North American Journal of Fisheries Management
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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Published online: 01 Jul 2015.

To cite this article: Martin K. Koenig, Kevin A. Meyer, Joseph R. Kozfkay, Joseph M. DuPont & Edward B. Schriever (2015) Evaluating the Ability of Tiger Muskellunge to Eradicate Brook Trout in Idaho Alpine Lakes, North American Journal of Fisheries Management, 35:4, 659-670, DOI: 10.1080/02755947.2015.1035467

To link to this article: http://dx.doi.org/10.1080/02755947.2015.1035467

North American Journal of Fisheries Management 35:659–670, 2015

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2015.1035467

ARTICLE

Evaluating the Ability of Tiger Muskellunge to Eradicate Brook Trout in Idaho Alpine Lakes

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Abstract

In western North America, nonnative Brook Trout *Salvelinus fontinalis* in alpine lakes threaten the persistence of native trout and often offer limited sport fishing opportunity as they are prone to stunting. Stocking tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*), which are reproductively sterile, may be an option to eradicate Brook Trout in some alpine lakes. We used floating gill nets to survey 17 alpine lake Brook Trout populations, then stocked 13 lakes with tiger muskellunge, with four additional lakes serving as controls. Tiger muskellunge were stocked at a mean TL of 317 mm and a density of 40 fish/ha. Brook Trout were resampled for 4 or 5 years after stocking to evaluate changes in Brook Trout TL and CPUE (fish/net-night). Declines in CPUE were substantial for both treatment and control lakes but were significantly greater in treatment lakes. Mean Brook Trout CPUE in treatment lakes declined from 23.1 fish/net-night to 2.3 fish/net-night 5 years after stocking tiger muskellunge, whereas in control lakes, CPUE declined from 25.5 fish/net-night to 7.8 fish/net-night 5 years later. Complete eradication appeared to occur in two lakes within 2 years, and in two more lakes by year 5. In lakes where tiger muskellunge were stocked, the proportion of Brook Trout ≥250 mm TL in the catch increased significantly in years 1, 2, and 4 after stocking (compared with prestocking data), whereas no increase occurred in control lakes. Tiger muskellunge were most successful in reducing Brook Trout CPUE in lakes with no inlets or outlets, while elevation and lake area may also have played a role. Our results suggest tiger muskellunge can improve the size structure and potentially eradicate Brook Trout populations from some alpine lakes. However, we recommend combining any tiger muskellunge stocking with other conventional removal methods to increase the likelihood of successful eradication.

During the early 20th century, Brook Trout *Salvelinus fontinalis* were introduced as sport fish to many high alpine lakes across western North America, including in Idaho. As a result, Brook Trout have established self-sustaining populations in some alpine lakes, most of which were historically fishless (Bahls 1992). Stocking fishless alpine lakes has been linked to lake-specific declines in native amphibian abundance (Pilliod and Peterson 2001; Knapp et al. 2007). Additionally,

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Received October 27, 2014; accepted March 22, 2015

nonnative Brook Trout in alpine lakes threaten native salmonid populations downstream (Dunham et al. 2004). High-elevation headwater streams below alpine lakes frequently contain some of the strongest remaining populations of native Cutthroat Trout *Oncorhynchus clarkii* and Bull Trout *S. confluentus* (Rieman et al. 1997; Dunham et al. 2004). In streams where Brook Trout occur, they often outcompete Cutthroat Trout (reviewed in Dunham et al. 2004) and may eventually eliminate some Cutthroat Trout populations (Kruse et al. 2000; Peterson et al. 2004; Shepard 2004). Additionally, Brook Trout may hybridize with or displace Bull Trout, thereby reducing or eliminating some Bull Trout populations (Kitano et al. 1994; Kanda et al. 2002).

Attempts to eliminate unwanted fish populations in alpine lakes have become more common as resource managers increase efforts to reduce site-specific, fish-related impacts on native fish and amphibian populations. To remove trout populations from alpine lakes, biologists have traditionally used several methods, of which high-intensity gill netting and chemical treatment were the most common. Physical removal with nets can be effective in smaller lakes (<3 ha), but requires considerable effort and usually takes months or years to remove all fish (Knapp and Matthews 1998; Parker et al. 2001). Chemical treatment with piscicides can be effective, and results are obtained quickly (Walters and Vincent 1973; Gresswell 1991). However, biologists may be hesitant to use chemical piscicides in alpine lakes due to cost, difficult access, impacts to nontarget species, and concern over negative public perception of applying chemicals in pristine alpine settings (Finlayson et al. 2010b; Billman et al. 2012).

Stocking tiger muskellunge (Northern Pike *Esox lucius* × Muskellunge *E. masquinongy*) as a biological control may be another option for managing unwanted Brook Trout in alpine lakes. Biological control offers some advantages over conventional methods, including reduced labor, no chemical piscicides, little specialized equipment, and a low cost/benefit ratio when effective (Hoddle 2002). Alpine lakes have simple fish communities, often consisting of only one trout species, which increases the likelihood that introduced predators will be strongly linked to salmonid prey (Hoddle 2002). Because tiger muskellunge are a reproductively sterile cross between Northern Pike and Muskellunge, the risk of establishing a self-sustaining exotic predator is eliminated. When present in high densities, esocids can limit densities of prey species such as White Sucker *Catostomus commersonii* and Black Crappie *Pomoxis nigromaculatus* (Siler and Beyerle 1986). Tiger muskellunge are highly effective predators on a variety of fish, especially soft-rayed fusiform prey (Tomcko et al. 1984) and thus show promise as a means of managing undesirable Brook Trout populations.

Brook Trout populations in alpine lakes often reach high densities as a result of a combination of abundant natural reproduction, early age at maturity, and few predators. Under such conditions, they are prone to becoming stunted (Donald and Alger 1989; Hall 1991a; Parker et al. 2001), at which point they are of marginal interest to most anglers (Rabe 1970; Donald et al. 1980; Donald and Alger 1989). In alpine lakes where eliminating unwanted Brook Trout is unachievable, shifting the size structure towards a higher proportion of quality fish (i.e., ≥250 mm TL) may be a practical secondary objective. In this study, we investigated the effectiveness of introducing tiger muskellunge to reduce or eliminate Brook Trout populations in alpine lakes in Idaho. Specifically, our objectives were to (1) determine whether tiger muskellunge stocked at densities of 40 fish/ha into alpine lakes could eliminate Brook Trout within 4–5 years, (2) document changes in the size structure of Brook Trout in response to stocking tiger muskellunge, and (3) determine lake characteristics that influenced the success of Brook Trout eradication using tiger muskellunge.

METHODS

Between 1998 and 2005, the Idaho Department of Fish and Game (IDFG) and U.S. Forest Service personnel collected alpine lake information to facilitate the selection of a study site. We preferentially selected lakes that were documented to have naturally reproducing Brook Trout populations, had limited inlet–outlet habitat, and did not lie in designated wilderness areas. Steep drainages were preferred, as they most likely possessed barriers that would prevent recolonization from Brook Trout found downstream. Based on preliminary data, we selected 13 alpine lakes for tiger muskellunge stocking and selected four additional lakes as control lakes that did not receive tiger muskellunge stocking (Figure 1).

