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Trophic biology and migratory patterns of sympatric Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*)

A.M. Dennert, S.L. May-McNally, M.H. Bond, T.P. Quinn, and E.B. Taylor

Abstract: The trophic ecology (diet and head morphology) and migration patterns of two closely related salmonid fishes, Arctic char (*Salvelinus alpinus* (L., 1758)) and Dolly Varden (*Salvelinus malma* (Walbaum, 1792)), were examined in tributaries of Lake Aleknagik, southwestern Alaska, to test for differentiation between species. Schoener's index of proportional overlap and multivariate analyses of diets suggested that these species had significantly different trophic niches. Arctic char and the largest individuals of both species had the most diverse diets, and sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) eggs dominated the diet of both species, especially Arctic char. Arctic char had larger jaws and wider heads than Dolly Varden of similar body length, which may contribute to interspecific diet difference. The species also differed in migration patterns; otolith microchemistry indicated that juvenile Arctic char were produced by nonanadromous mothers, whereas the mothers of the Dolly Varden had been to sea in the season prior to spawning. The species also segregate in spawning habitat (Arctic char in the lakes and Dolly Varden in streams), as well as in juvenile rearing habitat. Our study provides the first evidence of divergent feeding and migratory ecology between sympatric juvenile Arctic char and Dolly Varden, differences that may constrain hybridization and introgression between them.

Key words: competition, life history, diet analysis, sympatry, Arctic char, Dolly Varden, *Salvelinus alpinus*, *Salvelinus malma*.

Résumé : L'écologie trophique (régime alimentaire et morphologie de la tête) et les motifs de migration de deux salmonidés étroitement reliés, l'omble chevalier (*Salvelinus alpinus* (L., 1758)) et le Dolly Varden (*Salvelinus malma* (Walbaum, 1792)), ont été examinés dans des affluents du lac Aleknagik, dans le sud-ouest de l'Alaska, pour vérifier s'il y avait différenciation entre ces espèces. L'indice de chevauchement proportionnel de Schoener et des analyses multivariées des régimes alimentaires donnent à penser que ces espèces occupent des niches trophiques significativement différentes. Les ombles chevaliers et les plus grands individus des deux espèces présentaient l'alimentation la plus variée, les œufs de saumon sockeye (*Oncorhynchus nerka* (Walbaum, 1792)) dominant l'alimentation des deux espèces, particulièrement celle des ombles chevaliers. Ces derniers présentaient de plus grandes mâchoires et des têtes plus larges que les Dolly Varden de taille du corps semblable, ce qui pourrait contribuer à expliquer les différences entre leurs régimes alimentaires. Les motifs de migration des deux espèces différaient également; la microchimie des otolites indique que les ombles chevaliers juvéniles étaient produits par des mères non anadromes, alors que les mères de Dolly Varden avaient séjourné en mer durant la saison précédant le frai. Les espèces diffèrent également en ce qui concerne l'habitat de frai (des lacs pour l'omble chevalier, des cours d'eau pour le Dolly Varden) et l'habitat de grossissement des juvéniles. L'étude offre les premières preuves des écologies alimentaires et migratoires différentes d'ombles chevaliers et de Dolly Varden juvéniles sympatriques, une différence qui pourrait limiter leur hybridation et leur introgression. [Traduit par la Rédaction]

Mots-clés : concurrence, cycle biologique, analyse du régime alimentaire, sympatrie, omble chevalier, Dolly Varden, *Salvelinus alpinus*, *Salvelinus malma*.

Introduction

Ecological segregation between coexisting species in diet, habitat use, diel activity, or life history (e.g., extent or timing of migrations) is one of the fundamental characteristics of communities. For instance, there is a long history of research on the comparative ecology of stream fishes, including the extent and patterns of differential resource use during coexistence (Shelford 1911; Hartman 1965; Ross 1986; Mookerji et al. 2004; Herder and Freyhof 2006). Furthermore, and more recently, comparative ecological studies of fishes have explored the role of specialization to alternative ecological niches as a form of adaptation and its role in constraining gene flow between hybridizing species (Schluter 2000, 2001; Nosil et al 2005; Taylor et al. 2012).

Dolly Varden (*Salvelinus malma* (Walbaum, 1792)) and Arctic char (*Salvelinus alpinus* (L., 1758)) are two species of salmonid fishes native to the Northern Hemisphere that are estimated to have diverged from a common ancestor between 215 000 and 458 000 years ago (Taylor et al. 2008). Arctic char occur in sympatry with Dolly Varden in many freshwater habitats of western Alaska (DeLacy and Morton 1943; Mecklenburg et al. 2002). These fishes were both previously considered to constitute part of the *S. alpinus* "complex" and are often taxonomically and morphologically confused with one another (McPhail 1961; Taylor 2016). Historical and current hybridization occurs between the species, yet they maintain clear distinctions in sympatry (Gharrett et al. 1991; Taylor et al. 2008; May-McNally et al. 2015a). Despite their broadly sympatric distributions in western

A.M. Dennert, S.L. May-McNally, and E.B. Taylor. Department of Zoology, Biodiversity Research Centre, and Beaty Biodiversity Museum, The University of British Columbia, 6270 University Avenue, Vancouver, BC V6T 1Z4, Canada.
**M.H. Bond.** School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA; Fish Ecology Division, Northwest Fisheries Science Center, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112, USA.
T.P. Quinn. School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA.
Corresponding author: E.B. Taylor (email: etaylor@zoology.ubc.ca).

Fig. 1. A map of Lake Aleknagik, Bristol Bay, Alaska. The sampling sites are (1) Happy Creek, (2) Yako Creek, (3) Whitefish Creek, and (4) Silver Salmon Creek.
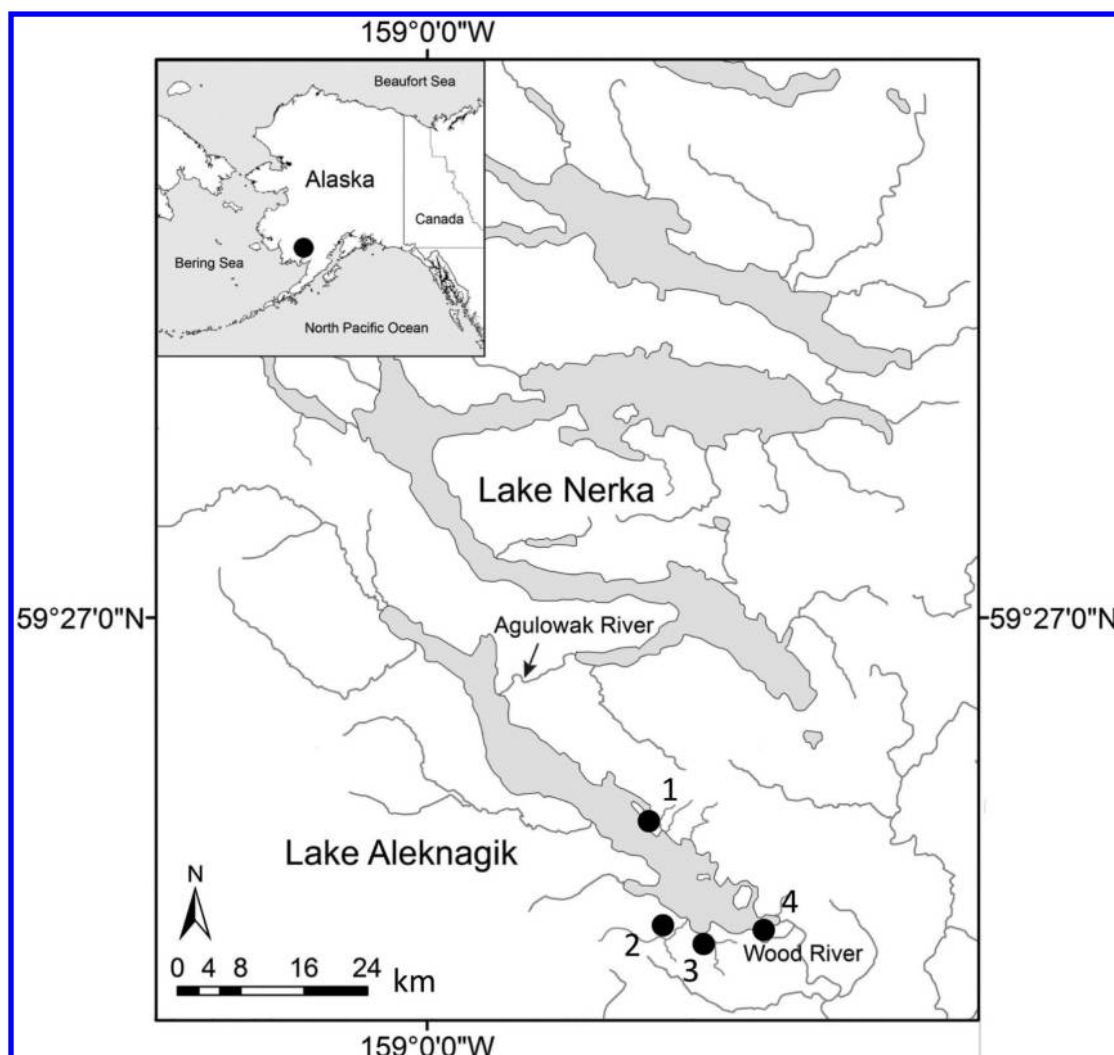
Alaska, their occasional co-occurrence in streams as juveniles (May-McNally et al. 2015a), and their ability to hybridize with one another, very little is known of their comparative ecology in sympatry. DeLacy and Morton (1943) studied the two species in Karluk Lake, on Kodiak Island in the Gulf of Alaska, and noted that they had broad ecological differences at least as subadults and adults. Arctic char were permanent residents of the lake where they spawned on submerged beaches, whereas Dolly Varden were anadromous, and spawning and early growth of juveniles took place in streams (DeLacy and Morton 1943). The difference in spawning habitats suggests that there is strong premating isolation between the species. The broad differences in habitat used (streams versus lakes), life history (freshwater resident versus anadromous), feeding ecology, and migratory behaviour also suggest that Dolly Varden and Arctic char may differ in physiological traits that may represent adaptations to alternative niches.

