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ARTICLE

A Comparative and Experimental Evaluation of Performance of Stocked Diploid and Triploid Brook Trout

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Abstract

Despite numerous negative impacts, nonnative trout are still being stocked to provide economically and socially valuable sport fisheries in western mountain lakes. We evaluated relative performance and potential differences in feeding strategy and competitive ability of triploid versus diploid brook trout *Salvelinus fontinalis* in alpine lakes, as well as behavioral and performance differences of diploid and triploid brook trout in two controlled experimental settings: behavioral experiments in the laboratory and performance evaluations in ponds. Across lakes, catch per unit effort (CPUE) and relative weight (W_r) were not significantly different between ploidy levels. Mean sizes were also similar between ploidy levels except in two of the larger lakes where diploids attained slightly larger sizes (approximately 20 mm longer). We observed no significant differences between diploids and triploids in diet, diet preference, or trophic structure. Similarly, growth and condition did not differ between ploidy levels in smaller-scale pond experiments, and aggressive behavior did not differ between ploidy levels (fed or unfed fish trials) in the laboratory. Independent of ploidy level, the relative performance of brook trout varied widely among lakes, a pattern that appeared to be a function of lake size or a factor that covaries with lake size such as temperature regime or carrying capacity. In summary, we observed no significant differences in the relative performance of brook trout from either ploidy level across a number of indices, systems, and environmental conditions, nor any indication that one group is more aggressive or a superior competitor than the other. Collectively, these results suggest that triploid brook trout will offer a more risk-averse and promising management opportunity when they are stocked to these lakes and elsewhere to simultaneously meet the needs for the sport fishery and conservation objectives.

The introduction of nonnative species to aquatic ecosystems has had numerous negative impacts, including direct predation on native species (Ruzycki et al. 2003; Pelicice and Agostinho 2009), dramatic changes to community structure (Reissig et al. 2006), altered energy flow (Sousa et al. 2008; Nalepa et al. 2009), and increased pathogen transmission to water bodies and native species (Minchin 2007). Specifically, the introduction of nonnative fishes to historically fishless, alpine lakes has had profound effects, including the downstream dispersal and invasion of streams and lakes that contain native fish populations (Adams et al. 2001; Knapp et al. 2001), shifts 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 et al. 2001; Dunham et al. 2002). Despite these ubiquitous negative impacts, nonnative fishes are still being stocked to provide and sustain both economically and socially valuable sport fisheries in western mountain lakes (e.g., Halverson 2008).

Reproductively sterile fish may provide a more ecologically risk-averse alternative to stocking fertile fish. Sterility may prevent genetic introgression with native fishes and reduce the risk of creating self-sustaining nonnative populations. Sterilization programs have been successful in closed environments and with nonanadromous fishes (Johnston et al. 1993; Dillon et al. 2000; Kozfkay et al. 2006). Sterility can be induced by several techniques, including the production of triploidy by pressure- or

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heat-shocking the eggs (Donaldson 1986; Feist et al. 1996). Sterile triploid fishes are already widely used both in commercial aquaculture and in sport fish hatcheries as an alternative to diploid (i.e., fertile) fish (O'Keefe and Benfey 1999; Hyndman et al. 2003; Koenig and Meyer 2011). Thus, stocking sterile fish in natural lakes may provide a way to balance the interests of native fish conservation with those of sport fishery management (Kozfkay et al. 2006).

Although the sterility of triploid fish provides an ecological advantage, fitness relative to diploid fish can very greatly among species and environmental conditions, which is an important consideration for establishing viable fisheries. For example, theoretically female triploid fish should have higher growth rates because they demonstrate fewer physiological changes associated with sexual maturation (e.g., inhibited muscle development; Thorgaard and Gall 1979), changes that can result in significant losses in production (Wlasow et al. 2004). Furthermore, female triploid fish should be able to allocate more energy to somatic growth than to reproduction (Hyndman et al. 2003). Higher growth rates of female triploid fishes have been shown for rainbow trout *Oncorhynchus mykiss* (Suresh and Sheehan 1998; Sheehan et al. 1999) and turbot *Psetta maxima* (Cal et al. 2006). In contrast, however, Koenig and Meyer (2011) observed no differences in length, weight, or dressed weight between diploid and triploid rainbow trout within a year of being stocked in 13 Idaho reservoirs.

In addition to potential differences in growth rates, triploids may also respond differently to some physiologically stressful environmental conditions (Galbreath et al. 2006). For example, triploid shi drums *Umbrina cirrosa* demonstrated lesser ability to tolerate stressors relative to diploid shi drums due to larger cell sizes, altered metabolic rates, and an increased sensitivity to elevated water temperatures, all of which lower their competitive ability under suboptimal conditions (Ballarin et al. 2004). In contrast, others have suggested that because triploid fish may experience a lower metabolic rate, they have a greater ability to tolerate lower concentrations of dissolved oxygen and other physical stressors (Stillwell and Benfey 1997). Triploid brook trout *Salvelinus fontinalis*, Atlantic salmon *Salmo salar*, and rainbow trout all demonstrated similar stress responses as diploids (Benfey and Biron 2000; Sadler et al. 2000; Maxime 2008), and other studies have observed no difference in critical thermal maxima or swimming velocity between triploid and diploid brook trout (Benfey et al. 1997; Stillwell and Benfey 1997). Nonetheless, if significant, altered performance due to physiological or metabolic differences in triploids could lead to a decrease in growth and increased mortality relative to diploids (Suresh and Sheehan 1998; Hyndman et al. 2003; Atkins and Benfey 2008). Clearly, based on these fitness-related measures alone, the performance of triploids relative to diploids may be highly dependent on environmental conditions such that the capacity for replacing diploids with triploids in popular fisheries remains uncertain (Koenig and Meyer 2011).

In summary, true differences in fitness and behavior between triploid and diploid fish appear to be highly variable, species-specific, and poorly understood in many natural settings. Furthermore, in addition to the factors that may determine the relative differences between diploids and triploids, there are a number of other factors that can influence the stocking success of fishes in general, including fish health, domesticated behavior, fish handling and transport, size at stocking, diet conversion, and habitat and environmental factors in the target water body (see reviews by Cresswell 1981; Cresswell et al. 1982; Kerr 2000). Collectively, these uncertainties highlight the need to evaluate performance of triploid and diploid fish prior to the initiation of a widespread and potentially costly or risky stocking program (Kozfkay et al. 2006).

Although not endemic to the western U.S., brook trout have been stocked throughout the region since the mid-1800s (Tyus et al. 1982). Past stocking has greatly expanded the distribution of brook trout outside their native range such that they are now among the most common salmonids in western streams (MacCrimmon and Campbell 1969; Fuller et al. 1999). Self-sustaining nonnative brook trout populations are widespread and abundant in mountain lakes of Colorado and Wyoming where they are considered nuisance species that threaten populations of the native cutthroat trout *O. clarkii* via cross-breeding and competition for resources (Hirsch et al. 2006). Nevertheless, brook trout are still currently managed as a game fish stocked for recreational fishing in several states (Ficke et al. 2009).

Due to their popularity among anglers, brook trout have been stocked in Utah lakes for over a century. Other previously stocked species include cutthroat trout, rainbow trout, and Arctic grayling *Thymallus arcticus* (Sigler and Sigler 1996). As a result of this long stocking history, brook trout have become established in many cold mountain lakes and streams throughout the state, including those in the Uinta Mountain range of northeastern Utah. Presently, approximately 60 lakes in the Uinta Mountains support wild brook trout populations (Carlisle and Hawkins 1998), and more than 100 Uinta Mountain lakes are stocked regularly with brook trout by the Utah Division of Wildlife Resources (UDWR). Uinta Mountain lakes are extremely popular for brook trout fishing and provide an important recreational, cultural, and economic resource to the state of Utah. However, naturally reproducing populations of brook trout have overpopulated many natural lakes, threatening native fish populations. Thus, in recent years UDWR has begun to consider a strategy of stocking only sterile triploid brook trout in an effort to maintain these economically valuable sport fisheries while protecting native cutthroat populations (W. Pearce, UDWR, personal communication).

