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Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*

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ABSTRACT: Chinook salmon is an anadromous species that varies in size at freshwater emigration, which is hypothesized to increase population resiliency under variable environmental regimes. In California's Central Valley (USA), the majority of naturally spawned juveniles emigrate in 2 pulses: small juveniles (referred to as fry), typically ≤55 mm fork length (FL), emigrate from natal streams in February–March, whereas larger juveniles (smolts), typically >75 mm FL, emigrate in mid-April–May. In some river systems, there is a smaller pulse of emigrants of intermediate size (parr), typically 56 to 75 mm FL. Although the relative contribution of these migratory phenotypes to the adult population is unknown, management activities focus on survival of larger emigrants and most artificially produced fish (98%) are released from hatcheries at parr and smolt sizes. We reconstructed individual length at freshwater emigration for a sample of adult Central Valley Chinook salmon from 2 emigration years using chemical (Sr:Ca and Ba:Ca) and structural otolith analyses. The adult sample was comprised of individuals that emigrated as parr (mean = 48%), followed by smolts (32%) and fry (20%). Fry-sized emigrants likely represent natural production because fish ≤55 mm FL comprise <2% of the hatchery production. The distribution of migratory phenotypes represented in the adult sample was similar in both years despite apparent interannual variation in juvenile production, providing evidence for the contribution of diverse migratory phenotypes to the adult population. The contribution of all 3 migratory phenotypes to the adult population indicates that management and recovery efforts should focus on maintenance of life-history variation rather than the promotion of a particular phenotype.

KEY WORDS: Chinook salmon · Migratory phenotype · Otolith chemistry

INTRODUCTION

Many diadromous fishes display variation in juvenile migratory behavior. Individuals with distinct migratory phenotypes may experience differential survival and thus contribute to a population's resiliency, defined as its ability to persist following disturbances across variable environmental conditions (Holling 1973, Stearns 1992, Hilborn et al. 2003, Secor 2007, Bottom et al. 2009). Chinook salmon *Oncorhynchus tshawytscha* is an anadromous species that displays extensive variation in the size at, and timing of, freshwater emigration (Taylor 1990, Healey 1991, Quinn 2005, Waples et al. 2009). However, limited empirical data on the contribution of distinct migratory phenotypes to adult populations across years prevents a robust evaluation of the resiliency hypothesis. Certain approaches, such as artificial tagging studies and scale analyses, can be used to determine the contribution of migratory phenotypes; however, each of these methods has substantial

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logistic and interpretive limitations. Chemical and structural analyses of fish otoliths, which hold a record of aspects of an individual's environment, provide an alternative approach to generating empirical data on the contribution of migratory phenotypes without the need to recapture individuals (Campana 1999, Campana & Thorrold 2001).

Extensive agricultural land use conversion and water development within California's Central Valley (USA) (Fig. 1) have impacted the region's fall Chinook salmon (Moyle 2002), which are listed as a species of concern under the Endangered Species Act (Good et al. 2005). The majority of naturally spawned juveniles emigrate in 2 pulses: small juveniles (referred to as fry), typically ≤55 mm fork length (FL), emigrate from natal streams in February–March, whereas larger juveniles (smolts), typically >75 mm FL, emigrate in mid-April–May (Brandes & McLain 2001) (Fig. 2a–f). In some river systems, there is a smaller pulse of emigrants of intermediate size (parr), typically 56 to 75 mm FL (Fig. 2g–h). The movement patterns of these emigrant size classes are not well described, but it has been suggested that individuals remain in freshwater portions of the Sacramento–San Joaquin River Delta until they attain sizes >70 mm FL, at which point they enter the ocean (MacFarlane & Norton 2002). Additionally, although there is no information on the relative survival of these emigrant size classes, water and hatchery management strategies within the Central Valley focus on maximizing survival of smolt-sized emigrants (Brandes & McLain 2001, Williams 2001). For example, in-river flows are regulated to maximize survival during smolt emigration and >50% of hatchery juveniles are released as smolts and 2% as fry.

