Pacific Fisheries Resource Conservation Council

Does Over-Escapement Cause Salmon Stock Collapse?

Technical Paper

Prepared by
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ABSTRACT

The impact of "over-escapement", the spawning of an unusually large number of salmon from a given population or run, is examined in data for 21 British Columbia sockeye stocks and two pink salmon stocks. While there is evidence of a decrease in spawning efficiency at high spawning numbers, there is no evidence for anything like a "collapse" or "near-collapse" of production following runs with very large numbers of spawners. Recent information on lake fertilization by salmon carcasses on fry production, a potentially positive impact of large numbers of spawners, is also discussed.

This technical paper was prepared on behalf of the Pacific Fisheries Resource Conservation Council by two Council members, Carl Walters and Paul LeBlond, and its science advisor, Brian Riddell. It was instigated by a request from the Minister of Fisheries and Oceans Canada for a review and information on the notion of over-spawning as it relates to fisheries management strategies.

RÉSUMÉ

Nous examinons l'impact d'une échappée excessive—le frai d'un nombre singulièrement élevé de saumons au sein d'une population ou d'une remonte spécifique—à travers les données concernant 21 stocks de saumons rouges et 2 stocks de saumons roses de la Colombie-Britannique. Bien que ces données montrent que l'efficacité du frai diminue lorsque la densité des géniteurs atteint un seuil élevé, rien ne prouve que de telles densités entraînent un effondrement ou un quasi-effondrement de la production. Nous discutons également d'informations récentes concernant l'influence de la fertilisation des lacs par les carcasses de saumons sur la croissance des alevins, une retombée potentiellement positive des densités élevées de géniteurs.

Cet article spécialisé a été préparé pour le Conseil de conservation des ressources halieutiques du Pacifique par deux membres du Conseil, Carl Walters et Paul LeBlond, et par le conseiller scientifique du Conseil, Brian Riddell. Sa rédaction a été motivée par une demande émanant du ministère des Pêches et des Océans concernant le besoin de présenter des informations sur la notion de frai excessif et sur les retombées éventuelles que pourrait avoir ce phénomène sur les stratégies mises en place pour la gestion des pêches.

1. OVERVIEW

Recent years have seen some severe restrictions on British Columbia salmon fisheries, leading in some cases to the highest spawning escapements for nearly a century. These restrictions have had a variety of objectives, ranging from protection of stocks that have experienced poor marine survival (Rivers and Smith Inlets, PFRCC 2004), to protection of weak stocks that migrate through fisheries at the same time as the more productive ones (Fraser River – DFO 2003a; Skeena – DFO 2003b), to deliberate management experiments aimed at determining whether or not recruitment could be further increased by allowing more spawners (Rivers Inlet and Fraser River sockeye).

The very large escapements of sockeye and pink salmon have led some fishermen to raise a concern about "over-spawning[1]". Their opinion was described in the following way to the House of Commons Standing Committee on Fisheries and Oceans (June 2003 report):

> *"There's a high correlation between over-escapement and poor return, particularly for sockeye. Every major over-escapement event since 1956 has resulted in a near-collapse in the Skeena, in Rivers Inlet, and in the Fraser River. But our managers go on dumping more and more fish on the spawning grounds."*

It is difficult to see how statements like this could be generally true, considering how much larger both salmon runs and escapements would have been before development of commercial fishing (see Ricker 1987). Nevertheless, there are reasons to be concerned for spawning populations that are limited by available spawning area and/or rearing habitats and could produce relatively poor returns per spawner due to competition effects. For example, the eggs of early-spawning adults could be destroyed by the crowding of large numbers of later-spawning fish. Excessively large numbers of spawners could deplete gravel oxygen supplies, raise the risk of pre-spawning mortality[2], and in some cases might be capable of exhausting food resources in rearing lakes.

It is worth noting that there are other views on the impact of over-escapement. Other interest groups emphasize the ecological value of higher spawning escapements, regardless of salmon production efficiency. Salmon carcasses serve purposes ranging from food for terrestrial animals (such as bears) to fertilization for forest ecosystems and aquatic rearing environments. Larger escapements through harvest restrictions have been argued as a means to conserve diversity and to promote re-colonization of habitats or dispersal of salmonids. The evaluation of tradeoffs between fishery benefits and possible ecological values is beyond the scope of this technical paper. However, there is a considerable body of historical data that can be used to evaluate the hypothesis that high escapements could lead to increased aquatic fertility and salmon production. Some of these data are discussed here.

This technical paper reviews the historical evidence from large spawning runs of sockeye and pinks, with data on catch and spawning escapement that can be associated to a spawning year. We show that:

- There is good evidence that high escapements are unlikely to produce proportionally more recruitment (returning adult production) for the next generation.
- But, there is no evidence that high spawning runs place stocks at risk of collapse.

[1] In many articles or comments, "over spawning" or "over escapement" are used synonymously; both refer to the presence on spawning grounds of mature salmon in such high numbers as to result in reduced numbers of progeny produced per spawning adult.
[2] Pre-spawning mortality refers to the death of mature fish that returned to freshwater systems but died before completion of reproduction. The term is generic in that it applies to any source of mortality during this period.

We also note that, in these data, there is little evidence that high escapements have had a beneficial effect on juvenile productivity. A recent study by Hume et al. (2004) on the ecosystem impacts of lake fertilization by decaying carcasses, included in Appendix 1, provides additional support for this statement.

2. A More Precise Definition of "Over-Escapement"

In a seminal 1954 paper, Canadian fisheries scientist W. E. Ricker wrote that even in the absence of fishing, fish populations tend to fluctuate about some level maintained by natural controls. Leading up to this paper, biologists increasingly considered "competition" to be one natural control, including "any factor whose effectiveness increases with stock density." However, Ricker pointed out that the relationship between the number of mature adults and the number of resulting progeny (the reproduction curve) was not well defined. Ricker (1954) reported:

> *"Plotting net reproduction (reproductive potential of the adults obtained) against the density of the stock which produced them, for a number of fish and invertebrate populations, give a domed curve whose apex lies above the line representing replacement reproduction. At stock densities beyond the apex, reproduction declines either gradually or abruptly." (Abstract, page 559)*

Ricker suggested that as the spawning density increased, density-dependent mortality mechanisms become more effective and would limit the number of juveniles produced in the next generation. These mortality factors, also called "compensatory" (Neave 1953), may involve predation on juveniles, cannibalism and competition when spawning areas are limited. The effect of the competition would be to reduce the number of progeny produced per adult spawner as the number of spawners increased.

Ricker (1954) expressed his findings as a "stock/recruitment" (S/R, reproduction curve) function. An example is shown in Figure 1A. The actual shape of the curve would vary with the species and habitats, but each curve would be characterized by a positive slope at lower spawning abundances (progeny produced exceed the number of spawners), a peak of production at some intermediate level of spawners, and then a declining rate of production at higher spawning densities (the slope becomes negative and progeny produced may be fewer than the number of spawners). In Figure 1A, the horizontal axis represents the numbers of spawners (for this example, the axis is standardized and without units, but densities could be measured in total numbers of spawners, numbers of females, or total numbers of eggs deposited). The vertical axis is the resulting production or progeny from the spawners and may be referred to as "recruits": the number of adult fish returning to the coast to spawn before they may be caught in fisheries (i.e., recruits to the fishery). That number of recruits thus reflects all sources of mortality from spawning and rearing in freshwater habitats to life stages in the ocean until they become vulnerable to the fisheries. The actual shape of a reproduction curve will vary between stocks; it also assumes stable environmental conditions during the period of observations (e.g., habitat, climate, fishing conditions).

Slightly after Ricker's 1954 paper, another reproduction curve was proposed by two British scientists, R. H. Beverton and S.J. Holt (1957). Their curve (Figure 1B) was based on similar logic, but at larger spawning densities the compensatory effects are not as great and the reproduction curve becomes asymptotic to a constant value instead of decreasing.

In terms of over-spawning, however, these two curves would have very different expectations. The Ricker curve implies that a population could decline rapidly at very high numbers of spawners, whereas the Beverton-Holt (B-H) curve implies that the population would stabilize near some maximum level of production or recruitment. Note though, that the B-H curve also implies reduced progeny produced per spawning salmon at high spawning population sizes. Thus, both theoretical curves predict reduced rates of production (recruit per spawner) at large number of spawners.

The Ricker curve was widely adopted as a fundamental guide in the management of Pacific salmonids. Typical recruit-against-spawner curves for Pacific salmon have the apex of the Ricker curve to the left of the intersection of the replacement line and the reproduction curve (the box in Figure 1A). There is thus some number of spawners that would be expected, on average, to produce the maximum number of fish that could be harvested in a sustainable way. In Figure 1A, point 'C' is the target number of spawners for which the difference between the expected recruitment (point 'A') and the replacement line (point 'B', on the line S = R where each spawner produces one recruit) is maximized. The difference between point A and point B is referred to as the maximum sustained yield (MSY) and the management target value (Spawners = 'C') is referred to as the optimum escapement[3] goal. Consequently, on the left of the intersection point, the difference between the recruitment curve and the replacement line (R = S) has been referred to as surplus production, since it is "surplus" to replacing the required number of spawners.

