The utilization of a Pacific salmon *Oncorhynchus nerka* subsidy by three populations of charr *Salvelinus* spp.

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The L_F-at-age trajectories differentiated two populations of Dolly Varden charr *Salvelinus malma* and a population of Arctic charr *Salvelinus alpinus* from the eastern end of Iliamna Lake, Alaska. *Salvelinus malma* from the Pedro Bay ponds were the smallest for a given age, followed by *Salvelinus alpinus* from the lake, and *S. malma* from the Iliamna River were much larger. The utilization of a large sockeye salmon *Oncorhynchus nerka* subsidy by the three *Salvelinus* spp. populations was then investigated by comparing diet data and mixing model (MixSIR) outputs based on carbon and nitrogen stable isotopes. Stomach contents indicated that both *S. malma* populations fed on *O. nerka* products, especially eggs and larval Diptera that had scavenged *O. nerka* carcasses, whereas *S. alpinus* fed on a variety of prey items such as three-spined sticklebacks *Gasterosteus aculeatus* and snails. Stable-isotope analysis corroborated the diet data; the two *S. malma* populations incorporated more *O. nerka*-derived nutrients into their tissues than did *S. alpinus* from the lake, although all populations showed substantial utilization of *O. nerka*-derived resources. *Salvelinus alpinus* also seemed to be much more omnivorous, as shown by stable-isotope mixing models, than the *S. malma* populations. The dramatic differences in growth rate between the two *S. malma* populations, despite similar trophic patterns, indicate that other important genetic or environmental factors affect their life history, including proximate temperature controls and ultimate predation pressures. © 2010 The Authors

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Key words: Iliamna Lake; length at age; MixSIR; polymorphism; stable isotopes.

INTRODUCTION

Salmonids of the genus *Salvelinus*, commonly known as charr, exhibit phenotypic plasticity and genetic differentiation in a wide variety of traits (Jonsson & Jonsson, 2001). Sympatric populations of Arctic charr *Salvelinus alpinus* (L.), in particular, express variation in colour (Hindar & Jonsson, 1982; Fraser *et al.*, 1998), morphology (Snorrason *et al.*, 1994; Reist *et al.*, 1995; Adams *et al.*, 1998) and life history (Jonsson *et al.*, 1988; Adams *et al.*, 1998). Smith & Skulason (1996) have hypothesized that much of this variation is a consequence of differences in food and habitat use.

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Variation of length at age in *Salvelinus* is particularly well studied and is often linked to resource partitioning, as the consumption of different prey leads to variation in growth rates and subsequent differentiation of body size (Jonsson *et al.,* 1988; Reist *et al.,* 1995; Adams *et al.,* 1998; Power *et al.,* 2002, 2005). Thingvallavatn, Iceland, for example, has four different *S. alpinus* morphs, three of which demonstrate distinct and unique feeding ecologies and trophic positions (Malmquist *et al.,* 1992; Sandlund *et al.,* 1992). Consequently, the morphs differ in growth rates and asymptotic body sizes (Jonsson *et al.,* 1988).

Life-history variation can be effective in identifying polymorphisms in fish populations, but diet and stable-isotope analysis are necessary to determine trophic segregation among sympatric populations. Diet analysis provides accurate short-term information, whereas stable isotopes provide integrated, long-term information on diet assimilation (Fry, 2006). Stable isotopes have been used to study aquatic food webs in general (Hobson & Welch, 1995; Vander Zanden *et al.,* 1999) and specifically to differentiate dietary niches among sympatric *Salvelinus* species (Power *et al.,* 2002) and among morphotypes within species of *Salvelinus* (Adams *et al.,* 2003; McCarthy *et al.,* 2004; Power *et al.,* 2009). For example, Adams *et al*. (2003) used nitrogen and carbon isotopes to reveal ecological segregation between two sympatric *S. alpinus* morphs that also differed in growth rate.

Although niche partitioning and sympatric ecotypes have often been studied in *S. alpinus*, they may also occur in other species of *Salvelinus* and between sympatric species. For example, in Iliamna Lake, Alaska, Dolly Varden charr *Salvelinus malma* (Walbaum) reside mainly in tributaries of the lake whereas *S. alpinus* are found in the lake itself (Taylor *et al.,* 2008). In addition, there appears to be at least two morphotypes of *S. malma*. Small-bodied (<350 mm fork length, L_F) *S. malma* are found in a series of spring-fed ponds that flow into the lake and much larger bodied conspecifics (<650 mm L_F) are found in the Iliamna River, a tributary to the lake in the same vicinity.

Iliamna Lake is a particularly interesting setting for a study of *Salvelinus* trophic ecology because it supports very large sockeye salmon *Oncorhynchus nerka* (Walbaum) populations (Hilborn *et al.,* 2003). When these fish return to fresh water, they release vast amounts of marine-derived nutrients into the ecosystem during spawning and after their death in the form of eggs and carcasses (Schindler *et al.,* 2003). Pacific salmon *Oncorhynchus* spp.-derived nutrients are important for resident fishes, increasing their body condition and growth rates (Bilby *et al.,* 1998; Wipfli *et al.,* 2003; Denton *et al.,* 2009). Their nutrients can be assimilated by resident fishes by two distinct pathways: directly, by consumption of eggs, adult muscle tissue and fry, or indirectly, by taxa that feed on *Oncorhynchus* spp. carcasses (Scheuerell *et al.,* 2007). For example, decaying *Oncorhynchus* spp. are scavenged by larval terrestrial blowflies (Meehan *et al.,* 2005), which are consumed by resident fishes (Denton *et al.,* 2009). Diet analysis can identify which of these two pathways a particular resident fish population utilizes at a particular time, but stable isotopes can provide an overall picture of the long-term assimilation of *Oncorhynchus* spp. resources by resident fishes because nitrogen and carbon from spawning and decaying *Oncorhynchus* spp. have unique and traceable isotopic signatures. For example, Kline *et al*. (1993) used stable-isotope techniques to show that all trophic levels of the Iliamna Lake food web were enriched in N^{15} compared to nearby lakes devoid of *O. nerka*.

The goals of this study were to (1) compare L_F at age between two populations of *S. malma* and a proximate *S. alpinus* population, (2) characterize and compare diets of the different morphotypes and species based on their degree of consumption of *O. nerka* products and 3) use stable isotopes to determine the extent to which these fishes rely on the *O. nerka* subsidy.