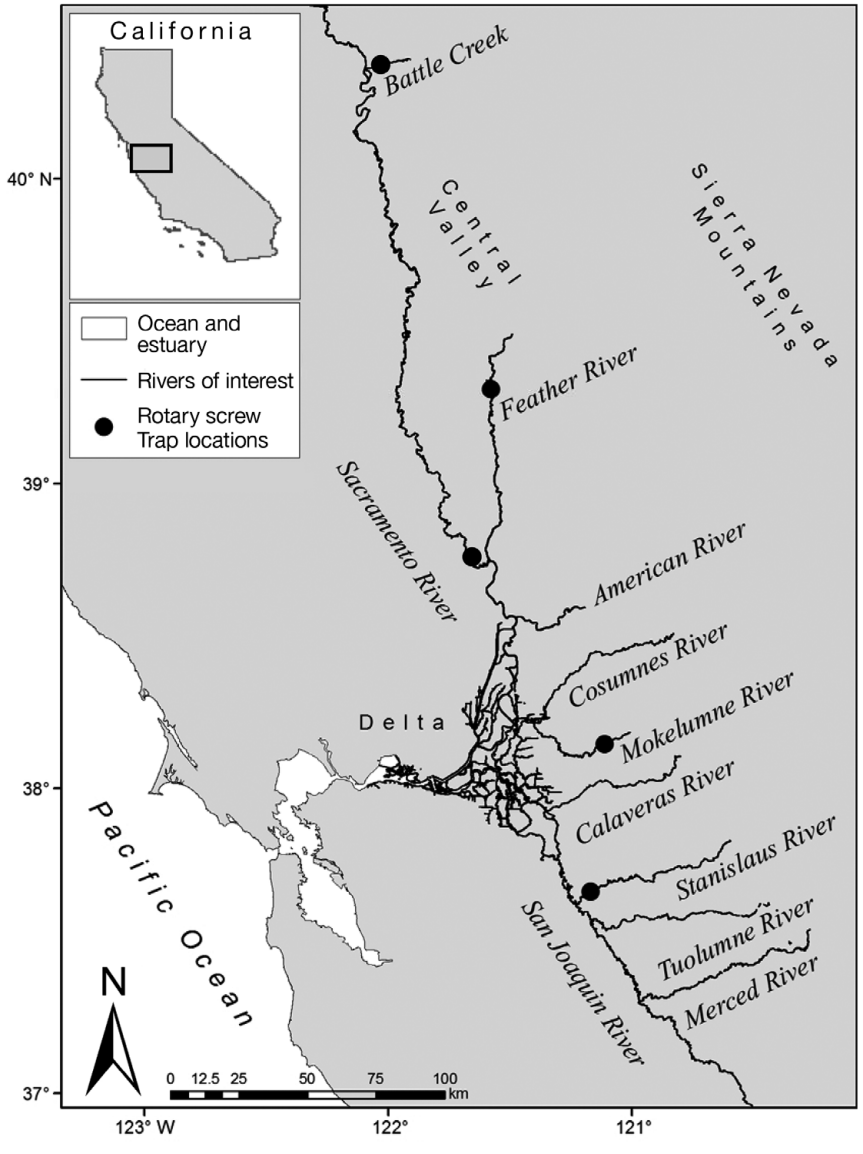

Fig. 1. General location of the Central Valley, California (inset). Major rivers, approximate rotary screw trap locations (●), and the Delta region are also identified

