

An analysis of 2004 smolt trap data from the Hovander smolt trap

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Executive Summary

Total production estimates for Chinook fry outmigrating from the Nooksack River in 2004 ranged from 803,968 (ACCE) to 990,215 (YCCE) individuals. 857,300 Chinook fry were released into the Nooksack between Feb 29 and May 24. Wild production estimates ranged from as low as 18,215 (ACCE) to as high as 132,195 (YCCE). However, the ACRM method (that is probably the most reliable of the three methods) gave estimates of **966,026** (total) and **108,726** (wild-origin) respectively. If hatchery-origin fry suffer mortality before reaching the trap site then these estimates are likely to be too high. This low-level of wild-production in 2004 is consistent with the hypothesis that severe hydrological events that occur in fall have a large adverse effect on wild production.

Residence time modeling for Chinook fry in 2004 supported the hypothesis that early release dates give rise to longer residence times prior to outmigration. Average residence times for an early-released group of marked hatchery-origin smolts was 28 days, and for a second group that was released later the average residence times was c. 19 days.

The total production estimate for Coho smolts was **2,693,075** smolts (ACRM). 1,241,005 smolts were released from hatcheries between May 3 and May 20. The wild production estimate is therefore **1,452,070** smolts, assuming no mortality occurs for hatchery-origin smolts prior to reaching the trap site. If mortality does occur for hatchery-origin smolts, then the wild production estimate will be too high.

Residence time modeling for Coho smolts was confounded by too-high daily production estimates derived using ACCE or YCCE methods. Modeled residence times for one group of marked smolts was 11 days, and was 4 days for a second, larger group of marked smolts. This compares to previous year's data that suggested an average residence time of just 2 to 3 days. The difference is probably a failure of the ACCE and YCCE methods to correctly determine daily production rates for Coho. This failure is probably due to a combination of diurnal differences in Coho smolt catchability, and relatively low nighttime sampling effort in 2004.



Introduction

Lummi Natural Resources operates a rotary screw smolt trap on the Nooksack River in the lower mainstem, near Ferndale. The goals of the sampling program are to develop accurate estimates of the annual production of outmigrating wild-origin salmon fry and smolts. The emphasis of the program is to quantify wild Chinook production for the endangered North Fork stock but secondary objectives include stock assessment for other native salmonids such as Coho. Data analyses of data from the Lummi screwtrap have been previously conducted in both 2002 and 2003 (Dolphin, 2002; 2003).

In 2004 the screwtrap was operated from January 15 through to August 10, although sampling intensity was highest from early April through to early-July (Fig. 1).

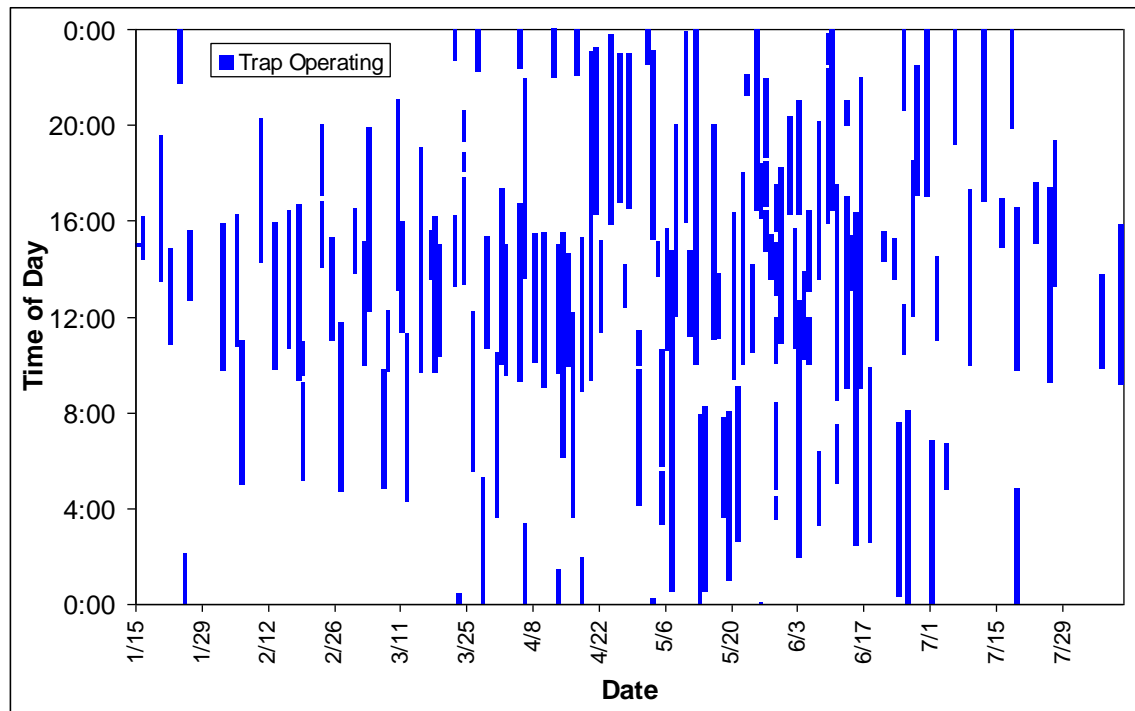


Figure 1. Daily sampling effort on the Lummi smolt trap in 2004.

This report aims to report the results of the sampling program in 2004, summarize the principle findings, and compare these results to previous data (where available) for Chinook fry (age 0+) and Coho smolts (age 1+). No analysis of the data for Chum or Pink salmon has been made to date.

Field Methods

The full methodology for the operation of the smolt trap is not given here but interested readers are referred to Conrad & MacKay (2000) for a full description of the site, sampling apparatus, and field protocols. A summary of the field data for each set and subset is provided in Appendix A.

Chinook

Results

Figure 2 shows the average daily catch per hour for age zero Chinook smolts based on trap data and linear interpolation between sample measurements. Table I outlines the timing, magnitude, and details of hatchery releases in 2003.

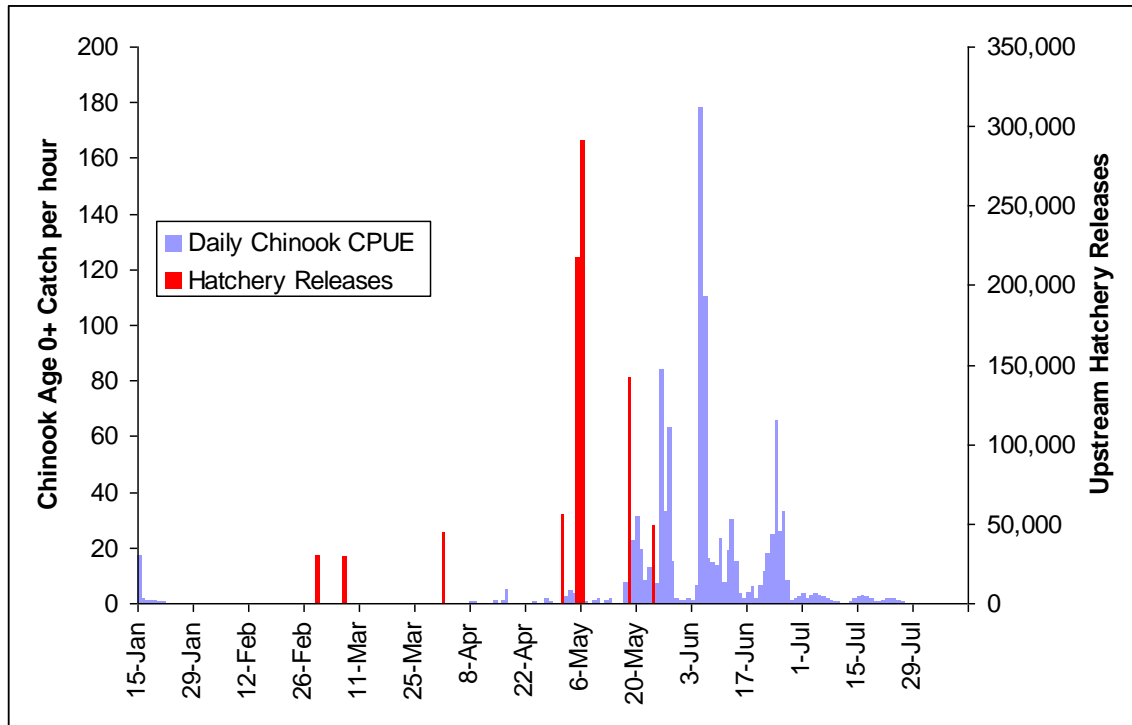


Figure 2. Average daily catch per hour for age-zero Chinook smolts in 2003

Table I. Details of Hatchery releases of age-zero Chinook Fry in 2004

Release Date	Release Site	Total Adipose Clip	Total CWT	Total Release
2/29/04	Maple Creek	0	0	30,400
3/7/04	Maple Creek	0	0	29,300
4/1/04	Kendall Hatchery	0	0	44,100
5/1/04	Kendall Hatchery	0	0	55,300
5/5/04	Middle Fork	0	0	217,000
5/6/04	North Fork	136,000	272,300	290,300
5/18/04	N. Fork	67,200	134,400	142,300
5/24/04	Kendall	0	48,600	48,600
Totals		203,200	455,300	857,300

Chinook Production Estimate Methods

Method 1. Ad-Clipped Hatchery smolts recapture ratio method (ACRM)

Traditional mark-recapture models use the ratio of marked individuals in the total catch, along with the original number of marked individuals that were released, to provide an estimate of how many individuals are represented by the catch. Several models have been developed for a range of scenarios where multiple releases of marked individuals and multiple catches are made. However, the simple Peterson estimate (single release, single recapture) is most appropriate in this case because outmigrating smolts are assumed to be catchable only once as they move out of the river. Assumptions made when making Peterson mark recapture estimates include the following:

1. The population under study should be both *geographically closed* and *demographically closed*.
2. Each member of the population has the same probability of being captured, and this capture probability does not change over time.
3. Marked and unmarked individuals randomly mix between samples.
4. Marks are permanent and always recognizable.

The formula used in the Peterson mark-recapture method is shown in 1 below:

$$\hat{N}_P = \frac{N_2 N_1}{M_2} \quad (1)$$

Where N_1 = the number of marked smolts released, N_2 is the total number of smolts caught during sampling, M_2 is the number of marked smolts caught at the trap during sampling, and N_P is the estimated size of the total population.

