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Trophic relationships between a native and a nonnative predator in a system of natural lakes

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Abstract –Bull trout, a species of char listed as threatened under the US Endangered Species Act, have been displaced from portions of their historic range following the introduction of nonnative lake trout. It has been suggested that competitive exclusion as a result of trophic overlap between bull trout and lake trout may be the causal mechanism associated with displacement of bull trout. This study used stable isotope data to evaluate trophic relationships among native bull trout, nonnative lake trout and other fishes in seven lakes in Glacier National Park (GNP), Montana. Bull trout and lake trout had greater δ^{15}N values relative to other fishes among lakes ($\delta^{15}N \geq 3.0‰$). Lake trout had greater δ^{15}N values relative to bull trout ($\delta^{15}N = +1.0‰$). Bull trout had greater δ^{13}C values relative to lake trout in six of the seven lakes examined. Although both bull trout and lake trout had greater δ^{15}N values relative to other fishes within lakes in GNP, differences in δ^{15}N and δ^{13}C between bull trout and lake trout suggest that they are consuming different prey species or similar prey species in different proportions. Therefore, displacement of bull trout as a direct result of complete overlap in food resource use is not anticipated unless diet shifts occur or food resources become limiting. Additionally, future studies should evaluate food habits to identify important prey species and sources of partial dietary overlap between bull trout and lake trout.

Key words: trophic relationship; stable isotope analysis; bull trout; lake trout; competitive exclusion

Introduction

Introduced species can directly affect native species through competition, predation, disease and hybridisation (Moyle & Cech 1996). Species introduction may occur both inadvertently and intentionally; however, the resulting outcome on native communities is often negative, regardless of initial intent. For example, the intentional introduction of *Mysis diluviana* has been shown to alter occurrence and composition of native zooplankton assemblages (Rieman & Falter 1981; Spencer et al. 1999; Vander Zanden et al. 2003; Ellis et al. 2011), growth rates of fish species (Tohtz 1993; Stafford et al. 2002) and fish assemblage structure (Spencer et al. 1991; Vander Zanden et al. 2003; Ellis et al. 2011). Intentional nonnative fish introductions have occurred globally for over 3000 years (Li & Moyle 1999) in an attempt to increase food supply, enhance fishing opportunities, manipulate aquatic systems and change aesthetics (Li & Moyle 1999). Unintentional introduction and invasions may also occur as a result of other activities. For example, sea lampreys (*Petromyzon marinus*), native to Lake Ontario, invaded the upper four Laurentian Great Lakes after the Welland Canal was constructed to allow shipping among the lakes (Smith 1971). Predation on native fishes by sea lampreys is considered to be one of the causes of the decimated fisheries in the Laurentian Great Lakes. However, this is not an isolated event, as introduced species have been implicated in contributing to a majority of the fish extinctions in the United States (Li & Moyle 1999).

Lake trout (*Salvelinus namaycush*) are top-level predators that have been introduced outside of their

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historic range throughout much of the western United States (Crossman 1995; Martinez et al. 2009). Lake trout have been introduced into many lakes and reservoirs because of their popularity as a sport fish (Martinez et al. 2009). Lake trout were introduced into the Flathead Lake-River system in 1905 (see Spencer et al. 1991). Since this introduction, lake trout have colonised lakes throughout the upper Flathead Drainage, including many lakes in Glacier National Park (GNP), Montana, west of the Continental Divide (Fredenberg 2002; Meeuwig et al. 2008). Within GNP, lake trout were first documented in Lake McDonald in 1959, Bowman Lake and Kintla Lake in 1962, Logging Lake in 1984, Harrison Lake in 2000, Lower Quartz Lake in 2003 and Quartz Lake in 2005 (Fredenberg 2002; Meeuwig & Guy 2007). These lakes are within the historic range of bull trout (*Salvelinus confluentus*), a species listed as threatened under the US Endangered Species Act. Many bull trout populations within GNP exhibit a lacustrine-adfluvial life history in which lake environments are occupied during much of their life history other than for spawning and rearing of juveniles. This results in spatial overlap with invasive lake trout, which generally exhibit a purely lacustrine life history. Within GNP, both bull trout and lake trout can attain large sizes; for example, mean, upper quartile and maximum total lengths were 380, 468 and 714 mm for bull trout and 422, 544 and 829 mm for lake trout among lakes (this study). Bull trout and lake trout are both generalist predators that feed on a variety of available aquatic taxa with diets that generally reflect food availability (e.g. see Martin 1966; Scott & Crossman 1973; Donald & Alger 1993; Wilhelm et al. 1999; Beauchamp & Van Tassell 2001); however, when present, fish compose the majority of bull trout and lake trout diets (Donald & Alger 1993). Therefore, bull trout and lake trout in many GNP lakes are likely piscivorous because of the availability of a variety of prey fish (Meeuwig et al. 2008). Additionally, fish (i.e. salmonids, cyprinids and catostomids) composed the majority of lake trout diets by weight in Lake McDonald within GNP (Dux 2005), and fish (i.e. salmonids, percids, cyprinids and catostomids) composed the majority of bull trout diets in nearby Flathead Lake and Libby Reservoir (Leathe & Graham 1982; Dalbey et al. 1998).

The number of bull trout has declined concomitantly with an increase in the number of lake trout in four lakes in GNP; Kintla Lake, Bowman Lake, Logging Lake and Lake McDonald (Fredenberg 2002). Similarly, introduced lake trout displaced native bull trout in Bow Lake and Hector Lake, Alberta (Donald & Alger 1993). Donald & Alger (1993) suggested that competition may have resulted in the observed displacement of bull trout and cite Gause's principle (i.e. competitive exclusion; Hardin 1960). Bull trout and lake trout had similar growth rates, gape limitations and mouth morphology and had similar food habits in Bow Lake and Hector Lake (Donald & Alger 1993); consequently, Donald & Alger (1993) further speculated that dietary overlap may limit the ability for these two species to establish sympatric populations. Studying trophic relationships between bull trout and lake trout can help elucidate whether competition for food resources is common in lakes where the distribution of native bull trout and nonnative lake trout overlaps.

Food habits studies can be used to examine trophic relationships within species assemblages. Food habits studies are often performed through gut content analyses, which entail collecting fish, removing their gut contents and quantifying the diet of the fish. Fish can be collected and gut contents removed by a variety of techniques, and there are a number of metrics for describing and comparing diet composition (see Bowen 1996). Gut content analyses can provide fine taxonomic resolution with respect to food habits; however, this method does have limitations. Stressful sampling techniques (e.g. gill netting, electrofishing) may cause fish to regurgitate gut contents (Bowen 1996). The composition of gut contents may be daily or seasonally variable; therefore, researchers must consider the timing of sampling when designing a study to examine food habits. Digestive rates may differ among different prey items, which may bias an analysis of gut contents towards prey items that are more difficult to digest (Bowen 1996).