Numerous studies have used otolith Sr:Ca to reconstruct aspects of migratory history (e.g. Elsdon & Gillanders 2006, Thibault et al. 2007, Volk et al. 2010) and Sr:Ca and Ba:Ca have been combined to examine diadromous migrations (e.g. McCulloch et al. 2005, Bradbury et al. 2008, Crook et al. 2008, Milton et al. 2008). Such reconstructions are possible because otoliths grow continuously throughout the life of a fish and certain elements, such as Sr, are incorporated into an otolith in proportion to their water concentration. The ratio of Sr to Ca (Sr:Ca) is typically greater in marine waters (~8.5 mmol mol^{-1}) than in freshwater (<5 mmol mol^{-1}) although elevated values can occur in freshwater (Kraus & Secor 2004, Brown & Severin 2009). Therefore, variation in otolith Sr:Ca is often used to reconstruct diadromous migrations (e.g. Limburg 1995, Secor et al. 1995, Daverat et al. 2005). However, the utility of using otolith Sr:Ca is limited; the reason being that Sr and Ca water concentrations vary linearly (conservatively) along a salinity gradient, while Sr:Ca ratios display a curvilinear relationship with salinity which results in minimal variation in Sr:Ca above salinities of ~8 to 10 (Kraus & Secor 2004, Zimmerman 2005). Otolith Ba to Ca (Ba:Ca), which is also positively related to water Ba:Ca, may provide greater dis-

