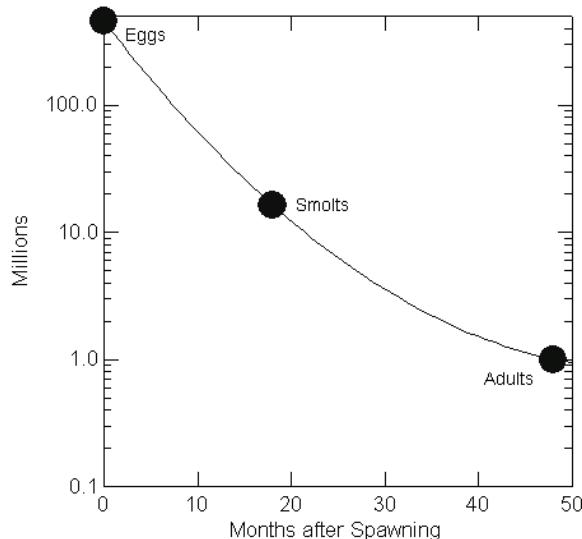


## 5 Survival

### 5.1 Productivity and Survival

The theoretical maximum abundance that a cohort of sockeye salmon can have is determined by the number of fertilized eggs produced by its parents. The abundance of the cohort begins to decline immediately as eggs are eaten or damaged or die from any number of causes (Fig. 48). The expected schedule for the eventual disappearance of a cohort is called a life table. It documents the average probability of dying during various intervals between birth and the maximum age that the species can achieve. Births and deaths of human populations, for example, are so well documented that the probabilities of dying at any particular age are relatively well known.



**Fig. 48** Abundance of an idealized sockeye salmon cohort, approximated from Chilko Lake statistics of average numbers of female spawners, fecundity, freshwater survival, and smolt-to-adult survival. Minor ecotypes (*e.g.*, age-2.x smolts, jacks, 5- and 6-year old adults) are not shown. Note that abundance is plotted on a logarithmic scale.

*“...it is evident that if we had some accurate method of determining from year to year the number of fish on the spawning grounds, this would afford data for prophecy”*

Charles H. Gilbert, 1923

When Gilbert made the comment above, he was under contract to the Province of British Columbia to report on the returns of sockeye salmon to the major rivers of British Columbia. He was the professor of zoology at Stanford University from its inception. He was arguably the most influential Pacific salmon biologist during the first quarter of the 20<sup>th</sup> century, and perhaps not coincidentally, a colleague and friend of J. Pease Babcock, Deputy Commissioner of Fisheries for British Columbia. One can imagine that Gilbert’s wishes for spawning ground censuses reflected the aspirations of salmon population biologists of the time. The key to building a life table is the census of population abundance. As late as the 1940s, salmon escapement was referred to as “seeding” and records of abundance were ordinal (Brett, 1950) but by the 1950s, the estimates became more quantitative.

## 5.2 Difficulties Estimating Salmon Abundance

The abundance of a salmon cohort is rarely taken by census. More often, it is the sum of an *estimate* of spawner abundance in a stream or lake plus an *estimate* of the catches of that population in the fisheries it encounters on its return migration. The reliability of the estimate of spawner abundance is determined by many factors but the counting fence has traditionally been considered to be the most reliable because an attempt is made to account for every individual migrating past a fixed point in the spawning migration. In the majority of cases, population abundance is estimated by stream walks, tagging and recapturing spawners, or some other method that relies on assumptions and inferences of varying reliability to produce an estimate of abundance.

The difficulties are relatively well known. One of the best documented examples of underestimating sockeye salmon abundance comes from the Babine River, part of the Skeena River drainage in northern British Columbia. The installation of a counting fence on the Babine River by the Fisheries Research Board of Canada in 1946 demonstrated that the estimate of abundance of sockeye salmon spawners, determined by walking streams and counting fish, was less than 50% of the total number reported migrating past the Babine River fence in the years 1946 and 1947, despite a conscientious effort of stream surveys.

*“That stream counts will be minimal is apparent by their very nature, but the discrepancy [at Babine Lake] is beyond such expectations”*

J. Roly Brett, 1952

Even an accurate census of spawner abundance each year allows only one element of a life table to be approximated: *total survival*. This is the proportion of a cohort surviving from hatching to maturity and spawning. But even this calculation requires an assumption about the average number of eggs that was fertilized by the spawning adults. That number varies from year to year and stock to stock, and from the age composition of the spawners (older females are usually larger and have more eggs). As a consequence, analysts typically avoid computing the initial size of a cohort from the number of fertilized eggs, but use instead the number of spawners (or number of female spawners) and assume that it will be a good index of the number of progeny. Compared to other sources of measurement error, this is likely a relatively small contributor.

