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Non-indigenous brook trout and the demise of Pacific salmon: a forgotten threat?

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Non-indigenous species may be the most severe environmental threat the world now faces. Fishes, in particular, have been intentionally introduced worldwide and have commonly caused the local extinction of native fish. Despite their importance, the impact of introduced fishes on threatened populations of Pacific salmon has never been systemically examined. Here, we take advantage of several unique datasets from the Columbia River Basin to address the impact of non-indigenous brook trout, *Salvelinus fontinalis*, on threatened spring/summer-run chinook salmon, *Oncorhynchus tshawytscha*. More than 41 000 juvenile chinook were individually marked, and their survival in streams without brook trout was nearly double the survival in streams with brook trout. Furthermore, when brook trout were absent, habitat quality was positively associated with chinook survival, but when brook trout were present no relationship between chinook survival and habitat quality was evident. The difference in juvenile chinook survival between sites with, and without, brook trout would increase population growth rate (λ) by *ca.* 2.5%. This increase in λ would be sufficient to reverse the negative population growth observed in many chinook populations. Because many of the populations we investigated occur in wilderness areas, their habitat has been considered pristine; however, our results emphasize that non-indigenous species are present and may have a dramatic impact, even in remote regions that otherwise appear pristine.

Keywords: chinook salmon; population growth rate; habitat quality; endangered species; non-indigenous species

1. INTRODUCTION

Human activities now routinely defeat natural barriers to species dispersal, resulting in rapid homogenization of the earth's biota. Accidental and deliberate species introductions are now occurring at unprecedented rates (D'Antonio & Vitousek 1992), and may be the most severe environmental threat the world now faces (Vitousek 1994; Kareiva 1996). Although as few as 10% of introduced species become established (Williamson 1996), non-indigenous species have the potential to severely alter the structure and function of native communities (Miller 1989; Vitousek 1990; Spencer *et al.* 1991; Grosholz *et al.* 2000). Even in designated wilderness areas or nature reserves, the effects of exotic species are pronounced. In fact, non-indigenous species are established in virtually every wilderness area in the United States (Cole & Landers 1996).

Freshwater systems have experienced a rapid decline in their native biota, with at least some of this decline attributable to non-indigenous species (Moyle *et al.* 1986). Fishes, in particular, have been intentionally introduced worldwide, usually to improve local fisheries or enhance recreational opportunities (Gido & Brown 1999; Rahel 2000). Such tinkering with fish faunas through species transfers dates back at least three millennia (Courtenay 1995). In North America, at least 140 species of freshwater fishes have had their ranges artificially expanded through 901 successful introductions (Rahel 2000). Most successful introductions of fishes in North America have occurred in species-depauperate regions in the west, where exotic species comprise up to 59% of the fish fauna (Moyle *et al.* 1986; Gido & Brown 1999). Because non-indigenous fishes are so ubiquitous and successful, they may alter communities at regional scales.

In the Columbia River Basin, the century-long decline of anadromous Pacific salmon towards extinction has been well documented and is now one of the United States' most contentious environmental issues (Mann & Plummer 2000; Levin & Schiewe 2001). The misuse of fish hatcheries, dams, over-exploitation and habitat degradation have all been implicated in the demise of salmon in the Columbia River Basin (NRC 1996). However, the impact of introduced fishes on native salmon has never been systemically examined, even though introduced fishes have commonly caused the local extinction of native fishes elsewhere (Moyle *et al.* 1986). Since the late 1800s, over 20 species of fishes have been introduced into the Columbia River Basin, and some of these fish have become well established (Poe *et al.* 1994). At present, 20% of the fish fauna of streams located in designated wilderness areas are introduced species (e.g. Achord *et al.* 1997). Non-indigenous fishes present a potential risk to endangered salmon, and should be part of discussions of the 'salmon problem'.

