Isolation Management with Artificial Barriers as a Conservation Strategy for Cutthroat Trout in Headwater Streams

DOUGLAS C. NOVINGER* AND FRANK J. RAHEL

Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071-3166, U.S.A.

Abstract: *We evaluated the effectiveness of isolation management and stocking to meet protection and enhancement goals for native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in Wyoming (U.S.A.). As a management strategy of the Wyoming Game and Fish Department, cutthroat trout were isolated upstream of artificial barriers in small headwater streams. Non-native trout that might have hybridized, competed with, or preyed upon cutthroat trout were removed from the isolated reaches, and then cutthroat trout of hatchery origin were stocked to augment populations. We monitored the abundance and body condition of cutthroat trout for 4–7 years following isolation in four streams with barriers and in two reference streams without barriers. Barriers limited new invasions by non-native trout, and removals of non-native trout greatly reduced their abundance but did not eliminate them (mainly brook trout [*Salvelinus fontinalis*]). Wild cutthroat trout persisted in low numbers upstream of barriers, but there was no evidence of enhancement of populations. Stocked cutthroat trout did not persist upstream of barriers, and many moved downstream over barriers. The body condition of wild cutthroat trout was comparable among populations upstream and downstream of barriers and in reference streams. Isolation management provided only short-term benefits by minimizing the risks of hybridization and allowed populations to persist during the study. Removal of non-native trout and stocking did not enhance wild cutthroat trout populations, however, likely because the isolated reaches lacked critical habitat such as the deep pools necessary to sustain large fish. Also, barriers disrupt migratory patterns and prevent seasonal use of headwater reaches by adult cutthroat trout. Longer-term consequences of isolation include vulnerability to stochastic processes and loss of genetic diversity. Where non-native species pose an immediate threat to the survival of native fishes, isolation in headwater streams may be the only conservation alternative. In such situations, isolated reaches should be as large and diverse as possible, and improvements should be implemented to ensure that habitat requirements are met.*

El Aislamiento con Barreras Artificiales como una Estrategia de Conservación para la Trucha (*Oncorhynchus clarki pleuriticus*) en Arroyos de Cabecera

Resumen: *Evaluamos la efectividad del aislamiento y de la repoblación para alcanzar las metas de protección y mejoramiento de la trucha nativa del río Colorado,* Oncorhynchus clarki pleuriticus, *en Wyoming (EE.UU.). Como una estrategia de manejo del Departamento de Caza y Pesca de Wyoming, se aislaron las truchas nativas aguas arriba de barreras artificiales, en arroyos de cabecera. Se removieron de estas zonas aisladas las truchas no nativas que pueden hibridizar, competir o depredar a la trucha nativa y se sembraron estas zonas con truchas de criadero para aumentar las poblaciones. Hicimos un seguimiento de la abundancia y la condición corporal de las truchas por 4 a 7 años después del aislamiento en cuatro arroyos con barreras y en dos arroyos sin barreras como referencia. Las barreras limitaron nuevas invasiones de truchas no nativas, y las remociones de truchas no nativas redujeron su abundancia pero no las eliminaron (*principalmente Salvelinus fontinalis*). Las truchas nativas silvestres persistieron en pequeño número aguas arriba de las barreras; sin embargo, no hubo evidencia de incrementos de sus poblaciones. Las truchas sembradas no persisti-*

*Current address: Missouri Department of Conservation, Conservation Research Center, 1110 S. College Avenue, Columbia, MO 65201, U.S.A., email novind@mdc.state.mo.us

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eron aguas arriba de las barreras y muchas se desplazaron aguas abajo cruzando las barreras. La condición corporal de las truchas nativas era similar entre las poblaciones aguas arriba y aguas abajo de las barreras y en los arroyos sin barreras. El aislamiento como herramienta de manejo solo proporcionó un beneficio a corto plazo al minimizar los riesgos de la hibridación y permitió que las poblaciones persistieran durante el estudio. Sin embargo, la remoción de truchas no nativas y la siembra no mejoró las poblaciones de truchas nativas silvestres, debido probablemente a que las áreas aisladas carecían del hábitat crucial tal como pozos profundos necesarios para proveer sustento a los peces de mayor tamaño. Además, las barreras desestabilizan los patrones migratorios e impiden que las truchas adultas hagan un uso estacional de los arroyos de cabecera. Las consecuencias a largo plazo del aislamiento incluyen la vulnerabilidad a procesos estocásticos y la pérdida de diversidad genética. El aislamiento de arroyos de cabecera puede ser la única alternativa de conservación en la que las especies no nativas son una amenaza inmediata para la supervivencia de peces nativos. En tales situaciones, las áreas aisladas deben ser tan extensas y diversas como sea posible, y se deben implementar mejoras para asegurar que se cumplan los requerimientos de hábitat.

