Ecological Applications, 14(3), 2004, pp. 754–772
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POPULATION ECOLOGY OF AN INVASION: EFFECTS OF BROOK TROUT ON NATIVE CUTTHROAT TROUT

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Abstract. Invasion by nonnative brook trout (*Salvelinus fontinalis*) often results in replacement of cutthroat trout (*Oncorhynchus clarki*) in the inland western United States, but the underlying mechanisms are not well understood. We conducted a four-year removal experiment to test for population-level mechanisms (i.e., changes in recruitment, survival, emigration, and immigration) promoting invasion success of brook trout and causing decline of native Colorado River cutthroat trout (*O. c. pleuriticus*). We chose 700–1200 m segments of four small mountain streams where brook trout had recently invaded cutthroat trout populations, two each at mid elevation (2500–2700 m) and high elevation (3150–3250 m), and annually removed brook trout from two streams (treatments), but not the other two (controls). We used depletion electrofishing, two-way fish weirs, and mark–recapture methods to estimate abundance, movement, and survival of trout. At mid elevation, age-0 and age-1 cutthroat trout survived at 13 times and two times higher rates on average, respectively, where brook trout were removed. At high-elevation sites, recruitment of cutthroat trout failed despite brook trout removals, apparently because of cold water temperatures. In contrast, age-2 and older cutthroat trout survived at similar rates, whether brook trout were removed or not and regardless of elevation. Summer movement by cutthroat trout was unaffected by removal of brook trout. We conclude that brook trout depress cutthroat trout populations at mid elevation through age-specific biotic interactions that reduce juvenile cutthroat trout survival, whereas populations restricted to high-elevation sites by invasion continue to decline because an abiotic factor (low temperature) causes recruitment failure. In comparison, brook trout survived at the same or higher rates than same-aged cutthroat trout. High immigration by brook trout recolonized depleted segments, and may help sustain invasions in sink habitats where environmental conditions limit recruitment. In streams similar to those we studied, eradication of brook trout is likely necessary to eliminate the threat to native cutthroat trout, but selective removal regimes that capture a high percentage of the brook trout population for least three consecutive years, repeated periodically, may permit cutthroat trout populations to persist with brook trout. To identify underlying mechanisms responsible for successful invasion by mobile, age-structured vertebrates such as stream fishes, experiments conducted at realistic spatial and temporal scales and including multiple age classes will be required.

Key words: brook trout; Colorado River cutthroat trout; demography; interspecific interactions; invasion biology; Oncorhynchus clarki pleuriticus; *population biology; recruitment; salmonids;* Salvelinus fontinalis; *species conservation; survival.*

Introduction

Invasions by nonnative organisms can harm ecosystems at many ecological levels (Parker et al. 1999), and are regarded as one of the most significant global challenges facing resource managers (Vitousek et al. 1996, Byers et al. 2002). For example, invasions by Nile perch (*Lates nilotica*), sea lamprey (*Petromyzon marinus*), and zebra mussel (*Dreissena polymorpha*) have produced major economic and social impacts (Moyle 1986, Mack et al. 2000). Moreover, aquatic invasions often cause the decline and imperilment of native species (Allan and Flecker 1993), and a general homogenization of freshwater faunas (Rahel 2000, 2002, Marchetti et al. 2001).

Invasions are fundamentally population-level phenomena (Parker 2000), but they are seldom studied as such. Success of an invasion is defined in terms of establishment and growth of a population (Vermeij 1996), which is a function of the ultimate population-level mechanisms of births and immigration (inputs B and I), and deaths and emigration (outputs D and E; Gotelli 2001). Accordingly, declines in native species can be described in similar terms. Identifying the population-level mechanisms of invasion is difficult (Holway 1999, Kiesecker et al. 2001), particularly where populations are age or stage structured (e.g., Kiesecker and Blaustein 1998, Neubert and Caswell 2000).

Manuscript received 12 December 2002; revised 7 August 2003; accepted 13 August 2003; final version received 26 September 2003. Corresponding Editor: F. J. Rahel.

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A comprehensive understanding of the population-level mechanisms underpinning invasion success and effects is necessary to design control, mitigation, and recovery plans (Parker et al. 1999, Sakai et al. 2001, Byers et al. 2002). However, comprehensive studies on the population biology of invasions are rare, and experimental evidence has only recently begun to accumulate despite its relevance to understanding invasion dynamics (Kareiva 1996). Population-level approaches have been applied to the study of plant invasions (Dayton and Primack 1999, Parker 2000) and some simple organisms (e.g., protozoans and rotifers; Miller et al. 2002). In contrast, most research on effects of invasive species has been done at the individual level, including studies on insects (Juliano 1998, Holway 1999), gastropods (Byers and Goldwasser 2001), crustaceans (Hill and Lodge 1999), amphibians (Kupferberg 1997, Kiesecker and Blaustein 1998, Kiesecker et al. 2001) and reptiles (Petren and Case 1996). Results are then scaled up to explain population-level declines in native species.

Salmonine fishes (trout, salmon, and charr) are a widely introduced group of mobile vertebrates known to negatively affect native aquatic fauna (Krueger and May 1991, Welcomme 1992, Fuller et al. 1999). For example, introductions and invasions by nonnative trout and charr have been implicated in the decline of native cutthroat trout (*Oncorhynchus clarki*) in the inland western United States (Gresswell 1988, Behnke 1992). Cutthroat trout are subject to genetic introgression with rainbow trout (*O. mykiss*) and other cutthroat trout subspecies (Allendorf and Leary 1988, Kanda et al. 2002), predation by lake trout (*Salvelinus namaycush*; Ruzycki et al. 2003), and competition with brook trout (*S. fontinalis*; Novinger 2000) and brown trout (*Salmo trutta*; Wang and White 1992). All subspecies of inland cutthroat trout are considered sensitive, threatened, or endangered, making their recovery a biological and legal imperative (Young and Harig 2001).

Brook trout invasions replace inland cutthroat trout in many streams (Dunham et al. 2003), and are viewed as a major impediment to cutthroat trout recovery (Behnke 1992, Young 1995, Harig et al. 2000). Despite this repeated pattern of replacement, the underlying population-level mechanisms that promote invasion by brook trout and harm cutthroat trout, and the life stages at which they operate, are not known. In contrast, most studies to date have been of individual-level (proximate) mechanisms, such as competition or predation, advanced to explain why brook trout replace cutthroat trout populations (Griffith 1970, Novinger 2000). These factors have been tested in small-scale laboratory or field-enclosure experiments, but results depended on the ages or sizes of individuals tested suggesting that some studies focused on life stages other than those at which effects occur (Peterson and Fausch 2003*a*). Moreover, many mechanisms driving stream salmonid populations are believed to operate at large spatial and long temporal scales (Gowan and Fausch 1996*a*, Rieman and Dunham 2000, Fausch et al. 2002), so individual-level studies at small scales may not scale up to explain population patterns (Peckarsky et al. 1997). Likewise, fishery biologists, who focus on the status of populations as their benchmark of success, are uncertain how to apply information at the individual level to management. Thus, we argue that identifying the existence and outcome of biotic interactions, measured at the population level as changes in demographic rates for each life stage, should precede more detailed tests of proximate-level mechanisms.

Our goal in this study was to measure the demography of a salmonine invasion at an appropriate scale using a field removal experiment of nonnative brook trout that recently invaded populations of native Colorado River cutthroat trout (*O. c. pleuriticus*) in streams. We identified factors promoting invasion success by brook trout and leading to declines in invaded cutthroat trout populations by estimating the population parameters (B, I, D, and E) of recruitment, survival by age class, and movement during a four-year study. Survival and abundance of cutthroat trout of each age class were compared between treatment streams where sympatric brook trout were removed vs. controls where they were not to determine at which life stages brook trout invasion caused effects. We also compared survival of brook trout and cutthroat trout to identify reasons for invader success. Movement of both species was measured to determine the relative contributions of emigration and immigration to local abundance and invasion dynamics. Integrating these results, we suggest removal strategies to help biologists managing cutthroat trout populations to counteract effects of brook trout invasions or facilitate coexistence. Finally, we discuss why population-level experiments are important to reveal underlying mechanisms of invasion by an age- or size-structured population.

Methods

Study sites

We selected four study streams in northern Colorado containing sympatric populations of nonnative brook trout and native Colorado River cutthroat trout (Table 1; Peterson 2002). They were selected from 12 streams surveyed during 1998 in which historical fish distribution data from natural resource agencies indicated long (>1 km) zones of sympatry (e.g., Colorado River Cutthroat Trout (CRCT) Task Force 1998), and were representative of headwater streams in the central Rocky Mountains where cutthroat trout populations are invaded by brook trout. Selection criteria also included no physical barriers to movement, a sufficient abundance of genetically pure cutthroat trout for mark–recapture analysis, and a remote location with low levels of angling. Based on published literature (Fausch 1989) and unpublished records from the Colorado Division of Wildlife, U.S. Bureau of Land Management, and

TABLE 1. Physical characteristics of the four study streams in north-central Colorado during 1998–2001.

Stream	Category†	Location‡	Elevation range (m)	Segment length (m)§	Mean bankfull width (m)
East Fork Parachute	mid CTL	39°34′50″ N, 107°55′31″ W	2542–2560	700–800	1.6
Little Muddy	mid TRT	39°56′59″ N, 106°02′46″ W	2658–2694	877–944	3.1
Indiana	high CTL	39°25′38″ N, 106°59′44″ W	3194–3246	950–1090	3.2
Willow	high TRT	40°28′12″ N, 105°46′48″ W	3188–3219	950–1200	2.3

† Elevation strata categories: mid elevation (mid) = 2500–2700 m, high elevation (high) = 3150–3250 m elevation. Treatment groups: treatment (TRT) = brook trout removed; control (CTL) = brook trout not removed.

‡ Location is the study segment's median north latitude and west longitude.

§ Study-segment lengths are presented as ranges because survey lengths were shorter in 1999 than in the other three years.