What then is over-escapement? The term implies a surplus of spawning fish. It would, as a minimum, refer to the number of spawners lying to the right of the intersection point (box in Figure 1A), since the expected recruitment would then become less than the number of spawners in the parental generation. In a more restricted and generally accepted way, over-escapement describes a spawning population size that is larger than the optimal escapement goal (point 'C' in Figure 1A) since the rate of return per spawner begins to decline after that point. However, as will be seen in the examples shown below, recruits-against-spawner data for Pacific salmon are notoriously variable and an optimal escapement goal is very difficult to estimate. Any consideration of the over-escapement concept should be limited to escapements substantially greater (50 to 100%) than the estimated escapement goal.

The Ricker curve is used to describe the concept of over-escapement because it indicates that returns per spawner are expected to decline at higher spawning population sizes. However, the primary thesis of Ricker's (1954) theory is that there are natural controls that allow recovery of those populations to more productive spawner levels. Thus, any notion that over-escapement will cause a population to collapse, even to go extinct, cannot be associated with Ricker's stock-recruitment theory. The actual origin of this notion is difficult to determine and may simply be inferred or assumed from an extrapolation of these curved reproduction relationships.

[3] Escapement refers to the fish that survive (i.e., escape from) fishing activities. In the context of optimal escapement goals, the fish must survival all fishing pressures and successfully reproduce (spawn).

3. The Relationship Between Spawner Abundance and Reproductive Success in Sockeye and Pink Salmon

For the major Fraser River sockeye stocks, there have been extensive statistical analyses of the historical relationship between spawning stock size and reproductive success, as measured by the recruits produced per spawner (Walters and Staley 1987; Cass and Wood 1994; Cass et al. 2000; Collie and Walters 1987; Welch and Noakes 1990,1991; Myers et al. 1998). These analyses have been based on half a century of reasonably accurate enumerations of spawning numbers and subsequent recruitments (catch plus spawners). Spawning abundance has varied widely over the years, providing good statistical contrast to determine how average recruitment is affected by low versus high spawning situations. A key focus of these analyses has been to understand the phenomenon of "cyclic dominance", where high spawning runs tend to produce high recruitments and low runs tend to stay low, and have involved many cross-correlation analyses that should have revealed effects such as improved fertility of rearing lakes if such effects have been important. Less accurate data are available over the same time period for Fraser River pink salmon and a few other examples used for the coast (Babine Lake sockeye, Rivers Inlet and Smith Inlet sockeye, and Bella Coola Area 8 pink salmon).

Data in Figures 2A and 2B are limited to 23 sockeye and pink salmon stocks that have annual quantitative estimates of spawners (reproductive effort in the parental generation) and the estimated catch and spawning escapement produced by the parental generations. A consistent time series of these data requires a long-term commitment to monitoring and limits the number of stocks that could be included in this review. Programs of artificial enhancement, such as spawning channels or lake fertilization programs, are likely to influence the shape of the reproduction curves and must be considered when comparing populations. Figure 2A shows the number of recruits against the numbers of spawners for 23 stocks of BC sockeye and pink salmon. Neither the Ricker nor B-H curves have been fitted to the data presented. Only the replacement line R = S has been shown, as a dotted line, so that the reader can visually assess at a glance the reproductive success of each spawning group. In examining these plots, note that the reproduction curves presented in Figures 1A and 1B are theoretical models of these relationships. Whenever data are collected in natural systems, however, extensive annual variability in environmental conditions, biological interactions, and developmental events over time will tend to mask any true reproduction relationship.

An important point about the analysis of historical stock and recruitment data that span a wide range of spawning stock sizes is that the recruitment and recruit-per-spawner observations reflect (i.e., contain) *all short-term* (one generation) effects of spawner abundance on productivity. It is not possible for an effect such as enhanced juvenile survival due to food production derived from spawner carcasses to somehow be an important concern for productivity, without that effect already being represented in the historical recruitment data. The only major effect of spawning stock size on long-term production and population viability that might not be reflected in historical data is the effect of crowding at high (e.g. "natural") spawning abundances on straying (dispersal) and colonization rates. One of the arguments for experimental increases in Fraser River sockeye escapements has been to see if high escapements will trigger some fish to stray and recolonize spawning and rearing areas that were depopulated after the 1912 Hell's Gate disaster. Efforts to restock such areas have not been very successful, and the natural recolonization of the river above Hell's Gate by pink salmon in the late 1940s hints that it may be better to let the fish do it on their own.

These analyses have produced a clear and relatively simple conclusion: For the sockeye or pink stocks examined here, there is a negative relationship between recruitment produced per spawner (total survival rate from egg to recruitment) and spawner abundance (Figure 2B). The relationship is nearly linear, implying a dome-shaped (Ricker's curve) relationship between spawner abundance and mean resulting recruitment. This implies the existence of an "optimum" spawning stock size at which the average difference between recruitment and the spawning stock needed to sustain that recruitment is largest and represents the maximum sustainable average yield for the stock.

There is no evidence of catastrophic decrease or collapse in recruitment per spawner at the highest spawning stocks. For instance, the Skeena River Babine stock produced two relatively poor (just break-even) returns at high spawning runs, but one very large return from an equally high spawning. The Adams (Late Shuswap) stock returned at a rate of less than 1:1 from one of its highest spawning runs, but then had good returns from two equally high spawning runs. The Chilko stock had just breakeven (1:1) returns for each of the five years of highest spawning runs, somewhat below the best returns observed at intermediate spawning stocks but nothing like a stock collapse. About the only consistent pattern that is evident at high spawning stocks in the data in Figure 2 is that recruitment becomes more unpredictable than at low spawning stocks.

However, there is clear evidence that recent spawning results for the dominant cycle lines on some stocks (Adams, Chilko, Late Stuart, Stellako, Pitt, Bowron, and Birkenhead) have been larger than the optimum for producing maximum average harvest. That is, there has been over-spawning in the sense of producing fewer additional recruits than would be needed to justify continuing to allow such high spawning runs in order to maximize future harvest opportunities. On this point, fishers have been correct in expressing concerns about "waste of fish" in the sense of spawning efficiency. It remains to be seen whether or not the high escapements have triggered dispersal and recolonization of habitats that would ultimately result in higher total production, and/or that there are significant ecosystem benefits not assessed in these data.

The spawning-recruitment analyses have failed to provide a satisfactory explanation for the phenomenon of cyclic dominance for Fraser River sockeye. Juvenile production per spawner is apparently quite high for the small "off-cycle" spawning runs, and these juveniles typically appear to be healthier (larger) than the juveniles produced under more crowded, competitive conditions. It has been calculated that if those off-cycle runs had been protected completely from harvest during the early 20th century and resulted in recovery to near the abundance of dominant cycle runs, the economic value of the fishery would have been increased by around $1 billion (Walters and Staley 1987; Cass et al. DFO report in preparation). Such considerations support continuing efforts to rebuild off-cycle runs through escapement controls.

Data collected on Rivers Inlet sockeye spawning and recruitment prior to the mid 1980s produced an ambiguous picture about whether or not higher spawning targets would produce improved recruitment (Fig. 2, Rivers Inlet sockeye). There was an explicit decision to close the fishery as an experiment to gather recruitment information on high spawning runs (Walters et al. 1993). In the years following that closure, only average recruitments and spawning runs were observed, and in 1991 there was a catastrophic decrease in marine survival rate that does not appear to be related to the size of those experimental escapements, given that the same decrease occurred in the nearby Smith Inlet run, for which there had been no deliberate attempt to increase spawning.

The interpretation of spawning and recruitment information for the Skeena River (Babine River) is greatly complicated by large production from the Fulton and Pinkut River spawning channels. There is some indication that higher juvenile abundances produced from the channels led to decreased survival in Babine Lake and may reflect that the lake has a limited capacity to produce sockeye smolts (PFRCC 2004). However, as in Rivers Inlet, the survival rates from spawning to recruitment have been so variable as to preclude any definitive statement about the best number of spawners to allow, except in the spawning channels where capacity to accommodate them is well understood.

One limitation of comparing adult recruitment to parental spawners, as in Figure 2, is that adult recruitment reflects the total of past mortality sources and does not allow inspection of freshwater versus marine factors. For example, in Figure 2 there is no means to assess if increased spawning stock has resulted in any improvement in performance per spawner (recruitment per spawner) as would be expected if fertilization from salmon carcasses were important to production[4]. But are there examples where production in freshwater and marine environments can be examined separately? We are aware of three such datasets for Fraser River sockeye salmon, plus the Bowron Lake sockeye example discussed below. It is worthwhile examining the juvenile production data for these stocks, as many of the large spawning escapements have occurred in recent years when marine survival rates have been relatively poor. Any assessment of over-escapement based on adult return data for the 1990s will therefore have two factors confounded – any potential impact of over-escapement, as well as reduced marine survival rates.

