = 399-10,238) for the SRTZ reach (Table 3). Using the catch equation, with a mean calculated q of 4.65, the abundance estimate for the CRTZ was 498 bass (95% CI = 143-1,736) or 0.07 bass/m.

Diet

Gastric lavage removed 99.8% of stomach contents from smallmouth bass ranging from 151 to 316 mm TL. Of the 53 fish examined for lavage effectiveness, 49 had 100% of their stomach contents removed by lavage. Contents not removed by lavage comprised (by weight) 69% unidentifiable fish parts, 17% crayfish parts, and 14% unidentifiable material.

We captured 694 smallmouth bass for dietary analysis from April through September. Prey items were present in the stomachs of 603 smallmouth bass. Smallmouth bass were similar in size between the three study reaches and weekly mean sizes were typically between 200 and 300 mm TL (Table 4). Over all reaches and weeks, bass averaged 219 mm and about 150 g. The most common prey in smallmouth bass stomachs (based on frequency of occurrence) were insects, crayfish, salmonids, and non-salmonid fishes (Table 5). In the SRTZ reach, salmonids were found in 36% of stomachs in late June and other fish were present in one-third to one-half of stomachs during most sampling weeks. In the CON reach, salmonids were present in 22% of stomachs in early June, but few bass contained salmonids in other sampling weeks. Many bass contained insects and crayfish in the CON reach particularly later in the year when fish were less frequently found in stomachs (Table 5).

Table 3. Estimates of population abundance of smallmouth bass >150 mm TL in study reaches in Lower Granite Reservoir in 2012-13. Abbreviations are as follows: SRTZ = Snake River transition zone, CON = confluence, and CRTZ = Clearwater River transition zone.

Reach	Estimated abundance	95% confidence intervals
SRTZ	4,348	399-10,238
CON	8,188	1,295-25,328
CRTZ	498	143-1,736

Table 4. Seasonal lengths and weights of smallmouth bass collected for diet analysis from study reaches in Lower Granite Reservoir in 2012.

Week Beginning	*N*	Total Length (mm)			Weight (g)		
		Mean	SD	Range	Mean	SD	Range
Snake River Transition Zone							
23 Apr	2	261	62	217-305	245	177	120-370
14 May	12	244	63	174-380	235	202	60-750
4 Jun	65	217	39	150-305	156	89	40-410
25 Jun	67	225	44	150-398	162	120	30-840
16 Jul	27	201	39	152-282	102	58	40-230
All	173	220	44	150-398	156	113	30-840
Confluence							
23 Apr	1	285	--	285	330	--	--
14 May	7	271	48	176-317	246	130	60-420
4 Jun	82	223	47	150-383	154	121	30-750
25 Jun	159	202	36	150-364	105	78	30-630
16 Jul	27	223	38	165-320	158	91	40-490
6 Aug	48	225	38	161-316	149	81	40-380
27 Aug	121	228	45	153-430	161	106	40-870
10 Sep	52	223	41	154-319	154	76	40-390
All	497	218	43	150-430	141	99	30-870
Clearwater River Transition Zone							
4 Jun	3	308	88	249-409	383	449	90-900
25 Jun	9	196	49	150-304	106	94	30-330
16 Jul	3	220	32	200-257	130	78	80-220
6 Aug	2	180	42	150-210	80	42	40-120
All	17	218	66	150-409	156	206	30-900

Table 5. Seasonal variation in diet composition (percent frequency of occurrence of non-empty stomachs) of smallmouth bass in three reaches of Lower Granite Reservoir in 2012. *N*s indicate the number of smallmouth bass with empty and non-empty stomachs.

Week beginning	*N* (empty)	*N* (non-empty)	Prey			
			Insects	Crustaceans	Salmonid	Other fish
Snake River Transition Zone						
23 Apr	0	2	0	100	0	50
14 May	3	9	22	22	22	56
4 Jun	12	53	40	30	15	36
25 Jun	7	59	75	39	36	32
16 Jul	5	22	86	36	0	9
Confluence						
23 Apr	0	1	0	0	0	100
14 May	3	4	25	100	0	25
4 Jun	4	79	46	68	22	19
25 Jun	32	128	36	42	5	45
16 Jul	1	26	69	42	4	15
6 Aug	5	43	65	58	5	23
27 Aug	13	108	43	89	0	7
10 Sep	4	54	46	87	0	6
Clearwater River Transition Zone						
4 Jun	1	2	0	0	0	0
25 Jun	1	8	25	12	25	63
16 Jul	0	3	33	0	67	0
6 Aug	0	2	50	0	0	100

The dominant prey (by weight in the stomach) in the SRTZ reach from April through late June was salmonid and non-salmonid fishes (Figure 2). The smallest smallmouth bass that contained a salmonid in the SRTZ was 159 mm. During this time, the contribution of non-salmonid fishes (mainly sand rollers *Percopsis transmontana*) to bass diets decreased from 88 to 34% while the contribution of salmonids (mainly Chinook salmon) increased from 0 to 48% (Table 6). By mid-July, prey fish were nearly absent from smallmouth bass diets and insects and crustaceans composed 35 and 63% of the diet, respectively. In the CON reach, from May through mid-July, prey fish again were important to smallmouth bass diets (non-salmonids: 15-57%; salmonids: 0-53%; Figure 2, Table 6). Salmonids (mainly Chinook salmon) composed 53% of the smallmouth bass diet during the week of 4 June. In the CON reach, crustaceans (primarily crayfish) composed the majority of the diet during most sampling weeks, particularly later in the summer when few prey fish were consumed. In the CRTZ reach, prey fish were predominant in the diets of the few smallmouth bass collected (Figure 2, Table 6). After fish, crayfish was the next most important prey composing 33% of the diet during the week of 25 June.

Based on the size of ingested Chinook salmon, it is likely that most were fall Chinook salmon (Figure 3). Estimated mean size of Chinook salmon consumed in the SRTZ reach was 73 mm (SD = 16.6 mm, N = 34, range = 43-121 mm) which was similar to the mean size of 72 mm (SD = 11.1 mm, N = 37, range = 48-93 mm) for ingested Chinook salmon in the CON reach. Only 4 Chinook salmon were found in smallmouth bass stomachs in the CRTZ reach and their mean length was 73 mm (SD = 2.9 mm, range = 70-77 mm). The maximum relative length of salmonids consumed by bass (prey FL/bass TL*100) was 53.1% (mean= 29.6%) and for all prey fish was 63.4% (mean= 29.5%).

A total of 32 PIT tags were found in smallmouth bass stomachs (Table 7). Most of the tagged fish were initially released at Big Canyon Creek on the Clearwater River and at Couse Creek on the Snake River. Most of the PIT-tagged fish from the Clearwater River were consumed in the CRTZ reach whereas most of the tagged fish released in the Snake River were consumed in the SRTZ reach. A total of 7 smallmouth bass had multiple PIT tags in their stomachs which ranged from 2 to 5 tags (Table 7). Smallmouth bass that consumed PIT-tagged Chinook salmon ranged in size from 175 to 318 mm TL.

Other salmonids such as juvenile steelhead and mountain whitefish were also occasionally consumed (Table 8). Only 1 juvenile steelhead was consumed and was not used in consumption and loss estimates. The most common non-salmonid prey fishes were sand rollers followed by sculpin *Cottidae* spp., northern pikeminnow *Ptychocheilus oregonensis*, and chiselmouth *Acrocheilus alutaceus* (Table 8). Crayfish was the predominant crustacean consumed followed by the opossum shrimp *Neomysis mercedis*. The main insects consumed were dragonflies and mayflies (Table 8).

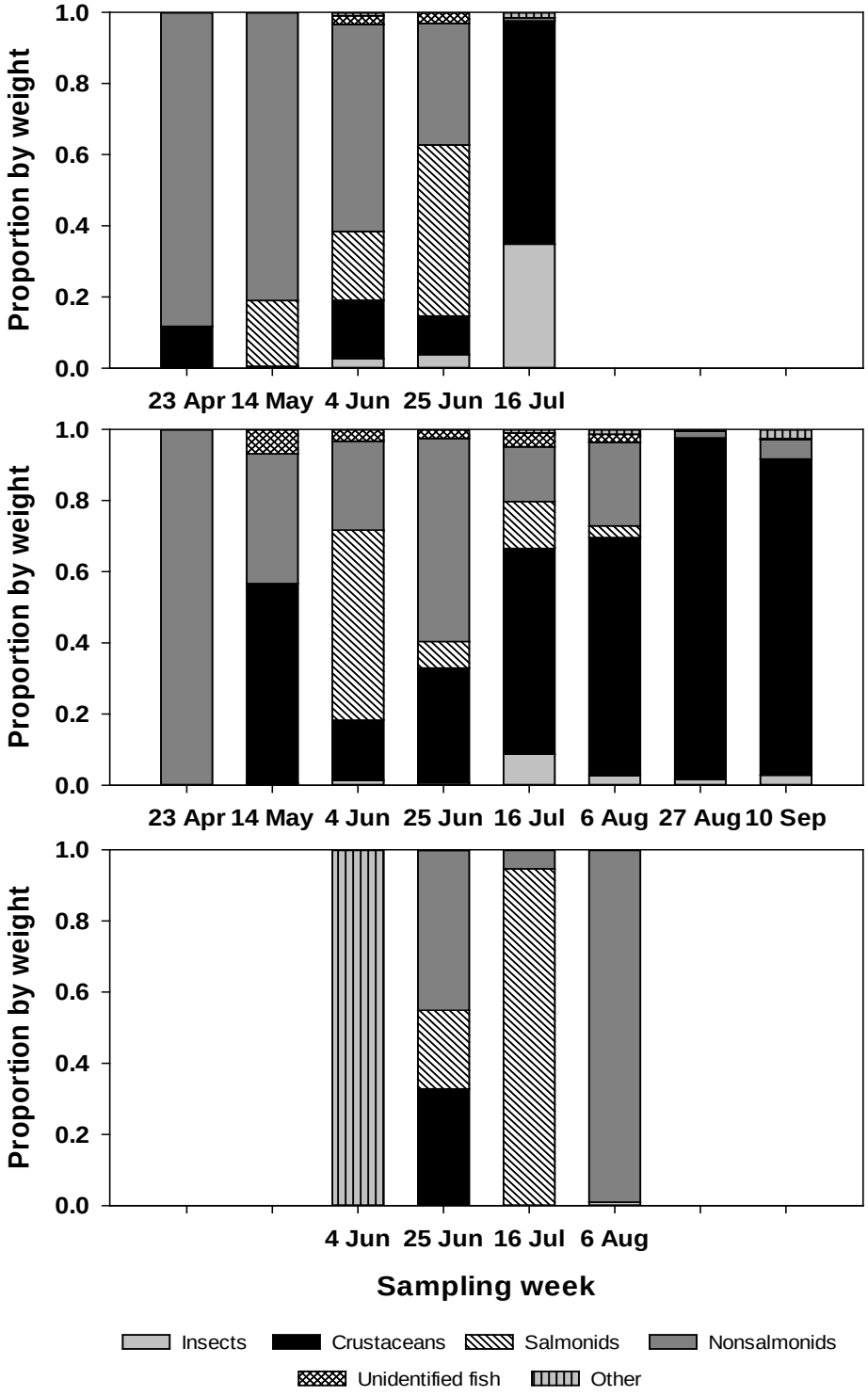

Figure 2. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in the Snake River Transition Zone reach (top panel), the Confluence reach (middle panel), and the Clearwater River Transition Zone reach (bottom panel) of Lower Granite Reservoir in 2012.

Table 6. Seasonal variation in diet composition (percent weight based on non-empty stomachs) of smallmouth bass in three reaches of Lower Granite Reservoir in 2012. *N*s indicate the number of smallmouth bass with empty and non-empty stomachs.

Week beginning	*N* (empty)	*N* (non-empty)	Prey					
			Insects	Crustaceans	Salmonid	Other fish	Unidentified fish	Other
Snake River Transition Zone								
23 Apr	0	2	0	12	0	88	0	0
14 May	3	9	0	0	19	81	0	0
4 Jun	12	53	3	16	19	58	3	1
25 Jun	7	59	4	11	48	34	3	0
16 Jul	5	22	35	63	0	1	0	1
Confluence								
23 Apr	0	1	0	0	0	100	0	0
14 May	3	4	1	56	0	36	7	0
4 Jun	4	79	1	17	54	25	3	0
25 Jun	32	128	1	32	7	57	3	0
16 Jul	1	26	9	58	13	15	4	1
6 Aug	5	43	3	67	3	24	2	1
27 Aug	13	108	2	96	0	2	0	0
10 Sep	4	54	3	89	0	5	0	3
Clearwater River Transition Zone								
4 Jun	1	2	0	0	0	0	0	100
25 Jun	1	8	0	33	22	45	0	0
16 Jul	0	3	0	0	95	5	0	0
6 Aug	0	2	1	0	0	99	0	0

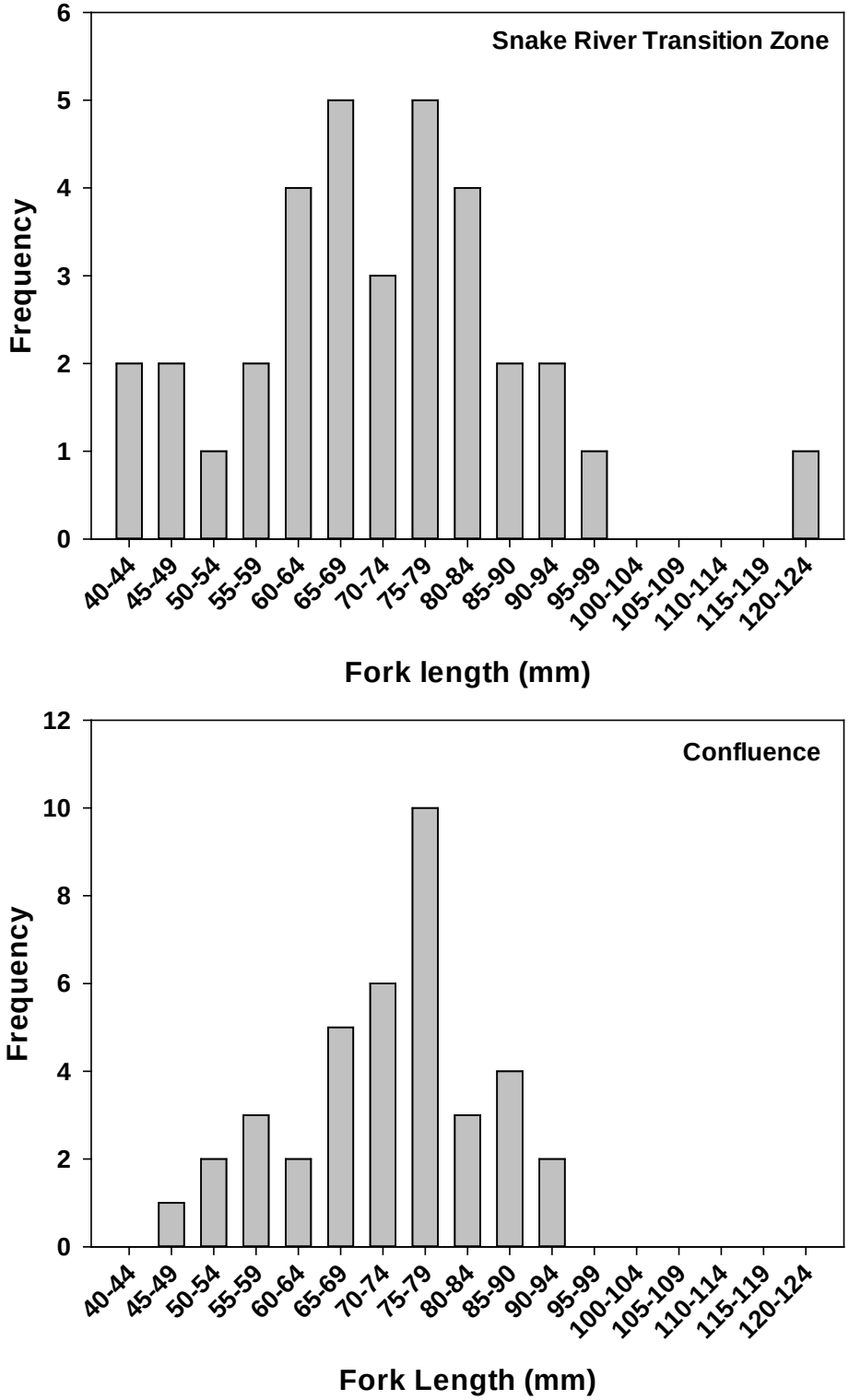

Figure 3. Size distribution of Chinook salmon consumed by smallmouth bass in the Snake River Transition Zone and Confluence reaches in Lower Granite Reservoir, 2012.

Table 7. Histories of PIT-tagged Chinook salmon consumed by smallmouth bass in Lower Granite Reservoir in 2012. Release site abbreviations: GRR = Grande Ronde River, BCCCAP = Big Canyon Creek Acclimation Pond on the Clearwater River, and SNAKE3 = Couse Creek on the Snake River. Recovery reach abbreviations: CON = confluence, SRTZ = Snake River transition zone, and CRTZ = Clearwater River transition zone. Tags highlighted in the same color were found in the same smallmouth bass. Non-highlighted tags were found in different bass. Chinook salmon and smallmouth bass (SMB) lengths are in millimeters.

Tag code	Release site	Release date	Run	Rear type	Release FL	Recovery date	Recovery reach	SMB TL
3D9.1C2DE00553	GRR	5/24/2012	Fall	Hatchery	85	5/31/12	CON	318
3D9.1C2DED4248	GRR	5/24/2012	Fall	Hatchery	81	5/31/12	CON	264
3D9.1C2DE0097F	BCCAP	6/18/2012	Fall	Hatchery	73	6/26/12	CRTZ	175
3D9.1C2DD0CC17	BCCAP	6/19/2012	Fall	Hatchery	69	6/27/12	CON	293
3D9.1C2DE6D2D5	BCCAP	6/20/2012	Fall	Hatchery	68	8/8/12	CON	304
3D9.1C2DEE444E	BCCAP	7/2/2012	Fall	Hatchery	74	7/16/12	CRTZ	257
3D9.1C2DEC8F93	BCCAP	7/5/2012	Fall	Hatchery	67	7/16/12	CRTZ	257
3D9.1C2DE6B4C5	BCCAP	7/6/2012	Fall	Hatchery	69	7/16/12	CRTZ	257
3D9.1C2DE6D28F	BCCAP	7/6/2012	Fall	Hatchery	73	7/9/12	CON	214
3D9.1C2DDE3FE8	SNAKE3	5/21/2012	Fall	Hatchery	70	6/6/12	SRTZ	266
3D9.1C2DDE59DF	SNAKE3	5/22/2012	Fall	Hatchery	69	6/6/12	SRTZ	266
3D9.1C2DECDB71	SNAKE3	5/21/2012	Fall	Hatchery	75	6/26/12	SRTZ	283
3D9.1C2DED393D	SNAKE3	5/21/2012	Fall	Hatchery	68	6/25/12	SRTZ	264
3D9.1C2DD15F90	SNAKE3	5/22/2012	Fall	Hatchery	73	6/25/12	SRTZ	190
3D9.1C2DDEB266	SNAKE3	5/22/2012	Fall	Hatchery	74	6/25/12	SRTZ	303
3D9.1C2DD1E593	SNAKE3	5/23/2012	Fall	Hatchery	84	6/25/12	SRTZ	256
3D9.1C2DDE6D6B	SNAKE3	5/23/2012	Fall	Hatchery	65	6/5/12	SRTZ	191
3D9.1C2DE606E1	SNAKE3	5/28/2012	Fall	Hatchery	68	6/5/12	SRTZ	191
3D9.1C2DD0666F	SNAKE3	5/30/2012	Fall	Hatchery	65	6/5/12	SRTZ	191
3D9.1C2DDE46C0	SNAKE3	5/30/2012	Fall	Hatchery	68	6/5/12	SRTZ	191
3D9.1C2DDEDA3D	SNAKE3	5/30/2012	Fall	Hatchery	66	6/5/12	SRTZ	191
3D9.1C2DDEB217	SNAKE3	5/23/2012	Fall	Hatchery	69	6/5/12	CON	262
3D9.1C2DE06AF5	SNAKE3	5/28/2012	Fall	Hatchery	71	6/6/12	SRTZ	194
3D9.1C2DE645E3	SNAKE3	5/28/2012	Fall	Hatchery	73	6/6/12	SRTZ	194
3D9.1C2DD28F3C	SNAKE3	5/29/2012	Fall	Hatchery	73	5/31/12	CON	289
3D9.1C2DDE4671	SNAKE3	5/29/2012	Fall	Hatchery	75	5/31/12	CON	289
3D9.1C2DDEC898	SNAKE3	5/29/2012	Fall	Hatchery	62	6/25/12	SRTZ	198
3D9.1C2DDDFA98	SNAKE3	5/30/2012	Fall	Hatchery	65	6/4/12	SRTZ	227
3D9.1C2DD281D8	SNAKE3	5/31/2012	Fall	Hatchery	79	6/4/12	SRTZ	227
3D9.1C2DD259EA	SNAKE3	6/5/2012	Fall	Hatchery	74	6/7/12	CON	236
3D9.1C2DD27B7F	SNAKE3	6/6/2012	Fall	Hatchery	72	6/7/12	CON	236
3D9.1C2DD22963	SNAKE3	6/6/2012	Fall	Hatchery	71	6/25/12	SRTZ	205

Table 8. Summary of prey items obtained from all smallmouth bass stomachs sampled in Lower Granite Reservoir in 2012.

Category	Taxon	Total mass (g)	Percent
Insects	Unidentifiable parts	5.9	32
	Odonata	4.4	23
	Ephemeroptera	3.5	19
	Plecoptera	2.0	11
	Diptera	1.4	7
	Trichoptera	0.6	3
	Orthoptera	0.3	2
	Hemiptera	0.2	1
	Hymenoptera	0.2	<1
	Lepidoptera	0.1	<1
	Coleoptera	<0.1	<1
	Homoptera	<0.1	<1
	Dermaptera	<0.1	<1
Crustaceans	Crayfish	328.5	93
	Neomysis mercedis	24.7	7
	Corophium spp.	0.1	--
	Amphipoda	<0.1	--
	Isopoda	<0.1	--
	Siberian prawn	<0.1	--
Salmonids	Chinook salmon	172.4	87
	Steelhead	13.4	7
	Unknown	10.0	5
	Mountain whitefish	1.4	1
Other fish	Sand roller	246.6	81
	Sculpin spp.	22.3	7
	Northern pikeminnow	16.2	5
	Chiselmouth	15.2	5
	Sucker spp.	1.2	<1
	Black crappie	0.8	<1
	Smallmouth bass	0.2	<1
	Catfish spp.	0.2	<1
	Bluegill	0.1	<1
	Peamouth	<0.1	<1
Unidentifiable fish	Parts	19.1	91
	Fry	1.8	9
Other	Rock	1.5	39
	Unknown	0.9	24
	Vegetation	0.8	22
	Eggs	0.5	13
	Centipede	<0.1	1
	Arachnida	<0.1	<1
	Oligochaeta	<0.1	<1

Consumption and loss

Salmonids.—Total loss of salmonids to smallmouth bass predation within our study area in 2012 was estimated to be 109,887 individuals (95% CI = 15,285-311,127; Table 9). Coincident to the abundance estimates, the highest total consumption occurred in the CON reach (62,894 salmonids) followed by the SRTZ reach (41,753 salmonids), but the highest consumption rates (salmonids/bass/day) occurred in the CRTZ reach, followed by the SRTZ reach. Total salmonid loss in the CRTZ reach was estimated at 5,240 fish, however data should be interpreted with caution as sample sizes were very low (only 17 samples examined). Consumption was first observed in the SRTZ reach during the week of 14 May, when 3,667 salmonids were consumed (0.04 salmonids/bass/day), and this gradually increased until the week of 25 June when a peak of 29,434 fish was consumed (0.32 salmonids/bass/day). Consumption was not documented in the SRTZ reach during the week of 16 July and the reach was not sampled during the week of 6 August because water temperatures exceeded 21°C and most subyearlings had emigrated. Consumption in the CON reach was observed from the week of 4 June through the week of 6 August. The highest estimated consumption of salmonids in the CON reach occurred during the week of 4 June (34,515 salmonids; 0.20 salmonids/bass/day). Consumption in the CRTZ was only documented during the weeks of 25 June and 16 July.

Non-salmonids.—Total loss of sand rollers to smallmouth bass predation during the study was estimated at 369,637 fish (95% CI = 52,406-1,078,062), and loss of sculpins was 84,899 fish (95% CI = 13,762-261,175; Table 9). Predation on sand rollers was only documented in the SRTZ and CON reaches while predation on sculpin occurred in all three reaches. Consumption of sand rollers occurred during most sampling occasions in the CON reach except during the weeks of 16 July, 6 August, and 10 September when sculpin consumption increased. It should be noted that sand rollers were present in 16 July stomach samples but in every instance were >90% digested so they were not included in consumption estimates. In the SRTZ, consumption of sand rollers was highest in the weeks of 23 April and 14 May, and then decreased while salmonid consumption increased. The highest weekly consumption of sculpin occurred in the CON reach (29,168 fish) during the week of 16 July and was documented in all weeks except during the weeks of 23 April and 14 May.

The predicted length at ingestion of sand rollers ranged from 21 mm to 99 mm (mean FL = 69 mm, SD = 21.0) while the length of sculpin ranged from 48 mm to 100 mm (mean FL= 60mm, SD = 17.3). The size distribution of sand rollers consumed shifted from larger fish (FL range = 43 mm to 99 mm) in the first four sampling occasions (23 April to 25 June) to mainly smaller fish (FL range = 21 mm to 77 mm) later in the summer (16 July to 27 August; Figure 4). The estimate of 43,599 sand rollers consumed in the week of 27 August was largely influenced by one individual bass with 10 small (FL range 21mm to 29mm) individuals in its stomach. No patterns in size distribution of sculpin were documented.

Table 9. Estimated losses (95% CI) of juvenile salmonids, sand rollers, and sculpin spp. in study reaches in Lower Granite Reservoir in 2012.