Brook Trout populations were sampled before tiger muskellunge were stocked (from July to late September in either 2005 or 2006) to estimate initial catch rates and size structure. Fish were sampled with floating gill nets that were 46 m long and 1.5 m deep, and had 19-, 25-, 30-, 33-, 38-, and 48-mm bar mesh panels. During the initial sampling, four gill nets were typically set in the early afternoon and fished overnight. Brook Trout captured in gill nets were counted and measured for TL (mm). Other fish species such as Cutthroat Trout and Rainbow Trout *O. mykiss* comprised <1% of the total fish catch among all lakes and therefore were not considered in our study.

We sampled the study lakes for four or five additional years after stocking tiger muskellunge to monitor changes in Brook Trout catch rates and size structure. Fish were sampled as described above, except that only one or two gill nets were deployed at each lake to reduce netting mortality. Additional tiger muskellunge were collected by angling with lures, measured to the nearest millimeter TL, and released. We used CPUE, calculated as fish/net-night, to compare relative abundance of Brook Trout before and after tiger muskellunge were stocked.

Tiger muskellunge were reared at IDFG's Hagerman State Fish Hatchery. Tiger muskellunge were transitioned from

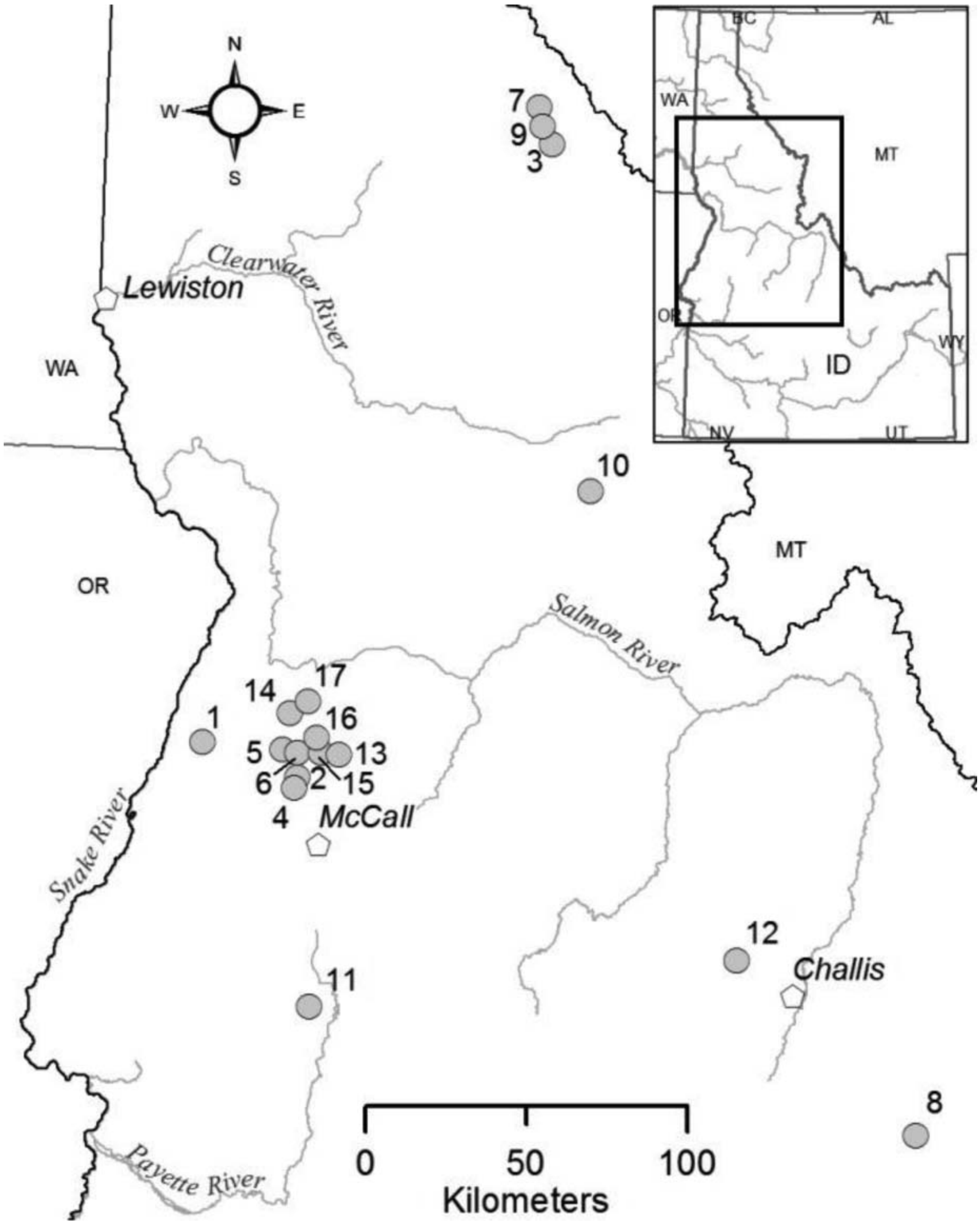

FIGURE 1. Location of selected alpine lakes in Idaho in a study designed to evaluate whether tiger muskellunge could eradicate Brook Trout populations. Numbers correspond to the lake names listed in Table 1.

pellet feed to live Brook Trout 2 weeks prior to stocking to familiarize them with natural prey and increase their predatory effectiveness (Gillen et al. 1981). At the time of stocking, tiger muskellunge TL averaged 317 mm, and ranged from 160 to 400 mm. Tiger muskellunge were stocked by helicopter using an adjustable-volume fire bucket set at 946 L. Tiger muskellunge were hand-counted and loaded before each flight to ensure stocking density was held constant among lakes at

40 fish/ha (Table 1). Densities in the fire bucket did not exceed 0.53 fish/L to reduce transport stress. We stocked four lakes on June 29, 2006, while the remaining lakes were stocked on June 12, 2007. Four additional control lakes did not receive any stocking (numbers 14–17, Table 1).

We measured several habitat features that we hypothesized might affect the ability of tiger muskellunge to eradicate Brook Trout from study lakes. Lake elevation (m) was recorded with a handheld GPS unit. Lake area (ha) was calculated by tracing a polygon over aerial photos with a GIS (ArcGIS 10). Lake inlets and outlets were visually inspected to assess whether these areas were accessible to lake-dwelling Brook Trout and whether they provided useable spawning and/or rearing habitat that could provide potential refuge from tiger muskellunge predation. We considered inlets and outlets as useable if there were no barriers to Brook Trout access and they appeared to provide perennial flow at the time lakes were sampled. We categorized lakes accordingly as (1) containing no useable inlets or outlets, (2) containing either a useable inlet or outlet, or (3) containing both. Depth (m) was measured from a float tube with a handheld sonar unit at five equidistant points along each of five transects placed at equal distances perpendicular to the long axis of the lake with the aid of a laser rangefinder. Maximum depth was estimated using the deepest of these measurements. The amount of littoral zone in each lake was defined as the percentage of the lake less than 3 m deep based on the depth data from the transects. These data were plotted over satellite images in ArcGIS 10 to create bathymetric maps from which the percent littoral zone was estimated. We were also interested in whether vegetative cover would improve the ability of tiger muskellunge to prey upon Brook Trout, so we visually estimated the percent of the lake containing submerged aquatic vegetation.

