Response by trout populations in alpine lakes to an experimental halt to stocking

Trip W. Armstrong and Roland A. Knapp

Abstract: Trout are often stocked into alpine lakes based on the generally untested assumption that resident populations would go extinct without stocking. The objectives of our study were to estimate the proportion of currently or formerly stocked alpine lakes in the Sierra Nevada, California, containing naturally reproducing trout populations (*Oncorhynchus mykiss*, *Oncorhynchus mykiss aguabonita*, *Oncorhynchus clarki henshawi*), identify characteristics of lakes associated with successful reproduction, and quantify the effects of stocking termination on trout density and individual growth rates in reproducing populations. We surveyed trout populations in 95 lakes in the John Muir Wilderness before and after a 4- to 8-year stocking halt and in 84 lakes in Sequoia–Kings Canyon National Park after a ≥20-year stocking hiatus. Based on recruitment during the no-stocking period, 70% and 68% of study lakes in the John Muir Wilderness and Sequoia–Kings Canyon National Park, respectively, contained reproducing populations. Results indicated that lakes with >2.1 m^2 of spawning habitat and at elevations <3520 m nearly always showed evidence of reproduction. For reproducing populations, stocking termination did not result in significant changes in population density, but may have increased individual growth rates. We conclude that most trout stocking in Sierra Nevada alpine lakes could be permanently halted with only minimal impact on the recreational fishery.

Résumé : Il arrive souvent que l'on ensemence des truites dans les lacs alpins, parce que l'on croit, généralement sans preuves, que les populations résidantes pourraient disparaître sans ces ensemencements. Les objectifs de notre étude sont d'estimer la proportion de lacs alpins dans la Sierra Nevada, Californie, contenant des populations de truites à reproduction naturelle (*Oncorhynchus mykiss*, *O. m. aguabonita*, *O. clarki henshawi*) qui sont actuellement ensemencés ou qui l'ont été dans le passé; nous voulons aussi identifier les caractéristiques des lacs dans lesquels la reproduction est réussie et étudier quantitativement les effets de l'arrêt des ensemencements sur la densité des truites et les taux individuels de croissance dans les populations qui se reproduisent. Nous avons fait l'inventaire de 95 lacs dans la région sauvage John Muir (JMW) avant et après un arrêt de 4–8 ans des l'ensemencements et de 84 lacs du parc national de Sequoia–Kings Canyon (SEKI) après un arrêt de ≥20 ans. D'après le recrutement observé durant l'arrêt des ensemencements, 70 % des lacs étudiés à JMW et 68 % de ceux de SEKI maintiennent des populations qui se reproduisent. Les lacs qui possèdent >2,1 m^2 d'habitat de fraye et qui sont situés à <3520 m d'altitude montrent presque toujours des indices de reproduction. Chez les populations qui se reproduisent, l'arrêt des ensemencements ne cause pas de changement significatif de la densité de population et peut augmenter les taux individuels de croissance. En conclusion, la plupart des ensemencements de poissons dans les lacs alpins de la Sierra Nevada peuvent être abandonnés de façon permanente et l'impact sur la pêche sportive sera minime.

[Traduit par la Rédaction]

Introduction

The stocking of non-native trout into naturally 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 fewer 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 non-native 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

Received 31 July 2003. Accepted 31 May 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 15 January 2005.
J17679

T.W. Armstrong.[1,2] Wildlife, Fish, and Conservation Biology, University of California, Davis, 1 Shields Avenue, Davis, CA 95616, USA.
R.A. Knapp. Sierra Nevada Aquatic Research Laboratory, University of California, HCR 79, Box 198, Mammoth Lakes, CA 93546, USA.

[1] Corresponding author (e-mail: twarmstrong@ucdavis.edu).

[2] Present address: Sierra Nevada Aquatic Research Laboratory, University of California, HCR 79, Box 198, Mammoth Lakes, CA 93546, USA.

doi: 10.1139/F04-144

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 USA estimated that only 25% of high-elevation lakes harboring introduced trout populations showed levels of natural reproduction 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 that already contain self-sustaining fish populations may provide little or no benefit to these fisheries (Parsons and Pereira 2001).

The objectives of this study were to (*i*) use an experiment in which lakes were subjected to a 4- to 8-year stocking hiatus to determine what proportion of currently stocked lakes in the John Muir Wilderness (JMW) study area (California, USA) contain naturally reproducing populations of introduced trout (rainbow trout, *Oncorhynchus mykiss*; golden trout, *Oncorhynchus mykiss aguabonita*; Lahontan cutthroat trout, *Oncorhynchus clarki henshawi*), (*ii*) determine what proportion of *Oncorhynchus* spp. populations in lakes in Sequoia–Kings Canyon National Park (SEKI; California, USA) show evidence of natural reproduction following a ≥20-year stocking hiatus, (*iii*) identify the habitat factors associated with successful reproduction in the JMW study lakes, and (*iv*) quantify the effects of halting stocking in the JMW study area on density and individual growth rates of naturally reproducing populations. Based on our common observation of young-of-the-year trout in lakes in both study areas, we hypothesized that a majority of currently stocked trout populations are in fact at least partially maintained by natural reproduction. We included the data from SEKI to determine whether the rates of natural reproduction by trout populations observed in the JMW study area were similar to those in other parts of the high-elevation Sierra Nevada. We also hypothesized that the probability of successful natural reproduction is directly related to the total spawning area available to trout populations. For trout populations showing evidence of successful natural reproduction, 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).

Materials and methods

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 in the Inyo and Sierra national forests; the center of the study area is at 37°20′N, 118°48′W; SEKI study area: 348 833 ha, the center of the study area is at 36°45′N, 118°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 (Melack et al. 1985; Knapp and Matthews 2000). They are located in the alpine and subalpine zones (>2800 m), remain ice-free for approximately 4 months each year, are oligotrophic, and rarely reach maximum temperatures greater than 17 °C (Melack et al. 1985; 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 (young-of-the-year 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).