To test for specialization to alternative food resources, we compared the trophic ecology of juvenile Dolly Varden and Arctic char sampled together in streams. We also compared their trophic morphology to see if any diet differences between species were associated with traits related to feeding capacity, especially gape size, that may influence the size of food that can be ingested and thus dietary habits (e.g., Bozek et al. 1994; Krebs and Turingan 2003; Carroll et al. 2004). Finally, we used otolith microchemistry analysis to test the

hypothesis that the two species exhibit different migratory histories.

Materials and methods

Study area

The study area, Lake Aleknagik (area = 83 km², maximum depth = 110 m, mean depth = 43 m; 59°16′03″N, 158°49′51″W; Burgner 1991), is located near Dillingham, Alaska, in the Wood River Lakes system that drains into Bristol Bay (Fig. 1). This lake presents a diversity of stream habitats, ranging in gradient, size, temperature, and other physical features, and many are used for spawning by sockeye salmon, *Oncorhynchus nerka* (Walbaum, 1972) (Pess et al. 2014). Other than adult sockeye salmon, which are present at high densities in the July–August spawning period, the stream communities primarily consist of Dolly Varden and juvenile Arctic char, juvenile coho salmon (*Oncorhynchus kisutch* (Walbaum, 1972)), rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)), coastrange sculpin (*Cottus aleuticus* Gilbert, 1896), and slimy sculpin (*Cottus cognatus* Richardson, 1836), as well as smaller numbers of other species, depending on the habitat features. Juvenile sockeye salmon migrate to the lake from the spawning streams upon emergence from their gravel nests. The diets of these fishes are typically composed of freshwater insects and other invertebrates. Salmonids, however, are largely opportunistic

Table 1. The total number of Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*) that were sampled for stomach contents across four sampling sites in Lake Aleknagik, southwestern Alaska.

Sampling site	Arctic char	Dolly Varden	Total
Happy Creek	24	12	36
Yako Creek	36	41	77
Whitefish Creek	23	4	27
Silver Salmon Creek	0	5	5
Total	83	62	145

feeders (e.g., Dill and Fraser 1984; Cada et al. 1987; Keeley and Grant 1997; Hagen and Taylor 2001; Gallagher and Dick 2010), and Dolly Varden and Arctic char feed seasonally on the flesh and eggs of salmon and other fishes during and after the spawning period (Denton et al. 2009; Armstrong et al. 2010).

Four permanent streams were selected for study (Fig. 1). Happy Creek contained both species in the same areas of the stream near the mouth, Yako Creek contained both species in a gradient from the mouth to mid-way up the stream; only Arctic char were found at the mouth, and the creek gradually transitioned to exclusively Dolly Varden several kilometres upstream (May-McNally et al 2015a). Whitefish Creek contained almost exclusively Arctic char, but a few Dolly Varden were found at the mouth. Sampling in Silver Salmon Creek revealed only Dolly Varden. This stream also differs from the other three, as it drains directly into the Wood River rather than into Lake Aleknagik (May-McNally et al 2015a). Consequently, Silver Salmon Creek lacks an annual sockeye salmon run and the opportunity to feed on eggs that they provide.

Fish sampling

Juvenile fishes were sampled in Happy, Yako, Silver Salmon, and Whitefish creeks in July 2014 ($n = 145$; Table 1). A short reach (~100 to 150 m) of each stream was sampled using a 2.5 m long × 1.5 m deep pole seine. The reaches sampled were those where preliminary sampling had indicated that the likelihood of sampling both species within similar habitats was high. After each reach was sampled, fish were sedated with MS-222 in fresh water before processing. We recorded global positioning system (GPS) data at the upstream end of each sample reach, as well as fork length, an adipose fin-clip sample (for DNA verification of species identity), and stomach contents by gastric lavage (Gallagher and Dick 2010) from each individual.

A subset ($n = 104$; 72%) of the total number of fishes sampled had their field identification confirmed by DNA analysis. Genomic DNA of each individual was extracted from the adipose fin clips and polymerase chain reaction (PCR) assays of three microsatellite DNA loci with fixed or nearly fixed differences between Dolly Varden and Arctic char (*Smm-21*, *Sfo-18*, and *Sco-202*) were conducted following methods outlined by May-McNally et al. (2015a). Ninety-nine percent (103 of 104 fish) of the samples tested had DNA-based and field-based species identifications that matched each other. Furthermore, a subset of 11 small Dolly Varden and 15 small Arctic char were collected and used in otolith microchemistry analyses (see below). The Arctic char used for otolith analysis were sampled opportunistically from three different sites around Lake Aleknagik using a 32 m long × 5 m deep beach seine and from a pool in the lower portion of Bear Creek using the pole seine. The Dolly Varden used for otolith analysis were collected from two sites in Yako Creek (upper and mid-Yako Creek) and Happy Creek. The fork lengths of all fish used in the analysis of otoliths were very similar and they were considered to be young of the year given their mean (SD) fork length of 38.6 (3.63) mm.

Diet analyses

Stomach contents were preserved in 95% ethanol at room temperature and subsequently identified to the lowest possible taxonomic level using dichotomous keys found in Merritt and Cummins (2008) and IOWATER (2005). In addition, data from the University of Washington's Fisheries Research Institute on the common benthic stream invertebrates in the region were used (J. Carter, University of Washington, personal communication). The number of sockeye salmon eggs in the diets was determined by counting the number of whole eggs or egg fragments that constituted more than 50% of the egg sphere.

Statistical analyses of diet data

We estimated the extent of trophic niche segregation between Dolly Varden and Arctic char by calculating diet overlap using two approaches. First, Schoener's index of proportional overlap (SI) provided the basis for tests for significance of diet differences (Bozek et al. 1994; Hagen and Taylor 2001; Gallagher and Dick 2010):

$$SI_{xy} = 100\left(1 - \tfrac{1}{2}\sum\nolimits^{n} |p_{xi} - p_{yi}|\right)$$

where n is the number of prey categories and p_{xi} and p_{yi} represent the proportional contribution of the *i*th prey item in species x and y, respectively (Schoener 1970).

We tested the null hypothesis of no differences between intraspecific and interspecific SI values in the following manner. We made independent pairwise comparisons of the mean interspecific SI (i.e., between Dolly Varden and Arctic char) and the mean intraspecific SI (i.e., within Dolly Varden and Arctic char), which represents a comparison of the relative strengths of intra- and interspecific diet overlap (cf. Abrams 1980), using Wilcoxon signed-rank tests. We sampled subsets of individuals such that no individual fish was used in more than one test of pairwise comparison of interspecific SI versus intraspecific SI and repeated this analysis using different subsets 10 times. The α value that determined the threshold significance of each test was adjusted using a sequential Bonferroni correction (Rice 1989) and was carried out in the program PAST version 3.04 (Hammer et al. 2001).

We next used multivariate analyses to evaluate trophic niche overlap. Data on the proportional representation of each prey item were transformed using a square-root ($x + 1$) transformation and the fork length of each fish was placed into a size class based on length-frequency distributions (May-McNally et al. 2015a). We included size-class comparisons to examine diet variation with size. Size class 1 contained individuals with a fork length of <100 mm, size class 2 contained 100–149 mm, size class 3 contained 150–199 mm, and size class 4 contained >200 mm. Then, a set of nonmetric multidimensional scaling (NMDS) analyses using the Euclidean distance measure were plotted to demonstrate the ranked dissimilarity between individuals. The stress value of the NMDS plots was assessed to ensure that the two-dimensional plot was an accurate representation of the multivariate data. Stress is calculated by assessing the amount of scatter the data set creates around a 1:1 line on a Shepard diagram, which is a diagram that plots the true distance among data points against its distance in two-dimensional space (Clarke 1993; Greenacre and Primicerio 2013). The stress value indicates how well the data are represented in two dimensions. When the stress value is lower, the two-dimensional representation of the true relationships between data points is greater (Greenacre and Primicerio 2013).

