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BRIEF COMMUNICATION

Gill raker and pyloric caeca counts differ between Arctic char (*Salvelinus alpinus*) and Dolly Varden (*S. malma*) populations across their ranges

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Abstract

Meristic characters are often used to differentiate between closely related forms, morphs, and species of fishes, and lend insight into ecology and post-glacial recolonization in taxa with complicated or contentious phylogenies, including the genus *Salvelinus*. Previous studies of meristics in *Salvelinus* have focused mostly on individual populations. We collated data from 456 populations/systems across the North American and Russian Arctic and sub-Arctic, and found that counts of pyloric caeca and gill rakers differed consistently between fish visually and/or genetically identified as Arctic char and Dolly Varden across their distributional ranges.

KEYWORDS
meristics, *Salvelinus alpinus*, *Salvelinus malma*, species differentiation

For over a century, scientists have used meristics—countable characteristics—to differentiate between different forms and species of fishes (Fowler, 1970; Jordan & Gilbert, 1882). Meristic characters can be affected by genetics and/or the environment, and commonly analysed characters include fin [branchiostegal] rays, vertebrae, scales along the lateral line, gill rakers, and pyloric caeca (Fowler, 1970). Even after the advent and widespread application of genetic techniques to study inter- and intraspecific differences between and among closely related species, analyses of meristic characters remain an effective and efficient—in terms of both time and cost—method to investigate differences among species, morphs, forms, and life-history types of highly diverse fishes, such as chars (*Salvelinus* spp.). Analyses of meristic characters can be conducted in the field or lab without any elaborate equipment and with minimal training, and are thus accessible to community partners and researchers working in remote locations, such as the Arctic.

Within the genus *Salvelinus*, meristic characters have long been used in attempts to differentiate Dolly Varden (*Salvelinus malma*) from bull trout (*Salvelinus confluentus*) in British Columbia, and to differentiate Arctic char (*Salvelinus alpinus*) from Dolly Varden in Alaska and Russia (Behnke, 1980; Behnke, 1984; DeLacy & Morton, 1943; McPhail, 1961; Morrow, 1980; Reist & Sawatzky, 2010). Given the

Meristic characters have long been used to differentiate forms, morphs, and species of chars (*Salvelinus* spp.), including the closely related Arctic char (*S. alpinus*) and Dolly Varden (*S. malma*). We collated existing data to investigate differences in pyloric caeca and gill raker counts over the distributional ranges of both species. An analysis of 456 populations and time points found that meristic characters differed consistently between fish visually and/or genetically identified as Arctic char and Dolly Varden.

complicated taxonomy of *Salvelinus* fishes and because individual meristic counts can overlap between Arctic char and Dolly Varden, researchers have long debated (i) the validity of considering Dolly Varden a distinct species and (ii) whether and which meristic characters could be used to effectively and consistently differentiate between the two species (e.g., Barsukov, 1960; Behnke, 1980; Savvaitova, 1980). Reist et al. (1997) showed that, when analysed together, total gill raker counts (i.e., the total number of gill rakers along the first gill arch) and pyloric caeca counts could effectively and consistently distinguish Arctic char from Dolly Varden in the western and central North American Arctic; Dolly Varden tended to have lower gill raker and pyloric caeca counts than Arctic char in the studied region. As gill rakers and pyloric caeca are involved in feeding and digestion, this variation could point to interspecific differences in prey preference. In addition to differentiating between closely related *Salvelinus* species, researchers have also used meristics in efforts to differentiate among sympatric forms, morphs, and life-history types of both Arctic char and Dolly Varden within systems and populations across their ranges (e.g., Alekseyev et al., 2013; Alekseyev et al., 2014; Alekseyev et al., 2019; Hesthagen et al., 1995).

