

The influence of population dynamics and environmental conditions on pink salmon (*Oncorhynchus gorbuscha*) recolonization after barrier removal in the Fraser River, British Columbia, Canada

G.R. Pess, R. Hilborn, K. Kloehn, and T.P. Quinn

Abstract: When barriers are removed, what biotic and abiotic factors determine how fish populations will colonize newly available habitats? We used counts of adult pink salmon (*Oncorhynchus gorbuscha*) from 1947 to 1987 in 66 streams of the Fraser River system, British Columbia, Canada, to determine when colonizing pink salmon populations became self-sustaining after a long-term migration blockage at Hell's Gate (river kilometre 209) was reduced. The abundance of salmon in available habitats were largely controlled by extrinsic factors such as an initially large source population, high intrinsic growth rates linked to favorable climate-driven conditions, a constant supply of dispersers, and large amounts of newly available habitat. Temporal variation in flows at Hell's Gate also affected recolonization success. Self-sustaining populations were developed within years of barrier removal and have continued to help expand the overall population of Fraser River pink salmon. However, pink salmon were considerably more abundant in the early 1900s than in the 1980s (~48 million vs. ~2.7 million), and the majority of spawning shifted from the historic areas above Hell's Gate prior to the rockslide to below Hell's Gate in the lower Fraser River after the long-term blockage was reduced, so the system has not returned to the former abundance and distribution patterns.

Résumé : Quels facteurs biotiques et abiotiques déterminent comment des populations de poissons coloniseront des habitats nouvellement disponibles quand les barrières en sont retirées? Les nombres de saumons roses (*Oncorhynchus gorbuscha*) adultes recensés de 1947 à 1987 dans 66 cours d'eau du réseau du fleuve Fraser (Colombie-Britannique, Canada) ont été utilisés pour déterminer à quel moment les populations colonisatrices de saumons roses deviennent autosuffisantes après la réduction d'un obstacle de longue durée à la migration à Hell's Gate (kilomètre fluvial 209). L'abondance des saumons dans les habitats disponibles était en bonne partie dictée par des facteurs extrinsèques tels qu'une importante population source initiale, de forts taux de croissance intrinsèque associés à des conditions favorables découlant du climat, un apport constant d'individus se dispersant et l'abondance d'habitats nouvellement disponibles. Les variations temporelles des débits à Hell's Gate influaient également sur le succès de recolonisation. Des populations autosuffisantes s'étaient établies après quelques années suivant le retrait des barrières et ont continué de contribuer à l'augmentation de la population globale de saumons roses du fleuve Fraser. Cela dit, ces derniers étaient beaucoup plus abondants au début du 20^e siècle que dans les années 1980 (~48 millions contre ~2,7 millions) et la majeure partie de l'activité de fraie s'est déplacée des frayères historiques situées en amont de Hell's Gate avant le glissement de terrain vers des frayères en aval de Hell's Gate, dans le bas Fraser, après la réduction de l'obstacle de longue durée, de sorte que l'abondance et la répartition antérieures des saumons dans le système n'ont pas été rétablies.

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Introduction

Barriers can limit the ability of fish populations and especially anadromous species to expand and occupy the full

range of suitable habitats within river basins. Barriers can be permanent and physical, such as impassable waterfalls in a river system that prevent fishes from reaching spawning grounds, and thus limit their distribution to downriver loca-

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tions (Quinn 2005; Waples et al. 2008). However, there can also be more subtle barriers to migration, dispersal, or population productivity. For example, adverse environmental conditions such as temperature (Major and Mighell 1967; Goniea et al. 2006), dissolved oxygen (Priede et al. 1988), and flow (Reiser et al. 2006) can delay migration or increase mortality during the returning adult life stage (e.g., Johnson et al. 1996) and limit recruitment (Martins et al. 2011). Predation by other freshwater fishes can lead to population fragmentation and limit interaction between spawning populations (Fraser et al. 1995). Management actions such as the amount and location of harvest activities may also limit populations over time (Ricker 1987). The common thread in each example is increased mortality in returning adults affecting the recruitment of progeny. The consequences of a life-stage specific "barrier" can thus limit future population levels to the point of extinction (Pimm and Pimm 1982; Underwood 1994; Knapp et al. 2001).

River systems throughout the world have been fragmented by human activities, and there is now widespread interest in reconnecting them by removing or modifying barriers to migration. Some barriers can be modified by natural processes or human intervention, leading to recolonization by returning adults (Anderson et al. 2010). When barriers are removed, what factors determine how a population will respond? Specifically, what is the role of biotic factors such as the size of the downstream (source) population and local competition and abiotic factors (e.g., quantity and quality of habitat above the barrier, river discharge during migration, ocean conditions, harvest) in controlling the rate and extent of colonization or recolonization by anadromous spawning populations? Subsequently, when does a recolonizing salmon population become self-sustaining, and what are the key variables that determine recolonization success? Very little is known about the processes and rates of recolonization by salmonids. While there are theoretical and modeled studies of salmon recolonization (Cooper and Mangel 1999; Schick and Lindley 2007), there are few empirical examples where we can quantitatively identify when a colonizing salmonid population becomes self-sustaining. Furthermore, there are no examples that have identified the relative importance of source populations and newly opened habitat characteristics to self-sustaining colonizing salmonid populations. There is also little consideration of the fact that a modest dispersal rate from a large source population may create the appearance of a population in some nearby stream that is in fact a sink that does not sustain itself.

In this paper we examined pink salmon (*Oncorhynchus gorbuscha*) populations within a large watershed in British Columbia to quantify key variables that determined the success of recolonizing salmon after a passage barrier was eased. Pink salmon are anadromous and semelparous; adults lay their eggs in the gravel of streams and rivers during late summer and fall (Heard 1991; Quinn 2005). Fry emerge from the gravels the following winter–spring and immediately migrate downstream to salt water where they spend a year feeding and growing. Adults migrate back into fresh water during summer, complete maturation, and then make the final upstream migration to their natal sites during the late summer and fall where they breed and inevitably die. Virtually without exception, pink salmon spawn at age 2, and so those

spawning in odd- or even-numbered years are isolated from cohorts spawning in the subsequent or prior year. For reasons that are not entirely clear, pink salmon populations in the southern portion of their overall range typically spawn in odd years, whereas northern populations are dominated by even-year spawners (Heard 1991; Krkošek et al. 2011).

Pink salmon were abundant (~48 million adults prior to 1915) in the Fraser River system of British Columbia until a rockslide in a canyon known as Hell's Gate created a hydraulic barrier to migration in 1913 (Ricker 1989; Roos 1996). For over three decades the species was absent from the river above the site of the rockslide until fishways were completed in 1947, and the species was once again recorded in its former habitat (Withler 1982; Ricker 1989). However, the presence of large numbers of pink salmon in the river below Hell's Gate (~12 to 8 million returning adults from 1947 to 1955; Ricker 1989; Beamish 2002) raised the question of whether all or any of the new populations were actually self-sustaining or merely dispersers (i.e., "strays") from the larger, productive populations downriver. Accordingly, our first goal was to identify and quantify key variables that determined pink salmon population establishment, including the source population's size, distance, dispersal rate, quantity and quality of the newly available habitat, barriers to connectivity, and environmental conditions. We then determined which pink salmon populations were self-sustaining (defined as those populations with a population growth rate of greater than 1.0) and which were "sinks" for more productive populations (Pulliam 1988). Lastly, we compared current and historic population abundance and spatial structure to determine if the Fraser River pink salmon populations have returned to prerockslide levels.

