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Distribution and Biology of Bull Trout (*Salvelinus confluentus*) in the Mackenzie Valley, Northwest Territories, with Notes on Sympatry with Dolly Varden (*Salvelinus malma*)

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ABSTRACT. Streams were surveyed along the Mackenzie Valley, Northwest Territories, to investigate the distribution and biology of riverine char. Bull trout (*Salvelinus confluentus*) were captured in 24 of 43 streams sampled from three watersheds: the Kotaneelee River, the South Nahanni River, and the Central Mackenzie Mountains. The first confirmed sympatric bull trout and Dolly Varden (*Salvelinus malma*) populations in the Northwest Territories are reported from the Gayna River (~65˚17′ N, 129˚21′ W). This location represents a geographical range extension for bull trout approximately 200 km northwest of the previous northernmost published location in the central Northwest Territories (~64˚30′ N and 125˚00′ W, Great Bear River). It also extends the geographical range of Dolly Varden south approximately 300 km from the closest known populations located in the Peel River basin. The identification of this geographic range expansion is a result of extending both our sampling range and our ability to identify riverine chars accurately. In bull trout, we observed two different growth patterns, which correspond to non-migratory and migratory life histories. Northern bull trout populations are relatively small and widespread, and they are separated from one another by large distances and in some cases by natural barriers. Although these populations share similar biological traits with their southern counterparts, the northern fish mature later and do not spawn as often, which increases their sensitivity to exploitation and other anthropogenic perturbations.

Key words: bull trout, *Salvelinus confluentus*, Dolly Varden, *Salvelinus malma*, Mackenzie River, riverine char, Gayna River, Northwest Territories

RÉSUMÉ. Des cours d'eau du long de la vallée du Mackenzie, dans les Territoires du Nord-Ouest, ont fait l'objet d'un relevé visant à étudier la répartition et la biologie des ombles fluviaux. Des ombles à tête plate (*Salvelinus confluentus*) ont été capturés dans 24 des 43 cours d'eau échantillonnés à partir de trois bassins hydrographiques : la rivière de Kotaneelee, la rivière Nahanni Sud et les monts Mackenzie centraux. Les premières populations sympatriques confirmées d'ombles à tête plate et de Dolly Varden (*Salvelinus malma*) dans les Territoires du Nord-Ouest proviennent de la rivière Gayna (~65˚17′ N, 129˚21′ O). Cet emplacement représente une extension de la portée géographique de l'omble à tête plate dans une mesure d'environ 200 kilomètres au nord-ouest de l'emplacement le plus au nord précédemment publié, dans le centre des Territoires du Nord-Ouest (~64˚30′ N et 125˚00′ O, rivière Great Bear). Les relevés ont également permis de constater que la portée géographique du Dolly Varden s'étend vers le sud, dans une mesure d'environ 300 kilomètres des populations connues les plus près, dans le bassin de la rivière Peel. Cette expansion de la portée géographique est attribuable à la fois à l'extension de notre aire d'échantillonnage ainsi qu'à notre aptitude à identifier les ombles fluviaux avec précision. Chez l'omble à tête plate, nous avons observé deux schémas de croissance différents, qui correspondent aux cycles biologiques non-migratoires et migratoires. Les populations d'ombles à tête plates du nord sont relativement petites et généralisées, et elles sont séparées les unes des autres par de grandes distances et, dans certains cas, par des barrières naturelles. Bien que ces populations possèdent des caractéristiques biologiques similaires à celles des populations d'ombles à tête plate du sud, celles du nord mûrissent plus vite et ne frayent pas aussi souvent, ce qui a pour effet de les rendre plus sensibles à l'exploitation et à d'autres perturbations anthropiques.

Mots clés : omble à tête plate, *Salvelinus confluentus*, Dolly Varden, *Salvelinus malma*, fleuve Mackenzie, omble fluvial, rivière Gayna, Territoires du Nord-Ouest

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INTRODUCTION

Our understanding of the biology for most fish populations from remote areas of northern Canada is poor (McPhail and Lindsey, 1970; Scott and Crossman, 1974), and lack of data is even more prevalent for populations at the northern extent of their range (Reist et al., 2002), which are separated geographically from those more centrally located in the distribution. These peripheral populations are considered to be most vulnerable to local extirpation because they often occupy marginal habitats; however, they warrant significant conservation efforts since they are expected to be genetically distinct from central populations (Lesica and Allendorf, 1995). Accurate knowledge of fish distributions and biology is important for effective management of peripheral populations, especially in areas with high risk of impacts from human activities.

Arctic char, *Salvelinus alpinus* (Linnaeus), bull trout, *Salvelinus confluentus* (Suckley), and Dolly Varden, *Salvelinus malma* (Walbaum), all occur north of the 60th parallel in North America, and both bull trout and Dolly Varden are at the northern extent of their range (McPhail and Lindsey, 1970; Scott and Crossman, 1974; DeCicco and Reist, 1999). In the past, these three species were often confused with one another because of their similar appearance (Behnke, 1980, 2002) and the lack of clear, easily applied field identification criteria (Reist et al., 2002). However, recent work has confirmed that Dolly Varden is a distinct species from Arctic char (Reist et al., 1997; Behnke, 2002; Taylor et al., 2008), and the southern group originally thought to be Dolly Varden is actually two distinct species: Dolly Varden and bull trout (Cavender, 1978; Haas and McPhail, 1991; Phillips et al., 1995; Reist et al., 2002).

Chars found across North America display a wide variety of migratory patterns. These include movements within a single stream (stream-resident; Jakobar et al., 1998), between rivers (fluvial; Hogan and Scarnecchia, 2006), between rivers and lakes (adfluvial; Watry and Scarnecchia, 2008), and between rivers or lakes and the sea (anadromy; Sandstrom and Harwood, 2002; Brenkman and Corbett, 2005). These migration patterns can be more broadly categorized into non-migratory and migratory life history strategies, with the former corresponding to stream-resident populations and the latter to fluvial, adfluvial, and anadromous populations. Migratory fish grow faster than non-migratory fish and are larger once sexually mature (Adams, 1994; Boag and Hvenegaard, 1997; Reist et al., 1997; Spangler, 1997; Swanberg, 1997; Johnston et al., 2007).

Bull trout is a char indigenous to western North America, inhabiting cold, clear, high-gradient mountain streams. Anadromous populations occur in streams across the northwestern United States (~42˚ N) and British Columbia. Inland populations, which include fluvial and adfluvial life history types, are distributed within interior drainages of western Alberta, British Columbia, the southern Yukon, and the Mackenzie River Valley in the Northwest Territories (Haas and McPhail, 1991; Reist et al., 2002; Fig. 1).

Dolly Varden populations are found primarily in coastal and inland rivers across British Columbia, the Yukon Territory, Alaska, and the Northwest Territories (Lee et al., 1980; Reist et al., 1997; Fig. 1). Populations occupying lakes are not as common as the fluvial type (McPhail, 1961; McCart, 1980; Morrow, 1980; Reist et al., 1997). Dolly Varden is now formally recognized as two subspecies in North America: a southern form (*S. malma lordi*) and a northern form (*S. malma malma*), which can be differentiated from one another by gill raker counts, vertebral number, and genetic analyses (Behnke, 1980; Phillips et al., 1999). The southern form is distributed along the Pacific coast from Washington to the Gulf of Alaska and the extreme southwestern Yukon Territory, whereas the northern form occurs from the north side of the Alaskan Peninsula and the Aleutian Islands north to the Mackenzie River in Canada (DeCicco and Reist, 1999).