Next, two-way analysis of similarity (ANOSIM) tests were carried out to account for the influence of species, as well as the coincident influence of sampling site and size on each individual's diet. The ANOSIM analyses used the Euclidean distance as a measure of diet difference. The ANOSIM tests the null hypothesis that any treatment groups are the same based on multivariate diet data (Clarke 1993; Anderson 2001; Anderson and Walsh 2013). An interaction be-

tween treatment groups (i.e., species, size class, stream of origin) is inherent in a crossed two-way ANOSIM design, so an interaction term cannot be partitioned out statistically as in multifactor ANOVA (Clarke 1993). Consequently, three separate ANOSIM tests were performed across the three treatments. We did not use multifactor ANOVA owing to the highly non-normal distributions of the proportional diet composition data, either as single variables or when summarized by ordination using principal components analysis. By contrast, ANOSIM is a distribution-free multivariate procedure.

In ANOSIM, the null hypothesis of no difference between treatment groups can be rejected both by a consistent difference in response variables across group levels and by differential effect sizes of response variables across group levels (Clarke 1993). As such, multiple tests of treatment groups may be beneficial to discern which are significant across all levels or just across some (i.e., if a significant interaction between treatment groups might be occurring). Here, a measure of the degree of influence of both treatment groups (e.g., species and size class) is represented by the relative R values associated with each.

A similarity percentage (SIMPER) analysis was carried out using the Euclidean distance measure to account for each prey item's influence on the dissimilarity between individuals. The SIMPER analysis examines which response variables are responsible for any dissimilarities found in a multivariate data set (Greenacre and Primicerio 2013). We used logistic regression to examine the relationship between fish length and the probability of consuming salmon eggs for each species. We did not use the five Dolly Varden sampled from Silver Salmon Creek in the ANOSIM, SIMPER, or logistic regression analyses because there were no sockeye salmon spawning in that stream and hence no salmon eggs on which to feed. All diet-related statistical analyses were carried out in the program PAST version 3.04 (Hammer et al. 2001).

Morphological analyses

To see if Dolly Varden and Arctic char differed in trophic characters that might influence diet, a morphological analysis was carried out upon samples of both species collected from Yako Creek, Happy Creek, and Whitefish Creek and contained in the fish collection at The University of British Columbia's Beaty Biodiversity Museum ($n = 38$; Supplementary Table S1[1]). These samples represented a range of collections from July 2013 and 2014 and from all four of the streams (Supplementary Table S1).[1] Dial calipers were used to measure the fork length, upper jaw length, the distance from the tip of the snout to the anterior portion of the eye, and the distance between the centers of each eye when measured dorsally. All distances were measured in millimetres (mm) on the left side of each individual, with the exception of the distance between the eyes (measured on the dorsal surface of each fish). Measuring fork length allowed for standardizing measurements to a common body size, upper jaw length was a proxy for gape size, and the eye measurements were proxies for reaction distance (Dunbrack and Dill 1984; Mazur and Beauchamp 2003).

Statistical analyses of morphological data

Fork length was positively correlated with the size of individual body parts or dimensions (i.e., $r^2 > 0.94$ in all cases). Consequently, all distances were scaled to the overall mean fork length by transforming the data using the allometric size removal function in PAST (Hammer et al. 2001). Three two-sample Student's t tests were carried out on size-standardized body part measurements to test for differences in trophic morphology. The α value that determined the threshold significance of each test was adjusted using a sequential Bonferroni correction (Rice 1989) using JMP version 9.0.2 (SAS Institute, Inc. 2010).

Otolith microchemistry analyses

Otolith chemistry of juveniles may be used to determine maternal anadromy in species where resident and migratory fish are sympatric (Kalish 1990). Commonly, the ratio of strontium (Sr) to calcium (Ca) in the otolith core, that region formed very early in larval development, is used to determine whether the natal portion of the otolith originates from fresh or marine water because Sr:Ca varies substantially between the two environments (Zimmerman and Reeves 2002; Donohoe et al. 2008; Zimmerman et al. 2009; Mills et al. 2012). High Sr:Ca ratios indicate residence in marine waters (Gillanders 2005; Elsdon et al. 2008); this is transferred maternally to the core of the otoliths of offspring being nourished by yolk (Kalish 1990). Therefore, in fresh waters with low Sr concentrations (≤5 mmol·mol^{-1}; Kraus and Secor 2004), maternal anadromy in the season preceding spawning can be assessed because the composition of the otolith core is derived from the maternal environment experienced during vitellogenesis or egg yolk formation (Riva-Rossi et al. 2007; Donohoe et al. 2008). Consequently, if the anadromous (Dolly Varden) versus lake resident (Arctic char) difference reported elsewhere (DeLacy and Morton 1943; McPhail 1961) is a general phenomenon, then the core of the otoliths of Dolly Varden would have levels of Sr:Ca indicative of some period of marine residence by their mothers, but this would not be the case for Arctic char.

In the laboratory, one otolith from each of 11 Dolly Varden and 15 Arctic char was rinsed in de-ionized water, dried, and then mounted in thermoplastic resin in the sagittal plane on a glass slide. Chemical data for each otolith were collected with laser ablation – inductively coupled plasma – mass spectrometry (LA–ICP–MS) at the Keck Collaboratory, Oregon State University. A Thermo X-Series II ICPMS (Thermo Fisher Scientific, Waltham, Massachusetts, USA) with a Photon Machines Analyte G2 (Photon Machines, Bozeman, Montana, USA) 193 nm laser set at a pulse rate of 10 Hz with a 85 µm ablation spot was used to ablate a hole from the surface through the core of the otolith for 1000 pulses. We continuously measured Sr, Mn, and Ca and used NIST-612 glass to transform ion ratios to elemental ratios and measure the mean percent relative standard deviations for each element (all less than 6%). Elemental ratios were converted to molar ratios using the molar mass of each element. Final analyses were computed on the element:Ca in mmol·mol^{-1}. A calcium carbonate standard with known concentration (USGS MACS-1) was used to determine the accuracy of the element:Ca ratio (>95% for all element:Ca). During ablation, we monitored the data for a rapid increase in the concentration of Mn, which indicates the core region had been reached (Ruttenberg et al. 2005; Miller and Kent 2009). The Sr:Ca data collected during the increase in Mn provided the maternally derived core signal, whereas the data collected during the initial abalation formed the freshwater edge value. We used a Student's t test to compare the edge and core Sr:Ca data for each fish. Those with significantly higher Sr:Ca in the core were considered to be offspring of anadromous mothers, whereas those with cores that were lower or not different were considered to have had resident mothers (Zimmerman and Reeves 2000).

Results

Diet analysis

We obtained stomach contents from 62 Dolly Varden and 83 Arctic char (Table 1) that were very similar in mean (±SD) size (fork length = 156.5 ± 50.5 versus 150.0 ± 51.1 mm for Arctic char and Dolly Varden, respectively; Student's t test, $p = 0.37$). The 10 independent pairwise comparisons of stomach contents between species yielded mean SI values of between 26.8% and 34.5% (Table 2). By contrast, the pairwise comparisons within species yielded means of 48.2% similarity between individual Arctic char and 51.3% similarity between individual Dolly Varden. There was significantly more

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Table 2. A summary table of one-sample Wilcoxon signed-rank tests comparing 10 permutations of independent pairwise comparisons of Schoener's index of proportional diet overlap between Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*) to mean intraspecific proportional diet overlap.

Permutation	Mean (%)	Comparison to mean index within Arctic char (48.2%)			Comparison to mean index within Dolly Varden (51.3%)			
		W	Z	p	W	Z	p	α
1	31.3	1278	2.6738	0.0075*	1365	3.3146	0.0009*	0.05
2	27.8	1258	2.8191	0.0048*	1317	3.2651	0.0011*	0.025
3	30.1	1271	3.2197	0.0013*	1323	3.6226	0.0003*	0.0167
4	28.9	1247	3.3458	0.0008*	1313	2.8709	0.0001*	0.0125
5	30.0	1191	3.2106	0.0013*	1256	3.7416	0.0002*	0.01
6	34.5	1134	2.7441	0.0061*	1215	3.4057	0.0007*	0.0083
7	33.9	1137	2.7672	0.0057*	1207	3.3386	0.0008*	0.0071
8	31.0	1116	2.9038	0.0037*	1181	3.4493	0.0006*	0.0063
9	26.8	1182	3.7906	0.0002*	1213	4.058	0.00005*	0.0056
10	33.3	968	2.2385	0.0252	1023	2.7261	0.0064	0.005

Note: The mean index of proportional diet overlap within Arctic char was 48.2%, whereas the mean index of proportional diet overlap within Dolly Varden was 51.3%. The *p* values presented are the large-sample approximations given by the Wilcoxon signed-rank test. Asterisks indicate a significant difference between the mean intraspecific index and the mean interspecific index of proportional diet overlap, where *α* to reject the null hypothesis is adjusted by a sequential Bonferroni correction.

diet similarity within species than between species; the interspecific SI values were significantly lower than the intraspecific value for both species in 9 out of 10 comparisons (Wilcoxon signed-rank tests; Table 2).