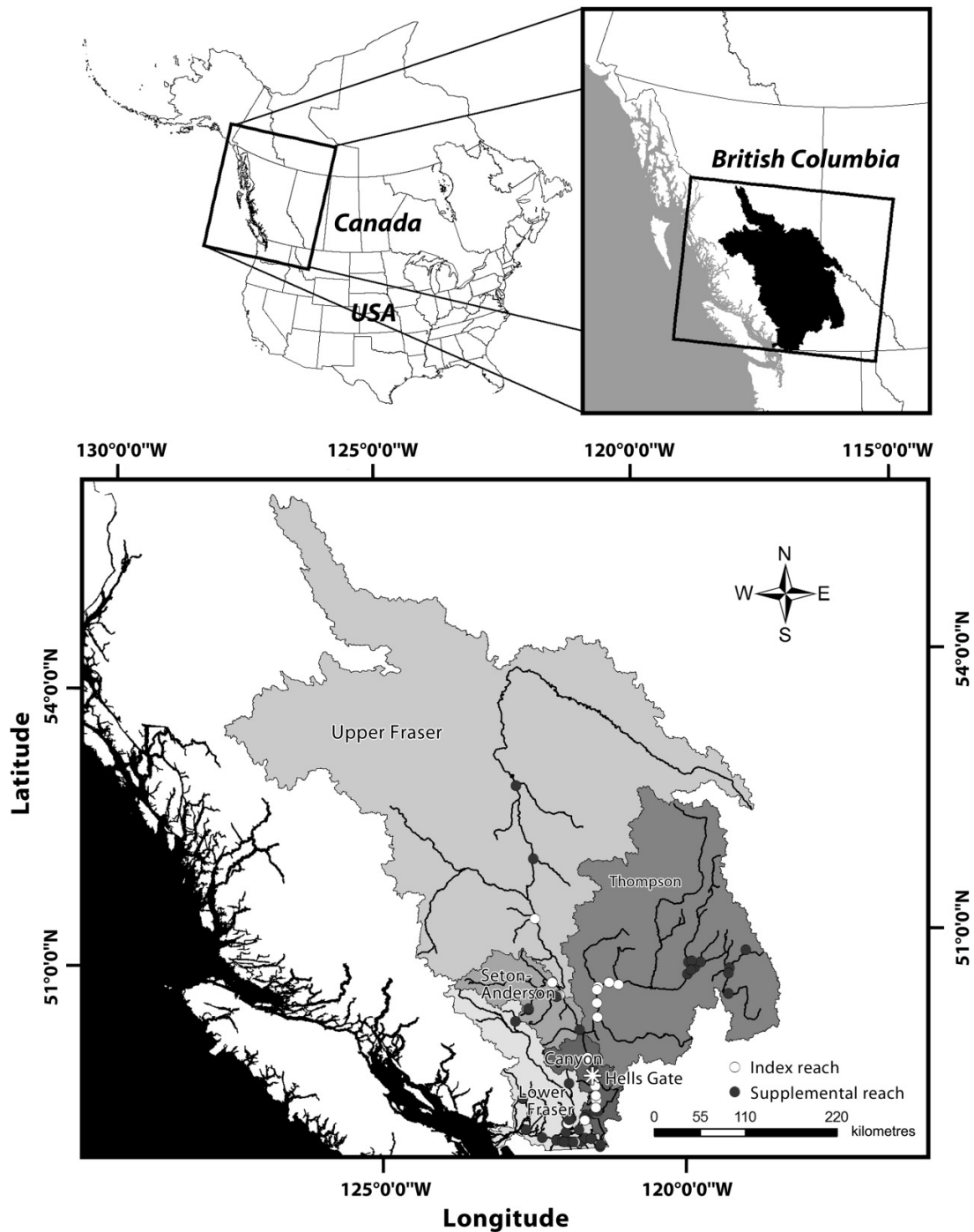
Materials and methods

Study area

The Fraser River is the fourth largest watershed in the Pacific Rim behind the Amur, Yukon, and Columbia (Fig. 1). It has a drainage area of 231 313 km² and 1370 km of riverine habitat. The Fraser River has many salmonids, including the five semelparous Pacific salmon species (Chinook (*Oncorhynchus tshawytscha*), sockeye (*Oncorhynchus nerka*) coho (*Oncorhynchus kisutch*), chum (*Oncorhynchus keta*), pink salmon), as well as and the iteroparous steelhead–rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*Oncorhynchus clarkii*), Dolly Varden (*Salvelinus malma*), and bull trout (*Salvelinus confluentus*). The populations of sockeye, Chinook, and pink salmon are the largest in Canada (Parken et al. 2008).

The total Fraser River pink salmon adult return averaged 11 500 000 ($\pm 6\,218\,360$ standard deviation (SD)) adults from 1947 to 1987, with an average of 2 241 342 ($\pm 1\,451\,741$ SD) adults escaping the fisheries and spawning in the watershed. Pink salmon were cut off from most of the watershed from 1913 until the late 1940s after a railroad construction-induced rockslide at river kilometre (rkm) 209 (Hell's Gate) altered flow conditions and made adult fish passage exceedingly difficult (Roos 1996). Pink salmon were able to pass above Hell's Gate in some years between 1913 and 1947 such as 1923 and 1927, but their presence was not consistent (Roos 1996). Other salmon species such as Chinook salmon and

Fig. 1. Map of the Fraser River watershed, British Columbia, Canada.



coho salmon were able to pass above Hell’s Gate during that time period (Roos 1996). Main stem and tributary pink salmon spawning populations above the rockslide area disappeared.

A joint Canadian–United States “convention” was signed in 1930 to “protect, preserve, and extend” sockeye salmon (the most important commercial species), and other salmonids such as pink salmon, in the Fraser River system above Hell’s Gate (Roos 1996). Another rockslide occurred in 1941 and the Commission recommended in 1944 the construction of fishways, which were completed in 1947 (Roos 1996). After fish passage facilities were constructed, adult

pink salmon migrated past the flow barrier and reestablished spawning areas above Hell’s Gate in one to two generations (Withler 1982; Roos 1996).

Data

Pink salmon populations for the Fraser River were estimated using mark–recapture techniques and foot surveys (Fisheries and Oceans Canada (DFO)). From 1957 to 1987, foot surveys were conducted in 66 streams distributed throughout the Fraser River basin (Appendix A, Table A1). Surveys were conducted every 7 to 10 days from August through October, the spawning period for this species in this

system. Each of the 70 survey reaches (more than one reach was surveyed in several streams) was identified as a primary (21) or supplemental (49) reach, and the typical survey method (e.g., foot survey vs. mark and recapture) was noted. Primary reaches were consistently surveyed on an annual basis, whereas supplemental reaches were periodically, but not consistently, surveyed from 1957 to 1987. The survey reach locations were verified on maps by the individuals who conducted the majority of the surveys over the 30-year time period. The 70 survey reaches can be classified into several watersheds designated “spawning population complexes”, including the Lower Fraser River, the Fraser River Canyon, the Seton–Anderson, the Thompson River, and the Uppermost Fraser River (Fig. 1). Each of the watersheds included more than one breeding location. We aggregated these data to estimate the number of adult pink salmon returning to spawn in each complex (i.e., after fishing had occurred). Methods for estimating the number of returning pink salmon changed after 1987; spawner surveys were terminated and the only approach was mark–recapture in the Lower Fraser River below Hell’s Gate (Schubert et al. 1997), so the reach-specific time series ended in 1987.

Pink salmon population estimates were also developed for the years 1947 to 1955 by Ricker (1989) and Beamish (2002) (Table 1) for the Lower Fraser River and by Withler (1982) for the Fraser River above Hell’s Gate (Table 1). Data from 1947 to 1955 do not include watershed-specific population estimates, but estimates were identified as below and above Hell’s Gate. Estimated overall harvest rate was then used to calculate the total return for each complex using harvest rate data gathered and compiled by the Pacific Salmon Commission (http://www.psc.org/publications_annual_fraserreport.htm).

We used geographic information systems (GIS) to help identify spawner survey index reaches and quantify habitat variables that were important to interpreting pink salmon recolonization of the Fraser River above Hell’s Gate. Distance measurements were generated by creating routes from an existing DFO 1:50 000 scale hydrography polyline layer and were expressed in river kilometres (rkm). The hydrography route layer was used to quantify the distance of each river and spawner survey reach to the confluence with the main stem Fraser River and to Hell’s Gate. Watershed boundaries distinct to Fraser River pink salmon populations were delineated by dissolving sub-basins defined by an existing 1:50 000 scale watershed polygon layer.

Approach and analysis

We developed a metapopulation model that was fit to observed spawning population size for each watershed. In the years 1947 to 1955, the data consisted only of counts below and above Hell’s Gate, but from 1957 to 1987 the spawning counts were by major complex. The assumptions of the model were as follows: (i) The number of fish produced from each population was a population-specific rate of increase times the number of spawners as modified by density dependence (Ricker 1954) and as modified by either a year-specific survival effect or a flow-specific survival effect. (ii) A fraction of the returning fish was always harvested. This harvest fraction is always known and changed on an annual basis. The harvest rate was the same for all spawning populations in a given year. (iii) Of those surviving harvest,

Table 1. Data on estimated numbers of pink salmon returning to the Fraser River (1947 to 1955; Ricker 1989; Beamish 2002) and on estimated numbers of pink salmon returning to the Fraser River above Hell’s Gate (1947 to 1955; Withler 1982).

