



Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence

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ABSTRACT: Selective mortality during early life history stages can have significant population-level consequences, yet critical periods when selective mortality occurs, the strength of selection, and under what environmental conditions can be difficult to identify. Here, we used otolith microstructure and chemistry to examine the factors potentially linked to selective mortality of juvenile fall-run Chinook salmon *Oncorhynchus tshawytscha* from California's Central Valley during early ocean residence. Back-calculated size and growth rates of the population were compared across 3 sample periods: as juveniles exited the San Francisco Bay estuary (estuary-exit), after their first month at sea (summer-ocean) and 5 mo after ocean entry (fall-ocean). We compared mortality dynamics during years of exceptional recruitment (addition of individuals to harvestable population; 2000 and 2001) to a year of poor recruitment (2005). Otoliths from 2005 were also analyzed for sulfur isotopes to discern hatchery from naturally spawned stock. Significant size and growth-rate selective mortality were detected during the first month at sea in the low recruitment year of 2005, but not in 2000 and 2001. Individuals that were larger and growing faster during freshwater and estuarine rearing were more likely to survive to summer and fall in the low recruitment year. There was a slight, but insignificant, increase in the proportion of hatchery to naturally spawned individuals from estuary-exit to fall-ocean, suggesting that fish from neither origin were overwhelmingly favored. Our results suggest that Central Valley Chinook salmon can be subject to significant size and growth-rate selective mortality resulting in low adult abundance, and this mortality appears independent of origin.

KEY WORDS: Critical period · Otolith · California Current · Hatchery · Gulf of the Farallones

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INTRODUCTION

Fish populations typically experience their highest mortality rates during the early life-history stages (Anderson 1988, Pearcy 1992, Sogard 1997). In many salmonid species the transition from the estuarine to ocean environment as juveniles is considered a critical period of high mortality (Parker 1968, Pearcy

1992, Beamish & Mahnken 2001, Wells et al. 2012). This mortality can be non-random, with the smaller, slower-growing individuals lost to predation or starvation (Parker 1971, Shepherd & Cushing 1980, Miller et al. 1988). Understanding the factors responsible for selective mortality and its timing is critical for accurate estimates of recruitment (addition of individuals to a harvestable population) and year-

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class strength (Hjort 1914, Gulland 1965, Houde 1987, Crowder et al. 1992). Changes in the distribution of population traits (e.g. body size) during early life-history stages can provide insight into selective mortality processes. If we can identify and measure the traits associated with survival, we may be able to better anticipate the success or failure of particular cohorts and consider harvest management actions relevant to all cohorts in the stock (Crowder et al. 1992).

Empirical data quantifying the mechanism and timing of selective mortality are often difficult to obtain. Fish otoliths present an opportunity to address these questions by allowing retrospective analysis of size and growth distributions of the population. Otoliths are calcified structures that grow by accreting permanent layers of calcium carbonate and protein (Campana & Neilson 1985). The otolith radius is significantly related to fish body size (e.g. fork length), and daily increments record growth rate, with larger increments accumulating in periods of faster growth (Neilson & Geen 1982, Campana & Neilson 1985, Bradford & Geen 1987, Campana 1990, Titus et al. 2004). Otoliths, therefore, allow us to back-calculate the body sizes and growth rates of surviving members of a population, and compare them to those previously sampled from the same population. A shift in the distribution of these traits may indicate selective mortality, and the timing of the shift may indicate when in the life history the selective mortality occurred (Grimes & Isely 1996).

Differences in juvenile salmon body size and growth rates also vary as a function of their rearing origin (Barnett-Johnson et al. 2007). Hatchery salmon generally grow faster and reach a larger size at release, which may increase the survival rates of hatchery individuals compared with those of natural origin (Unwin 1997, Reinhardt et al. 2001). Production hatcheries release a significant number of unmarked salmon in many regions, therefore there is great interest in understanding whether selective mortality processes in years of poor overall survival bias the population composition towards hatchery-origin fish. Specifically, there is evidence that the presence of hatchery fish reduces the marine survival of naturally spawned individuals, probably due to competition and their larger body size (Levin et al. 2001, Ruggerone et al. 2010). Conversely, decreased survival rates have also been shown in hatchery fish as a result of asynchronous release timing with peak prey abundance and marine productivity (Beamish et al. 2008, 2012), as well as due to domestication (Fritts et al. 2007).

In 2007, California's Central Valley fall-run Chinook salmon *Oncorhynchus tshawytscha* population of returning adults was at an historic low (Lindley et al. 2009) resulting in a closure of the fisheries in 2008 and 2009. Poor marine survival of juveniles that entered the ocean in 2005 was thought to have contributed to this collapse (Lindley et al. 2009). In general, it was observed that in the spring of 2005 juveniles were not unlike those in more successful cohorts, such as years 2000 and 2001, with regards to body size and lipid content on estuary-exit. However, by their first month at sea, juveniles from 2005 were smaller and had lower lipid concentrations, which implicates factors in the ocean as driving differences in mortality across years (Fig. 1; data from MacFarlane 2010). In the central California coastal system, upwelling dynamics were similar during the spring of 2000 and 2001, and were characterized by produc-

