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Differences in the impacts of dams on the dynamics of salmon populations

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Abstract

Modern concrete dams have devastated fish populations world-wide. However, dams vary greatly in how they are engineered and operated, and thus pose a range of threats to riverine fauna. Understanding the differences in the impacts of dams is critical for setting conservation priorities. We used a modified BACI (before-after-control-impact) sampling design as a means to quantify the effects of dams on spring/summer chinook salmon in two watersheds (Snake and Upper Columbia Rivers) of the Columbia River Basin, USA. The construction of four dams in the Columbia River Basin from 1966 to 1975 allowed us to test the hypothesis that the presence of these dams does not affect the abundance, survival and population growth of chinook salmon. In both the Snake and Upper Columbia Rivers, there was a significant decline from the period before dams were constructed (1959–65) to the period after dams were constructed (1980–90). In the Upper Columbia River, declines in productivity or population performance (measured as recruits per spawner or Ricker function residuals) were greater than in the control region. On the other hand, patterns of fish productivity in the Snake River were similar to those seen in the control region. The disparity between fates of Upper Columbia and Snake River populations points to the differences between regions in current efforts to reduce fish mortality associated with dams. Our analysis suggests that dams in the Upper Columbia River, but not Snake River, are a potential force preventing recovery of endangered salmon populations.

INTRODUCTION

The damming of rivers profoundly affects the integrity of riverine ecosystems (Pielou, 1998). After first drowning the original terrestrial and aquatic habitat, dams degrade water quality by altering flow regimes, increasing sedimentation and changing nutrient fluxes (Ligon, Dietrich & Trush, 1995; Power *et al*., 1996). Such changes produce extensive ecological disruptions, including modification of stream-channel morphology, spatial decoupling of rivers and their associated wetlands, disruption of food webs, and fragmentation and loss of habitat (e.g., NRC, 1992; Ligon *et al*., 1995; Power *et al*., 1996). Hydrological and ecological changes associated with dams have contributed substantially to the destruction of populations of migratory diadromous (migrating between ocean and freshwater) and potamodromous (migratory within freshwater) fishes, a variety of small-bodied riverine fishes and invertebrates, and numerous taxa dependent on flooding or freshwater inflows to estuarine habitats (Pringle, Freeman & Freeman, 2000)

The pace of dam construction has increased dramatically over the last 50 years. World-wide, fewer than 1000 'large' (≥ 15 m high from foundation to crest) dams were constructed in each decade prior to 1950; however, the rate of dam construction accelerated in the 1950s, peaking in the 1970s, with 5415 dams erected in the 1970s alone (Rosenberg, McCully & Pringle, 2000). By 1996, about half of all accessible global freshwater was impounded in reservoirs behind approximately 42,000 large dams and 800,000 'small' (< 15 m high) dams (ICOLD, 1998; Rosenberg *et al*., 2000). The extent of hydrologic alteration in single river basins can be enormous. For instance, the basins of the Columbia (North America), Danube (Europe) and Volga–Kama (Europe) rivers each include nearly 200 large dams (Rosenberg *et al*., 2000).

Dams vary greatly in how they are engineered and operated and thus pose a wide range of threats to riverine fauna. In the United States, there are 1825 hydropower projects (out of a total 6375 large dams in the US), that are operated by the US Federal Energy

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Commission (FERC, 1992). Of these, 10% have facilities in place that allow migratory fish to pass upstream and 13% have structures in place to facilitate downstream migration (Pringle *et al.*, 2000). Additionally, the effects of dams are likely to vary depending on their purpose. In the Columbia River Basin, the magnitude of the change in the natural hydrography required to meet irrigation needs is much less than that needed for the generation of hydropower (since peak demand for irrigation water is typically in the midsummer, just after the natural hydrograph peak) (NRC, 1996). Thus, dams used to generate hydropower may impact anadromous fish to a greater extent than dams used for irrigation.

Although it is clear that dams can have dramatic effects on aquatic fauna, it is valuable to determine when in an organism's life-cycle dams do the greatest damage. To answer this question, we explored the impact of dams on chinook salmon populations in the Columbia River Basin. The dams in the Columbia River Basin of North America have been implicated as a major contributor in dramatic decline of Pacific salmon populations (NRC, 1996). Since the 1980s alone, wild salmon populations in the Columbia River Basin have declined by more than 90%, and 12 Evolutionarily Significant Units (ESUs) of Pacific salmon in the Columbia Basin are now listed as threatened or endangered under the United States Endangered Species Act. An ESU is any group of populations that is substantially reproductively isolated from other conspecifics and represents an important component of the evolutionary legacy of the species (Waples, 1995).