There has been long-standing and widespread interest in the use of meristics to investigate phylogenetic and ecological relationships and char diversity within the Arctic char species complex, and in studies of the broader "char problem" (i.e., the intraspecific diversity char populations display over limited geographic areas; Klemetsen, 2010; Skreslet, 1973). Most individual studies have analysed meristic characters in char species over a geographic range that is limited relative to the overall species' distributions (see Table S1), though previous researchers have attempted to collate and analyse meristic data from different geographic areas (e.g., Alekseyev et al. 2000; Gordeeva et al., 2021; Savvaitova & Volobuyev, 1978). Building on this previous work, we identified a need to incorporate more recently published data, previously unpublished data, and older published data from a broader geographic area than had been included in previous collation efforts. Consequently, our objective was to investigate differences in meristic characters over the distributional ranges of Arctic char and Dolly Varden; this work represents the most comprehensive range-wide assessment of meristic differences between the two species. As the distributions of, and interactions between, Arctic char and Dolly Varden are changing in response to climate change and many populations inhabit remote systems where advanced technologies are unavailable, the need to accurately and consistently identify and differentiate the species using accessible, effective, and inexpensive techniques is, and will continue to be, highly relevant for conservation and management of critically important char fisheries.

We searched Web of Science, Google Scholar, and Canada's Federal Science Libraries Network for papers that reported both total gill raker and pyloric caeca counts for one or more populations of Arctic char and/or Dolly Varden. We used the search strings "('Arctic char*' OR 'Dolly Varden') AND ('gill raker*' AND caeca)"; "'Arctic char*' AND 'meristics'"; and "'Dolly Varden' AND 'meristics.'" We also searched the references of resulting papers for any literature that may have been missed in initial searches. Additionally, we collated data from published books, such as *Charrs: Salmonid fishes of the genus* Salvelinus (Balon & Penczak, 1980). Only papers published in English or translated into English were included. Papers were excluded if mean counts of both total gill rakers and pyloric caeca were not provided or could not be calculated, including if only upper or lower gill raker counts were presented. After screening, 47 papers published between 1943 and 2024 were included; some of these papers included data from previously published works. We also included previously unanalysed data collected by Fisheries and Oceans Canada and by the authors between 1987 and 2020 (CPG, 2002, 2004, 2017, 2018, 2019; HKS, 2006; SYW and community research assistants, 2019 and 2020). For data collected by the authors, pyloric caeca were counted by separating and removing each from the cecal mass, and all gill rakers, including rudimentary rakers, along the first left gill arch were counted. For fish sampled in Kugluktuk, Nunavut, in 2019 and 2020, the care and use of experimental animals complied with animal welfare laws, guidelines, and policies as approved by University of Waterloo Animal Use Protocol #30071. All char were caught by subsistence fishers, and following scientific sample collection, fish were returned to the subsistence fishers for consumption. Data included in this analysis represent average (at the level of the population) gill raker and pyloric caeca counts that were collated and/or calculated (from raw data) for 456 populations (Table S1). Study systems and water bodies are represented more than once if multiple papers were published on the system, or if average values were provided for multiple years.

Char included in the analysis were coded as either Arctic char or Dolly Varden based on designations used in the original papers, with some important exceptions. Prior to 1980, char populations located as far south as the lower Kuskokwim River, Alaska, and extending north and east to the lower Mackenzie River basin, Canada, were classified as western Arctic-Bering Sea Arctic char. These char, however, overlapped morphologically and ecologically with the northern form Dolly Varden (McPhail, 1961; Morrow, 1980). Species classifications presented in papers published before 1980 were thus examined and, where appropriate, species were reclassified (Table S1) based on currently accepted criteria, as per Morrow (1980). Some researchers through the mid-20th century also believed that Dolly Varden were synonymous with and/or a subspecies of Arctic char (e.g., Barsukov, 1960), meaning that species designations in the original papers were often convoluted; in those cases, subsequently published literature on char from the same systems was assessed to determine the species designation of the population in question. We also removed populations identified as Dolly Varden that may actually be bull trout (e.g., populations included in McPhail [1961] that should be reclassified based on Cavender [1978]). Additionally, in areas supporting multiple forms of char, or with taxonomically unresolved populations, researchers often used meristic characters to identify individuals to the species level (e.g., Behnke, 1972; McPhail, 1961); this would result in circularity in our analyses. We thus cross-checked the species designations of those populations with more recently published literature that included non-meristic information, and ensured that, to the best of our knowledge, classifications aligned with