Multivariate analyses

An NMDS analysis using the Euclidean distance measure represented the dissimilarity between the species' diets with a modest stress value (stress = 0.1765; Fig. 2A), i.e., the NMDS was a good representation of the dissimilarities in two dimensions. Arctic char consumed a wider variety of prey items than did Dolly Varden as reflected in a higher intraspecific dissimilarity between points within Arctic char (Fig. 2A). When individuals were grouped by size class, the smallest individuals (fork length <100 mm) consumed the narrowest range of prey (Fig. 2B). Larger individuals consumed an increasingly wider variety of prey and were the most dissimilar from the smallest size classes (Table 3).

An ANOSIM on transformed absolute value data indicated that species and size class both significantly contributed to the variation in diets (species: $R = 0.093$, $p = 0.0117$; size: $R = 0.302$, $p = 0.0001$). Similarity between species was lower than the similarity within species, but the species factor accounted for a lower degree of the variation in diets relative to size class as indicated by the smaller R value attributed to the species factor. A second two-way ANOSIM indicated no significant effect of sampling site (i.e., stream) or size class when these two factors were examined together across species (stream: $R = 0.034$, $p = 0.2135$; size: $R = 0.171$, $p = 0.1675$). A third two-way ANOSIM resulted in significant effects of both stream and species with the latter effect being slightly greater (stream: $R = 0.146$, $p = 0.0006$; species: $R = 0.175$, $p = 0.0097$).

The SIMPER analyses revealed differences in diets both among size classes and between species (Table 3). The most dissimilar comparisons occurred between fish from the smallest and largest size classes (89.6%; Table 3). The SIMPER analysis between species indicated an overall average dissimilarity of 43.3% between Dolly Varden and Arctic char (Table 3), and four prey items accounted for 90.4% of the dissimilarity between the stomach contents of Dolly Varden and Arctic char (Table 4). These prey items were sockeye salmon eggs, which contributed to 71.7% of the dissimilarity; Chironomidae (midges), which contributed to 9.8% of the dissimilarity; Baetidae (mayflies), which contributed to 5.5% of the dissimilarity; and Trichoptera (caddisflies), which contributed to 3.3% of the dissimilarity (Table 4). Arctic char consumed more sockeye salmon eggs, on average, than did Dolly Varden, whereas Dolly Varden consumed more Chironomidae, Baetidae, and Trichoptera (Table 4). There was a significant relationship between fork length and proba-

bility of consuming sockeye salmon eggs in Arctic char ($\beta = 0.017$, $p = 0.0017$), but not in Dolly Varden ($\beta = -0.0001$, $p = 0.924$).

Morphological analysis

Arctic char had larger mouths and heads than Dolly Varden when measurements were standardized by fork length (Table 5). Upper left jaw length, the distance from the anterior portion of the left eye to the tip of the snout, and the distance between the center of each eye when measured dorsally were all significantly larger in Arctic char when adjusted for multiple comparisons ($p = 0.0009$, 0.0026, and 0.0368, respectively; Table 5).

Otolith microchemistry

Analysis of otolith microchemistry indicated maternal anadromy in Dolly Varden, but not in Arctic char. Of the 15 Arctic char otoliths we examined, all had cores that were not significantly different ($P \geq 0.05$) or were significantly lower ($P < 0.05$) in Sr:Ca than the freshwater edge region, indicating that the mothers had not been to sea in the season prior to spawning. In contrast, all 11 of the Dolly Varden examined had core Sr:Ca values that were significantly higher than the freshwater edge region (all $p < 0.00001$), indicating that their mothers had been to sea. Moreover, differences in Sr:Ca ratios between species were limited to the core region of the otoliths (the region whose composition results from the maternal environment experienced during vitellogenesis). Average core Sr:Ca value of Dolly Varden (mean = 1.17 mmol·mol^{-1}) was significantly higher than that of Arctic char (mean = 0.63 mmol·mol^{-1}; Student's t test, $t = -16.68$, $p < 0.00001$). By contrast, when we compared the averaged Sr:Ca values for each growth region (core versus edge) between Dolly Varden and Arctic char, we found no difference in edge chemistry between Dolly Varden (mean = 0.84 mmol·mol^{-1}) and Arctic char (mean = 0.92 mmol·mol^{-1}; Student's t test, $t = 1.67$, $p = 0.11$).

Discussion

If, when, and how sympatric species partition available resources has been a central area of investigation in ecology (Schoener 1974; Nakano et al. 1992; Hagen and Taylor 2001) and is increasingly viewed as important to understanding the role of ecology in speciation and the maintenance of genetic distinction in the face of gene flow (Schluter 2000; Nosil et al. 2005; Svanbäck and Bolnick 2007). Here, we demonstrated that juveniles of two species of sympatric char differed in (*i*) trophic ecology during a critical period of summer growth, (*ii*) aspects of head morphology that are plausibly linked to the observed diet differences, and (*iii*) whether or not their mothers were anadromous. Combined with other information on the spatial

Fig. 2. A nonmetric multidimensional scaling (NMDS) analysis using the Euclidean distance measure on square-root (x + 1) transformed absolute value diet composition data from Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*). (A) Stomach contents plotted in two-dimensional space coded by species and (B) stomach contents plotted in two-dimensional space coded by size class. Size class 1 contains individuals with a fork length of <100 mm, size class 2 contains individuals with a fork length of 100–149 mm, size class 3 contains individuals with a fork length of 150–199 mm, and size class 4 contains individuals with a fork length of individuals with a fork length of >200 mm. Stress = 0.1765; axis 1: R^2 = 0.81; axis 2: R^2 = 0.10.
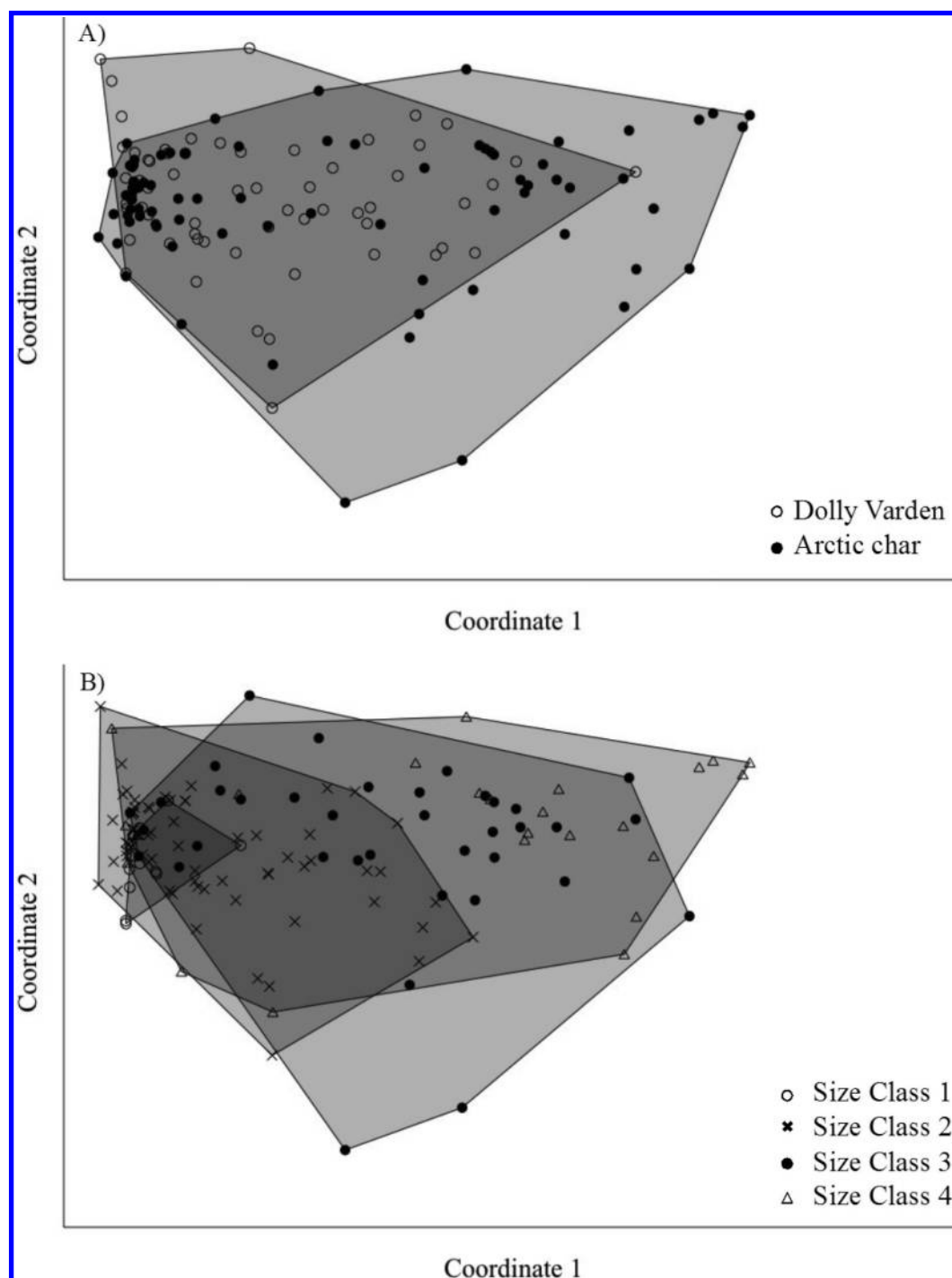
distributions of the species in this system (May-McNally et al. 2015*a*), our results suggest that Dolly Varden and Arctic char, although they may coexist as juveniles, are characterized by alternative trophic niches and migratory behaviour.