Here we adopt a modified BACI (before-after-control-impact) sampling design (Bernstein & Zalinski, 1983; Stewart-Oaten *et al.*, 1986; Underwood, 1991, 1994) as a means to quantify the effects of dams on salmon populations of the Columbia Basin. Using a unique 40-year time series of 16 chinook salmon (*Oncorhynchus tshawyscha*) populations, we test the null hypothesis that the presence of dams does not affect the abundance, survival and population growth of salmon.

METHODS

Study species

We focused on 16 chinook salmon populations from two ESUs in the upper and middle reaches of the Columbia River (Upper Columbia and Middle Columbia ESUs) as well as one from the Snake River (Snake River ESU), the largest tributary of the Columbia River (Fig. 1). Chinook in the Upper Columbia ESU are currently listed as endangered under the US Endangered Species Act, and those in the Snake River ESU are considered threatened. Chinook in the Middle Columbia ESU are presently not listed. Depending upon their natal river, Upper Columbia River chinook must negotiate three to

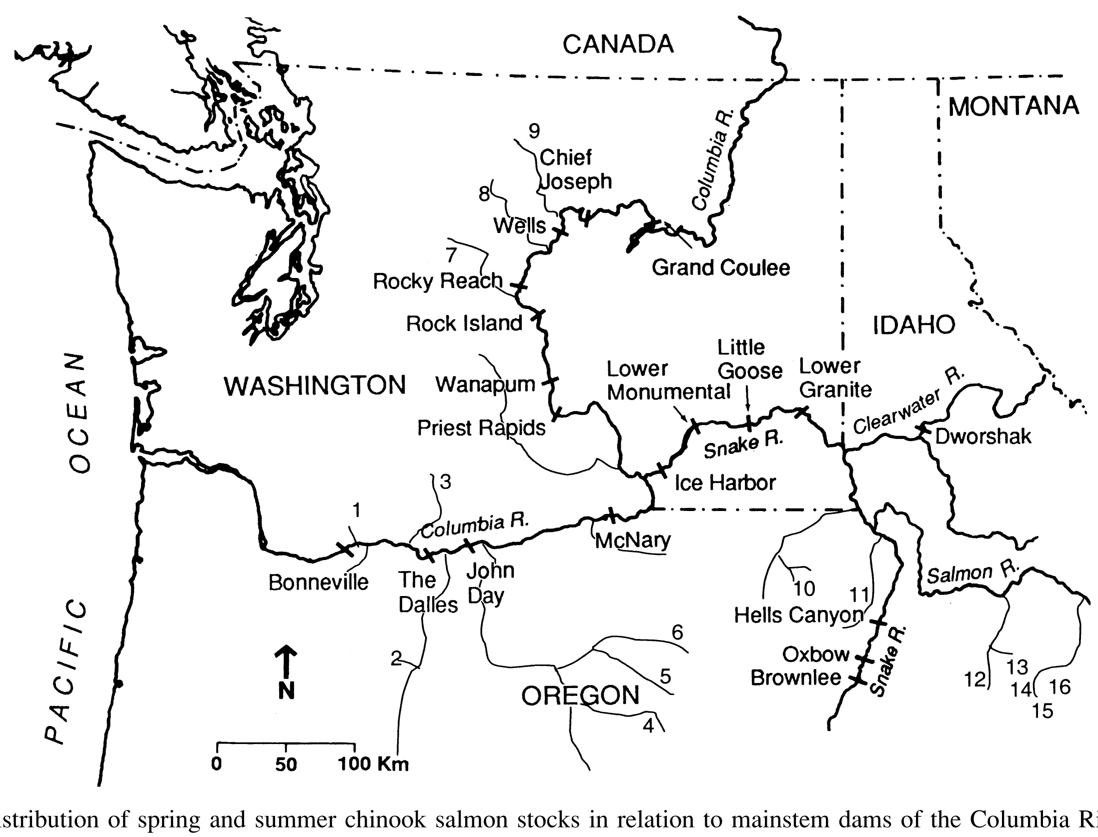

Fig. 1. Distribution of spring and summer chinook salmon stocks in relation to mainstem dams of the Columbia River Basin. Stock locations are indicated with numbers as follows: (1) Wind, (2) Warm Springs, (3) Klickitat, (4) Mainstem John Day, (5) Middle Fork John Day, (6) North Fork John Day, (7) Wenatchee, (8) Entiat, (9) Methow, (10) Minam, (11) Imnaha, (12) Poverty Flat, (13) Johnson, (14) Sulphur, (15) Bear Valley, (16) Marsh. Stocks 1 to 6 are in the Middle Columbia River ESU; stocks 7 to 9 are in the Upper Columbia River ESU; and stocks 10 to 16 are in the Snake River ESU.