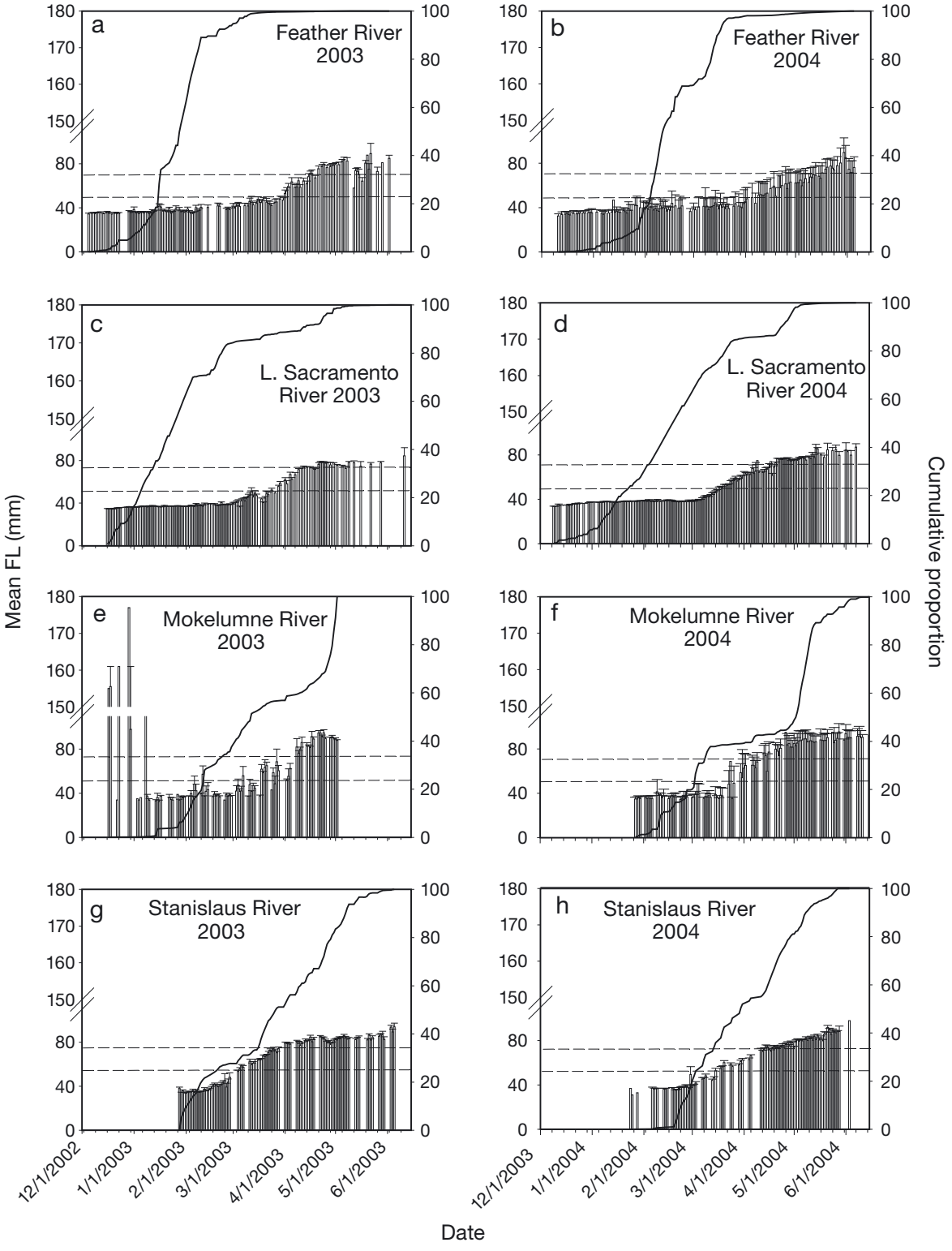

Fig. 2. *Oncorhynchus tshawytscha*. Size and timing of juvenile Chinook salmon emigration in the Central Valley, California. Mean (±SE) fork length (FL, mm; bars) and cumulative percent frequency of the total catch (solid line) are plotted against day of year (mo/d/yr). Data are from in-river rotary screw traps collections. In all cases, traps were placed in-river immediately prior to the first date with data presented. Data are included for 2003 and 2004 for (a,b) Feather River; (c,d) Lower Sacramento River; (e,f) Mokelumne River; and (g,h) Stanislaus River. Size designations for fry (≤55 mm FL), parr (56 to 75 mm FL), and smolt (>75 mm FL) are indicated by dashed lines

crimination between estuarine and marine habitats because Ba:Ca is often much greater (>50×) in freshwater compared with marine waters (Elsdon & Gillanders 2005, Hamer et al. 2006). Additionally, Ba displays non-conservative mixing behavior, which results in regions of enrichment at low salinities due to several processes, including desorption and resuspension (Coffey et al. 1997, Colbert & McManus 2005). Otolith Sr:Ca and Ba:Ca may be more useful in combination when discriminating among freshwater, estuarine, and marine residence than either elemental ratio alone, and allow for more detailed reconstruction of migratory phenotypes.

Few studies have used otolith Sr:Ca to quantify the relative contribution of juvenile migratory phenotypes in an adult population (Limburg 2001, Kraus & Secor 2004, Chino & Arai 2009) and, to our knowledge, none have evaluated the combined potential of Sr:Ca and Ba:Ca in such an approach. The primary objective of the present study was to reconstruct the juvenile migratory phenotypes of adult Central Valley fall Chinook salmon using otolith elemental (Sr:Ca and Ba:Ca) and structural analysis and determine the proportion of each phenotype present in a sample of adults that emigrated in 2003 or 2004. Given that rates of otolith elemental incorporation can vary among species, with temperature and possibly with salinity (Campana 1999, Elsdon & Gillanders 2003, Miller 2009), we developed species-specific models for the otolith incorporation of Sr:Ca and Ba:Ca to accomplish this objective. Furthermore, as noted by Elsdon et al. (2008), it is important to examine spatial patterns in water chemistry to confirm interpretations of otolith composition. Therefore, we also compiled data on water Sr:Ca and Ba:Ca throughout the Central Valley and coastal ocean. Finally, we obtained information on the relative abundance of migratory phenotypes observed in the juvenile emigrant population in 2003 and 2004 to compare with our adult reconstructions.

MATERIALS AND METHODS

Otolith incorporation of Sr and Ba in juvenile Chinook salmon. Species-specific models that describe the relationship between metal:calcium (Me:Ca) ratios of water and biogenic carbonates, such as those for corals and bivalves, are often used in palaeological and modern applications (e.g. Swart et al. 1999, Wei et al. 2000, Gaetani & Cohen 2006). In these cases, the relationships between water and carbonate Me:Ca are quantified under controlled laboratory conditions, and those relationships are used to interpret variations observed in field-collected individuals. However, we are aware of only one study that developed a species-specific model of otolith elemental incorporation to address a specific ecological question (see Kraus & Secor 2004). In previous studies, information from otoliths of other species were used to generate threshold levels indicative of habitat transitions for the species of interest (e.g. Hedger et al. 2008) or the species of interest was collected from representative locations to generate a baseline of otolith Me:Ca values (e.g. Daverat et al. 2005).

