Self-sustainability of trout populations in currently-stocked alpine lakes in California's Sierra Nevada

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Abstract: Trout are often stocked into alpine lakes based on the assumption that resident trout populations are not self-sustaining and would go extinct without regular stocking. However, this assumption has not been rigorously tested. The objectives of our study were to (1) estimate the proportion of currently-stocked alpine lakes in California's Sierra Nevada (USA) that contain self-sustaining trout populations, (2) identify the characteristics of lakes associated with self-sustainability, and (3) quantify the effects of stocking termination on trout density and individual growth rates in self-sustaining populations. We surveyed trout populations in 95 John Muir Wilderness (JMW) lakes before and after a 4-8 year stocking halt and 111 Sequoia/Kings Canyon National Park (SEKI) lakes after a ≥ 20 year stocking hiatus. Seventy-two percent of JMW study lakes and 66% of SEKI study lakes contained self-sustaining trout populations based on evidence of successful recruitment during the no-stocking period. Regression analysis identified spawning habitat area and lake elevation as significant factors influencing trout population persistence. Trout populations in lakes with >2.1 m^2 of spawning habitat and located at elevations <3520 m were nearly always self-sustaining. For self-sustaining populations, the termination of stocking did not result in significant changes in population density or individual growth rates. We conclude that most trout stocking in Sierra Nevada alpine lakes could be permanently halted without negatively impacting these fisheries.

Introduction and Problem Statement

The stocking of nonnative trout into historically fishless alpine lakes of western North America has been a common fisheries management practice for the past century. The fundamental motivation behind this practice is the creation and maintenance of recreational fisheries where none formerly existed (Cowx 1994). Although it is estimated that less than 5% of high elevation lakes in western North America originally contained fish, more than 95% of the larger (>2 ha surface area) and deeper (>3 m maximum depth) lakes now contain nonnative trout populations as a result of these stocking programs (Donald et al. 1980, Bahls 1992). Since the introduction of aerial stocking in the early 1950s, the majority of lakes capable of supporting trout populations have been stocked on a regular basis (Bahls 1992, Pister 2001). A central assumption underlying this intensive stocking program is that most introduced trout populations would disappear if stocking was halted. For example, fisheries managers in the western U.S. estimate that only 25% of high elevation lakes that contain introduced trout populations show levels of natural recruitment sufficient to maintain these populations without supplemental stocking (Bahls 1992). The assumption that most trout populations are not self-sustaining has rarely been tested, however, despite the fact that continued supplemental stocking of lakes with self-sustaining fish populations may provide little or no benefit to these fisheries (Parsons and Pereira 2001).

Objectives

The objectives of this study were to (1) determine what proportion of currently-stocked lakes in our John Muir Wilderness (JMW) study area contain self-sustaining populations of rainbow trout (*Oncorhynchus mykiss*), golden trout (*O. mykiss aguabonita*), or Lahontan cutthroat trout (*O. clarki henshawi*), (2) determine what proportion of formerly stocked lakes in Sequoia/Kings Canyon National Park (SEKI) contain self-sustaining *Oncorhynchus* spp. populations, (3) identify the habitat factors that influence trout population self-sustainability in the JMW, and (4) quantify the effects of halting stocking on density and individual growth rates of self-sustaining populations in the JMW study area. Based on our common observation of reproduction by trout populations in both study areas, we hypothesized that a majority of currently-stocked trout populations are in fact self-sustaining. We included the data from SEKI to determine whether the rates of self-sustainability observed in the JMW study area were similar to those in other parts of the high elevation Sierra Nevada. We also hypothesized that total spawning area is an important factor influencing trout population self-sustainability. For self-sustaining trout populations, we predicted that halting stocking would have either no effect or a positive effect on fish growth rates. A positive effect on growth rates might occur if halting stocking reduced fish densities (Donald and Anderson 1982).

Procedures

Study area

This study was conducted in the southern Sierra Nevada of California, and included lakes on both the east and west sides of the Sierra Nevada crest (JMW study area: 67,125 ha on the Inyo and Sierra National Forests: center of study area = 37º 20'N, 118º 48' W; SEKI: 348,833 ha, center of study area = 36º 45'N, 118º 30' W). All of the study lakes are of glacial origin and are located primarily within watersheds composed of intrusive igneous bedrock (California Division of Mines and Geology 1958). As a result, these lakes all have similar physical and chemical properties (Knapp and Matthews 2000, Melack et al. 1985). They are located in the alpine and subalpine zones (>2800m), remain ice free for approximately 4 mo/year, are oligotrophic, and rarely reach maximum temperatures greater than 17ºC (Melack et al. 1985, Stoddard 1987, Bradford et al. 1998, Knapp and Matthews 2000). Most of the precipitation entering these lakes is in the form of snow which falls from November to April. All lakes in the JMW and SEKI study areas were historically fishless, but most have been stocked repeatedly with fingerlings (trout < 50 mm fork length) since at least the 1950s as part of the aerial stocking program conducted by the California Department of Fish and Game (CDFG) (Knapp 1996). The JMW study area contains 216 lakes (water bodies with surface area ≥1.0 ha, and maximum depth ≥ 3 m), 173 of which harbor introduced trout populations (80%). Thirty-two lakes contain only self-sustaining brook trout populations (*Salvelinus fontinalis*), 109 contain only *Oncorhynchus* spp. populations, and 32 contain both *Oncorhynchus* spp. and self-sustaining brook trout. During 1990-2000, 118 (84%) of the lakes containing *Oncorhynchus* spp. were stocked with either *O. mykiss* (10 lakes), *O. m. aguabonita* (84 lakes), or *O. c. henshawi* (1 lake). The median number of times each lake was stocked during this period was four (range = 1-11), and the median stocking density was 553 fish/ha (range = 57 to 6289 fish/ha). In SEKI, the National Park Service began phasing out all fish stocking in 1977, and only 23 lakes continued to be stocked between 1977 and 1988. All stocking was halted in 1988, and the median final stocking year for SEKI lakes was 1970 (range = 1960 - 1988). Between 1962 and 1977, 111 lakes were stocked with only *O. mykiss* (50 lakes), only *O. m. aguabonita* (59 lakes), or with both species (2 lakes). During this period, the median number of times each lake was stocked was two (range = 1-4), and the median stocking density was 658 fish/ha (range = 46-12623 fish/ha).

