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Stable isotope evaluation of population- and individual-level diet variability in a large, oligotrophic lake with non-native lake trout

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Abstract – Non-native piscivores can alter food web dynamics; therefore, evaluating interspecific relationships is vital for conservation and management of ecosystems with introduced fishes. Priest Lake, Idaho, supports a number of introduced species, including lake trout *Salvelinus namaycush*, brook trout *S. fontinalis* and opossum shrimp *Mysis diluviana*. In this study, we used stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) to describe the food web structure of Priest Lake and to test hypotheses about apparent patterns in lake trout growth. We found that isotopic niches of species using pelagic-origin carbon did not overlap with those using more littoral-origin carbon. Species using more littoral-origin carbon, such as brook trout and westslope cutthroat trout *Oncorhynchus clarki lewisi*, exhibited a high degree of isotopic niche overlap and high intrapopulation variability in resource use. Although we hypothesised that lake trout would experience an ontogenetic diet shift, no such patterns were apparent in isotopic signatures. Lake trout growth rates were not associated with patterns in $\delta^{15}N$, indicating that variation in adult body composition may not be related to adult diet. Understanding trophic relationships at both the individual and species levels provides a more complete understanding of food webs altered by non-native species.

Key words: stable isotopes; individual variability; trophic position; niche space

Introduction

Trophic interactions are one of the fundamental mechanisms by which niche partitioning occurs in aquatic environments. Predators can have strong effects on ecosystem structuring through both direct (Goldschmidt et al. 1993) and indirect (Hölker et al. 2007) pathways, especially in lentic ecosystems (Northcote 1988; Jackson et al. 2001). Therefore, introduced predators can have an outsized effect on lacustrine systems (Sala et al. 2000; Eby et al. 2006; Mitchell & Knouft 2008), causing cascading effects on ecosystems (Carpenter et al. 2001; Sakai et al. 2001; Cucherousset & Olden 2011). Evaluating interspecific trophic relationships is therefore vital for conservation and management of ecosystems where introduced species have altered dynamics between coevolved native species.

Understanding how individual trait variation leads to population-level patterns can provide further insight into the dynamics of introduced species (Bolnick et al. 2003, 2011; Ruffino et al. 2011; Svanbäck et al. 2015). For example, individuals of an introduced species may not equally contribute to negative interactions (e.g. predation) with other species. Individuals can respond differently to competition and novel environmental conditions (Araújo et al. 2008) due to differences in phenotype and behaviour (Svanbäck & Bolnick 2007). Furthermore, feedback between behaviour and growth rate can reinforce individual foraging patterns (Huss et al. 2008), leading to correlation between phenotype and diet. As a

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result, generalist and specialist (e.g. piscivorous) individuals may exist within non-native fish populations and contribute disproportionally to negative interactions with native species. These individuals may be identifiable by growth rates, body condition or other phenotypic traits (Svanbäck et al. 2015). Therefore, linking dietary and phenotypic patterns at the individual level may provide a more complete understanding of the population-level effects of non-native species.

Lake trout *Salvelinus namaycush* have been introduced widely, often to provide a trophy component to recreational fisheries (Crossman 1995; Martinez et al. 2009). Lake trout are apex predators (Ryder et al. 1981) and introductions often cause conflicts with other sport fish and fishes of conservation concern (Ruzycki et al. 2003; Quist & Hubert 2004; Martinez et al. 2009; Syslo et al. 2011). Conflicts may be direct, via predation (Eby et al. 1995; Schoen et al. 2012), or indirect, via niche partitioning and competition with other predators (Donald & Alger 1993; Meeuwig et al. 2011). Over longer periods of time, the introduction of lake trout can cause trophic cascades (Tronstad et al. 2010), especially in systems with introduced opossum shrimp *Mysis diluviana* (Bowles et al. 1991; Ellis et al. 2011).

Lake trout were introduced to Priest Lake, Idaho, in 1925, but remained at low abundance until *M. diluviana* were established in the early 1970s. As a result, kokanee *Oncorhynchus nerka*, bull trout *Salvelinus confluentus* and westslope cutthroat trout *O. clarki lewisi* abundance declined dramatically (Venard & Scarnecchia 2005; Mallet 2013). Despite these changes, little is known about the current trophic relationships between species in Priest Lake. Lake trout are also known for their plasticity (Pazzia et al. 2002; Zimmerman et al. 2006; McDermid et al. 2010; Muir et al. 2015) and undergo ontogenetic diet shifts (Martin & Olver 1980); therefore, individuals are not expected to contribute equally to effects on other species. Phenotypic or behavioural traits may also affect individuals' ability to respond to reduced prey fish abundance (Stafford et al. 2013), further contributing to divergence in diet and ultimately interspecific interactions in Priest Lake.