[4]With the possible exception of Smith Inlet sockeye salmon (Fig 2B). However Smith Inlet sockeye rear in Long Lake which has been part of the Lake Enrichment Program (Canadian Salmonid Enhancement Program) since 1976. The objective of this program is to supplement food production in the lake by addition of chemical nutrients to increase survival and growth of juvenile sockeye salmon. This lake is thus not comparable to untreated lakes where the natural nutrient cycle prevails.

4. BOWRON LAKE SOCKEYE

Dr. Jim Woodey (pers. comm.[5]) identified this example to the authors. The Bowron Lake sockeye data is included in Figure 2B and shows six data points above the regression line at higher escapement values. While the juvenile data are not available for this stock, these data points result from dominant cycle years in a sockeye stock that usually was **not** cyclic. Starting with the 1959 spawning year, and lasting for six cycles (1959 through 1982), sockeye production switched to a four-year cycle with one strong year (the 1959 line). The upper panel of Figure 3 shows the number of female spawners for each year, identifying the 1959–1982 'cycle' years. The middle panel is a typical stock-recruitment plot, showing on the vertical axis the estimated adult recruitment as a function of the number of female spawners (on the horizontal axis). The larger escapement values have been identified by year of spawning.

The bottom panel presents the same data as in the middle panel but expressed as the rate of production (natural logarithm of recruitment divided by the number of female spawners) versus the number of female spawners. The straight line in this figure is the regression relation between these the two variable; its negative slope implies that the rate of return declined as the number of female spawners increased, a behaviour consistent with both Ricker's and B-H curves.

However, what is most interesting is that the two years with the largest numbers of spawners (1959 and 1979) are the start and finish of the cycle years, and the four dominant cycle years (1963, 1967, 1971, 1975) have large positive deviations from the regression at their spawning population sizes. These deviations imply that the rate of production for these years was greater than expected but the mechanism cannot be determined. Was the increase in production due to improved survival and growth of the juveniles in freshwater, or was it associated with good marine survival? If it were associated with increased numbers of spawners and improved freshwater production, then the response was apparently limited to the next summer and it may have established between-cycle interactions.

[5]Dr. Jim Woodey was a biologist with the International Pacific Salmon Fisheries Commission and the Pacific Salmon Commission for many years and has in-depth knowledge of Fraser River sockeye and pink salmon. He can be contacted through the Pacific Salmon Commission (www.psc.org).

5. CHILKO LAKE SOCKEYE

The assessment of Chilko Lake sockeye is unique in the Fraser River. Since 1949, juvenile sockeye smolts emigrating from the lake have been enumerated at a counting fence established by the International Pacific Salmon Fisheries Commission (Roos 1991). Chilko Lake is also the only Fraser basin lake to have been fertilized by Fisheries and Oceans Canada's Lake Enrichment Program (Bradford et al. 2000). Smolts have been counted every year except for the spring of 1991 when floods prevented a complete count. The lake was partially treated during 1988 (fry from 1987 spawning year) and then fully treated during 1989 through 1992. Figure 4 presents data from Chilko Lake. Data points from the spawning years that involved lake fertilization have been noted by open squares; other years in the 1990s by full circles, and all other years by full diamonds.

The data in Figure 4 demonstrate that there is much less variability in the number of smolts produced than in the adult production (adult recruitment in bottom panel, Figure 4). Also, in two of the five fertilization years, a substantial increase in smolt production resulted. Bradford et al. (2000) reported a significant but highly variable increase in productivity for the five treated years. While the largest returns for the fertilized years occurred for 1990 and 1991 spawning years, two of the largest spawning escapements on record, it is unlikely that the increased numbers of carcasses would contribute to the smolt production since the spawning reach at Chilko Lake is in the outlet river and few of the carcasses would mix into the lake system where the juveniles rear.

It is notable in the Chilko Lake data that for effective females spawners greater than 300,000[6] there is an apparent decrease in the smolts produced (middle panel, Figure 4), and that this relation is also apparent (but less so) in the adult data (bottom panel). Chilko Lake sockeye data are one of the best sets of stock-recruitment data on the Pacific coast, and for these data, there is an apparent density-dependence in the production relationship. While the presentation in Figure 4 is strengthened by the inclusion of the smolt production data, overall it does not change the conclusions for this stock based on Figure 2A, B.

[6] The value 300,000 effective female spawners would equate to approximately 700,000 total spawners after adjusting for spawning effectiveness and the sex ratio of adults.

6. Shuswap and Quesnel Lake Studies

Since the mid-1980s, a Fraser lakes program conducted by the Science Branch of Fisheries and Oceans Canada has included enumeration of sockeye fry in Chilko, Quesnel, and Shuswap lakes, plus monitoring of other trophic levels and physical parameters. Hume et al. (1996) used these data to estimate the optimal spawning escapement goals for sockeye salmon in these lakes, and provide a basis for comparison with recent escapements. Sockeye spawning escapements to Quesnel Lake (Figure 5, 2001 and 2002) and Shuswap Lake in 2002 (Figure 6) were the largest recorded spawning escapements for these lake systems.

Hume et al. (2004, included here as Appendix 1), in an update on their 1996 paper, present fry enumerations and fry sizes from these record large escapements. In both lakes, sockeye fry enumerations in the autumn show a leveling off (i.e., a plateau) of fry production compared to preceding years but do not indicate any evidence for a collapse of production at these high escapement values (see figures 1 and 2 in Appendix 1). The authors also provide fry size data (figure 3 in Appendix 1). Fry size does decrease slightly at high escapements, but the deviations for these recent escapements is not substantial (the deviations were not tested statistically), although the size of the Quesnel Lake fry in 2003 (2002 spawners) was smaller. It is also noteworthy that the smaller-sized Quesnel fry in 2003 could reflect an inter-year effect of two consecutive years of very large fry production, an event that has not occurred in the period of record for this lake.

While this work is limited to sockeye salmon, it is building strong evidence for a carrying capacity limit to sockeye production in the Fraser lakes. This would add further indications that over-spawning is not likely to lead to collapse of a sockeye salmon stock, but rather the lake system will provide the “natural controls” on production.

7. PRE-SPAWNING MORTALITY AND OVER-SPAWNING

While this report does not find evidence of stock collapse from excessively large escapements, the concern about the topic is understandable given past management emphasis on "optimizing" the escapement numbers. Furthermore, there are two related issues that may have heightened peoples' concerns for stock collapse:

1. the recent conservation actions for late-run Fraser sockeye salmon and the severe limitations placed on sockeye fisheries, and

2. a belief that the risk of disease outbreaks and pre-spawning mortality[7] increases greatly with increasing numbers of spawners in freshwater systems. Losses attributed to disease have been documented in a few Fraser sockeye salmon examples (Gilhousen 1990, Roos 1991) and for the artificial spawning channels in Babine Lake.

The issues associated with conservation of late-run Fraser sockeye salmon were clearly a concern during 2002, and have been the subject of a Minister's review committee (DFO 2003a). The basis of these actions was the assumption, based on trends evident in previous years, that early migration of the late-run Fraser sockeye salmon could result in upwards of 90% pre-spawning mortality. Restrictions were introduced in 2002 to maximize escapement. However, the pre-spawning mortality did not occur that year, and very large numbers of spawners reached the spawning grounds. Sampling reported by Hume et al. (2004, Appendix 1) demonstrates, at least to the fall fry stage, that the large number of spawners did not result in a collapse of the lake system or of the stock.

The coincidence of disease and large numbers of spawning fish does present a risk of major losses, but the incidence of this is very rare. As noted above, there are well-documented cases of this situation occurring, but when considered over all Fraser sockeye populations and years of monitoring (since 1948 in many lakes), three results are apparent:

i) When considered for all naturally-spawning populations (i.e., excluding spawning channels), the extent of pre-spawning mortality (including disease as a cause) rarely exceeds 50% of the returning adults (only 1.2% of 946 samples since 1948, based on the sockeye production database provided by the Pacific Salmon Commission). All samples include 100 or more females.

ii) The incidence of pre-spawning mortality is not related to the size of the spawning population. Figure 7 presents all 946 samples and plots them by spawning population size and the estimated pre-spawning mortality rate recorded in the Pacific Salmon Commission production database.

iii) The incidence of pre-spawning mortality was greater in the populations associated with spawning channels (12.5% of 96 observations had 50% or greater pre-spawning mortality rates). Sockeye populations included were Gates, Nadina, and Weaver after spawn-channel construction.

The incidence of pre-spawning mortality is largely a function of environmental conditions (Gilhousen 1990) and the development of stress in the mature adults. The actual cause of death could involve disease expression, but the development of disease at high spawning escapement levels should not simply be assumed. For example, the largest observed pre-spawning mortality at a large escapement level occurred in the Chilko Lake sockeye in 1963 (upper right corner, Figure 7). This extreme mortality event was associated with a large escapement, but the very early run timing, warm water temperatures, and virulent bacterium combined to contribute to the loss of spawners (page 30, Gilhousen 1990). However, during the 1990s period of large escapements to Chilko Lake (Figure 3), pre-spawning mortality has not exceeded 10% in any year.