Study design

Our overall study design in the JMW involved the survey of trout populations in a series of lakes during 1995-1996, use of these data to select experimental lakes (in which stocking was temporarily halted) and control lakes (in which regular stocking continued), and then the resurvey of the trout populations in the experimental and control lakes in 2001 and 2002 (Figure 1). To select experimental lakes, we used CDFG stocking records and data from field surveys to identify all lakes (n = 61) that met the following requirements: (1) contain only *Oncorhynchus* spp. (*O. mykiss, O. m. aguabonita*, or *O. c. henshawi*), (2) stocked at least biennially, and (3) separated from other stocked lakes located upstream or downstream by natural barriers or ≥0.5 km of stream. The first requirement was necessary to eliminate the potentially confounding effect of brook trout presence, because this species generally precludes self-sustainability by *Oncorhynchus* spp. in Sierra Nevada lakes (Boiano 1999). The second requirement was necessary to ensure that stocking frequencies prior to the stocking halt were high enough to allow us to test the effect of halting stocking on fish population densities and growth rates. The third requirement was necessary to ensure that fish population dynamics in the experimental lakes would not be influenced by stocking in adjacent populations (e.g., stocked fish moving into adjacent unstocked lakes). The CDFG supported this study and agreed to cease stocking in experimental lakes for the duration of the experiment. As a result of this cooperation, all experimental lakes experienced a stocking hiatus for at least four consecutive years between 1994 and 2001 (range = 4-8 yrs, median = 5 yrs). Control lakes (n = 34) were randomly chosen from the pool of lakes that met requirements 1 and 2, but not 3. These lakes continued to be regularly stocked for the duration of the experiment. Control lakes were used for two reasons in this study: 1) to assess the effects of halting stocking on population densities and individual growth rates, and 2) to apply our model of self-sustainability to a broader subset of JMW lakes. In addition to the short term experiment in the JMW, we also evaluated the self-sustainability of introduced *Oncorhynchus* spp. populations after a long term halt to stocking in Sequoia-Kings Canyon National Park. We identified 110 lakes in Sequoia-Kings Canyon National Park that had been stocked at least once between 1962 and 1977 and that contained only *Oncorhynchus* spp. We used the results of this analysis to evaluate the generality of our findings in the JMW study area.

Fish population sampling

We sampled fish populations in JMW and SEKI lakes using gill nets. Fish populations in JMW lakes were surveyed at the initiation of this study (1995-1996) and again at the end of the study (2001-2002), while those in SEKI were surveyed in 1997, 2000, 2001, and 2002. During the JMW resurveys, gill nets were set in the same locations and generally during the same time of day as sets made during the initial surveys. Gill nets used in all surveys were identical and were sinking monofilament nets 36 m long and 1.8 m tall. Each net had six 6 m long panels with bar mesh sizes of 10, 12.5, 18.5, 25, 33, and 38 mm. Nets were set so that the smallest mesh size panel was closest to shore, and the largest mesh size panel was farthest out in the lake. This arrangement was chosen to allow the capture of young trout (<100 mm) that are generally found primarily in near-shore habitats. Nets were anchored to shore and set perpendicular to the lake shoreline. We set gill nets either in the early morning or late evening and pulled them after 8-12 hours. Every captured fish was weighed to the nearest gram and measured to the nearest millimeter (fork length).

We used sagittal otoliths to age fish captured during the 2001-2002 JMW resurveys (Campana and Neilsen 1985). In 70 lakes, we captured < 40 fish and in these cases we removed the pair of sagittal otoliths from all captured fish. In 25 lakes, we captured > 40 fish. For these lakes, otoliths were extracted from 40 fish that represented the full range of size classes captured in the gill net. Otoliths were taken to the laboratory where they were cleaned, mounted on a glass microscope slide sulcus-side up, ground to the sagittal midplane, polished, and aged using the methods of Secor et al. (1992).

Annuli on sagittal otoliths are commonly used to age fish from a wide variety of salmonid species (Hall 1991, Toetz et al. 1991, Kruse et al. 1997, Hining et al. 2000) including trout from alpine lakes (Hall 1991, Boiano 1999). Golden trout from the Sierra Nevada are hybridized with coastal rainbow trout (Cordes et al 2001), yet are more phenotypically golden trout, and are referred to as such. Annular increment formation has been validated in *O. mykiss* (Graynoth 1996), suggesting the same for the hybrids. However, annular increment formation has yet to be validated in *O. m. aguabonita*, In order to test the hypothesis that increments from golden trout in our JMW study lakes are in fact produced annually, we conducted a validation experiment using one of our control lakes. In August 1999, we clipped adipose fins from 2000 golden trout fingerlings (~30 days old) prior to their being stocked into Summit Lake (37º 14’ N, 118º 41’ W). When the Summit Lake fish population was surveyed in 2002 using gill nets, fish without adipose fins were identified and otoliths from all captured fish were returned to the laboratory for aging. Aging was conducted without any information on whether or not the fish being aged had or did not have an adipose fin. Based on the assumption that sagittal otoliths from golden trout contain increments produced annually, we expected that these adipose-clipped fish would contain otoliths with three annuli.

Habitat characterization

In addition to resurveying fish populations in 2001 and 2002 in the JMW, we also characterized physical lake properties for each of the 95 JMW study lakes. Maximum lake depth was measured by sounding with a weighted line, and lake area was obtained from USGS 1:24000 topographic maps. We characterized littoral zone substrate composition by visually estimating the dominant substrate type along approximately 50 3-m long shoreline transects that were evenly spaced around the lake perimeter and were perpendicular to shore. Substrates were categorized as silt (<0.5 mm), sand (0.5-2 mm), gravel (<2-75 mm), cobble (>75-300 mm), boulder (>300 mm), or bedrock. To assess the amount of potential spawning habitat available to each trout population, we measured the area of suitable spawning habitat in the first 100 m of each inlet and outlet stream. Suitable spawning habitat was defined as gravel particles 0.5-4 cm in diameter and not cemented into the streambed, water depths of 10-50 cm, and water velocities of 20-60 cm/s (Bjornn and Reiser 1991, Knapp and Preisler 1999). We also measured the average width and depth of the first 100 m of each inlet and outlet stream (Donald 1987).

Data analysis

Determination of self-sustainability

We used two different criteria to categorize JMW trout populations as self-sustaining or non-self-sustaining. Under the first criterion, a trout population was categorized as self-sustaining if the gill net catch from the 2001-2002 fish surveys included one or more fish with ages indicating that they recruited during the stocking hiatus. Because low levels of reproduction might not be sufficient to maintain trout populations over the long term, we also included a second, more conservative criterion. Under this criterion, a trout population was categorized as self-sustaining only if the mean number of captured fish that recruited per year of the stocking hiatus was >1. This division point was chosen based on an obvious break in the distribution of the mean number of captured fish recruited per year of the stocking hiatus for all experimental lakes (Fig. 2). Because SEKI lakes had not been stocked for >10 years and *Oncorhynchus* spp. in Sierra Nevada alpine lakes rarely live longer than 10 years (Knapp et al. 2001), fish populations in SEKI lakes were categorized as self-sustaining if one or more trout were captured during the gill net survey.

Habitat effects on self-sustainability

We used stepwise logistic regression and tree regression to model the effect of physical lake characteristics on trout population self-sustainability in the JMW. Independent variables used in both models included maximum lake depth, elevation, total area of spawning habitat, total width of all inlet and outlet streams, and substrate composition. Before including the littoral zone substrate data in the regression analyses, we used principal components analysis to reduce their dimensionality to two principal components. Although tree regression is still rarely used in ecological studies, it is a useful method to identify the relationships between predictor variables and the response variable by producing an easily interpretable hierarchy of decision processes, as well identifying at what levels these variables become important (De'ath and Fabricius 2000). Because both regression models produced similar results (see Results), we used the tree regression results to estimate the level of self-sustainability for control lakes. By combining this estimate of self-sustainability with our determination of self-sustainability data from the experimental lakes, we obtained a single estimate of self-sustainability for all currently-stocked lakes in the study area.

