# Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington

**Elisabeth J Duffy and David A Beauchamp**

**Abstract:** We examined the effect of early marine entry timing and body size on the marine (smolt-to-adult) survival of Puget Sound Chinook salmon (*Oncorhynchus tshawytscha*). We used data from coded wire tag release groups of hatchery Chinook salmon to test whether hatchery release date, release size, and size in offshore waters in July and September influenced marine survival. Marine survival was most strongly related to the average body size in July, with larger sizes associated with higher survivals. This relationship was consistent over multiple years (1997–2002), suggesting that mortality after July is strongly size-dependent. Release size and date only slightly improved this relationship, whereas size in September showed little relationship to marine survival. Specifically, fish that experienced the highest marine survivals were released before 25 May and were larger than 17 g (or 120 mm fork length) by July. Our findings highlight the importance of local conditions in Puget Sound (Washington, USA) during the spring and summer, and suggest that declines in marine survival since the 1980s may have been caused by reductions in the quality of feeding and growing conditions during early marine life.

**Résumé :** Nous examinons les effets d'une entrée en mer hâtive et de la taille corporelle sur la survie en mer (saumoneau à adulte) chez les saumons chinook (*Oncorhynchus tshawytscha*) de Puget Sound. Nous avons utilisé des données provenant de groupes de saumons chinook libérés de pisciculture et marqués de fils de fer codés afin de tester si la date de libération de la pisciculture, la taille à la libération et la taille dans les eaux du large en juillet et en septembre influencent la survie en mer. La survie en mer est reliée le plus fortement à la taille corporelle moyenne en juillet et les tailles plus fortes sont associées à une survie plus grande. Cette relation s'est maintenue au cours de plusieurs années (1997–2002), ce qui laisse croire que la mortalité après le mois de juillet est fortement dépendante de la taille. L'addition de la taille à la libération et de la date de la libération n'améliore que peu la relation, alors que la taille en septembre est peu reliée à la survie en mer. Plus précisément, les poissons qui connaissent la survie en mer la meilleure sont ceux qui sont libérés avant le 25 mai et qui ont atteint une taille supérieure à 17 g (ou 120 mm de longueur à la fourche) au mois de juillet. Nos résultats soulignent l'importance des conditions locales dans Puget Sound durant le printemps et l'été et laissent croire que les déclins de la survie en mer depuis les années 1980 peuvent être dus à une réduction dans la qualité des conditions d'alimentation et de croissance durant le début de la vie en mer.

[Traduit par la Rédaction]

## Introduction

Marine survival of Pacific salmon (*Oncorhynchus* spp.) is believed to be strongly dependent on the "critical" (Hjort 1914) early marine period when both larger size (Ward et al. 1989; Henderson and Cass 1991; Mortensen et al. 2000) and faster growth have been associated with elevated overall marine survival for several species (Tovey 1999; Beamish et al. 2004; Cross et al. 2008). Timing of marine entry can also have a strong effect on marine survival (Blackbourn 1976; Bilton et al. 1982). In their "critical size and period" hypothesis, Beamish and Mahnken (2001) suggested that the regulation of salmon abundance through ocean mortality occurs in two stages, both of which are highly size-dependent. In the first stage, which occurs soon after juvenile salmon enter the estuarine or nearshore marine environment, mortality is hypothesized to be mainly predation-based. Size at this stage is critical because it partially determines the amount of predation risk (Parker 1971; Duffy and Beauchamp 2008). Size-spectrum theory states that larger fast-growing individuals should be vulnerable to the many gape-limited predators for shorter periods than their smaller and slower-growing

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conspecifics (Sogard 1997). The second stage of significant mortality is hypothesized to come in the late fall and winter of their first marine year and is a function of the condition of the juvenile. It is the growth preceding this stage, mainly during the summer (a "critical period"), which is vital in ensuring the juvenile reaches a size and condition that will increase its chances of surviving the first marine winter.

It has been particularly difficult to quantify stage-specific marine growth and size-selective mortality rates for individual salmon stocks because of the challenges associated with recapturing and distinguishing between highly mobile populations during their wide-ranging marine life. Therefore, calcified structures like scales and otoliths are useful tools because they record information on the size and growth history of salmon throughout their life (Fisher and Pearcy 1990; Fukuwaka and Kaeriyama 1997; Courtney et al. 2000). Individual salmon cohorts can also be identified relatively simply through coded wire tags (CWTs), which are typically used to identify (a variable proportion of) hatchery releases. By comparing stage-specific size and growth of juveniles and adults from known cohorts, it should be possible to identify if and when size- (and growth-) selective mortality events occur during marine life. Using this approach, researchers have found that early marine size and growth rates are highly correlated to survival rates for chum (*O. keta*, Healey 1982), Chinook (*O. tshawytscha*, Reimers 1973; Tovey 1999), coho (*O. kisutch*, Beamish et al. 2004), and pink salmon (*O. gorbuscha*, Moss et al. 2005; Cross et al. 2008).