Year	Total return to Fraser River ^a	Total return above Hell’s Gate ^b
1947	12 290 000	1 525
1949	9 430 000	1 225
1951	7 970 000	19 000
1953	9 090 000	62 150
1955	8 820 000	129 000

^aRicker 1989; Beamish 2002.

^bWithler 1982.

all returned to their natal site except a constant fraction that disperse to other sites. (iv) The fraction of dispersers straying to other sites is a decreasing function of the distance between the natal site and the place of actual spawning times a site-specific probability of straying to a site.

This model can be written as

$$(1) \quad \hat{R}_{j,t+2} = \left[\alpha_j N_{j,t} \exp\left(-\frac{N_{j,t}}{K_j}\right) y_{t+2} \quad \text{or} \quad \text{HA}_t, \text{HB}_t \right] \\ \hat{N}_{j,t+2} = \hat{R}_{j,t+2}(1-s)(1-\mu_{t+2}) + I_{j,t+2} \\ E_{j,t+2} = \hat{R}_{j,t+2}(1-\mu_{t+2})s$$

where $\hat{R}_{j,t+2}$ is the number of adult salmon that will return from the ocean from population j in year $t+2$, α_j is the population growth rate for population j , $N_{j,t}$ is the escapement in area j at time t , K_j is habitat capacity for population j , y_{t+2} is a year-specific impact on survival, and HA_t , HB_t is an annual flow effect multiplier attempted to capture freshwater conditions affecting upriver migration of spawning populations either above (HA_t) or below (HB_t) Hell’s Gate (see eq. 3). $\hat{N}_{j,t}$ is the predicted colonizing population size for population j at time t , s is the straying rate, μ_t is the harvest rate in year t , and $I_{j,t+2}$ is the number of immigrants to population j at time t (Table 2). Lastly $E_{j,t+2}$ is the number of individuals that will return to the Fraser River and who can stray from their natal spawning grounds. We defined habitat capacity as the total amount of habitat area under flow conditions at the time of spawning, irrespective of habitat preference or quality. The allocation of immigrants to each population was calculated with a distance-dependent dispersal equation:

$$(2) \quad I_{j,t} = \sum_{i=1}^n E_{i,t} \mathbf{p}_{i,j} \\ \mathbf{p}_{i,j} = \frac{\exp(-cd_{i,j})g_j}{\sum_{j=1}^n [\exp(-cd_{i,j})g_j]}$$

where $I_{j,t}$ is the number of fish from the “stray” pool that return to spawn in area j . While we call these fish strays, they are really potential strays, and some of them may return to their area of birth by chance as one of a number of possible return locations. $\mathbf{p}_{i,j}$ is the proportion of emigrants from area i that return and spawn in area j , c is a parameter describing how probability of colonization decreases with distance, $d_{i,j}$ is the distance from area i to area j , and g_j is a parameter describing the relative desirability of site j as a straying destination.

Table 2. Derivation of variables used in population dynamics model for Fraser River pink salmon 1947 to 1987.

Variable	Data and associated source	Estimated parameter	Model output
Initial population size (N_{1945})	Fisheries and Oceans Canada (DFO) spawner survey data (Tracy Cone, DFO, 100 Annacis Parkway, Unit 3, Delta, British Columbia; Tracy.Cone@dfo-mpo.gc.ca); Withler 1982; Ricker 1989; Beamish 2002	Treated as known	
Estimated population size ($\hat{N}_{j,t+2}$)			×
Carrying capacity (K)		×	
Population growth rate (α)		×	
Year effect (y)		×	
Flow (F)	Hope (08MF005) (National water data archive, Hydrometric program, Water Survey of Canada, http://www.wsc.ec.gc.ca/applications/H2O/index-eng.cfm)	Treated as known	
Flow effect intensity (q)		×	
Harvest rate (μ)	Pacific salmon commission Fraser River annual reports (http://www.psc.org/publications_annual_fraserreport.htm)	Treated as known	
No. of emigrants ($E_{j,t+2}$)			×
Straying rate (S)		×	
No. of immigrants ($I_{j,t}$)			×
Probability matrix ($\mathbf{p}_{i,j}$)			×
Distance-dependent dispersal coefficient (c)		×	
Relative desirability of site j as straying destination (g_j)		×	
Distance between source and colonizing population ($d_{j,i}$)	DFO Fish and Stream Information Summary System (http://www-heb.pac.dfo-mpo.gc.ca/maps/fiss_e.htm)	Treated as known	
Sigma (σ)		×	

The relative success migrating above Hells Gate in year t (y_t) was either estimated directly for each year or made a function of flow shown below as eq. 3. The year effect was an indicator of other factors that can affect annual population size, including initial survival in freshwater, estuarine, and ocean environments. The annual flow effect multiplier (HA_t or HB_t) attempted to capture freshwater conditions affecting upriver migration of adult salmon at Hell's Gate. This is not only the site of difficult passage, but even with fishways it remains a site of very high water velocities and difficult passage (Crossin et al. 2003). These and other studies (Rand and Hinch 1998; Rand et al. 2006) led us to hypothesize that higher mean monthly flow during the adult spawning migration period (October) would delay and possibly inhibit passage of adult pink salmon above Hell's Gate and decrease the number of spawners above Hell's Gate.

To capture the effect of flow at Hell's Gate, we used data from the Fraser River gage station at Hope (08MF005; na-

tional water data archive, hydrometric program, Water Survey of Canada, <http://www.wsc.ec.gc.ca/applications/H2O/index-eng.cfm>) to develop relationships between mean monthly flow in October and each spawning population complex. We estimated different relationships for spawning populations above (HA_t) and below Hell's Gate (HB_t) (eq. 3), because while the fishways were designed to facilitate fish passage for the majority of flows, high discharges can still delay and even block migration for spawning population complexes above Hell's Gate. Mean October flow ($\text{cm}\cdot\text{s}^{-1}$) was used as the returning freshwater condition because peak spawning typically occurred during mid- to late October (DFO, personal communication). We assumed that increased flow at Hell's Gate would be positively related to the number of pink salmon spawning in the Lower Fraser River and Canyon population complexes but negatively related to the number of pink salmon spawning in the Uppermost Fraser River, Thompson River, and Seton-Anderson watersheds (Fig. 2).

$$(3) \quad \begin{aligned} HA_t &= \exp[-q(F_t - \bar{F})] \quad \text{if the spawning population is above Hell's Gate} \\ HB_t &= \exp[q(F_t - \bar{F})] \quad \text{if the spawning population is below Hell's Gate} \end{aligned}$$

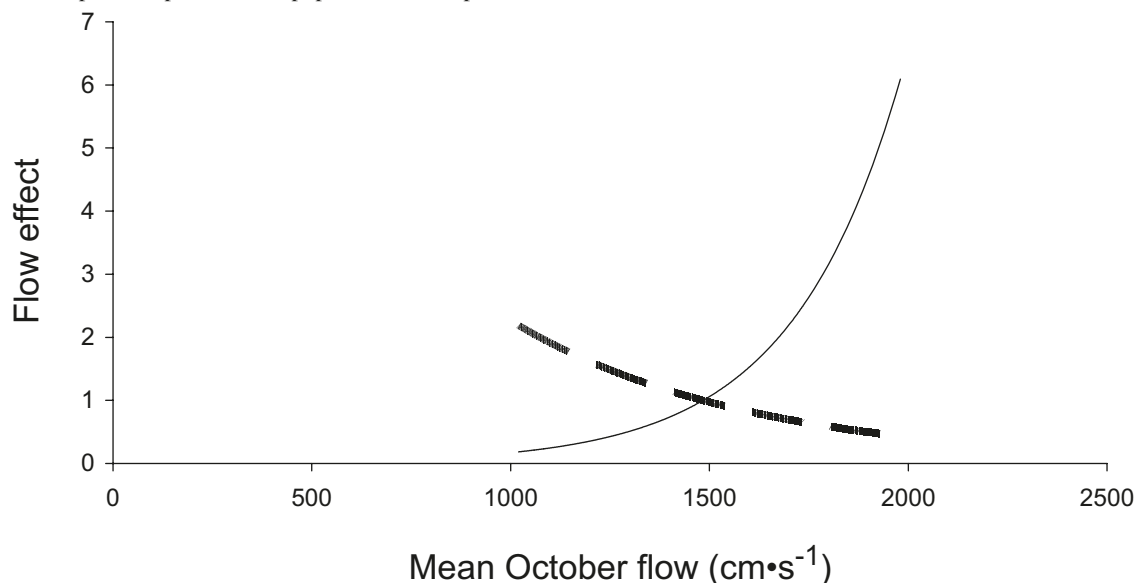
where F_t is the mean October flow at Hell's Gate at time t , \bar{F} is the average mean October flow at Hell's Gate from 1912 to 1987, and q is a parameter to be estimated that determines the intensity of the flow effect.