In this study, we used stable isotopes to describe current food web characteristics in Priest Lake and to test hypotheses about patterns in individual lake trout diets. Specifically, we hypothesised that lake trout would experience ontogenetic shifts from a diet dominated by *M. diluviana* to one that included more littoral prey fishes (Vander Zanden & Rasmussen 1996). We also hypothesised that the shift in diet would result in increasing trophic position of lake trout with increasing length. Finally, we hypothesised that fast-growing lake trout would have elevated $\delta^{15}N$ values relative to slow-growing individuals.

Methods

Priest Lake is a 9,461-ha oligotrophic, dimictic lake located in the Columbia River basin of northern Idaho (Fig. 1). Thermal stratification generally occurs mid-July through the end of October, with a thermocline at a depth of about 35–50 m and summer surface water temperatures reaching 26 °C in shallow areas (Kemmerer et al. 1924; Bjornn 1957; Rieman et al. 1979). The native fish assemblage includes bull trout, westslope cutthroat trout, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *P. coulterii*, largescale sucker *Catostomus macrocheilus*, longnose

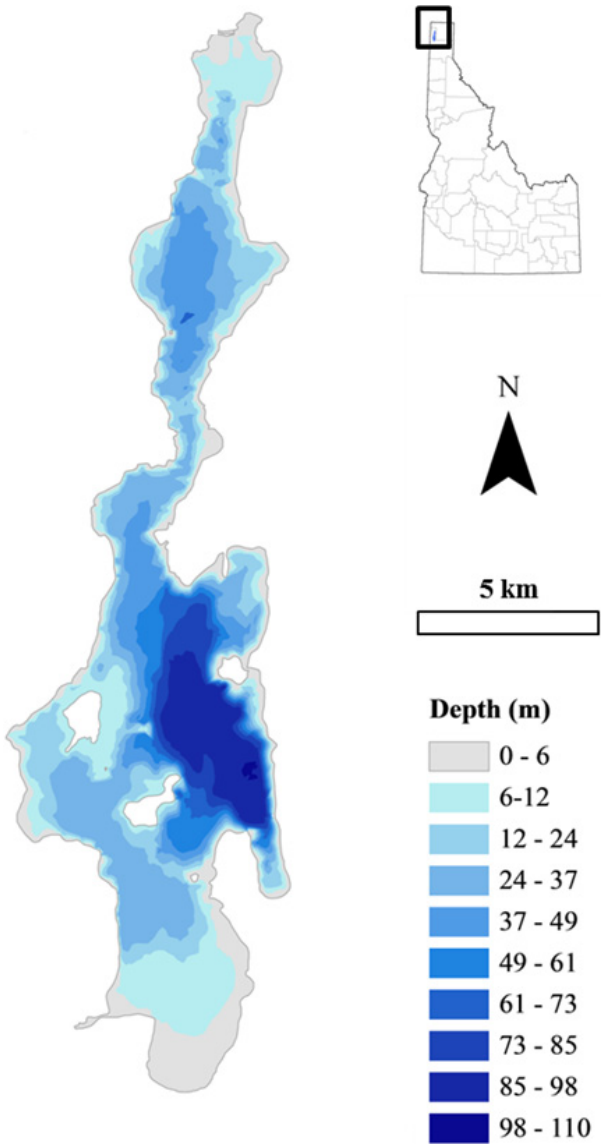

Fig. 1. Location of Priest Lake in the northern Panhandle of Idaho.

sucker *C. catostomus*, northern pikeminnow *Ptychocheilus oregonensis*, redside shiner *Richardsonius balteatus*, peamouth *Mylocheilus caurinus* and slimy sculpin *Cottus cognatus* (Bjornn 1957; Rieman et al. 1979; Maiolie et al. 2011). In addition to lake trout and kokanee, at least seven other fish species have been introduced: brook trout *S. fontinalis*, tench *Tinca tinca*, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieui*, northern pike *Esox lucius*, green sunfish *Lepomis cyanellus* and yellow perch *Perca flavescens* (Fredericks et al. 2009).

