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AN EVALUATION OF THE RELATIVE PERFORMANCE OF DIPLOID VERSUS
TRIPLOID BROOK TROUT WITH CONSIDERATION OF THE INFLUENCE
OF LAKE CHARACTERISTICS

by

Andy Dean

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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Logan, Utah

2014

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ABSTRACT

An Evaluation of the Relative Performance of Diploid versus Triploid Brook Trout with
Consideration of the Influence of Lake Characteristics

by

Andrew T. Dean, Master of Science

Utah State University, 2014

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

Triploid (sterile) trout potentially offer a more risk-averse option for stocking popular non-native sport fish; however the relative performance (e.g., survival and growth) of triploid versus diploid fish in natural settings is not well understood. I evaluated the relative performance of triploid versus diploid brook trout (*Salvelinus fontinalis*) stocked in high mountain Uinta lakes in response to food availability and lake morphology. I chose a set of 9 lakes that included a range of elevation and lake morphology. I observed no difference in CPUE or relative weight (W_r) of both types of trout in all lakes. Food availability (e.g., zooplankton and macroinvertebrates) varied substantially among lakes; however I observed no discernible difference between diploid and triploid diets, diet preference, or isotopic trophic signatures. Physical lake characteristics (e.g., dissolved oxygen [DO, mg/L] and temperature [$^{\circ}$ C]) were within or near optimal brook trout conditions (metabolically beneficial range) during the summer,

but over-winter DO reached near lethal levels under the ice. In sum, between the two strains, I did not observe any significant differences in relative performance measured across a number of indices; however the size distribution of diploid fish was marginally (20 mm) skewed towards larger fish (a difference likely not great enough to be detectable by the average angler). In contrast to the similarity in performance between strains, I did observe considerable variability in performance of brook trout across lakes as a function of lake productivity, food availability, and most importantly fish density. Fish performance was greater in lakes with a lower density of stocked fish. Overall, the results from this study indicate triploid brook trout offer a viable and risk-averse alternative to stocking diploid fish in Uinta mountain lakes. Stocking triploid fish should decrease the threat of uncontrolled expansion into adjacent water bodies, while still allowing managers to maintain a popular non-native sport fishery.

(52 pages)

PUBLIC ABSTRACT

An Evaluation of the Relative Performance of Diploid versus Triploid Brook Trout with
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Brook trout are native to the east and Midwestern United States. Brook trout have become a popular sport fish in the western United States and are currently widely stocked to provide sport fishing opportunities throughout the west. The Utah Division of Wildlife Resources (UDWR) regularly stocks brook trout into high mountain lakes in the Uinta Mountains to provide one of these popular fisheries. Stocking non-natives to high mountain lakes can cause competition with native species for food and habitat resources and provides source populations for dispersal of non-natives downstream. Triploid (sterile) fish may provide an opportunity to stock non-native fish to potentially sensitive environments like high mountain Uinta lakes. The UDWR stocked triploid and diploid (fertile) brook trout into nine lakes in the Uinta Mountains as a part of this study.

In this study, I examined the potential differences in growth and survival (relative performance) of stocked triploid and diploid brook trout. I also developed two models to

explain the factors that may limit relative performance of stocked brook trout, independent of ploidy (triploid or diploid) level in high mountain Uinta lakes. I did not find any differences in relative performance of triploid compared with diploid brook trout based upon indices of diet, growth and survival. The models indicated that factors associated with lake size and fish density affected relative performance of stocked brook trout. Lakes with higher fish densities contained brook trout in poor condition versus lakes with lower fish densities. Additionally, smaller shallower lakes contained very few fish compared to larger deeper lakes of this study. These findings suggest that brook trout may survive better and grow larger if stocked at lower densities. The results also suggest that survival is low in small shallow lakes. Harsh over-winter conditions in high mountain Uinta lakes may provide an explanation of poor survival in these small shallow lakes. Results of this study provide evidence that triploid brook trout are a viable alternative to stocking diploid, fertile brook trout to diminish the potential negative effects of stocking a non-native species. This study also suggests an evaluation of the stocking regime in high mountain Uinta lakes in order to improve the size and survival of stocked brook trout.

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Andrew T. Dean

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INTRODUCTION

The effects of non-native introductions on aquatic ecosystems (e.g., loss of biodiversity, spread of disease, altered energy pathways) have been extensive and well documented. These impacts include, but are not limited to, direct predation on native species (Ruzycki et al. 2003; Pelicice and Agostinho 2009), alterations of the plankton community (Parker et al. 2001; Eby et al. 2006; Reissig et al. 2006), and increased pathogen transmission to water bodies and native species (Minchin 2007). More specifically, the introduction of non-native fishes to historically fishless, alpine lakes has resulted in several potential negative outcomes including uncontrolled downstream dispersal into other streams and lakes with native fish populations (Adams et al. 2001; Knapp et al. 2001), a shift in size structure and abundance of zooplankton species (Eby et al. 2006; Latta et al. 2007; Knapp and Sarnelle 2008), and hybridization with native species (Knapp 1996; Dunham et al. 2002). Yet, despite these well-documented and ubiquitous negative impacts on aquatic ecosystems, non-native fishes are currently still being stocked to provide sport fisheries deemed economically and socially important by state management agencies. Sterile fish may provide a more ecologically risk-averse alternative to stocking fertile fish as well as potentially providing improvements to growth and production of non-native stocked fish.

Triploid fishes, which are reproductively sterile, are being considered as a promising replacement for diploid (fertile) fish in aquaculture and for human consumption (O'Keefe and Benfey 1999; Hyndman et al. 2003) due to purported higher growth rates and the inability to reproduce. The growth advantage of triploids has been

documented in numerous studies of a variety of different species. Suresh and Sheehan (1998) provided empirical evidence suggesting that triploid rainbow trout (*Oncorhynchus mykiss*) exhibit higher growth rates than diploid rainbow trout of adult size classes, an advantage attributed to the ability of triploid fish to allocate most energy towards growth, rather than reproduction and growth (Hyndman et al. 2003). Cal et al. (2006) similarly observed significantly higher growth in triploid turbot (*Psetta maxima*) than diploid turbot, with the difference in growth becoming more significant after each spawning season. Triploid fish also demonstrated fewer physiological changes typically associated with sexual maturation (e.g., inhibited muscle development; Thorgaard and Gall 1979), a physiological change that may significantly reduce somatic growth (Boulanger 1991). In theory, triploid fish have the potential to experience an extended period of maximum growth due to the reduction of muscle loss and minimized growth rate retardation. As such, if the theory holds, sterile fish offer an additional benefit to minimizing conservation risk. In most regularly-stocked sport fisheries, bigger fish (i.e., greater fish growth rates) is one of the primary objectives and can contribute to the greater goal of maintaining and improving angler's attitudes towards the fishery.

Although triploid and diploid fish have demonstrated similar performance (Benfey and Biron 2000; Sadler et al. 2000; Maxime 2008), triploid fish may also be physiologically intolerant to some physiologically stressful environmental conditions. However, these differences may be very species-specific (Peruzzi et al. 2005). For triploid rainbow trout, for example, lower tolerance to elevated water temperatures (Galbreath et al. 2006) resulted in less efficient metabolic and physiologic function (e.g.,

fewer erythrocytes and increased anaerobic respiration) relative to diploid fish. Similarly, Ballarin et al. (2004) demonstrated that triploid shi drums (*Umbrina cirrosa*) have a lower ability to tolerate stressors, relative to diploid shi drums due to: 1) fewer circulating blood cells, possibly affecting immunosurveillance; 2) a decrease in intercellular communication, which may affect signal transduction, cell movement, and other important processes; and 3) decreased aerobic metabolism, leading to an increase in energy store depletion. In contrast, however, others have suggested that because triploid fish may experience a lower metabolic rate, they have a greater ability to tolerate lower concentrations of oxygen and other physical stressors (Stillwell and Benfey 1997). As noted earlier, these differences in tolerance may be species specific and may also be influenced by the stocked environment.

Additionally, despite the theoretical advantages of stocking triploid fish, observed differences in the survival, growth (referred to here as relative performance), and behavior of triploid fish appears to be highly variable (see O'Keefe and Benfey 1999; Kerby et al. 2002; Oppedal et al. 2003). Hyndman et al. (2003) demonstrated that triploid brook trout (*Salvelinus fontinalis*) experience higher temperature-related rates of mortality compared with diploid brook trout. Similarly, triploid Atlantic salmon (*Salmo salar*) and brook trout also exhibited higher mortality and decreased performance compared with their diploid siblings. These triploid trout demonstrated a lower thermal optimum and an inability to sustain high metabolic demand, resulting in increased cardiac output and ultimately failure (Atkins and Benfey 2008). In addition to these potential differences in adult performance, there is some evidence that triploid fish may experience

lower growth and survival rates at early life stages (Suresh and Sheehan 1998), differences, however, that may be compensated for at later life stages (i.e., while diploid fish are sexually maturing).

Nonetheless, perhaps the most important reason for considering the use of triploid fish is the elimination of the potential for hybridization with native species and the uncontrolled expansion of these introduced fishes into areas where they are not desired. In sum, the effect triploidy has on fish performance in general appears to be highly variable, species-specific and poorly understood in a natural setting (Small and Randall 1989). Thus these uncertainties highlight the need to evaluate relative differences in performance of triploid and diploid fish prior to the initiation of a widespread and potentially costly stocking program. In this context, the experimental inclusion of triploid brook trout into the regular stocking program of the Uinta Mountains began in 2006 as a potentially more risk-averse alternative to stocking diploid brook trout. This large-scale experiment provided a unique opportunity to expand on the currently sparse understanding and quantification of triploid performance in a natural setting.