five privately owned dams above the confluence of the Snake River (Fig. 1), and then pass through an additional four federally owned dams on the Columbia River below the Snake confluence during downstream migration. In contrast, Snake River fish encounter four federally owned dams on the Snake River itself, and then pass the same four dams on the Lower Columbia River that fish from the upper Columbia traverse (Fig. 1). Middle Columbia fish must traverse from one to three of the dams on the Lower Columbia that both Upper Columbia and Snake River fish must also pass. The dams encountered by all three ESUs of chinook are equipped for the upstream passage of adults, but differ in how they handle juvenile fish migrating downstream. Although Snake River chinook encounter up to eight dams, about 75% of juvenile migrants are presently transported around these dams. For the 25% of fish remaining in the river, all dams encountered (four Snake River and four Columbia River dams) include facilities to enhance the passage of juvenile fish migrating downstream. Fish from the Middle Columbia also experience the passage facilities of the Lower Columbia dams. In contrast, few juvenile fish from the Upper Columbia ESU were transported during the study period (none are presently transported), and only one of the dams on the upper Columbia above its confluence with the Snake River is equipped with facilities to help the passage of juvenile migrants.

All populations used in this analysis were 'stream-type' chinook salmon, which typically produce juveniles that migrate downstream to the sea 1 year after hatching (Healey, 1991). Chinook salmon return to freshwater to spawn at 2–6 years of age, with most individuals returning at ages 4–5 (Healey, 1991). Populations in each region are affected by a range of habitat conditions and hatchery influences, but these effects do not appear to vary systemically among regions (Beamesderfer *et al.*, 1997).

Table 1. Summary of key attributes of spring/summer run chinook salmon stocks used in this paper

Index stock	ESU	Number of dams passed	Years of data used (brood years)
Bear Valley	Snake River	8	1959–90
Marsh	Snake River	8	1959–90
Sulphur	Snake River	8	1959–90
Poverty Flat	Snake River	8	1959–90
Johnson	Snake River	8	1959–90
Minam	Snake River	8	1959–90
Imnaha	Snake River	8	1959–90
Methow	Upper Columbia	9	1960–90
Entiat	Upper Columbia	8	1959–90
Wenatchee	Upper Columbia	7	1959–90
Mainstem John Day	Middle Columbia	3	1959–90
Middle Fork John Day	Middle Columbia	3	1959–90
North Fork John Day	Middle Columbia	3	1959–90
Warm Springs	Middle Columbia	2	1966–90
Mainstem Klickitat	Middle Columbia	1	1966–90
Wind	Middle Columbia	1	1970–90

Characterization of populations

State fishery agencies have monitored the number of spawning fish in most of the 16 populations we used in our analyses for *c*. 40 years. Years of data available for each of the 16 populations are provided in Table 1. We used three measures derived from spawner counts to characterize salmon populations. The first and simplest measure was standardized spawner number. Annual spawner counts for each population were standardized by subtracting the mean and dividing by the standard deviation. However, abundance alone cannot reflect per capita productivity. Thus, to assess effects on salmon production, we used two additional measures. Because estimates of both spawner numbers and age structure were available for the populations, it was possible to obtain a time series of the number of recruits per spawning adult. Recruits are defined as fish returning to the spawning grounds after 3–4 years at sea. Finally, although density-dependence is weak to non-existent in these populations because they are currently at such low densities (Kareiva, Marvier & McClure, 2000), some fisheries biologists still advocate first fitting recruits per spawner data to a Ricker stock-recruitment function (Ricker, 1975), and then using residual scatter about that fit as a measure of density-independent survival (Peterman *et al.*, 1998).

The data we used were derived from 'run-reconstructions' performed by Beamesderfer *et al.* (1997). Briefly, numbers of naturally occurring (i.e., not hatchery) spawners were estimated as the product of peak redd (nest) counts and the estimated number of fish per redd (Beamesderfer *et al.*, 1997). Spawner numbers were adjusted to account for harvest rates and natural mortality rates. Additional details of the procedures used to estimate spawner and recruit numbers are provided by Beamesderfer *et al.* (1997). Residuals were calculated by fitting a linear regression of natural log recruits per spawner vs. spawner abundance and then calculating deviations from that line.

Estimation of dam impacts

The first step in estimating the impacts of dams is to determine what constitutes a control for the treatment of the hydropower system. One approach is to use fish stocks residing in the Middle Columbia River Basin, an area with fewer dams, as controls for stocks from upstream regions of the basin with greater numbers of dams. However, because stocks within regions are clumped rather than interspersed, stocks within regions are pseudoreplicates, making the separation of location from treatment effects problematic (Hurlbert, 1984). Additionally, stocks from different regions are genetically distinct (Mathews & Waples, 1991; Myers *et al.*, 1998). Such genetic differences are strongly concordant with ecological and life history traits of chinook (Myers *et al.*, 1998). The presence of differences between down- and upriver stocks, therefore, is inconclusive because differences among regions may arise from many factors that vary among locations, only one of which is the number of dams (Zabel & Williams, 2000).