Both bull trout and Dolly Varden exhibit migratory and non-migratory life histories; however, individuals from all populations grow slowly, mature late, and do not always spawn in consecutive years (McPhail and Baxter, 1996; Reist et al., 1997). These biological characteristics make both species sensitive to anthropogenic impacts and environmental perturbations (Baxter and McPhail, 1996; Reist et al., 1997; Baxter et al., 1999; Ripley et al., 2005). Impacts contributing to the decline of bull trout populations in the southern portion of the range include over-harvesting, fragmentation and isolation of populations by both natural (e.g., unsuitable habitat) and man-made structures, habitat loss caused by industrial development, interaction with exotic species, exposure to contaminants, and the cumulative effects of these activities (Ford et al., 1995; Baxter et al., 1999; Hansen et al., 2002a, b; Palace et al., 2004; Ripley et al., 2005). Similarly, exploitation and changes to habitat are suspected as primary factors responsible for the decline of northern Dolly Varden populations (Sandstrom and Harwood, 2002; Stewart et al., 2010). As a result of these declines, the Committee on the Status of Endangered Wildlife in Canada assessed both the Alberta-Northwest Territories unit of bull trout and the Yukon-Northwest Territories unit of Dolly Varden as "Special Concern" (COSEWIC, 2011, 2012).

With development activities continuing at a rapid pace in the Northwest Territories (Cott et al., 2008), fish habitat could be compromised, which suggests the need to improve our understanding of the distribution and biology of riverine chars in this area. Several self-sustaining bull trout populations have been documented in the Northwest Territories at the northern extent of their range (Reist et al., 2002). Given that few of these remote areas have been disturbed (e.g., minimal harvest or development) or properly surveyed, we suspect that other populations exist. The objectives of this work are to 1) update the distribution of bull trout and Dolly Varden in the Northwest Territories, 2) describe the life history and biology of bull trout and Dolly Varden populations found in this area, and 3) describe the contact region for these two species, including confirmation of strict sympatry.

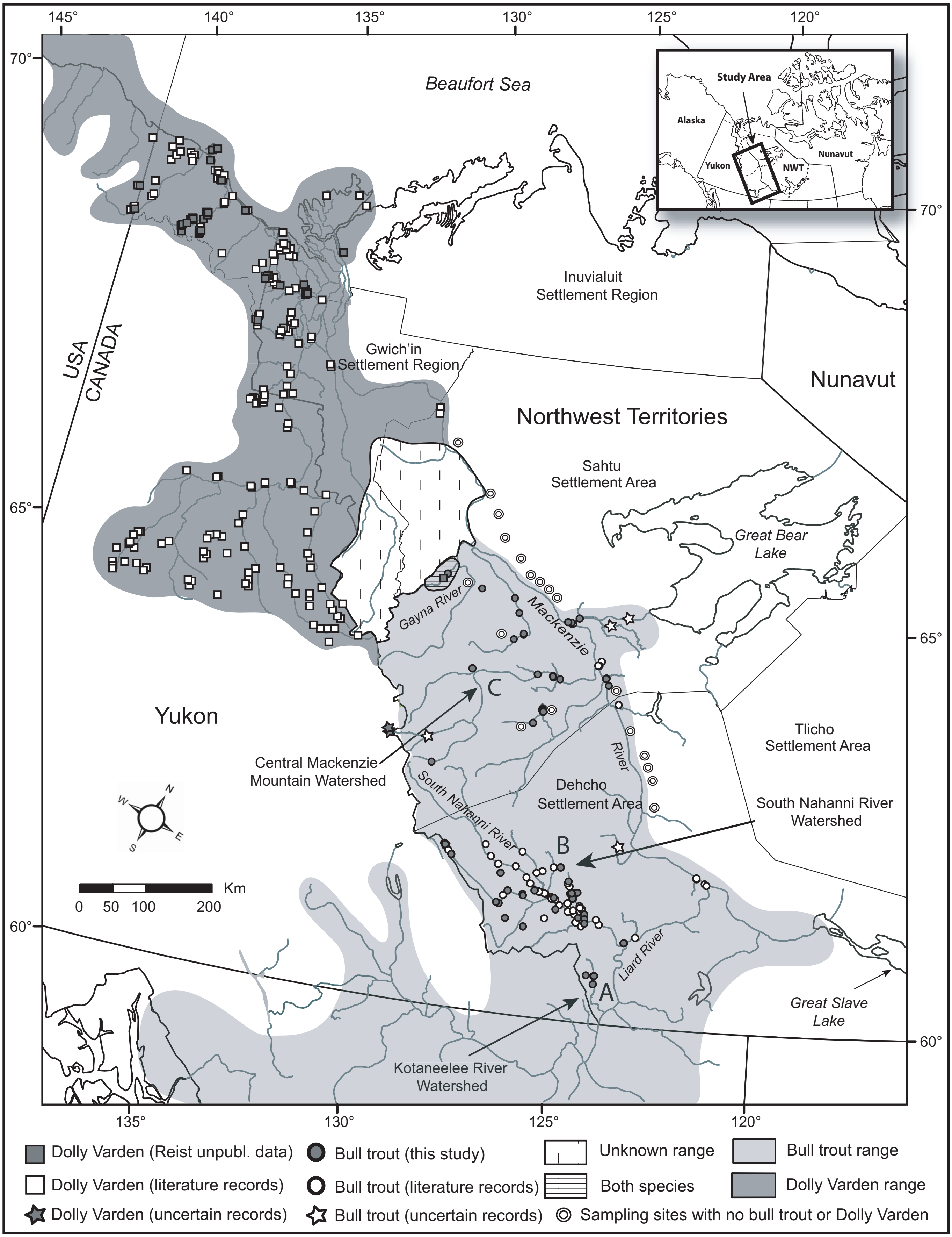

FIG. 1. Distribution of bull trout and northern Dolly Varden, showing new records from this study and point distributions from known and uncertain literature records. General distributions follow drainage basins and thus may be inaccurate, but they include accurate known point distributions. Only partial drainages are shown.

MATERIALS AND METHODS

Study Area

The Mackenzie River is the largest north-flowing river in North America, draining one-fifth of Canada's landmass (1.8 million km^2), with a mean annual flow of approximately 10 000 m^3/s (Rosenberg and Barton, 1986). Freshwater and anadromous fish use the Mackenzie River for feeding, overwintering, and as a migration corridor to access spawning tributaries in the spring or fall (Hatfield et al., 1972; Dryden et al., 1973). Resident fish populations, which carry out their entire life cycle in one stream, are found in many tributaries of the Mackenzie River (Dryden et al., 1973; Mochnacz et al., 2009a).