My overall goal was to gain a better understanding of the general performance of triploid brook trout compared with diploid brook trout stocked in high mountain Uinta lakes. In addition, I used this understanding of triploid and diploid performance to identify options for meeting both management and conservation goals of stocking non-native brook trout. My objectives were to 1) evaluate how the relative performance of triploid brook trout compared with that of diploid brook trout using a suite of performance measures including indices of abundance, size and condition, and 2) identify

which lake characteristics (e.g., lake morphology, productivity) most limit stocked brook trout performance in high mountain Uinta lakes, independent of ploidy group, to help guide more lake-specific stocking recommendations.

METHODS

Overall approach

I sampled fish three times throughout the summer months in nine lakes in 2008 and 2009 to compare the relative performance of diploid and triploid brook trout. To evaluate relative performance of triploid and diploid brook trout, I used catch per unit effort (CPUE) as an index of abundance and survival and relative weight (W_r) as a measure of condition. In addition, I measured, weighed, and collected stomach and tissue samples of marked (fin clipped) brook trout from each ploidy group to assess size structure, diet preference, and isotopic signatures for longer-term diet assessment. Lastly, I measured limnological and morphometric characteristics and sampled macroinvertebrates at each lake to identify factors potentially limiting the overall performance of triploid and diploid brook trout stocked in these high elevation lakes.

Study site description

I conducted my research in nine lakes (Alexander Lake, Blue Lake, Clegg Lake, Crystal Lake, Haystack Lake, Hoover Lake, Marshall Lake, Ruth Lake, and Spectacle Lake) located along the Mirror Lake Corridor of the Uinta Mountains, northeast Utah (Figure 1). These lakes were chosen from a larger set of candidate lakes, *a priori* based on three criteria: 1) lakes should span a wide range of lake elevations within the Uinta

range, 2) lakes should span the range of lake morphology present, and 3) lakes must be reasonably accessible (for stocking and sampling). For this large-scale experiment, the Utah Division of Wildlife Resources (UDWR) Kamas Hatchery, Utah, stocked these lakes with an equal ratio of diploid to triploid brook trout from 2006 through 2008 (Table

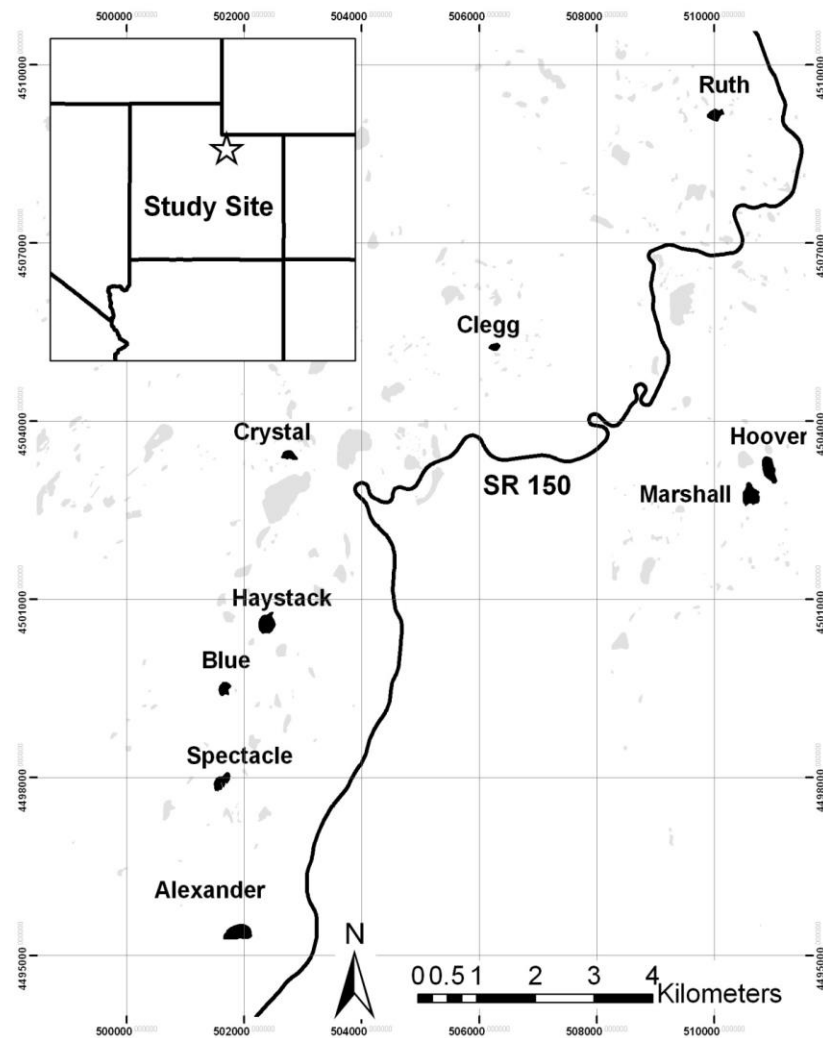


Figure 1. Study area map of our nine study lakes in the western portion of the Uinta Mountains along the Mirror Lake Corridor of northeastern Utah.

1). Lakes ranged in elevation from 2,853 m (Alexander) to 3,188 m (Clegg) (Table 1). The high elevation of these lakes results in short summer growing seasons, generally beginning in late June and ending in mid October, and a long winter season (all lakes are ice covered). The deeper lakes (e.g., Alexander, Blue, Haystack, Hoover, Marshall, and Ruth) typically stratify for a short period of time during mid summer (late July to mid August) and mix again during late August. The shallow lakes (< 5 m) typically do not completely stratify over the summer.

Uinta lakes are widely stocked with brook trout to provide a popular sport fishery. Uinta lakes formed following the recession of glaciers from the Pleistocene era (Laabs and Carson 2005), most of which were historically fishless. Since the advent of aerial stocking, over 70% of Uinta lakes were stocked regularly or contained reproducing populations of brook trout and cutthroat trout (*Oncorhynchus clarkii*) by the 1980's (Wilson 1979). Today, lakes along the Mirror Lake Corridor are extremely popular for their brook trout fishery and thus provide an important tourist and economic resource to the state of Utah.

Fish sampling

I captured brook trout using gill nets three times throughout the summer months (early, middle, and late summer) of 2008 and 2009 to estimate indices of survival, growth, abundance, and size structure. The gill nets consisted of seven 7.62 m panels with mesh sizes of 1.27 cm – 5.08 cm bar length in 0.64 cm increments randomly ordered throughout each net. Nets were set overnight to maximize brook trout captures. I calculated CPUE from the number of fish caught per unit gill net soak time (e.g.,

Table 1. Nine stocked lakes chosen *a priori* for this study in the western portion of the Uinta Mountains, Utah. The lakes range in morphometric characteristics (e.g., elevation, maximum depth, mean depth, surface area, and volume) and were chosen to span the environmental gradient present in the high mountain Uinta Lakes. Equal ratios of diploid (2N) and triploid (3N) brook trout were stocked by the Utah Division of Wildlife Resources from 2006 – 2008. Quotas were estimated at 100 fish per acre for brook trout and were adjusted throughout the years based on condition (Fulton’s K or W_r) and angling pressure, and matched to a cycle. The cycle determined the frequency of stocking (e.g., every 1 yr or every 2 yr) to meet sport fish needs as well as conservation objectives.

Lake	Lake Elevation (m)	Max. depth (m)	Mean depth (m)	Area (ha)	Volume (m ³)	Stocking Quotas					
						2006		2007		2008	
						2N	3N	2N	3N	2N	3N
Alexander	2,853	8.5	4.6	9.3	426,000	1113	1148	1152	1150	1210	1226
Blue	2,950	7.9	3.0	3.2	99,000	305	294				
Clegg	3,188	3.7	2.1	2.1	44,000	504	504				
Crystal	3,109	3.0	1.4	4.0	54,000	504	504	498	498	498	504
Haystack	3,030	8.8	3.4	6.9	231,000	452	448			454	447
Hoover	3,017	8.5	3.0	7.5	229,000	945	952	948	948	943	950
Marshall	3,045	11.0	4.6	7.3	333,000	903	896				
Ruth	3,152	9.1	3.7	3.9	144,000	252	252	252	252	249	247
Spectacle	2,969	5.2	1.8	3.8	69,000	704	700				

number/net/soak hour) for each sampling period and sampling year. I measured total length (TL) and weighed all brook trout to obtain size structure and an index of body condition (W_r). Relative weight was calculated using the common equation:

$$W_r = (W/W_s) * 100,$$

where, W is the individual fish weight and W_s is a standard length-specific weight based on a predicted weight of a developed length-weight regression (see Murphy et al. 1991) that represents the specific species of concern. The W_r metric uses 100 as a baseline for fish in good condition. Deviations lower than 95 indicate the fish is in poor condition and a W_r above 105 indicates the fish is in very good condition (Pope and Kruse 2007). I used paired Student's t-tests to test for statistical differences in CPUE and condition (W_r) and pooled data across lakes.

I compared relative size and age structure of diploid and triploid brook trout based on length-frequency data for each ploidy level within and among lakes. I tested for statistical differences in length frequencies using a Kolmogorov-Smirnov test (Neumann and Allen 2007) of diploid and triploid brook trout. For analysis I also pooled data across lakes.

Food availability and diet preference

To describe pelagic food availability, I collected zooplankton samples from at least one shallow site and one deep site in all lakes during the three summer fish sampling periods and once during the winter period. I sampled two vertical tows of the total water column between 1000 and 1600 hours with 80 μm and 500 μm Wisconsin-style zooplankton nets. If the lake was stratified, two additional zooplankton tows were taken through the epilimnion. In cases where density appeared high, I subsampled zooplankton in 2 mL aliquots using a Hensen Stempel pipette from a known volume of water. I

calculated zooplankton density for each zooplankton taxon adjusting the number of individuals enumerated to the total water column sampled (number of individuals/L).