Introduction

The intentional isolation of populations of threatened native species is an extreme measure to protect them from the negative effects of non-native species (Moyle & Sato 1991; Melvin et al. 1992; Shafer 1995). Isolation approaches to conservation management have been utilized most frequently in aquatic systems where movement corridors are well defined and the passage of animals is easier to control (Moyle & Sato 1991; Rinne & Turner 1991; Thompson & Rahel 1998). For example, cyprinodontid fishes in the southwestern United States (e.g., desert pupfishes [*Cyprinodon macularius*]) persist only in isolation from non-native mosquitofish (*Gambusia affinis*) and largemouth bass (*Micropterus salmoides*) (Minckley et al. 1991). Although isolation may confer short-term benefits by minimizing external threats, longer-term conservation success requires sufficient ecological and genetic resources to sustain or enhance populations in the isolated habitat fragments (Saunders et al. 1991; Wiens 1997). Undesirable consequences of isolation may include increased intraspecific competition, high levels of inbreeding, and susceptibility to chance catastrophes that can lead to population bottlenecks or local extirpation (Wilcox & Murphy 1985; Simberloff et al. 1992).

Isolation management is being employed by resource managers to protect threatened populations of cutthroat trout (*Oncorhynchus clarki*) in Rocky Mountain streams (Stuber et al. 1988; Propst et al. 1992; Young et al. 1996). Various subspecies of cutthroat trout have declined dramatically throughout the western United States following degradation of critical habitat, exploitation, and invasions of non-native trout species (Griffith 1988). Introduced rainbow trout (*Oncorhynchus mykiss*) and other subspecies of introduced cutthroat trout may hybridize with and threaten the genetic integrity of native cutthroat trout (Behnke 1992). Introduced brook trout (*Salvelinus fontinalis*) are hypothesized to compete with and prey upon cutthroat trout (Fausch 1989; Young 1995; Dunham et al. 1997; Harig et al. 2000). The mechanisms underlying these species interactions in natural populations are not clear. However, empirical studies suggest that brook trout could limit the downstream distribution of cutthroat trout through temperature-mediated competition, where brook trout have increased competitive abilities at warmer temperatures associated with lower elevations (De Staso & Rahel 1994; Novinger 2000), and via demographic effects in which brook trout tolerate higher population densities and may thereby exclude cutthroat trout from complex habitat (Schroeter 1998). Size-selective predation on age-0 cutthroat trout may also be a significant source of mortality (Gregory & Griffith 2000; Novinger 2000).

Conservation goals for cutthroat trout include protection and enhancement of genetically pure populations of the Colorado River subspecies of cutthroat trout (*O. c. pleuriticus*) that have declined and disappeared in many Wyoming streams. To eliminate immediate threats believed to be posed by non-native trout, the Wyoming Game and Fish Department initiated isolation management, beginning with installation of migration barriers on several high-elevation headwater streams in western Wyoming. Following completion of the barriers, they used intensive electrofishing to remove non-native fishes, mainly brook trout, and stocked the isolated stream reaches with cutthroat trout of hatchery origin in an attempt to augment populations. It was hoped that these activities would protect cutthroat trout from the negative effects of hybridization and competition and allow populations to increase (Wyoming Game and Fish Department 1987). Initial surveys showed that removal efforts greatly reduced the abundance of brook trout upstream of barriers and achieved the short-term benefit of protecting cutthroat trout from threats posed by non-native species (Thompson & Rahel 1996). Subsequent annual surveys were implemented to gauge the continued effectiveness of the barriers and monitor the success of isolation management and stocking in protecting and enhancing cutthroat trout populations.

Our purpose was to evaluate the effectiveness of this isolation-management approach for protecting and enhancing cutthroat trout following isolation for periods of 4 to 7 years. By definition, the process of isolation should exclude non-native trout that might hybridize or compete with native populations, but it also should not impede the potential recovery of populations. Elimination of brook trout, a potential competitor and predator, should enhance cutthroat trout populations by promoting increased growth and survival. Augmentation of wild populations of cutthroat trout by stocking should enhance spawning and facilitate population growth. We assessed the success of isolation management in achieving these aims by comparing the characteristics of cutthroat trout populations located upstream of barriers, where non-native trout were removed and hatchery cutthroat trout were stocked, with populations located downstream of barriers, where no such manipulations occurred. We also examined cutthroat trout populations in reference streams that lacked barriers and had sympatric populations of brook trout. Our assessment provided insight into the long-term potential for successful isolation management of cutthroat trout in Rocky Mountain headwater streams.

Methods

We performed annual monitoring surveys to assess temporal changes in cutthroat trout populations in response to isolation upstream of barriers, removal of non-native trout, and enhancement through stocking. We sampled four streams with barriers ("treatment" streams): Irene and Nylander creeks in the North Cottonwood Creek watershed (Sublette County, Wyoming) and Clear and Nameless creeks in the LaBarge Creek watershed (Lincoln County, Wyoming) (Table 1; Fig. 1). Two to four monitoring sites were established upstream of each barrier to the farthest extent of fish occurrence (Thompson & Rahel 1996). One monitoring site was established immediately downstream from each barrier. We also sampled sites on two reference streams in the LaBarge Creek watershed that lacked barriers: Spring Creek and Trail Creek. Two monitoring sites were on Spring Creek, one downstream near the stream's mouth and the other upstream near the spring source. Only one site near the mouth of Trail Creek was sampled because upstream reaches were intermittent (Table 1; Fig. 1). Monitoring surveys on treatment streams were performed for periods of 4 to 7 years between 1992 and 1999. The first year of data for each treatment stream represented fish abundances prior to removal of non-native trout. Sampling on the reference streams commenced in 1994. The streams we studied were typical of first-order, headwater streams in the Rocky Mountains of western Wyoming, with significant spring inputs and wetted widths of 1–3 m. All the streams were within the boundaries of Bridger National Forest and the Green River watershed.