‖ Deep pools were defined as those with ≥30 cm residual depth (cf. Harig and Fausch 2002; residual depth = maximum depth minus maximum tail crest depth at the downstream hydraulic control forming the pool) during baseflow in 2000 based on the median residual depth of all pools in all streams. Shallow pools were those with residual depth between 18 and 29 cm.

¶ Large woody debris (LWD) is defined as woody debris pieces ≥15 cm diameter and ≥3 m long at least partially in or suspended over the bankfull channel.

Thermographs were not deployed until fall 1998, so summer 1998 temperatures were not available.

U.S. Forest Service, brook trout invasion was ongoing in all streams and had progressed since the 1970s (see Appendix A for additional information on invasion progress). Study segments either spanned the leading edge of the invasion front (Indiana Creek), or included the most recently invaded stream habitat in the headwaters of each system (East Fork Parachute, Little Muddy, and Willow creeks).

Study segments in each stream ranged from 2500 to 3250 m in elevation, and ranged from 700 to 1200 m in length (Table 1). Streams were first or second order, averaged 1.6–3.2 m wide, and had average gradients of 2.3–4.7 %, gravel and cobble substrate, and less than 0.05 m^3/s base flow. Overstory vegetation in watersheds consisted of mixed stands of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and aspen (*Populus tremuloides*). Stream habitat alternated between higher-gradient forested segments and lower-gradient meadow segments where willow (*Salix* sp.) was the dominant riparian vegetation. Beaver (*Castor canadensis*) inhabited all streams except Willow Creek.

Study design and predictions

Streams were divided into mid-elevation (2500–2700 m) and high-elevation (3150–3250 m) strata on the a priori assumption that higher sites would be colder, which might affect demographic rates. Streams were randomly assigned to treatment (TRT) or control groups (CTL) within each elevation stratum, and brook trout populations were removed annually from treatment streams. This removal experiment employed an additive design appropriate for studies of nonnative species invasions where the goal is to demonstrate the existence of interspecific biotic interactions (Fausch 1998). Removing the nonnative population is the appropriate manipulation when conducting population-level field experiments of an invasion, because introducing nonnative species is unethical and contrary to management strategies for preserving native species (Peterson and Fausch 2003*a*).

We used current knowledge about brook trout invasions to develop specific predictions to test using a removal experiment (Peterson and Fausch 2003*a*). Based on the pattern of replacement of cutthroat trout by brook trout, we hypothesized that brook trout cause cutthroat trout populations to decline by depressing recruitment, reducing survival of one or more age classes, or forcing emigration. Given this, we predicted that removing brook trout from treatment streams would increase cutthroat trout recruitment, increase survival of one or more age classes, or reduce emigration rates, relative to control streams where brook trout were not removed. Moreover, we predicted that if one or more of these events occurred, then the abundance of cutthroat trout would increase in treatment streams as a result of brook trout removal. If none of these responses occurred, then we would infer that some other factor besides biotic interactions with brook trout causes cutthroat trout populations to decline (Fausch 1998). In addition to comparing cutthroat trout demographic rates in treatment vs. control streams, we also predicted that in control streams, recruitment, survival by age class, and immigration rates of brook trout would be equal to or higher than those of cutthroat trout, thereby allowing brook trout to successfully invade and persist while forcing cutthroat trout to decline or remain at low abundance.

Temperature and physical habitat characteristics

Water temperature and physical habitat are critical factors affecting persistence of cutthroat trout populations in central Rocky Mountain streams (Harig and Fausch 2002), and may set the context for their response to brook trout invasion. Water temperature was measured (to the nearest 0.2°C; every 20–72 min) during autumn 1998 to autumn 2001 by placing a TidBit thermograph (Onset Computer Corporation, Pocassett,

TABLE 1. Extended.

No. pools/100 m‖			Mean temperature (°C)#		
Deep	Shallow	LWD per 100 m¶	May	July	Conductivity (μS)
0.4	0.4	0.3	6.3	12.4	460
2.5	4.3	24.4	3.3	12.7	101
1.4	1.6	1.8	1.3	6.6	174
0.8	1.8	0.0	0.1	6.9	17

Massachusetts, USA) in a deep pool (>30 cm) in the study segment of each stream. Habitat surveys, adapted from Harig and Fausch (2002), were conducted during fall 2000 to measure physical characteristics, such as pool width, number of deep pools, and in-stream structure (e.g., large woody debris), known to influence trout populations (Gowan and Fausch 1996*a*). Temperature and physical habitat data were subsequently used as covariates to estimate survival and electrofishing capture probabilities.

Trout sampling

Two-pass removal electrofishing was used to obtain annual estimates of trout abundance and recruitment and to remove brook trout from treatment streams. In turn, mark–recapture techniques were used to measure changes in trout survival across years (see *Model fitting*). Streams were sampled annually during 1998 to 2001 at base flow, usually in early August to late September, depending on flow and temperature. During sampling, sections of 200–400 m were enclosed with block nets (5-mm mesh) and were electrofished in an upstream direction using a backpack electrofishing unit (Mark 10, Coffelt Manufacturing, Flagstaff, Arizona, USA) operated at 30 Hz, 150–450 V pulsed DC.

All trout captured during electrofishing were anesthetized (MS-222; Argent Chemical Laboratories, Redmond, Washington, USA), measured (fork length [FL], nearest 1 mm), and weighed (nearest 0.1 g). Trout were assigned to one of three age classes (ages 0, 1, and 2 and older) based on length, using a combination of length–frequency histogram and otolith data (Kennedy et al. 2003; D. Peterson and K. Fausch, *unpublished data*). All trout returned to streams were marked using a combination of finclips, individual tags, and color batch marks based on age, species, and year, which permitted constructing capture histories of individual fish during the experiment. Age-0 (young-of-the-year) and age-1 trout were given left- and right-pelvic finclips, respectively. Age-2 and older cutthroat trout (i.e., adults; age 2+ hereafter), which were ≥85 mm FL, were marked with alphanumeric coded passive integrated transponder (PIT) tags (Biomark, Boise, Idaho, USA) in 1998 or fluorescent visual implant (VI) tags (Northwest Marine Technology, Shaw Island, Washington, USA) during 1999–2001. Use of PIT tags was discontinued because of potential tag loss by spawning females. Instead, we implanted VI tags in the opaque tissue covering the lower (dentary) jawbone of trout, which permitted putting two tags in each fish to prevent loss of capture information if one tag was lost. In control streams, adult brook trout, which were ≥110 mm, received dark green Floy Fine Fabric Anchor tags (Floy Tag, Seattle, Washington, USA). To identify subsequent tag loss, the adipose fin was excised from all trout given unique tags. Florescent elastomer (Northwest Marine Technology) was injected into fin rays or the tissue covering the dentary or maxillary bones to denote the year of initial capture. Recaptured trout that had lost tags were retagged, and juvenile trout that grew sufficiently since their previous capture to warrant tagging also were tagged.

Marked trout were released within 25 m of their initial capture location. Prior to release, trout >75 mm were held overnight in live baskets placed in deep pools, but smaller trout were released on the day of capture to avoid potential predation in live wells. Cumulative handling mortality, the sum of electrofishing, measuring, tagging, and overnight mortality, was 9% for cutthroat trout (n = 2904) and 3% for brook trout (n = 5778). Overnight mortality was low, only 2.1% for cutthroat trout and 0.4% for brook trout, indicating little latent mortality after fish recovered from anesthesia. Survival estimates were based only on live releases, so they remain unbiased with respect to this mortality. Brook trout in treatment streams were euthanized with an overdose of anesthetic (MS-222; Animal Care and Use Committee protocol 98–067A, Colorado State University, Fort Collins, Colorado, USA), preserved in 10% formalin, and saved for further analysis.

Fish movement

Fish weirs were used to measure movement of trout into and out of study segments of three streams during 1999–2001 (all except East Fork Parachute Creek, the mid-elevation control stream). Weirs consisted of a two-way trap box with side panels covered with 6-mm black plastic mesh that funneled trout into the traps (see Gowan and Fausch 1996*b* for similar design). Trap boxes consisted of a 0.9 m long × 0.8 m wide × 0.6 m tall frame of PVC pipe covered with the same plastic mesh, and were divided longitudinally to separate fish moving upstream from those moving down. Velocity refuges (large cobble) were provided for trout in each side. Trap openings were 6 cm wide, and a 20 cm wide

board was placed inside the trap box 10 cm from the entrance to obscure the opening from trout already inside the trap. Tests in 1999 showed that trout could exit traps through the opening. Therefore, beginning in 2000 entrances were constricted into a 5 × 8 cm opening and through an angled section of plastic rain gutter fitted with a 10-cm length of flexible nylon stocking, which collapsed after trout passed through it and obscured the exit.

Weirs were placed at the upstream and downstream margins of the study segments in the three streams, with additional weirs placed inside or outside the study area. Weirs were secured using steel posts, and a 25-cm mesh skirt extending from the bottom of the apparatus was buried in stream gravel to prevent trout from passing beneath the weir. Snorkeling was used to confirm that the weir was closed to all trout >75 mm FL, which are primarily age 1 and older. Weirs were typically installed when snowmelt runoff subsided in mid June and removed in early October when streams froze. They could be monitored only from summer to fall because sites could not be reached during winter. Weirs were visited every other day, and captured trout were measured and weighed as above and given batch marks to indicate weir location and direction of travel. Fish were marked using various colors of nontoxic Liquitex acrylic paint (Binney and Smith, Easton, Pennsylvania, USA) injected into postorbital adipose tissue using a sterile insulin syringe. Larger trout were given the same tags and adipose finclips used during electrofishing if they met the same size criteria described above. After recovery from anesthesia, all cutthroat trout and brook trout in the control stream were released in the direction they were traveling, at least 10 m away from the weir. In treatment streams, brook trout entering the study segment were euthanized to maintain the experimental treatment, but those leaving the segment were released. Weir entrances were closed during electrofishing surveys. Capture data from weirs at the study segment boundaries were analyzed to determine how emigration and immigration of cutthroat trout varied between treatment and control streams. Movement direction by brook trout could be analyzed only in the control stream that had weirs (Indiana Creek), because in treatment streams their source population on one side of the weir was being removed.