I also sampled benthic macroinvertebrates to describe benthic food availability. I used a modified Hess sampler at four randomly-selected locations in the littoral zone during the mid-summer sampling period, placing the sampler approximately 5 cm into the substrate, and disturbing the substrate for 90 seconds. After the substrate was completely suspended within the sampler, I flushed all suspended contents into a 500 μm collection bucket. I immediately placed all contents from the collection bucket in a sample jar and preserved them in 95% ethanol for later identification and enumeration in the lab. In the lab, I pooled all four samples from each lake, and identified all sampled invertebrates to taxonomic order for estimates of relative abundance (number of individuals of each order/ m^2) in each lake.

To compare diet preference between ploidy groups, I removed stomachs from all marked fish and preserved them in 95% ethanol. In the lab, prey items were classified into aquatic invertebrates (to order), terrestrial invertebrates, fish (to species), or zooplankton (to genera). Invertebrate taxa were enumerated, blotted dry, and weighed en masse to the nearest 0.001 g. Zooplankton were weighed en masse by genus to the nearest 0.001 g, and the percent wet weight of each prey item for each individual fish and the percentage of each prey item of all items consumed was calculated. I used an electivity index (e.g., Strauss's L, Strauss 1979) to describe diet preference for both triploid and diploid brook trout (unidentifiable contents and organic matter were not included). To calculate diet overlap, I pooled diet samples across sample periods within

each lake for each year to compensate for unequal sample sizes among sampling periods (32 total diet samples in 2008, and 203 total diet samples in 2009). Then, I used Schoener's D (Schoener 1970) and compared diet overlap across lakes in both 2008 and 2009. Schoener's D values range from 0-1 in which 0 represents no diet overlap while 1 represents complete diet overlap. A threshold of 0.6 is considered significant diet overlap, above which competition for limited prey resources may occur (Schoener 1982).

In addition to analyses of stomach content and diet analyses, I analyzed isotope signatures (C, N) of both ploidy groups to assess potential differences in long-term feeding strategies and trophic position. I removed muscle tissue from a subsample of fish in each ploidy group from each lake and preserved tissue in 95% ethanol for later isotope analysis. I later dried tissue samples in an oven at 75° C for at least 24 hours, removed the tissue from the oven and pulverized each sample with a mortar and pestle. Samples were sent to the UC-Davis Stable Isotope Facility for analysis. I used a paired Student's t-test to compare overall ^{13}C and ^{15}N isotope signatures of diploid and triploid brook trout (across lakes, n = 53).

Other biotic and abiotic factors

I measured temperature, DO, light intensity, and water transparency during each fish sampling period, and once over the winter, to identify other factors potentially limiting the relative overall performance of brook trout. I measured temperature (°C), DO (mg/L) and light (lux) profiles at the deepest site in each lake. I recorded values of each variable from the surface every 0.5 m to the bottom of the lake (or until 5% surface intensity lux was reached for light). In addition, I placed one or two temperature loggers

in each lake, depending upon lake depth, one near the bottom (~2 m from the bottom) and the other approximately mid-lake depth (~3 m from the surface). Loggers were anchored to a buoy and continuously recorded hourly temperatures over a full year. Lastly, I recorded the mean depth (m) of disappearance and reappearance of a Secchi disk as an index of water transparency at the deepest site in each lake.

*Assessing factors potentially limiting
brook trout performance*

I used two statistical models to assess potential limiting factors on overall brook trout performance. First, I used a Random Forest (RF) model as a variable selection tool of all abiotic and biotic predictor variables. The top variables from this model were used in a hierarchical mixed model (see below) to test for significant relationships. Random Forest is ideal for this type of field data as it offers a reliable method for detecting relationships between numerous predictor variables and a response variable when sample size is small (e.g., nine lakes; Cutler et al. 2007). For inputs into the original RF model, I used fish condition (W_r) as the response variable and indices of lake productivity and food availability, environmental variables such as DO and temperature, and characteristics of lake morphology as predictor variables. Zooplankton density (number/L) represented pelagic food availability, and macroinvertebrate abundance (number/m²) represented benthic food availability. I assumed brook trout occupied waters at the theoretical optimal temperature or waters nearest to the optimum temperature in which DO concentrations were also suitable for brook trout growth. Therefore, I chose the temperature (°C) closest to the theoretical optimal temperature and

minimum DO concentrations (mg/L) to characterize abiotic conditions at each lake and sampling event.

Next, I used four of the unique (i.e., not redundant or covarying) top predictor variables from the RF model as inputs to a hierarchical-mixed model, to test for significant effects of each predictor variable on fish condition (W_r). For this study, a hierarchical mixed model provides an appropriate fit to the data structure as the observations measured within one or more higher levels (e.g., sample period and lake) are likely to be more similar than observations between levels (e.g., lake; Wagner et al. 2006). In addition to the four potential predictor variables identified in the RF analysis, I included two levels, Lake and Sample period, with sample period nested within lake:

$$\text{Fish Condition } (W_r) = \text{Lake} * \text{Sample period} + \text{CPUE} + \text{Zooplankton density} + \\ \text{Hectares} + \text{Macroinvertebrate Abundance} + \text{Optimal Temperature}$$

All results are presented as either or both relative (triploid fish versus diploid fish), and overall (i.e., fish performance across lakes, independent of ploidy level).

RESULTS

Relative performance

Total catch of all brook trout (BKT) and of marked trout (2N = diploid, 3N = triploid) was extremely variable across our study lakes. I captured the greatest number of brook trout overall in Crystal, Hoover and Ruth lakes (Table 2). I captured the lowest number of fish overall in Clegg and Marshall lakes (Table 2). All unmarked brook trout

Table 2. Number of captured brook trout and catch per unit effort (CPUE) from each lake in 2008 and 2009. Numbers are arranged by the number of brook trout captured followed by CPUE (i.e., number of fish/CPUE). Total in 2008 and 2009 includes marked fish (i.e., diploid and triploid) and unmarked fish.

Lake	2008			2009			Overall Total	Total Diploid	Total Triploid
	Total	Diploid	Triploid	Total	Diploid	Triploid			
Alexander	71/10	25/3	26/3	138/6	49/2	48/2	209/16	74/5	74/5
Blue	36/7	10/2	8/1	61/2	30/1	11/1	97/9	40/3	19/2
Clegg	8/1	5/1	1/1	3/1	1/1	2/1	11/2	6/2	3/2
Crystal	89/10	3/1	5/1	160/6	12/1	10/1	249/16	15/2	15/2
Haystack	54/6	1/1	0/0	151/5	3/1	3/1	205/11	4/2	3/1
Hoover	118/21	16/3	22/6	172/9	53/3	38/2	290/30	69/6	60/8
Marshall	11/1	2/1	0/0	78/4	14/1	1/1	89/5	16/2	1/1
Ruth	96/11	15/2	11/1	122/6	9/1	4/1	218/17	24/3	15/2
Spectacle	29/5	10/2	12/1	63/3	0/0	0/0	928	10/2	12/1

were either previously stocked or from naturally reproducing populations.

CPUE was highest in Alexander and Hoover lakes in both 2008 and 2009, and capture rates were lowest in Clegg Lake in both 2008 and 2009 (Table 2). Spectacle Lake also had relatively low capture rates in both years of the study with no marked fish captured in 2009 (Table 2, Figure 2). CPUE of marked fish was consistently greatest in Alexander and Hoover lakes and lowest in Clegg and Marshall lakes (Table 2, Figure 2).

When pooled across lakes, CPUE did not differ statistically between diploid and triploid brook trout ($t = 0.57$, $p = 0.57$, $df = 53$).

Size structure and condition

Across lakes, diploid brook trout demonstrated a size frequency distribution marginally but still significantly skewed towards larger fish as compared to triploid brook trout (mean 2N = 262.5 mm; mean 3N = 241.6 mm; $p < 0.05$, $D_{KS} = 0.24$; Figure 3). However, the larger size structure of diploid brook trout was really only evident in a couple lakes. Only a couple size classes representing two age groups were present in both years. In general, the size structure remained fairly consistent across lakes where only Alexander and Hoover lakes contained fish that experienced noticeable shifts in size from 2008 to 2009 (Figure 3).

Although highly variable across lakes, mean W_r was not different between diploid and triploid brook trout within lakes (mean 2N = 100.6; mean 3N = 96.7; $p = 0.052$, $df = 32$; Figure 4). Diploid brook trout W_r ranged from 75.2 – 165.3, and triploid fish W_r ranged from 70.4 – 156.3 across lakes. Mean W_r of diploid and triploid trout (127.0, 135.1, respectively) was highest in Marshall Lake in both years.

Food availability and diet

Diet composition was generally similar between ploidy groups. Stomach contents of diploids and triploids consisted primarily of Diptera, Mollusca and terrestrial invertebrates. I observed little variability in diet between both ploidy groups among lakes in 2008 (range = 0.50% – 0.67% overlap). Diet overlap between the ploidy groups was

highly variable among some lakes in 2009 (range = 0.07% -- 0.76% overlap). When pooled across lakes, percent diet overlap was not significantly different between ploidy groups in either 2008 or 2009 (0.82% and 0.77% overlap; respectively).