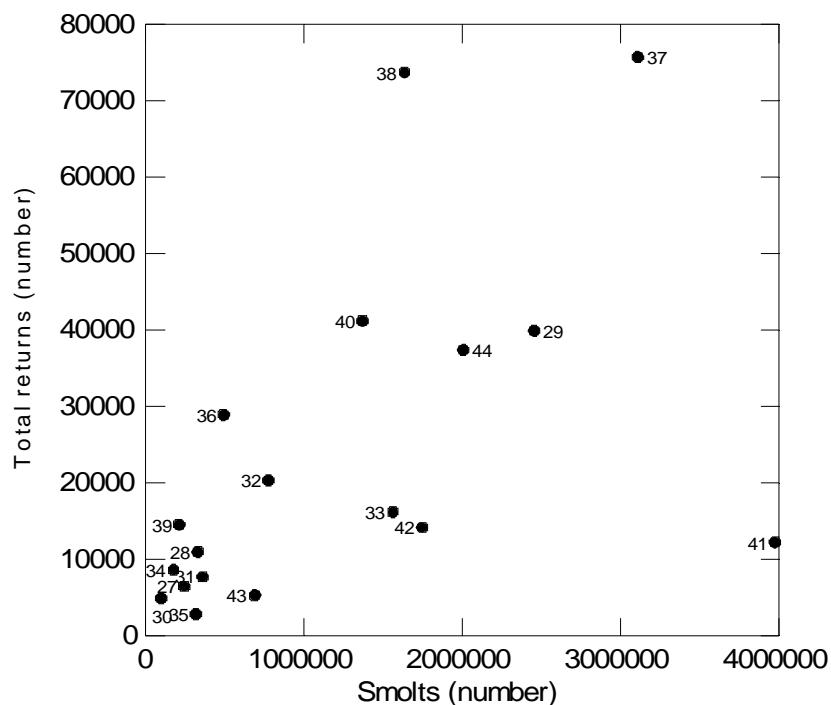
## 5.3 Smolt-to-Adult Survival

One consequence of determining only *total survival* is that when the average survival changes, it is very difficult to determine where the change occurred. As Fraser River sockeye salmon spend their lives divided almost equally between freshwater and saltwater habitats, scientists who are interested in distinguishing how salmon survive in these environments must take a census of the population as it leaves freshwater. Ideally this would occur immediately upstream of an estuary but the mixing of many populations from many nursery lakes within the watershed, and an inability (historically) to identify them to population of origin in a mixture, has made it easier to census sockeye salmon populations as they leave the nursery lake. Mortality of sockeye salmon between the nursery lake and the estuary is normally included in marine mortality although it is understood that some mortality occurs in the river (Ricker, 1966).

Ricker (1962) described how marine survival of sockeye salmon generally increased from 4% to 30% as the mean size of the smolts increased from 70 to 140 mm, but then he pointed out that the mean size of Chilko Lake sockeye salmon smolts varies little from year to year and with no apparent relation to average size (Ricker, 1966), a situation that continues to the present. The first comprehensive study of smolt-to-adult survival patterns in sockeye salmon was conducted using data that had been produced by a long history of study at Cultus Lake (Foerster, 1954). From the 1927 to 1944 ocean entry years, smolt-to-adult survival varied

from a low of 0.31% (1941) to a high of 5.78% (1936). Here, there was a significant positive relation between smolt size (both weight and length were measured) and survival, and Foerster (1954) described how 56% of the variation in adult returns was explained by the number of smolts emigrating and their average weight. Ricker's (1976) review of growth and survival in salt water has not been surpassed by any other work on the topic. The average of several methods of estimating natural mortality of Pacific salmon at sea, that were thought by Ricker (1976) to be without bias and had small or moderate sampling errors, in the last year at sea was  $0.015 \text{ m}^{-1}$  or  $18\% \text{ y}^{-1}$ .

One pattern that the smolt-to-adult survival time series in Cultus Lake shares with its mid-Fraser neighbour, Chilko Lake, since the 1950s is that the worst survival occurred at the highest smolt abundance. Both lakes feature an underlying pattern of increasing returns from increasing numbers of smolts until a dramatic decline occurs. In Chilko Lake, all of the major deviations from this pattern are strongly negative at the highest smolt abundances. However, with only one year to make this point (Fig. 49), it is not possible to know whether or not this is a general characteristic of the Cultus Lake population. In both cases, density-dependent survival is suggested. It is a general pattern, observed in nature, where the capacity of nature to support an abundance of animals is limited by some or several resource limitations.