Model Fitting

Models used to estimate abundance and survival

Survival and abundance estimates were calculated for three age classes of each species (age 0, age 1, and age 2+). We analyzed trout capture histories with maximum-likelihood estimators using two sets of multinomial models in the program MARK (White and Burnham 1999). This software package incorporates a linear modeling framework (i.e., design matrix) which allows the user to construct models that evaluate how given factors influence the estimated parameters. First, data for cutthroat trout, and for brook trout in control streams, were analyzed using Pollock's robust design with Huggins' population estimator. The robust design model is a combination of a demographically open live-recapture model (Cormak-Jolly-Seber [CJS]) and a closed-capture model (Kendall et al. 1995). Survival is estimated across the primary sampling periods (between years; i.e., 1 = 1998–1999, 2 = 1999–2000, and 3 = 2000–2001), whereas population size is estimated during secondary sampling sessions when the population is effectively closed (during electrofishing surveys; i.e., 1998, 1999, 2000, and 2001). Huggins' population estimator has better statistical properties than other population estimators when the number of captures is low because it is conditional on only the animals captured (Huggins 1991).

In this analysis, the robust design model was used to estimate apparent survival (ϕ), abundance (N), and electrofishing capture probabilities (p). Because trout were able to move into and out of the study areas during winter and spring, we were able to model apparent survival (ϕ) whereby a marked fish that left the study area and is not at risk of capture is statistically equivalent to a fish that died. Movement and recapture parameters were fixed at zero because movement was explicitly measured (see *Methods: Fish movement*) and no recaptures were possible during secondary sampling sessions because we conducted removal electrofishing. For a given species and stream, the estimated abundance of age groups 1 and 2+ during 1999–2001 represents a sum of the estimated abundance of different cohorts derived using a common electrofishing capture probability. For example, total abundance of age-2+ brook trout in the mid-elevation control stream during 2000 is composed of the sum of the abundances of individuals initially captured as (a) age 2+ in 2000, (b) age 1 in 1999, and (c) age 0 in 1998. Since abundance of these component groups in 2000 was estimated using a common electrofishing capture probability, the individual abundance estimates are not independent and covariances among the abundance estimates must be considered to properly estimate the variance of the sum. A large-sample approximation of the covariance between the component abundance estimates was derived using the delta method (Seber 1982) as

$$\widehat{\mathrm{cov}}(\hat{N}_1\hat{N}_2) = \frac{\hat{N}_1\hat{N}_2\widehat{\mathrm{var}}(\hat{p}^*)}{(\hat{p}^*)^2}$$

where $\hat{N}_1$ and $\hat{N}_2$ are the abundance estimates and $\hat{p}^*$ is the estimated common capture probability (K. Burnham, *personal communication*). Thus, the variance of the sum of these estimates becomes the sum of the variance–covariance matrix.

A second model, the generalized removal estimator for closed captures (White et al. 1982), was used to estimate abundance of brook trout in treatment streams at the time of removal. In addition, in the mid-elevation

treatment stream single-pass electrofishing was conducted in early July during 1999 to 2001 to remove brook trout before emergence of age-0 cutthroat trout (hereafter, additional electrofishing). This additional removal reinforced the treatment effect in this stream. Additional electrofishing was not done in the high-elevation treatment stream because annual two-pass surveys were conducted in early August as soon as streamflow permitted efficient electrofishing.

Model selection criteria

Data for brook trout and cutthroat trout were analyzed separately. First, a general linear model including effects of treatment group (treatment vs. control), age (ages classes 0, 1, and 2+), time (year), elevation stratum (mid vs. high), and their interactions was fit to the data. This ''global model'' included all the main factors and interactions of interest, and thus was the most highly parameterized model constructed in the design matrix of the program MARK. The global model should contain all relevant factors and probable causal mechanisms based on the study design, and can serve as a baseline for model selection and inference (Burnham and Anderson 2002). Subsequently, a series of reduced candidate models were fit to test a priori hypotheses about how the variables (e.g., treatment, age, etc.) influenced survival and electrofishing capture probabilities. Environmental and biological covariates, such as pool density, large woody debris density, water temperature, and competitor density, were included in some reduced models. Covariates for individual trout, such as body length, were not used because the data included batch-marked (juvenile) trout as well as individually tagged (adult) trout. Model structure notation follows Lebreton et al. (1992), with modifications, where ''+'' denotes factors which are additive in the logit scale, and ''×'' represents an interaction.

One or more best-approximating models were selected for inference from among candidate models using Akaike's Information Criterion corrected for small-sample bias (AIC_c; Burnham and Anderson 2002). Models were ranked and compared using ΔAIC_c and AIC_c weights, where ΔAIC_c estimates the relative difference between the top ranked model and each other model, and AIC_c weights measure the weight of evidence in favor of a model given the data. When the top-ranked model contributed at least 75% of the total AIC_c weight and was at least twice as likely as the next best model, parameter estimates and inferences were based on this single model. However, in all other cases parameters and associated variances were calculated as a weighted average across models based on AIC_c weights, and were used to make inferences (i.e., model averaging; Burnham and Anderson 2002). Modeling strategy for the robust design followed Lebreton et al. (1992), whereby electrofishing capture probabilities were initially modeled with survival held constant, then the best model structure of capture probabilities was used to model survival. In treatment streams where brook trout were removed, we modeled only electrofishing capture probabilities because survival was zero.

Model selection results

Cutthroat trout.—We fit 66 candidate models to estimate apparent survival (ϕ), after selecting a model structure for electrofishing capture probabilities (Lebreton et al. 1992; see Peterson 2002 for details). Variables included treatment group, age, time, trends (T = linear trend in the logit scale), elevation stratum, and body size. Body size may affect survival independent of age, so fish were divided into small vs. large groups at 71 mm. The small group included both age-0 cutthroat trout in mid-elevation streams and age-1 trout in high-elevation streams. Covariates, alone or in combination with other factors in models, included (a) temperature effects (mean July temperature, sum of mean daily temperature >0°C from May through August [summer degree days], and annual degree days; and (b) biotic interaction effects (density of same-age or same-size brook trout in a given stream).

Model selection indicated that survival of cutthroat trout varied by age, time, and treatment, but the effect of treatment differed between the two elevation strata (i.e., the treatment × elevation interaction was included in all the top models, whereas neither treatment nor elevation alone were). The data supported a complex model structure, and seven models were selected for inference (Table 2). Models 1 and 2 were considered closely competing models and contributed >80% of the AIC_c weight, but model averaging was used to derive all parameter estimates. Models explicitly testing the effect of brook trout competitor density ranked very low and do not appear in Table 2. The interaction of treatment with elevation was likely caused by cold water temperature depressing or eliminating cutthroat trout recruitment in the high elevation streams (see *Results*), so the main comparisons of survival for each age class were made within each elevation stratum. For each elevation, we contrasted survival differences between treatment and control streams by taking simple averages of model-averaged parameter estimates across years, calculating differences, using the delta method to derive variance estimates (Seber 1982, Burnham et al. 1987), and comparing overlap of 95% confidence intervals.

Brook trout in control streams.—We fit 41 candidate models to estimate apparent survival, after selecting an appropriate model structure for electrofishing capture probabilities. Variables and covariates were the same as for cutthroat trout. Survival of brook trout in control streams also varied by age, time, and elevation (Table 2). A single model (ϕ[age × time, age × elev, elev × time]) was nearly six times more likely than the next best model and was used for inference. Survival of brook trout and cutthroat trout were compared using

TABLE 2. Multinomial models used for inference of apparent survival (ϕ) and abundance (N) for cutthroat trout in all streams, and brook trout in control (CTL) streams, under Pollock's robust design with Huggins's population estimator. For cutthroat trout, model averaging was used to estimate parameters used for inference.

Model	Hypothesized model structure†	K‡	AIC_c	ΔAIC_c	w_i	Deviance	Description of survival probabilities
Cutthroat trout							
1	ϕ(age × t × TG × elev)	55	5282.78	0.00	0.478	18 827.6	Survival by age varies by time, treatment group, and elevation.
2	ϕ(age × t, age × TG × elev, TG × elev × t)	53	5283.52	0.74	0.330	18 832.5	Survival by age varies by time; survival by age varies by treatment group and elevation; survival by treatment group varies by elevation and time.
3	ϕ(age × TG × elev, TG × elev × t)	48	5285.84	3.06	0.103	18 845.3	Survival by age varies by treatment group and elevation; survival by treatment group varies by elevation and time.
4	$\phi_{JUVENILES}$(t × TG × elev) ϕ_{ADULTS}(TG × elev)	44	5286.97	4.19	0.059	18 854.7	Juvenile (ages 0 and 1 combined) survival varies by time, treatment group, and elevation; adult (age-2+) survival varies by treatment group and elevation.
5	ϕ(age × t × TG × elev) p(age × t × TG × elev)	62	5288.94	6.16	0.022	18 819.1	''Global model'' (all possible interactions of primary factors) for both survival and electrofishing capture probabilities.
6	ϕ(age × t, TG × elev × t)	47	5290.92	8.14	0.008	18 852.4	Survival by age varies by time; survival by treatment group varies by elevation and time.
7	$\phi_{JUVENILES}$(t × TG × elev) ϕ_{ADULTS}(t)	43	5304.02	21.24	0.00001	18 873.8	Juvenile (ages 0 and 1 combined) survival varies by time, treatment group, and elevation; adult (age-2+) survival varies by time.
Brook trout							
1	ϕ(age × t, age × elev, elev × t)	32	11 747.44	0.00	0.819§	66 013.8	Survival by age varies by time; survival by age varies by elevation; survival by elevation varies by time.