Tributaries to the Mackenzie River flow either year-round or seasonally, with peak discharge occurring after the spring freshet. Water levels decline throughout the summer and early fall, with some streams running dry by mid to late summer; however, fish may use these ephemeral streams seasonally for spawning, rearing, or feeding. Most tributaries in the central and upper Mackenzie Valley west of the Mackenzie River are high-gradient mountain streams that run clear after the spring freshet. This area, classified as the Taiga and Boreal Cordillera Ecoregion, has mean daily air temperatures between 16˚C and 17˚C in July and -24˚C and -30˚C in January (Ecosystem Classification Group, 2010). Discharge is lowest in the winter (Water Survey of Canada, 2011), which may last for up to eight months. During the winter, small tributaries (< 20 m wide) may freeze completely to the bottom; however, larger rivers and tributaries with perennial groundwater springs have sections that are ice-free or have floating ice (Prowse et al., 2006). Groundwater is prevalent in many streams found across this area and provides thermal refugia for cold-water species in the summer and winter (N.J. Mochnacz, unpubl. data). During the open-water season, water temperatures can be as low as 3.6˚C and as high as 17.7˚C; however, they do not exceed 10˚C in most spring-fed mountain streams (Mochnacz et al., 2004, 2009a, b). Stream discharge is governed primarily by snowmelt in the spring and precipitation during the open-water season, but groundwater also contributes to base flow throughout the year.

Fish Sampling

Sampling took place during the summer and fall from 2000 to 2008. A total of 43 streams were surveyed from the Kotaneelee River watershed, South Nahanni River watershed, and Central Mackenzie Mountains watershed (A, B, and C on Fig. 1). Sampling locations were selected on the basis of literature reports, local knowledge of char in the area, and the presence of suitable habitat. Tributaries of main-stem rivers and lakes were stratified into lower, middle, and upper sections according to stream elevation. We assumed that similar gradients within a stream provided homogenous habitat for fish. In each section, randomly selected reaches (200 – 500 m) were electrofished in an upstream fashion using a Smith-Root Type VII POW backpack electrofisher. Streams that were too deep to walk across were fished using barbless hooks, setlines, and gill nets. Barbless hooks were used to minimize injuries to fish that were released. A combination of live-sampling and limited dead-sampling was conducted to minimize impacts on populations.

Live Sampling

Each fish was identified to species using key external characteristics (Cavender, 1978; Haas and McPhail, 1991; Reist et al., 2002). Fork length (mm) and weight (g) were recorded, and sex and maturity were determined where possible. All bull trout and Dolly Varden larger than 200 mm were tagged with an individually numbered T-bar tag to gather information on growth and movement. Tags were inserted at the base of the dorsal fin between the posterior basal pterygiophores. A portion of the adipose fin was removed and stored in a 20% dimethyl sulfoxide/salt solution for genetic analysis and to evaluate tag loss. The first fin ray was removed from the left pelvic fin to evaluate the suitability of this structure for non-lethal age determination.

Fish were classified as juveniles or adults and assigned a life history (non-migratory, migratory) on the basis of capture location (e.g., river, lake, headwater stream), general body size, general body form, non-spawning color, the presence of parr marks, and sexual maturity.

Dead Sampling

Of the char captured (n = 289), 130 were sacrificed, frozen whole in the field, and transported to the Freshwater Institute Laboratory in Winnipeg for biological processing, which included meristic counts and morphometric measurements as per Reist et al. (1997), age determination from whole and sectioned otoliths as per Secor et al. (1992), sex and maturity determination as per McGowan (1992), and stomach content analyses. Fish were initially sorted into two groups: small fish (< 400 mm) and large fish (≥ 400 mm). Individuals were then subdivided into juvenile, non-migratory, migratory, and unknown categories using the following qualitative criteria: capture location (i.e., lake, river, headwater stream), general body size, dorsal and ventral non-spawning body color, presence of parr marks, and sexual maturity. A subset of these char (n = 89) was selected to confirm species identity using qualitative morphological characters and a linear discriminant function (LDF) (Haas and McPhail, 1991). The LDF is based on three morphometric and meristic characters: total branchiostegal ray count, principal anal ray count, and the ratio of upper jaw length to standard length.

Genetic Analysis

Assays using seven genetic markers diagnostic for bull trout and Dolly Varden were used to confirm the identity of all chars that were captured and to evaluate agreement between fish identifications from genetic data and those from morphological data. DNA was extracted from adipose fins, using commercial kits (DNeasy® Blood and Tissue Kit; Qiagen Inc.) according to manufacturer's instructions. The left domain of the mitochondrial DNA (mtDNA) control region was examined to identify collected specimens to species. Sequencing of 500 bp of the left domain of the mtDNA control region was performed as per Alekseyev et al. (2009). Although mtDNA is haploid, maternally inherited in most species, and susceptible to introgression between closely related species (Bernatchez et al., 1995; Wilson and Bernatchez, 1998; Redenbach and Taylor, 2002), it is capable of providing genetic information that can identify the direction of hybridization, if present.

Growth hormone 2 (GH2) and the first internal transcribed spacer region (ITS1) of the ribosomal DNA were also used to distinguish between bull trout and Dolly Varden. The GH2 assay (Taylor et. al., 2001; Redenbach and Taylor, 2002) genetically differentiates bull trout from Dolly Varden through a detectable length difference of the polymerase chain reaction (PCR) amplification product based on an indel mutation within the intron region. The ITS1 assay (Baxter et al., 1997) makes use of the presence of a diagnostic restriction site sequence, recognized by the restriction enzyme *SmaI* (Pleyte et al., 1992; Baxter et al., 1997), that is present in bull trout but absent in Dolly Varden. Specimens that display fragment patterns consistent with both Dolly Varden and bull trout can then be identified as hybrids. The restriction enzymes *Bsu36I* or *HpyCH4V*, with recognition sequences present in Dolly Varden but absent in bull trout (Pleyte et al., 1992), were used to confirm the results from the *SmaI* digest and detect interpretation errors potentially due to incomplete digestion. A survey of all bull trout in this study and of the northern form of Dolly Varden from several locations across the Alaskan North Slope and entire Canadian distribution confirmed the utility of *Bsu36I* and *HpyCH4V* for discrimination between the two species (data not shown).

Four microsatellite loci that are diagnostic for differentiating between Dolly Varden and bull trout (*Sco214,* Dehaan and Ardren, 2005; *Smm3* and *Smm5*, Crane et al., 2004; and *Omy301*, Jackson et al., 1998; results not shown) were assayed for variation across all bull trout samples in the current study and for a subset of Dolly Varden across the known Yukon and Northwest Territories distribution (data not shown). PCR reactions were run using "tailed" primer pairs (Brownstein et al., 1996). PCR amplifications were carried out in a single 10 µL multiplex reaction containing approximately 50 ng DNA, consisting of 0.20 µM each *Sco214* forward and reverse primer, 0.16 µM *Smm3*, 0.12 µM *Smm5*, 0.40 µM *Omy301*, 200 µM each dNTP, 1.5 mM MgCl2, 1X GeneAmp 10X PCR Gold Buffer (Applied Biosystems, Foster City, CA), and 0.5 U AmpliTaq Gold® polymerase (Applied Biosystems, Foster City, CA). Cycling parameters included a single cycle of 95˚C for 5 minutes, followed by 35 cycles of 94˚C for 30 seconds, 55˚C for 30 seconds, and 72˚C for 45 seconds. A final extension at 72˚C for 30 minutes completed the amplification. PCR products were run on an Applied Biosystems ABI Prism® 3130xl genetic analyzer (Foster City, CA) and manually genotyped using Genemapper® Software version 3.7 (Applied Biosystems, Foster City, CA).