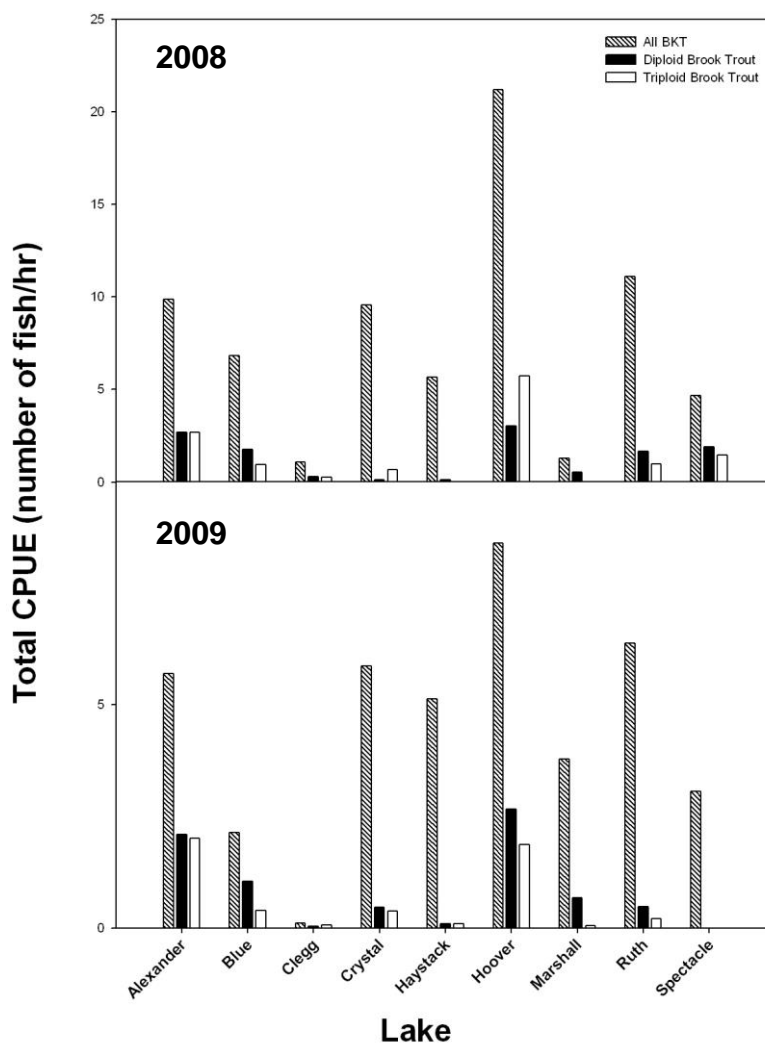


Figure 2. Catch per unit effort (CPUE) of total captured brook trout and marked brook trout within each lake (top panel = 2008 and bottom panel = 2009). No marked fish were captured in Haystack Lake in 2008, and no marked fish were captured in Spectacle Lake in 2009.

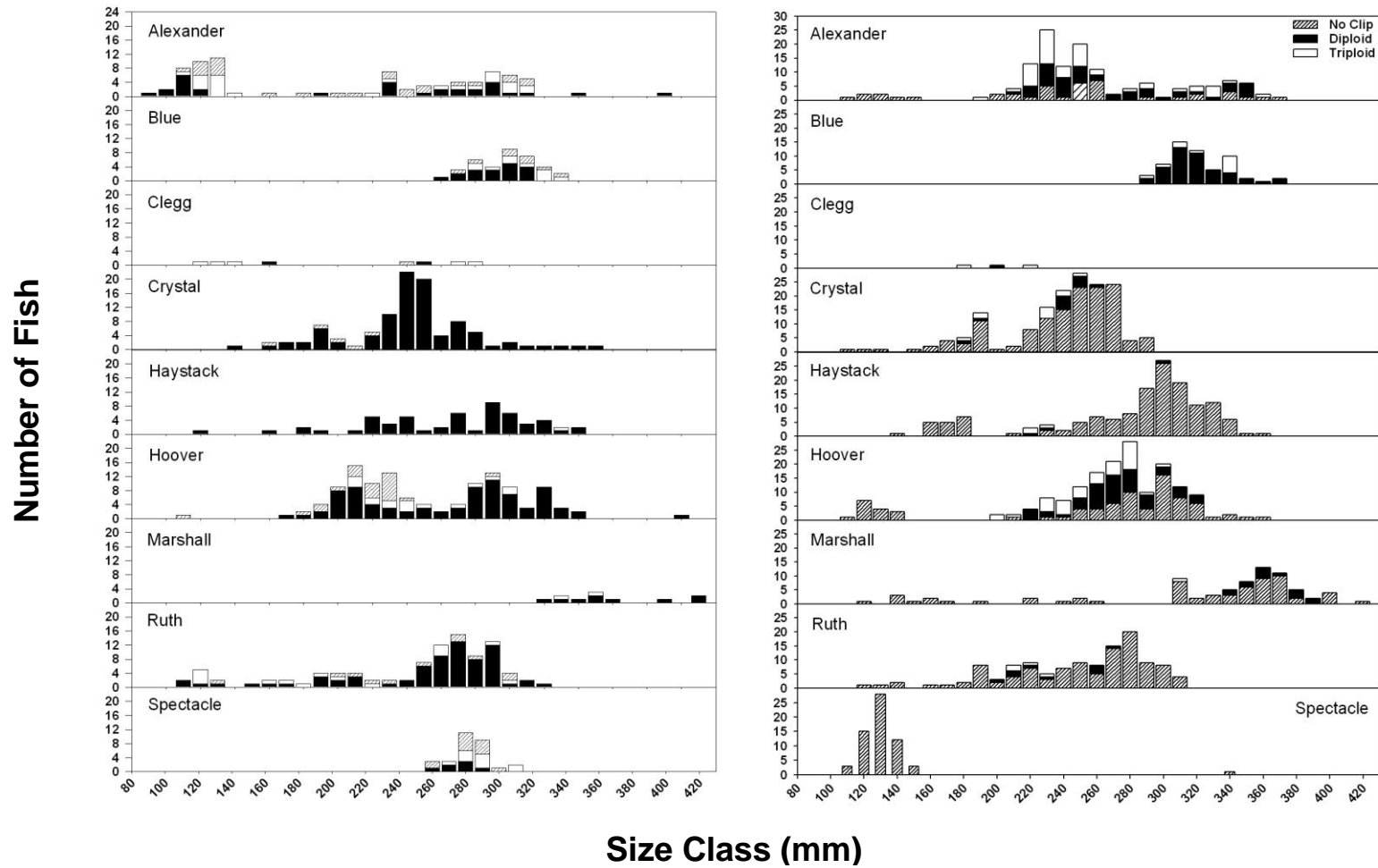


Figure 3. Size-frequency histograms (total length, mm) of triploid, diploid, and unmarked brook trout captured in 2008 (left panel) and 2009 (right panel). Note changes in y-axis ranges between two panels.

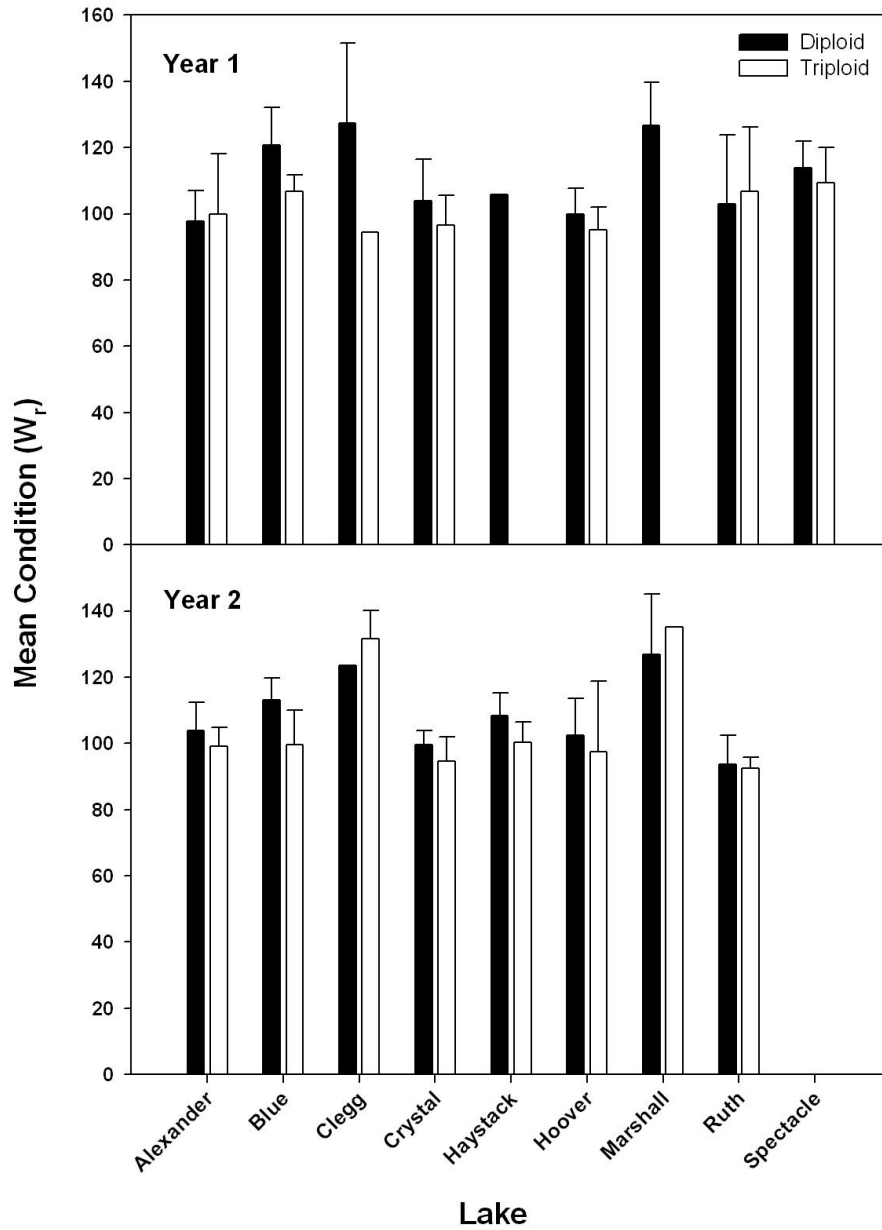


Figure 4. Mean condition (W_p , ± 1 SE) of diploid and triploid estimated in each lake (top panel = 2008 and bottom panel = 2009). No triploid fish were captured in Haystack and Marshall Lakes in 2008, and no marked fish were captured in Spectacle Lake in 2009.