95% confidence intervals for N_P can be calculated using a variety of probability distributions. However, when the percent of marked individuals (M_2/N_1) is less than 10%, and the number of recaptures, M_2 , is greater than or equal to 50, a confidence interval based on the Normal distribution is the most appropriate method. Consequently, confidence intervals for the ACRM method are calculated using equation 2:

$$N_P \pm 1.96 * \sqrt{\text{Var}(N)} \quad (2)$$

...where N_P is the population estimate, and the variance of N_P is determined using equation 3.

$$\text{Var}(N_P) = \frac{(N_1 + 1)(N_2 + 1)(N_1 - M_2)(N_2 - M_2)}{(M_2 + 1)^2(M_2 + 2)} \quad (3)$$

Table II shows the total number of hatchery Chinook that had their adipose fins clipped and were released, as well as the number of adipose fin clipped smolts that were recaptured, and the total number of Chinook smolts captured in the same sampling program. Hatchery-origin fish with coded wire tags are not similarly used to estimate recapture rates because of the possibility that detection rates are lower than for adipose fin clipped, thereby artificially lowering the recapture ratio and biasing the final estimate too high. Similarly, if any marked hatchery fish die, or do not pass the trap site, then the final estimate of total production is likely to be too high because the true recapture rate will be higher than calculated in Table II.

Table II. Chinook clipped adipose fin smolts recapture rate details for 2003.

	2003	
Number of Adipose fin-clipped smolts released	203,200	N_1
Number of Adipose fin-clipped smolts recaptured	1,045	M_2
Marked Smolt Recapture Ratio	0.51%	
Total number of smolts caught	4,968	N_2
Estimated Total production of Chinook smolts in 2003	966,026	N_P
Upper 95% Confidence Limit	1,017,847	
Lower 95% Confidence Limit	914,206	

The results of using this method suggest that a total of **966,026** smolts migrated downstream past the Screwtrap in 2004. Since we know that 857,300 smolts were released from the hatchery, the difference (**108,726**) could be interpreted as wild-origin smolts. However, this does not incorporate any loss of hatchery fish due to mortality prior to their arrival at the trap site. The magnitude of any bias caused by wrongly assuming no mortality occurs when using the ACRM method is discussed further in the Coho production estimate results section but, overall, this error would lead to overly optimistic estimates for wild-origin Chinook production.

Time-series based production estimate methods...

Other methods to estimate annual production of Chinook smolts attempt to create a time series of catch-per-hour measurements for the entire outmigration period, and then convert this time-series into production (all fish passing the trap site) per day using a trap-specific catch efficiency estimate. Summing the daily production estimates over the entire outmigration period provides an estimate of total production. All of the methods that use this time series as a basis explicitly make predictions as to the magnitude and timing of outmigration past the trap site.

The time-series of catch per hour data for Chinook is created using trap catch rates stratified by dawn, day, dusk and night sampling periods. Intervals between sampling periods for which no data are available are assumed to be related primarily to catch rates during other portions of the same 24-hour period. That is, if night time sampling data is available for a particular 24-hour period, then the day time value is assumed to be a function of the night time sample. This relationship is derived from a regression of a scatter plot of day versus night (or day versus dawn, day versus dusk, etc as appropriate) catch rates. For days in which no sampling data is available at all, catch rates are interpolated linearly within sampling strata between known days for which data is available. As an example, if catch rates during the day on May 12th were 4 fry per hour, and catch rates during the day on May 14th were 2 fry per hour, then the rate used for daytime on May 13th would be 3 fry per hour.

Three methods have been used to derive an estimate for the trap catch efficiency. One method uses a secchi-depth reading to estimate the trap's catch efficiency during each sampling period. However, application of this method in previous years has proven to provide very poor results and, consequently, it has been abandoned.

Method 2. Summed Daily Production Estimates – Year-Specific Constant Catch Efficiency method (YCCE)

One indirect measure of trap efficiency can be obtained using the percentage of marked hatchery Chinook that are recaptured, along with the proportion of time that was spent sampling. The recapture percentage is a

function of trap catch efficiencies that vary from day-to-day, fish migration timing, sample timing, and overall hours fished. To measure catch efficiency it is necessary to isolate catch efficiency from sample timing and amount of effort. Because we cannot measure the actual numbers of fish moving past the trap site we cannot directly measure catch efficiencies on a day-to-day basis, so the most we can do is to estimate 'average' catch efficiency for the whole season. For this 'average' value to be useful for converting catch per hour values into production per hour values, it is necessary to assume that trap catch efficiencies are constant throughout the diurnal cycle and throughout the sampling season. Since we do not see consistent differences in catch per hour between day versus night sampling times, it is likely that trap catch efficiency is similar for both time periods. However, catch rates do appear to be slightly higher around dawn and dusk which may indicate either higher catch efficiency during these times, or else higher outmigration rates at these times. Any error created by failing to differentiate sampling efficiencies for these time periods is likely to be reduced by the short time periods involved for these sampling periods.

We know that if the trap were not operated at all (effort = zero hours) then no fish would have been recaptured at all. We also know that we caught a certain percentage of the marked hatchery fish after sampling a known proportion of the total time possible (and the effort was spread throughout the season). Assuming that the number of marked fish recaptures is *linearly* related to hours of effort, then the slope of the line joining these two points is the average trap catch efficiency during that sampling season. Clearly, this extrapolation will be most convincing when the actual sample effort is a large proportion of the overall time.

If we assume that trap catch efficiencies during the outmigration period of the marked fish are also representative for the remainder of the outmigration season, and are similar for unmarked fish, then the estimate of average trap catch efficiency for marked hatchery fish can be extrapolated to unmarked hatchery fish, and possibly wild-origin smolts also.

Figure 3 shows the relationship between the recapture rate of marked hatchery smolts, versus the proportion of time sampled during their outmigration period, for the past five years. An analogous value is also shown based on an identical screwtrap operating in the Skagit River mainstem. Based on the larger volume of water in the Skagit you would expect that the Skagit trap would have a lower catch efficiency rate.

Overall, 1999, 2002, 2003, and 2004 show very similar average catch efficiencies (~2.6 - 3.3%) after extrapolating based on sampling effort, whereas recapture rates were below expectations in 2001 (1.73%) and much higher in 2000 (7.3%). Flows in 2001 were quite low, possibly explaining the reduced catch efficiency, but no such explanation is known for the 2000 data when river flows and secchi depth were moderate but catch efficiencies much higher than expected.

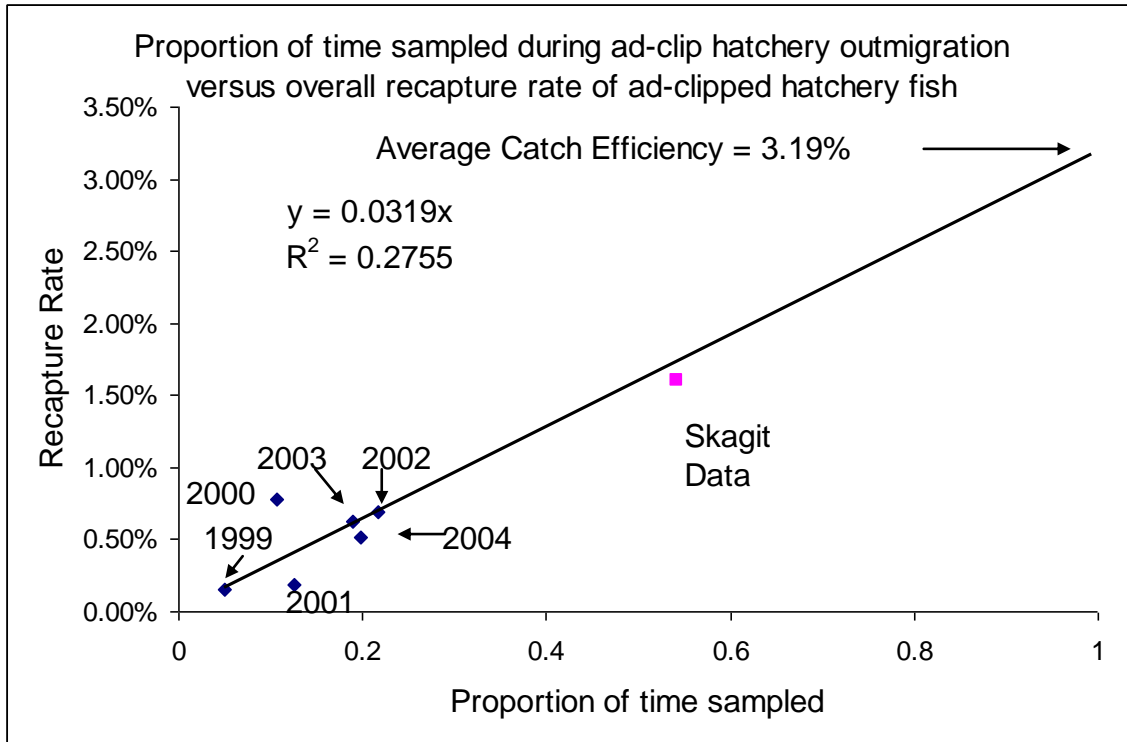


Figure 3. Season wide recapture rates of marked hatchery Chinook smolts versus the proportion of time sampled between May 15 and July 1.

Based on the 2004 season catch efficiency of 2.59%, daily production estimates were derived using the interpolated daily catch-per-hour data shown in Fig. 2. The results of this analysis are shown in Figure 4. The total number of age zero Chinook smolts outmigrating past the trap-site was estimated to be **990,215** smolts. However, it should be remembered that this estimate assumes that no mortality occurs between release and recapture for marked smolts. Mortality rates ought to be low, but if wrong then this assumption will tend to artificially reduce the catch efficiencies estimated in Figure 3. Underestimating the true catch efficiency of the trap would cause production estimates to be biased upward. Assuming the above estimate for total smolt production is correct, and also that no mortality exists in hatchery fish before they reach the trap site, then the total wild production for 2004 would be **132,915** smolts using the YCCE method.