Samples were genetically identified as bull trout, Dolly Varden, or hybrid from the combined genetic profile present at the mitochondrial, ITS1, GH2, and microsatellite assays.

Of the seven markers examined, at least four were required for coarse classification of individuals (Boecklen and Howard, 1997). Samples were considered pure species if there was concurrence across markers. Hybrids were identified if any combination of diagnostic markers specific for bull trout and Dolly Varden was present in a single specimen.

Analyses

Size-at-age data from 130 char were used to compare growth between non-migratory and migratory groups. The growth curves for each group were fitted to the von Bertalanffy growth model (VBGM):

$$L_{(t)} = L_{\infty} (1\text{-}e^{-K(t-t_0)})$$

where $L_{(t)}$ is the estimated length at age t, L_{∞} is the asymptotic average maximum length, K is the body growth coefficient, and t_0 is the hypothetical age at age zero length (Jones, 2000). Analysis of residual sum of squares (Haddon, 2001) was used to determine whether there were any differences in growth between non-migratory and migratory groups. The Mann-Whitney U test was used to compare branchiostegal ray and principal anal fin ray counts between bull trout and Dolly Varden. The upper jaw length to standard length ratio and LDF scores were compared using two-sample independent t-tests. For all statistical tests significance was assessed at $\alpha < 0.05$.

RESULTS

Distribution

Bull trout were captured from 24 of 43 streams surveyed across the southern and central Northwest Territories (Table 1; Fig. 1).

In the Kotaneelee River watershed, 18 bull trout were captured from an unnamed creek flowing east to the Kotaneelee River (Table 1). Fish were caught approximately 14 km upstream near the headwaters of this unnamed creek and also at several sites in the lower reach near the confluence with the Kotaneelee River (Fig. 1).

In the South Nahanni River watershed, 146 bull trout were captured during the summer and fall. Most were from Funeral Creek (n = 88) and the Flat River (n = 33) while the remaining 25 fish were collected from various watercourses across the watershed (Table 1; Fig. 1).

TABLE 1. Total number of bull trout captured from the Northwest Territories (NT) by location with corresponding mean fork length and age and length distributions. The values of known bull trout populations are summarized from the available literature.

Location	Co-ordinates	Life history[1]	No.	Length Distribution (mm)	Mean Fork length in mm (SD)	Age distribution in years (median)
Canada and United States						
Various systems across the range	(~ 49–56˚N)	SR	–	140–410	–	–
		F	–	410–730	–	–
		AF	–	508–824	–	–
Kotaneelee River Watershed (NT)						
Unnamed Creek (Kotaneelee River)	60˚36.136′ N, 124˚01.311′ W	SR	18	202–400	286.4 (± 57.9)	7–9 (8)
South Nahanni Watershed (NT)						
Funeral Creek	61˚36.375′ N, 124˚44.123′ W	SR	88	35–370	152.6 (± 90.8)	0–11 (2)
Galena Creek	61˚32.433′ N, 124˚47.032′ W	SR	1	321	–	–
Jorgenson Creek	61˚31.466′ N, 126˚05.440′ W	SR	3	245–336	300.3 (± 48.6)	–
Marengo Creek	61˚35.321′ N, 125˚48.026′ W	SR	1	359	–	–
Prairie Creek	61˚36.293′ N, 124˚49.139′ W	SR	7	175–430	300.5 (± 104.2)	2–9 (5)
South Nahanni River	61˚14.578′ N, 124˚24.293′ W	SR	3	281–402	337 (± 60.9)	11
Flat River	61˚54.440′ N, 128˚05.880′ W	F	33	35–167	54.8 (± 28.5)	0–2 (0)
Irvine Creek	61˚45.161′ N, 126˚44.467′ W	F	3	243–626	441.7 (± 191.9)	5–12 (10)
South Nahanni River	61˚30.403′ N, 126˚05.073′ W	F	1	510	–	–
Mary River	61˚23.180′ N, 125˚11.716′ W	SR	1	309	–	9
Bennett Creek	61˚22.856′ N, 126˚41.931′ W	UK	1	344	–	–
Meilleur River	61˚07.676′ N, 125˚59.450′ W	UK	1	259	–	6
Wrigley Creek	61˚55.101′ N, 125˚59.450′ W	UK	1	226	–	5
Borden Creek	61˚23.342′ N, 126˚45.603′ W	SR	1	280	–	9
Lower Skinboat Creek	61˚12.046′ N, 126˚29.320′ W	UK	1	193	–	4
Central Mackenzie Mountains Watershed (NT)						
Unnamed Creek (Redstone River)	63˚39.001′ N, 126˚23.691′ W	F	2	576–605	590.5 (± 20.5)	16
Little Keele River	64˚42.566′ N, 126˚58.207′ W	F	1	603	–	12
Carcajou River	65˚19.000′ N, 127˚30.000′ W	F	6	472–662	573.2 (± 68.6)	6–14 (12)
Gayna River (reach 2)	65˚17.892′ N, 129˚21.340′ W	F	9	468–730	604.6 (± 85.6))	9–18 (14)
Keele River	64°14.593′ N, 125˚59.444′ W	F	14	432–636	534.5 (± 53.5)	9–10 (10)
Trout Creek	64˚11.691′ N, 126˚14.285′ W	F	2	432–594	513.0 (± 114.6)	9–14 (11)
Gayna River (reach 1)[2]	65˚17.455′ N, 129˚21.480′ W	SR	49	215–339	258.7 (± 27.9)	4–10 (7)
Gayna River (reach 2)[2]	65˚17.892′ N, 129˚21.340′ W	SR	2	248–378	313.0 (± 91.9)	8
Doris Lake outlet	65˚10.888′ N, 128˚19.162′ W	AF	1	487	–	9
O′Grady Lake outlet	63˚00.231′ N, 128˚59.861′ W	AF	9	294–825	537.4 (± 183.9)	6–18 (11)
Drum Lake outlet	63˚49.043′ N, 126˚11.084′ W	AF	30	49-711	548.2 (± 147.6)	1–18 (11)

[1] SR = stream-resident, F = fluvial, AF = adfluvial, UK = unknown.
[2] These fish are Dolly Varden.

In the Central Mackenzie Mountains watershed, 74 bull trout were captured. More than half were taken from three locations: Drum Lake (n = 30), O'Grady Lake (n = 9), and the Keele River (n = 14). The remaining 21 fish were collected from Doris Lake, Trout Creek, Carcajou River, Little Keele River, Gayna River, and an unnamed tributary of the Redstone River (Table 1).