Notes: Factors are age (ages 0, 1, and 2+), time (t = year), treatment group (TG), and elevation stratum (elev). Multiplier ×'s denote interactions between factors. Separate abundance estimates (N) for each combination of age, time, treatment group, and elevation (i.e., N [age × t × TG × elev]) were generated using each model. Akaike's Information Criterion, corrected for small sample size (AIC_c) based on the log likelihood and number of parameters (K), was used to select models for inference (see *Model fitting*: *Model selection criteria*). The difference in AIC_c between the highest ranking and subsequent models (ΔAIC_c) and AIC_c weights (w_i) provide an index of relative support for each model. Deviance is defined as the difference in −2log(likelihood model|data) of the current model and −2log(likelihood model|data) of the saturated model, which has the number of parameters equal to the sample size.

† With the exception of cutthroat trout model 5, models have the same structure for electrofishing capture probabilities (p[age × t, age × TG × elev, TG × elev × t]) but varied in their model structure for survival. Cutthroat trout model 5 is the ''global model,'' which included all possible interactions of the primary factors for both survival and electrofishing capture probabilities.

‡ Parameter counts (K) include only survival and electrofishing capture probabilities. Abundance parameters are not counted under the Huggins' population size estimator because it is a ''derived'' parameter calculated outside of the likelihood framework.

§ Model 1 was almost six times more likely than the next best model, so it was used for inference.

the same method used to compare cutthroat trout survival across treatment groups.

Brook trout in treatment streams.—We fit 14 candidate models using primary factors (age, time, and elevation) to select a model structure for electrofishing capture probabilities from which abundance was estimated (Table 3). Ten models had some degree of support (i.e., AIC_c weight > 0), but age was clearly the single most important factor predicting capture probability and appeared in all 10 models. Model averaging was used to derive parameter estimates based on the top 10 models.

TABLE 3. Multinomial models used for inference of abundance (N) of brook trout in treatment (TRT) streams using the generalized removal estimator for closed captures. Model averaging was used to account for model uncertainty and to calculate parameter estimates.

Model	Hypothesized model structure for electrofishing capture probabilities	K	AIC_c	ΔAIC_c	w_i	Deviance	Description of electrofishing capture probabilities
1	p(age)	26	−12 765.38	0.00	0.453	98.1	Capture varies by age.
2	p(age + elev)	27	−12 764.46	0.92	0.286	97.0	Capture by age has constant (additive) elevation effect.
3	p(age × elev)	29	−12 762.66	2.72	0.116	94.7	Capture by age varies by elevation.
4	p(age + t)	29	−12 761.19	4.19	0.056	96.2	Capture by age has constant time effect.
5	p(age × elev + t)	31	−12 760.16	5.22	0.033	93.1	Capture by age varies by elevation; constant time effect.
6	p(age + t + elev)	30	−12 759.00	5.39	0.031	95.3	Capture by age has constant time and elevation effects.
7	p(elev × t + age)	33	−12 758.50	6.88	0.015	90.7	Capture by elevation varies by time; age effect is constant.
8	p(age × t)	35	−12 756.70	8.64	0.006	88.3	Capture by age varies by time.
9	p(age × elev, elev × t)	35	−12 756.08	9.30	0.004	89.0	Capture by age varies by elevation; capture by elevation varies by time.
10	p(age × t × elev)	46	−12 748.00	16.39	0.0001	73.3	Capture by age varies by time and elevation (all interactions of primary factors).

Notes: Factors and model-selection criteria are as in Table 2. A ''+'' denotes factors with a constant (additive) effect in the logit scale. For example, in model 2, capture probabilities differ both by age (ages 0, 1, and 2+) and elevation (mid-elevation and high-elevation treatment streams) such that the difference between ages is constant across the two elevation strata. Abundance estimates (N) for all models included separate values for each combination of age, time, and elevation (i.e., N(age × t × elev), and are based on the electrofishing capture probabilities (p) for the given model and the number of individuals captured (n), such that $\hat{N} = n/p$. Parameter counts (K) include both electrofishing capture probabilities and abundance estimates.

RESULTS

Trout captures and population structure

We used the 11 241 trout captured during multipass electrofishing during 1998–2001 to estimate survival and abundance. Brook trout (n = 6425 in controls, n = 1983 in treatments) were more abundant that cutthroat trout (n = 2833), and represented nearly 75% of the trout captured. We removed an additional 606 brook trout from the mid-elevation treatment stream by additional electrofishing in July during 1999–2001, but these fish were not included in calculating the abundance estimates. Electrofishing capture probabilities were high ($\bar{p}$ = 0.68, range 0.25–0.97), and similar for both species (cutthroat $\bar{p}$ = 0.66, brook $\bar{p}$ = 0.70; see Appendix B). Survey lengths were shorter in 1999 than in the other three years because expansion of beaver pond habit at one stream made electrofishing unsafe and because of insufficient manpower to complete the most upstream 70–200 m in the other streams. Consequently, trout captured at locations during 1998 that were not resampled in 1999 were excluded from the data to avoid a downward bias in survival estimates. Abundances are presented as densities to adjust for differences in survey lengths among years.

Trout population structure differed between mid- and high-elevation streams. All age classes of trout (e.g., ages 0, 1, and 2+) were present in mid-elevation streams each year, but juveniles were often absent from high-elevation streams. Age-0 and -1 cutthroat trout were never captured during electrofishing surveys in the high-elevation treatment stream (Willow Creek). Age-0 cutthroat trout were never captured in the high-elevation control stream (Indiana Creek), and age-0 brook trout and age-1 trout of both species were found only in low numbers.

Juvenile brook trout were larger than cutthroat trout of the same age in a given stream and year, as indicated by data from the first survey in 1998 (Table 4). The magnitude of this difference varied by stream and year, but overall, age-0 and age-1 brook trout averaged 21.9 and 28.8 mm larger than cutthroat trout, respectively.

Trout survival

Age-0 cutthroat trout in the mid-elevation treatment stream survived at a rate 13 times greater on average than age-0 cutthroat trout in the mid-elevation control stream (Fig. 1A, Table 5; mean difference [95% confidence limits; CL]: 0.294 [0.208, 0.380]). Moreover, in the mid-elevation control stream, age-0 brook trout survived at a rate 10 times greater than age-0 cutthroat trout (mean difference: 0.210 [0.185, 0.236]), although survival rate of both species declined through time. Only two survival estimates for age-0 cutthroat trout were possible in the mid-elevation treatment stream because this age class was inadvertently not marked in 1998. No estimates of age-0 survival were possible for

TABLE 4. Fork length (mean, with 1 SE in parentheses) by age class of trout captured during 1998 electrofishing surveys.

Stream (category)	Survey dates	Fork length (mm)					
		Cutthroat trout age class			Brook trout age class		
		0	1	2+	0	1	2+
East Fork Parachute (mid CTL)	24–27 Sep	68.5 (0.48)	128.4 (1.09)	197.2 (4.23)	87.1 (0.39)	142.4 (0.58)	193.4 (0.87)
Little Muddy (mid TRT)	10–13 Sep	42.3 (0.43)	77.3 (0.53)	130.1 (2.12)	64.8 (0.41)	116.9 (0.85)	174.3 (1.83)
Indiana (high CTL)	20–23, 29 Aug	†	56.2 (0.58)	188.7 (5.61)	41.3 (1.6)‡	···	244.0 (4.10)
Willow (high TRT)	17–20 Sep	†	†	230.0 (8.12)	44.5 (0.48)	85.2 (1.49)	201.2 (1.41)

Notes: Ellipses (···) indicate that no trout were captured in 1998. Length data from 1998 are presented because brook trout lengths in treatment streams from 1999–2001 were potentially influenced by removals in prior years. Age-2+ trout are age 2 and older.

† No individuals of this age class were ever captured during electrofishing surveys from 1998–2001, although a few age-0 trout were captured in October some years. Recruitment to age 1 was absent (Willow Creek) or low (Indiana Creek) every year.

‡ Sample size was small ($n = 4$) for this estimate.

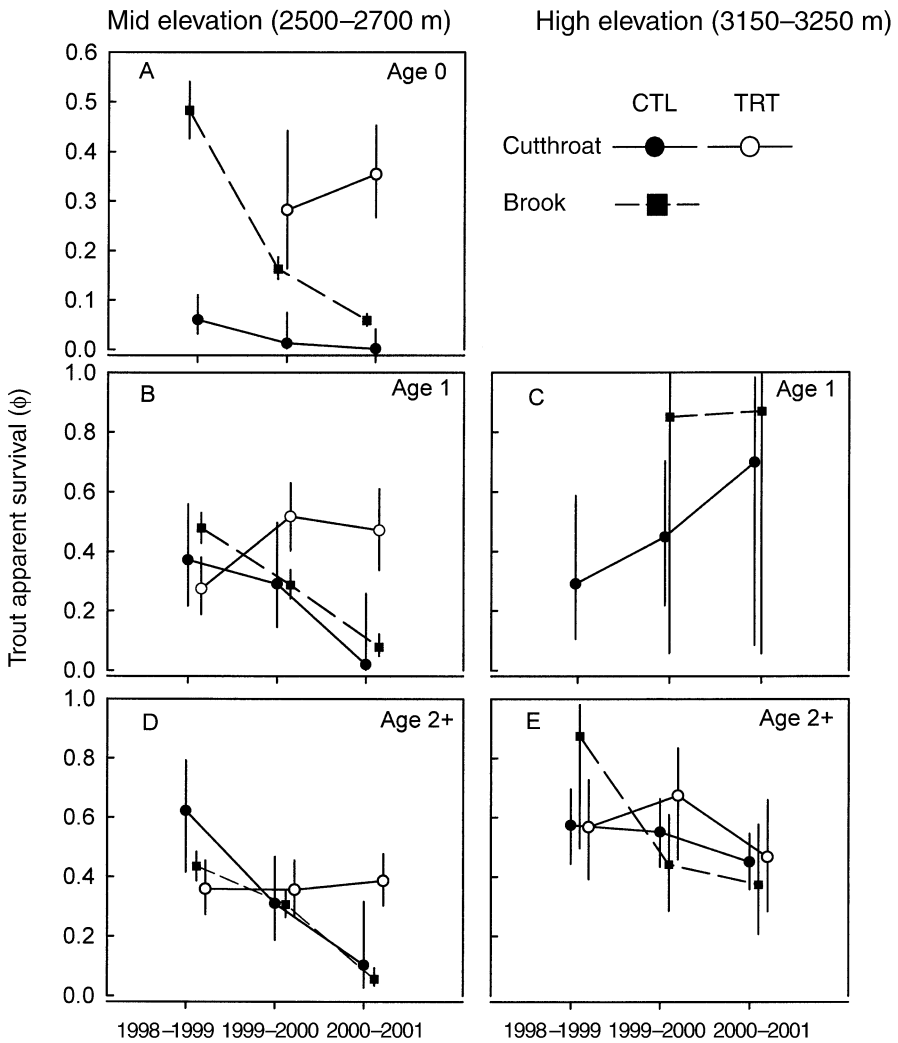

FIG. 1. Apparent survival of cutthroat trout and brook trout in study streams during 1998–2001. Key to abbreviations: CTL = control stream, TRT = treatment stream where brook trout were removed, age 2+ = trout age 2 and older. No age-0 cutthroat trout were captured or marked in high-elevation streams, and no estimates were possible for brook trout in treatment streams. Error bars show 95% confidence intervals.