Stable isotope analysis provides an indirect method for examining trophic relationships. Elements such as carbon and nitrogen have more than one isotope (Peterson & Fry 1987). The ratio of heavy to light isotopes in a sample can be compared to a standard and then expressed in terms of a δ value (e.g. δ^{13}C and δ^{15}N), which is used to quantify the isotopic composition of the sample (Peterson & Fry 1987). Empirical evidence has shown that δ^{15}N of a consumer is generally greater than that of its diet (see Martínez del Rio et al. 2009). The difference in δ^{15}N between a consumer and its diet is a result of isotopic discrimination (Martínez del Rio et al. 2009), which has also been referred to as isotopic fractionation (Hobson & Clark 1992). General trends in isotopic discrimination between diet and consumer make measurements of δ^{15}N useful for examining the trophic position of species within an assemblage. For example, Minagawa & Wada (1984) observed an average discrimination of 3.4‰ between δ^{15}N values of diet and consumer among a variety of taxa. However, isotopic discrimination of δ^{15}N can vary considerably depending on diet (e.g. 1.4‰ for consumers raised on invertebrate diets and 3.3‰ for consumers raised on high-protein diets; McCutchan et al. 2003). Conversely, there is little isotopic discrimination of δ^{13}C between diet and consumer [e.g. 0.2‰ in freshwater systems (France & Peters 1997); 0.5‰ among non fluid-feeding consumers (McCutchan et al. 2003)]; additionally, studies have shown that δ^{13}C values of littoral primary producers are greater than those of pelagic primary producers in aquatic systems (France 1995; Hecky & Hesslein 1995). Therefore, δ^{13}C measurements have been used for inferring where, or on what group of species, a consumer is feeding (e.g. Vander Zanden et al. 1999).

Stable isotope analysis provides a time-integrated estimate of food habits because δ^{13}C and δ^{15}N represent the average diet consumed over periods of weeks to months, depending on the turnover rate of the tissue examined (e.g. Tieszen et al. 1983). This is in contrast to gut content analysis that provides a point-in-time estimate of diet. Relatively few individuals of a species are needed to examine trophic relationships using stable isotope analysis (e.g. <10; Vander Zanden & Rasmussen 2002), unlike gut content analysis that may require the sampling of larger numbers of consumers to achieve an adequate sample size of nonempty stomachs. For example, 27% of bull trout and 18% of lake trout had empty stomachs in Lake Pend Oreille, Idaho (Vidergar 2000), and the per cent of empty lake trout stomachs varied from 19% to 70% among seasons in Lake McDonald, Montana (Dux 2005).

The objective of this study was to evaluate trophic relationships between bull trout and lake trout in lakes of GNP. Relationships between fish length and δ^{13}C and fish length and δ^{15}N were examined among species and lakes to determine whether δ^{15}N and δ^{13}C were dependent on individual size and to evaluate the potential for ontogenetic trophic shifts. Comparisons were performed using analysis of variance (ANOVA) models to evaluate complete overlap in δ^{15}N and δ^{13}C values between bull trout and lake trout. Complete overlap in δ^{15}N and δ^{13}C values between bull trout and lake trout would provide support for the hypothesis that these species are complete competitors for food resources (Donald & Alger 1993).

Methods

Study system

The study system consisted of seven lakes located in GNP west of the Continental Divide (Fig. 1). The selected lakes have sympatric populations of native bull trout and nonnative lake trout and vary in species richness and composition (Meeuwig et al. 2008). Other native fish species present within the study system include cutthroat trout (*Oncorhynchus clarkii*), mountain whitefish (*Prosopium williamsoni*), pygmy whitefish (*Prosopium coulterii*), largescale sucker (*Catostomus macrocheilus*), longnose sucker (*Catostomus catostomus*), northern pikeminnow (*Ptychocheilus oregonensis*), peamouth (*Mylocheilus caurinus*), redside shiner (*Richardsonius balteatus*), mottled sculpin (*Cottus bairdi*) and slimy sculpin (*Cottus cognatus*). Other nonnative fish species present in the study system include brook trout (*Salvelinus fontinalis*), kokanee (*O. nerka*) and lake whitefish (*Coregonus clupeaformis*).

Field methods

Gill net and hook and line surveys were conducted during the summer of 2005 in the seven study lakes. Gill net surveys were also conducted during the summer of 2006 in Quartz Lake and Lower Quartz Lake to increase sample sizes of target species. Gill net surveys were conducted with sinking, experimental gill nets that were 38 m long, 2 m deep and constructed of multifilament nylon with five panels: 19-, 25-, 32-, 38- and 51-mm bar mesh. The number of gill nets set varied among lakes according to scientific collection permit requirements, which allowed incidental mortality of ≤10 bull trout. Hook and line surveys were conducted concurrently with gill net surveys.

Fish were anesthetized with 30 mg·l^{-1} clove oil (Prince & Powell 2000), identified to species, measured for length (total length; mm) and released. A minimum of 100 individuals were measured if >100 individuals of a given species were sampled within a lake. A 14-gauge soft tissue biopsy needle (Achieve Soft Tissue Biopsy Needle; Cardinal Health, McGaw Park, IL, USA) was used to nonlethally extract a sample of white muscle (2 mm diameter by 15 mm long) from a subsample of fish at each lake for stable isotope analysis (δ^{15}N and δ^{13}C) prior to release. White muscle was selected as it exhibits lower within tissue variance in δ^{13}C than other tissues, such as red muscle, heart and liver and has been suggested as an appropriate tissue for examining trophic relationships among fishes (Pinnegar & Polunin 1999). Muscle samples were collected by inserting the needle into the dorsal musculature near the insertion of the dorsal fin in a posterior to anterior direction. Muscle samples were placed in a portable cryogenic freezer (model CX100; Taylor Wharton, Theodore, AL, USA) and transported to Montana State University.

Sample storage capacity at the study sites was limited to 80 samples based on equipment limitations; therefore, subsampling was used to provide a representative sample of fish species present within each lake. Fish were subsampled at each lake as follows: (i) up to 10 bull trout were sampled, (ii) up to 10 lake