In Puget Sound, most Chinook salmon are "ocean-type," migrating to saltwater immediately after emergence or following up to several months of freshwater rearing. Most of these juvenile Chinook salmon enter Puget Sound and occupy nearshore waters during the spring and early summer (Brennan et al. 2004; Duffy et al. 2005; Toft et al. 2007). By midsummer, large numbers of Chinook salmon are caught offshore by midwater trawl surveys, and catches remain high at least through early fall (Beamish et al. 1998). Puget Sound Chinook salmon were listed as threatened under the Endangered Species Act (ESA) in 1999 (NMFS 1999), and at least half of the approximately 29 stocks of Chinook salmon in the Puget Sound basin have been influenced or supported by hatcheries (NRC 1996). Hatchery influence varies regionally, ranging from approximately 40% of the juvenile Chinook salmon population in the northern region to up to 98% of juvenile Chinook salmon in the southern region (Duffy et al. 2005). Up to 37 artificial propagation programs, state-run and tribal, produce approximately 30 million Chinook salmon in Puget Sound annually (NMFS 2004; RMPC 2010). Each hatchery follows its own practices, and several hatcheries release multiple cohorts, often at different dates and body sizes, and the fish are subjected to different rearing and release strategies. Puget Sound hatcheries typically release large pulses of ocean-type Chinook salmon between mid-April and late June, although releases as late as September have been reported. Hatchery-produced smolts enter Puget Sound at a larger size than wild counterparts, and size differences persist in nearshore habitats through the spring (Duffy et al. 2005).

Poor marine survival has been identified as one factor contributing to the decline of Chinook salmon in Puget Sound (Greene et al. 2005); however, little is known about the mechanisms and timing associated with high marine mortality. The goal of this study was to examine factors affecting marine survival, and specifically, to determine if and when timing and size during early marine life affected marine survival of Chinook salmon in Puget Sound. Since 1997, the abundance and distribution of juvenile salmon in offshore waters has been sampled during the summer (July) and early fall (September). This sampling program provided information on the inter- and intra-annual variation in sizes of fish in offshore waters that we could compare with marine survival estimates. To address the high degree of variability in the Chinook salmon population, we used CWTs to track specific Chinook salmon release groups through their first spring and summer in Puget Sound. We then examined specific factors that were hypothesized to affect marine survivals. These included release date (day of the year), size at release, and average masses in July and September. We performed a linear regression analysis on different combinations of these variables and used Akaike's information criterion (AIC) to find the most parsimonious model. We hypothesized that larger sizes at each stage would correlate with higher marine survivals, and expected the effect of release date on marine survival to be less clear due to interannual differences in environmental conditions.

## Materials and methods

### Study area

Puget Sound (Washington, USA) is a deep, elongated glacial fjord composed of underwater valleys, ridges, and basins with an average depth of 135 m (Burns 1985). We divided Puget Sound into three regions: North, from Admiralty Inlet south to Edwards Point; Central, from Edwards Point south to the Tacoma Narrows, and South, waters south of the Tacoma Narrows (Fig. 1). We examined data from Chinook salmon released from hatcheries in each of these regions: Wallace River (WR) and Bernie Gobin (BG) in the North; Grover's Creek (GC), Gorst Creek Pond (GO), Soos Creek (SC), White River (WH) and Puyallup Tribal (PT) in the Central Region; and Hupp Springs (HS), Kalama Creek (KC), and Nisqually River (NR) in the South (Fig. 1).

### Fish sampling

Midwater rope trawling was conducted in the North and Central regions of Puget Sound during 2 d trips in July and September 1997–2007. The rope trawl had an effective opening of 14 m deep × 30 m wide when fishing (Beamish et al. 2000) and was operated in offshore waters (generally greater than 30 m bottom depth). On average, 30 trawls were conducted per year. The average tow lasted for 20 min at 4.4 knots, covering a distance of 2687 m. Approximately two thirds of the trawls sampled the upper 30 m of the water column, with occasional deeper tows ranging between 30–120 m. All sampling occurred during daylight hours.

For each trawl, total counts were recorded for each species. For Chinook salmon, hatchery-origin fish were identified by adipose fin clips and CWTs; unmarked Chinook salmon were assumed to be of natural origin. Marking of all hatchery Chinook salmon has been required since 2000; however, marking errors and use of nonvisible marks (thermal otolith marks) on some hatchery release groups (particularly experimental and "wild recovery" fish) contributed an unknown but likely small percentage of hatchery origin fish to the unmarked fraction. On average, unmarked fish represented 18% of the Chinook salmon catch in July and 29% in September.

Individual fork lengths (FL, to the nearest 1 mm) were recorded for at least 60 fish per species, when available, and all CWT salmon. Wet mass (to the nearest 0.1 g) were recorded for a smaller subsample of Chinook salmon (typically 20–40 fish per trawl), and many but not all CWT salmon. We pooled data from 2001–2007 to develop a length–mass regression for fish lacking mass measurements:

$$\text{Mass of Chinook salmon (g)} = 0.000004 \times \text{FL(mm)}^{3.1808}$$

$r^2 = 0.99$; $n = 4422$, 86–844 mm, 2001–2007.

Since mass measurements can be less accurate at sea (especially in rough seas, although those are rare in Puget Sound), regression-derived masses provided more consistent values representative of the average fish.