For the 13 treatment lakes in which tiger muskellunge were stocked, we evaluated multicollinearity between the physical habitat variables collected at each lake, and determined that maximum depth was positively correlated with lake area ($r = 0.73$). Since maximum depth was based on limited measurements, we surmised that lake area was a more reliable variable and removed maximum depth from our analyses. Control lakes were not included in these analyses because some of the physical habitat data were not collected at these lakes.

We compared mean TL of Brook Trout in lakes before stocking with each year after stocking tiger muskellunge using grand means across treatment and control lakes. Similarly, we compared the proportion of Brook Trout in the catch that were ≥250 mm TL. Both comparisons were made using *t*-tests (at $\alpha = 0.05$).

We assessed whether Brook Trout CPUE changed across years after stocking tiger muskellunge using repeated-measures ANOVA. The experimental unit was Brook Trout CPUE (fish/net-night) for each annual sample at each lake. A statistically significant interaction term ($\alpha = 0.05$) between stocking treatment (i.e., treatment versus control lakes) and year was used to indicate a stocking effect on Brook Trout CPUE.

If this test showed that stocking tiger muskellunge reduced Brook Trout CPUE, we subsequently wished to evaluate how lake habitat characteristics influenced the magnitude of the change in Brook Trout CPUE. For this analysis, we used a general linear model (GLM) to relate the percent change in Brook Trout CPUE (comparing prestocking to year-4 CPUE) to the physical habitat variables collected at each lake. We chose to use catch rate data from year 4 as the response variable for two reasons. First, we assumed it might take several years for tiger muskellunge to eradicate Brook Trout. Second, one lake was missing data in year 5, so we used year 4, which had a more complete data set. We selected the best GLM models from all possible subsets based on the lowest Akaike information criterion (AIC) scores (Akaike 1973) corrected for small sample sizes (AIC_c; Burnham and Anderson 1998). We determined the most plausible models as those with AIC_c scores within 2.0 of the best model (Burnham and Anderson 2004). We used AIC_c weights (w_i) to assess the relative plausibility of each model and R^2 to show the amount of variation explained by each model. We examined diagnostics of model residuals for both the repeated-measures ANOVA and the GLM analysis to ensure model aptness for the data at hand. All statistical analyses were performed with SAS statistical software (SAS Institute 2009).

RESULTS

Relative abundance of Brook Trout varied widely among study lakes and years, but declined quickly in most of the 13 lakes stocked with tiger muskellunge. In treatment lakes, Brook Trout CPUE declined 33–98% from before stocking tiger muskellunge to 4 years after, except for one lake where catch rate increased by 35% (Figure 2). On average, Brook Trout CPUE across all treatment lakes declined from 23.1 fish/net-night before stocking tiger muskellunge to 8.3 fish/net-night 1 year after stocking, and to 2.3 fish/net-night 5 years later. During the same period, Brook Trout CPUE in control lakes declined 11–66% and increased 50% in one lake. Mean Brook Trout CPUE in control lakes declined from 25.5 fish/net-night to 15.3 fish/net-night 1 year later, and to 7.8 fish/net-night 5 years later. Thus, while Brook Trout catch declined for both treatment and control lakes, the decline in CPUE was significantly greater for treatment lakes, as indicated by a significant treatment × year interaction term in the repeated-measures ANOVA ($F = 5.94$, df = 11, $P = 0.01$). Complete eradication appeared to occur in two lakes (Black and Corral lakes) within 2 years and in two more lakes (Granite Twin and Shirts lakes) by year 5.

Changes in Brook Trout TL varied across lakes, but increased at most treatment lakes where Brook Trout were still

TABLE 1. Physical description of Idaho alpine lakes stocked with tiger muskellunge (13 lakes) or used as controls (four lakes) to eradicate Brook Trout; % littoral was the estimated percentage of lake area classified as littoral habitat (i.e., <3 m deep); % vegetation was the estimated percentage of littoral habitat containing submerged aquatic vegetation; and % change in Brook Trout CPUE corresponds to 4 years after stocking tiger muskellunge. Lake numbers correspond to those in Figure 1.

							Accessible habitat in			
Lake number	Lake name	Lake elevation (m)	Lake size (ha)	Maximum depth (m)	% littoral habitat	% vegetative habitat	Inlet	Outlet	Tiger muskellunge stocked	% change in CPUE
1	Black	2,199	10.5	37.8	26	10	No	Yes	420	−100
2	Corral	2,085	2.6	7.3	39	40	No	No	104	−100
3	Fly	1,652	1.0	3.3	85	0	No	No	41	−96.4
4	Granite Twin	2,183	16.1	20.4	37	10	No	Yes	656	−97.5
5	Grass Mountain 1	2,238	5.1	6.1	74	0	No	No	206	−89.3
6	Grass Mountain 2	2,263	5.1	3.7	82	15	Yes	No	225	−97.1
7	Heather	1,875	2.6	9.0	50	0	Yes	Yes	106	−73.1
8	Merriam	2,926	2.6	10.4	31	5	Yes	Yes	107	35.1
9	Platinum	1,753	1.0	4.1	60	0	No	Yes	40	−85.7
10	Running	2,008	8.4	14.0	15	0	Yes	Yes	349	−23.4
11	Shirts	2,254	3.5	3.1	100	10	No	Yes	140	−86
12	Spruce Gulch	2,698	10.9	13.0	45	10	No	No	439	−93.7
13	Upper Hazard	2,294	15.8	21.4	30	5	Yes	Yes	632	−61.1
14	Black #2	2,177	2.6				Yes	Yes	control	50.0
15	Hard Creek	2,262	3.5	5.5			Yes	Yes	control	−66.1
16	Lloyds	2,092	2.9				Yes	Yes	control	−71.7
17	Rainbow	2,150	8.8				Yes	Yes	control	−11.7

