DIET OF JUVENILE BURBOT AND INSIGHT INTO GAPE LIMITATION

Zachary B. Klein*, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho, 83844-1141, 303-249-4190

Ryan S. Hardy, Idaho Department of Fish and Game, 2885 West Kathleen Avenue, Coeur d'Alene, Idaho, 83815

Michael C. Quist, U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Sciences, University of Idaho, 875 Perimeter Drive, Moscow, Idaho, 83844-1141

ABSTRACT

Throughout much of their distribution, Burbot (*Lota lota*) populations are declining or have been extirpated. Burbot in the Kootenai River, Idaho represent one such imperiled population. In an effort to restore Burbot in the Kootenai River, managers have turned to conservation aquaculture. However, no appreciable increase in natural recruitment has been observed in the system. The lack of natural recruitment is believed to be partly due to a deficiency of high-quality prey. As a result, we sought to i) describe the diet of juvenile Burbot, ii) evaluate the influence of Burbot mouth gape on diet and iii) estimate prey availability at release locations. Burbot were stocked into two earthen ponds at the Boundary Creek Wildlife Management Area (BCWMA) and sampled weekly to evaluate diet. Zooplankton were sampled weekly from each pond and from release locations of hatchery-reared Burbot (i.e., Kootenai River, Goat River, Boundary Creek, Deep Creek) to quantify prey availability. Over the course of the study (~3 months), Burbot primarily fed on Cyclopoida. Burbot never appeared to be gape limited and exhibited little variability in the size of zooplankton ingested. Zooplankton densities at stocking locations were relatively low in comparison to BCWMA ponds. Low zooplankton densities at release sites indicate that alternative management actions may need to be considered to enhance Burbot recruitment in the Kootenai River drainage.

Key words: Burbot, Diet, Kootenai River, Gape

INTRODUCTION

Burbot (*Lota lota)* are the only freshwater member of the family Gadidae (Howes 1991). They have a holarctic, circumpolar distribution that rarely extends below 40°N latitude. Throughout much of their distribution, Burbot populations are either declining or have been completely extirpated (Arndt and Hutchinson 2000; Paragamian et al. 2000). Declines are especially evident in populations at the southern extent of the species' distribution (Dixon and Vokoun 2010). In Idaho, the Kootenai River (Kootenay in Canadian waters) represents one such imperiled population. Historically, the Kootenai River supported subsistence, commercial and recreational fisheries for Burbot. In the later part of the 20th century, Burbot populations began to decline resulting in the eventual closure of the fishery in the 1990s (Paragamian et al. 2000). Burbot numbers continued to decline and a committee, the Kootenai Valley Resource Initiative (KVRI), was created and tasked with developing a conservation strategy to restore Burbot in the Kootenai River (KVRI Burbot Committee 2005). One of the primary restoration measures identified by the KVRI was the use of conservation aquaculture to reverse population declines of Burbot. Although the conservation strategy outlined rehabilitation actions, it did not provide population-level targets that were necessary to restore Burbot in the Kootenai River. In response, Paragamian and Hansen (2009) used density-dependent population models to define management targets necessary to recover Burbot in the system. The authors suggested that 17,500 individuals (143 fish/km) producing 1.1 recruits/year was necessary to achieve a self-sustaining population. However, the management goals outlined by Paragamian and Hansen (2009) assumed the occurrence of natural recruitment. Although over 1,500,000 hatchery-reared Burbot have been released in the Kootenai River drainage from 2009–2015, no appreciable increase in natural recruitment has been observed.

Low availability of quality prey has been suggested as contributing to the lack of natural recruitment of Burbot in the Kootenai River. Prey limitations have been considered to be one of the major causes of recruitment failure in fishes for over a century (Hjort 1914). Cushing (1969, 1990) hypothesized that a asynchrony between peak larval fish abundance and their prey would result in decreased recruitment success (Match-Mismatch Hypothesis). Although the Match-Mismatch Hypothesis (and similar hypotheses) has been extensively investigated, the exact mechanisms underlying recruitment success of larval fishes are rarely identified (Anderson 1988). Notwithstanding, the significance of appropriate prey to larval and juvenile fish is an important consideration with regard to growth, survival and recruitment to a population (Crowder et al. 1987; Graeb et al. 2004; Garvey and Chipps 2012). If one assumes that prey availability is at least partially responsible for regulating recruitment in fish populations, then the identification of available and appropriate prey in natural environments is critically important for the management of imperiled fishes. Therefore, the goals of the current study were to i) describe the diet of juvenile Burbot, ii) evaluate the influence of Burbot mouth gape on diet and iii) estimate prey availability at release locations.

METHODS

The Kootenai River is the second largest tributary to the Columbia River and supports Idaho's only native Burbot population. The Kootenai River originates in Kootenay National Park, British Columbia, Canada. From its origin, the river flows south into the United States where it is impounded by Libby Dam near Jennings, Montana forming Lake Koocanusa (Knudson 1994). Thereafter, the river flows through the northwest corner of Idaho before returning to Canada. In Idaho, three major tributaries of the Kootenai River (Boundary Creek, Deep Creek, Goat River) have been identified as important rearing habitats for juvenile Burbot. As such, each tributary has been the focus of intensive stocking of juvenile Burbot. Burbot were released in Boundary Creek less than 1 km from its confluence with the Kootenai River near the Canada-Idaho border. In Deep Creek, Burbot are stocked 21–33 km from its confluence with the Kootenai River near Bonners Ferry, Idaho. Burbot have been released at various locations throughout the Goat River.

In February 2012, adult Burbot were sampled from Moyie Lake, British Columbia using baited cod traps and angling (Spence 2000; Neufeld and Spence 2004). Burbot were spawned on site and fertilized eggs were transported to the University of Idaho's Aquaculture Research Institute, Moscow, Idaho. Burbot were reared using standard techniques (Jensen et al. 2008) and hatched from March 20–26, 2012. Burbot were reared for approximately 40 days and then transferred to the Boundary Creek Wildlife Management Area (BCWMA) ponds. The ponds are located on the west side of the Kootenai River valley near Porthill, Idaho. Each pond (*n* = 2) was excavated in 2010 and measures approximately 25 × 15 m. Both ponds are roughly 3.5 m deep and fill naturally through run off and seepage. On May 1, 2012, about 10,500 larval Burbot (~10.0 mm total length) were stocked in each pond (0.01 fish/L). From May–July, up to ten juvenile Burbot were sampled weekly to evaluate diet and growth. Juvenile Burbot were sampled with vertical hauls of a D-ring net (750 µm mesh) and preserved in 90% ethanol. Concurrently, zooplankton were sampled in triplicate from each pond to evaluate prey availability. Zooplankton were sampled using vertical tows of a Wisconsin-style plankton net. The net measured 0.3 m in diameter and was constructed of 80 µm mesh. Additional zooplankton samples were collected from the Kootenai River and Boundary Creek to evaluate prey availability at release locations. Zooplankton in the Kootenai River and Boundary Creek were collected in triplicate using 18.9 L grab samples, that were filtered through 80 µm mesh. All zooplankton samples were immediately preserved in 10% Lugol's solution. Burbot and zooplankton samples were transported to the University of Idaho for analysis. In July 2012, both ponds were drained and remaining Burbot were removed and released into Boundary Creek. In 2013, adult Burbot were collected and juveniles were reared following the same techniques used in 2012. Burbot hatched from March 27–April 5 and were transferred to the BCWMA ponds approximately 50 days later. On May 22, 2013, approximately 50,000 larval Burbot were stocked into each pond (0.04 fish/L). Larval Burbot and zooplankton were sampled in the same manner as in 2012. Ponds were drained in late July and remaining Burbot were released into Boundary Creek. Zooplankton samples were collected from the Kootenai River, Boundary Creek, Deep Creek and the Goat River in the same manner as in 2012.

