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Factors affecting size of trout in high mountain lakes

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Abstract

Trout were captured using gill nets at 206 mountain lakes to assess whether lake access difficulty or other abiotic lake characteristics influenced fish size. Lakes were 1,338–3,165 m in elevation and 0.2–22.9 ha in surface area; to reach them, off-road travel was 0–25.4 km in distance and 0–2,627 m in cumulative elevation gain, and the percent of off-road travel that was on a trail ranged from 0% to 100%. Cutthroat trout (*Oncorhynchus clarkii*) were similar in size ($\overline{X}$ = 273 mm) to rainbow trout (*O. mykiss*) ($\overline{X}$ = 260 mm) and rainbow × cutthroat hybrids ($\overline{X}$ = 259 mm) but larger than brook trout (*Salvelinus fontinalis*) ($\overline{X}$ = 218 mm). Trout were larger in lakes with an underlying shield lithology rather than acid volcanic, shale, and sedimentary rock lithologies, perhaps reflecting differences in rock weathering and therefore dissolved nutrients and minerals leaching into lakes. Trout were also larger in larger, higher elevation, southern-facing lakes with a more uniform shoreline. Larger lakes may provide more heterogeneous habitat, less overlap in habitat use between life stages (minimizing cannibalism), and more diverse, abundant, and stable food supplies. Geographical relief and aspect influence solar radiation, which in turn affects snowmelt, water temperature, and phytoplankton growth. The smallest effect size was for how much off-road travel was on a trail, perhaps because angling effort is so diffuse in high mountain lakes, and because contemporary anglers harvest few of the fish they catch in such settings, rendering angler access difficulty relatively unimportant to fish size structure.

Keywords: Alpine lake, Brook trout, Cutthroat trout, Rainbow trout

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Introduction

The Rocky Mountain region of western North America contains thousands of high mountain lakes, the majority of which were naturally fishless[1]. However, for well over a century, various species of salmonid have been stocked (usually as fry) in countless high mountain lakes across this region to diversify angling opportunities; in many instances, these lakes now support self-sustaining wild populations of fish[2−4]. Relatively high angler catch rates[5−7] and the scenic backdrop often experienced in such remote alpine settings compel most anglers to express high levels of satisfaction with their fishing experience at mountain lakes in the Rocky Mountain region[8,9].

Catch rates and aesthetics are only two of the myriad determinants of angler satisfaction[10] and choice of fishing locations[11]. The size of fish that anglers encounter while fishing also influences where they exert angling effort[12] and how satisfied they are with their angling experience[13]. Consequently, fisheries managers and anglers alike are interested in understanding what affects fish size in high mountain lakes. Historically, angler harvest was an important factor affecting abundance and size structure in many trout fisheries[14,15]. In Wyoming high mountain lakes, lake accessibility was reported to be the primary factor affecting size structure of cutthroat trout (*Oncorhynchus clarkii*)[16]. However, a catch-and-release mentality has become more pervasive among trout anglers in recent decades in North America[17] and beyond, including in high mountain lakes[18], suggesting that contemporary anglers are likely having minimal influence on trout size structure in such fisheries. Nevertheless, population-level effects in freshwater fisheries can occur at relatively low harvest rates[19−21], thus my first objective was to determine if lake access difficulty affected the size of trout in Idaho high mountain lakes.

Besides angling effects, the size structure of trout populations in lacustrine waters can be influenced by many other biotic and abiotic factors. For example, in aquatic ecosystems, lithology influences water chemistry[22,23], which can affect primary productivity[24] and therefore fish production[25]. High mountain lakes generally have low concentrations of dissolved nutrients[26], but there is substantial variation in weathering between rock types[27]. Moreover, altitude mediates rock weathering[27] as well as the length of the growing season for fish[28,29]. Additional factors that may affect the size structure of lacustrine fish populations include the species of consideration[30,31], gear used to sample the population[32], and lake morphology[33] and aspect[34], among others. A better understanding of the influence these and other factors have on the size of salmonids residing in high mountain lakes would benefit fisheries managers tasked with setting angling regulations and communicating such regulations to the general public. Therefore, a second objective of my study was to determine what other factors besides lake access difficulty might be influencing the size of trout in Idaho high mountain lakes.