Snouts from all CWT salmon were removed and sent to the Washington Department of Fish and Wildlife (WDFW) where each CWT was read (Lynn Anderson, WDFW, Olympia, Washington). We retrieved information associated with each CWT from the Regional Mark Processing Center's CWT recovery online database (RMIS Database 1977). CWT fish are released primarily by state and tribal run hatcheries and sampled at various commercial, recreational, and escapement fisheries coast-wide by sampling agencies. Each unique CWT code is associated with release, catch, and recovery information.

Release information includes hatchery and stock information, location and date of release, numbers released, and average size at release. Catch information includes the sampling area, number caught, percent of catch that was sampled, and related information.

Recovery information includes the date and specific location of catch, fishery, and related biological data. Where possible, the ratio of the number of fish sampled to the total catch is multiplied by the total number of tags extracted to form the "estimated number of fish" (RMIS Web Site User Manual 2006).

To obtain estimates of marine survival (Survival, %) for the CWT Chinook salmon from our midwater trawl surveys (Table 1), we ran survival analysis (SA1) queries (RMIS Survival Analysis Report, 4 August 2010). The ratio of the total estimated number of fish recovered to the total number of juveniles released is used to estimate marine survival:

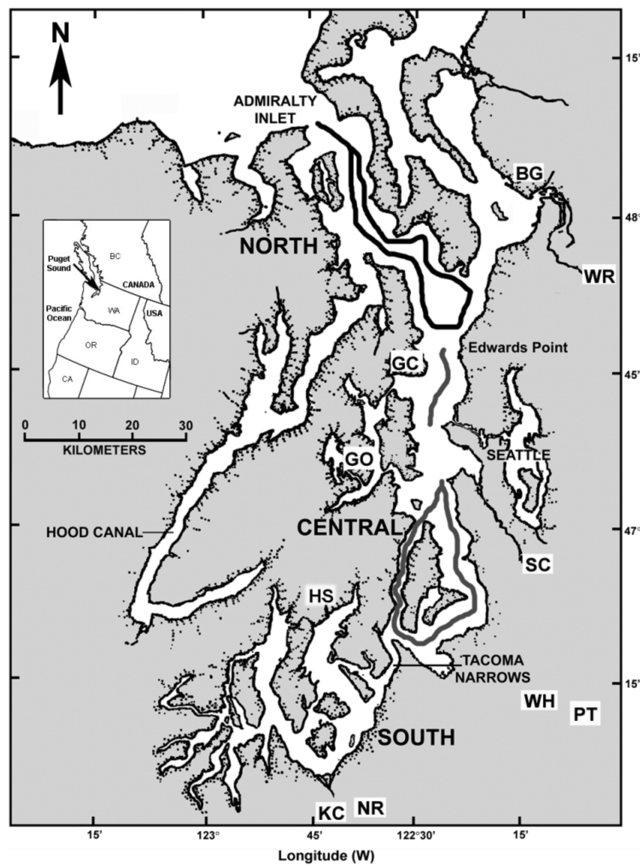
$$\text{Survival}_{\text{CWT}} = (\text{total estimated no. of recoveries} \times 100)/\text{total no. of juveniles released}$$

Average marine survivals since 1998 ranged from 0.3% to 1.0%, and were similar to values since 1983 (Fig. 2). Higher marine survival values were observed in the 1970s and in previous decades (Fig. 2; Ruggerone and Goetz 2004).

## Linear regression analysis of marine survival

We limited our regression analysis of marine survival to CWT-specific release groups of Chinook salmon that were released in April–June of their first year, were captured in both July and September trawls during a given year, and were released no later than 2002 (since marine survival data for more recent brood years was considered incomplete). To increase sample sizes for an individual release group, we pooled CWT codes from hatcheries that released multiple groups of fish (each with a unique CWT code) at identical release dates and masses. Based on these criteria, we were able to examine 5–10 CWT release groups per year from four different brood years (Table 1). We calculated average sizes of each release group in July and September based on FL, and then used the length–mass regression to estimate average mass, because several fish lacked individual mass data.

**Fig. 1.** Puget Sound map showing regions (North, Central, South), midwater trawl survey areas, and approximate locations for hatcheries of origin for Chinook salmon (identified by fin clips and coded wire tags, CWT) examined in this study. Unbroken lines indicate typical routes surveyed by midwater trawl in North (black) and Central (gray) regions. Hatcheries include Wallace River (WR) and Bernie Gobin (BG) in the North; Grover's Creek (GC), Gorst Creek Pond (GO), Soos Creek (SC), White River (WH), and Puyallup Tribal (PT) in the Central region; and Hupp Springs (HS), Nisqually River (NR), and Kalama Creek (KC) in the South.