To assess the effectiveness of a triploid-only management strategy, we evaluated the relative (triploid versus diploid) and overall (independent of ploidy level) performance of stocked brook trout in Uinta Mountain lakes. Specifically, we tested for differences in the relative performance, feeding strategy, and competitive ability of triploid and diploid brook trout stocked

TABLE 1. Physical conditions, water quality variables, and zooplankton densities for the nine study lakes in the western portion of the Uinta Mountains, Utah. Water quality values are means determined from a vertical profile of each lake during three summer sampling periods in 2008 and 2009 (average of all sampling periods in both years). T = temperature, DO = dissolved oxygen (range of minimum to maximum), Secchi = Secchi disk depth, Chl a = chlorophyll a concentrations.

Lake	Elevation (m)	Maximum depth (m)	Mean depth (m) (m)	Surface area (ha)	Volume (m^3)	T (°C)	DO (mg/L)	Secchi (m)	Chl a (μg/L)	Zooplankton (number/L)
Alexander	2,853	8.5	4.6	9.3	425,551	8.13	0.80–7.53	3.63	46.78	294.8
Blue	2,950	7.9	3.0	3.2	98,679	7.05	1.10–7.72	2.98	4.58	127.0
Clegg	3,188	3.7	2.1	2.1	44,035	13.48	2.88–7.67	3.10	6.82	159.2
Crystal	3,109	3.0	1.4	4.0	54,397	16.85	5.27–7.52	2.28	2.86	216.9
Haystack	3,030	8.8	3.4	6.9	230,661	7.31	1.37–8.55	3.49	3.11	235.0
Hoover	3,017	8.5	3.0	7.5	229,427	7.19	0.58–8.68	4.82	15.73	380.4
Marshall	3,045	11.0	4.6	7.3	333,040	6.95	1.38–10.18	6.25	4.96	187.2
Ruth	3,152	9.1	3.7	3.9	143,577	7.25	0.63–8.10	3.51	6.76	308.5
Spectacle	2,969	5.2	1.8	3.8	68,828	11.89	1.48–7.13	2.83	5.41	240.4

in high mountain lakes, and behavioral and performance differences of diploid and triploid brook trout in two controlled settings: behavioral experiments in the laboratory and performance evaluations in ponds.

METHODS

Performance Evaluations in Lakes

Study lakes.—The nine study lakes (Alexander, Blue, Clegg, Crystal, Haystack, Hoover, Marshall, Ruth, and Spectacle lakes) are located along the Mirror Lake corridor of the Uinta Mountains in northeastern Utah (Figure 1; Table 1). We selected these nine lakes from a larger set of high Uinta Mountain lakes because they represented a large range of elevations, lake morphologies, and associated abiotic conditions found in the Uinta range and could be stocked with an equal ratio of uniquely marked (e.g., fin-clipped) triploid and diploid brook trout. Lake elevations range from 2,845 to 3,180 m above sea level, maximum depths range from 3.0 to 10.9 m, mean depths range from 1.4 to 4.6 m, and lake sizes range from 2.1 to 9.3 ha (Table 1). The high elevations of these lakes result in a short summer growing season (late June to mid-October) and long winter season. Deeper lakes in the range usually stratify for a short period of time during midsummer (late July to mid-August) and become mixed again during late August, whereas shallow lakes (<5 m maximum depth) typically do not stratify over the summer due to complete solar heating throughout the day.

From 2006 to 2008, UDWR (Kamas State Fish Hatchery) stocked an equal ratio of age-0 (~7 month old) triploid and diploid mixed-sex brook trout in the nine study lakes (Table 2). At the time of stocking, diploids were on average 198 mm total length (TL) and 86 g, and triploids were 209 mm TL and 104 g. Fish were stocked at a quota of approximately 247 fish/ha (100 fish/acre) for brook trout that was adjusted throughout the years based on fish condition (Fulton's condition factor [K] or relative weight [W_r]) at the time of sampling and angling

TABLE 2. Annual stocking records for diploid (2N) and triploid (3N) brook trout, stocked by the Northern Region of Utah Division of Wildlife Resources, 2006 – 2008, for nine study lakes in the western portion of the Uinta Mountains, Utah. "Pressure" refers to the angler pressure, where L = light, M = moderate, H = heavy, and VH = very heavy. "Quota" refers to the total number of trout stocked (both ploidy levels), whereas "rate" refers to the stocking quota per hectare of both ploidy levels; quota is matched to a "cycle" that determines the frequency of stocking (e.g., every 1, 2, or 3 years)

				Rate	2006		2007		2008	
Lake	Pressure	Quota	Cycle	(number/ha)	2N	3N	2N	3N	2N	3N
Alexander	H	2,300	1	247.3	1,113	1,148	1,152	1,150	1,210	1,226
Blue	M–H	600	3	187.5	305	294				
Clegg	M	500	2	238.1	504	504			249	247
Crystal	H	1,000	1	250.0	504	504	498	498	498	504
Haystack	H	900	2	130.4	452	448			454	447
Hoover	VH	1,400	1	186.7	945	952	948	948	943	950
Marshall	H	1,800	2	246.6	903	896				
Ruth	H	500	1	128.2	252	252	252	252	249	247
Spectacle	L	1,400	3	368.4	704	700				