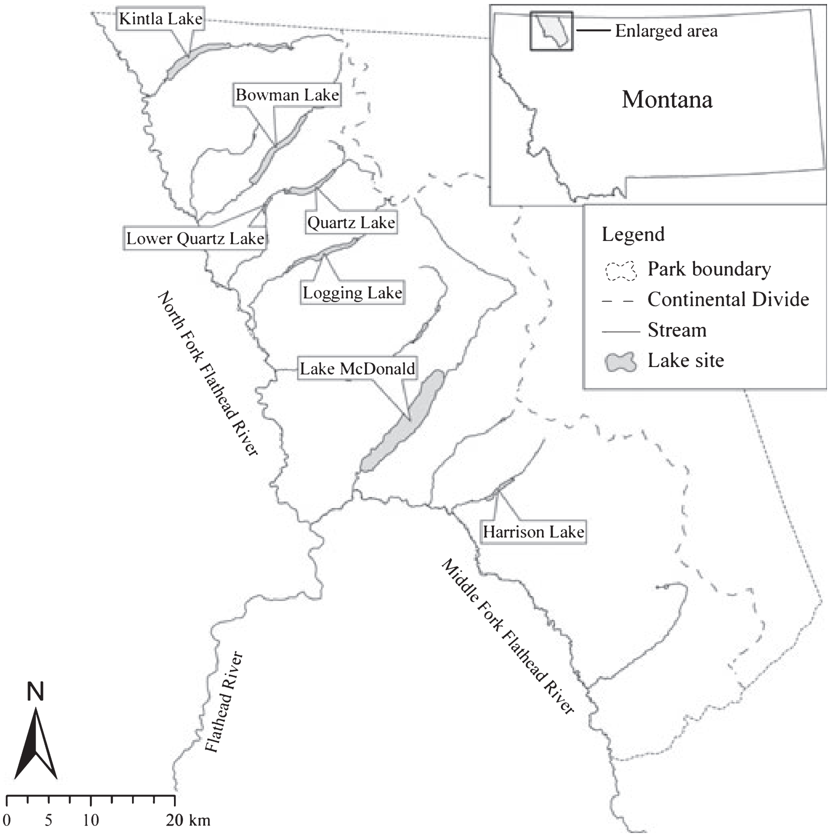

Fig. 1. Location of seven lakes in Glacier National Park, Montana, inhabited by sympatric populations of native bull trout and nonnative lake trout.

trout were sampled and (iii) up to five individuals of each other fish species present were sampled. Two sets of samples were collected from Quartz Lake, one in 2005 and one in 2006. These samples were pooled for analyses (see below for between year comparisons) resulting in a larger sample size for Quartz Lake. Additionally, muscle samples were only collected from bull trout and lake trout individuals large enough to be considered likely piscivores (i.e. ≥200 mm; McPhail & Baxter 1996).

A two-sample t-test ($\alpha = 0.05$; PROC TTEST; SAS Institute 1989) was used to evaluate whether the mean length of individuals subsampled for stable isotope analysis was representative of the mean length of all individuals sampled by lake and species (Table 1). The mean length of redside shiner differed between the subsample and the total sample of all individuals in Bowman Lake ($t = 2.18$, d.f. = 28, $P = 0.038$), Lower Quartz Lake ($t = 3.31$, d.f. = 38, $P = 0.002$) and Logging Lake ($t = 2.61$, d.f. = 18, $P = 0.018$); probability values for all other species by lake comparisons varied from 0.064 to 1.000. A two-sample t-test was used to compare the mean lengths of bull trout and lake trout subsampled for stable isotope analysis by lake. Mean lengths of bull trout and lake trout did not differ within lakes with the exception of Lower Quartz Lake ($t = 6.52$, d.f. = 11, $P < 0.001$); probability values for all other comparisons within lakes varied from 0.104 to 0.724.

Laboratory methods

Muscle samples were dried for 48 h at 60 °C and ground to a fine powder with a mortar and pestle (Jardine et al. 2003). About 2–3 mg of the prepared sample was placed into a 4- by 6-mm tin capsule and shipped to South Dakota State University (Department of Plant Science, Brookings, SD, USA) for stable isotope analysis using an Europa ANCA-GSL 20-20 IRMS mass spectrometer. Isotope δ values were calculated following Peterson & Fry (1987).

Data analysis

Pearson product-moment correlations (PROC CORR; SAS Institute 1989) were calculated between fish length and δ^{13}C and between fish length and δ^{15}N for each species by lake to examine trends in δ^{13}C and δ^{15}N for the lengths of fish sampled. Correlation analyses were performed when at least three individuals per species by lake were sampled, resulting in 50 species by lake correlation analyses for each of the isotopes examined. Values for δ^{13}C and δ^{15}N were plotted against length when correlations were significant ($\alpha = 0.05$).

An analysis of variance (ANOVA) was used to examine differences in δ^{15}N among bull trout, lake trout and all other sampled fish species combined (hereafter referred to as other fishes) among lakes.

Table 1. Lake, species, sample size (*N*) and length (total length; mean ± standard deviation) of the total sample of individuals measured by lake, and sample size, length, δ^{13}C (mean ± standard error) and δ^{15}N (mean ± standard error) of individuals used for stable isotope analysis. Species within lakes followed by an asterisk had lengths that differed significantly between the subsample used for stable isotope analysis and the total sample. Descriptive statistics for the total sample of bull trout and lake trout are based on individuals ≥200 mm; however, an addition eight bull trout varying from 124 to 198 mm and an additional five lake trout varying from 132 to 197 mm were sampled among lakes.