In addition, triploid and diploid brook trout appeared to select similar prey items among lakes. Diptera dominated macroinvertebrate abundance across lakes (63.1 %), and Amphipoda and Isopoda ranked second (15.8%) and third (11.1%) in total macroinvertebrate abundance. Both ploidy groups typically selected for Coleoptera, Odonata, Amphipoda, and Diptera, as indicated by Strauss's L electivity index (Table 3).

Similarly, isotopic signatures indicated significant diet overlap and trophic position for both triploids and diploids across lakes in 2008. Carbon isotopic signatures ($\delta^{13}\text{C}$) were similar between diploid (mean \pm 2SE = -24.10 ± 1.14) and triploid (-24.91 ± 1.28 , Figure 5), as were nitrogen isotopic signatures ($\delta^{15}\text{N}$) between diploid (8.02 ± 0.51) and triploid (7.32 ± 0.46 , Figure 5) brook trout. Based on a paired Student's t-test, there was no significant difference in $\delta^{13}\text{C}$ between diploid and triploid isotopic signatures ($\delta^{13}\text{C}$, $t = 0.96$, $p = 0.35$, $df = 50$). However $\delta^{15}\text{N}$ signatures were significantly different between diploids and triploids ($\delta^{15}\text{N}$, $t = 2.01$, $p = 0.04$, $df = 50$).

Factors potentially limiting brook trout overall performance

Based on the variables I measured (Table 1), there appeared to be no abiotic conditions (e.g., DO and temperature) lethal to brook trout across all nine study lakes and in both years of the study. Temperature and DO remained within nonlethal limits (e.g., $4.5\text{-}23^\circ\text{C}$ and $> 5\text{ mg/L}$, respectively) for brook trout in all lakes throughout the summer (Figures 6 and 7). Minimum DO levels fell below the optimal range (9-15 mg/L; Raleigh 1982) for brook trout in all but two lakes over the summer months, yet these suboptimal

limits were never low enough to be lethal for brook trout (Figure 6). Over the summer, temperatures remained within the optimal range for brook trout growth in all lakes except

Table 3. Feeding electivity (Strauss's L) by diploid and triploid brook trout from five high mountain Uinta lakes in 2008. Greater values indicate preference and lower values indicate avoidance. The most preferred diet items are highlighted in bold. Only macroinvertebrates are shown, as extremely few zooplankton were found in diets.

Triploids		Lake			
Invertebrate taxa	Alexander	Blue	Hoover	Ruth	Spectacle
Amphipoda	-0.519	-0.181	-0.233	0.182	-0.005
Coleoptera	0.000	0.351	0.160	0.001	0.000
Diptera	0.407	-0.630	-0.430	-0.049	0.025
Ephemeroptera	0.000	0.000	-0.001	0.000	-0.002
Hemiptera	0.000	0.000	0.000	-0.002	0.000
Isopoda	0.000	-0.109	0.000	-0.143	0.000
Mollusca	-0.037	-0.008	-0.116	-0.039	0.000
Odonata	0.185	0.646	0.747	0.085	-0.002
Oligochaeta	-0.037	-0.068	-0.119	-0.067	-0.017
Trichoptera	0.000	0.000	0.000	0.035	0.000
Trombidiformes	0.000	0.000	-0.007	-0.004	0.000
Diploids		Lake			
Invertebrate taxa	Alexander	Blue	Hoover	Ruth	Spectacle
Amphipoda	-0.519	-0.165	-0.052	0.218	-0.005
Coleoptera	0.000	0.000	0.471	0.000	0.005
Diptera	0.741	-0.167	-0.430	0.334	-0.480
Ephemeroptera	0.000	0.000	-0.001	0.000	-0.002
Hemiptera	0.000	0.000	0.000	-0.002	0.000
Isopoda	0.000	-0.109	0.000	-0.439	0.000
Mollusca	-0.037	-0.008	-0.116	-0.040	0.000
Odonata	-0.148	0.496	0.255	0.000	0.498
Oligochaeta	-0.037	-0.068	-0.119	-0.067	-0.017
Trichoptera	0.000	0.021	0.000	0.000	0.000
Trombidiformes	0.000	0.000	-0.007	-0.004	0.000

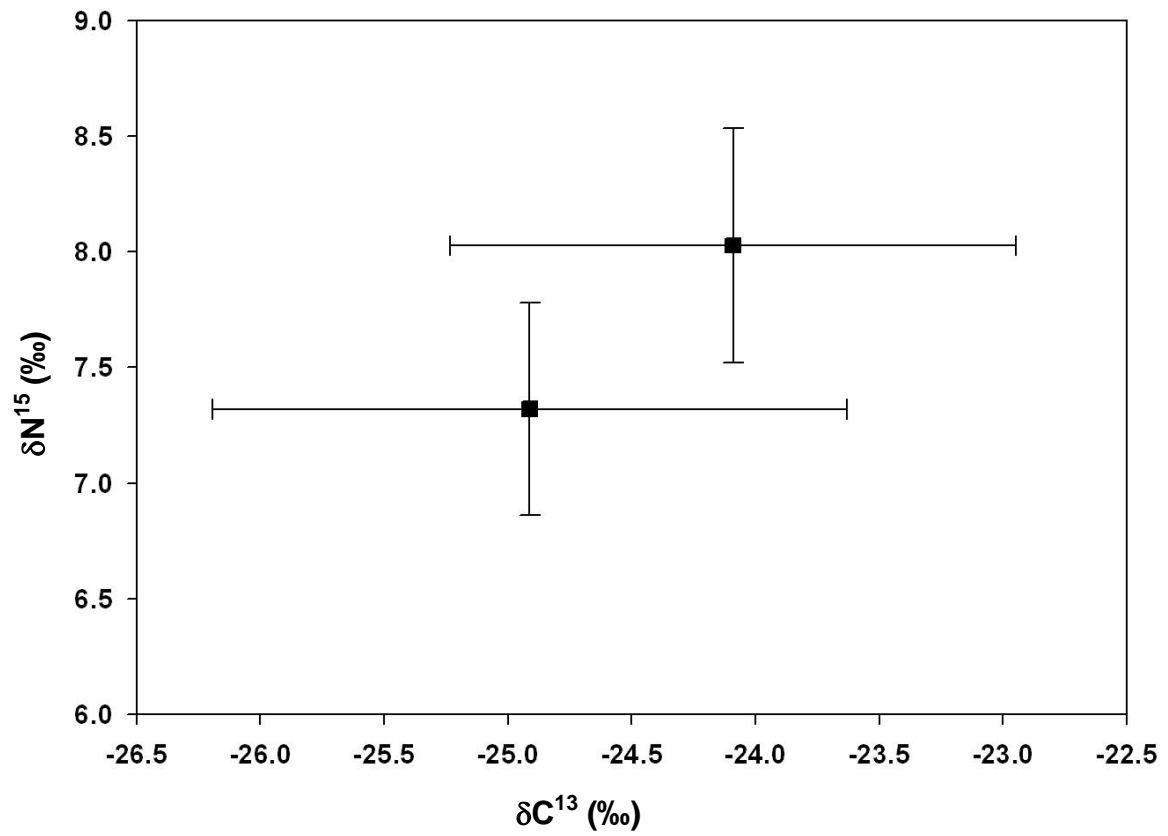


Figure 5. Mean δN^{15} and δC^{13} (± 2 SE) of triploid and diploid brook trout across the nine study lakes in 2008.

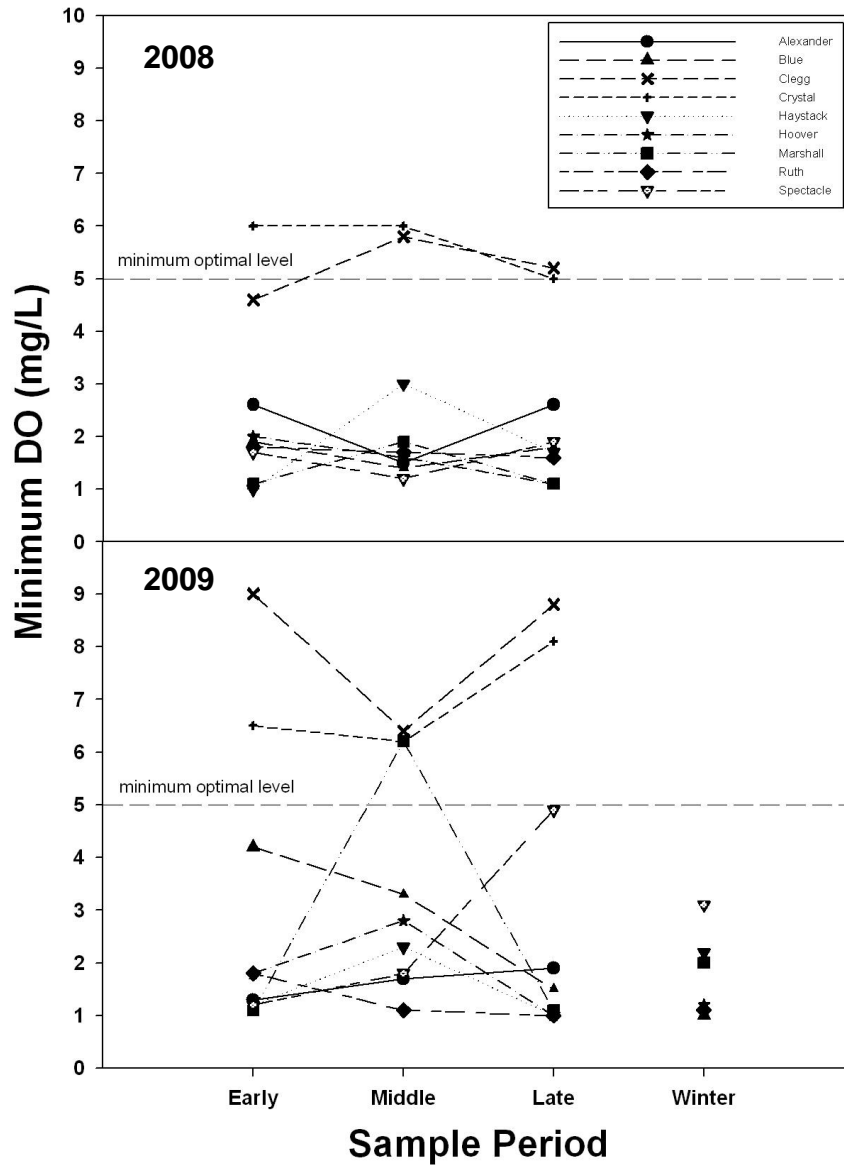


Figure 6. Minimum dissolved oxygen (mg/L) levels recorded during the three summer sampling periods in 2008 (top panel) and the three summer and one winter in 2009 (bottom panel). Dashed line represents the minimum DO (mg/L) threshold for optimal brook trout growth. Minimum DO concentrations were measured 1-2 meters from the bottom.