Week	Salmonids	Sand rollers	Sculpin spp.
		Snake River Transition Zone	
23 Apr	0	29,216 (2,620-68,797)	0
14 May	3,667 (337-8,635)	30,357 (2,722-71,484)	0
4 Jun	8,652 (794-20,374)	12,234 (1,097-28,809)	0
25 Jun	29,434 (2,702-69,310)	16,638 (1,492-39,180)	4,579 (420-10,782)
16 Jul	0	0	0
Total	41,753 (3,833-98,319)	88,445 (7,931-208,270)	4,579 (420-10,782)
		Confluence	
23 Apr	0	171,953 (27,197-531,890)	0
14 May	0	12,774 (2,020-39,512)	0
4 Jun	34,515 (5,459-106,762)	9,426 (1,491-29,158)	4,226 (668-13,073)
25 Jun	5,288 (836-16,355)	43,440 (6,871-134,369)	2,257 (357-6,981)
16 Jul	13,884 (2,196-42,945)	0	29,168 (4,613-90,224)
6 Aug	9,207 (1,456-28,478)	0	17,339 (2,742-53,632)
27 Aug	0	43,599 (6,896-134,863)	2,970 (470-9,187)
10 Sep	0	0	19,410 (3,070-60,040)
Total	62,894 (9,947-194,540)	281,192 (44,475-869,792)	75,370 (11,920-233,137)
		Clearwater River Transition Zone	
4 Jun	0	0	0
25 Jun	604 (174-2,106)	0	3,068 (881-10,694)
16 Jul	4,636 (1,331-16,162)	0	0
6 Aug	0	0	1,882 (541-6,562)
Total	5,240 (1,505-18,268)	0	4,950 (1,422-17,256)
		All Reaches	
Total	109,887 (15,285-311,127)	369,637 (52,406-1,078,062)	84,899 (13,762-261,175)

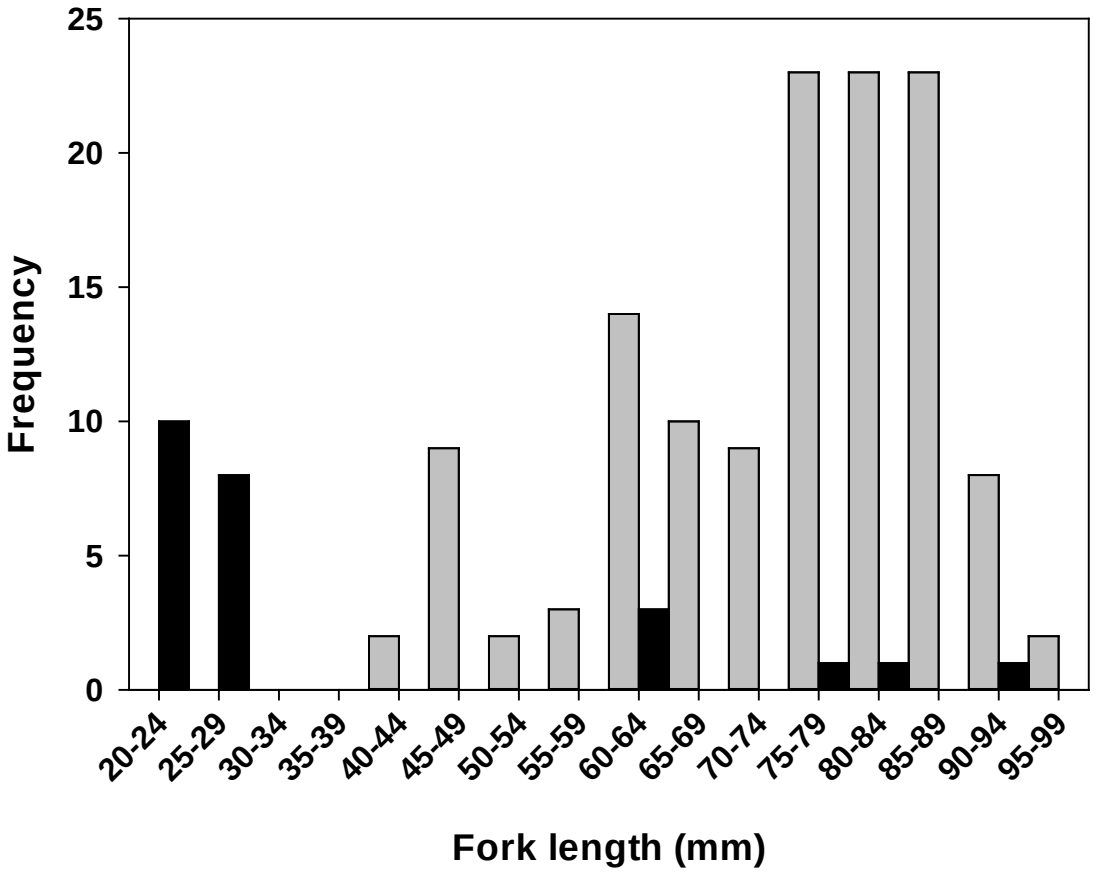

Figure 4. Length frequency of sand rollers consumed by smallmouth bass in Lower Granite Reservoir from 23 April to 25 June (gray bars) and from 16 July to 27 August (black bars), 2012.

DISCUSSION

Consumption of salmonids

Juvenile salmonids were a major component of smallmouth bass diets at times in 2012, with the majority likely being subyearling fall Chinook salmon. Salmonids composed up to 54% of the diet by weight in the CON reach and 48% in the SRTZ reach during June when peak consumption occurred. Frequencies of occurrence were also high, with up to 36% of the bass sampled in June containing salmonids in the SRTZ. Excluding the CRTZ because of low sample sizes, the highest consumption rate (0.32 salmonids/bass/day) occurred in the SRTZ reach during the week of 25 June.

These estimates are much higher than those reported by Naughton et al. (2004), who estimated that only 10% of smallmouth bass diets were composed of salmonids in the Snake River arm in 1997. Our estimates are more consistent with Tabor et al. (1993) who found that salmonids composed up to 59% of the diet of smallmouth bass in the upper end of McNary Reservoir in the Columbia River. In terms of total loss of salmonids in 2012, we estimated 109,887 fish were consumed within our reaches. This estimate was the second highest of all prey fish found in stomachs. In the SRTZ reach alone, we estimated that 41,753 salmonids were consumed, a 6-fold increase from that estimated in 1997 by Naughton et al. (2004). Conversely, the abundance estimates of smallmouth bass (>150 mm) in the SRTZ reach (418 fish/rkm) and CRTZ reach (108 fish/rkm) were much lower than reported by Naughton et al. (2004), who reported 3,820 smallmouth bass (>175 mm TL) in the first 6 rkms of the CRTZ (637 fish/rkm) and 11,877 bass in the first 12 rkms of the SRTZ reach (990 fish/rkm). About 20% of our catch throughout the study was composed of fish between 150 to 175 mm TL which would make our estimates even lower. The increase in total salmonid loss, but decrease in abundance, indicates that the increase is due to a large increase in daily consumption rates (prey/bass/day).

There are several reasons for the increase in daily consumption rates of subyearlings by smallmouth bass that we observed. First, the run size of subyearlings has increased dramatically since 1996. Hatchery supplementation has directly increased the population via annual releases of juveniles and indirectly as a result of increased production from natural spawners (Connor et al. 2013). Naughton et al. (2004) concluded that the increase in consumption from 1996 to 1997 was due, in part, to the increase in the number of subyearlings that passed Lower Granite Dam during outmigration (from 1 April to 1 October; 18,066 fish in 1996, 97,985 fish in 1997). In 2012, 1,069,525 subyearlings were estimated to have passed the dam (DART 2014). Second, river flows were lower in 2012 than in 1996-1997, especially in June when peak consumption occurred (Figure 5). Mean daily discharge in June 2012 was 47.8 kcfs, less than one-half of that in June 1997 (117.8 kcfs). The lower river flows, and less turbid water usually associated with low flows, may provide higher foraging efficiency for smallmouth bass (Sweka and Hartman 2003) and also affect prey selectivity (Carter et al. 2010). Lower velocities in the

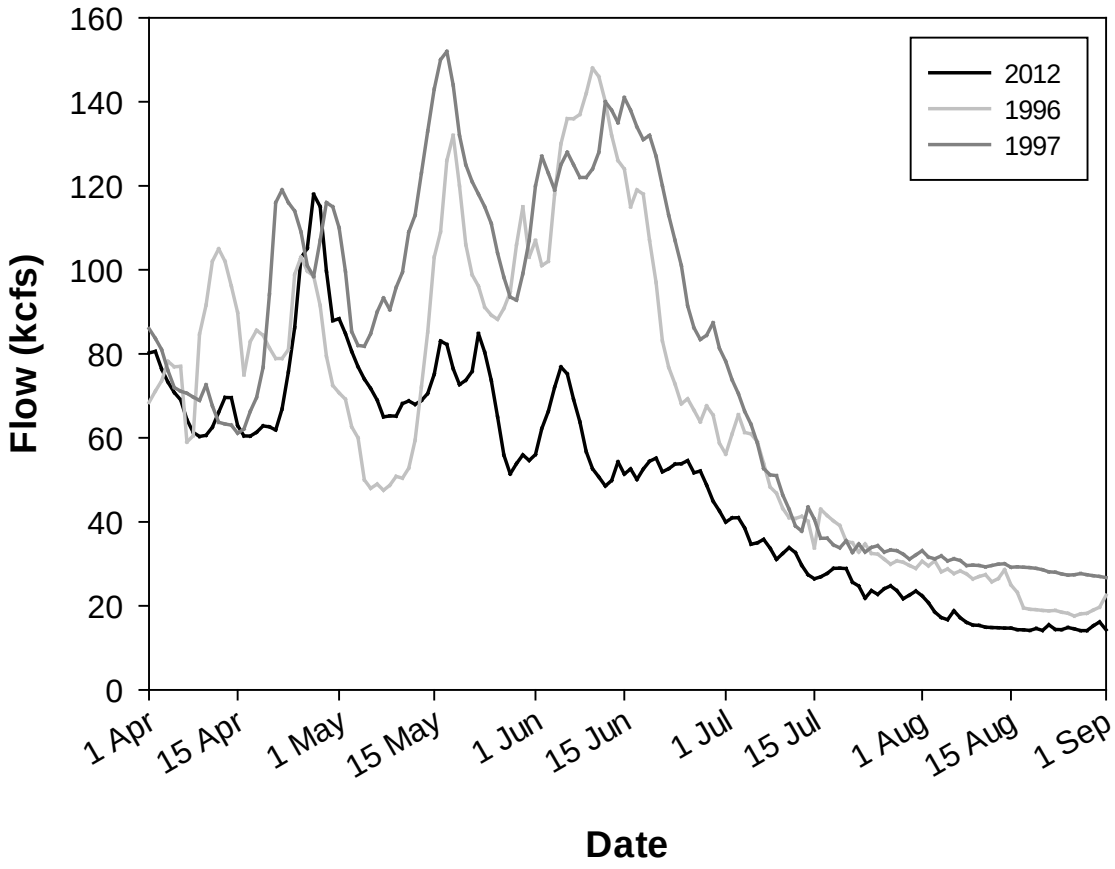

Figure 5. Snake River flows measured at the Anatone gage for 1996, 1997, and 2012.

transition areas between the free-flowing river and reservoir of the Snake River have also been linked to decreased migratory cues for subyearlings, which may influence migration delay and increase subyearling susceptibility to predation within these areas (Tiffan et al. 2009). Although higher water temperatures, which are usually associated with lower river flows, can increase evacuation rates of smallmouth bass and subsequently increase consumption (Rogers and Burley 1991), we did not find temperature differences between the years. Lower flows in 2012 were also evident during May-June in the CRTZ reach; however abundances and CPUE from electrofishing were low, making it difficult to assess the current impact predation has on subyearlings within this reach.

Temperatures and use of angling early in the season affected our catch of smallmouth bass and our ability to accurately assess predation on subyearlings. Water temperatures were cool in April and May and our catches of smallmouth bass using angling were relatively low which affected our consumption estimates. We estimated 3,667 salmonids were consumed in the SRTZ reach during the week of 14 May; however this was based on a sample of only 12 bass stomachs. Poor angling success during early sampling occasions could be the result of several factors: (1) lower water temperatures may limit feeding activity of smallmouth bass, (2) feeding efficiency may be low because of high water flows and turbidity, (3) bass may not have been recruited to our angling gear, or (4) bass may not have been present in the habitats we sampled during those occasions. Temperatures collected at the time of sampling were around 12.8°C in the SRTZ reach and 12.2°C in the CON reach during the week of 23 April and around 13.8°C and 11.9 °C in these reaches during the week of 14 May. This is near the lower range of preferred water temperatures for smallmouth bass (Ferguson 1958, Barans and Tubb 1973). Temperatures in the CRTZ during these weeks were 8.0°C and 10.0 °C, below the preferred temperature.

We initially used angling to minimize capture impacts to juvenile salmon as angling specifically targeted smallmouth bass. We switched to electrofishing to increase our catch of smallmouth bass in late May and June but had to switch back to angling in late June when water temperatures exceeded 18°C. Angling was not effective when water temperatures were cool and turbidity was high. Later in the summer in the CON reach, angling was more effective but CPUEs were still lower than that of electrofishing. We acknowledge that angling targets actively feeding fish and this may biased consumption results upward; however, this sampling collected fish from a broader range of water depths that may have been more representative of the population at large. Also, most fish did not contain fish in their stomachs which indicated that angling did not just catch bass that were feeding on fish. Although the use of multiple gear types may have biased consumption estimates, we believe that differences in our sampling gears may be minimal and consumption estimates may be conservative because both gear types are active and we were able to collect bass as small as 150 mm with both gears. Beamesderfer and Rieman (1988) studied size selectivity of smallmouth bass between gear types in John Day Reservoir in

the Columbia River and found that angling selected towards larger individuals but captured bass as small as 150 mm, whereas electrofishing caught bass over a broader size range. We did not attempt to determine if there were dietary differences between bass captured by angling and electrofishing in our study because we were unable to control for interactions related to sampling period and habitat type. However, we do acknowledge that this assessment would be worthwhile and would likely provide additional insights into results collected during our study.

Variation in smallmouth bass abundance and consumption between study reaches was likely influenced by subyearling presence and habitat differences. Subyearlings are present first in the SRTZ reach as they disperse downstream from release and production areas in Hells Canyon. By the end of June most subyearlings have left this reach, however, because water temperatures typically exceed 22°C in the reach (DART 2014). Smallmouth bass abundance may have been lower in the SRTZ reach than in the CON reach due to higher velocities in the former (Tiffan et al. 2009). However, the concentration of subyearlings in this reach may increase their vulnerability to predation. By July and August, consumption of subyearlings in the CON reach may be lower because there are fewer subyearlings in the system as many fish from the Snake River have emigrated seaward by this time. Most subyearlings in this reach during this time probably originate from the Clearwater River, where emergence is later than in the Snake River. The CON reach had a higher bass abundance and a higher total salmonid loss even though consumption rates were lower overall. A main difference between the reaches was the difference in abundance of bass between the habitat types. The CON reach had much higher densities of bass in riprap habitat (0.78 fish/m) than in non-riprap habitat (0.36 fish/m) whereas the SRTZ reach had similar densities in these habitats (riprap: 0.21 fish/m, non-riprap: 0.21). The different habitat preferences of subyearlings and smallmouth bass may ultimately affect predation loss estimates. Although smallmouth bass densities in riprap habitat were much higher in the CON reach, subyearlings do not prefer this habitat (Garland et al. 2002). Total loss of salmonids within the CON reach could potentially be much lower if a majority of the consumption is occurring in non-riprap habitat. Future research should estimate consumption in these two habitat types given the impact the overall abundance estimates have on the total loss of salmonid calculations.

The low abundance of smallmouth bass in the CRTZ precluded reliable estimation of salmonid consumption in the reach. Our estimates of smallmouth bass abundance in the CRTZ reach were much lower than those reported by Naughton et al. (2004). The reason for this is unknown, but may be related to cool water temperatures provided by summer flow augmentation from Dworshak Reservoir. Anecdotal evidence suggests that a large number of subyearlings are present in the CRTZ reach during July and August, and these fish may be vulnerable to predation if smallmouth bass abundance increases in this reach.

We found that subyearling likely comprised the majority of the salmonids that were consumed by smallmouth bass. Subyearlings may be more vulnerable to predation in transitional and reservoir habitats because of their small size. We found that smallmouth bass as small as 160 mm TL contained subyearlings as large as 74 mm FL, which suggests that even small bass may pose a predation threat. Fritts and Pearsons (2006) found that 150-199 mm smallmouth bass accounted for 42.9% of the salmonid consumption in the Yakima River, and that decreasing relative length of salmonid prey increased with bass size. In our study, the maximum relative length of salmonids (salmonid FL/bass TL * 100) consumed by 150-199 mm smallmouth bass was 47.2%, suggesting that subyearling susceptibility to predation based on size alone is very high because of the high abundance of small-sized (<200 mm) bass in Lower Granite Reservoir. Conversely, Anglea (1997) found that smallmouth bass ranging in size from 250-389 mm had the highest salmonid consumption in Lower Granite Reservoir in 1994-1995.

The most influential component of our total salmonids loss estimate was the abundance estimate of smallmouth bass. For example, in the SRTZ reach we observed that decreasing the bass abundance by 1,000 fish (4,348 to 3,348) resulted in a decreased consumption estimate of almost 10,000 juvenile salmonids (41,753 to 32,154). We believe that our estimates are conservative because studies conducted in the Columbia River have shown that smallmouth bass abundance estimates are negatively biased (Beamesderfer and Rieman 1998). We used the POPAN parameterization of the Jolly-Seber model for abundance estimates instead of the Jolly-Seber Lambda model that Naughton et al. (2004) used because we were unable to get model convergence in program MARK. It is common for the MARK program to have difficulty converging on parameter estimates because of the penalty constraints necessary to keep parameters consistent with each other. We acknowledge that the catchability variable (p) for POPAN is fundamentally different than q, but is at least suggestive that using q may be feasible and meet some of the catch model assumptions. We also acknowledge that estimating q at lower abundance levels would be beneficial and improve the abundance estimate for the CRTZ.

Laboratory factors may also have influenced our estimates of consumption. First, all samples were stored in 90% ethanol which may have affected the length and weight measurements of digested fish. Whole sockeye salmon *O. nerka* fry preserved in 95% ethanol lost 19.7% of mean fresh weight after 16 days (Shields and Carlson 1996). Weight loss due to ethanol preservation would increase the percent digested calculation and lead to underestimates of consumption because fish would not be included if they were now more than 90% digested. Second, the presences of unidentifiable fish parts in samples presented an analytical complication. They often comprised a large portion of percent diet by weight at times, and may have amplified the conservative estimates of consumption. Many of the unidentifiable parts that we encountered were digested fish without heads. This limited our ability to identify diet items because the diagnostic bones are located in the fish's head. In samples containing fish without heads or only bones, the main diagnostic bone present was usually a sculpin cleithrum. There

were only a few instances where unidentifiable bones from salmonids were present under these circumstances. This would imply that a greater portion of the unidentifiable fish parts were likely salmonids, or at the least not from sculpin.

Consumption of non-salmonids

We found that smallmouth bass consumed large numbers of non-salmonids. Whereas salmonids consumption rates were periodically high, non-salmonid consumption rates were routinely high. For example, sand rollers were the predominant non-salmonid species that was consumed (by weight) in the SRTZ and CON reaches. For context, smallmouth bass consumed more than twice as many sand rollers as salmonids. Sculpin spp. was the second most consumed non-salmonid, and high consumption occurred when sand roller consumption decreased in July and August. It should be noted that the estimates of consumption of sand rollers and sculpin are likely biased because we used the evacuation rate model (Rogers and Burley 1991) that was developed for salmonids. With the overall high frequency of occurrence, percent weight in diet, and high consumption rates it is likely they are a preferred prey species for bass and are highly susceptible to predation except in mid-summer. The shift in size distribution of sand rollers present in bass stomachs indicated that spawning potentially occurred during the summer months or some ontogenetic habitat shift occurred. The prevalence of small (~25 mm) sand rollers in the 27 August samples indicate that spawning may have occurred during late July-early August and post-spawn adults dispersed to different habitats, or bass showed selection for juveniles. A July spawn timing would be consistent with populations in the central Columbia River (Gray and Dauble 1979). With the high consumption estimates of sand rollers in 2012, it is possible that annual sand roller abundance fluctuations may even impact predation on salmonids.

In conclusion, smallmouth bass predation on salmonids during our study was highest during June, when conditions were conducive for efficient feeding and temporal and spatial overlap of bass and salmonids occurred. We believe our estimates of consumption and abundance are conservative and further research should be directed towards determining salmonid loss across a range of river flows and water temperatures. In 2012, June flows were lower than they were in 1996 and 1997, when the last predation study was conducted in this area. The increase in subyearling abundance since ESA listing has been identified as a factor contributing to density-dependent changes in growth and timing of reservoir entry (Connor et al. 2013). Early reservoir entry and smaller size may put subyearlings at a higher risk if smallmouth bass abundance and consumption are higher in the reservoir than in the river. Further research should be conducted to estimate consumption in the riverine sections as well as further downstream in Lower Granite Reservoir where Naughton et al. (2004) found their highest consumption.

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CHAPTER TWO

Predation Susceptibility of Juvenile Fall Chinook Salmon Exposed to Sudden Temperature Changes and Slightly Supersaturated Dissolved Gas

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ABSTRACT

High mortality of hatchery-reared juvenile fall Chinook salmon emigrating from the Clearwater River was previously measured at the confluence of the Snake and Clearwater rivers; however, the causative mechanism of mortality is unknown. To elucidate potential mechanisms, the predation susceptibility of juvenile fall Chinook salmon was assessed during simulated passage from the Clearwater River and through the confluence of the Clearwater and Snake rivers, with and without cool water provided by flow augmentation. Emigrant-sized juvenile salmon were acclimated to temperatures typical of the Clearwater River when cool water augmentation is discharged from Dworshak Dam (10°C to 17°C) and during temperatures that would be present without augmentation (17°C to 24°C). They were then exposed to smallmouth bass within temperatures typical of the Snake River in summer (17°C to 24°C). Slightly supersaturated total dissolved gas concentrations of 105% were also simulated to more closely approximate gas conditions of both rivers in summer. Predation susceptibility of juvenile salmon acclimated at 10°C or 17°C and exposed to predators at 17°C did not differ. However, for salmon exposed to predators at 24°C, predation susceptibility was arguably higher for juvenile salmon acclimated at 10°C (a 14°C increase) than for salmon acclimated at 17°C or 24°C (7°C and 0°C increases, respectively). These results indicate that predation susceptibility may be higher when a relatively large temperature difference exists between the Clearwater and Snake rivers; that is, when cool water flow augmentation occurs in summer. However, further research is needed to determine if the mortality near the confluence measured in previous studies is related to cool water augmentation and, ultimately, whether or not this mortality has a population-level effect on natural Snake River fall Chinook salmon.

INTRODUCTION

The consequences of anthropogenic water management of rivers include changes in physical habitat that may increase the invasion success of introduced species (Bunn and Arthington 2002). Artificial management of river flows can alter water temperature and modify total dissolved gas (TDG) concentrations, both of which are significant controls of aquatic system health (Johnson and Rinne 1982). Water temperature can be increased by thermal effluents released into rivers from electricity-generating facilities (Ebel et al. 1971; Coutant 1973; Prats et al. 2010) or from warm, eplimnetic discharge from temperature-stratified reservoirs; or cooled by hypolimnetic discharge from temperature-stratified reservoirs (Johnson and Rinne 1982; Olden and Naiman 2010; Prats et al. 2010). Changes in river water temperature due to water management can also create gas-supersaturated conditions when waters of different temperatures are mixed (Colt 1984). Consequently, changes in river conditions may lead to improvement of the habitat for non-native fishes, which may then increase predation on native fishes such as salmonids in the Pacific Northwest, U.S.A. (Carey et al. 2011), or relatedly, may affect the behavior of native salmonids (Bellgraph et al. 2010), which may make them more susceptible to predation by non-native species.

In the Snake River basin of the northwestern United States, hypolimnetic water is released from Dworshak Dam on the north fork of the Clearwater River to cool the four reservoirs on the lower Snake River (Figure 1) during late summer with the goal of improving juvenile salmon emigration survival (Connor et al. 1998; Connor et al. 2003). Although this water release, often called 'flow augmentation', has been shown to speed the emigration of juvenile salmon (Connor et al. 2003) and increase juvenile salmon survival while emigrating through the reservoirs (Connor et al. 1998), the introduction of unnaturally cooled Clearwater River water into warm Snake River water can result in a 15°C temperature change in late summer where the two rivers meet, potentially impacting survival of juvenile salmonids migrating through the confluence (Tiffan et al. 2009a, 2009b, 2010). Without flow augmentation from Dworshak Dam, this temperature difference would not exist or would be more gradual. Recent studies have measured very low survival probabilities of hatchery juvenile fall Chinook salmon *Oncorhynchus tshawytscha* emigrating through a 13-km reach from the lower Clearwater River and into the Snake River when a temperature difference existed between the rivers (~0.30–0.60 survival in 2007, Tiffan et al. 2009a; 0.30–0.35 survival in 2009, Tiffan et al. 2010). Previously tested hypotheses to determine the potential explanation for this low survival indicated that it is likely not caused solely by temperature shock (Bellgraph et al. 2010) or by gas bubble disease incurred during confluence passage (Tiffan et al. 2012). However, it is possible that the combination of sub-lethal stress incurred by juvenile salmon during the temperature transition and potential additional stress from naturally occurring, slightly supersaturated dissolved gas concentrations of both rivers (diel fluctuations ~102–108%; Tiffan et al. 2012) may make juvenile salmon more susceptible to predation than under natural thermal conditions (i.e., no flow augmentation). Additionally, confluence passage may expose juvenile salmon to

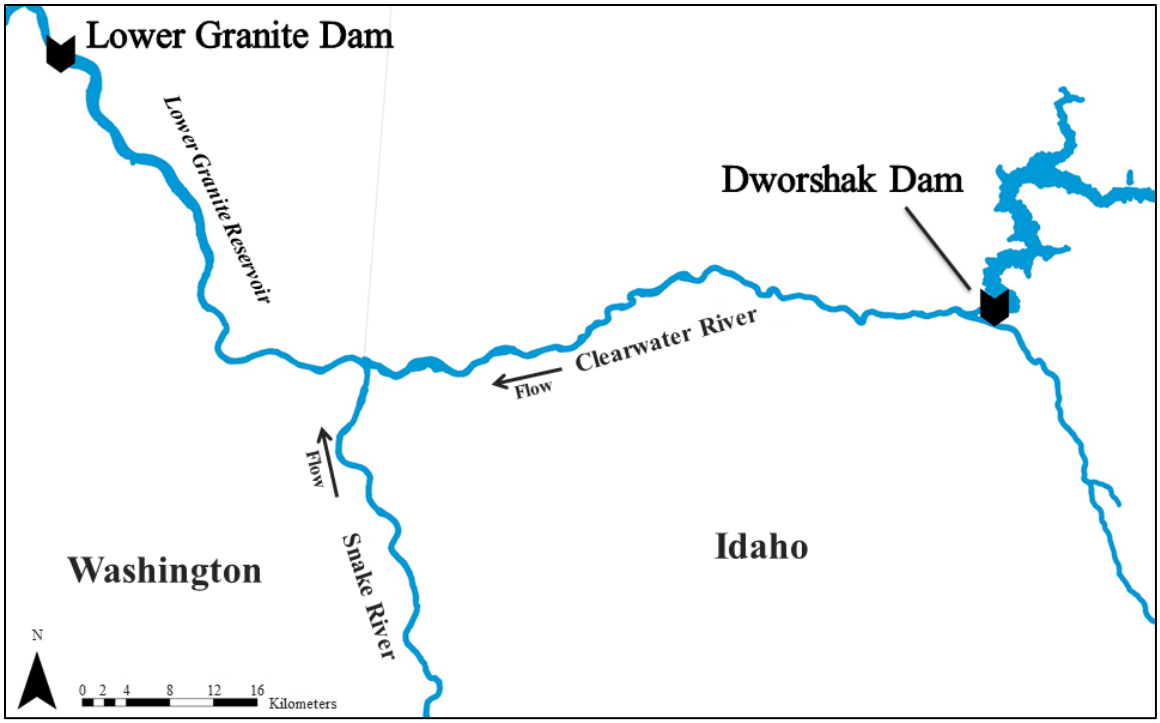

Figure 1. Location of the confluence of the Snake and Clearwater rivers in relation to Dworshak Dam, which releases cool water during summer to reduce water temperatures in the Snake River, including Lower Granite Reservoir.

very high concentrations of TDG due to mixing of waters of different temperatures. For example, in late summer when water temperature differed by 8°C between the two rivers, a TDG concentration of 122.5% was recorded (Tiffan et al. 2012). According to equations by Colt (1984), the TDG concentration at the confluence could be even greater when the temperature difference is greater.