In the Gayna River, 49 Dolly Varden were captured from a large pool below a set of impassable falls (> 15 m, Gayna River, reach 1; Table 1). Below this pool was a series of riffles extending 500 m, which then transitioned into a narrow canyon opening that created a hydraulic drop (~5 m). In the pool at the base of that canyon, we captured nine bull trout and two Dolly Varden (Gayna River, reach 2; Table 1). No char were captured upstream of the first set of impassable falls.

Identification

All "unknown" char retained from the field exhibited morphological features consistent with either bull trout or Dolly Varden. Of the 89 specimens that we analyzed using the LDF, genetic assays, and quantitative characters, 74 were identified as bull trout and 15 as Dolly Varden.

The LDF was used to confirm field identifications based on qualitative characters for "unknown" char (n = 89). The agreement rate between char identifications using the LDF and those using qualitative characters (field identification) was 95.5%. Four fish from Funeral Creek were identified as bull trout both in the field and using genetic analyses but scored as Dolly Varden using the LDF ([online] Appendix 1; Fish ID: 47332, 47335, 47263, 47264). These four fish had a median total branchiostegal ray count of 26. The median total branchiostegal ray count for all "unknown" char was consistent with reported values for either Dolly Varden or bull trout, but the principal anal ray count differed (Haas and McPhail, 1991; Fig. 2). Significant differences in total branchiostegal ray count (U = 120.0: $p = < 0.001$, Mann-Whitney U test) and linear discriminant scores ($t(87) = 11.747$, $p = < 0.001$, two-sample t-test) were detected between bull trout and Dolly Varden (Fig. 2).

Genetic analyses were successfully completed on 258 of the 289 char captured and revealed that 178 were bull

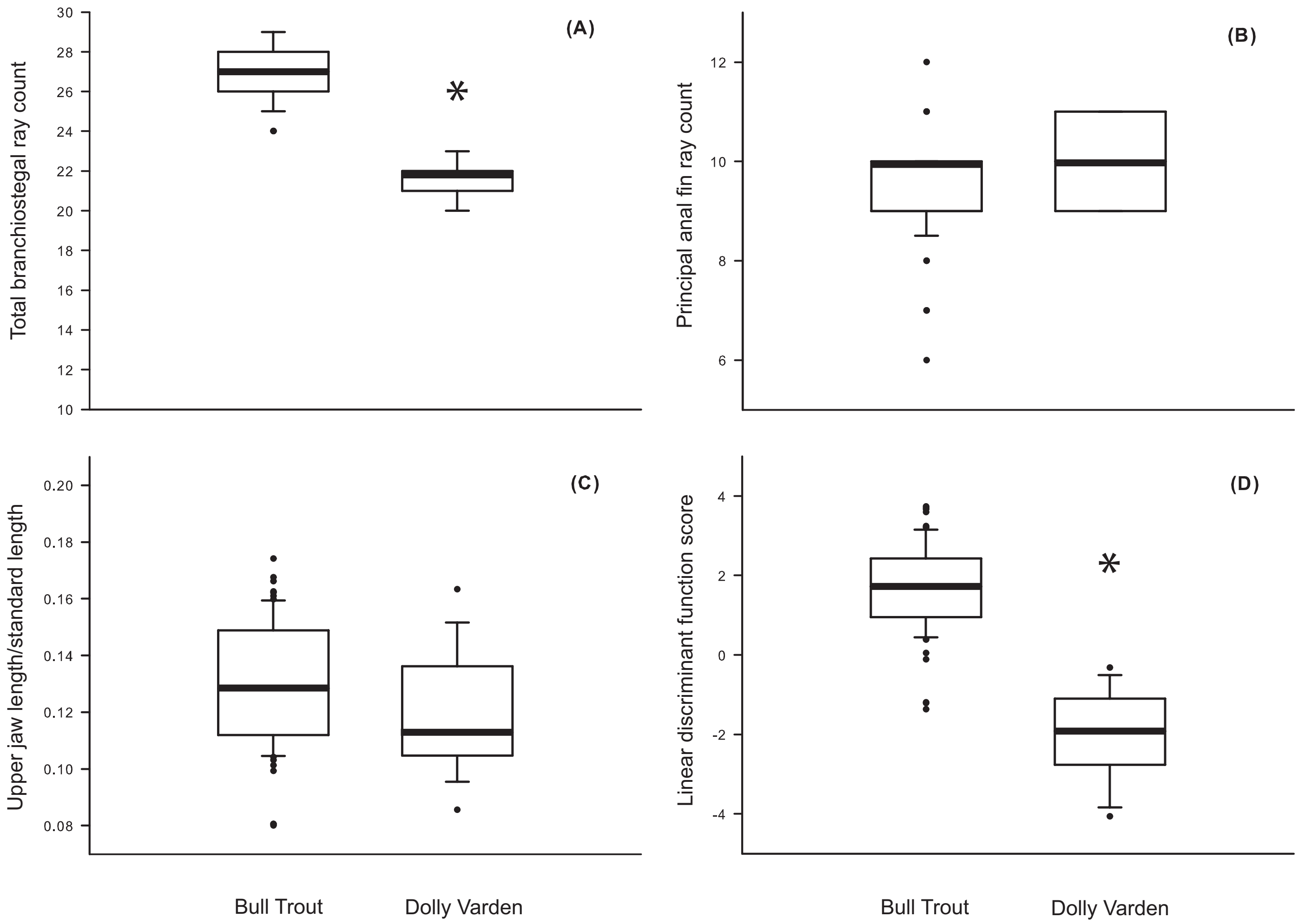

FIG. 2. Box plots of morphological characters (A–C) used to discriminate between bull trout (n = 74) and Dolly Varden (n = 15) and their multivariate combination (D) (Haas and McPhail, 1991). For each box, the thick horizontal line represents the median, and values within the box represent the interquartile range. Whiskers below and above the boxes represent the 10th and 90th percentiles and observations falling outside these percentiles are shown as points. Asterisks denote significant differences between bull trout and Dolly Varden for each character or combination of characters examined.

trout, 51 were Dolly Varden, and 29 were unresolved ([online] Appendix 1). All samples successfully profiled at the genetic assays were identified as pure bull trout or Dolly Varden; there was no evidence of hybrid individuals present. The agreement rate between identifications of fish by genetic assays and those by LDF was 95.5%, and agreement between field identifications and genetic assays was 100.0%.

Sequence data for a 500 bp fragment of the left domain of the mtDNA control region displayed two haplotypes, BLTR_dlp01 (Genbank accession number JQ436479) and BER12 (EU310902; previously reported in Alekseyev et al., 2009), which are commonly found in bull trout and Dolly Varden, respectively. Sequence divergence between the two haplotypes was 2.6%. No Dolly Varden haplotypes were found outside of the Gayna River ([online] Appendix 1). In the Gayna River, all specimens collected from reach 1 exhibited Dolly Varden haplotype BER12, the most common haplotype found in Dolly Varden of the Yukon and Northwest Territories (data not shown). In reach 2, two individuals exhibited the BER12 haplotype and seven contained the bull trout haplotype BLTR_dlp01. These results are consistent with both the field and morphological results.