Burbot were measured to the nearest 0.5 mm (total length). Gape was measured to the nearest 0.001 mm using a gape micrometer (Arts and Evans 1987). A metal cone was inserted into the mouth of each Burbot until the mouth was fully extended (maximum gape). The cone diameter was measured at the point of full, natural extension of the mouth (Arts and Evans 1987; DeVries et al. 1998). Care was taken to avoid over-extending or otherwise distorting the mouth.

Following body measurements, Burbot were dissected and stomachs were excised. Stomachs were opened and contents were removed. All prey items were identified to the lowest possible taxon and enumerated. Taxa included *Bosmina* spp., Calanoida, *Ceriodaphnia* spp., *Chydorus* spp., Coleoptera, Cyclopoida, *Daphnia* spp., *Diaphanosoma* spp., Diptera, Ephemeroptera, Gastropoda, nauplii, Odonata, Ostracoda, *Polyphemus* spp. and Rotifera. In addition, up to 20 prey items from each taxon were measured along their longest axis to the nearest 0.001 mm using an ocular micrometer (Bremigan and Stein 1994; Garvey and Chipps 2012). For instance, *Daphnia* spp. were measured from the anterior portion of the carapace to the base of the posterior spine (DeVries et al. 1998). If prey items were partially digested, taxa were identified using diagnostic structures, but were not measured for total length. For example, partially digested dipterans were identified and enumerated using identifiable heads.

Zooplankton sampled from release locations were identified to the lowest possible taxon and enumerated. Two hundred to four hundred of the most abundant taxa were identified and enumerated to ensure the identification of rare taxa (DeVries et al. 1998; Bunnell et al. 2011). In addition, zooplankton were measured along their longest axis. Densities of all taxa in the environment were estimated as the total number of a given taxon sampled by the volume of water sampled. Analysis of Burbot diet and zooplankton data was conducted by year due to disparate sampling periods between years (May–July 2012; June–July 2013). In addition, prey use was not compared to prey availability because certain taxa (e.g., Diptera, Odonata, Coleoptera) were not effectively sampled with the Wisconsin-style plankton net. The ratio between maximum length of ingested prey and available prey was regressed against Burbot mouth gape to identify periods of potential gape limitation. Burbot with empty stomachs were removed from the analysis.

RESULTS

Over the course of the study, 223 Burbot were sampled and 23 (12 in 2012; 11 in 2013) had empty stomachs. Burbot growth differed between ponds in both years (Fig. 1). In pond 2, Burbot averaged about 66.0 mm of growth over 77 days; whereas, Burbot in pond 1 averaged approximately 44.0 mm of growth over the same time period. In 2013, Burbot in pond 2 averaged 16.0 mm of growth from June 14–July 10; whereas, Burbot in pond 1 averaged 10.5 mm of growth over the same period.

Temporal patterns in zooplankton density and assemblage were similar between ponds (Fig. 2). In May 2012, Cyclopoida and nauplii accounted for 53–64% of the zooplankton in each pond. The ponds were not sampled in May 2013; thus, comparisons across years were not possible. During both years, *Bosmina* spp. had the highest density in each pond and composed 37–79% of the zooplankton assemblage from June to July. Rotifera and cladocerans (e.g., *Ceriodaphnia* spp., *Daphnia* spp.) were nearly always present, but at relatively low densities. For example, at their highest density *Daphnia* spp. accounted for less

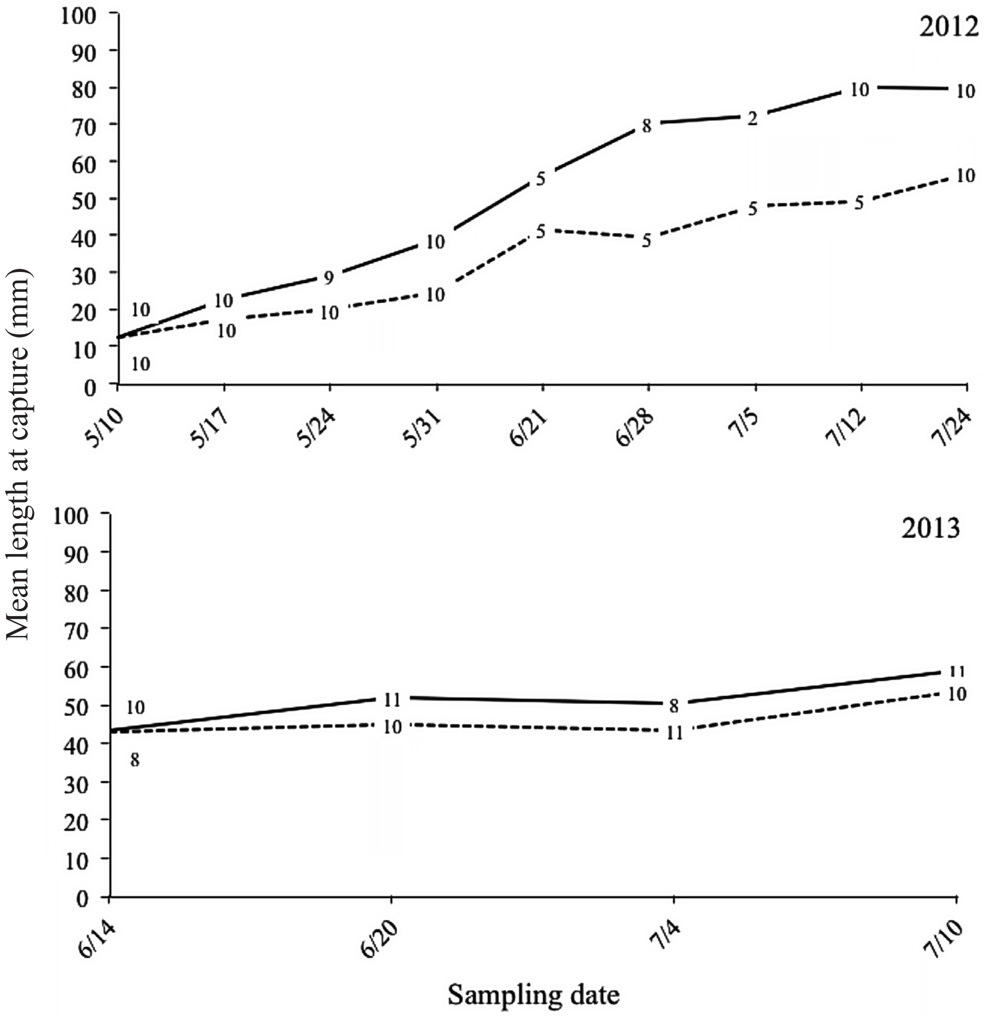

Figure 1. Mean length at capture for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho in 2012 and 2013. Dashed lines represent Burbot sampled from pond 1 and solid lines represent Burbot sampled from pond 2. Numbers along each line indicate the number of Burbot sampled on a given date.