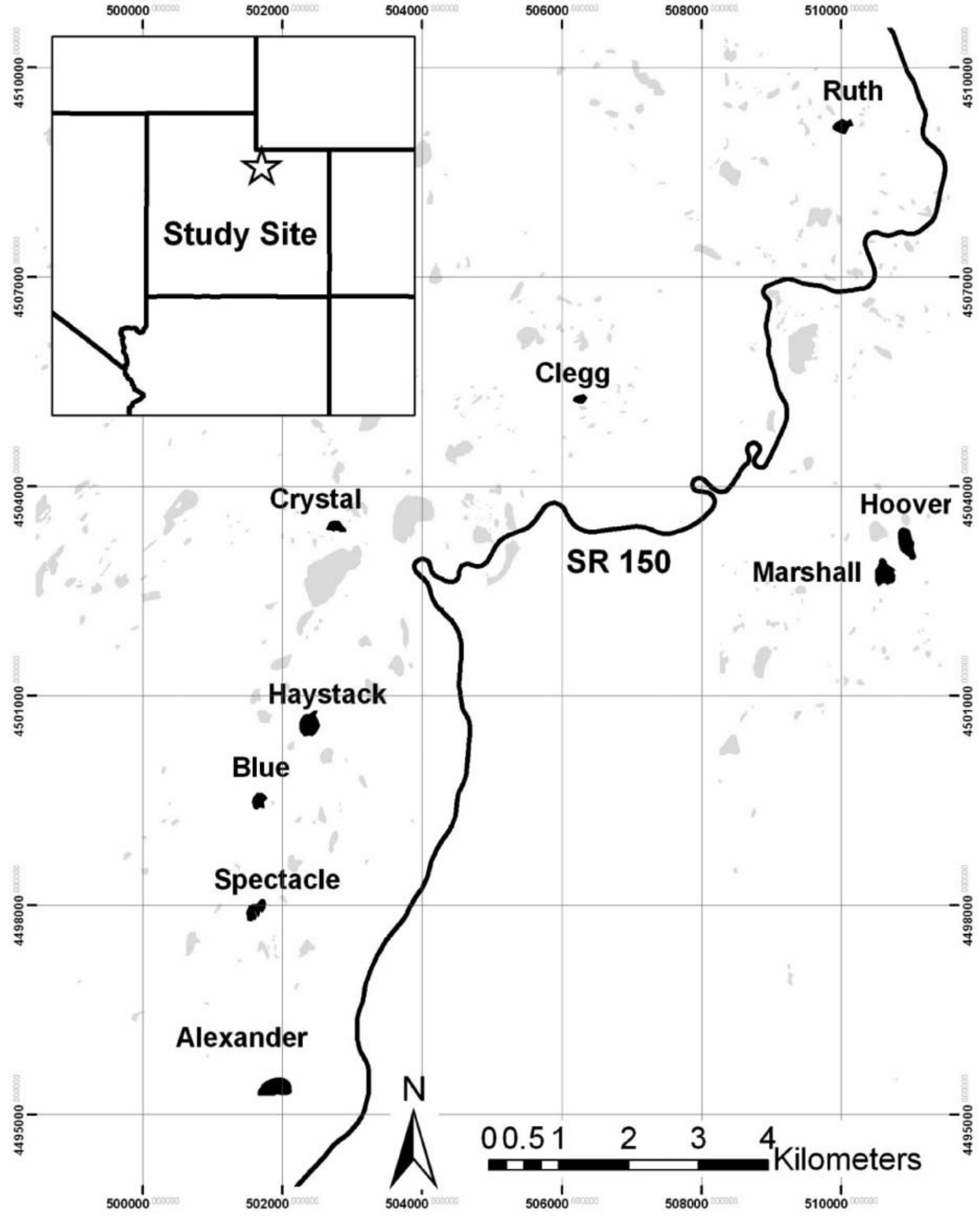

FIGURE 1. Study area of the nine study lakes in the western portion of the Uinta Mountains along the Mirror Lake Corridor of northeastern Utah.

pressure at lakes along the Mirror Lake Highway. Adjustments to stocking rates have been made by UDWR based on more than 30 years of gill-net surveys and qualitative assessments of fishing pressure (R. Wilson, UDWR, personal communication). Quotas were also matched to a "cycle" that determines the frequency of stocking (e.g., every 1 or 2 years).

All brook trout in this study came from the UDWR Egan Hatchery brood stock and the Owhi strain, which was introduced to Utah in 1979 and is the only brook trout strain in the state. Fish stocked in 2006 and 2007 were from the same parents, whereas the 2008 fish were from one year-class younger. Triploids are produced in all UDWR hatcheries by pressure-shocking the eggs (9,500 psi for 4 min). A large number of efficacy fish were retained after stocking to evaluate posttagging and handling mortality, and the mortality rate for these fish was near zero (T. Hallows, UDWR, personal communication). In each year, UDWR randomly samples lots from the different hatcheries for blood testing; the triploid percentage varies between 75% and 100%, depending on the year and hatchery. In 2007 and 2008 the triploid percentage from the Kamas Hatchery was 100%; data for Kamas Hatchery in 2006 are not available. Left and right pelvic fin clips were used to distinguish the diploid and triploid groups, respectively, and all fish stocked during these years were marked

Relative abundance, size structure, and condition.—In 2008 and 2009, we captured brook trout three times throughout the summer months (early, 1–8 July; middle, 21–28 July; and late, 18–25 August) using experimental monofilament floating gillnets set overnight. Gill nets consisted of seven 7.6-m panels, each of a different mesh size (ranging from 1.27 to 5.08 cm in 0.635-cm increments), placed in random order throughout the net. Two nets were used per lake. We measured (nearest 1 mm TL) and weighed (mass to nearest 0.1 g) all captured fish to determine population size structure and fish condition. We assessed fish condition using W_r, the ratio of the measured weight to the expected weight for a healthy brook trout of the same length (i.e., standard weight). We used the standard weight (W_s) equation for brook trout of Hyatt and Hubert (2001) based on TL (mm): $\log_{10} W_s = -5.186 + 3.103 \log_{10}\mathrm{TL}$. We calculated the relative abundance of both triploid and diploid brook trout using catch per unit effort (CPUE; fish/h) of gill nets for each sampling period and year.

Statistical analysis: lake performance.—We tested the effects of "ploidy", "year" and sampling "time" (early, mid, late) on CPUE using a randomized block design with lake as the random blocking factor. "Year" and "time" were fixed-effects factors that were repeated measures on lake. We partitioned residual variance into separate estimates for each sampling time (i.e., variance was heterogeneous for "time"). We log transformed CPUE prior to analysis to better meet assumptions of normality and homogeneity of variance; due to zero values, a small increment was added to each observation prior to transformation. Similarly, we assessed the effects of "ploidy" and "year" on mean W_r using an ANOVA of a randomized block design where "lake" was again the random blocking factor. Both "ploidy" and "year" were fixed-effects factors associated with repeated measures within "lake". We partitioned residual variance into heterogeneous variances for ploidy level, where the triploid variance was greater than the diploid variance. In addition, we compared the relative size structure and growth of diploid and triploid brook trout based on length-frequency histograms for each ploidy level within and among lakes. We evaluated statistical differences in the length distributions of diploid and triploid brook trout using a Kolmogorov–Smirnov test (D_{KS}; Neumann and Allen 2007) across lakes.

Limnology and food availability.—We measured several water quality characteristics during each fish sampling period in all nine lakes and once over the 2009 winter in six lakes (reported in Budy et al. 2011) to identify abiotic factors that potentially limit the performance of brook trout. We measured temperature (°C) and dissolved oxygen (DO; mg/L) profiles at 0.5-m increments from the surface to the bottom of the lake. In addition, we placed temperature loggers in each lake near the bottom (approximately 2 m from the bottom) and approximately midlake depth (approximately 3 m from the surface) with an anchored buoy to continuously record hourly temperatures over a full year. We recorded Secchi disk depth as an index of water transparency at the deepest site. We collected water samples for chlorophyll *a*, as an indicator of phytoplankton biomass, at the midpoint of each lake using an integrated 8-m plastic tube throughout the water column. We placed all collected matter in an opaque bottle until we returned to shore. We filtered a known volume of each sample in the field though a glass-fiber filter, which we then wrapped in aluminum foil and kept frozen until analysis. Chlorophyll *a* was extracted in the laboratory in a known volume of ethanol for 24 h and then measured with a flourometer to obtain chlorophyll *a* concentrations (μg/L).

To assess pelagic food availability, we 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. We performed two vertical tows of the total water column between 10:00 and 16:00 hours with 80- and 500-μm Wisconsin-style zooplankton nets. If the lake was stratified, we took two additional zooplankton tows through the epilimnion. We preserved all samples in Lugol's solution for later examination. In the laboratory, we enumerated and identified zooplankton to genus and measured 30 individuals per taxa per sample to estimate density and biomass. We calculated zooplankton density for each zooplankter, correcting the number of individuals enumerated by the total water column sampled (number of individuals per liter), and determined individual zooplankton weights using length–weight regressions (McCauley 1984) for an estimate of total biomass.

To assess benthic food availability, we sampled benthic macroinvertebrates using a modified Hess sampler at four randomly selected locations in the littoral zone during the midsummer sampling period in 2008. We pooled all four samples from each lake and identified all invertebrates to order level to obtain estimates of relative abundance (number of each order per square meter) in each lake.

Feeding strategy and competitive ability.—To characterize fish diet and evaluate diet preference and overlap between the two ploidy levels, we removed stomachs from fish and classified prey items as aquatic invertebrates (to order), terrestrial invertebrates (explicitly), fish (to species), or zooplankton (to genera). For zooplankton and invertebrate prey, we weighed each invertebrate order or zooplankton genus en masse to the nearest 0.001 g blot-dry wet weight. We then calculated the percent wet weight of each prey item for each individual fish.

