North American Journal of Fisheries Management 23:109–119, 2003

Can Anglers Influence the Abundance of Native and Nonnative Salmonids in a Stream from the Canadian Rocky Mountains?

ANDREW J. PAUL* AND JOHN R. POST

Department of Biological Sciences,
University of Calgary,
Calgary, Alberta T2N 1N4, Canada

JIM D. STELFOX

Alberta Sustainable Resource Development,
Number 100, 3115 12th Street Northeast,
Calgary, Alberta T2E 7J2, Canada

Abstract.—The proliferation of nonnative fishes throughout North America is a major concern for fisheries managers. In this paper, we evaluate the efficacy of selective harvest in reducing nonnative brook trout *Salvelinus fontinalis* and restoring native cutthroat trout *Oncorhynchus clarki* and bull trout *S. confluentus* populations in a small stream in the Canadian Rocky Mountains. From 1998 through 2000, groups of anglers have been involved in an organized program to selectively harvest brook trout from Quirk Creek, Alberta. Annual population estimates conducted by electrofishing indicate that selective harvest has had little effect on the brook trout population. Bayesian estimates of species catchability (i.e., proportion of vulnerable population caught per unit of angling effort) differed significantly between native and nonnative species, the catchability of native species being 2.5-fold greater than that for nonnatives. Using population models, we show that the lower catchability of brook trout coupled with their fast growth and early maturity make them resilient to angling exploitation. Higher catchability, slower growth, and later maturity of the native species make them extremely sensitive to overexploitation. Furthermore, the increased angling effort associated with a brook trout suppression program may be accompanied by sufficient incidental mortalities of native species as to prevent their recovery or lead to further declines. We conclude that the use of selective harvest to reduce nonnative brook trout populations in western North America requires further study before being accepted as an effective method.

Nonnative salmonids have been introduced into western North America since the latter part of the 19th century (Rahel 1997). Although some introductions had limited success in establishing wild populations, many introductions established naturally reproducing populations and have threatened regional biodiversity (Rahel 1997, 2000). At about the same time that fish introductions began in the Rocky Mountains of western Canada, declines of native salmonids were being recognized (Prince et al. 1912). Hypothesized mechanisms for the decline included overfishing, entrainment of fish in irrigation canals, and pollution (Prince et al. 1912). These factors read as a litany of hypotheses that could have been drafted nearly 100 years later, with one notable exception: competition from nonnative fishes.

The replacement of native fish populations by nonnatives may have been first recognized in western North America during the 1930s, associated with the disappearance of the once famous cutthroat trout *Oncorhynchus clarki* fishery in Lake Tahoe and the simultaneous proliferation of nonnative lake trout *Salvelinus namaycush* (Cordone and Frantz 1966). Direct competition among fishes has been hypothesized as a mechanism behind such species shifts (Griffith 1988), but conclusive studies are lacking (Fausch 1988). Fausch (1988) argued that empirical experiments to test the effects of introduced fishes on native species would require the comparison of interspecific versus intraspecific competition under relevant conditions; such studies are few (e.g., Byorth and Magee 1998).

Other studies have noted that anglers may be important in influencing the distribution of native and nonnative fishes because native fishes tend to be more susceptible to angling (MacPhee 1966; Marshall and MacCrimmon 1970). Conversely, reduction of nonnative fishes through their selective harvest by anglers has been proposed as a mechanism for increasing the abundance of native fishes (Larson et al. 1986). Although angling harvest is acknowledged as a potential mechanism in deter-

* Corresponding author: ajpaul@ucalgary.ca

Received July 26, 2000; accepted May 7, 2002

mining species distributions (Fausch and White 1981; Griffith 1988), it rarely has been assessed in the fisheries literature (e.g., Larson et al. 1986; Beamesderfer et al. 1996).

The objective of the present study was to quantitatively assess the ability of anglers to reduce nonnative brook trout *S. fontinalis* populations in streams from the Canadian Rocky Mountains. To address the problem, we used empirical data from a brook trout suppression project (BTSP; Stelfox et al. 2001) and age-structured population models. The BTSP relied on anglers attending organized trips to selectively harvest brook trout from Quirk Creek in southwestern Alberta. The models used data derived from the project (and other sources where necessary) to evaluate the potential success of the suppression program. Success was defined as a decrease in brook trout abundance and an increase in native salmonid populations.

Study Area

Quirk Creek drains into the upper Elbow River, which forms part of the Bow River drainage in southern Alberta. The creek originates at an elevation of 1,640 m and flows for 11.6 km before joining the Elbow River at an elevation of 1,530 m (Figure 1). The lower reach of the creek (reach 1) flows through forest with overhanging willow *Salix* spp. and alder *Alnus* spp. (Tripp et al. 1979). The upper two reaches (reaches 2 and 3) form the majority of Quirk Creek and flow through a large meadow dominated by grasses and shrubs. The mean wetted width in these upper reaches is approximately 3.6 m. The gradient of the upper reaches is 1.5% and increases in the lower reach (A. J. Paul, unpublished data). The fish community of Quirk Creek consists of two native species, cutthroat trout *Oncorhynchus clarki* and bull trout *S. confluentus*, and the nonnative brook trout. Brook trout were first introduced into the Elbow River drainage in 1940. Despite this early introduction into the upper Elbow River, brook trout were present only in reach 1 of Quirk Creek in 1978 (Tripp et al. 1979). Cutthroat trout and bull trout were the only fish species present in the upper two reaches in 1978.