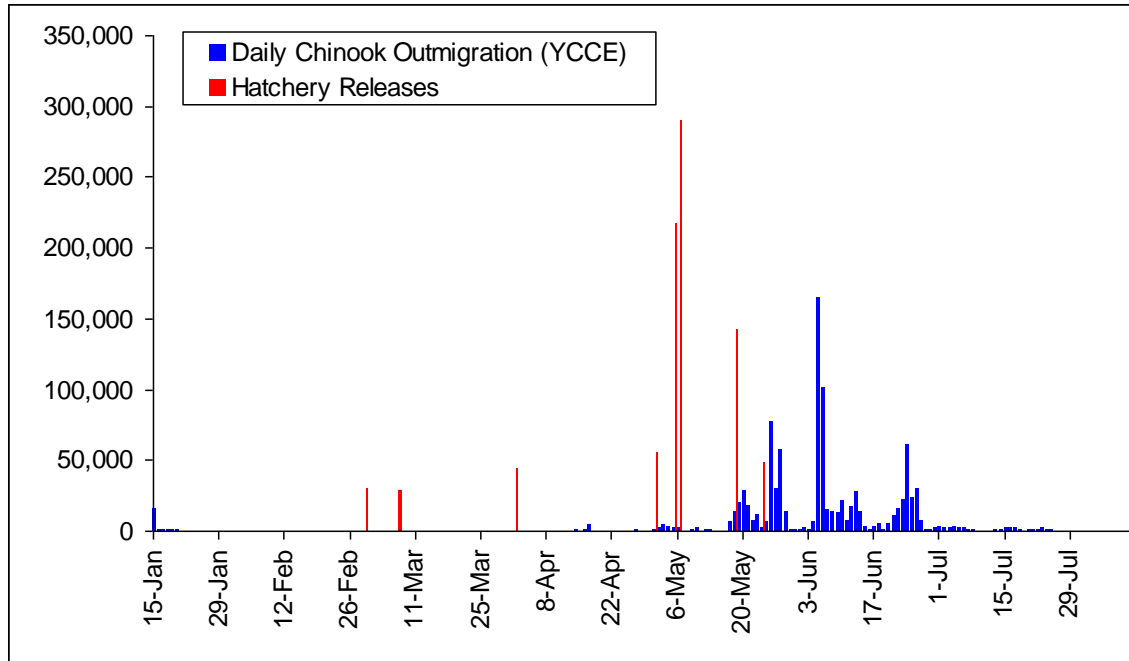


Figure 4. Daily production estimates in 2004 for age-zero Chinook smolts calculated from daily catch per hour and using a constant catch efficiency of 2.59% (YCCE)

Method 4. Summed Daily Production Estimates – Average Constant Catch Efficiency method (ACCE)

This method is identical to the year-specific constant catch efficiency method except that, instead of using different constant catch efficiencies for each outmigration season, the long-term average catch efficiency across all seasons is used. This long-term average catch efficiency is represented as the slope of the trendline shown in Figure 3. Overall, the average catch efficiency for the Lummi screw trap is estimated to be 3.19% based on the past 6-year’s data.

The results of this method for 2004 suggest that the total production of age-zero Chinook smolts was **803,968** smolts. The overall pattern of outmigration is shown in Figure 5.

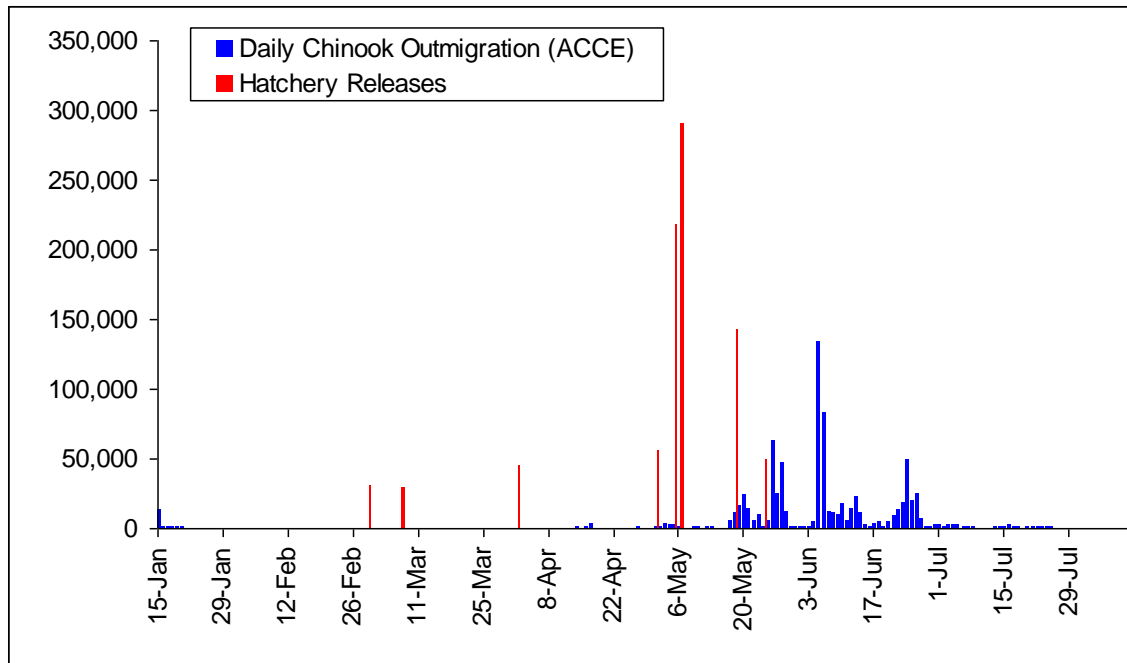


Figure 5. Daily production estimates in 2004 for age-zero Chinook smolts calculated from daily catch per hour and using a constant catch efficiency of 3.19% (ACCE)

We know that at 857,300 hatchery-origin smolts were released into the Nooksack in 2004 but this model predicted a total outmigration of only 803,968 smolts. If this is accurate, then some of the hatchery origin smolts must have died prior to reaching the trap site (or else they remained upstream all year). Because the mortality rate is unknown, it is impossible to determine if there were any wild-origin smolts at all other than those captured prior to the first hatchery release. Approximately **18,215** wild-origin smolts were estimated to have outmigrated prior to the first hatchery release date on Feb 29.

Comparison of the three production estimates

Results from 1999 – 2004 that were obtained using the three methods presented here are shown in Figure 6 and compared to the known hatchery releases in each year. Note that the absolute values in this graphic will differ slightly from those presented in the 2003 report because the ACCE catch efficiency value has changed slightly with the inclusion of the 2004 data in Figure 3.

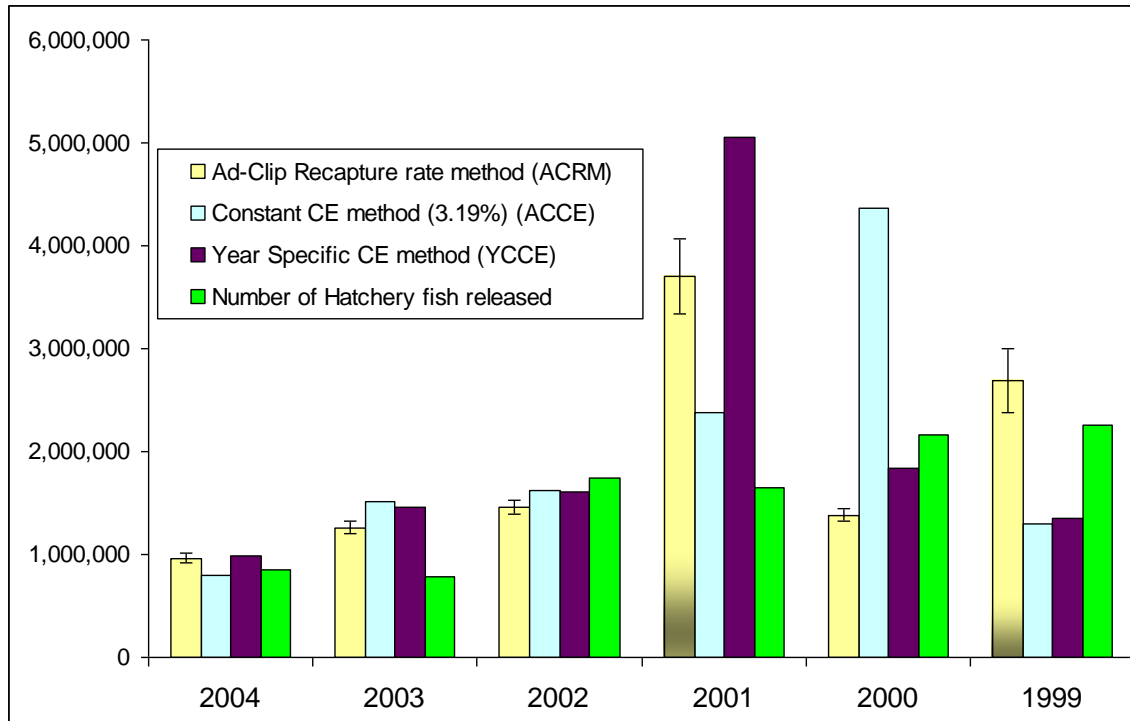


Figure 6. Three alternative production estimates for age zero Chinook smolts outmigrating from the Nooksack River from 1999 – 2003, compared with the number of hatchery-origin smolts released in each year (green). Shading of the two ACRM bars in 2001 and 1999 indicates that many fewer marked hatchery smolts were caught relative to other years, and the ACRM estimate might be more prone to large error because of the increased scaling factors. This may also result from unusually high mortalities of marked hatchery smolts prior to recapture.

Marked Hatchery Chinook Residence Time Modeling

One of the concerns associated with a hatchery program releasing smolts into the upper watershed of a river system is whether the presence of hatchery fish might have adverse impacts on wild-origin Chinook smolts. Such impacts could, hypothetically, come about through predation (i.e., large hatchery smolts eating small wild-origin smolts), competition for food (e.g., aquatic stages of stream insects, drift of aerial insects, etc), competition for space (e.g., prime holding habitat, flood refugia, etc), and possibly transmission of diseases from hatchery-origin smolts to wild smolts. To evaluate the likelihood of predatory and competitive interactions, as well as the potential for disease transmission, it is necessary to understand the behavior of hatchery smolts after their release. Logically, there is less opportunity for competitive/predatory interactions if hatchery smolts head downstream until they reach the estuary immediately upon release. Conversely, if hatchery-origin smolts prefer to spend long periods of time in the upper watershed they will have to eat suitable food and spend time in suitable micro-habitats that afford predator protection, foraging opportunities, and

refuge from flood water velocities. Obviously this strategy increases the potential for interaction between hatchery and wild-origin smolts.