Differences in diet and morphology

Colwell and Futuyma (1971) cautioned against sampling bias when calculating SI values, noting that closely spaced sampling sites could overestimate niche overlap due to the potential for spatial similarity in certain resource environments and habitats. We were unable to balance sampling among streams and stream reaches evenly. As such, it is plausible that our estimates of niche overlap are conservative and the actual inferred niche overlap between these species is lower than given here. Despite this uncertainty, the SI values that we estimated are broadly consistent

Table 3. A summary table of a SIMPER analysis dissimilarities on square-root $(x + 1)$ transformed prey abundance data for diets of Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*).

Group 1	Group 2	Overall average dissimilarity (%)
Dolly Varden	Arctic char	43.29
Size class 1	Size class 2	18.30
Size class 1	Size class 3	53.33
Size class 1	Size class 4	89.55
Size class 2	Size class 3	43.86
Size class 2	Size class 4	74.92
Size class 3	Size class 4	56.38

Note: Overall average dissimilarity between species and size classes is shown. Size class 1 contains individuals with a fork length of <100 mm, size class 2 contains 100–149 mm, size class 3 contains 150–199 mm, and size class 4 contains >200 mm. An expansion on the specific dissimilarities between Dolly Varden and Arctic char can be seen in Table 4.

with those reported for stream salmonids, although there are cases where dietary overlap can be substantially higher (i.e., >0.6; Muir and Emmett 1988; Hagen and Taylor 2001; Hilderbrand and Kershner 2004). For instance, Mookerji et al. (2004) studied diet overlap in allopatric and sympatric populations of Atlantic salmon (*Salmo salar* L., 1758) and brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) sampled from two streams in Quebec. In the most direct comparison between the two species collected from the same stream and across the same time periods, the estimated interspecific diet overlap was between 0.22 and 0.25. These estimates were lower than intraspecific comparisons (collected for brook trout only) in only one of the three time periods sampled, but the intraspecific comparisons (0.12–0.38) in brook trout involved samples from different streams (Mookerji et al. 2004). Similarly, Dineen et al. (2007) reported mean numerically based SI values between sympatric juvenile brown trout (*Salmo trutta* L., 1758) and Atlantic salmon ranging between 0.35 and 0.67 across three Irish streams and three seasons, with only one value exceeding the commonly accepted threshold for "significant" overlap of 0.6 (Wallace 1981).

Hurlbert (1978) discussed some limitations of metrics such as SI and suggested that these indices may lack clear biological interpretation because they distill the ecological niche to a single value and ignore variation in "resource states" such as seasonal abundance or variability. The purpose of our study, however, was to examine trophic niche overlap during a particular "resource state", because the annual sockeye salmon run is likely to be a key time of year for these juvenile fishes in terms of resource acquisition (Denton et al. 2009). Consequently, a metric such as SI is appropriate in our case.

Our ANOSIM analyses found that diet varied during a period in July between the char species and among streams. At least some of the differences that we observed between Dolly Varden and Arctic char, however, may be attributable to differences in food availability or other factors that influence feeding (e.g., stream flow) among streams because our sampling was not balanced in terms of the numbers of each species sampled among streams. Furthermore, it is possible that differences in density of one or either species across stream could contribute to some of the differences in diet (cf. Svanbäck and Bolnick 2007). Species, however, was the only factor that was significant across both ANOSIM tests where it was tested, and size class and species both had consistently higher R values than sampling stream. This suggests that species and the size of an individual played larger roles in determining diet than the immediate stream environments that we sampled. Similarly, we were unable to record the exact GPS location of each fish sampled, just the location at the upper end of each stream reach. Consequently, microspatial differences in prey distribution or differences in microhabitat use between Dolly Varden and Arctic char within stream reaches could

contribute to the observed interspecific differences between their diets within a reach.

The SIMPER analyses demonstrated that largest differences in stomach contents were present between individuals of the largest and smallest size classes, and that diets expanded as the fish grew. This is likely due to the larger mouth, more efficient predation, and greater stomach volume in larger individuals (Van Valen 1965; Wankowski 1979; Scharf et al. 2000). The interspecific differences between Dolly Varden and Arctic char were similar in magnitude to the differences between individuals of size class 2 (100–149 mm) and size class 3 (150–199 mm) within the species (cf. Polis 1984). This suggests that the dissimilarity between species might be based on divergent trophic morphology, particularly in the size of mouth parts that typically increases as fish grow (see below). The SIMPER analysis that compared interspecific differences found that four prey items made up 90% of the dissimilarity between species and 70% of the dissimilarity was made up of a single prey item (i.e., sockeye salmon eggs). Because all fish used in the SIMPER analyses were collected in areas that had spawning sockeye salmon (and hence, access to eggs), our results suggest a greater ability to exploit, or stronger preference for, sockeye salmon eggs by Arctic char. Sockeye salmon eggs also contributed greatly to the variation between size classes; the opportunity or capacity to eat eggs may be an important part of diet separation between species and size classes during the spawning season.

The logistic regression showed that Arctic char increased their exploitation of sockeye salmon eggs as they grew, but Dolly Varden did not. Armstrong et al. (2010) demonstrated an increase in feeding on sockeye salmon eggs with increasing size in juvenile coho salmon, and they estimated that coho salmon, Arctic char, and Dolly Varden first began eating eggs at between 60 and 70 mm. When scaled to a common fork length, Arctic char had significantly larger mouth and head morphology than Dolly Varden. Furthermore, both the distance between the eyes and the distance from snout to eye were larger in Arctic char. These latter trait values are associated with a greater reaction distance that may be important in the detection of drifting eggs (Dill and Fraser 1984; Dunbrack and Dill 1984; Scharf et al. 2000; Mazur and Beauchamp 2003). Head and mouth morphology may influence the size, quantity, and diversity of prey items consumed between species and individuals (Van Valen 1965; Wankowski 1979; Langeland et al. 1991; Nakano et al. 1992; Lu and Bernatchez 1999; Scharf et al. 2000) and, in particular, may contribute to the increase in sockeye salmon eggs in the diet with increasing size in Arctic char relative to Dolly Varden (e.g., Adams and Huntingford 2002; Krebs and Turingan 2003).

Snorrason et al. (1994) suggested that the development of divergent Arctic char morphotypes were driven by variation in diet and habitat use. Woods et al. (2013) and May-McNally et al. (2015b) demonstrated that sympatric morphs of Arctic char were characterized by differences in diet and habitat use and that the morphs were genetically distinct from one another. This is consistent with the idea that chars, and Arctic char in particular, are predisposed to divergence via trophic specialization (Klemetsen 2010). The ability to exploit a wide variety of resources depending on environmental conditions, including the presence of a congener, may, therefore, be a key factor explaining the coexistence of Dolly Varden and Arctic char. Nonetheless, it would be important to understand if coexistence between the two species and differences in diet that we have demonstrated extend to other parts of the year when sockeye salmon eggs are not such a dominant prey item. For instance, some studies have reported that seasonal coexistence and the extent of diet overlap between species can be influenced by levels of food abundance, which is higher during periods of increased food abundance (Nilsson 1960; Nummi and Väänänen 2001).

Our study did not resolve prey item identity to a lower taxonomic level than family and in some cases prey were only identified to order: Trichoptera, Plecoptera, Hymenoptera. The Trichoptera (caddisflies) were among the four prey items that contributed to a com-

Table 4. The results of a SIMPER analysis on square-root ($x + 1$) transformed prey abundance data comparing diets of sympatric Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*).