We performed linear regression analyses to determine whether early marine sizes and timing affected marine survivals (Survival). The explanatory variables we tested were the first release date (RelDate; day of the year), average mass at release (RelWt), average mass in July midwater trawl surveys (JulWt), and average mass in September surveys (SepWt). We inspected the individual parameter plots

**Table 1.** Information on Chinook salmon (identified by fin clips and coded wire tags, CWT) captured by midwater trawl in Puget Sound (PS) during their first marine summer (July and September).

| | | Release | | | July | | | | September | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | Hatchery | Survival (%) | Date | Mass (g) | *n* | FL (mm) | SE | Mass (g) | *n* | FL (mm) | SE | Mass (g) |
| Central | SC | 0.50 | 9 May 1997 | 6.2 | 15 | 119.5 | 4.8 | 16.2 | 6 | 153.5 | 5.3 | 35.9 |
| Central | GC | 1.21 | 30 Apr. 1997 | 7.1 | 21 | 144.8 | 3.8 | 29.8 | 6 | 166.3 | 4.9 | 46.4 |
| Central | WH | 0.10 | 5 June 1997 | 5.5 | 7 | 98.6 | 2.4 | 8.8 | 10 | 143.8 | 3.0 | 29.2 |
| South | HS | 0.40 | 29 May 1997 | 9.4 | 24 | 123.9 | 1.5 | 18.2 | 21 | 156.4 | 2.6 | 38.2 |
| South | NR | 1.52 | 6 May 1997 | 11.1 | 16 | 150.3 | 3.1 | 33.6 | 4 | 203.8 | 17.4 | 88.5 |
| North | BG | 0.55 | 24 May 1999 | 5.82 | 5 | 122.4 | 3.9 | 17.5 | 3 | 167.0 | 8.7 | 47.0 |
| Central | SC | 1.12 | 5 May 1999 | 5.7 | 20 | 126.1 | 2.4 | 19.2 | 10 | 158.6 | 4.4 | 39.9 |
| Central | GC | 1.89 | 15 Apr. 1999 | 9.1 | 16 | 153.7 | 4.1 | 36.1 | 6 | 211.8 | 10.5 | 100.1 |
| South | KC | 1.04 | 18 May 1999 | 8.4 | 5 | 132.4 | 5.4 | 22.5 | 6 | 156.0 | 4.0 | 37.8 |
| South | NR | 0.73 | 7 May 1999 | 8.7 | 9 | 136.4 | 3.1 | 24.7 | 3 | 156.7 | 4.3 | 38.4 |
| South | NR | 0.90 | 11 May 1999 | 9.1 | 7 | 131.3 | 3.8 | 21.9 | 3 | 173.3 | 3.8 | 52.9 |
| North | BG | 0.72 | 8 May 2001 | 5.7 | 4 | 123.5 | 3.1 | 18.0 | 1 | 148.0 | — | 32.0 |
| North | WR | 0.28 | 29 June 2001 | 7.8 | 13 | 106.6 | 2.0 | 11.3 | 9 | 142.0 | 2.1 | 28.1 |
| Central | SC | 0.33 | 18 May 2001 | 6.0 | 13 | 115.6 | 2.9 | 14.6 | 19 | 144.8 | 9.6 | 29.8 |
| Central | GC | 0.63 | 11 May 2001 | 5.2 | 8 | 134.4 | 1.8 | 23.5 | 7 | 152.1 | 1.7 | 34.9 |
| Central | PT | 0.14 | 12 June 2001 | 6.8 | 2 | 106.5 | 1.5 | 11.2 | 3 | 148.7 | 7.2 | 32.5 |
| Central | PT | 0.38 | 15 June 2001 | 8.4 | 1 | 114.0 | — | 14.0 | 8 | 141.8 | 3.0 | 27.9 |
| Central | WR | 0.32 | 25 May 2001 | 7.1 | 10 | 117.7 | 2.3 | 15.4 | 14 | 147.2 | 2.0 | 31.5 |
| South | HS | 0.38 | 25 May 2001 | 9.1 | 3 | 124.7 | 3.2 | 18.5 | 6 | 159.0 | 4.8 | 40.2 |
| South | KC | 0.76 | 16 May 2001 | 8.6 | 3 | 128.3 | 5.9 | 20.3 | 3 | 147.7 | 3.2 | 31.8 |
| South | NR | 1.04 | 8 May 2001 | 8.4 | 14 | 143.1 | 2.4 | 28.8 | 8 | 154.6 | 5.6 | 36.8 |
| North | BG | 0.50 | 14 May 2002 | 5.7 | 8 | 117.4 | 1.7 | 15.3 | 2 | 173.5 | 26.5 | 53.1 |
| North | WR | 0.18 | 15 June 2002 | 6.3 | 10 | 95.2 | 1.3 | 7.9 | 7 | 141.6 | 3.0 | 27.8 |
| Central | SC | 0.13 | 3 June 2002 | 6.1 | 13 | 95.1 | 1.2 | 7.8 | 1 | 158.0 | — | 39.4 |
| Central | GC | 0.46 | 20 May 2002 | 6.8 | 39 | 117.4 | 1.3 | 15.3 | 7 | 161.1 | 6.6 | 42.0 |
| Central | GO | 0.21 | 20 May 2002 | 6.7 | 11 | 106.4 | 2.1 | 11.2 | 6 | 144.5 | 6.4 | 29.7 |
| Central | WH | 0.19 | 29 May 2002 | 5.0 | 11 | 98.7 | 2.1 | 8.8 | 3 | 150.3 | 6.6 | 33.6 |
| Central | WH | 0.33 | 17 May 2002 | 11.1 | 9 | 124.8 | 2.5 | 18.6 | 4 | 154.5 | 8.5 | 36.7 |
| South | HS | 0.22 | 3 June 2002 | 9.4 | 21 | 114.0 | 1.1 | 14.0 | 5 | 160.2 | 17.4 | 41.2 |
| South | KC | 0.46 | 23 May 2002 | 7.2 | 9 | 113.0 | 2.5 | 13.6 | 3 | 159.3 | 9.9 | 40.5 |
| South | NR | 0.35 | 7 May 2002 | 8.1 | 52 | 119.9 | 0.9 | 16.4 | 7 | 168.6 | 8.3 | 48.4 |