MATERIALS AND METHODS

STUDY SITES

Pedro Bay ponds

The Pedro Bay ponds are a series of *c*. 15 spring-fed ponds that drain into the north-east end of Iliamna Lake near the village of Pedro Bay, in the Bristol Bay region of south-west Alaska (59° 47′ 25″ N; 154° 06′ 58″ W) (Fig. 1). The ponds vary in size from *c*. 100 to almost 2000 m^2 and are relatively uniform in depth (*c*. 0·2–0·4 m; Quinn & Kinnison, 1999). The substratum is dominated by sand (*c*. 1 mm in diameter; Quinn *et al.,* 1995), over a bed of medium sized cobble. The riparian zone is dominated by small spruce, alder and willow, with some grasses. The ponds are connected by a series of very small streams (*c*. 1 m wide and 0·2 m deep), combining to form a larger depression, 3 m wide and 1–2 m deep, which flows into Iliamna Lake. The ponds are 1 to 2 km from the lake. Seven of the ponds were sampled, the others lack active springs, have silty substrata, are not used for spawning by *O. nerka* and are seldom visited by *S. malma*. The ponds that were sampled have all had spawning *O. nerka* at least once in the past 5 years (T. P. Quinn & H. B. Rich Jr., unpubl. data). *Oncorhynchus nerka* are the only species of *Oncorhynchus* seen consistently in these habitats, and *S. malma* is the only other common salmonid species. *Oncorhynchus nerka* densities vary widely among years and among ponds in a given year, with an average of *c*. 0·1 fish m^{-2}. *Salvelinus malma* also inhabit the ponds for at least a portion of the year. They range in size from young-of-the-year (YOY) *c*. 25 mm, to *c*. 365 mm (Denton *et al.,* 2009).

Iliamna River

The Iliamna River flows into the eastern corner of Iliamna Lake (59° 44′ 12″ N; 153° 58′ 06″ W) and differs from the Pedro Bay ponds in many respects. It drains a glacial valley with an area of 520 km^2. The average width is *c*. 30 m and the average depth is 1·2 m, with an average summer flow of 7 m^3 s^{-1} (Demory *et al.,* 1964). Riparian vegetation consists primarily of spruce, cottonwood, alder, birch and willow. The substratum is mainly sand in the lower river until a major *O. nerka* spawning tributary, Chinkelyes Creek enters 10 km up from the mouth, after which, the substratum is composed mostly of gravel with some sand and bedrock. The main river forks 18 km up from the mouth. The majority of *O. nerka* spawning occurs between Chinkelyes Creek and the forks, and all *S. malma* sampling occurred in this reach.

Iliamna Lake

At 2622 km^2, Iliamna Lake is the largest lake in Alaska and has a maximum depth of 393 m. Historically it has supported total runs of up to 44 million *O. nerka*, although in recent years returns have been smaller (Hilborn *et al.,* 2003). It is generally covered in ice from January to May (Poe, 1980). Lake levels are at their lowest in April to May and increase through the summer due to glacial melt, reaching their peak in September (Donaldson, 1967). The catchment basin is home to 24 resident fish species, including *S. malma* and *S. alpinus*, rainbow trout *Oncorhynchus mykiss* (Walbaum), three-spined stick-lebacks *Gasterosteus aculeatus* L., coastrange sculpin *Cottus aleuticus* Gilbert and slimy sculpin *Cottus cognatus* Richardson (Bond & Becker, 1963). *Salvelinus alpinus* were collected near Fuel Dump Island in front of the University of Washington's field camp (59° 44′ 15″ N; 154° 12′ 29″ W; Fig. 1).
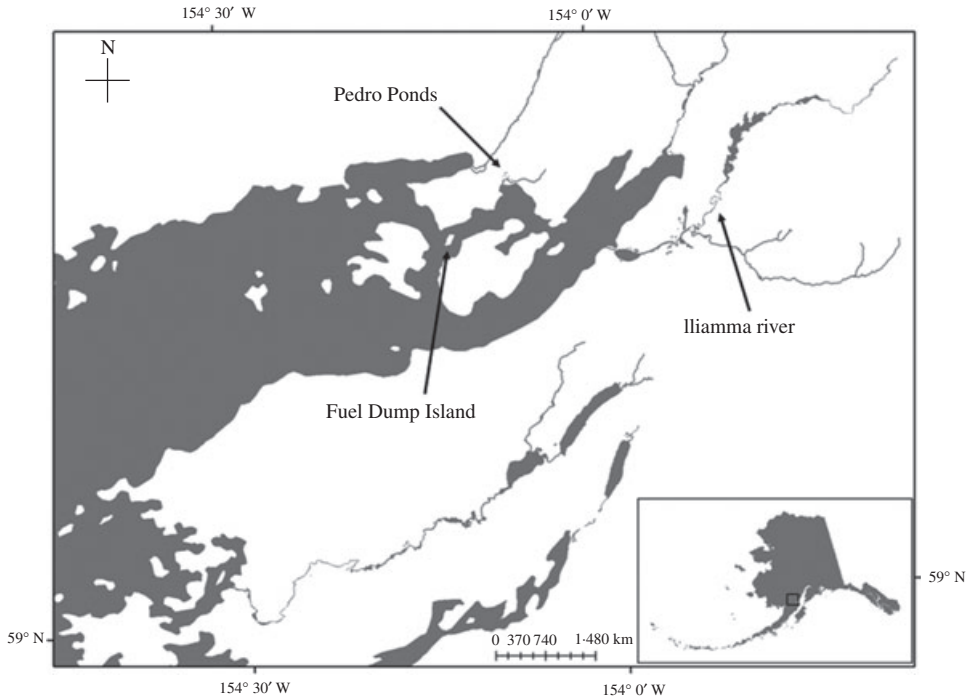
Fig. 1. Map of the east of Iliamna Lake, indicating the three sampling sites. *Salvelinus malma* were collected from the Pedro Ponds and the Iliamna River while *Salvelinus alpinus* were collected near Fuel Dump Island.

FIELD PROTOCOLS

Salvelinus malma were collected from the Pedro Bay ponds complex with a 10 m stick seine and from the Iliamna River by hook and line and minnow traps. *Salvelinus alpinus* were captured from Iliamna Lake using a 30 m beach seine. None of these gear types are unbiased with respect to size but the goal was to obtain specimens over a range of sizes rather than to determine the overall size distribution of the populations. All specimens were sacrificed, measured (L_F) to the nearest mm, weighed to the nearest g and brought back to the laboratory for otolith, diet and stable-isotope processing. *Salvelinus malma* and *S. alpinus* are morphologically similar species, but identification of the individuals was validated by genetic techniques (Taylor *et al.,* 2008).