than 5% of the total zooplankton (June 2012). Macroinvertebrates (e.g., Diptera, Coleoptera, Ephemeroptera) were poorly represented in zooplankton samples; but, this was likely due to sampling technique and not low densities.

Zooplankton at release locations showed similar patterns in zooplankton density and assemblage structure to the BCWMA ponds (Fig. 2). However, zooplankton densities were much lower among all release location than those observed in the BCWMA ponds. Boundary Creek had a mean density of approximately 30 zooplankton/L in 2012. *Bosmina* spp., *Daphnia* spp. and Cyclopoida were the most abundant zooplankton sampled in Boundary Creek in 2012 and represented 82% of the zooplankton present. Similarly, Cyclopoida and *Bosmina* spp. composed about 77% of the zooplankton present in the Kootenai River in 2012. Zooplankton densities were much lower across all release locations in 2013. The Kootenai River had the highest

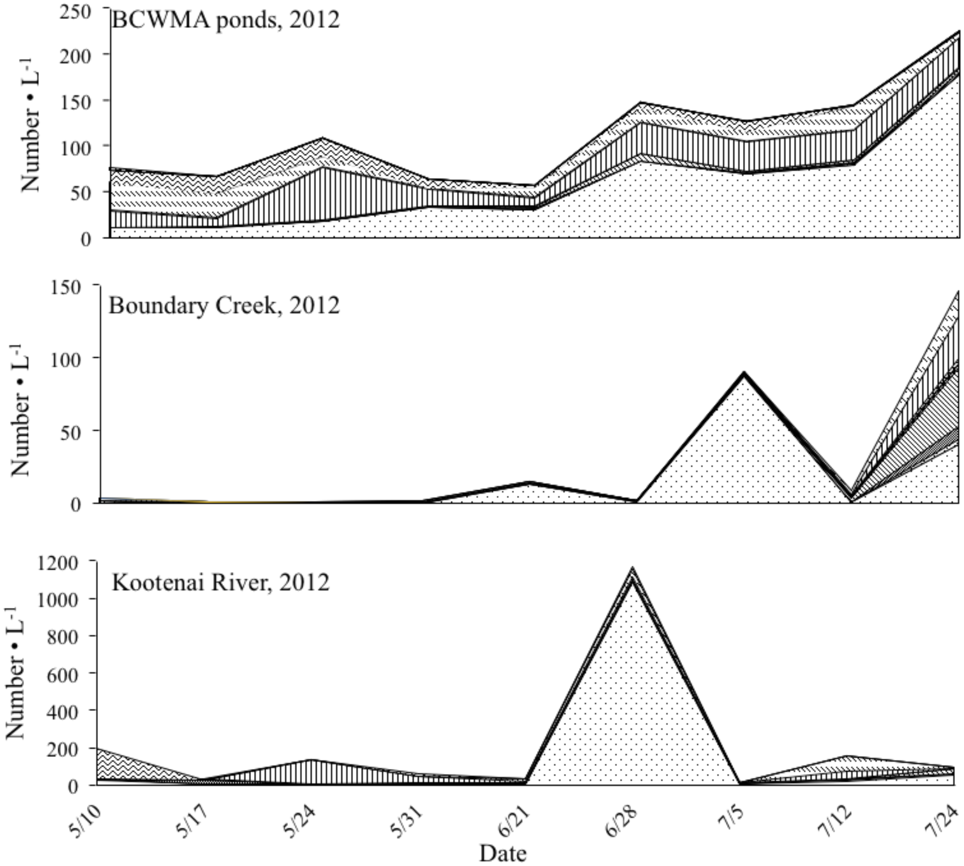

Figure 2. Zooplankton densities for Boundary Creek Wildlife Management Area ponds and stocking locations (i.e., Boundary Creek, Kootenai River, Goat River, Deep Creek). Prey categories include *Bosmina* spp. (⬚), Calanoida (▤), *Ceriodaphnia* spp. (▩), *Chydorus* spp. (░), Coleoptera (▣), Collembola (▦), Cyclopoida (▥), *Daphnia* spp. (▧), *Diaphanosoma* spp. (▪), Diptera (▫), Ephemeroptera (▒), Harpacticoida (⊠), Hemiptera (■), Hydrachnidae (▞), nauplii (◩), Ostracoda (▓), Plecoptera (▨), *Polyphemus* spp. (◫), Rotifera (◪), *Scapholeberis* spp. (▚).