To determine prey selection (electivity) by each ploidy level, we calculated Chesson's α (Chesson 1978) as:

$$\alpha = r_i p_i^{-1}\left(\Sigma r_i p_i^{-1}\right)^{-1},$$

where r is the proportion of prey type i in the diet of fish and p is the proportion of prey type i in the environment. Random feeding occurs at values of $1/n$ (where $n =$ the number of food items available), with values $>1/n$ indicating preference and values $<1/n$ indicating avoidance (Chesson 1978). Due to low fish catches or low abundance of some invertebrate taxa in samples, we determined prey electivity for five of the nine study lakes that had adequate data: Alexander, Blue, Hoover, Ruth, and Spectacle lakes.

In parallel with the electivity analyses, we also compared diet overlap between diploid and triploid brook trout in eight study lakes (all except Clegg Lake) in 2008, 2009, or both using Schoener's index (D) of diet overlap,

$$\mathrm{D} = 1 - 0.5\sum_{i=1}^{n} |p_{x,i} - p_{y,i}|,$$

where $p_{x,j}$ and $p_{y,j}$ are proportions of prey item i found in x and y populations (e.g., diploids and triploids) and n is the total number of prey items. Values of D range from 0 (no overlap) to 1 (complete overlap; Schoener 1970), and biologically significant overlap was defined as any value greater than 0.6. To compensate for different sample sizes in the 2 years and natural variability in the diet overlap analysis (32 diet samples in 2008 and 203 diet samples in 2009), we first combined data by averaging the percent composition of each invertebrate species across sample periods within each lake for each year. We then compared brook trout diet overlap across all lakes in both 2008 and 2009.

We analyzed isotopic signatures of both ploidy levels to assess potential differences in long-term feeding strategies and trophic position. We removed muscle tissue in the field and sent prepared samples to the UC-Davis Stable Isotope Facility, University of California Davis, for natural abundance analyses of ^{13}C and ^{15}N. Isotopic signatures are reported in δ-notation, where:

$$\delta^{13}\mathrm{C} \text{ or } \delta^{15}\mathrm{N} = [(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1{,}000,$$

and where R is the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. The standard for δ^{13}C is PeeDee belemnite and for δ^{15}N is atmospheric nitrogen. We compared δ^{13}C and δ^{15}N of diploid and triploid brook trout from isotope samples pooled across lakes ($n = 53$) using a paired Student's t-test ($\alpha = 0.05$).

Performance Evaluations in Ponds

We conducted performance evaluations on age-0 brook trout in five experimental ponds, each of which had a surface area of 500 m^2, volume of 1,050 m^3, and average depth of 2 m. Ponds were filled in early spring with 10°C well water and subsequently inoculated with zooplankton. By late June 2009, the zooplankton community in ponds was well developed; average zooplankton density for all ponds was 36 daphnids/L, 75 ceriodaphnids/L, 43 calanoids/L, and 37 cyclopoids/L, which are densities comparable with those found in the Uinta Mountain study lakes in 2008 (Budy et al. 2011). At the start of the evaluation on 16 June 2009, average Secchi disk depth was 2.2 m (SE = 0.1), surface water temperature was 20.2°C (SE = 0.3), and average DO was 10.8 mg/L (SE = 0.7), conditions well suited for brook trout (Raleigh 1982). Temperature loggers were deployed in all ponds in July. Throughout the summer, well water was periodically added to ponds to maintain water levels.

We stocked each pond with 25 diploid and 25 triploid age-0 brook trout (148 d old) supplied by the UDWR Kamas State Fish Hatchery, based roughly on the maximum stocking quota used in the mountain lakes. For this component of the study, only triploids were marked with a pelvic fin clip. At the time of stocking, diploids were on average 75 mm TL and 4.5 g, and triploids were 73 mm TL and 4.3 g. At the end of the evaluation (14 October 2009), we sampled all ponds by pulling a 6-mm-mesh seine across the entire pond length four times. We noted length, weight, and ploidy level (based on fin clip) for each captured fish. One week before sampling fish, we measured abiotic variables that may affect fish performance (e.g., temperature, dissolved oxygen, pH) and collected zooplankton samples in each pond. We evaluated statistical differences for length, weight, and W_r between diploid and triploid brook trout within each pond with paired Student's t-tests ($\alpha = 0.05$).

Laboratory Behavioral Experiments

For our behavioral experiments, age-0 diploid and triploid brook trout were supplied by the UDWR Kamas State Fish Hatchery, the same facility that rears and stocks fish into Uinta Mountain lakes. For these experiments, a left pelvic fin clip identified the diploid trout and the triploid trout had no fin clip. Brook trout used in this experiment were spawned on 9 December 2008, hatched around 27 January 2009, and transferred to our experimental facility on 24 June 2009. We housed the two ploidy levels of fish separately in 750-L capacity tanks containing flow-through 10°C well water with 25 fish per tank, and fed fish commercially available trout feed daily prior to experiments. In preliminary trials, we determined that two pairs of fish filled the 106-L glass aquaria at a density where individual fish behavior was observable in real time. Fresh well water in each aquarium ranged from 13°C to 15°C and DO levels never dropped below 5 mg/L during trials.

TABLE 3. Diploid (2N) and triploid (3N) brook trout population information for nine study lakes in the western portion of the Uinta Mountains, Utah, sampled three times each during the summers of 2008 and 2009, including total catch, catch per unit effort (CPUE), mean condition (W_r), mean total length (TL), and Schoener's index (D) of diet overlap (for select lakes). Total catch is for all sampling periods combined in a given year; CPUE, W_r, and TL are the average of all sample periods in a year. NA indicates insufficient data were available for computing a given metric.

	Total catch				CPUE (number/h)				W_r				TL (mm)					
	2008		2009		2008		2009		2008		2009		2008		2009		D	
Lake	2N	3N	2N	3N	2N	3N	2N	3N	2N	3N	2N	3N	2N	3N	2N	3N	2008	2009
Alexander	25	26	49	48	8.9	8.9	3.1	3.4	97.8	99.8	103.8	99.0	201.2	195.7	265.7	251.1	0.67	0.57
Blue	10	8	30	11	5.9	3.2	3.5	2.3	120.7	106.8	113.1	99.5	301.4	300.0	317.6	319.7	0.50	0.42
Clegg	5	1	1	2	0.9	0.8	1.3	2.2	127.4	94.5	123.5	131.5	183.2	236.0	208.0	194.0	NA	NA
Crystal	3	5	12	10	0.4	2.2	3.6	3.3	103.9	96.7	99.5	94.5	201.7	190.6	230.6	217.4	NA	0.47
Haystack	1	0	3	3	0.4	0.0	3.3	3.3	105.8	NA	108.5	100.2	325.0	NA	244.7	221.0	NA	0.48
Hoover	16	22	53	38	2.3	3.2	4.3	2.5	99.9	95.1	102.4	97.4	242.5	211.0	360.7	251.6	0.51	0.54
Marshall	2	0	14	1	3.0	0.0	2.3	1.6	126.6	NA	127.0	135.1	339.0	NA	360.7	323.0	NA	0.07
Ruth	15	11	9	4	5.6	3.3	6.1	6.8	103.0	106.7	93.8	92.6	193.1	237.2	230.0	213.8	0.58	0.76
Spectacle	9	12	0	0	3.4	1.6	0.0	0.0	113.8	109.4	NA	NA	283.3	278.3	NA	NA	0.50	NA

Before behavioral observations, we weighed trout to the nearest 0.1 g and measured TL to the nearest 1 mm, which allowed us to pair similarly sized fish and thus remove any potential size bias on aggressive behavior (T. Wagner et al. 2006). We marked fish by injecting acrylic latex paint subcutaneously with a 3-mL syringe and a 22-gauge hypodermic needle at the base of the caudal fin of each trout (Goforth and Folts 1998) to allow us to immediately identify the ploidy level of the fish.