		Total sample		Stable isotope analysis			
Lake	Species	*N*	Length (mm)	*N*	Length (mm)	δ^{13}C	δ^{15}N
Kintla Lake	Bull trout	12	353 ± 101	10	347 ± 111	−23.66 ± 0.34	10.77 ± 0.18
	Lake trout	34	451 ± 178	10	421 ± 102	−22.53 ± 0.40	11.94 ± 0.25
	Cutthroat trout	50	194 ± 74	5	176 ± 12	−23.05 ± 0.70	7.69 ± 0.25
	Mountain whitefish	100	228 ± 45	5	239 ± 22	−25.58 ± 0.79	7.34 ± 0.38
	Longnose sucker	250	135 ± 118	5	201 ± 29	−21.87 ± 0.92	7.25 ± 0.43
	Peamouth	47	110 ± 34	5	119 ± 4	−26.88 ± 0.35	7.79 ± 0.26
	Redside shiner	8	145 ± 24	4	141 ± 35	−24.59 ± 0.87	7.16 ± 0.19
Bowman Lake	Bull trout	12	370 ± 156	10	351 ± 117	−22.62 ± 0.63	10.56 ± 0.32
	Lake trout	47	422 ± 155	10	415 ± 76	−24.95 ± 0.65	10.90 ± 0.35
	Cutthroat trout	23	155 ± 67	5	132 ± 5	−25.18 ± 1.15	7.44 ± 0.30
	Mountain whitefish	104	276 ± 63	5	251 ± 45	−24.83 ± 0.42	7.76 ± 0.28
	Longnose sucker	55	148 ± 68	5	158 ± 32	−20.82 ± 0.49	7.38 ± 0.20
	Redside shiner*	26	85 ± 22	4	110 ± 6	−22.64 ± 0.90	7.54 ± 0.80
Quartz Lake	Bull trout	59	393 ± 133	20	416 ± 94	−23.51 ± 0.32	11.12 ± 0.26
	Lake trout	4	394 ± 111	3	342 ± 47	−25.43 ± 1.08	12.37 ± 0.25
	Cutthroat trout	29	320 ± 74	10	335 ± 40	−24.37 ± 0.32	8.21 ± 0.17
	Mountain whitefish	178	219 ± 41	10	214 ± 12	−27.24 ± 0.52	8.66 ± 0.17
	Largescale sucker	9	237 ± 86	5	197 ± 13	−20.48 ± 0.33	7.95 ± 0.26
	Longnose sucker	121	218 ± 152	10	271 ± 109	−22.82 ± 0.68	8.52 ± 0.35
	Redside shiner	27	97 ± 24	5	118 ± 8	−20.67 ± 0.39	8.75 ± 0.26
Lower Quartz Lake	Bull trout	13	434 ± 121	10	414 ± 79	−23.21 ± 0.57	10.79 ± 0.20
	Lake trout	3	727 ± 33	3	727 ± 33	−25.77 ± 0.84	11.49 ± 0.36
	Cutthroat trout	61	244 ± 87	5	231 ± 64	−24.30 ± 1.00	8.10 ± 0.35
	Mountain whitefish	144	194 ± 46	5	184 ± 36	−24.89 ± 1.50	8.50 ± 0.30
	Longnose sucker	120	214 ± 87	5	157 ± 66	−22.02 ± 0.72	7.55 ± 0.49
	Redside shiner*	36	56 ± 21	4	92 ± 16	−24.93 ± 0.82	8.42 ± 0.99
Logging Lake	Bull trout	6	322 ± 120	6	322 ± 120	−22.54 ± 0.52	11.44 ± 0.27
	Lake trout	26	416 ± 149	10	410 ± 84	−23.71 ± 0.47	12.01 ± 0.17
	Cutthroat trout	39	273 ± 88	5	288 ± 71	−24.59 ± 0.81	8.56 ± 0.54
	Mountain whitefish	102	194 ± 49	5	191 ± 15	−25.28 ± 0.65	9.09 ± 0.19
	Longnose sucker	100	297 ± 137	5	326 ± 158	−20.48 ± 0.36	7.96 ± 0.33
	Northern Pikeminnow	126	132 ± 56	5	131 ± 2	−21.04 ± 0.21	8.97 ± 0.08
	Redside shiner*	15	78 ± 23	5	105 ± 6	−21.63 ± 0.21	8.82 ± 0.20
Lake McDonald	Bull trout	8	417 ± 81	8	417 ± 81	−23.10 ± 0.63	10.14 ± 0.28
	Lake trout	32	382 ± 137	10	405 ± 60	−25.56 ± 0.37	11.48 ± 0.31
	Cutthroat trout	4	187 ± 141	2	308 ± 45	−26.26 ± 1.21	7.38 ± 0.39
	Kokanee	8	406 ± 18	5	409 ± 13	−29.26 ± 0.69	6.16 ± 0.70
	Mountain whitefish	68	267 ± 77	5	266 ± 41	−26.11 ± 0.95	5.88 ± 0.21
	Pygmy whitefish	10	139 ± 32	5	132 ± 4	−26.89 ± 0.24	9.49 ± 0.30
	Lake whitefish	71	311 ± 180	4	383 ± 118	−25.92 ± 0.48	7.38 ± 0.78
	Largescale sucker	21	222 ± 104	5	199 ± 20	−19.15 ± 0.31	8.38 ± 0.29
	Longnose sucker	43	265 ± 88	5	263 ± 35	−21.33 ± 0.93	8.36 ± 0.11
	Northern pikeminnow	120	184 ± 61	5	194 ± 9	−20.61 ± 0.65	8.55 ± 0.38
	Peamouth	103	155 ± 40	5	167 ± 26	−21.38 ± 0.75	7.74 ± 0.37
	Redside shiner	23	83 ± 19	4	98 ± 4	−23.13 ± 0.40	7.72 ± 0.20
Harrison Lake	Bull trout	9	467 ± 125	8	471 ± 133	−24.02 ± 0.66	10.96 ± 0.37
	Lake trout	10	521 ± 112	10	521 ± 112	−27.30 ± 0.30	12.22 ± 0.55
	Cutthroat trout	22	272 ± 71	5	289 ± 25	−25.10 ± 0.47	9.11 ± 0.34
	Brook trout	2	139 ± 84	1	198	−22.54	8.23
	Kokanee	4	305 ± 68	4	305 ± 68	−31.05 ± 0.22	9.93 ± 0.87
	Mountain whitefish	147	208 ± 42	5	211 ± 17	−28.86 ± 0.60	9.07 ± 0.58
	Longnose sucker	53	213 ± 92	5	192 ± 16	−25.68 ± 0.74	7.85 ± 0.29

Prior to this analysis, differences in δ^{15}N for the pooled sample from Quartz Lake were examined and model assumptions were evaluated. δ^{15}N did not differ between years for bull trout ($F_{1,17} = 0.28$, $P = 0.601$) and other fishes ($F_{1,37} = 1.81$, $P = 0.187$) for the pooled sampled from Quartz Lake. Only three lake trout were sampled between years in Quartz Lake (one in 2005, two in 2006); therefore, a similar analysis was not performed for lake trout. However, the range of δ^{15}N for the three lake trout was less than that of bull trout and other fishes. No trends were observed for deviation from normality for δ^{15}N (Shapiro–Wilk Statistic; Shapiro & Wilk 1965), and experimental error variance of δ^{15}N did not differ among bull trout, lake trout and all other fishes combined within lakes based on a Brown–Forsythe test for homogeneity of variance (Brown & Forsythe 1974). The ANOVA model used was a randomised complete block design with subsampling where lakes were treated as random blocks, the fixed factor had three levels (bull trout, lake trout and other fishes), individual fish were treated as subsample units and fish length was included as a covariate to account for differences in δ^{15}N associated with fish length ($\alpha = 0.05$; PROC GLM; SAS Institute 1989). Blocking by lake was used to account for differences in δ^{15}N among lakes because primary consumers were not sampled to provide a way of standardising δ^{15}N among lakes (e.g. Vander Zanden & Rasmussen 1999). There was no interaction between the random block and the fixed factor showing that differences in δ^{15}N among levels of the fixed factor were systematic among lakes. Therefore, the randomised complete block design provided a valid method for standardising comparisons among δ^{15}N values of bull trout, lake trout and other fishes. Preplanned comparisons were made to test the following predictions: (i) bull trout and lake trout will have similar δ^{15}N values, (ii) bull trout will have greater δ^{15}N values relative to other fishes and (iii) lake trout will have greater δ^{15}N values relative to other fishes. Significant differences in δ^{15}N between bull trout and lake trout were used to infer incomplete overlap in δ^{15}N.

A similar procedure was used to examine differences in δ^{13}C between bull trout and lake trout among lakes. δ^{13}C did not differ between years for bull trout sampled from Quartz Lake ($F_{1,17} = 0.16$, $P = 0.698$). The range of δ^{13}C of the three lake trout sampled from Quartz Lake was less than that of bull trout. No trends were observed for deviation from normality for δ^{13}C (Shapiro–Wilk Statistic; Shapiro & Wilk 1965), and experimental error variance of δ^{13}C did not differ between bull trout and lake trout within lakes based on a Brown–Forsythe test for homogeneity of variance (Brown & Forsythe 1974). Preliminary analyses indicated an interaction between the random block (i.e. lake) and the two levels of the fixed factor (i.e. bull trout and lake trout). Consequently, separate ANOVA models were used to examine differences in δ^{13}C between bull trout and lake trout for each lake separately. Significant differences in δ^{13}C between bull trout and lake trout were used to infer incomplete overlap in δ^{13}C.

Results

Bull trout δ^{13}C values were generally greater than lake trout δ^{13}C values among lakes with the exception of Kintla Lake, and δ^{13}C values of bull trout and lake trout were generally intermediate within the distribution of other fishes sampled by lake (Table 1). Lake trout δ^{15}N values were greater than bull trout δ^{15}N values among lakes, and δ^{15}N values of both bull trout and lake trout were greater than δ^{15}N values of other fishes among lakes (Table 1).