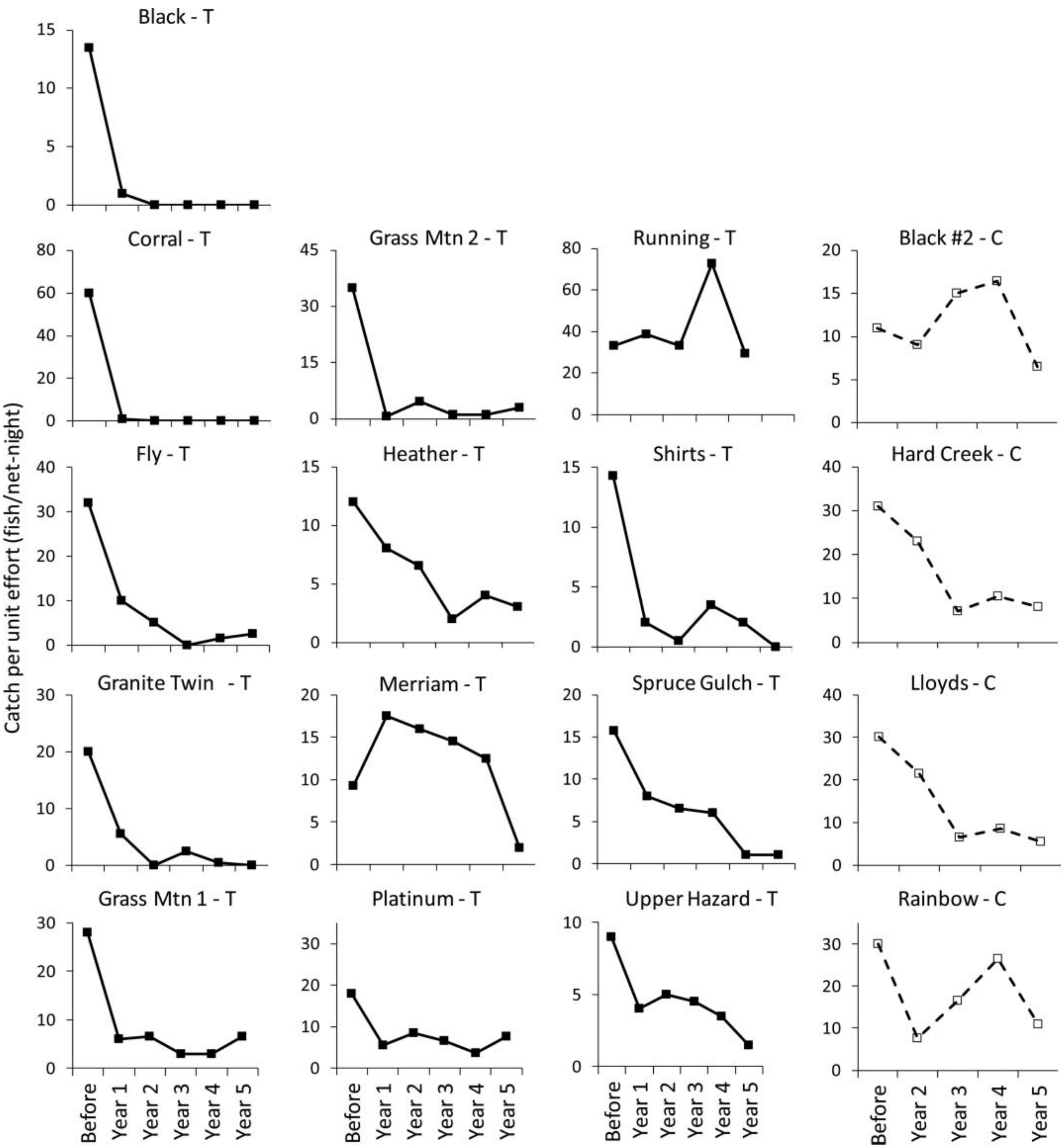

FIGURE 2. Annual gill net CPUE for Brook Trout caught in 13 alpine lakes in Idaho where tiger muskellunge were introduced and four control lakes where no stocking occurred. Treatment lakes are shown by black lines, solid symbols, and "T" following the lake name, while control lakes are shown by dashed lines, open symbols, and "C" following the lake name.

sampled. Grand mean TL for Brook Trout increased significantly 1 year ($t = -4.15$, df $= 24$, $P < 0.001$), 2 years ($t = -3.77$, df $= 21$, $P = 0.001$), and 4 years ($t = -2.61$, df $= 22$, $P = 0.02$) after stocking tiger muskellunge (Figure 3). In contrast, grand mean TL for Brook Trout only increased significantly in year 2 for control lakes ($t = -2.45$, df $= 6$, $P = 0.05$). The proportion of Brook Trout ≥ 250 mm TL in the catch increased significantly 1 year ($t = -3.46$, df $= 24$, $P =$

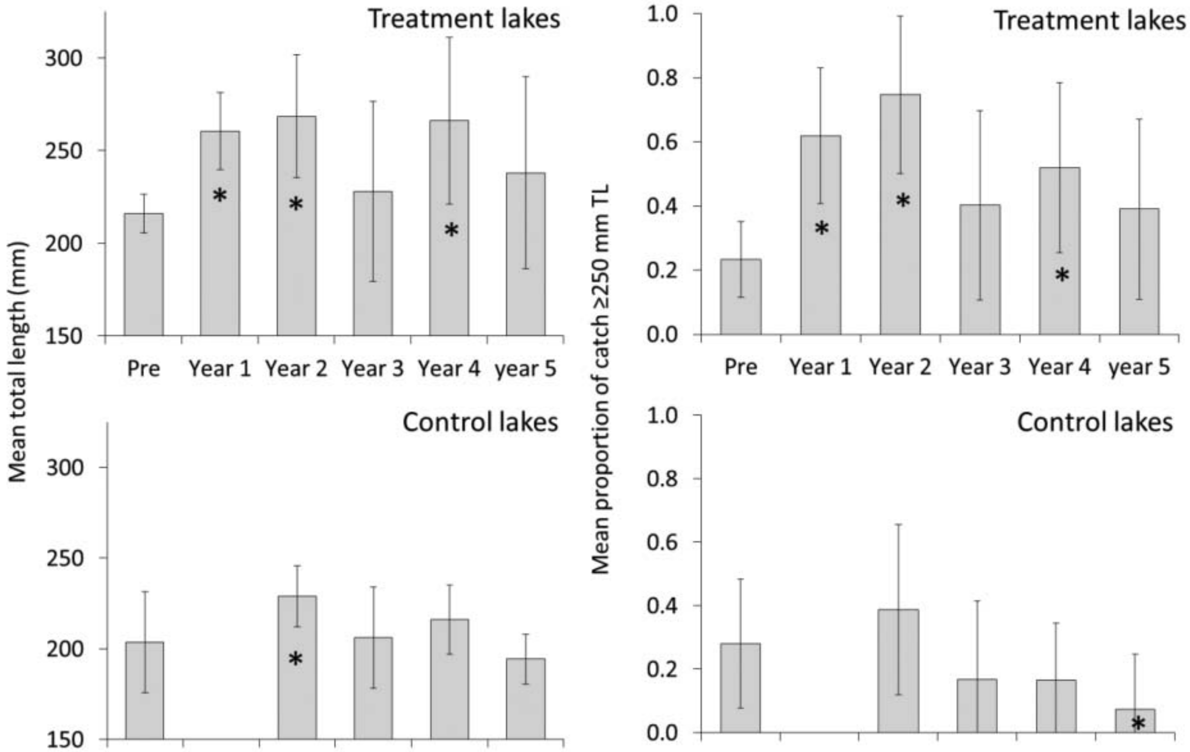

FIGURE 3. Grand mean (±95% CIs) for Brook Trout TL and proportion of catch ≥ 250 mm in 13 alpine lakes in Idaho where tiger muskellunge were stocked and four control lakes where no stocking occurred. Asterisks denote years that differ significantly from the prestocking sample data (*t*-test, $\alpha = 0.05$).