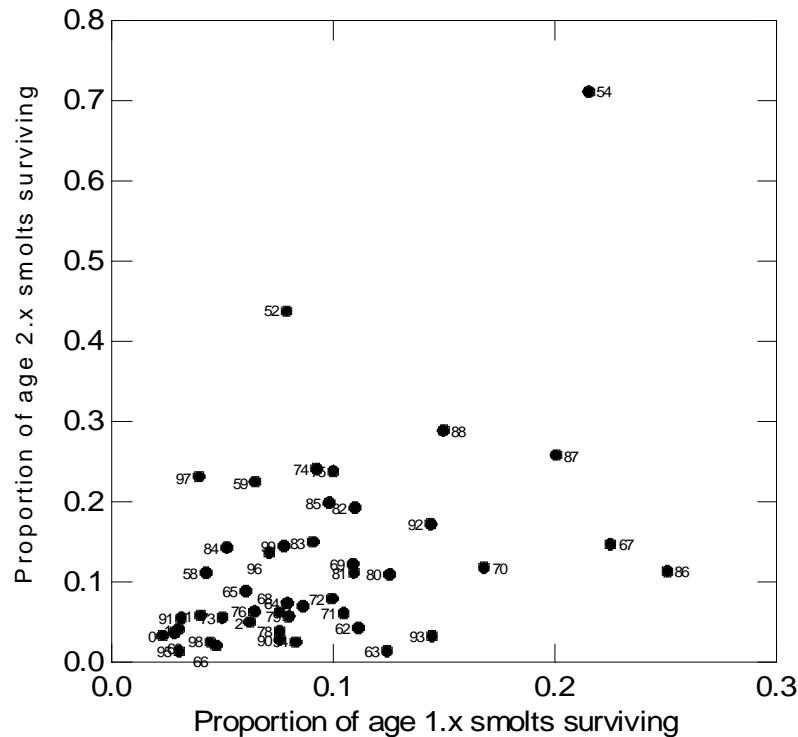


**Fig. 49** Adult returns of sockeye salmon (ordinate) from the abundance of smolts of the same cohort (abscissa) at Cultus Lake, 1927 to 1944 ocean entry years.

The 1941 (ocean entry year) outlier was also the year of smallest mean size of smolts emigrating from Cultus Lake. It has been shown that smaller sockeye salmon smolts from Chilko Lake have greater mortality than larger individuals when a single cohort is examined (Henderson and Cass, 1991) but the principle does not apply to differences in mean smolt size among years in Chilko Lake. In Cultus Lake, however, there was a significant relationship between mean smolt size and smolt-to-adult survival during the years from 1927 to 1944. Years with smaller average smolt size have poorer smolt-to-adult survival. The 1941 anomaly in smolt-to-adult survival did not appear so unusual when considered within this framework. Why Chilko Lake and Cultus Lake should differ so clearly on this point is not known, other than to note that Chilko Lake is the most productive sockeye salmon population, on average, and Cultus Lake is the least productive of the Fraser River

populations (McKinnell, 2008). Perhaps there are significant differences between the two populations in the energy density of smolts of equivalent size.

On average, 96% of the smolts leaving Chilko Lake are age-1.x and the remainder are age-2.x. Therefore, postsmolts of a single cohort can experience very different environmental conditions upon entering the sea. As a consequence, the marine survival of age-1.x smolts leaving Chilko Lake in any year is more similar to the marine survival of age-2.x smolts of the previous cohort than to the survival experienced by their siblings which leave one year later (Fig. 50). The correlation of the former is 0.45 ( $P < 0.01$ ), whereas there is no correlation of the latter ( $P > 0.05$ ). However, despite sharing a common ocean entry year and location, the amount of interannual variation in marine survival shared by the two groups entering the sea in the same spring is weak ( $R^2 = 20\%$ ), and this drops to 16% if the calculation is made using only 44 years of data that exclude the two anomalous survivals in 1952 and 1954 at the earliest part of the time series. Without the two early outliers, the mean survival of age-2.x smolts across all other years was 12% and the mean survival of age-1.x smolts was 9% for calculations up to, and including, the 2004 brood year. Some of the poor correlation between groups that enter the sea in the same year may be due to inadequate biological sampling of age-2.x groups in the catch or on the spawning grounds. Because they are relatively rare, an inadequate sample of the adult returns can affect the survival estimates.