Here, we take advantage of several unique datasets from the Columbia River Basin to address the impact of non-indigenous fishes on the survival of juvenile chinook salmon. We focus on the impact of brook trout, *Salvelinus fontinalis*. Brook trout are the most abundant exotic fishes in the spawning and rearing habitat of threatened spring/summer-run chinook salmon (Hall-Griswold & Petrosky 1996; Achord *et al.* 1997). They appear to easily outcompete anadromous salmon (Hutchison & Iwata 1997) and may be important predators of salmon eggs and juveniles (Johnson & Ringler 1979; Johnson 1981).

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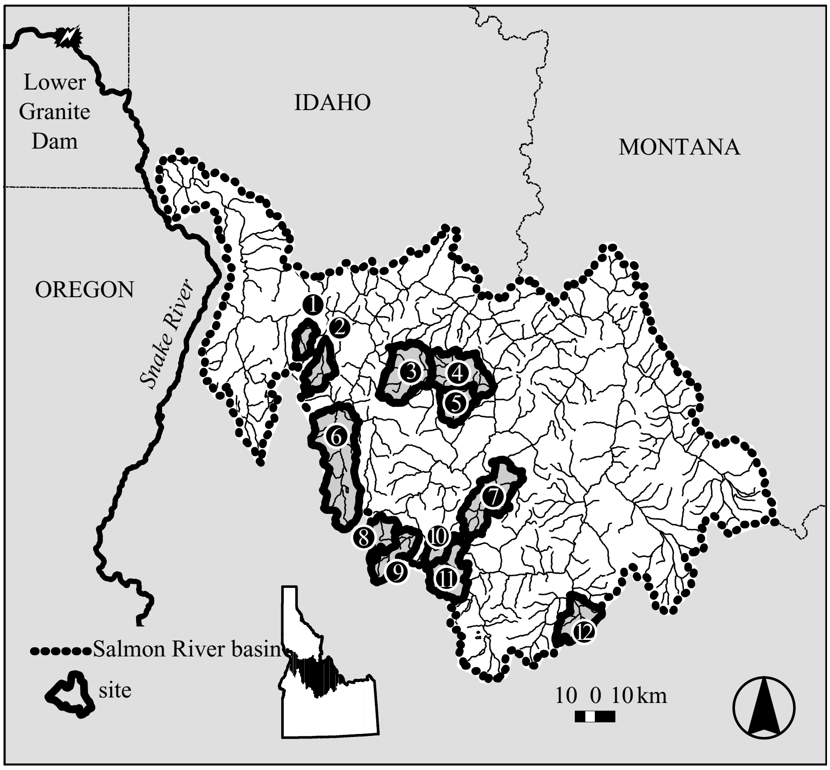

Figure 1. Twelve study sites. 1, Lake Creek; 2, Secesh River; 3, upper Big Creek; 4, lower Big Creek; 5, Rush River; 6, south fork Salmon River; 7, Loon Creek; 8, Elk Creek; 9, Bear Valley Creek; 10, Marsh Creek; 11, Valley Creek; 12, Herd Creek.

Specifically, we (i) document the distribution and relative abundance of brook trout in 12 streams in the Columbia Basin; (ii) examine the impact of brook trout on the survival of juvenile chinook salmon; and (iii) estimate the potential effects of brook trout removal on population growth of chinook salmon.

2. MATERIAL AND METHODS

(a) *Study sites*

The 12 study sites were located in the *ca.* 36 000 km^2 Salmon River basin (figure 1). The mainstem of the Salmon River drains into the Snake River, at 303 river km (measured along the length of the river) above the mouth of the Snake River. All sites were similarly situated within the basin averaging about 428 river km (s.d. = 86.4) above the mouth of the Snake River. Sites with brook trout present (see below) averaged 428.12 km (s.d. = 90.22) from the mouth of the Snake River; sites where brook trout were present averaged 428.10 km (s.d. = 95.20) from the Snake River mouth. This difference was not significant ($p = 0.99$). Human population density is low and timber harvesting, mining and agriculture (50% of the basin is allotted to livestock grazing) are the dominant land-use practices. Agriculture is particularly concentrated in the eastern part of the basin, and 600 water diversions for irrigation are associated with agricultural activities. There are 85 986 mining claims and 2789 mining hazard sites (ICBEMP 1999), but most mining activity ended decades ago. The US Forest Service and the Bureau of Land Management manage 89% of the basin, with 27% of the basin designated and managed as wilderness area.