We observed brook trout in the aquarium under natural lighting through a gap in a black curtain blocking the aquarium from possible external visual stimuli in the room (Kraft 2009). We also took video recordings of each treatment so that we could reexamine a treatment if necessary. During each treatment, we tallied attacks made by the two diploid and two triploid fish separately. Behavior constituting an attack included fin nipping, chasing, biting, and any action that produced a fleeing response in another fish (Kudoh and Yamaoka 2004).

We allowed fish to acclimate to the aquarium for 30 min, after which we observed the fish for 20 min in prefood treatment trials. We then fed the fish and observed them for an additional 10 min to investigate whether food would affect aggression as well as to mimic a typical pellet-feeding occurrence at a hatchery. We conducted 10 trials using new fish in each trial.

We assessed the effects of ploidy level and period (pre- versus postfeeding) on the number of aggressive attacks using a two-way factorial ANOVA, in a split-plot ANOVA with plots (fish: diploid versus triploid) within blocks (trials). Repeated measures on a fish were subplots; the subplot factor was period (pre- versus postfeeding). Counts were log transformed before analysis to better approximate the assumptions of normality and homogeneity of variance. An increment of 0.5 was added to each count before log transformation to accommodate zero counts. We analyzed data using the GLIMMIX procedure in SAS (SAS Institute 2005) using a normal distribution and an identity link ($\alpha = 0.05$).

RESULTS

Performance Evaluation in Lakes

Relative abundance, size structure, and condition.—The total catch of all brook trout (triploid, diploid, and no mark) was extremely variable among study lakes (Table 3). We captured the greatest total number of brook trout (marked and unmarked) in Crystal ($n = 249$), Hoover ($n = 290$), and Ruth ($n = 218$) lakes and the lowest number in Clegg ($n = 11$) and Marshall ($n = 89$) lakes (both years combined). In both 2008 and 2009, CPUE of marked fish was greatest in Alexander and Hoover lakes and lowest in Clegg and Marshall lakes (Table 3; Figure 2). Spectacle Lake also demonstrated relatively low CPUE in both years of the study, with no marked fish captured in 2009.

The CPUE did not differ significantly between diploid and triploid brook trout nor did we observe any significant effects of "year" or sampling "time" ($P > 0.55$; Figure 2; Tables 3, 4) or significant interactions among factors ($P > 0.06$; Tables 3, 4). Similarly, we observed no significant difference in the mean W_r of diploids versus triploids nor a significant "year" effect ($P > 0.46$; Figure 2; Tables 3, 4). On average, the size distribution of diploid brook trout was skewed toward larger fish compared with triploid brook trout: mean diploid TL = 262.5 mm and mean triploid TL = 241.6 mm ($D_{KS} = 0.24$, $P < 0.05$; Figure 3); however, the actual size difference was quite small (~20 mm) and the sample size was large. In some individual lakes (e.g., Alexander Lake), the frequency of larger fish increased from year 1 to year 2 (Figure 3). In all other lakes, the size structure was relatively similar in year 1 and year 2.

Limnology and food availability.—In 2008 and 2009, minimum DO levels over the summer months were below the

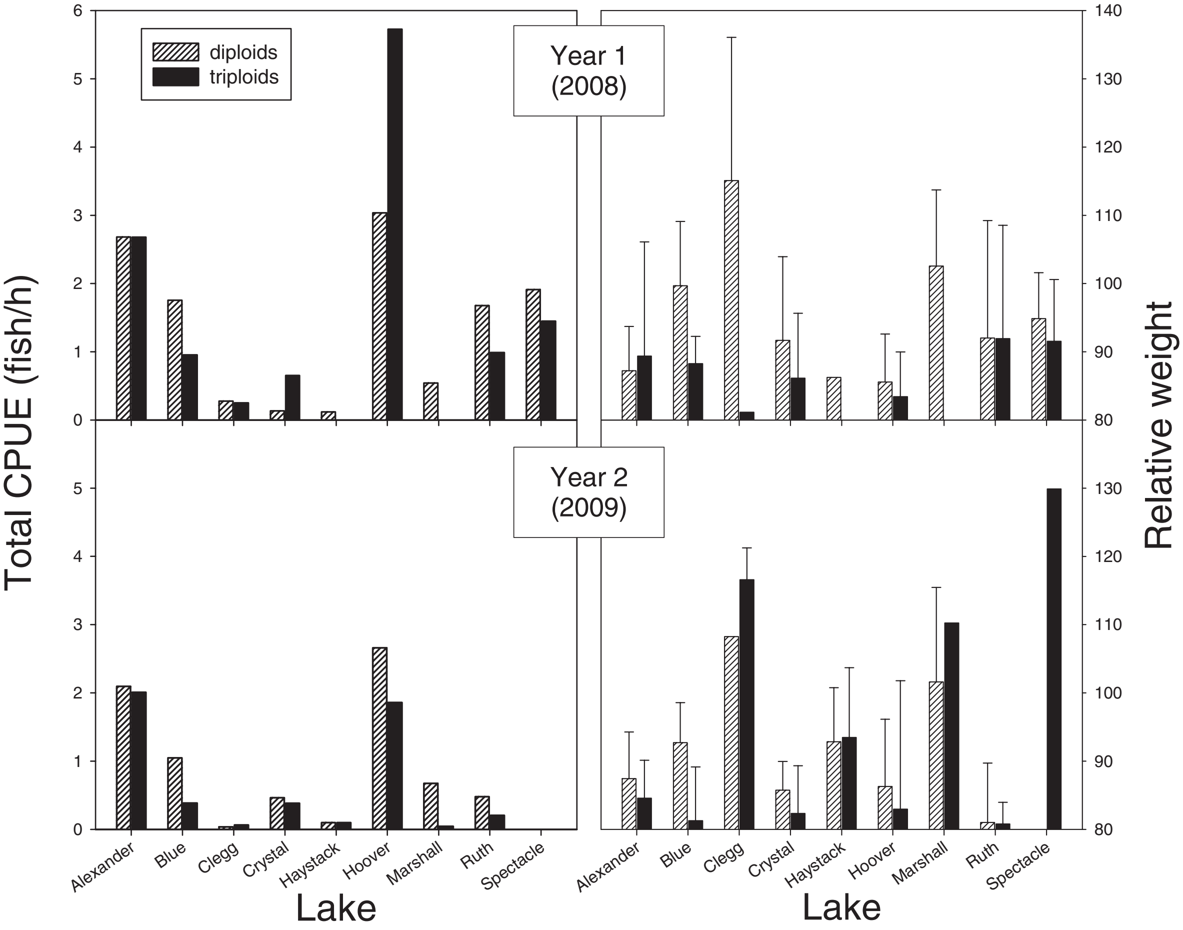

FIGURE 2. Total catch per unit effort (CPUE) of diploid and triploid brook trout within each lake in year 1 (top left panel) and year 2 (bottom left panel), and average relative weight (W_r) (±1 SD) for diploid and triploid brook trout for each lake during year 1 (top right panel) and year 2 (bottom right panel). No triploid fish were captured in Haystack Lake and Marshall Lake in year 1; one marked fish was captured in Spectacle Lake in year 2.

TABLE 4. Results of statistical analyses of the relative performance of the two strains in lakes for catch per unit effort (CPUE) and condition (relative weight, W_r). Results are based on type III tests of fixed effects from randomized block designs; "lake" was the random blocking factor. See text for additional information describing statistical methods.