Materials and methods

The study was conducted in the state of Idaho in the western United States. There are over 3,000 high mountain lakes in Idaho, approximately 1,000 of which contain salmonids[35]. The Idaho Department of Fish and Game (IDFG) stocks about 680 of these lakes on either an annual, 2-, or 3-year interval. Most stocked fish are cutthroat trout or rainbow trout (*O. mykiss*), and they are generally stocked in late summer from fixed-wing aircraft as 40-mm fry. Because fish are stocked as fry, they cannot be distinguished from wild fish. Consequently, whether cutthroat trout, rainbow trout, or cutthroat × rainbow hybrids captured in the present study were of wild or hatchery origin was unknown. However, prior research indicates that the vast majority (> 80%) of these taxa encountered in high mountain lakes in

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Idaho that are stocked with trout are wild[4,6]. Moreover, brook trout (*Salvelinus fontinalis*) have not been stocked in Idaho high mountain lakes for decades, but they too have established self-sustaining populations in numerous Idaho high mountain lakes; thus, they were all wild in the present study. Although stocked fish comprise a small fraction of fish encountered in Idaho high mountain lakes, the stocking program continues due to a low cost to stock lakes (US$ 250/lake; M. Koenig, IDFG, personal communication) and to prevent fish winterkills from eliminating fishing opportunities at lakes currently supporting fisheries.

High mountain lakes in Idaho are generally managed with a six-trout daily harvest limit with no size restriction. For brook trout, the daily harvest limit is 25 fish with no size restriction. Two lakes had a more restricted two-fish daily bag limit.

High mountain lake fish surveys were conducted between 2001 and 2023. Fish were captured using floating or sinking experimental gill nets (46 m long and 2 m deep, with nylon mesh panels of 19-, 25-, 32-, 38-, 51-, and 64-mm bar mesh). Nets were generally set perpendicular to the shore with the smaller mesh along the shore. The number and type of nets set at each lake were at the discretion of the lead biologist, but in general, one to four nets were used, with more nets used at larger lakes. Nets were generally set in mid- to late afternoon and were retrieved the next morning. In many instances, net type (i.e., floating or sinking) was not recorded during data collection; for this reason, net type during analyses was categorized as floating (49% of fish caught), sinking (15%), or unknown (36%).

Captured fish were identified to species and measured for total length to the nearest mm. Cutthroat trout, rainbow trout, cutthroat × rainbow hybrids, and brook trout comprised > 99% of the catch; the few other salmonids that were captured were not included in the analyses. Also ignored (and not recorded) were the few fish < 150 mm in length that were captured in nets. I assumed that for fish > 150 mm, gill net catch using the nets noted above was relatively unbiased with regard to fish size in high mountain lakes, as demonstrated in other Idaho mountain lakes[36].

Several lake characteristics were measured (Table 1) that have been previously shown to be related to trout size or abundance (which can affect fish size via competition) in high mountain lakes[16,34,37,38]. Elevation (m), surface area (ha), aspect, and shoreline development ratio were determined using Google Earth Pro[39]. I included elevation because it directly affects how long a high mountain lake is covered with ice and snow, which directly affects the length of the growing season for trout[40]. Surface area affects how much of the lake can be effectively fished by anglers, since most high mountain lake anglers fish from shore. Aspect (i.e., azimuth angle) of the lake affects solar radiation, which in turn affects the length of the growing season and phytoplankton growth[41]; rather than attempting to estimate the radian aspect of each lake, I categorized the lakes (in relation to surrounding ridges) as southern facing (S, SW, and SE), northern facing (N, NW, and NE) or laterally facing (E and W). The shoreline development ratio was calculated as:

Table 1. Characteristics of high mountain lakes in Idaho where trout were sampled with gill nets from 2001 to 2023.