Our regression analyses indicated that amount of spawning habitat was of primary importance in determining self-sustainability (see Results). However, measuring this variable requires visits to each lake and measurements of spawning habitat availability are therefore not widely available for lakes outside of our study area. During the 1950s and 1960s, the CDFG conducted qualitative habitat and fish population surveys for many of the lakes on national forest lands in the Sierra Nevada (including nearly all of our JMW study lakes). These surveys included a categorization of trout spawning habitat as "none", "poor", "fair", "good", or "excellent". These CDFG estimates were available for 55 of the 61 experimental lakes. Only one lake had been categorized as having "excellent" spawning habitat, so we combined this category with the "good" category. To determine whether this widely available measure of spawning habitat could be used to predict trout population self-sustainability, we used a chi-square test to quantify the strength of the association between the CDFG spawning habitat categories and our lake-specific determination of trout population self-sustainability in the experimental lakes from our JMW study area.

Effects of halting stocking on densities and growth rates

We quantified the effect of halting stocking on trout populations in the JMW by comparing population densities and lake-specific individual fish growth rates in control and experimental lakes before and after the stocking hiatus. We used maximum fish size as a proxy for individual growth rates (Donald et al. 1980). We used catch per unit effort (CPUE: number of fish caught per gill net per hour) as a measure of fish density. The validity of this method of estimating population density is suggested by the results of Schindler et al. (2001) that demonstrate a positive linear relationship between CPUE (as measured by gill net catches) and actual population density in *O. m. aguabonita* in high elevation Sierra Nevada lakes. We used two different comparisons to determine whether the halt to fish stocking resulted in changes in population density and growth rate. First, we used two-sample t-tests to compare the CPUE and maximum fish size in experimental versus control lakes using data collected after the several year halt to stocking (2000-2001 survey). We predicted that fish densities in experimental lakes would be lower and maximum fish size would be greater than in control lakes after the several year stocking hiatus. To determine whether observed differences in CPUE and maximum fish size were likely a consequence of the halt to stocking and not attributable to preexisting differences between fish populations in experimental and control lakes, we also used two-sample t-tests to compare CPUE and maximum fish size in experimental and control lakes before the stocking hiatus began (using data from the 1995-1996 survey). We predicted that there would be no significant difference in CPUE or maximum fish size between control and experimental lake populations before the stocking hiatus. Second, we used paired t-tests to compare CPUE and maximum fish size measured for each fish population before and after the stocking hiatus. Only those experimental lakes categorized as containing self-sustaining trout populations were included in this analysis. Our expectation was that there would be a decrease in CPUE after the stocking hiatus.

We also hypothesized that if there was a decrease in density, this might result in an increase in maximum fish size in self-sustaining experimental populations.

To determine whether these statistical tests had the ability to identify potential changes in population density and maximum fish size given our study design, we conducted power analyses. Power analysis allowed us to determine whether a lack of statistically significant changes in CPUE and maximum fish size was the result of a lack of real change in these metrics or an inability to detect such a change as a consequence of small sample sizes and/or high variability. For all power analyses, we measured our ability to identify a change in mean values of at least 25% ($\alpha = 0.05$). High power (≥ 0.8) indicates that the sampling design used was likely sufficient to allow us to detect significant changes in CPUE and maximum fish size. Low power indicates that statistical results revealing no significant changes may be the result of low sample size and/or high variance and not a true lack of differences (Steidl et al. 1997). All statistical analyses were conducted using S-Plus (S-Plus 1999) and the α-level for all statistical tests was 0.05.

Results

Validation of annular increment formation

In the 2002 gill net sample from Summit Lake, we captured six golden trout lacking adipose fins. Independent counts of increments on sagittal otoliths from these fish made by both authors indicated that otoliths from all six fish contained three obvious increments. Therefore, increments in these otoliths appear to be produced annually.

Fish population self-sustainability

Trout populations in forty-four of our 61 JMW experimental lakes showed evidence of natural reproduction during the stocking hiatus. Therefore, under our first criterion for categorizing populations as self-sustaining (any evidence of natural reproduction during the stocking hiatus), 72% of the experimental lakes contained self-sustaining populations. For calculation of self-sustainability using our second criterion, we identified those populations that experienced abundant reproduction during the stocking hiatus. The gill net catches from 37 of our experimental lakes contained a mean of >1 fish per year recruited into the population during the stocking hiatus. Using this second criterion, 61% of the experimental populations were self-sustaining. Taken together, these two criteria produce a range of self-sustainability in the experimental lakes of 61-72%. For the SEKI lakes, 73 of 111 (66%) lakes contained self-sustaining trout populations. This level of self-sustainability is in the middle of the range determined for trout population self-sustainability in the JMW lakes.

Factors influencing population self-sustainability

Regression analyses of the factors that influence self-sustainability and the analyses of the effects of stocking termination on CPUE and fish size were conducted on data categorized using both criteria. Regression results were very similar regardless of which criterion was used, and we therefore present only the results from the more conservative (61%) estimate of self-sustainability. The principal component analysis we conducted to reduce the dimensionality of littoral zone substrate data indicated that the first two axes (PC1, PC2) together explained 53% of the variation in littoral zone substrate characteristics. Axis loadings (Table 1) suggested the strong negative influence of percent gravel and strong positive influence of percent boulder on scores for PC1. PC2 was strongly negatively influenced by silt and positively influenced by sand.

Logistic regression indicated that the probability of trout population self-sustainability was a positive function of the total amount of spawning habitat and a negative function of lake elevation (Table 2). The effects of maximum lake depth, littoral zone substrate composition (PC1, PC2), and stream width on population self-sustainability were not significant. The tree regression yielded similar results to the logistic regression, again indicating the positive influence of the amount of spawning habitat and the negative influence of elevation on population self-sustainability (Fig. 3). Ninety-five percent of lakes with >2.1 m^2 of spawning habitat contained self-sustaining trout populations while only 41% of lakes with <2.1 m^2 of spawning habitat contained self-sustaining trout populations. For lakes with <2.1 m^2 of spawning habitat, none of the ten trout populations occurring in lakes above 3520 m were categorized as self-sustaining while 55% of those below 3520 m were self-sustaining (Fig. 3).

Before using the tree regression model to predict self-sustainability of the control lakes, we compared physical habitat characteristics of experimental and control lakes to ensure that they were similar. We compared experimental and control lakes using Wilcoxon rank-sum tests and found the two groups were not significantly different for any of the measured habitat variables, including maximum depth (Fig 4A), total stream width (Fig. 4B), elevation (Fig. 4C), lake surface area (Fig. 4D), total spawning area (Fig. 4E), PC1 (Fig. 4F), and PC2 (Fig. 4G). Therefore, despite the fact that experimental lakes were not chosen at random, they were physically similar to the randomly chosen control lakes. We next applied the results from our tree regression model to all 34 control lakes used in our JMW study area. Our model predicted that 19 of these populations were self-sustaining. We combined these predictions with our determination of self-sustaining populations in the experimental lakes, which resulted in an overall level of self-sustainability of 59% within our JMW study area. Therefore, the majority of lakes that were stocked during the previous decade in our JMW study area contain self-sustaining *Oncorhynchus* populations and any supplemental stocking was therefore unnecessary.

After determining which of the experimental lake populations were self-sustaining, we analyzed whether qualitative CDFG estimates of spawning habitat quality could also be used to predict population self-sustainability. The qualitative spawning habitat categories were significantly associated with trout population self-sustainability (Pearson's chi square test: $\chi^2 = 10.79$, df = 3, $P = 0.013$; Fig. 5). Of the lakes with "poor", "fair", or "good/excellent" spawning habitat, 71% contained self-sustaining trout populations. In contrast, of the 20 lakes with spawning habitat categorized as "none", only 25% contained self-sustaining trout populations (Fig. 5). These results suggest that the qualitative CDFG estimates of spawning habitat quality that are currently available for many Sierra Nevada lakes could be used to identify self-sustaining trout populations.