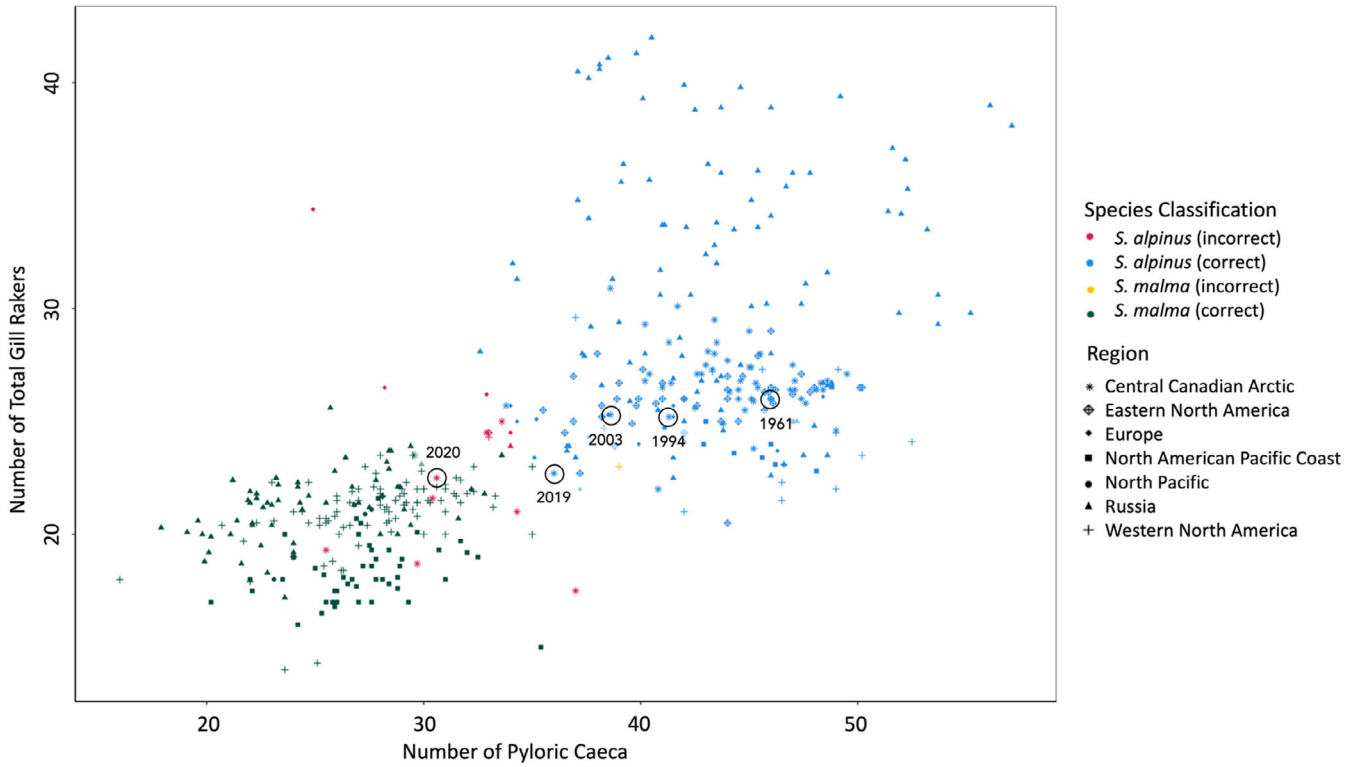

FIGURE 1 Average gill raker and pyloric caeca counts for 456 Arctic char and Dolly Varden populations across several geographic regions. Symbol colors represent correct or incorrect linear discriminant function analysis (LDA) classification. Five years of data for the Coppermine River are circled; these data suggest a shift in *Salvelinus* species composition in the system over time.

currently accepted designations. We recognize that there is ongoing scientific debate about whether Arctic char and Dolly Varden can validly be considered two species; this analysis, however, is founded on conventional species designations used in the current literature.

