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ARTICLE

Temporal Population Trends and Habitat Associations for Mountain Whitefish in Central Idaho

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Abstract
Mountain Whitefish *Prosopium williamsoni* have failed to garner the same level of attention as other members of the salmonid family in terms of scientific investigations, especially with regard to habitat associations and population status. Consequently, we used snorkel survey data from 1985 to 2019 to relate a suite of environmental factors to Mountain Whitefish occupancy and abundance and to estimate population growth rates in central Idaho. Mountain Whitefish population growth rates in the majority of subbasins in central Idaho appear to be stable or increasing over the past several decades, but more so in the Salmon River basin than in the Clearwater River basin. Mountain Whitefish occupancy and abundance were higher in stream reaches that were lower in elevation and gradient and larger in size, with an occupancy rate of <0.10 in stream reaches that were <6 m average wetted width but >0.50 in stream reaches that were ≥9 m average wetted width. Road density was positively associated with the occupancy and abundance of Mountain Whitefish, contrasting previous studies that generally report negative associations between road density and salmonid population metrics. While this relationship may simply be correlative in nature, in the relatively sterile lotic environment of central Idaho, such anthropogenic disturbance may inadvertently result in nutrient enrichment, potentially benefitting the forage base of Mountain Whitefish. We also observed that conductivity positively influenced Mountain Whitefish abundance, likely stemming from its direct effect on stream productivity. Although the status of Mountain Whitefish in central Idaho appears generally stable, the paucity of studies reporting on the status of this species highlights the need for additional research devoted to a better understanding of trends in Mountain Whitefish abundance across their range.

Mountain Whitefish *Prosopium williamsoni* are one of the most widely distributed (Behnke 2002) and abundant (Meyer et al. 2009) species of salmonids in western North America. However, unlike other members of the salmonid family, they have failed to garner much attention from fisheries managers (Brown 2010), likely because anglers generally do not target them. Limited interest in Mountain Whitefish from these groups has resulted in a shortage of studies targeted at understanding the ecology of the species (Northcote and Ennis 1994).

Although studies focusing on Mountain Whitefish are relatively scarce compared with other salmonids, attempts have been made to address this knowledge gap. For example, it has been established that Mountain Whitefish primarily occupy riverine habitat (Northcote and Ennis 1994; Sigler and Zaroban 2018), are broadcast spawners in autumn (Sigler 1951; Northcote and Ennis 1994; Boyer et al. 2017), can achieve lengths exceeding 600 mm (Taylor et al. 2012), commonly live from 8 to 24 years (Thompson and Davies 1976; Meyer et al. 2009; Watkins et al. 2017), and feed almost exclusively on aquatic insects (Sigler 1951; DosSantos 1985). These and other studies have also investigated Mountain Whitefish behavior (DosSantos 1985; Taylor et al. 2012), fecundity (Sigler 1951; Brown 1952;

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Wydoski 2001; Meyer et al. 2009; Boyer et al. 2017), growth (Pettit and Wallace 1975; Benjamin et al. 2014), movement (Pettit and Wallace 1975; Davies and Thompson 1976; Benjamin et al. 2014), recruitment (Watkins et al. 2017), and survival (Thompson and Davies 1976; Meyer et al. 2009; Watkins et al. 2017).

What has rarely been evaluated is population growth rates for Mountain Whitefish, though there is anecdotal information that some populations across western North America are in decline (Boyer et al. 2017). Also lacking are studies investigating factors that limit the distribution and abundance of Mountain Whitefish, although habitat alterations (Erman 1973; Northcote and Ennis 1994; Paragamian 2002; Brinkman et al. 2013) and water temperature thresholds (Quinn et al. 2010) have been shown to influence their distribution. To help fill these knowledge gaps, our first objective was to use data from a long-term, broadscale snorkeling program to evaluate trends in Mountain Whitefish abundance across central Idaho. Our second objective was to investigate environmental factors influencing the contemporary distribution and abundance of Mountain Whitefish in the study area.

METHODS

Study area.— Data for the current study were collected from the Clearwater River and Salmon River basins in central Idaho (Figure 1). The Clearwater River originates in the Bitterroot Mountains and has a drainage area of approximately 25,000 km^2 and a mean basin elevation of 1,311 m. Originating in the Sawtooth Mountains, the Salmon River has a larger drainage area of approximately 37,000 km^2 and a higher mean basin elevation of 2,020 m. In addition to Mountain Whitefish, other salmonids in these basins include Bull Trout *Salvelinus confluentus*, Brook Trout *S. fontinalis*, Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *O. kisutch*, Westslope Cutthroat Trout *O. clarkii lewisi*, Lake Trout *S. namaycush*, and resident and anadromous forms of Rainbow Trout *O. mykiss* and Sockeye Salmon *O. nerka*.