Effects of halting stocking on self-sustaining populations

Prior to the stocking hiatus, neither CPUE (two-sample t-test: $t = 0.049$, df = 93, $P = 0.96$; Fig. 6A) nor maximum fish size (two-sample t-test: $t = 0.824$, df = 93, $P = 0.412$; Fig. 6B) was significantly different between control and experimental lakes. Based on a hypothetical difference of 25% between the means, the power of these tests was high (CPUE t-test: power = 0.7; maximum fish size t-test: power = 1.0), indicating that both statistical tests had a relatively strong ability to detect a difference, given the sample sizes and sample variances that characterized these data. After the stocking hiatus, neither CPUE (two-sample t-test: $t = 0.646$, df = 93, $P = 0.520$; Fig 6C) nor maximum fish size (two-sample t-test: $t = -1.036$, df = 93, $P = 0.303$; Fig. 6D) was significantly different between control and experimental lakes. The power of these tests was also high (CPUE t-test: power = 0.7, maximum fish size t-test: power = 1.0). These high power values suggest that we likely would have been able to detect a difference in maximum fish size and CPUE of 25% had there been a real difference of this magnitude.

Comparing CPUE and maximum fish size before and after the stocking hiatus indicated no significant change in CPUE (paired t-test: $t = 2.1$, df = 35, $P = 0.978$, Fig. 7A) or maximum fish size (paired t-test: $t = -1.82$, df = 35, $P = 0.962$, Fig. 7B). The power of these tests was also relatively high (maximum fish size t-test: power = 1.0; CPUE t-test: power = 0.64), indicating that the paired t-tests had a relatively strong ability to detect a difference of 25% between the means given the sample size of 36 populations and sample variances that characterized these data. We conclude that the experimental halt to stocking had no effect on the densities or individual growth rates of self-sustaining populations in our study.

Conclusion

The practice of supplemental stocking in high elevation lake fisheries in the Sierra Nevada of California and elsewhere in western North America has historically been predicated on the assumption that few or none of these introduced trout populations are self-sustaining (Bahls 1992). However, the results from our experiment indicate that the majority of *Oncorhynchus* spp. populations in our JMW and SEKI study areas were in fact self-sustaining. Based on the two criteria we used to categorize experimental lakes as self-sustaining, we estimated that 61-72% of our JMW study lakes and 66% of our SEKI study area lakes contained self-sustaining trout populations. We chose the conservative end of this estimate and developed a tree regression model to predict factors that influence self-sustainability. This model predicted that 19 of the control lakes in the JMW also contained self-sustaining populations. Adding our determinations of self-sustainability in experimental lake populations to our predictions from the control lake populations resulted in an overall estimate of self-sustainability in the JMW study area of 59%. It is important to note that this value is based on the conservative definition of self-sustainability, and is therefore potentially an underestimate. The high degree of concordance between estimates of self-sustainability in JMW and SEKI populations suggests the results from the JMW can be extrapolated across both a longer time scale as well as a broader spatial scale. Taken together, the results from both study areas indicate that a complete halt to stocking in the JMW would result in little change to the existing fisheries. These results indicate that a re-evaluation of self-sustainability in other high elevation lake systems may be necessary. This study suggests that a majority of high elevation lakes in the western states may be stocked unnecessarily. One of the most effective methods to determine the proportion of self-sustaining populations in high elevation areas, as demonstrated in our experiment, is to halt fish stocking for several consecutive years. In addition to being a simple tool for evaluating self-sustainability, halting stocking is inexpensive and the effects (if any) are reversible.

The logistic regression and tree regression models both identified the amount of spawning habitat and elevation as being the only two factors from our study that contributed significantly to trout population self-sustainability. Results from the tree regression further suggested that only 2.1 m^2 was sufficient to produce self-sustaining trout populations. Donald (1987) found that for trout in high elevation lakes, the probability of suitable spawning (and therefore natural recruitment) was directly related to size of outlet streams. Boiano (1999) also identified spawning habitat area as a significant factor in determining trout population self-sustainability for high elevation rainbow trout populations in Yosemite National Park. Most high elevation Sierra Nevada lakes contain at least some spawning habitat (R.A. Knapp, unpublished data), which supports the idea that the majority of currently-stocked trout populations are in fact self-sustaining and would not require additional stocking to persist. It is important to note that that measures of spawning habitat vary from year to year depending upon amount of winter precipitation as well as the time of year the lake is surveyed. As a result of this inter-annual variation, the minimum amount of spawning habitat we identified in this study as important to determining population self-sustainability is unlikely to be an absolute limitation, but rather a relative number indicating the small area actually required by trout populations. We also identified a significant association between self-sustainability and qualitative estimates of spawning habitat quality in our study area. These results show that visual identification of spawning habitat in a lake indicates a strong likelihood that the resident population is self-sustaining. The fact that qualitative assessments of spawning habitat availability provided a reasonably accurate assessment of self-sustainability suggests that simply assigning all populations in lakes with any spawning habitat as self-sustaining may be a prudent management strategy in the absence of quantitative measures of recruitment magnitude and habitat characteristics.

In addition to spawning habitat, our regression models also suggest that the probability of population self-sustainability decreases with elevation. Specifically, the tree regression indicated that lakes above 3520 m were very unlikely to contain self-sustaining trout populations. One possible explanation for this inability of trout populations at the highest elevations to become self-sustaining is that the ice-free growing season in these lakes may be too short to allow successful recruitment. Lakes at these high elevations usually remain ice-free for only a few weeks each summer. A short ice free season forces spawning to occur later in the summer, which would likely result in a truncated growing season for emerging fry (Donald et al. 1980). In addition, West and Larkin (1987) identified size-selective mortality in *Oncorhynchus nerka* fry as occurring most intensely during the late summer and fall. If emerging rainbow and golden trout fry in our high elevation lakes are subject to slow growth and size-selective mortality based on some minimum size threshold, then it is possible that fish in the highest elevation populations are spawning successfully but that this spawning results in little or no recruitment.

For the self-sustaining populations in our JMW study area, the results of our experiment show no effects of a halt to stocking on population density or maximum fish size. These results suggest that supplemental stocking of lakes provides no benefit when populations are self-sustaining. Several other studies have examined the effects that stocking can have on existing fish populations in species other than *Oncorhynchus* spp. and have also concluded that supplemental stocking may often contribute little to fishery quality. Cortes Rui et al. (1996) and Bohlin et al. (2002) found that stocking brown trout (*Salmo trutta*) into stream resident brown trout populations increased mortality resulting from intraspecific competition. Stocking walleye (*Stizostedion vitreum*) into self-sustaining populations in Minnesota lakes resulted in decreases in adjacent year class abundance and decreased the weights of resident fish (Li et al. 1996b) yet had no effect on overall population abundance (Li et al 1996a). Similarly, Parsons and Pereira (2001) concluded that the stocking of walleye fingerlings into self-sustaining walleye populations was ineffective in boosting year class strength.

