Notes

Diet Overlap of Top-Level Predators in Recent Sympatry: Bull Trout and Nonnative Lake Trout

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Abstract

The establishment of nonnative lake trout *Salvelinus namaycush* in lakes containing lacustrine–adfluvial bull trout *Salvelinus confluentus* often results in a precipitous decline in bull trout abundance. The exact mechanism for the decline is unknown, but one hypothesis is related to competitive exclusion for prey resources. We had the rare opportunity to study the diets of bull trout and nonnative lake trout in Swan Lake, Montana during a concomitant study. The presence of nonnative lake trout in Swan Lake is relatively recent and the population is experiencing rapid population growth. The objective of this study was to evaluate the diets of bull trout and lake trout during the early expansion of this nonnative predator. Diets were sampled from 142 bull trout and 327 lake trout during the autumn in 2007 and 2008. Bull trout and lake trout had similar diets, both consumed *Mysis diluviana* as the primary invertebrate, especially at juvenile stages, and kokanee *Oncorhynchus nerka* as the primary vertebrate prey, as adults. A diet shift from primarily *M. diluviana* to fish occurred at similar lengths for both species, 506 mm (476–545 mm, 95% CI) for bull trout and 495 mm (470–518 mm CI) for lake trout. These data indicate high diet overlap between these two morphologically similar top-level predators. Competitive exclusion may be a possible mechanism if the observed overlap remains similar at varying prey densities and availability.

Keywords: bull trout; diet overlap; kokanee; lake trout; mysis; nonnative; predators

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Introduction

Lake trout *Salvelinus namaycush* (Figure 1) introductions and invasions have been implicated in declines of bull trout *Salvelinus confluentus* (Figure 1), a federally threatened species, native to numerous lakes in the Intermountain West (Donald and Alger 1993; Fredenberg 2002; Martinez et al. 2009). Lake trout were widely introduced outside their native range beginning in the early 1900s, particularly in the Intermountain West, to create commercial fisheries or to provide anglers with opportunities to catch an additional top-level predator

Figure 1. Lake trout *Salvelinus namaycush* (**top panel**) and bull trout *Salvelinus confluentus* (**bottom panel**) from Quartz Lake, Glacier National Park, Montana, in 2006.

(Crossman 1995; Martinez et al. 2009). Lake trout distribution continues to expand throughout the western United States due to invasions of interconnected waterways and illegal introductions (Martinez et al. 2009). Unfortunately, range expansion of lake trout has often led to the declines in native salmonid populations in many western North American lakes (Fredenberg 2002; Koel et al. 2005), and altered trophic dynamics in aquatic and terrestrial ecosystems (Spencer et al. 1991; Koel et al. 2005; Tronstad 2008; Ellis et al. 2011).

The mechanism causing the decline in native salmonids once lake trout are established is typically unknown. In Yellowstone Lake, it is believed that lake trout predation is the mechanism for the decline in Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* (Ruzycki et al. 2003). In lentic ecosystems where nonnative lake trout and bull trout are sympatric top-level predators, the mechanism for the decline in bull trout abundance has been hypothesized to be more closely linked to predation (Beauchamp et al. 2006), competition for food (Donald and Alger 1993), and varying life-history traits (Martinez et al. 2009). Thus, better understanding the ecology of lake trout and bull trout in sympatry will help elucidate the mechanisms for declines in bull trout abundance.

The objective of this study was to evaluate the diet overlap and, hence, potential diet competition between lake trout and bull trout in Swan Lake, Montana. This study provides a rare case history of the diets of bull trout and nonnative lake trout in sympatry, where the lake trout population is undergoing rapid population growth (Cox 2010). This information is important given that several lakes in the Intermountain West contain *Mysis diluviana*, lake trout, and bull trout (Bowles et al. 1991; Hansen et al. 2008; Cox 2010; Ellis et al. 2011). Further, we conducted a diet analysis to determine the body length at which bull trout and lake trout shift their diet from primarily invertebrates to fish (i.e., switch to piscivory). Several studies have described the diets of bull trout and lake trout in sympatry and allopatry, with similar results. One common thread is that kokanee *Oncorhynchus nerka* are a preferred prey for adult lake trout and bull trout, but both species are opportunistic and will switch to other prey if kokanee decline (Jeppson and Platts 1959; Bjornn 1961; Martin and Olver 1980; Fraley and Shepard 1989; Spencer et al. 1991; Donald and Alger 1993; Beauchamp and Van Tassell 2001; Dux 2005; Meeuwig 2008). *M. diluviana* is common prey for juvenile lake trout (Martin and Olver 1980), but less is known about predation by bull trout. We hypothesized that diets would be similar given the presence of *M. diluviana* and kokanee, and the switch to piscivory would occur at similar body lengths, given the similarities in morphology and behavior as outlined by Donald and Alger (1993).