Taxon	Average dissimilarity (%)	Variation		Mean abundance	
		Contributive (%)	Cumulative (%)	Arctic char	Dolly Varden
Sockeye salmon[a] eggs	31.04	71.70	71.70	24.0100	13.3956
Chironomidae	4.26	9.84	81.55	2.5921	2.8224
Baetidae	2.39	5.51	87.05	0.2304	0.3364
Trichoptera	1.45	3.34	90.40	0.0169	0.2704
Plecoptera	1.01	2.32	92.72	0.3249	0.3136
Nematoda	0.44	1.01	93.73	0.1089	0.0036
Hirudinea	0.43	1.00	94.73	0.0225	0.0000
Heptageniidae	0.42	0.97	95.70	0.0121	0.0784
Hymenoptera	0.41	0.94	96.64	0.0324	0.0009
Unidentified species	0.29	0.66	97.30	0.0225	0.0049
Drosophilidae	0.17	0.39	97.69	0.0064	0.0064
Elmidae	0.16	0.37	98.06	0.0016	0.0036
Simuliidae	0.16	0.37	98.43	0.0064	0.0009
Gastropoda	0.16	0.37	98.80	0.0049	0.0004
Empididae	0.07	0.16	98.96	0.0004	0.0025
Haliplidae	0.06	0.15	99.11	0.0016	0.0004
Ceratopogonidae	0.06	0.14	99.25	0.0036	0.0000
Scirtidae	0.06	0.14	99.38	0.0016	0.0000
Culicidae	0.06	0.13	99.51	0.0004	0.0009
Oligochaetae	0.05	0.11	99.62	0.0016	0.0000
Hydracarina	0.04	0.10	99.72	0.0001	0.0009
Syrphidae	0.04	0.10	99.82	0.0001	0.0009
Tipulidae	0.04	0.08	99.91	0.0016	0.0000
Dryopidae	0.03	0.06	99.97	0.0001	0.0004
Odonata	0.01	0.03	100.00	0.0001	0.0000

Note: Average dissimilarity, the percentage of contributive and cumulative variation, and the mean abundance of each prey item that occurred within the diets are given. The analysis used a Euclidean distance measure and the overall average dissimilarity was 43.3%.

[a]*Oncorhynchus nerka.*

Table 5. Left upper jaw length (as a proxy for gape width), distance from tip of the snout to anterior eye margin, and the distance between the eyes standardized by fork length in sympatric samples of Dolly Varden (*Salvelinus malma*) and Arctic char (*Salvelinus alpinus*).

Phenotype	Upper jaw length (mm)[a]	Distance from snout to eye (mm)[b]	Distance between eyes (mm)[c]
Arctic char	15.4±0.28	9.1±0.14	13.6±0.25
Dolly Varden	14.1±0.25	8.5±0.13	12.4±0.23

Note: The standardized fork length was 152.8 mm. All values are expressed as transformed mean ± SE and are significant at $p < 0.0368$ ($n = 17$ Arctic char and $n = 21$ Dolly Varden).

[a]$p = 0.0009$.
[b]$p = 0.0026$.
[c]$p = 0.0368$.

bined 90% of the trophic dissimilarity between these species (3.4% for Trichoptera). Furthermore, sample sizes were not equally distributed across each sampling stream. This may have resulted in conservative analysis of sampling stream as an influential factor. All of our data were obtained during the period of sockeye salmon spawning. As such, there was no control for the effect of the sockeye salmon (e.g., the presence of eggs and also the disturbance of insects caused by their digging; Field-Dodgson 1987; Peterson and Foote 2000), and our diet data therefore may apply only to this particular time of year and sockeye salmon density. Salmon eggs, however, play a large role in the growth of juvenile fishes that feed on them (Denton et al. 2009; Armstrong et al. 2010; Bentley et al. 2012) and to have avoided sampling during the salmon spawning period would have been unrepresentative of the trophic ecology in these streams. Indeed, although Arctic char appear to reside largely in Lake Aleknagik, their seasonal appearance in streams is probably driven by the temporary availability of salmon eggs there because Arctic char may feed on eggs (e.g., Hindar and Jonsson 1982) and make well-marked habitat shifts to

exploit seasonal growth opportunities (e.g., Näslund 1990; Klemetsen et al. 2003). Furthermore, characterization of the mean size of the prey items examined would help to further test for differences in the trophic ecology of Dolly Varden and Arctic char, and stable isotope analysis could provide a longer term perspective on the trophic ecology of these species (Bootsma et al. 1996; Bearhop et al. 2004). Finally, there is a strong need for a better understanding of how the species behave when sympatric, especially in terms of the behavioural aspects of trophic interactions (e.g., Schutz and Northcote 1972; Jonsson et al. 2008).

Differences in migratory life history

Our analysis of Dolly Varden and Arctic char otoliths revealed a distinct separation in the migratory histories of the parents of the juvenile fishes assayed. All the Dolly Varden had been produced by mothers that had been to sea in the season prior to spawning, while none of the Arctic char had been produced by anadromous mothers. Needless to say, a greater sample size is required to determine if all Arctic char are resident in this system and if all Dolly Varden are anadromous. The fry we assayed, however, represented a mix of collections from streams and beaches, in the case of the Arctic char, and from several streams, in the case of the Dolly Varden. Given the complete separation between the migratory histories of these samples, selected "blind" with respect to any information on their parents, it seems likely that the Dolly Varden in this system, or at least the females, are primarily anadromous (cf. Hart et al. 2015), and the Arctic char are primarily resident. This conclusion is consistent with the results of other forms of sampling with beach seines, gill nets, and hook and line (Taylor et al. 2008; May-McNally et al. 2015*a*), all of which can produce large-bodied Arctic char throughout the summer in this system, whereas adult-sized Dolly Varden are seldom encountered until the fall during what is presumably their upstream migration from the sea. In addition, there is segregation of spawning

sites between the two species as determined by direct observations and as inferred from catches of young-of-the-year fish. Dolly Varden have been observed spawning in streams, whereas Arctic char have been observed spawning in the lake on submerged beaches in Lake Aleknagik (C. Schwanke, Alaska Department of Fish and Game, Dillingham, Alaska, USA) and also in Karluk Lake, Alaska (DeLacy and Morton 1943). Newly emerged Arctic char are routinely caught in the lake beaches in mid-summer, whereas young-of-the-year Dolly Varden are only found in streams. Consequently, it seems likely that young Dolly Varden result from adults that spawn in streams and that juveniles grow there until they are large enough to migrate to sea, although there may also be some nonanadromous males as reported elsewhere (e.g., Maekawa et al. 1993). In contrast, after adult Arctic char spawn in lakes, the young of the year emerge on lake beaches, but then ascend the lower reaches of streams, overlapping spatially with juvenile Dolly Varden (May-McNally et al. 2015a). After a few years, when the juvenile Dolly Varden are migrating to sea, the older juvenile Arctic char move into deep areas of the lake where they feed and grow for several years until they are large enough to feed in shallower water, where they routinely eat juvenile sockeye salmon in the early summer (Ruggerone and Rogers 1984; May-McNally et al. 2015a).

Our work has provided the first estimates of the degree to which sympatric Arctic char and Dolly Varden differentially use trophic and spatial resources in freshwater habitats. Further work is required to understand the generality of these differences across other systems and the extent of seasonal variation in resource use, particularly for trophic biology and during times when sockeye salmon eggs are not available. More generally, and if our results are consistent across systems and seasons, they may contribute to constraining gene flow between Dolly Varden and Arctic char when they do hybridize (Taylor et al. 2008; May-McNally et al. 2015a). For instance, morphologically intermediate hybrids may show reduced feeding performance, in terms of food acquisition and growth, relative to parental species in fishes (e.g., Schluter 1995). Furthermore, the behavioural and physiological differences associated with freshwater residency (Arctic char) versus anadromy (Dolly Varden) may reduce survival of hybrids and explain their rarity in nature (Taylor et al. 2008; May-McNally et al. 2015a; cf. Foote et al. 1992; Taylor and Foote 1991; Moore et al. 2010).

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References

Abrams, P. 1980. Some comments on measuring niche overlap. Ecology, 61: 44–49. doi:10.2307/1937153.

Adams, C.E., and Huntingford, F.A. 2002. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. Evol. Ecol. 16: 15–25. doi:10.1023/A:1016014124038.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26: 32–46. doi:10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J., and Walsh, D.C.I. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83: 557–574. doi:10.1890/12-2010.1.

Armstrong, J.B., Schindler, D.E., Omori, K.L., Ruff, C.P., and Quinn, T.P. 2010. Thermal heterogeneity mediates the effects of pulsed subsidies across a landscape. Ecology, 91: 1445–1454. doi:10.1890/09-0790.1. PMID:20503876.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., and MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Anim. Ecol. 73: 1007–1012. doi:10.1111/j.0021-8790.2004.00861.x.

Bentley, K.T., Schindler, D.E., Armstrong, J.B., Zhang, R., Ruff, C.P., and Lisi, P.J. 2012. Foraging and growth responses of stream-dwelling fishes to interannual variation in a pulsed resource subsidy. Ecosphere, 3: doi:10.1890/ES12-00231.1.

Bootsma, H.A., Hecky, R.E., Hesslein, R.H., and Turner, G.F. 1996. Food partitioning among Lake Malawi nearshore fishes as revealed by stable isotope analyses. Ecology, 77: 1286–1290. doi:10.2307/2265598.

Bozek, M.A., DeBrey, L.D., and Lockwood, J.A. 1994. Diet overlap among size classes of Colorado River cutthroat trout (Oncorhynchus clarkii pleuriticus) in a high-elevation mountain stream. Hydrobiologia, 273: 9–17. doi:10.1007/BF00126765.

Burgner, R.L. 1991. Life history of sockeye salmon (Oncorhynchus nerka). In Pacific salmon life histories. Edited by C. Groot and L. Margolis. The University of British Columbia Press, Vancouver. pp. 3–117.

Cada, G.F., Loar, J.M., and Cox, D.K. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. Am. Midl. Nat. 117: 374–385. doi:10.2307/2425980.