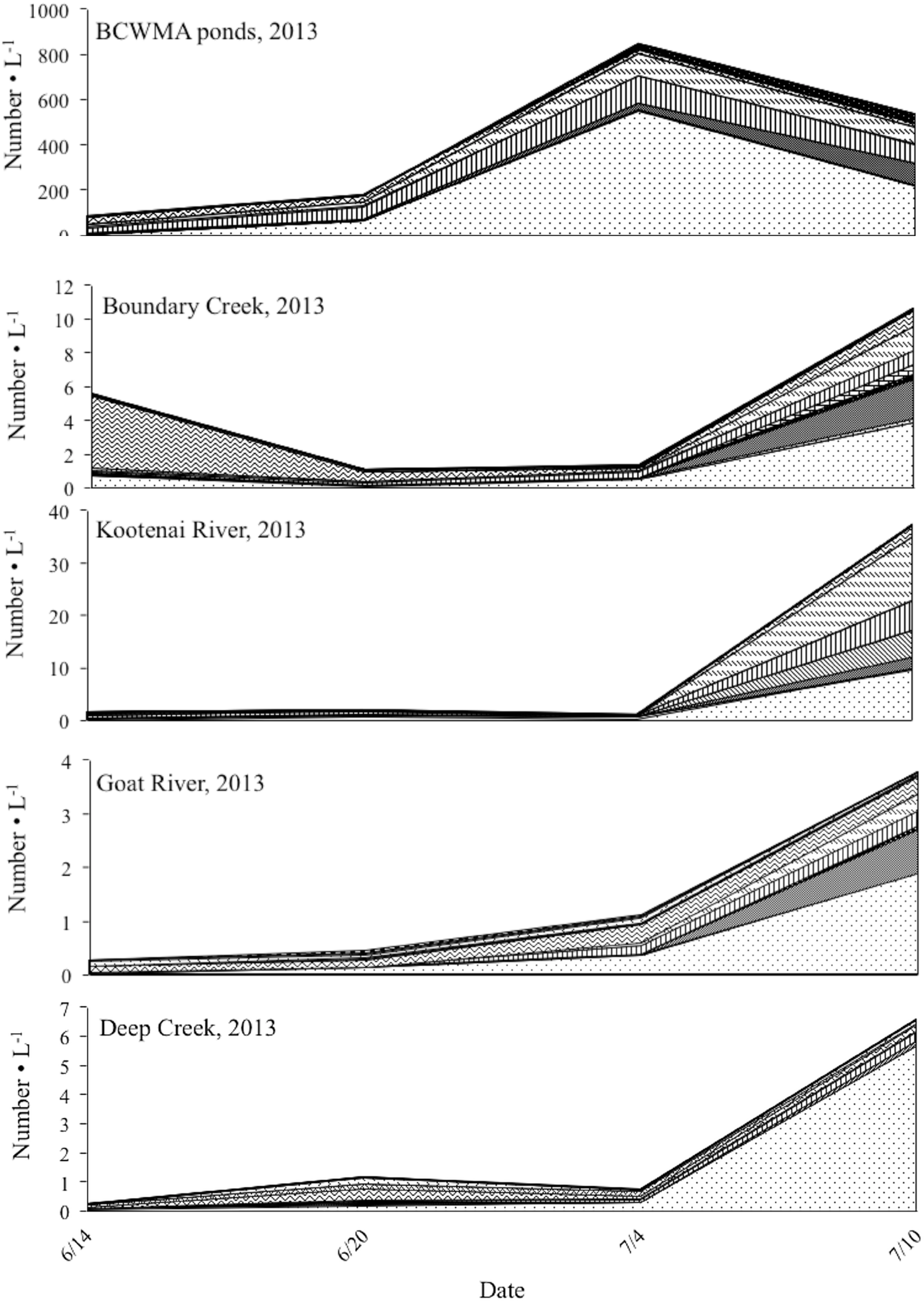

Figure 2. (continued) Zooplankton densities for Boundary Creek Wildlife Management Area ponds and stocking locations (i.e., Boundary Creek, Kootenai River, Goat River, Deep Creek). Prey categories include *Bosmina* spp. (⬚), Calanoida (▦), *Ceriodaphnia* spp. (▓), Chydorus spp. (▒), Coleoptera (◘), Collembola (▣), Cyclopoida (▥), *Daphnia* spp. (▧), *Diaphanosoma* spp. (■), Diptera (◲), Ephemeroptera (▣), Harpacticoida (⊠), Hemiptera (■), Hydrachnidae (▚), nauplii (▨), Ostracoda (▓), Plecoptera (▩), *Polyphemus* spp. (▥), Rotifera (▧), *Scapholeberis* spp. (▩).

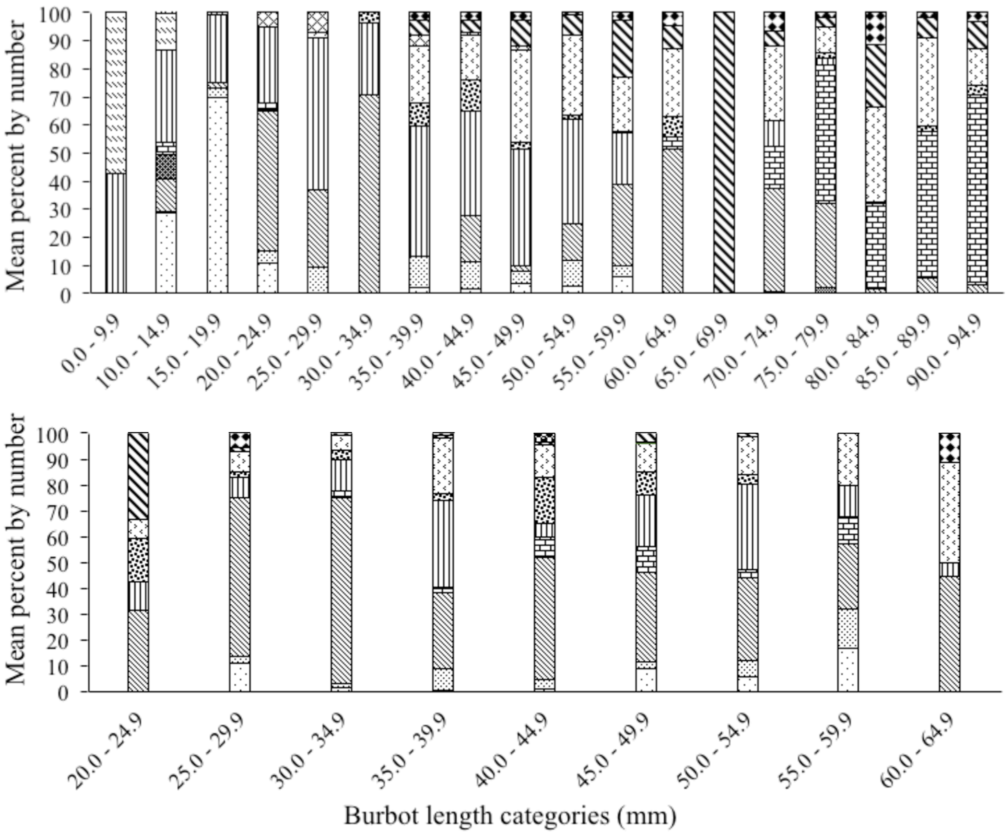

Figure 3. Diet composition by length category for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho. The top panel represents Burbot sampled in 2012 and the bottom panel represents Burbot collected in 2013. Prey categories include *Bosmina* spp. (░), Calanoida (▦), *Ceriodaphnia* spp. (▩), *Chydorus* spp. (░), Coleoptera (◆), Cyclopoida (▥), *Daphnia* spp. (▧), *Diaphanosoma* spp. (■), Diptera (░), Ephemeroptera (▩), Gastropoda (▩), nauplii (▤), Odonata (▨), Ostracoda (▧), *Polyphemus* spp. (▩) and Rotifera (▨).

density of all stocking locations (~10 zooplankton/L) in 2013. Larger zooplankton (e.g., Cyclopoida, *Daphnia* spp.) were poorly represented in 2013 with *Bosmina* spp. representing the highest densities across all sites.

Cyclopoida were common in the diet of juvenile Burbot (Fig. 3 and 4). At small sizes (<20.0 mm), juvenile Burbot predominantly fed on *Bosmina* spp., Cyclopoida and nauplii. *Bosmina* spp. and Cyclopoida accounted for 61% of the diet of 10.0–14.9 mm Burbot and 94% of the diet of 15.0–19.9 mm Burbot. Burbot greater than 20.0 mm consumed larger zooplankton such as *Daphnia* spp. However, Cyclopoida were always present in the stomachs of 20.0–59.9 mm Burbot and accounted for an average of 36% of their diet. Burbot greater than 59.9 mm had varied diets that were primarily composed of *Daphnia* spp., Calanoida and macroinvertebrates.