0.002), 2 years ($t = -4.55$, df = 21, $P < 0.001$), and 4 years ($t = -2.31$, df = 22, $P = 0.03$) after stocking tiger muskellunge (Figure 3). The proportion of Brook Trout ≥ 250 mm TL did not increase in control lakes.

Initially, tiger muskellunge TL increased quickly after stocking, but slowed in subsequent years. At the time of stocking, tiger muskellunge averaged 317 mm TL ($n = 26$). Mean TL of tiger muskellunge increased to 460 mm ($n = 49$) in year 1, 534 mm ($n = 17$) in year 2, 644 mm ($n = 4$) in year 3, and 638 mm ($n = 8$) by year 4. Angling and visual observations indicated tiger muskellunge persisted in at least five of the lakes at least 4 years after stocking (Table 2).

For the 13 treatment lakes stocked, the percent reduction in Brook Trout CPUE 4 years after stocking was most strongly correlated with lake elevation (correlation coefficient, $r = -0.50$) and percent littoral habitat ($r = 0.45$), and less correlated with lake area ($r = 0.05$) and percent vegetation ($r = 0.26$). In regards to categorical habitat variables, declines in Brook Trout CPUE were more pronounced at lakes with no inlet or outlet (mean = 95%) and at lakes with one or the other (92%) than at lakes with both inlets and outlets (26%; Figure 4).

The GLM model results indicated that the percent change in Brook Trout CPUE 4 years after stocking tiger muskellunge was best explained by inlet–outlet habitat, lake elevation, and lake area. The most parsimonious model included only one variable (usable inlets or outlets) and explained 48% of the variation in changes in Brook Trout CPUE (Table 3). Two other plausible models included elevation and lake area, suggesting these factors may also have been important in determining the relative success of reducing Brook Trout abundance (Table 3). A model including inlets–outlets, elevation, and lake area improved model fit from $R^2 = 0.48$ to $R^2 = 0.62$, compared with the single variable model, but w_i of the three-variable model was less than half of the single variable model, indicating the three-variable model was less plausible (Table 3).

DISCUSSION

Our results suggest tiger muskellunge can be an effective biological control for undesirable Brook Trout populations in some alpine lakes. Most lakes showed substantial declines immediately after stocking, indicating Brook Trout reductions occurred quickly. This is consistent with several studies that have demonstrated esocids readily consume soft-rayed fusiform prey fish (Mauck and Coble 1971; Weithman and Anderson 1977; Goddard and Redmond 1978; Gillen et al. 1981). The effectiveness of tiger muskellunge at controlling Brook Trout was likely improved by their large average size at the time of stocking (>300 mm) and their exposure to live Brook

TABLE 2. Number of tiger muskellunge stocked and captured or observed in subsequent years in 13 Idaho alpine lakes.

Lake name	Initial number stocked	Number of tiger muskellunge observed or captured				
		Year 1	Year 2	Year 3	Year 4	Year 5
Fly	41	4	1	0	0	
Heather	106	2	0	0	0	
Platinum	40	0	0	0	0	
Running	349	0	2	0	0	
Black	420	26	10	2	10	1
Corral	104	7	10	0	2	0
Granite Twin	656	2	6	6	0	1
Grass Mountain 1	206	2	1	0	0	0
Grass Mountain 2	225	1	0	0	1	0
Merriam	107	2	1	0	0	0
Shirts	140	0	7	2	5	0
Spruce Gulch	439	32	4	10	2	2
Upper Hazard	632	4	1	0	0	0

Trout prior to stocking. In general, hatchery esocids survive better and have higher foraging success when (1) reared on a diet of live fish, (2) stocked at larger sizes (>250 mm) in the spring, and (3) stocked in lakes with high densities of suitable prey (Storck and Newman 1992; Szendrey and Wahl 1996; Larscheid et al. 1999; Wahl 1999). This corresponds well with the design of our study and the characteristics of these lakes.

Tiger muskellunge were not only able to reduce Brook Trout abundance significantly, but they completely eradicated them from four lakes within 5 years of being stocked. We anticipated some successful eradications based on results from a 1998 IDFG pilot study at Ice Lake (0.54 ha) in central Idaho. Brook Trout were eliminated from Ice Lake within 3 years of stocking tiger muskellunge (41 fish/ha). Unlike the lakes in our study, Brook Trout at Ice Lake were also actively removed with electrofishing from the inlets and outlets to reduce recolonization, which probably contributed to the extirpation achieved there (E. B. Schriever, unpublished data). Despite the success we observed at some lakes, four lakes in the current study showed little if any change in catch rates or length of Brook Trout, indicating impacts from tiger muskellunge stocking were sometimes negligible. We saw no effect at our highest elevation and coldest site, Merriam Lake, where few tiger muskellunge were observed after the first year of sampling. At this lake, Brook Trout CPUE was high until collapsing in year 5, most likely the result of some natural event unrelated to stocking tiger muskellunge. This disparity in success suggests the ability of tiger muskellunge to eradicate Brook Trout will vary among lakes, probably as a function of habitat and survival after stocking.

Surprisingly, Brook Trout CPUE declined substantially in the control lakes as well, although not as precipitously as in treatment lakes. One explanation for this decline is the

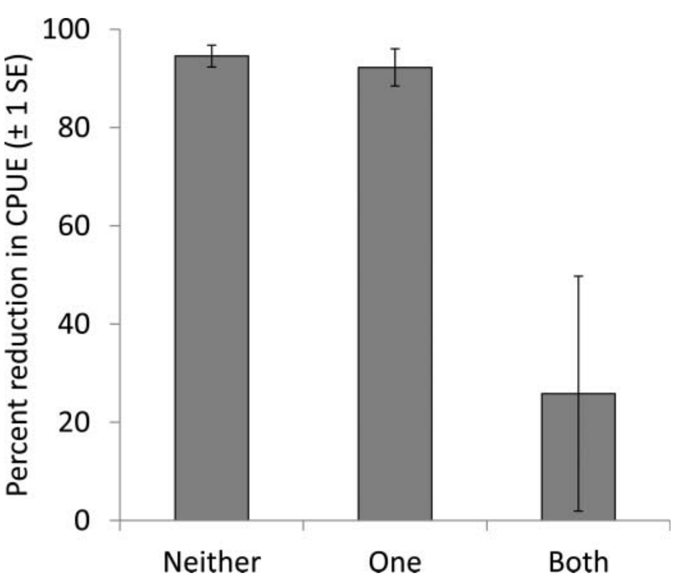

FIGURE 4. Mean percent reduction (±SE) in Brook Trout CPUE 4 years after tiger muskellunge were stocked in lakes with or without inlets and outlets accessible to Brook Trout. Lakes were divided into those with useable inlets and outlets (both), those with neither (none), and those with one or the other (one).