With the purpose of directly augmenting isolated cutthroat trout populations, the Wyoming Game and Fish Department stocked each of the four treatment streams three times during 1990–1998. Stocking efforts involved the release upstream of barriers of approximately 500–2000 juvenile fish 120 mm in length. Each stocking was marked with a distinctive fin clip.

To sample fish populations, we used a single backpack unit and methods described by Thompson and Rahel (1996) to conduct three-pass, depletion-removal electrofishing. We sampled in August when streams were at base flow. Block nets (1-cm mesh) were set at upstream and downstream extents of each 100-m site to ensure closure of the sample reach. Following each electrofishing pass, all trout captured were counted, measured for total length to the nearest 1 mm, weighed to the nearest 1 g, and placed in a holding cage outside of the site. Age-0 cutthroat trout (young-of-year; length $<$ 50 mm) were rarely observed because sampling dates occurred just prior to emergence. Hence, our samples reflect only the abundance of one-year-old and older ($\geq$age 1) cutthroat trout. We counted stocked cutthroat

Table 1. Characteristics of streams in western Wyoming, where isolation management of cutthroat trout populations was monitored, including stream length (upstream of barriers or from mouth for reference streams), number of 100-m sampling sites, range in elevation from most downstream to most upstream site, and years sites were sampled.*

Stream	*Stream length (km)*	*Number of sites*	*Elevation range (m)*	*Years sampled*
Treatment streams (migration barriers)				
Clear Creek	1.5	3	2540–2550	1994–1998
Irene Creek	3.6	5	2425–2500	1993–1999
Nameless Creek	2.9	5	2455–2510	1992–1998
Nylander Creek	1.2	3	2470–2485	1992–1999
Reference streams (no barriers)				
Spring Creek	6.0	2	2495–2585	1994–1998
Trail Creek	4.5	1	2550	1994–1998

**On the four streams with a barrier (treatment streams), one site was immediately downstream of the barrier, whereas the remainder of sites were distributed upstream (Fig. 1). For comparison, upstream and downstream sites on two streams without barriers (reference streams) were sampled.*

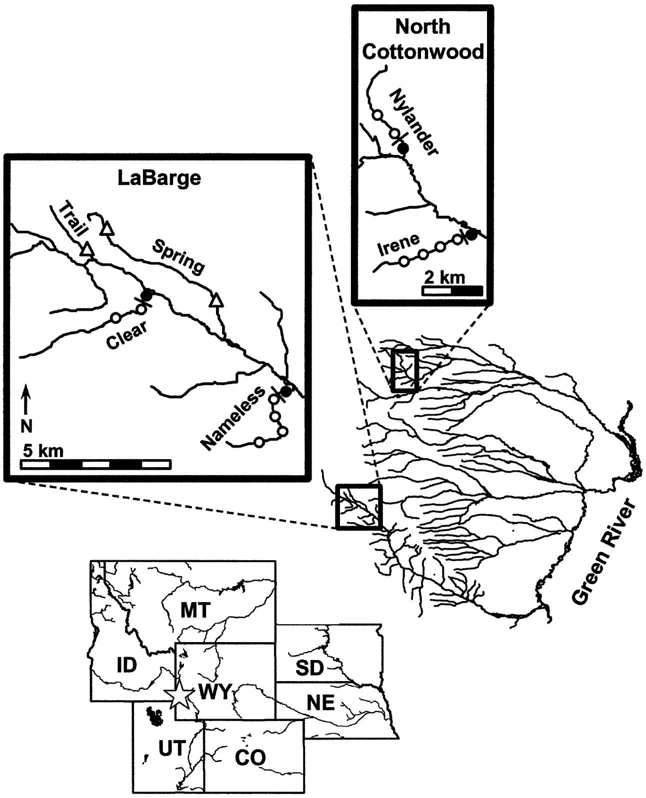

Figure 1. Study sites on headwater streams in the Green River watershed of western Wyoming. Sites were located both upstream (open circles) and downstream (closed circles) of fish migration barriers on Clear and Nameless creeks in the LaBarge Creek watershed and Nylander and Irene creeks in the North Cottonwood Creek watershed. Reference sites (triangles) were located on two streams without fish migration barriers in the LaBarge Creek watershed: Spring and Trail creeks.

trout separately. Age-0 brook trout (length 50–90 mm) had emerged the previous spring and were distinguished from older, larger brook trout (≥age 1). Following processing, brook trout collected upstream of barriers were either euthanized or marked with a visual implant tag and released downstream of the barrier to aid in documenting upstream movement past barriers (Thompson & Rahel 1998). We used Zippen model M_b in the program Capture (White et al. 1982) to calculate probabilities of capture, population estimates, and upper 95% confidence intervals when a descending pattern of removal was achieved. When a descending pattern of removal was not achieved, we used the total number of fish caught during the three electrofishing passes as the population estimate. This occurred at only a few sites with low trout abundance, where few or no trout were captured on each electrofishing pass.