Carroll, A.M., Wainwright, P.C., Huskey, S.H., Collar, D.C., and Turingan, R.G. 2004. Morphology predicts suction feeding performance in centrarchid fishes. J. Exp. Biol. 207: 3873–3881. doi:10.1242/jeb.01227. PMID:15472018.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18: 117–143. doi:10.1111/j.1442-9993.1993.tb00438.x.

Colwell, R.K., and Futuyma, D.J. 1971. On the measurement of niche breadth and overlap. Ecology, 52: 567–576. doi:10.2307/1934144.

DeLacy, A.C., and Morton, W.M. 1943. Taxonomy and habits of the charrs, Salvelinus malma and Salvelinus alpinus, of the Karluk drainage system. Trans. Am. Fish. Soc. 72: 79–91. doi:10.1577/1548-8659(1942)72[79:TAHOTC]2.0.CO;2.

Denton, K.P., Rich, H.B., and Quinn, T.P. 2009. Diet, movement, and growth of Dolly Varden in response to sockeye salmon subsidies. Trans. Am. Fish. Soc. 138: 1207–1219. doi:10.1577/T09-006.1.

Dill, L.M., and Fraser, A.H.G. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (Oncorhynchus kisutch). Behav. Ecol. Sociobiol. 16: 65–71. doi:10.1007/BF00293105.

Dineen, G., Harrison, S.S.C., and Giller, P.S. 2007. Diet partitioning in sympatric Atlantic salmon and brown trout in streams with contrasting riparian vegetation. J. Fish Biol. 71: 17–38. doi:10.1111/j.1095-8649.2007.01441.x.

Donohoe, C.J., Adams, P.B., and Royer, C.F. 2008. Influence of water chemistry and migratory distance on ability to distinguish progeny of sympatric resident and anadromous rainbow trout (Oncorhynchus mykiss). Can. J. Fish. Aquat. Sci. 65(6): 1060–1075. doi:10.1139/F08-029.

Dunbrack, R.L., and Dill, L.M. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (Oncorhynchus kisutch). Can. J. Fish. Aquat. Sci. 41(8): 1176–1182. doi:10.1139/f84-139.

Elsdon, T.S., Wells, B.K., Campana, S.E., Gillanders, B.M., Jones, C.M., Limburg, K.E., Secor, D.H., Thorrold, S.R., and Walther, B.D. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanogr. Mar. Biol. 46: 297–330. doi:10.1201/9781420065756.ch7.

Field-Dodgson, M.S. 1987. The effect of salmon redd excavation on stream substrate and benthic community of two salmon spawning streams in Canterbury, New Zealand. Hydrobiologia, 154: 3–11. doi:10.1007/BF00026826.

Foote, C.J., Wood, C.C., Clarke, W.C., and Blackburn, J. 1992. Circannual cycle of seawater adaptability in Oncorhynchus nerka: genetic differences between sympatric sockeye salmon and kokanee. Can. J. Fish. Aquat. Sci. 49(1): 99–109. doi:10.1139/f92-012.

Gallagher, C.P., and Dick, T.A. 2010. Trophic structure of a landlocked Arctic char Salvelinus alpinus population from southern Baffin Island, Canada. Ecol. Freshw. Fish 19: 39–50. doi:10.1111/j.1600-0633.2009.00387.x.

Gharrett, A.J., Goto, A., and Yamazaki, F. 1991. A note on the genetic contrast of sympatric Dolly Varden (Salvelinus malma) and Arctic charr (S. alpinus) in the Karluk River system, Alaska. In Reproductive biology and population genetics of Dolly Varden (Salmonidae). Edited by F. Yamazaki. Report of Overseas Work Supported by Grant-in-Aid for Overseas Scientific Survey of the Ministry of Education, Science, and Culture of Japan, Tokyo. pp. 37–48.

Gillanders, B.M. 2005. Otolith chemistry to determine movements of diadromous and freshwater fish. Aquat. Living Resour. **18**: 291–300. doi:10.1051/alr:2005033.

Greenacre, M., and Primicerio, R. 2013. Multivariate analysis of ecological data. Fundación BBVA, Bilbao, Spain.

Hagen, J., and Taylor, E.B. 2001. Resource partitioning as a factor limiting gene flow in hybridizing populations of Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). Can. J. Fish. Aquat. Sci. **58**(10): 2037–2047. doi:10.1139/f01-141.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica, **4**: 1–9.

Hart, L.M., Bond, M.H., May-McNally, S.L., Miller, J.A., and Quinn, T.P. 2015. Use of otolith microchemistry and stable isotopes to investigate the ecology and anadromous migrations of Northern Dolly Varden from the Egegik River, Bristol Bay, Alaska. Environ. Biol. Fishes, **98**: 1633–1643. doi:10.1007/s10641-015-0389-1.

Hartman, G.F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. **22**(4): 1035–1081. doi:10.1139/f65-095.

Herder, F., and Freyhof, J. 2006. Resource partitioning in a tropical stream fish assemblage. J. Fish Biol. **69**: 571–589. doi:10.1111/j.1095-8649.2006.01126.x.

Hilderbrand, R.H., and Kershner, J.L. 2004. Influence of habitat type on food supply, selectivity, and diet overlap of Bonneville cutthroat trout and non-native brook trout in Beaver Creek, Idaho. N. Am. J. Fish. Manage. **24**: 33–40. doi:10.1577/M02-192.

Hindar, K., and Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet Lake, western Norway. Can. J. Fish. Aquat. Sci. **39**(7): 1030–1045. doi:10.1139/f82-138.

Hurlbert, S. 1978. The measurement of niche overlap and some relatives. Ecology, **59**: 67–77. doi:10.2307/1936632.

IOWATER. 2005. Benthic macroinvertebrate key. Iowa Department of Natural Resources, Des Moines.

Jonsson, B., Jonsson, N., Hindar, K., Northcote, T.G., and Engen, S. 2008. Asymmetric competition drives lake use of coexisting salmonids. Oecologia, **157**: 553–560. doi:10.1007/s00442-008-1103-1. PMID:18629544.

Kalish, J.M. 1990. Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. Fish. Bull. (Wash., D.C.), **88**: 657–666.

Keeley, E.R., and Grant, J.W.A. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **54**(8): 1894–1902. doi:10.1139/f97-096.

Klemetsen, A. 2010. The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. Freshw. Rev. **3**: 49–74. doi:10.1608/FRJ-3.1.3.

Klemetsen, A., Knudsen, R., Staldvik, F.J., and Amundsen, P.-A. 2003. Habitat, diet and food assimilation of Arctic charr under the winter ice in two subarctic lakes. J. Fish Biol. **62**: 1082–1098. doi:10.1046/j.1095-8649.2003.00101.x.

Kraus, R.T., and Secor, D.H. 2004. Incorporation of strontium into otoliths of an estuarine fish. J. Exp. Mar. Biol. Ecol. **302**: 85–106. doi:10.1016/j.jembe.2003.10.004.

Krebs, J.M., and Turingan, R.G. 2003. Intraspecific variation in gape–prey size relationships and feeding success during early ontogeny in red drum, *Sciaenops ocellatus*. Environ. Biol. Fishes, **66**: 75–84. doi:10.1023/A:1023290226801.

Langeland, A., L'Abee-Lund, J.H., Jonsson, B., and Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. J. Anim. Ecol. **60**: 895–912. doi:10.2307/5420.

Lu, G., and Bernatchez, L. 1999. Correlated trophic specialization and genetic divergence in sympatric lake whitefish ecotypes (*Coregonus clupeaformis*): support for the ecological speciation hypothesis. Evolution, **53**: 1491–1505. doi:10.2307/2640895.

Maekawa, K., Hino, T., Nakano, S., and Smoker, W.W. 1993. Mate preference in anadromous and landlocked Dolly Varden (*Salvelinus malma*) females in two Alaskan streams. Can. J. Fish. Aquat. Sci. **50**(11): 2375–2379. doi:10.1139/f93-261.

May-McNally, S.L., Quinn, T.P., and Taylor, E.B. 2015a. Low levels of hybridization between sympatric Arctic char (*Salvelinus alpinus*) and Dolly Varden char (*Salvelinus malma*) highlights their genetic and spatial distinctiveness. Ecol. Evol. **5**: 3031–3045. doi:10.1002/ece3.1583. PMID:26356310.

May-McNally, S.L., Quinn, T.P., Woods, P.J., and Taylor, E.B. 2015b. Evidence for genetic distinction among sympatric ecotypes of Arctic char (*Salvelinus alpinus*) in south-western Alaskan lakes. Ecol. Freshw. Fish, **24**: 562–574. doi:10.1111/eff.12169.

Mazur, M.M., and Beauchamp, D.A. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environ. Biol. Fishes, **67**: 397–405.

McPhail, J.D. 1961. A systematic study of the *Salvelinus alpinus* complex in North America. J. Fish. Res. Board Can. **18**(5): 793–816. doi:10.1139/f61-053.

Mecklenburg, C.W., Mecklenburg, T.A., and Thorsteinson, L.K. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Md.