Stable-isotope analyses were used to illuminate the reliance of different *Salvelinus* populations on different food resources, and specifically, the contribution of *O. nerka*-derived food sources (*e.g.* eggs). While diet composition may change immediately after the arrival of adult *O. nerka*, stable-isotope signatures take time to equilibrate to a change in diet and the length of time depends primarily on the tissue sampled (Pinnegar & Polunin, 1999). Pinnegar & Polunin (1999) recommended using muscle tissue, and various experiments have indicated that, in fishes, muscle tissue equilibrates with a change in diet in *c*. 3–4 weeks (Herzka, 2005). Therefore, *Salvelinus* spp. samples were collected between 14 August and 4 September in 2007 and 2008, at least 4 weeks after the long-term average arrival of adult *O. nerka* (Demory *et al.,* 1964). Samples from the two consecutive years were grouped for isotope analysis because of the almost identical *O. nerka* escapements to Iliamna Lake in 2007 and 2008, 2·76 million and 2·81 million, respectively.

Preliminary analysis of *Salvelinus* spp. diets from the three areas was used to identify the taxa needed as end members or inputs into the mixing model. Because turnover

rates of isotopes in prey items are probably more rapid than in consumers, non-*O. nerka*-derived items were collected both before and after *O. nerka* arrival and subsequently pooled (Cabana & Rasmussen, 1996; Vander Zanden & Rasmussen, 1999; O'Reilly *et al.,* 2002; Post, 2002). Pooling these time periods integrates prey isotope signatures across the period during which *O. nerka* subsidies could elevate prey isotope signatures. This potentially increased the variance associated with these end members and is thus a conservative approach. These non-*O. nerka* end members were collected and analysed for each of the three areas, minimizing possible complications associated with local differences. *Oncorhynchus nerka* fry were only present before adults arrived and maggots were only available after *O. nerka* arrived, died and the maggots had fed on the carcasses. Stable-isotope signatures of *O. nerka* eggs and flesh were obtained from the literature and represent a relatively proximate population in Bristol Bay (Moore & Semmens, 2008). Previous studies indicated that *S. malma* from both the Pedro Bay ponds and the Iliamna River consumed *O. nerka* fry in early July, but fry had never been recorded in their diets for at least a 4 week period before stable-isotope collection began on 14 August. *Oncorhynchus nerka* fry migrate out of these systems in the spring; thus, *O. nerka* fry were not included in the isotope analysis for the *S. malma* populations (Denton *et al.,* 2009; K. P. Denton, unpubl. data). Although *O. nerka* fry were never recorded in the limited number of *S. alpinus* diets collected from Iliamna Lake, the abundance of fry in the lake during the course of sampling warranted their inclusion as an end member in the isotope analysis.

LABORATORY PROTOCOL

Length at age and diets

Otoliths were removed from all fishes and aged; only those receiving duplicate-independant readings were included for analysis. Fishes were dissected and stomach contents were removed. All items were separated into categories: benthic invertebrates, terrestrial invertebrates, *O. nerka* fry, *O. nerka* eggs, terrestrial Diptera larvae (maggots) and unidentifiable material. All items were then dried at $60°$ C until a constant mass was reached and weighed to the nearest 1 mg. All diet masses were then standardized by dividing the total mass of a particular diet category by the mass of the fish.

Stable isotopes

Muscle tissue for stable-isotope analysis from the fish was taken directly anterior to the dorsal fin, between the lateral line and the dorsal fin. Samples of taxa that were represented in the diets from each of the three *Salvelinus* populations were also processed. Samples were freeze dried for 48 h, pulverized with a mortar and pestle into an homogenized powder, and *c*. 1 mg was measured into small tin capsules. All samples were sent to the University of California (UC) Davis Stable Isotope Facility (http://stableisotopefacility.ucdavis.edu) and were analysed for both carbon and nitrogen stable-isotope ratios with a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer (www.sercongroup.com).

Stable-isotope ratios are expressed as delta values (δ) and measured as the parts per thousand (‰) difference between the sample and that of an international standard according to the formula: $\delta = 1000[(R_{sample} - R_{standard})R_{standard}^{-1}]$, where R = the carbon (^{13}C:^{12}C) or nitrogen (^{15}N:^{14}N) of the sample or the standard. UC Davis used three secondary standards to normalize the carbon isotope data on the Pee-Dee belemnite scale for δ^{13}C (Craig, 1957) and the atmospheric nitrogen scale for δ^{15}N (Mariotti *et al.,* 1983): ammonium sulphate–sucrose, bovine liver (NIST Reference 1577b) and peach material (NIST Reference 1547). These laboratory standards were calibrated against IAEA standards USGS-40 and USGS-41. UC Davis long-term S.D. for their secondary standards are 0·2‰ C and 0·3‰ N.

DATA ANALYSIS

The L_F-at-age plots were fit to the von Bertalanffy growth equation: $\hat{L}_i = L_\infty(1 - e^{[-k(a_i - t_0)]})$, where $\hat{L}_i$ is the predicted L_F of a fish number i, L_∞ is the asymptotic average maximum L_F, k is a coefficient determining how quickly the fish grow, t_0 is

the time when $L_F = 0$ and a_i is the age of the ith fish. Best-fit coefficients were found by minimizing the sum of squares for each population.

Analysis of the stable-isotope data considered the fact that diet-tissue fractionation occurs and therefore measured $\delta^{13}C$ values, vary among tissues, particularly as a function of lipid content, and that studies incorporating organisms exhibiting a wide range of lipid content should account for this variation (Deniro & Epstein, 1977; McConnaughey & McRoy, 1979; Focken & Becker, 1998; Thompson *et al.,* 2000). To deal with the potential influence of lipid variation on $\delta^{13}C$ values of *Salvelinus* spp. and end members, all $\delta^{13}C$ values were corrected with mathematical lipid normalization using the equation for animals from aquatic ecosystems from Post *et al.* (2007).

The potential contributions of specific end members to the diet assimilation of *Salvelinus* spp. were evaluated using a Bayesian mixing model, MixSIR (Semmens & Moore, 2008). MixSIR incorporates the variance associated with predator and prey diet-tissue signatures and of the isotopic fractionation values. MixSIR was run to determine prey contributions to the diets of each of the three *Salvelinus* populations. In addition, distinct L_F classes, based on otolith ages, were investigated to determine size-dependant incorporation of *O. nerka* nutrients. Pedro Pond *S. malma* were divided into three L_F classes, and Iliamna River *S. malma* and Iliamna Lake *S. alpinus* were divided into two L_F classes each. Separate MixSIR runs were performed for the Pedro Pond *S. malma* <70 mm (age 1 year), 70–125 mm (ages 2–3 years) and >125 mm (>3 years). Iliamna River *S. malma* were separated into fish >100 mm and <100 mm. *Salvelinus alpinus* from Iliamna Lake included those 150–350 mm and those >350 mm. The only *S. alpinus* sampled that were <150 mm were YOY <40 mm, which primarily feed on zooplankton and therefore were not included in the MixSIR runs. Previously published values of diet-tissue fractionation were used: $2·3 \pm 1·6$ for $\delta^{15}N$ and $0·4 \pm 1·2$ for $\delta^{13}C$ for aquatic organisms were used (mean $\pm$ S.D.; McCutchan *et al.,* 2003). End member and fractionation stable-isotope ratios are shown in Table I.