Fishes were collected from Priest Lake in spring and summer 2013 and 2014, and in autumn 2013. Profundal fishes were sampled using bottom-set monofilament gill nets (depth: 20–240 m; Ng 2015). Nearshore areas were sampled with overnight-set floating monofilament experimental gill nets (1.8 m deep × 45 m long; 38, 50, 64, 76, 102, and 128-mm stretch mesh) and with night-time boat-mounted electrofishing (Smith-Root Inc., Vancouver, WA, USA). Samples of kokanee were also collected during a creel survey. Finally, a large trap net was used to collect spawning lake trout.

Zooplankton was sampled from Priest Lake in summer 2013 and 2014. In August 2013, *M. diluviana* were collected during a sampling effort targeting kokanee with a midwater trawl (Rieman & Myers 1992). In June 2014, a 500-μm mesh (0.5 m diameter) plankton net and a 300-μm mesh (0.2 m diameter) plankton net were used to sample *M. diluviana* and zooplankton in Priest Lake. Vertical tows were conducted at night through the layer of *M. diluviana* that was identified with sonar.

Captured fish were measured and a small sample of white muscle tissue was removed from the anterior dorsal musculature. Samples were placed on ice during field processing and immediately frozen (−24 °C) in the laboratory until further processing. *M. diluviana* were isolated from other zooplankton in the laboratory, then separated by length (small, <1 cm; large >1 cm), as diets can vary by size (Chipps & Bennett 2000). Individual *M. diluviana* were combined to reach a mass of approximately 5 g wet weight per sample. Bulk zooplankton samples (with *M. diluviana* removed) were separated into samples of roughly 5 g. Observation of bulk samples indicated that they were composed primarily of cladocerans and copepods.

All samples were processed for stable isotope analysis by the Washington State University Stable Isotope Core Laboratory. Samples were dried at 60 °C to constant mass and ground to a fine powder. One to 2 mg of each sample was placed into a tin cup and processed for $\delta^{13}C$ and $\delta^{15}N$ values using an elemental analyzer (ECS 4010; Costech Analytical, Valencia, CA, USA) and a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen; Brenna et al. 1998; Qi et al. 2003). Results were expressed as the relative difference between isotope ratios of the sample and a standard:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \times 1,000$$

where δ (‰) is the difference, R_{sample} is the isotopic ratio of the sample, and R_{standard} is the isotopic ratio of the standard (Vienna Pee Dee Belemnite for $^{13}C/^{12}C$ and atmospheric N_2 for $^{15}N/^{14}N$). Samples were checked for calibration using three running standards: acetanilide, corn *Zea mays* and keratin. Because lipids are generally depleted in ^{13}C relative to proteins and carbohydrates, variation in fat content can bias estimates. We therefore used a mathematical normalisation for lipid content using the C:N ratio (Post et al. 2007).

Priest Lake trophic structure was evaluated qualitatively by comparing individual and average $\delta^{13}C$ and $\delta^{15}N$ values using bi-plots (France 1995; Vander Zanden et al. 1997). Sample sizes for individual taxa precluded statistical tests of differences between seasons and years, but visual observation indicated no major differences among sampling events. Therefore, all analyses were conducted with samples pooled across time and location. Trophic position of individual taxa and overall food chain length was estimated by converting $\delta^{15}N$ values to trophic position. We assumed that zooplankton fed at trophic position 2 and determined successively higher trophic positions using the following equation:

$$\text{TP}_i = \frac{\delta^{15}\text{N}_i - \delta^{15}\text{N}_{pc}}{3.4} + 2$$

where TP_i is the trophic position of the *i*th taxon, $\delta^{15}\text{N}_i$ is the nitrogen signature of the *i*th taxon, and $\delta^{15}\text{N}_{pc}$ is the nitrogen signature of primary consumers (zooplankton; Post 2002). Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) were used to estimate standard ellipse area (i.e. niche size) for members of the Priest Lake food web because they are robust to differences in sample size. In addition to niche size, we also evaluated the area of niche overlap between taxa in Priest Lake.