**Note:** Chinook salmon originated from 10 hatcheries: Wallace River (WR) and Bernie Gobin (BG) in the North; Grover's Creek (GC), Gorst Creek Pond (GO), Soos Creek (SC), White River (WH), and Puyallup Tribal (PT) in the Central region; and Hupp Springs (HS), Nisqually River (NR) and Kalama Creek (KC) in the South. Survival (%) refers to the smolt-to-adult survival of a group of CWT Chinook salmon released from a hatchery on a specific date. Release date refers to the first day of release from the hatchery. Mass at release (wet mass, g) refers to the average size at hatchery release. Information on releases and survival of CWT salmon was obtained from the RMIS database. Sample sizes (*n*) and average lengths (FL, mm, ± 1 SE) are listed for salmon caught in July and September. Average lengths were converted to mass (wet mass, g) using a length–mass regression derived from this study (see Materials and methods).

(diagnostic residual and probability plots) to confirm that the values were normally distributed. Survival data were log-transformed to avoid predicting negative survival values. We used the following equation to model marine survival:

$$\log_{10}(\text{survival}) = \beta_0 + \beta_i X_i \ldots + \beta_4 X_4 + \epsilon$$

where $\beta_0$ is the intercept, $\beta_i$ are the parameters, $X_i$ are the explanatory variables (RelDate, RelWt, JulWt, SepWt), and $\epsilon$ is the error term.

We used Akaike's information criterion (AIC) to evaluate which sets of possible candidate models might best explain survival rates (model selection). AIC scores, which balance model complexity (no. of parameters) with goodness of fit (likelihood), were determined for all model parameter combinations, and then corrected for the effects of small sample sizes ($AIC_c$; Burnham and Anderson 1998). The difference between each model's $AIC_c$ and the lowest overall $AIC_c$ score, the ΔAIC, was used to rank the models. By convention, models with ΔAIC scores lower than 2 are considered to perform equally well. Models with ΔAIC scores between 2 and 10 are considered to have moderate value, whereas ΔAIC scores greater than 10 are considered to have poor approximations to the data (Burnham and Anderson 1998).

We calculated additional AIC metrics to help interpret the model selection analysis. The AIC weight ($w_i$) is the relative weight of an individual model compared with all of the models:

$$w_i = \exp(-0.5 \times \Delta AIC_i) / \Sigma[\exp(-0.5 \times \Delta AIC_i)]$$

The AIC weight can be interpreted as the weight of evidence that a given model is the best approximating model. Importance weight, the sum of AIC weights for each model that contains the parameter of interest, gives an indication of the relative importance of individual variables (Burnham and Anderson 1998).

We used AIC model averaging to incorporate model selection uncertainty (using AIC weights) into our calculations of parameter estimates and associated variances. For model-averaged parameter estimates, we calculated $\widehat{\beta}$ , where parameter estimates are averaged over only the models in which the predictor occurs:

$$\widehat{\beta}\text{JulWt} = \sum w_\text{i} \times \beta\text{JulWt}_\text{i}$$

Model averaging was also used to calculate associated error (SE) and 95% confidence intervals (CI, based on $t$ = 1.95 for 95% CI with 20+ samples) associated with these parameter estimates (Burnham and Anderson 1998).

## Results

### CWT Chinook salmon

During this study, an average of 147 (July) and 99 (September) CWT Chinook salmon were caught each year. CWT fish accounted for approximately 8% of the catch of juvenile Chinook salmon. The average residence time (days between capture and first release date) of these CWT Chinook salmon was 60 days in July (range: 20–110 days) and 128 days in September (range: 80–195 days). Most CWT Chinook salmon originated from hatcheries in the Central and South regions (74%–94%), with a smaller proportion from the North (4%–17%). We caught a small number of CWT Chinook salmon from distant locales, including Hood Canal and British Columbia.

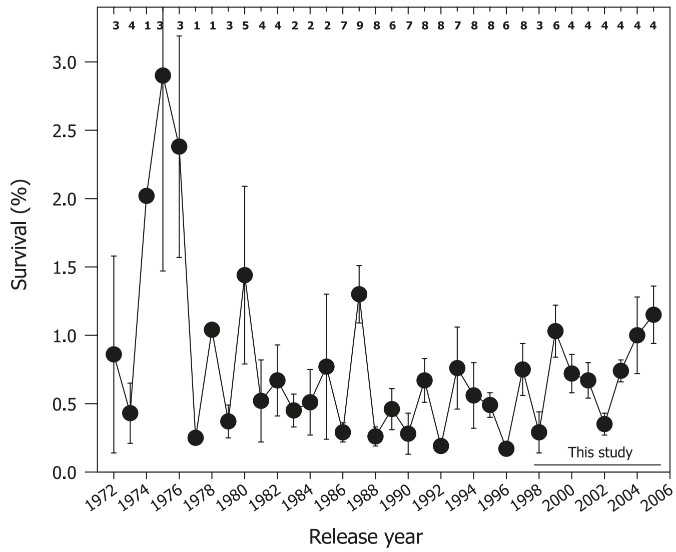
### Linear regression analysis of marine survival

We identified 5–10 CWT release groups in four release years (1997, 1999, 2001, and 2002) that could be tracked through consecutive catches (Table 1). Each release group had a minimum of five and up to 59 captures. Release groups originated from 10 different hatcheries, with at least 2 in each region of Puget Sound. These Chinook salmon were released (date of first release) between mid-April and late June, mass at release ranged from 5 to 11 g.