Using the R package "MASS" and IBM SPSS Statistics (version 29.0.2.0), we performed a linear discriminant function analysis (LDA) using the two meristic characters of interest—total gill raker counts and pyloric caeca counts—as independent variables, and species classification as the dependent variable. To evaluate the efficacy of using the meristic characters to differentiate between the two species, we also calculated the misclassification rate. To investigate whether the ability to discriminate between Arctic char and Dolly Varden using counts of pyloric caeca and total gill rakers varies among regions, LDA analyses were performed on the full dataset and on data subsets for the following regions: (i) central Canadian Arctic (Mackenzie River, NT, east to Cambridge Bay, NU); (ii) eastern North America (east of Cambridge Bay, NU); (iii) North Pacific; (iv) Europe; (v) Russia; (vi) western North America (north of the Alaska Peninsula and east to the Mackenzie River); and, (vii) North American Pacific Coast (Alaska Peninsula and south).

Consistent with Reist et al. (1997), we found distinct clustering between populations of Arctic char and Dolly Varden when using counts (arithmetic means for each population/system) of both total gill rakers along the first left gill arch and pyloric caeca (Figure 1). In North America, northern form Dolly Varden (*S. m. malma*; "western North America" and "central Canadian Arctic") and southern form Dolly Varden (*S. m. lordi*; "North American Pacific Coast") also appear to be meristically distinct, with southern form Dolly Varden displaying fewer gill rakers along the first left gill arch (Figure 1; Table S1). The two Asian forms of Dolly Varden (*S. m. kraschenninnikovi*/*S. m. curilus* and *S. malma*; Table S1) also appear to be distinct from each other, with *S. m. kraschenninnikovi*/*S. m. curilus*, the southern Asian Dolly Varden, displaying fewer pyloric caeca than *S. malma* individuals (Esin, 2015; Pichugin et al., 2008).

The majority of populations represented in this analysis are from Arctic and sub-Arctic North America and Russia; the searches we employed yielded data from comparatively few ($n = 17$) European char populations, only one of which was from a non-Norwegian system (Dösener Lake; Balon & Penczak, 1980). Although additional studies conducted on European Arctic char populations have presented meristic data, no others captured by our search included both gill raker and pyloric caeca data, instead including alternative characteristics, such as the number of branchiostegal rays (e.g., Doherty & McCarthy, 2004).

Perhaps the most interesting system for which we have meristic data is the Coppermine River in Nunavut, Canada. For this river, we were able to collate meristic data gathered in 1961 ("Bloody Falls"; McPhail, 1961), 1994, 2003, 2019, and 2020 (data provided and/or collected by authors; Figure 1; Table S1). In 1961, the mean meristic counts for *Salvelinus* captured from this river were situated within the

TABLE 1 Region-specific species classification accuracy using a linear discriminant function analysis applied to total gill raker and pyloric caeca counts that were averaged for populations.

Region	Number of populations	Number correctly classified	Percentage correctly classified
Central Canadian Arctic	61	53	86.9
Eastern North America	44	43	97.7
North Pacific	5	5	100
Europe	17	13	76.5
Russia	166	164	98.8
North American Pacific Coast	56	56	100
Western North America	107	105	98.1

Arctic char cluster (Figure 1). With each successive time point, however, the mean counts shift toward the cluster of fish that is meristically Dolly Varden (Figure 1; Table S1). This aligns with observations of fishers in the community of Kugluktuk (a hamlet located at the mouth of the Coppermine River) who report that they catch more Dolly Varden–like chars now than they did in previous decades (17 knowledge holders [harvesters and fishers] identified by Kugluktuk Hunters and Trappers Organization, Kugluktuk, NU, oral interviews, May 2022 and January 2023 [unpublished data]).