It is not possible to directly observe the behavior of individual hatchery smolts after release because radio/acoustic tagging is not presently possible with Chinook smolts in the size range released. However, a small proportion of the hatchery smolts are marked in one of two ways. Some hatchery smolts have a coded wire tag (CWT) inserted into their snout, some have their adipose fin clipped (this fin does not re-grow), and some have both CWT and the adipose clip. In theory, we know when and where the marked smolts are released, and we can identify marked smolts amongst the smolts caught in the trap. Essentially, we ought to be able to measure the length of time taken for the marked fish to leave their release site and reach the trap (i.e., the residence time). This information should provide an indication of hatchery fish residence times in general (if you assume that marked hatchery fish behave in the same way as unmarked hatchery fish).

Unfortunately, this is not as simple in practice as in theory; and there are several reasons for this difficulty.

Firstly, we are not intercepting all marked fish that are going down the river but instead are catching an unknown (and potentially variable) proportion on a daily basis. This problem can be resolved somewhat by making assumptions about the catch efficiency of the trap from day-to-day (that is, we can assume it is constant).

Secondly, the timing of hatchery smolt release is sometimes complicated by an extended volitional release strategy. This is where the smolts are kept in a holding pond and an opening is made between the pond and the river itself, and the smolts allowed to emerge from the pond at their leisure. At some point, the last smolts are eventually driven from the pond. Sometimes this 'volitional release' period may last for as long as a week. This issue could be remedied for by counting smolts as they leave the pond but, unfortunately, no such counts are made. As a result, it becomes necessary to assumptions regarding the rate of smolt departure from the holding ponds.

A third problem arises when more than one group of marked smolts is released into the river at different times/locations. This is especially problematic when marked smolts from one group are still arriving at the screw trap when another marked group is released somewhere upstream. Once you have two groups of identically marked smolts in the river above the trap, it is impossible to know whether a marked fish arriving at the trap has been in the river for a short time (second release group) or a long time (first release group). Consequently, it becomes necessary to make assumptions about the proportion of marked fish arriving in the trap that belong to each of the two (or more) groups of marked smolts that may be present in the river upstream.

A fourth arises when the summed daily production estimates for marked hatchery smolts do not tally with the number of marked smolts released. In some case, these discrepancies suggest that fewer marked fish are moving downstream past the trap site than were originally released. This problem can be overcome by assuming that a number of marked hatchery fish die (or else decide to outmigrate as yearlings the following year). Skalski (1998) suggested that survival of marked hatchery smolts in the Snake River remained relatively constant throughout the outmigration period. Consequently, a constant daily survival rate may be a reasonable solution, although it is likely that survival would also depend on fluctuations in the environmental conditions experienced by the smolts. However, if the summed daily production estimates exceed the known size of the release group then no model can be developed that would be reasonable for speculating on the residence times of released smolts.

In 2004 two groups of ad-clipped Chinook smolts from Kendall Hatchery were released into the North Fork of the Nooksack River (Table I). The first group (136,000 smolts) was volitionally released starting on May 6. The second group (67,200 smolts) was volitionally released starting on May 18.

The first marked smolts ($n=2$) were caught at the screw trap around dusk on May 10 (see Appendix A). No marked smolts were caught during 5 hours of sampling on May 6th, 14 hours of sampling on May 7th, or 8 hours of sampling on May 8th. No sampling was conducted on May 9th, and no smolts were caught in the afternoon set on May 10th. I am assuming that the two smolts caught at dusk on May 10th represent the first smolts to reach the trap site. The last marked smolts ($n=2$) were caught at the trap site on July 18th. Assuming that these represent the last outmigrating marked smolts, this suggests that the minimum residence time is between 3 and 4 days, and the maximum residence time observed may be as high as 61 - 73 days (depending on which group these last 2 fish originally came from).

To estimate the average residence time for hatchery fish it is necessary to model the two groups individually and make some assumptions regarding their actual release times, daily mortality rate, and what proportion of the fish from mixed groups arriving at the trap belong to each group.

Critical assumptions used in residence time models

1. All smolts left the holding pens on the first day of their volitional release period. This may result in overestimating the actual residence times if smolts entered the river at a later date. Unfortunately, no end dates for volitional release were reported by the hatcheries this year
2. Daily survival/mortality is fixed and constant throughout the season. This is a variable that can be manipulated until model output matches daily production estimates for marked hatchery smolts.

3. The number of fish from one group that is caught in the screw trap catch is assumed to be directly proportional to the percentage of the total marked fish population made up by that group at the start of the day. That is, if 30% of all marked fish upstream from the trap belong to 'Group 1', then 30% of the fish caught in the trap that day are assumed to be from 'Group 1'. If this number exceeds the total number of smolts remaining in that group, then the actual number remaining is used and the remainders of the captured smolts are split proportionally amongst any remaining groups.
4. ACCE daily production estimates for marked smolts are accurate.

In essence, the model works by establishing 6 columns for each group of marked hatchery fish that were released, with a separate column containing the ACCE daily production estimates for each calendar date (rows).

The first column for each group of smolts simply records the number of days since that group was released. For example, The first group of marked smolts that were released were considered to be caught 0 days after release if they were caught on May 6, 1 day after release if they were caught on May 7, and so on.

The second column records the number of fish in that group alive and upstream from the trap site at the beginning of the day. This value corresponds exactly to the number remaining alive in the river at the end of the previous day, except for day 0 when this is the number of smolts released (another column elsewhere in the spreadsheet).

The third column indicates how many of those smolts will die that day. This is simply the number of smolts alive at the start of the day, multiplied by a constant mortality rate.

The fourth column is the estimated number of marked smolts *from that group* that outmigrate past the trap site during that day. This is a function of the total daily production estimate for that day, multiplied by the proportion of all marked fish, that are alive and upstream of the trap, that belong to that group at the start of that day (calculated in column 6).

The fifth column is the number of fish remaining alive and upstream from the trap site at the end of the day (= number alive at start of day, minus the number dying, minus the number outmigrating.)

The last column calculates what proportion of all marked fish in the river above the trap site, at the beginning of each day, that group of fish represents.

The sum of each group's outmigrant column must equal the ACCE daily production estimate for marked smolts. The only variable that can be altered is

the daily mortality rate (a constant). An iterative process varies the mortality rate until the model output exactly matches the ACCE daily production estimate and all remaining fish are accounted for by mortality.

Now we have an approximation of the daily outmigration and mortalities for each group of marked fish. The average residence time is calculated by multiplying the combined mortalities and outmigrants for each day, by the number of days that have passed since release (the first column for each group). These values are summed for each group and then divided by the number of smolts in that group that were originally released.

Overall group survival (to the trap site) can also be estimated by summing the total number of modeled outmigrants for that group and dividing this by the number of smolts that were originally released.

A summary of the table showing the final model for marked hatchery smolts in 2003 is presented in Appendix B. The results for 2003 are shown in Figure 7.

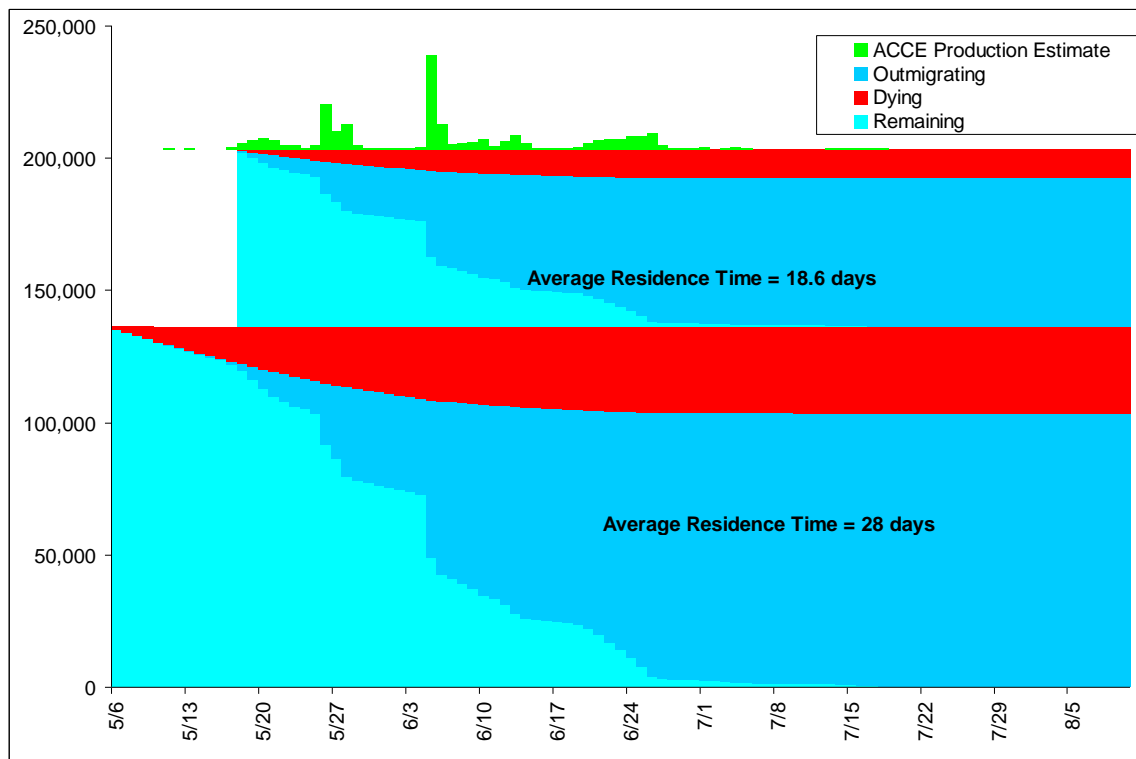


Figure 7. Model output showing cumulative outmigration, mortality, and ACCE daily production estimates for two groups of ad-clipped hatchery-origin Chinook smolts in 2004.

Similar modeling was also conducted using historical data for 2003, 2002, 2001, and 1999. Modeling could not be conducted for 2000 data because ACCE production estimates for marked fish in 2000 was nearly double that of the

number of marked fish that were released. The reason for this discrepancy is not known at this time, but one potential explanation could be that hatchery records may be erroneous for that year. Alternatively, low sampling effort combined with poor survival of marked hatchery fish may have strongly affected the measured recapture rate for ad-clipped fish in 2000. The results of the model for 1999 differ markedly from those of 2001 – 2003 but this may be a result of the poor sampling effort in 1999, which is discussed further in the section comparing the three methods of determining production estimates.