Size in July (JulWt) was the most plausible explanatory variable for marine survival, appearing in all of the top candidate models ($\Delta$AIC < 5, Table 2), and ranking highest in importance weight (1.0, Table 3). Size at release and date of release were also included in the most plausible models ($\Delta$AIC < 2) and had similar importance weights (Table 3), though they did not perform well as the sole explanatory variable ($\Delta$AIC > 20, Table 2). None of the most plausible models ($\Delta$AIC< 2) included size in September.

The relationship between size and survival was positive at all stages we considered, though most evident in July, while release date showed a negative relationship to survival (Fig. 3). Specifically, Chinook salmon that were larger than 17 g (120 mm FL) in July experienced the highest marine survivals (>0.5%), while fish released later than 25 May experienced the lowest marine survivals (<0.5%, Table 1). Only release groups that were substantially larger than typical sizes in September (>80 g outliers) experienced consistently high marine survivals (Fig. 3).

**Fig. 2.** Average marine survivals (percentage ± 1 SE) of juvenile Chinook salmon (identified by adipose fin clips and coded wire tags, CWT) released from Puget Sound hatcheries in 1972–2005. The number of CWT release groups included each year is listed above each point. This figure is adapted from Ruggerone and Goetz (2004), with data added for release years 1998–2005. Survival data were obtained from the Regional Mark Information System database.




## Discussion

For hatchery Chinook salmon in Puget Sound, marine survival was most strongly explained by the average body size in July, with larger sizes associated with higher survivals. Size at, and date of release from hatcheries, helped to better explain marine survival, although only slightly, whereas size in September showed a much weaker relationship to marine survival. Specifically, fish that experienced the highest marine survivals were released before 25 May and were larger than 17 g by July. This relationship was consistent over multiple years (1997–2002), and suggests that mortality after July was strongly size-dependent.

Our study provides strong evidence that rapid growth during the early marine period (through at least mid-July) is critical for improved marine survival of Chinook salmon. Therefore, factors affecting early marine growth, like water temperature and the abundance and quality of prey, are likely to affect marine survival. The importance of body size in July to marine survival also supports the hypothesis that significant size-selective mortality occurs at some point during or after the first marine summer. This corresponds to a second stage of early marine mortality hypothesized by Beamish and Mahnken (2001) in the critical size and period hypothesis. Recent research suggests that this second stage of size-selective mortality occurs over the late fall and winter of the first marine year (Tovey 1999; Beamish et al. 2004; Moss et al. 2005), and that this mortality is linked primarily to growth rates preceding this stage. While this study establishes a strong link between size and survival, future work should focus on the timing and mechanism behind significant marine mortality events for Puget Sound Chinook salmon to help guide recovery and management efforts.

**Table 2.** Results of Akaike's Information Criteria model selection for factors affecting marine survival (Survival, Table 1) of hatchery Chinook salmon (identified by adipose fin clips and coded wire tags, CWT) from Puget Sound (released in 1997, 1999, 2000, 2001).

| Model | Explanatory variables | df | AICc | ΔAIC | $w_i$ | Adj $R^2$ | $\beta_{RelWt}$ | $\beta_{RelDate}$ | $\beta_{JulWt}$ | $\beta_{SepWt}$ | $\beta_0$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *n*+1+3 | JulWt, RelWt | 28 | –28.09 | 0.00 | 0.24 | 0.812 | –0.028 | | 0.044 | | –0.919 |
| *n*+1 | JulWt | 29 | –27.85 | 0.24 | 0.21 | 0.802 | | | 0.041 | | –1.071 |
| *n*+1+4 | JulWt, RelDate | 28 | –27.57 | 0.52 | 0.19 | 0.809 | | –0.010 | 0.034 | | –0.441 |
| *n*+1+3+4 | JulWt, RelWt, RelDate | 27 | –26.19 | 1.91 | 0.09 | 0.810 | –0.021 | –0.002 | 0.039 | | –0.560 |
| *n*+1+2 | JulWt, SepWt | 28 | –25.92 | 2.18 | 0.08 | 0.799 | | | 0.043 | –0.002 | –1.050 |
| *n*+1+2+3 | JulWt, SepWt, RelDate | 27 | –25.80 | 2.30 | 0.08 | 0.807 | | –0.004 | 0.037 | –0.002 | –0.369 |
| *n*+1+2+4 | JulWt, SepWt, RelWt | 27 | –25.78 | 2.31 | 0.08 | 0.807 | –0.027 | | 0.046 | –0.001 | –0.908 |
| *n*+1+2+3+4 | JulWt, SepWt, RelWt, RelDate | 26 | –23.90 | 4.19 | 0.03 | 0.806 | –0.019 | –0.003 | 0.041 | –0.002 | –0.487 |
| *n*+3+4 | RelWt, Rel Date | 28 | –6.02 | 22.07 | 0.00 | 0.617 | 0.046 | –0.015 | | | 1.431 |
| *n*+4 | RelDate | 29 | –4.01 | 24.09 | 0.00 | 0.573 | | –0.016 | | | 1.871 |
| *n*+2+4 | SepWt, RelWt, RelDate | 27 | –3.90 | 24.19 | 0.00 | 0.610 | 0.039 | –0.014 | | 0.002 | 1.224 |
| *n*+2 | SepWt, RelDate | 28 | –3.78 | 24.31 | 0.00 | 0.589 | | –0.013 | | 0.004 | 1.332 |
| *n*+2+3 | SepWt | 29 | 10.05 | 38.14 | 0.00 | 0.328 | | | | 0.012 | –0.843 |
| *n*+3 | SepWt, RelWt | 28 | 11.99 | 40.08 | 0.00 | 0.316 | 0.022 | | | 0.011 | –0.968 |
| *n* | RelWt | 29 | 19.60 | 47.69 | 0.00 | 0.085 | 0.066 | | | | –0.841 |
| | Null (Intercept) | 30 | 21.13 | 49.22 | 0.00 | | | | | | –0.349 |