Mouth gape was positively related to Burbot length (Fig. 5) across both years. As mouth gape increased, the maximum length of ingested zooplankton remained

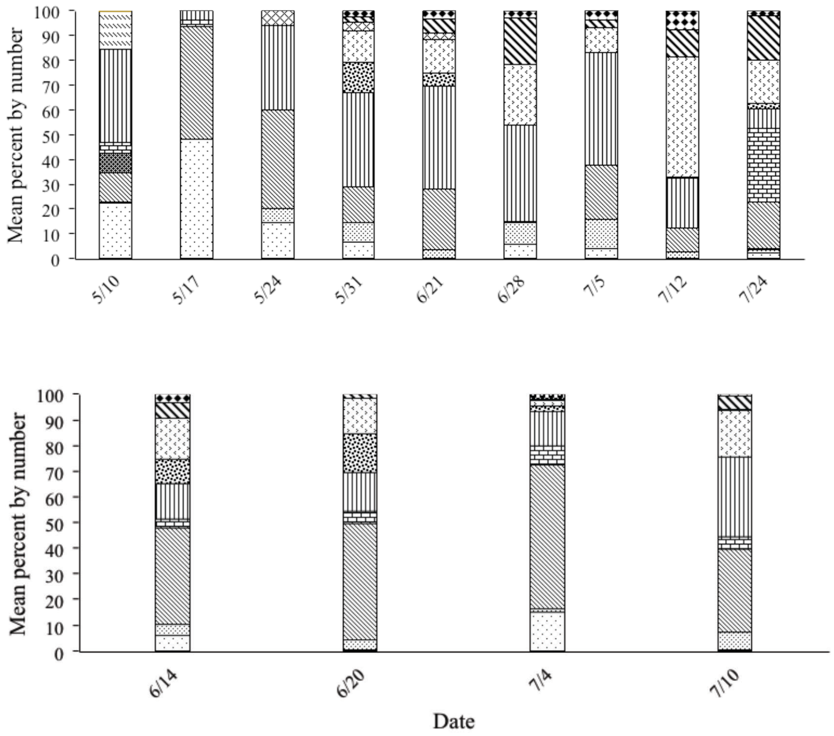

Figure 4. Mean percent by number of prey by date for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho. The top panel represents Burbot sampled in 2012 and the bottom panel represents Burbot collected in 2013. Prey categories include *Bosmina* spp. (⁚), Calanoida (▦), *Ceriodaphnia* spp. (▩), *Chydorus* spp. (▒), Coleoptera (◘), Cyclopoida (▥), *Daphnia* spp. (▧), *Diaphanosoma* spp. (■), Diptera (⁘), Ephemeroptera (▓), Gastropoda (◙), nauplii (▤), Odonata (⊠), Ostracoda (◪), *Polyphemus* spp. (▩) and Rotifera (▨).

relatively constant (Fig. 6). In 2012, mouth gape showed a weak, positive relationship with mean, minimum and maximum length of ingested zooplankton prey. Interestingly, mean and maximum length of ingested zooplankton were negatively related to mouth gape in 2013 (Fig. 6).

Across years, Burbot consumed the largest zooplankton available (Fig. 7). For instance, Burbot consumed zooplankton that were on average 50% larger than free-swimming zooplankton sampled in the BCWMA ponds in 2012. In 2013, Burbot consumed zooplankton that were on average 60% larger than free-swimming zooplankton sampled in the BCWMA ponds. Furthermore, mouth gape did not appear to influence the size of ingested zooplankton at any time during the study. For instance, Burbot with a gape less than 0.75 mm (SD = 0.06 mm) consumed zooplankton that averaged 1.12 mm (0.44 mm) in length. Burbot transitioned to macroinvertebrates when they reached approximately 60.0 mm in length, but measurement of macroinvertebrate prey was not possible due to partial digestion.

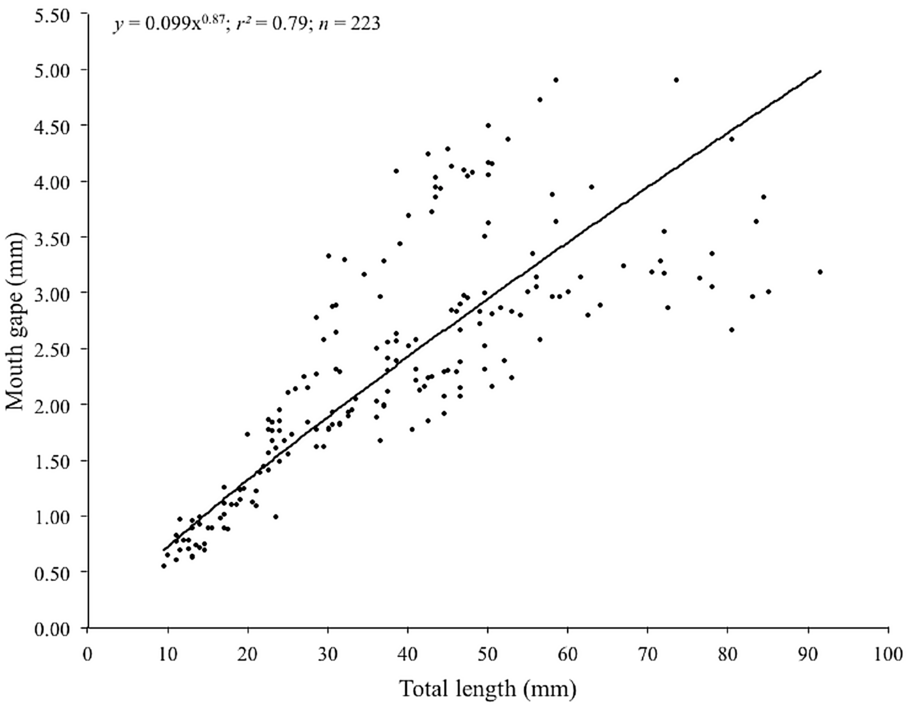

Figure 5. Mouth gape as a function of total length for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho in 2012 and 2013.

DISCUSSION

The diet of juvenile Burbot in the BCWMA ponds was consistent with that reported in the literature. Ghan and Sprules (1993) evaluated diet of larval and juvenile Burbot in Oneida Lake, New York. Rotifera (*Asplanchna* sp.) and nauplii were the primary prey of 4.0–10.0 mm Burbot. Ten to fifteen millimeter Burbot predominantly fed on Cyclopoida and then transitioned to a greater diversity of prey items (*Daphnia* spp., Cyclopoida, Calanoida) after they reached 15.0 mm. In Lake Constance (Germany, Austria, Switzerland), 10.0 mm Burbot primarily fed on Cyclopoida and nauplii (Probst and Eckmann 2009). Thereafter, Cyclopoida accounted for about 40% of Burbot diet. George et al. (2013) reported that juvenile Burbot in Lake Huron, Michigan fed almost exclusively on copepods. Furthermore, Cyclopoida were the dominant prey item and accounted for 43% of Burbot diet from April–July. Cyclopoida accounted for about 30% of the diet of Burbot from May–July in the current study. Although juvenile Burbot appear to select for Cyclopoida, it is unclear which factors (e.g., prey size, spatial overlap) contribute to prey choice in juvenile Burbot.