Length and δ^{13}C were negatively correlated for bull trout in Kintla Lake, Bowman Lake, Quartz Lake and Logging Lake (Fig. 2), cutthroat trout in Lower Quartz Lake and Harrison Lake and lake whitefish in Lake McDonald (Fig. 3). Length and δ^{15}N were positively correlated for cutthroat trout and mountain whitefish in Quartz Lake, redside shiner in Lower Quartz Lake and kokanee in Lake McDonald (Fig. 4).

Lake trout δ^{15}N was estimated to be 1.0‰ greater than bull trout δ^{15}N ($F_{1,12} = 26.88$, $P = 0.001$; Fig. 5). Lake trout δ^{15}N was estimated to be 4.0‰ greater than δ^{15}N of other fishes ($F_{1,12} = 303.65$, $P < 0.001$; Fig. 5). Bull trout δ^{15}N was estimated to be 3.0‰ greater than δ^{15}N of other fishes ($F_{1,12} = 268.91$, $P < 0.001$; Fig. 5). Bull trout δ^{13}C was greater than lake trout δ^{13}C in all lakes except Kintla Lake, where lake trout δ^{13}C was greater; differences between bull trout δ^{13}C and lake trout δ^{13}C were significant in four of the seven lakes examined (Fig. 6).

Discussion

Dietary overlap between bull trout and lake trout has been suggested as a causal mechanism for the displacement of bull trout under conditions of limited food supply where the distribution of these species is sympatric (e.g. northern Montana, south-western Alberta and east-central British Columbia; Donald & Alger 1993). Analyses of δ^{13}C and δ^{15}N provide little evidence for complete trophic overlap between bull trout and lake trout among lakes sampled in this study. However, data needed to determine whether food is limiting within this study system are unavailable (e.g. bull trout and lake trout consumption estimates, prey species abundance and biomass, lake productivity). Patterns observed in this study may be a consequence of diet shifts associated with colonisation by nonnative lake trout. For example, lake trout shifted from a largely littoral, fish-based diet to a largely pelagic, zooplankton-based diet following invasions by non-native smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) in Canadian lakes (Vander Zanden et al. 1999). This conclusion was based on a comparison between stable isotope analyses of invaded (bass present) and reference lakes

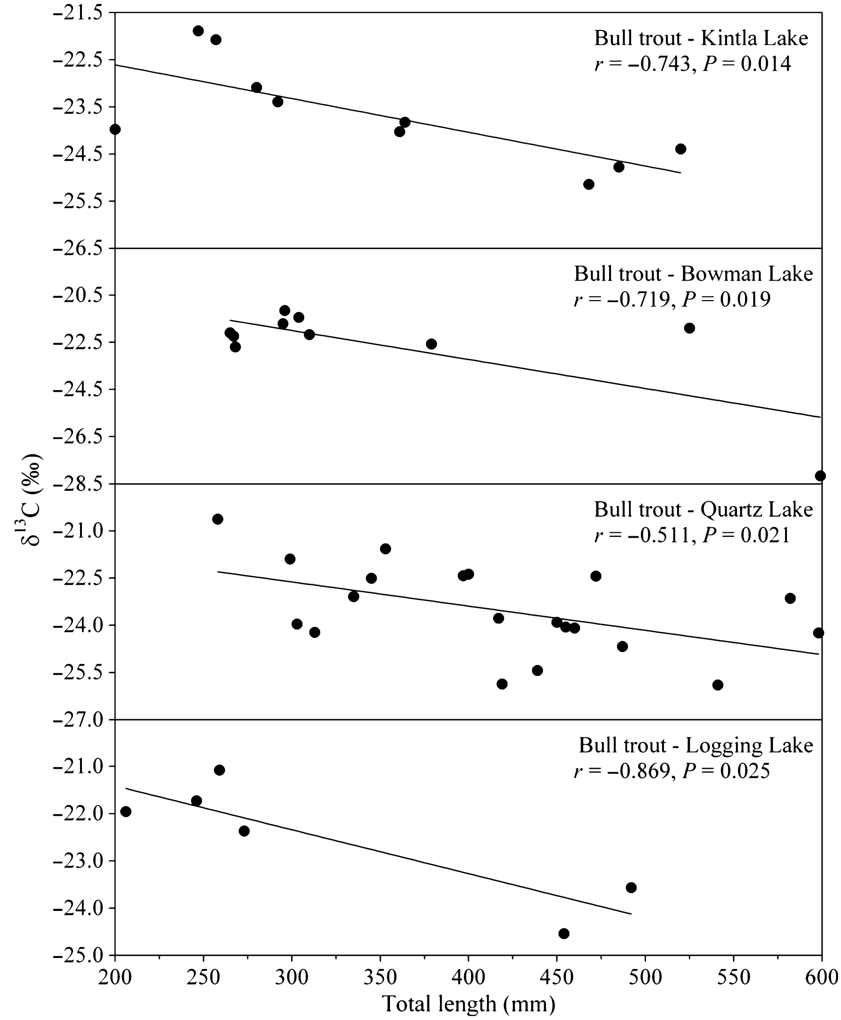

Fig. 2. Correlation between length and δ^{13}C for bull trout in Kintla Lake, Bowman Lake, Quartz Lake and Logging Lake, Glacier National Park, Montana. Trend lines were calculated using linear regression.

(bass absent) and on long-term studies of two invaded lakes (Vander Zanden et al. 1999).

It is difficult to determine whether the δ^{13}C and δ^{15}N values observed for bull trout among lakes in GNP are a result of diet shifts associated with colonisation by nonnative lake trout. Lakes in GNP that have not been colonised by nonnative lake trout are more depauperate in fish species richness (Meeuwig et al. 2008), and bull trout food habits often differ among lakes with different species assemblages (e.g. Leathe & Graham 1982; Donald & Alger 1993; Dalbey et al. 1998; Wilhelm et al. 1999; Vidergar 2000; Beauchamp & Van Tassell 2001; Clarke et al. 2005). Therefore, these lakes would be poor references as the influence of species assemblage could not be controlled.