Data collection.— From 1985 to 2019, 11,692 fish surveys were conducted at 2,935 sites across the Clearwater River and Salmon River basins, from which Mountain Whitefish occupancy, abundance, and population growth rates were determined. Fish surveys were conducted via daytime snorkeling from 0900 to 1800 hours when the sun was overhead, typically from June to August of each year. The length of stream snorkeled at each location averaged 97 m (range = 40–300 m). Protocols for snorkel surveys (Apperson et al. 2015) were similar to those established by Thurow (1994). Prior to the start of each survey, underwater visibility (i.e., distance to distinguish patterns on an object [e.g., boot or tape measure], used as a surrogate for spotting patterns on fish) was measured before each survey

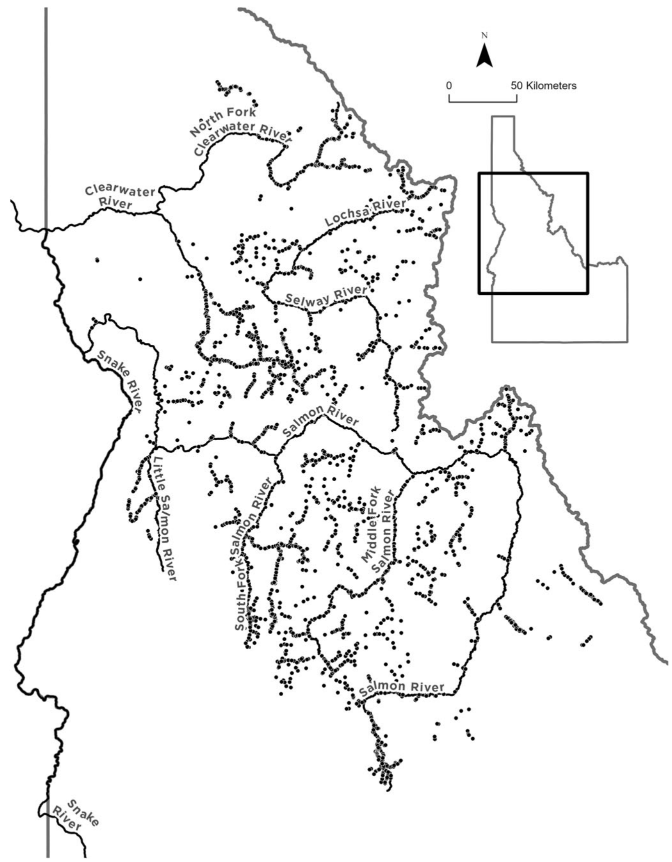

FIGURE 1. Map of the Clearwater River and Salmon River basins of central Idaho. Black dots represent locations where snorkel surveys were conducted during 1985–2019.

and averaged 2.5 m. Visibility was measured to determine the number of snorkelers required to survey the site so that the distance between snorkelers did not exceed the visibility. The majority of surveys (~90%) were conducted in an upstream manner, but water conditions (e.g., high water velocities or deep water) occasionally required the snorkelers to move in a downstream direction. Salmonids >50 mm were identified to species, and total lengths were estimated to the nearest 25 mm in total length. Salmonids <50 mm were not recorded due to the difficulty in identifying some of those fish to species using phenotypic characteristics.

To evaluate factors that influenced Mountain Whitefish occupancy and abundance, various environmental data for each site that was snorkeled (Table 1) were collected using field measurements or a geographic information system (GIS). Field measurements were collected at the time of snorkeling. Average stream width for each site was calculated by averaging wetted width measurements collected every 20 m throughout the survey site and was included in our analyses because stream size can influence Mountain Whitefish occupancy (Meyer et al. 2009). Instantaneous

TABLE 1. Summary of environmental data (i.e., conductivity, elevation, road density, and stream slope) and survey data (water temperature and average wetted width) collected either with geographic information system analysis or during snorkel surveys from 2010 to 2019 in the Clearwater River and Salmon River basins of central Idaho. Data were divided into sites where Mountain Whitefish were either absent or present.

	Absent				Present			
Variable	Mean	SD	Minimum	Maximum	Mean	SD	Minimum	Maximum
Conductivity (μS/cm)	73	39	28	327	67	30	29	260
Elevation (m)	1,410	455	278	2,431	1,292	400	413	2,229
Road density (m)	8,515	9,389	0	57,885	10,135	9,098	0	48,385
Slope (%)	2.4	2.0	0.0	14.8	0.8	0.9	0.0	11.8
Temperature (°C)	12.4	3.1	4.0	24.0	14.3	2.7	8.0	22.0
Wetted width (m)	7.3	5.8	0.8	55.3	16.2	10.0	2.6	52.7

water temperature (°C) at the time of the snorkel survey was collected because it can affect detection probability for salmonids during snorkel surveys (O'Neal 2007). The area of the snorkel survey (m^2) was quantified to account for differences in effort among surveys.