Exposure to sudden temperature changes has been shown to increase predation susceptibility of many fish species during their early life history stages. Four- to six-week-old larval Atlantic silverside *Menidia menidia* were more susceptible to predation by striped killifish *Fundulus majalis* after sudden exposure to a 10°C increase for 10–15 min (Deacutis 1978). Fry of lake whitefish *Coregonus clupeaformis* were also significantly more vulnerable to predation by yellow perch *Perca flavescens* after a sudden increase of 10°C for 1-min duration—as compared to control fry that did not undergo a temperature change (Yocom and Edsall 1974). Predation susceptibility of whitefish also increased when predators were acclimated to warmer temperatures (Yocom and Edsall 1974). Among Pacific salmon species, fry of sockeye salmon *O. nerka* were more susceptible to predation by juvenile coho salmon *O. kisutch* after a sudden increase ≥10°C for durations of 5 or 60 s (Sylvester 1972). Increased acclimation temperature of predators also increased predation rates (Sylvester 1972). Additionally, juvenile rainbow trout

O. mykiss were significantly more vulnerable to predation by adult rainbow trout, as compared to controls, after about 90 s of exposure to 30.5°C, and juvenile fall Chinook salmon were significantly more vulnerable after only about 30 s of exposure to 28°C (Coutant 1973). Although not extensively studied, increased predation susceptibility following a sudden decrease in temperature is also possible. Age-0 flannelmouth sucker *Catostomus latipinnis* were more vulnerable to predation by rainbow trout following a sudden 10°C decrease in temperature (Ward and Bonar 2003).

The potential impact of predation by nonnative species, particularly by smallmouth bass *Micropterus dolomieu*, on threatened and endangered juvenile salmon has become a topic of concern for fisheries scientists and managers in the Columbia River Basin (Tabor et al. 1993; Carey et al. 2011; Hughes and Herlihy 2012; Lawrence et al. 2012). In particular, Lower Granite Reservoir on the Snake River may be considered a "hotspot" for smallmouth bass predation (Curet 1993; Zimmerman and Parker 1995; Anglea 1997; Naughton et al. 2004). Curet (1993) suggested that smallmouth bass were "the most serious predator" of subyearling fall Chinook salmon in Lower Granite Reservoir, having higher predation rates on juvenile salmon than native northern pikeminnow *Ptychocheilus oregonensis*. Zimmerman and Parker (1995) noted that relative abundance of smallmouth bass was higher in Lower Granite Reservoir than other reservoirs in the Columbia Basin. Naughton et al. (2004) estimated the loss of subyearling fall Chinook salmon to smallmouth bass predation in Lower Granite Reservoir to be highest in the Snake River just upstream of the Clearwater River confluence as compared to the lower Clearwater River and forebay and tailrace of Lower Granite Dam, but juvenile salmon were still not considered a major prey item at any of these locations. Additionally, Naughton et al. (2004) suggested that between-year variability in temperature may be positively related to predation potential; predation was six times higher in 1997 than in 1996 when August water temperatures were 20.6°C and 16.7°C, respectively.

We evaluated the predation susceptibility of juvenile fall Chinook salmon emigrating from the Clearwater River, through the confluence with the Snake River, and into Lower Granite Reservoir during simulated periods of with and without flow augmentation. We performed a controlled laboratory experiment that acclimated juvenile fall Chinook salmon to simulated Clearwater River conditions and then subjected them to predation by smallmouth bass in simulated Snake River conditions. The specific objective was to compare predation susceptibility of juvenile salmon after acclimation to temperatures of 10, 17, or 24°C (range of Clearwater River temperatures with and without augmentation) followed by exposure to predators that were acclimated at 17°C or 24°C (summer temperature range of the Snake River). This resulted in a total of five temperature-change combinations—10°C to 17°C, 17°C to 17°C, 10°C to 24°C, 17°C to 24°C, and 24°C to 24°C. The acclimation conditions simulating the Clearwater River represented the typical temperature range during flow augmentation from Dworshak Dam (10–17°C) and more natural temperatures that would be present if flow augmentation did not occur (17–24°C). Because the Snake River is typically warmer than the

Clearwater River, it was assumed that in the wild smallmouth bass would choose the warmer Snake River water in order to maximize predatory effectiveness (Bevelhimer 1995). Due to the concern that multiple stressors could contribute to increased predation susceptibility (Mesa 1994; Mesa et al. 2002), a TDG concentration of 105%, which is the approximate daily mean of natural conditions found in both the Clearwater and Snake rivers during late summer, was used in all experimental conditions to make the experimental conditions more applicable to fish in the wild.

METHODS

Study Animal Acquisition and Care

Juvenile fall Chinook salmon embryos from the Hanford Reach population of the Columbia River were acquired from Priest Rapids Hatchery in Mattawa, Washington, and transported to the Aquatic Research Laboratory (ARL) at the Pacific Northwest National Laboratory (PNNL) in Richland, Washington, in fall 2011. Juvenile fall Chinook salmon from the Hanford Reach population were used as surrogates of Snake River fall Chinook salmon from the Clearwater River due to the threatened status of the Snake River population and the potential difficulties associated with obtaining eggs from this population. However, we reasoned that Hanford Reach juveniles were the most suitable surrogates based on the proximal geographic location and similar temperature tolerance of juveniles from both populations. Juvenile Hanford Reach fall Chinook salmon acclimated to 10°C experienced 100% mortality after 37 min of exposure to 26.7°C (Snyder and Blahm 1970). Similarly, Geist et al. (2010) calculated the upper lethal temperature of juvenile Snake River fall Chinook salmon to be 26.8°C. Although the experimental methods used to calculate these temperature-related mortality rates differ, we believe these similar mortality estimates indicate similar temperature tolerances between juvenile Snake and Hanford Reach fall Chinook salmon and that Hanford Reach fish were a suitable surrogate to examine predation susceptibility related to temperature changes.

Embryos were raised in egg trays until hatch, and then about 2,000 juveniles were transferred to a 600-L circular tank for rearing in preparation for the experiment. The water used from embryo acquisition through early juvenile rearing was withdrawn directly from the Columbia River adjacent to the ARL and was at ambient temperature. Water temperature was manipulated beginning in March 2012 to simulate the approximate temperature regime of the Clearwater River and to ultimately grow juvenile salmon to a fork length of 60–100 mm (mean of about 80 mm) for the experiment. This length range represents the approximate length of wild juveniles emigrating from the Clearwater River in July through September when flow augmentation occurs (Table 3 in Arnsberg et al. 2010). Salmon were initially fed ad libitum at least daily with size-specific feeding pellets manufactured by Bio-Oregon (Longview, Washington) to grow fish to the desired size. Just prior to the beginning of the experiment when salmon reached the required size, water temperature was held constant at 10°C and salmon were fed once daily to satiation to reduce growth rates in order to reduce the potential for differences

in mean size between replicates during the experimental period. Study fish in acclimation chambers prior to predation trials were fed once daily to satiation during the experimental period.

Smallmouth bass (n = 27; total lengths varying from 185 mm to 390 mm) were captured in April 2012 by hook-and-line or electrofishing in the lower Yakima River near the confluence with the Columbia River, transported by truck to the ARL in a 50-L aerated cooler, and housed within two 600-L circular flow-through tanks. Newly acquired bass were combined with 12 smallmouth bass captured by hook-and-line in fall 2011, and all bass were held in ambient Columbia River water. Several days prior to the experiment, a subset of 10 bass was randomly assigned to each of the two tanks with the ultimate experimental predation temperatures of 17°C and 24°C; bass were temperature-acclimated at no more than 2°C per day (to minimize temperature-associated stress) to the ultimate experimental temperatures. The number of bass within each predation tank (n = 10) was chosen to balance the expected consumption potential of the predators with prey availability, with the ultimate intent of being able to stop the experiment when about 50% of the total prey were consumed. The predation experiment was stopped at 50% total consumption of prey due to statistical concerns (per recommendations by Coutant 1973 and Mesa and Warren 1997) and because we wanted to be able to measure an effect (i.e., if all or none of the prey were eaten, an effect would be immeasurable). We reasoned that 10 bass in each tank was an appropriate number to start with, but we reserved the ability to increase or decrease the abundance of predators if predation occurred too fast or too slow during the first replicates. Initially, bass were fed to satiation about once every three days with live juvenile fall Chinook salmon to ensure that bass remained accustomed to eating live prey. Throughout the experiment, bass were fed live prey ad libitum up to 3 days prior to each predation replicate in order to maintain predator health but also to ensure adequate predator hunger during the predation trials.

Experimental System Setup

Eight experimental tanks were used to contain the predation (two tanks) and acclimation (six tanks) conditions throughout the experiment (Figure 2). Predation tanks had target temperatures of 17°C or 24°C, and target temperatures of acclimation tanks varied from 10°C to 24°C, depending on the temperature "step" of the acclimation. The temperature step was increased either 1°C or 2°C per acclimation day to acclimate juvenile salmon from the 10°C stock tank to the specified acclimation temperatures of 10, 17, or 24°C. All tanks had target TDG concentrations of 105% to simulate slightly supersaturated dissolved gas conditions that are present in both the Snake and Clearwater rivers in summer. About 10 medium-size cobble stones (~10–20-cm in diameter) and two plastic aquarium plants were placed in each predator tank to provide refuge to prey during the predation trials. Real-time video cameras and monitors were also installed at each predator tank so that predation trials could be viewed remotely. The entire experimental area was enclosed within a temporary wall of opaque plastic to reduce disturbance and minimize potential bias on fish behavior. All tanks and components were

Figure 2. Experimental tanks included two larger circular tanks (left; light blue) used to house predators and conduct predation trials and six smaller acclimation tanks (right; dark blue) used for acclimation of juvenile Chinook salmon from the stock-tank temperature of 10°C to the ultimate acclimation temperatures of 10, 17, or 24°C.

monitored and cleaned as needed throughout the experiment to minimize the risk of study-fish infection.

Tank conditions were maintained using a managed system consisting of a water supply, water heater and chiller, sensors, and a gas-supersaturation column. During the experiment, ambient Columbia River water up to 100% TDG was divided into two head tanks and chilled or heated to 10°C and 24°C. Both head tanks were aerated after heating or cooling to maintain TDG at approximately 100%. To obtain supersaturated gas of 105% for experimental conditions, a third head tank with 10°C water was used to supply a gas supersaturation column (Specific Mechanical Systems Ltd., Saanichton, British Columbia, Canada; Figure 3) that consisted of a 2-m-high × 20-cm-diameter stainless steel column with inflow lines for both compressed air and water. Water to the supersaturation column was delivered by a centrifugal pump, while a gate valve at the bottom of the tank controlled the outflow rate and internal tank pressure. Compressed air, regulated with a sensor and flow control valve, was injected to the top of the column to increase the TDG pressure in the water entering the column. A sight glass at the side of the column with a water-level float switch maintained a constant air-to-water volume ratio inside the column. The supersaturation level of the outflow from the column was maintained at approximately 130% TDG by manipulating the water inflow, water outflow, and column water level.

Figure 3. Column used to supersaturate the total dissolved gas concentrations of water entering the experimental tanks.

Water from the three head tanks was then mixed using an integrated temperature and TDG sensing and control platform to obtain target conditions within each predation and acclimation tank. Three solenoid valves (Irritrol Utra Flow 700-1, Irritrol Systems, Riverside, California; Figure 4) controlled the proportion of water entering each experimental tank from each of the three head tanks. The TDG levels were monitored by a TDG sensor (Model T507, In-Situ Inc., Fort Collins, Colorado) at the outlet of each tank. A barometric pressure sensor (Model CS100, Campbell Scientific Inc., Logan, Utah), data logger (Model CR1000, Campbell Scientific Inc.), and two controllers (model SDM-CD16AC, Campbell Scientific Inc.) maintained the TDG level within each tank (± SD ≤ 4.8 mmHg). The TDG sensors were initially calibrated using a pressure calibrator (Fluke-719-30G, Fluke Corporation, Everett, Washington). The gas sensors had an accuracy of ± 2 mmHg over the range of 400 to 1400 mmHg. Gas levels of each tank were controlled by a computer program (written in CRBasic and implemented via LoggerNet; Campbell Scientific Inc.) that operated the three valves for each tank (Figure 4). The valves controlled delivery of the gas supersaturated water and the heated and chilled saturated water as needed to maintain target gas and temperature levels. Gas- and temperature-level data were checked against the target value once per second and recorded to the data logger once per minute. Dissolved oxygen was checked daily in all eight tanks using a handheld meter (Model 85, YSI Incorporated, Yellow Springs, Ohio).

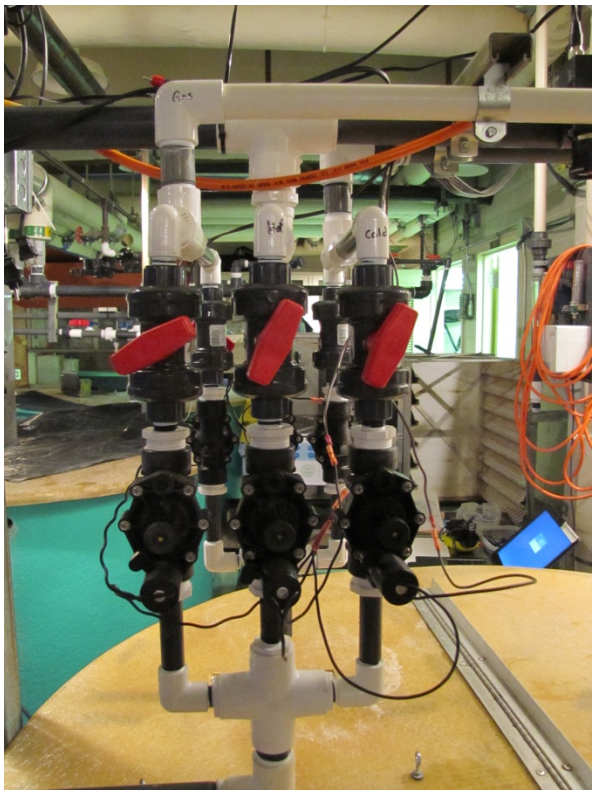

Figure 4. Solenoid valves used to control conditions within each experimental tank from three separate water inputs.

Predation Susceptibility Trials

Groups of juvenile salmon were temperature-acclimated from the stock-tank temperature of 10°C to the ultimate acclimation temperatures of 10, 17, or 24°C during a 10-day period prior to each of the predation trials. To begin an acclimation, 30, 30, and 15 juvenile salmon from the stock tank were randomly divided into three separate acclimation tanks with ultimate temperatures of 10, 17, and 24°C, respectively. Fifteen salmon were used for each of the five acclimation-predation combinations; only 15 prey fish were needed for the 24°C acclimation because transfer from 24°C to 17°C was not applicable to fish in the wild. Groups of salmon were then steadily acclimated by +2°C (or +1°C from 16 to 17°C for the 17°C acclimation group) per day to a target "step" temperature; this increase in acclimation step temperature was increased until the ultimate acclimation temperatures were reached for each tank. On the seventh day following the beginning of an acclimation, all three salmon groups were at their ultimate temperatures, which were then held steady for three more days until the predation trials were conducted. Predation trials occurred once every 5 days throughout the experiment; thus, two separate sets of three acclimation tanks were needed to offset the timing of acclimation groups. For example, groups of salmon to be used for subsequent predation trials began acclimating on

day 1 and 6 of the experiment and were used for predation trials on day 11 and 16 of the experiment, respectively.

Juvenile salmon were measured and marked on the seventh day following the beginning of an acclimation, 3 days prior to the predation trials. The order of acclimation groups to be measured and marked was randomly chosen. Salmon were removed from an acclimation tank by dip net and held temporarily in an opaque 20-L plastic bucket with a lid and aerated acclimation water (taken from the acclimation tank) to minimize stress during handling. The temperature of the bucket was monitored to ensure that temperatures did not deviate from the assigned ultimate acclimation temperature. Individual salmon were then removed from the temporary holding bucket to an opaque bucket containing an anesthetic of 80 mg/L tricaine methanesulfonate (MS-222) buffered with 80 mg/L sodium bicarbonate, and salmon remained until Stage 4 anesthesia (loss of equilibrium and slowing of opercular movements) was reached. Once anesthetized, juvenile salmon fork length (mm) and weight (g) were measured and salmon were given a unique adipose-fin clip corresponding to their acclimation temperature: 10°C-acclimated fish were given a single vertical cut in their adipose fin; 17°C-acclimated fish had their entire adipose fin removed; and 24°C-acclimated fish had half of their adipose fin removed (Figure 5). Following the marking procedure, juvenile salmon were recovered from anesthesia and returned to their respective acclimation tanks.

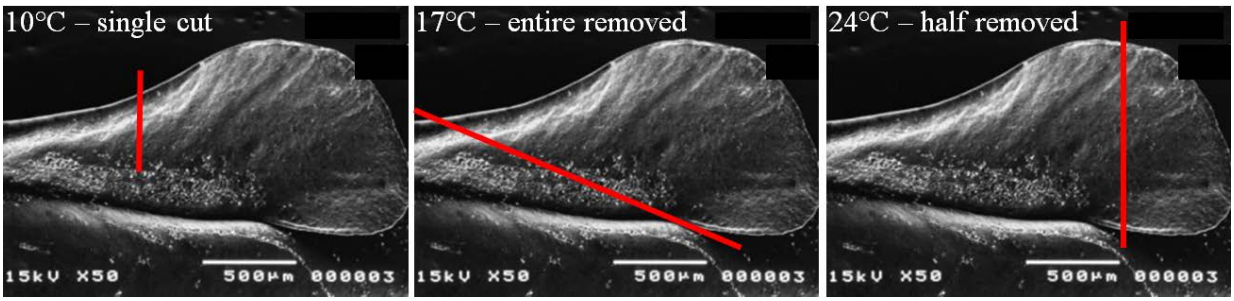

Figure 5. Unique adipose-fin clips to identify groups of salmon acclimated at 10°C (single vertical cut, left panel), 17°C (entire removed, middle panel), and 24°C (half removed, right panel). Red lines indicate the clipping region.

Predation susceptibility trials were conducted simultaneously for the 17°C and 24°C predation temperatures, and predation tanks contained juvenile fall Chinook salmon that were acclimated to two or all three of the acclimation temperatures, respectively (Figure 6). First, juvenile salmon from the three acclimation temperatures were transferred to individual 20-L opaque buckets with lids and water from the respective acclimation tanks. All ordering of salmon transfers between tanks/buckets and buckets/predation tanks was randomized. A coin was flipped to determine which of the 17°C or 24°C predation temperatures to begin first. The buckets containing the three temperature-acclimated groups were then emptied within 30 s into a large dip net located within the 17°C or 24°C predation tank to separate juvenile salmon

temporarily from predators. The dip net was then overturned in the direction of a floating mass of plastic plants, which allowed prey to seek refuge, if able. Predation by smallmouth bass continued until about 50% of the salmon had been consumed, as determined by an observer viewing the predation trial through the remote video monitor, or until 90 min had passed. All remaining juvenile salmon were removed from the predation tanks by dip net and immediately euthanized in a solution of 250 mg/L MS-222 buffered with 250 mg/L sodium bicarbonate. Unconsumed salmon were then enumerated by acclimation group based on the adipose fin clip. The experiment was replicated a total of six times for each predation temperature (17°C and 24°C).

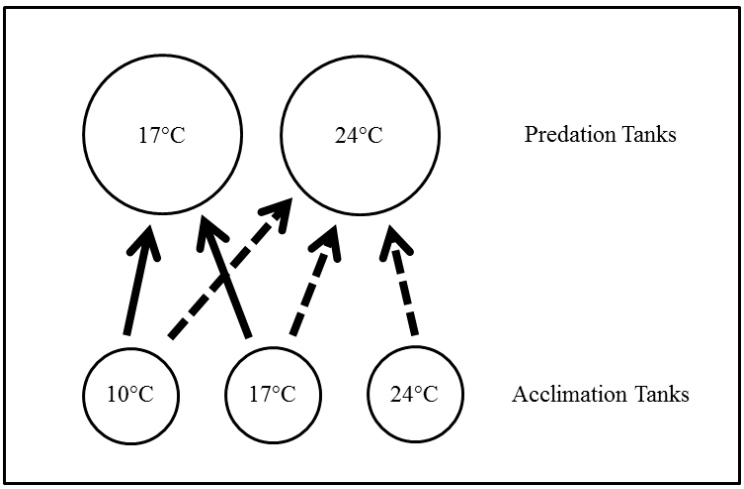

Figure 6. Transfer procedure of juvenile fall Chinook salmon from acclimation tanks to predation tanks containing smallmouth bass. Solid arrows indicate simultaneous transfer of 10°C- and 17°C-acclimated salmon to the 17°C predation tank; dashed arrows indicate simultaneous transfer of all three temperature-acclimated groups of salmon to the 24°C predation tank. Two sets of three acclimation tanks were used to stagger the 10-day acclimation procedure so that predation trials could occur every 5 days.

Statistical Analysis

Juvenile salmon length and weight were compared between replicates and acclimation conditions using two-way analysis of variance (ANOVA), and individual and interaction effects were examined to determine if fish growth was an influential factor in the analysis. Pairwise comparisons were made using Tukey's Honestly Significant Difference (HSD) test.

Predation susceptibilities were calculated separately for the 17°C and 24°C predation temperatures using ratios of the number of fish consumed from one acclimation temperature to the number of fish consumed from the other acclimation temperature(s). For the 17°C predation

temperature, the number of salmon consumed from the 10°C acclimation and 17°C acclimation were compared using a ratio to test the hypothesis:

H_{017}: predation susceptibility of 10°C- and 17°C-acclimated salmon was equal (i.e., number of 10°C consumed:number of 17°C consumed = 1)

H_{A17}: predation susceptibility of 10°C-acclimated salmon was greater than 17°C-acclimated salmon (i.e., number of 10°C consumed:number of 17°C consumed > 1).

The alternative hypothesis was set as a one-way test (>1) because it was assumed that predation susceptibility would be greater for salmon exposed to the greater temperature change and also to increase statistical power to detect a difference; in reality, this assumption was affirmed. The Wilcoxon signed-rank test was used to test whether the median consumption ratio for the 17°C predation temperature was equal to or greater than 1. A ratio statistically equal to 1 (failure to reject the null hypothesis) would indicate that juvenile salmon acclimated at either 10°C and 17°C had equal predation susceptibility. Conversely, a median consumption ratio statistically greater than 1 would reject the null hypothesis and indicate greater predation susceptibility of 10°C-acclimated than 17°C-acclimated salmon.

For the 24°C predation temperature, a consumption ratio was calculated for each acclimation-temperature group of juvenile salmon in comparison to the total consumed from the other two acclimation groups (hereafter called "consumption ratio combinations"). The three consumption ratio combinations were 1) number consumed from 10°C:number consumed from 17°C + 24°C, 2) number consumed from 17°C:number consumed from 10°C + 24°C, and 3) number consumed from 24°C:number consumed from 10°C + 17°C. A hypothesis was then tested to compare predation susceptibility of each acclimation-temperature group of salmon to the predation susceptibility of the other acclimation-temperature groups (i.e., consumption ratio combinations 1 to 3 as shown above). For example, the null and alternative hypotheses for consumption ratio combination 1 were:

H_{024}: predation susceptibility of 10°C-acclimated salmon was equal to the predation susceptibility of 17°C- *and* 24°C-acclimated salmon (number of 10°C consumed: number of 17°C *and* 24°C consumed = 0.5)

H_{A24}: predation susceptibility of 10°C-acclimated salmon was greater than 17°C- *and* 24°C-acclimated salmon (number of 10°C consumed:number of 17°C *and* 24°C consumed > 0.5).

The hypotheses were then tested for consumption ratio combinations 2 and 3. The Wilcoxon signed-rank test was used to test whether the median consumption ratio was equal to or greater than 0.5. In other words, the consumption ratio combinations were calculated by comparing the number of prey consumed from one acclimation temperature (e.g., "Group 1"; n = up to 15 fish) to the number of prey consumed from the other two acclimation temperatures (e.g.,

"Group 2"; n = up to 30 fish) such that a ratio of 0.5 (e.g., 15/30) would indicate equal predation susceptibility of Group 1 and Group 2. Due to simultaneous testing of three consumption ratios (i.e., one for each acclimation temperature), we used a Bonferroni-corrected α of 0.017 (i.e., $\alpha = 0.05/3$). A ratio equal to 0.5 (failure to reject the null hypothesis) would indicate that juvenile salmon acclimated at one of the three specified temperatures had predation susceptibility equal to the sum of the two remaining acclimation groups. Rejection of the null hypothesis would indicate that predation susceptibility was greater for an acclimation group than the sum of the two remaining acclimation groups. To determine the detectable difference of the predation susceptibility ratio, post-hoc power analyses were performed using a power of 0.8 and an alpha of 0.05 and 0.017 for the 17°C and 24°C predation temperatures, respectively. All statistical analyses were performed using JMP Version 7.0 (SAS Institute, Inc., Cary, North Carolina) with an alpha of 0.05.