Angling regulations governing Quirk Creek have varied substantially over the years. The daily bag limit for all trout captured from Quirk Creek before 1974 was 10, reduced to 5 in 1976, with no size limit. For bull trout, the daily bag limit was reduced to five in 1974 and to two in 1984. In 1987, minimum size limits of 25 and 40 cm were implemented for cutthroat trout and bull

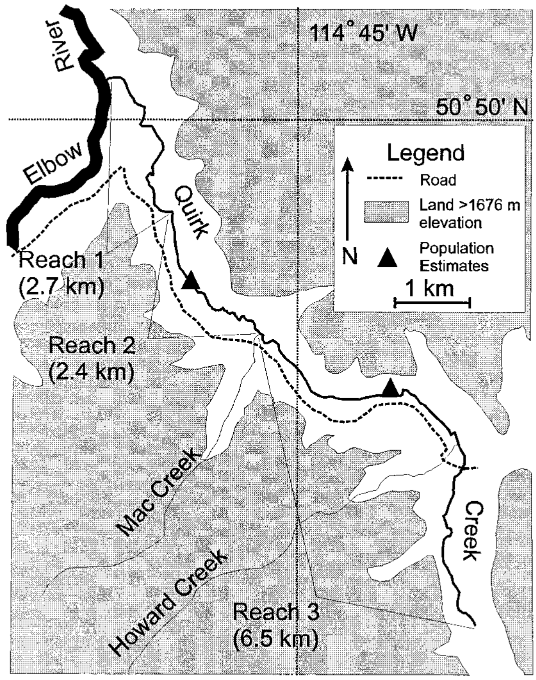

FIGURE 1.—Map of Quirk Creek (Alberta, Canada), showing locations of the reaches and sites used for population estimates.

trout, respectively. Then in 1995, provincewide regulations prohibited any harvest of bull trout. Finally, in 1998 the entire length of Quirk Creek was designated as catch-and-release fishing for all fishes. This latter regulation was implemented as part of the BTSP described below.

Methods

Brook trout suppression.—From 1998 through 2000, the BTSP was carried out to assess the efficacy of anglers in removing brook trout from Quirk Creek. From July to October, groups of anglers were taken on organized trips to participate in the program. Only anglers who had passed a detailed fish identification test were allowed to participate in the program. The fish identification test consisted of 17 photographs (decreased to 16 in 1999) of the three salmonid species at various life stages. Anglers had to achieve a grade of 100% to pass the test. Anglers who passed the test and attended an organized trip harvested all brook trout they captured in Quirk Creek. In 1998 and 1999, the BTSP was confined to the uppermost reach of Quirk Creek (reach 3). The remaining reaches (1 and 2) were still catch-and-release only. By 2000, the BTSP was expanded so that anglers harvested brook trout from reach 2 as well. For the purpose of this study, we focus on the angling data obtained only from reach 3 because of the 3-year time series for this reach. Movement of brook trout, as determined by the recapture of marked fish, from reach 2 to reach 3 during the summer was negligible and probably was restricted by the small beaver dams separating the reaches (Stelfox et al. 2001). A summary of angling data for all reaches can be found in Stelfox et al. (2001).

Anglers participating in the program kept careful records of their total time fishing and the number and estimated length (nearest 5 cm) of all cutthroat trout and bull trout they had caught and released throughout the day. At the completion of the day's fishing, all anglers reported to a designated station where they turned in their brook trout harvest for counting and measuring. Brook trout were measured for fork length (FL; mm) and weight (g).

Population estimates.—Population estimates were conducted at two sites on Quirk Creek by electrofishing (Figure 1). Population estimates in reach 2 were carried out in 1987 and from 1995 to 2000. Population estimates in reach 3 were done from 1998 to 2000. The electrofishing took place during mid-August to early September. In 1987, a mark–recapture study design was used in reach 2 over 1,033 m with 5 days separating the marking and recapture phases. The remainder of the estimates used a depletion design, with at least three removal passes completed for each estimate. The reach length for the depletion estimates ranged from 380 to 500 m. Fish were identified and measured. Some of the brook trout and cutthroat trout sampled in 1987 were collected for aging (by means of otoliths) and determining age at maturity.

The mark–recapture estimate used Chapman's modification of the Petersen–Lincoln estimator (White et al. 1982). A 95% confidence interval for this estimate was determined by using likelihood profiles and assuming that the number of marked recaptures followed a binomial distribution (Hilborn and Walters 1992). Depletion estimates were based on the generalized removal model of Otis et al. (1978). The 95% confidence intervals for these estimates were also constructed by using likelihood profiles that assumed a binomial distribution for each removal pass (Otis et al. 1978). We generated abundance estimates for different size (FL) groupings of fish, including all sizes combined, smaller than 101 mm, 101–150 mm, 151–200 mm, and larger than 200 mm. Abundance estimates from the size groupings were used in calculating total vulnerable population (see equation [3]).

Population model and parameter estimation.—Age-structured population models were used to simulate the effects of the BTSP on the three fish species present in Quirk Creek. The models were formulated in discrete time, with each age-class being updated annually. We assumed the modeled population occupied a 5-km stretch of stream similar to reach 3 of Quirk Creek (Figure 1). The biological component of the model consisted of growth, natural mortality, fecundity, and egg survival. The fishery component consisted of size-dependent vulnerability, catchability, total angling effort, legal harvest, and hooking mortality.