Individual growth rates and population density are often negatively correlated in stream and lake-dwelling salmonids (Donald et al. 1980, Donald and Anderson 1982, Elliot 1993, Bohlin et al. 1994, Jenkins et al. 1999, Schindler et al. 2001). Therefore, if the halt to stocking in our experimental lakes resulted in a decrease in population density, we would expect to see an increase in maximum fish size. Densities in self-sustaining populations did not change even after several years without supplemental stocking. This response suggests that at higher trout densities (resulting from the stocking of fry) an increasing mortality rate compensates for the increase in density. This results in an essentially constant number of adult fish within each population, and therefore also a relatively constant maximum fish size. This compensating density dependent mortality likely only affects those populations with abundant spawning habitat availability. In lakes with insufficient spawning habitat to sustain populations in the long term, stocking termination would likely eventually lead to changes in both density and maximum fish size. Other salmonid populations have been shown to exhibit density dependent compensatory behavior as well. Ferreri and Taylor (1996) showed that increasing density in lake trout resulted in compensatory changes in fecundity and growth rates. Experiments with steelhead trout demonstrate that in the absence of emigration, increasing density leads to increasing levels of food competition, increased mortality, and decreased growth (Ferreri and Taylor 1996, Keeley 2001). In addition, Jenkins et al. (1999) and Vollestad et al. (2002) found that brown trout growth rate decreased as population density increased. Future studies could increase our understanding of how self-sustaining fish populations respond to stocking termination by examining the population-level consequences of halting stocking in fish populations regulated by density dependent mortality.

In conclusion, the majority of lake-dwelling *Oncorhynchus* spp. populations in our JMW and SEKI study areas are self-sustaining and few will revert to a fishless condition even with a complete halt to stocking. The findings that cessation of stocking had no effect on population density or individual growth rates, should encourage fisheries managers to re-evaluate current stocking strategies. Although our study was limited to trout populations in high elevation areas of the Sierra Nevada, the high levels of self-sustainability are likely not limited only to populations in this geographic area. Our results suggest that the level of trout population self-sustainability in other high elevation lakes in western North America is likely considerably higher than is currently believed (e.g., Bahls 1991).

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Table 1. Loadings for the first two principal component axes of littoral zone substrate composition. PC1 and PC2 explained 29% and 24%, respectively, of the variance in littoral zone substrate characteristics.

Substrate type	PC1	PC2
Silt	-0.269	-0.749
Sand	-0.262	0.474
Gravel	-0.469	0.354
Cobble	0.000	0.119
Boulder	0.691	0.230
Bedrock	0.390	-0.151

Table 2. Results of the stepwise logistic regression analysis of the effect of lake habitat characteristics on trout population self-sustainability, showing regression coefficients and *P*-values for each independent variable.

Variable	Coefficient	*P*-value
Total spawning habitat area	0.383	0.0004
Elevation	-0.007	0.006
Maximum depth	0.004	0.773
Total stream width	-0.0002	0.657
PC1	-0.009	0.967
PC2	-0.261	0.420

Fig. 1. Map of the John Muir Wilderness study area showing locations of the experimental and control lakes. Inset map shows the state of California (black), the Sierra Nevada (white), and the location of the study area within the Sierra Nevada (black dot).

Fig. 2. Histogram of the mean number of fish captured in the gill net sample that were recruited in the lake per year of the stocking hiatus.

Fig. 3. Tree regression results for all 61 experimental lakes. Significant factors influencing self-sustainability of trout populations are total spawning habitat and lake elevation. The number of self-sustaining populations (Y) and the number of non-self-sustaining (N) populations is given at each node as Y/N, as is the percent of lakes that were self-sustaining.

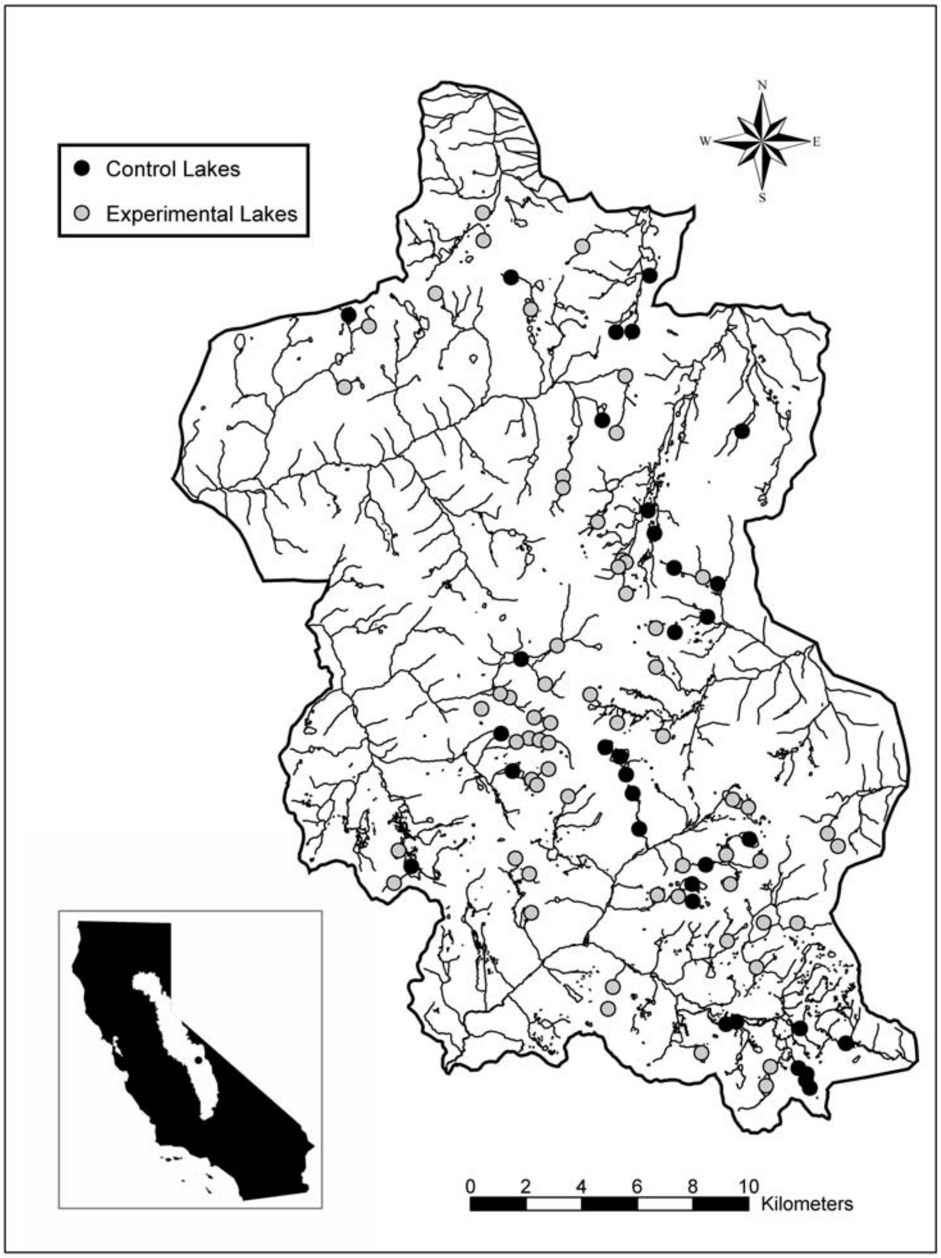
Fig. 4. Box plots showing (A) maximum lake depth, (B) total stream width, (C) lake elevation, (D) lake surface area, (E) total area of spawning habitat, (F) littoral zone substrate principle component axis 1 (PC1), and (G) littoral zone substrate principle component axis 2 (PC2) for control and experimental lakes. The line within each box represents the median, the bottom and top of each box indicate the 25^{th} and 75^{th} percentiles, the whiskers represent the 10^{th} and 90^{th} percentiles, and the points above and below the whiskers indicate values outside the 10^{th} and 90^{th} percentiles. Sample sizes for