RESULTS

The computer and sensor-controlled system performed well in producing repeatable tank conditions between acclimation levels, tanks, and replicates (Table 1). Mean tank temperatures among replicates were typically within 0.5°C of the target temperatures, and mean TDG concentrations among replicates were typically within 1.0% of the target TDG (Table 1). Mechanical failure of the gas compressor on 26 June 2012 allowed TDG concentrations to remain over 110% for a 64-min period (with a peak of 141%) in one of the 24°C acclimation tanks; however, the gas concentration quickly returned to the targeted 105% once a new compressor was installed. Following the high TDG concentration, the exposed acclimating salmon remained within the tank at 105% TDG for 3 more days before the predation trial. Predation susceptibility results (as discussed below) did not differ markedly from the other replicates; thus, we believe any effects of the short-duration TDG spike were negligible in the study's outcome. Total dissolved gas concentrations exceeding 110% in tanks 2–8 were due to anomalous readings when the TDG sensors were out-of-water for weekly cleaning (Figure 7). Mean dissolved oxygen differed somewhat between tanks throughout the experiment, varying from a mean of 90.9% in the 24°C predator tank to a mean of 98.9% in one of the 10°C acclimation tanks (Figure 8); however, empirical values were within acceptable limits for rearing healthy juvenile salmon (Westers and Pratt 1977).

Table 1. Summary of temperature and total dissolved gas (TDG) conditions within acclimation and predation tanks. The "Target Temperatures" field indicates the "ultimate" acclimation temperature reached prior to the predation trials and each temperature-acclimation "step" to reach the ultimate temperature; predation tanks were kept at a consistent target temperature throughout the experiment. The target TDG in all experiments was 105%. The range of mean temperature and mean TDG among replicates are shown.

Tank Type	Target Temperatures (°C; Ultimate-Step)	Mean Empirical Temperatures (°C)	Mean Empirical TDG (%)
Acclimation	10-10	9.6–10.5	105.1–105.5
	17-10	10.1–10.2	104.9–106.7
	17-12	12.0–12.2	105.2–106.6
	17-14	13.5–14.2	105.3–106.1
	17-16	16.0–16.1	105.3–106.2
	17-17	17.0–17.1	105.1–106.3
	24-10	9.9–10.5	105.3–106.0
	24-12	12.1–12.2	105.3–106.1
	24-14	14.0–14.2	105.0–106.2
	24-16	16.0–16.1	105.4–106.5
	24-18	18.0–18.1	105.7–106.6
	24-20	20.1–20.3	105.9–106.5
	24-22	21.9–22.1	106.1–107.1
	24-24	23.8–24.0	106.2–106.9
Predation	17	17.1–17.1	105.3–105.5
	24	24.0–24.2	106.0–106.6

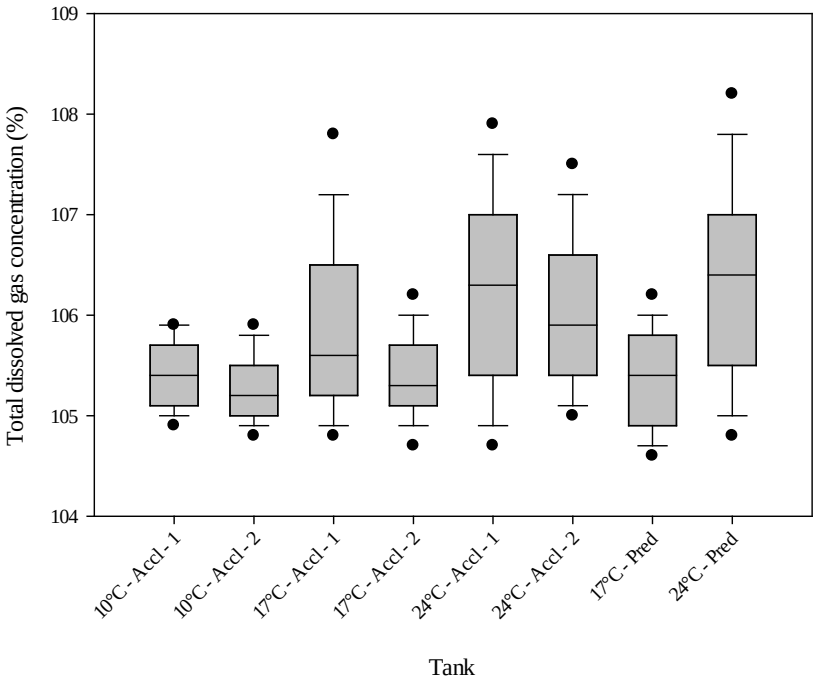

Figure 7. Percentage of total dissolved gas (TDG) of acclimation (Accl) and predation (Pred) tanks throughout the experiment. There were a total of 8 tanks maintained at a target 105% TDG including two tanks for each prey acclimation temperature of 10°C, 17°C, and 24°C and two tanks for the predators. Lines within boxes denote the median; boxes denote the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles.

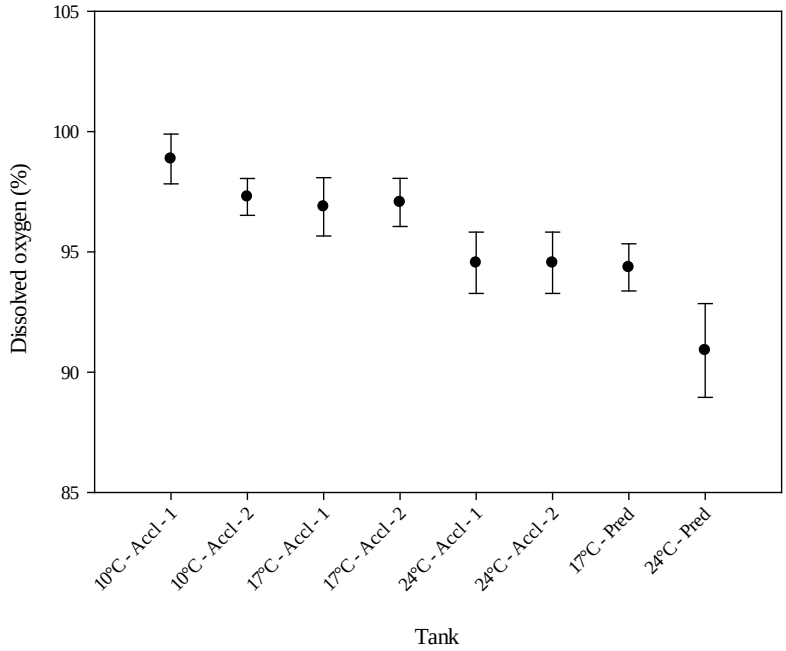

Figure 8. Percentage of dissolved oxygen of acclimation (Accl) and predation (Pred) tanks through the experimental period. There were a total of 8 tanks monitored for dissolved oxygen including two tanks for each prey acclimation temperature of 10°C, 17°C, and 24°C and two tanks for the predators. Error bars are two standard errors of the mean.

Juvenile salmon fork length did not differ among acclimation groups within replicates ($P = 0.4698$); however, fork length differed among replicates (ANOVA, $P < 0.0001$), increasing from a mean of 81 mm in the first replicate to 94 mm in the sixth replicate (Figure 9). There was no significant interaction effect of juvenile salmon length between replicate and target acclimation temperature ($P = 0.8234$). Juvenile salmon weight differed also among replicates (ANOVA, $P < 0.0001$), but there was no statistical difference in fish weight among acclimation groups within replicates ($P = 0.1857$). Juvenile salmon weight increased from a mean of 6.0 g in the first replicate to a mean of 9.0 g in the sixth replicate (Figure 10), and there was no interaction effect of fish weight between replicate and acclimation group ($P = 0.4535$).

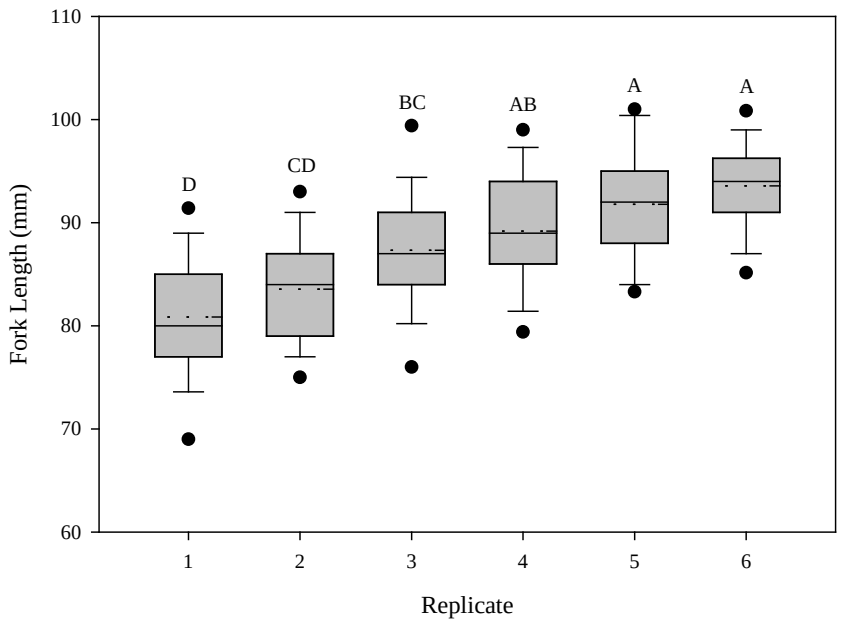

Figure 9. Fork length (mm) of acclimating juvenile fall Chinook salmon prior to each experimental predation susceptibility replicate. Solid lines within boxes denote the median; dashed lines indicate means; boxes denote the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles. Non-similar letters above individual plots indicate statistically significant differences at an alpha of 0.05.

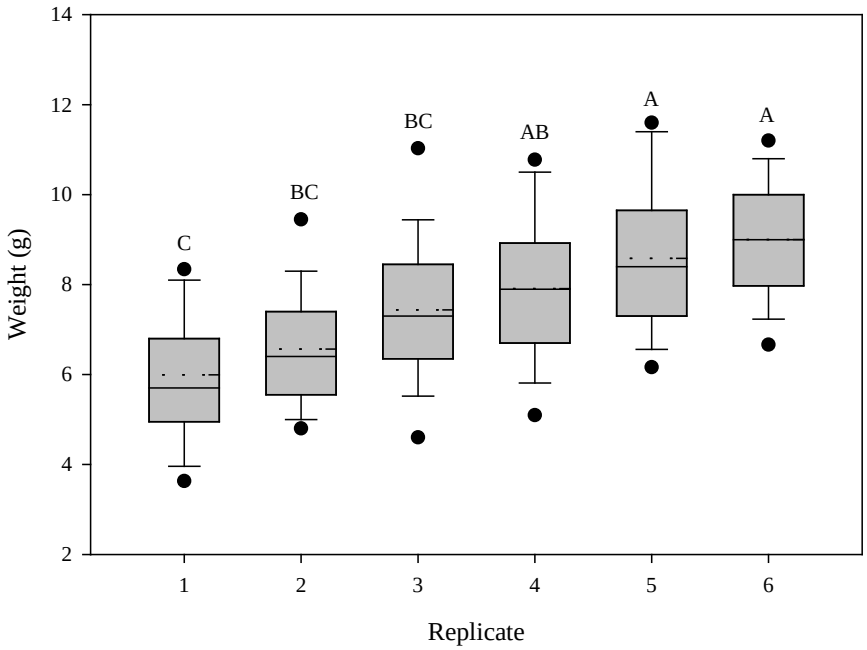

Figure 10. Weight (g) of acclimating juvenile fall Chinook salmon prior to each experimental predation susceptibility replicate. Solid lines within boxes denote the median; dashed lines indicate means; boxes denote the 25th and 75th percentiles, whiskers the 10th and 90th percentiles, and dots the 5th and 95th percentiles. Non-similar letters above individual plots indicate statistically significant differences at an alpha of 0.05.

The proportion of salmon consumed varied from 0.35 to 0.75 in the 17°C predation temperature and 0.4 to 0.47 in the 24°C predation temperature. Mean predation replicate duration was 31.3 min (SD = 46.2) for 17°C and 4.5 minutes (SD = 5.1) for 24°C; however, because of considerable variability in predation durations these means were not statistically different (*t*-test, $P = 0.1879$). The maximum predation duration at 24°C was 14 min, whereas two of the 17°C predation replicates used the maximum 90-min predation period and were subsequently terminated. All other predation replicates at 17°C or 24°C (n = 9, 75%) lasted 5 min or less.

Predation susceptibility did not differ statistically among temperature-acclimated prey groups in the 17°C or 24°C predation trials (Figure 11). However, within the 24°C predation temperature, predation susceptibility of consumption ratio combination 3 (24°C:10°C + 17°C) was nearly significantly lower for salmon that did not experience a temperature change (Wilcoxon signed-rank test, $P = 0.018$ with Bonferroni-corrected $\alpha = 0.017$; Figure 11 and Table 2). A post-hoc power analysis indicated that only one more experimental replicate at the 24°C predation temperature would have improved the ability to detect a consumption-ratio difference of 0.08 (the detectable difference was 0.16 for 6 replicates), assuming similar experimental error. Predation susceptibility at 24°C of consumption ratio combination 1 (10°C:17°C + 24°C) or

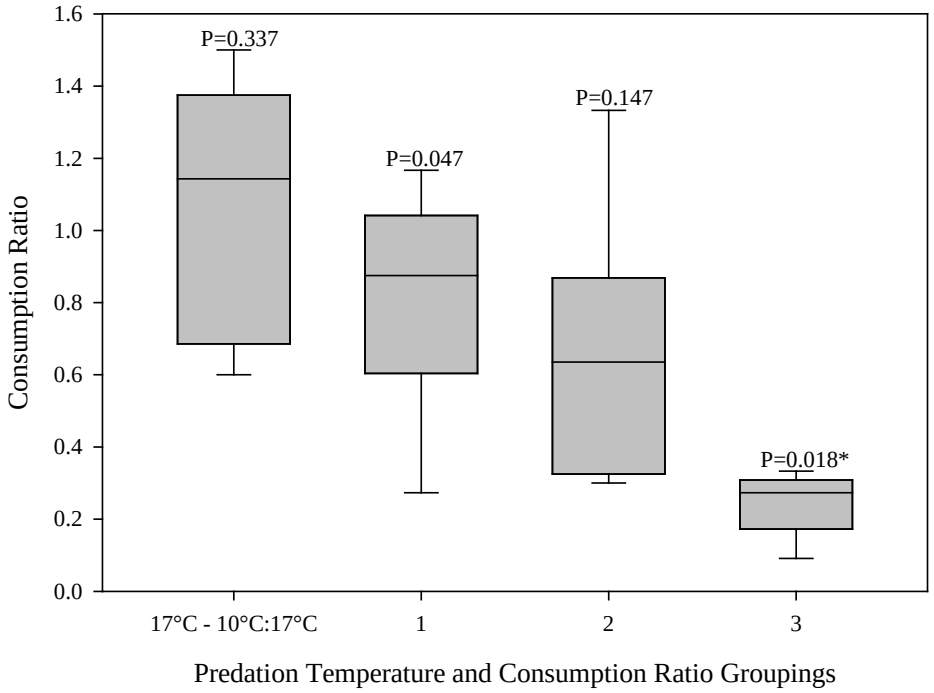

Figure 11. Consumption ratios (i.e., predation susceptibility) of juvenile salmon exposed to predators at 17°C (10°C:17°C) and 24°C (consumption ratio combination 1, 2, and 3; see Methods section for details). The null hypotheses for the 17°C and 24°C predation temperatures were that the median consumption ratio = 1.0 and 0.5, respectively; failure to reject the null indicated equal predation susceptibility between groups. Alternative hypotheses were the consumption ratio was > 1.0 and > 0.5, respectively, for the 17°C and 24°C predation temperatures; rejection of the null hypotheses would indicate unequal predation susceptibility among compared groups. Lines within boxes denote the median and the box denotes the 25th and 75th percentiles. An asterisks indicates a nearly significant different at the Bonferroni-corrected alpha value of $\alpha = 0.05/3 = 0.017$.

Table 2. Predation on juvenile fall Chinook salmon by smallmouth bass after sudden transfer to 24°C from 10°C, 17°C, and 24°C acclimation temperatures. The three consumption ratio combinations were: 1) number consumed from 10°C:number consumed from 17°C + 24°C, 2) number consumed from 17°C:number consumed from 10°C + 24°C, and 3) number consumed from 24°C:number consumed from 10°C + 17°C. The null hypothesis was that the median ratio would be equal to 0.5 if predation susceptibility existed within a consumption ratio combination.

Replicate	Number Eaten			Consumption Ratio Combinations		
	10°C	17°C	24°C	1	2	3
1	3	8	3	0.273	1.333	0.273
2	6	5	1	1.000	0.714	0.091
3	5	5	2	0.714	0.714	0.200
4	7	3	3	1.167	0.300	0.300
5	6	3	3	1.000	0.333	0.333
6	6	5	3	0.750	0.556	0.273

consumption ratio combination 2 (17°C:10°C + 24°C) were not statistically significant (P = 0.147 and P = 0.047, respectively; Figure 11 and Table 2). Within the 17°C predation temperature, predation susceptibility also did not differ between the 10°C and 17°C acclimation groups (P = 0.337; Figure 11 and Table 3).

DISCUSSION

Juvenile fall Chinook salmon acclimated to 24°C and exposed to predators at 24°C had an arguably lower predation rate (P = 0.018 at α = 0.017) than salmon transferred from 10 to 24°C or 17 to 24°C. The lower predation susceptibility of fish exposed to this treatment suggests that without cool water augmentation from Dworshak Dam and a more natural thermal regime of the lower Clearwater River during a relatively warm water year (24°C), juvenile fall Chinook salmon emigrating from the Clearwater River may be less susceptible to predation than when flow augmentation occurs. Predation susceptibility of juvenile salmon acclimated to 17°C and

Table 3. Predation on juvenile fall Chinook salmon by smallmouth bass after sudden transfer to 17°C from 10°C and 17°C acclimation temperatures. The null hypothesis was that the median ratio would be equal to 1.0 if predation susceptibility existed between acclimation temperatures.

Replicate	Number Eaten		Consumption Ratio
	10°C	17°C	10°C:17°C
1	4	3	1.333
2	8	7	1.143
3	8	7	1.143
4	3	5	0.600
5	5	7	0.714
6	6	4	1.500

exposed to predators at 17°C did not differ significantly from salmon transferred from 10 to 17°C, which may indicate that when the waters of both rivers are relatively cool, predation susceptibility at the confluence may not differ within the range of expected temperatures. It is important to note that cool water flow augmentation from Dworshak Dam begins on 5 July of each year and is regulated to maintain the temperature of the Snake River at Lower Granite Dam at 20°C or lower; thus, this latter scenario applies to predation susceptibility prior to and after augmentation occurs each year or in very cool years when flow augmentation is not needed to cool the Snake River. Unfortunately, we were not able to compare predation susceptibility between the 17°C and 24°C predation exposure temperatures due to the structure of the experimental design, so it is unknown whether predation susceptibility differed between these predation temperatures.

Several characteristics of the lower Clearwater River and confluence likely make this stretch of river particularly attractive to predatory fishes and may increase the predation susceptibility of emigrating juvenile fall Chinook salmon from the Clearwater River. Experiencing multiple acute stressors has been implicated in increasing predation susceptibility of emigrating juvenile Chinook salmon (Mesa 1994; Mesa et al. 2002). Acute stressors in the lower Clearwater River and confluence include 1) thermal stress due to passage from the cool Clearwater River to the warmer Snake River; 2) chronic exposure to slightly supersaturated TDG concentrations in both the Clearwater and Snake rivers (100–110%; Tiffan et al. 2012); 3) potential of very high TDG concentrations created by mixing of the cool Clearwater River and warm Snake River (e.g., 122.5% documented on 9 August 2011, Tiffan et al. 2012; concentrations up to 137.5% are possible with 15°C difference based on +~2.5% TDG per +1°C "rule" proposed by Nebeker et al. 1978); and 4) agricultural and urban development, including channelization, diking, and bank stabilization of the lower Clearwater River that has decreased water quality and reduced habitat complexity (USFWS 2002). Shively et al. (1996) attributed

high rates of predation on juvenile fall Chinook salmon in the lower Clearwater River to the high density of hatchery-released fish and the change in physical characteristics of the river as it transitions from free flowing to impounded (as it enters Lower Granite Reservoir). As juvenile fall Chinook salmon density increased in the lower Clearwater River, driven by hatchery releases, a functional response by northern pikeminnow resulted in almost exclusive predation on juvenile salmon during their peak density (Shively et al. 1996). Northern pikeminnow also preferentially selected the smallest juvenile fall Chinook salmon available (Shively et al. 1996), which may increase the susceptibility of wild juveniles, which are generally smaller than hatchery-released fish.

The presence of nonnative smallmouth bass throughout the Clearwater and Snake rivers, as opposed to the co-occurring native northern pikeminnow, may also increase the predation potential on both wild and hatchery juvenile fall Chinook salmon emigrating from the Clearwater River. Exposure of juvenile Chinook salmon to odors of smallmouth bass and northern pikeminnow indicated that Chinook salmon did not exhibit an antipredator response (Kuehne and Olden 2012). Conversely, exposure to chemical cues of northern pikeminnow elicited an antipredatory response including motionless behavior and/or a panic response (Kuehne and Olden 2012). If wild and hatchery fall Chinook salmon are not able to sense the odor of smallmouth bass in the lower Clearwater River, particularly after experiencing multiple stressful environmental conditions during confluence passage, it is possible that predation susceptibility may be increased during these conditions.

A few study caveats should be considered when applying the results of this laboratory study to the Clearwater-Snake confluence. First, this study is applicable to conditions when the temperature difference between the Clearwater and Snake rivers are different and when juvenile salmon are actively emigrating through this area. The temperature differentiation typically occurs for only a few months of the year, whereas juvenile fall Chinook salmon migrate through this area several weeks prior to and after this thermal differentiation. This study also assumed that at the confluence, juvenile salmon are exposed to sudden increases in temperature, but it is known that in some cases, juvenile salmon will choose to reside in relatively cool water within the water column (Tiffan et al. 2009c). However, based on the potential of juvenile salmon to use the upper water column as a foraging area or to regulate their depth to obtain neutral buoyancy (Pflugrath et al. 2012), it is a reasonable assumption that juvenile fall Chinook salmon emigrating from the Clearwater River experience, for an unknown period of time, the warm surface layer of Snake River origin water. Coutant (1973) indicated that only a 33-s exposure was needed to increase predation susceptibility of juvenile Chinook salmon that encountered a 13°C increase (from 15°C to 28°C). Further, Mesa (1994) indicated that juvenile salmon exposed to multiple stressors were more likely to be preyed upon within a 1-h period following the stressors. These previous studies provide support that predation susceptibility of juvenile Chinook salmon from the Clearwater River may have increased predation susceptibility while emigrating through the Clearwater-Snake confluence in summer. Finally, it is important to note

that hatchery-raised juvenile salmon were used for this study and that their behavior may not represent the behavior of wild fish. Several previous studies have suggested that hatchery salmonids and other species have maladaptive predator avoidance behaviors as compared to those of wild fish (Huntingford 2004; Houde et al. 2010; Jackson and Brown 2011); similarly, it is possible that hatchery salmon used in this study had higher predation susceptibility than would be expected for wild fish with predator experience. However, the mortality related to predation susceptibility of wild versus hatchery juvenile fall Chinook salmon through the confluence during the same temporal period is currently unknown.

The increase in mean size (length and weight) of study fish between experimental replicates was significantly different but likely did not have a biological effect on the study results. Within a replicate, fish size did not differ among the three acclimation groups, and thus prey size did not have an effect on predation susceptibility. Ideally, equal size of juvenile salmon throughout all predation susceptibility replicates would have provided support that all replicates were truly replicated; however, all the ranges of mean fish length between replicates (mean 80–94 mm, Figure 9) were within the upper size range of wild juvenile fall Chinook salmon sampled in the lower Clearwater River (Table 3 in Arnsberg et al. 2010). Thus, we believe that all replicates were valid in describing relative predation susceptibility for similarly sized wild-emigrating salmon.

The consumption ratios used to compare predation susceptibility were chosen as the metric for comparison to meet the assumption of independence of sampling units and because they account for the variability in the total fish consumed between replicates. Predation susceptibility data in similar studies have been analyzed using Chi-squared analysis (see Mesa and Warren 1997); however, data from these experiments were retained for analysis only when 30–70% of fish were consumed, in order to account for changing prey availability throughout the predation period. Thus, to maintain the best sample size possible for the current study (i.e., not wanting to remove replicates because they did not meet the 30–70% consumption assumption as in Mesa and Warren 1997), consumption ratios were used rather than proportional data.

The confluence of the Clearwater and Snake rivers is an environmentally complex area with changes in temperature, velocity, supersaturated TDG concentrations, and channel modifications related to urbanization that may synergistically interact to cause high mortality of emigrating juvenile fall Chinook salmon in summer. The results of the current study indicate that predation susceptibility may be increased when a relatively large temperature change interacts with other hydrological conditions present at the confluence. However, predation may not be the only factor explaining the high mortality rates measured in previous years of this project. Further research is needed to determine if mortality is related to cool water augmentation and, ultimately, whether or not this mortality has a population-level effect on the dynamics of Snake River fall Chinook salmon.

MANAGEMENT IMPLICATIONS AND FUTURE RESEARCH

The potential for high mortality of emigrating juvenile fall Chinook salmon from the Clearwater River during their passage through the Clearwater–Snake confluence in summer should be of concern to fisheries managers tasked with restoring threatened Snake River fall Chinook salmon. Since the Endangered Species Act listing of this stock in 1992 (NMFS 1992), the proportion of the population spawning in the Clearwater River has grown markedly; consequently, the potential for confluence conditions to affect this population has also grown. In 1991, the Clearwater River contained only 7% (n = 4) of the spawning redds throughout the population's distribution; in 2011, the Clearwater River contained 34% (n = 1,611) of the population's spawning redds (IPC 2013). The increase in the number of redds built in the Clearwater River, the likely increase in juvenile production, and the potential for wild-produced fish to be especially affected due to their emigration in summer necessitate a more thorough understanding of mortality rates and the sources of mortality of emigrating wild and hatchery fish through the confluence of the Snake and Clearwater rivers.