To determine the relative importance of the *O. nerka* subsidy to the three different *Salvelinus* spp. populations, the carbon and nitrogen stable-isotope ratios for fish from each location were plotted. Confidence regions (95%) for the population centriods were included using the ordiellipse function from the R vegan package (Oksanen *et al.,* 2008). A permutation test, as implemented in the envfit function (also part of the vegan package) was used to test for differences between the groups. To control for length differences among populations and the associated size-dependant variation in isotope ratios, only *Salvelinus* spp. between the ages of 3 and 5 years, inclusive, were included in this analysis.

RESULTS

LENGTH AT AGE

The L_F-at-age plots revealed clear differences among the three sampled populations of *Salvelinus*. For a given age, *S. malma* from the Iliamna River were the largest, followed by *S. alpinus* from the lake, and *S. malma* from the ponds were the smallest (Fig. 2). When fit to the von Bertalanffy equation, all coefficient estimates followed the same pattern, the Iliamna River *S. malma* exhibited the largest theoretical maximal L_F and growth rate, followed by *S. alpinus* from the lake and then *S. malma* from the ponds.

DIETS

A total of 387 diets were collected, 360 from the *S. malma* in the Pedro Bay ponds, 18 from *S. malma* in the Iliamna River and 16 from *S. alpinus* in Iliamna Lake. Diet analysis revealed that *S. malma* from the Iliamna River and the Pedro Bay ponds not only consumed different prey than *S. alpinus* from the lake but the

TABLE I. End member and fractionation inputs for the MixSIR model. Pond DV and River DV are *Salvelinus malma* and Lake AC are *Salvelinus alpinus*

		Mean ± s.d.	n
Pond DV			
Fractionation	$\delta^{15}N$	2·30 ± 1·61	Literature
	$\delta^{13}C$	0·40 ± 1·21	Literature
Eggs and maggots	$\delta^{15}N$	12·25 ± 1·00	Literature
	$\delta^{13}C$	−20·88 ± 0·90	Literature
Benthic insects	$\delta^{15}N$	2·98 ± 3·07	5
	$\delta^{13}C$	−28·46 ± 3·60	5
Terrestrial insects	$\delta^{15}N$	3·20 ± 0·16	5
	$\delta^{13}C$	−22·64 ± 0·34	5
River DV			
Fractionation	$\delta^{15}N$	2·30 ± 1·61	Literature
	$\delta^{13}C$	0·40 ± 1·21	Literature
Eggs and maggots	$\delta^{15}N$	12·25 ± 1·00	Literature
	$\delta^{13}C$	−20·88 ± 0·90	Literature
Benthic insects	$\delta^{15}N$	4·21 ± 0·33	5
	$\delta^{13}C$	−27·09 ± 0·35	5
Lake AC			
Fractionation	$\delta^{15}N$	2·30 ± 1·61	Literature
	$\delta^{13}C$	0·40 ± 1·21	Literature
Eggs and flesh	$\delta^{15}N$	11·17 ± 0·58	Literature
	$\delta^{13}C$	−21·15 ± 0·78	Literature
Gasterosteids	$\delta^{15}N$	7·75 ± 1·25	5
	$\delta^{13}C$	−24·61 ± 2·19	5
Snails	$\delta^{15}N$	3·49 ± 0·05	5
	$\delta^{13}C$	−10·65 ± 0·02	5
Cottids	$\delta^{15}N$	9·10 ± 1·66	5
	$\delta^{13}C$	−14·28 ± 3·11	5

average standardized mass of their diets also differed significantly (Table II). Four weeks after adult *O. nerka* arrived, *S. malma* diets from the Iliamna River and the Pedro Bay ponds consisted primarily of *O. nerka* eggs, with some Diptera larvae in the Pedro Bay pond fish. At that time, diets of *S. alpinus* included many different prey items; *G. aculeatus* were the most common prey. Standardized diet masses for all three populations differed significantly, with *S. malma* from the Pedro Bay ponds having the heaviest (1·89 mg g^{-1} fish), followed by *S. malma* from the Iliamna River (0·79 mg g^{-1} fish). *Salvelinus alpinus* from the lake had the lowest average standardized diet mass, 0·04 mg g^{-1} fish (ANOVA, $F_{2,381} = 12·24$, $P < 0·001$) (Table II).

STABLE ISOTOPES

A total of 66 fish were sampled for stable-isotope analysis, 20 *S. malma* from the Pedro Bay ponds, 26 *S. malma* from the Iliamna River and 20 *S. alpinus* from Iliamna Lake. Carbon and nitrogen stable-isotope plots and the MixSIR model runs
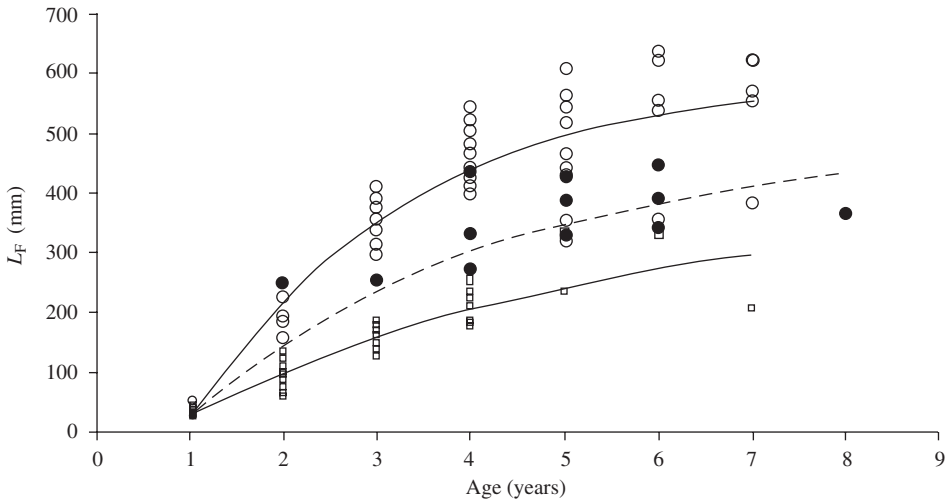
FIG. 2. Fork length (L_F)-at-age plots for three different *Salvelinus* populations from Iliamna Lake and its tributaries: *Salvelinus malma* from the Iliamna River (○), *Salvelinus alpinus* from the lake (●) and *S. malma* from the Pedro Bay ponds (□). Curves represent best-fit lines derived from the von Bertalanffy growth equation.

indicated that all three *Salvelinus* populations incorporated significant amounts of *O. nerka*-derived nutrients but *S. malma* from the Pedro Bay ponds and Iliamna River had higher levels than the *S. alpinus* (Fig. 3).