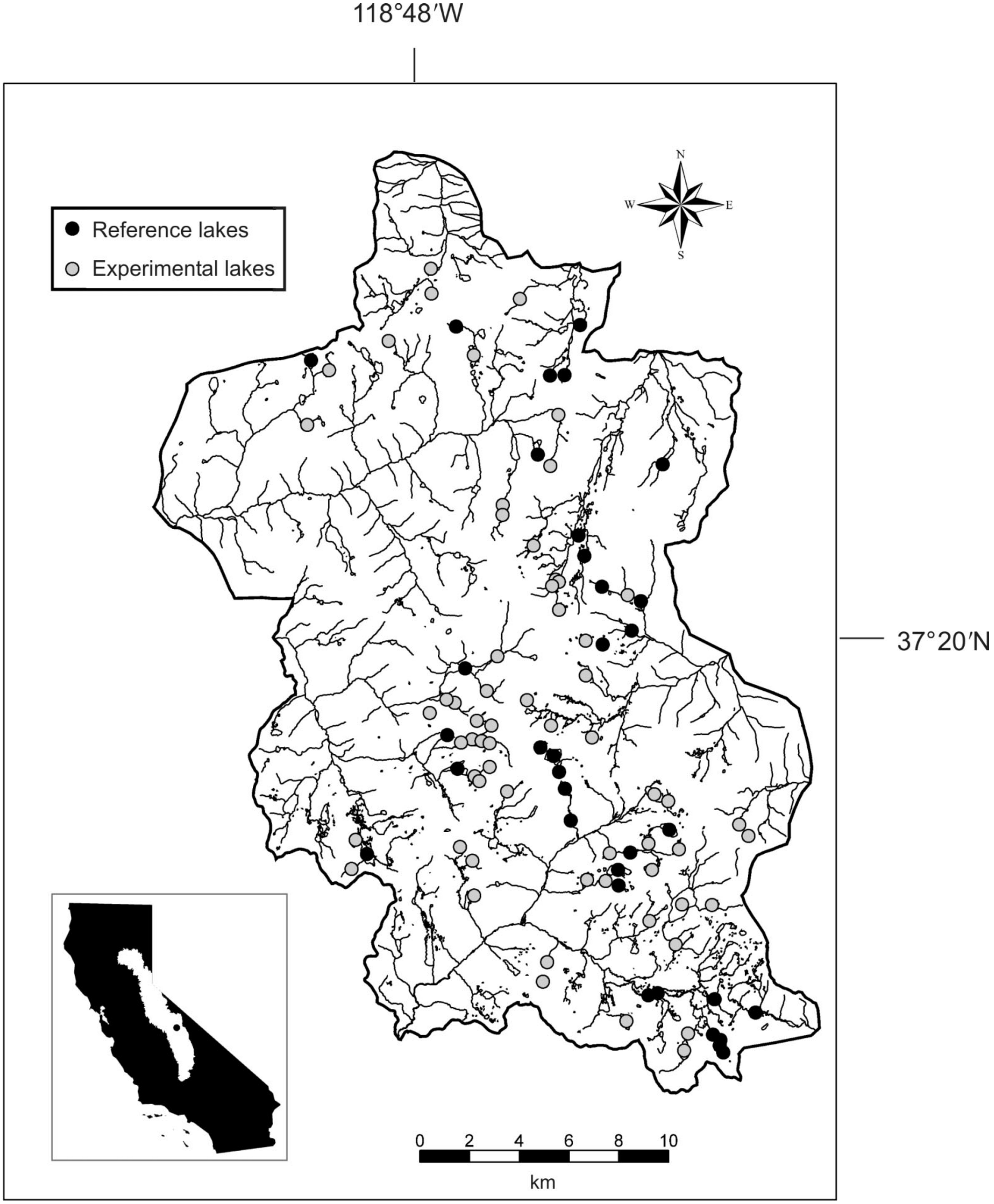
The JMW study area contains 216 lakes (water bodies with surface area ≥1.0 ha; maximum depth ≥3 m), 173 of which harbor introduced trout populations (80%; R.A. Knapp, unpublished data). During 1990–2000, 118 (84%) of these lakes were stocked with either *O. mykiss* (10 lakes), *O. m. aguabonita* (84 lakes), or *O. c. henshawi* (1 lake). The median number of times each lake was stocked during this period was 4 (range = 1–11) and the median stocking density was 553 fish·ha^{-1} (range = 57–6289 fish·ha^{-1}). Of the 1157 lakes in SEKI, 548 lakes harbor introduced trout populations (47%; R.A. Knapp, unpublished data). Although the National Park Service discontinued nearly all stocking in 1977, 84 lakes were stocked with either *O. mykiss* (29 lakes), *O. m. aguabonita* (53 lakes), or both species (2 lakes) between 1960 and 1977. During this period the median number of times each lake was stocked was 2 (range = 1–4) and the median stocking density was 988 fish·ha^{-1} (range = 91–9886 fish·ha^{-1}).

Most golden trout in the Sierra Nevada are actually golden trout × rainbow trout hybrids (R.A. Knapp, personal observation; Cordes 2001; Cordes et al. 2003). Because they are phenotypically more similar to golden trout, we refer to them as such throughout this paper.

Study design

The portion of our study conducted in the JMW involved the survey of trout populations in a series of lakes during 1995–1996, the use of these data to quantify premanipulation characteristics of fish populations and to select experimental lakes (in which stocking was temporarily halted) and reference lakes (in which regular stocking continued), and then the resurvey of trout populations in the experimental and reference lakes in 2001 and 2002 (Fig. 1). Trout captured during the lake resurveys were aged using otoliths, and the presence of fish born during the stocking hiatus was used as evidence of successful natural reproduction by the resident trout population. 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: (*i*) contained only *Oncorhynchus* spp. (*O. mykiss*, *O. m. aguabonita*, or *O. c. henshawi*), (*ii*) were stocked at least biennially, and (*iii*) were separated from other stocked lakes located upstream or downstream by natural barriers or ≥500 m of stream. The first requirement was necessary to eliminate the potentially confounding effect of the presence of brook trout (*Salvelinus fontinalis*), 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 mini-

Fig. 1. Map of the John Muir Wilderness (JMW) study area showing the locations of the experimental lakes (solid circles) and reference lakes (shaded circles). The inset map shows the State of California, USA (solid), the Sierra Nevada (open), and the location of the study area within the Sierra Nevada (●).



mize the possibility that fish population dynamics in the experimental lakes would be influenced by stocking in adjacent lakes (e.g., stocked fish moving into adjacent unstocked lakes). While some literature suggests that trout are able to move distances >2000 m through streams (Gowan and Fausch 1996), golden trout in Sierra Nevada streams have only been documented moving relatively short distances (<600 m; Matthews 1996). Trout populations in 54 (89%) of our experimental lakes were isolated from other stocked trout populations by impassible barriers. In the remaining seven experimental lakes (11%), trout populations were separated from adjacent stocked trout populations by 500–3600 m (median = 500 m). As a consequence of the generally high degree of isolation of trout populations in our experimental lakes from any stocked lakes, stocking of reference lakes during the study should have had little or no influence on the structure of trout populations in the experimental lakes. Following the initial sampling of fish populations in all JMW study lakes, the CDFG ceased stocking experimental lakes for at least 4 consecutive years between 1994 and 2001 (range = 4–8 years, median = 5 years).

Reference lakes ($N = 34$) were randomly chosen from the remaining lakes that met requirements *i* and *ii* but not *iii*. These lakes continued to be regularly stocked for the duration of the experiment. Reference lakes were used for two reasons in this study: (1) to facilitate assessment of the effects of halting stocking on population densities and individual growth rates, and (2) to allow us to apply our model of those factors determining whether or not trout populations were able to reproduce naturally to a broader subset of JMW lakes.

In addition to the short-term experiment in the JMW, we also conducted a longer term study in which we evaluated whether introduced *Oncorhynchus* spp. populations in SEKI lakes had maintained themselves through natural reproduction after a ≥20-year halt to stocking. We identified 84 lakes in SEKI that were not stocked after 1977, had been stocked at least once between 1962 and 1977, and contained only *Oncorhynchus* spp. Fish populations in these lakes were sampled in 1997, 2000, 2001, or 2002, and the capture of any trout was taken as evidence of successful natural reproduction. We used the results of this analysis to evaluate the generality of our findings regarding the rate of successful natural reproduction in the JMW study area.

Fish-population sampling

We sampled fish populations in JMW and SEKI lakes using gill nets. 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 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. The five largest mesh size panels are effective at catching >120 mm long trout, while the smallest mesh size panel can successfully capture trout as small as 80 mm (Hall 1991*b*). A single net was set in each lake 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 trout <120 mm in length, fish that are found primarily in nearshore habitats (Landry et al. 1999). Nets were anchored to shore and set perpendicular to the lake shoreline. We set gill nets in either the early morning or the late evening and pulled them after 8–12 h. Every captured fish was weighed to the nearest gram and measured to the nearest millimetre (fork length). Catch per unit effort (CPUE; i.e., the number of fish captured per hour in each net) from nets set during the day versus at night were similar ($X_{\text{day}} = 3.1$, $X_{\text{night}} = 2.6$; two-sample *t* test, $t = 0.628$, df = 93, $P = 0.532$).