(b) *Study species*

Brook trout are native to eastern North America, from Newfoundland to Hudson Bay and south to Georgia. They have been introduced for sport fishing by fishery agencies and private recreational fishing organizations since the 1800s and are now established in every western state in the US (Fuller *et al.* 1999). Generally, brook trout are among the most abundant fishes in the streams in which they occur (Hall-Griswold & Petrosky 1996; Achord *et al.* 1997; Maret *et al.* 1997).

Brook trout occur in clear, cool, well-oxygenated creeks, small to medium rivers, and lakes. They feed on a wide range of organisms including worms, leeches, crustaceans, insects, molluscs, fishes, amphibians and small mammals (Sigler & Sigler 1987; Karas 1997). They reach a maximum size of 860 mm; at our sites they averaged *ca.* 80 mm in length with a maximum of *ca.* 450 mm (Hall-Griswold & Petrosky 1996).

Adult chinook from the populations we examined migrate up the Snake River in March–July to spawn and produce juveniles that migrate downstream to the sea one year after emergence. These populations are referred to as 'spring/summer' because of the timing of adult migration. They are also categorized as 'stream-type' because they spend at least their first year of life in freshwater. We selected these populations (listed as threatened under the Endangered Species Act) because the National Marine Fisheries Service has tagged wild chinook parr with passive integrated transponder (PIT) tags since 1988. An expansion of this programme in 1992 provided data that allowed us to estimate rates of juvenile survival of the salmon (see below).

(c) *Brook trout distribution and relative abundance*

The distribution and abundance of brook trout have not been systematically investigated in the Columbia River Basin; however, independent research efforts conducted by the National Marine Fisheries Service (NMFS) and Idaho Department of Fish and Game (IDFG) designed to sample chinook parr also enumerated brook trout (and other fish species) as a routine part of their sampling in the Salmon River basin. Both of these efforts provided data that allowed us to document the distribution and relative abundance of brook trout in the Salmon River basin.

Idaho Department of Fish and Game has monitored juvenile spring/summer chinook salmon throughout the Salmon River basin since 1984, with data publicly available up to 1997. Fish are sampled in late summer and autumn following procedures similar to those described by Hankin & Reeves (1988). Several 100 m reaches within streams were delineated with flagging tape. Trained snorkelers then entered the water downstream of the selected reach and swam slowly upstream counting numbers of chinook salmon, brook trout and other fish species. Sampling was conducted by 1–5 snorkelers depending on the size of the stream. Petrosky & Holubetz (1984) and Hall-Griswold & Petrosky (1996) provide detailed descriptions of the IDFG sampling methods.

NMFS began a study in 1988 to PIT tag wild chinook parr in tributaries of the Snake River. During the late summer and early autumn of each year, NMFS electro-fished stream reaches in an effort to collect chinook salmon for tagging with minimal impact on the fishes. Electro-fishing was concentrated in areas within each stream where chinook abundance was highest. In addition to collecting juvenile chinook, all other species that were stunned by the electro-fisher were enumerated. Streams were only sampled in years when chinook abundance was relatively high (IDFG did not grant collection permits when chinook abundance was low). Data are available for our study sites in 1992, 1993, 1994, 1998 and 1999. Because this collection scheme was not designed to estimate abundances of fishes and also targeted areas of high chinook density, the numbers of brook trout generated by this effort are suspicious. Nonetheless, these data, in concert with those from IDFG, provided a relative index of brook trout distribution and abundance. A detailed description of NMFS sampling procedure is provided by Achord *et al.* (1994).