## 5.4 Variability at Different Temporal Frequencies

The statistics of Fraser River sockeye salmon population biology are, for the most part, summarized as annual values. The degree to which finer scale within-year statistics can be computed depends on the frequency of observation. Repeated measurements of the same features using the same, or very similar, methods lead to the establishment of time series of the annual characteristics of salmon biology. Statistics that appear to vary randomly from year to year are described as having interannual variation. Should a time series of seasonal observations have a trend or cycle, or some other longer-term pattern, variations of these kinds are often referred to as decadal-scale or even multi-decadal frequencies. A common approach in trying to understand the cause of variation in salmon biology is to see what other physical, chemical, or biological time series share the same pattern of variation. The physical effects of some cycles, such as the annual cycle of warming and cooling at higher latitudes, are well known so their effects on a time series is often removed to reveal the variation that is not related to the seasonal cycle of the Sun.

The scale of an effect can be an important clue to its origin. The cause of variation in a time series that has no apparent relation to environmental variation of other nearby measurements might arise from a local effect, whereas a pattern of variation in a time series that is shared regionally may have a regional origin. A technique used to study variation in time series is to understand the spatial scale of variation as a clue to its source. Time series that are a result of multiple influences present even greater challenges, particularly when the observations themselves are imprecise or biased by the methods used to make the original observations. The latter, if an important characteristic of a time series, means that weak sources of variation will be difficult to detect.

### 5.4.1 Interannual

The coefficient of variation (magnitude of variability in a time series in relation to its mean value) in the number of smolts produced per effective female spawner in Chilko Lake is 47%. The coefficient of variation of age-1.x adult returns per age-1.x smolt is 60%. The coefficient of variation of total returns per effective spawner in Chilko Lake is 96%. The latter is larger because it includes variation from both sources. The important result of this comparison is that returns per spawner, the normal measure of Fraser River sockeye salmon productivity, includes significant year-to-year variability from both freshwater and ocean sources. Because it has not been measured routinely at other lakes, the relative influence of each habitat on total survival cannot be determined. Returns per spawner is the measurement of choice (or default) for most Fraser River sockeye salmon populations because only adults are censused in every population.

For comparison, smolt-to-adult survival of age-1.x sockeye salmon from Babine Lake (Skeena River) had a coefficient of variation of 70% for brood years 1961 to 1977 (McDonald and Hume, 1984). This study evaluated four major assumptions surrounding the construction of spawning channels to increase adult sockeye salmon production. Assumptions about freshwater production were largely met, *i.e.*, more spawning habitat created by the channels provided for more eggs to survive, and this translated into more fry in the lake and more smolts emigrating to sea. Only during odd years did greater numbers of adults return from the increased numbers of smolts. There was no average increase in adult returns during even brood years (McDonald and Hume, 1984). The difference between odd/even brood year marine survival in Babine Lake is not apparent in more recent data (brood years 1970–2000). There is no significant difference between odd and even brood year smolt-to-adult survival in Chilko Lake sockeye salmon (1-way ANOVA,  $P > 0.9$ ) over the period of record, but a more thorough analysis of this topic is warranted in the future because of its appearance in other species using the Strait of Georgia (Ruggerone and Goetz, 2004).

### 5.4.2 Decadal

Significant changes occurred in the North Pacific ocean-climate system around 1977 (Mantua *et al.*, 1997) and around 1989 (Hare and Mantua, 2000), so these years are often used to delimit climate and productivity regimes. The local expressions of these phenomena vary around the North Pacific. Spring and summer SSTs at Kains Island on the northwest coast of Vancouver Island, for example, were significantly warmer (by 0.8°C) in August after 1989. In studies of Fraser River sockeye salmon productivity and climate, Beamish *et al.* (1997, 2004a) found a statistically significant change (increase) in Fraser River sockeye salmon productivity following the 1976/77 climate regime shift in a subset of the time series. However, using the entire period of record and a different analytical approach, no statistically significant change in total survival was found up to the 1999 brood year McKinnell (2008). In Chilko Lake, where freshwater and postsmolt survival can be distinguished, he found that average freshwater survival had declined after 1989 (up to the 1999 brood year) but he found no statistical evidence of a significant decline in average postsmolt survival during the same period. This result was likely due to having few complete years of data after the decline in survival, and by not recognizing 1992 as the year when the change occurred. However, by extending the time series to the 2004 brood year, using 1992 as the ocean entry year of change in mean survival ( $\sqrt$  transformed), a significant decrease ( $P < 0.05$ ) was found for both smolt ages. The difference in average freshwater survival seems to have disappeared because of recent, unexplained high freshwater survival of the 2005 and 2006 brood years in Chilko Lake.