Size-dependent growth and fecundity estimates for each species were based on empirical data collected from Quirk Creek. We assumed that growth followed a von Bertalanffy growth curve (Ricker 1975). The growth curve was fit to age-at-length data from Tripp et al. (1979), a subsample of fish collected during the 1987 population estimates, and a sample of brook trout captured by angling in 1998. Growth curves were fit to the empirical data by using least-squares regression. Using the same data sources, we determined age at maturity for each species as the year in which more than 95% of females reached maturity. We also noted the proportion of females that matured in the previous year and assumed a similar proportion of spawning females in the model.

The length–fecundity relations for female brook trout and cutthroat trout were based on the data of Tripp et al. (1979) collected from Quirk Creek and other nearby streams. Because there was no significant difference between the relations for these species (Tripp et al. 1979), we used the equation for brook trout (eggs $= 7.0 \cdot \mathrm{FL}$ [mm] $- 819$) for both species. This relation does not differ significantly from that reported in Goetz (1989) for bull trout and Dolly Varden *S. malma*. Therefore, the one length–fecundity equation was used for all three species. We also assumed a 1:1 sex ratio for each species and assumed that, once mature, all individuals spawned in consecutive years.

Natural mortality and egg survival were determined heuristically and from the literature. Yearly mortality for salmonids age 1 and older is on the order of 0.30–0.70 (cf. Rieman and McIntyre 1993), so we adjusted the natural mortality rates within this range for each of the three species such that their average lifetime reproductive outputs were similar (Gurney and Nisbet 1998). Essentially we imposed the condition that neither early or late maturity would result in females of any species producing more eggs over their expected lifetime when fishing mortality was absent. The number of eggs that successfully hatched to form an age-0 cohort was modeled as an asymptotic function of initial egg number. We assumed the maximum number of age-0 for a species in a given year to be 3,250 (or 650 age-0 fish/km). This value was based on back-calculating age-0 densities from observed maximum densities of age-1 brook trout in Quirk Creek, assuming mortality in the first year was 70%. The initial steepness of the curve was set such that half the maximum age-0 density is achieved when egg deposition equals 62,500 eggs, which is the estimated egg production of 110 adult brook trout 200 mm FL. We assumed the same egg survival curve for each species.

Our models assume no interactions among species. We wanted to answer the primary question as to whether observed growth, fecundity, and maturity coupled with angling could result in differential population effects among species. The introduction of interspecies interactions would result in an added and unwarranted level of complexity. First, interactions among native and nonnative salmonids are poorly understood (Fausch 1988), which leaves us with little guidance for constructing functional relations that would describe species interactions. Second, we think that what can be learned from direct fish–angler interactions is itself informative without having to introduce interactions among fishes.

We assumed the total angler's catch (C) for a given species in a year could be described by the equation

$$C = qEV, \tag{1}$$

where q is catchability (fish caught/[fish vulnerable · unit effort]), E is the measure of effort (rod-hours/year), and V is the size of the vulnerable population. The vulnerability (v) of an individual fish to anglers was assumed to increase sigmoidally with size according to the function

$$v = \alpha(1 - e^{-\beta(\mathrm{FL})})^{\gamma}, \tag{2}$$

where α, β, and γ are empirically fitted parameters and FL is fork length. We constrained size-dependent vulnerability to range from 0 to 1, with 0 being completely invulnerable and 1 fully vulnerable. Under this condition, the parameter α equals 1. Parameters for equation (2) were determined from the size distribution of brook trout in the electrofishing catch and in the angler's catch taken within 1 week of the electrofishing (reach 3 only). This approach assumes that electrofishing provides an unbiased size distribution for fish greater than the minimum size caught by anglers (>120 mm). Brook trout were broken down into 10-mm size-groups; for each group the number in the angling catch was divided by the electrofishing catch. This was repeated for all size-groups and the final proportions were standardized to range between 0 and 1. In cases where a size-group appeared in the angling catch but not in the electrofishing catch, the standardized proportion was set to 1. Equation (2) was then fit to the standardized proportions by using least-squares regression. Data for cutthroat trout and bull trout were not directly used for fitting equation (2) because sizes from the angling catches would have been based on imprecise visual estimates at 5-cm increments. However, we did plot standardized proportions for these two species to see if they were similar to the brook trout data.

Once the size-dependent vulnerability (v) is determined, the total vulnerable population (V) for a species can be estimated from

$$V = \sum_{i=1}^{s} v_i N_i \tag{3}$$

where s is the maximum number of size classes and N_i is the abundance of size-class i. The values for N_i were determined from the electrofishing data. The catchability parameter q from equation (1) can now be solved directly for each species. However, to both address uncertainty in our species-specific estimates of q and effectively incorporate data collected from reach 3 over the 3 years, we used a Bayesian approach to define a probability density function (PDF) for q. Assuming that C, E, and V for each year are known with certainty and that C follows a Poisson process, then the posterior PDF for q can be determined (see Appendix) as

$$f_{\mathrm{post}}(q) = \frac{\exp\left(-q \sum_{j=1}^{y} E_j V_j\right)\left(q \sum_{j=1}^{y} E_j V_j\right)^{\Sigma_{j=1}^{y} C_j}\left(\sum_{j=1}^{y} E_j V_j\right)}{\Gamma\left[\left(\sum_{j=1}^{y} C_j\right) + 1\right]} \tag{4}$$

where y is the total number of sampling events for which C, E, and V were determined. Our derivation of equation (4) assumes that the PDF for q remains

TABLE 1.—Variables whose values change with implementation of the brook trout suppression program (BTSP) during model simulations. Pre-BTSP and BTSP values are shown for each of the three species; n.a. = not applicable.