All three populations showed size-dependant isotopic variation, indicating ontogenetic diet shifts (Fig. 4). Larger fishes incorporated more *O. nerka*-derived nutrients than smaller fishes; this phenomenon was more pronounced for *S. malma* than *S. alpinus*. For example, stable-isotope signatures indicated that all three L_F classes of *S. malma* from the Pedro Bay ponds complex incorporated marine-derived nutrients but larger fish apparently consumed more *O. nerka* products. Model results

TABLE II. Diet composition of *Salvelinus malma* from the Pedro Ponds (Pond DV, $n = 350$) and the Iliamna River (River DV, $n = 18$) and *Salvelinus alpinus* from Iliamna Lake (Lake AC, $n = 16$) expressed in mg dry mass of category g^{-1} fish and in frequency of occurrence (F_o). Both *Gasterosteus aculeatus* and *Pungitius pungitius* were found in Lake AC diets, but combined for analysis. Seven of the 16 Lake AC diets were analysed qualitatively and therefore are only included in the F_o calculations

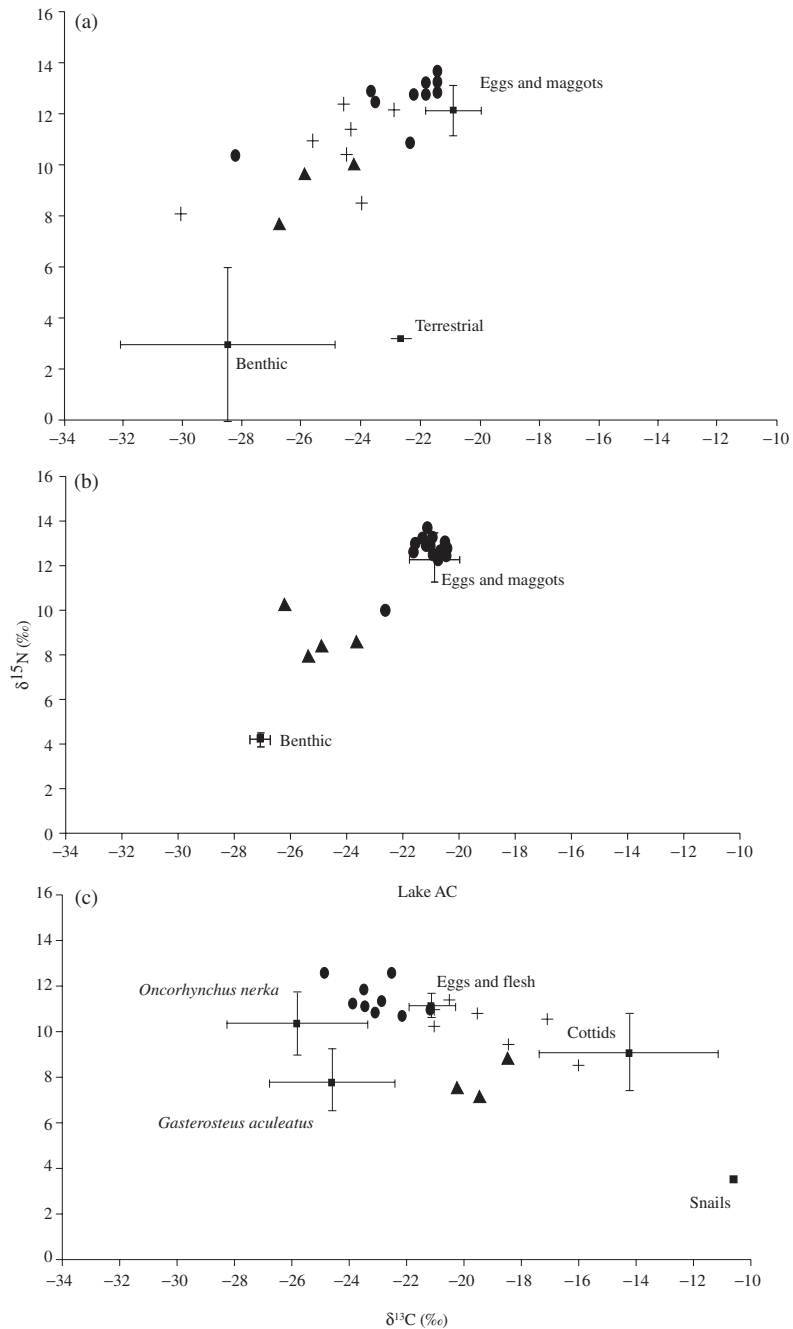|	Pond DV		River DV		Lake AC	
	mg^{-1} g fish	F_o	mg^{-1} g fish	F_o	mg^{-1} g fish	F_o
Oncorhynchus nerka eggs	1·81	0·75	0·78	1·00	0·00	0·00
Maggots	0·03	0·36	<0·01	0·39	0·00	0·00
Insects	0·05	0·41	0·01	0·06	0·00	0·00
Gasterosteids	0·00	0·00	0·00	0·00	0·04	0·50
Snails	0·00	0·00	0·00	0·00	<0·01	0·38
Total	1·89		0·79		0·04	

FIG. 3. Carbon and nitrogen stable-isotope plot for (a) *Salvelinus malma* from the Pedro Ponds and (b) from the Iliamna River and (c) *Salvelinus alpinus* from Iliamna Lake indicating end members (means ± S.D.), and different fork-length (L_F) classes of *Salvelinus*. Benthic and terrestrial refer to invertebrates from those habitats. Eggs are *Oncorhynchus nerka* eggs and maggots are terrestrial Diptera larvae that colonize *O. nerka* carcasses. (a) <75 mm (▲), between 75 and 125 mm (+) and >125 mm (●); (b) <100 mm (▲) and >100 mm (●); (c) <50 mm (▲), between 50 mm and 350 mm (+) and >350 mm (●).