Maximum gape is often considered to be a principal feature contributing to prey choice in juvenile fishes (Mills et al. 1984; Miller et al. 1988; Schael et al. 1991). Fish typically consume progressively larger prey items as gape increases (O’Brien 1979; O’Brien 1987; Schael et al. 1991). In the current study, Burbot did not show a strong relationship between gape and prey size as has been reported for other fishes. In fact, Burbot in the BCWMA ponds never appeared to be gape limited for zooplankton and consistently ate similarly sized zooplankton. For example, Burbot in BCWMA ponds regularly ate zooplankton with lengths that exceeded their maximum mouth gape when gape was between 0.5–2.0 mm. Once mouth gape was greater than 2.0 mm, Burbot continued to eat zooplankton that were similar in length to those consumed at smaller gape sizes. Ghan and Sprules (1993) reported similar findings in regard to maximum gape and prey length. For example, Burbot in Oneida Lake with mouth gapes between 0.25–2.0

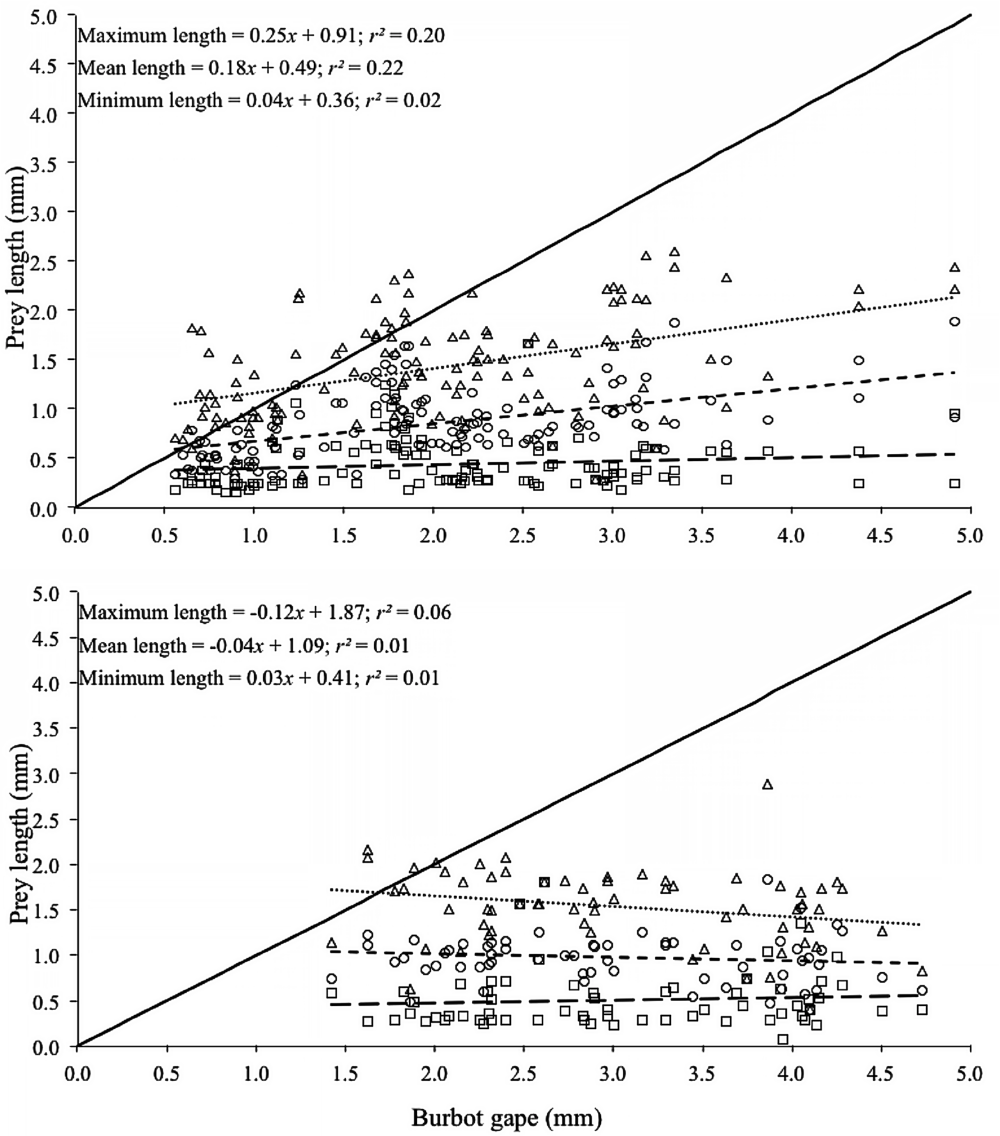

Figure 6. Length of ingested prey versus mouth gape for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho in 2012 and 2013. Stomach contents are represented as the mean (open circle), maximum (open triangle) and minimum (open square) length of prey found in each Burbot stomach ($n = 200$). Regression equations for maximum (dotted line), mean (dashed line) and minimum (long-dashed line) ingested prey length are presented. Solid lines denote mouth gape equal to ingested prey length. The top panel represents Burbot sampled in 2012 and the bottom panel represents Burbot sampled in 2013.

mm often consumed prey items with lengths greater than maximum mouth gape (Ghan and Sprules 1993). However, the authors noted that prey width rather than prey length limited the size of prey ingested by larval and juvenile Burbot. When mouth gape was less than 0.35 mm, the width of ingested prey approached or equaled gape. Once maximum gape exceeded 0.75 mm, Burbot consumed prey with widths considerably smaller than their maximum gape (Ghan and Sprules 1993). Prey width was not measured in the current study; however, the work conducted by Ghan and Sprules (1993) suggests that Burbot are briefly gape limited during early development. Although prey choice appears to be partly dictated by gape, it remains unclear why Burbot select specific