Variable	Brook trout		Cutthroat trout		Bull trout	
	Pre-BTSP	BTSP	Pre-BTSP	BTSP	Pre-BTSP	BTSP
Effort (rod-hours/year)	200	656	200	656	200	656
Size limit (mm)	None	None	250	n.a.	400	n.a.
Bag limit	None	None	2	0	2	0

stationary with respect to changes in V. The maximum likelihood estimate of q (q_{MLE}) can be determined by differentiating equation (4) and solving at 0, which leaves

$$q_{\mathrm{MLE}} = \frac{\sum_{j=1}^{y} C_j}{\sum_{j=1}^{y} E_j V_j}. \tag{5}$$

The q_{MLE} for each species was used in the population models. Because q can be difficult to interpret, we defined one final parameter, E_v, which is the effort required to catch the vulnerable population. The parameter E_v is the inverse of q and has the units of rod-hours.

Simulations were run such that, prior to time zero, the model was at equilibrium conditions under the pre-BTSP harvest regulations and levels of angling effort (Table 1). After $t = 0$, the BTSP was implemented in the model (Table 1). The maximum effort of 656 rod-hours/year came directly from the angling effort in 1999. The preprogram effort was arbitrarily set at one-third of this maximum effort (Table 1). The model was qualitatively insensitive to the value of preprogram effort (provided this effort was sufficiently low to permit population persistence); however, the preprogram effort did affect the magnitude of model predictions. Size and bag limits were based on provincial regulations that governed the fishery in Quirk Creek before the start of the removal program. We assumed that the hooking mortality rate for fish that were caught and released ranged from 1% to 5%, which represents relatively low rates from the literature (Muoneke and Childress 1994). We also assumed no illegal harvest. Finally, the simulations were run for 5 years after the start of the suppression program.

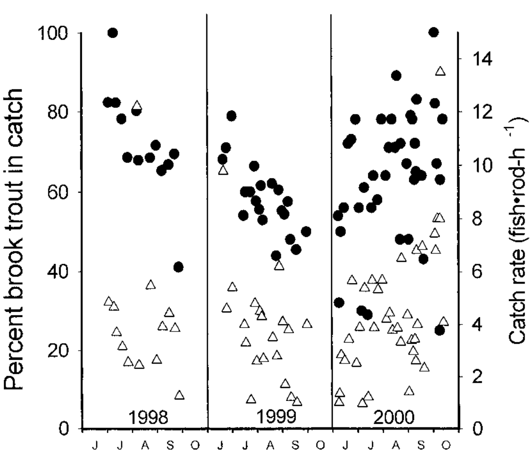

FIGURE 2.—Observed catch rates for all species (triangles; right scale) and percentage of brook trout in the angling catch (circles; left scale) for the first 3 years of the brook trout suppression program in Quirk Creek. The letters along the horizontal axis designate the months June through October.

Results

Brook Trout Suppression Program

A total of 436, 656, and 477 rod-hours per summer of effort (reach 3 only) were used in the BTSP from 1998 to 2000, respectively. This effort resulted in anglers harvesting 1,076, 1,412, and 1,128 brook trout in each of the respective years. Anglers caught 349, 735, and 522 cutthroat trout and 63, 161, and 68 bull trout, respectively, in those years. The percentage of brook trout in anglers' catches declined over the first 2 years of the program from more than 80% in 1998 to around 50% by 1999 and increased again in 2000 (Figure 2). Catch rates for all species combined remained relatively constant at approximately 3.5 fish/rod-hour (Figure 2).

Population Estimates

Cutthroat trout were the most abundant species in 1987, followed by brook trout and then bull trout (Figure 3a). The 1987 finding was the first report of brook trout presence in the upper two reaches of Quirk Creek. From 1995 on, brook trout were the most abundant species in the creek, followed by cutthroat trout and then bull trout. Brook trout densities for reach 2 increased from 76 fish/km (all

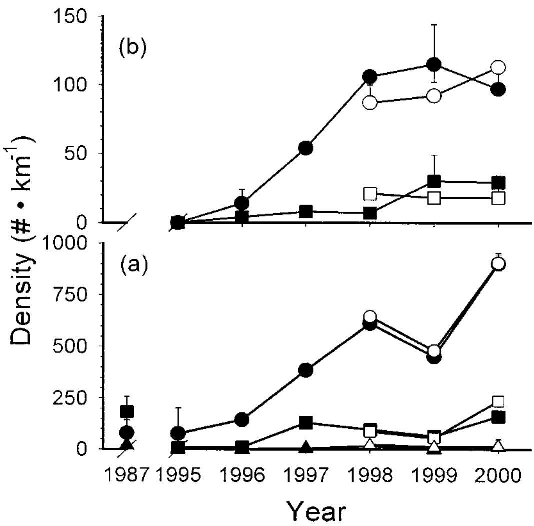

FIGURE 3.—Estimated densities of fishes in Quirk Creek as determined by electrofishing. Panel **(a)** is for all fish captured, panel **(b)** for fish larger than 200 mm FL. Error bars are 95% confidence intervals. Brook trout are represented by circles, cutthroat trout by squares, and bull trout by triangles. Closed symbols are for estimates from reach 2 and open symbols for estimates from reach 3. Missing symbols for bull trout in some years indicate that too few fish were captured to obtain a population estimate.