indicated that *S. malma* <70 mm consumed *c*. 65% invertebrates and 35% *O. nerka* eggs and Diptera larvae whereas the intermediate and largest L_F classes consumed 50 and 70% *O. nerka* eggs and Diptera larvae, respectively [values represent the median posterior probability; Fig. 4(a)]. Similar trends were seen between smaller and larger fishes from both Iliamna River [Fig. 4(b)] and Iliamna Lake [Fig. 4(c)]. In general, the fishes from Iliamna Lake were more omnivorous, and isotope mixing models
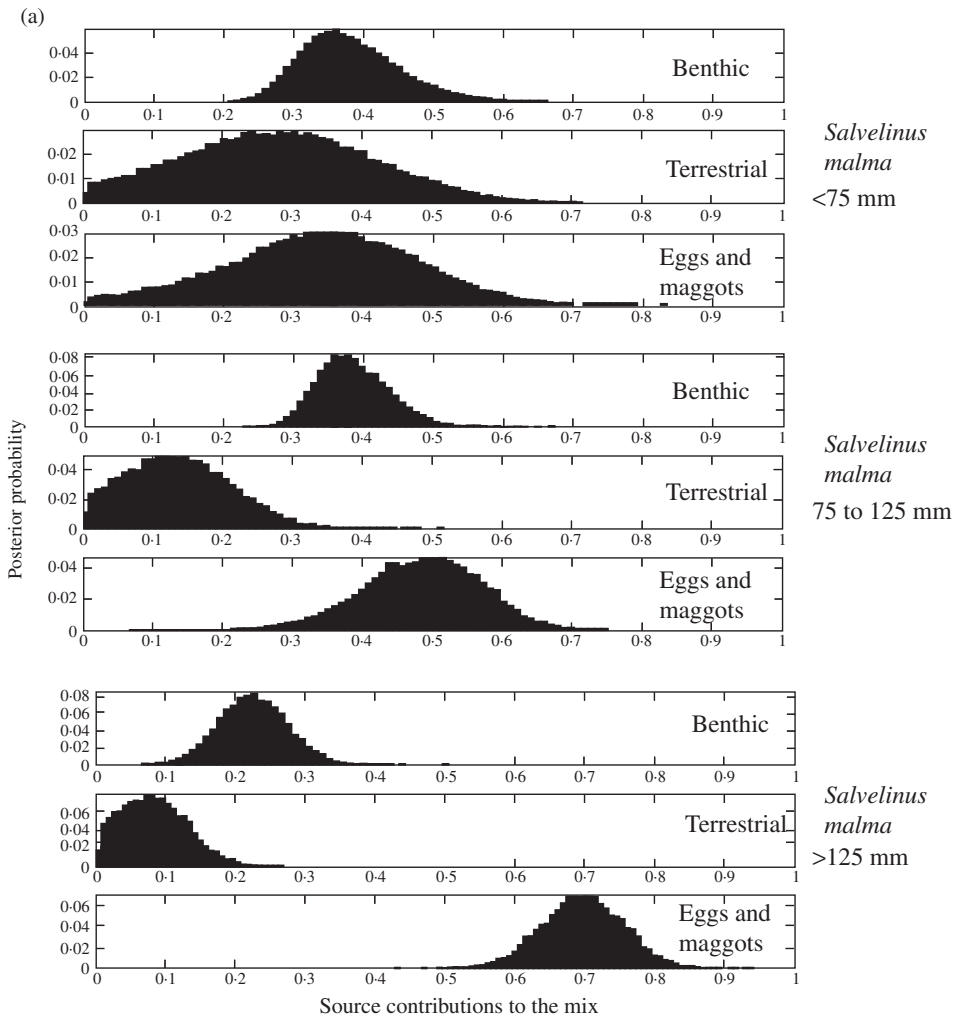