Another approach is to compare time periods before dams were constructed to time periods with the current hydropower configuration. The historical river with fewer dams thus serves as a control for the modern river. Unfortunately a major shift in oceanographic conditions, accompanied by substantial decreases in marine primary production (Mantua *et al.*, 1997), was coincident with the completion of the Federal Columbia River Power System in 1975 (corresponding to outmigration year 1977). Also in 1975, completion of the Libby and Mica dams in the upper reaches of the Columbia Basin nearly doubled storage capacity in the river at the same time that climate shifts decreased annual average run-off. Thus, there was a significant decrease in freshwater discharge after 1975, and comparisons before and after completion of the hydropower system are confounded by these massive changes in oceanography and hydrography. Although there may be differences in population parameters of Snake and Upper Columbia ESUs before and after the hydropower system was completed, the many other factors that changed at this time confound this simple comparison.

A before-after-control-impact (BACI) approach provides a partial solution to the problems highlighted above. Stewart-Oaten *et al.* (1986) suggested that, to judge whether an impact has occurred, one should calculate the difference in the variate of interest between control and putative impact sites before and after the onset of the potential disturbance. A significant change in the mean difference (delta) between populations after the onset of the perturbation is strong evidence of an effect of the environmental impact. In an ANOVA context, this manifests as a significant interaction between impact status (Control/Impact sites) and time (Before/After impact). That is, control and impact sites respond differently to the disturbance regardless of their initial relationship. The approach of comparing upriver to downriver regions is clearly imperfect as discussed above. None the less, the absence of differences among regions that vary in dam number would be strongly suggestive that passage through the hydropower system is not the leading determinant of population size or dynamics.

The basic BACI approach (Steward-Oaten *et al.*, 1986) is designed for the comparison of one impact and one control site. Because we had two impact sites and one control, we adopted a slightly different analysis based on Underwood's 'Beyond BACI' approach (Underwood, 1991, 1994). We used the modified BACI approach to test the effects of Columbia River dams on salmon populations as follows. We defined the 'before' period as brood years 1959–65 and the after period as 1980–90. In 1959–65 fish from the Snake and Upper Columbia Rivers had to pass four dams versus the seven to nine dams they currently have to pass. We used ANOVA and a priori contrasts to test for an effect of the four additional hydropower projects that were constructed between 1966 and 1975. In the analysis, ESU and before/after (B/A) are the main effects. The effect of the dams is addressed by using a priori contrasts or asymmetrical ANOVA (Underwood, 1994). The interaction between ESU status (downstream/control vs. upstream/impact) and B/A demonstrates that the relationship between control sites and impact sites changed with the building of the dams, thereby indicating a potential dam effect. Additionally, a comparison of the two putative impact sites is also suggested a priori because of the difference in transport of the outmigrating fish. This comparison is investigated by examining the interaction between upstream ESUs (Snake vs. Upper Columbia) and B/A. When this interaction term was significant, we performed separate *t* tests comparing delta values between the Middle Columbia ESU (control) and the Snake or Upper Columbia ESUs (impact). Because two *t* tests were performed, a Bonferonni adjustment (SYSTAT 2000) was performed to protect the experiment-wise α; consequently, P values less than 0.025 were considered significant. Since populations within ESUs may not be independent replicates, we used the mean standardized spawner counts, recruits per spawner and Ricker function residuals for each ESU as a response datum for each year. For visual comparison, we calculated mean differences (deltas) between Middle Columbia, Upper Columbia and Snake River ESUs for each variable.

Recruits per spawner data were natural log transformed. Standardized spawner counts and Ricker residuals were square root transformed; however, because these data included negative values, simple square-root transforms were impossible. Consequently, we calculated the square root of the absolute value and then reassigned the sign. Prior to analysis, data were assessed with Bartlett's test and QQ plots to assure they met the assumptions of parametric statistics. We also tesed for autocorrelation in the time series using the Durbin–Watson test (Wilkinson, Blank & Gruber, 1996). We did not detect autocorrelation in the standardized spawner data. However, both recruits per spawner and Ricker residuals showed autocorrelation. Because autocorrelation can arise from missing terms in the model, we added census number (i.e., time) as a covariate in these models (Dillon & Goldstein, 1984). Slopes were homogeneous for the recruits per spawner data, and this covariate removed the autocorrelation. For Ricker residuals slopes were not homogeneous, so the covariate was not used. Therefore, significant results from analyses of Ricker residuals should be interpreted cautiously (Dillon & Goldstein, 1984).