Methods

Swan Lake is located in northwest Montana (47.9628°N, 113.9033°W) near Flathead Lake, Montana.

Swan Lake is 1,335 ha with a mean depth of 16 m, maximum depth 43 m, total dissolved solids 112 mg/L, and is dimictic. The fish assemblage consists of 10 native (westslope cutthroat trout *Oncorhynchus clarkii lewisi*, bull trout, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulterii*, northern pikeminnow *Ptychocheilus oregonensis*, peamouth *Mylocheilus caurinus*, redside shiner *Richardsonius balteatus*, longnose sucker *Catostomus catostomus*, largescale sucker *Catostomus macrocheilus*, and slimy sculpin *Cottus cognatus*) and at least seven nonnative species (lake trout, kokanee, rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis*, northern pike *Esox lucius*, brook stickleback *Culaea inconstans*, and central mudminnow *Umbra limi*).

We collected bull trout in 2007 using a stratified random sampling design that was developed to sample lake trout in a concurrent study (see Cox 2010 for more details). We sampled all bull trout and lake trout using gill nets from 19 September to 4 October (see Cox 2010); gill nets were set in the morning and evening, and fished on average for 2.4 h. Sinking gill nets consisted of three 91.4-m-long by 2.4-m-deep monofilament panels of 2.5, 3.2, 3.8, 4.5, and 5.1-cm bar mesh. We collected lake trout from 9 September through 25 September in 2008 using the same sampling design (see Cox 2010 for more details). However, the length of the gill net was doubled and an additional six panels of 91.4-m, 1.9-cm bar mesh were added. We fished gill nets for an average of 3.5 h in 2008.

All bull trout mortalities, a function of gill-netting bycatch, were frozen and transported to the laboratory at Montana State University. We were unable to conduct diet analyses on live bull trout sampled because of constraints included in our Endangered Species Act as amended (ESA 1973) permit. Thus, live bull trout captured in the gill net were returned immediately to the lake. Regardless of this constraint, the length range of bull trout represented in this study (295–732 mm) was similar to the length range of all bull trout sampled (191–765 mm; Rosenthal and Fredenberg 2009; *Supplemental Material*, Report S1; http://dx.doi.org/10.3996/012011-JFWM-004.S2).

We analyzed 142 bull trout for diet contents (*Supplemental Material*, Table S1; http://dx.doi.org/10.3996/012011-JFWM-004.S1). We measured standard length (mm) because bull trout were frozen whole and subsequently some fish had damaged caudal fins. In 2010, we measured standard length and total length on 31 bull trout from the Swan Lake population, to develop a relationship between standard length and total length. Thus, all bull trout standard lengths were converted to total length using the equation

$$\text{total length} = 4.403 + 1.118(\text{standard length})$$

where $P < 0.001$, $df = 29$, $r^2 = 0.99$. We measured weight (g) on all thawed bull trout. We removed stomach contents and placed them in 80% ethanol for further processing.

We obtained lake trout lengths (total length, mm) and weights (g) in the field from five fish per cm length category. Stomachs were removed and frozen in the field and transported to the laboratory at Montana State University for analysis. We analyzed 327 lake trout stomachs (*Supplemental Material*, Table S1; http://dx.doi.org/10.3996/012011-JFWM-004.S1).

We separated stomach contents of lake trout by family for invertebrates (except for mysid shrimp *M. diluviana*, and the fingernail clam *Pisidium adamsi*, which were identified to species) and by individual species for fish. Bull trout stomach contents were only identified as *M. diluviana*, other invertebrates, and fish. Thus, a complete list of invertebrate diet items for bull trout was unavailable. We estimated frequency of occurrence and volume by taxon (Chipps and Garvey 2007). Frequency of occurrence and volume were only analyzed for *M. diluviana*, Diptera spp., and fish because those taxa represented 99% of the diet contents by volume for both species. Unfortunately, there was a lack of historical zooplankton data; thus, evaluating the temporal responses of the zooplankton assemblage to changes in the top-level predator assemblage was not practical. We did not incorporate rainbow trout in the diet study because they are relatively uncommon and are spatially segregated from lake trout and bull trout during much of the year. Further, we believe that rainbow trout have a minor influence on the food web in Swan Lake. Analysis of mean proportion by volume followed methods outlined by Chipps and Garvey (2007) for mean proportion by weight (MW_i). Mean proportion by volume was analyzed by length category. We subjectively delineated length category based on the logistic switch-to-piscivory curve (see above). We calculated proportion by number of fish species in the diet for lake trout and bull trout (Chipps and Garvey 2007). We estimated body length at switch to piscivory using logistic regression for binary response data. Binary response data were lake trout and bull trout with stomach contents composed of either fish or invertebrates. The switch to piscivory was compared at the length wherein 50% of the diet was composed of fish as estimated as the 0.5 value on the logistic regression curve. We calculated confidence intervals (CI; 95%) for logistic regression models from the standard error of the predicted value. All statistical analyses were conducted using R 2.10.1 (R Core Development Team 2010).