(d) *Survival rates of chinook salmon*

We estimated survival of chinook salmon from the summer of their first year when they were tagged to the following spring as they migrated downstream to the sea. Because only fishes larger than 55 mm in length can be PIT tagged (Achord *et al.* 1994, 1997), our survival estimates do not include smaller fishes. Our method for estimating survival relies on equipment at Lower Granite Dam (and dams downstream from Lower Granite Dam; figure 1) that automatically detects PIT-tagged fishes as they migrate downstream (Prentice *et al.* 1990). Survival can thus be estimated from the point of release in streams to Lower Granite Dam using the Cormack–Jolly–Seber (CJS) procedure (Cormack 1964; Jolly 1965; Seber 1965). A feature of the CJS release–recapture method is that not all individuals are detected at the site of interest, but subsequent detections allow for estimation of the probability of detection at that site. Survival from point of release to Lower Granite Dam was estimated as

$$\hat{S} = \frac{n/\hat{p}}{R},$$

where n is the number of fish detected at Lower Granite Dam, $\hat{p}$ is the probability of detection there and R is the release number. The probability of detection for each population and year was based on the number of individuals not detected at Lower Granite Dam and subsequently detected downstream, and the number of individuals detected at Lower Granite Dam and subsequently detected downstream (Burnham *et al.* 1987). Standard errors of the survival estimates were also calculated as described by Burnham *et al.* (1987, pp. 112–116).

The CJS method requires the assumptions that (i) the fate of each individual is independent of all others; (ii) all fishes in a group have equal survival and detection probabilities; and (iii) prior detection history has no effect on subsequent survival and detection probabilities (Skalski *et al.* 1998). Although we did not have enough downstream detections to test these assumptions explicitly, Skalski *et al.* (1998) found the survival estimates robust to many violations of assumptions.

(e) *Estimating effects of brook trout on juvenile survival and population growth of chinook salmon*

We used a general linear model to test the hypothesis that the presence of brook trout does not affect the survival of chinook salmon. We used average survival at each site as the response variable in this analysis because within-site survival may not be independent from year to year. Because we did not have absolute faith in the estimates of brook trout density produced by either NMFS or IDFG (see § 3), we categorized sites as those with or without brook trout. The presence or absence of brook trout and year were considered main effects in our model. As populations of chinook and brook trout may be affected by habitat quality, we included a conglomerate constructed by using principal component analysis on seven diverse measures of habitat as a covariate in our model. We characterized the habitat for each of the 12 sites using existing geospatial datalayers (table 1).

We chose seven measures of habitat based on available data (table 1). We defined the area of influence for each site as aggregations of catchments, similar in size to United States Geologic Survey 6th field hydrologic units that directly contacted any given site (figure 1). We carried out our geospatial data overlays in ARC/INFO using the INTERSECT command.

We then characterized each habitat class/sub-class in the watershed and reach analysis areas using an area-weighted mean for continuous variables, or by fraction of total area for categorical variables. Using principal component analysis, we reduced these seven variables and used the first principal component (which explained more than 50% of the variance) as a descriptor of habitat quality. Prior to analysis we tested for homogeneity of variances using Levene's test (Wilkinson *et al.* 1996), and we found no evidence of heteroscedasticity.

3. RESULTS

The abundance of brook trout varied significantly among our study sites using data gathered either by NMFS or IDFG (figure 2; for NMFS data, Kruskal–Wallis test statistic = 53.03; $p < 0.001$; for IDFG data, Kruskal–Wallis test statistic = 20.48; $p = 0.015$). Estimates of brook trout abundance by NMFS and IDFG were not significantly correlated ($r = 0.14$, $p = 0.50$); however, the rank order of brook trout abundance was correlated ($r = 0.70$, $p < 0.001$). These analyses suggest that estimates of brook trout densities were unreliable, but that we could separate sites into two categories for subsequent analyses: those sites with brook trout and those sites without brook trout (figure 2).