sizes combined) in 1995 to 900 fish/km in 2000 (903 fish/km in reach 3). This peak in 2000 was largely the result of a strong year-class of age-0 brook trout. Bull trout densities ranged from too few to detect to a high of 21 fish/km (reach 3) in 1998. There was little within-year variability between reaches 2 and 3 for estimated densities of cutthroat trout or brook trout. For cutthroat trout, the largest coefficient of variation (CV; = SD/mean) in population estimates between reaches was 27% (2000), the average CV over the 3 years being 15%. This variability was even lower for brook trout, the maximum CV being 4.3% and the average CV 2.7%.

Densities of large brook trout (>200 mm FL) increased from 1996 to 1998, leveling off at 100 fish/km from 1998 to 2000 (Figure 3b). Although no data exist for reach 3 before 1998, both reaches showed roughly similar trends in densities of large brook trout from 1998 onward, even though reach 2 had no angling harvest during 1998 and 1999. Except in 1998, densities of large cutthroat trout also showed similar trends between reaches 2 and 3.

Population Models

Parameterization.—Age-at-length data for Quirk Creek indicated that brook trout growth rates were faster than those of either cutthroat trout or bull trout (Figure 4). Age-1 and age-2 brook trout reached mean sizes of 127 and 210 mm FL, respectively, whereas cutthroat trout or bull trout at similar ages were smaller. The estimated mean asymptotic size for brook trout (297 mm FL) was smaller than that of cutthroat trout (317 mm FL) or bull trout (339 mm FL); however, the differences were not statistically significant (standard errors 20–30 mm).

Age-at-maturity data for Quirk Creek showed that female brook trout matured at an earlier age than did female cutthroat trout or bull trout (Figure 4). Data collected in 1978 (Tripp et al. 1979), 1987, and 1998 indicated that more than 95% of female brook trout had matured by age 2. In contrast, 95% of female cutthroat trout matured by age 5 and bull trout by age 6. No female brook trout were mature at age 1. We used age 2 as the threshold for the entrance of brook trout into the spawning population. Cutthroat trout and bull trout, on the other hand, showed a proportion of females (range, 20–70%) maturing 1 year earlier than their respective maturity ages stated above. To account for this, we assumed in our models that 50% of the female cutthroat trout matured at age 4 and 50% of the female bull trout matured at age 5.

Size-dependent vulnerability for brook trout indicated they first become vulnerable to angling at about 125 mm FL and are fully recruited to the angling catch at sizes larger than 270 mm FL (Figure 5). Data for cutthroat trout and bull trout showed a size and angling relation similar to that for brook trout (Figure 5); thus, we utilized the relationship for brook trout to describe size-dependent vulnerability for all three species in the population models.

The angler catch, made within 1 week of the population estimates, indicated that many of the vulnerable cutthroat trout and bull trout were caught and released during this period (Table 2). In contrast, only one-quarter to one-half of the vulnerable brook trout were caught during the same period. These differences indicate that the catchability of cutthroat trout and bull trout was 2.5-fold greater than that for brook trout (Figure 6). The maximum likelihood estimate for E_v, the effort needed to catch the vulnerable population, was 259 rod-hours for brook trout. In contrast, the estimates were 90 and 109 rod-hours for cutthroat trout and bull trout, respectively. Although we had only 3 years of data, we saw no indication that catchability for any species showed a directional change among years (Table 2).