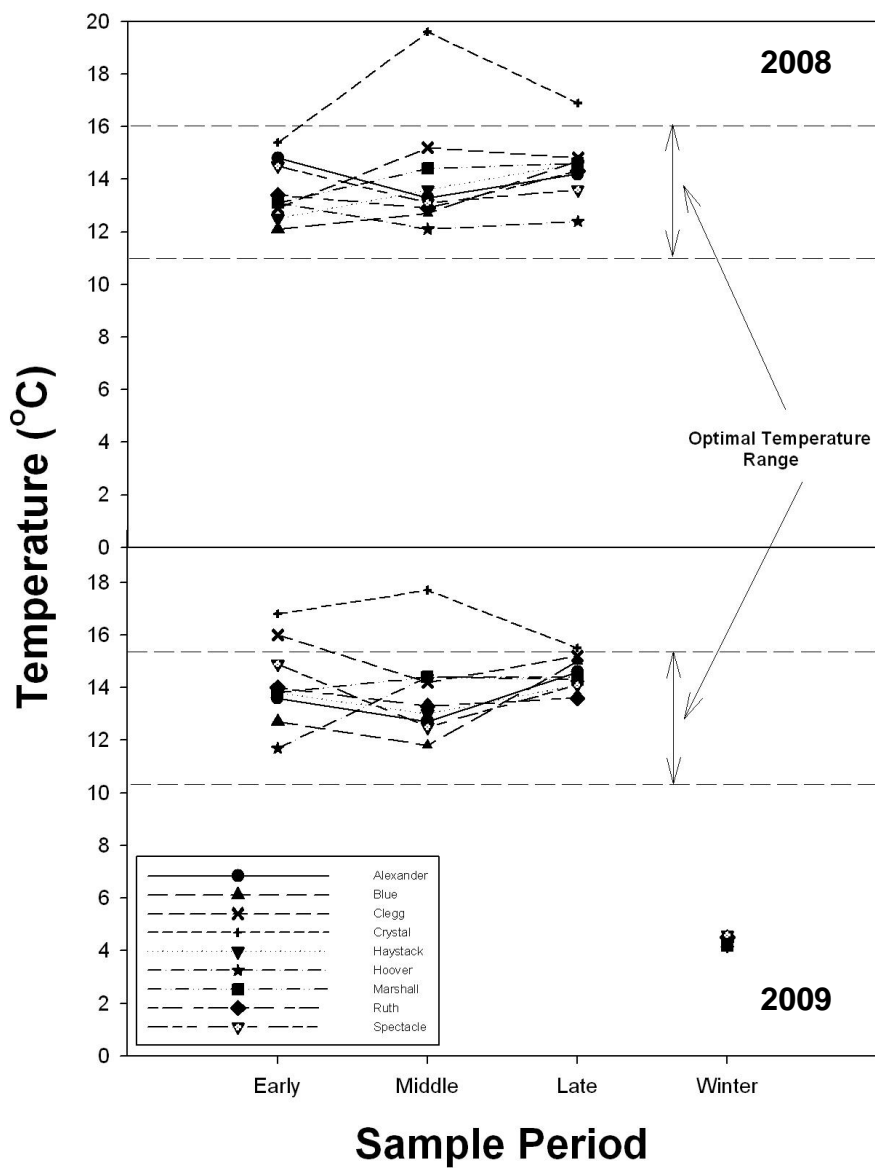


Figure 7. Observed temperature ($^{\circ}$ C) closest to the optimal temperature range for brook trout growth in 2008 (top panel) and 2009 (bottom panel). Winter measurements were only taken in 2009. In both panels, the optimal temperature range for brook trout growth is indicated by the band within the two horizontal dashed lines.

one, in which temperatures were consistently above the optimal range, but still not lethal for brook trout (Figure 7).

Indices of food availability were highly variable across lakes and in both years of the study. Total macroinvertebrate abundance ranged from 95 individuals/m² to 4686 individuals/m² (Figure 8). Dipterans and amphipods dominated the macroinvertebrate community in all lakes sampled in 2008 (range, 44% - 98% relative abundance). Zooplankton density ranged from 876 individuals/L to 2328 individuals/L (Figure 9).

Assessing factors potentially limiting brook trout performance: Random forest analysis

Overall (independent of ploidy group) and across all lakes the top four predictive variables of fish condition (W_r) based on Random Forest were: 1) total brook trout CPUE; 2) maximum depth; 3) surface area (ha); and 4) optimal temperature (percent variance explained = 25.6; Figure 10). Only three of these variables were significant in the hierarchical mixed model: CPUE (number of fish/net soak hour, $p < 0.0001$, $df = 34$), maximum depth (m, $p = 0.02$, $df = 6$) and optimal temperature (°C, $p = 0.01$, $df = 34$).

Partial dependence plots illustrate the effects of each of these top four predictor variables on relative weight while averaging the effects of all other variables of the Random Forest model. Relative weight decreased as CPUE and hectares increased (Figure 11). Inversely, relative weight increased as maximum depth and optimal temperature increased (Figure 11). However, an extreme outlier in the residuals of maximum depth appeared to influence the model, thus substantially minimizing the confidence that can be placed on this explanatory variable.

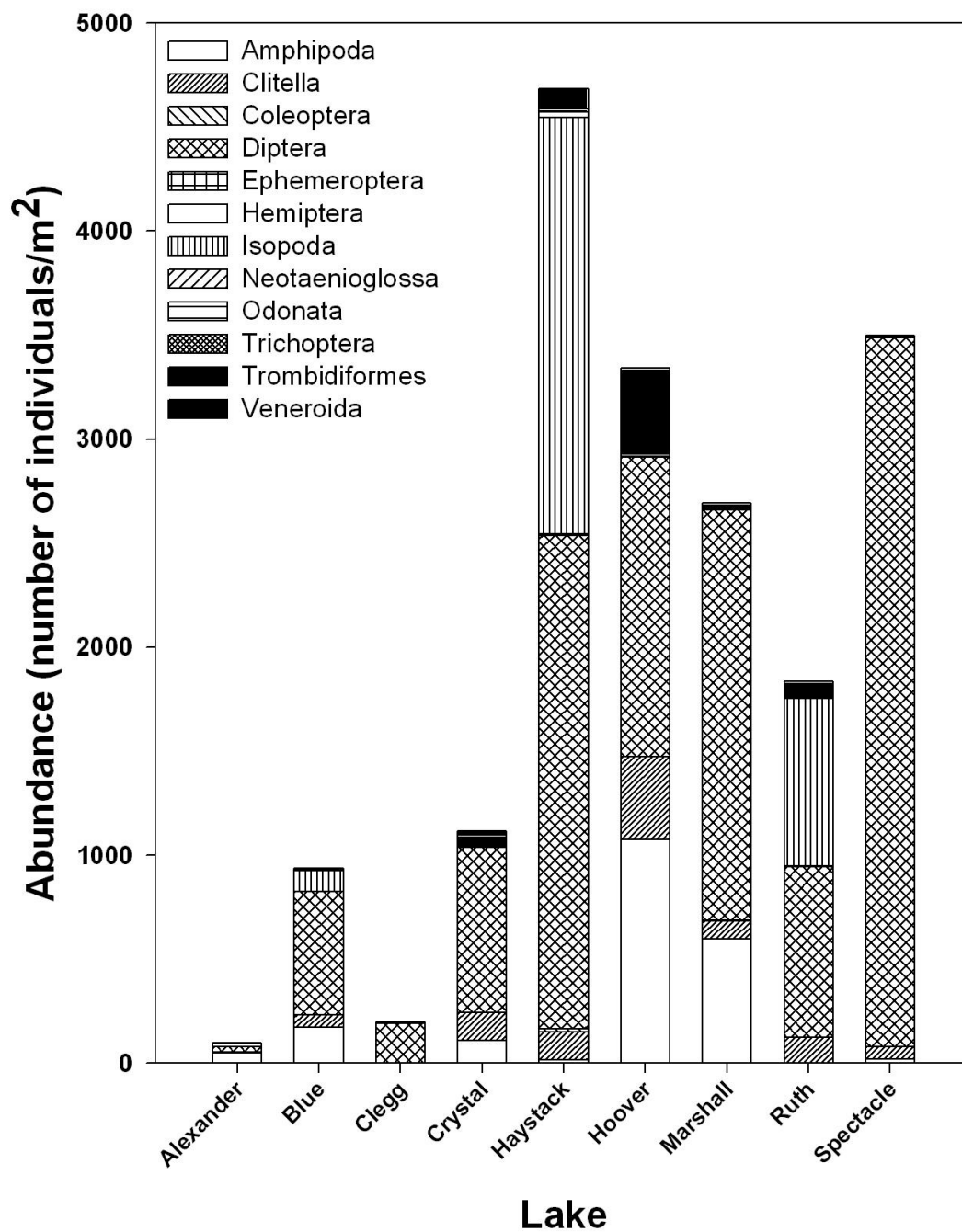


Figure 8. Macroinvertebrate abundance (number/m²) sampled in each lake.