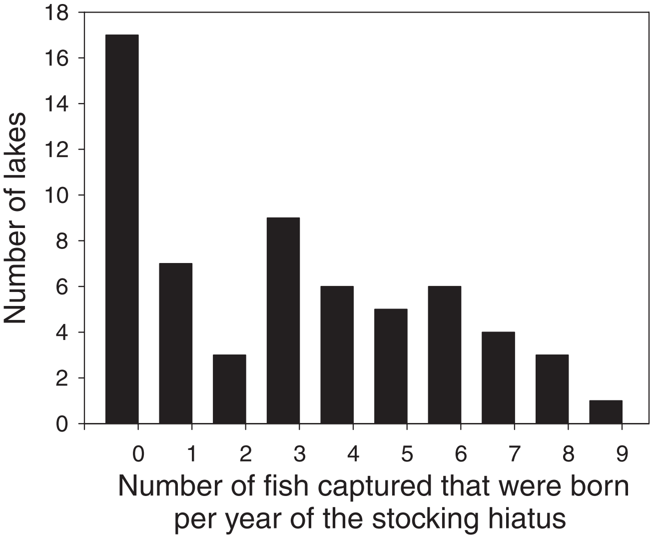
We used sagittal otoliths to age fish captured during the 2001–2002 JMW lake resurveys (Campana and Neilsen 1985). In 70 lakes, we captured <40 fish and in these cases we removed the pair of sagittal otoliths from all captured fish. In 25 lakes, we captured >40 fish. For these lakes, otoliths were extracted 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 (Kruse et al. 1997; Hining et al. 2000), including trout from alpine lakes (Hall 1991*a*; Boiano 1999). Annular-increment formation has been validated in *O. mykiss* (Graynoth 1996) but not in *O. m. aguabonita*. 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 reference lakes. In August 1999, we clipped adipose fins from 2000 golden trout fingerlings (~30 days old) immediately prior to their being stocked into Summit Lake (37°14′N, 118°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-fin-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 US Geological Survey 1 : 24 000 topographic maps. We characterized littoral zone substrate composition by visually estimating the dominant substrate type along approximately fifty 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 diameter), 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, as well as of in-lake spawning habitat associated with inlet and outlet streams. We focused spawning-habitat measurements on stream and stream-associated habitats because successful embryo development in *Oncorhynchus* spp. depends on continuous water flow (Bjornn and Reiser 1991). For the stream portion of surveys, we limited our measurements to the first 100 m of stream because analysis of preliminary spawning-habitat data collected during the 1995–1996 lake surveys indicated a significant association between the amount of spawning habitat in the first 100 m of stream and successful natural reproduction by lake-resident trout. 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 $\text{cm}\cdot\text{s}^{-1}$ (Bjornn and Reiser 1991; Knapp and Preisler 1999). We also estimated the average width and depth of the first 100 m of each inlet and outlet stream.

Fig. 2. Frequency histogram showing the amount of trout (*Oncorhynchus* spp.) reproduction that occurred in the JMW experimental lakes during the stocking hiatus. The *x* axis shows the number of trout captured in the gill net whose ages indicated that they were born during the stocking hiatus. The number of trout captured was divided by the number of years of the stocking hiatus to standardize the catch amongst lakes subject to no stocking for differing numbers of years. The number of captured fish that were born per year of the stocking hiatus ranged from 0 to 9.



Data analysis

Determination of reproductive status

We used two different criteria to categorize JMW trout populations as reproductive or non-reproductive. Under the first criterion, a trout population was categorized as reproductive if the gill-net catch from the 2001–2002 fish surveys included any trout whose age indicated that it was born during the stocking hiatus, and non-reproductive if no such trout were captured. Because low levels of successful natural 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 reproductive only if the gill-net catch included an average of >1 fish born per year of the stocking hiatus. This division point was chosen based on an obvious break in the distribution of the number of captured fish born per year of the stocking hiatus for all experimental lakes (Fig. 2). The number of fish is expressed on a per-year basis to standardize the numbers captured from lakes with different durations of stocking termination. Because SEKI lakes had not been stocked for ≥20 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 reproductive if 1 or more trout were captured during the gill-net survey and non-reproductive if no trout were captured.

Habitat effects on reproductive status

We used stepwise logistic regression and tree regression to model the effect of physical lake characteristics on the reproductive status of trout populations 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 littoral zone 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 (PC1, PC2), which together explained 53% of the variation in substrate characteristics (Table 1). 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 as identifying the levels at which these variables become important (De'ath and Fabricius 2000). Because the two regression models produced similar results (see Results), we used the tree-regression results to estimate the proportion of naturally reproducing populations in reference lakes. We then combined this estimate with the number of experimental lakes with naturally reproducing populations to obtain a single estimate of the proportion of naturally reproducing trout populations for all currently stocked lakes in the study area.

Table 1. Loadings for the first two principal component axes of littoral zone substrate composition.

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

Note: PC1 and PC2 explained 29% and 24%, respectively, of the variance in littoral zone substrate characteristics.

Our regression analyses indicated that the amount of spawning habitat was of primary importance in determining population reproduction (see Results). However, measuring this variable requires visits to each lake, and measurements of spawning-habitat quantity are therefore not widely available for lakes outside 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 reproduction, we used a χ^2 test to quantify the strength of the association between the CDFG spawning-habitat categories and our lake-specific determination of trout population reproductive status 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 reference and experimental lakes before and after the stocking hiatus. We used two different measures to quantify individual fish growth: size-at-age and maximum fish size. For size-at-age analyses, we used age-4 fish because this was the most frequently encountered age class. All age-4 fish from each gill-net sample were used in these growth-rate determinations. Although size-at-age is a commonly used measure of salmonid growth rate (Quinn and Deriso 1999), this analysis was dependent on having fish from a particular age class present in every gill-net sample. Therefore, we used maximum fish size as a second measure of individual growth rate because it allowed us to include every JMW study lake in our analyses. Although maximum fish size is only rarely used as a measure of individual growth rate, based on our study data, average size of age 4 fish and maximum fish size were highly correlated ($N = 42$, $r = 0.56$, $P < 0.0001$). We used CPUE 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), which demonstrate a positive linear relationship between CPUE (measured as gill-net catches) and actual population density for *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 CPUE, size-at-age, and maximum fish size in experimental versus reference lakes using data collected after the several-year halt to stocking (2000–2001 survey). To determine whether observed differences in CPUE, size-at-age, 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 reference lakes, we also used two-sample *t* tests to compare CPUE, size-at-age, and maximum fish size in experimental and reference lakes before the stocking hiatus began (using data from the 1995–1996 survey). Second, we used paired *t* tests to compare CPUE, size-at-age, and maximum fish size for each fish population measured before and after the stocking hiatus. Only those experimental lakes containing trout populations categorized as reproductive were included in this analysis.

To determine whether these statistical tests could 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, size-at-age, 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 (Steidl et al. 1997). 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. 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 6 golden trout lacking adipose fins. Independent counts of increments on sagittal otoliths from these fish made by both authors indicated that otoliths from all 6 fish contained three obvious increments. Therefore, increments in these otoliths appear to be produced annually.

Fish population reproductive status

Trout populations in 43 of our 61 JMW experimental lakes (70%) contained trout with ages which indicated that they were born during the stocking hiatus. Therefore, based on our first criterion for determining reproductive status, 70% of the experimental lakes contained trout populations that were categorized as reproductive. Using our second, more conservative criterion to identify only those lakes with abundant natural reproduction, in 37 of 61 experimental lakes (61%) we captured an average of >1 fish born per year of the stocking hiatus (Fig. 2). The age structure of two representative trout populations that were categorized as nonreproductive and reproductive are provided (Fig. 3). For the SEKI lakes, 57 of 84 lakes (68%) contained trout populations categorized as reproductive. Therefore, the majority of study lakes in the JMW and SEKI showed evidence of substantial natural reproduction. In SEKI, the fact that trout populations persisted after ≥20 years of no stocking suggests that the level of natural reproduction in lakes categorized as reproductive is sufficient to maintain these populations over the long term.