We calculated the model parameters for each spawning population within a likelihood framework where the best model fit for the years 1947 to 1987 for all the spawning populations was provided by minimizing the negative log-likelihood of each population in each year (Hilborn and Man-

gel 1997). We assumed an observation error model with log-normally distributed errors about the counts. We calculated the negative log-likelihood (l) of the predicted colonizing population size ($\hat{N}_{j,t}$) given the observed colonizing population size ($N_{j,t}$):

$$(4) \quad l(N_{j,t} | \hat{N}_{j,t}) = -\ln \left[\left(\frac{1}{\sigma\sqrt{2\pi}} \right) \right] + \left[\frac{(N_{j,t} - \hat{N}_{j,t})^2}{2\sigma^2} \right]$$

Fig. 2. Graphic representation of flow effect variable on estimated number of Fraser River pink salmon population complexes above and below Hell's Gate. High flows can deter upriver pink salmon migration and potentially increase the number of pink salmon counted on spawning sites below Hell's Gate. The dashed line represents the flow effect on pink salmon populations that spawn upstream of Hell's Gate, and the solid line represents pink salmon populations that spawn below Hell's Gate.



where σ is the standard deviation of the process error for all the spawning populations. We summed the individual negative log-likelihoods generated for each spawning population in a given year to calculate the total log-likelihood to represent how well the model fits the data, where smaller total negative log-likelihood corresponds to a better fit.

We constructed a set of nested models based upon examining all possible combinations of main effects. The first model was the null model, where we assumed only a population effect with no immigration, year, or flow effect. The second model included a population effect and an effect from one of the three main variables: immigration, year, or flow. In this case we hypothesized that one of these variables alone dominated and aids in better predicting spawning population size over time. The third model included a population effect and two additional effects from immigration, year, or flow. The last model included all four variables: population, immigration, year, and flow effect (i.e., all of the variables were important in predicting pink salmon spawning population size in the Fraser River).

All combinations of main effects were plausible hypotheses and were therefore competed using Akaike's information criterion adjusted for small sample sizes (AIC_c) to compare how well each of the models trade off between model fit and complexity (Burnham and Anderson 2002). The difference between the AIC_c of a candidate model and the one with the lowest AIC_c provided the ranking metric (ΔAIC_c). Generally speaking, ΔAIC_c between 0 and 4 indicates substantial support for a model being the most likely approximating model given the trade-off between fit and complexity. A ΔAIC_c between 4 and 7 represents less support, and ΔAIC_c of greater than 7 indicates very little support (Burnham and Anderson 2002). Akaike weights (w_i) were calculated, representing the strength of evidence in favor of model i being the most likely model. The ratio of Akaike weights (w_i/w_j) indicated the plau-

sibility of the most likely model compared with other models (Burnham and Anderson 2002).

Results

As reported by Withler (1982), 1525 adult pink salmon were estimated above Hell's Gate in 1947, with increases to 19 000 by 1951 and 129 000 in 1955, an increase of two orders of magnitude in four generations (Table 1). During this time period the total returns of pink salmon to the Fraser River system were 8–12 million (Table 1). In addition to the numerical increase above Hell's Gate, there was a spatial expansion pattern, particularly in the Thompson River and Seton–Anderson watersheds, where spawner estimates were generally increasing from 1957 to 1981 (Table 3). A reduction in the number of pink salmon in each of those watersheds occurred between 1983 and 1987, with an increase in the number of pink salmon below Hell's Gate in the Lower Fraser River and Canyon tributaries (Table 3).

Two models were most likely to predict pink salmon spawning population dynamics in recently colonized habitats (Table 4), and their parameter estimates were similar (Table 5). The most likely model included a dispersal effect, a year effect, and a flow effect on migration at Hell's Gate (Fig. 3). The model fit was seven times more plausible than the next best candidate model, which included all the same variables with the exception of a dispersal effect (Table 4). The models with only one of the three single parameters or a different combination of two of the three variables were less plausible than the models including year and flow or year, flow, and dispersal (emigration and immigration) (Table 4).

The two most likely models distinguished themselves from the next models by capturing the downward trend in the overall population prior to the mid 1960s and the large-scale shift in abundance between populations that occurred in 1985 (Fig. 3). We hypothesize that a large number of pink salmon

Table 3. Estimated numbers of adult pink salmon spawning in regions of the Fraser River system, British Columbia, Canada.

Year	Lower Fraser River	Canyon streams	Thompson River	Seton–Anderson	Uppermost Fraser River
1957	1 073 904	12 660	269 332	60 820	263
1959	733 933	28 862	87 224	16 153	62
1961	547 850	15 290	69 411	62 175	83
1963	516 831	21 832	285 243	136 562	723
1965	543 757	7 798	233 100	125 458	3 180
1967	785 797	7 942	450 487	239 720	3 015
1969	848 532	4 894	248 900	212 980	0
1971	928 046	22 549	258 203	308 241	5 346
1973	766 053	18 237	283 504	249 058	0
1975	315 059	9 516	480 350	280 860	36
1977	775 016	9 276	978 325	435 341	3 444
1979	1 523 458	25 610	891 191	712 840	1 846
1981	2 255 753	43 234	1 166 348	626 402	5 532
1983	3 310 999	46 456	512 398	501 475	1 721
1985	5 254 163	164 437	193 448	274 120	530
1987	1 066 032	11 736	253 109	743 286	496

Table 4. Model selection results for factors that affected pink salmon recolonization of the Fraser River above Hell’s Gate from 1957 to 1987.

Candidate models	Log-likelihood	<i>p</i>	ΔAIC_c	Akaike weight (<i>w_i</i>)	<i>w_i</i> / <i>w₁</i>
Year, dispersal, flow	29.87	40	0.00	0.874	1
Year, flow	35.82	36	3.9	0.124	7
Year	42.82	34	13.9	0.001	1 043
Year, dispersal	39.94	38	16.1	0.000	3 197
Flow	81.87	15	54.0	0.00	532 048 240 602
Flow, dispersal	78.83	19	55.9	0.00	1 389 548 513 671
Dispersal	81.66	17	57.6	0.00	3 186 677 646 907
Null	86.20	13	58.7	0.00	5 468 360 709 664

Note: Models are ranked from most plausible ($\Delta AIC_c = 0$) to least plausible; *p* is the number of parameters. The ratio of Akaike weights (*w_i*/*w₁*) indicates the plausibility of the most likely model (*w₁*) compared with other models (*w_i*).

that typically had spawned upstream of Hell’s Gate did not gain access to the these areas in 1985 because of difficult flow conditions and thus spawned below Hell’s Gate. The variation prior to 1977 was predominantly captured with the year effect, whereas the variation seen since 1977 was captured by the flow effect. The initial increase in Thompson and Seton–Anderson populations since 1947 was captured with the dispersal effect in the most likely model (Figs. 3c and 3d).

The initial population size estimates were within 1% of both of the most likely models. However, carrying capacity estimates were considerably larger than actual population sizes for the Lower Fraser River and Canyon stream populations (Table 5). Carrying capacity estimates were similar to actual spawning population sizes for the Thompson River and Seton–Anderson populations (Table 5). The dispersal probability to a spawning population varied considerably, ranging between none to almost 75% (Table 5). A continual source of dispersers from the source (~2.5%) combined with a large initial source population resulted in a large estimated number of dispersers (strays) ($17\,535 \pm 4089$) to colonize newly opened habitats irrespective of model fit (Fig. 4). Estimated numbers of recruits per spawners > 1.0 occurred con-

sistently in each of the spawning population complexes from 1957 to 1987, with the exception of the Uppermost Fraser River (Table 5; Fig. 5). The estimated numbers of recruits per spawner were two times greater for the Thompson River and Seton–Anderson than for the Lower Fraser River and Canyon streams (Table 5; Fig. 5). The Uppermost Fraser River did not establish a self-sustaining spawning population during the observed timeframe and could not be modeled as a population because the abundance estimates were zero for some years between 1957 and 1987.