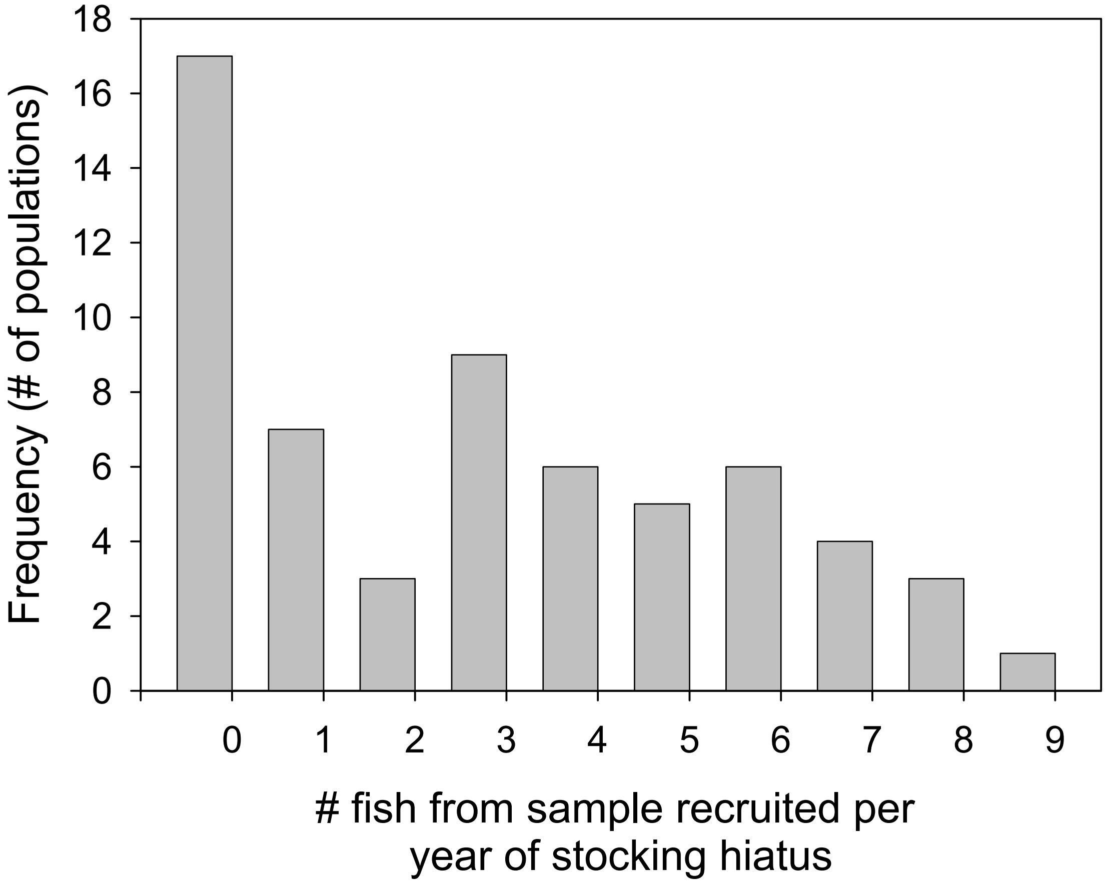
all tests were $n_{control}$ = 34 and $n_{experimental}$ = 61. "NS" indicates the difference between samples is not significant (P >0.05). All statistical results were obtained using Wilcoxon rank-sum test.

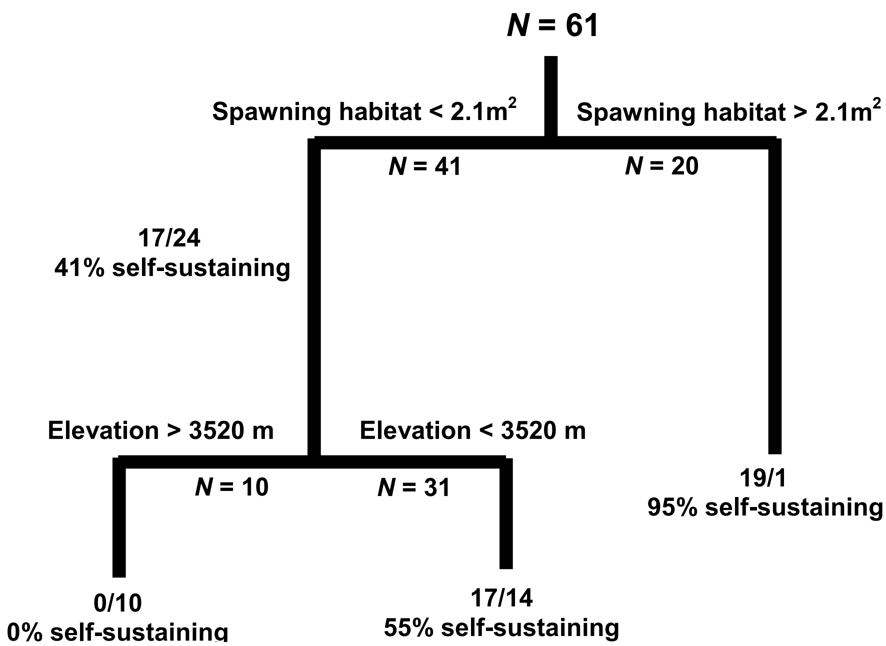
Fig 5. The percent of experimental lakes that contained self-sustaining trout populations as a function of qualitative categories of spawning habitat suitability. Sample sizes are given at the base of each bar.