Habitat factors influencing reproductive status

Regression analyses of the factors that influence trout population reproductive status and the analyses of the effects of stocking termination on CPUE and fish size were conducted on data categorized using both criteria for determining trout population reproductive status. Results were similar regardless of which criterion was used, and we therefore present only the results from the more conservative estimate of the percentage of populations categorized as reproductive (61%).

Logistic regression indicated that the probability of trout population reproduction 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 reproduction were not significant. The tree regression yielded similar results, again indicating the positive influence of the amount of spawning habitat and the negative influence of elevation on population reproduction (Fig. 4). Ninety-five percent of lakes with >2.1 m^2 of spawning habitat contained reproductive trout populations, while only 41% of lakes with <2.1 m^2 of spawning habitat contained reproductive trout populations. For lakes with <2.1 m^2 of spawning habitat, none of the 10 trout populations occurring in lakes above 3520 m were reproductive, while 55% of those in lakes below 3520 m were reproductive (Fig. 4).

Before using the tree-regression model to predict natural reproduction in the reference lakes, we compared the physical habitat characteristics of experimental and reference lakes to ensure that they were similar. Experimental and reference lakes were compared using Wilcoxon's rank-sum tests and showed no significant differences in any of the measured habitat variables, including maximum depth (Fig. 5*a*),

Fig. 3. Age–frequency histograms for two JMW experimental lakes, (*a*) Jawbone Lake and (*b*) Upper Honeymoon Lake, chosen to illustrate trout (*Oncorhynchus* spp.) populations with different levels of natural reproduction. The solid box above the bars indicates the period during which the lake was stocked and the open box indicates the period of the stocking hiatus. The trout population depicted in *a* shows no evidence of natural reproduction, while the trout population depicted in *b* shows substantial natural reproduction during the stocking hiatus.

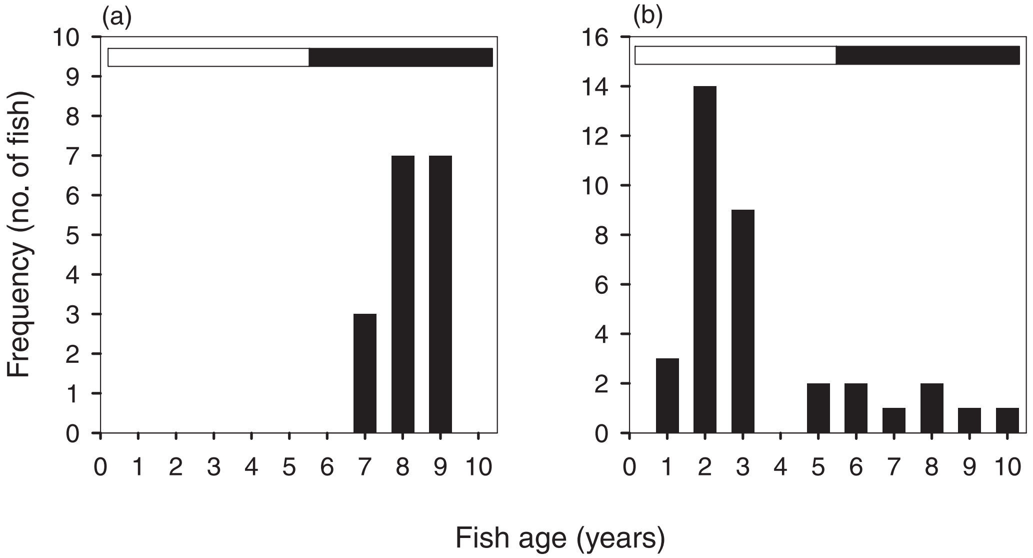
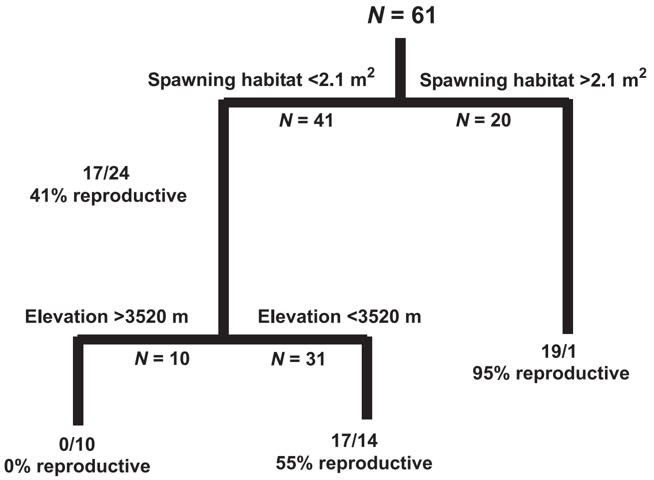


Table 2. Results of stepwise logistic regression analysis of the effect of lake habitat characteristics on the reproductive status of trout (*Oncorhynchus* spp.) populations in the experimental lakes (reproductive, non-reproductive) in the John Muir Wilderness.

Variable	Regression coefficient	*P*
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

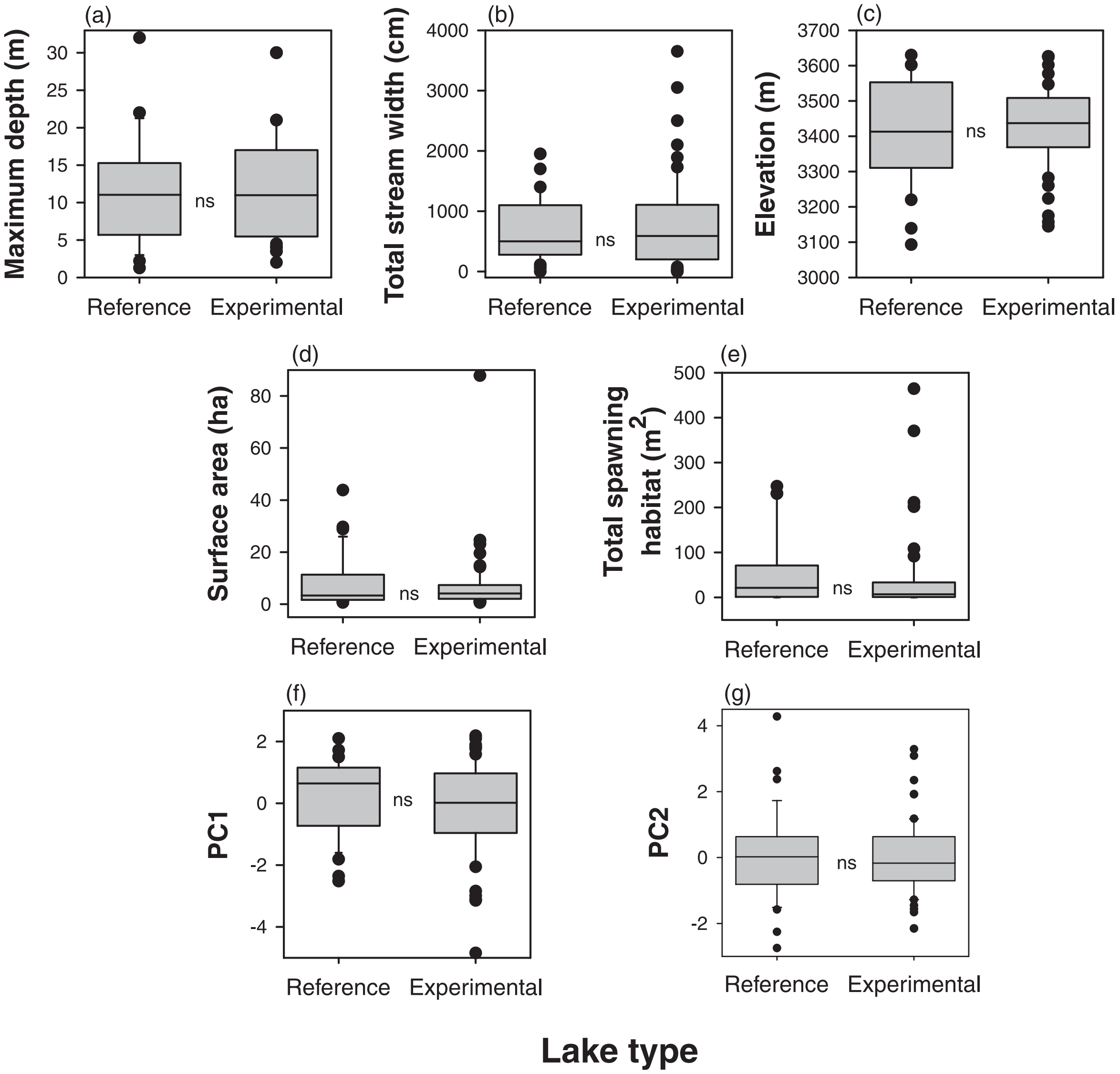
total stream width (Fig. 5*b*), elevation (Fig. 5*c*), lake surface area (Fig. 5*d*), total spawning area (Fig. 5*e*), PC1 (Fig. 5*f*), and PC2 (Fig. 5*g*). Therefore, despite the fact that experimental lakes were not chosen at random, they were physically similar to the reference lakes. We next applied the results from our tree-regression model to all 34 reference lakes used in our JMW study area. Our model predicted that 19 of these populations would be reproductive (56%). We combined these predictions with our determination of reproductive populations in the experimental lakes (based on the more conservative criterion), which resulted in 59% of our JMW study lakes being categorized as reproductive. Therefore, the majority of lakes that were stocked during the past decade in our JMW study area contain naturally reproductive *Oncorhynchus* spp. populations.