Results

Bull trout length varied from 295 to 732 mm and lake trout length varied from 166 to 945 mm. Bull trout weight varied from 129 to 2,630 g and lake trout weight varied from 36 to 10,680 g. Similar proportions of bull trout and lake trout had empty stomachs (Table 1). For both species, frequency of occurrence was highest for *M. diluviana* and fish (Table 1). Mean proportion by volume for *M. diluviana* and fish varied among length categories (Table 2). Volume of *M. diluviana* was highest in length categories ≤300 mm and 301–500 mm for both species. Volume of fish was highest in length categories 501–700 mm and ≥700 mm for both species. Kokanee were the dominant fish prey of both species (Table 3). Other fish species comprised only 0.02 to 0.07 of the total

Table 1. Proportion of empty stomachs and frequency of occurrence of *Mysis diluviana*, Diptera spp. larvae, and fish in diets of 142 bull trout *Salvelinus confluentus* and 327 lake trout *Salvelinus namaycush* sampled in Swan Lake, Montana in 2007 and 2008.

	Species	
Metric	Bull trout	Lake trout
Empty stomachs	0.32	0.29
Frequency of occurrence		
Mysis diluviana	0.68	0.59
Diptera spp. larvae[a]	—	0.24
Pisidium adamsi	—	0.12
Other invertebrates	0.09	—
Fish	0.39	0.43

[a] Diptera spp. were pooled in the "Other invertebrates" category in bull trout diet analyses.

Table 3. Proportion by number for identifiable fish in the diets of 13 bull trout *Salvelinus confluentus* and 43 lake trout *Salvelinus namaycush* sampled in Swan Lake, Montana in 2007 and 2008.

	Species	
Diet item	Bull trout	Lake trout
Kokanee *Oncorhynchus nerka*	0.86	0.88
Pygmy whitefish *Prosopium coulterii*	0.07	0.02
Salvelinus spp.	0.07	0.04
Largescale sucker *Catostomus catostomus*	—	0.02
Redside shiner *Richardsonius balteatus*	—	0.05

number of fish in the diet. Body length at switch to piscivory (0.5 proportion with fish in the diet) was nearly identical: 506 mm (476–545 mm CI) for bull trout and 495 mm (470–518 mm CI) for lake trout, and confidence intervals overlapped at all lengths (Figure 2).

Discussion

Diet composition and body length at which bull trout and lake trout became predominantly piscivorous in Swan Lake were remarkably similar, supporting our hypothesis of high potential for diet overlap between these two morphologically similar top-level predators. To our knowledge, these data represent the largest diet sample of sympatric bull trout and lake trout, and largely corroborate previous diet studies conducted on bull trout and lake trout.

For example, in Flathead Lake, Montana, large bull trout (>550 mm) and lake trout (>500 mm) fed almost exclusively on kokanee and mountain whitefish (Leathe and Graham 1982) prior to the introduction of *M. diluviana* and collapse of kokanee, and bull trout were the predominant *Salvelinus* spp. in the lake. The contemporary diet of lake trout, now the dominant predator in Flathead Lake, is mostly composed of *M. diluviana* and lake whitefish following the collapse of the kokanee population (Ellis et al. 2011). Kokanee composed 66% of the bull trout ($N = 11$, ≥406 mm) diet and 87% of the lake trout ($N = 195$, ≥406 mm) diet by weight in Lake Pend Oreille, when bull trout and Kamloops *Oncorhynchus mykiss kamloops* were the dominant predators (Clarke et al. 2005). In Lake Billy Chinook, where lake trout are absent, kokanee represented the largest fraction of the fish prey in bull trout diets (Beauchamp and Van Tassel 2001). Kokanee, when present even at low abundances, appear to be preferred prey for adult lake trout and bull trout (Jeppson and Platts 1959; Bjornn 1961; Martin and Olver 1980; Fraley and Shepard 1989; Spencer et al. 1991; Beauchamp and Van Tassell 2001; Clarke et al. 2005). Adult lake trout and bull trout are opportunistic predators and will prey on other species if kokanee are extirpated from a waterbody or were never historically present (Martin and Olver 1980; Donald and Alger 1993; Dux 2005; Meeuwig 2008). Lake whitefish *Coregonus clupeaformis*, mountain whitefish, and pygmy whitefish composed 95% of the prey by weight in adult lake trout diets in Lake McDonald, where kokanee and bull trout are extant at low abundance (Dux 2005).