RESULTS

Standardized spawner counts fluctuated greatly over the last 40 years in all ESUs (Fig. 2). None the less, while Middle Columbia River populations have generally varied around their long-term average, both Snake and Upper Columbia River populations have declined markedly. While ANOVA found a significant B/A effect, the significant interaction indicated that the three

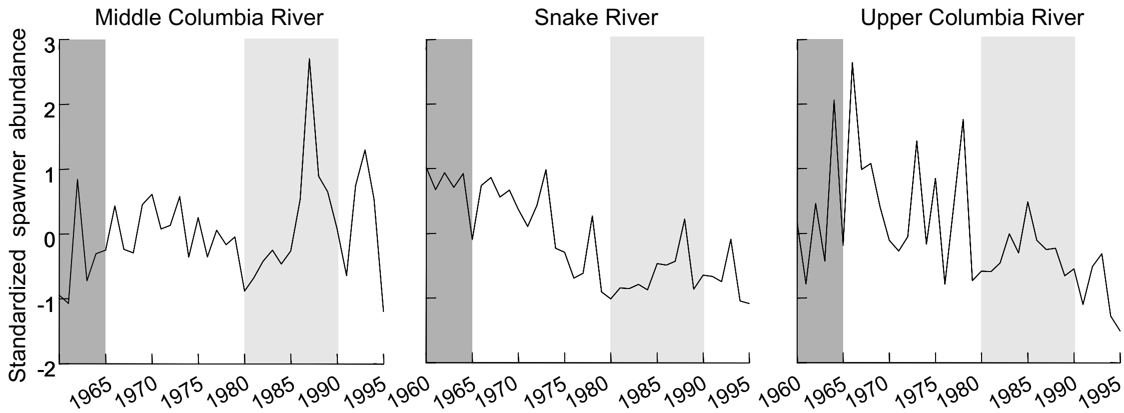

Fig. 2. Time series of spawner abundance from 1959 to 1995. The 'before' period (when four mainstem dams were present in the Columbia River Basin) is shaded dark grey and the 'after' period (when Snake River salmon passed eight dams and Upper Columbia river salmon passed seven to nine dams) is shaded light grey.

ESUs did not respond similarly to the construction of dams (Table 2). In particular, the a priori contrast, Control/Impact*B/A, indicates that spawner counts decreased more in the Upper Columbia and Snake River ESUs (upstream/impact sites) than in the Middle Columbia River ESU (downstream/control site) (Figs 3(a), 4(a)). In both instances mean delta values (defined as Upper Columbia or Snake River minus Middle Columbia River spawner counts) were positive in the before period and declined significantly to negative values in the after period (Figs 3(a), 4(a)). Thus, upstream ESUs initially had greater standardized spawner numbers than the Middle Columbia ESU, but in the after period had fewer spawners than downstream ESUs.

Like spawner counts, the number of recruits per spawner and residuals from Ricker functions varied greatly over the 40-year study period (Fig. 5). However, differences between the Snake and Upper Columbia ESUs emerged in these analyses (Tables 3 and 4). For recruits per spawner, we did not detect a significant Control/Impact*B/A interaction (Table 3), suggesting that upriver ESUs did not respond strongly to the dams

Table 2. Results of ANOVA and a priori contrasts on salmon spawner numbers. Both ESU and Before/After were treated as fixed factors. Data were square root transformed prior to analysis. Spawner data were not autocorrelated (Durbin–Watson test, $P > 0.05$)

Source	d.f.	*MS*	*F*	*P*
ESU	2	0.050	0.12	0.88
Before/After (B/A)	1	1.944	4.60	0.037
ESU*B/A	2	4.174	9.86	< 0.001
Control/Impact*B/A	1	6.497	15.35	< 0.001
Snake/UC*B/A	1	1.851	4.37	0.042
ERROR	48	0.423		