Merritt, R.W., and Cummins, K.W. 2008. An introduction to the aquatic insects of North America. Kendall Hunt Publishing Co., Dubuque, Ia.

Miller, J.A., and Kent, A.J.R. 2009. The determination of maternal run time in

juvenile Chinook salmon (*Oncorhynchus tshawytscha*) based on Sr/Ca and Sr-87/Sr-86 within otolith cores. Fish. Res. **95**: 373–378. doi:10.1016/j.fishres.2008.09.030.

Mills, J.S., Dunham, J.B., Reeves, G.H., McMillan, J.R., Zimmerman, C.E., and Jordan, C.E. 2012. Variability in expression of anadromy by female *Oncorhynchus mykiss* within a river network. Environ. Biol. Fishes, **93**: 505–517. doi:10.1007/s10641-011-9946-4.

Mookerji, N., Weng, Z., and Mazumder, A. 2004. Food partitioning between coexisting Atlantic salmon and brook trout in the Sainte-Marguerite River ecosystem, Quebec. J. Fish Biol. **64**: 680–694. doi:10.1111/j.1095-8649.2004.00333.x.

Moore, M.E., Goetz, F.A., Van Doornik, D.M., Tezak, E.P., Quinn, T.P., Reyes-Tomassini, J.J., and Berejikian, B.A. 2010. Early marine migration patterns of wild coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. PLoS ONE, **5**: e12881. doi:10.1371/journal.pone.0012881. PMID:20862225.

Muir, W.D., and Emmett, R.L. 1988. Food habits of migrating salmonid smolts passing Bonneville Dam in the Columbia River, 1984. Regul. Rivers Res. Manage. **2**: 1–10. doi:10.1002/rrr.3450020102.

Nakano, S., Fausch, K.D., Furukawa-Tanaka, T., Maekawa, K., and Kawanabe, H. 1992. Resource utilization by bull char and cutthroat trout in a mountain stream in Montana, U.S.A. Jpn. J. Ichthyol. **39**: 211–217. doi:10.1007/BF02905478.

Näslund, I. 1990. The development of regular seasonal habitat shifts in a landlocked Arctic charr, *Salvelinus alpinus* L., population. J. Fish Biol. **36**: 401–414. doi:10.1111/j.1095-8649.1990.tb05620.x.

Nilsson, N.-A. 1960. Seasonal fluctuations in the food segregation of trout, char, and whitefish in 14 north-Swedish lakes. Rep. Freshw. Inst. Drottingholm, **41**: 185–202.

Nosil, P., Vines, T.H., and Funk, D.J. 2005. Reproductive isolation caused by natural selection against immigrants from divergent habitats. Evolution, **59**: 705–719. doi:10.1111/j.0014-3820.2005.tb01747.x. PMID:15926683.

Nummi, P., and Väänänen, V.M. 2001. High overlap in diets of sympatric dabbling ducks — an effect of food abundance? Ann. Zool. Fenn. **38**: 123–130.

Pess, G.R.,., Quinn, T.P., Schindler, D.E., and Liermann, M.C. 2014. Freshwater habitat associations between pink (*Oncorhynchus gorbuscha*), chum (*O. keta*), and Chinook salmon (*O. tshawytscha*) in a watershed dominated by sockeye salmon (*O. nerka*) abundance. Ecol. Freshw. Fish, **23**: 360–372. doi:10.1111/eff.12088.

Peterson, D.P., and Foote, C.J. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. Trans. Am. Fish. Soc. **129**: 924–934. doi:10.1577/1548-8659(2000)129<0924:DOSSHB>2.3.CO;2.

Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? Am. Nat. **123**: 541–564. doi:10.1086/284221.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**: 223–225. doi:10.2307/2409177.

Riva-Rossi, C., Pascual, M.A., Babaluk, J.A., Garcia-Asorey, M., and Haldenk, N.M. 2007. Intra-population variation in anadromy and reproductive life span in rainbow trout introduced in the Santa Cruz River, Argentina. J. Fish Biol. **70**: 1780–1797. doi:10.1111/j.1095-8649.2007.01449.x.

Ross, S.T. 1986. Resource partitioning in fish assemblages: a review of field studies. Copeia, **1986**: 352–388. doi:10.2307/1444996.

Ruggerone, G.T., and Rogers, D.E. 1984. Arctic char predation on sockeye salmon smolts at Little Togiak River, Alaska. Fish. Bull. (Wash., D.C.), **82**: 401–410.

Ruttenberg, B.I., Hamilton, S.L., Hickford, M.J., Paradis, G.L., Sheehy, M.S., Standish, J.D., Ben-Tzvi, O., and Warner, R.R. 2005. Elevated levels of trace elements in cores of otoliths and their potential for use as natural tags. Mar. Ecol. Prog. Ser. **297**: 273–281. doi:10.3354/meps297273.

SAS Institute, Inc. 2010. JMP®. Version 9.0.2 [computer program]. SAS Institute Inc., Cary, N.C.

Scharf, F.S., Juanes, F., and Rountree, R.A. 2000. Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar. Ecol. Prog. Ser. **208**: 229–248. doi:10.3354/meps208229.

Schluter, D. 1995. Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth. Ecology, **76**: 82–90. doi:10.2307/1940633.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, New York.

Schluter, D. 2001. Ecology and the origin of species. Trends Ecol. Evol. **16**: 372–380. doi:10.1016/S0169-5347(01)02198-X. PMID:11403870.

Schoener, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology, **51**: 408–418. doi:10.2307/1935376.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science, **185**: 27–39. doi:10.1126/science.185.4145.27. PMID:17779277.

Schutz, D.C., and Northcote, T.G. 1972. An experimental study of feeding behavior and interaction of coastal cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). J. Fish. Res. Board Can. **29**(5): 555–565. doi:10.1139/f72-092.

Shelford, V.E. 1911. Ecological succession. I. Stream fishes and the method of physiographic analysis. Biol. Bull. (Woods Hole), **21**: 9–35. doi:10.2307/1535983.

Snorrason, S.S., Skulason, S., Jonsson, B., Malmquist, H.J., Jonasson, P.M., Sandlund, O.T., and Lindem, T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus*

(Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. Biol. J. Linn. Soc. **52**: 1–18. doi:10.1111/j.1095-8312.1994.tb00975.x.

Svanbäck, R., and Bolnick, D.I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. Proc. R. Soc. B Biol. Sci. **274**: 839–844. doi:10.1098/rspb.2006.0198.

Taylor, E.B. 2016. The Arctic char (*Salvelinus alpinus*) "complex" in North America revisited. Hydrobiologica. [Published online Dec. 2015.] doi:10.1007/s10750-015-2613-6.

Taylor, E.B., and Foote, C.J. 1991. Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). J. Fish Biol. **38**: 407–419. doi:10.1111/j.1095-8649.1991.tb03130.x.

Taylor, E.B., Lowery, E., Lilliestråle, A., Elz, A., and Quinn, T.P. 2008. Genetic analysis of sympatric char populations in western Alaska: Arctic char (*Salvelinus alpinus*) and Dolly Varden (*Salvelinus malma*) are not two sides of the same coin. J. Evol. Biol. **21**: 1609–1625. doi:10.1111/j.1420-9101.2008.01603.x. PMID:18771450.

Taylor, E.B., Gerlinsky, C., Farrell, N., and Gow, J.L. 2012. A test of hybrid growth disadvantage in wild, free-ranging species pairs of threespine stickleback (*Gasterosteus aculeatus*) and its implications for ecological speciation. Evolution, **66**: 240–251. doi:10.1111/j.1558-5646.2011.01439.x. PMID:22220878.

Van Valen, L. 1965. Morphological variation and width of ecological niche. Am. Nat. **99**: 377–390. doi:10.1086/282379.

Wallace, R.K., Jr. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. **110**: 72–76. doi:10.1577/1548-8659(1981)110<72:AAODI>2.0.CO;2.

Wankowski, J.W.J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. J. Fish Biol. **14**: 89–100. doi:10.1111/j.1095-8649.1979.tb03498.x.

Woods, P.J., Young, D., Skúlason, S., Snorrason, S.S., and Quinn, T.P. 2013. Resource polymorphism and diversity of Arctic charr *Salvelinus alpinus* in a series of isolated lakes. J. Fish Biol. **82**: 569–587. doi:10.1111/jfb.12011. PMID:23398069.

Zimmerman, C.E., and Reeves, G.H. 2000. Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry. Can. J. Fish. Aquat. Sci. **57**(10): 2152–2162. doi:10.1139/f00-192.

Zimmerman, C.E., and Reeves, G.H. 2002. Identification of steelhead and resident rainbow trout progeny in the Deschutes River, Oregon, revealed with otolith microchemistry. Trans. Am. Fish. Soc. **131**: 986–993. doi:10.1577/1548-8659(2002)131<0986:IOSARR>2.0.CO;2.

Zimmerman, C.E., Edwards, G.W., and Perry, K. 2009. Maternal origin and migratory history of steelhead and rainbow trout captured in rivers of the Central Valley, California. Trans. Am. Fish. Soc. **138**: 280–291. doi:10.1577/T08-044.1.