We also assessed the body condition of cutthroat trout to test for the effects of brook trout removal on factors related to the length-weight relationship of individual fish. To describe body condition, we calculated relative weight (W_r; Kruse & Hubert 1997), an index widely used to assess the body form or plumpness of fishes relative to an average length-weight relationship for the species. Values of W_r close to 100 are assumed to reflect good body condition.

We evaluated the effectiveness of isolation management to enhance cutthroat trout populations by testing for evidence of temporal trends in abundance and body condition attributable to non-native trout removal and supplemental stocking. We assessed changes in the longitudinal difference in trout abundance (estimated population size per 100 m) in upstream and downstream sites by calculating the following metric: longitudinal difference = (mean number of trout/100 m in upstream sites) − (number of trout/100 m in downstream site).

We expected to see an increase in the longitudinal difference over time if removal of non-native trout and supplemental stocking were effective at increasing the abundance of wild cutthroat trout above the isolation barriers. Using Kendall's τ (tau), a nonparametric rank correlation procedure robust to small sample sizes (Sokal & Rohlf 1981), we performed separate tests on data from each stream for an association between the longitudinal difference in abundance and the number of years after removal of non-native fishes. This test is appropriate given our limited time series and lack of evidence for serial correlations in residuals from regression of the longitudinal difference on time. We assessed temporal trends in trout abundance in each site on reference streams (two sites on Spring Creek, one site on Trail Creek) by submitting the actual population estimates to the same test for correlation. Comparisons between treatment and reference streams were done visually. We used similar procedures to assess temporal patterns in the body condition of cutthroat trout by utilizing longitudinal differences in relative weight and calculating Kendall's correlation coefficient. We performed all analyses using SAS (SAS Institute 1999) and $\alpha = 0.05$ to judge statistical significance.

Results

Depletion-removal electrofishing was an effective census method, and reliable population estimates with 95% confidence intervals were possible for 135 of 152 samples (89%). Nondescending removal patterns occurred when the total number of fish captured was low (<6) and more individuals were collected during the second or third pass. Mean probabilities of capture (±1 SD) were highest for cutthroat trout (0.82 ± 0.18) and brook trout at ≥age 1 (0.77 ± 0.19), whereas brook trout at age 0 were only slightly more difficult to collect (0.74 ± 0.20). Of 268 brook trout tagged and released downstream of barriers between 1992 and 1994, 19 (7%)

were subsequently recaptured upstream of barriers; however, we did not recapture additional tagged brook trout upstream of barriers during the remainder of the study (1995–1999). One rainbow trout (length = 171 mm) was removed from upstream of the barrier on Nameless Creek during the first year of sampling on that stream (1992).

Initial removal efforts greatly reduced brook trout abundance upstream of barriers, although the species was not eliminated. Abundances of brook trout at ≥age 1 upstream of barriers declined by 75–96% following the first year of removal and remained depressed relative to downstream sites in subsequent years (Fig. 2). The brook trout population downstream of the barrier on Nylander Creek was especially dense and increased markedly across 8 years of sampling. Abundances of age-0 brook trout declined by similar amounts upstream of barriers following initial removals and remained low (<1 fish/100 m; Fig. 3). In Clear and Nameless creeks, brook trout at age 0 were not observed in upstream sites after 1995 and disappeared from both upstream and downstream sites by 1997 and 1998. Trends in abundance of brook trout in the reference streams appeared stable during the study and were comparable to trends in most sites downstream of barriers. We consistently observed higher fish densities in the downstream sites on Spring Creek and Trail Creek (also at a site downstream) relative to the upstream site on Spring Creek. Brook trout at age 0 were never observed in this latter site.