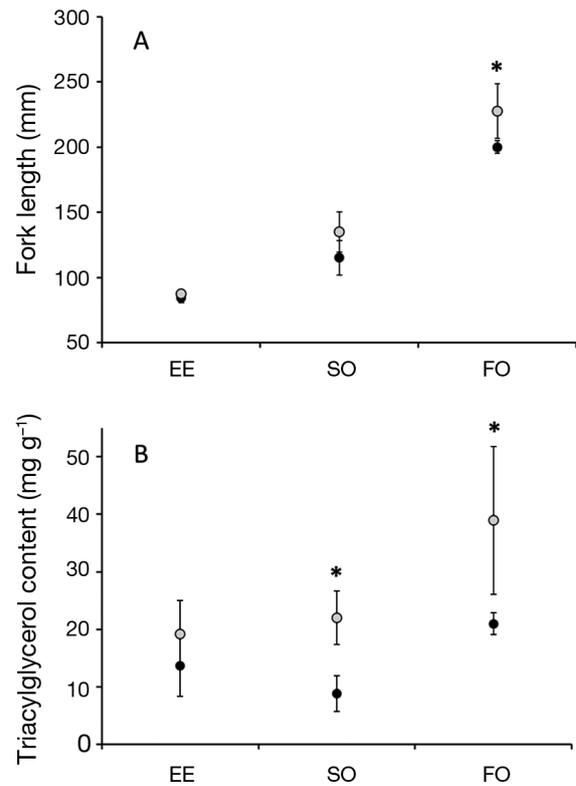


Fig. 1. Means and 95% confidence intervals of (A) measured fork length (mm) and (B) measured triacylglycerol content (mg g⁻¹) at capture across 3 sample periods: estuary-exit (EE), summer-ocean (SO), and fall-ocean (FO). In both cases, fish from 2005 (black) were significantly smaller and lower in lipid content than fish from 2000 and 2001 (grey) by fall-ocean. Stars denote significant differences (ANOVA) with $p < 0.001$. Data from MacFarlane (2010)

tive conditions with normal to high abundances of zooplankton and forage fish (Durazo et al. 2001, Schwing et al. 2002). In contrast, the late onset of upwelling in 2005 resulted in anomalously low abundances of salmon prey items during the time period when juvenile Chinook salmon were entering the ocean (Peterson et al. 2006, Schwing et al. 2006, Barth et al. 2007, Lindley et al. 2009), which relates directly to the ultimate condition and later abundance of Central Valley Chinook salmon (Wells et al. 2012). Subsequently the subyearling cohorts of 2000 and 2001 recruited as adults in high numbers, unlike the subyearlings from 2005.

Here, we used otolith microstructure and chemistry to evaluate the factors linked to potential selective mortality of juvenile fall-run Chinook salmon from California's Central Valley during contrasting years of recruitment. Retrospective changes in the frequency distributions of body sizes, growth rates, and proportion of hatchery-born individuals in the population were assessed across 3 time periods within the critical early ocean period: first as they exited the San Francisco Bay estuary (estuary-exit), again 1 mo after ocean entry (summer-ocean), and approximately 5 mo after ocean entry (fall-ocean).

High rates of mortality on smaller, slower-growing individuals following ocean entry has been previously documented in other species and stocks of juvenile salmon using mark-recapture techniques (Parker 1968, Bilton et al. 1982, Bax 1983, Duffy & Beauchamp 2011), back-calculated size and growth estimates with scales (Healey 1982, Ward et al. 1989, Holtby et al. 1990, Cross et al. 2008), and otoliths (Neilson & Geen 1986, Good et al. 2001). Despite previous studies of this kind on other salmonid species and stocks, no similar work has been done for California's Central Valley Chinook salmon—the overwhelming contributor to the commercial and recreational salmon fisheries off California. Importantly, California's Central Valley Chinook salmon originate from the extreme southern end of the species distribution (MacFarlane & Norton 2002), suggesting that previous studies on populations more centrally or northerly distributed may not suffice to capture the dynamics of this population. In addition, unlike most previous studies, our sampling design explicitly captured the period of ocean entry by sampling the population as it exited the estuary, thus enabling us to evaluate selective mortality at the earliest time at sea. This study is also unique in that we used an innovative approach to evaluate the extent to which hatchery versus natural rearing influences selective mortality.

We tested for evidence of selective mortality on juvenile fall-run Chinook salmon from California's Central Valley in years of contrasting recruitment (exceptionally high versus exceptionally low). We hypothesized that, if present, selective mortality would be greater during 2005 than during the more productive ocean years of 2000 and 2001, and that survivorship may be influenced by rearing origin.

MATERIALS AND METHODS

Sample collection

Subyearling Chinook salmon were collected as part of an annual trawl survey conducted by the National Oceanic and Atmospheric Administration Southwest Fisheries Science Center. These surveys sampled subyearling Chinook salmon spatially and temporally over their early ocean residence. The subyearling population was first sampled beneath the Golden Gate Bridge in May and June as it exited the estuary (estuary-exit; Fig. 2). A broader range of stations in the coastal ocean were sampled during June and July (summer-ocean) and again during October (fall-ocean) (Fig. 2). These sampling periods coincided with the documented juvenile emigration timing of California's Central Valley fall-run Chinook

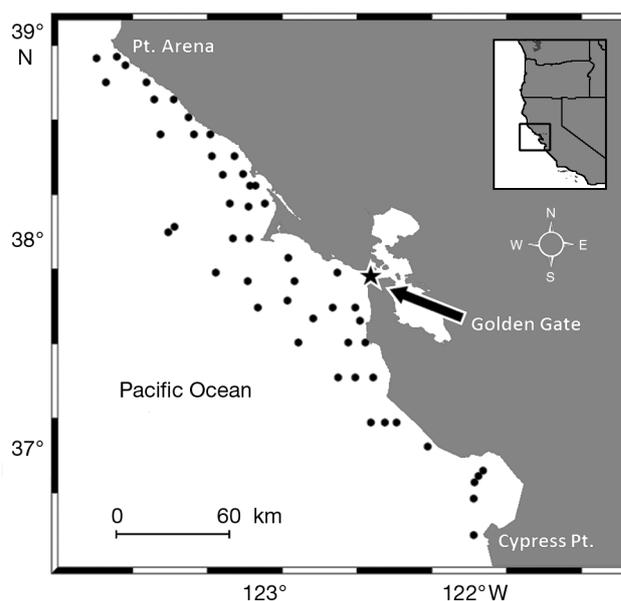


Fig. 2. Sampling locations. Estuary-exit trawls were conducted beneath the Golden Gate Bridge (star). Coastal ocean stations were sampled during summer- and fall-ocean sample periods

Table 1. Sampling dates and available sample sizes for each year of interest at estuary-exit (EE), summer-ocean (SO), and fall-ocean (FO). Sample sizes do not reflect abundance

