# Critical Periods in the Marine Life History of Pacific Salmon?

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It is now exactly one century since the great Norwegian fisheries biologist Johan Hjort proposed his "critical period" hypothesis: That very early in the life history of marine fish such as cod, a single short period largely determined the major fluctuations in recruitment evident in fish populations (Hjort 1913). Hjort was an excellent scientist, and his original conjecture was that such a critical period might exist just after cod hatched from their eggs, when he viewed the larvae as particularly frail and thus especially vulnerable to environmental variability. However, Hjort also made clear in his writings that he viewed this hypothesis as merely a simple working theory and that research would have to move on to look at later phases in the life history if this initial simplifying theory was not supported. Unfortunately, such was rarely the case and many biologists came to state Hjort's theory as a fact, and used it as a powerful rationale to justify focussing research efforts on the earliest life history phases, which were typically viewed as more tractable subjects for study than the later life history stages. For salmon populations, this typically meant proposing that the "salmon problem" (poor smolt to adult survival rates) was determined either in freshwater or in the first few days or weeks of life in the ocean. Although a second "critical period" has been proposed to occur in the first winter at sea (Beamish and Mahnken 2001) for salmon, the issue of whether specific critical periods actually exist (and thus make the recruitment problem potentially more tractable) has never been formally examined. After a century of research, there continues to be a persistent effort to simplify research on salmon by assuming that there is a critical period in the freshwater or early marine life history (and to propose large-scale research programs to study it) before actually establishing its existence. The consequences are important because, if the early marine phase is simply studied to assess the drivers of salmon returns without formally testing the theory that this life history period has the dominant role in determining recruitment, research programs may potentially continue for decades without ever establishing that they are studying the "wrong" period, wasting both intellectual and financial resources—and the opportunity to actually identify where the recruitment problem actually lies.

The advent of prototype large-scale freshwater and marine telemetry systems, such as the POST array, now provides an opportunity to formally assess the critical period theory as it applies to Pacific salmon, as a large number of populations have now been tagged and their freshwater and marine survival followed for 1-2 months after release. A 10-fold decline in survival of many Pacific salmon populations occurred over the last three decades, with smolt-to-adult return rates dropping from >10% to ~1%. Using the POST telemetry array we tested whether mortality in the earliest life history phases is large enough to form the primary driver of adult recruitment rates, and whether the survival measured during the early marine period is now small enough to explain a ten-fold decline in smolt-to-adult recruitment.

*Size-related effects on smolt survival*

Until very recently, current telemetry tags were too large to be implanted into the entire size range of salmon smolts, raising the question of whether telemetry-based survival measurements are representative. Welch et al. 2011 found that in British Columbia studies of sockeye, Chinook, coho salmon, and steelhead, no distortion in the size spectrum of initially tagged smolts relative to that of the survivors 1-2 months later was evident. A similar result is found in our studies of tagged yearling Chinook salmon smolts from the Columbia River (Fig. 1).

It is also possible to compare downriver survival to Bonneville Dam of acoustically tagged smolts with that of smolts tagged with PIT tags, a much smaller tag that is applicable to the entire size range of migrating smolts in the Columbia River (Fig. 2). Survival with distance is indistinguishable, suggesting that neither the larger size of acoustically tagged smolts or higher tag burdens are major contributory factors to survival where it can be compared. This result fits with the one survival study we have conducted where we directly measured the survival to adult return (SAR) of Cultus Lake sockeye using specially programmed acoustic tags (Welch et al. 2011); the resulting survival of the tagged smolts (2/200=1% ±1.4%; mean ±2SE) compared very favourably with the survival rate of wild (1.5%) smolts.