Fig 4. Tree-regression results for all 61 JMW experimental lakes, displaying the effects of habitat variables on the reproductive status of trout (*Oncorhynchus* spp.) populations (reproductive, non-reproductive). The number of reproductive populations (*Y*) and the number of non-reproductive (*N*) populations is given at each node as *Y*/*N*, together with the percentage of lakes that were reproductive.



After determining which of the experimental-lake populations were reproductive, we analyzed whether qualitative CDFG estimates of spawning-habitat quality could also be used to predict successful population reproduction. The qualitative spawning-habitat categories were significantly associated with population reproductive status (Pearson's χ^2 test, $\chi^2 = 10.79$, df = 3, $P = 0.013$; Fig. 6). Of the lakes with poor, fair, or good/excellent spawning habitat, 71% contained trout populations categorized as reproductive. In contrast, of the 20 lakes with spawning habitat categorized as none, only 25% showed evidence of natural trout reproduction (Fig. 6). 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 naturally reproductive trout populations.

Fig. 5. 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 principal component axis 1 (PC1), and (*g*) littoral zone substrate principal component axis 2 (PC2) for reference ($N = 34$) and experimental ($N = 61$) lakes. The line within each box represents the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, and the data points below and above the whiskers indicate values outside the 10th and 90th percentiles; "ns" indicates that the difference between reference and experimental lakes is not statistically significant (Wilcoxon's rank-sum test, $P > 0.05$).

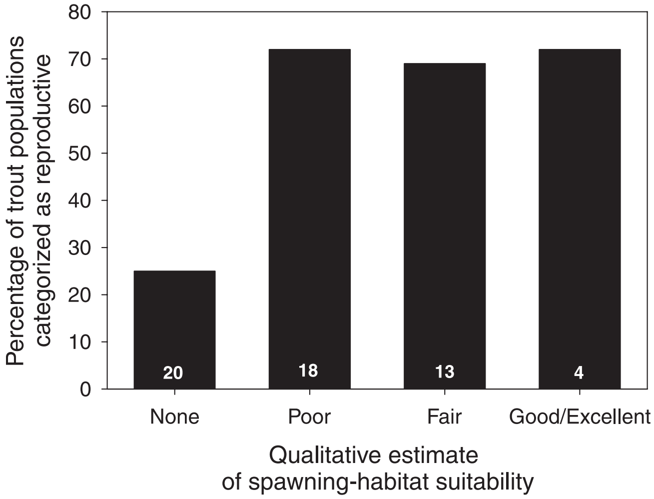


Effects of halting stocking on reproducing populations

Prior to the stocking hiatus, neither CPUE (two-sample *t* test, $t = 0.049$, df = 93, $P = 0.96$; Fig. 7*a*), size at age 4 (two-sample *t* test: $t = -0.595$, df = 64, $P = 0.554$; Fig. 7*b*), nor maximum fish size (two-sample *t* test, $t = 0.824$, df = 93, $P = 0.412$; Fig. 7*c*) differed significantly between reference and experimental lakes. Based on a hypothetical difference of 25% between the means, the power of these tests was high in two cases (CPUE: power = 0.7; maximum fish size: 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. The power of the size-at-age test was relatively low (0.12), which was likely a result of a smaller sample size. After the stocking hiatus, CPUE (two-sample *t* test, $t = 0.646$, df = 93, $P = 0.520$; Fig. 7*d*), size-at-age (two-sample *t* test, $t = -0.638$, df = 41, $P = 0.267$; Fig. 7*e*), and maximum fish size (two-sample *t* test: $t = -1.036$, df = 93, $P = 0.303$; Fig. 7*f*) again did not differ significantly between reference and experimental lakes. Again, the power of two of these tests was high (CPUE: power = 0.7; maximum fish size: power = 1.0), whereas the power of the third test was relatively low (size-at-age: power = 0.16). The high power values suggest that we likely would have been able to detect a difference of 25% in CPUE and maximum fish size had there been a real difference of this magnitude. The low power in the size-at-age *t* test is also likely a result of the smaller sample size.

For experimental lakes categorized as reproductive, comparisons of CPUE and maximum fish size for the same lakes before and after the stocking hiatus indicated no significant change in CPUE (paired *t* test, $t = 2.1$, df = 36, $P = 0.978$; Fig. 8*a*) or maximum fish size (paired *t* test, $t = -1.82$, df =

Fig 6. Percentages of JMW experimental lakes that contained reproductive trout (*Oncorhynchus* spp.) populations as a function of qualitative categories of spawning-habitat suitability obtained from the California Department of Fish and Game. The number at the base of each bar is the sample size.



36, $P = 0.962$; Fig. 8*c*). However, size at age 4 was significantly higher after the stocking hiatus (paired *t* test, $t = 2.99$, df = 21, $P = 0.0035$; Fig. 8*b*). The power of the CPUE and maximum fish size tests was also relatively high (CPUE: power = 0.64; maximum fish size: power = 1.0), 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 37 lakes and sample variances that characterized these data. We conclude that while the experimental halt to stocking had no effect on population densities, individual growth rates of naturally reproducing trout populations increased after stocking was halted, at least when the growth rate was measured as size at age 4.