Year	EE	N	SO	N	FO	N
2000	May 17–18, 23–24 Jun 5–6	35	Jun 20–30	32	Sep 26–29 Oct 2–6	2
2001	May 22–23 Jun 12–13	35	Jul 24–Aug 5	25	Oct 19–26	10
2005	May 10–11 Jun 7–8	84	Jun 18–25	87	Oct 5–13	80

salmon (Fisher 1994) and allowed us to track changes in the population over the critical period of early ocean residence. We focused on 3 years of sampling from this annual survey that captured differing ocean conditions and overall recruitment (Table 1). Years 2000 and 2001, combined to increase sample size, were years of productive ocean conditions (Durazo et al. 2001, Schwing et al. 2002) that resulted in similarly exceptional adult abundance 2 yr later (second and fourth greatest adult abundances on record; Pacific Fisheries Management Council 2013). Otolith data from 2000 and 2001 were part of an historical data set, and few physical otoliths were available to us. The springs and summers of 2000 and 2001 represented similar ocean conditions and high salmon recruitment to adulthood, therefore, while not ideal, we felt there was sufficient support that combining the otolith data between these collections would not bias our study results. Year 2005 was a year of poor ocean conditions and resulted in low adult abundance in the ocean and historically low returns to the river in 2007 (Lindley et al. 2009). This was not a study to compare the specific oceanic conditions that lead to potential selective mortality but, rather, to simply evaluate whether contrasting years of recruitment could have resulted, in part, from selective forces. However, as 2000 and 2001 also represented generally productive conditions and 2005 did not, we have the opportunity to qualitatively evaluate the impact of environmental conditions on mortality dynamics.

The estuary-exit station was located beneath the Golden Gate Bridge in San Francisco, California (Fig. 2) and was sampled with a midwater trawl towed at the surface for durations of 15 to 30 min at speeds of 2 to 3 knots. The net was 20 m long with 10 m head and foot ropes, and sampled the top 10 m of water. The nylon mesh had a gradient of 1.6 cm at the head rope to 0.4 cm at the codend. The codend itself was fitted with a 1.27 cm knotless mesh liner.

Further detail of the estuary-exit trawling process can be found in MacFarlane et al. (2005).

Coastal ocean stations (summer- and fall-ocean) were located between Point Arena, California (38° 55' N, 123° 44' W) and Cypress Point, California (36° 34.5' N, 122° 00' W) (Fig. 2). The coastal stations were sampled with a Nordic 264 rope trawl towed at the surface for 6 to 40 min (average 22 min) at a speed of 3 to 4 knots. The net was 27 m wide and 194 m long, and sampled the top 14 m of water. The mesh gradient ranged from 163 to 9 cm in the codend. The codend liner was 6 × 10 mm knotless nylon. Further detail of the coastal ocean trawling process can be found in MacFarlane (2010).

Sample preparation and analysis

All fish were measured, weighed, and then kept frozen or under ice until their otoliths were removed. After removal, otoliths were rinsed with deionized water and cleaned of adhering tissue. Dry otoliths were stored in microcentrifuge tubes until they were prepared for increment analysis. Otoliths were mounted in Crystalbond™ resin and polished using a succession of lapping films (600 grit, 1500 grit, 3 μm and 1 μm) until the primordia were exposed and daily increments were clearly visible.

Daily otolith increments were counted and measured along standardized transects from the post-rostrum primordia in the dorsal direction (Fig. 3). Daily increment measurements began at the exogenous feeding check (Marshall & Parker 1982) and continued to the outer edge. Otoliths from 2000 and 2001 were archived samples previously measured along the 30° transect. More recently, the 90° transect has become the accepted standard assessment practice for Chinook salmon otoliths across multiple labs (Titus et al. 2004), and otolith samples from 2005 were measured along the 90° transect. Unfortunately the archived samples were prepared to maximize readability along the 30° transect, leaving very few samples that could be re-read along the 90° transect. It is important to note that the increment widths between the 2 transects, and in our case years, are not directly comparable due to the shape of the otolith; increments along the 30° transect will always be larger than those along the 90° transect.

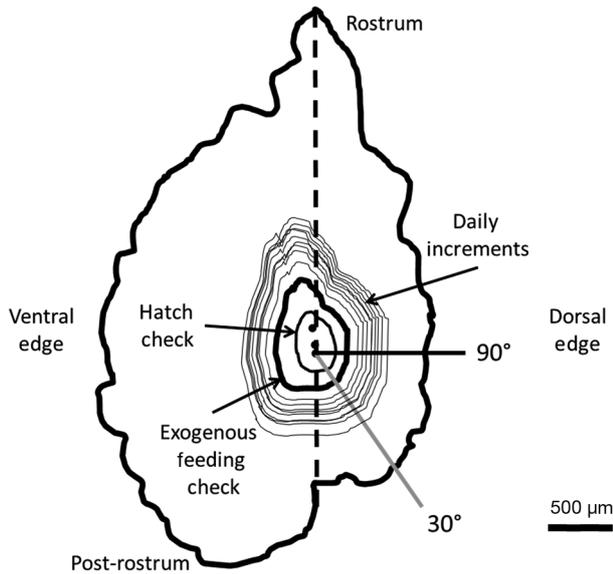


Fig. 3. Increment measurement transects differed between years. Otoliths from 2000 and 2001 were measured along the 30° transect. Otoliths from 2005 were measured along the 90° transect. Transects originated at the primorida closest to the post-rostrum and were oriented in the dorsal direction. Measurements began at the exogenous feeding check and continued to the outer edge. Daily increments were measured and counted

For juvenile Chinook salmon, a strong relationship exists between otolith radius and fork length (Neilson & Geen 1982, Bradford & Geen 1987, Titus et al. 2004). To make the data both comparable between years and maintain adequate sample size, back-cal-

culated otolith radii (μm) and increment widths ($\mu\text{m d}^{-1}$) were converted to fork length (mm) and growth rates (mm d^{-1}). These conversions were done using otolith radius to fork length regressions defined for each transect type (Fig. 4). To confirm that both the 30° and 90° transect measurements appropriately represented fork length, a subset of readable otoliths that had been previously read along the 30° transect were re-read along the 90° to compare the 2 transects. Actual fork lengths at capture were regressed against the calculated fork lengths from the 30° transect conversion and had a good linear fit ($N = 58, R^2 = 0.83, p < 0.001$). The same was done for the 90° transect subset, which also had a good linear fit ($N = 58, R^2 = 0.82, p < 0.001$). A regression between the fork lengths calculated from the 30° and 90° transects for the same fish showed good linear agreement ($N = 58, R^2 = 0.79, p < 0.001$). In all 3 cases, residuals were randomly distributed. We are, therefore, confident that both transects may be used to convert to fork length, and after doing so, are comparable.