[7] See footnote 2 page 5 of this report

8. PERSPECTIVES AND GUIDANCE

Our ability to test for effects of over-escapement remains limited, but the examples compiled in this technical paper do not indicate any evidence of stock collapse after large spawning escapements. There is, however, evidence of declining rates of production (recruits per spawner) at high escapement levels. There is also increasing evidence of a carrying capacity limitation to sockeye production in the large Fraser basin lakes. Our ability to assess over-escapement in other sockeye systems is much more limited and even more so for other species. While the very large escapements of the past couple of years have further confirmed these observations, the results are not particularly new nor provide a basis for additional insights.

The concerns expressed that over-escapement has lead to stock collapse are not supported by available data on Pacific salmon. There is a valid concern for the efficiency of salmon production at higher spawning population sizes, but this could have been surmised from Ricker's original 1954 paper, and is the basis for efforts to determine an intermediate spawning level that both supports harvesting and sustains the fish population. However, we must also note the advocacy for larger spawning escapements (regardless of production efficiency) for ecological values. It is also argued that larger escapements through lower harvest rates may be necessary to conserve salmon biodiversity, and that large escapements may be necessary to promote re-colonization of habitats or dispersal of salmonids. For Fraser River sockeye salmon, Fisheries and Oceans Canada's current review of a long-term escapement may provide the appropriate forum for consideration of these latter values and related issues.

Since 1995, concerns about high pre-spawning mortality (and hence lower recruitment per spawner), particularly for the Adams River run that has exhibited abnormal migration behavior, have led to a policy of trying to protect every potential spawner. The wisdom of this trade-off argument (today's catch versus future recruitment and catch) may be questioned, but the recent high pre-spawning mortality rates may presage a decrease in production rates per spawner and hence also a reduction in the exploitation rate to sustain a long-term harvest. There are not yet enough observations of recruitments from such "impaired" spawning runs (such as the Adams) to calculate what their optimum exploitation rates should be, but some precautionary reduction in rates would be justified for such stocks if this pre-spawning mortality persists.

In the Fraser sockeye case, Fisheries and Oceans Canada has apparently made a strategic change in policy to deal with variation in recruitment in what fisheries scientists term "fixed escapement control". Historically, management was based primarily on control of fishing rates (fixed exploitation rate control), where a relatively stable percentage of each returning run was harvested. There was an evolution towards fixed escapement goals following the 1985 Pacific Salmon Treaty and the need to define annually the total allowable catch for both countries. This technical paper on over-escapement has relevance to the strategies underlying these harvest options, but there are significant practical and conservation consequences associated with both approaches that require further consideration.

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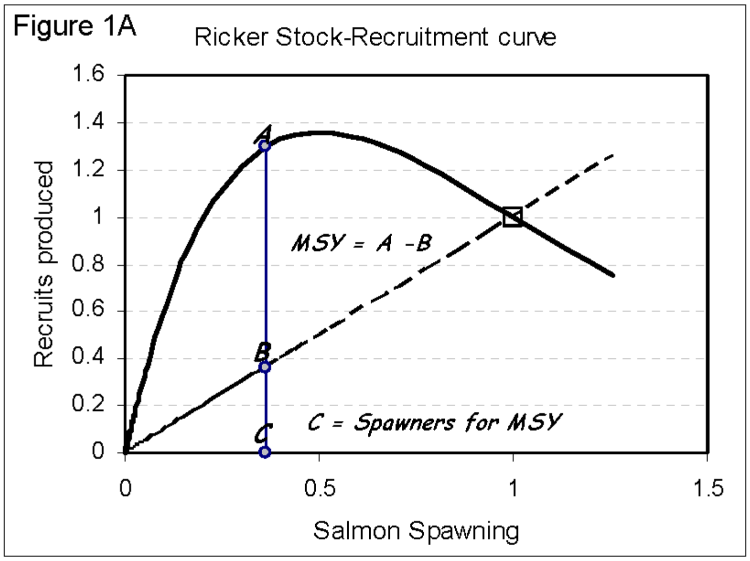
CAPTIONS AND FIGURES

Figure 1. Model relationships between the number of spawners (S) in a generation and their progeny produced (recruits to the fishery, R).

Fig. 1A: Ricker's dome -shaped curve [R = a S exp(-bS)]. The difference between the number of recruits indicated by Ricker's curve (point A) and a number of recruits equal to the number of spawners, as given by the one-to-one replacement dotted line (point B) is the "surplus production" available to the fishery. It reaches a maximum value, called the Maximum Sustainable Yield, for an optimum number of spawners (point C). Beyond the intersection of Ricker's curve with the replacement line (small box), there are fewer recruits than spawners and the population declines.

Fig. 1B: An alternate model is the Beverton-Holt curve, where the number of recruits for large numbers of spawners tends to a constant maximum value rather than declining.

For both curves, the ratio R/S of number of recruits per spawner decreases as the number of spawners becomes large; it does so more rapidly for Ricker's curve than for the Beverton-Holt curve.



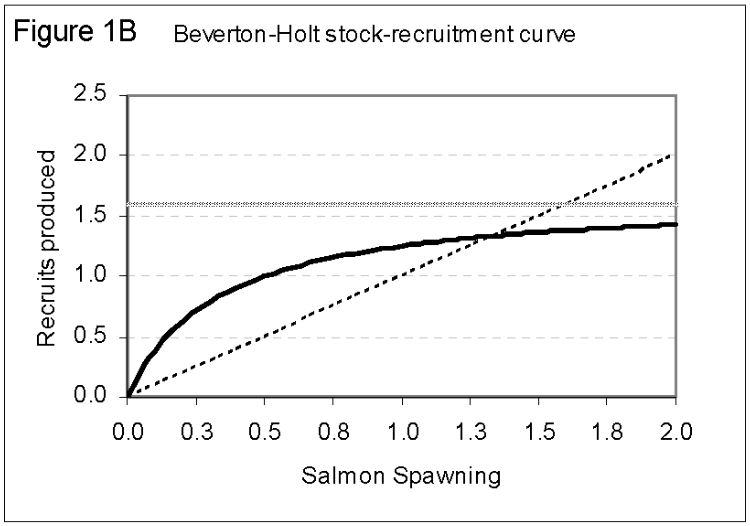


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Figure 2. Recruitment data for sockeye and pink salmon stocks.

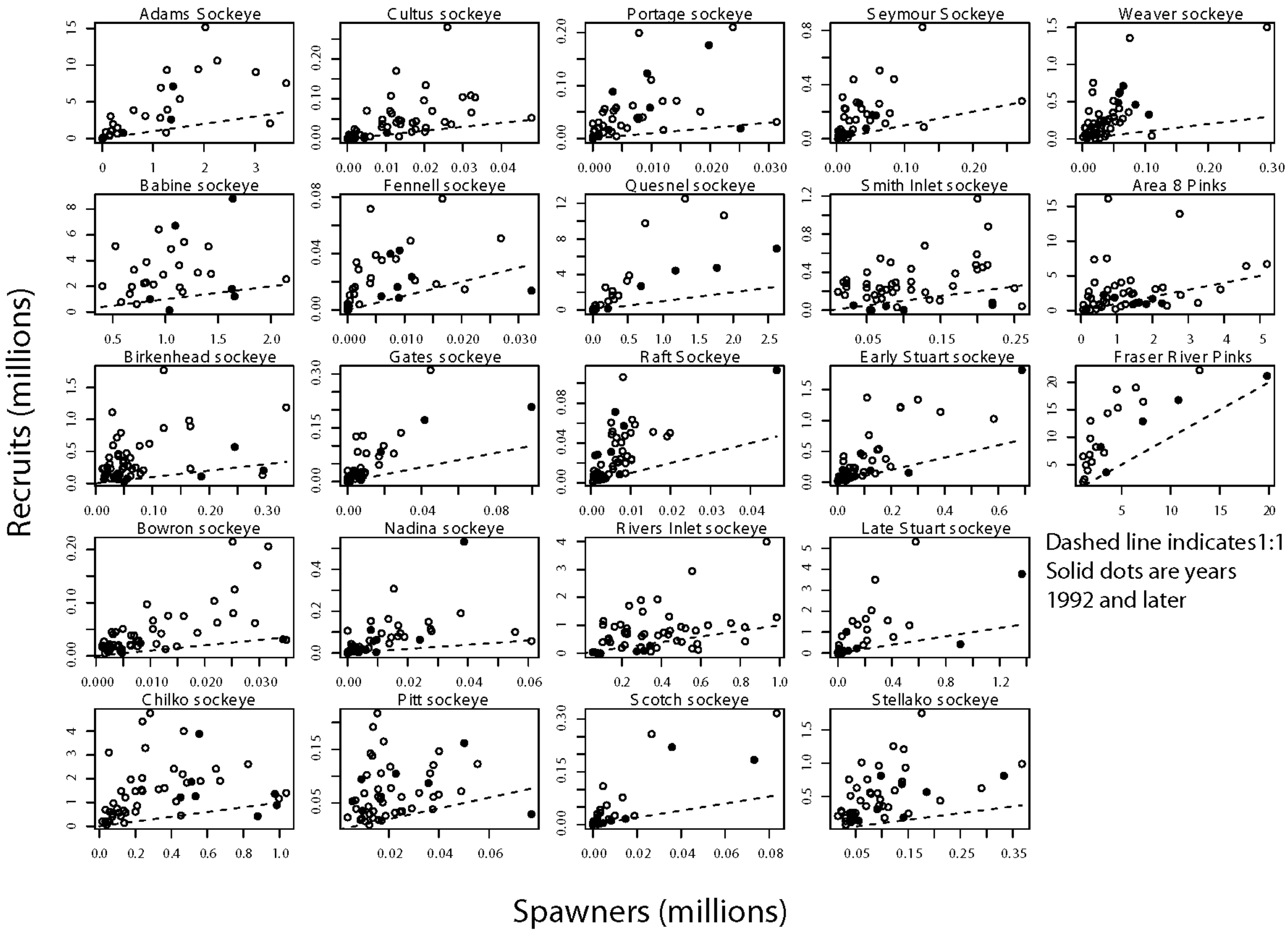
Data provided by the Pacific Salmon Commission (Fraser sockeye and pink data) and the Department of Fisheries and Oceans, Canada.