Bull trout and lake trout have been shown to be generalist and opportunistic predators in many studies. The diet of bull trout in Lake Billy Chinook, Oregon, was variable seasonally and among size classes, and included kokanee, bull trout, rainbow trout (*O. mykiss*), mountain whitefish, other salmonids, cyprinids, cottids, catostomids and invertebrates (Beauchamp & Van Tassell 2001). Bull trout predation on three aquatic invertebrates in Harrison Lake, Alberta, varied seasonally and was similar to the seasonal abundance of the prey species (Wilhelm et al. 1999). Bull trout and lake trout fed on a wide range of available taxa, including aquatic and aerial insects and fishes in lakes varying in trophic complexity in northern Montana, south-western Alberta and east-central British Columbia; however, when present, fish composed the majority of bull trout and lake trout diets (Donald & Alger 1993). Dietary differences were observed between small (i.e. 177–406 mm) and large (i.e. >406 mm) lake trout in Lac la Ronge, Saskatchewan, where small lake trout fed on invertebrates (especially *Mysis relicta*), ciscoes (*Coregonus zenithicus* and *Coregonus artedi*), sculpins (*Myoxocephalus thompsonii* and *C. cognatus*) and ninespine sticklebacks (*Pungitius pungitius*) and large lake trout fed on ciscoes, lake whitefish, ninespine stickleback, longnose sucker, yellow perch (*Perca flavescens*), sculpins, burbot (*Lota lota*), walleye (*Sander vitreum*), spottail

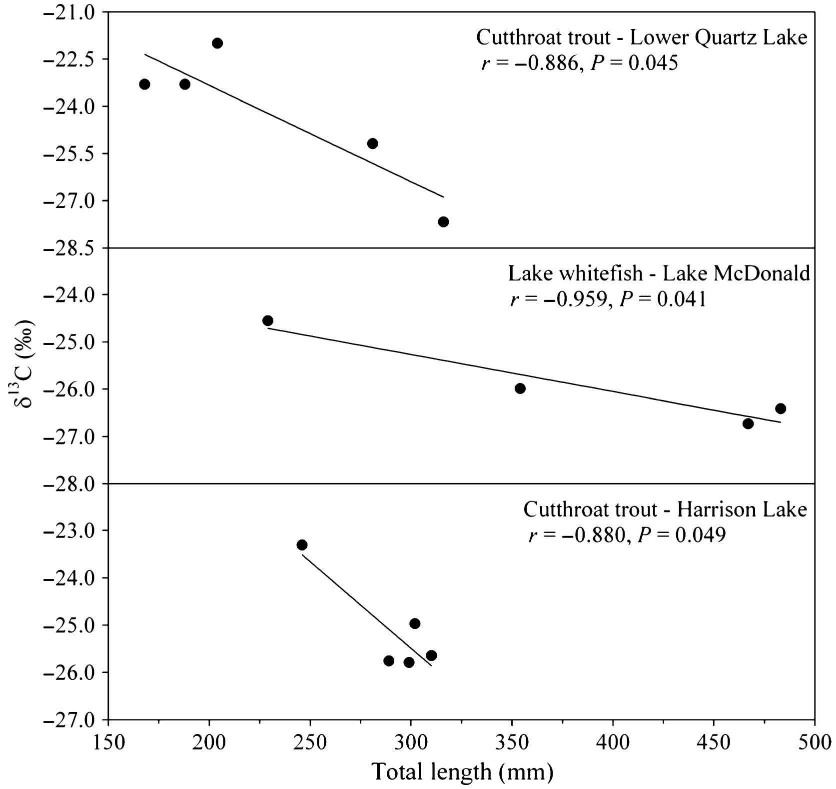

Fig. 3. Correlation between length and $\delta^{13}C$ for cutthroat trout in Lower Quartz Lake, lake whitefish in Lake McDonald and cutthroat trout in Harrison Lake, Glacier National Park, Montana. Trend lines were calculated using linear regression.

minnow (*Notropis hudsonius*), lake trout and small numbers of invertebrates (<11% of diet; Rawson 1961). Lake trout in Algonquin Park, Ontario, may feed on fishes or plankton, depending on their availability (Martin 1966). Lake trout diet varied with habitat (i.e. nearshore and offshore) and was related to prey abundance in Lake Michigan (Miller & Holey 1992). These studies suggest that differences in $\delta^{13}C$ and $\delta^{15}N$ between bull trout and lake trout in GNP could result from partitioning of prey resources associated with species-specific habitat use and prey availability rather than from diet shifts.

In six of the seven lakes examined in this study, the average bull trout $\delta^{13}C$ value was greater than the average lake trout $\delta^{13}C$ value (significantly greater in three of the seven lakes), and in four of the seven lakes, there was a negative relationship between bull trout length and $\delta^{13}C$. Studies have shown that $\delta^{13}C$ of littoral consumers in lakes is often greater than $\delta^{13}C$ of pelagic or profundal consumers as a result of a benthic algae $\delta^{13}C$ being greater than $\delta^{13}C$ of planktonic algae (France 1995; Hecky & Hesslein 1995; Vander Zanden & Rasmussen 1999). For example, $\delta^{13}C$ of primary consumers was −23.8‰ in littoral area, −28.4‰ in pelagic areas and −30.5‰ in profundal areas among 14 lakes in Ontario, Quebec (Vander Zanden & Rasmussen 1999), and a mean difference of 1.7‰ between $\delta^{13}C$ values for lake trout in bass invaded lakes and noninvaded lakes was used to infer greater dependence on littoral prey in noninvaded lakes (lake trout $\delta^{13}C = -27.5$‰) and a greater dependence on pelagic prey in invaded lakes (lake trout $\delta^{13}C = -29.2$‰). Among the study lakes where bull trout $\delta^{13}C$ values were greater than those of lake trout, mean differences varied from 1.17‰ to 3.28‰ (see Table 1). Therefore, the observed trends are suggestive of bull trout foraging in littoral habitat more than lake trout and of bull trout shifting from foraging in littoral habitat to foraging in pelagic or profundal habitat as they increase in length. Similarly, bull trout have been observed to be spatially segregated based on size in Harrison Lake, Alberta, with smaller bull trout (i.e. ≤250 mm fork length) observed in shallow water (i.e. <1 m) and larger bull trout observed in the profundal offshore waters (Wilhelm et al. 1999). However, additional information is necessary to determine whether there are differences in baseline $\delta^{13}C$ values between littoral and pelagic habitat within GNP lakes (e.g. see Vander Zanden & Rasmussen 1999).

Lake trout had greater $\delta^{15}N$ values relative to bull trout among lakes. This may be the result of consuming different prey species or similar prey species in different proportions, but the possibility that lake trout are receiving some dietary contribution from bull trout should not be disregarded. Lake trout can consume prey fish with lengths about 50% their own length (Ruzycki 2004). Therefore, it is possible that bull trout are contributing to the diet of lake trout even within the size range of individuals examined in this study.