Lake characteristic	Mean	SE	Minimum	Maximum
Elevation (m)	2,396	24	1,338	3,165
Lake size (ha)	4.15	0.28	0.16	22.87
Shoreline development ratio	1.22	0.01	1.05	2.35
Hiking distance (km)	7.8	0.4	0	25.4
Cumulative elevation gain (m)	821	44	0	2,627
Percent of hike on trail	76	2	0	100

$$L/(2\sqrt{\pi A})$$

where, L is the length of the shoreline, and A is the lake surface area; the ratio is a unitless index of lake shape irregularity, with perfectly circular lakes having a value of 1.0. The shoreline development ratio affects an angler's ability to effectively fish the lake, since an irregular shoreline provides peninsulas from which anglers can cast more effectively; it also influences lake complexity and littoral habitat.

Lithology influences water chemistry such as nitrogen and phosphorus levels as well as conductivity and pH, which in turn influence primary productivity[42,43], a driver of fish production[25]. The predominant lithology at each lake was estimated using the Geologic Map of Idaho at a scale of 1:750,000[44] and was categorized as acid volcanic (rhyolite), basalt, sedimentary (including alluvium, sandstone, and quartzite), shale, and shield (metamorphic and plutonic rock)[45].

I also included three measures of lake access difficulty as predictor variables. First, I estimated off-road travel distance (km) from the nearest road to the lake by tracing the likely travel route using US Geological Survey 1:24,000-scale digital topographical maps. The off-road travel route often followed trails, but where trails were absent, I traced what I assumed to be the most likely route of travel. Using the same digital maps, I estimated the proportion of the off-road travel distance that was on a trail and the cumulative gain in elevation (m) during the off-road travel. I used cumulative gain (rather than net gain) to account for instances in which the off-road travel required passing over a series of one or more elevational gains. In the few instances where the lake was lower in elevation than the starting point of off-road travel, I used the cumulative loss in elevation instead of the gain because the return travel from the lake to the vehicle would comprise the same amount of cumulative gain in elevation.

Statistical analyses

I conducted all statistical analyses using SAS[46]. I used general linear models to evaluate what factors were related to fish length at high mountain lakes using Proc GLMSELECT. Each fish was the experimental unit, with the response variable being the fish's length. Predictor variables included net type, all the lake characteristics and lake access difficulty metrics, and species. To specifically evaluate whether lake access difficulty influenced fish size at these lakes, the following candidate models were considered: a model with all predictor variables except the lake access difficulty parameters; models with these same parameters in addition to 1 of the 3 lake access difficulty indices; and a null model. Indications of collinearity between continuous predictor variables included in the same model were absent (i.e., absolute values for all pairwise Pearson correlation coefficients < 0.48).

I ranked models using Akaike's information criterion (AIC)[47], and I considered the most plausible models to be those with AIC scores within 2.00 of the best model[48]. I used AIC weights (w_i) to assess the relative plausibility of each of the most plausible models, and adjusted coefficients of determination to describe the amount of variation in fish length that was explained by the parameters in the models. I report parameter estimates with 95% confidence intervals (CIs) only for the most plausible models, and I considered only those parameters with 95% CIs that did not overlap zero as influential in a model, regardless of their inclusion.

Results

From 2001 to 2023, a total of 336 surveys were conducted across 206 high mountain lakes. Lake characteristics varied substantially (Table 1), with lakes ranging from 1,338 to 3,165 m in elevation

($\overline{X}$ = 2,396 m), 0.2 to 22.9 ha in surface area ($\overline{X}$ = 4.2 ha), and 1.05 to 2.35 in shoreline development ratio ($\overline{X}$ = 1.22). Hikes to access these lakes ranged from 0 to 25.4 km in distance ($\overline{X}$ = 7.8 km), and 0 to 2,627 m in cumulative elevation gain ($\overline{X}$ = 821 m), and the percentage of off-road travel distance that was on a trail ranged from 0 to 100% ($\overline{X}$ = 76%).