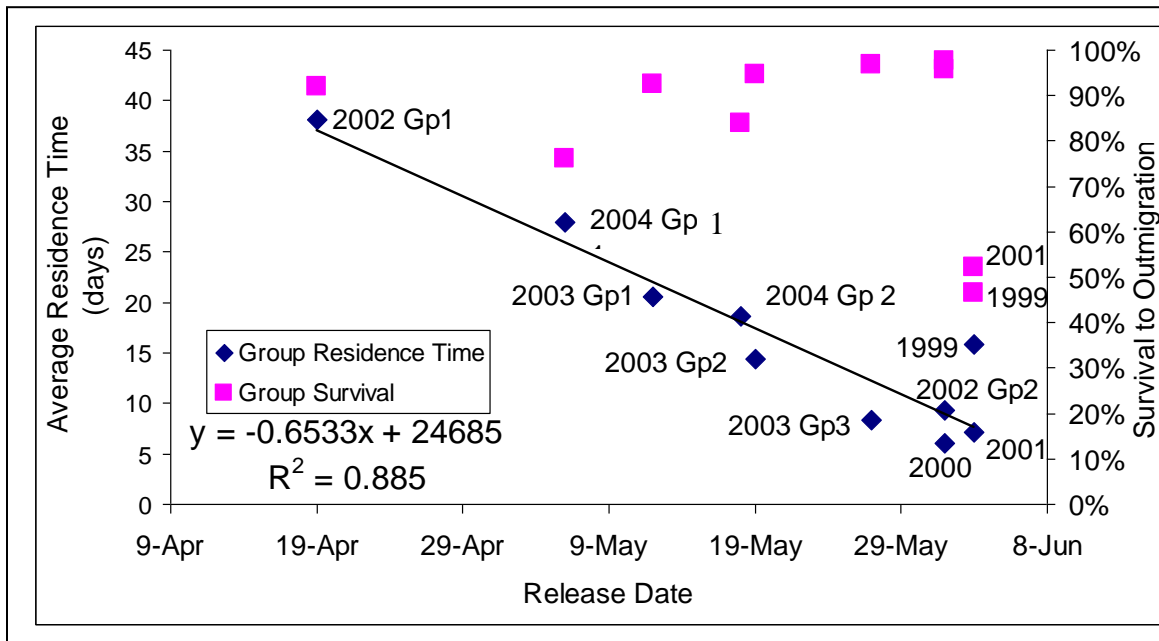


Figure 8. Modeled average residence time and group survival versus group release date for groups of marked hatchery Chinook smolts released in 1999, 2001, 2002, 2003, & 2004.

Figure 8 shows the group residence times and survival rate versus the release date based on historical trap data. Clearly there appears to be a relationship between the timing of release and the modeled length of time that hatchery-origin smolts take to reach the trap site after release. Unfortunately, multiple groups being released into the river at different times confound the data from 2002, 2003, and 2004.

If you were to assume that all fish caught in the trap were from the first group released, regardless of other groups being introduced before the first group had cleared the system, then the average residence time for the first group would be shortened, but the average residence time for subsequent groups would increase commensurately. However, this would be an unlikely scenario because fish from the second or third groups would probably not delay their outmigration solely because of the lingering presence of some fish from the first group.

Modeling hatchery introductions in 2004 using parameters developed in the 2004 residence time model

Ultimately we are interested in estimating what the annual production of Spring Chinook smolts is from the Nooksack River. Unfortunately, we currently have no direct means of counting these, as they are indistinguishable from wild-origin Fall Chinook or unmarked hatchery-origin Chinook caught in screw trap operations. Consequently, we need to devise some means of indirectly separating wild-origin from hatchery-origin smolts, and then further subdividing the wild-origin component into the Spring and Fall stocks. At the present time there is no way to separate wild-origin Spring smolts, unmarked hatchery-origin Spring smolts, and wild-origin Fall smolts from each other, save by comprehensive DNA analysis (to ascertain stock) and Otolith examination (to determine wild or hatchery origin). Unfortunately, this kind of analysis would be prohibitively expensive and would mean killing listed fish.

An indirect means of separating hatchery-origin from wild-origin smolts can be made by modeling the total Chinook smolt population to match two parameters. The first parameter is the YCCE daily production estimates for all Chinook smolts combined (measured from trap data). The second parameter is the estimated daily mortality rate of marked hatchery Chinook smolts that was derived in the residence time modeling section above. If we assume that the last Chinook smolt caught in the trap represents the last day of outmigration, then we assume that the number of smolts remaining alive upstream from the trap site is zero at the end of that last day. We have an estimate of how many fish outmigrated on the last day, and we know what the daily mortality rate is, so we can back-calculate the number of fish that must have been alive upstream of the trap that morning. The number alive at the start of the last day is also the number alive at the end of the penultimate day. In the same way as for the last day, we can then estimate how many must have been alive at the start of the penultimate day by factoring in that day's outmigrants and allowing for mortality once again. Essentially we can back calculate the entire outmigration season, remembering to deduct hatchery groups from the modeled starting population on the dates that they were released.

We know that all outmigrants prior to the first release of hatchery smolts are wild-origin. If we assume that the proportion of hatchery smolts in the trap's catch is identical to the proportion of hatchery fish in the total pool of smolts alive and upstream of trap site, then we can split the hatchery-origin and wild-origin components out of the total daily production estimate based on the relative proportion of each group alive and upstream of the trap at the start of each day. Modeling hatchery fish separately from the main model can be done because we know their relative proportion in the main model's population and we know their daily mortality rate (from the residence time model). Consequently, we can subtract the modeled daily production of hatchery-origin fish from the total

production of all Chinook smolts combined, to finally arrive at a modeled daily production estimate for wild-origin smolt throughout the season.

Once again there are some critical assumptions in arriving at the daily production estimate of wild-origin smolts. These assumptions are essentially the same as those in the residence time model section above except that the YCCE daily production estimates are not exclusive to marked hatchery fish, and there is the further assumption that unmarked hatchery fish exhibit the same mortality rate as marked hatchery fish. One final assumption also exists. This is that the modeled mortality rate of marked hatchery smolts is also true for wild-origin smolts.

Appendix C details the results of the model for each day of the outmigration season. The breakdown of daily production estimates generated from the model are presented in Figure 9. Overall, this model predicts that 633,662 hatchery-origin smolts outmigrated past the trap site and 168,457 wild-origin smolts outmigrated past the trap site.

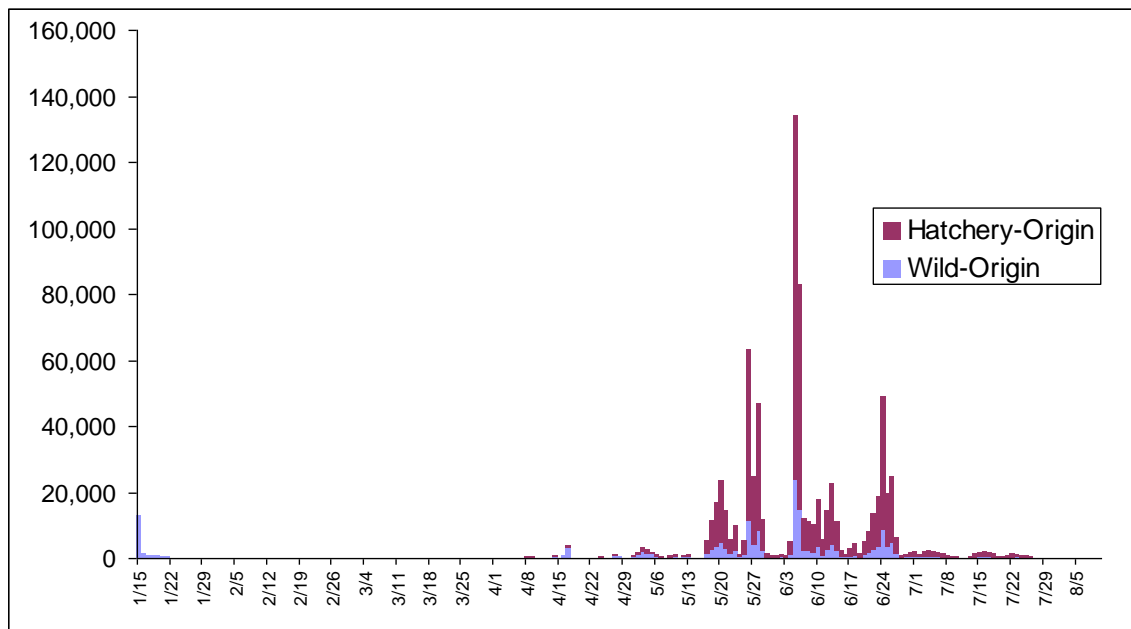


Figure 9. Hatchery-origin and wild-origin daily production estimates derived from daily modeling using daily mortality rates from the 2004 residence time model.

Chinook Discussion

Comparison of Production Estimate Methods over Time

It is difficult to assess the relative merits of each of the three estimation methods without knowing the true number of smolts outmigrating in any given year, or knowing the width of confidence intervals around each estimate.

The only confidence interval available for any of the estimates is the ACRM (Peterson) method. In 2003, 2002, and 2000 the confidence intervals were remarkably tight (<5%) around the estimate. The estimates for 1999 and 2001 had relatively worse intervals, but they remained surprisingly narrow (11% and 10% respectively). However, it should be remembered that this method makes some critical assumptions that could easily be violated in this application. For example, marked fish could not mix with fish that were caught prior to their release. Also, marked fish may not behave identically to unmarked hatchery fish, and hatchery fish overall may not behave like wild-origin fish, leading to differences in trap catch efficiency. That is, not all fish may have had an equal chance of being sampled. Consequently, I would treat the ACRM estimate and the associated confidence intervals with due caution.

The only reference value that we know with reasonable certainty is the number of hatchery fish that were released into the river. An unknown (but probably large) proportion of the hatchery-origin fish survive to reach the trap site, and an unknown number of wild-origin fish presumably also outmigrate past the trap site. Consequently, we would expect that a good production estimation method would not result in values markedly below the known release of hatchery smolts. We also believe that, historically, the number of wild-origin smolts wouldn't be all that high in relation to the hatchery-production since we believe that wild-origin adults have typically been a small proportion of the total adult return. Figure 6 shows the production estimates for the last 5 years that were derived by using each of the three methods detailed above, as well as the number of hatchery-origin smolts released each year.