Owing to differences in diets, hatchery and naturally produced salmon can be distinguished by quantifying the sulfur isotope ratio $^{34}\text{S}/^{32}\text{S}$ within the juvenile portion of the otolith (Weber et al. 2002, Johnson et al. 2012). The $^{34}\text{S}/^{32}\text{S}$ ratio is expressed in delta notation $\delta^{34}\text{S}$, where $\delta^{34}\text{S} = [(^{34}\text{S}/^{32}\text{S})_{\text{meas}} / (^{34}\text{S}/^{32}\text{S})_{\text{CDT}} - 1] \times 1000 \text{‰}$, $(^{34}\text{S}/^{32}\text{S})_{\text{meas}}$ is the measured sulfur isotope ratio and $(^{34}\text{S}/^{32}\text{S})_{\text{CDT}}$ is the Canyon Diablo Troilite reference ratio, 0.044163 (Ding et al. 2001). For the poor recruitment year of 2005, a subset of the

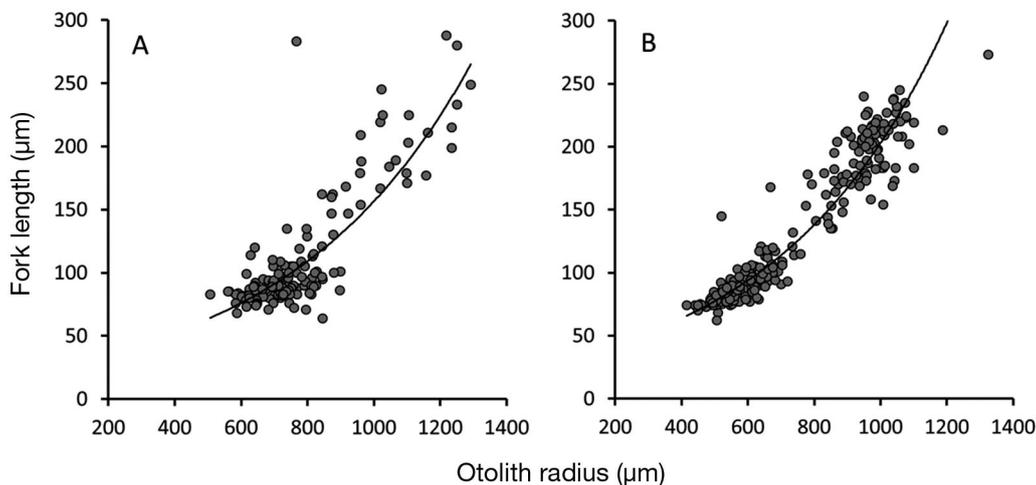


Fig. 4. Regressions between otolith radius and fork length at capture yielded exponential relationships that were used to convert back-calculated otolith radii into fork lengths. Regressions were done within year to account for the different otolith measurement transects: (A) 2000 and 2001, $y = 25.76e^{0.0018x}$, $R^2 = 0.71$; (B) 2005, $y = 29.535e^{0.0019x}$, $R^2 = 0.92$

otoliths was selected for sulfur isotope analysis. Otoliths were randomly chosen from the estuary-exit ($N = 61$) and fall-ocean samples ($N = 66$) to determine whether there was a change in the proportion of hatchery and naturally spawned fish following ocean entry. Otolith sulfur isotopes were measured using an ion microprobe at the University of California at Los Angeles (Cameca IMS 1270, National Ion Microprobe Facility). Techniques are described in Weber et al. (2002) and Johnson et al. (2012). Sulfur isotopes were measured in 3 spots of $\sim 30 \mu\text{m}$ diameter (~ 6 to 10 d of growth) in the core of the otolith and in the portion of the otolith deposited just after yolk absorption but before outmigration (post exogenous feeding, PEF). The difference in the mean $\delta^{34}\text{S}$ between the core and PEF were determined for sample classification (Weber et al. 2002, Johnson et al. 2012). Individuals that had differences in the mean $\delta^{34}\text{S} \pm 1$ standard error between the core and PEF of greater than 6.5 were considered to be naturally spawned. The difference in $\delta^{34}\text{S}$ of 6.5 corresponds to a PEF value of $\sim 8.5\%$, with fish exhibiting greater PEF values to be hatchery fish receiving isotopically heavier marine protein in their feed (Weber et al. 2002).

Statistical analysis

For each sample period (estuary-exit, summer-ocean, and fall-ocean) we back-calculated the average fork length (mm) at given ages (i.e. increments) and means were compared at 10 d increment steps (e.g. at ages 10, 20, 30 d, etc.). Age categories with fewer than 10 otolith samples were not included in the analysis. Significant differences in mean fork length indicate shifts in the body size at a given age and may indicate size-selective mortality at that age. A repeated-measures ANOVA was used, as increments in otoliths for individual fish are measured over time and are potentially correlated and non-independent.

In addition to comparing back-calculated size at different ages, we also compared back-calculated size frequency distributions at ocean entry. Using the average age (days post exogenous feeding) at estuary-exit (2000 and 2001 mean = 104 d, SD = 23; 2005 mean = 93 d, SD = 20) as our ocean-entry benchmark, we calculated the fork length at the corresponding age for each fish to construct a size distribution of the population at ocean entry for all 3 sample periods within each year. Changes observed in the ocean-entry size distribution between any of the sample periods (estuary-exit, summer-ocean, fall-ocean) would

suggest size-selective mortality. Following Claiborne et al. (2011) we used a Wilcoxon rank sum test to compare distributions.