Fig. 2A: Production of adult offspring (Recruitment) from the number of parents (Spawners) in the spawning year (numbers are in millions of fish). Each point on a plot is the estimated offspring produced from each spawning year, typically from the early 1950s through returns in 2002, for 23 populations for which we could collate the data. The dashed straight line is the "replacement line" when the recruits produced equal the number of fish in the spawning population. Data points above the line indicate recruitment surplus to replacing the number of spawners, and points below the line indicates a loss of production relative to the spawners. Solid dots indicate spawning years from 1992 and later during to a period of reduced marine productivity.

Fig. 2B: Adult offspring produced per parent (Recruits/Spawner, R/S) versus the number parents (Spawners) in each spawning year (numbers are in millions of fish). The R/S axis (vertical) is expressed as the natural logarithm (ln) of the ratio to present the linear form of the Ricker S/R curve. Each point on a plot is the estimated offspring per spawner for each spawning year, typically from the early 1950s through to returns in 2002, for 23 populations for which we could collate the data. The dashed straight line is a regression line that estimates the rate of change in recruitment per increment in the parental spawning population size. Data points above the line indicate recruitment at a higher productivity rate than expected on average, and data points below the line indicate the converse. Solid dots indicate spawning years from 1992 and later during a period of reduced marine productivity.

Populations included in Figures 2A, B were:

1) *Adams Sockeye—late run Fraser River sockeye to the Adams River, Shuswap Lake*
2) *Babine Sockeye—total sockeye in Babine Lake, including spawning channels, Skeena River*
3) *Birkenhead Sockeye—late summer run, lower Fraser River, above Lillooet Lake*
4) *Bowron Sockeye—early summer run, upper Fraser River*
5) *Chilko Sockeye—summer run, central Fraser basin (see Appendix 2)*
6) *Cultus Sockeye—late run, lower Fraser River (listed as Endangered, May 2003)*
7) *Fennell Sockeye— early summer run, North Thompson River, North Barriere Lake*
8) *Gates Sockeye—early summer run, central Fraser above Anderson Lake, includes channel*
9) *Nadina Sockeye—early summer run, upper Nechako River & Francois Lake, includes channel*
10) *Pitt Sockeye—early summer run, Pitt Lake in lower Fraser, includes hatchery and incubation.*
11) *Portage Sockeye—late summer run, above Seton Lake in mid-Fraser*
12) *Quesnel Sockeye—summer run, two major tributaries (Horsefly and Mitchell rivers), upper Fraser basin in Quesnel Lake*
13) *Raft Sockeye—early summer run, upper North Thompson River*
14) *Rivers Inlet Sockeye—Owikeno Lake complex of sockeye spawning streams, central BC*
15) *Scotch Sockeye—early summer run to Shuswap Lake, South Thompson River*
16) *Seymour Sockeye—early summer run to Shuswap Lake, South Thompson River*
17) *Smith Inlet Sockeye—Long Lake in central BC, lake enriched since late 1970s.*
18) *Early Stuart Sockeye—early returns to Stuart Lake in upper Fraser River, multiple streams*
19) *Late Stuart Sockeye—late summer run to Stuart Lake in upper Fraser River, multiple streams*
20) *Stellako Sockeye—summer run to upper Fraser River and Fraser Lake (Nechako River)*
21) *Weaver Sockeye—late run sockeye to lower Fraser (Harrison River), includes channels*
22) *Area 8 Pinks—pink salmon in Bella Coola River and local steams (even and odd years)*
23) *Fraser Pinks—odd-year pink salmon in Fraser River, multiple spawning locations*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Weaver sockeye
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Fennell sockeye
Quesnel sockeye
Smith Inlet sockeye
Area 8 Pinks
Birkenhead sockeye
Gates sockeye
Raft Sockeye
Early Stuart sockeye
Fraser River Pinks
Bowron sockeye
Nadina sockeye
Rivers Inlet sockeye
Late Stuart sockeye
Chilko sockeye
Pitt sockeye
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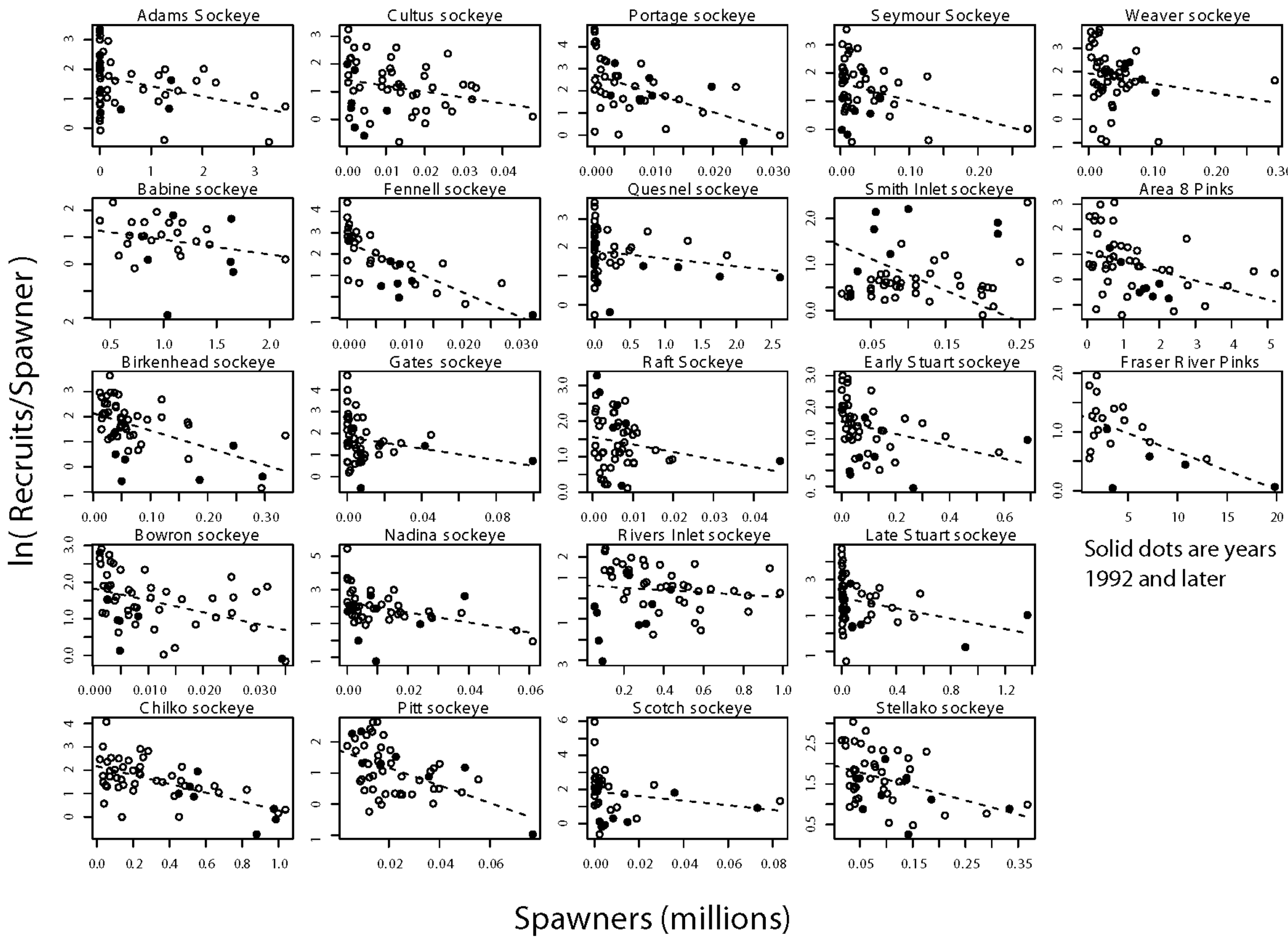
Solid dots are years
1992 and later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Quesnel sockeye
Smith Inlet sockeye
Area 8 Pinks
Birkenhead sockeye
Gates sockeye
Raft Sockeye
Early Stuart sockeye
Fraser River Pinks
Bowron sockeye
Nadina sockeye
Rivers Inlet sockeye
Late Stuart sockeye
Chilko sockeye
Pitt sockeye
Scotch sockeye
Stellako sockeye
Solid dots are years 1992 and later
ln(Recruits/Spawner)
Spawners (millions)

Figure 3. Production dynamics for Bowron Lake sockeye.