Simulation.—The results from the model sim-

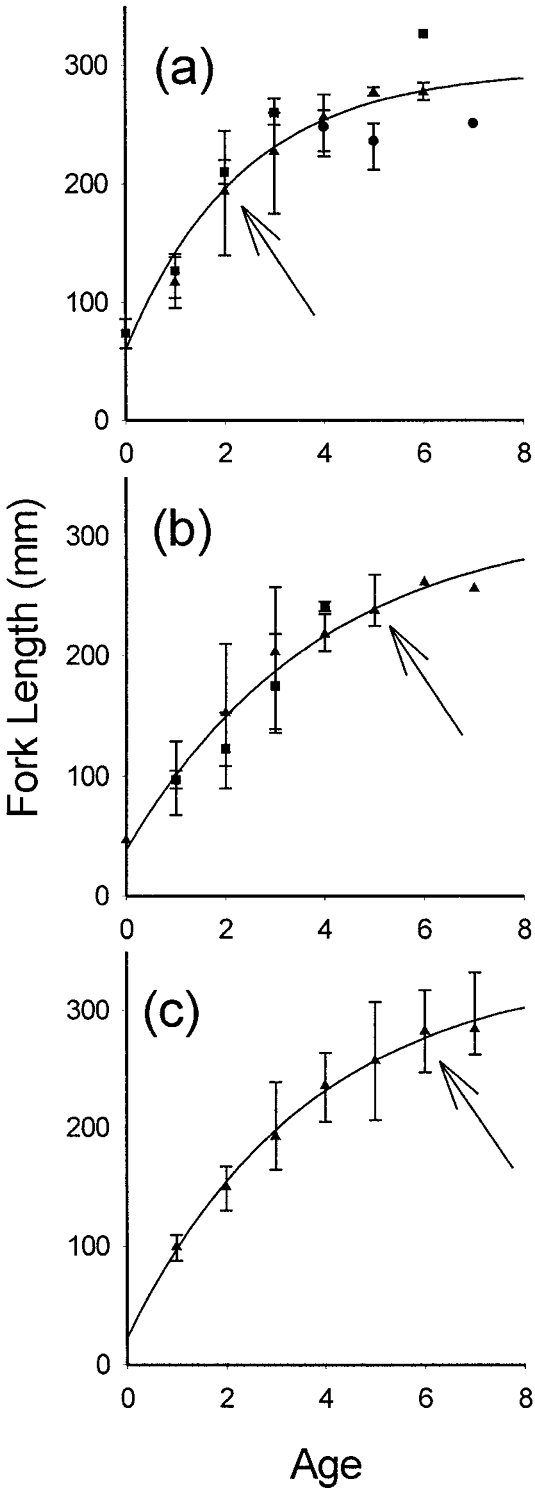

FIGURE 4.—Age at length and maturity for **(a)** brook trout, **(b)** cutthroat trout, and **(c)** bull trout in Quirk Creek. Vertical bars show the ranges. Triangles are for

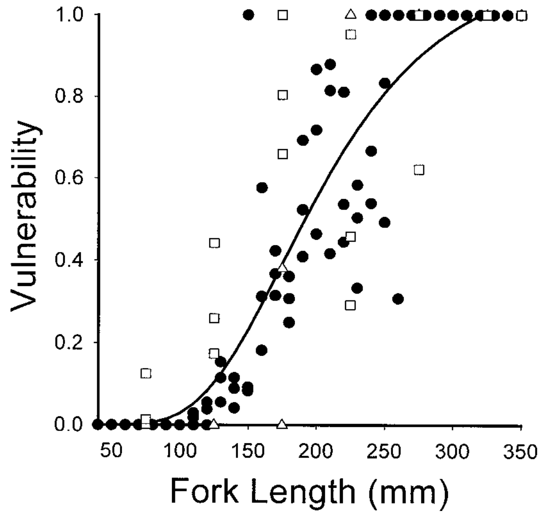

FIGURE 5.—Size-dependent vulnerability of fishes to anglers in Quirk Creek for 1998–2000. Circles are for brook trout, squares for cutthroat trout, and triangles for bull trout. The line shows the nonlinear regression fit of equation (2) to the brook trout data.

ulations show that the proportion of brook trout in the angling catch would decrease over the first 2 years of the simulated BTSP, from 31% of the catch at time zero to 25% after 2 years (Figure 7). After year 2, the modeled percentage of brook trout in the angler catch increased to 30% by year 5. Catch rates decreased slowly over the first 5 years of the project, from a high of 10 fish/rod-hour of effort in the first year to 6 fish/rod-hourof effort by year 5 (Figure 7).

Densities of all fishes could decrease under the simulated BTSP (Figure 8). Densities of age-1 and older brook trout decreased by approximately 8% after 5 years, most of the decrease occurring within the first year. For adult brook trout, the decrease was by about 50% from the initial adult population (Figure 8). However, despite more restrictive regulations on cutthroat trout and bull trout (Table 1), the populations of those fish declined or remained stable after the program started. At hooking mortality rates of 5%, populations of bull trout and

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data presented in Tripp et al. (1979). Squares are for brook trout and cutthroat trout collected from reach 2 during the 1987 population estimate. Circles are for brook trout collected by anglers in 1998 from reach 3. The solid line is the von Bertalanffy model fit to the data. Arrows indicate when more than 95% of females were mature.

TABLE 2.—Catch, effort, size of the vulnerable population (V), and catchability (q) for brook, cutthroat, and bull trout in Quirk Creek from 1998 to 1999. The vulnerable population was determined from population estimates (four size-classes; see Methods) for reach 3 expanded over the 6.5 km of that reach and corrected for size-dependent vulnerability (equation 2; Figure 5). Catch (numbers) and effort (rod-hours) are based on angler creel surveys conducted within 1 week of the population estimate for a given year.

Species	Year	Catch	Effort	V	q
Brook trout	1998	203	79.5	687	3.72×10^{-3}
	1999	258	124.75	529	3.91×10^{-3}
	2000	206	62	842	3.95×10^{-3}
Cutthroat trout	1998	78	79.5	85	1.15×10^{-2}
	1999	133	124.75	83	1.28×10^{-2}
	2000	77	62	151	8.22×10^{-3}
Bull trout	1998	19	79.5	36	6.64×10^{-3}
	1999	43	124.75	19	1.81×10^{-2}
	2000	7	62	37	3.05×10^{-3}

cutthroat trout would decline by 62% and 30%, respectively, within 5 years. Although not shown, hooking mortality rates of 10% or more would result in extinction of the simulated bull trout and cutthroat trout populations. Even at hooking mortality rates of 1%, native populations would not increase under the BTSP but rather would either remain stable or decline slowly.