Macroinvertebrates were only collected in 2008 for logistical and cost reasons.

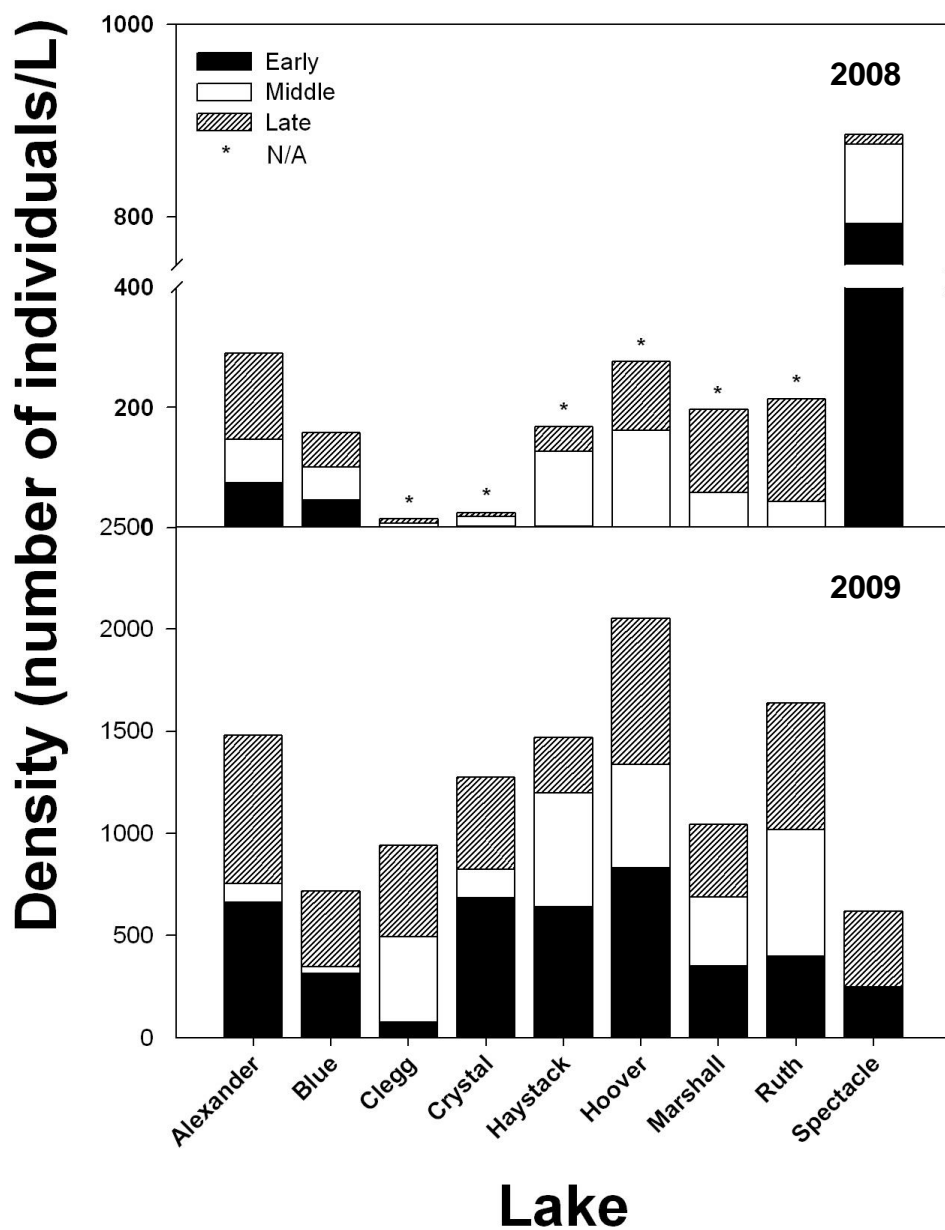


Figure 9. Zooplankton density (number of individuals/liter) for each lake from the early, middle and late sample periods of 2008 (top panel) and 2009 (top panel). N/A (*) indicates early sample date (black) was not available. Note the scale differences between the two sample years and the break in the y-axis of the top panel.

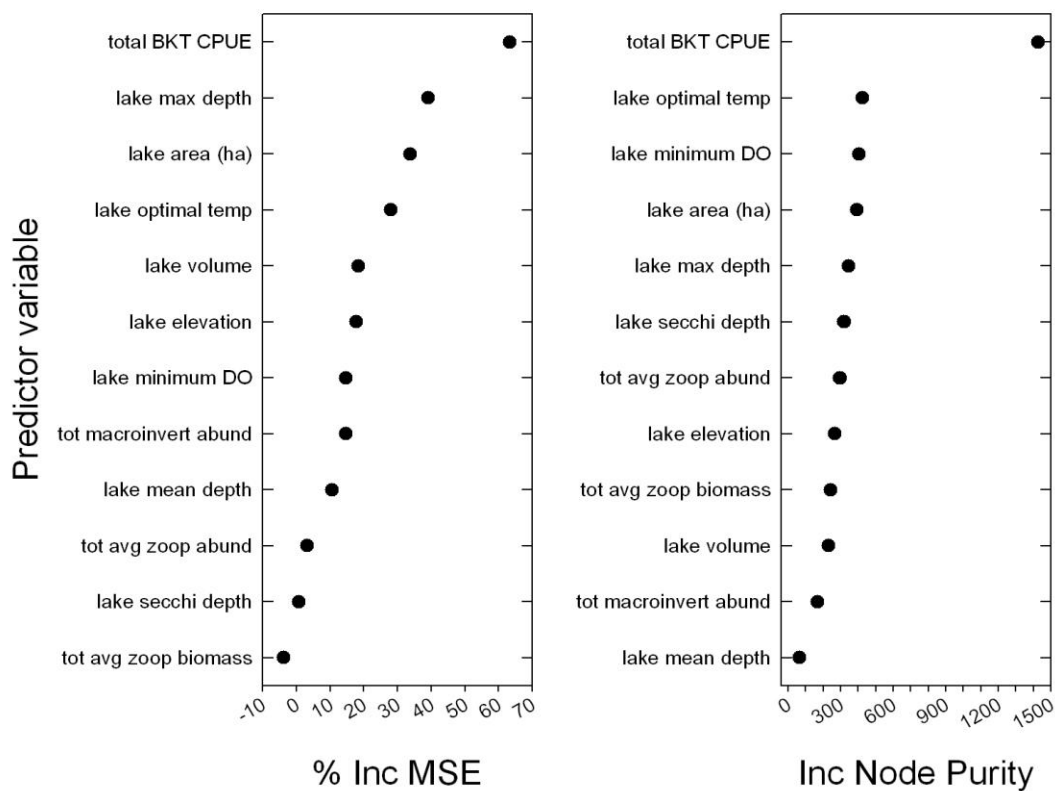


Figure 10. Variable importance plots from the Random Forest model used to determine average prediction error and assess variable importance in predicting brook trout relative weight among measured predictor variables of all nine study lakes. Increase in mean square error (accuracy) explained by each variable is shown in the left panel. the increase in node purity (influence) for each variable is shown in the right panel ($r^2 = 25.6$).