TABLE 5. Apparent survival, ϕ (mean with 1 SE in parentheses), of trout in four study streams in northern Colorado from 1998 to 2001.

	Cutthroat trout				Brook trout	
Age class (years)	Mid TRT (Little Muddy)	Mid CTL (East Fork Parachute)	High TRT (Willow)	High CTL (Indiana)	Mid CTL (East Fork Parachute)	High CTL (Indiana)
0	0.318 (0.0433)†	0.0247 (0.0075)	‡	‡	0.235 (0.0107)	‡
1	0.421 (0.0349)	0.227 (0.0442)	‡	‡	0.281 (0.0135)	‡
2+	0.367 (0.0269)	0.345 (0.0483)	0.569 (0.0556)	0.525 (0.0332)	0.266 (0.0121)	0.563 (0.0527)

Notes: Table values are the means of three interannual survival estimates across years using model-averaged values (cutthroat trout) or values from a single model (brook trout) from each year. Key to abbreviations: Mid = mid elevation (2500–2700 m), High = high elevation (3150–3250 m), CTL = control stream (brook trout populations not manipulated), TRT = treatment stream (i.e., brook trout removed). Variances of means for maximum-likelihood estimators were calculated using the formula for sampling variance of the average where $\hat{\text{var}}(\bar{\hat{\phi}}) = \Sigma_{i=1,j=1}^{n}\hat{\text{cov}}(\hat{\phi}_{ij})/n^2$ (e.g., Burnham et al. 1987), whereby the variance of the mean is the sum of the variance–covariance matrix for the parameters divided by the square of the sample size. When calculating the mean values for a given species, interannual survival estimates for age-0 and age-1 trout within a stream were treated as independent (covariance = 0) because individuals moved to the next age class at the end of the interval. In contrast, interannual survival estimates for age-2+ trout within a stream were not independent (covariance $\neq$ 0) because individuals could ''recycle'' within this terminal age class if they survived.

† This value is the mean of two years of data (n = 2). Only two survival estimates for age-0 cutthroat trout were possible in the mid-elevation treatment stream because this age class was inadvertently not marked in 1998.

‡ No estimate was made because of no or sparse data.

either species at high-elevation sites because either few or no age-0 trout were produced or they emerged in late fall after surveys were completed.

Overall, age-1 cutthroat trout in the mid-elevation treatment stream survived at a rate about twice that of age-1 cutthroat trout in the mid-elevation control stream (Fig. 1B; Table 5; mean difference: 0.194 [0.083, 0.304]), primarily because of the difference during 2000–2001. However, in the mid-elevation control stream, age-1 cutthroat trout survived at a similar rate to age-1 brook trout across all years (mean difference: 0.054 [−0.037, 0.144]), and survival of both species decreased as brook trout density increased (Fig. 1B). In the high-elevation control stream, low abundance of age-1 trout resulted in large confidence intervals for survival estimates, making comparison difficult (Fig. 1C), and no age-1 cutthroat trout were captured in the high-elevation treatment stream.

Age-2+ cutthroat trout survived at similar rates in treatment and control streams at each elevation (Fig. 1D and 1E, Table 5; mean differences: mid elevation, 0.022 [−0.086, 0.131]; high elevation, 0.044 [−0.083, 0.171]), and survived at a similar rate to age-2+ brook trout in control streams (mean differences: mid elevation, 0.079 [−0.019, 0.176]; high elevation, −0.038 [−0.16, 0.083]). Age-2+ survival of both species remained relatively constant over time in three streams, but declined in the mid-elevation control stream as trout density increased. Overall, adult trout survival was greater in high- than in mid-elevation streams (mean differences: cutthroat trout, 0.191 [0.108, 0.275]; brook trout, 0.297 [0.191, 0.403]), probably due to greater trout longevity in populations at cold, high-elevation sites (Kennedy et al. 2003).

Trout abundance

Electrofishing removal was effective at reducing recruitment and abundance of juvenile brook trout in treatment streams, especially at the mid-elevation site, but adult brook trout were more difficult to control. Given the average capture probability (brook $\bar{p} = 0.70$), more than 90% of brook trout were estimated to have been removed during each survey by two electrofishing passes. Brook trout recruitment was reduced to very low levels after two consecutive years of removals in both treatment streams, and remained so in the mid-elevation treatment stream (Fig. 2A and 2B). Although some recruitment was expected in treatment streams because adult brook trout may have immigrated and spawned after removal treatments each year, the increase in brook trout recruitment in the high-elevation treatment stream during 2001 was unexpected. Warm water temperatures during autumn 2000 and spring–summer 2001 probably caused high overwinter egg survival, earlier fry emergence, and higher fry survival.

Relatively high abundance of adult brook trout in both treatment streams each year indicated that substantial immigration occurred between late fall, after electrofishing removal was completed and the weirs were removed, and the following summer when weirs were installed. Adult brook trout density in the high-elevation treatment stream was reduced to ~40% of its initial level during 1999–2001 (Fig. 2F), but was not markedly altered in the mid-elevation treatment stream (Fig. 2E). In fact, adult brook trout density in the latter increased during 1999–2001 if fish captured during additional electrofishing in July are added to the two-pass abundance estimate in September.

Age-0 cutthroat trout abundance generally increased over time in the mid-elevation treatment stream, but declined in the mid-elevation control stream (Fig. 3A). The effect of removing brook trout on recruitment of age-0 cutthroat trout was delayed two years after the pretreatment sample in 1998, most likely because eggs already laid by brook trout before their removal in fall

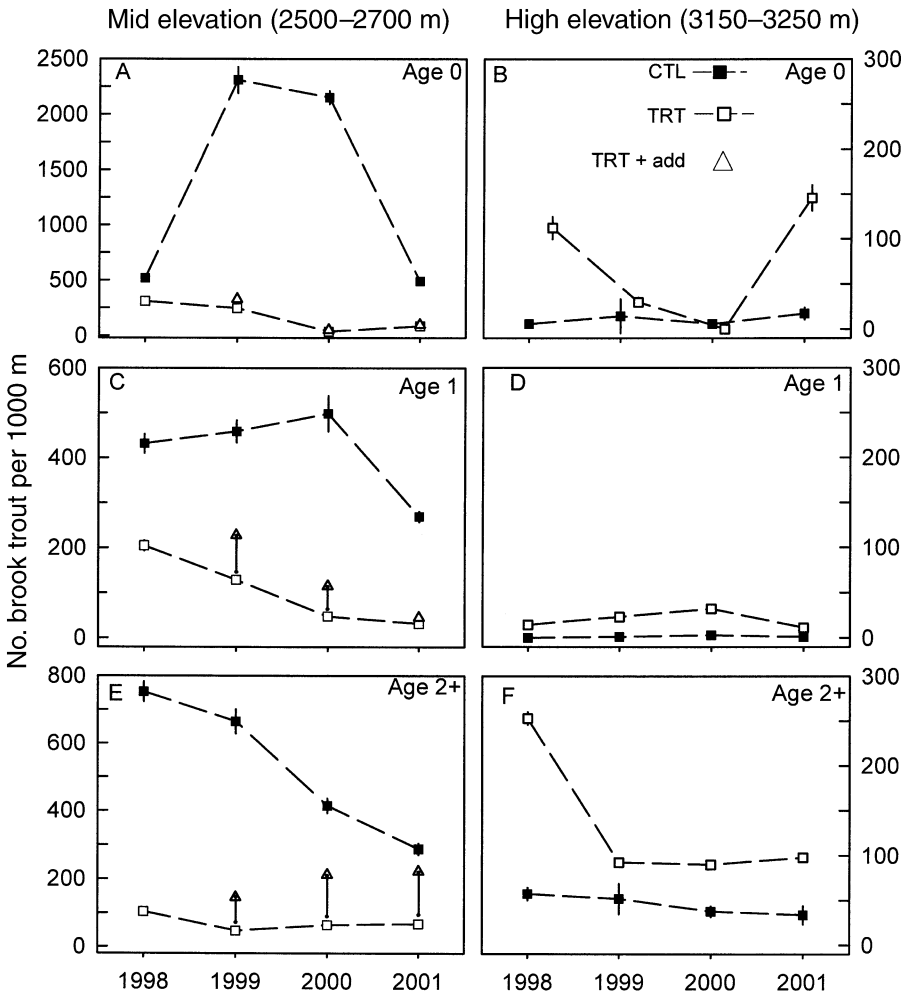

FIG. 2. Density of brook trout in study streams during 1998–2001. Abundance estimates from 1998 are pretreatment values. Abbreviations are as in Fig. 1, and error bars show 95% confidence intervals. The age-1 estimates in the high-elevation control stream (D) are the actual number captured because of low numbers. The scale of *y*-axes differs between mid- and high-elevation streams. Open triangles on stalks above density estimates in the mid-elevation treatment stream (TRT + add) include the additional brook trout removed during July electrofishing.