Sustained reductions in brook trout abundance, com-

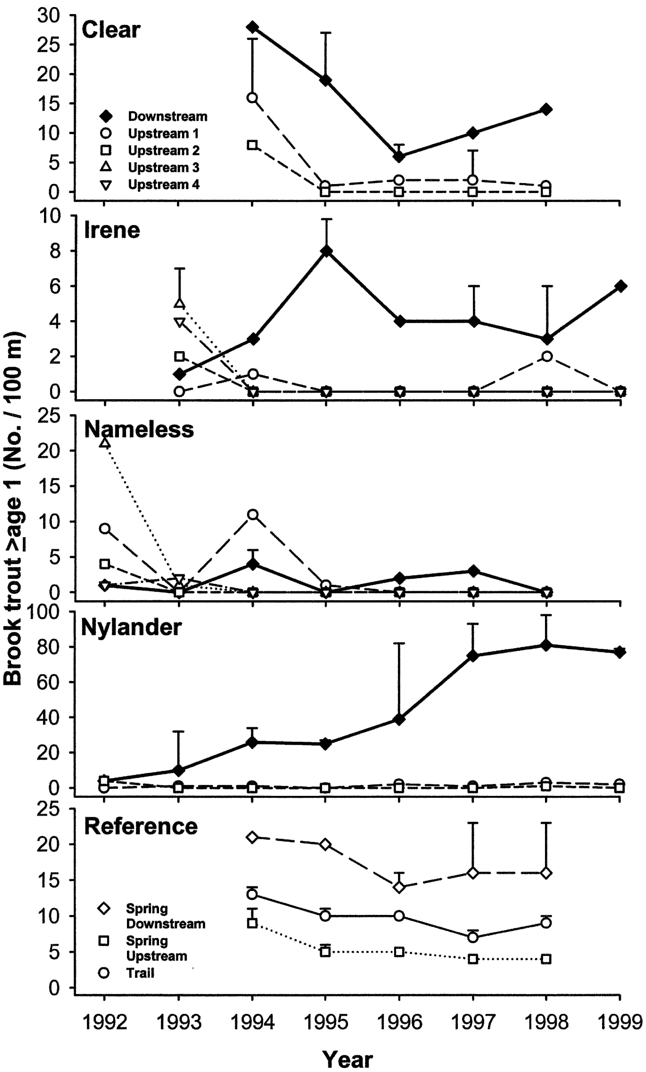

Figure 2. Population estimates (+95% C.I.) for brook trout aged 1 year and older (≥age 1) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

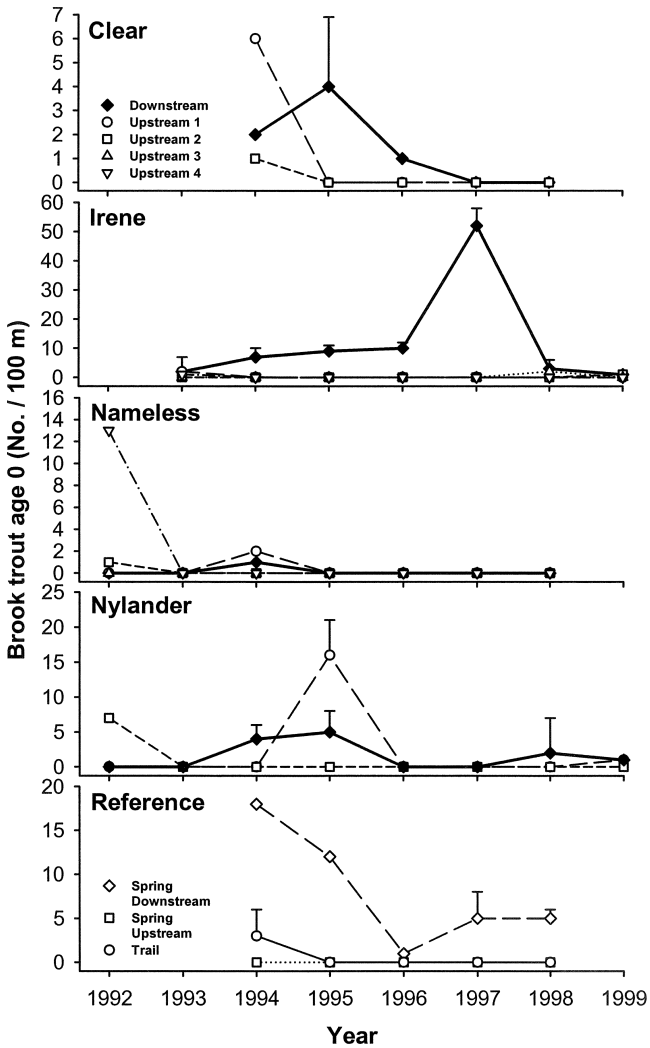

Figure 3. Population estimates (+95% C.I.) for young-of-year brook trout (age 0) in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992 through 1999. The y-axis scaling is different among streams.

bined with isolation upstream of the barriers, did not correspond with enhancement of wild cutthroat trout populations. In Clear and especially Irene and Nylander creeks, the post-removal abundance of cutthroat trout was generally greater downstream, not upstream, of barriers (Fig. 4). However, abundances of cutthroat trout in downstream sites tended to be lower than the abundances of the co-occurring brook trout population (Fig. 2). Other than an initial decline in Trail Creek, we did not observe notable temporal patterns in abundances of cutthroat trout in the reference streams, and the magnitude of population estimates was similar to population estimates in treatment streams (Fig. 4). Longitudinal differences in cutthroat trout abundance (upstream - downstream) did not increase as hoped for under an isolation-management strategy (Fig. 5). We did not detect significant correlations between longitudinal differences in abundance and the number of years after removal of non-native fishes in any of the four treatment or reference streams. Values for Kendall's τ ranged from -0.20 (Clear Creek, $p = 0.62$) to 0.29 (Nameless Creek, $p = 0.36$), confirming the absence of significant enhancement of wild cutthroat trout. The statistical power ($1 - \beta$) of these correlation tests averaged 0.81 (range $0.56 - 0.99$). The best response occurred in Nameless Creek, where there was a relative increase in the initial abundance of cutthroat trout upstream of barriers from a low difference of -4.5 to a high of 2.75 (+7.25 fish/100 m 2 years after removal). In years 2 through 6, however, the longitudinal difference remained relatively constant at only 1.6 fish/100 m.