Calculating survival rates of wild-produced juvenile fall Chinook salmon through the Clearwater–Snake confluence has been impossible to date due to their small size and relatively low abundance, but this information is needed to determine if wild fish have high mortality and if this is affected by confluence conditions. The small size of emigrating wild fish (individuals < 95 mm fork length) has restricted survival studies to the use of passive integrated transponder (PIT) technology, which requires large sample sizes to produce survival estimates with reasonable accuracy and precision; capturing sufficient individuals to determine a statistically acceptable survival estimate of juvenile fall Chinook salmon emigrating from the Clearwater River has not been possible to date. Active telemetry (using radio or acoustic transmitters) requires a smaller sample size to estimate survival than PIT technology (McMichael et al. 2010); however, the larger size of historic active telemetry transmitters has not allowed implantation of these tags in juvenile salmon less than approximately 95 mm in fork length. Despite this previous inability, technology is improving at a marked rate. There is currently a prototype Juvenile Salmon Acoustic Telemetry System (JSATS) acoustic transmitter weighing 0.22 g with dimensions of 15-mm length and 3.4-mm diameter that will soon be available for assessing survival rates of smaller (<95 mm fork length) wild juvenile fall Chinook (Figure 12). The development of this transmitter has been funded by the U.S. Army Corps of Engineers, Portland District, and is expected to be commercially available in early 2014. Ongoing laboratory and field trials at PNNL are being used to determine the minimum salmonid tagging size, and results should be available in fall 2013.

Figure 12. Prototype downsized Juvenile Salmon Acoustic Telemetry System (JSATS; right) transmitter as compared to a full duplex passive integrated transponder (PIT) tag (left).

Ideally, survival of wild emigrating juvenile fall Chinook salmon through the Clearwater–Snake confluence and through the lower Snake River reservoirs could be assessed during both current cool water augmentation conditions from Dworshak Dam and during more naturally occurring conditions with more similar temperatures between the lower Clearwater River and Snake River (i.e., without flow augmentation). Such a study would provide information needed to assess the potential trade-off between mortality at the confluence due to cool-water augmentation versus mortality caused by higher water temperatures of the lower Snake River reservoirs. Although speculative, it is possible that cool-water augmentation conditions may be causing a higher-than-desired mortality rate of wild juvenile fall Chinook salmon that are more likely to emigrate through the confluence during cool-water augmentation conditions.

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CHAPTER THREE

Distribution and Abundance of Potential Invertebrate Prey for Juvenile Fall Chinook Salmon in the Snake River

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INTRODUCTION

Many Snake River fall Chinook salmon *Oncorhynchus tshawytscha* use lower Snake River reservoirs, particularly Lower Granite Reservoir, for rearing before migrating seaward as subyearlings (Connor et al. 2002). The impoundments used by rearing subyearlings are fundamentally different from the riverine Hells Canyon Reach where most natural subyearlings are produced. In Hells Canyon, subyearlings rely on lotic food webs that are mainly composed of aquatic macroinvertebrates. By contrast, impounded habitats are characterized by lentic food webs composed of phytoplankton, zooplankton, and other invertebrates that are more adapted to low water velocities (Tiffan et al. 2014). These reservoir food webs have changed over the past 20 years with the colonization of introduced species that may influence subyearling productivity.

One non-native invertebrate that has recently become very abundant in Lower Snake River reservoirs is the estuarine opossum shrimp, *Neomysis mercedis* (hereafter, *Neomysis*; Figure 1). Subyearlings prey heavily on this relatively large (~15 mm, total length) species when both are present in shallow water habitats during the spring (Tiffan and Connor 2012; Tiffan et al. 2014). Although *Neomysis* is omnivorous, it can prey heavily on zooplankton (Murtaugh 1981a; Cooper et al. 1992; Haskell and Stanford 2006), which subyearlings also prey on in reservoir habitats. The consumptive demand that *Neomysis* exerts on lower trophic levels is unknown, but warrants investigation given their relatively high biomass. Furthermore, the habitat use and population ecology of *Neomysis* in lower Snake River reservoirs remain largely unexplored.

Another recent invasive species that has colonized the lower Snake River reservoirs is the Siberian prawn *Exopalaemon modestus* (hereafter, prawns; Figure 2). This species was first documented in the Snake River at fish collection facilities at main-stem dams in the late 1990s and has since increased exponentially in abundance (Haskell et al. 2006). However, virtually nothing is known about this species' distribution, abundance, reproductive biology, food habits, and role in the food web in the lower Snake River reservoirs. The Siberian prawn is a large (~60 mm, total length) benthic organism that is omnivorous (Bell and Coull 1978). Given that *Neomysis* is also a benthic species, it is probable that prawns prey upon *Neomysis* and other taxa such as *Corophium* spp. (hereafter, *Corophium*; Figure 3), oligochaetes, and benthic aquatic insects. The role of prawns in the food web that ultimately supports subyearlings is unknown but should be cause for concern given the limited data on their effects.

Both *Neomysis* and prawns have the potential to directly and indirectly impact subyearling feeding and growth opportunity if their proliferation causes changes to the food web. In 2011, we began sampling Lower Granite and Little Goose reservoirs to collect basic information on these species. In addition, we also collected data on primary productivity,

Figure 1. Pictures of *Neomysis mercedis*.

Figure 2. Pictures of Siberian prawns *Exopalaemon modestus*.

Figure 3. Pictures of *Corophium* spp.

zooplankton, and surface drift. For this report, our objectives were to 1) describe the seasonal abundance and spatial distribution of *Neomysis* and prawns, 2) describe the seasonal changes in prawn population size structure, 3) describe the reproductive timing of prawns, and 4) describe the diet of prawns. This report summarizes data analyzed through November 2012.

METHODS

Sampling design and locations

We collected monthly samples in Lower Granite and Little Goose reservoirs from May 2011 to March 2013. Each reservoir was divided into an upper, middle, and lower reach to ensure that samples were collected over a broad spatial area. Within each reach, we established systematic sampling sites that were sampled each month. At these systematic sites, 100-m transects were initially selected at random and these sites became the fixed sampling transects. Roughly one-half of the transects was located in shallow water (<12 m) and one-half was located in deep water (>12 m). Systematic sites in Lower Granite Reservoir included Silcott Island (river kilometer [rkm] 211), Centennial Island (rkm 193), Wawawai (rkm 178.5), and Offield Landing (rkm 174.5). Systematic sites in Little Goose Reservoir included Illia (rkm 163), Tucker Bar (145.5), and New York Island (rkm 126.5). Additional sites were regularly sampled in each reservoir during the first year of sampling, but during the second year of sampling additional sites were selected randomly and sampled without replacement to increase our spatial variability.

Sample collection

We collected epibenthic invertebrates along 100-m transects using a beam trawl, also known as an epibenthic sled (Figure 4). The trawl had a rectangular opening that measured 2 m × 0.5 m and a net that was 3.7 m long, which tapered to a cod end. The trawl was constructed of 6.3 mm nylon delta mesh. The last 1.2 m of the cod end contained an internal liner constructed of 1.6-mm nylon delta mesh. Heavy nylon mesh was attached around the outside of the cod end to reduce chafing. The trawl frame had curved skids that allowed it to ride more smoothly along the reservoir bottom without getting snagged. A tickle chain was attached across the inside of the bottom of the frame in front of the trawl lead line to move benthic organism off the bottom during trawling so they could more easily be captured by the net.

The trawl was fished from an 8-m prop-driven boat equipped with two hydraulic winches, spools containing metered cable, and an A-frame and stantion support structure for deploying and retrieving the trawl (Figure 5). Beginning and ending waypoints for each transect were input in a GPS, which was used for navigation and to record the distance trawled. The trawl was deployed until it reached the bottom, which was determined based on the depth of the

Figure 4. Pictures of the 2-m beam trawl used to collect benthic invertebrates in Lower Granite and Little Goose reservoirs during 2011-2013.

Figure 5. Picture of the boat used to deploy a beam trawl to sample benthic invertebrates in Lower Granite and Little Goose reservoirs during 2011-2013.

water, the amount of cable deployed, and the angle of cable. The trawl was then towed a distance of 100 m along the bottom, and then retrieved. The trawl sample was poured through either a 500 or 600 μm sieve to remove silt and debris and then preserved in 90% ethanol. On many occasions when a large trawl sample was collected, a random subsample was preserved. In these instances, both the subsample and the remainder of the total sample were weighed (wet).

In each reservoir reach (upper, middle, lower) a water sample from the surface was collected monthly (May, 2011 to April, 2012) to measure turbidity in nephelometric turbidity units (NTU) with a portable turbidity meter. We also measured water clarity with a 20-cm Secchi disk. We pooled all data between the two reservoirs and expressed mean (±SE) turbidity and Secchi depth by month. These data were only collected during the first year of sampling.

We measured chlorophyll-a concentrations in the water during each month of sampling as an indicator of primary productivity of the pelagic habitats. Monthly water samples were collected in each reach of each reservoir. A volume of 100 ml of water was collected, stored in a light-proof container, and stored on ice until processing at the end of each day. Each water sample was concentrated onto a glass fiber filter paper by low vacuum filtration then frozen. In the laboratory, pigments were extracted in 90% acetone, for 24 hours at -20°C, then the extracted slurry was removed and its fluorescence was measured with a fluorometer. The concentration of chlorophyll-a was then calculated in μg/L.

Sample processing and analysis

Prawns.—All prawns were blotted to remove excess ethanol and then weighed individually (±0.001 g, wet). A subsample of prawns, encompassing a broad range in sizes, was selected to develop a carapace length-weight regression. These prawns were weighed and initially measured (±0.001 mm) from the tip of the rostrum to the back of the carapace at the dorsal midline. However, the rostrum was often broken, so we switched to measuring from the posterior margin of the eye orbit to the medial posterior margin of the carapace. Based on this measurement, weight could be predicted from measurements of carapace length (CL; eye orbit to posterior margin of the carapace), or vice versa, with the following equation:

$$\text{Weight} = 0.0006*\text{CL}^{3.0296}. \quad (1)$$

The R^2 for this regression was 0.97 (N=1,664). CLs based on rostrum measurements were converted to CLs based on the eye orbit measurements with the following regression:

$$\text{CL}_{\text{eye orbit}} = 0.5271*\text{CL}_{\text{rostrum}} - 0.1091. \quad (2)$$

The R^2 for this regression was 0.98 (N=555). All CLs referred to hereafter are based on the eye orbit measure.

The weights of all individual prawns within a sample were summed to determine the total weight of prawns for each sample. If the processed sample was a subsample, then its weight was multiplied by the subsampling rate to estimate a total sample weight. We pooled data within each reach (i.e., upper, middle, or lower), depth strata (i.e., deep or shallow), and by reservoir. We calculated and plotted mean monthly prawn density (#/m^2) and biomass (g wet/m^2). We then binned prawn carapace length data into 1-mm intervals for the two reservoirs and constructed monthly length-frequency histograms by depth strata to examine trends in size distributions.

We randomly selected 128 ovigerous prawns collected from July through December to estimate fecundity. We removed eggs from individual females, counted them, and weighed the total number (g, wet). We also weighed each prawn after the eggs had been removed to determine the percentage of the prawn weight (without eggs) that the eggs represented. This is analogous to the reproductive output calculation made for Siberian prawns by Oh et al. (2002).

We determined the monthly sex ratios of prawns collected in Little Goose Reservoir. We selected this reservoir because prawns are generally more abundant there than in Lower Granite Reservoir. We randomly selected 30-70 prawns (>10 mm CL) from samples collected primarily at systematic sites. Each prawn was measured and then two different morphological features were examined to differentiate between males and females. Females were distinguished by having a smooth ventral surface between the pleopods on the first two abdominal segments (Figure 6, panel A). In addition, the posterior-most pair of walking legs on the thorax was more widely spaced than on males and lacked a short ridge-like protuberance oriented along the ventral midline between this pair of legs (Figure 6, panel A). In contrast, males had pronounced protuberances oriented perpendicular to the ventral midline between the pleopods on the first two abdominal segments (Figure 6, panel B). The posterior-most pair of walking legs on the thorax was also more closely spaced than on females and there was a short ridge-like protuberance oriented along the ventral midline between this pair of legs (Figure 6, panel C). Sex ratios were plotted to show monthly trends over the two years of sampling.

Sex ratios were also determined for prawns collected at Lower Granite and Little Goose dams in 2013. Annual peak passage at the dams occurred during September and October. Personnel at the juvenile fish collection facilities saved the entire daily prawn sample at least once a week (sometimes daily) from mid-September to the end of October. All prawns were measured and had sex determined as described above. Plots were made of the weekly percent of females and males passing each dam.

The diet of prawns was summarized for Lower Granite Reservoir from samples collected monthly from May 2011 to March 2013. We randomly selected up to 48 prawns in each of three size classes (<4.3 mm CL, 4.3-9.1 mm CL, >9.1 mm CL); however, some size classes were not

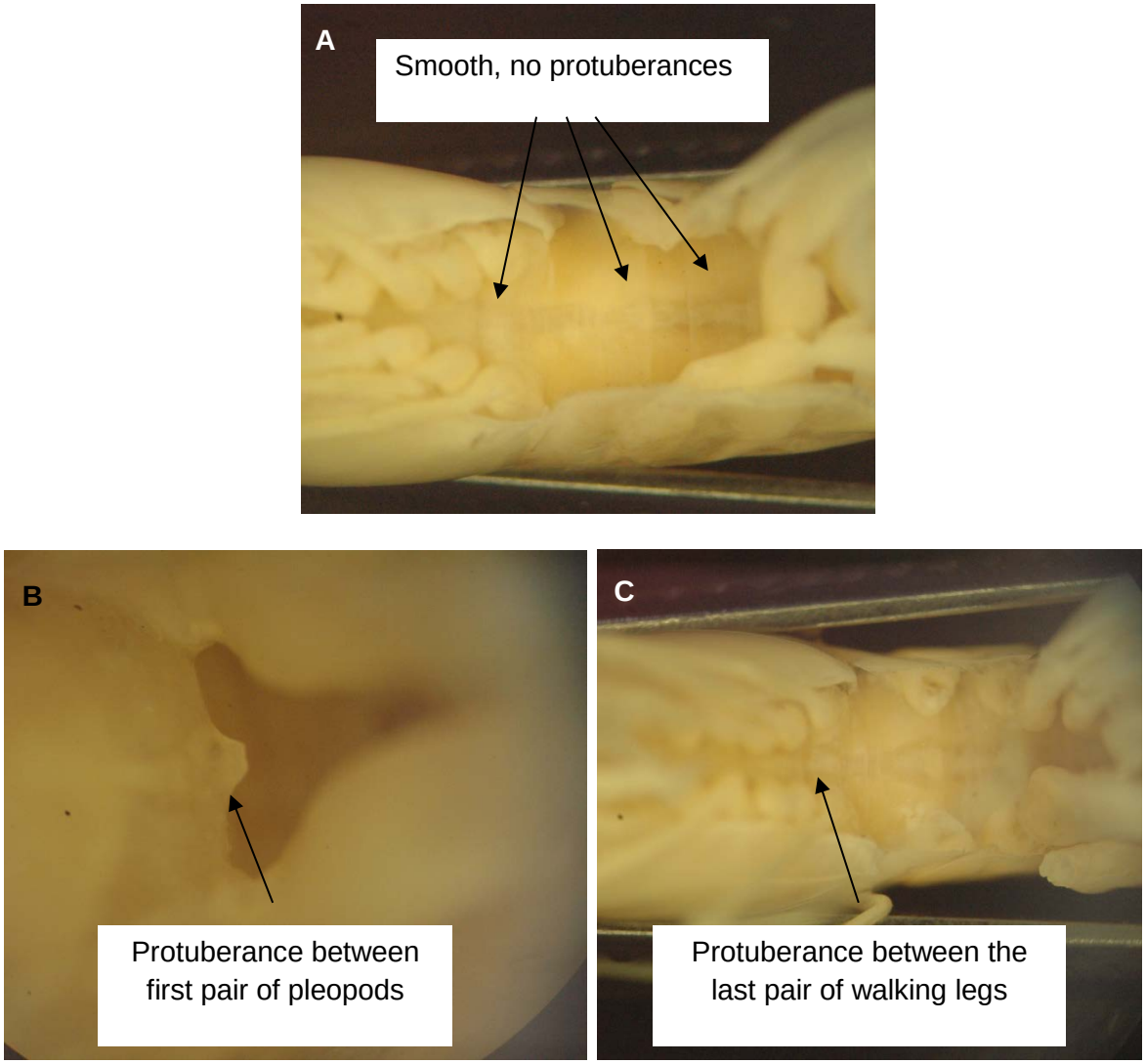

Figure 6. Characteristics used to distinguish between female (panel A) and male (panels B and C) Siberian prawns. All views are of the ventral surface. Each prawn is oriented with its head on the left side of the picture. Some of the pleopods have been removed to improve viewing.

present every month. Individual prawns were weighed, measured (CL), and had their stomach contents removed following carapace removal. Individual taxa were identified under a dissecting scope to the lowest practical level and each taxon was placed in a separate vial. The prey from different prawns were pooled by taxon within each sampling category (i.e., month and size category) to obtain sufficient mass for subsequent weighing. Each pooled taxon was dried at 60°C for 24 h and dry weights were recorded to the nearest 0.00001 g. Diet composition results were summarized by the proportion (by weight) of different prey taxa consumed, and examined for general seasonal and ontogenetic patterns.

Neomysis and Corophium.—All *Neomysis* from a given sample were blotted to remove excess ethanol and then weighed (±0.001 g, wet) collectively. *Neomysis* were counted and weighed collectively in each sample. If the processed sample was a subsample, then its weight was multiplied by the subsampling rate to arrive at a total sample weight. The number of *Neomysis* per gram of subsample was then multiplied by the total sample weight to determine the number of individuals in the sample. The same procedure was used to process *Corophium* in each sample. Densities and biomass of *Neomysis* and *Corophium* were calculated in the same manner as for prawns. Other invertebrate taxa that were collected were removed from each sample, identified to the lowest practical taxon, counted, and weighed.

RESULTS

Flows and temperatures were similar in Lower Granite and Little Goose reservoirs during our sampling (Figure 7). Flows were highest from May through July, decreased during winter, and then increased again the following spring. Temperatures increased from about 10°C in early May to a peak of around 20°C by August and then declined to a low of about 2.5°C during winter in both years (Figure 7). In 2011, turbidity was highest (17.8±0.25 NTU) in June coinciding with high flows and then declined thereafter to a low of 2.28±0.11 NTU in December (Figure 8). Similarly, water clarity was lowest (0.67±0.065 m) in June, 2011 and highest (3.61±0.17 m) in December, 2011 (Figure 8).

Chlorophyll-a concentrations showed seasonal trends at sampling sites in each reservoir. In Lower Granite Reservoir, chlorophyll-a concentrations increased from low levels in spring and early summer then peaked (depending on the site) in early autumn, and declined thereafter (Figure 9). Chlorophyll-a concentrations were generally highest at Offield (lower reach) during the summer and fall with the exception of August and September, 2012 when concentrations were higher at Centennial Island (middle reach). Chlorophyll-a concentrations were generally lowest at Silcott Island (upper reach; Figure 9). In Little Goose Reservoir, chlorophyll-a results were less clear due to times when samples were not collected. Chlorophyll-a concentrations increased from low levels in spring to peaks in the summer and autumn in both years but the magnitude of the peak at New York Island could not be fully ascertained in 2011. In both

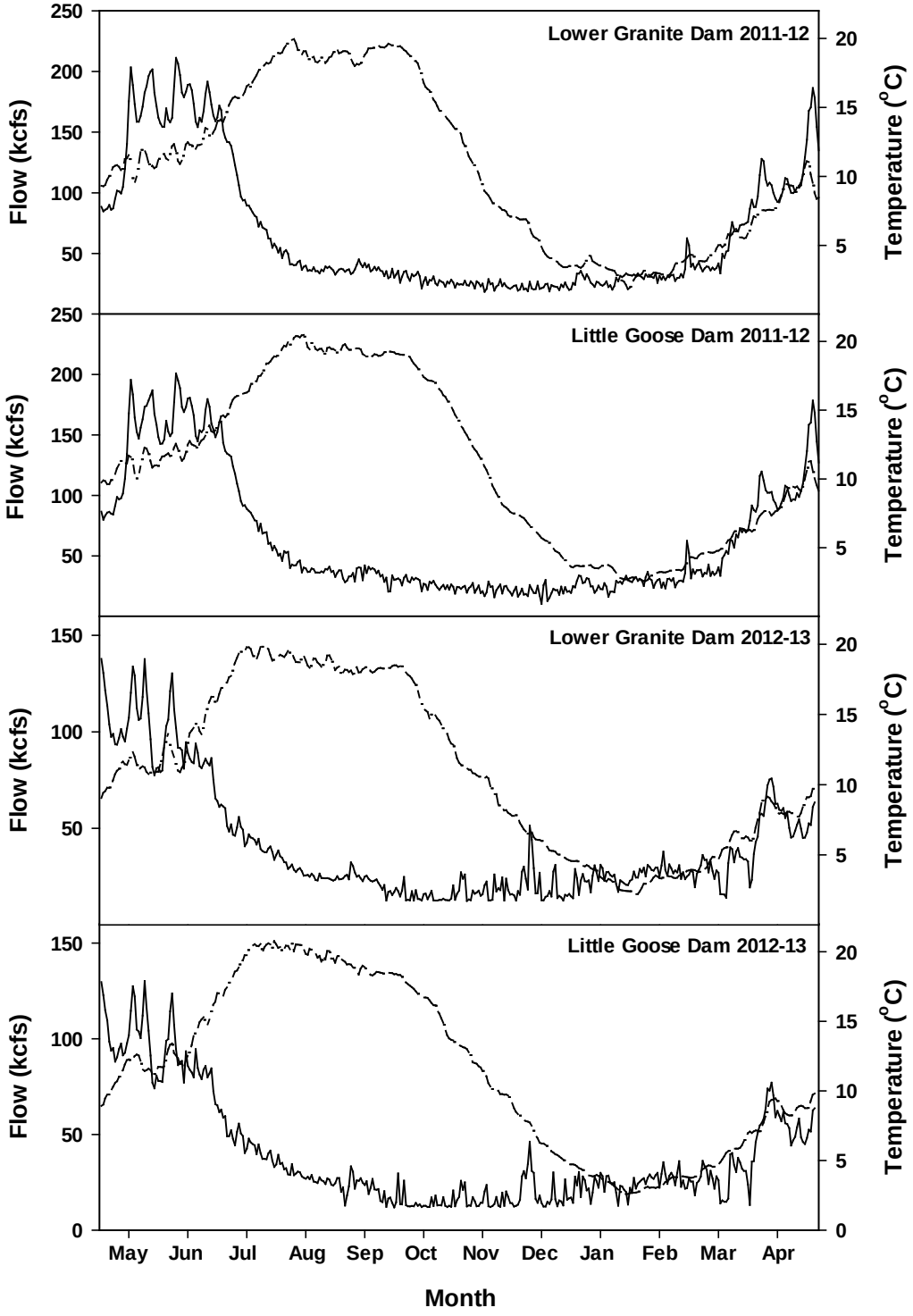

Figure 7. Daily mean flows (solid lines) and temperatures (dashed lines) recorded at Lower Granite and Little Goose dams from May, 2011 through April, 2012 (top two panels) and from May, 2012 through April, 2013 (bottom two panels).

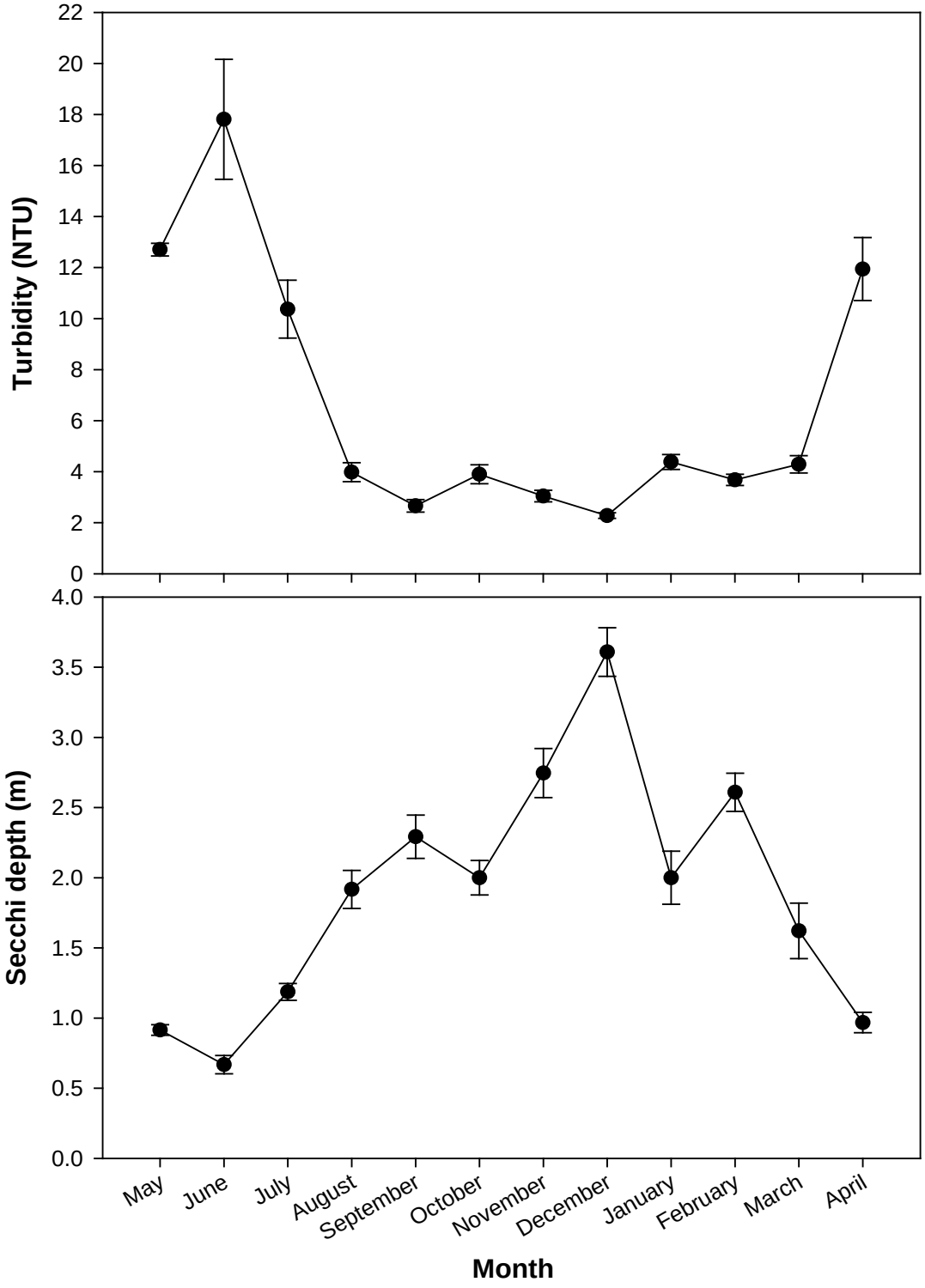

Figure 8. Monthly mean turbidity (±SE; top panel) and Secchi depth (±SE; bottom panel) measured in Lower Granite and Little Goose reservoirs (data pooled) from May, 2011 through April, 2012.