Growth was calculated by subtracting the consecutive back-calculated fork lengths (FL) (e.g. $\text{Growth}_{\text{age } x} = \text{FL}_{\text{age } x} - \text{FL}_{\text{age } x-1}$, where 'age x ' is the otolith growth increment sampled). Specific growth rates were then calculated (total growth in 50 d divided by initial size before that 50 d period) in overlapping 50 d intervals (i.e. Days 1–50, 25–75, 50–100, etc.), as 50 d is optimal for resolving differences in growth (Bradford & Geen 1987). Means were then compared (ANOVA) across the 3 sample periods (estuary-exit, summer-ocean, fall-ocean) for each year. Intervals with fewer than 10 samples were not included in the analysis. Divergence in the mean back-calculated growth rate between sample periods would suggest selection on growth rate. The 50 d window in which a divergence occurs may indicate the window over which faster growth was important.

In addition to examining size and growth, we explored whether there was selective mortality in the poor survival year of 2005 as a function of whether fish spent their early life in a river or a hatchery. A change in the proportion of hatchery and naturally spawned fish from estuary-exit to fall-ocean (chi-square) may indicate a survival advantage of rearing origin in a poor survival year. To determine the most accurate proportions of hatchery and natural individuals we used Laplace's procedure (Laplace 1812) to produce 95% confidence intervals (Johnson et al. 2012). The confidence intervals were governed by binomial statistics and were calculated using the adjusted Wald estimate modified for small sample sizes (Lewis & Sauro 2006, Johnson et al. 2012). This analysis was not done for the 2000 and 2001 samples as these were part of an historical data set and we were limited by the number of physical otoliths available to us.

RESULTS

Size

In 2005, significant divergence in back-calculated fork length was observed as early as 60 d post exogenous feeding (Fig. 5). Tukey's post hoc test revealed that estuary-exit fish were significantly smaller than the survivors in the fall sample had been at age 60 d (repeated-measures ANOVA, $p < 0.05$) and significantly smaller than both the summer- and fall-ocean populations at ages 70 to 110 d (repeated-measures

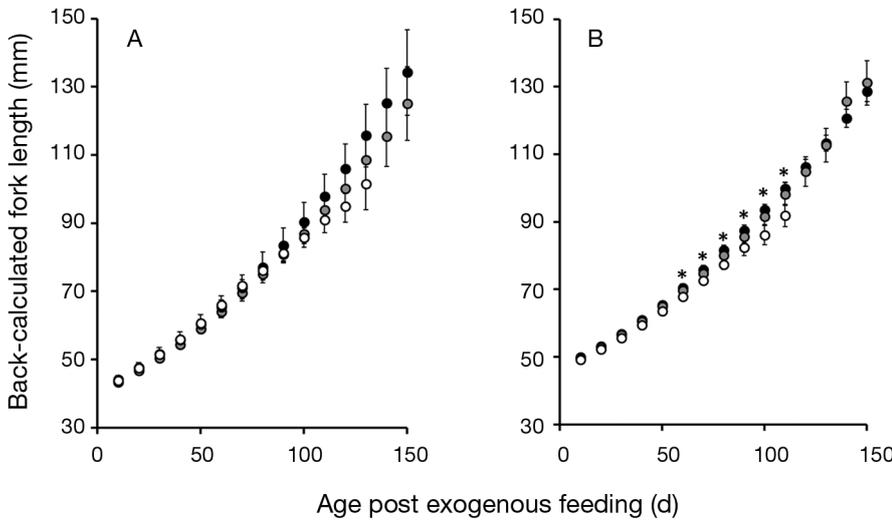


Fig. 5. Average back-calculated fork lengths (mm) and 95% confidence intervals at age post exogenous feeding for estuary-exit (white), summer-ocean (grey), and fall-ocean (black) in (A) 2000 and 2001 and (B) 2005. Stars denote ANOVA significance with $p < 0.05$

ANOVA, $p < 0.01$). Summer and fall samples were not different from each other. There was no difference in back-calculated fork length between any of the sample periods in 2000 and 2001.

In 2005, the back-calculated size distribution at the ocean-entry benchmark of juveniles sampled at estuary-exit was significantly different from juveniles collected in the summer- and fall-ocean periods (Fig. 6; Wilcoxon rank sum test, $p < 0.01$). The shift in distribution was to the right, suggesting that the larger individuals at ocean entry had a survival advantage in 2005. The backcalculated size distributions at ocean entry of the summer and fall populations were not different. In contrast, in 2000 and 2001 there was no significant shift in the distribution of fork lengths between any of the sample periods at the ocean-entry benchmark.

Growth rate

In 2005, significant differences in retrospective specific growth rate were detected as early as 1–50 d (ANOVA, $p = 0.046$) with the most compelling evidence of selective mortality related to growth rate observed at intervals of 25–75 and 50–100 d (ANOVA, $p < 0.001$) (Table 2, Fig. 7), which encompass the period of freshwater and estuarine growth before ocean entry. Fish collected in the

ocean during summer and fall exhibited faster retrospective growth relative to the population when sampled at estuary-exit. As with body size in 2005, a Tukey's post hoc test revealed no differences in growth rate between the summer and fall populations. In 2000 and 2001 no significant differences in specific retrospective growth rate were observed between any of the sample periods.

Rearing origin

Sulfur isotope analysis indicated that at estuary-exit 60% (confidence interval = 42 to 72%) of our sample was comprised of hatchery fish (hatchery $N = 32$, natural $N = 21$). By fall, only a modest increase in the proportion of hatchery fish was observed at 67% (confidence interval = 54 to 79%; hatchery $N = 35$, natural $N = 17$), however this increase was not statistically significant ($\chi^2 = 0.55$, $p = 0.46$).