Linear regression was used to test hypotheses regarding patterns in the lake trout population. Specifically, we tested for significant increases in $\delta^{13}C$ and $\delta^{15}N$ with length to evaluate dietary partitioning by lake trout that may undergo ontogenetic diet shifts. All analyses were conducted in R (version 3.1.2; R Core Team 2014). Finally, we evaluated the relationship between lake trout growth and trophic position. Sagittal otoliths and fin rays were collected from lake trout sampled in 2013. Otoliths were

mounted in epoxy, thin-sectioned with a low speed saw (Buehler, Lake Bluff, IL, USA) and viewed under a dissecting scope using transmitted light (Quist et al. 2012). A von Bertalanffy growth model was fit to observed length-at-age at capture data:

$$L_t = L_\infty[1 - e^{-k(t-t_0)}]$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is a growth constant, and t_0 is the theoretical age when length is 0 mm (Gallucci & Quinn 1979). Standardised residuals were used as an indicator of individual growth rate. We compared the mean $\delta^{15}N$ values of lake trout in the upper versus lower 25th percentiles of growth by age.

Results

Over the course of the study, 15 taxa were sampled from Priest Lake (Table 1). The food chain was relatively short, with a difference of only 2.3 trophic positions between zooplankton and the highest member, lake trout (Table 2). Trophic position of bull trout (4.1) was nearly as high as for lake trout. *M. diluviana* had an average trophic position of 2.7, but trophic position of smaller individuals (2.3) was lower than for large individuals (2.8).

Little niche overlap occurred between species using pelagic versus littoral carbon sources (Fig. 2; Table 3). Organisms collected in predominantly pelagic areas, including zooplankton, *M. diluviana*, kokanee

Table 1. Month and year of collection of stable isotope samples from taxa in Priest Lake, Idaho, along with length range (total length, mm) for fishes.

Taxa	Year	Month	*n*	Length
Brook trout	2014	June	6	119–308
Bull trout	2013	May	2	244–551
		October	1	
Cutthroat trout	2013	November	1	165–482
	2014	June	15	
Kokanee	2013	May	2	240–410
		October	3	
		November	8	
	2014	May	4	
		June	3	
Lake trout	2013	April	97	257–932
		May	273	
	2014	May	46	
Largescale sucker	2013	April	4	293–585
		May	1	
		November	2	
	2014	June	1	
Longnose sucker	2013	May	2	280–452
		November	1	
Mountain whitefish	2013	October	6	295–460
		November	10	
	2014	June	1	
Mysis	2013	August	8	
	2014	June	15	
Northern pikeminnow	2013	May	5	178–491
		November	1	
	2014	June	12	
Peamouth	2014	June	10	197–349
Smallmouth bass	2014	June	1	270
Tench	2013	November	1	374–457
	2014	June	4	
Yellow perch	2013	November	1	318
Zooplankton	2014	June	11	
Total			558	

Taxa were collected by gill nets, electrofishing, angling, trawling and zooplankton tows.

Table 2. Trophic position of taxa sampled from Priest Lake listed by decreasing mean trophic position with lower (LCB) and upper (UCB) 95% confidence bounds.

	Tropic position		
Taxa	Mean	LCB	UCB
Lake trout	4.2	4.1	4.4
Bull trout	4.1	2.7	5.6
Northern pikeminnow	3.8	3.2	4.4
Yellow perch	3.8	–	–
Brook trout	3.8	2.7	4.8
Mountain whitefish	3.7	3.1	4.3
Smallmouth bass	3.6	–	–
Longnose sucker	3.5	2.1	5.0
Cutthroat trout	3.5	2.9	4.2
Largescale sucker	3.5	2.5	4.4
Kokanee	3.4	2.9	4.0
Peamouth	3.4	2.6	4.2
Tench	3.1	2.0	4.2
Adult *Mysis diluviana*	2.8	2.2	3.4
Juvenile *Mysis diluviana*	2.3	1.2	3.4
Zooplankton	2.0	–	–