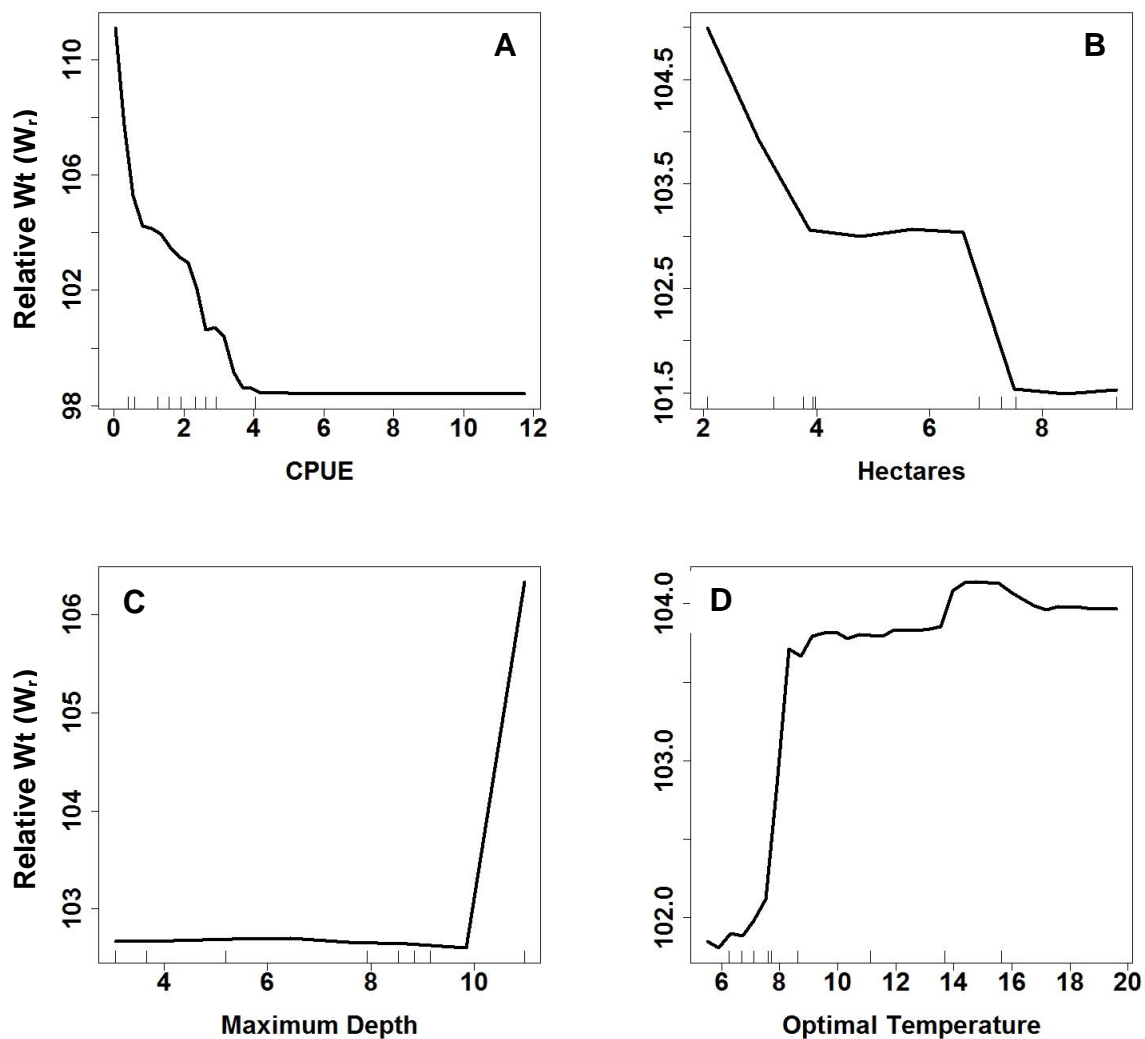


Figure 11. Partial dependence plots of the top four variables of the Random Forest model; relative weight (W_r) of all captured brook trout was the response variable. Partial dependency plots illustrate the effect of one predictor variable on the response variable. Partial dependence is represented by the effect on relative weight of catch per unit effort (A), hectares (B), maximum depth (C), and optimal temperature (D). Note the difference in scale of the y-axes.

DISCUSSION

A common trend in comparisons of the performance of sterile versus reproductively viable fish is a considerable degree of variability in results across studies. This variability may stem from the systems within which the ploidy groups are compared, the species studied, or both (Kerby et al. 2002; Peruzzi et al. 2005). Despite such variability, the few studies to date that have compared the performance of triploid and diploid salmonids generally reveal similar performance among the two ploidy groups as well as similar responses to potentially limiting physical conditions (Oppedal et al. 2003; Stillwell and Benfey 1997; Galbreath et al. 2006). Accordingly, I compared the relative performance of diploid and triploid brook trout in high mountain lakes and overall performance across a suite of biotic and abiotic measures.

The similarity in condition (W_r) of diploid and triploid fish observed here has been noted elsewhere in both related and more distant species (Chiasson et al. 2009, McGeachy et al. 1995; Xiaoyun et al. 2010). I did not observe any differences in fish condition between triploid and diploid stocked brook trout, also documented by Wagner et al. (2006), for rainbow trout, for example. This similarity of condition between the two ploidy groups was also noted in an outdoor pond experiment of the same strain of brook trout by Budy et al. (2012). However, although condition was not different between the two ploidy groups, overall condition was very poor, independent of ploidy group. Poor fish condition is not entirely surprising in these high elevation, cold mountain lakes, as the growing season is short, and the lakes are generally oligotrophic, with low food availability (Lienesch et al. 2005). Nonetheless, strong signals of density

dependence (discussed below) observed in these lakes indicate that poor growth conditions in these types of lakes may be exacerbated by high stocking densities (see below).

In contrast to considerable similarity in relative condition, the size structure of diploid brook trout was significantly, although marginally, skewed towards larger sizes relative to triploids in some lakes. Simon et al. (1993) similarly noted larger sizes of diploids compared with triploids, a difference they attributed to physiological differences due to ploidy level. Diploid brook trout are likely reaching larger sizes as a result of faster growth rates prior to sexual maturation. In contrast, triploid brook trout of the same strain used in stocking Uinta lakes attained similar sizes in outdoor ponds (Budy et al. 2012), although those trout only represented a single age class. Across my study lakes, there appear to be three size classes present, representing age classes 1, 2, and 3. Assuming they can survive over the winter, as more diploid fish age, mature sexually, and reproduce, I would expect this modest size advantage to disappear (Hyndman et al. 2003). In addition, it is important to note that the slightly larger size of diploids may be biologically insignificant and simply an artifact of the very large sample size. Lastly, the mean difference (~ 20 mm) in size between ploidy groups was small and may be a negligible difference to the average, weekend angler who commonly uses this fishery.

Differences in diet preference and trophic position between ploidy groups could indicate differences in feeding strategy or that one ploidy group was a superior competitor for space or food (Hilderbrand and Kershner 2004). However, based on the extensive similarities in diet between ploidy groups and the similarity in trophic position,

it appears that both ploidy groups are consuming the same diet items and feeding at a similar trophic position. Although $\delta^{15}\text{N}$ signatures were significantly different between diploids and triploids, the difference is likely not biologically significant given a change of 3.4 ‰ trophic fractionation between each trophic level increase (Minagawa and Wada 1984). Furthermore, in lakes with adequate sample sizes of marked fish, diet preference was also similar between ploidy groups. Of the five lakes for which I compared diet preference (Strauss's L electivity index), diploid and triploid diet preference was nearly identical. And, in four of the five lakes, both triploids and diploids selected for at least one (e.g., Diptera) of the two most common benthic invertebrates, suggesting both ploidy groups are generally opportunistic feeders (Allan 1981; Morinville and Rasmussen 2006). In sum, the lack of difference in diet, diet preference, and trophic position between ploidy groups parallels the similarity in fish performance overall, between ploidy groups.

*Factors potentially limiting growth
and survival overall*

As has been observed elsewhere, the factors that appear to be most influential in determining the performance of stocked trout and salmonids in high elevation lakes were associated with lake size and total fish density (Post et al. 1999, Buktenica et al. 2007), not ploidy group. Lachance and Magnan (1990) reported poorer return yield and weight of brook trout stocked into lakes with high fish densities. Comparatively, my results illustrate poorer condition of brook trout stocked in high density environments. Lakes with higher fish density were also the larger lakes sampled in this study. The poor condition of brook trout in the larger lakes of my study suggests the possibility of inter

and intraspecific competition for food resources. Competition for food resources has been noted in other oligotrophic, mountain lakes where food resources were limited (Cavalli et al. 1998). In general, large lakes with high CPUE contained fish with lower body condition, and smaller lakes with low CPUE contained fish with higher body condition. This pattern suggests CPUE and condition (W_r) may be a function of lake size, or a function of a factor driven by or co-varying with lake size, such as habitat availability, food availability or temperature.

Both statistical models used in this study indicated strong signals of density dependent effects on fish performance. Independent of ploidy group, CPUE, maximum lake depth and lake size (area) were the top three predictor variables of W_r across lakes and years in a Random Forest model. CPUE and maximum lake depth were the only significant variables in the hierarchical-mixed model as well. These strong signals of density-dependent effects are often found in oligotrophic lakes, where greater growth rates occur when fish densities are low. Amundsen et al. (2007) found that lowering densities of Arctic char (*Salvelinus alpinus*) in lakes similar to my study lakes decreased intra-specific competition for food resources. Similarly, higher densities of steelhead trout (*Oncorhynchus mykiss*) increased competition by for food resources and habitat in artificial stream segments (Keeley 2001). Lake size (ha) and depth likely influenced fish densities in this study and subsequently fish condition.

Furthermore, this general pattern of lower condition and higher CPUE could not be explained based on density-dependent effects or temperature alone. Generally, larger lakes experience thermal stratification allowing cold-water species such as salmonids to

persist even when epilimnion temperatures approach or exceed upper thermal limits (Jackson and Harvey 1989). In the larger lakes of my study, brook trout were able to persist lower in the water column where temperatures were more optimal for survival and growth during the summer. Additionally, the larger deeper lakes likely also provided ample areas where brook trout were able to survive throughout winter conditions (ice depths reached nearly one meter). In the smaller lakes, the lesser proportion of the lake suitable for brook trout during the summer may similarly contribute to low over-winter survival, where ice likely reached the bottom or very near the bottom throughout most of the lake. Therefore, in addition to density effects, some of the difference in CPUE across lakes is likely the result of harsh over winter conditions, when habitat (e.g., anoxia) and food availability are already low (Bystrom et al. 2006). These over-winter conditions may also explain the poor overall condition of stocked brook trout that over-wintered.

In addition to a relationship between lake size, CPUE and condition (W_r), connectivity between lakes may also influence condition and CPUE. Crystal Lake is connected to another lake, Washington Lake, a larger, deeper lake a few hundred meters to the south that remains connected to Crystal Lake through a small stream throughout the spring and most of the summer months. Fish have the opportunity to move freely between lakes during spring run-off and early summer, potentially supplementing fish populations in Crystal Lake from Washington Lake. All other large lakes in my study generally remain disconnected from other source populations. These remaining larger lakes had high CPUE in both years of my study. Consequently, condition of brook trout within these larger lakes was consistently lower than lakes with low CPUE, again

suggesting density-dependent effects.

Management implications

These findings have important implications for management of high mountain Uinta lakes as well as important broader implications for the conservation of native fishes and their aquatic ecosystems. First, marked variability in relative performance of stocked brook trout across lakes, independent of ploidy level, calls for a reevaluation of which lakes to stock and at what densities. Strong signals of density dependence indicate these lakes are food limited and that stocked brook trout could potentially survive better and attain larger sizes if stocked at lower densities. Second, consistent similarities in relative performance between triploid and diploid brook trout stocked in Uinta lakes suggest triploids may offer a more risk averse and promising opportunity when stocking non-native brook trout to these and other lakes. The opportunity to stock sterile fish in ecosystems similar to Uinta lakes will prevent hybridization with native species and prevent the establishment in other downstream water bodies. The benefits of stocking sterile triploid brook trout allow State agencies to simultaneously maintain a non-native sport fishery as well as meet conservation goals.

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