TABLE 3. General linear model results relating lake habitat characteristics to percent change in Brook Trout CPUE 4 years after introducing tiger muskellunge. Only the most plausible models (those with AIC_c scores within 2.0 of the best model) are shown.

Variables	R^2	AIC_c	ΔAIC_c	w_i
Inlets–outlets	0.48	108.51	0.00	0.32
Elevation, area	0.51	109.63	1.12	0.18
Elevation, area, inlets–outlets	0.62	110.37	1.86	0.13

repeated gill netting we conducted at the lakes, which may have reduced Brook Trout abundance through time. However, we believe gill netting had little impact on Brook Trout CPUE (at control or treatment lakes) because on average we only caught 20 Brook Trout per lake per year of sampling. In comparison, mark–recapture Brook Trout population estimates were made at the start of the study in three lakes, and abundance averaged 1,279 Brook Trout per lake (J. M. DuPont, unpublished data). It seems unlikely that removing a few dozen Brook Trout with gill nets each year would have noticeably reduced overall abundance. More plausibly, declines in Brook Trout CPUE at all the lakes (control and treatment) might have been related to some regional factor such as changes in annual precipitation or temperature. Such bioclimatic factors can synchronously affect stream-dwelling salmonid populations in Idaho (Copeland and Meyer 2011). That Brook Trout declined at significantly greater rates in treatment lakes suggests that the additional decline in CPUE in treatment lakes compared with control lakes was attributable to the stocking of tiger muskellunge.

Increasing mean TL is a common response after reducing densities of stunted Brook Trout populations. Hall (1991b) used removal experiments to demonstrate that change in Brook Trout size in alpine lakes was proportional to population density, with the change in length being proportional to the change in density. Similarly, Parker et al. (2001) found a rapid increase in Brook Trout body condition following removal by gill net in a Canadian alpine lake. Donald and Alger (1989) reported increased mean weight for all age-classes of Brook Trout in a Canadian alpine lake when subjected to only 20% exploitation, a rate much lower than the level of tiger muskellunge predation at most of the lakes in our study. Mean TL in our treatment lakes was significantly different in the first 2 years after stocking (Figure 4). This pattern may have been a result of tiger muskellunge consuming small Brook Trout initially, increasing mean TL quickly as densities were reduced (Anderson 1973; Hall 1991b). The largest remaining individuals may have escaped predation through avoidance or by exceeding the gape limitation of the tiger muskellunge. Managers interested in improving trout size structure should carefully consider tiger muskellunge stocking densities. For instance, stocking tiger muskellunge near 40 fish/ha will likely improve size structure of the trout population, but the resulting trout densities may be so low that catch rates will disappoint anglers.

Our results suggest that inlet–outlet habitat was the single most influential variable in determining the ability of tiger muskellunge to reduce Brook Trout CPUE. Generally, there was less change in Brook Trout CPUE in lakes with inlets and outlets (Figure 4). Indeed, the four lakes where tiger muskellunge were least effective all contained both useable inlets and outlets. The inlets and outlets in the alpine lakes we studied were generally narrow (<2 m wide) and shallow (<10 cm deep). Nevertheless, they were apparently large enough for Brook Trout to find refuge from tiger muskellunge predation, and they may have provided additional recruitment to the lentic portion of the Brook Trout population. Use of inlet–outlet streams or drainage channels as a means of escaping piscivorous fish is common among fish prey species (Borcherding et al. 2002; Jepsen and Berg 2002; Skov et al. 2008). However, these habitats may be seasonably unsuitable, such as in summer (due to high water temperatures or inadequate flow) or winter (due to frazil ice, anchor ice, collapsing snow banks, or ice shelves), which could force Brook Trout back into alpine lakes where they become vulnerable to tiger muskellunge predation.

Lake elevation was another factor that influenced the success of tiger muskellunge in reducing Brook Trout CPUE, with reductions in CPUE declining as elevation increased. Tiger muskellunge may have experienced higher winter mortality at higher elevations, while lower water temperatures and reduced metabolic demand may have lowered predation rates. The importance of the remaining variables was inconclusive, possibly for several reasons. For example, percent vegetative cover (estimated visually) was a subjective measurement that may have precluded significant correlation with declines in Brook Trout catch rates if the measurements were inaccurate. Additionally, our limited sample size ($n = 13$) may not have provided adequate power to detect other potentially meaningful relationships. For instance, lake area was not strongly correlated with change in Brook Trout CPUE but was included in the second- and third-best models, whereas other more strongly correlated variables (such as percent littoral habitat and percent vegetative cover) were not included in any of the most plausible models. Although Brook Trout likely occupied pelagic areas in our study lakes in order to avoid tiger muskellunge, they may have periodically entered littoral areas where food sources were more abundant. Concentrating Brook Trout eradication efforts in small, shallow alpine lakes, especially those with a higher percent coverage of aquatic vegetation, may force more overlap in habitats used by tiger muskellunge and Brook Trout and increase the likelihood of eradication success (Tomcko et al. 1984). Although we did not address it in this study, future studies might examine how other habitat features such as large woody debris and boulders might influence how successful tiger muskellunge are at controlling Brook Trout in alpine lakes.

Three years after stocking, tiger muskellunge were not caught or observed in more than half the stocked lakes; although in lowland lakes, tiger muskellunge commonly live longer than 10 years (Fitzgerald et al. 1997). The rarity of tiger muskellunge encounters may have been due in part to low sample effort (to avoid netting mortality). However, the high-elevation, oligotrophic waters and simple habitat of most alpine lakes are not ideal tiger muskellunge habitat. Rather, esocids generally prefer warm, low-elevation lakes and slow-moving rivers with shallow habitat (2–4 m deep) that contain submerged or emergent vegetation and numerous piscine prey species (Scott and Crossman 1973; Hanson and Margenau 1992; Tipping 2001). Nevertheless, exotic fish species often thrive in novel environments as long as they can take advantage of vulnerable prey or a lack of competitors (e.g., Moyle 1986; Witte et al. 1992). In most of the alpine lakes in our study, tiger muskellunge presumably found ample prey, adequate “lie-and-wait” cover, and at least a tolerable ambient environment that met their basic physiological needs. If tiger muskellunge exhausted their food resources, they may have starved before completely removing Brook Trout in some lakes. In such cases, additional years of stocking tiger muskellunge may help complete eradications, but cannibalism from any remaining large tiger muskellunge could negate benefits from additional tiger muskellunge stocking in subsequent years.