Using the subset of otoliths of known origin we were able to compare body size and growth rate

Table 2. Mean specific growth rate ANOVA results for each 50 d window across all 3 sample periods (estuary-exit, EE; summer-ocean, SO; fall-ocean, FO) in both 2000 and 2001 and 2005

Days post exogenous check	2000 and 2001			2005			
	N	Mean	SD	N	Mean	SD	
1–50	EE	70	0.491	0.09	83	0.364	0.08
	SO	57	0.467	0.09	87	0.387	0.08
	FO	12	0.482	0.09	80	0.392	0.08
		$p = 0.31$		$p = 0.05$			
25–75	EE	63	0.507	0.11	75	0.396	0.06
	SO	56	0.494	0.09	85	0.422	0.08
	FO	12	0.497	0.09	80	0.440	0.08
		$p = 0.78$		$p < 0.001$			
50–100	EE	35	0.478	0.10	28	0.370	0.06
	SO	46	0.479	0.08	54	0.415	0.07
	FO	12	0.502	0.08	80	0.436	0.07
		$p = 0.67$		$p < 0.001$			
75–125	EE	16	0.436	0.09	–	–	–
	SO	24	0.455	0.08	26	0.382	0.06
	FO	11	0.505	0.06	80	0.398	0.06
		$p = 0.08$		$p = 0.06$			
100–150	EE	–	–	–	–	–	
	SO	17	0.444	0.09	13	0.372	0.05
	FO	10	0.492	0.06	80	0.379	0.05
		$p = 0.31$		$p = 0.22$			

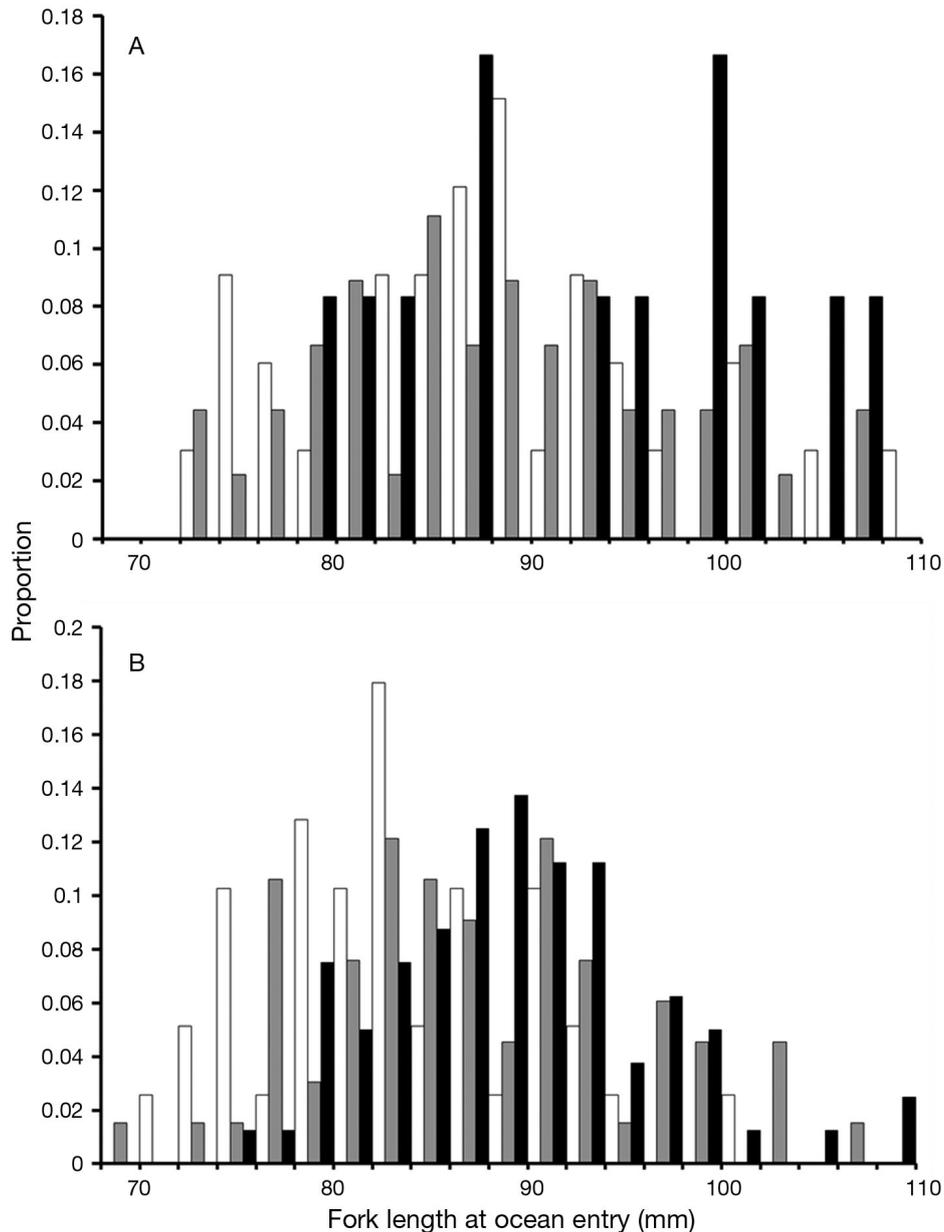


Fig. 6. Normalized fork length distributions (probability density function) at ocean entry for all 3 sample periods: estuary-exit (white), summer-ocean (grey), and fall-ocean (black). (A) There was no significant shift in size distribution in 2000 and 2001. (B) A significant shift (Wilcoxon rank sum test) was detected between estuary-exit and summer ($p = 0.01$), and estuary-exit and fall-ocean ($p < 0.01$) in 2005, but not between summer- and fall-ocean in 2005

between hatchery and naturally spawned individuals from 2005. Of the fish collected during the estuary-exit period, the average measured fork length (at capture) of hatchery individuals was significantly larger (mean = 89.8 mm, SD = 14.3) than the natural individuals (mean = 81.8 mm, SD = 10.0) (ANOVA, $p = 0.03$). By the fall-ocean period, hatchery individuals remained slightly larger (mean = 206.69 mm, SD = 20.6) than the natural individuals (mean = 193.12 mm, SD = 21.6) (ANOVA, $p = 0.02$).