FIG. 4. MixSIR results for three fork-length (L_F) classes of *Salvelinus malma* collected from the Pedro Ponds. Benthic and terrestrial refer to invertebrates from those habitats. Eggs are *Oncorhynchus nerka* eggs and maggots are terrestrial Diptera larvae that colonize the *O. nerka* carcasses. (b) MixSIR results for *S. malma* of two different L_F classes collected from the Iliamna River. Benthic refers to aquatic invertebrates and eggs refer to *O. nerka* eggs, maggots are terrestrial Diptera larvae that colonize the *O. nerka* carcasses. (c) MixSIR results for *Salvelinus alpinus* of two different L_F classes sampled from Lake Iliamna. Gasterosteids include *Gasterosteus aculeatus* and *Pungitius pungitius*; fry refer to *O. nerka* fry and eggs; flesh refers to the eggs and flesh of *O. nerka*.
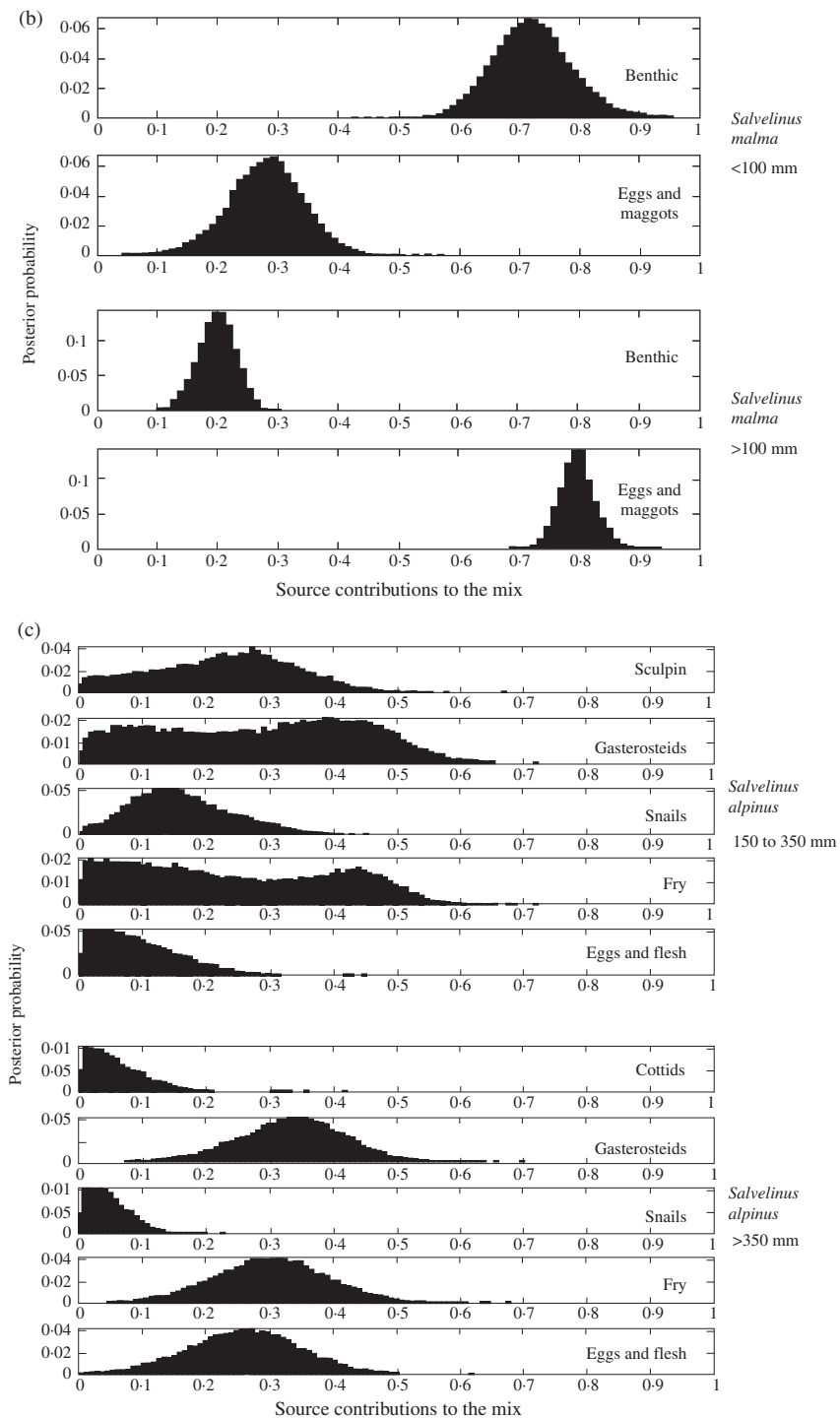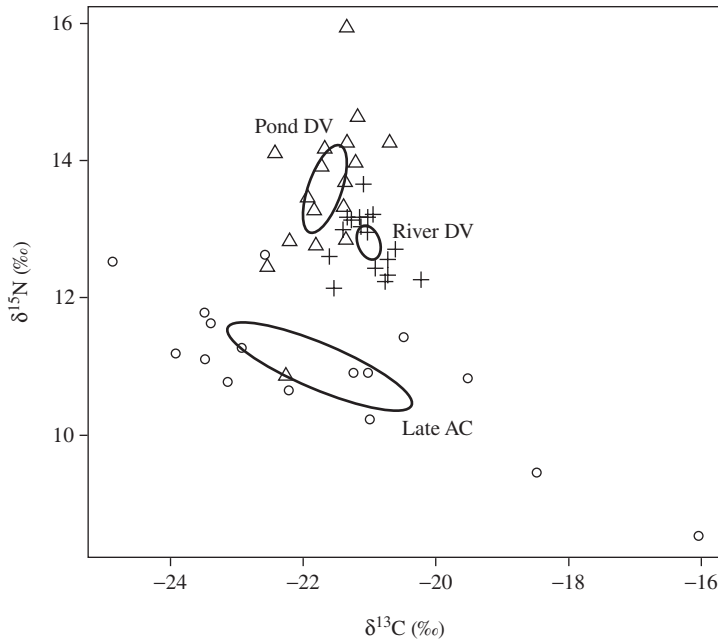
FIG. 4. Continued

FIG. 5. Carbon and nitrogen stable-isotope plot of three different *Salvelinus* populations in Iliamna Lake and its tributaries at least 4 weeks after the arrival of adult *Oncorhynchus nerka*. Fishes from the lake are *S. alpinus*, while those from the ponds and river are *S. malma*. Each ellipse is centred at the mean value of the population and represents a 95% CI of that mean. Symbols depict *S. malma* from the Pedro Ponds ($\triangle$), *S. malma* from the Iliamna River ($+$) and *S. alpinus* from Iliamna Lake ($\bigcirc$). If fishes only ate *O. nerka* products, it would be predicted that *Salvelinus* isotopic signatures would be δ^{13}C c. $-20 \cdot 5$ and δ^{15}N c. $14 \cdot 0$, after consideration of isotopic discrimination.

revealed that they probably consumed a mixture of fishes such as gasterosteids, cottids and *O. nerka* fry, as well as benthic invertebrates such as snails [Fig. 4(c)].

Comparison of isotopic ratios among the three populations revealed significant differences in the incorporation of the *O. nerka* subsidy, with the most striking being the elevated δ^{15}N enrichment of the two *S. malma* populations compared to the *S. alpinus* population (Fig. 5). This enrichment is probably because the two *S. malma* populations incorporated more *O. nerka* products, as quantified by the mixing models (Fig. 4). There was no overlap between the three ellipses and the envfit permutation test indicated significant differences between the three populations (centroids: lake = $-21 \cdot 74$ δ^{13}C (‰), $11 \cdot 00$ δ^{15}N (‰); ponds = $-21 \cdot 67$ δ^{13}C (‰), $13 \cdot 57$ δ^{15}N (‰); river = $-21 \cdot 01$ δ^{13}C (‰), $12 \cdot 81$ δ^{15}N (‰); $P < 0 \cdot 001$).

DISCUSSION

The L_F-at-age patterns revealed the existence of two ecologically distinct *S. malma* populations in the eastern tributaries of Iliamna Lake. An additional population of *S. alpinus*, sampled from the lake itself, had still another L_F-at-age trajectory, intermediate between the two *S. malma* populations. The L_F-at-age variation has

been used to delineate populations of sympatric *Salvelinus* populations in other lacustrine systems (Nordeng, 1983; Jonsson *et al.,* 1988; Reist *et al.,* 1995; Power *et al.,* 2005). Jonsson *et al*. (1988) distinguished four different *S. alpinus* morphs in Thingvallavatn, Iceland, based on L_F-at-age differentiation, which were linked to food and habitat segregation. Without further sampling it is not possible to determine which, if either, of these *S. malma* populations is typical of the lake system, and how many other populations exist. Preliminary sampling in Knutson Creek, near the Pedro Bay ponds, also has revealed small-bodied *S. malma*, closer in size to those from the ponds than the Iliamna River fish.