Discussion

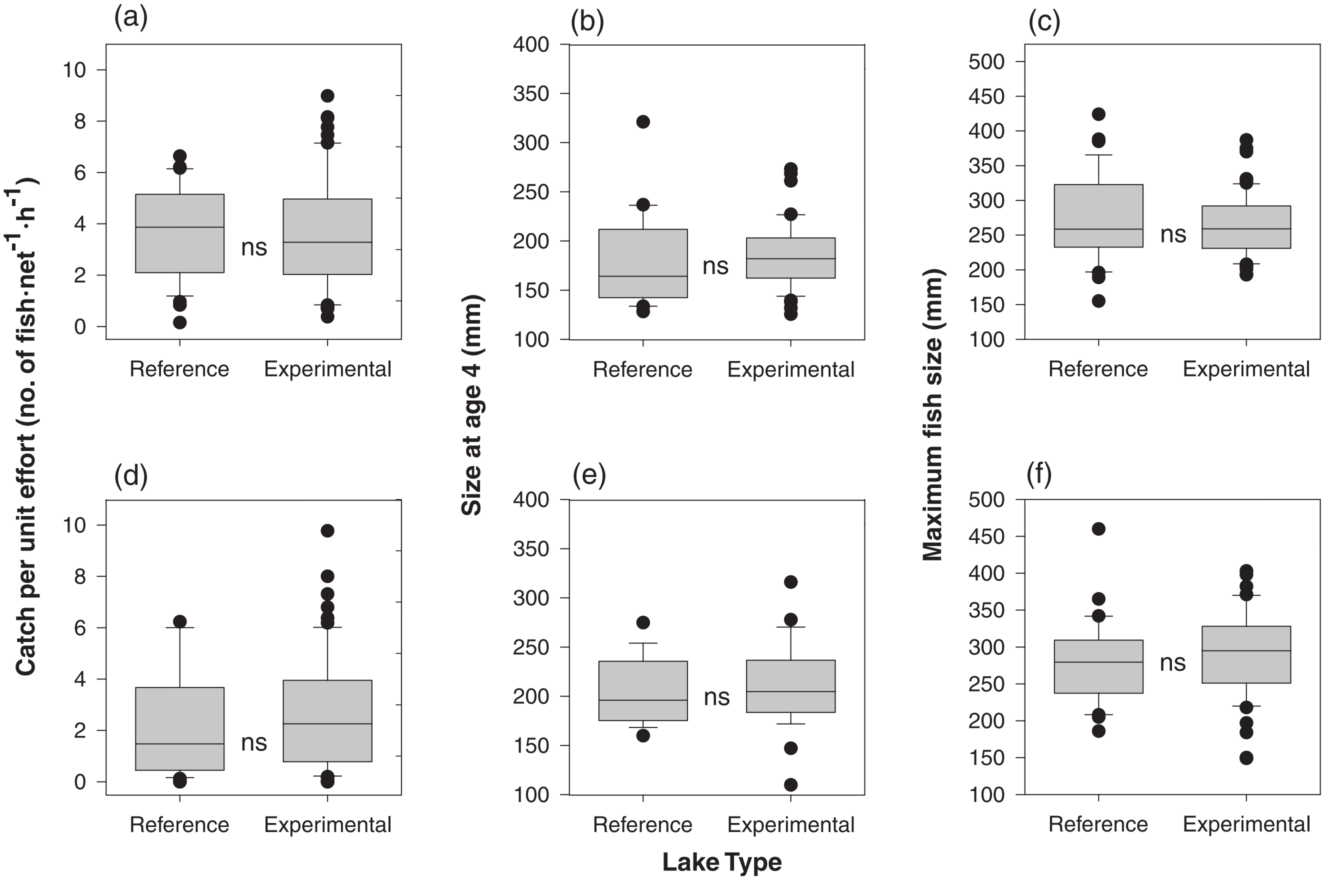
The practice of supplemental stocking in high-elevation lakes in the Sierra Nevada of California and elsewhere in western North America has historically been predicated on the assumption that few or none of these introduced trout populations are self-sustaining (Bahls 1992). However, results from our stocking-termination experiment indicate that the majority of *Oncorhynchus* spp. populations in our JMW and SEKI study areas showed evidence of substantial natural reproduction. Based on the more conservative criterion that we used to categorize experimental lakes as reproductive, we estimated that 61% of our JMW experimental lakes and 68% of our SEKI study area lakes contained naturally reproductive trout populations. The tree-regression model predicted that 56% of the reference lakes in the JMW also contained reproductive populations. Adding our determinations of reproduction in experimental-lake populations to our predictions from the reference-lake populations resulted in an overall estimate of natural reproduction in the JMW study lakes of 59%. The high degree of concordance between estimates of natural reproduction in JMW and SEKI populations suggests that the results from the JMW can be extrapolated across both a longer time scale and a broader spatial scale.

The relatively short time scale of the experimental halt to stocking in the JMW study area was not sufficient to allow a definitive determination of self-sustainability in these populations. In contrast, the much longer (20+ years) halt to stocking in SEKI lakes was likely sufficient for determining population self-sustainability. Many of these populations in SEKI experienced low levels of natural reproduction (measured as CPUE), yet the populations remained self-sustaining over a long period of time. In addition, the presence of fish populations in SEKI lakes indicates that angling pressure probably has little or no effect on population self-sustainability. These low levels of reproduction in SEKI populations suggest that most or all of the JMW populations identified as reproductive are likely to be self-sustaining over the long term as well.

Given that the majority of currently stocked lakes in the JMW study area show evidence of successful natural reproduction, the consequences to the recreational fishery of even a complete and permanent halt to stocking in this area are likely to be small. For example, there are 216 large lakes (≥1 ha, ≥3 m deep) in the JMW study area, 173 of which contain trout populations. Sixty-three of these lakes contain self-sustaining S. fontinalis populations and are not stocked, while another 15 contain *Oncorhynchus* spp. populations and are not stocked for various reasons. Our results predict that of the remaining 95 *Oncorhynchus* spp.-containing lakes (all of which were stocked until our study began), approximately 39 are non-reproductive and will likely revert to a fishless condition without supplemental stocking and 56 are reproductive and would maintain themselves in the absence of any further stocking. The 39 populations that would disappear represent only 23% of the total fish populations ($N = 173$) in the JMW study area. Therefore, the results from both study areas indicate that even a complete halt to stocking in the southern Sierra Nevada would likely result in only a relatively small decrease in the overall number of fish-containing lakes. These results suggest that a reevaluation of the need for continued fish stocking to maintain trout fisheries in other high-elevation lake systems may be necessary. One of the most effective methods to determine the proportion of naturally reproducing fish populations in high-elevation areas, as demonstrated in our experiment, is to halt stocking for several consecutive years. In addition to being a simple tool for evaluating reproductive potential, halting stocking is inexpensive and any negative effects are easily 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 significantly influenced the reproductive status of trout populations. Results from the tree regression further suggested that as little as 2.1 m^2 of spawning habitat was sufficient to produce naturally reproducing trout populations. Other studies have also documented the overriding importance of spawning habitat in allowing successful reproduction by trout introduced into mountain lakes. For example, Donald (1987) reported that the probability of trout populations becoming established after being introduced into naturally fishless alpine lakes was directly related to the size of outlet streams, presumably because the amount of available spawning habitat is an increasing function of outlet size. Boiano (1999) also identified

Fig. 7. Box plots showing (*a*) catch per unit effort (CPUE), (*b*) size at age 4, and (*c*) maximum fish size for reference and experimental lakes in 1995–1996 (i.e., before the stocking hiatus), and (*d*) catch per unit effort (CPUE), (*e*) size at age 4, and (*f*) maximum fish size for reference and experimental lakes in 2001–2002 (i.e., after the stocking hiatus). The line within each box represents the median, the bottom and top of each box indicate the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, and the data points below and above the whiskers indicate values outside the 10th and 90th percentiles; "ns" indicates that the difference between reference and experimental lakes is not statistically significant (two-sample *t* test, $P > 0.05$). In the comparisons between CPUE and maximum fish size, sample sizes are 34 and 61 for reference and experimental lakes, respectively. Sample sizes for size-at-age before the stocking hiatus are 20 and 46 for reference and experimental lakes, respectively; sample sizes for size-at-age after the stocking hiatus are 15 and 28 for reference and experimental lakes, respectively.