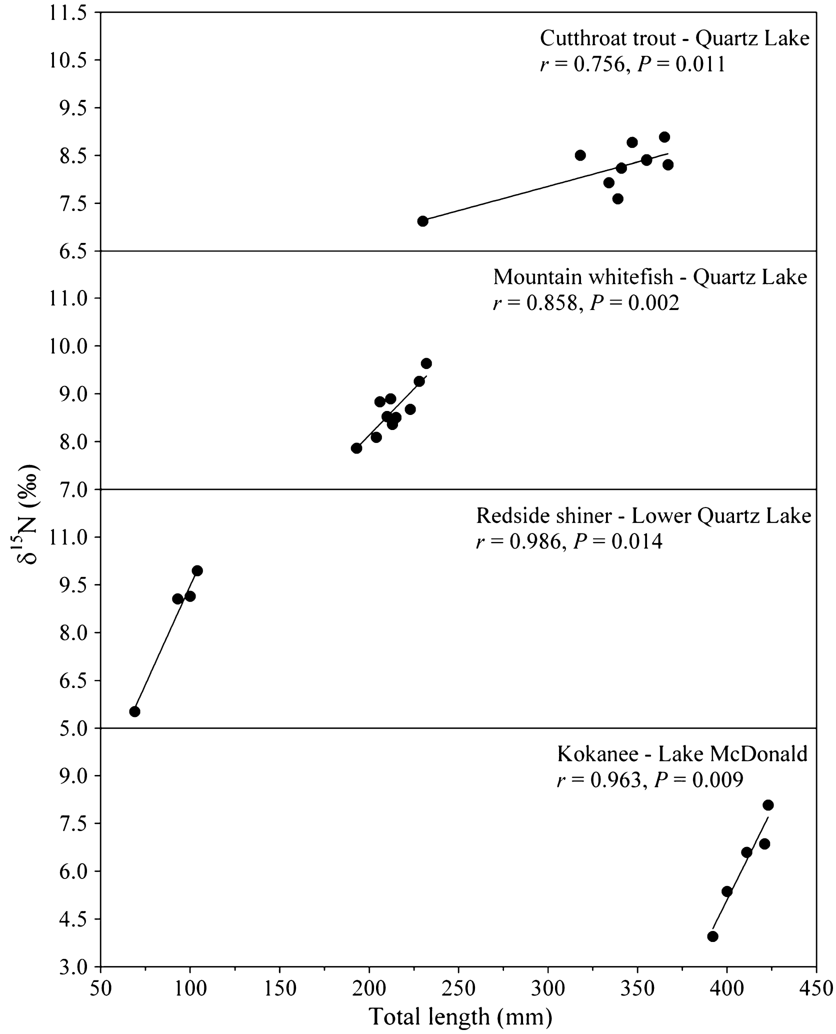

Fig. 4. Correlation between length and $\delta^{15}N$ for cutthroat trout in Quartz Lake, mountain whitefish in Quartz Lake, redside shiner in Lower Quartz Lake and kokanee in Lake McDonald, Glacier National Park, Montana. Trend lines were calculated using linear regression.

For example, the length of the smallest bull trout sampled in this study was <50% the length of the largest lake trout sampled within lakes with the exceptions of Quartz Lake and Lake McDonald.

This study shows that bull trout and lake trout have greater $\delta^{15}N$ values than other fishes in GNP lakes. This suggests that these species are top-level predators and indicates the potential for competition for prey resources; however, these species differed in levels of naturally occurring stable isotopes commonly used to examine trophic relationships (Martínez del Rio et al. 2009). Differences between these species in $\delta^{13}C$ in the majority of lakes examined and $\delta^{15}N$ among lakes may be the result of consuming different species or different proportions of similar species. Therefore, there is little evidence for complete trophic overlap between bull trout and lake trout in GNP, which has been suggested as a causal mechanism for population-level declines and extirpation of bull trout following the introduction of lake trout (Donald & Alger 1993). However, the magnitude of difference in trophic characteristics required for bull trout and lake trout to coexist is unknown. Although bull trout and lake trout differed in $\delta^{13}C$ in the majority of lakes and $\delta^{15}N$ among lakes, both species were more similar to each

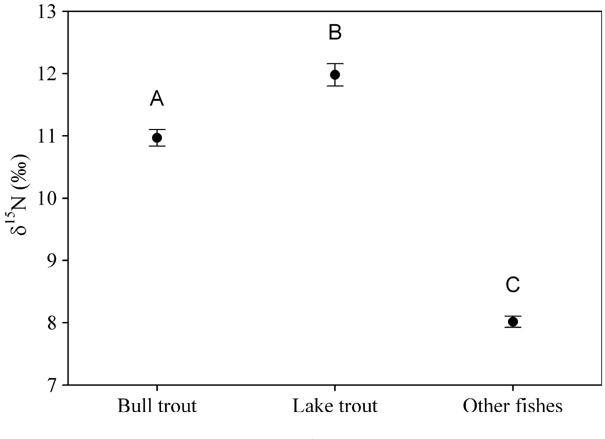

Fig. 5. Mean (±standard error) $\delta^{15}N$ of bull trout, lake trout and other fishes among seven lakes in Glacier National Park, Montana. Comparisons that were significantly different are indicated by different letters.

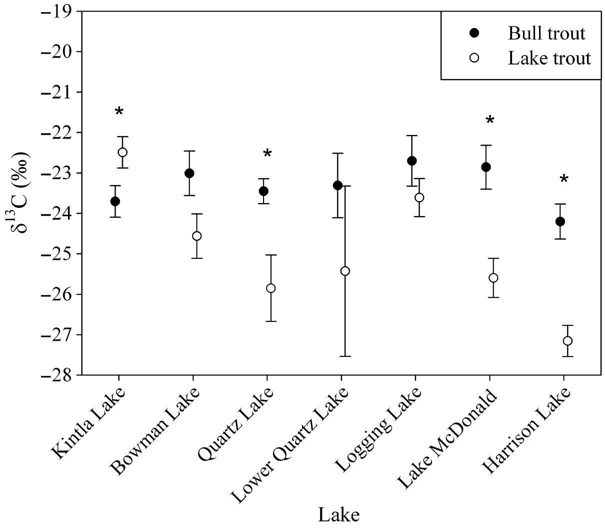

Fig. 6. Mean (±standard error) δ^{13}C of bull trout (filled circles) and lake trout (open circles) among seven lakes in Glacier National Park, Montana. Lakes where comparisons between bull trout and lake trout were significantly different are indicated by an asterisk.

other in δ^{15}N than they were to other species within lakes Therefore, some level of competition for food resources between these species is likely. This study did not evaluate trophic overlap between bull trout and lake trout <200 mm so it is unknown if competition for food resources at earlier life stages may result in exclusion of bull trout. Additionally, implicit in this 'competitive exclusion' hypothesis is the requirement of limited food supply. No data are available with respect to food abundance or consumption rates of bull trout and lake trout within GNP. Resources may be sufficient to allow partitioning of prey between two top-level predators within GNP. Additional research such as quantitative gut content analyses, bioenergetics modelling, and abundance and biomass estimates for predator and prey species to complement stable isotope data will help elucidate whether population-level declines in bull trout are likely to occur as a result of diet overlap with lake trout. Additionally, future stable isotope analyses should evaluate bull trout and lake trout <200 mm and examine habitat-specific, baseline isotopic values within lakes of GNP to provide a finer-scale analysis of trophic relationships and foraging habitat use among fishes.

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References

Beauchamp, D.A. & Van Tassell, J.J. 2001. Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130: 204–216.

Bowen, S.H. 1996. Quantitative description of the diet. In: Murphy, B.R. & Willis, D.W., eds. Fisheries techniques, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 513–532.

Brown, M.B. & Forsythe, A.B. 1974. Robust tests for the equality of variances. Journal of the American Statistical Association 69: 364–367.

Clarke, L.R., Vidergar, D.T. & Bennett, D.H. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14: 267–277.

Crossman, E.J. 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside of its native distribution: a review. Journal of Great Lakes Research 21(Suppl. 1): 17–29.