Sampling effort in 1999 was much lower than other years, and featured very few nighttime samples. Inadequate nighttime sampling might considerably under-estimate the total number of fish if smolts are more likely to outmigrate, or be caught by the trap, at night. Consequently, it is likely that the most useful production estimate for the 1999 season will be the Ad-Clip Recapture Ratio method. Supporting this contention, both the YCCE and ACCE methods estimate a number that is approximately one half of the known hatchery release in 1999. Unless the hatchery releases were subject to drastic mortality (disease perhaps?), these numbers are unlikely to be realistic.

Since 1999, the proportion of sampling effort conducted at night has increased considerably, particularly in 2002, 2003, and 2004. The ACRM, YCCE, and ACCE methods all agree fairly closely for 2002, 2003, and 2004. By contrast,

the three methods provide far less consistency during the 2000 and 2001 seasons. Both the ACRM and YCCE methods produced estimates that are reasonably similar in magnitude, but the ACCE method differs strongly in both years. Why does the ACCE method diverge from the other two methods during 2000 and 2001?

River flows during the outmigration in 2001 were considerably lower than usual which could explain why the catch efficiency of the trap differed from 'normal' conditions during that season. Since there is an environmental explanation for unusual trap catch efficiency in 2001, it is likely that the ACRM and YCCE estimates are probably more reliable than the estimate based on long-term trap catch efficiencies (because long term averages are most useful in 'typical' circumstances). However, river flows in 2000 were not unusually low, and secchi-depth readings didn't deviate from the normal range either. There doesn't appear to be an environmental explanation for the extremely high recapture rate of marked hatchery-origin smolts (nearly double what was expected given the amount of sampling effort). One possible explanation could be erroneous records of how many marked hatchery-origin fish were released in 2000. Given that there is no readily apparent environmental explanation, it may be that the long-term catch efficiency estimate (ACCE) may be more realistic for the 2000 season. Also, although the sampling effort in 2000 was higher than 1999, it was still short of the effort expended in the following seasons. Consequently, large gaps in the sampling record may have resulted in pulses of fish being missed altogether as they migrated downstream.

In 1999 (ACRM only), 2001, 2003, and 2004 (barely), both the ACRM and YCCE methods estimated that the total production of Chinook fry from the river exceeded the number of hatchery-origin fry that were released. However, in 2000 and 2002 both of these methods estimated that the total production of fry from the river was *lower* than the number of hatchery-origin fry that were released. If true, then these production estimates for 2000 and 2002 are surprising, since we had assumed that hatchery-origin fry would have a fairly short stay in the river and experience only minimal mortality. Also, there ought to be at least *some* wild-origin fry outmigrating as well. This raises some serious questions about these assumptions, or about the accuracy of the production estimates.

Obviously, the first question is whether these estimates are even in the right ballpark. As has been discussed, the ACCE method may prove to be a better method for estimating the production in 2000. Using this method, the resulting production estimate does exceed the known release groups in 2000. However, there is still a question mark over the 2002 estimate since the ACCE estimate agrees very closely with both of the other methods. Leaving aside the question as to the accuracy of the production estimates, is it possible that some of the assumptions made regarding residence times, mortality, or wild production are erroneous? Unfortunately, most of these assumptions are difficult to test directly.

One hypothesis could be that some of the released hatchery-origin smolts died prior to reaching the trap. Muir *et al.* (1999) showed that that daily survival rates for marked hatchery-origin Chinook fry (c. 80mm FL) released into the Snake River was c. 98.2% per day. Although conditions in the Nooksack are probably less hostile than the highly regulated (i.e., dammed) Snake River, it is still reasonable to assume that some mortality occurs between release sites and the Lummi screw trap. Mortality of Chinook released into the Nooksack River might be due to handling stress, disease (perhaps exacerbated by stress), starvation, predation, or stranding in off-channel habitat when river waters drop suddenly after high-flow conditions.

Another possible reason for the production estimate being lower than the number of hatchery fish released in a year could be that some of the hatchery-origin fish had not moved downstream past the trap site by the end of sampling. In other words, some hatchery fish might over-winter in the river and outmigrate as yearlings the following year. Arguing against this hypothesis is the fact that no ad-clipped yearling Chinook smolts have ever been caught in the screw trap (except when clipped yearlings were also released that same year). However, the number of yearling Chinook caught in the trap is typically very small (10-30 fish per year) so the chances of catching a marked yearling would be very low even if they were present in the river. Interestingly, two adipose-clipped yearling Chinook were caught in beach seines in the Nooksack Estuary in 2003. If these fish were released into the Nooksack as zeroes then we may have an indication that some hatchery fish may over-winter either in the river or in the estuary. However, the possibility also exists that these yearling Chinook could have been released elsewhere and were simply migrating along the shore from their release site, and happened to be caught as they passed the Nooksack estuary. No further information is available to evaluate the likelihood or proportion of hatchery fish that could be accounted for in this way.

Based on the preceding, and with the exception of the 1999 and possibly 2000 estimates, it seems that the most plausible production estimators currently available are the YCCE and ACRM methods. Of these, the YCCE method provides the most information since it can be used to look at daily outmigration rates. However, the ACCE estimate does provide a 'ballpark' comparison that can be useful for corroboration. If the ACCE and YCCE results disagree by a large margin then there ought to be a close examination of the data to explain how the difference arose and which method is likely to be at fault. A good example is 2001 where unusually low flows probably invalidated using the ACCE method. Similarly, the ACRM method provides a good comparison for the YCCE method. Where these two methods differ strongly there ought to be a close examination of the data to determine why. In 1999, for example, inadequacies in the sampling program probably lead to underestimation of the number of outmigrating smolts using daily catch-per-hour values obtained almost solely during daylight sets. This probably means that the ACRM method performed better than either the YCCE or ACCE methods in 1999.

The three production estimate methods used here have agreed very closely for the last three years. This is probably a good indication that we have a pretty good indication of the true magnitude of production of Chinook fry from the Nooksack from 2002, 2003, and 2004. This validates the change in sampling protocols that has increased the overall effort, begun to stratify sampling by dawn, day, dusk, and night, and to minimize the length of the gaps in the sampling effort to avoid missing pulses of fish moving downstream.

Hatchery Chinook Residence Times

In 2004 the shortest residence time was 3 - 4 days, and the longest residence time observed may have been as long as 73 days. Modeling results suggest that the average residence time for the first group was around 28 days, and the last group averaged somewhere around 19 days. These results are consistent with trends in the 2003, 2002 and 2001 data where early-release groups tend to stay in the upper watershed for a longer time than those released later in the season. This behavioral difference has also been noted in the Snake River, albeit for yearling Chinook smolts (Smith *et al.*, 2002), so the modeling results for age-zero Chinook are within the realm of possibility. If the model findings are true, then there are obviously implications for the scheduling of hatchery releases. Delaying hatchery releases until the end of May/start of June should minimize the duration for whatever interactions exist between hatchery-origin and wild-origin smolts.

Residence time modeling has provided a consistent pattern of residence times versus release date over several years of data. Better release rate information for extended volitional releases would probably result in only minor adjustments to the model results. Significant changes to the model output will probably only arise if day-by-day trap catch efficiency information becomes available so that changes in environmental conditions are *reliably* taken into account (e.g., secchi depth, flow patterns, etc) each day.

Modeled daily survival rates of age-zero Chinook smolts in 2001, 2002, 2003, and 2004 were 99.21%, 99.66%, 99.43% and 99.17% respectively. These survival rates are all better than those for outmigrating age-zero Chinook smolts in the Snake River (98.16% surviving per day; Muir *et al.*, 1999). This is likely because age-zero Chinook outmigrating from the Nooksack River do not have to contend with predator-filled impoundments or additional mortality associated with hydroelectric schemes present on the Snake River (e.g., turbine damage, oxygen-super-saturation, spillway turbulence, etc).

Modeling Wild-origin Chinook production

Two approaches were used to try to split the overall YCCE production estimate into wild-origin and hatchery-origin components.

The first method attempts to reconstruct the daily population dynamics occurring upstream from the trap site, based on daily YCCE production estimates, hatchery release timing, and the constant daily mortality rate derived from the residence time modeling. Then it makes assumptions regarding the proportion of the two components (wild vs. hatchery) in the screw trap catch, based on the relative proportions of the two population components that remain upstream. Based on all of the above, it then constructs a model of the hatchery outmigration. The difference between the hatchery-only model and the total Chinook model is assumed to represent the daily wild-origin outmigration.

The second method uses the relationship shown in Figure 8 to predict the survival of groups of released smolts, based on residence time modeling for 4 years of data. This process results in a point estimate of how many hatchery smolts outmigrate each year, and the difference between this value and the total YCCE production estimate is assumed to be the number of wild-origin smolts outmigrating. This approach provides less information than the other method, but also requires less detailed information and, consequently, has less risk of going astray.

The two methods respectively provide estimates of **168,457** and 326,906 wild-origin smolts outmigrating in 2004. Given that we have no data on survival of marked hatchery fry in February or March, it is unlikely that the relationship shown in Figure 8 can be reliably extrapolated. Of these two values, I believe that the lower value is more likely to be correct.

The low level of wild production in 2004 is consistent with predictions of low egg survival in the fall of 2003. These predictions were based on the timing and magnitude of three large-scale flood events in the Nooksack during October and November of 2003 when most of the eggs would have been at their most vulnerable. By contrast, no large scale flood events have occurred so far this year (as of 11/15) and egg survival is expected to be good. This suggests that next year's wild Chinook production should be relatively high provided that sufficient spawners returned to the Nooksack in 2004. However, if a serious flood event occurs within the next two to three weeks then survival may still be diminished.

Coho

Coho Production Estimate Methods

There are four potential methods for quantifying Coho production based on smolt trap data.

Adipose-fin Clipped Recapture Method (ACRM)

The first method is to use the percentage of marked (adipose fin-clipped) hatchery smolts that were captured in the trap after being released upstream, to convert the number of all smolts that were caught in the trap to an estimated total production assuming that the recapture rate is the same for marked and unmarked smolts. The calculations and assumptions underlying this method have been previously described in the Chinook methodology section. Using this method allows you to calculate a total production estimate but does not provide any information on the timing of migration during the season.

Time-series based production estimate methods...

The remaining three methods attempt to create a time series of catch-per-hour measurements for the entire outmigration period, and then convert this time-series into production (all fish passing the trap site) per hour using a trap-specific catch efficiency estimate that is derived in different ways. Summing the hourly production estimates over the entire outmigration period provides an estimate of total production. All of the methods that use this time series as a basis explicitly make predictions as to the magnitude and timing of outmigration past the trap site.