A total of 6,889 fish were captured during the 336 high-mountain lake surveys (Fig. 1). Cutthroat trout were slightly larger in size ($\overline{X}$ = 273 mm; maximum = 555 mm) than rainbow trout ($\overline{X}$ = 260 mm; maximum = 610 mm) and rainbow × cutthroat hybrids ($\overline{X}$ = 259 mm; maximum = 480 mm), and were much larger than brook trout ($\overline{X}$ = 218 mm; maximum = 447 mm). Thirteen percent of cutthroat trout were ≥ 350 mm, compared to 7% for rainbow trout, 9% for rainbow × cutthroat hybrids, and only 1% for brook trout.

The most plausible candidate model contained all parameters related to lake characteristics, plus the percentage of off-road travel distance that was on a trail for the lake access difficulty parameter (Table 2). This model explained 18% of the variation in size of fish captured in high mountain lakes, and no other candidate models were considered plausible based on AIC scores and weights. Parameter estimates and their 95% CIs (Table 3) indicated that, for categorical variables: (1) fish size did not differ between floating and sinking nets; (2) trout in lakes located in areas with an underlying shield lithology were estimated to be 23, 19, and 15 mm larger than in lakes with underlying lithologies of acid volcanic, shale, and sedimentary rock, respectively; (3) trout residing in lakes with a southern-facing aspect (S, SE, or SW) were estimated to be 13 and 21 mm larger than those residing in lakes with a northern-facing (N, NE, or NW) or lateral-facing (E or W) aspect; and (4) cutthroat trout were estimated to be 10 mm larger than rainbow trout, 14 mm larger than cutthroat × rainbow hybrids, and 55 mm larger than brook trout.

Effect sizes differed greatly between continuous predictor variables, as indicated by parameter estimates and their 95% CIs (Table 3). Fish length was predicted to increase by 0.5 mm for every 1 ha increase in lake size and 15 mm for every 1,000 m increase in elevation. In contrast, fish length was predicted to decrease by 18 mm for every 1.0 increase in shoreline development ratio. The smallest effect size was for the percentage of the off-road travel distance that was on a trail, which was predicted to decrease fish length by only 10 mm for lakes that could be accessed entirely by trail compared to access being entirely off trail.

Discussion

My primary objective was to determine if lake access difficulty affected the size of trout residing in high mountain lakes, and the results of this study suggest that poorer trail access indeed had a slight positive influence on trout size. A similar but much stronger relationship was demonstrated in Wyoming mountain lakes, where a 17% increase in proportional stock density for cutthroat trout was observed for every 1 km increase in off-trail travel distance to access a lake[16],