Dalbey, S., DeShazer, J., Garrow, L., Hoffman, G. & Ostrowski, T. 1998. Quantification of Libby Reservoir levels needed to maintain or enhance reservoir fisheries: methods and data summary, 1988–1996. Portland, OR: Bonneville Power Administration. Project Number 83–467.

Donald, D.B. & Alger, D.J. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71: 238–247.

Dux, A.M. 2005. Distribution and population characteristics of lake trout in Lake McDonald, Glacier National Park: implications for suppression. Bozeman, MT: Master's thesis, Montana State University.

Ellis, B.K., Stanford, J.A., Goodman, D., Stafford, C.P., Gustafson, D.L., Beauchamp, D.A., Chess, D.W., Craft, J.A., Deleray, M.A. & Hansen, B.S. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences of the United States of America 108: 1070–1075.

France, R.L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. Limnology and Oceanography 40: 1310–1313.

France, R.L. & Peters, R.H. 1997. Ecosystem differences in the trophic enrichment of ^{13}C in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences 54: 1255–1258.

Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in mountain lakes. Intermountain Journal of Sciences 8: 143–152.

Hardin, G. 1960. The competitive exclusion principle. Science 131: 1292–1297.

Hecky, R.E. & Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14: 631–653.

Hobson, K.A. & Clark, R.G. 1992. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. The Condor 94: 189–197.

Jardine, T.D., McGeachy, S.A., Paton, C.M., Savoie, M. & Cunjak, R.A. 2003. Stable isotopes in aquatic systems: sample preparation, analysis, and interpretation. Fredericton, NB: University of New Brunswick, Canadian Rivers Institute. Canadian Manuscript Report of Fisheries and Aquatic Sciences No. 2656.

Leathe, S.A. & Graham, P.J. 1982. Flathead Lake fish food habits study. Denver, CO: US Environmental Protection Agency.

Li, H.W. & Moyle, P.B. 1999. Management of introduced fishes. In: Kohler, C.C. & Hubert, W.A., eds. Inland fisheries management in North American, 2nd edn. Bethesda, MD: American Fisheries Society, pp. 345–374.

Martin, N.V. 1966. The significance of food habits in the biology, exploitation, and management of Algonquin Park, Ontario, lake trout. Transactions of the American Fisheries Society 95: 415–422.

Martínez del Rio, C., Wolf, N., Carleton, S.A. & Gannes, L.Z. 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biological Reviews of the Cambridge Philosophical Society 84: 91–111.

Martinez, P.J., Bigelow, P.E., Deleray, M.A., Fredenberg, W.A., Hansen, B.S., Horner, N.J., Lehr, S.K., Schneidervin, R.W., Tolentino, S.A. & Viola, A.E. 2009. Western lake trout woes. Fisheries 34: 424–442.

McCutchan Jr, J.H., Lewis Jr, W.M., Kendall, C. & McGrath, C.C. 2003. Variation in trophic shifts for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102: 378–390.

McPhail, J.D. & Baxter, J.S. 1996. A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities. Bancouver, BC: University of British Columbia, Department of Zoology. Fisheries Management Report No. 104.

Meeuwig, M.H. & Guy, C.S. 2007. Evaluation and action plan for the protection of 15 threatened adfluvial populations of bull trout in Glacier National Park, Montana: final scientific report. Bozeman, MT: Montana Cooperative Fishery Research Unit.

Meeuwig, M.H., Guy, C.S. & Fredenberg, W.A. 2008. Influence of landscape characteristics on fish species richness among lakes of Glacier National Park, Montana. Intermountain Journal of Sciences 14: 1–16.

Miller, M.A. & Holey, M.E. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. Journal of Great Lakes Research 18: 51–60.

Minagawa, M. & Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta 48: 1135–1140.

Moyle, P.B. & Cech Jr, J.J. 1996. Fishes: an introduction to ichthyology, 3rd edn. Upper Saddle River, NJ: Prentice-Hall, Inc.

Peterson, B.J. & Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18: 293–320.

Pinnegar, J.K. & Polunin, N.V.C. 1999. Differential fractionation of δ^{13}C and δ^{15}N among fish tissues: implications for the study of trophic interactions. Functional Ecology 13: 225–231.

Prince, A. & Powell, C. 2000. Clove oil as an anesthetic for invasive field procedures on adult rainbow trout. North American Journal of Fisheries Management 20: 1029–1032.

Rawson, D.S. 1961. The lake trout of Lac la Ronge, Saskatchewan. Journal of the Fisheries Research Board of Canada 18: 423–462.

Rieman, B.E. & Falter, C.M. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Transactions of the American Fisheries Society 110: 613–620.

Ruzycki, J.R. 2004. Impact of lake trout introductions on cutthroat trout of selected western lakes of the continental United States. Logan, UT: Ph.D. dissertation, Utah State University.

SAS Institute. 1989. SAS/STAT user's guide, version 6, Vols 1–2, 4th edn. Cary, NC: SAS Institute.

Scott, W.B. & Crossman, E.J. 1973. Freshwater fishes of Canada. Ottawa, Canada: Fisheries Research Board of Canada.

Shapiro, S.S. & Wilk, M.B. 1965. An analysis of variance test for normality (complete samples). Biometrika 52: 591–611.

Smith, B.R. 1971. Sea lampreys in the Great Lakes of North America. In: Hardisty, M.W. & Potter, I.C., eds. The biology of lampreys, Vol. 1. New York, NY: Academic Press, pp. 207–247.

Spencer, C.N., McClelland, B.R. & Stanford, J.A. 1991. Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. BioScience 41: 14–21.

Spencer, C.N., Potter, D.S., Bukantis, R.T. & Stanford, J.A. 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research 21: 51–64.

Stafford, C.P., Stanford, J.A., Hauer, F.R. & Brothers, E.B. 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: a retrospective analysis using otoliths. Transactions of the American Fisheries Society 131: 994–1003.

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G. & Slade, N.A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ^{13}C analysis of diet. Oecologia 57: 32–37.

Tohtz, J. 1993. Lake whitefish diet and growth after the introduction of *Mysis relicta* to Flathead Lake, Montana. Transactions of the American Fisheries Society 122: 629–635.

Vander Zanden, M.J. & Rasmussen, J.B. 1999. Primary consumer δ^{13}C and δ^{15}N and the trophic position of aquatic consumers. Ecology 80: 1395–1404.

Vander Zanden, M.J. & Rasmussen, J.B. 2002. Food web perspectives on studies of bass populations in north-temperate lakes. In: Philipp, D.P. & Ridgway, M.S., eds. Black bass: ecology, conservation, and management. Bethesda, MD: American Fisheries Society, pp. 173–184.

Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401: 464–467.

Vander Zanden, M.J., Chandra, S., Allen, B.C., Reuter, J.E. & Goldman, C.R. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) Basin. Ecosystems 6: 274–288.

Vidergar, D.T. 2000. Population estimates, food habits and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Moscow, ID: Master's thesis, University of Idaho.

Wilhelm, F.M., Parker, B.R., Schindler, D.W. & Donald, D.B. 1999. Seasonal food habits of bull trout from a small alpine lake in the Canadian Rocky Mountains. Transactions of the American Fisheries Society 128: 1176–1192.