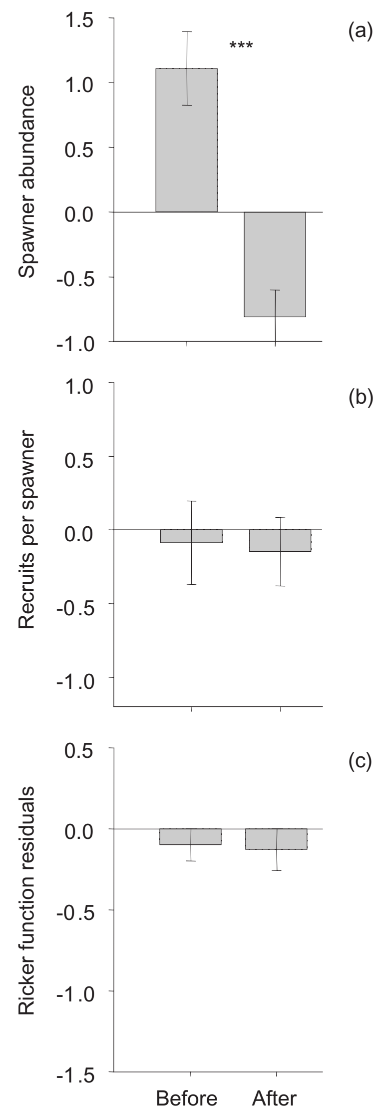

Fig. 3. (Right) Mean differences between Snake and Middle Columbia Rivers (delta values) in spawner abundance, recruits per spawner and and residuals from Ricker functions from 1959–65 (before) and 1980–90 (after). *** indicates significance at $P < 0.001$. Error bars are 1 SE.

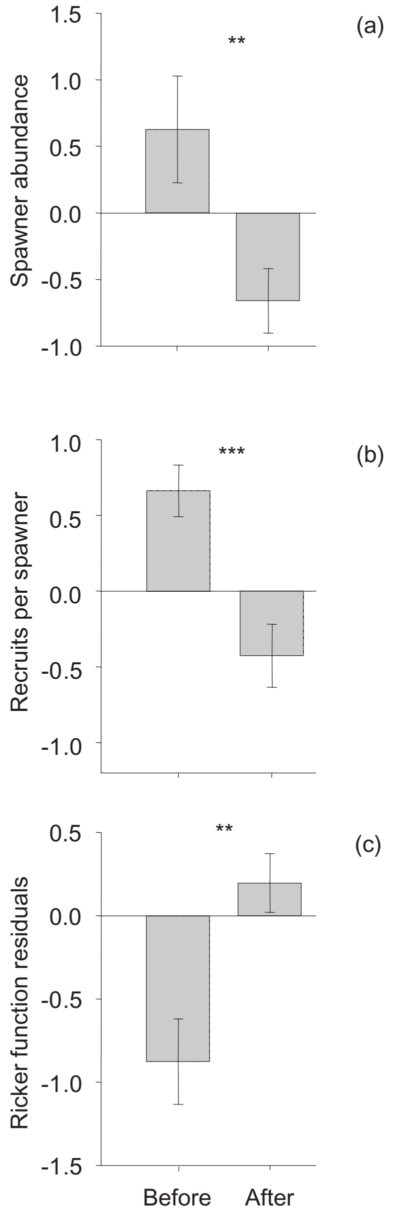

Fig. 4. Mean differences between Upper and Middle Columbia Rivers (delta values) in spawner abundance, recruits per spawner and residuals from Ricker functions from 1959–65 (before) and 1980–90 (after). ** indicates significance at $P < 0.01$ and *** at $P < 0.001$. Error bars are 1 SE.

Table 3. Results of ANOVA and a priori contrasts on number of recruits per spawner. Data were natural log transformed prior to analysis. Both ESU and Before/After were treated as fixed factors. Addition of the census number covariate removed autocorrelation (Durbin–Watson test, $P > 0.05$).

Source	d.f.	*MS*	*F*	*P*
ESU	2	0.066	0.43	0.665
Before/After (B/A)	1	0.659	4.24	0.045
ESU*B/A	2	0.712	4.53	0.016
Control/Impact*B/A	1	0.414	2.67	0.109
Snake/UC*B/A	1	0.991	6.39	0.015
Census number	1	7.573	48.81	< 0.001
ERROR	47	0.155		

Table 4. Results of ANOVA and a priori contrasts on residuals from Ricker functions. Data were square root transformed prior to analysis. Both ESU and Before/After were treated as fixed factors. Data were autocorrelated (Durbin–Watson test, $P < 0.05$)

Sources	d.f.	*MS*	*F*	*P*
ESU	2	0.021	0.04	0.96
Before/After (B/A)	1	14.862	28.77	<0.001
ESU*B/A	2	0.931	1.80	0.176
Control/Impact*B/A	1	0.914	1.36	0.191
Snake/UC*B/A	1	2.464	3.66	0.181
ERROR	48	0.517		

(although power was low, $1\text{-}\beta < 0.3$). However, a significant Snake/Upper Columbia*B/A interaction indicated the response of the upstream populations was inconsistent (Table 3). Indeed, we were unable to detect a difference between Snake and Middle Columbia populations (Fig. 3(b); $t = 0.164$; $P = 0.87$) in the delta value, while the difference in delta between the Upper Columbia and Middle Columbia ESUs was highly significant (Fig. 4(b); $t = 4.061$; $P = 0.001$).