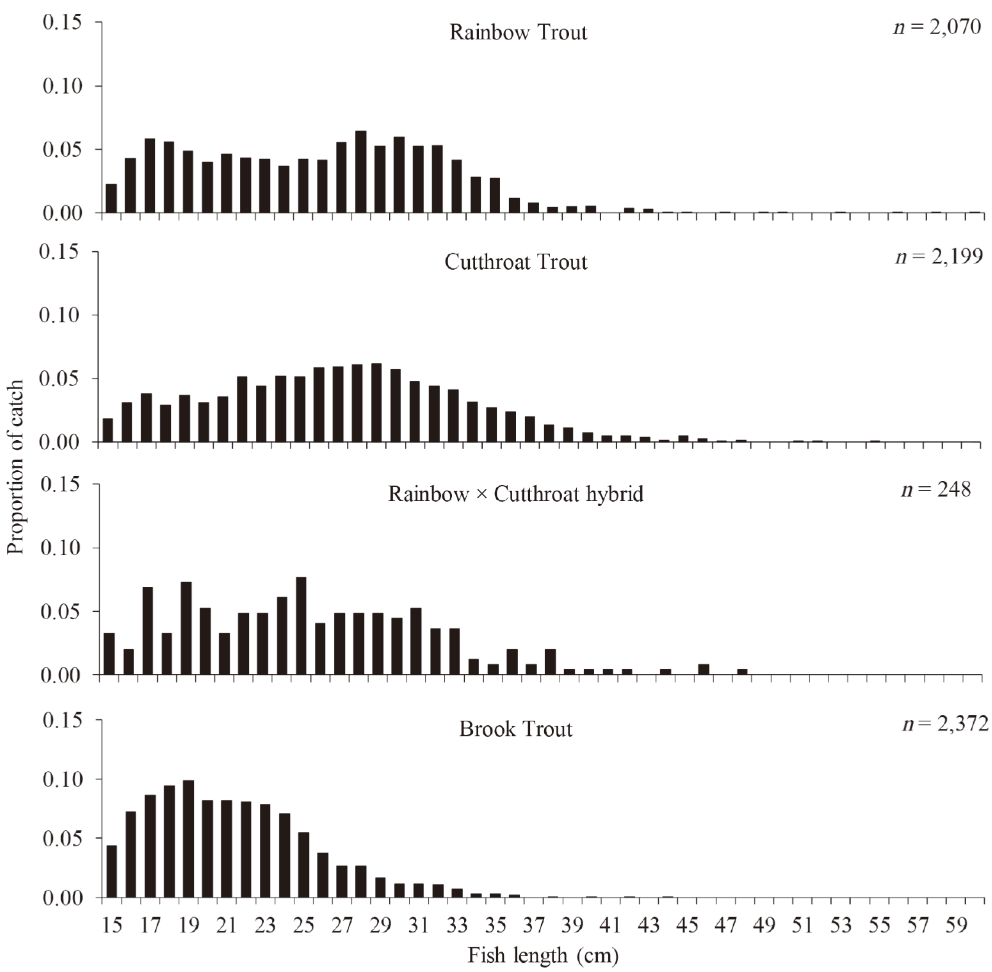

Fig. 1 Length frequency of various trout species caught in gill nets at high mountain lakes in Idaho from 2001 to 2023. Sample size is given for each species.

Table 2. Candidate general linear models relating lake characteristics to the size of trout captured with gill nets at high mountain lakes in Idaho from 2001 to 2023.

Model	AIC	ΔAIC	w_i	Adj r^2
Species + lithology + elevation + shoreline development ratio + net type + lake size + aspect + percent of hike on trail	62,697.62	0.00	0.99	0.18
Species + lithology + elevation + shoreline development ratio + net type + lake size + aspect + cumulative hiking elevation gain	62,706.38	8.75	0.01	0.18
Species + lithology + elevation + shoreline development ratio + net type + lake size+ aspect	62,711.12	13.49	< 0.01	0.18
Species + lithology + elevation + shoreline development ratio + net type + lake size + aspect + hiking distance	62,712.30	14.67	< 0.01	0.18
Null	64,041.34	1,343.72	< 0.01	–

Plausible models were considered to be those with Akaike's information criterion (AIC) scores within 2.00 of the best model. Akaike weights (w_i) were used to rank the relative plausibility of the candidate models, and adjusted coefficients of determination (r^2) were used to assess the amount of variation explained by the models.

Table 3. Parameter estimates and lower (LCI) and upper (UCI) 95% confidence intervals for the most parsimonious general linear model relating lake characteristics to the size of trout captured with gill nets at high mountain lakes in Idaho from 2001 to 2023.

Parameter	Estimate	SE	LCI	UCI
Intercept	270.522	8.561	253.742	287.302
Net type - floating	−0.234	2.249	−4.642	4.173
Net type - unknown	9.731	2.329	5.165	14.297
Lithology - acid volcanic	−23.226	3.441	−29.970	−16.483
Lithology - basalt	−1.308	4.965	−11.039	8.422
Lithology - sediment	−15.146	3.059	−21.142	−9.150
Lithology - shale	−19.260	4.471	−28.024	−10.497
Lake size (ha)	0.514	0.158	0.204	0.823
Elevation (m)	0.015	0.002	0.010	0.019
Shoreline development ratio	−17.606	3.798	−25.051	−10.161
Species - Brook trout	−46.372	1.957	−50.207	−42.537
Species - Cutthroat trout	9.571	2.035	5.582	13.560
Species - Rainbow × Cutthroat hybrid	−4.671	3.997	−12.505	3.163
Aspect - lateral (i.e., E or W)	−20.827	2.696	−26.112	−15.542
Aspect - northern	−13.373	2.326	−17.932	−8.814
Percent of hike in trail	−0.102	0.026	−0.153	−0.051