Correlations in abundance between the spawning population complexes varied. The greatest degree of correlation was between the Lower Fraser River and Canyon streams population complex (Table 6). The Seton–Anderson and Thompson River population complexes were also highly correlated, suggesting an exchange between the two populations or common environmental influences affecting them more than other pairs of populations. The Thompson River and Uppermost Fraser River spawning population complexes were also highly correlated. Spawning populations above and below Hell’s Gate were not closely correlated in abundance, even though the initial source population complex for above Hell’s Gate was the Lower Fraser River. In some cases there

Table 5. Parameter estimates for the two most plausible pink salmon recolonization models.

	Year, dispersal, flow	Year, flow
Initial population size (N_{1945})		
Lower Fraser River	5 202 939	5 243 721
Canyon streams	54 198	13 275
Thompson River	0	590
Seton–Anderson	5	225
Recruits per spawner (α)		
Lower Fraser River	6.0	6.9
Canyon streams	5.9	5.8
Thompson River	10.2	12.8
Seton–Anderson	10.6	11.8
Carrying Capacity (K)		
Lower Fraser River	22 532 077	5 548 989
Canyon streams	517 653 643	8 651 919 684
Thompson River	769 664	511 381
Seton–Anderson	712 352	551 076
Dispersal probability (p_{ij}) to a spawning population		
Lower Fraser River	0.74	
Canyon streams	0.00	
Thompson River	0.21	
Seton–Anderson	0.05	
Straying rate (s)	2.47%	

was a negative correlation between the spawning population complexes above and below Hell’s Gate, which could be due to factors such as the opposite effects of flow conditions (Fig. 2).

The average historic pink salmon population size in the Fraser River system prior to the 1915 rockslide was estimated to be ~48 (±4.6) million, with the majority (77%) spawning above Hell’s Gate (~37 ± 3.6 million) versus below it (~11 ± 2.4 million; Ricker 1989; Beamish 2002). During the 1980s, there were ~1.2 million (±212 693) above Hell’s Gate in the Thompson River and Seton–Anderson systems, a decrease of 97% from historical population estimates. Lower Fraser River pink salmon during the 1980s numbered ~2.7 million (±690 854), which was a 12.5% increase compared with estimates prior to the rockslide. Almost 70% of pink salmon in the Fraser River in the 1980s spawned in the lower river, with the remaining 30% spawning above Hell’s Gate.

Discussion

Barriers to migration that vary temporally can have pronounced effects on fish population dynamics and can lead to recolonization and the restructuring of spawning populations. A hydrologic barrier at Hell’s Gate on the Fraser River had negative effects on pink salmon spawning populations above the barrier, preventing them from using the vast majority of the historic habitat area and dramatically decreasing the number of returning adults to the overall Fraser River pink salmon population complex.

The subsequent release of the migration barrier at Hell’s Gate allowed for the natural reestablishment of self-sustaining upstream pink salmon spawning populations

within one to two decades after construction of passage facilities. Compared with other species of Pacific salmon, pink salmon are (i) more numerous, (ii) apparently more prone to stray, (iii) less variable in life history, (iv) have a short period of freshwater residence, and have (v) a shorter generation time and (vi) higher but more variable population productivity (e.g., recruits per spawner) (Myers et al. 1995; Hendry et al. 2004; Krkošek et al. 2011). All of these attributes make them likely to colonize new habitats and expand quickly. Consistent with this perspective, pink salmon were the first salmonid to colonize recently opened–created streams in southeast Alaska after decades of glacial retreat (Milner and Bailey 1989). Pink salmon recolonized 25 streams that changed elevation by over 4 m in Prince William Sound within 6 years of the 1964 earthquake (Roys 1971). Pink salmon in the Fraser River system are an excellent example of the establishment of self-sustaining, tributary-specific spawning populations that responded to a barrier removal owing to their energy efficient migrations and overall swimming performance (Standen et al. 2002; Crossin et al. 2003; MacNutt et al. 2006). Fraser River pink salmon were able to colonize above a barrier and adapt to differences in source population distance, habitat characteristics, and competition from other salmonid species.

All estimated Fraser River pink salmon spawning populations, excluding the Uppermost Fraser River, consistently had population growth rates >1.0. Two of those are above the historic barrier at Hell’s Gate, and thus by our definition these are all self-sustaining spawning populations. The combination of large numbers of individuals and relatively high and consistent population productivity is a primary foundation for potential colonization of newly opened habitats. Another critical attribute to recolonization by pink salmon in the Fraser River was a continual source of dispersers from highly productive spawning populations downriver. We estimated a constant dispersal rate (2.5%) from a large initial source population in the lower river that resulted in persistently large numbers of colonizing pink salmon to the newly opened habitats. This estimate is quite plausible based on other estimates of pink salmon straying rates (Hendry et al. 2004). It is important to note that while we modeled constant dispersal, there are other types of dispersal such as density-dependent dispersal due to population size and resource competition that might influence straying rates among salmon populations and over time. Lastly, the ability of Fraser River pink salmon to migrate long distances efficiently also led to recolonization of the Fraser River above Hell’s Gate (Standen et al. 2002; Crossin et al. 2003; MacNutt et al. 2006).

Pink salmon became abundant in the Fraser River above Hell’s Gate in a few generations (e.g., decades) but have not approached the estimated levels prior to the rockslide (Ricker 1989). In addition, the proportion of pink salmon above and below the rockslide has shifted since recolonization, and most pink salmon now occur below the rockslide’s site. Shifts in the relative abundance between spawning salmon populations across a watershed or region over time have been documented elsewhere. For example, in Bristol Bay, Alaska, the productivity and relative abundance of sockeye salmon populations shifted with climatic conditions that favored specific life history patterns and geographic regions (Hilborn et al. 2003). The change in the population structures

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Fig. 3. Observed (circles) and modeled (line) data of pink salmon spawning populations 1947 to 1987 in the Fraser River, British Columbia, Canada, following removal of a flow barrier at Hell’s Gate. Modeled data is from the most likely candidate model and includes dispersal, year, and a flow effect. (a) Lower Fraser, (b) canyon streams, (c) Thompson, (d) Seton–Anderson, (e) Fraser River below Hell’s Gate, (f) Fraser River above Hell’s Gate.