The pattern with residuals from Ricker functions was similar to that of recruits per spawner (Fig. 6). While there was a general B/A effect, we did not detect a dam effect as evidenced by the non-significant Control/Impact*B/A term in Table 4 (although power was low, $1\text{-}\beta < 0.3$). In this case, Snake/Upper Columbia*B/A was not significant, suggesting that the response of these two upstream ESUs was consistent. Delta values for Ricker residuals did not vary between Snake and Middle Columbia Rivers (Fig. 3(c); $t = 0.083$; $P = 0.73$), but did vary significantly between the Upper and Middle Columbia Rivers (Fig. 4(c); $t = 3.57$; $P = 0.003$). Because Ricker residuals were autocorrelated, these results should be viewed with caution.

DISCUSSION

Modern concrete dams now exist by the thousand. It is clear that the extensive hydrologic modifications caused by dams have devastated fish populations world-wide (Pringle *et al*., 2000). In North America, where the most information is available, numerous examples of dams directly or indirectly contributing to the demise of fishes have been documented (Pringle *et al*., 2000). Although the hundreds of thousands of dams around the globe are obviously not good for fish, they may vary in how bad they are. Understanding the differences in the impacts of dams is crucial for setting conservation priorities.

The erection of dams along the Columbia and Snake Rivers clearly affected anadromous salmon in the Columbia River Basin (Raymond, 1988; Williams & Tuttle, 1992). The significant decline in spawner numbers from the before to after period in the Snake and Upper Columbia Rivers but not in the Middle Columbia River suggests that the development of hydropower strongly impacted salmon stocks (see also Williams, Smith & Muir, 2001). Although dams contributed to the severe declines in Snake and Upper Columbia River

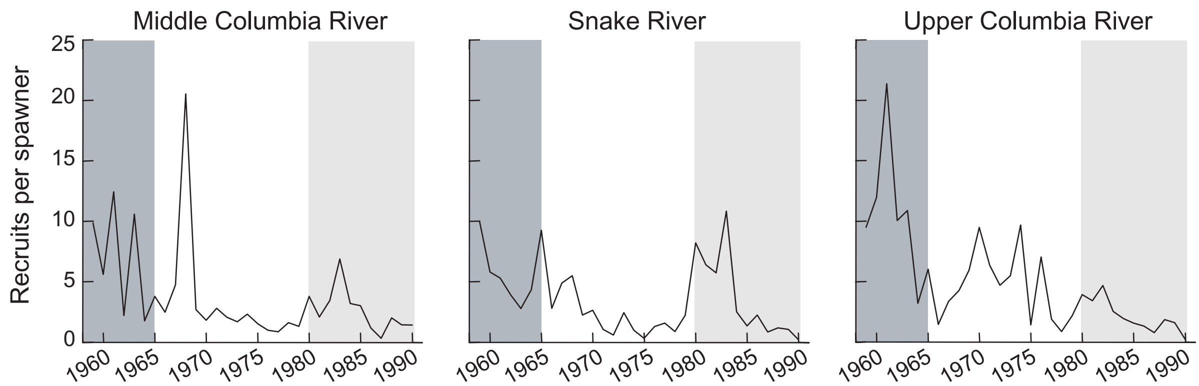

Fig. 5. Time series of recruits per spawner from 1959 to 1990. The 'before' period (when four mainstem dams were present in the Columbia River Basin) is shaded dark grey and the 'after' period (when Snake River salmon passed eight dams and Upper Columbia River salmon passed seven to nine dams) is shaded light grey.

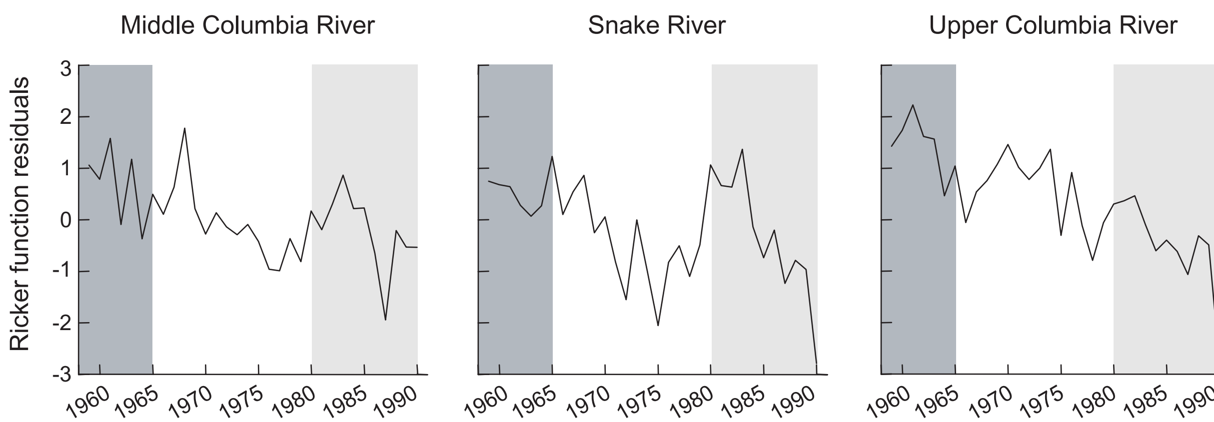

Fig. 6. Time series of residuals from Ricker functions from 1959 to 1990. The 'before' period (when four mainstem dams were present in the Columbia River Basin) is shaded dark grey and the 'after' period (when Snake River salmon passed eight dams and Upper Columbia River salmon passed seven to nine dams) is shaded light grey.