The seven habitat attributes we used to characterize sites, and thus our estimate of habitat quality, varied greatly among sites (table 1). The percentage cover of riparian wetlands, for example, ranged from a high of

Table 1. Habitat attributes of study sites.

site	riparian wetlands (non-forested)	1989 maximum temperature	diversions per 10 km^2	fraction of rangeland	cumulative annual precipitation (mm)	fraction of granitic bedrock	fraction of hillslope $< 1.5\%$
Bear Valley Creek	0.08	9.17	0.00	0.10	991.33	0.69	0.18
lower Big Creek	0.00	11.00	0.00	0.14	668.79	0.73	0.02
upper Big Creek	0.01	10.10	0.00	0.05	1231.78	0.49	0.04
Elk Creek	0.08	9.37	0.00	0.07	1002.70	0.76	0.19
Herd Creek	0.00	8.18	0.55	0.57	568.31	0.00	0.02
Lake Creek	0.01	10.80	0.00	0.03	1218.85	0.94	0.12
Loon Creek	0.01	9.06	0.44	0.17	553.31	0.37	0.01
Marsh Creek	0.06	9.69	2.00	0.12	698.12	0.81	0.17
Rush Creek	0.00	9.75	0.00	0.11	708.49	0.26	0.00
Secesh River	0.01	10.72	0.00	0.06	1319.37	0.94	0.09
south fork Salmon River	0.01	10.05	0.00	0.02	976.21	0.96	0.05
Valley Creek	0.05	9.72	4.12	0.15	621.10	0.50	0.17

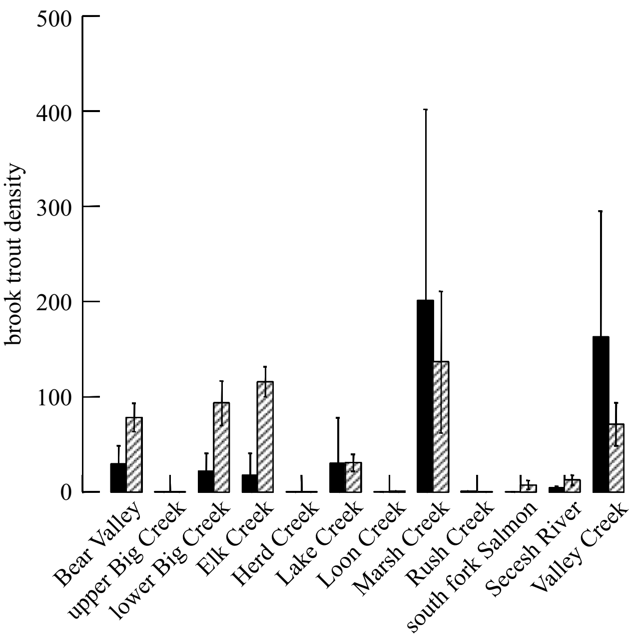

Figure 2. Average brook trout density (+1 s.e.) in 12 streams in the Snake River Basin as estimated by the Idaho Department of Fish and Game (IDFG; black histograms, number per 100 m^2) and the National Marine Fisheries Service (NMFS; hatched histograms, number per km^2).

nearly 9% at Elk Creek to a low of 0.23% at lower Big Creek. When we reduced these habitat attributes, using principal component analysis, to generate a single index of habitat quality, the component loadings for the first principal component suggested our habitat index represented a contrast between temperature, precipitation and geological features versus the percentage of rangeland and number of water diversions (table 2).

At our study sites, a total of 41 540 juvenile chinook were uniquely marked with PIT tags during the 5 years of our examination. Our estimates of survival of these juvenile chinook varied greatly among sites (table 3). Our estimates of survival, averaged across years, ranged from a low of 0.12 (s.e. = 0.02) in Valley Creek to 0.33 (s.e. = 0.02) at lower Big Creek. Over all sites, survival averaged 0.186 during the years that we investigated. Our point estimates of survival ranged from a low of 0.067 (s.e. = 0.007) in Valley Creek in 1994 to a high of 0.48 (s.e. = 0.184) in Rush Creek in 1992.