Reference conditions for categorical variables were rainbow trout (for species), shield (for lithology), and sinking nets (for net type).

prompting the authors to assert that lake accessibility was the primary factor affecting cutthroat trout stock structure in the high mountain lakes they surveyed. In contrast, the most plausible model in the present study predicted that the size of trout would increase by only 10 mm for lakes entirely accessible by trail compared to lakes with no trail whatsoever. Although inclusion of either alternate access difficulty metric—total distance hiked or cumulative elevation gain—explained an equivalent amount of variation in fish size at lakes (Table 2), these models had virtually no support compared to the top model.

The influence access difficulty once had on trout size structure in high mountain lakes has presumably diminished over time because anglers now voluntarily release most of the fish they catch in such remote fisheries[18]. Moreover, the lake access difficulty metrics I used may no longer be a good indication of how difficult lake access is for many anglers. For example, anglers access Idaho high mountain lakes in a variety of ways, including by foot or by use of horses, all-terrain vehicles (ATVs), or backcountry airstrips, with ATV use in particular skyrocketing in recent decades[49,50]. Increased use of ATVs on trails that lead to remote lakes has likely diminished the importance of lake distance from roads and the elevation gain to get there in terms of angling pressure. Nevertheless, my detection of a weak access difficulty vs trout size structure relationship suggests angling pressure still has a minor impact on trout populations in remote mountain lakes. Anglers catch an estimated 14% of salmonids residing in Idaho mountain lakes[18], and although less than half of landed fish are estimated to be harvested, low levels of harvest coupled with catch-and-release angling can impact trout size structure under certain conditions[51,52].

The parameter with the largest effect on size of trout in Idaho high mountain lakes was species, with fish being largest in lakes containing cutthroat trout, intermediate-sized in lakes containing rainbow trout and cutthroat × rainbow hybrids, and smallest in lakes containing brook trout. It is well established that growth rates and size structure vary among salmonid species in lacustrine environments[30,53], including in high mountain lakes[54], and fish size plays an important role in angler effort[12,13] and harvest decisions[55]. However, size alone is not the only factor affecting angler interest in particular waters. Anglers may prefer to catch certain species based on real or perceived differences in beauty, fight quality, native status, taste, or other traits[56,57]. Fortunately, cutthroat trout are an appealing salmonid to target for anglers in the western US[56]. To avoid stunted fish populations, managers may be averse to managing for brook trout, which are known to grow slowly in high mountain lakes[36,58] and therefore are less desirable from a size standpoint[59,60]. Moreover, once wild brook trout populations have become established, they are difficult to remove[61], and they can have negative downstream impacts on a variety of native salmonids[62].

The relationship between rock type and fish size in Idaho high-mountain lakes likely stems in part from the fact that different lithologies weather differently, which can influence the availability of dissolved nutrients and minerals that leach into lakes, ultimately influencing primary productivity. Admittedly, it would have been more straightforward to measure water chemistry and primary productivity directly rather than using lithology as a surrogate, but this was impractical at hundreds of lakes located in remote roadless settings. Some nutrients in high mountain lakes may be influenced by anthropogenic sources (primarily, atmospheric deposition) as much as, or more than, rock weathering, including nitrogen[26,63] and phosphorus[64]. Nevertheless, rock weathering is clearly an important contributor to a variety of minerals and nutrients in aquatic ecosystems[65]. Rock weathering also affects substrate particle size in aquatic environments[66], which may be important in the present study considering that most fish were wild and thus likely produced by inlet, outlet, or lake-shore spawning[3,67,68]. It seems unlikely that rock type affected lake productivity by influencing terrestrial ecosystem processes, considering that mountain lakes typically rely very little on allochthonous input for primary production[69;but see70]. However, surprisingly little research has been conducted on the direct or indirect effects of lithology on fisheries, and more investigation is needed to establish causative links.