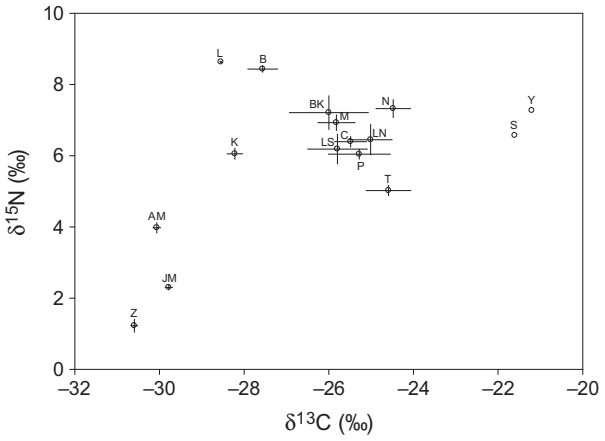

Fig. 2. Bi-plot of stable isotope values for members of the fish assemblage in Priest Lake, Idaho, sampled in 2013 and 2014. Vertical and horizontal lines represent 1 SE. Taxa represented are zooplankton (Z), juvenile *M. diluviana* (JM), adult *Mysis diluviana* (AM), kokanee (K), lake trout (L), bull trout (B), brook trout (BK), mountain whitefish (M), largescale sucker (LS), west-slope cutthroat trout (C), peamouth (P), northern pikeminnow (N), longnose sucker (LN), tench (T), smallmouth bass (S), and yellow perch (Y).

Table 3. Percent area of standard ellipse overlap for members of the Priest Lake food web. Standard ellipse areas were calculated from $\delta^{13}C$ and $\delta^{15}N$ signatures and represent isotopic niche space.

	Zoop	MD	LKT	KOK	BLT	BKT	MWF	LSS	WCT	PEA	LNS	TEN	NPM
Zoop	1												
MD		1											
LKT			1		0.10								
KOK				1									
BLT			0.11		1	0.16							
BKT					0.01	1	0.52	0.22	0.12	0.13	0.15		0.30
MWF						1	1	0.37	0.22	0.17	0.30		0.25
LSS						0.6	0.54	1	0.28	0.39	0.18	0.11	
WCT						0.79	0.79	0.69	1	0.52	0.59		
PEA						0.51	0.34	0.54	0.29	1	0.33		
LNS						0.69	0.68	0.29	0.39	0.39	1		0.05
TEN								0.29				1	
NPM						0.79	0.35				0.03		1

Percent area of overlap is given for each taxa by column; darker shading represents a higher per cent overlap. Overlap relative to taxa by column is given above the diagonal (which represents 1:1 relationships) and overlap relative to taxa by row is given below the diagonal. Taxa are organised by $\delta^{13}C$ (decreasing in enrichment from left to right and top to bottom): zooplankton (Zoop), *Mysis diluviana* (MD), lake trout (LKT), kokanee (KOK), bull trout (BLT), brook trout (BKT), mountain whitefish (MWF), largescale sucker (LSS), westslope cutthroat trout (WCT), peamouth (PEA), longnose sucker (LNS), tench (TEN) and northern pikeminnow (NPM).

and lake trout, tended to have depleted $\delta^{13}C$ values (Fig. 2). Pelagic species' standard ellipses did not overlap, except for the standard ellipse of lake trout, which overlapped 10% with the standard ellipse of bull trout (Table 3). Species with less enriched $\delta^{13}C$ also tended to have smaller niches; lake trout had the smallest niche area (Fig. 3). A cluster of species with more enriched $\delta^{13}C$ values was centred around $-25.0‰$ and included brook trout, mountain whitefish, westslope cutthroat trout, longnose suckers, largescale suckers, peamouth and tench. These species exhibited a high degree of niche overlap (Table 3), had the most variable $\delta^{13}C$ values and tended to have larger niche sizes (Fig. 3). Westslope cutthroat trout had an intermediate-sized niche area, but high overlap with six other species, including three non-native species (Table 3). Yellow perch and smallmouth bass had the most enriched $\delta^{13}C$ values (Fig. 2); however, low sample sizes precluded further analysis.