Discussion

The observed decline in native cutthroat trout and bull trout populations and the subsequent increase in brook trout for Quirk Creek through the late 1980s and 1990s are similar to trends observed in the United States (Gresswell 1988). In fact, it was this decline in native fishes from Quirk Creek that prompted the start of the BTSP in 1998. The mechanism behind the switch from native to non-native populations in Quirk Creek is not known and probably will never be known conclusively. Conditions in Quirk Creek may have favored the competitive dominance of brook trout over cutthroat and bull trout (Griffith 1972; De Staso and Rahel 1994). However, our results show that the high catchability of cutthroat trout and bull trout, coupled with their later maturity and larger size at maturity, renders them more susceptible to overfishing than brook trout are. This mechanism has been referred to as the species replacement hypothesis (Griffith 1988), in contrast to the displacement hypothesis, which would arise from direct competition between species. Further experimental work will be required to evaluate the relative importance of these hypotheses, which are not mutually exclusive (e.g., Volpe et al. 2001).

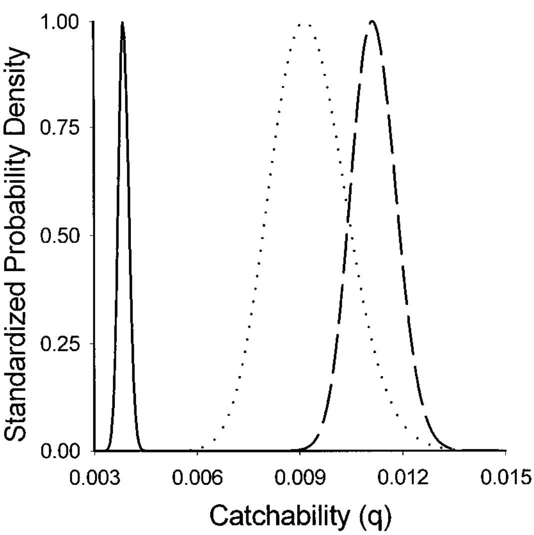

FIGURE 6.—Posterior probability distributions of catchability (q; fish caught/[fish vulnerable · rod-hours]) for brook trout (solid line), cutthroat trout (dashed line), and bull trout (dotted line). Probability densities were scaled to fall between 0 and 1.

An interesting aspect to the community structure of fishes in Quirk Creek is that brook trout were present in reach 1 but absent from reaches 2 and 3 (Figure 1) in 1978 (Tripp et al. 1979). By 1987, however, they were present in at least reach 2 and by 1995 were the dominant fish in both the upper reaches. If the species displacement hypothesis were true, then why were brook trout not present in the upper reaches until sometime during the 1980s? One hypothesis is that before the late 1970s, vehicle access to Quirk Creek was limited to off-road travel. Under these conditions, large populations of relatively unexploited cutthroat trout and bull trout may have prevented the successful colonization of brook trout into these upper reaches. In the late 1970s, a road was constructed that paralleled Quirk Creek along much of its length. This road, which bridged the Elbow River,

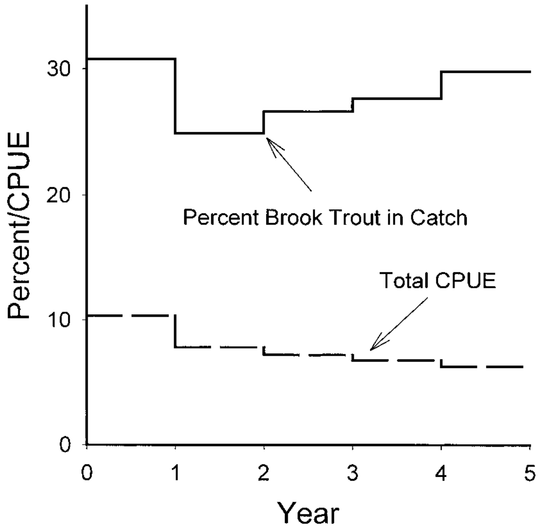

FIGURE 7.—Catch rates (CPUE; measured as fish/rod-hours) and percentage of brook trout in the angling catch for the first 5 years of simulated brook trout removal program.

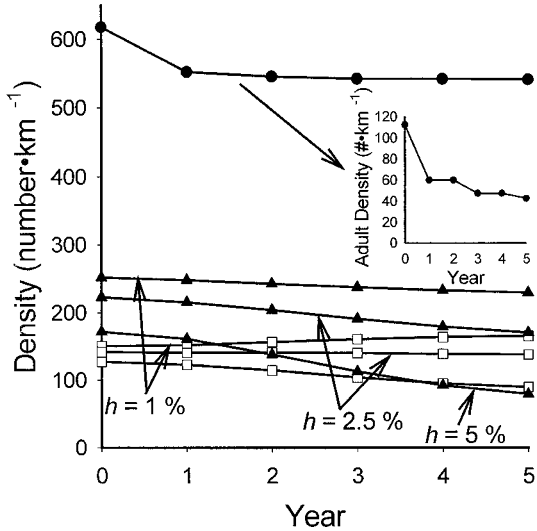

FIGURE 8.—Densities of age-1 and older brook (circles), cutthroat (squares), and bull (triangles) trout for the first 5 years of the simulated brook trout removal program. The densities of cutthroat and bull trout are shown under three different levels of hooking mortality (h). The inset graph shows results for adult brook trout only.

provided an easy means of vehicular access to Quirk Creek. Increased access may have pushed angling effort above sustainable levels for the native fishes, thereby allowing brook trout to occupy vacant niches.