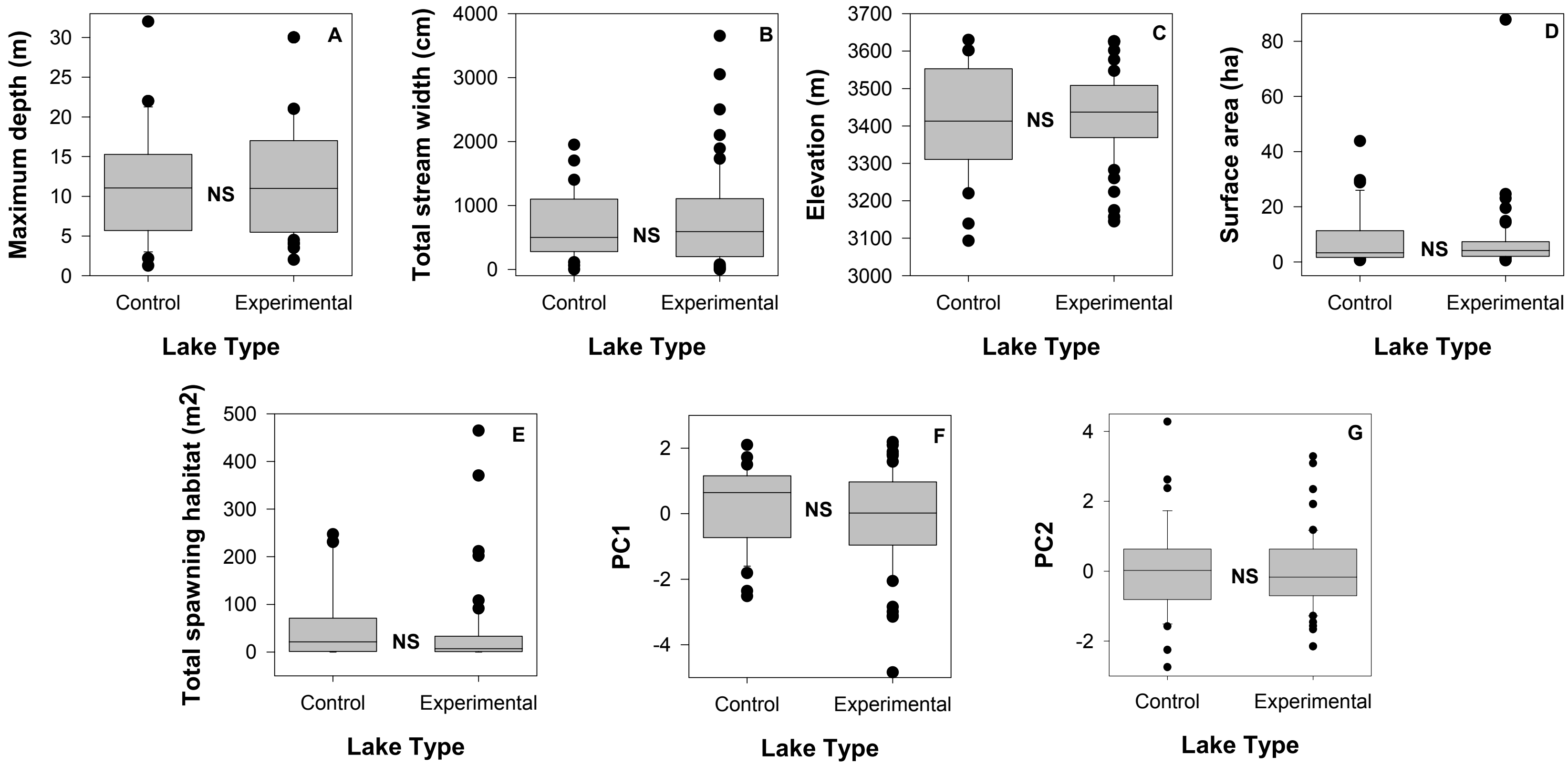
Fig. 6. Box plots showing (A) catch-per-unit-effort (CPUE) and (B) maximum fish size for control and experimental lakes in 1995-1996, and (C) catch-per-unit-effort (CPUE), and (D) maximum fish size and for control and experimental lakes in 2001-2002. The line within each box represents the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers below and above each box indicate the 10th and 90th percentiles, and the points below and above the whiskers indicate all points falling outside the 10th and 90th percentiles. Sample sizes are 34 and 61 for control and experimental lakes, respectively. Neither comparison is statistically significant (NS = not significant).

Fig. 7. Box plots showing (A) maximum fish size and (B) catch-per-unit-effort (CPUE) for self-sustaining populations from initial surveys (1995-1996) and resurveys (2001-2002). The line within each box represents the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers below and above each box indicate the 10th and 90th percentiles, and the points below and above the whiskers indicate all points falling outside the 10th and 90th percentiles. Sample sizes are 37 for both groups. Neither comparison is statistically significant (NS = not significant).