The genotype results from the ITS1 and GH assays supported the biological and mtDNA results. For samples successful at both assays, there was consensus between the ITS1 and GH2 results. The ITS1 assay showed that all samples identified as bull trout had a double band profile indicative of the species-specific restriction pattern produced by *SmaI*, whereas all Dolly Varden were unaltered. A separate restriction digest of ITS1 with *Bsu36I* or *HpyCHV* confirmed the results obtained with the *SmaI* assay, and the GH assay showed expected PCR amplified fragment sizes of the growth hormone locus corresponding to each respective species (Taylor et al., 2001). All samples exhibited a genetic profile consistent with a pure species, with no crossover of species-specific alleles or combination of expected species-specific banding patterns indicative of a hybrid.

Genotype profiles from the four microsatellite markers also confirmed results of the biological and genetic assays. The microsatellite loci reported in this study were

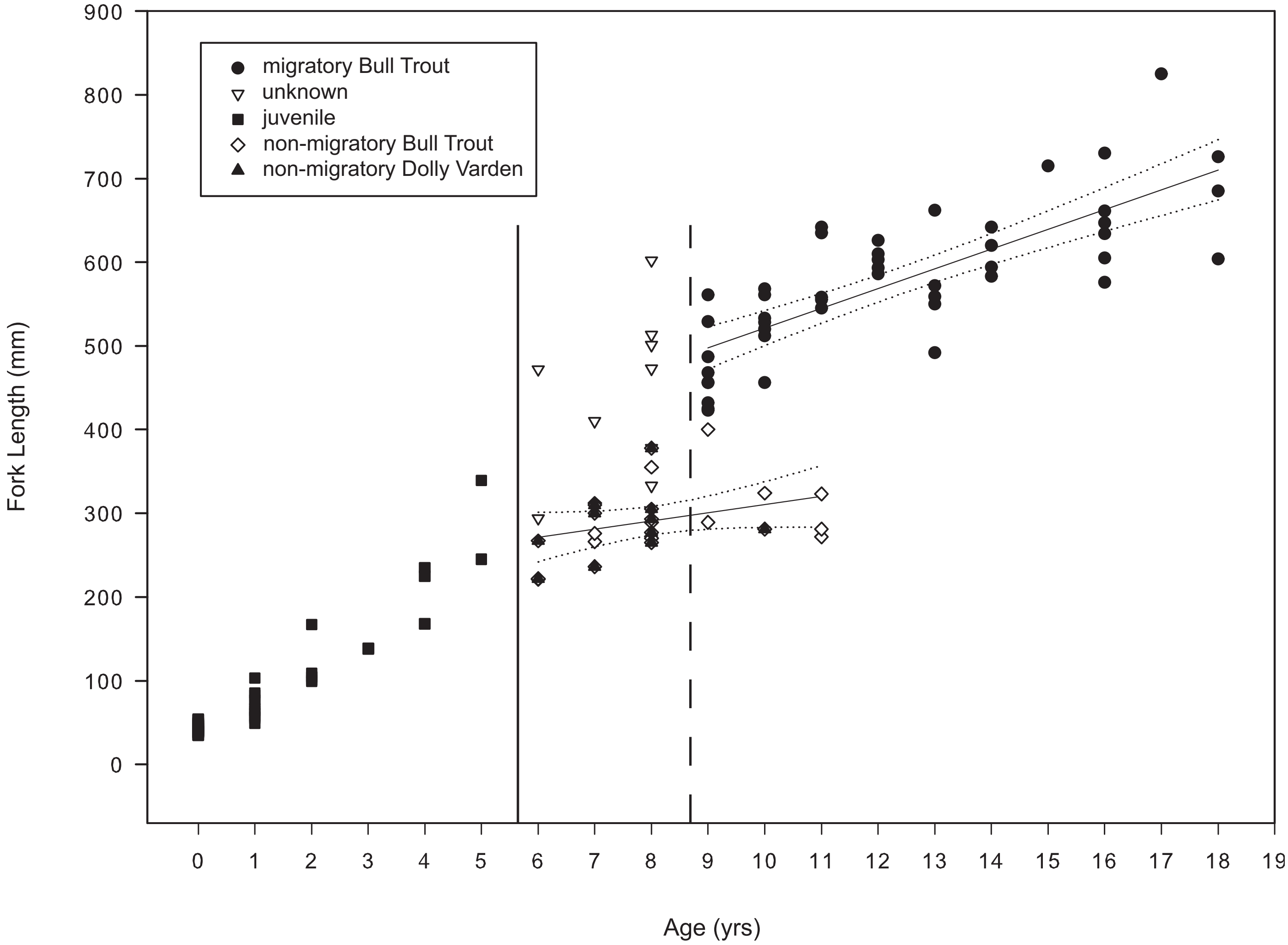

FIG. 3. Length-at-age plot of juvenile, non-migratory, migratory, and unknown bull trout and Dolly Varden from the Northwest Territories. Points to the right of the straight and dashed lines represent mature non-migratory and migratory fish, respectively. The regression equations for mature individuals from both non-migratory groups (both bull trout and Dolly Varden) and migratory groups (bull trout) were calculated separately. Dotted lines represent 95% confidence limits of the regression. Length-at-age comparison: migratory > non-migratory (F = 281.7; df = 22,25; $p < 0.001$).

considered to be diagnostic for the bull trout and northern form Dolly Varden samples used in this and other concurrent studies (data not shown). All bull trout specimens in this study were fixed at allele 104 for Omy301 and at allele 116 for *Smm3*. Locus *Sco214* was fixed at allele 161 across all analyzed Dolly Varden samples. There was no overlap in the allelic distribution across both species at any of the four microsatellites and no combination of both bull trout and Dolly Varden alleles in any single specimen.

Biology

Length-at-age data showed two types of growth patterns corresponding to our a priori designations of non-migratory and migratory fish (Fig. 3). The mean fork length was 298 mm for non-migratory fish compared to 571 mm for migratory fish, and significant differences in growth between these two groups were detected (Table 2). There was significant overlap between immature fish, and all unknowns were distributed across both the non-migratory and migratory groups (Fig. 3). Juveniles were immature fish with parr marks; non-migratory fish were adults that were less than 400 mm and either resting, mature, or running ripe; migratory fish were adults more than 400 mm; and unknown fish were those with uncertain maturity state.

TABLE 2. Parameters (K = growth coefficient; t_0 is the hypothetical age at age zero; L_∞ is the asymptotic average maximum length) of the von Bertalanffy growth equation for non-migratory and migratory char collected from streams in the southern and central Northwest Territories. Age ranges are presented with sample size (*n*) in parentheses. Length-at-age comparison: migratory > non-migratory (F = 281.7; df = 22,25; $p < 0.001$).

Group	K	t_0	L_∞	Age range (*n*)
Migratory	0.0106	1.533	825	0–18 (85)
Non-migratory[1]	0.1349	-1.355	400	0–11 (45)

[1] The non-migratory sample includes Dolly Varden captured in the Gayna River (n = 11).