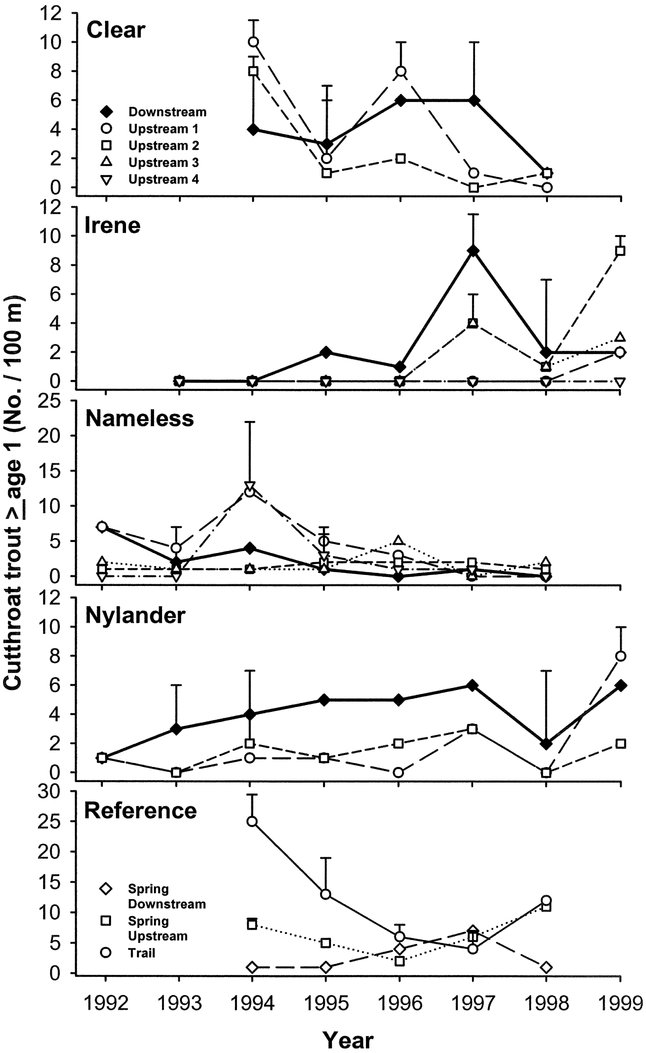

Figure 4. Population estimates (+ 95% C.I.) for wild cutthroat trout ≥ age 1 in sites upstream and downstream of barriers in treatment streams and in sites in reference streams in 1992–1999. The y-axis scaling is different among streams.

We found only limited evidence for increased body condition of cutthroat trout upstream of barriers. We did not detect significant trends in the longitudinal difference in relative weight of cutthroat trout in Nameless or Nylander creeks or in reference streams (τ ranged from -0.20 to 0.67; power ranged from 0.52 to 0.90). We did find a positive correlation between the longitudinal difference and number of years after removal of non-native fishes in Clear Creek ($\tau = 1.0$, $p = 0.04$, $n = 4$). The trend was for a consistent increase in the longitudinal difference from -15.3 in 1994 to 1.3 in 1998, suggesting that by the end of the study cutthroat trout upstream of the barrier increased from a marked deficit in condition to approximately equivalent condition relative to cutthroat trout downstream of the barrier. Sample sizes of cutthroat trout of sufficient size for reliable calculation of relative weight (Kruse & Hubert 1997) were too low for trend analyses in Irene Creek. Across the duration of the study, relative weights of cutthroat trout av-

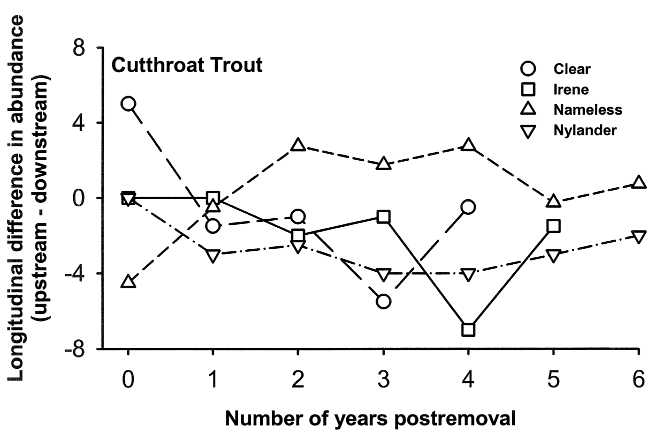

Figure 5. Longitudinal differences in abundance of wild cutthroat trout ≥ age 1 before and after removal of non-native trout, calculated by subtracting the population estimate (trout/100 m) in the downstream site from the mean population estimate of the upstream sites in each stream for each year.

eraged 94.1 (SE = 1.7, n = 66) in sites upstream of barriers, 92.1 (1.7, 47) downstream of barriers, and 95.4 (1.5, 43) in reference streams.