### 5.4.3 Evolutionary-scale

Selective pressures in the environment affect the evolution of heritable characteristics of sockeye salmon populations. Populations that are found in the Fraser River have evolved to their contemporary diversity over millennia, since the start of the retreat of the Laurentide ice sheet from the coastal region of British Columbia approximately 10,000 years ago. Hodgson (2000) concluded that variation in migratory timing among sockeye salmon populations was related to spawning time, migration distance, river temperature and flow regimes. She found that long delays between migration and spawning occurred in coastal areas, some of which had warm freshwater temperatures during the migration. She suggested that long delays provided the means to avoid higher temperatures which occur after migration in freshwater. For some populations, it was unclear why they should return early, with a long delay before spawning, rather than return on a date that would provide a shorter delay before spawning, after freshwater temperatures had declined from their peak.

An alternative (and at this point, speculative) idea that has not been considered previously, entertains the possibility that migration timing in sockeye salmon at the southern end of the species range has evolved to the present state by selective forces operating in the ocean, enroute to freshwater. It has the following logic:

1. Some populations of sockeye salmon, especially near their southern ocean entry locations, migrate from salt water to freshwater far sooner than is expected from time of spawning.
2. Populations that exhibit the most extreme form of this type of behaviour have a shared geography in the northern California Current region.
3. The northern California Current region is subject to large interannual variations in physics, chemistry, and biology because of its proximity to the North Pacific Transition Zone between the Subarctic and the Subtropic.
4. The migration timing anomalies occur with diminishing frequency northward.
5. Fraser River sockeye salmon do not exhibit this behaviour because the Johnstone Strait approach route provides relief from the evolutionary forces that affect west coast populations.
6. High northern diversion rates in warm years are the interannual response to oceanic selective pressure.
7. Migration timing is a highly heritable characteristic and early arrival occurs in affected populations because evolution has extinguished later arrivals, suggesting that the ocean is unsuitable for sockeye salmon migration when they might otherwise (based on spawn timing) appear in freshwater.
8. A seasonal northward expansion of the Subtropical/Transition Zone region is the cause for reasons that keep sockeye salmon from this region on the high seas.
9. A less drastic result of this pressure is the role of the ocean in determining a high northern diversion.
10. Any expansion of the inhospitable region will provide greater selective pressures to avoid it.

## 5.5 Tag Recapture Rates as a Proxy for Survival

It is not uncommon to attempt to estimate marine survival of salmon using the percentage of tags recaptured. Where the fishing effort is high and the probability of detection is high, the result can be a good approximation, if not an absolute estimate, of marine survival. Coded wire tags have been used routinely to understand the migration and survival of coho salmon and chinook salmon (Weitkamp and Neely, 2002; Daly *et al.*, 2009; Teo *et al.*, 2009). From 1964 to 1968, sockeye salmon postsmolts, potentially of any population, were tagged and released throughout coastal North Pacific Ocean, including the Bering Sea (Hartt and Dell, 1986). A total of 40, or 0.4% of the 9,883 tagged in these years was subsequently recovered after two or three years at sea.

Of the 40 recoveries of tagged age-x.0 sockeye salmon that have ever been recovered, six (14.6%) were taken in one seine set on the coast of Southeast Alaska on July 24, 1968. Hartt and Dell (1986) did not report the numbers caught on that specific day, but they made only four sets during a 10-day period, with a total of 59 sockeye salmon caught in the four sets. If all 59 sockeye were taken in only one of these four sets, the minimum survival rate from that one set would have been approximately 10%. If each of the four sets caught  $\frac{1}{4}$  of the 59 fish, the survival rate from the set with the tagged fish would be approximately 68%. Each of these six tagged sockeye salmon was recovered in fisheries along the British Columbia coast in 1970.

In general, however, the tag recapture rates measured in the seine operations from 1964 to 1968 were remarkably low, considering that the average smolt-to-adult survival for Chilko Lake sockeye salmon during brood years that correspond to these tagging years (~1961–1966) was approximately 8.5%. Why should the probability of survival of sockeye salmon tagged at sea at a later stage of life be more than an order of magnitude lower than the probability of survival of fish just leaving Chilko Lake? On average, it cannot be lower, so the results suggest either heavy mortality from tagging or a remarkably low probability of tag detection, or a combination of both. It suggests that reliable measures of survival will not be found in the existing high seas tagging data.