Idaho fishing regulations allow anglers to harvest two tiger muskellunge per day, with none under 1,016 mm (40 in) TL. Anecdotal evidence from some anglers suggests that many were not aware of the regulations, and illegal harvest of tiger muskellunge may have affected our efforts to remove Brook Trout at some lakes. However, we did not estimate angler effort at our study lakes and thus could not estimate angling mortality of tiger muskellunge. Future efforts to remove Brook Trout with tiger muskellunge should consider potential angling impacts when determining stocking densities.

Management Implications

Conventional methods to remove unwanted fish populations are typically costly and labor intensive. We estimated the cost to stock tiger muskellunge in 9 of the 13 lakes in our study was approximately US $22,000 (average of $2,444 per lake), of which helicopter flight time was the primary expense ($18,000), followed by the cost to purchase, raise, and transport the fish ($5.50/kg, $2,200). We did not include additional costs for monitoring Brook Trout population responses after stocking. Knapp and Matthews (1998) used gill nets to remove a low-density trout population from a small (1.6 ha) alpine lake, high (3,120 m) in the Sierra Nevada Mountains of California. They removed the entire Brook Trout population (97 fish) within 3 years during the ice-free period with 108 net-nights of effort. The authors estimated the cost of gill netting ($5,600) was slightly less than the projected cost of aerial rotenone application ($6,500). However, after the initial one-time purchase for a helicopter spraying rig, they estimated rotenone application would actually be more cost effective if multiple lakes were to be treated. Parker et al. (2001) successfully removed the entire Brook Trout population (261 fish) from a 2.1-ha alpine lake (9.2 m deep) using gill nets, but expended 10,000 net-nights over 3 years to do so in a relatively small lake. Similar to Knapp and Matthews (1998), those authors concluded that using gill nets would likely be impractical for lakes greater than 10 ha in size and 10 m in average depth. For larger lakes, Parker et al. (2001) recommended other control methods including electrofishing, trap netting on spawning grounds, lake drawdown, disturbing spawning areas, and applying chemical piscicides. Most of these alternate methods would be impractical for typical alpine lakes because of their remote locations and limited access. These studies indicate aerial rotenone application may be the most viable option for large, deep alpine lakes and those with self-sustaining trout populations in inlets or outlets (Knapp and Matthews 1998). However, applying rotenone in alpine lakes presents its own set of challenges. Rotenone is most effective when lakes are isothermal, suggesting treatments would have to occur in early summer or fall, when access and weather in alpine environments can be challenging. Alpine lakes often have low water temperatures, low alkalinity, and low organic matter, extending the time rotenone will remain toxic and prolonging the persistence of its toxic metabolite, rotenolone (Finlayson et al. 2010a). Carefully monitoring detoxification downstream and bioassays prior to restocking are essential.

Removing unwanted fish species with biological control methods offers some compelling benefits. Successful projects have low cost/benefit ratios, require little labor or specialized equipment, and may minimize mortality of nontarget organisms like invertebrates and amphibians associated with chemical piscicides (Hoddle 2002). Since nearly all alpine lakes throughout Idaho were historically fishless (Bahls 1992), there is little risk to native trout species in alpine lake watersheds. Moreover, introducing other piscivorous salmonids could negatively affect native trout downstream, while tiger muskellunge are poorly adapted to headwater streams typically found below alpine lakes. Despite these advantages, Meronek et al. (1996) reported that stocking fish species to remove other species was not as effective as physical or chemical methods. Those authors estimated that only 24% of such projects were successful, similar to the 31% success rate among lakes in our study. Meronek et al. (1996) found that chemical treatment was the most commonly used method (58%), and rotenone was successful in 48% of the projects. However, the authors found that the highest success rate for fish removal projects combined both physical and chemical removal techniques. Our study suggests that stocking tiger muskellunge in alpine lakes to eradicate unwanted Brook Trout populations may be successful in some cases but not in others. We recommend any tiger muskellunge stocking be combined with other conventional removal methods for greater chances of success.

Without additional effort to remove Brook Trout that persist in refuge habitats such as inlet or outlet streams, alpine lakes could be recolonized shortly after tiger muskellunge disappear. In larger, more complex lakes, additional effort may be needed to eliminate Brook Trout not accessible to tiger muskellunge. In the absence of substantial predation, Brook Trout may rebound quickly, so multiple suppression methods that target refuge habitats should be combined to maximize effectiveness. Finally, we analyzed only 13 alpine lakes in this study, and it appeared that tiger muskellunge were successful in eradicating unwanted Brook Trout in four of them. Additional research in alpine lakes is needed to better understand what lake characteristics allow tiger muskellunge to be most effective and at what stocking densities, and which conventional removal methods could be combined with tiger muskellunge stocking to improve the chances of successfully eradicating Brook Trout from alpine lakes.

ACKNOWLEDGMENTS

Joe Chapman and the staff at Hagerman Hatchery raised and transported the tiger muskellunge and were critical to the success of this project. We acknowledge the hard work and dedication of the many technicians that helped sample these lakes, especially Peter Gardner, Eric Herrera, Chris Sullivan, Alan Sievers, John Walrath, John Cassinelli, Lars Alsager, Bryan Cage, Karen Schnake, Tobyn Rhodes, John Earhart, Tim Kuzan, John McComas, and Josh Peterson. Funding for this work was provided by anglers and boaters through their purchase of Idaho fishing licenses, tags, and permits, and from federal excise taxes on fishing equipment and boat fuel through the Sport Fish Restoration Program.

REFERENCES

Anderson, R. 1973. Application of theory and research to management of warmwater fish populations. Transactions of the American Fisheries Society 102:164–171.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Second international symposium on information theory. Akademiai Kiado, Budapest.

Bahls, P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Science 66:183–193.

Billman, H. G., C. G. Kruse, S. St-Hilaire, T. M. Koel, J. L. Arnold, and C. R. Peterson. 2012. Effects of rotenone on Columbia spotted frogs *Rana luteiventris* during field applications in lentic habitats of southwestern Montana. North American Journal of Fisheries Management 32:781–789.

Borcherding, J., M. Bauerfeld, D. Hintzen, and D. Neumann. 2002. Lateral migrations of fishes between floodplain lakes and their drainage channels at the lower Rhine: diel and seasonal aspects. Journal of Fish Biology 61:1154–1170.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Copeland, T., and K. A. Meyer. 2011. Interspecies synchrony in salmonid densities associated with large-scale bioclimatic conditions in central Idaho. Transactions of the American Fisheries Society 140:928–942.

Donald, D. B., and D. J. Alger. 1989. Evaluation of exploitation as a mean of improving growth in a stunted population of Brook Trout. North American Journal of Fisheries Management 9:177–183.

Donald, D. B., R. S. Anderson, and D. W. Mayhood. 1980. Correlations between Brook Trout growth and environmental variables for mountain lakes in Alberta. Transactions of the American Fisheries Society 109:603–610.