The time-series of catch per hour data for Coho is created using trap catch rates stratified by day versus night sampling periods. Intervals between sampling periods are assumed to be related primarily to catch rates during other portions of the same 24-hour period. That is, if night time sampling data is available for a particular 24-hour period, then the day time value is assumed to be a function of the night time sample. This relationship is derived from a regression of a scatter plot of day versus night catch rates. For days in which no sampling data is available at all, catch rates are interpolated linearly within sampling strata between known days for which data is available. As an example, if catch rates during the day on May 12th were 4 smolts per hour, and catch rates during the day on May 14th were 2 smolts per hour, then the rate used for daytime on May 13th would be 3 smolts per hour.

Secchi Depth-Catch Efficiency Relationship Method (SDCE)

Trap catch efficiencies can be derived using any number of methods. Historically, it was thought that trap catch efficiencies were a function of smolt size and visibility through the water (i.e., unlit secchi depth readings). To

determine the relationship between secchi depth and catch efficiency for yearling smolts, marked hatchery smolts have been released about a mile above the trap site and the number of smolts that were recaptured after 24 hours was measured. However, catch efficiencies measured using this methodology for highly stressed smolts that were recaptured in the first 24 hours after release are unlikely to closely resemble those of wild fish, or even hatchery fish that have become acclimated to riverine conditions over time. Furthermore, as more trials were conducted it became apparent that no reliable relationship could be observed for any species. Finally, day time versus night time catch efficiencies are likely to exist for Coho due to the diurnal migratory behavior they exhibit. Consequently, the catch efficiencies measured in the small scale trials are also likely to be a function of both trap catch efficiency and diurnal timing of movement past the trap site. Because trap catch efficiencies based on the trials are extremely low (<0.5%), and likely to be unrealistic for fish accustomed to riverine conditions, the very large scaling factors will potentially magnify error up to 200 times! Unless you can really hang-your-hat on the secchi depth-catch efficiency relationship this is a recipe for disaster. Consequently, this approach to determining trap catch efficiencies has been abandoned for Coho.

Year-Specific Constant Catch Efficiency Method (YCCE)

Marked fish that are caught in the trap either have their adipose-fin clipped, or they have a coded wire tag implanted, or both, and are released from hatcheries in the upper watershed. The number of these released, marked fish are known and reported by the hatchery. Consequently, it is possible to determine what percentages of the released fish are recaptured at the trap over the period of the outmigration season. However, because the fish do not all go past the trap en-masse this value is unlikely to represent the true catch efficiency of the trap. Moreover, the trap does not operate 24-7 during the entire outmigration period and, consequently, many individuals that would have been caught if the trap were operating are never captured at all. Obviously, the actual recapture rate results from a combination of instantaneous trap catch efficiencies and the timing and duration of the trap sampling activities during the outmigration period. However, we do know exactly when the trap was operating and it is therefore possible to estimate the *average* instantaneous catch efficiency of the trap during the outmigration season.

- We know that if we did no sampling at all while the fish were outmigrating then we would have caught no fish.
- We know that we sampled a certain percentage of the possible time during the period when the marked smolts were outmigrating past the trap site (this period defined as beginning on the day that the first marked smolt is caught and ending on the day that the last marked smolt is caught).
- We also know what percentage of the marked fish was recaptured during the outmigration period.

- Generally we assume that the timing of sampling within the outmigration period is not important but would be better to sample evenly throughout the outmigration period for this number to be realistic.

By assuming that the number of fish captured is a linear function of how much time is spent sampling during the outmigration period, we can plot a line on a chart showing recapture rate versus the proportion of the outmigration period that was sampled. One end of the line would be at the origin (0% recaptured, 0 time sampled) and the other end of the line would be the actual recapture rate at the known proportion of time sampled. The slope of the line represents the average instantaneous catch efficiency of the trap for that year's outmigration period.

This value is calculated separately for each year's results, and then used to transform catch per hour data into production-per-day data separately for each year.

Average Constant Catch Efficiency Method (ACCE)

One of the problems from the YCCE method is that the timing of Coho outmigration is typically rapid for the majority of the hatchery production (2 - 6 days) with a few stragglers outmigrating in low numbers for the remainder of the outmigration period. If environmental conditions during that short period of high-intensity outmigration are unusual, or if the trap operating hours during that time period are greatly different than for the remainder of the outmigration period, then it is possible that the catch efficiency determined by the YCCE method could be unrealistic, and thus greatly distort the production estimate for that year.

One way to avoid year-specific problems with the timing and magnitude of sampling effort within the outmigration period would be to standardize effort at the highest level for the entire outmigration period. Unfortunately, that is logistically beyond our means. One alternative approach would be to step back from year-specific predictions of catch efficiency and use an average catch efficiency calculated using data from several year's YCCE method catch efficiencies. This can be done by plotting several years observed recapture percentage versus the proportion of the outmigration period sampled. Since we also know that no effort equals no fish, we regress the data points using a line that passes through the origin. This time, the slope of the line is the estimated average constant catch efficiency (ACCE) of the trap over a period of years.

This single catch efficiency value can then be used to transform catch per hour data for all years into production per hour data, and therefore total production estimates also. Obviously, with each new year's data, the average value will change and the production estimates for each year will then need to be recalculated.

The risk to this approach is that if actual trap catch efficiencies are non-average during the peak outmigration period then using an average catch

efficiency calculated across several years could strongly bias the resulting production estimates. The only way to remove this risk, and to simultaneously avoid the risk of differential sampling effort within the outmigration period, would be to use the YCCE method, but maintain consistent relative effort throughout the entire outmigration period. Of necessity, the amount of effort should be as high as possible.

Coho Production Estimate Results

Adipose-fin Clipped Recapture Method (ACRM)

Table III Results obtained using the ACRM method for smolt trap data from 1999 to 2004.

Year	2004	2003	2002	2001	2000	1999
Total Production Estimate (N_P)	2,693,075	1,988,042	2,077,633	2,162,813	2,260,919	4,640,808
Known Hatchery Releases (H)	1,241,005	1,403,100	1,304,831	1,230,747	1,429,200	2,669,737
Wild Production Estimate (N_P-H)	1,452,070	584,942	772,802	932,066	831,719	1,971,071
Ad-Clips Released (N_1)	1,193,205	1,353,300	1,225,031	1,170,747	1,365,635	320,465
Total Coho Caught (N_2)	2,898	4,056	5,997	3,946	2,937	782
Ad Clips Recaptured (M_2)	1,284	2,761	3,536	2,136	1,774	54
Observed Recapture Rate (M_2/N_1)	0.11%	0.20%	0.29%	0.18%	0.13%	0.02%
Variance (N_P)	3,133,772,188	455,562,613	499,032,987	1,001,065,168	1,137,357,243	345,516,755,075
95% Confidence Interval Width	109,721	41,834	43,785	62,014	66,100	1,152,101

Table III shows the parameters and results obtained using the ACRM/Peterson's Mark-Recapture method for smolt trap data in 2004 and earlier seasons. The production estimates are also presented graphically in Figure 10.

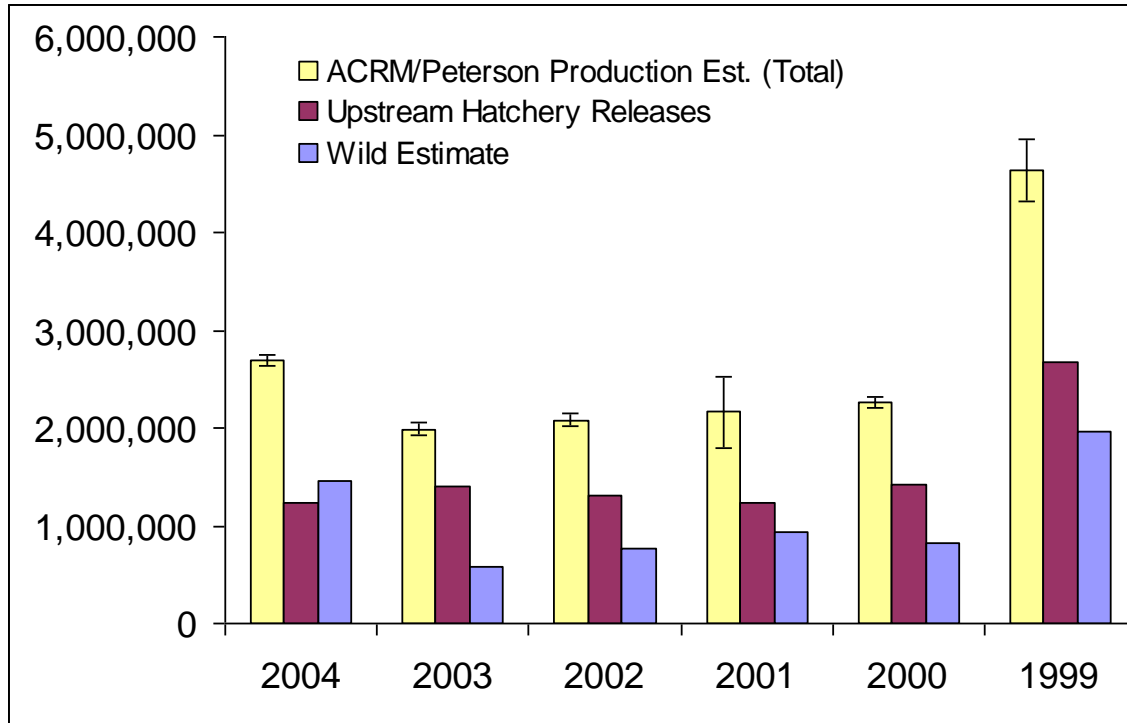


Figure 10. ACRM / Peterson Mark-Recapture Production Estimates for Coho Yearling smolts outmigrating from the Nooksack River (+/- 95% CL).