Broadscale GIS layers were linked to Mountain Whitefish occupancy and abundance data using Arcmap 10.6 (Environmental Systems Research Institute, Redlands, California). Using the GIS model constructed by Olson and Cormier (2019), conductivity was estimated for each site and was included in our analyses as a measure of stream productivity (McFadden and Cooper 1962; Scarnecchia and Bergersen 1987). Elevation at each site was calculated from a GIS digital elevation model and was included because it can influence Mountain Whitefish occupancy and abundance (Rahel and Hubert 1991). Underlying lithology was determined at each site using the GIS Idaho State Geologic Map at a scale of 1:750,000 (Lewis et al. 2012) and was categorized as acid volcanic (rhyolite), basalt, sedimentary (including alluvium, sandstone, and quartzite), shale, and shield (metamorphic and plutonic rock; Suchet et al. 2003). Lithology was included in our analyses due to its effect on water chemistry (Olson and Hawkins 2012), habitat complexity (Guy et al. 2008), and substrate size (Kaufmann et al. 2009), all of which can influence Mountain Whitefish occupancy and abundance (DosSantos 1985; Kennedy 2009; Smith et al. 2016).

Road density was included to account for the effect that road construction and maintenance often have on salmonids in general (Dunham and Rieman 1999; Valdal and Quinn 2011) and Mountain Whitefish in particular (Northcote and Ennis 1994). Estimates of road density at each site were calculated by mapping the roads in Idaho using the 2019 Topologically Integrated Geographic Encoding and Referencing database (U.S. Census Bureau 2019) and summing the total meters of road within 10 km^2 (i.e., within a 1.78-km radius) of each survey site. Stream slope and stream order (Strahler 1957) were estimated using National Hydrography Dataset Plus version 2 (https://nhdplus.com/NHDPlus/NHDPlusV2_home.php) and were included to account for their influence on Mountain Whitefish distribution and abundance (Platts 1979; Meyer et al. 2009). Conductivity, elevation, lithology, road density, and slope were all point estimates at the downstream end of the site.

Data analyses.— Temporal trends in Mountain Whitefish abundance in central Idaho were evaluated by estimating population growth rates (λ) individually for each of the major subbasins within the Clearwater River and Salmon River basins. Population growth rates were estimated for the entire long-term data set (1985–2019) and for a more contemporary time period (2010–2019). For both time frames, a site was only included in the trend analyses if Mountain Whitefish had been observed at the site at least once over the course of all surveys and a minimum of three surveys had been completed at the site. For long-term surveys, at least one survey had to be conducted at a site during 2000–2009 and 2010–2019. For contemporary surveys, three surveys must have occurred at a site during 2010–2019. Of the 2,935 sites surveyed by snorkelers, 286 sites met the long-term survey criteria and 308 sites met the contemporary survey criteria (Table 2), but sample size was inadequate to estimate λ for the Clearwater and the North Fork Clearwater subbasins. Sites were divided into headwater streams (stream orders 1–3; Vannote et al. 1980) and large rivers (stream orders >3) because Mountain Whitefish tend to occupy larger rivers (Platts 1979; Maret et al. 1997; Meyer et al. 2009), and headwater streams likely represent suboptimal habitat for the species.

Population growth rates were estimated by fitting snorkel count data to a linear regression model in Program R (R Core Team 2021). The independent variable within the model was the sample year, and the dependent variable was the $\log_e$ transformation of the mean Mountain Whitefish density (fish/100 m^2) from snorkel surveys conducted

TABLE 2. Mountain Whitefish population growth rates (λ) for major subbasins of the Clearwater River and Salmon River basins of central Idaho. The 95% confidence intervals are also included in parentheses. Survey sites were divided into headwater streams (stream orders 1–3) and larger rivers (stream orders >3). Abbreviations are as follows: SF is South Fork and MF is Middle Fork.