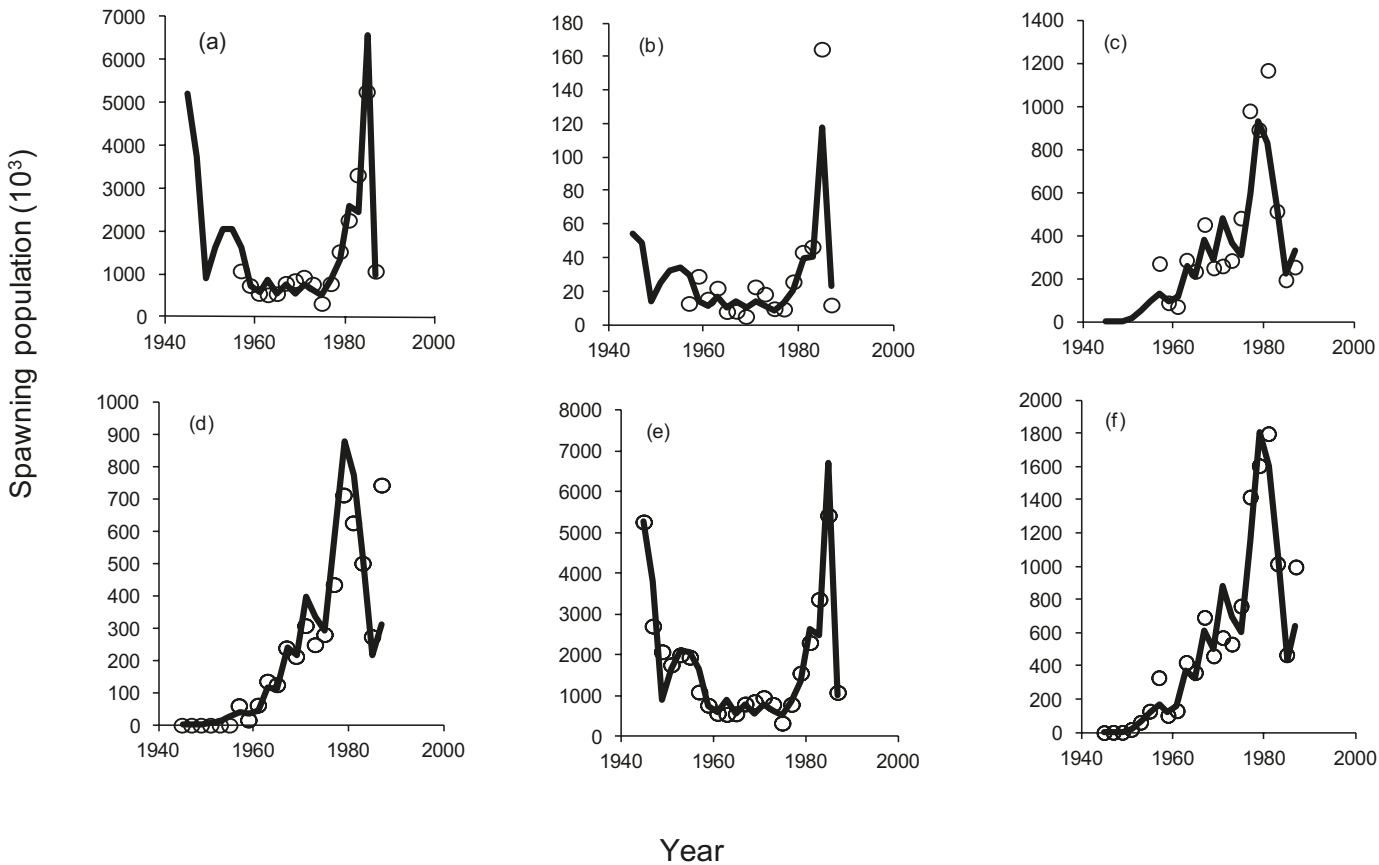
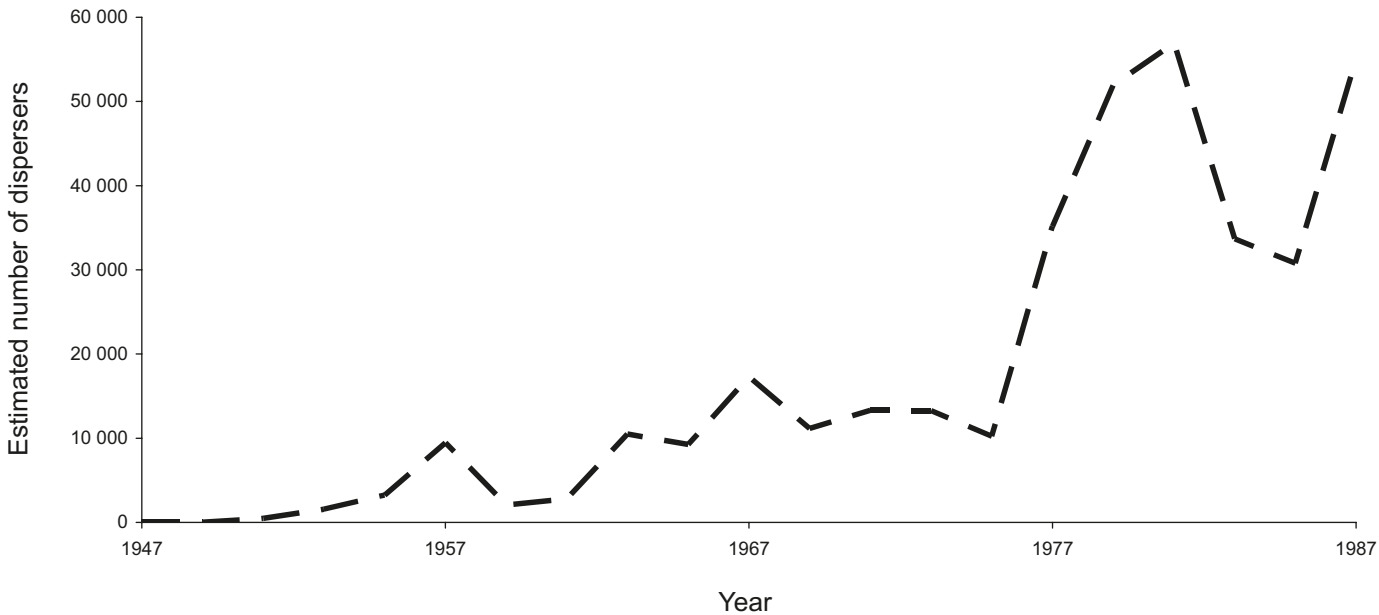


Fig. 4. Estimated number of pink salmon dispersers (strays) from source population complexes below Hell’s Gate to sites above Hell’s Gate in the Fraser River, British Columbia, Canada, 1947 to 1987. The dashed line represents straying rates of 2.5%.



above and below Hell’s Gate suggests that either habitat conditions have changed or that the genetically unique populations that evolved are lost and not reconstituted. If the latter,

it suggests that removal of barriers that caused local extirpation does not guarantee reestablishment of the same population structure; thus, the general assumption of reversibility of

Fig. 5. Estimated population growth rates from 1957 to 1987 for spawning populations of pink salmon in the Fraser River, British Columbia, Canada. Dark solid lines indicate median population growth rate. Box indicates 25th and 75th percentiles, while solid lines at the end of the hash marks perpendicular to the box are 5th and 95th percentiles.

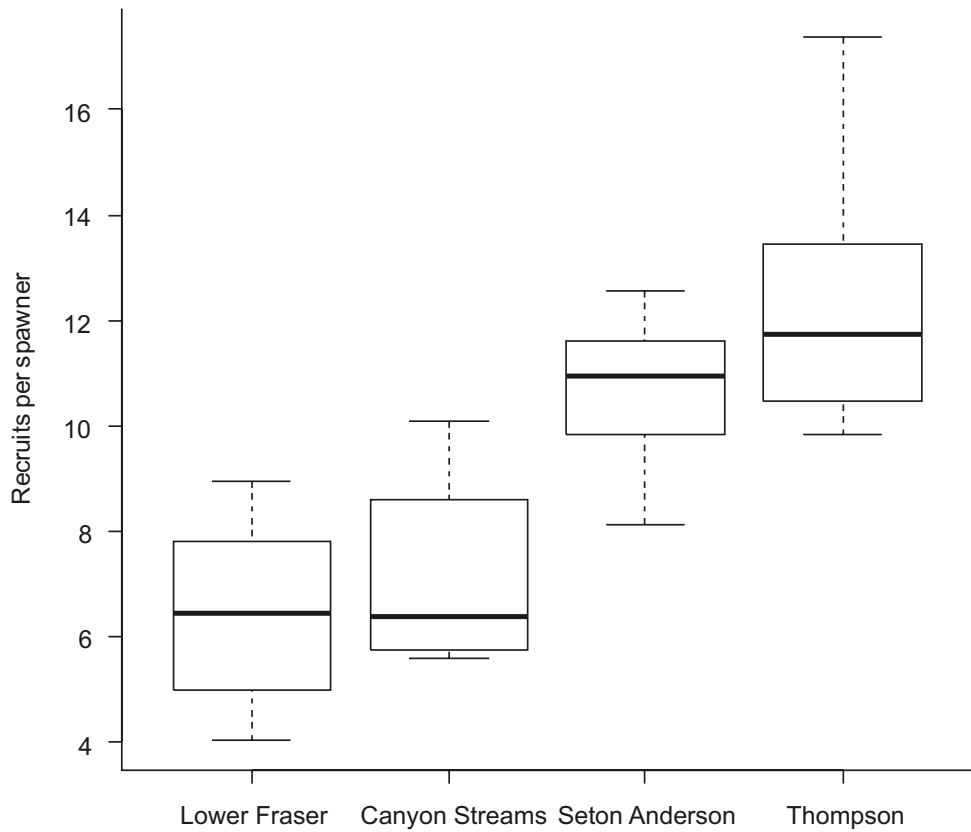


Table 6. Correlation coefficients between numbers of pink salmon spawning annually in regions of the Fraser River, British Columbia, Canada 1957–1987.

	Lower Fraser River	Canyon streams	Thompson River	Seton–Anderson	Uppermost Fraser River
Lower Fraser River	1.00				
Canyon streams	0.92	1.00			
Thompson River	0.12	−0.06	1.00		
Seton–Anderson	0.29	0.07	0.67	1.00	
Uppermost Fraser River	0.05	−0.05	0.59	0.36	1.00

effects may not be justified if populations with presumably uniquely adapted attributes are lost.