## 5.6 Leading Indicators of Survival

*In generating the 2009 forecast, long-term average productivities had been assumed, which seemed reasonable given that marine indicators suggested that conditions for salmon going to sea in 2007 would be relatively good.*

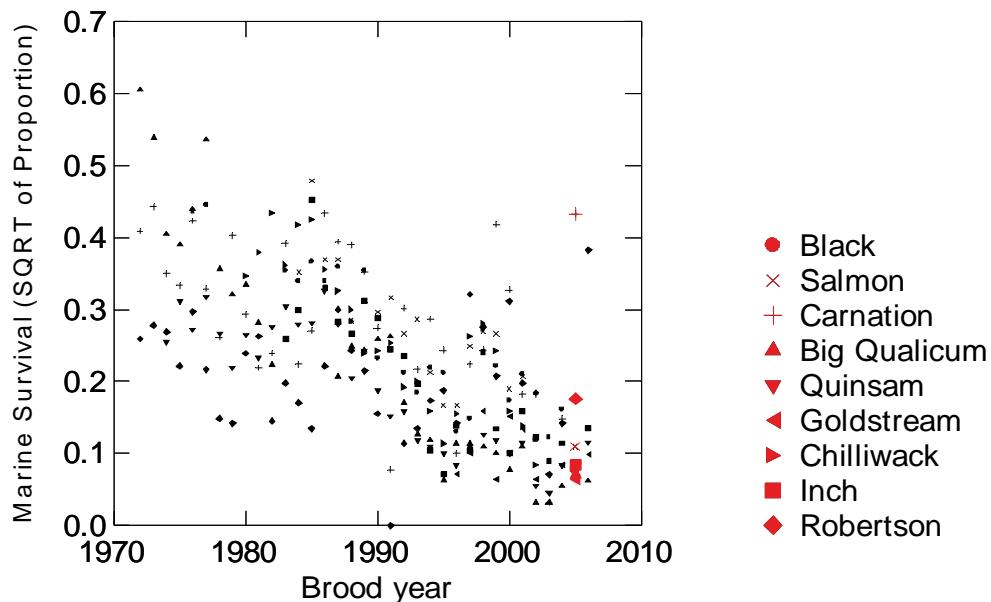
Crawford and Irvine, 2010

### 5.6.1 Comparisons with coho salmon survival

Most Fraser River sockeye salmon and most coho salmon rear in freshwater for one year before migrating to sea (Sandercock, 1991). The value of observing variations in the survival of coho salmon, for a study of sockeye salmon, is their habit of returning to spawn one year earlier than sockeye salmon of the same brood year. A large fraction of the year-to-year variation in marine survival of coho salmon is shared commonly with other coho stocks along the North American continent suggesting that a large-scale factor (or factors) is affecting all (Teo *et al.*, 2009). While the two species have different behaviours upon reaching the ocean, there is a potential for oceanic anomalies to affect both species, where they share a common environment. Indeed, this was the case for the 2003 brood year when both species entered a coastal ocean in 2005, which was not very hospitable for some salmonids (Mackas *et al.*, 2006, 2007).

Some experimental forecasts are beginning to consider how variation in the coastal oceanic environment affects salmon survival. Trudel *et al.* (2009), for example, described how low coho postsmolt growth is associated with poor coho marine survival. For the 2005 brood year (2007 ocean entry year), marine survival varied markedly among populations (Fig. 51). For the the Strait of Georgia populations, marine survival of the

2005 brood year was low but not the worst ever observed; that accolade belongs to the 2003 brood year. Marine survival of the 2005 brood year of Carnation Creek coho salmon near Barkley Sound was remarkably high, but this is (currently) a small run of coho salmon with few spawners where small changes in numbers can generate large changes in survival percentage. Marine survival of the larger Robertson Creek coho salmon population for the 2005 brood year was near the long-term average.