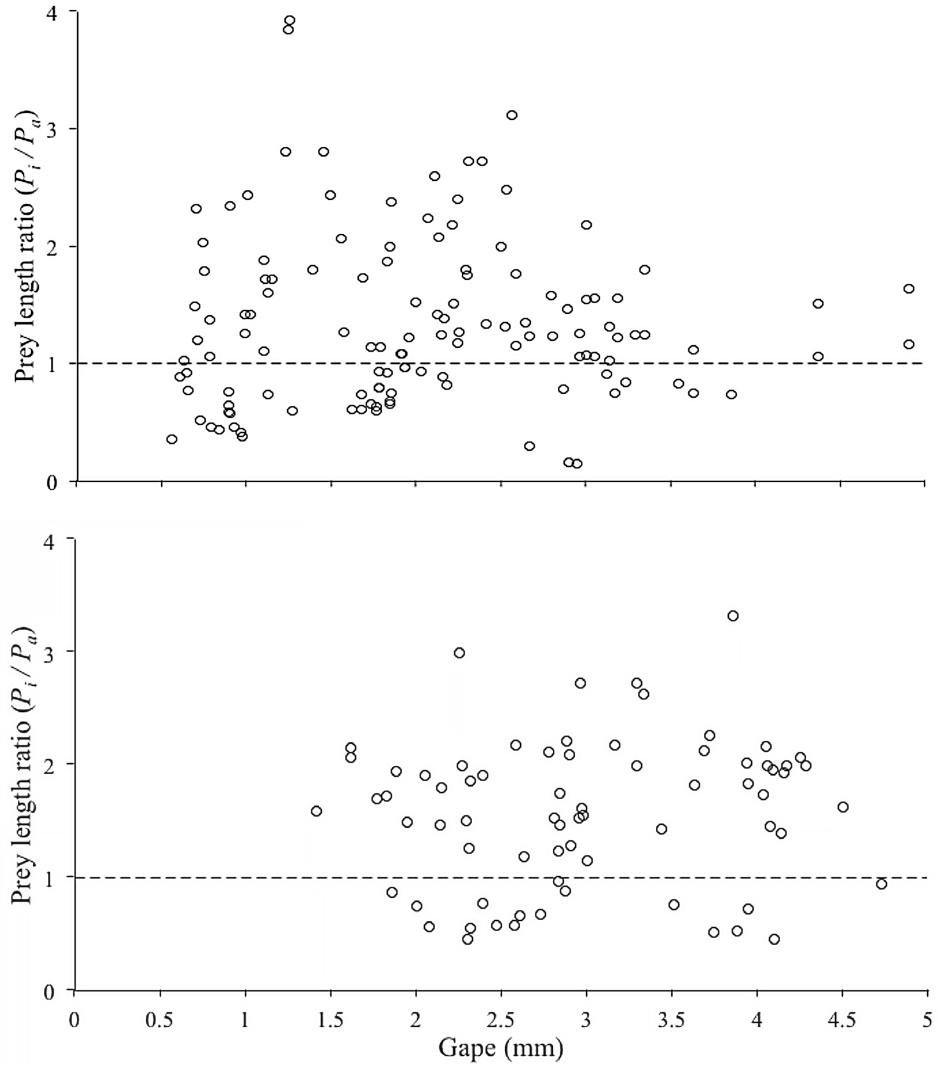

Figure 7. Ratio of maximum length of ingested prey (Pi) and available prey (Pa) versus gape for Burbot sampled from the Boundary Creek Wildlife Management Area ponds, Bonners Ferry, Idaho. The top panel represents Burbot sampled in 2012 and the bottom panel represents Burbot sampled in 2013. Dashed lines denote maximum length of ingested prey equal to maximum length of prey available in each pond.

prey taxa (copepods) over other, similarly sized prey items (daphnids).

The type of prey juvenile fish ingest can be determined by capture efficiency and handling time (Werner and Hall 1974; O'Brien et al. 1976; Gill 2003). Capture efficiency represents the success rate of capturing prey items (Gill 2003); whereas, handling time reflects the amount of time required to capture and swallow prey items (Sreekumari and Aravindan 1993). Intuitively, fish should maximize capture efficiency while reducing handling time (O'Brien 1979). Copepods generally have lower capture probabilities than cladocerans due to their quick, erratic movements (Drenner et al. 1980). Ghan and Sprules (1993) suggested that Cyclopoida are more visible to larval Burbot due to their irregular, darting movements. Additionally, George et al. (2013) posited that copepods are more visible than cladocerans because of their dark pigmentation. Burbot are visual feeders (Wocher et al. 2011) that exhibit crepuscular foraging behavior (Martin et al. 2011). Thus, fast moving, highly visible prey may be more readily identified and consumed than slow moving, lightly pigmented prey (e.g., *Daphnia* spp.). Regardless, Cyclopoida appear to be an important prey resource for larval and juvenile Burbot.

The impetus for the current study was that low prey availability was contributing to poor recruitment of Burbot in the Kootenai River. From 2009–2015, over 1,500,000 age-2 and younger Burbot were stocked into the Kootenai River and its tributaries. Of these, 1,328,538 Burbot were less than 60 days post hatch which roughly corresponds to a mean maximum length of 9.0 mm. Small Burbot (10.0–20.0 mm) predominantly fed on Cylopoida and *Bosmina* spp. in the current study. If Burbot stocked into the Kootenai River and its tributaries exhibit similar feeding habits, the majority of Burbot released will likely require high densities of zooplankton to avoid starvation. Unfortunately, identifying what constitutes a "high density" of zooplankton is difficult due to the paucity of data surrounding the food requirements of Burbot. Therefore, future research is needed to understand if current release locations support zooplankton densities sufficient to support larval and juvenile Burbot. Managers could also focus on releasing larger Burbot that do not require zooplankton prey. Our results indicate that Burbot transition from zooplankton prey to macroinvertebrates around 60.0 mm. A similar shift from zooplankton to macroinvertebrates has been reported in other studies. For instance, Ryder and Pesendorfer (1992) found that approximately 80% of the diet of 41.0–114.0 mm Burbot was composed of Amphipoda. Similarly, juvenile Burbot (51.0–102.0 mm) in the White River, Michigan primarily fed on Amphipoda and Ephemeroptera (Beeton 1956). If Burbot were stocked at larger lengths, they may benefit from abundant prey that has not been appropriately quantified in this and other studies. Regardless of the chosen release strategy, the identification of stocking locations with relatively high densities of high quality prey is necessary to ensure the rehabilitation of Burbot in the Kootenai River.

ACKNOWLEDGMENTS

We thank K. McBaine and M. Thomas for assistance with processing samples in the laboratory. We thank S. Young, C. Laude and J. Hughes for their help with Burbot stocking and sample collection. We also thank the University of Idaho's Aquaculture Research Institute for their support with intensive culture of Burbot. We thank J. Walrath and two anonymous reviewers who provided helpful comments on a previous version of the manuscript. Funding for the project was provided by Idaho Department of Fish and Game. Additional support was provided by the U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research Unit. The Unit is jointly sponsored by the U.S. Geological Survey, University of Idaho and Idaho Department of Fish and Game and Wildlife Management Institute. This project was conducted under the University of Idaho Institutional Animal

Care and Use Committee Protocol 2011-33. The use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

Anderson, J. T. 1988. A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. Journal of Northwest Atlantic Fisheries Science 8:55–66.

Arndt, S. and J. Hutchinson. 2000. Characteristics of a tributary-spawning population of burbot from Columbia Lake. Pages 48–60 *in* V. L. Paragamian and D. W. Willis, editors. Burbot biology, ecology and management. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, MD.