Stocking of hatchery-origin cutthroat trout upstream of barriers failed to enhance populations for more than 1 or 2 years after release (Table 2). Our recaptures of marked hatchery cutthroat trout suggested a rapid loss of stocked fish downstream over the barriers. Three separate stocking events occurred in each of the treatment streams (12 total), with initial stocking densities that ranged from 18 to 138 fish/100 m. Sampling in the year following release indicated that abundances of hatchery cutthroat trout stocked upstream of barriers declined by 87% to 100%, with <1% of the original stocks remaining after 3 years. In 1992 cutthroat trout stocked upstream of the barrier in Nameless Creek declined in abundance from 34 to 7 fish/100 m within 2 months. Stocked fish were, however, found downstream of the barrier at a density of 17 fish/100 m, suggesting significant downstream movement. Cutthroat trout stocked into Nylander Creek (42 fish/100 m in 1991) and Clear Creek (138 fish/100 m in 1995) were never recaptured at sites upstream of barriers in subsequent years. By contrast, stocked cutthroat trout were recaptured in sites downstream of barriers, particularly in Clear Creek. In several years, abundance estimates for stocked cutthroat trout in sites downstream of barriers exceeded abundance estimates for sites upstream of barriers.

Discussion

There was little evidence of enhancement of wild cutthroat trout populations upstream of barriers following isolation and removal of brook trout. In fact, average abundances of cutthroat trout upstream of barriers remained lower than downstream in three of the four treatment streams (negative longitudinal differences in abundance), indicating that fewer cutthroat trout persisted in isolation than coexisted with brook trout.

One explanation for this pattern is that brook trout had only a limited effect on cutthroat trout and that a significant release from competition did not occur. We consider this explanation unlikely for several reasons. Removal of brook trout from the study reaches decreased

Table 2. Decline in hatchery cutthroat trout stocked upstream of migration barriers in four streams in 1990 through 1999.[a]

			Abundance of hatchery cutthroat trout (number/100 m)									
Stream	*Fin clip*	*Number stocked (year)*	*1990*	*1991*	*1992*	*1993*	*1994*	*1995*	*1996*	*1997*	*1998*	*1999*
Clear Creek												
upstream	RP	2006 (1993)				134	8	2	0	0	0	
downstream							14	2	0	0	0	
upstream	LP	2006 (1994)					134	15	1	0	0	
downstream								10	1	0	0	
upstream	AD	2065 (1995)						138	0	0	0	
downstream									0	1	8	
Irene Creek												
upstream	RP	1003 (1990)	28	0	0	0.3	0	0	0	0	0	0
downstream				0	0	0	0	0	0	0	0	0
upstream	AD	2016 (1991)		56	0	0.5	0.3	0	0	0	0	0
downstream					0	0	0	0	0	0	0	0
upstream	LP	1007 (1998)									28	0
downstream												1
Nameless Creek												
upstream	RP	508 (1990)	18	0	0.5	0	0	0	0	0	0	
downstream				0	0	0	0	0	0	0	0	
upstream	AD	1008 (1991)		35	4.5	1.5	0.3	0.3	0	0	0	
downstream					2	0	0	1	0	0	0	
upstream	LP	1000 (1992)			34 (7)[b]	0.5	0.5	0	0	0	0	
downstream					(17)[b]	1	1	1	0	0	0	
Nylander Creek												
upstream	RP	1002 (1990)	84	ns	0	0	0	0	0	0	0	0
downstream				ns	0	0	0	0	0	0	0	0
upstream	AD	504 (1991)		42	0	0	0	0	0	0	0	0
downstream					2	0	0	0	0	0	0	0
upstream	LP	1540 (1998)									128	2
downstream												2

[a] *Stocks were identified by a fin clip (RP, right pelvic; LP, left pelvic; AD, adipose). Shown are the number of cutthroat trout stocked (year stocked) upstream of barriers and their subsequent abundance through time both upstream and downstream of the barriers (ns, not sampled).*
[b] *Abundance of stocked cutthroat trout determined 2 months after stocking.*

total trout numbers by 35% to 83%, a marked reduction in fish biomass in small, high-elevation streams that are generally considered resource-limited for trout (Fausch 1998). The regularity, intensity, and character of mechanisms underlying competition between cutthroat trout and brook trout are not clear. However, competitive interactions between the species have been hypothesized to contribute to the long-term decline of cutthroat trout in other systems and to determine patterns of distribution (Griffith 1972, 1988; Fausch 1989; Young 1995; Dunham et al. 1999; Kruse et al. 2000). Also, the presence of brook trout appears to limit reintroductions of cutthroat trout in mountain streams (Harig et al. 2000).

Another possibility is that there is a considerable time lag before a detectable response to isolation management occurs, given lengthy generation times for cutthroat trout in higher-elevation streams (4 years or longer; Gresswell 1988; Behnke 1992). The duration of our study might have been too short to allow depressed populations opportunity to recover (e.g., Clear Creek was sampled for 4 years following removal of non-native fishes), especially if the resilience of small populations was low in marginal headwater habitats. However, two of the four streams were sampled for 6 years following removal of non-native fishes; it seems unlikely that in this time evidence for numerical enhancement of cutthroat trout populations would remain absent.