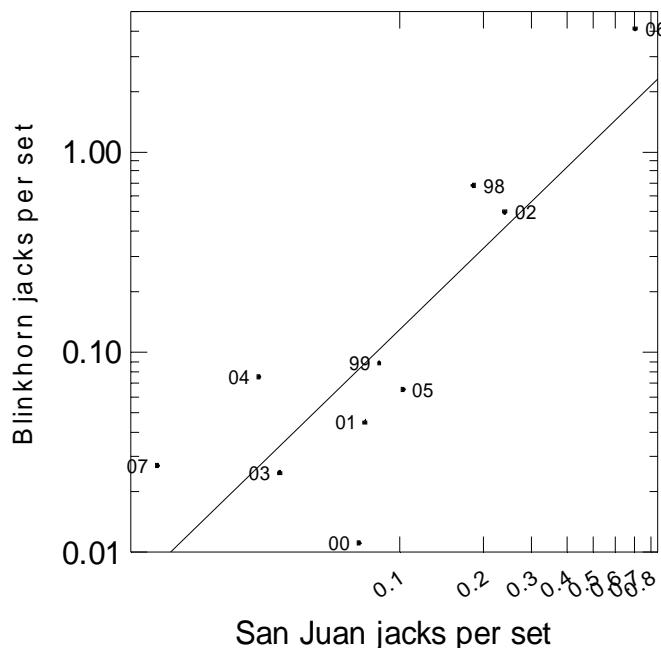
**Fig. 51** Marine survival ( $\sqrt{\cdot}$  transformed to emphasize variation at low survival) *versus* brood year for seven hatcheries in the Strait of Georgia and two (Robertson and Carnation) on the west coast of Vancouver Island. Marine survivals for the 2005 brood year (2007 ocean entry year) are highlighted in red.

Forecasts of survival and returns of Fraser River sockeye salmon have been made on the basis of the Strait of Georgia surveys by DFO but forecast performance has been highly variable during the short period it has been attempted. As the focus of sampling in the Strait of Georgia is coho and chinook salmon survival, its summer and fall sampling schedule captures only a fraction (probably variable from year to year) of the April–July migration of Fraser River sockeye salmon postsmolts from the Strait of Georgia. Nevertheless, these data were used to predict the returns of Fraser River sockeye salmon beginning in 2007 (DFO, 2008). The first forecast in 2007 was for above average marine survival and above average returns, based largely on the observation that the sockeye salmon postsmolts caught that year in the Strait of Georgia were larger than in previous years. Returns in 2007 were among the lowest observed, with the lowest marine survival ever recorded to that point in history. Likewise, sockeye salmon returns to the Fraser River in 2008, based on the Strait of Georgia sampling in 2006, were expected to provide above average returns. Returns in 2008 were below average, with no fishery permitted. The forecasts of Fraser River sockeye salmon returns in 2009, based on sampling in 2007, were expected to be extremely poor, and this was what occurred.

## 5.6.2 Preliminary signs of 2010 abundance<sup>7</sup>

Gillnet test fisheries in the approach routes to the Fraser River are augmented each year by purse seine test fisheries as the abundance of the annual return builds. They provide data on the abundance of maturing age-1.1 sockeye salmon (jacks) that the gillnet test fisheries miss. Jacks sockeye salmon spend only one year at sea before maturing and therefore are too small to be caught by the mesh size of commercial gillnets. Although they represent only a small fraction of the population each year, the value of jack abundance information, if a representative sample can be obtained, is a one-year look ahead at the magnitude of the cohort that will return the following year (assuming relatively constant age at maturity).

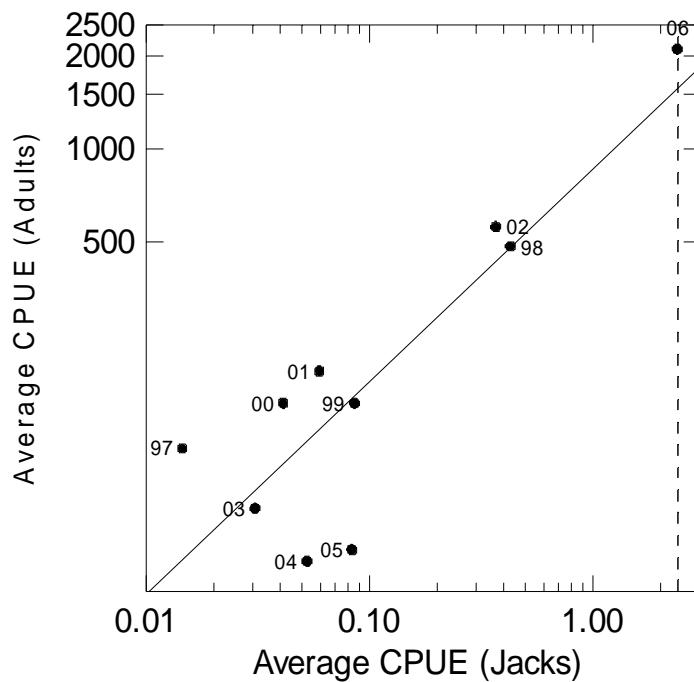
From 2000 to 2009, Fraser River sockeye salmon jacks in the Blinkhorn Island test fishery (upper Queen Charlotte Strait) are about twice as abundant as in the San Juan purse seine test fishery. Nevertheless, there is a highly significant positive correlation ( $r = 0.97$ ,  $P < 0.001$ ) between the aggregate annual CPUE of sockeye salmon jacks caught in the Blinkhorn Island purse seine test fishery and the same in the San Juan purse seine test fishery (Fig. 52). Although the magnitude of the correlation is heavily influenced by the high catches of jacks of the 2006 brood year, *i.e.*, jacks that returned in 2009, it suggests that over the range of observations the two independent purse seine test fisheries are detecting the same jack abundance signal. The correlation for older maturing sockeye salmon is 0.64.