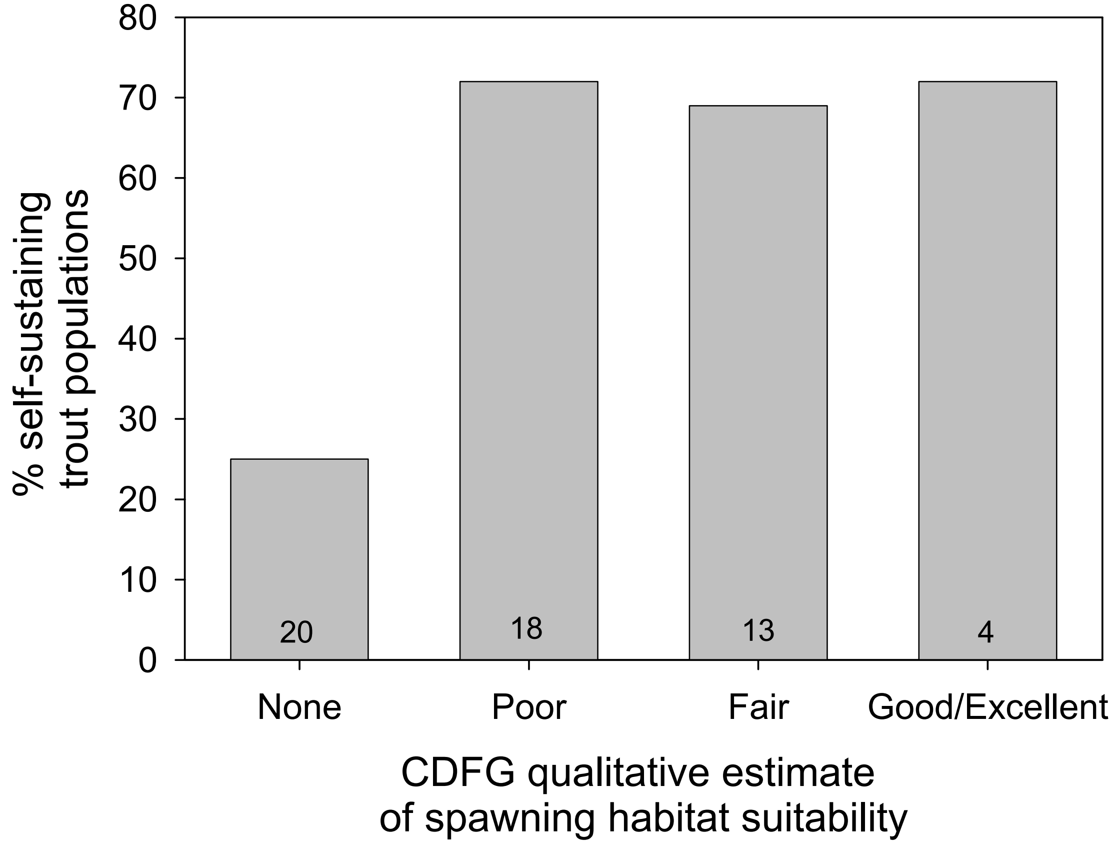

Control Lakes
Experimental Lakes
N
S
E
W
0 2 4 6 8 10 Kilometers

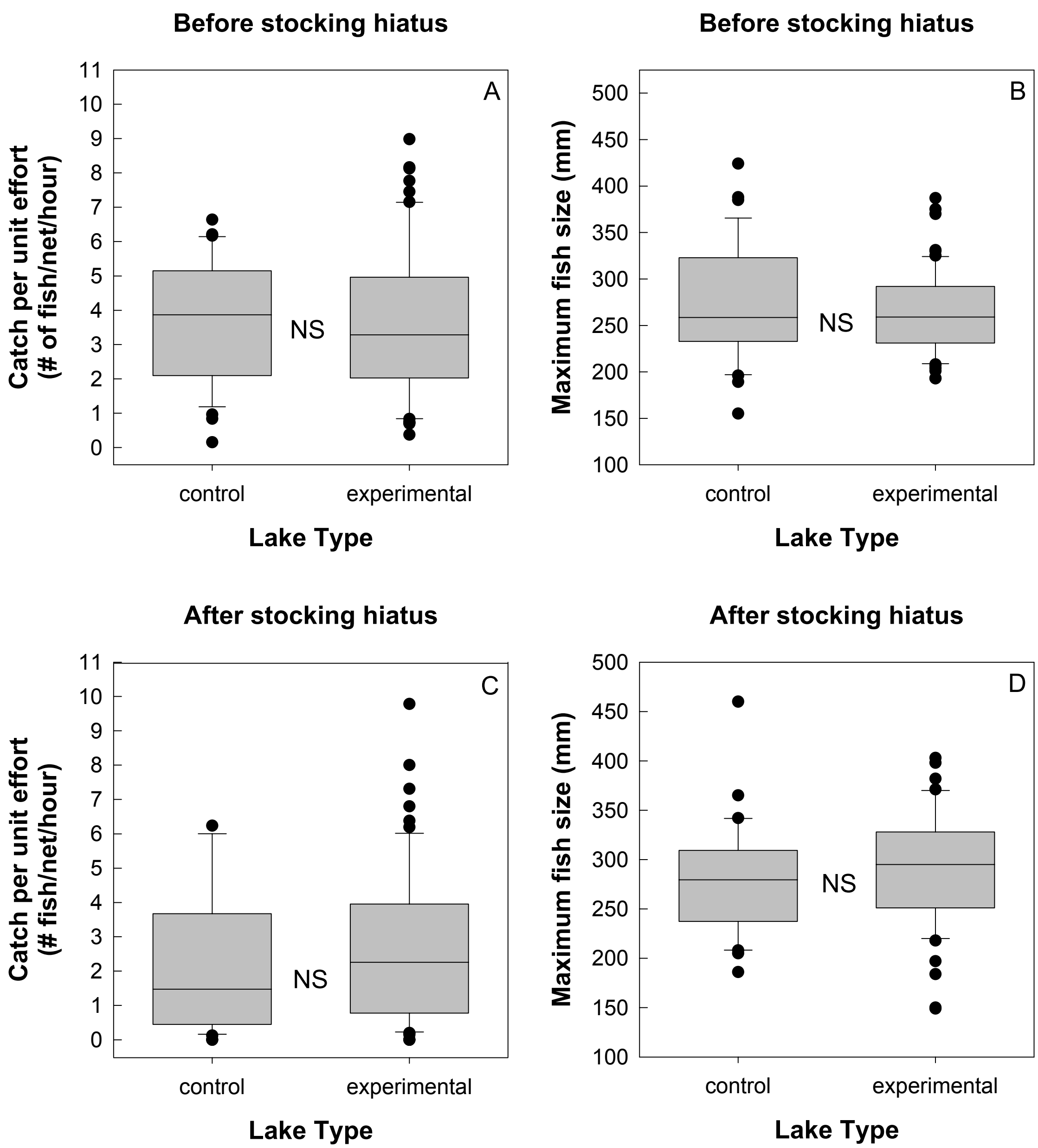

Frequency (# of populations)
18
16
14
12
10
8
6
4
2
0
0
1
2
3
4
5
6
7
8
9
fish from sample recruited per
year of stocking hiatus

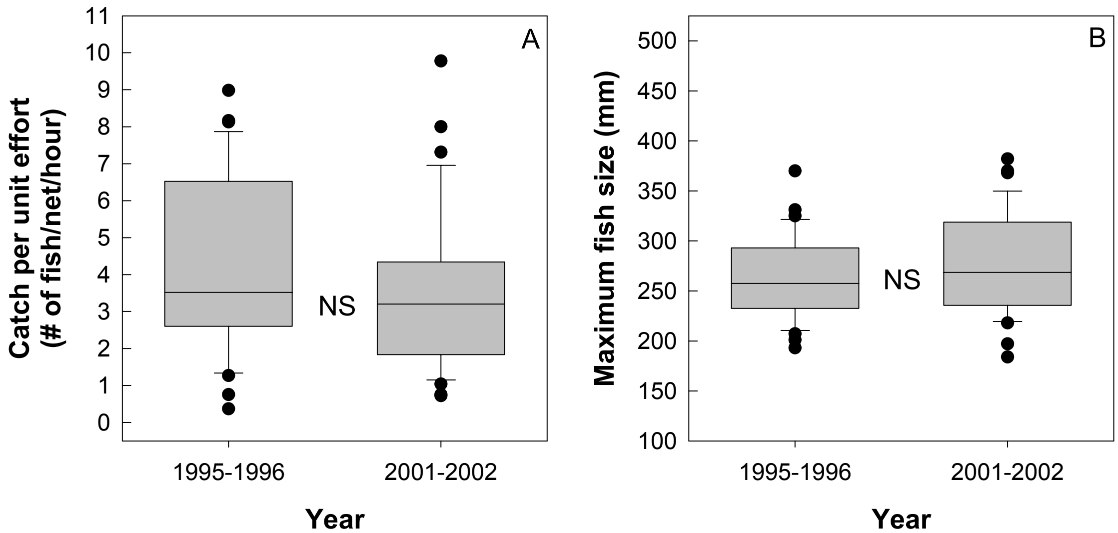

N = 61
Spawning habitat < 2.1m2
Spawning habitat > 2.1m2
N = 41
N = 20
17/24
41% self-sustaining
Elevation > 3520 m
Elevation < 3520 m
N = 10
N = 31
19/1
95% self-sustaining
0/10
0% self-sustaining
17/14
55% self-sustaining



Maximum depth (m)
A
NS
Control
Experimental
Lake Type
Total stream width (cm)
B
NS
Control
Experimental
Lake Type
Elevation (m)
C
NS
Control
Experimental
Lake Type
Surface area (ha)
D
NS
Control
Experimental
Lake Type
Total spawning habitat (m2)
E
NS
Control
Experimental
Lake Type
PC1
F
NS
Control
Experimental
Lake Type
PC2
G
NS
Control
Experimental
Lake Type


80
70
60
50
40
30
20
10
0
% self-sustaining
trout populations
20
18
13
4
None
Poor
Fair
Good/Excellent
CDFG qualitative estimate
of spawning habitat suitability


Before stocking hiatus
A
Catch per unit effort (# of fish/net/hour)
11
10
9
8
7
6
5
4
3
2
1
0
NS
control
experimental
Lake Type
Before stocking hiatus
B
Maximum fish size (mm)
500
450
400
350
300
250
200
150
100
NS
control
experimental
Lake Type
After stocking hiatus
C
Catch per unit effort (# fish/net/hour)
11
10
9
8
7
6
5
4
3
2
1
0
NS
control
experimental
Lake Type
After stocking hiatus
D
Maximum fish size (mm)
500
450
400
350
300
250
200
150
100
NS
control
experimental
Lake Type


A
Catch per unit effort
(# of fish/net/hour)
0
1
2
3
4
5
6
7
8
9
10
11
NS
1995-1996
2001-2002
Year
B
Maximum fish size (mm)
100
150
200
250
300
350
400
450
500
NS
1995-1996
2001-2002
Year

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