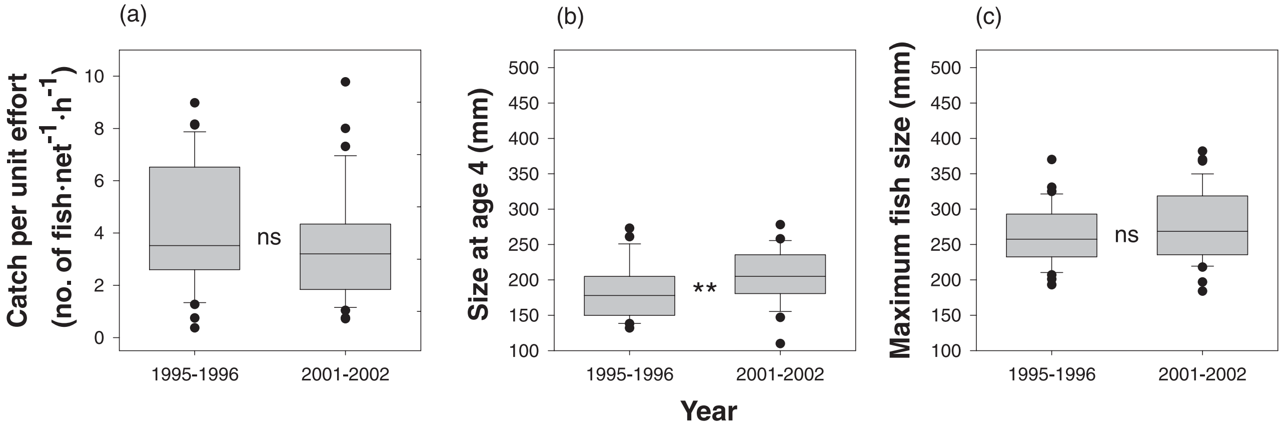


spawning-habitat area as a significant factor in allowing successful natural reproduction by introduced *O. mykiss* populations in high-elevation lakes in Yosemite National Park. Most high-elevation Sierra Nevada lakes contain at least some spawning habitat (R. Knapp, unpublished data), which supports the idea that the majority of currently stocked trout populations are in fact able to reproduce and would not require additional stocking to persist. Although our surveys included all spawning habitat in the first 100 m of each stream, as well as all in-lake stream-associated spawning habitat, it is important to note that measurements of the total amount of spawning habitat at each lake likely vary from year to year depending upon the amount of winter precipitation as well as the time of year the lake is surveyed. As a result of this interannual variation, the minimum amount of spawning habitat we identified in this study as necessary for successful reproduction is unlikely to be an absolute limitation, but rather a relative number indicating the small area actually required by trout populations. It should also be recognized that by restricting our measurements of stream spawning habitat to the first 100 m of stream, we undoubtedly missed some spawning habitat that was available to the trout populations.

The significant association we found between the likelihood of successful natural reproduction and qualitative estimates of spawning-habitat quality in our JMW study area suggests not only that qualitative estimates of spawning-habitat availability may provide a reasonably accurate means of categorizing the reproductive status of trout populations, but also that in the absence of quantitative measures of recruitment magnitude and habitat characteristics, a prudent management strategy may be to simply categorize those trout populations in lakes with any spawning habitat as reproductive. The qualitative assessments needed to make this determination are currently available for many Sierra Nevada lakes.

Our regression models also suggest that in addition to depending on the amount of spawning habitat, the probability of successful reproduction by trout populations decreases with increasing elevation. Specifically, the tree regression indicated that lakes above 3520 m were unlikely to contain reproductive trout populations. One possible explanation for

Fig. 8. Box plots showing (*a*) catch per unit effort (CPUE), (*b*) size at age 4, and (*c*) maximum fish size for trout (*Oncorhynchus* spp.) populations in JMW experimental lakes categorized as reproductive 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 represent the 10th and 90th percentiles, and the points below and above the whiskers indicate values outside the 10th and 90th percentiles; "ns" indicates that the difference between reference and experimental lakes is not statistically significant (paired *t* test, $P > 0.05$); ** indicates that the difference is significant (paired *t* test, $P < 0.005$). Sample sizes are 37 for the first two groups and 22 for the third group.



this inability of trout populations at the highest elevations to reproduce 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. These small fry may be subject to strong size-selective mortality, as has been documented for fry of other salmonids (e.g., West and Larkin 1987). If emerging 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 lakes are spawning successfully but that this spawning results in little or no recruitment.

For the naturally reproducing populations in our JMW study area, the results of our experiment show that there were no effects of a halt to stocking on population density or maximum fish size, but that there was an increase in fish growth rates as measured by size at age 4. Together, these results suggest that supplemental stocking of the study lakes provides no benefit when populations reproduce on their own, and in fact may reduce growth rates. 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 streams with resident S. trutta populations increased mortality resulting from intraspecific competition. Stocking walleye (*Stizostedion vitreum*) into Minnesota lakes with self-sustaining *S. vitreum* populations resulted in decreases in abundance of adjacent year classes and decreases in the weights of resident fish (Li et al. 1996*b*) yet had no effect on overall population abundance (Li et al. 1996*a*). Similarly, Parsons and Pereira (2001) concluded that the stocking of *S. vitreum* fingerlings into self-sustaining *S. vitreum* populations was ineffective in boosting year-class strength.

The lack of a density response following stocking termination in our study lakes that contained reproductive populations suggests that at higher trout densities (resulting from the stocking of fry) an increasing mortality rate may compensate for the increase in density. This compensation may result in an essentially constant number of adult fish within each population. Salmonid populations are well known to be subject to such density-dependent mortality (Elliot 1985; Keeley 2001). Studies of population regulation in salmonids have nearly all been conducted in streams, and in these habitats it seems likely that the mechanism underlying density-dependent mortality is territory formation by age-0 fish that places an upper limit on their density (Elliot 1990; Grant and Kramer 1990). Whether a similar mechanism is responsible for population regulation in lake-dwelling salmonids remains unknown.

Individual growth rates and population density are often negatively correlated in salmonids (e.g., Jenkins et al. 1999; Schindler et al. 2001; Vollestad et al. 2002). Although we did not detect a significant change in trout density and maximum fish size in our experimental lakes after stocking termination, size-at-age increased. One possibility as to why the two growth-rate measures responded differently to stocking termination is that a rapid response in maximum fish size was prevented by the presence of fish cohorts that remained from the prestocking-hiatus period. If competition for food is strongest within cohorts, then density and growth of cohorts from the stocking period may be relatively unaffected by changes in the density of younger cohorts resulting from the stocking hiatus. In contrast, growth of age-4 fish may have increased as a result of even slight decreases in the density of this cohort. Longer term studies will be necessary to elucidate whether stocking termination did in fact increase fish growth rates and if so, the mechanism underlying these changes.

In conclusion, the majority of lake-dwelling *Oncorhynchus* spp. populations in our JMW and SEKI study areas showed evidence of successful reproduction, and relatively few JMW lakes will revert to a fishless condition even with a complete halt to stocking. The findings from this study indicate that cessation of stocking had no effect on population density but may have had a positive effect on fish growth rates. These results should encourage fisheries managers to reevaluate current mountain lake stocking programs, as the level of successful natural reproduction by trout populations in other high-elevation lakes in western North America may also be considerably higher than is currently believed (e.g., Bahls 1992).