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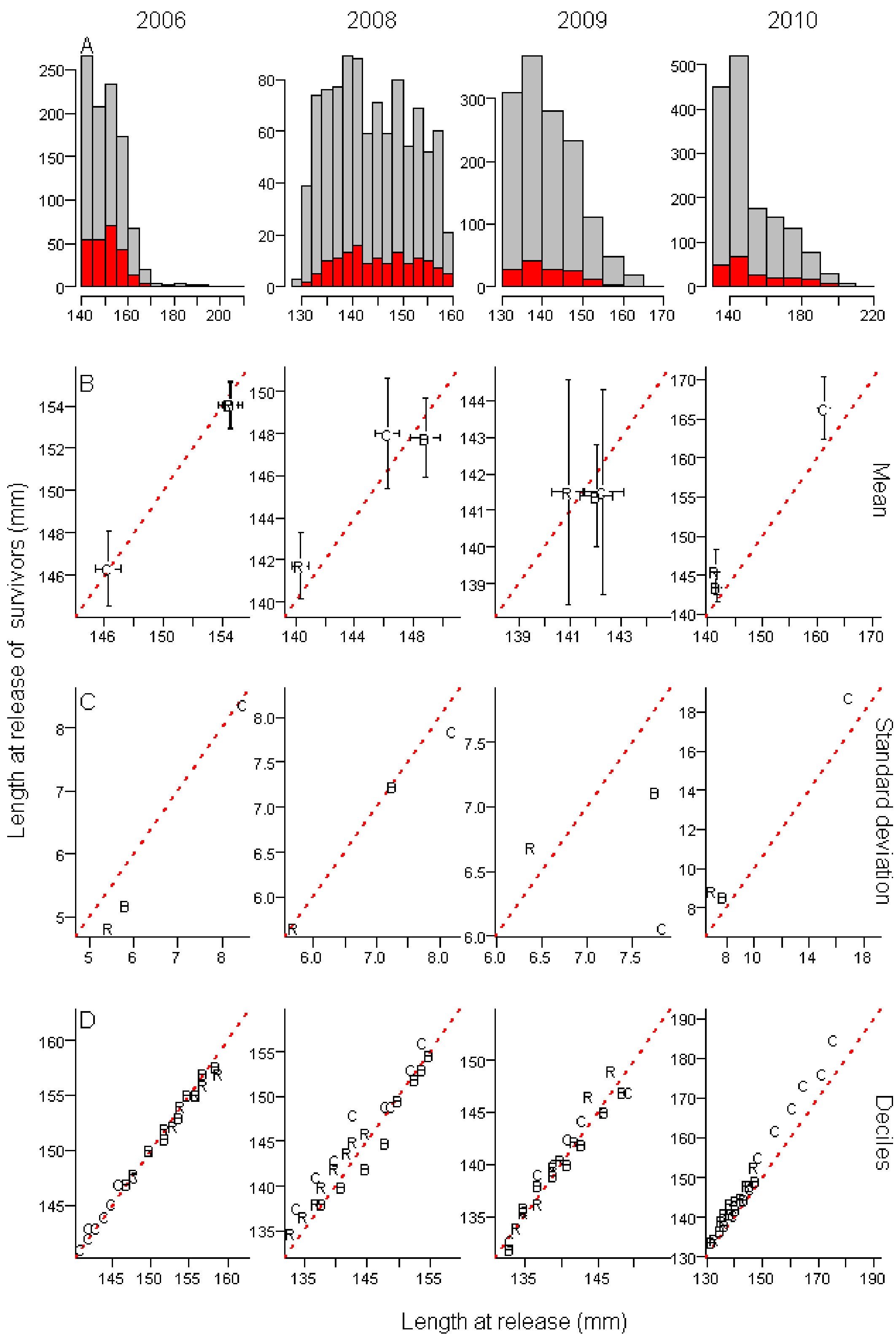


**Fig. 1.** (Top) Comparison of the size-at-release of all Columbia River tagged spring Chinook smolts released at their hatchery with the size-at-release of those tagged animals surviving to reach Willapa Bay ca. one month later. The middle two rows compare the mean size of smolts at release and of the survivors (±95% CI) and the variance around the mean; the bottom row shows the QQ plot. In each case there are no departures from 1:1 (dashed red line), indicating that over the size range of fish tagged significant distortions due to differential survival with size are not evident.