Effect	Number df	Density df	*F*	*P*-value
	CPUE			
Year	1	88	0.07	0.80
Time	2	88	0.60	0.55
Year × Time	2	88	2.96	0.06
Ploidy	1	88	1.48	0.23
Year × Ploidy	1	88	0.53	0.47
Time × Ploidy	2	88	0.03	0.97
Year × Time × Ploidy	2	88	0.07	0.93
	W_r			
Year	1	15.42	0.57	0.46
Ploidy	1	15.42	0.26	0.61

optimal range of 9–15 mg/L (Raleigh 1982) for brook trout in all but two lakes (Clegg and Crystal lakes). In February 2010, DO levels were below optimal in all for all six lakes sampled, with maximum DO values <7 mg/L and minimum DO values <1 mg/L for all lakes. Over the summer all lake temperatures remained within the optimal range of 11–16°C for brook trout growth (Raleigh 1982), with the exception of Clegg Lake, in which temperatures were consistently above the optimal range. Winter temperatures in all six lakes sampled were consistently well below the optimal range for trout growth, with temperatures <4.6°C throughout the water column of all lakes and mean temperatures ranging from 3.5°C to 3.8°C. Both winter DO and temperature were correlated with lake surface area and maximum depth ($r^2 = 0.45$–0.56). The small, shallow lake, Spectacle Lake, had the lowest mean DO concentrations and temperatures (minimum, mean, and maximum), and the larger, deeper lakes (Hoover, Haystack, and Marshall lakes) consistently demonstrated higher winter DO concentrations and temperatures.

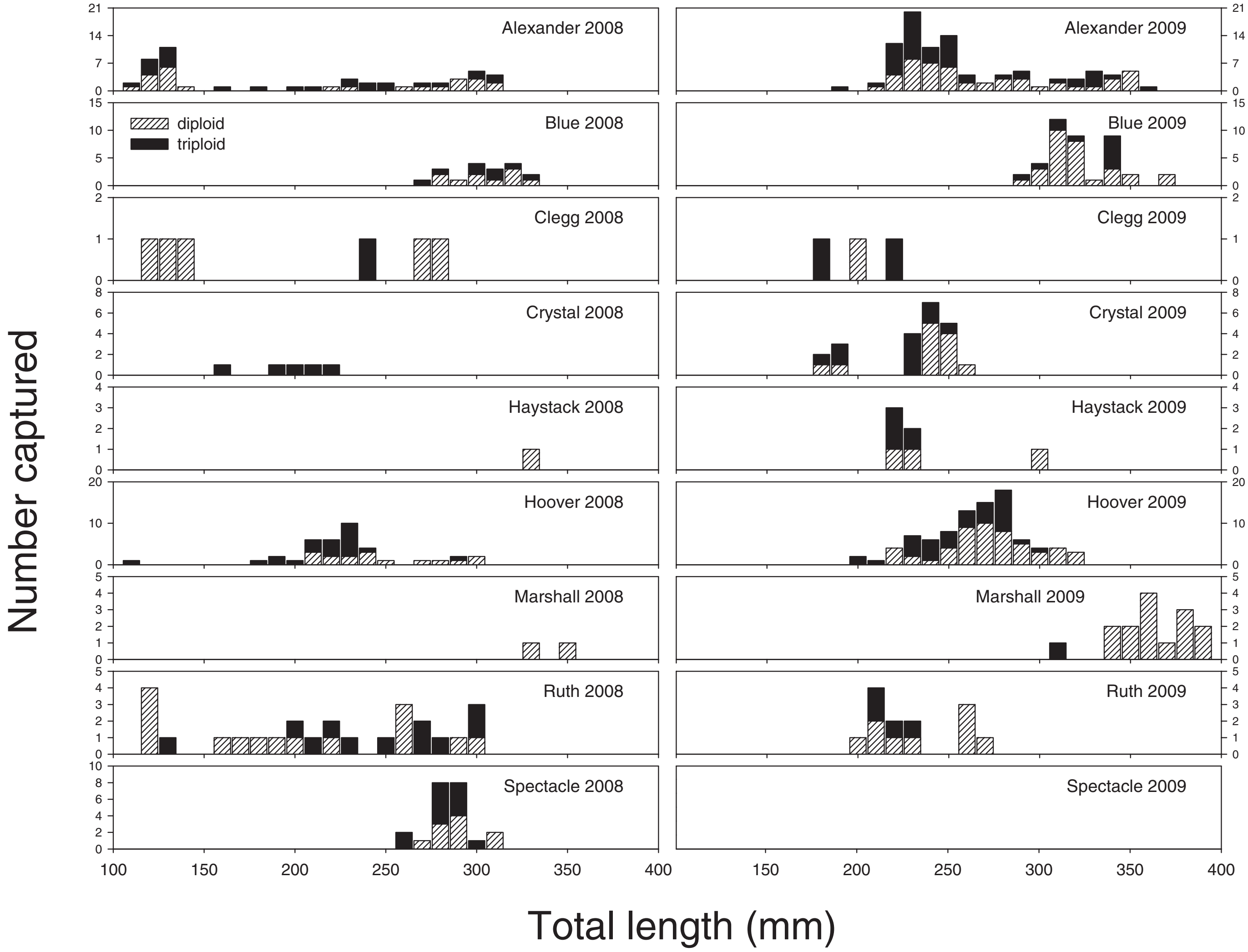

FIGURE 3. Length-frequency histograms (TL, mm) of triploid (black bars), diploid (hashed bars), and unmarked (no clip, white bars) brook trout from nine study lakes in the Uinta Mountains in 2008 (left panels) and 2009 (right panels). Note changes in *y*-axis labels.

In 2008, the benthic macroinvertebrate community was dominated by dipterans and amphipods. Total abundance ranged from 95 (Alexander Lake) to 4,686 individuals/m^2 (Haystack Lake) in 2008. In both years, the zooplankton community was dominated by *Holopedium*, *Daphnia*, and calanoid copepods, although densities of zooplankton were five times greater in 2009 than in 2008. Average chlorophyll *a* concentrations (an index of lake productivity) ranged widely from 0.7 to 74.9 μg/L (Table 1).

Feeding strategy and competitive ability.—In 2008 we observed biologically significant diet overlap (D > 0.6) between diploid and triploid brook trout in Alexander Lake (D = 0.67) and moderate overlap for all other lakes (D = 0.50–0.58) except Crystal, Haystack, and Marshall lakes (D < 0.5). In 2009, diet overlap was significant in Ruth Lake (D = 0.76) and moderate for all other lakes (D = 0.42–0.57) except Marshall and Spectacle lakes (Table 3). No or extremely low diet overlap was demonstrated in lakes with very small or asymmetric sample sizes.

When we compared diet overlap of the two ploidy levels for all study lakes combined in 2008 and 2009, we observed very high diet overlap between diploid and triploid brook trout in both years (D = 0.82 for 2008 and 0.77 for 2009). Both types of brook trout consumed primarily dipterans, amphipods and isopods, terrestrial invertebrates, and odonates. As zooplankton were only found in stomach samples of triploid fish in two of the lakes (Alexander and Ruth lakes, representing <1% of their diets overall), we did not consider zooplankton in our analyses of prey electivity. In all study lakes, diploid and triploid trout selected odonates and dipterans over other invertebrates based on Chesson's α. Brook trout avoided Amphipoda, Ephemeroptera, Hemiptera, Isopoda, Mollusca, and Trombidiformes in all lakes where they were found. Oligochaetes were available in the environment of all lakes, yet they were not found in the diets of any brook trout, suggesting avoidance or lack of benthic foraging.

Isotopic signatures also indicated significant diet overlap and similar trophic position for both ploidy levels in 2008. Carbon isotopic signatures (δ^{13}C) were not significantly different between diploids (−24.10 ± 1.14 [mean ± 2 SE]) and triploids (−24.91 ± 1.28) ($t = 0.96$, $P = 0.35$, df = 50). In contrast, mean δ^{15}N was significantly higher for diploid trout relative to triploids ($t = 2.01$, $P = 0.04$, df = 50), although the difference between mean values (diploid: 8.02 ± 0.51, triploid: 7.32 ± 0.46) is arguably not biologically significant given an assumed trophic fractionation of 3.4‰ per each trophic level increase (Minagawa and Wada 1984).