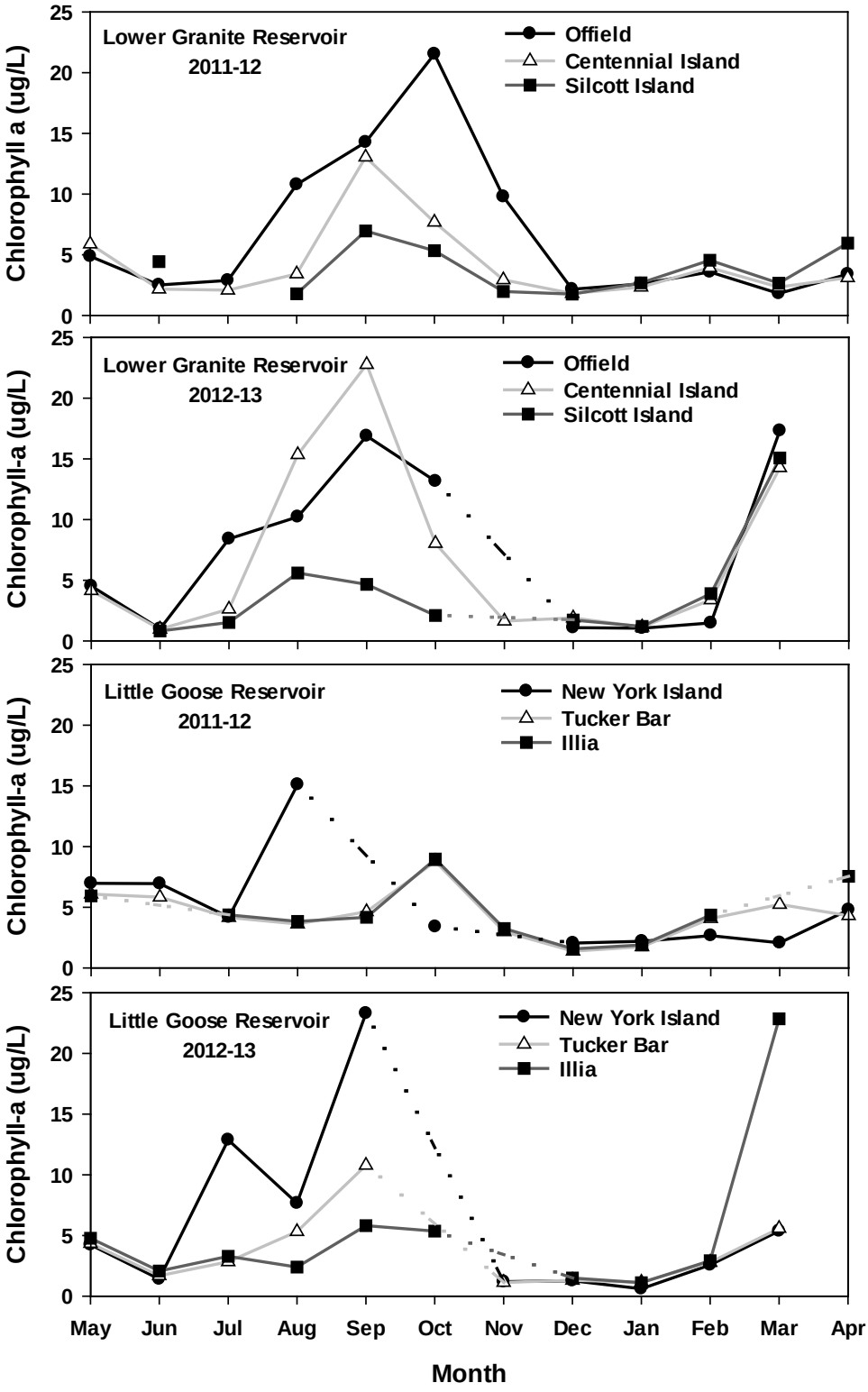

Figure 9. Monthly mean chlorophyll-a concentrations at three locations in Lower Granite Reservoir (top two panels) and Little Goose Reservoir (bottom two panels) in 2011-12 and 2012-13. Broken lines represent interpolations when data were missing.

reservoirs, chlorophyll-a concentrations began increasing in early spring 2013, at the end of our sampling.

We collected epibenthic invertebrates in 1,100 trawl samples from May, 2011 through November, 2012. Depth information on sample sites in Lower Granite and Little Goose reservoirs is shown in Table 1. *Neomysis* dominated the catch, composing 46-99% of samples in terms of both density and biomass (Table 2). At times we were not able to sample all sites within a month due to high winds, inclement weather, and unsafe trawling conditions.

Prawns

The presence of prawns was documented in all reaches of Lower Granite Reservoir, but their abundance showed considerable variation. Mean prawn densities in shallow sample sites were generally low in all reaches except on a few occasions in the middle and lower reaches (Figure 10). Prawns were generally more abundant at deep locations in the middle and lower reaches of Lower Granite Reservoir with peak densities occurring in August, November, February, and October (Figure 10). Prawns were never abundant at shallow or deep sites in the upper reach of Lower Granite Reservoir during all months sampled (Figure 10).

Trends in prawn abundance in Little Goose Reservoir were similar to those observed in Lower Granite Reservoir (Figure 10) and prawn presence was also documented in all reaches. Prawns were least abundant and sometimes absent in the upper portion of the reservoir. Abundances increased in a downstream direction and were generally highest in the lower reach (Figure 10). The highest densities were observed in autumn and winter months in the middle and lower reach. As in Lower Granite Reservoir, prawns were more abundant at deep locations in Little Goose Reservoir. On average, densities were over twice as high at deep compared to shallow sites (Figure 10). Prawns were generally more abundant in Little Goose Reservoir than in Lower Granite Reservoir. Grand mean density of prawns at deep sites in the lower reach of Little Goose Reservoir (0.492 prawns/m^2, SE=0.082) over all sampling months was four times higher than the mean density of prawns (0.121 prawns/m^2, SE=0.03) in the lower reach of Lower Granite Reservoir (Table 3). Grand mean density of prawns at deep sites in the middle reach of Little Goose Reservoir (0.127 prawns/m^2, SE=0.035) was almost two times higher than the mean density of prawns (0.069 prawns/m^2, SE=0.017) in the middle reach of Lower Granite Reservoir (Table 3).

Trends in prawn biomass generally followed those of prawn densities in both Lower Granite and Little Goose reservoirs (Figure 11). Prawn biomass was substantially higher at deep sample sites compared to shallow sample sites in both reservoirs (Figure 11). The biomass of prawns was generally higher in Little Goose Reservoir than in Lower Granite Reservoir. Grand mean biomass of prawns at deep sites in the lower reach of Little Goose Reservoir (0.214 g/m^2,

Table 1. Depth information on shallow and deep sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs that were sampled with a beam trawl from May, 2011 through November, 2012 to collect epibenthic invertebrates.

Site	N	Mean depth (m)	Standard deviation (m)	Minimum (m)	Maximum (m)
LGR Shallow	284	4.6	1.8	1.5	11.9
LGR Deep	248	22.3	6.2	12.2	36.0
LGO Shallow	318	7.1	2.6	2.4	11.9
LGO Deep	246	21.8	7.6	12.2	37.8

Table 2. Percent of catch of different epibenthic invertebrates based on density and biomass at shallow and deep sample sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs from May, 2011 through November, 2012.

Location	Prawns	Neomysis	Corophium	Corbicula	Other
Based on density (#/m^2)					
LGR Shallow	<1%	99%	<1%	<1%	<1%
LGR Deep	<1%	98%	1%	<1%	<1%
LGO Shallow	<1%	99%	<1%	<1%	<1%
LGO Deep	<1%	93%	4%	2%	<1%
Based on biomass (g/m^2)					
LGR Shallow	<1%	98%	<1%	<1%	<1%
LGR Deep	11%	83%	<1%	4%	1%
LGO Shallow	1%	97%	<1%	1%	<1%
LGO Deep	24%	46%	<1%	29%	<1%

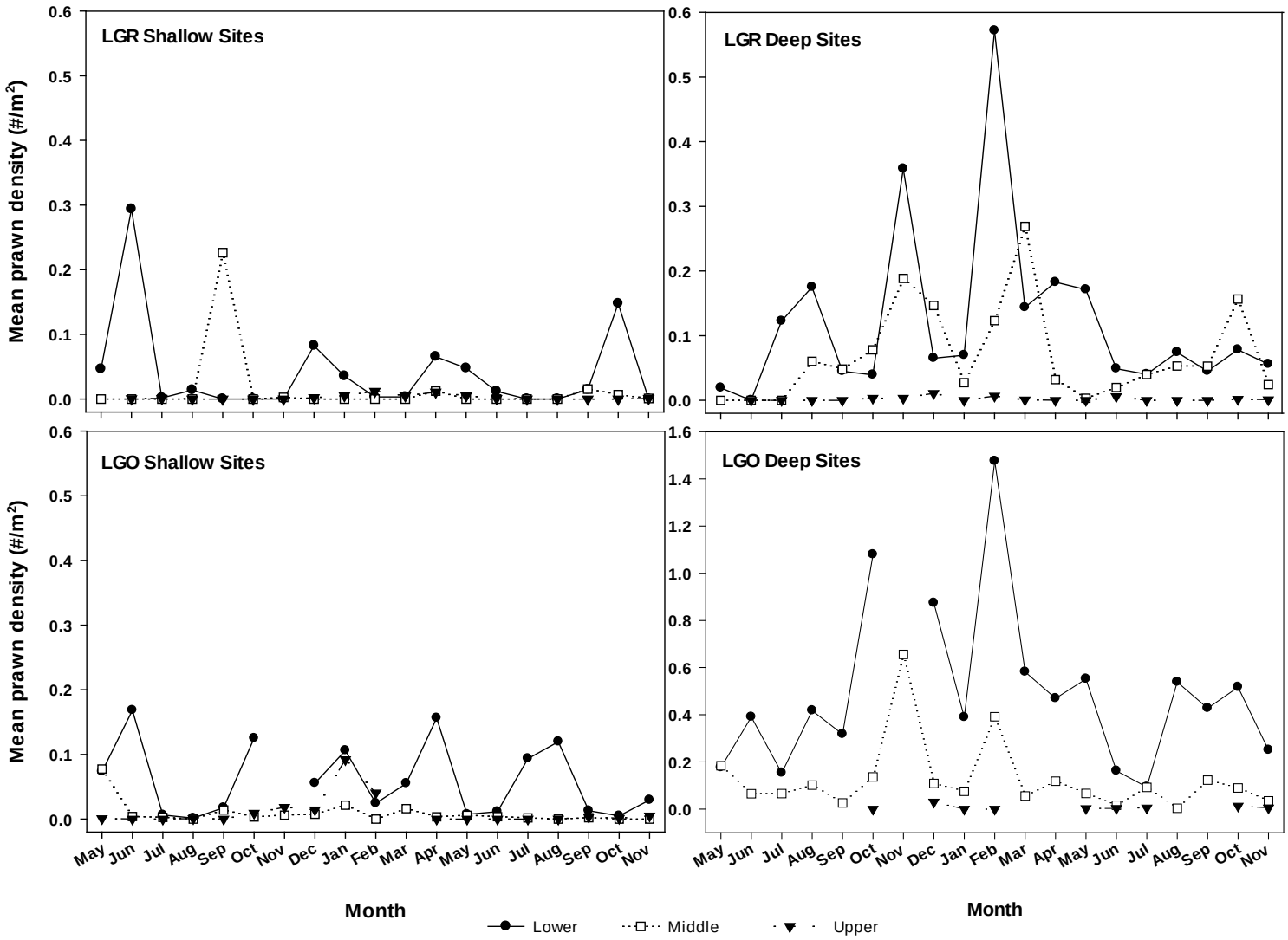

Figure 10. Monthly prawn densities at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Densities are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

Table 3. Densities and biomasses of Siberian prawns collected monthly with a beam trawl in Lower Granite (LGR) and Little Goose (LGO) reservoirs from May, 2011 through November, 2012. *N* is the number of monthly samples used to calculate grand means and standard errors (SE).

				Density (#/m^2)		Biomass (g/m^2)	
Reservoir	Depth stratum	Reach	*N*	Mean	SE	Mean	SE
LGR	Deep	Lower	19	0.121	0.031	0.074	0.018
		Middle	19	0.069	0.017	0.078	0.018
		Upper	18	0.002	0.001	0.001	0.0004
	Shallow	Lower	19	0.040	0.017	0.016	0.014
		Middle	19	0.014	0.012	0.001	0.0006
		Upper	18	0.002	0.001	0.001	0.0005
LGO	Deep	Lower	18	0.492	0.082	0.214	0.031
		Middle	19	0.127	0.035	0.084	0.018
		Upper	9	0.006	0.003	0.001	0.007
	Shallow	Lower	18	0.059	0.013	0.007	0.003
		Middle	19	0.009	0.004	0.006	0.004
		Upper	18	0.010	0.005	0.103	0.005

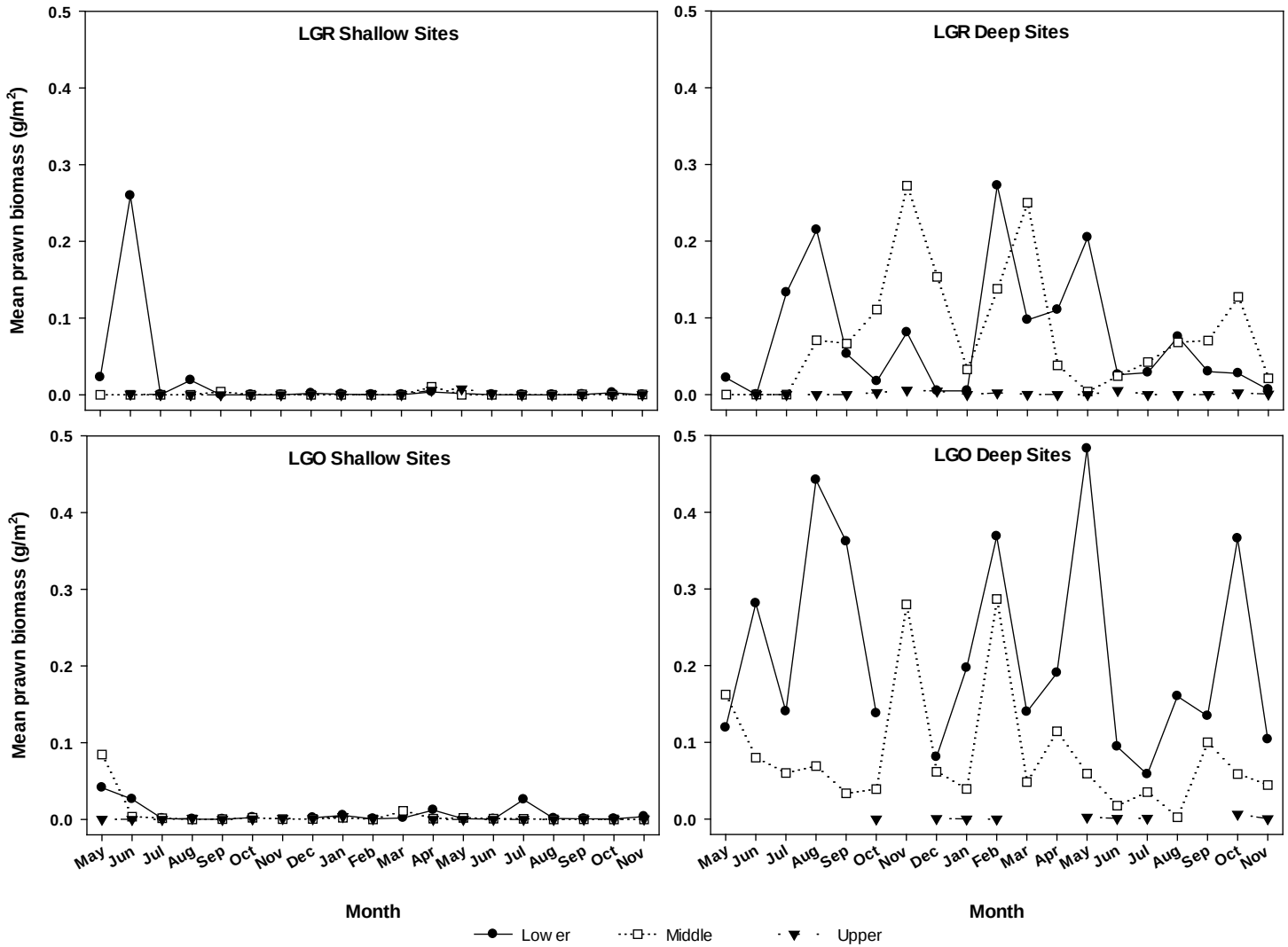

Figure 11. Monthly prawn biomass at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Biomasses are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

SE=0.031) over all sampling months was three times higher than the mean biomass of prawns (0.074 prawns/m^2, SE=0.018) in the lower reach of Lower Granite Reservoir (Table 3). Grand mean biomasses of prawns at deep sites in the middle reaches of Little Goose Reservoir (0.084 g/m^2, SE=0.018) and Lower Granite Reservoir (0.078 g/m^2, SE=0.018) were similar (Table 3).

Carapace length-frequency distributions showed seasonal variation in the presence of different size classes of prawns. For both reservoirs and depth strata combined, two apparent size classes of prawns became evident in September, 2011 and August, 2012 (Figure 12). The smaller prawns were the product of summer spawning that had recruited to the population while the larger prawns were adults. From October, 2011 through April, 2012, juvenile prawns were far more abundant than adults, whose abundance remained low (Figures 13 and 14). After April, 2012, the abundance of adult prawns increased as juvenile prawns recruited to the adult population, which was apparently complete by August 2012. Figures 13 and 14 show seasonal carapace length frequency distributions by depth stratum. When present, juvenile prawns were collected at both shallow and deep sites, but few adult prawns were collected at shallow sites by comparison. With the exception of May, 2011, most adult prawns were collected in deep water. Carapace length-frequency distributions suggest that the life span of prawns in lower Snake River reservoirs is little more than one year.

In 2011, ovigerous female prawns were first collected in Lower Granite Reservoir in July and in Little Goose Reservoir in May (Figure 15). In 2011, peak numbers of egg-bearing females occurred in July and August in Lower Granite Reservoir and were last collected in November. In Little Goose Reservoir, a peak of 135 ovigerous females were collected in September, and were present in collections through January, 2012 (Figure 15). In 2012, ovigerous females were first collected in July in both reservoirs, and the last ovigerous female was collected in October (Figure 15). Most females with eggs were collected during summer and early autumn months, suggesting that spawning occurs during this time. More ovigerous prawns were collected in Little Goose Reservoir than in Lower Granite Reservoir in 2011, but the opposite was true in 2012, with the exception of the month September (Figure 15). A total of 128 ovigerous females were examined for fecundity (Table 4). Ovigerous females had a mean carapace length of 12.7 mm (SD=1.5 mm; range 9–16.3 mm) and a mean total weight of 1.4 g (SD=0.4 g; range 0.7–2.4 g). The mean number of eggs per female was 189 (SD=55; range 66–332) and on average constituted 11.9% of total body weight (range 1.7–23.5%).

The ratio of female to male prawns showed consistent seasonal variation in Little Goose Reservoir between the two years of sampling (Figure 16). Male prawns were generally more prevalent except during the fall and winter months in 2011-12 and during September and October, 2012 (Figure 16). Of the prawns collected during the peak of passage at Lower Granite

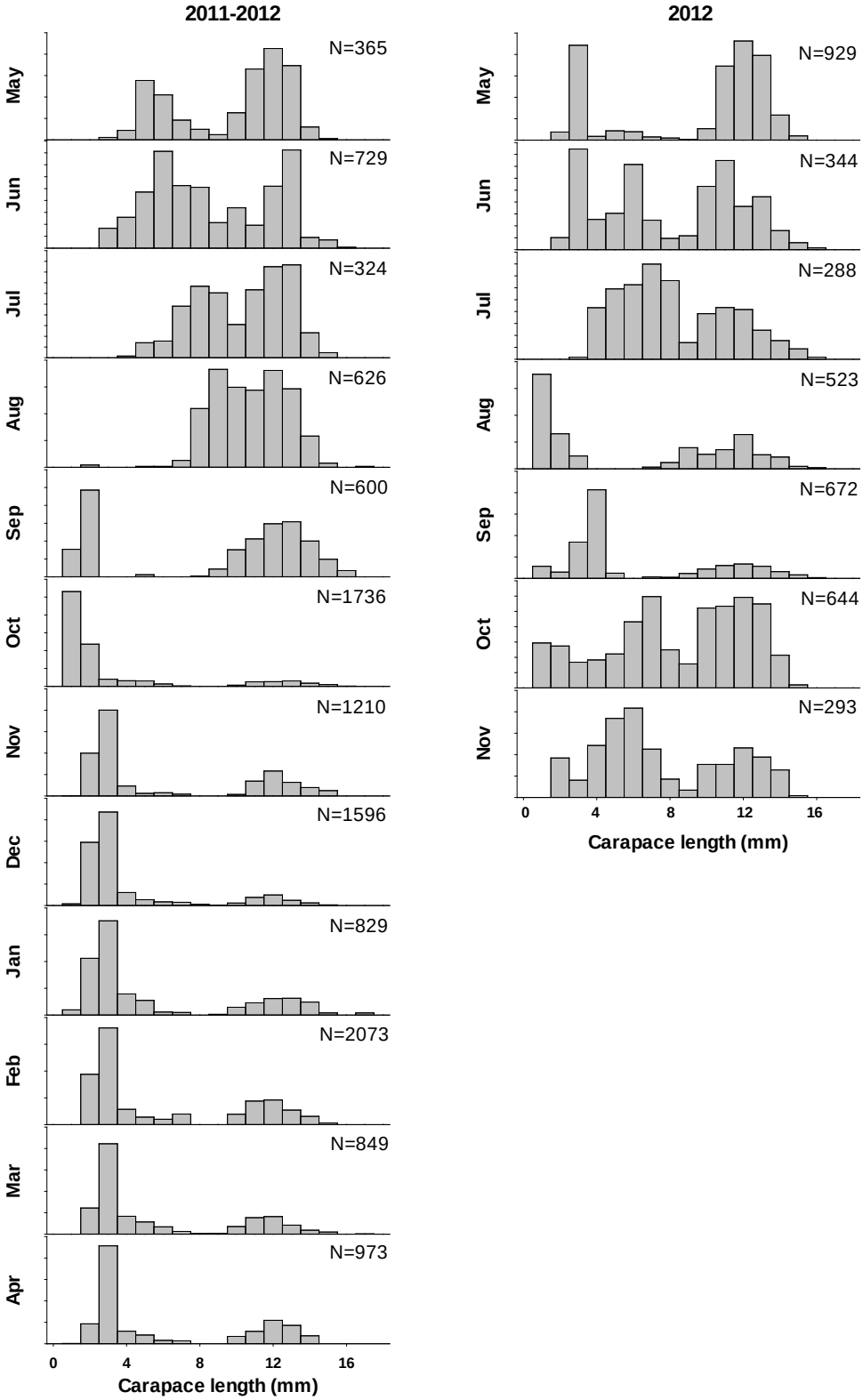

Figure 12. Relative length-frequency histograms of prawns collected from Lower Granite and Little Goose reservoirs (combined) from May, 2011 through November, 2012.

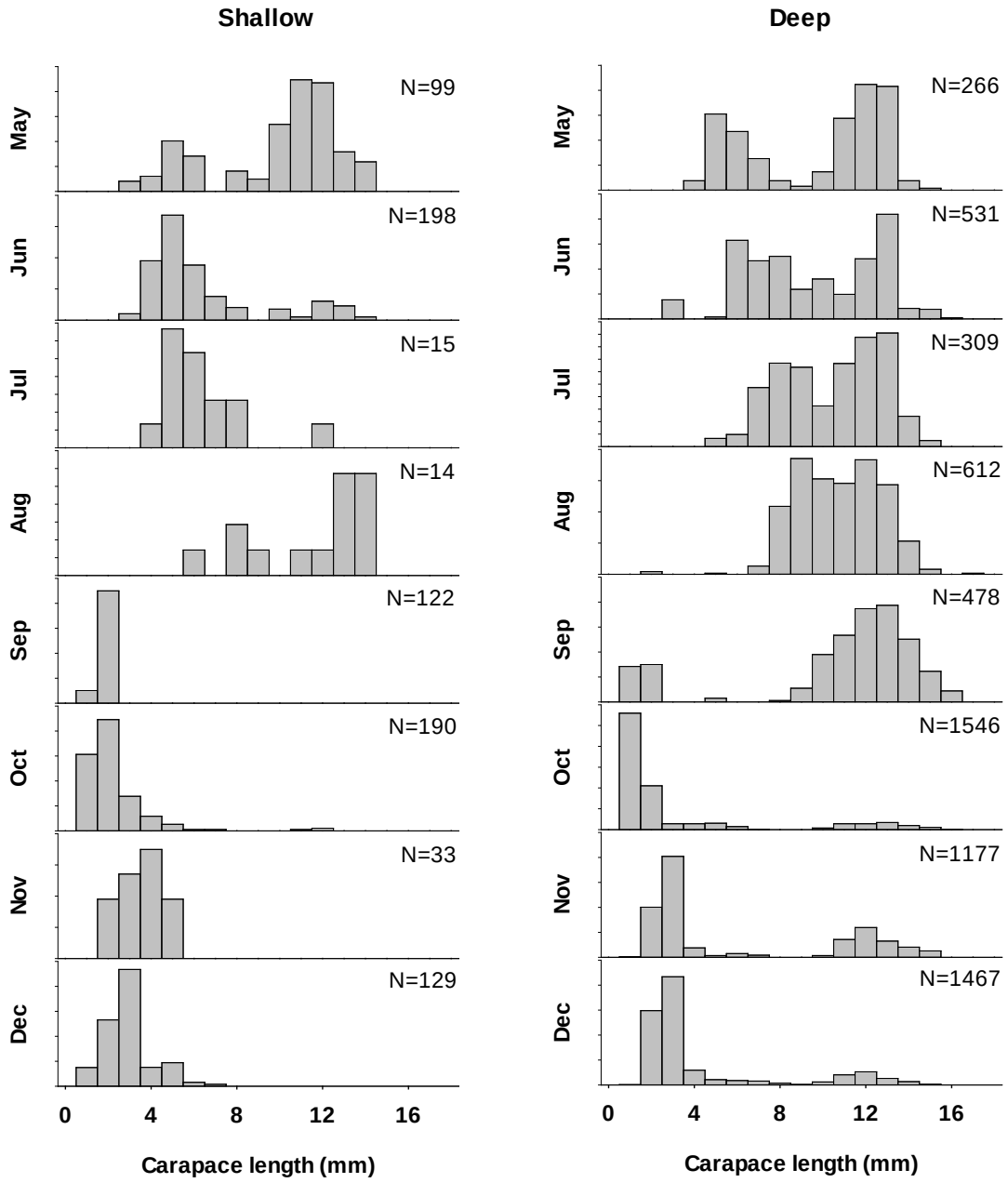

Figure 13. Relative length-frequency histograms of prawns collected from shallow and deep sites in Lower Granite and Little Goose reservoirs (combined) from May through December, 2011.