Table 2. Mean proportion of volume (ml; SE) by length category for 96 bull trout *Salvelinus confluentus* and 233 lake trout *Salvelinus namaycush* sampled in Swan Lake, Montana in 2007 and 2008.

		Length category (mm)			
Species	Prey	≤300	301–500	501–700	≥701
Bull trout		$N = 10$	$N = 69$	$N = 17$	
	Mysis diluviana	0.77 (0.13)	0.70 (0.05)	0.06 (0.06)	—
	Other invertebrates	0	0.01 (0.003)	0	—
	Fish	0.12 (0.09)	0.22 (0.05)	0.94 (0.06)	—
Lake trout		$N = 57$	$N = 89$	$N = 64$	$N = 23$
	Mysis diluviana	0.97 (0.01)	0.79 (0.04)	0.06 (0.03)	0
	Other invertebrates	0.02 (0.01)	0.02 (0.005)	0.01 (0.01)	0.05 (0.04)
	Fish	0	0.18 (0.04)	0.93 (0.03)	0.95 (0.04)

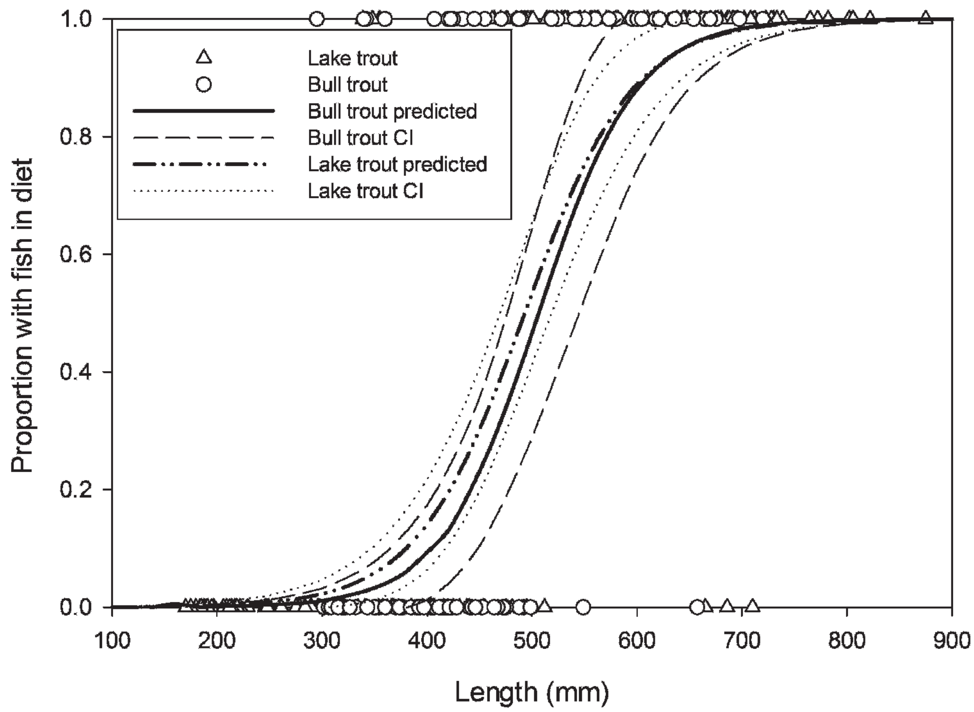

Figure 2. Logistic regression models of body length related to diet item (i.e., invertebrates or fish) and 95% confidence intervals (CI) for bull trout *Salvelinus confluentus* ($N = 96$) and lake trout *Salvelinus namaycush* ($N = 233$), sampled in Swan Lake, Montana in 2007 and 2008, where 1.0 equals only fish present and 0.0 equals only invertebrates present in the diet.

We found few *Salvelinus* spp. (none of the *Salvelinus* spp. could be identified to species) in the diets of lake trout or bull trout. Based on our results, the relatively low density of adult lake trout in Swan Lake (see Cox 2010) and the relatively abundant kokanee, we surmise that predation on bull trout by lake trout is biologically insignificant at this time. We believe kokanee serve as a prey-buffer to predation on bull trout by lake trout. If the kokanee population collapses under high lake trout predation, or the lake trout population continues to expand as observed in other lake systems, then it is possible that conspecific predation rates and predation on bull trout by lake trout will increase.