Performance Evaluations in Ponds

At the end of the performance evaluation period (14 October 2009), temperatures in the ponds ranged from 10.8°C to 11.5°C and DO ranged from 10.3 to 11.8 mg/L, values that are within the optimal range for brook trout growth and survival (Raleigh 1982). Turbidity in ponds was low (0.4–1.6 NTU) and pH ranged from 7.9 to 8.6. Zooplankton abundance was low: average zooplankton densities of ponds were 0.04 daphnids/L, 5.8 ceriodaphnids/L, 1.2 calanoids/L, and 0.05 cyclopoids/L.

Estimated survival at the end of the pond experiment, based on the number of recovered fish in each pond, was significantly better for diploids (mean = 18.4%; range, 0–48%) than for triploids (mean = 13.6%; range, 0–40%) ($t = 3.21$, $P = 0.03$ df = 4). However, it is important to note that survival event was extremely low for fish from both ploidy levels, indicating the data from this factor should be interpreted with caution. From the four ponds, we captured a total of 23 diploid trout ranging from 127 to 165 mm TL and from 10.5 to 39.6 g, and 17 triploid trout ranging from 119 to 190 mm TL and from 15.3 to 52.4 g (Figure 4). Although survival of diploid trout was higher than triploid trout, average W_r was not significantly different between ploidy levels ($t = -0.005$, $P = 0.50$, df = 38; diploid: 83.4 ± 10.1 [mean ± SE], triploid: 83.5 ± 7.9). Similarly, average growth over this 112-d interval was not significantly different between diploids (21.0 g and 67.4 mm TL) and triploids (24.1 g and 72.1 mm TL) ($t = -0.40$, $P = 0.71$, df = 4).

Laboratory Behavioral Experiments

Total lengths and weights of individuals used in behavioral evaluations ranged from 79 to 109 mm and from 6.2 to 12.0 g, respectively, with mean lengths of 93.4 mm for diploids and 95.1 mm for triploids. However, individuals paired within each trial never differed by more than 10 mm. In both the pre- and postfeeding trials, diploids on average performed more attacks than did triploid brook trout, but the variability in number of attacks was extremely high and the differences were not significant (Figure 5). In prefeeding trials, the number of diploid attacks ranged from 0 to 44 (mean ± SE, 6.7 ± 4.3), whereas the number of attacks made by triploid trout ranged from 0 to 4 (1.7 ± 0.4). No attacks from fish from either ploidy level occurred in 2 of the 10 trials. In the postfeeding trials, the number of diploid attacks ranged from 0 to 8 (2.3 ± 0.7) and the number of triploid attacks ranged from 0 to 5 (1.7 ± 0.4). Trout attacked conspecifics regardless of ploidy level (i.e., diploids attacked both diploids and triploids and vice versa). In summary, we observed no significant difference between diploid and triploid aggression ($F = 3.36$, $P = 0.10$, df = 9), no significant period effect for prefeeding versus postfeeding ($F = 1.37$, $P = 0.26$, df = 18), and no significant interaction effect ($F = 0.05$, $P = 0.83$, df = 18).

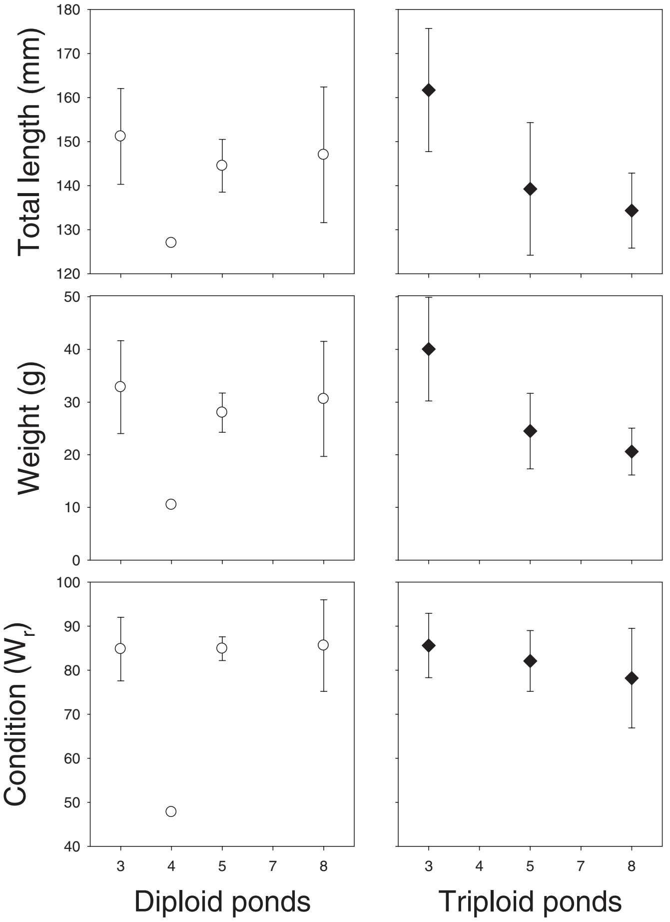

FIGURE 4. Length, weight, and condition (W_r) of diploid (left panels) and triploid (right panels) brook trout after 4 months (over summer) of rearing in five experimental ponds. No fish were recovered from pond 7 and no triploid trout were recovered from pond 4. Error bars represent ±1 SD.

DISCUSSION

Comparisons between Ploidy Levels

In order to provide a robust test of the potential differences in relative performance between triploid and diploid brook trout, we chose nine lakes for study that covered a large range of lentic conditions found in high mountain lakes. With a few minor

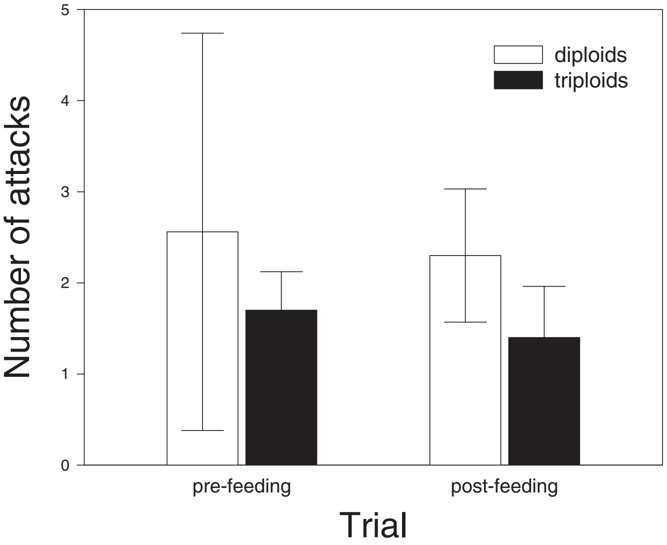

FIGURE 5. Average number of attacks (±1 SE) by diploid and triploid brook trout for behavioral observation trials in aquaria before (pre-) and after (post-) feeding.

exceptions, we observed very little difference in the relative performance between stocked diploid and triploid brook trout in our study lakes, a result that concurs with previous studies of diploid and triploid performance (E. J. Wagner et al. 2006; Chiasson et al. 2009). Conversely, Koenig et al. (2011) observed marked differences in the performance of diploid and triploid rainbow trout in alpine lakes.