1998 produced fry that affected cutthroat trout abundance in summer 1999. Thus, in the mid-elevation streams, the mean difference in density of age-0 cutthroat trout was greater during 2000 and 2001 compared to 1998 and 1999, indicating a treatment effect on density (one-tailed t test; $t = 4.55$, df $= 2$, $P = 0.02$). Age-0 cutthroat trout were much less abundant than age-0 brook trout in the mid-elevation control stream (cf. Figs. 2A and 3A).

Age-1 cutthroat trout abundance in the mid-elevation treatment stream increased markedly in 2001, in contrast to the mid-elevation control stream where abundance was low and declined through time (Fig. 3B). The effect of the brook trout removal treatment was delayed a year longer than for age-0 cutthroat trout, because the strong year class produced in 2000 did not recruit to age 1 until 2001. When this contrast was made, the difference in density of age-1 cutthroat trout between the two streams was greater during 2001 than in 1998–2000 (one-tailed t test; $t = 6.51$, df $= 2$, $P = 0.01$). However, in the high-elevation streams, age-1 cutthroat trout were absent (treatment) or present in low numbers (control), so no such comparisons were possible (Fig. 3C). Age-1 cutthroat trout were much less abundant than age-1 brook trout in the mid-elevation control stream (cf. Figs. 2C and 3B), but more abundant in the high-elevation control stream (Figs. 2D and 3C).

Abundance of age-2+ cutthroat trout did not increase in treatment streams and declined in all but the high-elevation control stream (Fig. 3D and 3E), indicating no effect of the treatment on adult cutthroat trout abundance. Adult brook trout were much more abundant than adult cutthroat trout in the mid-elevation control stream, but not in the high-elevation control stream (Figs. 2E, 2F, 3D, and 3E).

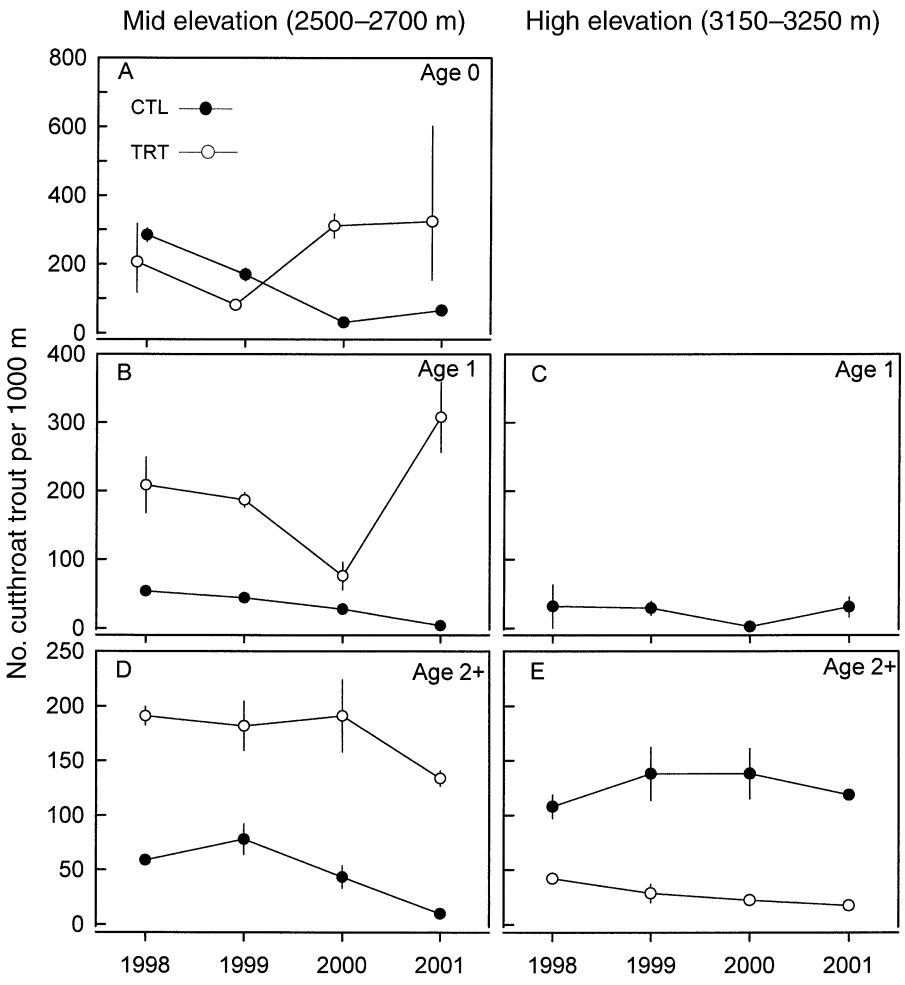

FIG. 3. Density of cutthroat trout in study streams during 1998–2001. Abundance estimates from 1998 are pretreatment values. Abbreviations are as in Figs. 1 and 2, and error bars show 95% confidence intervals. No age-0 cutthroat trout were captured or marked during fall electrofishing surveys in high-elevation streams.

Cutthroat trout survival related to brook trout density

Survival of juvenile cutthroat trout was inversely related to density of brook trout, the only other fish sympatric with cutthroat trout in these streams. Brook trout density varied widely among streams, so we plotted survival of cutthroat trout of a given age class against the estimated density of the same age or size class of brook trout during the interval over which survival was estimated (Fig. 4). Graphs revealed a negative relationship between survival of juvenile (age-0 and -1) cutthroat trout and juvenile brook trout density, but no such relationship for age-2+ cutthroat trout and age-2+ brook trout.

Movement through weirs

A total of 965 trout were captured in weirs at upstream and downstream ends of study areas in three streams from June through October of 1999–2001 (Fig. 5). Trout as small as 45 mm FL were captured, but most were >75 mm. Over 70% of all trout were captured in the mid-elevation treatment stream, where weirs were operated longer each year (range 100–123 d) than in the high-elevation sites (treatment [TRT] 62–74 d, control [CTL] 69–98 d), because streamflow permitted earlier installation. Brook trout (n = 647) were captured more frequently than cutthroat trout (n = 318).

Brook trout removal did not appear to affect the summer movement of cutthroat trout. Moreover, cutthroat trout in streams with weirs showed only a slight tendency toward net emigration. Logistic regression (PROC GENMOD; SAS 2001) was used to estimate the proportion of trout captured at weirs that were moving into or out of the study segments. The effect of brook trout removal (i.e., treatment effect) on cutthroat

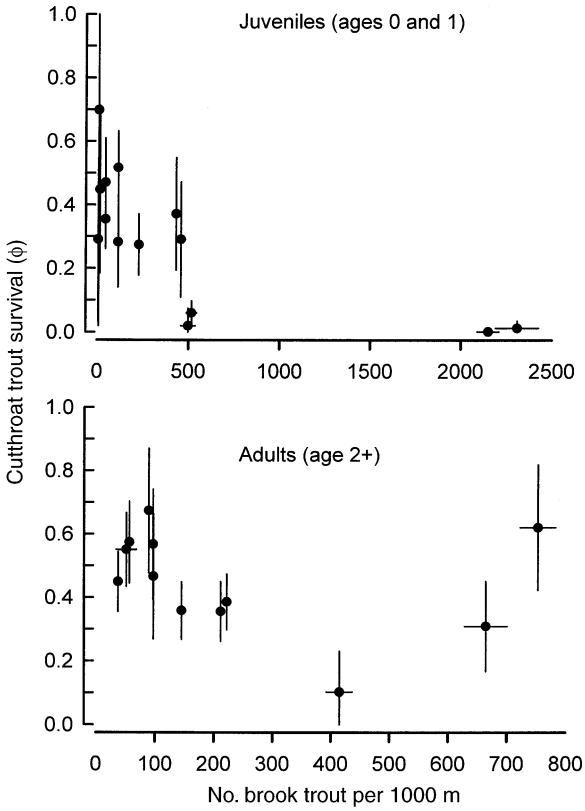

FIG. 4. Survival of cutthroat trout during 1998–2001 at different densities of nonnative brook trout. Cutthroat trout survival by age or size class was matched to brook trout density during the appropriate time interval. For example, in control streams, age-0 brook trout density in fall 1998 was paired with age-0 cutthroat trout survival during fall 1998–fall 1999. Error bars show 95% confidence intervals.

trout emigration was determined by fitting three logistic regression models that included an intercept parameter plus (a) treatment group, (b) treatment group + year, and (c) treatment group × year interaction. The model-averaged 95% confidence interval for the treatment parameter included zero, and these models estimated that 60% of cutthroat trout captured at weirs in treatment streams were emigrants, compared to 56% in the control stream (the 95% confidence interval for the difference was from −7% to 15%). Thus, there was no evidence for a difference in cutthroat trout emigration rates between treatment and control streams. The magnitude of net movement (i.e., net emigration or immigration) by cutthroat trout was determined by fitting five models, which included the three models used to measure the treatment effect plus two additional models: (a) intercept only and (b) intercept + year. Model-averaged estimates showed that about 58% of cutthroat trout captured at weirs in all streams emigrated during summer and 42% immigrated, but the lower 95% confidence level on emigration overlapped 50% in five of nine cases and the other four reached 51%, indicating no or very little net emigration. Moreover, of 76 individually tagged cutthroat trout that emigrated through weirs during 1999–2001, 22% returned to the study area the same year, 21% occupied the study area the following year, and 3% did both.

In the three streams with weirs, many more brook trout attempted to move into the study segments than leave them (Fig. 5). In the high-elevation control stream, logistic regression analysis of captures (n = 26) using two models (intercept only and intercept plus year) indicated that brook trout had a tendency to immigrate. Estimates based on model averaging showed that 67–86% of brook trout were immigrants during 1999–2001, and 95% confidence levels did not overlap 50% in 2000 or 2001. In treatment streams, statistical comparison of movement direction is biased because all immigrants (n = 500) were euthanized to maintain the treatment.