Acknowledgements

This research was supported by grants to R. Knapp from the California Department of Fish and Game (P0180021), the U.S. Forest Service (PSW-95-001-CCS, PSW-96-0007CA, PSW-98-0009CA), and the National Park Service (USDI NPS 8550-002), a donation to R. Knapp from Trout Unlimited, and a grant to P. Moyle from the University of California Water Resources Center (Project W-955). Numerous field assistants were critical to the success of this study and their diligence is much appreciated. Thanks are also extended to the California Department of Fish and Game for altering their stocking program to allow us to conduct the stocking-termination experiment in the John Muir Wilderness.

References

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

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. Am. Fish. Soc. Spec. Publ. No. 19. pp. 83–138.

Bohlin, T., Sundstrom, L.F., Johnsson, J.I., Hojesjo, J., and Pettersson, J. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. J. Anim. Ecol. **71**: 683–692.

Boiano, D.M. 1999. Predicting the presence of self-sustaining trout populations in high elevation lakes of Yosemite National Park, California. M.S. thesis, Humboldt State University, Humboldt, Calif.

Bradford, D.F., Cooper, S.D., Jenkins, T.M., Jr., Kratz, K., Sarnelle, O., and Brown, A.D. 1998. Influences of natural acidity and introduced fish on faunal assemblages in California alpine lakes. Can. J. Fish. Aquat. Sci. **55**: 2478–2491.

California Division of Mines and Geology. 1958. Geologic atlas of California. California Department of Conservation, Sacramento.

Campana, S.E., and Neilsen, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. **42**: 1014–1032.

Cordes, J.F. 2001. Genetic purity of California golden trout populations in the headwater of Golden Trout Creek. Available from the web site of the University of California Genomic Research Laboratory: http://genome-lab.ucdavis.edu/People/Jan's%20Web%20Pages/CGT%20-project%20page1.htm [accessed 5 May 2002].

Cordes, J.F., Stevens, M.R., and May, B.P. 2003. Genetic status of California golden trout in the South Fork Kern River and transplanted populations. Report to the Threatened Trout Committee, California Department of Fish and Game, Sacramento.

Cortes Rui, M.V., Teixeira, A., and Pereira, C.A. 1996. Is supplemental stocking of brown trout (*Salmo trutta*) worthwhile in low productive streams? Folia Zool. **45**: 371–381.

Cowx, I.G. 1994. Stocking strategies. Fish. Manag. Ecol. **1**: 15–30.

De'ath, G., and Fabricius, K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology, **81**: 3178–3192.

Donald, D.B. 1987. Assessment of the outcome of eight decades of trout stocking in the mountain national parks, Canada. N. Am. J. Fish. Manag. **7**:545–553.

Donald, D.B., and Anderson, R.S. 1982. Importance of environment and stocking density for growth of rainbow trout in mountain lakes. Trans. Am. Fish. Soc. **111**: 675–680.

Donald, D.B., Anderson, R.S., and Maywood, D.W. 1980. Correlations between brook trout growth an environmental variables for mountain lakes in Alberta, Canada. Trans. Am. Fish. Soc. **109**: 603–610.

Elliot, J.M. 1985. Population regulation for different life-stages of migratory trout *Salmo trutta* in a Lake District stream, 1966–1983. J. Anim. Ecol. **54**: 617–638.

Elliot, J.M. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behaviour. J. Anim. Ecol. **59**: 803–818.

Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Can. J. Fish. Aquat. Sci. **53**: 1370–1381.

Grant, J.W.A., and Kramer, D.L. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. Can. J. Fish. Aquat. Sci. **47**: 1724–1737.

Graynoth, E. 1996. Determination of the age of brown and rainbow trout in a range of New Zealand lakes. Mar. Freshw. Res. **47**: 749–756.

Hall, D.L. 1991*a*. Age validation and aging methods for stunted brook trout. Trans. Am. Fish. Soc. **120**: 644–649.

Hall, D.L. 1991*b*. Growth, fecundity, and recruitment responses of stunted brook trout populations to density reduction. Doctoral dissertation, University of British Columbia, Vancouver, B.C.

Hining, K.J., West, J.L., Kulp, M.A., and Neubauer, A.D. 2000. Validation of scales and otoliths for estimating age of rainbow trout from southern Appalachian streams. N. Am. J. Fish. Manag. **20**: 978–985.

Jenkins, T.M., Jr., Diehl, S., Kratz, K.W., and Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. Ecology, **80**: 941–956.

Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. Ecology, **82**: 1247–1259.

Knapp, R.A. 1996. Nonnative trout in natural lakes of the Sierra Nevada: an analysis of their distribution and impacts on native aquatic biota. Vol. III. Centers for Water and Wildlands Resources, University of California, Davis.

Knapp, R.A., and Matthews, K.R. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv. Biol. **14**: 428–438.

Knapp, R.A., and Preisler, H.K. 1999. Is it possible to predict habitat use by spawning salmonids? A test using California golden trout (*Oncorhynchus mykiss aguabonita*). Can. J. Fish. Aquat. Sci. **56**: 1576–1584.

Knapp, R.A., Matthews, K.R., and Sarnelle, O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecol. Monogr. **71**: 401–421.

Kruse, C.G., Hubert, W.A., and Rahel, F.J. 1997. Using otoliths and scales to describe age and growth of Yellowstone cutthroat trout in a high-elevation stream system, Wyoming. Northwest Sci. **71**: 30–38.

Landry, F., Post, J.R., and Parkinson, E.A. 1999. Spatial ontogeny of lentic age-0 rainbow trout, *Oncorhynchus mykiss*: whole-lake manipulations of population size structure. Can. J. Fish. Aquat. Sci. **56**: 1916–1928.

Li, J., Cohen, Y., Schupp, D.H., and Adelman, I.R. 1996*a*. Effects of walleye stocking on population abundance and fish size. N. Am. J. Fish. Manag. **16**: 830–839.

Li, J., Cohen, Y., Schupp, D.H., and Adelman, I.R. 1996*b*. Effects of walleye stocking on year-class strength. N. Am. J. Fish. Manag. **16**: 840–850.

Matthews, K.R. 1996. Diel movement and habitat use of California golden trout in the Golden Trout Wilderness, California. Trans. Am. Fish. Soc. **125**: 78–86.

Melack, J.M., Stoddard, J.L., and Ochs, C.A. 1985. Major ion chemistry and sensitivity to acid precipitation of Sierra Nevada lakes. Water Resour. Res. **21**: 27–32.

Parsons, B.G., and Pereira, D.L. 2001. Relationship between walleye stocking and year-class strength in three Minnesota lakes. N. Am. J. Fish. Manag. **21**: 801–808.

Pister, E. 2001. Wilderness fish stocking: history and perspective. Ecosystems, **4**:279–286.

Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Schindler, D.E., Knapp, R.A., and Leavitt, P.R. 2001. Alteration of nutrient cycles and algal production resulting from fish introductions into mountain lakes. Ecosystems, **4**: 308–321.

Secor, D.H., Dean, J.M., and Laban, E.H. (*Editors*). 1992. Otolith removal and preparation for microstructural examination. Can. Spec. Publ. Fish. Aquat. Sci. No. 117.

S-Plus. 1999. User's manual. Data Analysis Products Division, Math Soft, Seattle, Wash.

Steidl, R.J., Hayes, J.P., and Schauber, E. 1997. Statistical power analysis in wildlife research. J. Wildl. Manag. **61**: 270–279.

Vollestad, L.A., Olsen, E.M., and Forseth, T. 2002. Growth-rate variation in brown trout in small neighboring streams: evidence for density-dependence? J. Fish Biol. **61**: 1513–1527.

West, C.J., and Larkin, P.A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon *Oncohynchus nerka* in Babine Lake, British Columbia, Canada. Can. J. Fish. Aquat. Sci. **44**: 712–721.