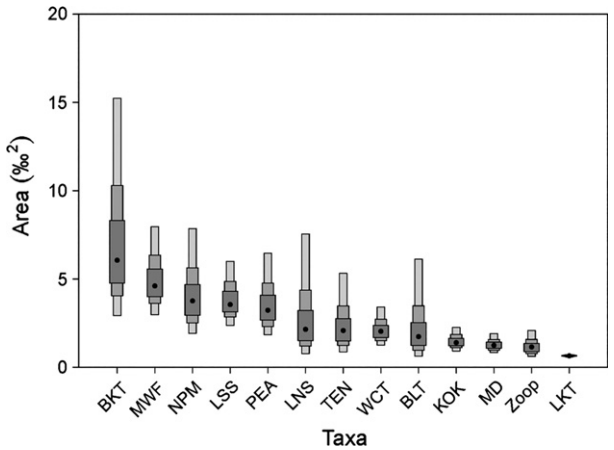

Fig. 3. Plot of 95% credible intervals for estimated ellipse area of taxa sampled in 2013 and 2014 from the Priest Lake food web. Shaded boxes (from dark to light) represent 50, 75 and 95% credible intervals. Taxa codes are brook trout (BKT), mountain whitefish (MWF), northern pikeminnow (NPW), largescale sucker (LSS), peamouth (PEA), longnose sucker (LNS), tench (TEN), westslope cutthroat trout (WCT), bull trout (BLT), Kokanee (KOK), *Mysis diluviana* (MD), zooplankton (Zoop), and lake trout (LKT).

Total length of lake trout was positively related to $\delta^{13}C$ value, but the relationship accounted for only 9% of the variability in $\delta^{13}C$ values ($P < 0.001$, $r^2 = 0.092$). Neither lake trout length ($P = 0.184$, $r^2 = 0.005$) nor growth rate (Fig. 4) indicated strong relationships with $\delta^{15}N$. Although not significantly different, faster growing individuals tended to have lower $\delta^{15}N$ values.

Discussion

Priest Lake was characterised by the presence of decoupled pelagic and littoral food webs; furthermore, species using littoral carbon sources fed at a similar trophic level and had higher diet variability and larger niche size than species using pelagic carbon sources. Diet breadth tends to increase with increasing competition for resources (Werner & Hall 1974) and may be highest at intermediate trophic levels (Svanbäck et al. 2015). Intraspecific diet variability coupled with a high degree of niche overlap potentially indicates the presence of competition among species using littoral carbon sources in Priest Lake. Similar patterns were observed in nearby Lake Pend Oreille, Idaho, which has a similar native and

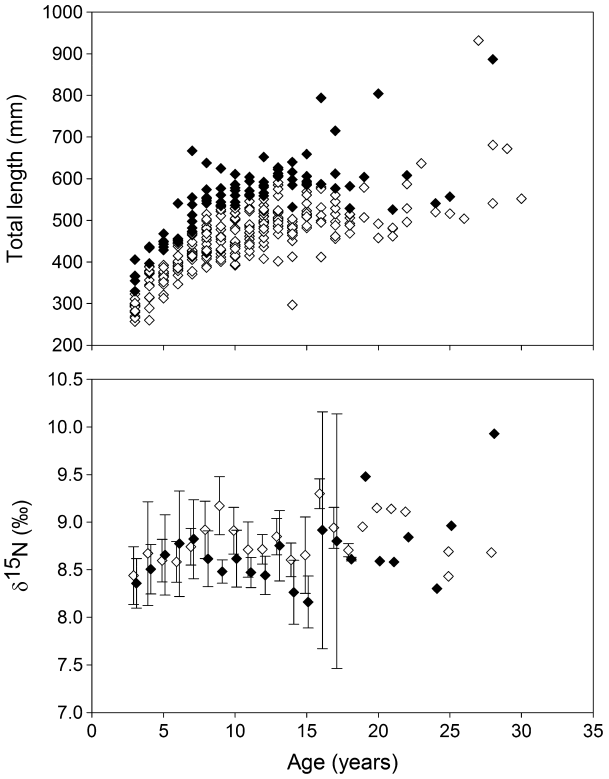

Fig. 4. Length-at-age at capture (top panel) and relationship between growth and $\delta^{15}N$ (bottom panel) for lake trout sampled from Priest Lake during spring 2013. A von Bertalanffy model was fit and individuals with growth in the upper 25th percentile (black diamonds) and lower 25th percentile (white diamonds) by age were isolated. Mean $\delta^{15}N$ with 95% confidence intervals was plotted for each group. Sample sizes after age 18 were insufficient to calculate confidence intervals ($N < 2$).

non-native species composition to Priest Lake (Clarke et al. 2005). Future studies could explore spatial, temporal and intraspecific (e.g. ontogenetic) resource partitioning (Bearhop et al. 2004; Matthews & Mazumder 2004) to better understand these interactions and the role of non-native species (e.g. brook trout, smallmouth bass, and yellow perch) in structuring the littoral fish assemblage.