Diet analysis indicated that the two *S. malma* populations utilized the *O. nerka* subsidy to a large degree, while no *O. nerka* products were found in the *S. alpinus* sampled from the Iliamna Lake. *Salvelinus malma* from the Pedro Bay ponds and the Iliamna River consumed large quantities of *O. nerka* eggs and terrestrial blowfly larvae, which colonize decaying *O. nerka* carcasses (Meehan *et al.,* 2005). *Salvelinus alpinus* in the lake had access to *O. nerka* fry rearing there during the entire sampling period, but fry were not detected in their diet, even though MixSIR results suggest that larger *S. alpinus* had fed on them to some extent. *Oncorhynchus nerka* fry occupy the littoral zone of Iliamna Lake for only a rather brief period each spring and had largely moved to the limnetic zone by the time *S. alpinus* were sampled (Rich, 2006). It is also possible that there are *S. alpinus* in the open waters of the lake, where juvenile *O. nerka* are found, but sampling was restricted to the littoral zone. Moreover, the *S. alpinus* may have acquired at least part of their enriched stable-isotope signatures through complex nutrient cycling processes. Previous studies dealing with the incorporation of marine-derived nutrients into freshwater food webs have indicated the importance of both bottom-up enrichment processes (Kline *et al.,* 1990, 1993; Bilby *et al.,* 1996, 1998) and direct consumption by higher trophic level consumers (Scheuerell *et al.,* 2007; Moore *et al.,* 2008; Denton *et al.,* 2009).

Stable-isotope analysis revealed that all three populations of *Salvelinus* were highly enriched in marine signatures of both carbon and nitrogen compared to systems without *O. nerka* present (Kline *et al.,* 1993). These results are consistent with Kline *et al*. (1993), who compared nitrogen and carbon isotope signatures of various organisms representing all trophic levels of the Iliamna Lake system food web to local, *O. nerka* free, control lakes. This study indicates that *O. nerka* enrichment of the Iliamna Lake food web extends into its tributaries as well.

Stable-isotope mixing models indicated that all three populations of *Salvelinus* consumed *O. nerka* products, but to varying degrees. *Salvelinus malma* from the Iliamna River and the large fish from the Pedro Bay ponds consumed 75 and 70% *O. nerka* products, respectively, whereas larger *S. alpinus* consumed 55%, on average. The MixSIR model generally agreed with the diet data for both *S. malma* populations, but it predicted a far higher proportion of *O. nerka* products in *S. alpinus* than were observed in the diets. As noted above, the peak availability of *O. nerka* fry in the littoral zone had passed, and the *S. alpinus* were mainly feeding on other fishes such *as G. aculeatus* and invertebrates (notably snails). Moreover, 56% of the *S. alpinus* in the lake had empty stomachs. Thus, the diet data did not capture the long-term perspective on trophic ecology that stable isotopes provided. In addition, MixSIR results suggested a high degree of omnivory by *S. alpinus*, displayed by larger spreads in predicted diet contributions of various prey items. Both populations of *S. malma* were more enriched in ^{15}N than *S. alpinus* in the

lake (Fig. 5). This is consistent with diet and MixSIR results, which indicate the *S. malma*'s direct consumption of *O. nerka* products, fry and eggs, as opposed to the bottom-up fertilization processes that may affect *S. alpinus*.

Stable-isotope C–N plots and mixing model results indicated size-specific variation in *O. nerka* subsidy utilization by both populations of *S. malma* and to some degree by *S. alpinus*. Smaller fishes relied more on benthic invertebrates, whereas direct consumption of *O. nerka* products increased with size. This phenomenon probably results from a combination of gape limitation (Armstrong *et al.,* 2010) and habitat segregation because the smallest *S. malma* occupy very small streams rather than the ponds where spawning *O. nerka* are concentrated (Denton *et al.,* 2009). Grey (2001) used stable isotopes of C and N in Loch Ness, Scotland, to determine that juvenile brown trout *Salmo trutta* L. consumed mainly early instars of benthic macroinvertebrates, whereas larger fish were more piscivorous and concluded that gape limitation was responsible for the ontogenetic shift.

Salvelinus populations also exhibited different patterns in intrapopulation isotopic variation. Both *S. malma* populations had relatively small ellipses, consistent with narrow diet breadth observed in the collections. In contrast, *S. alpinus*, inhabiting the lake and having a wide range of possible prey items, exhibited a wide range of both C and N signatures, indirect evidence of substantial individual specialization in diet. It is tempting to speculate that dominant food resources such as *O. nerka* eggs may decrease individual specialization as shown by the different ellipse sizes of the three study populations; however, it is difficult to quantitatively compare rates of specialization across populations (Semmens *et al.,* 2009) that experience different prey with vastly different isotope space. Based on previous studies that have observed that higher resource availability can decrease levels of individual specialization (Tinker *et al.,* 2008), it is likely that an abundant food resource such as *O. nerka* eggs would decrease levels of intrapopulation dietary specialization.

There are two probable causes for the differing L_F-at-age trajectories of the two *S. malma* populations. Large disparities in water temperatures during the summer growing season between the Pedro Ponds and the Iliamna River are a plausible, proximate explanation for the different growth rates. The spring-fed Pedro Bay ponds remain at a relatively constant $5°$ C throughout the summer (K. Denton, unpubl. data), while the snowmelt fed Iliamna River has summer temperatures of c. $10°$ C (USGS, unpubl. data). Thus, growth in the ponds may be limited by temperature rather than food. On the other hand, predation risk in the two habitats presents a plausible ultimate, evolutionary explanation. The Pedro Ponds are extremely shallow and clear, and the *O. nerka* population is subjected to intense, size-selective predation from brown bears *Ursus arctos* (Quinn & Kinnison, 1999). *Salvelinus malma* in the Iliamna River reach sizes, which are comparable to adult *O. nerka* and therefore would probably undergo extreme predation pressure in the Pedro Ponds. Although bear predation rates are not available for the Iliamna River, pool depths >2 m would probably provide refuge for large *S. malma* in that system, based on the relationship between stream size and predation rate observed in *O. nerka* (Quinn *et al.,* 2001).

In conclusion, L_F-at-age comparisons revealed two distinct populations of *S. malma* in the eastern tributaries of Iliamna Lake, Alaska. These two populations also differed in L_F-at-age from a sympatric *S. alpinus* population in the lake itself. Furthermore, diet composition and stable-isotope signatures indicated that the *S. malma* populations and the *S. alpinus* differed in their reliance on the lake's large

O. nerka subsidy. These results are significant because they are based on *S. malma* from only two of the lake's several dozen tributary systems, and only *S. alpinus* that were captured in the littoral zone of the lake in one specific location. Given the size and habitat diversity within the Iliamna Lake basin, it is likely that future research will uncover even more morphological and ecological diversity within *Salvelinus*. Finally, large *O. nerka* subsidies that are available to *Salvelinus* spp. throughout the north Pacific may influence their divergence.

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