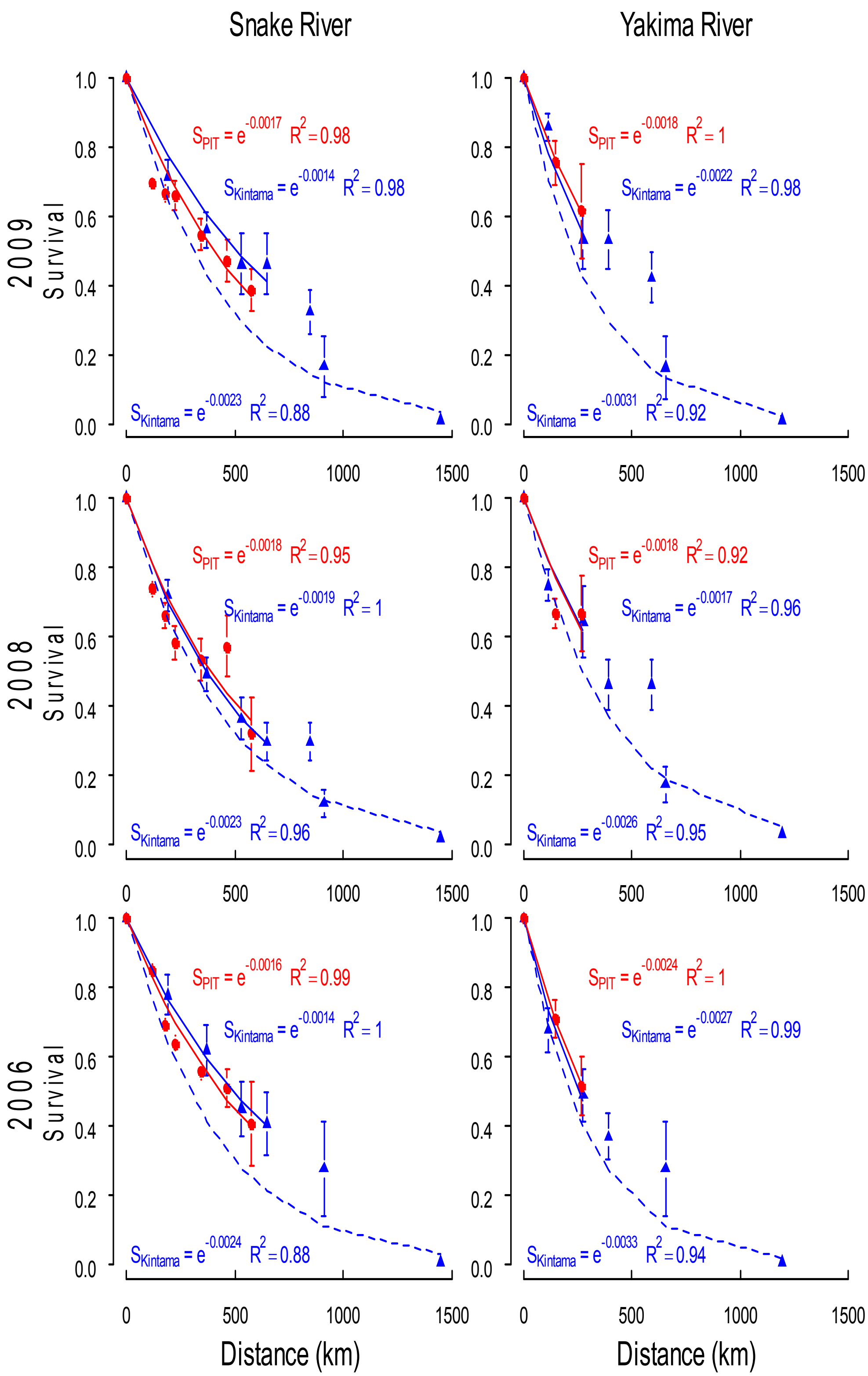


**Fig. 2.** Comparison of survival with distance from release for PIT and acoustically tagged smolts for two Columbia River spring Chinook stocks. Survival to Bonneville Dam (the last location where survival of PIT tagged fish can be measured) is indistinguishable.