For fish communities that have shifted to dominance by nonnatives, the question becomes, ''What tools does a resource manager have that could shift community structure back to dominance by the native species?'' If both species are strong competitors in the absence of angling effort, then closing the fishery will have no effect because the nonnative population will be resilient to reestablishment by the native community. However, the selective harvest of nonnative fishes by anglers may be a cost-effective tool for managers to reduce populations of nonnatives in mountain streams (Larson et al. 1986). If angling harvest for the native species goes to zero with selective harvest, then this technique can be used with little worry: Angling effort should simply be set as high as possible and everybody should hope that this is sufficient to reduce the nonnatives. However, angling harvest is unlikely to go to zero because hooking-related mortalities do occur. The manager is now faced with a dilemma: Is hooking mortality sufficient to result in declines of native populations? The answer to this question depends on three rates: those of hooking mortality, growth, and catchability. In the case of Quirk Creek, high catchability and low growth rate (i.e., late age-of-maturity) of native fishes means that hooking mortality will probably be a concern.

Model simulations for Quirk Creek support this concern. At hooking mortality rates exceeding 2.5%, native fishes declined under catch-and-release regulations because of the substantial angling effort in the BTSP (i.e., an average of 78 rod-hours $\cdot$ km^{-1} $\cdot$ year^{-1}). Although we did not explicitly consider the misidentification of fish species by anglers in our model simulations, such events would further increase the apparent hooking mortality rate. Therefore, levels of angling effort that may be utilized in BTSPs could have a detrimental effect on cutthroat trout and bull trout through increasing their hooking mortality.

Three years of brook trout removal by anglers and model simulations for Quirk Creek further suggest that brook trout populations may be extremely resilient to angling, given their ability to mature at small sizes and early ages. Similarly, Jensen (1971) and Donald and Alger (1989) observed that exploited populations of brook trout exhibited altered fecundity and maturity schedules that compensated for increased mortality. Donald and Alger (1989) also found that recruitment to age 1 increased under exploitation, which would further offset increased mortality from exploitation. Therefore, the selective harvest of brook trout by anglers may be ineffective in Quirk Creek, and similar streams, because of the resilience of these fish to angling exploitation.

In summary, 3 years of brook trout removal by anglers in a small, low-order stream from the foothills of the Canadian Rocky Mountains and model simulations suggest that these populations may be highly resilient to overexploitation. In contrast, native cutthroat trout and bull trout have higher catchabilities and mature at older ages than brook trout, which renders the former two species more susceptible to overexploitation than the latter. These differences in susceptibility to overexploitation could have shaped patterns of distribution between native and nonnative fishes at a regional scale, with native fishes persisting in areas that have always received low angling effort. The ability for selective harvest of brook trout by anglers to reverse this trend seems unlikely and may have an even further detrimental effect on native populations.

Acknowledgments

We are indebted to Dean Baayens (Trout Unlimited Canada) for organizing and overseeing the angler expeditions to Quirk Creek. We also thank the numerous volunteer anglers and students who have participated throughout the project. This research was financially supported by the Parks Venture Fund, Alberta Sustainable Resource Development, and the hunters and anglers of Alberta through the Challenge Grants in Biodiversity Program, Department of Biological Sciences, University of Alberta, and the Alberta Conservation Association.

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Appendix

Equation (4) arises from the notion that the gamma density function is the conjugate prior for a Poisson process (Hilborn and Mangel 1997). Although conjugate relations are well recognized in the statistical literature on Bayesian techniques, we feel it a useful exercise to derive equation (4), especially as it pertains to catch data. The PDF for a particular catchability q_i is

$$f_{\text{post}}(q_i \mid C, E, V) = \frac{\mathcal{L}(C \mid q_i, E, V) \cdot f_{\text{prior}}(q_i)}{\int_{q=0}^{\infty} \mathcal{L}(C \mid q, E, V) \cdot f_{\text{prior}}(q)\, dq} \qquad \text{(A.1)}$$

where C, E, V, and q are defined as before, $\mathcal{L}$ represents the likelihood of observing the data for a given value of q, and f_{prior} is the prior PDF for q. Assuming that the likelihood of observing C catches follows a Poisson process and that the prior probability for any q is uniform during the initial sampling event, then equation (A.1) becomes

$$f_{\text{post}}(q_i \mid C, E, V) = \frac{\dfrac{e^{-q_i VE}(q_i VE)^C}{C!} \cdot 1}{\displaystyle\int_{q=0}^{\infty} \dfrac{e^{-qVE}(qVE)^C}{C!} \cdot 1\, dq}. \qquad \text{(A.2)}$$

Writing the gamma function as

$$\Gamma(C) = \int_0^{\infty} e^{-r} \cdot r^{C-1}\, dr$$

and defining $r = qVE$ such that $dr = VE\, dq$, then after some algebra, equation (A.2) can be written

$$f_{\text{post}}(q_i \mid C, E, V) = \frac{e^{-q_i VE}(q_i VE)^C VE}{\Gamma(C + 1)}. \qquad \text{(A.3)}$$

If equation (A.3) is now used for the prior density function in equation (A.1), we can derive the general PDF of equation (4).