Several hypotheses have been proposed regarding the difference in population size before and after the rockslide (Ricker 1989). One hypothesis was that pink salmon populations above Hell’s Gate (e.g., Thompson River, Seton–Anderson, Uppermost Fraser River) were larger-bodied fish and stronger swimmers relative to those in the lower river, and these populations were lost after the slide (Ricker 1989). These populations were lost because of a combination of the selective removal of larger individuals from the population by gillnet and troll fisheries and by the rockslide, and the resulting colonization was from smaller-bodied, lower Fraser River pink salmon populations (Ricker 1989). The overall decrease in fish size has been hypothesized to make the migration through the canyon more difficult; thus, fewer fish can make the migration (Williams et al. 1986; Ricker 1989).

Several lines of evidence support this hypothesis, including

a 23% decrease in Fraser River pink salmon body size from 1951 to 1987 (0.46 kg; Ricker 1989). This change in size may have been due to other factors besides selective harvest, such as changing ocean conditions that affect growth rate and size (Beamish 2002). Interestingly, the Fraser River fish above Hell’s Gate are still larger than their Lower Fraser River counterparts and have higher maximum swimming speeds, allowing them to negotiate the Hell’s Gate rapids (Williams et al. 1986; Beacham et al. 1988; Ricker 1989). Other possible hypotheses put forth include longer migrations through more difficult rapids, regardless of the fish ladders, more severe habitat conditions during the egg to fry life stages owing to higher flow events and more extreme cold temperature conditions, and human impacts to spawning grounds (Ricker 1989). When colonization took place, the fish that were able to migrate above Hell’s Gate were presumably the most fit, in terms of swimming performance, and so were probably not a random sample from the lower

river. These “favored founders” (Quinn et al. 2001) have continued to experience selection from the rigorous migration, and some degree of adaptation is likely to have taken place in the 60 years or 30 generations since colonization.

Large-scale ocean and climate processes have affected Fraser River pink salmon during the period of recolonization above Hell’s Gate. Prior to 1976 the average annual Fraser River pink salmon run size (the number of spawners plus those caught in fisheries) was 6 840 375 ($\pm 3 413 970$), with the number of spawning pink salmon (escapement) averaging 1 565 375 ($\pm 391 901$). From 1977 to 2001, the Fraser River pink salmon run averaged 15 598 692 ($\pm 6 310 823$), and the escapement averaged 6 832 615 ($\pm 5 007 251$). The over two-fold increase in run size in the Fraser River after 1976 is comparable to the overall increase across the Pacific Rim. Prior to 1976, the annual average was about 151 million adult pink salmon across the entire Pacific Ocean, but from 1977 to 2001 the total population more than doubled to 323 million fish per year (Ruggerone and Nielsen 2004). The apparent shift to environmental conditions favoring pink salmon in general, including those in the Fraser River, probably facilitated the rapid recolonization of the Fraser River above Hell’s Gate, as it produced a large source population from which individuals might stray upriver, and it also provided high rates of survival and recruitment of the progeny of the strays. This phenomenon was, in part, captured with the model’s year effect on population dynamics.

Higher flows and water temperatures increase energy use by migrating salmon in the Fraser River (Rand and Hinch 1998), and conditions at Hell’s Gate can also delay migration or prevent passage (Macdonald and Williams 1998). Flows during the normal period of pink salmon migration can vary between 1000 and 2500 m³·s⁻¹ and can affect the timing of migration and spawning and en route mortality of salmonids (Rand et al. 2006). We found that flows can affect the relative bi-annual abundance of pink salmon spawning complexes above and below Hell’s Gate. Very high flows during migration seemed to deter pink salmon from spawning above Hell’s Gate and cause these fish to spawn in downriver streams. Capturing this temporal effect is important in understanding the bi-annual variation displayed in the population dynamics of pink salmon in the Fraser River.

Our results indicated that Fraser River pink salmon developed populations above Hell’s Gate from a combination of an initially large source population, high intrinsic growth rates linked to favorable climate-driven conditions, a constant supply of dispersers, and large amounts of newly available habitat. New spawning populations can help expand overall population size over time, as was the case with Fraser River pink salmon. These populations can vary in terms of relative productivity, the dispersal between populations, and relative contribution to the larger population. Analysis of the Fraser River pink salmon spawning populations revealed that some populations have higher productivity with this complex of populations, and magnitude of exchange among them is mediated in part by river conditions that influence passage. The spatial structure and relative abundance of the spawning populations can shift, relative to historic conditions, once a barrier is removed. In summary, self-sustaining anadromous salmon populations can develop within generations when ac-

cess to historically available habitat becomes available for recolonization.

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References

- Anderson, J.H., Faulds, P.L., Atlas, W.I., Pess, G.R., and Quinn, T.P. 2010. Selection on breeding date and body size in colonizing coho salmon, *Oncorhynchus kisutch*. *Mol. Ecol.* **19**(12): 2562–2573. PMID:20492523.
- Beacham, T.D., Withler, R.E., Murray, C.B., and Barner, L.W. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. *Trans. Am. Fish. Soc.* **117**(2): 109–126. doi:10.1577/1548-8659(1988)117<0109:VIBSME>2.3.CO;2.
- Beamish, R.J. 2002. Recent returns of pink salmon to the Fraser River indicate the importance of relating stock to recruitment on a regime scale. North Pacific Anadromous Fish Commission (NPAFC). Doc. 633, Fisheries and Oceans Canada, Science Branch – Pacific Region, Pacific Biological Station, Nanaimo, B.C.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- Cooper, A.B., and Mangel, M. 1999. The dangers of ignoring metapopulation structure for conservation of salmonids. *Fish Bull.* **97**(2): 213–226.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Whelly, M.P., and Healey, M.C. 2003. Pink salmon (*Oncorhynchus gorbuscha*) migratory energetics: response to migratory difficulty and comparison with sockeye salmon (*Oncorhynchus nerka*). *Can. J. Zool.* **81**(12): 1986–1995. doi:10.1139/z03-193.
- Fraser, D.F., Gilliam, J.F., and Yip-Hoi, T. 1995. Predation as an agent of population fragmentation in a tropical watershed. *Ecology*, **76**(5): 1461–1472. doi:10.2307/1938148.
- Gonia, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Trans. Am. Fish. Soc.* **135**(2): 408–419. doi:10.1577/T04-113.1.
- Heard, W.R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). In *Pacific salmon life histories*. Edited by C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 119–230.
- Hendry, A.P., Castaic, H.V., Kinnison, M.T., and Quinn, T.P. 2004. The evolution of philopatry and dispersal: homing versus straying in salmonids. In *Evolution illuminated: salmon and their relatives*. Edited by A.P. Hendry and S.C. Stearns. Oxford University Press, New York. pp. 52–91.
- Hilborn, R., and Mangel, M. 1997. The ecological detective: confronting models with data. Monographs in Population Biology 28. Princeton University Press, Princeton, N.J.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci. U.S.A.* **100**(11): 6564–6568. doi:10.1073/pnas.1037274100. PMID:12743372.
- Johnson, S.C., Blaylock, R.B., Elphick, J., and Hyatt, K.D. 1996. Disease induced by the sea louse (*Lepeophtheirus salmonis*) (Copepoda: Caligidae) in wild sockeye salmon (*Oncorhynchus*