Top panel: the effective number of female spawners for each year.

Middle panel: the number of recruits against the number of effective female spawners; the year of the run is indicated for the higher escapement years.

Bottom panel: the natural logarithm of the ratio of recruits to spawners against the number of effective female spawners. The negative slope of the regression line indicates that the productivity (recruits per spawner) decreases for large numbers of spawners.

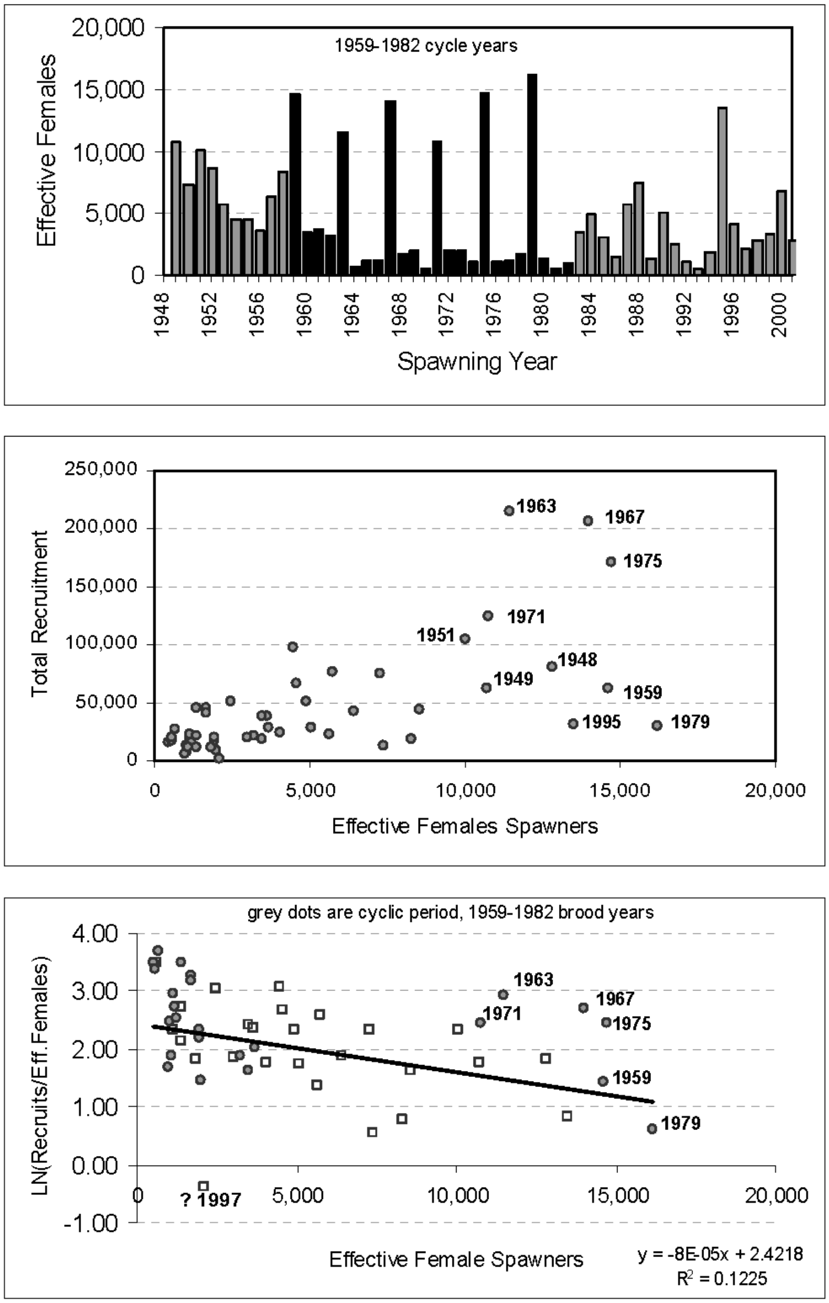

Figure 4. Production dynamics for Chilko Lake sockeye.

Top panel: the total spawning escapement since 1948 to 2002 and the estimated number of effective female spawners (lighter grey, lower portion of the columns). Note the extensive loss of spawners in the 1963 spawning year. Middle panel: the estimated number of sockeye smolts (in millions) emigrating from the lake and related to the number of effective female spawners in their parental generation. In this figure, the four squares labeled indicate the spawning years for those years of lake fertilization. Bottom panel: the estimated total adult production and related to the effective number of female spawners in their parental generation. In this figure, the 1989 year label indicates the adult return estimated for the spawning year that did not have a smolt estimate due to flooding. The other squares are as in the middle figure.

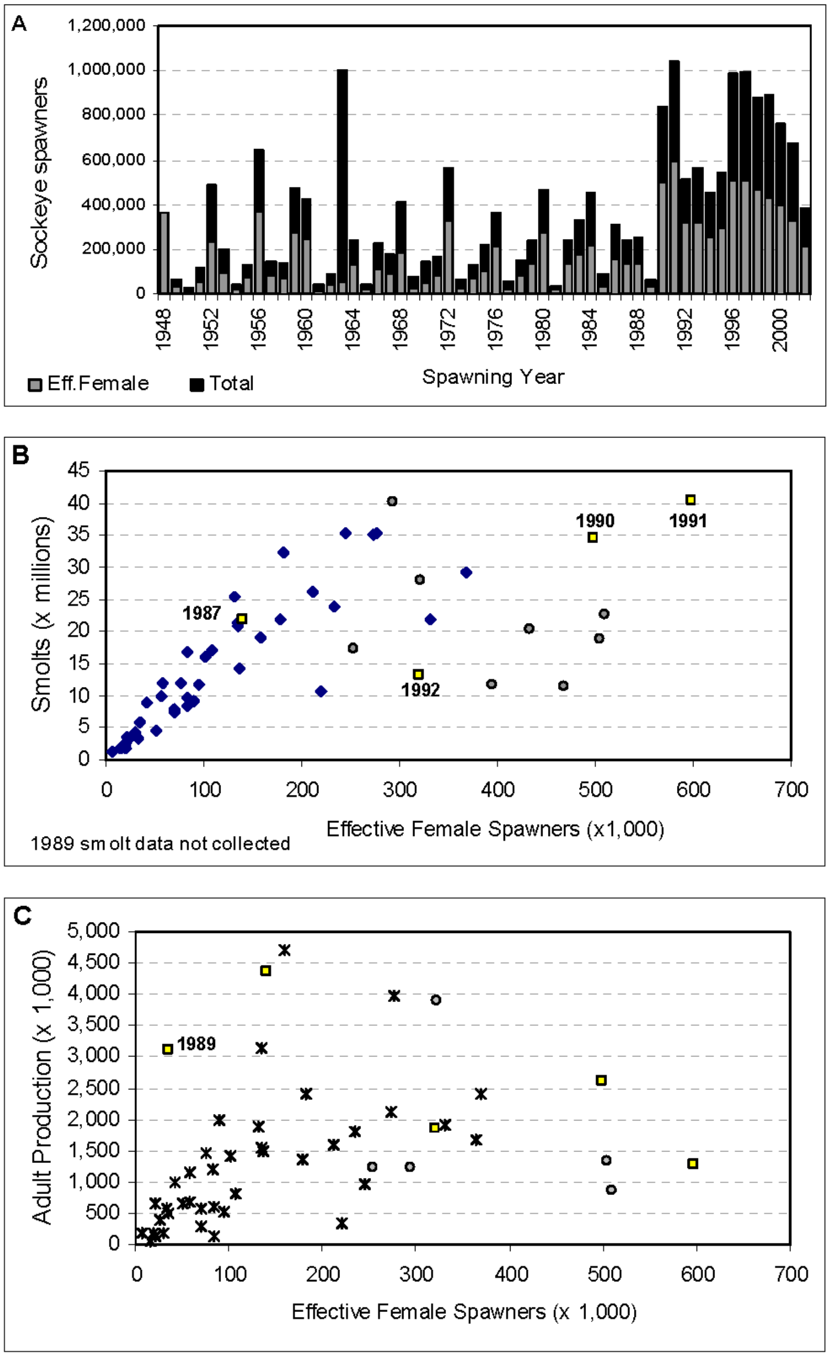

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Figure 5. Total sockeye salmon spawning escapements to the Horsefly and Mitchell rivers in the Quesnel Lake system.

Fraser River (1948–2003 escapements).