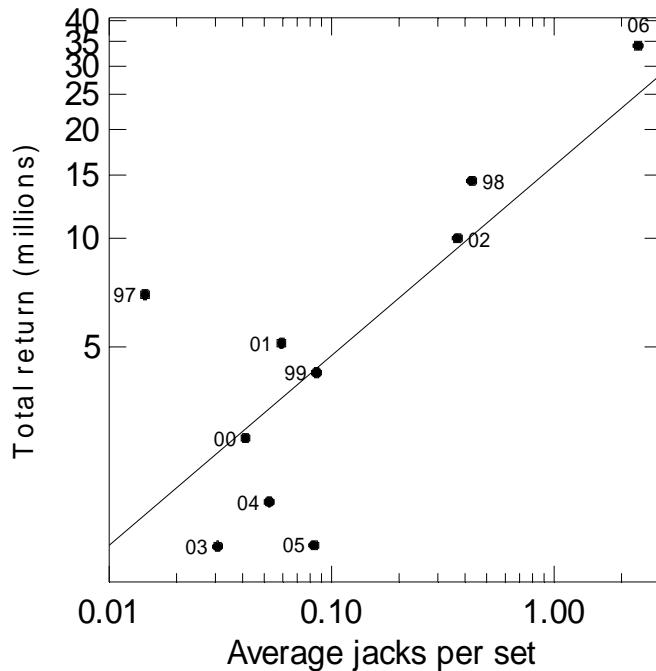
**Fig. 52** Comparison of Blinkhorn Island sockeye salmon jacks per set *versus* the same at San Juan, on a log scale.

The relationship between the average CPUE of sockeye salmon jacks in the test fisheries and the following year's CPUE of adult sockeye salmon (Fig. 53) or total brood year returns (Fig. 54) indicates that this measure may be useful for detecting some of the large-scale changes in abundance that have been observed from 2000 to 2010. The 2006 brood year outlier was evident in 2009, but because it was more than five-fold greater than the next highest value (1997 brood year), it was difficult to know how large the return would be. As there was no fishery in 2009, the purse seine test fisheries were one of the few sources of this information.

<sup>7</sup> Summary of a presentation to the DFO Fisheries Oceanography Working Group, February 16–17, 2010.



**Fig. 53** Average CPUE of adult sockeye salmon in the Blinkhorn Island and San Juan purse seine test fisheries *versus* the same measure for sockeye salmon jacks, by brood year. Vertical dashed line indicates the jack CPUE measured in 2009 for the 2010 adult return. Data are presented on a logarithmic scale to emphasize variation at low CPUE.



**Fig. 54** Total returns of Fraser River sockeye salmon *versus* the average numbers of jacks caught in Blinkhorn Island and San Juan purse seine test fisheries, by brood year. The 2006 brood year total return is the in-season abundance estimate from August 31, 2010 provided by the Pacific Salmon Commission.

Sockeye salmon jack CPUE in the purse seine test fisheries does not appear to be very reliable when jack CPUE is <0.1 per set. The total return the following year can vary from 1.5 to 7 million. Most of the signal in this relationship is related to the abundance of Late-run sockeye salmon (as indicated by the four-year interval between years of high CPUE and high total returns). The relatively good return of the 1997 brood year was not detected by the jack CPUE index because the dominant populations that made up the return in 2001 do not have populations with significant numbers of jacks.

**Summary** – The existence of a relationship between the abundance of age-1.1 sockeye salmon in one year and the abundance of returns of age-1.2 sockeye salmon the following year is an indication that the magnitude of the sockeye salmon return to the Fraser River was largely determined prior to the time when the age-1.1 returned. If the major cause of variation in survival occurred after the age-1.1 sockeye salmon returned, there would be little reason for them to correspond. However, because most of the signal in that relationship comes from the Late-run sockeye salmon, it is not possible to know if it applies only to this component or to the others as well. Clearly, it cannot apply to stocks that lack detectable numbers of jacks.