- nerka*) stocks of Alberni Inlet, British Columbia. Can. J. Fish. Aquat. Sci. **53**(12): 2888–2897. doi:10.1139/f96-226.
- Knapp, R.A., Matthews, K.R., and Sarnelle, O. 2001. Resistance and resilience of alpine lake fauna to fish introductions. Ecol. Monogr. **71**(3): 401–421. doi:10.1890/0012-9615(2001)071[0401:RAROAL]2.0.CO;2.
- Krkošek, M., Hilborn, R., Peterman, R.M., and Quinn, T.P. 2011. Cycles, stochasticity, and density dependence in pink salmon population dynamics. Proc. R. Soc. Lond. Ser. B Biol. Sci. **278**: 2060–2068.
- Macdonald, J.S., and Williams, I.V. 1998. Effects of environmental conditions on salmon stocks: the 1997 run of early Stuart sockeye salmon. In *Speaking for Salmon; Workshop Proceedings. Edited by P. Gallagher and L. Wood.* Institute of Fisheries Analysis, Simon Fraser University, Burnaby, B.C. pp. 46–51.
- MacNutt, M.J., Hinch, S.G., Lee, C.G., Phibbs, J.R., Lotto, A.G., Healey, M.C., and Farrell, A.P. 2006. Temperature effects on swimming performance, energetics, and aerobic capacities of mature adult pink salmon (*Oncorhynchus gorbuscha*) compare with those of sockeye salmon (*Oncorhynchus nerka*). Can. J. Zool. **84**(1): 88–97. doi:10.1139/z05-181.
- Major, R.L., and Mighell, J.L. 1967. Influence of Rocky Reach Dam and the temperature of the Okanogan River on the upstream migration of sockeye salmon. Fish Bull. **66**(1): 131–147.
- Martins, E.G., Hinch, S.G., Patterson, D.A., Hague, M.J., Cooke, S.J., Miller, K.M., Lapointe, M.F., English, K.K., and Farrell, A.P. 2011. Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River Sockeye salmon (*Oncorhynchus nerka*). Glob. Change Biol. **17**(1): 99–114. doi:10.1111/j.1365-2486.2010.02241.x.
- Milner, A.M., and Bailey, R.G. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. Aquacult. Fish. Manage. **20**(2): 179–192.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science, **269**(5227): 1106–1108. doi:10.1126/science.269.5227.1106. PMID:17755535.
- Parken, C.K., Candy, J.R., Irvine, J.R., and Beacham, T.D. 2008. Genetic and coded wire tag results combine to allow more-precise management of a complex Chinook salmon aggregate. Trans. Am. Fish. Soc. **28**(1): 328–340.
- Pimm, S.L., and Pimm, J.W. 1982. Resource use, competition, and resource availability in Hawaiian honeycreepers. Ecology, **63**(5): 1468–1480. doi:10.2307/1938873.
- Priede, I.G., Solbé, J.F.L.G., Nott, J.E., O'Grady, K.T., and Cragg-Hine, D. 1988. Behaviour of adult Atlantic salmon, *Salmo salar* L., in the estuary of the River Ribble in relation to variations in dissolved oxygen and tidal flow. J. Fish Biol. **33**(Suppl. sA): 133–139. doi:10.1111/j.1095-8649.1988.tb05567.x.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am. Nat. **132**(5): 652–661. doi:10.1086/284880.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle, Wash.
- Quinn, T.P., Kinnison, M.T., and Unwin, M.J. 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. Genetica, **112–113**(1): 493–513. doi:10.1023/A:1013348024063. PMID:11838785.
- Rand, P.S., and Hinch, S.G. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. Can. J. Fish. Aquat. Sci. **55**(8): 1832–1841. doi:10.1139/f98-068.
- Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., and Higgs, D.A. 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Trans. Am. Fish. Soc. **135**(3): 655–667. doi:10.1577/T05-023.1.
- Reiser, D.W., Huang, C.-M., Beck, S., Gagner, M., and Jeanes, E. 2006. Defining flow windows for upstream passage of adult anadromous salmonids at cascades and falls. Trans. Am. Fish. Soc. **135**(3): 668–679. doi:10.1577/T05-169.1.
- Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. **11**(5): 559–623. doi:10.1139/f54-039.
- Ricker, W.E. 1987. Effect of the fishery and of obstacles to migration on the abundance of Fraser River sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. 1522. Nanaimo, B.C.
- Ricker, W.E. 1989. History and present state of the odd-year pink salmon runs of the Fraser River region. Can. Tech. Rep. Fish. Aquat. Sci. 1702. Nanaimo, B.C.
- Roos, J.F. 1996. Restoring Fraser River salmon. Pacific Salmon Commission, Vancouver, B.C.
- Roys, R.S. 1971. Effect of tectonic deformation on pink salmon runs in Prince William Sound. In *The Great Alaska Earthquake of 1964.* National Academy of Sciences, (NAS) Publication 1604, Washington, D.C. pp. 220–237.
- Ruggerone, G.T., and Nielsen, J.L. 2004. Evidence of competitive dominance of pink salmon (*Oncorhynchus gorbuscha*) over other salmonids in the North Pacific Ocean. Rev. Fish Biol. Fish. **14**(3): 371–390. doi:10.1007/s11160-004-6927-0.
- Schick, R.S., and Lindley, S.T. 2007. Directed connectivity among fish populations in a riverine network. J. Appl. Ecol. **44**(6): 1116–1126. doi:10.1111/j.1365-2664.2007.01383.x.
- Schubert, N.D., Whitehouse, T.R., and Cass, A.J. 1997. Design and evaluation of the 1995 Fraser River pink salmon (*Oncorhynchus gorbuscha*) escapement estimation study. Can. Tech. Rep. Fish. Aquat. Sci. 2178. Fisheries and Oceans Canada, Science Branch, New Westminster, B.C.
- Standen, E.M., Hinch, S.G., Healey, M.C., and Farrell, A.P. 2002. Energetic costs of migration through the Fraser River canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry. Can. J. Fish. Aquat. Sci. **59**(11): 1809–1818. doi:10.1139/f02-151.
- Underwood, A.J. 1994. Spatial and temporal problems with monitoring. Vol. 2. In *The rivers handbook, hydrological and ecological principles.* Edited by P. Calow and G.E. Petts. Oxford, Blackwell Scientific, London, UK. pp. 227–253.
- Waples, R.S., Pess, G.R., and Beechie, T.J. 2008. Evolutionary history of Pacific salmon in dynamic environments. Evol. Appl. **1**(2): 189–206. doi:10.1111/j.1752-4571.2008.00023.x.
- Williams, I.V., Brett, J.R., Bell, G.R., Traxler, G.S., Bagshaw, J., McBride, J.R., Fagerlund, U.H.M., Dye, H.M., Sumpter, J., Donaldson, E.M., Bilinski, E., Tsuyuki, H., Peters, M.D., Choromanski, E.M., Cheng, J.H.Y., and Coleridge, W.L. 1986. The 1983 early run Fraser and Thompson River pink salmon: morphology, energetics and fish health. International Pacific Salmon Fisheries Commission, Bulletin 23, Vancouver, B.C.
- Withler, F.C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. 1079, Nanaimo, B.C.

Appendix A

Table A1 appears on the following page.

Table A1. Streams surveyed for pink salmon the in the Fraser River from 1957 to 1987 below and above Hell's Gate.

Below Hell's Gate			Above Hell's Gate			
Lower Fraser River			Fraser River Canyon	Thompson River	Seton–Anderson	Uppermost Fraser River
Early-run	Late-run	Fraser River Canyon	Fraser River Canyon	Thompson River	Seton–Anderson	Uppermost Fraser River
Main stem Fraser River	Main stem Fraser River	American Creek	Nahatlatch River	Adams River	Bridge River	Churn River
Johnson Slough	Big Silver Creek	Anderson Creek		Bonaparte River	Cayoosh Creek	Gaspard Creek
Ruby Creek	Birkenhead River	Coquihalla River		Deadman Creek	Gates Creek	Hawkes Creek
	Border Creek	Emory Creek		Eagle River	Seton Creek	Lower Chilcotin River
	Brown Creek	Flood Creek		Little River	Lower Seton Channel	Quesnel River
	Center Creek	Hunter Creek		Lower Shuswap River	Upper Seton Channel	Stein River
	Chilliwack–Vedder River	Jones Creek		Nicoamen Creek	Portage Creek	Watson Bar Creek
		Jones Creek Channel		Nicola River	Yalakum River	Williams Lake Creek
	Chipmunk Creek	Kawawa Creek		Thompson River		
	Coquitlam River	Lorenzetti Creek		North Thompson River		
	Depot Creek	Nine mile Creek		South Thompson River		
	Foley Creek	Popkum Creek				
	Harrison River	Ruby Creek				
	Johnson Slough	Sawmill Creek				
	Kanaka Creek	Spuzzum Creek				
	Little Chilliwack River	Stoyama Creek				
	Liumchen Creek	Texas Creek				
	Maria Slough	Yale Creek				
	Middle Creek					
	North Alouette River					
	Paleface Creek					
	Ryder Creek					
	South Alouette River					
	Silver Creek (Pitt River)					
	Silverdale Creek					
	Slesse Creek					
	Squakum Creek					
	Stave River					
	Steelhead Creek					
	Suicide Creek					
	Sweltzer Creek					
	Tamihi Creek					
	Upper Chilliwack River					
	Weaver Channel Artificial Spawning Channel					
	Weaver Creek					
	Whonnock Creek					

Note: These surveys occurred only below Hell's Gate. Data from Fisheries and Oceans Canada (DFO), Tracy Cone, Fraser River stock assessment data manager, 100 Annacis Parkway, Unit 3, Annacis Island, Delta, BC V3M 6A2, 604-666-7269, Tracy.Cone@dfo.mpo.gc.ca.