Results of the linear discriminant function analysis revealed that the combination of pyloric caeca and total gill raker counts correctly classified 96.3% of populations (439/456; LDA Axis 1 Wilks' $\lambda = 0.226$, $df = 2$, $p < 0.001$) relative to the classifications (sometimes updated to reflect current understanding, as detailed earlier) reported in original publications. One Dolly Varden population and 16 Arctic char populations were misclassified using pyloric caeca and gill raker counts (Figure 1). Though we sought to confirm the species identification of samples collected prior to 1980, this was difficult to achieve for populations that were not the focus of subsequent research. As such, it is possible that errors in the original species classifications of one char population each in Russia and western North America explain two of the misclassifications. The accuracy of classification also qualitatively varied among regions (Table 1). Four European populations were misclassified, as were eight populations from the central Canadian Arctic. The relatively high misclassification rate among char populations from the central Canadian Arctic is consistent with the observation that char diversity in the region is complex (Reist & Sawatzky, 2010). Continued work in systems and regions supporting sympatric Arctic char and Dolly Varden (i.e., systems in the central Canadian Arctic) should be performed to assess whether species identification using nuclear DNA, mtDNA, and meristics are aligned, or if there is evidence for introgression that has led to inconsistent results among methods. Additional future analyses, not limited to systems in the central Canadian Arctic and especially including representation of different regions in Russia, could link meristic data with phylogenetic data to further our understanding of meristic variability across phylogenetic lineages; this could provide insight into contemporary population dynamics, especially in systems that support multiple forms, morphs, or species of char.

In this analysis, we used meristic data that were averaged at the level of populations, and we acknowledge that this approach has limitations. Individuals within populations exhibit variability in gill raker and pyloric caeca counts. Variability will be greater and affect analyses and interpretations of mean data when Dolly Varden and Arctic char are sympatric. In the Coppermine River in the central Canadian Arctic, for example, previously published mtDNA data indicate that there are sympatric Arctic char and Dolly Varden in the system (Reist & Sawatzky, 2010). The presence of both species would not be captured with the population-level meristic data presented here, and may well have contributed to some of the misclassifications. Distribution and relative abundance of Dolly Varden in river systems in the central Canadian Arctic, including the Coppermine River, have previously been the subject of scientific discussion (Reist & Sawatzky, 2010), and our presentation of both historic and contemporary meristic population mean counts suggests that additional research on *Salvelinus* fishes in the region, using more advanced methods, is warranted. Given the information loss that comes with analysing population means, we caution against using the population mean data presented in this contribution to draw inferences about the species composition of a given population; to do that, individual-level meristic data or data collected from other analytical techniques must be used. The use of finer-scale meristic data remains highly relevant in the critical initial stages of examining diversity within and across systems and populations—especially given that the method can be easily applied anywhere by anyone—and initial hypotheses (e.g., that all char in a system are meristically the same and are the same species) can be further tested using additional independent methods, such as genomics.

This range-wide analysis of both Arctic char and Dolly Varden shows that the two species are largely distinct in their meristic characters across their distributional ranges, though there is variation among regions that may be driven by complex *Salvelinus* distributional patterns. Although both species display substantial intraspecific variation in population-level mean counts for the two meristic characters investigated (Figure 1; Table 1), Dolly Varden generally have fewer pyloric caeca and gill rakers than do Arctic char. Discussions around the diversity, phylogenetic history, and distribution of these two species are complex and can be contentious. We show that meristics represent a labor- and cost-efficient starting point for studying differences within contemporary populations and, if multiple years of data are

available, serve as a foundation for possible investigations of shifts and changes over time. This is especially relevant given the need for methods that allow for and facilitate community-based monitoring of subsistence fisheries in remote and underserviced northern communities.

AUTHOR CONTRIBUTIONS

TNL, JDR, CPG, and HKS provided archived data used in this work; SYW collected additional samples. SYW and HKS conceptualized this work, and conducted data analyses and performed data visualization. SYW wrote the original draft of this manuscript, which was reviewed and edited by HKS. All authors reviewed this manuscript and provided feedback.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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