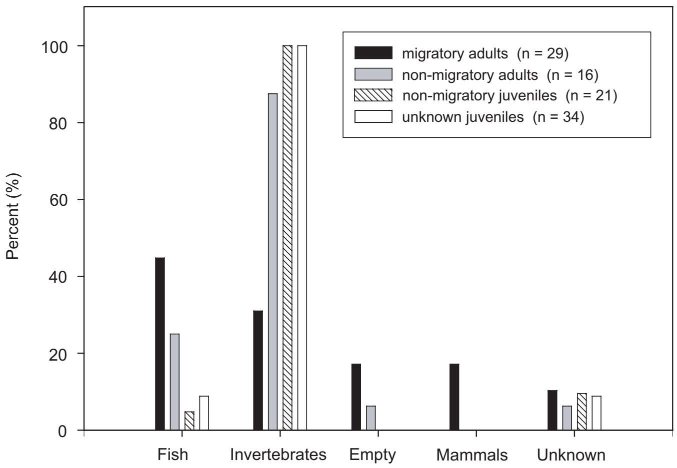

FIG. 4. Estimated relative volumes in gut content of adult migratory and non-migratory bull trout, juvenile non-migratory bull trout, and juveniles with unknown life history.

The estimated annual growth rate of juveniles captured from Funeral Creek (age 0–5) was 27.9 mm and 14.2 g; however, after age five the average annual weight gain increased to approximately 60 g. The density of juveniles captured from two reaches in Funeral Creek during September 2001 was 5.6 and 6.7 fish/100 m^2.

Sexually mature males and females in spawning and non-spawning (i.e., resting) condition were observed in all three areas. Resting females typically had ovaries that filled approximately half of the body cavity, eggs that were small and granular, and in some cases, retained residual eggs. Resting males had fully developed gonads that were the full length of the body, had no fluid in the center, and were purplish in color.

Stomach contents showed that adults consumed almost equal amounts of fish and invertebrates, whereas juveniles consumed mostly aquatic invertebrates (Fig. 4). The stomach contents of non-migratory fish were dominated by invertebrates, whereas stomachs of migratory fish contained a higher proportion of fish and terrestrial mammals (Fig. 4).

DISCUSSION

Distribution

Reist et al. (2002) confirmed the presence of bull trout in the Northwest Territories (~64˚30′ N, 125˚00′ W, Great Bear River) approximately 500 km north of the previous northernmost known occurrence (~61˚ N, N, 125˚ W, Prairie Creek, Liard River drainage). However, the range of this species remained uncertain in drainages to the north and south because of limited surveys in this remote area and the inability of non-experts to identify bull trout accurately in the field. We show that bull trout occur in multiple tributaries from interior drainages of the Kotaneelee River watershed, South Nahanni River watershed, and Central Mackenzie Mountains watershed. The population found in the Gayna River represents a range extension of approximately 200 km to the northwest of the Great Bear River, and the specimens from O'Grady Lake extend the range approximately 200 km to the southwest near the border of the Yukon. Our results provide further evidence that historical literature records for char in drainages west of the Mackenzie River and south of the Gayna River (e.g., Prairie Creek ~61˚ N, 125˚ W) that were identified as Dolly Varden likely represent bull trout.

The presence of bull trout populations exclusively in drainages west of the Mackenzie River implies that habitat attributes and landscape features (or a combination) influence habitat use in this region. Although many rivers on the east side of the Mackenzie River appear to provide suitable habitat for riverine char, we have very few records of bull trout occurring in the area (Reist et al., 2002) and no confirmed records of Dolly Varden. Furthermore, the numerous stream surveys conducted in this area have yielded no indication of self-sustaining populations (Reist et al., 2002; Mochnacz and Reist, 2007; Mochnacz et al., 2009a, b). This finding suggests that fish captured in tributaries east of the Mackenzie River are individuals from west-side drainages that have strayed from natal spawning streams in search of more productive feeding habitats or suitable overwintering areas. Both situations are possible, given that extensive migrations are common for this species (Ford et al., 1995; Baxter and McPhail, 1996; Swanberg, 1997). Many of the drainages to the east of the Mackenzie River are smaller, second- or third-order streams that drain directly into the Mackenzie River, whereas drainages that bull trout occupy to the west are high-gradient headwater tributaries that eventually drain into larger downstream rivers, such as the Keele and South Nahanni Rivers. Perennial groundwater sources, which have been linked to karst landforms in this area, appear to be more common in streams to the west than in those in the east, and perhaps their presence influences the distribution of bull trout in this region (N.J. Mochnacz, unpubl. data; Ford, 1983; Hamilton and Ford, 2002).

Sympatric bull trout and Dolly Varden were found in the Gayna River, a tributary of the Mountain River in the Central Mackenzie Mountains watershed. On the basis of recent proposed distributions (Reist and Sawatzky, 2010), we suspect that Dolly Varden from this river belong to the northern form subspecies, *S. malma malma*; however, this conclusion requires confirmation. This finding is significant because it represents the first known point of contact between these two taxa in the north and also extends the range of the proposed northern form Dolly Varden south by approximately 300 river kilometres from the closest known populations located in interior drainages of the Peel River basin (Reist et al., 1997; Anderton, 2006).

Both species were captured from a pool downstream of an impassable barrier in the Gayna River; however, we suspect that Dolly Varden inadvertently moved downstream during a high-water event. Determining whether these two taxa are syntopic—that is, whether they occupy the same discrete habitat in this watercourse—is important in the context of understanding the ecology of riverine chars in this area. More extensive fishing surveys should be conducted downstream from this area to the confluence with the Mountain River to determine species composition and potential hybridization in this river.

The low relative abundance of bull trout that we observed suggests that most populations are relatively small, widespread, and perhaps fragmented in our study area (Mochnacz et al., 2004, 2009a, b; Mochnacz and Reist, 2007). This finding is consistent with observations from other watersheds across the range (Goetz, 1989; Rieman and McIntyre, 1995; McPhail and Baxter, 1996; Swanberg, 1997; Baxter et al., 1999; Hvenegaard and Thera, 2001; Nelson et al., 2002). Such population structure and distributional patterns complicate management and conservation efforts. The distribution of bull trout in this region may be influenced by competition with other species for habitat and resources. For example, the density of Arctic grayling (*Thymallus arcticus*) was much higher than that of bull trout in streams where they co-occurred (Mochnacz et al., 2004, 2009a, b; Mochnacz and Reist, 2007). The availability of high-quality habitat may limit the productive capacity of bull trout populations in this region, especially in areas where they co-occur with other species that have similar habitat requirements (e.g., Dolly Varden). Future research should investigate areas north of the Gayna River, where bull trout and Dolly Varden may hybridize, occur in sympatry, or both, since these phenomena have been documented in British Columbia (Haas and McPhail, 1991; Baxter et al., 1997). If any of these scenarios occur, they will further complicate management and conservation by making field identification of riverine char by non-experts far more difficult.

Bull trout populations in the Northwest Territories are separated geographically within watersheds; however, in most situations they are not fragmented from one another by impassable barriers (e.g., the South Nahanni River watershed). Therefore, it is conceivable that individual fish from these seemingly isolated populations may interact, resulting in genetic exchange between populations. A group of populations with this type of spatial arrangement and connectivity is often referred to collectively as a metapopulation (Policansky and Magnuson, 1998) and has been documented in other watersheds where bull trout populations are found farther south (Dunham and Rieman, 1999; Hvenegaard and Thera, 2001; Warnock et al., 2010). These interactions, which involve genetic exchange between individuals, serve to strengthen regional populations by "re-founding" and protecting the genetic diversity that is necessary for long-term survival in varying environments (Quinn et al., 1991; NRC, 1996; Policansky and Magnuson, 1998). Metapopulation structuring complicates management and must be taken into account during consideration of potential development activities to ensure that barriers to fish migrations do not occur in these watersheds. Future research should focus on documenting movement patterns and genetic relationships among populations in watersheds where this species occurs in the Northwest Territories.