Dunham, J. B., D. S. Pilliod, and M. K. Young. 2004. Assessing the consequences of nonnative trout in headwater ecosystems in western North America. Fisheries 29:18–26.

Finlayson, B., R. Schnick, D. Skaar, J. Anderson, L. Demong, D. Duffield, W. Horton, and J. Steinkjer. 2010a. Planning and standard operating procedures for the use of rotenone in fish management–rotenone SOP manual. American Fisheries Society, Bethesda, Maryland.

Finlayson, B., W. L. Somer, and M. R. Vinson. 2010b. Rotenone toxicity to Rainbow Trout and several mountain streams insects. North American Journal of Fisheries Management 30:102–111.

Fitzgerald, T. J., T. L. Margenaue, and F. A. Copes. 1997. Muskellunge scale interpretation: the question of aging accuracy. North American Journal of Fisheries Management 17:206–209.

Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and Bluegills in experimental systems. Transactions of the American Fisheries Society 110:197–209.

Goddard, J. A., and L. C. Redmond. 1978. Northern Pike, tiger muskellunge and Walleye populations in Stockton Lake, Missouri: a management evaluation. Pages 313–319 *in* R. L. Kendall, editor. Selected coolwater fishes of North America. American Fisheries Society, Special Publication 11, Bethesda, Maryland.

Gresswell, R. E. 1991. Use of antimycin for removal of Brook Trout from a tributary to Yellowstone Lake. North American Journal of Fisheries Management 11:83–90.

Hall, D. L. 1991a. Age validation and aging methods for stunted Brook Trout. Transactions of the American Fisheries Society 120:644–649.

Hall, D. L. 1991b. Growth, fecundity and recruitment responses of stunted Brook Trout population to density reduction. Doctoral dissertation. University of British Columbia, Vancouver.

Hanson, D. A., and T. L. Margenau. 1992. Movement, habitat selection, behavior, and survival of stocked Muskellunge. North American Journal of Fisheries Management 12:474–483.

Hoddle, M. S. 2002. Restoring balance: using exotic species to control invasive exotic species. Conservation Biology 18:38–49.

Jepsen, N., and S. Berg. 2002. The use of winter refuges by roach tagged with miniature radio transmitters. Hydrobiologia 483:167–173.

Kanda, N., R. F. Leary, and F. W. Allendorf. 2002. Evidence of introgressive hybridization between Bull Trout and Brook Trout. Transactions of the American Fisheries Society 131:772–782.

Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of Bull Trout in the upper Flathead drainage, Montana, with special reference to hybridization with Brook Trout. Transactions of the American Fisheries Society 123:988–992.

Knapp, R. A., D. M. Boiano, and V. T. Vredenburg. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). Biological Conservation 135:11–20.

Knapp, R. A., and K. R. Matthews. 1998. Eradication of nonnative fish by gill netting from a small mountain lake in California. Restoration Ecology 6:207–213.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 2000. Status of Yellowstone Cutthroat Trout in Wyoming waters. North American Journal of Fisheries Management 20:693–705.

Larscheid, J., J. C. Christianson, T. Gengerke, and W. Jorgensen. 1999. Survival, growth and abundance of pellet-reared and minnow-reared Muskellunge stocked in northwestern Iowa. North American Journal of Fisheries Management 19:230–237.

Mauck, W. L., and D. W. Coble. 1971. Vulnerability of some fishes to Northern Pike (*Esox lucius*) predation. Journal of the Fisheries Research Board of Canada 28:957–969.

Meronek, T. G., P. M. Bouchard, E. R. Buckner, T. M. Burri, K. K. Demmerly, D. C. Hatleli, R. A. Klumb, S. H. Schmidt, and D. W. Coble. 1996. A review of fish control projects. North American Journal of Fisheries Management 16:63–74.

Moyle, P. B. 1986. Fish introductions into North America: patterns and ecological impact. Pages 27–43 *in* H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions in North America and Hawaii. Springer-Verlag, New York.

Parker, B. R., D. W. Schindler, D. B. Donald, and R. S. Anderson. 2001. The effects of stocking and removal of a nonnative salmonid on the plankton of an alpine lake. Ecosystems 4:334–345.

Peterson, D. P., K. D. Fausch, and G. C. White. 2004. Population ecology of an invasion: effects of Brook Trout on native Cutthroat Trout. Ecological Applications 14:754–772.

Pilliod, D. S., and C. R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322–333.

Rabe, F. W. 1970. Brook Trout populations in Colorado beaver ponds. Hydrobiologia 35:431–448.

Rieman, B. E., D. C. Lee, and R. F. Thurow. 1997. Distribution, status, and likely future trends of Bull Trout within the Columbia River and Klamath River basins. North American Journal of Fisheries Management 17:1111–1125.

SAS Institute. 2009. SAS/STAT 9.2 user's guide, 2nd edition. SAS Institute, Cary, North Carolina.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada Bulletin 184.

Shepard, B. B. 2004. Factors that may be influencing non-native Brook Trout invasion and their displacement of native Westslope Cutthroat Trout in three adjacent southwestern Montana streams. North American Journal of Fisheries Management 24:1088–1100.

Skov, C., J. Brodersen, P. A. Nilsson, L.-A. Hansson, and C. Brönmark. 2008. Inter- and size-specific patterns of fish seasonal migration between a shallow lake and its streams. Ecology of Freshwater Fish 17:406–415.

Siler, D. H., and G. B. Beyerle. 1986. Introduction and management of northern Muskellunge in Iron Lake, Michigan. Pages 257–262 *in* G. E. Hall, editor. Managing muskies: a treatise on the biology and propagation of Muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

Storck, T. W., and D. L. Newman. 1992. Contribution of tiger muskellunge to the sport fishery of a small, centrarchid-dominated impoundment. North American Journal of Fisheries Management 12:213–221.

Szendrey, T. A., and D. H. Wahl. 1996. Size-specific survival and growth of stocked Muskellunge: effects of predation and prey availability. North American Journal of Fisheries Management 16:395–402.

Tipping, J. M. 2001. Movement of tiger muskellunge in Mayfield Reservoir, Washington. North American Journal of Fisheries Management 21:683–687.

Tomcko, C. M., R. A. Stein, and R. F. Carline. 1984. Predation by tiger muskellunge on Bluegill: effects of predator experience, vegetation, and prey density. Transactions of the American Fisheries Society 113:588–594.

Wahl, D. H. 1999. An ecological context for evaluating the factors influencing Muskellunge stocking success. North American Journal of Fisheries Management 19:238–248.

Walters, C. J., and R. E. Vincent. 1973. Potential productivity of an alpine lake as indicated by removal and reintroduction of fish. Transactions of the American Fisheries Society 102:675–697.

Weithman, A. S., and R. O. Anderson. 1977. Survival, growth, and prey of esocidae in experimental systems. Transactions of the American Fisheries Society 106:424–430.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes 34:1–28.