**Note:** Candidate models took the following form: $\log_{10}(\text{Survival}) = \beta_0 + \beta_i X_i \ldots + \beta_4 X_4 + \epsilon$; where $\beta_0$ was the intercept, $\beta_i$ were the parameters, $X_i$ were the explanatory variables, and $\epsilon$ was the error term. Explanatory variables were release mass (RelWt), release date (RelDate), and masses in July (JulWt) and September (SepWt). Degrees of freedom (df), adjusted (Adj) $R^2$, intercept and parameter values ($\beta_i$) are listed for each model. AIC scores are reported as AICc, AIC corrected for small sample sizes, ΔAIC, the difference from the model with the lowest (best) AICc, and AIC weight ($w_i$), the weight of an individual model relative to all candidate models. Candidate models are ranked in order of fit (lowest to highest ΔAIC).

**Table 3.** Akaike's Information Criterion model-averaged parameter estimates ($\widehat{\beta}$), associated error (SE) and 95% confidence intervals (CI, based on $t$ = 1.95 for 95% CI with 20+ samples), for the composite model linking explanatory variables to marine survival of hatchery Chinook salmon (identified by adipose fin clips and coded wire tags, CWT) from Puget Sound (see Table 2).

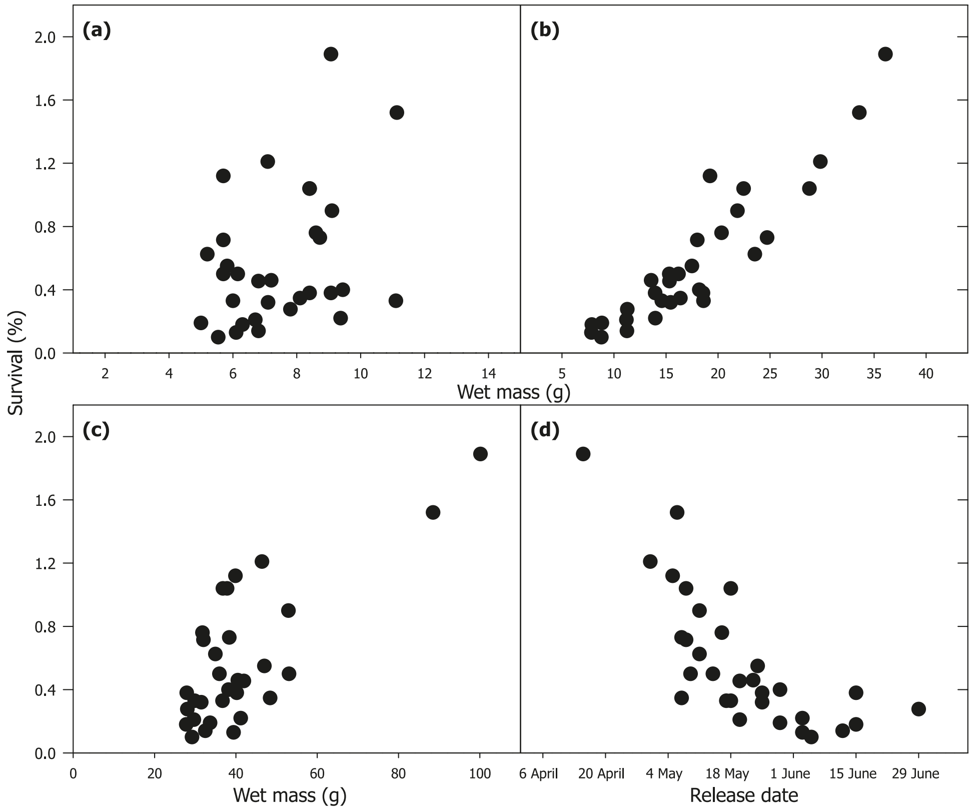
| | | | 95% CI | | |
|---|---|---|---|---|---|
| Explanatory variables | $\widehat{\beta}$ | SE | Upper | Lower | Importance Wt |
| JulWt | 0.040 | 0.006 | 0.052 | 0.028 | 1.00 |
| SepWt | –0.002 | 0.002 | 0.003 | –0.006 | 0.26 |
| RelWt | –0.026 | 0.019 | 0.011 | –0.062 | 0.44 |
| RelDate | –0.006 | 0.004 | 0.002 | –0.014 | 0.39 |
| Intercept | –0.784 | 0.359 | –0.084 | –1.484 | 1.00 |