The difference in body size between the 2 groups could relate to age differences. Specifically, hatchery fish were, on average, 20 d older than natural fish collected at the estuary exit. This difference in age prompted additional investigation in terms of growth rate. To examine growth rate before ocean entry, the final 50 d of growth before capture (last 50 d from edge of otolith) at the Golden Gate Bridge was compared between hatchery (mean = 0.43, SD = 0.16) and naturally spawned (mean = 0.27, SD = 0.12) fish

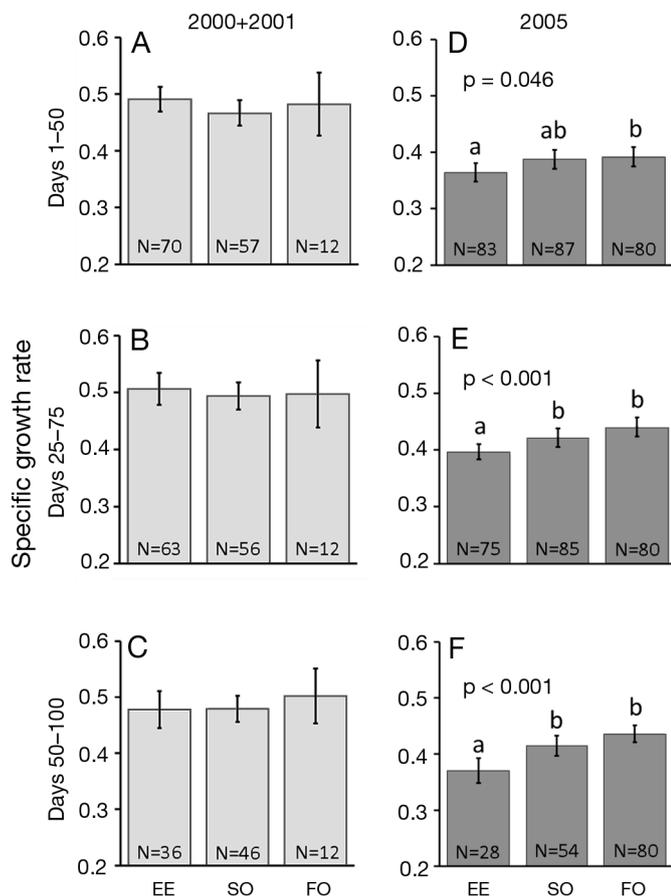


Fig. 7. Average specific growth rate over Days 1–50, 25–75, and 50–100 post exogenous feeding. (A–C) No significant differences in growth rate were observed between the sample periods (estuary-exit, EE; summer-ocean, SO; fall-ocean, FO) in 2000 and 2001. (D–F) In 2005, significant differences were observed between estuary-exit and summer- and fall-ocean (E,F), but not between summer- and fall-ocean

collected during the estuary-exit sample period. Hatchery individuals had significantly faster specific growth in the 50 d before ocean entry (ANOVA, $p = 0.001$). Notably, it appears that in 2005 hatchery individuals had faster growth rates before ocean entry and larger size on entering the ocean than natural fish, but the proportion of hatchery to naturally spawned individuals did not change greatly during early ocean residence.

DISCUSSION

Our results show statistically significant size and growth-rate selective mortality in 2005 that was not observed in 2000 and 2001. In years of improved ocean productivity and exceptional recruitment, such

as 2000 and 2001, selective mortality went undetected, as both large, fast-growing and small, slow-growing individuals survived the ocean entry period. The selective mortality detected in 2005 is similar to cases presented by Holtby et al. (1990), Blom et al. (1994), Saloniemi et al. (2004) and Cross et al. (2008), who observed an increased benefit of larger size to other juvenile salmonids in low survival years. Poor conditions, driven by the late onset of upwelling in 2005 (Lindley et al. 2009), may have created what Cushing (1990) described in the 'match-mismatch hypothesis'. Variability in the synchronicity during the timing of emigration and food availability will drive variable survival of cohorts. Limited by food, average growth rates are lower, mortality rates are higher, and often selective mortality is evident. In 2005, the majority of juveniles entered the ocean before the onset of spring-upwelling-driven ocean productivity. This food limitation potentially led to an increase in mortality that disproportionately removed the smaller, slower-growing individuals from the population. Individuals from 2005 were significantly smaller and of significantly lower lipid content following ocean entry than individuals from 2000 and 2001 (MacFarlane 2010), which further supports food limitation and starvation as a primary mechanism driving selective mortality in 2005. However, the increase in selective mortality on smaller individuals could also be driven by increased susceptibility to predation. Regardless of the ultimate mechanism, it is clear that only the larger, faster-growing individuals survived the first month at sea in 2005.

We also observed significant differences in average back-calculated body size at ages 60 to 110 d, and a shift in the distribution of back-calculated body sizes at the ocean-entry benchmark in 2005. In both cases, the average back-calculated fork length of the population at estuary-exit was smaller than the back-calculated fork length of the population by summer or fall in the ocean. Only the larger individuals survived following ocean entry. No differences in back-calculated size were observed between the sample populations in summer and fall, demonstrating that the mortality occurred during the first month at sea, between the estuary-exit and summer-ocean periods. Conversely, in 2000 and 2001 we did not see evidence of significant size-selective mortality when comparing average back-calculated fork lengths. There was no significant shift in the back-calculated size distribution at ocean entry between any of the 3 sample periods in 2000 and 2001.

Many factors determine ocean-entry timing, and variation exists around the age at which fish enter

the ocean. Ideally, an otolith mark or check formed on ocean entry could be used to provide information on age and size for each individual fish at ocean entry. However, no otolith markers have been validated for ocean entry in this system. Therefore, we applied the average age of fish caught at estuary-exit as the benchmark for when fish sampled in the summer and fall entered the ocean. This method assumes no variation in the age that fish entered the ocean. There is still the potential that back-calculated sizes could be over- or underestimated, as well as that survival may have been related to age as opposed to size. However, age and size are typically tightly coupled and difficult to separate. In our estuary-exit samples we found little variation in age (2000 and 2001 mean = 104 d, SD = 23; 2005 mean = 93 d, SD = 20) and therefore found this approach to be an adequate benchmark representing ocean entry.