Although we observed no differences in fish condition between stocked triploid and diploid brook trout, diploid brook trout did attain slightly larger average sizes in some lakes. Higher growth rates and size of diploids have been observed in previous studies (Simon et al. 1993), while similarity in size structure of diploid and triploid fish has been noted elsewhere (Xiaoyun et al. 2010; Koenig and Meyer 2011). In some cases the observed differences in size was only for smaller sizes-classes (McGeachy et al. 1995; Chiasson et al. 2009). In our study, diploids attained larger sizes in two large-sized lakes (Marshall and Haystack lakes), but the other lakes showed little difference in size between diploids and triploids. Furthermore, the average difference in size of fish between ploidy levels was small (approximately 20 mm) and is probably undetectable to the average angler. Often, differences in size between diploids and triploids often do no materialize until the onset of sexual maturity. Given that brook trout typically take 3 years to reach maturity (E. Wagner and T. Hallows, UDWR, personal communication), any potential size differences should have been evident in the older trout (i.e., those stocked in 2006), but perhaps not those stocked in 2008. Considering the similarity in size distribution across all sizes of fish and high overwinter mortality overall, the issue of sexual maturation does not appear to have affected the triploid–diploid comparison herein.

Based on observed diet similarities, diet overlap, and trophic position, we did not detect any differences in feeding strategy or evidence for competitive superiority between ploidy levels. Our diet results are novel in that few studies have directly measured the diet composition of trout in mountain lakes or other natural settings. Aquaculture studies support our finding that feeding and diet preferences of diploid and triploid trout are similar (Boulanger 1991; O'Keefe and Benfey 1999). However, in other species others have found evidence of lower performance of triploid versus diploid fish (rainbow trout, Simon et al. 1993; Atlantic salmon, Carter et al. 1994; Cotter et al. 2002) that could have resulted from some undocumented or unknown aspect of feeding ecology.

Similarly, we found similar growth and condition of diploid and triploid brook trout in controlled pond experiments of mixed ploidy levels, despite a wide range of thermal conditions. In our ponds, there was little difference between triploid and diploid trout growth, even when temperatures consistently exceeded 19°C. Previous studies have also found no effect of ploidy on critical thermal maxima (Benfey et al. 1997; Galbreath et al. 2006). In contrast, others have documented increased mortality of triploid brook trout as a result of chronically high temperatures (Hyndman et al. 2003). Despite similarities in growth and condition in pond experiments, average survival of diploids was significantly higher than that of triploids, perhaps due to elevated water temperatures (e.g., conferring an advantage to diploids; Hyndman et al. 2003). Midsummer water temperatures in the ponds occasionally reached 25°C and varied widely, probably as a function of pond seepage (and subsequent topping off with 10°C well water) or algal mat coverage and the resultant shading in some ponds. However, it is important to note that survival in ponds was extremely low overall, such that environmental conditions could be either masking ploidy effects or causing biologically unimportant, yet statistically significant, differences in survival between ploidy groups.

Based on laboratory behavioral experiments, we found no significant difference in aggressive behavior between diploids and triploids in pre- and postfeeding trials. Furthermore, in over one-half of the behavioral trials, no aggressive behavior was recorded, and there appeared to be no inherent difference in brook trout aggression based on ploidy level alone. Although we did find that, on average, diploids performed more attacks than did triploids, this difference was not significant. Statistically, it was just as likely that an aggressive individual was a diploid or triploid fish; aggressive individuals attacked fish from their own ploidy level as often as they attacked the other. In a similarly conducted feeding response trial of triploid and diploid brook trout, only one diploid group (size, 40–58 mm) was dominant over triploids (O'Keefe and Benfey 1999). Furthermore, this dominance difference diminished as the fish grew, and dominance was not observed in groups ranging in size from 99 to 204 mm. In contrast, our results differ from those of Carter et al. (1994) and Garner et al. (2008), who found that triploid trout were less aggressive than diploids.

Effects of Environmental Conditions on Trout Performance

Independent of ploidy level, the relative performance of brook trout varied widely among lakes, indicating that survival of stocked brook trout in high mountain lakes in general is highly lake-specific (Josephson and Youngs 1996). Larger deeper lakes generally demonstrated high CPUE, while smaller, shallower lakes demonstrated low CPUE (e.g., Clegg and Marshall lakes). Consistently high CPUE in the larger study lakes (Alexander and Hoover lakes) suggest that relative abundance may be influenced by lake size or by a factor that covaries with lake size (e.g., thermal stratification, carrying capacity; Amundsen et al. 2007). Although high CPUE was also observed in the relatively small-sized Crystal Lake, this may be due to overwinter refuge and supplementation from the larger, deeper Washington Lake through a small stream connection available in spring (e.g., Jackson and Zydlewski 2009). In contrast, the large lakes (Alexander and Hoover lakes) in this study are essentially disconnected from additional source populations.

Higher CPUE in larger lakes may be due to differences in the availability of thermal refugia in the summer or winter, or both. In mountain environs, deeper lakes commonly experience thermal stratification that allows coldwater fishes to persist even when surface temperatures approach or exceed upper or lower thermal limits (Jackson and Harvey 1989). In contrast, shallower lakes may never stratify; as a result, elevated temperatures through the full water column may persist throughout the summer. Empirical evidence suggests that temperatures near the upper limit for brook trout may lead to a decrease in growth and increased mortality in triploids (Hyndman et al. 2003; Atkins and Benfey 2008). We observed high temperatures in two of the nine study lakes (Clegg and Crystal lakes), but only near the lake surface. In these lakes, brook trout are likely able to seek out more thermally suitable conditions near the bottom or near stream inlets where temperatures measured seldom reached levels high enough to affect brook trout growth or survival (i.e., 19°C; Hyndman et al. 2003). Thus, it seems more likely that observed differences in CPUE among some lakes are the result of harsh winter conditions, which can be more severe in smaller lakes (Budy et al. 2011). Winter DO levels and temperatures were consistently below the optimal range for brook trout growth in the six lakes sampled, and the small, shallow lakes (e.g., Spectacle Lake) had lower DO and temperatures than did the larger, deeper lakes (e.g., Hoover, Haystack, and Marshall lakes). These severe overwinter conditions occur during a time period when habitat and food are already limited (Bystrom et al. 2006), in part explaining the poor overall condition (W_r) of all stocked brook trout in these high mountain lakes.

Although condition was low overall, the condition of brook trout in the large lakes with consistently high CPUE was lower than lakes with low CPUE, indicating a density-dependent effect. In a related study of these same lakes, CPUE, maximum lake depth, and lake area were the top three predictor variables explaining variation in stocked brook trout condition (W_r) independent of ploidy level (random forest analysis; Budy et al. 2011; also see Donald and Anderson 1982). Density-dependent effects are common in large oligotrophic lakes, where growth rates are higher at lower densities due to decreased intraspecific competition for limited food resources (Amundsen et al. 2007). Differences in stocking frequency could also account for some of the observed differences in catch rate among lakes. Alexander, Crystal, and Hoover lakes were stocked in all 3 years, whereas Clegg and Marshall lakes were stocked less frequently (twice and once, respectively). However, the small-sized Ruth Lake was stocked in all 3 years but had a much lower CPUE than the larger lakes stocked at the same frequency, suggesting that relative abundance and survival are at least partly a function of lake size, depth, or both.

Management Implications

In summary, we found very few significant differences in performance, feeding strategy, competitive ability, or aggression between diploid and triploid brook trout in both natural and controlled settings at three spatial scales. Our results show that triploid brook trout may provide a valuable management tool that will allow managers to provide a sport fishery in lakes where natural reproduction is not sufficient to maintain the fishery, while simultaneously minimizing the risk of nonnative expansion into other waters and the deleterious effects of negative interspecific interactions on native ecosystems (Knapp et al. 2001; Knapp and Sarnelle 2008). In addition, our findings have important implications for management of triploid brook trout in high mountain lakes in the Uinta Mountains. Large differences in relative performance among lakes calls for a reevaluation of which lakes to stock and at what density and frequency. Strong signals of density dependence indicate these lakes are food or space limited at current stocking densities, suggesting that stocked brook trout, independent of ploidy level, could potentially survive better and attain larger sizes if stocked at lower densities.

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