Table 2. Component loadings of the first principal component from principal component analysis of seven attributes used to characterize habitat quality.

habitat attribute	component loading
percentage of riparian wetland (non-forested)	0.265
maximum air temperature	0.757
number of diversions	−0.219
percentage of rangeland	−0.885
millimetres of precipitation	0.800
percentage of granitic bedrock	0.926
hillslope	0.465

Survival of chinook salmon nearly doubled from an average of 0.148 (s.e. = 0.007) in the presence of brook trout to 0.267 (s.e. = 0.02) in the absence of brook trout. Our general linear model revealed that survival of juvenile chinook was associated with the presence of brook trout, but that brook trout presence interacted with habitat quality to affect chinook survival (table 4; figure 3). In the presence of brook trout, mean survival of chinook was not related to habitat quality ($r^2 = 0.06$, $p = 0.56$). In contrast, when brook trout were absent, habitat quality was positively associated with average chinook survival ($r^2 = 0.97$, $p = 0.01$). Thus, when brook trout were present, chinook survival was depressed and not responsive to habitat quality, whereas in the absence of brook trout, survival was higher and positively associated with habitat quality.

4. DISCUSSION

Worldwide, freshwater ecosystems are among those habitats most affected by humans (Mooney & Hobbs 2000; Rosenberg *et al.* 2000). The damming and diversion of rivers, and the destruction of riparian habitats, have

Table 3. Estimates of juvenile chinook survival from the summer of their first year when they were tagged to the following spring.

site	1992			1993			1994			1998			1999		
	number released	estimated survival	s.e.	number released	estimated survival	s.e.	number released	estimated survival	s.e.	number released	estimated survival	s.e.	number released	estimated survival	s.e.
Bear Valley Creek	1014	0.160	0.026	856	0.215	0.020	1455	0.083	0.008	820	0.202	0.019	837	0.197	0.028
lower Big Creek	282	0.325	0.044	186	0.294	0.036	727	0.273	0.019	467	0.385	0.027	389	0.353	0.042
upper Big Creek	451	0.086	0.013	535	0.120	0.028	755	0.138	0.015	960	0.142	0.012	701	0.188	0.024
Elk Creek	628	0.116	0.017	998	0.158	0.016	1512	0.101	0.010	700	0.219	0.019	660	0.212	0.023
Herd Creek	224	0.150	0.035	119	0.168	0.037	534	0.148	0.020	959	0.186	0.014	315	0.201	0.032
Lake Creek	255	0.228	0.039	252	0.105	0.021	405	0.106	0.019	545	0.189	0.030	603	0.151	0.021
Loon Creek	261	0.347	0.136	396	0.259	0.038	964	0.189	0.016	1029	0.317	0.022	719	0.237	0.026
Marsh Creek	1000	0.133	0.014	944	0.183	0.019	1575	0.115	0.009	769	0.225	0.017	554	0.147	0.021
Rush Creek	25	0.480	0.184	10	0.200	0.126	15	0.267	0.114	27	0.259	0.084	0	—	—
south fork Salmon River	998	0.152	0.017	803	0.134	0.021	1571	0.090	0.009	998	0.120	0.012	1010	0.130	0.021
Secesh River	327	0.180	0.032	422	0.126	0.018	1549	0.128	0.011	936	0.144	0.015	907	0.158	0.018
Valley Creek	1026	0.080	0.012	848	0.132	0.017	1551	0.067	0.007	1001	0.188	0.014	1009	0.132	0.016

profoundly affected the integrity of freshwater systems (Kolar & Lodge 2000). The decline of aquatic and riparian communities of the Columbia River Basin could easily serve as an example of the severe problems challenging those charged with restoration of the flora and fauna of these systems. Although non-indigenous species may be the most important anthropogenic impact on freshwater systems (US Congress 1993; Naiman *et al.* 1995), their role in the demise of threatened salmon has been ignored (NRC 1996; ISG 1996). The evidence we present suggests that non-indigenous brook trout are abundant in at least a portion of the Columbia River Basin and have the potential to greatly affect efforts to restore populations of chinook salmon.