populations, the key unanswered question is whether dams are presently preventing the recovery of these populations. The situation faced by fish today is far different from that faced by those during the era of dam construction. Mitigation measures adopted after 1975, including fish-passage facilities, predator control, transportation and flow augmentation, have combined to improve conditions confronting salmon migrants (NRC, 1996).

In the Upper Columbia River, declines in productivity or population performance (measured as recruits per spawner) were greater than in the Middle Columbia. In contrast, patterns of fish productivity in the Snake River were similar to those seen in the Middle Columbia. Thus, these results support the hypothesis that dams, as currently operated, are limiting the recovery of fish in the Upper Columbia River. On the other hand, our analyses do not support the hypothesis that the hydropower system (in its current configuration) is preventing recovery of Snake River fish. Rather, other factors, or combinations of factors, such as poor ocean conditions, habitat degradation or the effects of hatchery fish may be more important to the continuing decline of Snake River populations (cf. Kareiva *et al.*, 2000).

The disparity in the fate of Upper Columbia and Snake ESUs points to differences between the regions in current efforts to reduce juvenile mortality. All dams on the Snake River under consideration in this study are operated by the US Federal Energy Commission and are equipped with elaborate structures to facilitate the migration of both adult and juvenile fish. During the 'after' period of this study, a large portion (~75%) of juvenile salmon emigrants was collected from fish bypass systems at Lower Granite, Little Goose and McNary Dams (Fig. 1) and transported below the lowest downstream dam (i.e., below Bonneville Dam, Fig. 1). Although collection methods do not capture all passing juveniles at any one dam, when fish are captured at several dams most migrants will eventually be collected, and only a small fraction will travel through all reservoirs and dams. In contrast, dams on the Upper Columbia River are privately owned and lack the juvenile bypass equipment found at the federal dams. Upper Columbia River salmon were collected only at McNary Dam (Fig. 1), after these fish had already transited up to five dams and reservoirs. Consequently, only a small proportion of Upper Columbia River fish were transported, and even those fish that were transported had encountered several dams without fish bypass facilities (Ceballos *et al*., 1993).

Alternatively, differences between the Upper Columbia and the other two ESUs may simply reflect geographic differences in how these populations respond to environmental change. For instance, Welch *et al*. (2000) suggest that steelhead trout from geographically separate populations responded differently to a large-scale climate event that occurred around 1990. Steelhead populations from northern British Columbia showed increasing recruitment, while recruitment in populations from southern British Columbia declined. These steelhead populations enter the ocean in different places, and thus patchiness in ocean conditions has an obvious effect. The chinook populations we examined all enter the sea at the same location. However, if fish from different ESUs have different marine distributions (Healey, 1991; Myers *et al*., 1998; Zabel & Williams, 2000), or if they enter the ocean at different times (Ryding & Skalski, 1999), they may respond differently to environmental change. Since analyses of genetic markers reveal that these populations are distinct (Mathews & Waples, 1991; Myers *et al*., 1998), it is also possible that fish from different ESUs respond differently to the same environmental conditions.

Dams have clearly disrupted populations of salmon and other migratory fishes. In the Columbia River Basin, there are now thousands of dams – some only a meter or two in height and others more than a 100 m high. While even smaller dams can block the movement of migratory fishes, these dams obviously vary in the extent of their impact. Additionally, of the nearly 200 dams > 15 m high in the Columbia Basin, fewer than 10% are equipped with structures to facilitate fish movements. While it is difficult to demonstrate clearly the magnitude of the impact of dams, our results indicate that the effects of dams will vary depending on how they are constructed and operated. There is plainly much scope for both scientific and policy debates concerning the impact of dams on the recovery of these salmon populations. Ideally, fisheries scientists can contribute to the determination of dam impacts by providing sound ecological data based on well-constructed analyses. Our analysis points to hydropower systems on the Upper Columbia River, but not the Snake River, as a potential force preventing recovery of endangered salmon populations. The impacts of different dams and operational schemes on organisms will vary, and careful comparison may allow the lessons learned from one location to be applied to other regions.

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