Based on the data in Table III it appears that c.2.7 millions coho smolts outmigrated in 2004. We know that 1.2 million smolts were released from hatcheries above the trap-site, and this suggests that the difference is comprised of wild-origin smolts (1.45 million). However, it is important to remember that one of the primary assumptions in this estimate is that the population is demographically closed: that is, no mortality occurs between release and recapture of the marked fish. Unfortunately we have no means to measure post-release mortality of marked hatchery fish in the river. In other river systems daily mortality rates of hatchery-released smolts are very low in unobstructed stretches of river. If this is true for the Nooksack River also, then it is likely that overall mortality of the fish is also low...especially since we are confident that their residence time is only a few days. However, it is likely that the measured recapture rate is probably biased slightly lower than the true recapture rate. This will have the effect of artificially biasing the final production estimate slightly too high which will artificially inflate the wild production estimate by an unknown amount. On the other hand, when we subtract the total hatchery release from the (presumably slightly too high) ACRM production estimate we do not factor in this mortality of hatchery-released smolts either. This would have the effect of artificially reducing the wild-production estimate but an amount directly related to the actual mortality of hatchery-released smolts. So, on one hand the faulty assumption of nil mortality would increase the wild-production estimate, and simultaneously it would decrease it by a different amount. To quantify which 'bias' would dominate requires a good understanding of daily mortality rates for hatchery-origin smolts as well as a thorough knowledge of residence times.

Lacking specific knowledge of true mortality rates, it is instead possible to model different scenarios to determine how sensitive the estimate is to varying levels of mortality. Accordingly, I have constructed a theoretical plot (Figure 11) showing the overall effect on the ACRM estimate when mortality ranges from 0% (no mortality) to 25% (25% of all hatchery-released smolts die before reaching the trap site).

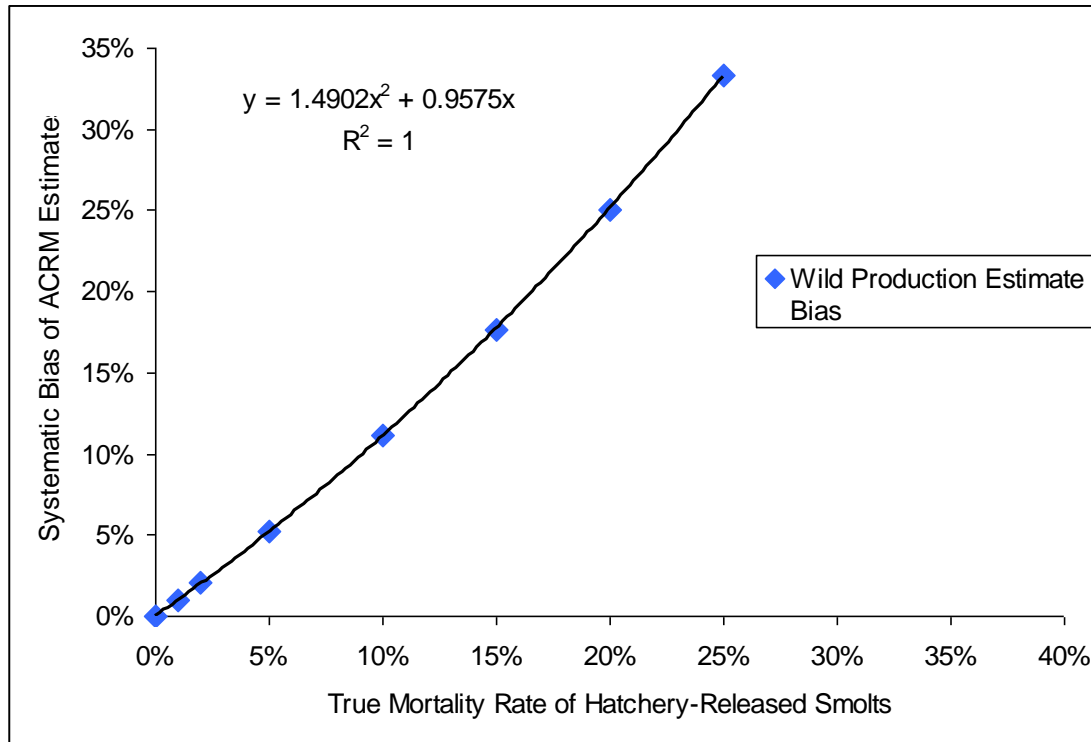


Figure 11. Plot of modeled ACRM bias magnitude compared to theoretical group mortality rates for hatchery-origin smolts prior to reaching the trap site.

Based on the modeling of hatchery-origin smolt group mortality rates, it appears that the ACRM estimate tends to over-estimate the true outmigration by a percentage that can be described by the equation $y = 1.49M^2 + 0.96M$; where y is the percentage bias, and M is the group mortality (%) of hatchery-origin smolts. This relationship also describes the bias of ACRM estimates for total Coho, hatchery Coho, and Chinook fry estimates as well. Consequently, if 5% of all hatchery smolts that are released were to die before reaching the trap (or else become resident upstream until after sampling ceases), then the overall ACRM production estimates for hatchery and wild-origin smolts would both be

$$\begin{aligned}
 \text{Bias} &= 1.49 * 0.05^2 + 0.96 * 0.05 \\
 &= 0.052 \text{ (3dp)} \\
 &= 5.2\%
 \end{aligned}$$

Residence Time Modeling for Coho

Using the ACCE daily production estimates (Figure 12), the average residence time of the first group of marked Coho was 11 days, and for the second groups the average residence time was 4 days (Figure 13).

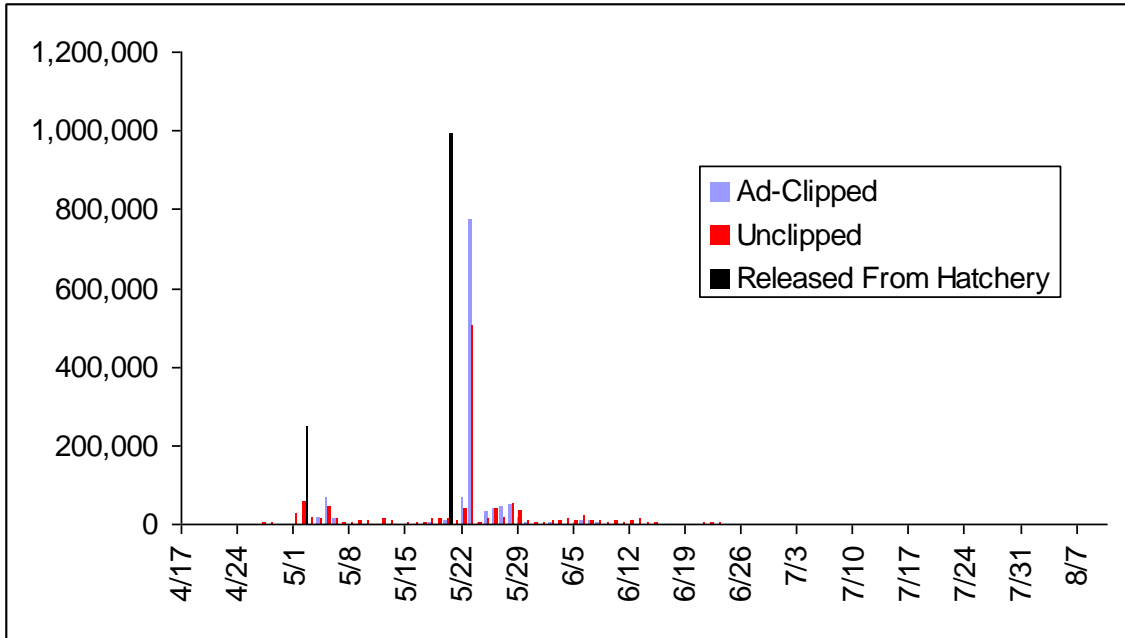


Figure 12. ACCE daily production estimates for Coho smolts in 2004 versus hatchery releases.

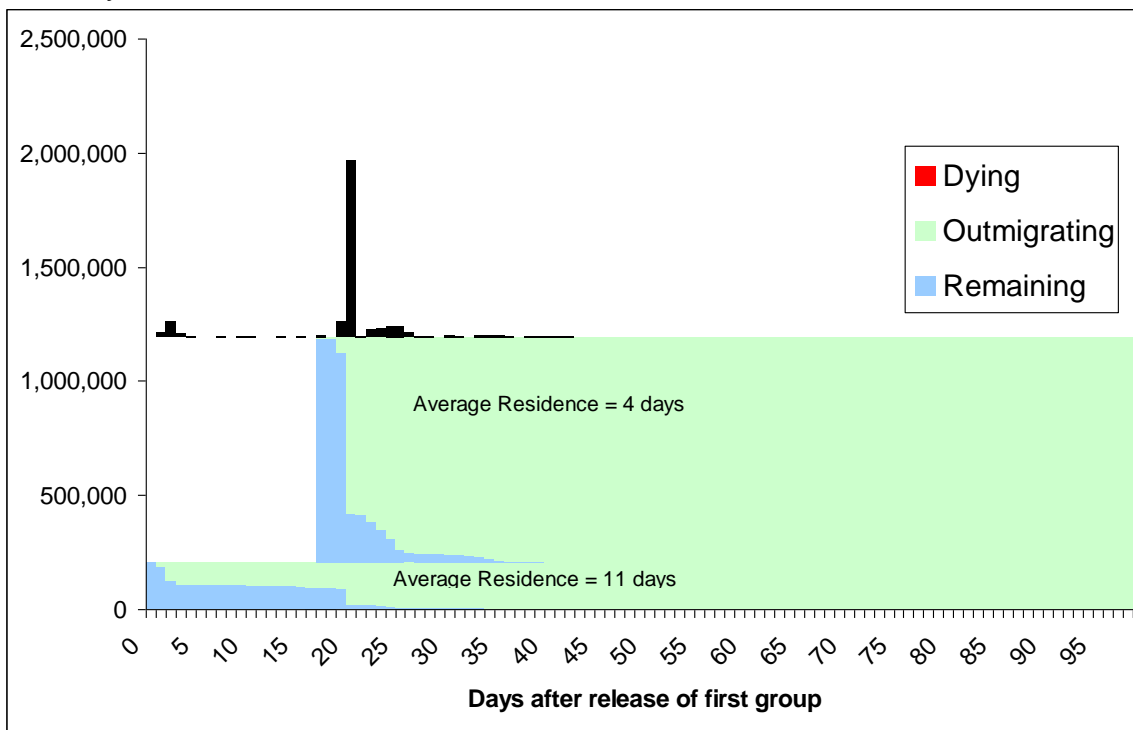


Figure 13. Average residence time modeling output based on 2004 ACCE daily production estimates.

However, since the summed daily production estimates exceed the number of hatchery-origin smolts that are known to have been released, it is likely that the true residence times differ from these estimates: particularly for the first group. Data from previous years indicates that Coho smolts typically have an average residence time of just 2 to 3 days.

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