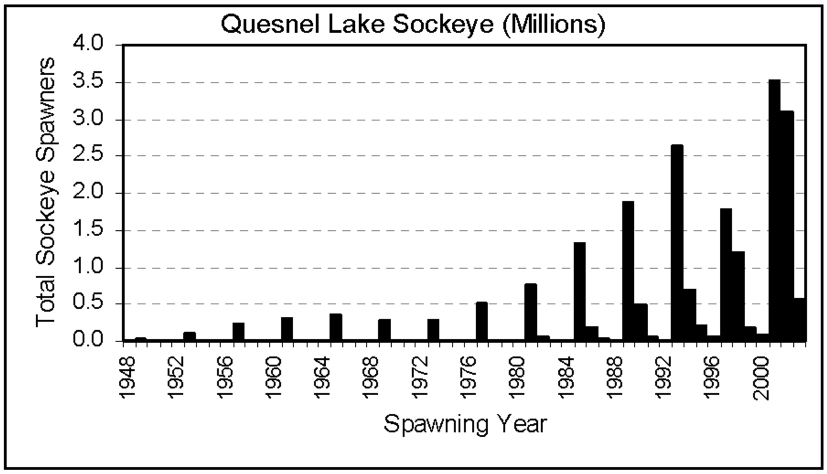


Figure 6. Total sockeye salmon spawning escapements to the Early and Late Shuswap Lake stocks (1948–2003 escapements).

These include returns to the Adams River sockeye stock.

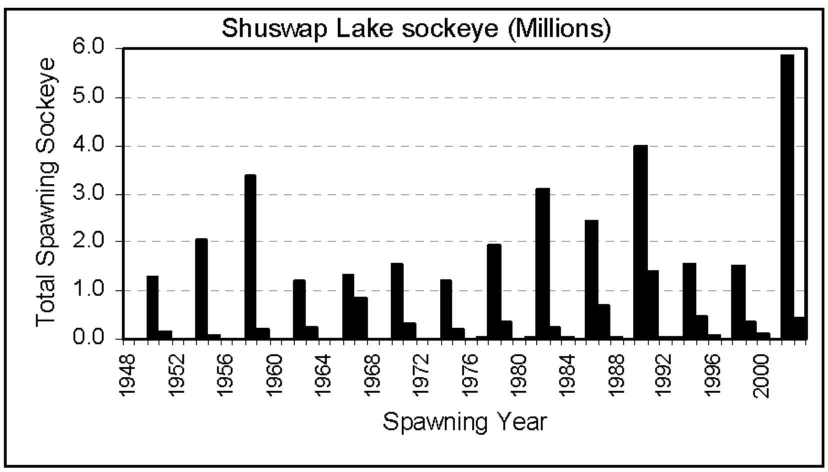
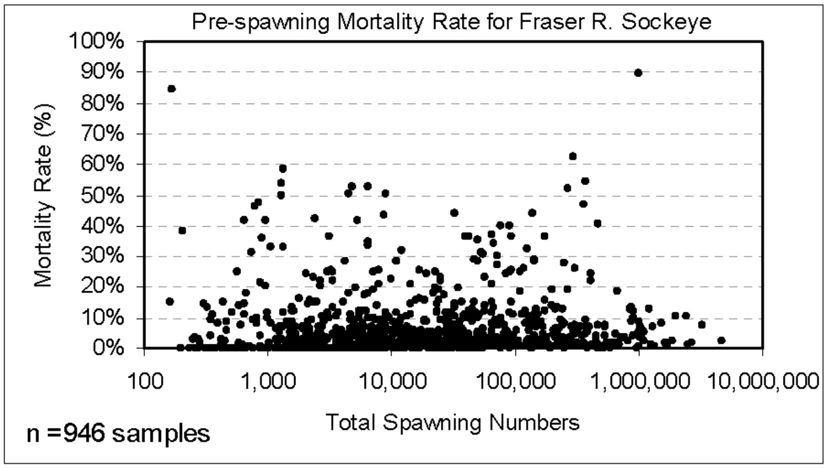


Figure 7. Distribution of estimated pre-spawning mortality rates for all Fraser River sockeye populations sampled since 1948.

Excluding populations associated with spawning channels or very small samples (<100 females recorded). The horizontal axis (total number of spawning sockeye) is presented on a logarithmic scale to increase contrast between the smaller population sizes (presented in multiples of ten on the scale).



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APPENDIX 1. PRELIMINARY REPORT ON SOCKEYE FRY IN QUESNEL AND SHUSWAP LAKES IN 2003

Jeremy Hume[8], Ken Shortreed, and Steve MacLellan
Fisheries & Oceans Canada Cultus Lake Laboratory February 19, 2004
Revised March 15, 2004

In 2002, the sockeye escapement of 5.5 million to Shuswap Lake was the highest ever recorded. Of this number, 2.9 million were females which spawned successfully (effective female spawners—EFS). In Quesnel Lake in 2002, a direct estimate of spawner numbers was obtained only for the Mitchell River. However, based on the Mitchell River escapement relative to the Horsefly River and other spawning areas in the previous year, we estimated the total escapement to Quesnel Lake in 2002 was 3.8 million. A slightly lower total escapement estimate of 3.1 million was developed by the Pacific Salmon Commission (PSC) using DNA analysis of Quesnel sockeye collected in the lower Fraser River at Mission (Steve Latham, PSC, personal communication). In this report, we used the PSC estimate of 3.1 million. Using this estimate as well as the EFS and prespawning mortality proportions in the Mitchell River in 2002, we estimate the total EFS to Quesnel Lake in 2002 was 1.3 million.

For a number of years we have been performing hydroacoustic and trawl surveys on Shuswap and Quesnel lakes to obtain estimates of numbers of juvenile sockeye in the lakes. These estimates are used through PSARC in stock forecasting (Cass et al. 1995 and Cass 1996 annually). They have also been used to develop and test fry-based and habitat-based (PR model) empirical models which predict rearing capacity of the lakes and the optimum escapement required to maximize production (Hume et al. 1996; Shortreed et al. 2000).

Given the high escapements to both lakes in 2002, we expected that fry recruitment to the lakes in 2003 would be very high, and would possibly greatly exceed the productive (rearing) capacity of both lakes. To test this, we obtained juvenile sockeye salmon population estimates by conducting acoustic and trawl surveys on Quesnel Lake in the summer (July 29) and fall (Sept 23) of 2003 and on Shuswap Lake in the fall (Oct 23) of 2003 (as in Hume et al. 1996). These surveys provided abundance, distribution, survival, size, and diet information of sockeye fry from the 2002 escapement. In conjunction with this study, we also carried out a limnological investigation of Quesnel Lake to determine the effects of the high escapements on lake productivity. In addition, the Provincial Ministry of Water, Land, and Air Protection (MWLAP) has been conducting surveys of the kokanee and rainbow trout in Quesnel Lake and have reported preliminary results (Sebastian et al. 2004). In this report, we compare the 2003 juvenile sockeye data with similar data collected from both these lakes for up to19 previous years, which include a wide range of spawner escapements.

Shuswap Lake

The escapement of 2.9 million EFS to Shuswap Lake was one million greater than in the previous record year (1990), but did not produce any more fall sockeye fry than in many years of lower escapements (Fig. 1). Densities were high in some parts of the lake (12,600/ha in one part of Salmon Arm) and were higher than previously observed in areas such as Anstey Arm, where densities are usually low. In the fall of 2003, we estimate there were a total of 132 million fry (+/− 95% C.I. = 18%) in Shuswap and Mara lakes. The data indicate that in Shuswap Lake, fall

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fry abundance peaks at escapements of about 1.0 million EFS (~2.0 million total escapement) and that fall fry numbers are the same or lower at all higher escapements (Fig. 1). While we didn't obtain a summer estimate in 2003, summer estimates from previous years also indicate no increase in fry abundance above an EFS of around 1.0 million. In Shuswap Lake, fall fry size changes relatively little over a wide range of spawner numbers (Fig. 3). Average size is about 2.3 g at escapements over 0.6 million EFS. In 2003, fry averaged 2.0 g, within the range of sizes previously observed.

Quesnel Lake

The estimated escapement of 1.3 million EFS to Quesnel Lake was the largest subdominant escapement ever recorded to that lake and it followed the highest dominant escapement ever recorded to Quesnel Lake. We estimate there were a total of 76.2 million fry (+/− 95% C.I. = 22%) in the lake in the summer of 2003 and 51.3 million fry (+/−95% C.I. = 22%) in the fall. Sockeye were distributed throughout the lake at moderate densities (max = 6,000/ha) and in some areas such as the East Arm, fish densities were higher than previously observed. The data indicate that in Quesnel Lake, maximum fry abundance is reached at an escapement of 0.75-1.0 million EFS (~1.5 to 2 million total escapement) (Fig. 2). Beyond these escapements, summer and fall fry numbers do not increase. In Quesnel Lake, fall fry average about 3.5 g at moderate escapements. At higher escapements, size is more variable (Fig. 3). Fry collected in the fall of 2002 and 2003 were among the smallest ever recorded (2.7 and 1.9 g, respectively) from Quesnel Lake. However, fall fry from the 1993 brood year, a year with a similar high escapement, averaged 4.0 g, larger than the long-term average fall fry size.

Discussion

Recent escapements to Shuswap and Quesnel lakes have been the highest or amongst the highest ever observed. The decomposing carcasses from these escapements have returned significant amounts of marine derived nutrients (MDN) to the South Thompson and Quesnel river watersheds. Carcasses in the Shuswap watershed will have increased nutrient loading to the lake somewhat but nutrients from carcasses in the Adams river (63% of the total in 2002) are mostly diverted downstream by prevailing currents into Little Shuswap Lake and the South Thompson River, where they mostly benefit species other than sockeye.