M. diluviana is a common diet item in native lake trout populations (Martin and Olver 1980). Lake trout of length $<$460 mm in Lake Pend Oreille fed exclusively on cottids (68%) and *M. diluviana* (32%; Clarke et al. 2005). *M. diluviana* was an important diet item for lake trout of length $\leq$625 mm in Flathead Lake (Beauchamp et al. 2006). *M. diluviana* is a highly used prey item by juvenile lake trout and bull trout in Swan Lake. *M. diluviana* were introduced in Swan Lake in 1975, were established by 1980, and were at peak densities of about 230 m^2 by the late 1980s (Rumsey 1988). Currently, densities have stabilized near 150 m^2 (L.R. Rosenthal, Montana Fish, Wildlife and Parks, personal communication). Our study is the first we are aware of that illustrates the high use of *M. diluviana*, specifically by juvenile bull trout in the presence of lake trout and kokanee, though this assemblage is present in several other lakes throughout the Intermountain West (Martinez et al. 2009). This may be partially a function of lake bathymetry because Swan Lake is relatively shallow. Therefore, *M. diluviana* may be more equally available to bull trout and lake trout than in deeper ecosystems. Angler-caught bull trout in Priest Lake, Idaho consumed *M. diluviana*, but the results were not delineated by length (Rieman et al. 1979).

Lake trout and bull trout appear to have similar diets in allopatry (Martin and Olver 1980; Beauchamp and VanTassell 2001) and in sympatry (Vidergar 2000). Thus, the presence of nonnative lake trout in waters containing bull trout does not cause a shift in food habits of either *Salvelinus* spp. Interestingly, native lake trout populations shifted food habits when nonnative smallmouth bass and rock bass were introduced (Vander Zanden et al. 1999). However, this occurred in lakes that did not contain pelagic prey species for lake trout.

Our results are founded on diet samples from a single season and could bias interpretations if these results are extrapolated for all seasons given the known temporal variability in bull trout and lake trout diets in other systems (Leathe and Graham 1982; Beauchamp and Van Tassell 2001; Beauchamp et al. 2006). For example, bull trout predation on kokanee was highest in the autumn in Lake Billy Chinook (Beauchamp and Van Tassell 2001). Thus, it is plausible that these data represent the season of highest overlap between lake trout and bull trout in Swan Lake. We surmise that the temporal variation in the diet of bull trout and lake trout in Swan Lake would not obscure the broad conclusions regarding diet overlap.

Empirically ascertaining the multiple mechanisms that likely interact to cause the decline of bull trout populations once lake trout are established is virtually impossible; nevertheless, the nearly complete overlap in diet items observed in this study suggests competition can play an important role, particularly given a scarcity in vertebrate prey resources for piscivorous adults. In several systems, bull trout and lake trout are currently coexisting, but bull trout are at greatly reduced abundances. This may be a function of the opportunistic nature of both species to prey on a variety of prey resources once kokanee are depleted. Further, several authors have illustrated that predators consuming the same prey can coexist when predator and prey densities vary and density dependence is not linear in predator populations (Armstrong and McGehee 1980; Abrams et al. 2003; Roos et al. 2008). An alternative hypothesis is that competitive exclusion between the species has not had enough time to be fully expressed. In most waterbodies, the effects of lake trout are studied after the bull trout population has waned. We believe Swan Lake will be an interesting case history to study in the future, given the recent expansion of lake trout.

Supplemental Material

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Table S1. Diet data for bull trout *Salvelinus confluentus* (BLT) and lake trout *Salvelinus namaycush* (LKT) sampled in Swan Lake, Montana. Bull trout were sampled in 2007 and lake trout were sampled in 2008. Diet headings are defined as: total volume (vol_ml), percent *Mysis diluviana* (per_mysis), percent other invertebrates (per_oi), percent fish (per_fish), *M. diluviana* volume (Mysis_vol), other invertebrate volume (oi_vol), fish volume (fish_vol), Diptera number (dipter_num), and *Pisidium adamsi* number (pisidium_num). Note: Bull trout length is standard length and lake trout is total length. To convert bull trout length to total length see publication for model.

Found at DOI: http://dx.doi.org/10.3996/012011-JFWM-004.S1 (119 KB XLS).

Report S1. Rosenthal LR, Fredenberg WA. 2009. Experimental removal of lake trout in Swan Lake, MT: 2009 Annual Report. Annual report for the Swan Valley bull trout working group.

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