**Note:** Importance weight (Wt, the sum of AIC weights, $w_i$, for each model that contains the parameter of interest) gives an indication of the relative importance of individual variables. Explanatory variables were release mass (RelWt), release date (RelDate), and masses in July (JulWt) and September (SepWt). The composite model for marine survival (Survival, %) of Puget Sound Chinook salmon was:
$\log_{10}(\text{Survival}) = -0.784 + 0.044 \times \text{JulWt} - 0.002 \times \text{SepWt} - 0.026 \times \text{RelWt} - 0.006 \times \text{RelDate} + \text{error}$.

Larger release size and earlier release date also conferred some benefit to marine survival of Chinook salmon. These benefits may be explained both by how release date and size affect early marine growth opportunities and by how they affect mortality before July. The period immediately after ocean entry is associated with high mortality rates, as high as 2%–8% per day for several Pacific salmon species (Parker 1968; Fisher and Pearcy 1988), compared with less than 1% per day later in life (Parker 1962; Pearcy 1992). Most of this mortality is hypothesized to be due to predation (Beamish and Mahnken 2001; Brodeur et al. 2003), and many gape-limited predators, like salmonids, exhibit negative size-selective predation (Parker 1971; Duffy and Beauchamp 2008). Larger release size can help to reduce initial susceptibility to these predators while release timing can affect temporal overlaps with predators. Earlier release from hatcheries can also serve to maximize growth opportunities in productive marine waters. Timing of marine entry has shown to impact marine survival for salmon in other systems (Blackbourn 1976; Bilton et al. 1982).

The relatively small effect of release size on marine survival in this study may be due to the small range of release sizes (5–11 g) in our analysis. Increased marine survival associated with larger release sizes have typically been observed in other salmon species, and over wider ranges in both sizes and marine survivals (e.g., masu salmon (*Oncorhyncous masou*), Miyakoshi et al. 2001; Atlantic salmon (*Salmo salar*), Kallio-Nyberg et al. 2004; coho salmon, Quinn et al. 2005). Quinn et al. (2005) did find that larger release size (range: 3–20 g) was associated with higher marine survival for Puget Sound Chinook salmon released from neighboring hatcheries in 1969–1998. However, they also found that annual differences in release size within a hatchery did not explain interannual variations in marine survival.

**Fig. 3.** The relationship between marine survival (%) and (*a*) average release size (body mass, *g*, (*b*) average size (*g*) in July, (*c*) average size (*g*) in September, and (*d*) release date for select groups (identified by adipose fin clips and coded wire tags, CWT) of Puget Sound hatchery Chinook salmon in 1997, 1999, and 2001–2002. Notice different scales on *x* axes.




This supports our finding that inter-annual patterns in marine survivals were influenced most by factors during early marine residence.

One limit of this study is its applicability to wild Chinook salmon. In the Baltic Sea, both hatchery and wild Atlantic salmon exhibited a positive relationship between smolt size and marine survival, but this relationship differed both by origin and year. Wild fish, despite being considerably smaller, experienced consistently higher survivals than hatchery fish, and the survival benefit conferred by larger size was especially strong for wild fish in poor survival years (Saloniemi et al. 2004). Though we do not know how marine survival of wild fish compares to hatchery fish in Puget Sound, we do know that wild Chinook salmon exhibit more variable marine entry timing than hatchery fish, (February–August; Simenstad et al. 1982; Brennan et al. 2004; Duffy et al. 2005), and enter Puget Sound at a smaller size than hatchery counterparts. These size differences persist in nearshore habitats through the spring (Duffy et al. 2005), but not in the midwater trawl surveys of July and September (R. Beamish, Fisheries and Oceans Canada, Pacific Biological Station, Hammond Bay Road, Nanaimo, British Columbia, unpublished data). This suggests that wild Chinook salmon experience higher early marine growth rates, that they experience stronger size-selective mortality, or that they exhibit different distribution patterns (e.g., different migration rates and habitat use). While it is important to learn more about factors affecting the marine survival of wild Chinook salmon, it is likely that efforts to improve early marine growth opportunities in Puget Sound will benefit both hatchery and wild fish.

This study suggests that much of the marine mortality of Chinook salmon is determined by local conditions during their first spring and early summer in Puget Sound. This early marine residence could be viewed as a critical period when Chinook salmon must maximize their size to minimize size-selective mortality associated with the remainder of their marine life. Our findings highlight the importance of Puget Sound as a rearing environment for juvenile salmon, and suggest that declines in marine survival since the 1980*s* may have been caused by reductions in the quality of feeding and growing conditions during early marine life.

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