*Survival in the early vs later phase of salmon migration*

Smolt to adult survival is now down to ca. 1% in many stocks of salmon in both southern British Columbia and the US Pacific Northwest region. The various survival studies conducted using the prototype POST array and reported in Welch et al. (2011) for British Columbia and in Porter et al. (2012a, b) for the Columbia River can be used to compare the magnitude of survival in the early and later phases of the migration. Although direct estimates of survival in the later marine phase are currently lacking, apart from the Cultus Lake study cited above, it is possible to compare the ratio of early to later survival necessary to achieve observed SARs.

We report (Table 1) British Columbia steelhead and sockeye salmon survival to the exit from the Salish Sea (Queen Charlotte Strait/Juan de Fuca Strait sub-arrays) as these two species consistently migrated out of the Salish Sea, while for coho and Chinook salmon stocks (primarily Fraser River) we report survival to the river mouth because these two species ceased migration after entering the ocean and remained resident in the Salish Sea for the remainder of the tag's lifespan. Migration to the river mouth after release typically takes one week in the Fraser River and in the Columbia River takes three weeks to reach Astoria (near the river mouth) and four weeks to reach Willapa Bay, which encompasses the Columbia River plume region.

**Table 1.** Summary of survival values by species using the prototype POST array. Values in the table are simple means of estimated "critical period" survival across all stocks of a given species. The final column compares survival in the first period to survival over the remainder of the life history necessary to achieve currently observed smolt-to adult return survival (SAR) of ca. 1%. Although the survival ratio is sensitive to the exact value of the SAR, it demonstrates that in all cases early phase survival is much higher and therefore the majority of overall survival to adult return is determined sometime after the first 1-2 months of smolt migration.

| Species | "Critical Period" Survival | Current SAR Rates | Survival Ratio (Early/Late) |
|---|---|---|---|
| **Southern British Columbia Stocks** | | | |
| Steelhead | 25% | ~1% | ~6X |
| Sockeye | 15% | ~1% | ~2X |
| Coho (River only) | 62% | ~1% | ~100X |
| Chinook (River only) | 27% | ~1% | ~6X |
| **Columbia R Spring Chinook** | | | |
| Release to River Mouth (Astoria) | 42% | 0.5%~1% | 100X~200X |
| Release To Willapa Bay | 22% | " | 9X~17X |
| Plume Only (Astoria-Willapa Bay) | 49% | " | 50X~100X |

In each case, survival in the first month of migration is much higher than the survival in the later phase necessary to result in the observed 1% overall SAR. (Note that freshwater survival to the mouth of the Fraser and Columbia rivers is particularly high compared to marine-phase survival).

*Discussion*

In all populations examined, survival beyond the current extent of the POST array must be substantially lower than survival within the geographic extent of the array. Two counterbalancing effects on survival during the early phases of salmon migration may occur in our telemetry studies that could potentially distort this conclusion: (1) Surgical implantation of tags may reduce survival in the earliest phases ("tagging effects") and thus inflate estimates of the importance of survival in the early phase; (2) use of larger hatchery smolts in many (but not all) of the studies may result in survival estimates higher than might be experienced by smolts currently too small to tag, deflating estimates of the magnitude of early phase survival.

To date, we have found little evidence that either process is likely to have a substantial influence on survival in the early phase. Overall, our results point to the majority of salmon survival being determined after the first 1-2 months of migration. Of particular importance, our direct measurements of survival in the early phase of the migration are too high to largely account for the 10-fold decline in SARs seen over the past 2-3 decades. Although we do not have direct measurements of survival for periods when survival was formerly much better, even the elimination of all possible sources of mortality in the early marine phase (i.e., raising survival to 100%) would be insufficient to increase SARs by a factor of ten. At best, elimination of all sources of mortality would raise SARs by a factor of 2-5 fold.

It may be appropriate to retire the concept of a single "critical" period and to consider all phases of the life history of salmon as important, rather than to start from the simplifying assumption that one period is of overriding importance and then build research programs on the basis of this assumption. From this perspective, the first phase of a scientific research program should be to evaluate whether a particular life history period is really "critically" important, rather than to simply assume it to be true. Our results using surgically implanted salmon smolts to date have found little evidence that there is sufficient mortality occurring in the first 1-2 months of migration to account for the very large declines in adult survival that have been observed, and there is good evidence that much of the determinants of recruitment occur later in the marine phase.

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