	Long term (1985–2019)				Contemporary (2010–2019)			
Subbasin	Time frame	Sites	Surveys	λ	Time frame	Sites	Surveys	λ
Clearwater River (headwater streams)								
Lochsa River	1988–2019	6	110	1.03 (0.94–1.14)	2010–2019	9	37	1.18 (0.76–1.85)
Selway River	1986–2019	7	119	0.93 (0.82–1.06)	2010–2019	7	35	0.59 (0.31–1.14)
SF Clearwater River	1986–2019	42	795	0.90 (0.82–1.00)	2010–2019	39	294	0.79 (0.49–1.26)
Overall	1986–2019	55	1,024	0.95 (0.93–0.98)	2010–2019	55	366	0.93 (0.81–1.08)
Clearwater River (larger rivers)								
Lochsa River	1988–2019	15	297	1.04 (0.99–1.10)	2010–2019	23	149	1.10 (0.88–1.37)
Selway River	1988–2019	19	329	1.01 (0.93–1.08)	2010–2019	14	88	1.00 (0.70–1.42)
SF Clearwater River	1986–2019	17	296	0.83 (0.77–0.90)	2010–2019	12	63	0.68 (0.47–0.98)
Overall	1986–2019	51	922	0.99 (0.95–1.02)	2010–2019	49	300	0.99 (0.85–1.16)
Salmon River (headwater streams)								
Lower Salmon River	1991–2017	1	19	0.93 (0.70–1.23)	2010–2017	1	3	0.85 (0.16–4.45)
Middle Salmon River	1987–2019	9	152	0.96 (0.85–1.09)	2010–2019	8	383	1.00 (0.53–1.92)
MF Salmon River	1985–2019	23	378	0.95 (0.86–1.06)	2010–2019	21	153	0.95 (0.58–1.57)
SF Salmon River	1986–2019	11	259	1.03 (0.93–1.16)	2010–2019	17	113	0.85 (0.51–1.44)
Upper Salmon River	1986–2019	15	266	1.01 (0.90–1.12)	2010–2019	29	147	1.15 (0.68–1.95)
Overall	1985–2019	59	1,074	1.07 (1.03–1.11)	2010–2019	76	799	1.30 (1.06–1.58)
Salmon River (larger rivers)								
Lower Salmon River	1987–2019	6	106	0.94 (0.85–1.05)	2010–2019	6	29	0.79 (0.47–1.31)
Middle Salmon River	1987–2019	11	197	1.09 (1.00–1.18)	2011–2019	8	37	1.07 (0.62–1.87)
MF Salmon River	1985–2019	66	1,099	1.00 (0.94–1.06)	2010–2019	65	481	1.16 (0.90–1.49)
SF Salmon River	1988–2019	15	309	1.05 (0.98–1.13)	2010–2019	26	137	1.13 (0.81–1.58)
Upper Salmon River	1987–2019	23	405	1.03 (0.96–1.10)	2010–2019	23	137	1.24 (0.87–1.76)
Overall	1985–2019	121	2,116	1.08 (1.04–1.12)	2010–2019	128	821	1.25 (1.04–1.50)

that year that met the criteria noted above. Density estimates were used rather than raw count data to account for differences in survey effort between surveys. When constructed in this manner, the slope of the model is equal to the intrinsic rate of change for the population (r; Morris and Doak 2002), which can be exponentiated to estimate λ. The 95% confidence intervals (CIs) were calculated using the error surrounding the estimate of λ from the linear regression (i.e., 95% CI = 1.96 × SE). Because values of zero cannot be $\log_e$ transformed, all surveys with a density of zero were replaced with 0.01 fish/100 m^2. These replacements altered the mean and standard error for these data sets by less than 0.01% compared with the unaltered trend data. Populations were considered stable when the 95% CIs overlapped 1, whereas they were considered to be increasing or decreasing when point estimates of λ were either >1 or <1, respectively, and 95% CIs did not overlap 1. Based on diagnostic analyses of model residuals, including the Kolmogorov–Smirnov test for normality, model fit was deemed acceptable (Neter et al. 1989).

Modeling factors that influenced Mountain Whitefish occupancy was conducted using logistic regression, with a dummy response variable of 1 if they were present and 0 if they were absent. For sites surveyed more than once, Mountain Whitefish were considered present if they were observed at least once at the site. Because preliminary analyses indicated that the fish count data were overdispersed, modeling factors that influenced Mountain Whitefish abundance was conducted using negative binomial regression. Both types of models were fit in program R (R Core Team 2021) using the MASS package (Venables and Ripley 2002). Because survey area (i.e., effort) was different between surveys, both types of models included survey area as an offset to control for this difference. Of the 11,692 snorkel surveys conducted over the entire study period, 3,516 surveys (at 1,293 sites) occurred during the contemporary time period (2010–2019) and were used in these analyses.