Identification

Although agreement was high between identifications of "unknown" char in the laboratory using qualitative morphological characters and field identifications, there were some discrepancies between LDF results and genetic and qualitative assessments. These discrepancies could be due to an inherent bias of the LDF that causes this method to misidentify bull trout more often than Dolly Varden. Since bull trout have higher counts and measurements than Dolly Varden, underestimation of meristic and morphometric characters often results in misidentification of bull trout as Dolly Varden or hybrids. This error is expected to increase for small fish and occurs most frequently with branchiostegal ray counts (Haas and McPhail, 2001). The dual identification of four fish from Funeral Creek, which were identified as Dolly Varden using the LDF but as bull trout using field and genetic markers, probably resulted from underestimation of meristic counts and characters. This explanation seems even more likely given the small size of these fish (< 75 mm). Furthermore, all three diagnostic tests were in agreement for other similar sized bull trout captured from this stream. To confirm "unknown" species, it is important to retain voucher specimens for subsequent identification by experts or acquire non-lethal tissue samples for genetic identification. Acquiring non-lethal tissue samples is especially important for small fish, since they are most susceptible to misidentification using quantitative morphological analyses.

The genetic data suggest that bull trout and Dolly Varden in this area remain reproductively isolated: there is no evidence of recent hybridization between bull trout and Dolly Varden. However, the presence of Dolly Varden with bull trout in reach 2 of the Gayna River system illustrates the possibility of gene flow between these two species, which has been documented farther south (Baxter at al., 1997; Leary and Allendorf, 1997; Redenbach and Taylor, 2003). Further sampling and investigation will be required to determine the effect that these incidences will have on these two populations.

Char Life History and Implications for Management

We observed clear differences in overall size, growth, and diet among bull trout captured during this study, which suggests that different life histories are present in this region. The two growth patterns observed are consistent with non-migratory (i.e., stream-resident) and migratory (i.e., fluvial, adfluvial) bull trout populations found farther south (Fraley and Shepard, 1989; Adams, 1994; Swanberg, 1997). The growth rate of bull trout observed in the migratory group was significantly greater than that in the non-migratory group, as demonstrated by the difference in the slopes of the regression lines. Such divergence in growth could be a result of the productivity in habitats that these fish occupy or trophic levels at which they feed. The diet data clearly showed differences for these two groups, supporting this hypothesis. For example, mature fish (> 9 yrs) from Funeral Creek were far smaller than individuals from downstream reaches of the South Nahanni River, and they consumed mostly invertebrates. Stream-resident bull trout populations have adapted to survive in less productive headwater areas, whereas fluvial and adfluvial populations inhabit more productive downstream areas (Fraley and Shepard, 1989; Adams, 1994; Swanberg, 1997). Fish captured in all three watersheds also exhibited alternate-year spawning patterns, which is consistent with other populations found farther south (McPhail and Baxter, 1996; Johnston et al., 2007). However, bull trout captured in this region did mature later (6–10 yrs) than most fish found in systems farther south (Baxter and McPhail, 1996).

These findings are significant from a management perspective because fish that mature late and spawn in nonconsecutive years are not as resilient to impacts as fish that mature earlier and spawn annually. Alternate-year spawning behaviour, which is also seen in some southern populations, is believed to be an adaptation to low-productivity environments (Goetz, 1989; McPhail and Baxter, 1996 and references therein; McCart, 1997; Reist et al., 1997). As latitude increases, productivity generally decreases as a result of colder temperatures and shorter growing seasons, which makes northern populations more susceptible to perturbations than those found farther south. The ability of individual populations to withstand impacts is further influenced by life history, since growth varies between stream-resident and adfluvial and fluvial types (McPhail and Murray, 1979; Fraley and Shepard, 1989; Adams, 1994; McPhail and Baxter, 1996; Ratliff et al., 1996; Spangler, 1997; Hvenegaard and Thera, 2001; Johnston et al., 2007). Managers must clearly understand the biology and life history of northern populations to ensure the implementation of conservative fishing quotas, including potential closures for some areas, as well as appropriate habitat protection measures. Designating appropriate harvest levels and mitigating development activities that could alter fish habitats will be especially important for small headwater populations or for those that require migratory behaviour in order to persist (metapopulations).

Understanding the ecology of bull trout and Dolly Varden in northern Canada is important in the context of existing and anticipated impacts of climate change and human activity. Both species have demonstrated an inherent vulnerability to a number of impacts, including over-harvesting, fragmentation and isolation of populations, habitat degradation and loss, interaction with exotic species, and the cumulative effects of these activities (McCart, 1997; Sandstrom et al., 2001; Reist et al., 2002, 2006; Ripley et. al., 2005). Climate trends show that hydro-ecological processes in the North have changed as a result of shifts in precipitation and temperature patterns (Prowse et al., 2006; Rosenzweig et al., 2007). For example, the stream base flow in most rivers has increased by 5% to 9% annually and by 25% to 90% in winter (Rosenzweig et al., 2007; Richter-Menge and Jeffries, 2011). Recent climate change projections indicate that both the frequency and the magnitude of precipitation events will increase, annual air temperatures will increase, and permafrost will degrade in the North (Rosenzweig et al., 2007). These changes will lead to an overall shift in the hydro-ecology of rivers, resulting in less intense earlier spring freshets, higher winter flows with less ice cover, and a decrease in water levels during the summer (Prowse et al., 2006; Reist et al., 2006). Survival during the winter may improve as habitat availability increases; conversely, pathways to critical habitat such as spawning and rearing areas could be impaired in areas where combinations of precipitation and evaporation lead to reductions in water levels. Also, the incidence of parasitism could increase, exotic species could move northward, and the existing permafrost could degrade, promoting slumping and infilling of essential habitat. Since both species have very specific spawning, rearing, and winter habitat requirements (McCart and Craig, 1973; Baxter and McPhail, 1999; Sandstrom et al., 2001; Mochnacz et al., 2010), care must be taken to mitigate degradation or destruction of these areas by human activity. Mitigation will be especially important for essential habitats, such as perennial groundwater upwellings, which maintain winter habitat and provide high-quality spawning habitat for both species (Baxter and McPhail, 1999; Sandstrom et al., 2001; N.J. Mochnacz, unpubl. data).

Future research should focus on improving our understanding of critical habitat use, population size and structure, life history, and distribution in areas of uncertainty for both species. Future research on bull trout in the Northwest Territories should be a high priority: as new information is gathered, it will serve to inform managers so that they can manage this sensitive species more effectively in the future. The sensitivity of bull trout to perturbations suggests that this species could be a good indicator of ecosystem health and may be a good candidate for long-term monitoring programs in this region.

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