In addition to size, growth-rate selective mortality was observed in 2005. Measured over 50 d intervals beginning at the exogenous feeding check, back-calculated specific growth rates were slower on average within the population at estuary-exit than within the populations that survived to summer and fall in the ocean. Individuals who were able to grow faster before ocean entry were more likely to survive to summer and fall under poor ocean conditions. The most compelling intervals were 25–75 and 50–100 d, which encompass the time period in the freshwater and estuary leading up to ocean entry.

Juvenile Central Valley Chinook salmon express a diversity of outmigration strategies that influence growth during their early life, and the habitats where they gain most of their growth are also variable. Some juveniles spend their early lives in hatcheries, others leave their natal rivers at a young age (<1 mo) and small size (<55 mm) growing mainly in the Sacramento and San Joaquin river mainstems, freshwater delta or bays before they enter the ocean, while others remain for a longer period of time in their natal rivers and then migrate rapidly to sea (Williams 2012). Regardless of where fish experience faster growth and achieve larger size before ocean entry, it appears that this early growth is important for success during unproductive ocean conditions. Individuals that were small, slow growers before ocean entry did not survive when ocean conditions were not sufficient. While the major factor in the declines of the 2005 cohort was probably ocean conditions, this finding highlights the importance of freshwater restoration efforts with regards to Central Valley Chinook salmon. Therefore, for natural fish, good growth during early life stages in the fresh-

water and potential access to good rearing habitats, such as floodplains or estuaries, may determine the success of a given outmigration strategy, especially in years of poor ocean conditions.

Duffy & Beauchamp (2011) found similar results with regard to Puget Sound Chinook salmon in that growth within the sound was positively related to early marine survival. In contrast, Zabel & Achord (2004), using mark-recapture techniques, found that downstream survival of spring and summer Chinook in the Snake River was poorly predicted by body size. However, Zabel & Achord (2004) are keen to point out that this does not suggest that size during the freshwater phase is not important for subsequent phases, such as ocean entry or early marine residence as in our study. Using techniques consistent with ours, Tomaro et al. (2012) determined that it was not growth in freshwater, but growth after a month at sea that best predicted adult abundance. However, their samples were all collected following ocean entry, and therefore did not capture the population at the critical estuary-exit period, which we were able to achieve.

It is worth noting that fish from 2000 and 2001 had faster growth rates while in freshwater and in the estuary compared with those fish from 2005. This is surprising, as conditions in the freshwater and estuarine environments were not largely atypical in 2005 (Lindley et al. 2009). This difference in pre-ocean growth rate between the 2 years could be driven by a difference in the proportion of larger hatchery and smaller naturally spawned individuals. This remains unknown as the proportion of hatchery and natural origin fish was only measured for 2005. Another unexplored explanation for the differences in growth before ocean entry could be an increase in freshwater selective mortality in 2000 and 2001 that removed the small, slower-growing individuals before we collected them at the estuary-exit. A third scenario involves access to floodplains. Previous work has shown that access to floodplains (i.e. the Yolo Bypass) during seaward migration has a positive impact on juvenile salmon growth and survival to adulthood (Sommer et al. 2001, Jeffres et al. 2008). The Yolo Bypass floodplain was open for a greater number of days in 2000 than both 2001 and 2005 (www.water.ca.gov) giving the fish from 2000 more access to floodplain rearing. This may have been sufficient to manifest the difference in pre-ocean growth rate seen when comparing the combined 2000 and 2001 samples to the 2005 samples.

The change in proportion of hatchery and naturally spawned individuals from estuary-exit to fall-ocean in 2005 was small and not statistically significant.

This was surprising due to the evidence for size and growth-rate selective mortality; hatchery individuals exhibited significantly larger body sizes and faster growth before ocean entry. Previous work has shown the majority of the Chinook salmon in California's ocean fishery were of hatchery origin, and therefore we focused on a sampling design with the power to statistically detect a >20% shift in composition between the estuary and those sampled in the fall in the ocean (Barnett-Johnson et al. 2007, Kormos et al. 2012). In addition, the high cost of sulfur analyses limited the number of samples ($N = \sim 100$) that were feasible for this study. Notably, the shift in hatchery fish composition from 60 to 67% was small enough that to deem it statistically significant (90% power, $\alpha 0.05$) would have required more than 2000 samples. It appears, then, that during 2005 (a year of poor ocean and salmon productivity) there was no highly favored benefit to being of hatchery or natural origin. This was surprising and prompts further investigation on additional selective factors, as our findings here suggest that hatchery individuals should have had a survival advantage in 2005 based on larger body sizes and faster growth rates.

CONCLUSIONS

We detected a significant effect of both size and growth-rate selective mortality on juvenile Central Valley fall-run Chinook salmon that appears independent of fish rearing origin. The effect was variable and only detected in a year of poor ocean conditions with low food availability and lower survival to adulthood. The mortality appeared to have occurred early in the ocean life history, predominantly between estuary-exit and the first month at sea. This significant mortality event preceded devastatingly poor adult returns in 2007, which then led to complete closures of the salmon fisheries off California in 2008 and 2009. To our knowledge, this is the first study of its kind to be done for California's Central Valley Chinook salmon, and one of the few to evaluate selective mortality over the earliest time at sea for a salmonid. We also used an innovative approach to evaluate the extent to which selective mortality acts on rearing origin. This study suggests that otoliths can be used to assess the degree of selective mortality following the critical period of ocean entry. The degree of selective mortality can then be used as an early indicator of the potential cohort success. Further work will be necessary to determine the strength and predictive ability of this indicator and the extent

to which growth in specific freshwater habitats, as well as ocean drivers, affect the degree of selective mortality and survival to adulthood. Quantifying the degree of mortality could be used to direct adaptive management of remaining cohorts (i.e. 1 and 2 yr olds) and buffering of potentially poor adult returns 2 years out.

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