Prior to logistic and negative binomial model fitting, collinearity was assessed between covariates, and highly correlated covariates (i.e., $r > 0.70$; Dormann et al. 2013) were not included in the same model. Both stream width and stream order were metrics of stream size; because stream width and survey area were highly correlated ($r = 0.84$) and not independent (i.e., surveyed area = width × reach length) and because survey area was needed in models as an offset, we only included stream order as a metric of stream size in our modeling efforts. To avoid pseudoreplication (Zar 1999) and temporal autocorrelation (Sokal and Rohlf 1995) in the fish count data, survey area, water temperature, and wetted width were averaged across all surveys at a site when sites were visited more than once during the entire study period. No changes were made to the remaining covariates (i.e., conductivity, elevation, lithology, road density, and stream order), as they did not differ between surveys.

All variables were included as fixed effects, and continuous variables were scaled (Schroeder et al. 1986) so that the mean was equal to zero and a one-unit increase in the variable was equal to one standard deviation. Variables were included as linear terms except for water temperature, which was included as a quadratic term due to the fact that salmonids, like nearly all poikilotherms, have an optimal temperature range, and outside this range, activity (and therefore detectability) may be diminished (Thurow 1994; O'Neal 2007). Because of inherent differences in Mountain Whitefish distribution and abundance between subbasins, subbasin was included as a fixed effect. Data from the Potlatch subbasin were discarded from our analyses because although Mountain Whitefish are present in the subbasin, they were entirely absent from the sites surveyed in this study. For each parameter estimate, 95% CIs were calculated via profiling (Venables and Ripley 2002). Parameter estimates and CIs were exponentiated to increase interpretability, and parameters were considered significant when the 95% CIs did not overlap 1 (for continuous variables) or each other (for discrete variables).

RESULTS

In the Clearwater River basin, Mountain Whitefish λ was stable in headwater streams for all subbasins except the South Fork Clearwater River, where λ declined over the entire study period but was stable in the past 10 years (Table 2; Figure 2). In larger rivers, λ was negative in the South Fork Clearwater across the entire study period. Combining data across subbasins to look at overall trends in the Clearwater River basin indicated that Mountain Whitefish λ in the past 10 years was stable in headwater streams and in larger rivers, but long-term λ declined in headwater streams. In the Salmon River basin, Mountain Whitefish λ—both contemporary and long term—was stable in headwater streams and in larger rivers for all subbasins. However, combining data across subbasins to assess overall trends in the Salmon River basin indicated that Mountain Whitefish λ was increasing in headwater streams and in larger rivers for long-term and contemporary time frames.

Mountain Whitefish were present during at least one visit at 561 (43%) of the 1,293 sites used to relate environmental conditions to their contemporary distribution and abundance in central Idaho. Where Mountain Whitefish were present at these sites, they were observed during every survey at 60% ($n = 337$) of the sites and sporadically at 40% ($n = 224$) of the sites. At sites where they were sporadically present, Mountain Whitefish were observed during 52% of the surveys. Their abundance averaged 1.02 fish/100 m^2 (range = 0.01–19.01 fish/100 m^2) at the 561 sites they occupied.

Mountain Whitefish occupancy was influenced by a variety of factors, including elevation, road density, slope, and stream order (Table 3). Parameter estimates indicated that Mountain Whitefish were more likely to occupy larger, lower-elevation stream reaches with a lower stream slope and a higher density of roads in the vicinity of the site. In comparison, parameter estimates from the Mountain Whitefish abundance model indicated that their density was higher in stream reaches with higher conductivity, lower elevation, a higher density of roads in the vicinity of the site, and lower water temperature at the time of the survey (Table 3). Additionally, Mountain Whitefish density was higher in stream reaches with sedimentary and shale lithologies than in reaches with an underlying lithology of basalt.

DISCUSSION

While this is apparently the first study to present broad-scale estimates of Mountain Whitefish λ, there is some evidence of population declines in various portions of their range (see Boyer et al. 2017), highlighting the need for a better understanding of trends in Mountain Whitefish abundance. Because Mountain Whitefish are sensitive to alterations in riverine habitat (e.g., Erman 1973; Northcote and Ennis 1994; Paragamian 2002; Brinkman et al. 2013), they are often used as an indicator species for local environmental assessments (e.g., Bergstedt and Bergersen 1997; McPhail and Troffe 1998; Cash et al. 2000; Quinn et al. 2010) despite the lack of trend data across their range. Based on results from the current study, the vast majority of Mountain Whitefish populations in central Idaho appear to be stable or increasing over the past several decades, although this is true more so in the Salmon River basin than in the Clearwater River basin. These results are not surprising given that more than one-third of central Idaho is designated or de facto wilderness and has been demonstrated to be a stronghold for other native resident salmonids (e.g., Meyer et al. 2014; Kennedy and Meyer 2015). Nevertheless, not all of these areas are pristine,