(a) *Potential mechanisms of brook trout impact*

We did not investigate the mechanisms underlying the patterns we observed, but several non-mutually exclusive processes may generate a negative relationship between brook trout and chinook salmon survival. Many of the systems where chinook spawn and rear are inherently nutrient poor (Bilby *et al.* 1996, 1998; Larkin & Slaney 1997; Wipfli *et al.* 1999), and the recent decline in nutrients provided by the carcasses of adults after they spawn has exacerbated this shortage (Gresh *et al.* 2000). It is possible that juvenile chinook survival is a function of food resources, and brook trout may intensify food limitation by competing with salmon. Additionally, brook trout aggressively defend feeding territories and appear to easily outcompete anadromous salmon (Hutchison & Iwata 1997). Because competition between brook trout and chinook parr has the potential to affect growth rates, and survival of juvenile salmon appears related to their size (Meekan *et al.* 1998; Einum & Fleming 2000), the patterns we report here may have been produced by competition for food.

Predation by brook trout on salmon eggs and parr may also underlie the patterns we observed (Krueger & May 1991). Brook trout are voracious predators, and they frequently consume juvenile salmonids (Sigler & Sigler 1987; Karas 1997). Additionally, brook trout appear to be important predators of salmon eggs (Karas 1997). Johnson (Johnson & Ringler 1979; Johnson 1981), for example, reported that salmon eggs comprised between 38 and 95% of the diet of brook trout in a tributary of Lake Ontario. The presence of brook trout may also indirectly increase predation rates on juvenile chinook by increasing numbers, or success, of other chinook predators (Holt 1984).

A final possibility is that what appears to be a brook trout impact is simply the effect of a covarying variable that we did not include in our analyses. For instance, it is not unreasonable to expect longer migrations to be associated with higher mortality. However, we selected sites that were in close proximity, and average survival was not associated with migration distance ($r^2 = 0.01$). Additionally, Paulsen & Fisher (2001) found a negative association between road density and the survival of juvenile chinook in the Snake River Basin. However, road densities did not differ among the sites we used in this study (ICBEMP 1999), and thus it seems unlikely that habitat degradation associated with roads caused the differences we saw. Nonetheless, experimental manipulations are clearly

Table 4. Results of analysis of covariance testing the null hypothesis of no difference in the association of chinook survival with the presence or absence of brook trout (main effect) and habitat quality (covariate).
(SS, sum of squares; MS, mean square.)

source	SS	d.f.	MS	F	P
brook trout	0.048	1	0.048	164.508	< 0.0001
habitat quality	0.008	1	0.008	26.568	0.0008
brook trout × habitat quality	0.005	1	0.005	17.580	0.003
error	0.002	8	0.0002	—	—

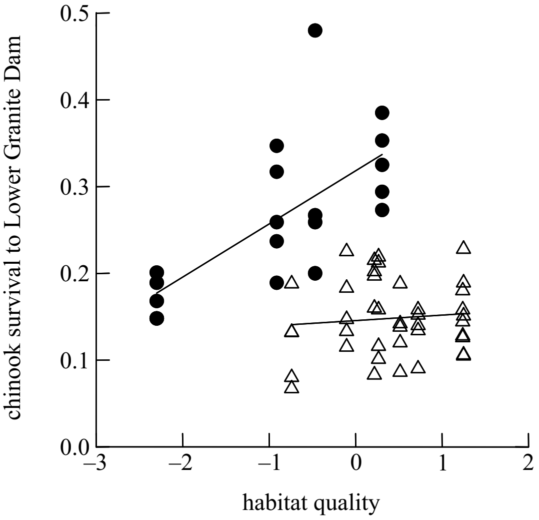

Figure 3. Survival of juvenile chinook salmon (from the summer of the first year when they were tagged to the following spring) as a function of habitat quality in sites in which brook trout were present (open triangles) or absent (filled circles). Each point represents an annual survival; however, statistical analyses were performed using average survival at each site as the response variable (see § 2).

necessary to isolate any effect of brook trout from that of other factors.

(b) *Do brook trout really matter?*

Our results suggest a difference of *ca.* 12% in average juvenile survival between sites with and without brook trout. However, the important question is whether such an increase in age-specific survival is likely to produce an increase in rates of population change (λ, cf. Dennis *et al.* 1991; McClure *et al.* 2002) sufficient to be a significant part of a recovery effort. Given a significant effect of brook trout on survival of chinook juveniles, we can convert survival improvements into increases in chinook λ that would be realized by brook trout removal. Such an estimate should be viewed with care since the differences between streams with and without brook trout may involve other differences, above and beyond the difference in the presence of brook trout.