Lake trout in Priest Lake were apex predators; however, their trophic position was lower than in other lakes containing *M. diluviana* and pelagic prey fishes. Trophic position of lake trout in Priest Lake was nearly half a trophic position lower than in Lake Pend Oreille, despite the presence of *M. diluviana* and kokanee in both lakes (Clarke et al. 2005). Similarly, lake trout in Priest Lake more closely resembled Canadian populations without access to pelagic prey fishes, which exhibited lower average trophic positions than those with access to prey fishes (Vander Zanden et al. 2000). Reduced lake trout trophic position is also associated with the establishment of *M. diluviana* (Vander Zanden et al. 2003), decreased fish species richness (Vander Zanden et al. 1999b) and increased diet generalisation (Post et al. 2000). Given the historical declines in kokanee abundance in Priest Lake (Bowles et al. 1991), these patterns may reflect low prey fish abundance and reliance of lake trout on *M. diluviana* in Priest Lake.

Previous work has found that ontogenetic niche shifts and intraspecific niche partitioning can be detected using stable isotopes, but we did not identify resource partitioning within the lake trout population in Priest Lake. We hypothesised that low pelagic prey fish abundance in Priest Lake would lead to increased use of littoral fish resources, especially for larger, piscivorous individuals (Vander Zanden & Rasmussen 1996). The poor relationship between length and $\delta^{13}C$ indicated that lake trout of all sizes feed consistently on prey of predominantly pelagic-origin carbon signatures. The narrow niche space of lake trout further supports the observation that individuals feed similarly. The lack of observed differences seen in our study contrasts with many other studies that identified patterns in $\delta^{13}C$ with length (Clarke et al. 2005; Keyse et al. 2007; Zimmerman et al. 2009; Power et al. 2012). Lake trout in Priest Lake either lack sufficient pressure to seek alternative prey resources (Svanbäck et al. 2015) or they may face cognitive limitations to prey switching (Ishii & Shimada 2010).

Lake trout in Priest Lake did not exhibit patterns in $\delta^{15}N$ enrichment with length or growth rate, which are commonly associated with ontogenetic diet shifts in a number of fish species (Grey 2001; Eloranta et al. 2010; Gallagher & Dick 2010). However, these patterns are not always identifiable in lake trout populations (Vander Zanden et al. 2000; Johnson et al. 2002; Clarke et al. 2005). Shifts in lake trout $\delta^{15}N$ signatures may be confounded by prey signatures (Vander Zanden et al. 2000; Keyse et al. 2007; Zimmerman et al. 2009) or may reflect dietary homogeneity. Reduced consumption of *M. diluviana* should be detectable with stable isotopes because of substantially different signatures from that of fish. Dietary homogeneity is the likely cause because prey resources are limited in Priest Lake (Bowles et al. 1991; Ng et al. in press) and intraspecific competition may prohibit individuals from increasing the proportion of fish in their diet. Field observations of lake trout stomach contents in Priest Lake indicate that many individuals, regardless of size, consumed *M. diluviana* (Ng 2015). Analysis of $\delta^{15}N$ values and growth rate provided further evidence that larger or faster growing lake trout do not exhibit dietary differences in Priest Lake. Other factors, such as early onset of piscivory (Mittelbach & Persson 1998) or the confounding effect of rapid growth (Hesslein et al. 1993), could be tested by examining isotopic signatures closer to the period of transition to piscivory.

Stable isotopes provide time-integrated perspectives on diet and niche partitioning, which can be used to evaluate the role of intra- and interspecific diet variability in food web structure and species interactions (Vander Zanden & Rasmussen 1999). As such, these methods provide considerable insight into the community- and individual-level effects of introduced species (Vander Zanden et al. 1999a; Svanbäck et al. 2015). We found disjoint trophic pathways based on pelagic and littoral carbon sources that also exhibited different underlying patterns in niche size and overlap. Although lake trout are a highly mobile predator, the narrow niche size and lack of trophic partitioning contributed to the isolation of the pelagic-based food web. Given the importance of piscivores in structuring lacustrine ecosystems, this information enhances understanding of the food web structure in systems with non-native piscivores.

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