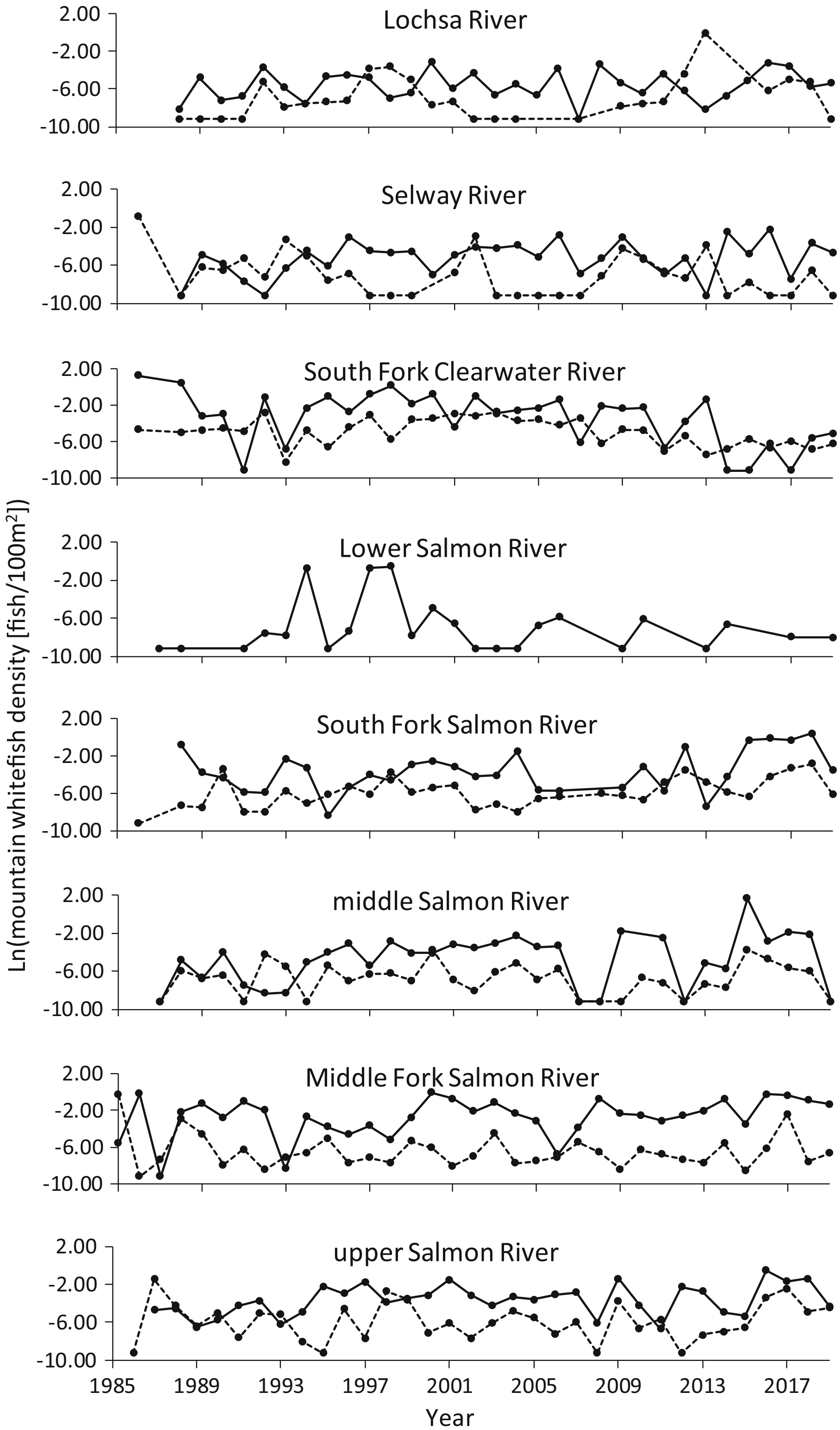

FIGURE 2. Trends in the density of Mountain Whitefish in various subbasins of the Clearwater River and Salmon River basins of central Idaho. Dashed lines are headwater streams (stream orders 1–3), whereas solid lines are large rivers (stream order >3).

TABLE 3. Parameter estimates from generalized linear models evaluating the distribution and density of Mountain Whitefish in the Clearwater River and Salmon River basins of central Idaho. Also included are lower and upper 95% confidence limits. Parameter estimates and confidence limits were exponentiated to increase interpretability. See Methods for complete variable and model descriptions.