McClure *et al.* (2002) calculated λ for seven of the populations of chinook salmon we investigated here and an additional eight populations in the same region we investigated (table 5). Using estimates of age structure from McClure *et al.* (2002) and Kareiva *et al.* (2000), we calculated the change in λ that might be expected by brook trout removal using the following relationship (Caswell 2000):

Table 5. The estimated increase in population growth rate (λ) following the removal of brook trout.

site	baseline λ	estimated λ in the absence of brook trout
Johnson Creek	1.01	1.04
Marsh Creek	0.99	1.01
Poverty Creek	1.01	1.03
Sulphur Creek	1.04	1.07
Bear Valley Creek	0.99	1.02
Camas Creek	0.92	0.94
Cape Horn Creek	1.05	1.08
Elk Creek	1.05	1.08
Knapp Creek	0.89	0.91
Lake Creek	1.06	1.08
south fork Salmon River	1.06	1.09
Secesh River	0.98	1.00
Big Creek	0.97	1.00
Yankee Fork	0.88	0.90
Yankee West Fork	0.99	1.01

$$\lambda_{\mathrm{nbt}} = \left(\frac{S_{\mathrm{nbt}}}{S_{\mathrm{wbt}}}\right)^{1/G} \times \lambda_{\mathrm{wbt}},$$

where S is the life-stage (yearly) survival, G is the mean generation time (stock specific) and the subscripts wbt and nbt refer to 'with brook trout' and 'no brook trout', respectively.

We estimate a *ca.* 2.5% increase in λ following removal of brook trout (table 5). Of the 15 populations McClure *et al.* (2002) investigated, eight are heading towards extinction (i.e. $\lambda \leqslant 1$), but a 2.5% increase in λ is sufficient to reverse the negative population growth for five of these populations. Other populations have only slightly positive growth (e.g. $\lambda = 1.01$), and given the uncertainty in estimates of λ, as well as demographic and environmental stochasticity, an increase is clearly beneficial for these populations. Thus, even the modest increase in λ we estimate from brook trout removal could be an important step in the recovery of these populations.

(c) *Interactive effects of brook trout with habitat*

The importance of freshwater habitat to chinook salmon has been appreciated for some time, and recent efforts documenting various landscape attributes to chinook abundance or survival have served to reinforce this understanding (Thompson & Lee 2000; Paulsen & Fisher 2001). Interestingly, our results suggest that the potential benefits of a high-quality habitat to juvenile chinook may be masked by brook trout. In the absence of brook trout, there was a positive association of chinook survival with habitat quality, but this relationship was absent when brook trout were present.

Habitat protection and restoration are the centrepieces of efforts to restore salmon populations in the Salmon River Basin (Mann & Plummer 2000). Our results, however, suggest that such efforts may not restore populations of chinook salmon unless brook trout are eliminated. It is also possible that habitat restoration aimed at improving salmon runs will enhance populations of brook trout and thus have a negative impact on salmon.

5. CONCLUSIONS

Demographic models show clearly that modest reductions in juvenile mortality of chinook salmon could reverse the current declines these populations are presently experiencing (Kareiva *et al.* 2000). However, because many of the populations we investigated occur in wilderness areas, their habitat has been considered pristine (Petrosky & Schaller 1996), and a perception exists that there is little scope for improving the survival of juvenile chinook while they rear in freshwater (e.g. Collie *et al.* 2000). Our results suggest that such perceptions of the Salmon River Basin are inaccurate. Non-indigenous brook trout are ubiquitous throughout 'pristine' regions of the Salmon and upper Snake River Basins (Hall-Griswold & Petrosky 1996; Achord *et al.* 1997; Maret *et al.* 1997), and clearly have the potential to have an impact on the survival of juvenile chinook. There is plainly a need to test experimentally the patterns we report here; nonetheless, our results emphasize that non-indigenous species are present and may have dramatic impacts even in remote regions that otherwise appear pristine.

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