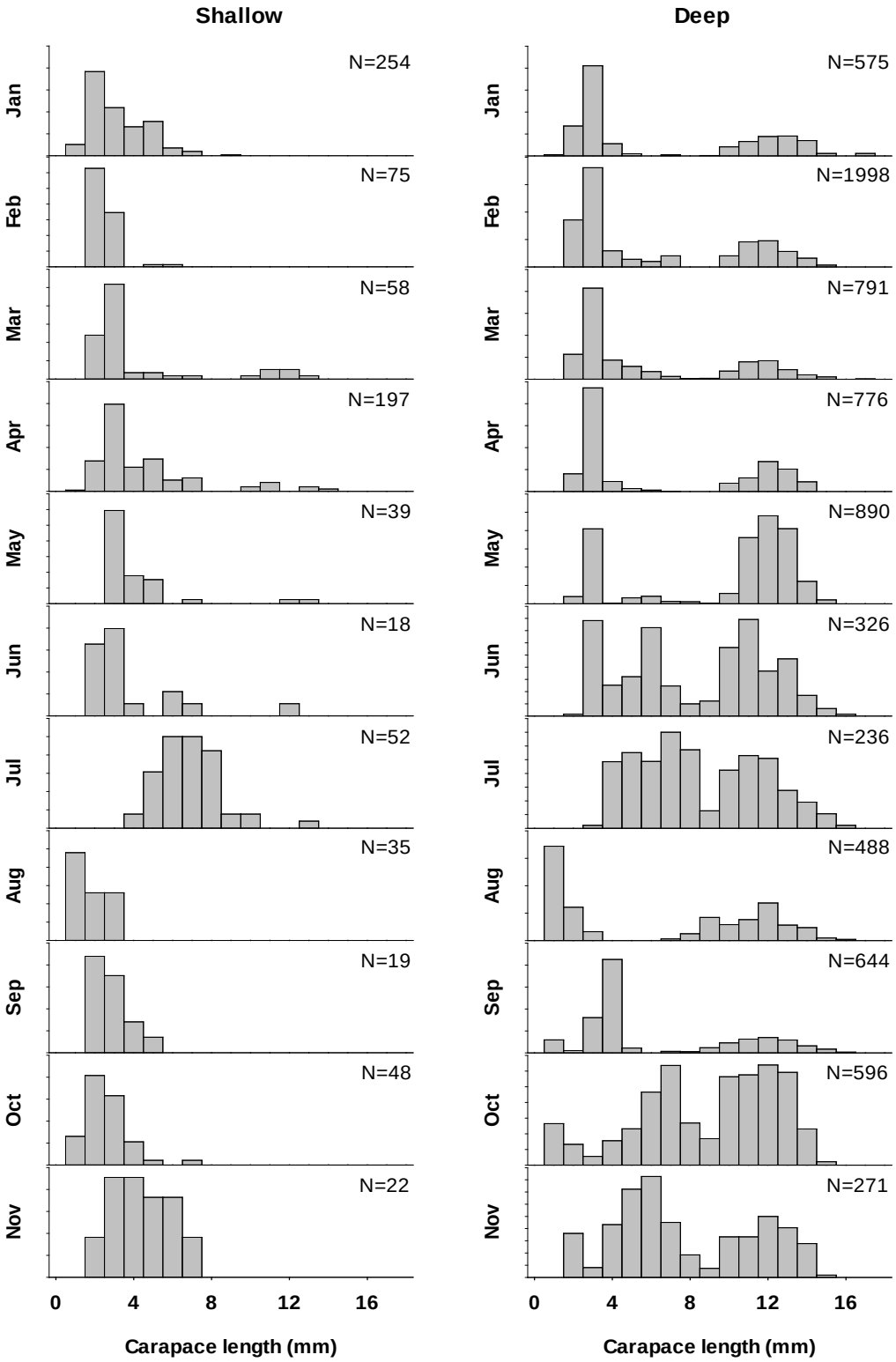

Figure 14. Relative length-frequency histograms of prawns collected from shallow and deep sites in Lower Granite and Little Goose reservoirs (combined) from January through November, 2012.

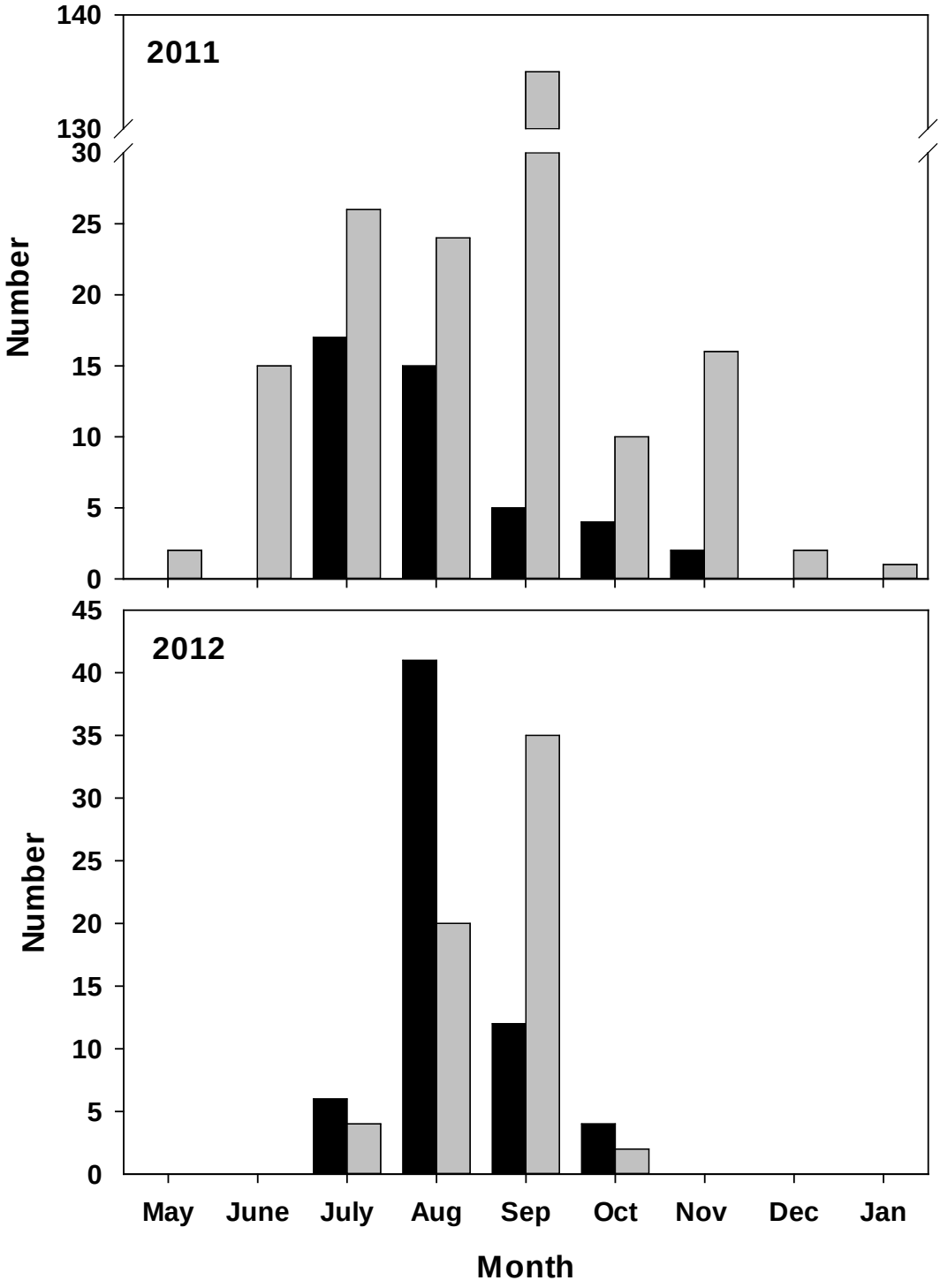

Figure 15. Number of ovigerous prawns collected in Lower Granite Reservoir (black bars) and Little Goose Reservoir (gray bars) from May to January, 2011 (top panel) and from May to November, 2012 (bottom panel).

Table 4. Summary of fecundity information from Siberian prawns collected in Lower Granite and Little Goose reservoirs during 2011-2012. *N* is the number of prawns examined.

Metric	*N*	Mean	SD	Range
Egg count	128	189	54.9	66-332
Percent egg mass[1]	122	11.9	4.6	2.6-20
Carapace length (mm)	127	12.7	1.5	9-16.3
Total prawn and egg mass (g)	129	1.4	0.4	0.7-2.4

[1] (egg mass / prawn mass without eggs) * 100

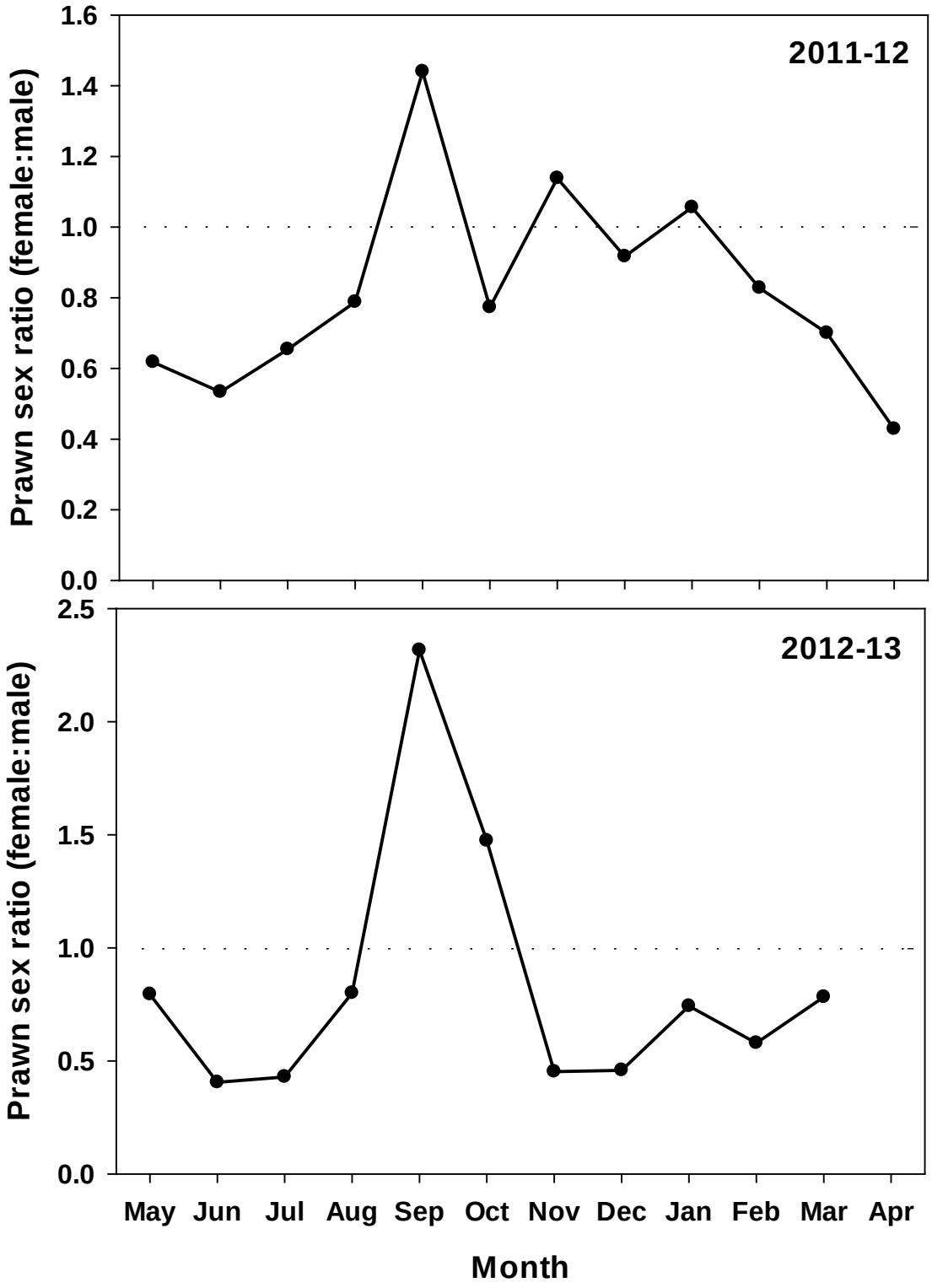

Figure 16. Monthly sex ratios of Siberian prawns collected in Little Goose Reservoir by beam trawling during 2011-12 (top panel) and 2012-13 (bottom panel). Data above the dashed reference line indicate more females than males in the population.

and Little Goose dams during September and October, 2013, the majority were females (Figure 17).

The stomach contents of 678 prawns were examined to describe their diet in Lower Granite Reservoir. Prawns primarily consumed *Neomysis*, detritus, dipterans, oligochaetes, and amphipods (Table 5). *Neomysis* composed the majority of the diet for all size classes. *Neomysis* composed 88% of the diet of large prawns (>9.1 mm CL), 69% of the diet of medium prawns (4.3-9.1 mm CL), and 59% of the diet of small prawns (<4.3 mm CL; Table 5). In contrast, the percentage of detritus and amphipods (Gammaridae) in the diet increased with decreasing prawn size. The highest percentage of dipterans (8.9) was consumed by medium-size prawns and large prawns consumed the most oligochaetes, albeit a low percentage (3.0). Other prey consumed were Bivalvia, Cladocera, *Corophium* spp., Ephemeroptera, Ostracoda, Polychaeta, Simuliidae, and Trichoptera.

Neomysis

Neomysis abundance varied considerably by season, depth, and reach in Lower Granite and Little Goose reservoirs (Figure 18). In both reservoirs, grand mean densities of *Neomysis* at shallow sites were often twice as high as at deep sites (Table 6). The highest mean densities of *Neomysis* in Lower Granite Reservoir were observed at shallow sites in the middle (grand mean = 135.2 mysids/m^2, SE = 24.7) and upper (grand mean = 74.6 mysids/m^2, SE = 14.7) reaches, whereas in Little Goose Reservoir, the highest densities were observed at shallow sites in the lower reach (grand mean = 51.9 mysids/m^2, SE = 15.0; Table 6). In Lower Granite Reservoir, *Neomysis* densities approached a maximum of nearly 400 mysids/m^2 at shallow sites in the middle reach in September, 2012 and a maximum of 230 mysids/m^2 at deep sites in the middle reach in November, 2011 (Figure 18). In Little Goose Reservoir, *Neomysis* densities approached a maximum of nearly 300 mysids/m^2 at shallow sites in the lower reach in September, 2012 and a maximum of 100 mysids/m^2 at deep sites in the lower reach in November, 2011 (Figure 18).

Neomysis were generally more abundant in Lower Granite Reservoir than in Little Goose Reservoir. Within shallow sites, grand mean density of *Neomysis* in the upper reach of Lower Granite Reservoir (74.5 mysids/m^2) was over four times higher than in the upper reach of Little Goose Reservoir (17.2 mysids/m2; Table 6). At shallow, middle reach sites, *Neomysis* densities were over five times higher in Lower Granite (135.2 mysids/m^2) than in Little Goose Reservoir (25.9 mysids/m^2). At shallow, lower reach sites, densities were only slightly higher in Lower Granite Reservoir (57.4 mysids/m^2) than in Little Goose Reservoir (51.9 mysids/m^2). Within deep sites, grand mean density of *Neomysis* in the upper reach of Lower Granite Reservoir (28.2 mysids/m^2) was over two and a half times higher than in the upper reach of Little Goose Reservoir (9.6 mysids/m2; Table 6). At deep, middle reach sites, *Neomysis* densities were about four times higher in Lower Granite (55.3 mysids/m^2) than in Little Goose Reservoir (14.1 mysids/m^2). At deep, lower reach sites, densities were only slightly lower in Lower Granite

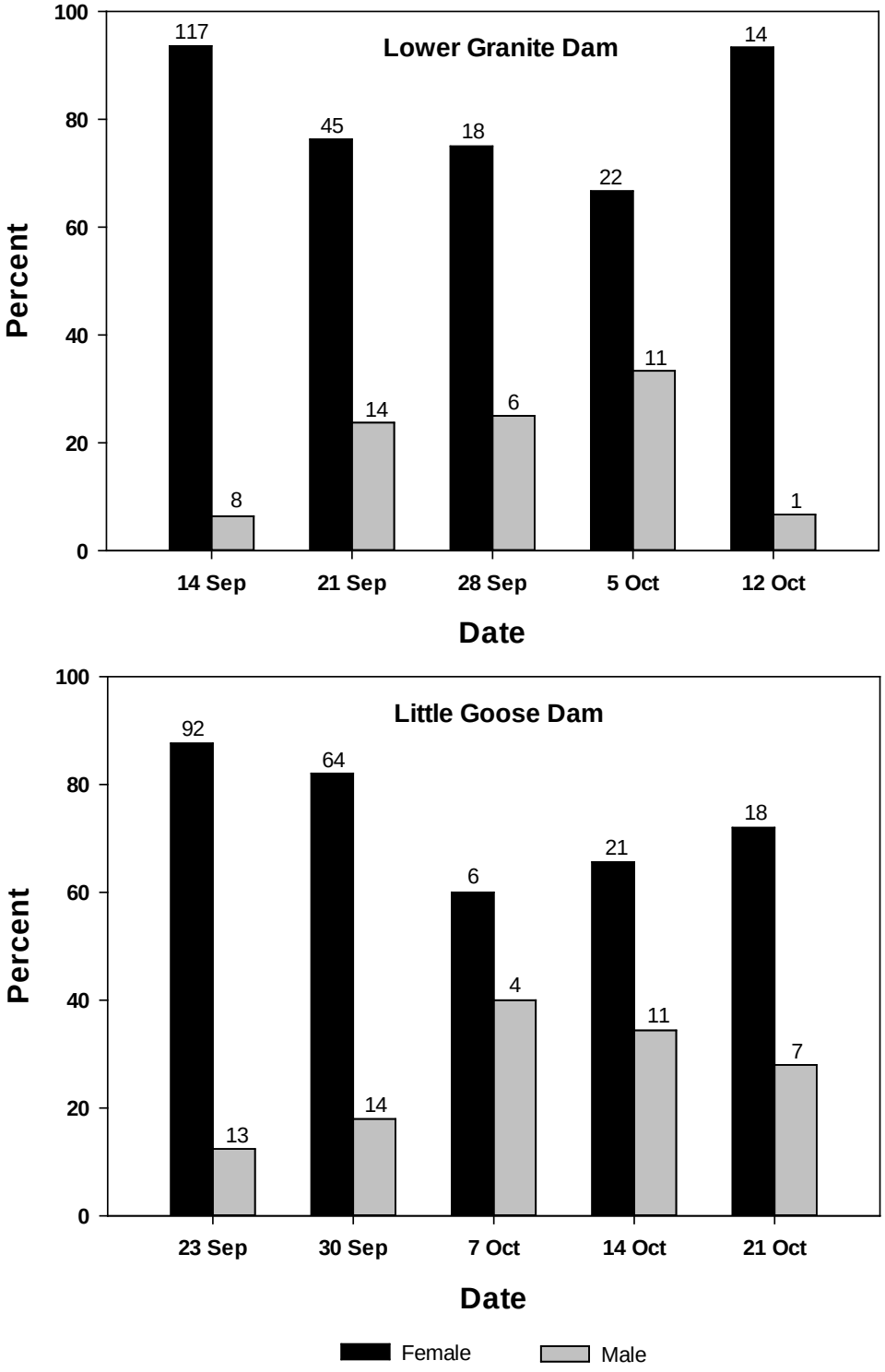

Figure 17. Percentages of female and male Siberian prawns collected at Lower Granite and Little Goose dams in 2013. The number above each bar represents the sample size.

Table 5. Contribution (percent by weight) of identifiable prey taxa to the diets of three size classes of Siberian prawns collected in Lower Granite Reservoir from May, 2011 through March, 2013. *N* is the number of prawns containing a specific prey.

	Large (>9.1 mm CL)		Medium (4.3-9.1 mm CL)		Small (<4.3 mm CL)	
Taxon or category	*N*	Percent	*N*	Percent	*N*	Percent
Neomysis	116	88.5	38	68.8	7	59.0
Detritus	33	2.9	23	12.5	5	15.3
Diptera	19	3.8	7	8.9	0	0
Oligochaeta	11	3.0	3	2.1	0	0
Amphipods	6	1.6	4	6.0	2	17.4
Other[1]	6	0.2	3	1.7	3	8.3
Unidentified	208		137		59	
Prawns containing identifiable food	191		78		17	
Empty	58		84		57	
Total examined	295		256		127	

[1] Includes Bivalvia, Cladocera, *Corophium* spp., Ephemeroptera, Ostracoda, Polychaeta, Simuliidae, and Trichoptera

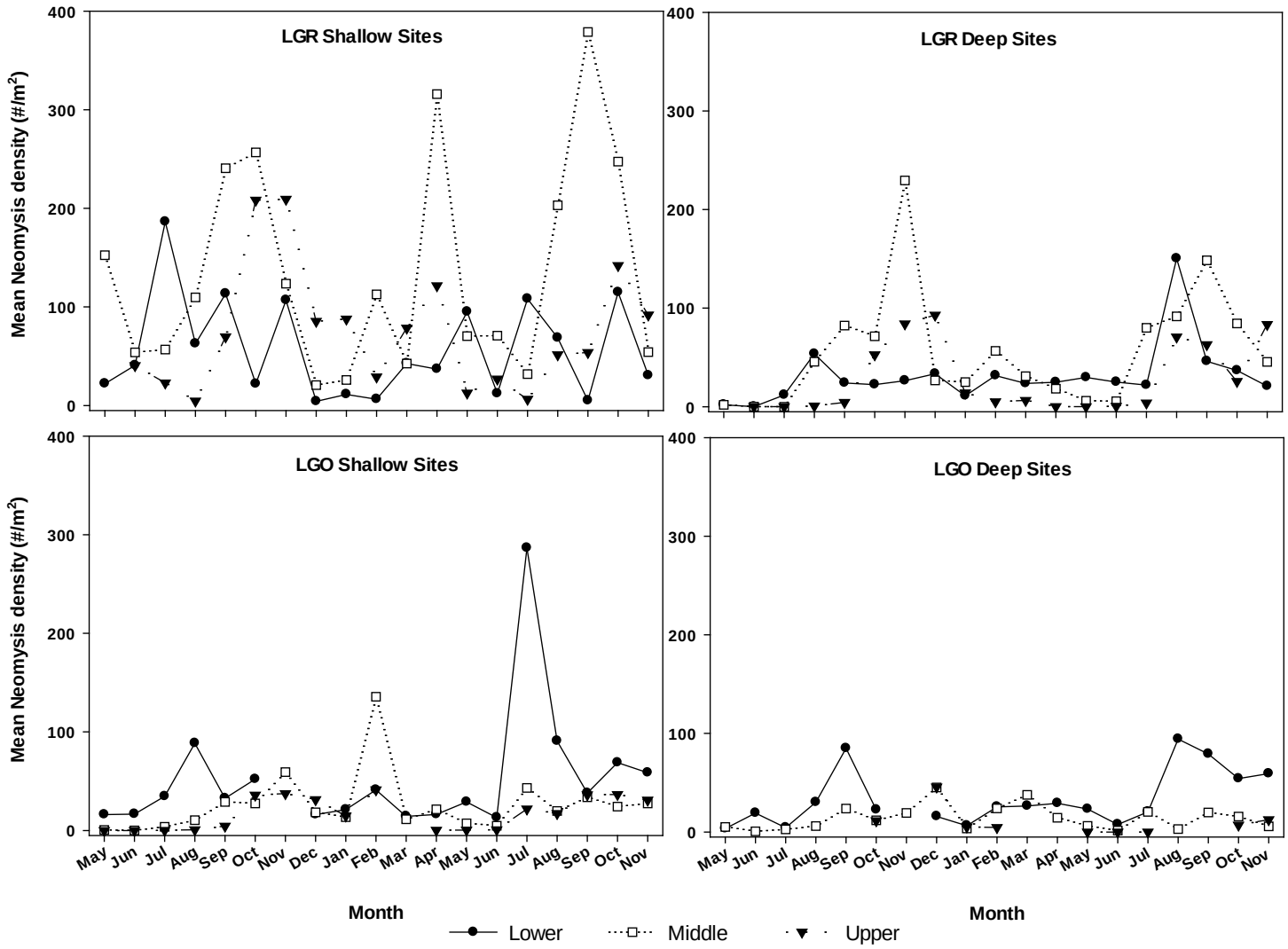

Figure 18. Monthly *Neomysis mercedis* densities at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Densities are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

Table 6. Densities and biomasses of *Neomysis mercedis* collected monthly with a beam trawl in Lower Granite (LGR) and Little Goose (LGO) reservoirs from May, 2011 through November, 2012. *N* is the number of monthly samples used to calculate grand means and standard errors (SE).