Parameter	Estimate	95% confidence limits	
		Lower	Upper
Distribution			
Intercept	0.00	0.00	0.00
Conductivity	1.01	0.81	1.25
Elevation	0.66	0.48	0.89
Lithology (acid volcanic)	1.79	0.34	9.16
Lithology (sedimentary)	2.86	0.59	13.15
Lithology (shale)	4.73	0.99	21.77
Lithology (shield)	3.17	0.69	14.02
Road density	1.40	1.15	1.70
Slope	0.42	0.28	0.60
Stream order	2.48	1.89	3.30
Temperature	0.98	0.80	1.19
Subbasin (SF Clearwater)	44.47	10.43	319.82
Subbasin (NF Clearwater)	279.22	47.20	2,621.69
Subbasin (Lochsa)	19.50	4.24	146.37
Subbasin (Selway)	32.35	6.95	246.51
Subbasin (lower Salmon)	9.94	1.62	88.08
Subbasin (SF Salmon)	57.40	12.24	436.92
Subbasin (middle Salmon)	69.23	14.42	538.37
Subbasin (MF Salmon)	95.55	19.02	765.83
Subbasin (upper Salmon)	123.47	24.49	981.61
Abundance			
Intercept	0.00	0.00	0.00
Conductivity	1.52	1.31	1.79
Elevation	0.84	0.71	0.99
Lithology (acid volcanic)	2.53	0.61	8.63
Lithology (sedimentary)	3.98	1.03	12.25
Lithology (shale)	4.19	1.09	12.83
Lithology (shield)	3.48	0.91	10.58
Road density	1.14	1.02	1.27
Slope	0.90	0.80	1.02
Stream order	1.07	0.95	1.20
Temperature	0.90	0.83	0.99
Subbasin (SF Clearwater)	3.42	0.42	22.89
Subbasin (NF Clearwater)	10.70	1.30	72.31
Subbasin (Lochsa)	4.13	0.49	28.69
Subbasin (Selway)	4.88	0.59	33.23
Subbasin (lower Salmon)	1.25	0.12	13.15
Subbasin (SF Salmon)	7.30	0.88	49.70
Subbasin (middle Salmon)	6.92	0.84	47.08
Subbasin (MF Salmon)	11.99	1.43	83.29
Subbasin (upper Salmon)	5.40	0.64	37.90

especially in the South Fork Clearwater River subbasin, where habitat alterations are more prevalent (Northwest Power and Conservation Council 2003) than in adjacent subbasins; this may explain the declining population growth rates for this subbasin. Considering that this is the first study we are aware of that has assessed Mountain Whitefish population growth rates, we encourage more research devoted to investigating trends in Mountain Whitefish abundance across their range so that their broadscale status is better understood.

Although elevation was inversely related to the occupancy and abundance of Mountain Whitefish, it is unlikely that this indicates a direct causative relationship. Rather, changes in elevation were likely correlated to changes in other environmental factors that more directly elicited behavioral or physiological responses in Mountain Whitefish. For example, lower elevation streams tend to be larger in size and lower in gradient, and we observed higher Mountain Whitefish occupancy in such conditions, as have others (Sigler 1951; Torgersen et al. 2006; Meyer et al. 2009). Stream width was not included in our models because (as mentioned above) stream width and survey area were highly correlated and not independent and survey area was needed to control for differences in snorkeling "effort" between sites. However, the relationship between stream width and Mountain Whitefish occupancy was striking (Figure 3), with an occupancy rate of <0.10 in reaches with stream width <6 m but >0.50 in reaches with average stream width ≥9 m. Relatively large, low-gradient stream reaches likely provide a more suitable thermal regime as well as better spawning, rearing, and overwinter habitat for Mountain Whitefish than narrower, steeper headwater reaches. Unfortunately, lower-elevation lotic habitats in the Intermountain West are more vulnerable to temperature warming due to climate change than are headwater streams (Isaak et al. 2016). Considering their aversion to smaller streams, the ability of Mountain Whitefish to colonize upstream habitat as temperatures warm in the lower-elevation reaches they currently occupy may be diminished compared with other native salmonids (e.g., Isaak et al. 2015).