Perhaps the most plausible hypothesis for failure of isolation management to enhance cutthroat trout is that isolated segments of headwater mountain streams lacked critical resources. Resources were apparently adequate to sustain populations at relatively low, pre-isolation levels, but the heterogeneity and connectivity of habitat needed to meet the seasonal requirements of cutthroat trout may be limited upstream of barriers, which could have inhibited population growth. Cutthroat trout in some stream systems migrate downstream to reach deep, low-velocity habitats to overwinter, then return to headwaters in search of spawning habitat (Jakober et al. 1998; Brown 1999; Schmetterling 2000). Lack of deep pools has been related to failure of translocations of greenback cutthroat trout (*O. c. stomias*) (Harig & Fausch 2002). The apparent loss of stocked cutthroat trout downstream over barriers in the present study is consistent with downstream migration to reach overwintering habitats. Loss to downstream emigration has similarly hampered establishment of arctic grayling (*Thymallus arcticus*) upstream of barriers in Yellowstone National Park (Kaya 2000).

Some immediate conservation benefits to cutthroat trout were realized as a result of isolation. Installation of the barriers and removal of non-native trout appeared to minimize the risk of hybridization with rainbow trout and generally inhibited reinvasion by brook trout (but regarding the efficacy of barriers, see Thompson & Rahel 1998). Rainbow trout and other non-native cutthroat trout exist in major tributaries of the Green River watershed; hence, continued maintenance of barriers will be necessary to exclude these species. Removal of non-native brook trout also greatly reduced the species' abundance upstream of barriers, although subsequent removals may be required because electrofishing did not eradicate brook trout from complex habitats (Thompson & Rahel 1996).

These successes need to be weighed against the potential for longer-term risks of isolation in apparently incomplete, fragmented habitats. The viability of small, isolated populations is threatened in the long term by stochastic processes and the potential loss of genetic heterogeneity (Wiens 1997). Extreme and fluctuating environmental conditions characterize headwater streams in mountainous regions, and chance phenomena including forest fires, freezing, and dewatering of stream channels could extirpate fish from isolated habitat fragments (Schlosser & Angermeier 1995; Rieman & Clayton 1997). Adequate levels of immigration are necessary to avoid the deleterious effects of inbreeding, including loss of genetic variation that could increase the risk of extinction (Saunders et al. 1991; Propst et al. 1992; Kruse et al. 2001). Actual population sizes of salmonids necessary for longer-term viability may be as high as 2500 individuals (Allendorf et al. 1997), and 8–25 km of stream may be required to encompass sufficient habitat to support a population of that size (Hilderbrand & Kershner 2000). Harig et al. (2000) determined that isolated reaches needed to exceed 5.7 km for successful establishment of greenback cutthroat trout in Rocky Mountain streams. The isolated populations we studied, however, occupied stream reaches ranging from 1.2 to 3.6 km in length, with estimated total population sizes of <200.

Isolation management at larger spatial scales in drainage networks might avoid potentially negative long-term effects by increasing habitat heterogeneity and connectivity and allowing for fluvial life histories (Dunham et al. 1997). But such strategies involve a tremendous effort to remove non-native fishes and to ensure that unwanted species do not recolonize. Habitat alteration such as increasing pool habitats and improving riparian conditions to benefit cutthroat trout in coordination with isolation also might promote enhancement of populations (Binns & Remmick 1994; Harig & Fausch 2002). Management agencies have been involved in reconnecting two isolated populations of Colorado River cutthroat trout in the Little Snake River drainage of Wyoming and Colorado by building a barrier to upstream fish migration downstream of the confluence of the streams and then poisoning non-native trout in the intervening waters (Young et al. 1996; Wyoming Game and Fish Department 1999). A similar project is now underway in the LaBarge Creek drainage of Wyoming, where several isolated populations of cutthroat trout (including those in Nameless and Clear creeks) will be united into a single, large population (Sexauer 2000).

Despite potentially serious drawbacks, isolation management may offer the only immediate solution for protection of native fishes that cannot withstand predation, hybridization, or competition with non-native species (Minckley et al. 1991; Shafer 1995). For example, native galaxiid fishes in New Zealand remain abundant only upstream of barriers that prevent colonization by non-native, piscivorous brown trout (Townsend 1996). Populations of genetically pure Yellowstone cutthroat trout may owe their persistence to irrigation diversion dams that prevent invasion by non-native trout (Kruse et al. 2000). Recovery of threatened greenback cutthroat trout has relied on establishing new populations isolated from non-native trout by natural or artificial barriers (Stuber et al. 1988; Harig et al. 2000).

However, an isolation approach combined with stocking did not achieve numerical enhancement of cutthroat trout populations during our study and may threaten longer-term viability by fragmenting populations of small size in restricted habitats. We urge careful consideration of the risks inherent in an isolation-management approach to the longer-term protection and enhancement of threatened populations prior to commitment of substantial resources to implement and maintain such a program. If isolation management of inland cutthroat trout appears to be the best option for immediate preservation of threatened populations, we suggest that isolated stream reaches be as long as possible and that habitat enhancements be considered to provide the full range of resources needed to sustain all life stages.

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