Lake morphology and orientation were also related to the size of fish encountered during gill netting, with larger, more uniform-shaped lakes with a southern aspect having larger fish. Just as larger rivers typically support larger trout, larger mountain lakes may generally provide salmonids with more heterogeneity in littoral and pelagic habitat, less overlap in habitat use between life stages (minimizing cannibalism), and more diversity, abundance, and stability in food supplies, all of which may increase survival and growth rates and, consequently, size structure[71,72]. Larger, more uniform-shaped high mountain lakes also tend to be deeper[6,73], and lake depth has been positively correlated to trout growth rates in high mountain lakes[73]. Geographical relief and aspect influence solar radiation in streams[74] and lakes[41], which in turn affect snowmelt, water temperature, and phytoplankton growth. However, aspect has rarely been empirically associated with population characteristics of fisheries. Our results indicate that southern-facing lakes indeed produce larger trout, likely due to a longer and more productive growing season.

The positive relationship I observed between elevation and fish size was surprising and contradicts prior research demonstrating an inverse relationship between elevation and growth for trout in high mountain lakes[73,74]. Although higher-elevation mountain lakes generally have shorter growing seasons, this may not necessarily reduce fish size, as evidenced by some Colorado high mountain lakes exhibiting larger average zooplankton size—a primary food source for trout—at higher-elevation lakes[75]. It is also possible that fish population densities or biomass were lower in the higher-elevation lakes in the present study, reducing competition. Hall[59] demonstrated that size differences between populations of brook trout in Sierra Nevada mountain lakes were inversely related to population density and biomass, and that density and biomass were inversely related to elevation, but these results were based on only eight lakes. Density and biomass data were unavailable for the present study, but future research on the effects of environmental conditions on trout size in mountain lakes would benefit from inclusion of density-dependent metrics.

Most of the variation in fish size in Idaho high-mountain lakes went unexplained by the few predictor variables included in the present study. Since fish were not aged but length ranged from 150–610 mm, the most obvious omitted explanatory variable was fish age. Prior research suggests that additional factors that may have influenced the size of trout I observed in high mountain lakes include: the abundance and type of zooplankton present (i.e., energy content and selectivity vary by species); density-dependent metrics (as mentioned above); water temperature; lake stratification, and depth; the amount of allochthonous input; and, disturbances such as landslides or fire[34,54,59,75−77]. In particular, wildfire may now be having an amplified influence on high mountain lake ecosystems, with wildfire intensity, frequency, and size rising across the western United States[78,79], including in Idaho, where 18% of the 33.6 million acres of federal land burned between 2007 and 2017 (Idaho Department of Lands, unpublished data); many of these burns were near mountain lakes included in the present study. Although the causative effects of wildfire on alpine lakes are not well studied, it is assumed that wildfires may alter levels of important nutrients and minerals in high mountain lakes, such as dissolved organic carbon[80]. Future research incorporating wildfire and other predictor variables would provide a more comprehensive assessment of factors limiting the size structure of trout in high mountain lakes.

Besides the above-mentioned inability to include a more comprehensive suite of predictor variables, the present study had two other limitations. First, I assumed that the size of trout encountered in study lakes was a function of growth and mortality rates[71], but growth and mortality were not measured directly, so whether the observed relationships between fish size and the predictor variables were indicative of influences on trout growth, mortality, or both cannot be ascertained. Second, I assumed that all trout captured in gill nets were wild, though a small percentage were likely of hatchery origin[4, 6], and wild and hatchery trout generally differ in growth[81] and survival[82] and, consequently, size structure. Notwithstanding study limitations, the present study suggests that trout are larger in Idaho high mountain lakes when lakes are larger and at higher elevation; are found in shield lithologies with a southern aspect; have less trail access; and hold cutthroat trout. Fisheries managers can use such information to adjust stocking strategies and to communicate with anglers on areas to target their fishing effort.

Ethical statements

There were no ethical guidelines applicable to this study.

Author contributions

The author confirms sole responsibility for the following: study conception and design, data collection, analysis and interpretation of results, and manuscript preparation.

Data availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Conflict of interest

The author declares that he has no conflict of interest.

Dates

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