DISCUSSION

Age-specific biotic interactions as a mechanism causing replacement of cutthroat trout

Results from this four-year field experiment provide new insight into the decades-long controversy about

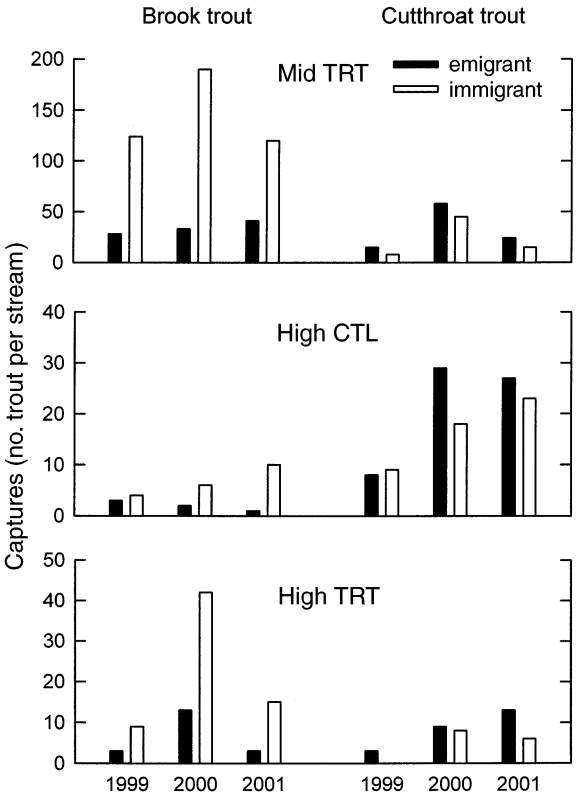

FIG. 5. Trout movement in three study streams during June–September of 1999–2001. Values are captures at two-way weirs of trout entering (immigrant) or leaving (emigrant) the study segments. Abbreviations are as in Figs. 1–3. Immigrant brook trout in treatment streams were removed to maintain the treatment, but emigrant brook trout were allowed to emigrate.

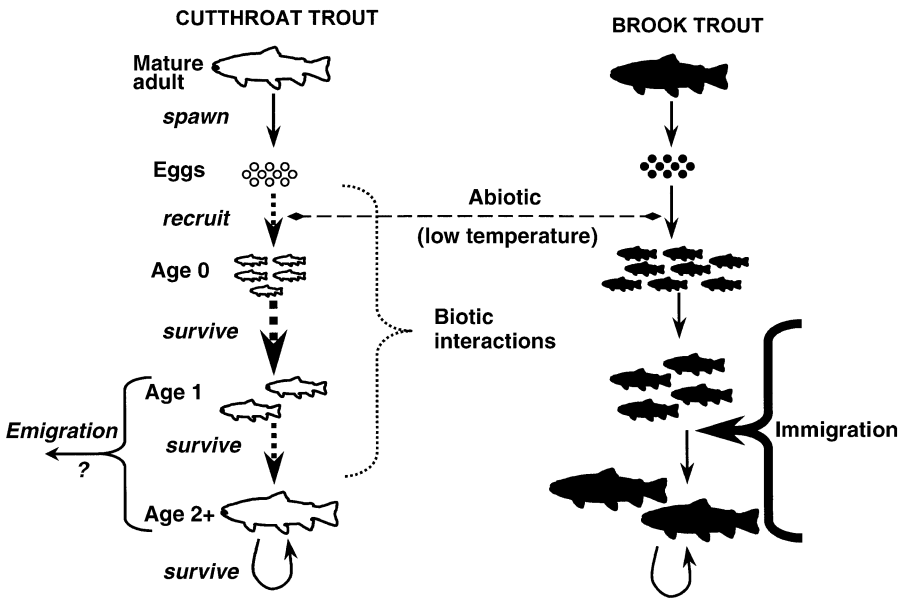

FIG. 6. Demography of brook trout invasion and effects on cutthroat trout in four Colorado streams. The conceptual diagram depicts the life stages of cutthroat trout and brook trout (e.g., eggs, age 0, age 1, etc.) and shows transitions between stages (e.g., spawning, recruitment, and survival) and movement (e.g., immigration and emigration) that are the mechanisms causing changes in abundance. Dashed arrows indicate demographic transitions for cutthroat trout that are affected by biotic interactions with brook trout, whereas solid arrows depict transitions unaffected by brook trout (adult survival) or for which no data are available (spawning). The width of dashed arrows indicates the magnitude of the biotic effect. Biotic interactions with brook trout affect cutthroat trout most strongly at the younger life stages, specifically at recruitment of age-0 and interannual survival of age-0 and age-1 individuals. Recruitment of both species is apparently depressed or eliminated by low summer water temperatures in high-elevation streams (horizontal dashed line). Cutthroat trout showed a slight tendency to emigrate from study segments during summers, but the effect size was small or not statistically significant (''?'' below thin arrow bracket). Moreover, some of the emigration that was measured may be part of an annual movement pattern and thus may be only temporary. In contrast, brook trout immigrated into study segments at high rates from source populations downstream (thick arrow bracket).

how nonnative brook trout replace native cutthroat trout in streams of the western United States (Griffith 1972, 1988, Fausch 1989). The data are consistent with the hypothesis that biotic interactions with brook trout suppress cutthroat trout populations, particularly during the first two years of life (Fig. 6). They also demonstrate that brook trout are adept invaders, capable of sustaining or rapidly increasing their abundance. However, abiotic factors that varied by elevation influenced the demographics of both trout species. Here we discuss the initial predictions we tested with the removal experiment, and the conclusions we can draw about mechanisms causing brook trout invasion and its effects on native cutthroat trout.

First, the experiment upheld the prediction that recruitment to age 0 by cutthroat trout would increase where brook trout were removed, which supported the hypothesis that brook trout cause declines in cutthroat trout populations by depressing reproduction. However, cutthroat trout recruitment in high-elevation streams was low or absent, and removal of brook trout did not ameliorate recruitment failures in the high-elevation treatment stream. Spawning habitat was available in this stream because brook trout recruited in the study segment, and age-0 cutthroat were present in low numbers in a warmer segment more than 2 km downstream. Thus, abiotic factors, primarily cold summer water temperatures, can apparently limit cutthroat trout recruitment in high-elevation streams of the central Rocky Mountains (Harig et al. 2000, Harig and Fausch 2002).

Second, as predicted, cutthroat trout survival increased after brook trout were removed, but only for juveniles, which supported the hypothesis that brook trout affect survival of some, but not all, age classes of cutthroat trout. Age-0 cutthroat trout survival was 13 times greater, on average, and age-1 cutthroat trout survival was two times greater, in the mid-elevation treatment stream compared to that in the mid-elevation control stream. In contrast, age-2+ cutthroat trout survival did not change in response to brook trout removal at either elevation. Moreover, age-0 and age-1, but not age-2+, cutthroat trout survival was inversely related to brook trout density (Fig. 4). Although we did not detect reduced survival of age-2+ cutthroat trout in response to brook trout, subtle sublethal effects such as reduced growth might lead to decreased fecundity that may have population-level implications (see Adams 1999 for example with brook trout). Overall, our results indicate that brook trout invasion can impose a

population bottleneck (Elliot 1994) on cutthroat trout by reducing their interannual survival at the juvenile life stage.

Apparent survival is generally biased low compared to true survival, because some emigrants survive elsewhere. However, this would only affect the conclusions of the experiment if apparent survival was biased differently in different streams (i.e., a different proportion of emigrants survived). In the three study streams with weirs, few cutthroat trout emigrated farther upstream, and in all streams those that emigrated downstream encountered higher densities of brook trout than in the study segments. Thus, age-0 and -1 cutthroat trout apparent survival should be relatively unbiased because few survive when brook trout density is high (Fig. 4). Age-2+ cutthroat trout apparent survival should be uniformly biased among streams because they survived at the same rate whether brook trout were removed or not (Table 5) and regardless of brook trout density (Fig. 4). Relatively few brook trout emigrated compared to the abundance in each stream (cf. Figs. 2 and 5), so brook trout apparent survival estimates should be relatively unbiased.

Third, our experiment upheld the prediction that cutthroat trout abundance would increase after brook trout removal because of changes in recruitment or survival. Greater age-0 cutthroat trout recruitment and survival in the treatment vs. control streams at mid elevation led to greater age-1 abundance in the final year of the study. However, latent brook trout reproduction caused lag effects in detecting these increases for juvenile cutthroat trout, and precluded detecting increases for adults. Consecutive years of electrofishing removal and weir operation were necessary to reduce brook trout reproduction to very low levels because adults immigrated into the study area and spawned after weirs were removed. As a result, relatively high densities of age-0 brook trout were produced during 1998 and 1999 in the mid-elevation treatment stream, so recruitment of age-0 cutthroat trout did not increase until the third and fourth years (2000 and 2001). Accordingly, we did not detect an increase in adult cutthroat trout abundance in treatment vs. control streams at mid elevation because more time would have been required to measure the entry of these large cohorts, caused by brook trout removal, into the age-2+ population.

Fourth, we confirmed the prediction that brook trout would survive at higher rates than cutthroat trout, which supported the hypothesis that higher survival by one or more age classes of brook trout can lead to successful invasion and replacement of cutthroat trout. However, this occurred only for age-0 brook trout in the mid-elevation control stream, which survived at a rate 10 times greater than age-0 cutthroat trout. In contrast, we did not detect any differences in survival between age-1 and age-2+ brook trout and cutthroat trout in any stream. Strong year classes (i.e., large cohorts) of age-0 brook trout during 1999 and 2000 in the mid-elevation control stream may have caused density-dependent declines in survival for all ages of both trout species. However, survival differences between age-0 trout of the two species remained consistent as age-0 brook trout density increased fivefold, indicating an invasion effect of brook trout on cutthroat trout irrespective of overall trout density.