				Density (#/m^2)		Biomass (g/m^2)	
Reservoir	Depth stratum	Reach	*N*	Mean	SE	Mean	SE
LGR	Deep	Lower	19	31.4	7.3	0.278	0.048
		Middle	19	55.3	13.3	0.482	0.112
		Upper	18	28.2	8.3	0.238	0.068
	Shallow	Lower	19	57.4	11.6	0.484	0.119
		Middle	19	135.2	24.7	1.088	0.230
		Upper	18	74.6	14.7	0.702	0.144
LGO	Deep	Lower	18	33.7	6.7	0.368	0.056
		Middle	19	14.1	2.9	0.161	0.036
		Upper	9	9.6	4.8	0.088	0.039
	Shallow	Lower	18	51.9	15.0	0.470	0.098
		Middle	19	25.9	7.0	0.253	0.079
		Upper	18	17.2	3.9	0.141	0.032

Reservoir (31.4 mysids/m^2) than in Little Goose Reservoir (33.7 mysids/m^2). *Neomysis* biomass followed trends similar to that of density in both reservoirs (Figure 19; Table 6).

Corophium

In contrast to *Neomysis*, *Corophium* were not very abundant in beam trawl catches in either reservoir (Figure 20). At shallow sites in Lower Granite Reservoir, *Corophium* densities were consistently low in all reaches, but some peaks were observed in the middle and lower reaches during the summer months. At deep sites in Lower Granite Reservoir, *Corophium* were generally more abundant in the lower and middle reaches, but the highest abundance was observed in the upper reach in December (Figure 20). In Little Goose Reservoir, *Corophium* were also generally not abundant at shallow sites, but peaks in abundance were observed in September, 2011 in both the lower and middle reaches (Figure 20). At deep sites in Little Goose Reservoir, the highest *Corophium* abundances were observed primarily in the lower reach in September, 2011 and May, 2012. Within shallow and deep sites in Lower Granite Reservoir, grand mean densities typically increased in a downstream direction with the exception of deep sites in the middle reach, which had the highest observed densities (0.41 organisms/m^2; Table 7). In both deep and shallow sites in Little Goose Reservoir, *Corophium* densities consistently increased from the upper to lower reservoir (Table 7).

Trends in *Corophium* biomass generally followed those of abundance in both reservoirs (Figure 21). Extremely high biomasses (>0.17 g/m^2) were observed at shallow sites in the middle reach of Lower Granite Reservoir in September, 2011 and March, 2012 and in the lower reach in July, 2011 (Figure 21). Otherwise, biomasses at shallow sites were generally <0.001 g/m^2. At deep sites in Lower Granite Reservoir, monthly biomasses were variable, and apart from a few peaks exceeding 0.002 g/m^2, most biomass estimates were lower than this. In Little Goose Reservoir, *Corophium* biomass peaked at shallow sites in the lower and middle reaches in September, 2011 (Figure 21). A similar peak was also observed during this month at deep sites, and then again during May, 2012.

DISCUSSION

In Lower Granite and Little Goose reservoirs, the seasonal abundance of prawns was highly variable which made it difficult to detect trends. Prawns were generally more abundant in deep water than in shallow water, but were present in both habitats throughout the year. Juvenile prawns were collected at both shallow and deep sites but juveniles composed the majority of the catch in shallow waters where adult prawns were largely absent during most months. It is possible that juvenile prawns used shallow water for rearing to a greater extent than deeper water. This is plausible since water velocities are probably lower in those areas which may make that habitat more suitable for juvenile prawns with lower swimming capacity. Larger prawns were mainly found in deep water suggesting that they may prefer that habitat once they become

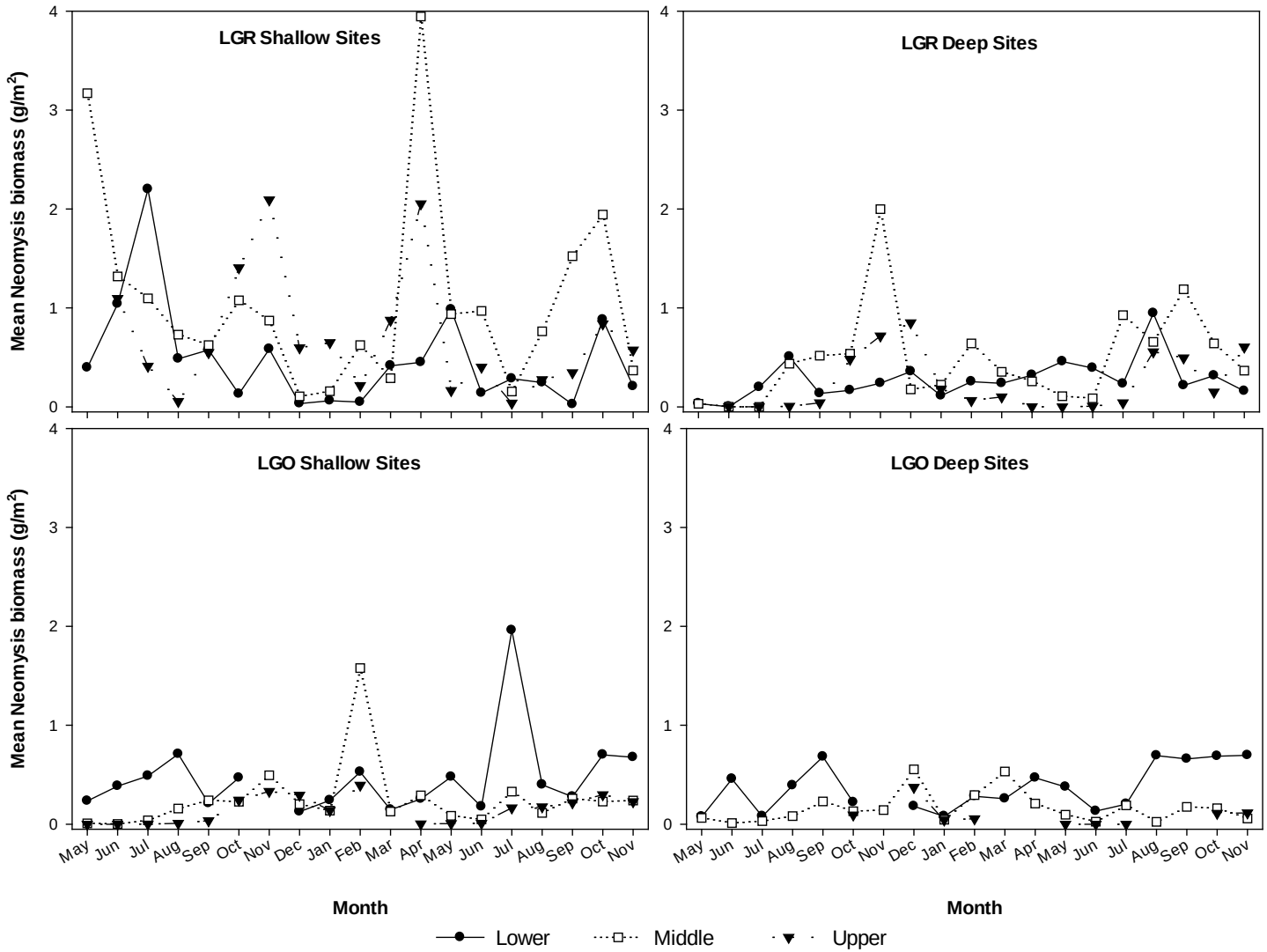

Figure 19. Monthly *Neomysis mercedis* biomass at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Biomasses are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

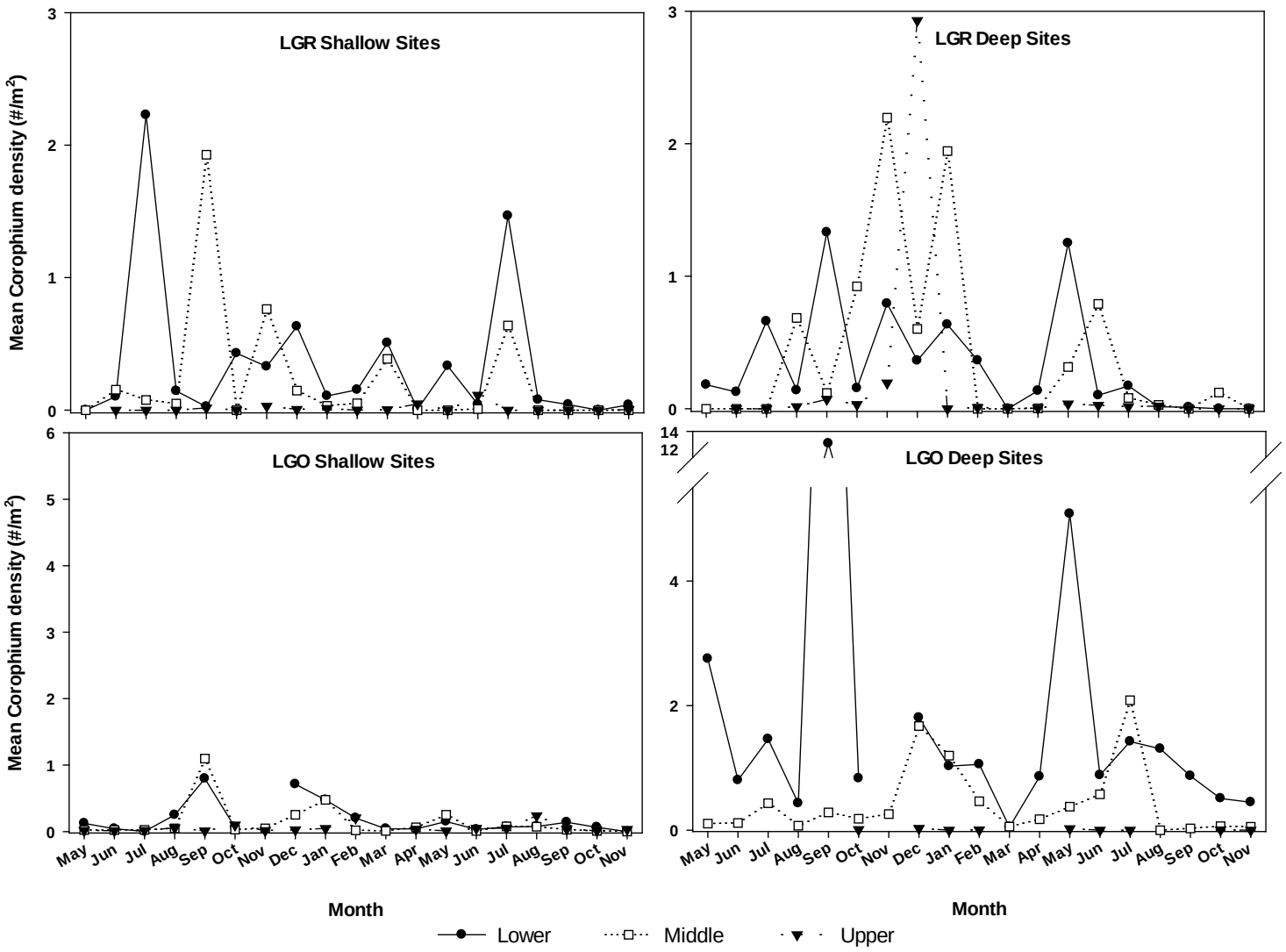

Figure 20. Monthly *Corophium* spp. densities at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Densities are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

Table 7. Densities and biomasses of *Corophium* spp. collected monthly with a beam trawl in Lower Granite (LGR) and Little Goose (LGO) reservoirs from May, 2011 through November, 2012. *N* is the number of monthly samples used to calculate grand means and standard errors (SE).

				Density (#/m^2)		Biomass (g/m^2)	
Reservoir	Depth stratum	Reach	*N*	Mean	SE	Mean	SE
LGR	Deep	Lower	19	0.34	0.09	0.0008	0.0003
		Middle	19	0.41	0.15	0.0006	0.0002
		Upper	18	0.19	0.16	0.0003	0.0002
	Shallow	Lower	19	0.35	0.13	0.0005	0.0002
		Middle	19	0.22	0.11	0.0110	0.0108
		Upper	18	0.01	0.01	0.00004	0.00003
LGO	Deep	Lower	18	1.90	0.68	0.0066	0.0024
		Middle	19	0.43	0.13	0.0007	0.0002
		Upper	9	0.01	0.004	0.00003	0.00001
	Shallow	Lower	18	0.18	0.06	0.0004	0.0002
		Middle	19	0.14	0.06	0.0003	0.0002
		Upper	18	0.05	0.02	0.00007	0.00002

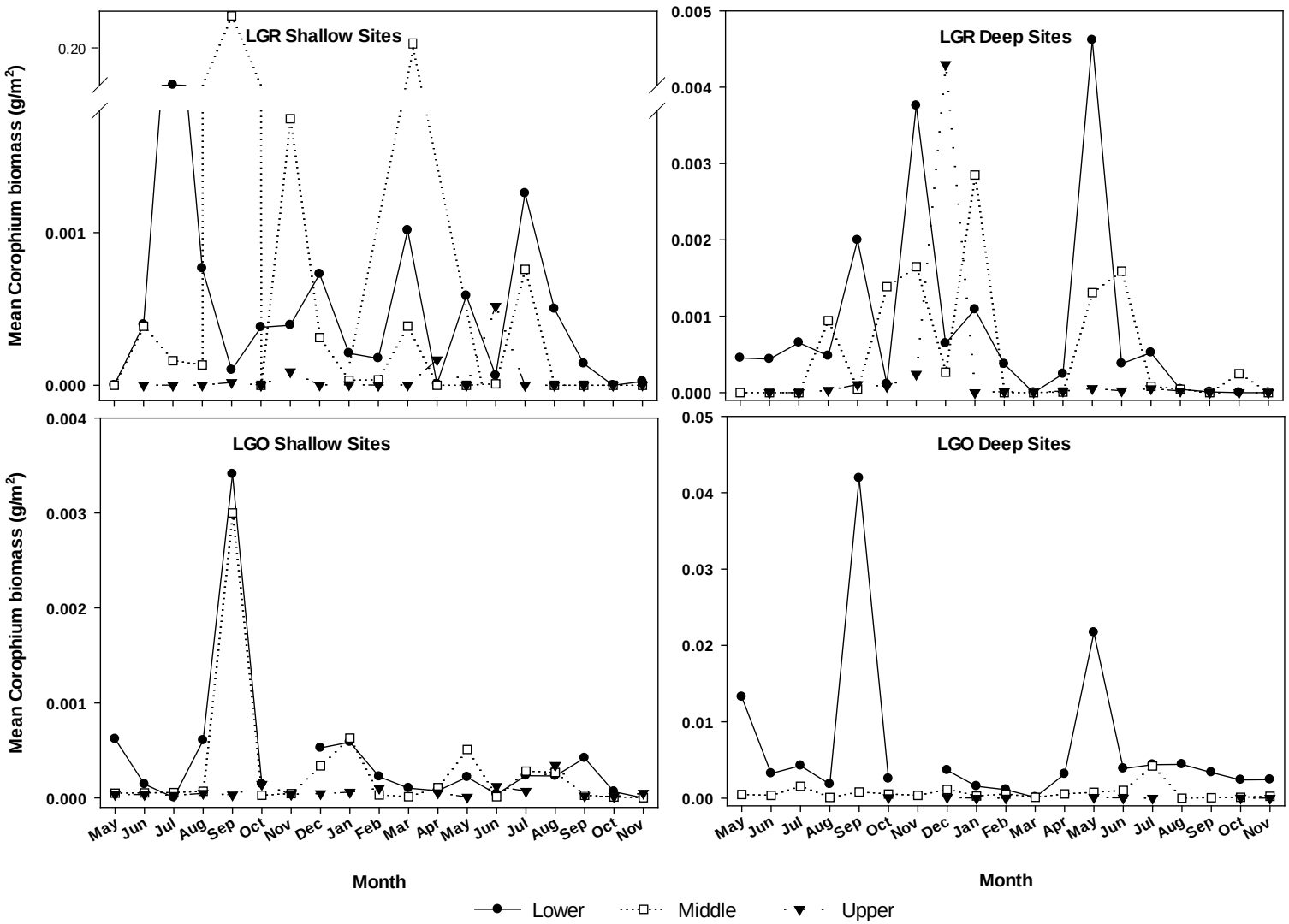

Figure 21. Monthly *Corophium* spp. biomass at shallow and deep sampling sites in Lower Granite (LGR) and Little Goose (LGO) reservoirs, May, 2011 through November, 2012. Biomasses are summarized for the lower (solid line), middle (dotted line), and upper (dashed line) reaches.

adults. Length-frequency plots suggest that many young-of-year prawns move to deep water in autumn, while some remain in shallow water.

The distribution of prawns in Lower Granite and Little Goose reservoirs may be controlled in part by water velocities. Prawns in both reservoirs were either absent, or present in low abundance, in most samples collected in the upper reaches regardless of the time of year, but were more abundant in lower reservoir reaches. Velocities are highest in the upper reaches of reservoirs (Tiffan et al. 2009), and it is plausible that velocity limits the upstream expansion of their range to these areas. The lower velocities in the lower reaches of both reservoirs may also explain why prawns were generally more abundant there.

Spawning by Siberian prawns in the lower Snake River appears to be a mid-summer to early autumn event. We first observed ovigerous females in May, 2011 but most were collected from July through September depending on the year and reservoir. Although we did find eggs into December and January, they did not appear to be viable. Female prawns carry their eggs on their abdomen until they hatch. We did observe some prawns with eggs on their abdomen as well as in their ovaries (under their carapace) suggesting they may be capable of spawning more than once in a season. During development, eggs are first orange to yellow in appearance and then eyes become visible as embryos develop. We did not distinguish between eyed and noneyed eggs in our fecundity estimates. The prawns we examined contained a mean of 189±55 eggs/female (range, 66-332). This is very similar to the fecundity information for Siberian prawns from a lake in Korea as reported by Oh et al. (2002). They reported a mean of 182±68 eggs/female and brood sizes ranging from 60-353. The size range of ovigerous females we measured (9-16.3 mm CL) was also similar to that reported by Oh et al. (2002), which ranged from 7.7 to 16.7 mm CL. The egg proportion of prawn body weight that we calculated (11.9%) was somewhat lower than the 17.4% reproductive output calculated by Oh et al. (2002), but may be due to the cooler temperatures in the Snake River compared to the Korean lake from which Oh et al. (2002) collected their prawns. Finally, our length-frequency data is similar to that reported by Oh et al. (2002) and suggests that prawns produced in the summer and autumn mature into reproductive adults by the following summer, but begin to die soon after. Oh et al. (2002) estimated that Siberian prawns live a maximum of 1.1-1.3 years. It is likely that prawns in the lower Snake River have a similar life span because there were never more than two size classes present. Our results suggest that prawn reproduction in the lower Snake River reservoirs is similar to that in their native range but may progress on a later, and perhaps shorter, time schedule due to cooler Snake River temperatures.

Although we collected both male and female prawns throughout the year, males were more abundant than females except in some autumn and winter months. Females were most abundant in September of each sampling year when spawning occurred. This is consistent with the data of Oh et al. (2002) who showed that males were often more prevalent than females, particularly outside of the spawning season. The reason for passage of primarily female prawns at Lower Granite and Little Goose dams during early autumn is puzzling. It may be due to a

post-reproductive behavior as many of the females no longer had eggs. Prawns are benthic, so to be entrained into the fish collection system at the dams, they must swim up into the water column a considerable distance. The reason for this behavior is currently unknown.

Although prawns are omnivorous (Bell and Coull 1978), our diet data showed they are primarily predators of other invertebrates in Lower Granite Reservoir. All size classes of prawns primarily consumed *Neomysis*, which is not surprising given their high abundance, but is interesting given their relatively high escape capacity (Irvine et al. 1990). It is noteworthy that the location of some of the highest prawn densities we observed (lower reach of Little Goose Reservoir) was the same for the highest *Corophium* densities we observed, yet there was little consumption of this invertebrate. Because *Corophium* are smaller than *Neomysis* and are tube-dwellers, they may be less noticeable to prawns. They are also fast swimmers. Apart from *Neomysis*, detritus and small amphipods were also important to the diets of the smallest prawns we examined. We speculate that *Neomysis*, as an abundant food source for prawns, may have contributed to the establishment and increase of the Siberian prawn population in lower Snake River reservoirs.

Neomysis densities were higher in Lower Granite than in Little Goose Reservoir. Mean densities were generally <100 mysids/m^2 in both reservoirs but maximum mean monthly densities in Lower Granite Reservoir ranged from 230 mysids/m^2 at deep sites to almost 400 mysids/m^2 at shallow sites. These densities were higher than reported for studies in oligotrophic systems but lower than densities reported in eutrophic systems (Table 5). It is somewhat difficult to compare our results to other studies because of differences in sampling methods. *Neomysis* are commonly collected in vertical net tows so aerial densities reported from that type of sampling represent the portion of the water column sampled. These tows are typically made at night because *Neomysis* are distributed throughout the water column at night (Cooper et al. 1992; Haskell and Stanford 2006). In contrast, we sampled during the day by towing a trawl along the bottom when *Neomysis* were concentrated there. We believe that most *Neomysis* were benthically (rather than pelagically) oriented during our daytime sampling and thus our density estimates should be somewhat comparable to other studies, at least at a coarse scale.

Neomysis densities were generally greater in shallow water than in deep water, which is consistent with findings of Murtaugh (1981b). One reason for this is that food may be more abundant in shallower areas. In Lower Granite Reservoir, the shallow sampling areas in both the upper and middle reaches were located behind islands away from the main river channel. These may be important zooplankton production areas because velocities are lower there, and zooplankton may be transported out of these areas at lower rates. The lower velocities in shallow habitats may also explain the higher *Neomysis* densities found there because *Neomysis* would also be less likely to be transported out of those habitats compared to deeper main-channel habitats where the velocities would be higher.

Table 5. A comparison of density (maximum seasonal estimate) and biomass (corresponding with maximum density) of *Neomysis* spp. in freshwater and estuarine systems. Much of this table was reproduced from Cooper et al. (1992). The results from our study are shown in bold and split out by shallow and deep sites. Lower Granite Reservoir is abbreviated as LGR.

Lake or estuary	Density (#/m^2)	Biomass (g/m^2)	Lake trophic status	Source
Kasumigaura	11,000	6.0	Ultra-eutrophic	Toda et al. (1981)
				Toda et al. (1982)
Sacramento-San Joaquin estuary	7,000	4.5	NA	Siegfried et al. (1979)
Fraser River estuary (side channel)	1,000	0.6	NA	Johnston and Northcote (1989)
Ferring	882	---	Ultra-eutrophic	Søndergaard et al. (2000)
LGR shallow	**548**	**2.3**	**Oligotrophic**	**This study**
LGR deep	**378**	**3.3**		
Washington	406	0.3	Eutrophic	Murtaugh (1981b)
				Edmondson and Lehman (1981)
Muriel	117	0.07	Ultra-oligotrophic	Nidle et al. (1984)
				Cooper (1988)
Kennedy (Clayoquot arm)	71	0.05	Ultra-oligotrophic	Nidle et al. (1984)
				Nidle and Shortreed (1985, 1987)
Fraser River estuary (main channel)	10	0.001	NA	Northcote et al. (1976)

We summarized data collected on *Corophium* because we routinely collected them during our sampling and they are seasonally important in the diet of rearing subyearling fall Chinook salmon (Tiffan et al. 2012). However, our beam trawl probably did not effectively sample them because they are tube dwellers and the trawl was most effective at collecting epibenthic invertebrates. In our collections, *Corophium* density was typically <1 organism/m^2. By comparison, Seybold and Bennett (2010) reported *Corophium* densities in excess of 1,500/m^2 in lower Snake River reservoirs while sampling with a Peterson dredge. One of the reasons that our *Corophium* density estimates could be low is that during some sampling events large samples of silt and debris over-filled the cod end of the net. During these instances, some smaller Corophium may have escaped through the large mesh while we worked to concentrate the sample to the cod end. Our analysis of benthic samples that were collected with a dredge in 2012 will enable us to better understand the abundance of *Corophium* and other benthic invertebrates in the soft substrates of Lower Granite and Little Goose reservoirs.

The proliferation of prawns and *Neomysis* in Lower Granite and Little Goose reservoirs has added a new dimension to the food web and their effects are not fully understood at this time. It is well known that *Neomysis* prey on zooplankton and can selectively prey upon larger *Daphnia* , thereby reducing their abundance (Murtaugh 1981b; Haskell and Stanford 2006). This is important because subyearling fall Chinook salmon also feed on zooplankton when they rear in reservoir habitats (Curet 1993; Rondorf et al. 1990; Tiffan et al. 2014). However, once subyearlings grow large enough, they begin to prey on *Neomysis*, and Tiffan et al. (2014) showed that *Neomysis* can compose up to 98% of subyearling diets in late spring in Lower Granite Reservoir. *Neomysis* are also consumed by larger reservoir-type fall Chinook salmon in autumn, but to a lesser extent (Tiffan and St. John 2011). It is likely that only larger subyearling smolts and reservoir-type juveniles in late summer and autumn would be capable of consuming prawns. However by this time, juvenile fall Chinook salmon typically use pelagic habitats and their use of benthic prey like prawns may be minimal, but no data exist to either reject or confirm this notion. Juvenile prawns in shallow habitats would be more vulnerable to juvenile salmon predation than larger prawns occupying deeper habitats. To date, prawn consumption by juvenile salmon has not been documented.

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Appendix C: List of Metrics and Indicators

Category	Subcategory	Subcategory Focus 1	Subcategory Focus 2	Specific Metric Title
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			

Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			

Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
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Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
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Fish	Mark/Tag Recovery or Detection			
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Fish	Origin			

Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
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Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			

Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
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Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
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Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators	Fish Life Stage: Adult Fish		Smallmouth bass abundance
Fish	Diet: Fish			Smallmouth bass diet

Fish	Mark/Tag Application			Smallmouth bass tagging
Fish	Mark/Tag Recovery or Detection			Smallmouth bass recapture
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		Smallmouth bass predation rate
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			

Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		

Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			

Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		
Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
Fish	Abundance of Fish Predators	Fish Life Stage: Adult Fish		Smallmouth bass abundance
Fish	Diet: Fish			Smallmouth bass diet
Fish	Mark/Tag Application			Smallmouth bass tagging
Fish	Mark/Tag Recovery or Detection			Smallmouth bass recapture
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		Smallmouth bass predation rate
Fish	Abundance of Fish Predators			
Fish	Growth Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Mark/Tag Application			
Fish	Mark/Tag Recovery or Detection			
Fish	Migration Pathways: Fish	Fish Life Stage: Juvenile Fish		

Fish	Origin			
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Migrant		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile - Ocean Type		
Fish	Predation Rate: Fish	Fish Life Stage: Juvenile Fish		
Fish	Prey Indices: Fish			
Fish	Timing of Life Stage: Fish	Fish Life Stage: Adult - Returner		
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Fish	Mark/Tag Recovery or Detection			
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Fish	Abundance of Fish Predators			
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