Not only are larger, lower-elevation river segments more vulnerable to climate change displacement of native salmonids, they also tend to be more heavily altered by anthropogenic disturbances, including road construction and maintenance. Considering that Mountain Whitefish were positively associated with such larger, lower-elevation streams, it should not be surprising that we also found positive associations between road density and their occupancy and abundance. In general, roads negatively affect salmonid populations through sedimentation and habitat alteration (Dunham and Rieman 1999), as well as by creating barriers to fish movement (Diebel et al. 2015). However,

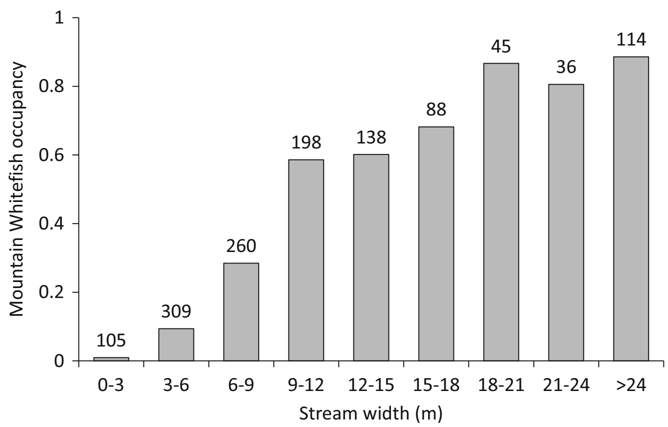

FIGURE 3. Observed occupancy rates of Mountain Whitefish in the Clearwater River and Salmon River basins, Idaho, in stream reaches with various average stream widths. Numbers on the top of bars indicate the sample size for each bin.

Mountain Whitefish differ from most other stream-dwelling resident salmonids in that they have a stronger tendency to school in deeper pool and run habitat, and they broadcast spawn rather than building redds; these behaviors may render Mountain Whitefish less vulnerable to impacts from roads. Alternatively, Scrimgeour et al. (2008) argued that the positive association they observed between Mountain Whitefish occupancy and road density may have been caused by road construction and maintenance creating a trophic cascade of nutrient enrichment mediated by forest land-use practices (e.g., Carignan et al. 2000; Lamontagne et al. 2000), resulting in increased invertebrate abundance. However, this explanation is not supported by the population growth rates we observed, which were lowest in the South Fork Clearwater River basin, perhaps the most disturbed watershed in the study area.

As with stream size, conductivity in streams also changes longitudinally, although not always in a linear manner (e.g., McGuire et al. 2014). We observed that conductivity positively influenced Mountain Whitefish abundance, as has been demonstrated for Mountain Whitefish in other portions of their range (Meyer et al. 2009). Such a relationship likely stems from conductivity directly affecting stream productivity (Rawson 1951; Welch 1952). Stream conductivity in our study area is relatively low (cf. Merovich et al. 2007) compared with other areas where Mountain Whitefish occur (e.g., Meyer et al. 2009; Boyer et al. 2017). As such, our results emphasize that in the relatively sterile lotic environments of the central Idaho mountains (Sanderson et al. 2009), higher stream productivity increases Mountain Whitefish productivity.

Lithology can have a profound effect on channel morphology (Minshall et al. 1985), water chemistry (Clow and Sueker 2000; Wanty et al. 2009), substrate composition (Connolly and Hall 1999), and habitat availability (Lanka and Hubert 1987; Baxter and Hauer 2000) within a stream. In the present study, lithology had no apparent influence on Mountain Whitefish occupancy and only limited influence on their abundance, with densities being highest in stream reaches with sedimentary and shale lithologies and lowest in stream reaches with basalt lithology. The fact that lithology was more influential for Mountain Whitefish abundance than their distribution suggests that lithology influenced habitat suitability more than their ability to fulfill a particular component of their life history. However, surprisingly little research has been conducted regarding the direct effects of lithology on fish distribution or abundance; thus, further research is needed to establish better causative links between lithology and fish ecology.

Our study had some important limitations that may have influenced our findings. First, snorkel data have been shown to be more prone to observation error than data generated from other traditional fish sampling techniques in streams, such as electrofishing, screw traps, and weirs (Meyer et al. 2014), likely because detection probability is less consistent between snorkel surveys. However, estimates of λ using linear regression are robust to the potential presence of observation error within the data (Humbert et al. 2009) and there is no reason to suspect directional bias in the relationships we observed between environmental factors and Mountain Whitefish occupancy or abundance. Second, although snorkel survey locations were not established randomly, we assume that the data they generated did not result in any directional bias in our results, based on the sheer volume of survey sites (nearly 3,000) included in the study (cf. Kadmon et al. 2003). Third, we only included a few of the myriad factors that could have influenced Mountain Whitefish occupancy and abundance in the study area, although this is an inherent weakness of most limiting-factor analyses conducted on fish populations. Notwithstanding these and other limitations, our results suggest that although Mountain Whitefish in central Idaho appear to be stable, conserving wider, lower-elevation stream reaches, especially in sedimentary and shale lithologies, would likely positively benefit Mountain Whitefish populations.

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