Fifth, emigration by cutthroat trout did not decrease where brook trout were removed, which did not confirm our prediction. Thus, we have no evidence to support the hypothesis that the presence of brook trout affects summer movement of cutthroat trout. Emigration rates did not differ between the treatment and control streams where we had weirs, and in all streams the statistical difference between emigration and immigration rates for age-1 and age-2+ cutthroat was either very small or nil, so these fish exhibited only a slight tendency, if any, to emigrate. Moreover, emigration was only temporary for some fish, suggesting that weirs operated from summer through fall measured only a portion of the annual movement of cutthroat trout in these streams. More thorough monitoring using telemetry would be necessary to define these patterns (e.g., Schmetterling 2001, Schrank 2002).

In contrast, high propagule pressure from immigrating brook trout supplemented invasions where conditions were favorable for recruitment (warmer mid-elevation streams) or helped sustain invasions in sink habitats where conditions for recruitment were unfavorable (colder high-elevation streams). Brook trout exhibited net immigration in every year that weirs were operated in three streams. However, results in treatment streams must be interpreted cautiously because electrofishing removals in the study segments reduced the supply of emigrants. Nevertheless, our results agree with the general pattern of brook trout tending to move upstream during summer in western United States mountain streams (Gowan and Fausch 1996*a*, Adams et al. 2000, Peterson and Fausch 2003*b*). In addition, downstream-directed invasions are common where brook trout have been introduced into headwater lakes (Adams et al. 2001). Brook trout captured immigrating through weirs in treatment streams during summer alone would have increased age-1 and older brook trout abundance in the study segments by 34%, on average, based on fall surveys ($n = 6$, 1 SE = 9.3%). Moreover, subsequent immigration replaced 40% to >100% of the pretreatment abundance of age-2 and older brook trout in treatment streams in the eight months between weir removal in the fall and installation the following summer. Similarly, Gowan and Fausch (1996*a*, *b*) observed rapid population turnover in brook trout caused by movement in other Colorado streams. Ultimately, propagule pressure is positively correlated with invasion success and impacts (Kolar and Lodge 2001), so high movement rates by brook trout undoubtedly contribute to their widespread invasions and frequent re-

placement of native cutthroat trout in the western United States.

An alternate hypothesis for cutthroat trout declines is that invading brook trout introduce debilitating or fatal diseases (e.g., whirling disease). However, disease assays in the study streams revealed no such diseases or pathogens, so the disease hypothesis was not supported in this case (see Peterson 2002).

Competition and predation are believed to be the individual-level mechanisms causing replacement of cutthroat trout by brook trout in western U.S. streams (Griffith 1988). Numerous individual-level studies have attempted to measure competition between these two species, but with varying success (Peterson and Fausch 2003*a*). Studies focusing on adult cutthroat trout found no evidence that brook trout were superior competitors (Griffith 1972, Cummings 1987), unless cutthroat trout faced a numerical disadvantage (Schroeter 1998). However, juvenile cutthroat trout interacting with brook trout shifted to energetically less favorable positions (Cummings 1987), were behaviorally subordinate (Griffith 1972, Novinger 2000), grew less and had depressed lipid reserves (Thomas 1996), and survived at a lower rate (Novinger 2000) than when in allopatry. Most of these studies mimicked the size advantage juvenile brook trout maintain over cutthroat trout during their first one or two years of life. In contrast, results of size-matched trials using age-1 and older trout depended on temperature, whereby brook trout dominated cutthroat trout at 20°C but not 10°C (De Staso and Rahel 1994). Our results at the population level indicate that brook trout affect cutthroat trout by reducing age-0 recruitment and age-0 and age-1 interannual survival, and thus strengthen the inferences from individual-level experiments of competition and predation that used juvenile age classes of cutthroat trout. The cumulative evidence indicates that age- (or size-) specific biotic interactions (competition or predation; e.g., Taniguchi et al. 2002), which decrease survival of the youngest life stages of cutthroat trout, are probable mechanisms by which brook trout replace cutthroat trout.

Bottlenecks caused by biotic interactions at juvenile life stages are predicted to have large effects on dynamics of size- or stage-structured populations (Werner and Gilliam 1984, Persson 1988, Persson et al. 1999), and appear to influence invasion dynamics between brook trout and cutthroat trout. Similarly, simulation modeling of brook trout populations subject to invasion by rainbow trout in the United States Appalachian Mountains, showed that these populations are also sensitive to variation in juvenile survival rates (Marschall and Crowder 1996, Clark and Rose 1997).

Management implications

Our study confirms earlier observations that brook trout are effective invaders of headwater streams in the central Rocky Mountains (Gresswell 1988, Behnke 1992) and can undermine cutthroat trout restoration and translocation efforts (e.g., Harig et al. 2000), although their invasion does not always result in extirpation of cutthroat trout throughout all watersheds (Fausch 1989, Dunham et al. 2003). In the stream segments we studied, we found that brook trout recruited and survived as well or better than native cutthroat trout, immigrated rapidly and even sustained invasion by immigration alone, and ultimately had large effects on the vulnerable juvenile life stages of cutthroat trout which would lead to population declines and replacement.

How can this information be used by managers in streams where brook trout are affecting native cutthroat trout? Clearly the highest priority is to prevent brook trout introductions, but managers are typically confronted with ongoing invasions. Complete eradication of brook trout above a barrier to immigration is the preferred option, provided that habitat in the segment upstream is sufficient for cutthroat trout persistence (Harig and Fausch 2002, Novinger and Rahel 2003), because this experiment demonstrated that recruitment and survival of cutthroat trout increased when brook trout were removed. Long-term, large-scale, electrofishing removals were successful in nearly eliminating nonnative trout and increasing abundance of native brook trout in southern Appalachian Mountain streams (Moore et al. 1986, Kulp and Moore 2000), and cutthroat trout in a Montana stream (Shepard et al. 2002). However, if seasonal movements of cutthroat trout like those we found are important to the long-term persistence of cutthroat trout populations, barriers may fragment populations and lead to declines (Novinger and Rahel 2003).

Although total removal of nonnative trout is often impossible because stream habitats are complex, selective removal strategies may allow cutthroat trout to persist. For example, our data show that three consecutive years of removing over 90% of the estimated brook trout population, in conjunction with a semipermanent barrier to fish movement (e.g., seasonally operated weirs), would permit a large cohort of cutthroat trout to survive from age 0 to age 2. After this, our results indicate they would be affected little by biotic interactions with brook trout. For central Rocky Mountain streams, at least two removals per year would also be required to produce the intended result (Thompson and Rahel 1996, Kulp and Moore 2000). The first removal in early summer could target age-0 brook trout so they would not interact with the age-0 cutthroat trout which emerge later, and the second removal in early fall could target adult brook trout that might spawn and produce offspring that would interact with young cutthroat trout the following summer. Where complete brook trout eradication is not feasible, two removals per year for three consecutive years should be repeated periodically to increase the probability of cutthroat trout persistence. Ultimately, constant vigilance and careful planning are necessary for effective conservation of native cutthroat trout populations confronted with invasion by nonnative brook trout.

Value of experiments on the demography of invasions

In a broader context, this study demonstrates that it can be difficult to determine the mechanisms underpinning success of invaders and impacts on native species without detailed population-level experiments. For example, if we had measured the response of only adult cutthroat trout to four years of brook trout removal, we would have concluded that brook trout had no effect and some other factor reduced cutthroat trout populations. Based on our findings, subsequent studies of brook trout interactions can focus on age-0 and -1 cutthroat trout to determine the relative importance of individual-level mechanisms like competition and predation on their survival (cf. Novinger 2000), and to identify age classes of brook trout causing the greatest effects.

Experiments on invading populations and host communities are rare, and have focused primarily on weeds (Shea and Kelly 1998, Dayton and Primack 1999). In contrast, most experiments on mobile, stage-structured organisms have been at the individual level, and comprehensive demographic approaches have seldom been used (but see Gabor and Hellgren [2000] and Moorhouse et al. [2003]). In one case, individual-level experiments successfully predicted the impacts of bullfrog invasion on native frogs, but further experiments in large-scale enclosures were required to isolate the individual-level and population-level mechanisms (Kupferberg 1997, Kiesecker and Blaustein 1998). Population-level experiments with stream fish invasions will be challenging because their ranging behavior, age structure, and longevity will require large scales of investigation to encompass (Fausch et al. 2002). Nonetheless, such large-scale studies will be needed to identify population-level mechanisms causing invasions, and to measure and understand their impacts on native species.

Acknowledgments

The manuscript was improved by helpful comments from Susan Adams, Colden Baxter, Kevin Bestgen, Amy Harig, LeRoy Poff, Frank Rahel, Mike Young, and an anonymous reviewer. Financial support was provided by the Colorado Division of Wildlife (CDOW), U.S. Department of Interior Central Utah Project Completion Act (CUPCA), USDA Forest Service Fish Habitat Relationships Program (FHR), and Trout Unlimited (TU). We thank Tom Nesler (CDOW), Ralph Swanson (CUPCA), Nick Schmal (FHR), Dave Winters (FHR), Mike Young (FHR), and Whit Fosburgh (TU) for administering these funds. D. Peterson was also supported by scholarships from the West Denver Chapter of Trout Unlimited, Cook Memorial Scholarship fund, Peters Scholarship fund, and the Western Division of the American Fisheries Society. We thank the dozens of technicians and volunteers who helped collect field data. P. Lucaks, A. Ellingson, and K. Burnham provided assistance with statistical analysis and program MARK.

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APPENDIX A

A description of the status of nonnative brook trout (*Salvelinus fontinalis*) in four streams in north central Colorado, USA, inhabited by Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) is presented in ESA's Electronic Data Archive: *Ecological Archives* A014-014-A1.

APPENDIX B

A table of parameter estimates for apparent survival, population size, and electrofishing capture probabilities for trout in the four study streams during 1998–2001 is presented in ESA's Electronic Data Archive: *Ecological Archives* A014-014-A2.