In contrast, almost all MDN in the Quesnel system circulates in the lake for some time and will directly affect lake productivity. Our limnological study of Quesnel Lake has shown increased productivity and biomass of lower trophic levels as a result of the recent very high escapements (Shortreed et al. in prep). Increases in phytoplankton and zooplankton biomass were observed in 2003 but there were no detectable increases in juvenile sockeye abundance or size. There are a number of possible reasons for this apparent “uncoupling” of fish production from the increased productivity of lower trophic levels. These could include spawning ground limitation, the high abundance of a phytoplankton species that is resistant to grazing by zooplankton, unusually warm water in the summer of 2003, or carry-over effects from the high fish densities in 2002. Further data and analysis are needed to better understand both this and the longer-term effects of the high escapements on Quesnel and Shuswap lakes.

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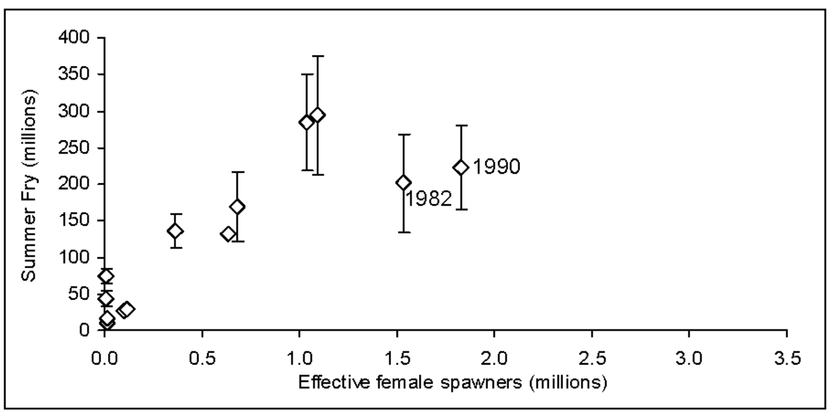
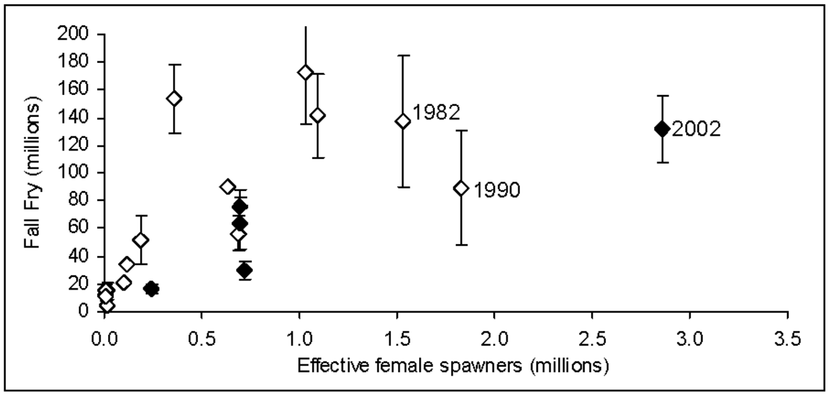
Figures

Appendix 1—Figure 1. Relationship between Shuswap Lake EFS and their subsequent offspring in the summer (upper) and fall (lower).

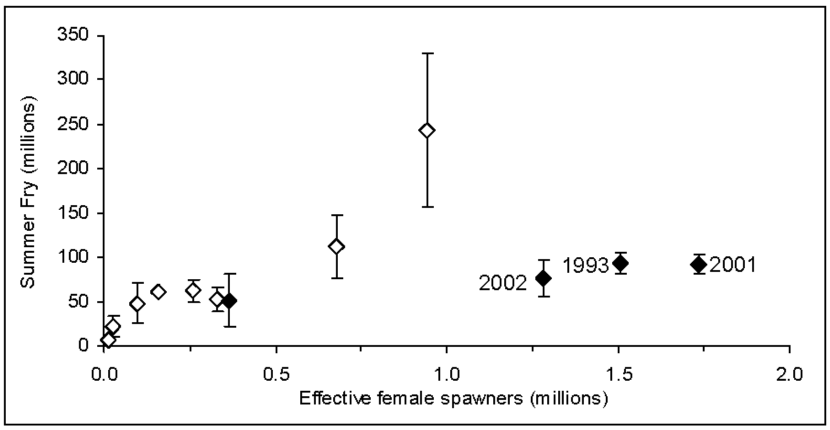
Open diamonds are from Hume et al. (1996), solid diamonds are new data from the 1994 and later brood years. 95% confidence intervals on each data point are shown by the vertical lines. Some brood years are indicated.

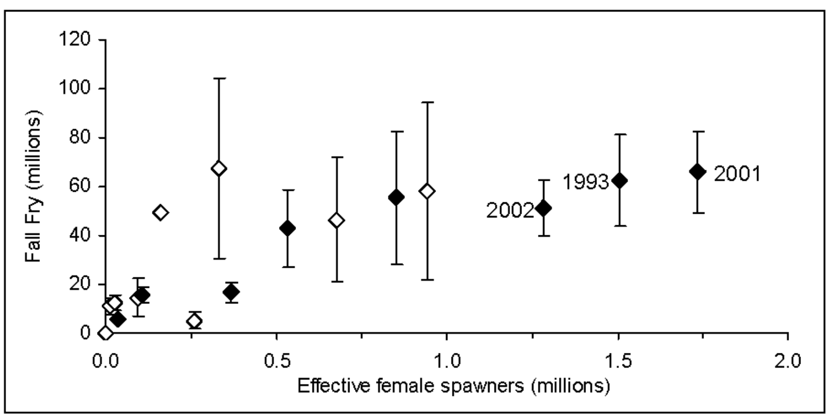




Appendix 1—Figure 2. Relationship between Quesnel Lake EFS and their subsequent offspring in the summer (upper) and fall (lower).

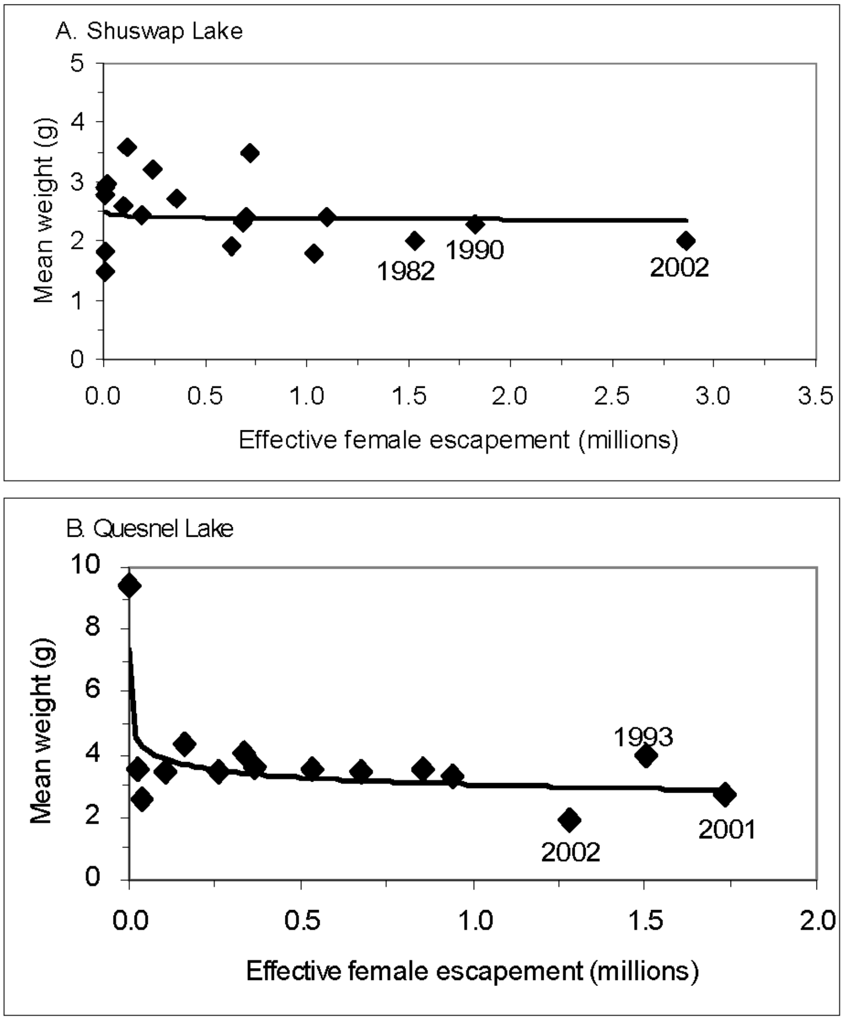
Open diamonds are from Hume et al. (1996), solid diamonds are new data from the 1993 and later brood years. 95% confidence intervals on each data point are shown by the vertical lines. Some brood years are indicated.





Appendix 1—Figure 3. Size of A) Shuswap Lake and B) Quesnel Lake fall fry in relationship to EFS.

Some brood years are indicated.



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