Arts, M. T. and D. O. Evans. 1987. Precision micrometer measurement of mouth gape of larval fish. Canadian Journal of Fisheries and Aquatic Sciences 44:1786–1791.

Bunnell, D. B., B. M. Davis, D. M. Warner, M. A. Chriscinske and E. F. Roseman. 2011. Planktivory in the changing Lake Huron zooplankton community: Bythotrephes consumption exceeds that of *Mysis* and fish. Freshwater Biology 56:1281–1296.

Beeton, A. M. 1956. Food habits of the Burbot (*Lota lota lacustris*) in the White River, a Michigan trout stream. Copeia 1:58–60.

Bremigan, M. T. and R. A. Stein. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51:913–922.

Crowder, L. B., M. E. McDonald and J. A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. Canadian Journal of Fisheries and Aquatic Sciences 44:141–147.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. Journal du Conseil International pour l'Exploration de la Mer 33:81–92.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Advances in Marine Biology 26:249–293.

DeVeries, D. R., M. T. Bremigan and R. A. Stein. 1998. Prey selection by larval fishes as influenced by the available zooplankton and gape limitation. Transactions of the American Fisheries Society 127:1040–1050.

Drenner, R. W. and S. R. McComas. 1980. The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. Pages 587–593 *in* W. C. Kerfoot, editor. Evolution and ecology of zooplankton communities. University Press of New England, Hanover.

Dixon, C. J. and J. C. Vokoun. 2010. Population structure and diet of burbot (*Lota lota*) in small streams near the southern extent of the species' range. Journal of Freshwater Ecology 25:49–58.

Garvey, J. E. and S. R. Chipps. 2012. Diet and energy flow. Pages 733–779 *in* A. V. Zale, D. L. Parrish and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

George, E. M., E. F. Roseman, B. M. Davis and T. P. O'Brien. 2013. Feeding ecology of pelagic larval Burbot in northern Lake Huron, Michigan. Transactions of the American Fisheries Society 142:1716–1723.

Graeb, B. D. S., J. M. Dettmers, D. W. Wahl and C. E. Cáceres. 2004. Fish size and prey availability affect growth, survival, prey selection and foraging behavior of larval Yellow Perch. Transaction of the American Fisheries Society 133:504–514.

Ghan, D. and W. G. Sprules. 1993. Diet, prey selection and growth of larval and juvenile Burbot *Lota lota* (L.). Journal of Fish Biology 42:47–64.

Gill, A. B. 2003. The dynamic of prey choice in fish: the importance of prey size and satiation. Journal of Fish Biology 63:105–116.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe, viewed in the light of biological research. Rapports et Procès Verbaux des Réunions du Conseil International pour l'Exploration de la Mer 20:1–228.

Howes, G. J. 1991. Biogeography of gadoid fishes. Journal of Biogeography 18:595–622.

IDEQ (Idaho Department of Environmental Quality). 2006. Assessment of water quality in Kootenai River and Moyie river subbasins (TMDL). Idaho Department of Environmental Quality, Couer d'Alene Regional Office, Coeur d'Alene, Idaho.

Jensen, N. R., S. C. Ireland, J. T. Siple, S. R. Williams and K. D. Cain. 2008. Evaluation of egg incubation methods and larval feeding regimes for North American Burbot. North American Journal of Aquaculture 70:162–170.

Knudson, K. 1994. Water quality status report: Kootenay (Kootenai) River Basin, British Columbia, Montana and Idaho. The Kootenai River Network, Libby, MT. and Ecological Resource Consulting, Helena, Montana.

KVRI (Kootenai Valley Resource Initiative) Burbot Committee. 2005. Kootenai River/Kootenay Lake Burbot conservation strategy. Kootenai Tribe of Idaho, Bonners Ferry.

Martin, B., S. Czesny and D. Wahl. 2011. Vertical distributions of larval fish in pelagic waters of southwest Lake Michigan: implications for growth, survival and dispersal. Journal of Great Lakes Research 37:279–288.

Miller, T. L., L. B. Crowder, J. A. Rice and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657–1670.

Mills, E. L., J. L. Confer and R. C. Ready. 1984. Prey selection by young yellow perch: the influence of capture success, visual acuity and prey choice. Transactions of the American Fisheries Society 113:579–587.

Neufeld M. D. and C. R. Spence. 2004. Evaluation of a simple decompression procedure to reduce decompression trauma in trap-caught Burbot. Transactions of the American Fisheries Society 5:1260–1263.

O'Brien W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton: recent research with plantivorous fish and their zooplankton prey shows the evolutionary thrust and parry of the predator-prey relationship. American Scientist 67:572–581.

O'Brien, W. J. 1987. Planktivory by freshwater fish: thrust and parry in the pelagia. Pages 3–16 *in* W. C. Kerfoot and A. Sih, editors. Predation, University Press of New England, Hanover.

Paragamian, V. L. 2000. The effects of variable discharges on burbot spawning migrations in the Kootenai River, Idaho, USA and British Columbia, Canada. Pages 111–123 *in* V. L. Paragamian and D. W. Willis, editors. Burbot biology, ecology and management. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.

Paragamian, V. L. and V. D. Wakkinen. 2008. Seasonal movement of Burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. American Fisheries Society Symposium 59:55–77.

Paragamian, V. L. and M. J. Hansen. 2009. Rehabilitation need for Burbot in the Kootenai River, Idaho, USA and British Columbia, Canada. North American Journal of Fisheries Management 29:768–777.

Probst, W. N. and R. Eckmann. 2009. Diet overlap between young-of-the-year perch *Perca fluviatilis* (L.) and burbot, *Lota lota* (l.), during earl life-history stages. Ecology of Freshwater Fish 18:527–537.

Ryder, R. A. and J. Pesendorfer. 1992. Food, growth, habitat and community interactions of young-of-the-year burbot, *Lota lota* L., in a Precambrian Shield Lake. Hydrobiologia 243:211–227.

Schael, D. M., L. G. Rudstam and J. R. Post. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*) and black crappie (*Pomoxis nigromaculatus*). Canadian Journal of Fisheries and Aquatic Sciences 48:1919–1925.

Sreekumari, T. and C. M. Aravindan. 1993. Influence of size, station time and satiation amount on the prey handling time in *Anabas testudineus* (Bloch). Journal of Indian Fisheries Association 23:105–108.

Spence, C. R. 2000. A comparison of catch success between two styles of burbot traps in lakes. Pages 165–170 *in* V. L. Paragamian and D. W. Willis, editors. Burbot: biology, ecology and management. American Fisheries Society, Fisheries Management Section, Publication 1, Bethesda, Maryland.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

Wocher, H., A. Harsányi and F. J. Schwarz. 2011. Larviculture of Burbot (*Lota lota* L.): larval rearing using *Artemia* and Weaning onto dry feed. Aquaculture Research 44:106–113.

Received 05 August 2016
Accepted 21 November 2016