Here we developed models for the otolith incorporation of Sr and Ba in juvenile fall Chinook salmon using data on water and otolith Sr:Ca and Ba:Ca that were collected from field collections and laboratory experiments. Data were included in models only if measurements of both water and otolith Me:Ca were available (Table 1). For water analyses, samples were collected, filtered (0.45 µm), and acidified using standard methods (Eaton et al. 2005). Standard calibrations were generated with SPEX Certiprep® Group certified reference materials, and Ca, Sr, and Ba concentrations were measured with a Teledyne Leeman Prodigy inductively coupled plasma-optical emission spectrometer. Samples of known concentration (National Institute of Standards and Technology [NIST]; Standard

Table 1. Sources of juvenile Chinook salmon otoliths used to determine relationships between water and otolith Sr:Ca and water and otolith Ba:Ca. Mean water temperature (°C), salinity, and Sr:Ca and Ba:Ca ratios associated with each source are included. n: number of juveniles included for each category; trt: salinity × water Me:Ca treatment combination; OR: Oregon; CV: Central Valley; CA: California; CLC: controlled laboratory conditions; nd: no data available

Source of juveniles	Date	Water temperature (°C)	Salinity	Water Sr:Ca		Water Ba:Ca	
				mmol mol^{-1}	n	µmol mol^{-1}	n
Trask River hatchery, OR	Apr 2006	nd	0	2.6	9	84	8
Merced River hatchery, CV	Feb 2008	nd	0	3.4	11	1600	7
Mokelumne River hatchery, CV	Feb 2008	nd	0	5.1	7	1100	11
Coastal ocean, Southern OR, Northern CA	Jul 2008	nd	32	8.6	16	5	16
J. A. Miller (unpubl. data), CLC	nd	8.8, 11.9, 15.3	0, 5, 10, 15	1.5, 7.2, 7.8, 8.2	4–6 fish/trt	30, 60, 75, 135, 230, 520, 1035	4–6 fish/trt
Zimmerman (2005), CLC	nd	4.9–10.7	0, 6.3, 12.7, 18.6, 15.5, 33.0	2.8, 6.4, 7.4, 7.7, 7.9, 8.4	12 fish/trt	nd	nd

Reference Material 1643e) were introduced throughout the run to estimate accuracy: measured concentrations were within 2.0, 1.3, and 2.4% of reported values for Ca, Sr, and Ba, respectively (n = 7). Precision was estimated with repeated measurements of the same sample (NIST 1643e) and varied by <2.5% for all 3 elements (n = 3). For otolith analyses, sagittae were prepared using standard methods to minimize contamination (e.g. Miller 2009). Otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were collected using a VG PQ ExCell inductively coupled plasma mass spectrometer (ICPMS) with a New Wave DUV193 excimer laser. The laser was set at a pulse rate of 10 Hz with a 40 µm diameter spot size and travelled at 5 µm s^{-1}. Limits of detection (ppm) were calculated as 3 standard deviations of background measurements: Ca = 0.02, Sr = 0.03, and Ba = 0.008. Normalized ion ratios were converted to elemental ratios as described in Miller (2007), converted to molar ratios based on the molar mass of Ca, Sr, and Ba, and presented as mmol mol^{-1} for Sr:Ca and µmol mol^{-1} for Ba:Ca. The mean percent relative standard deviations (%RSD) for NIST 612 glass during data collection were ^{43}Ca = 3.2, ^{86}Sr = 4.1, and ^{138}Ba = 4.4%. A calcium carbonate standard of known composition developed by the US Geological Survey (USGS MACS-2) provided an estimate of accuracy: measured values were within 2% of known values for both Sr:Ca and Ba:Ca. Linear and non-linear regression analyses were used to quantify the relationships between otolith and water Me:Ca using Statistica®. Data were examined for normality and homogeneity of variance prior to analysis.

Spatial patterns in water chemistry. In order to examine spatial patterns in water chemistry, we acquired existing data on Ca, Sr, and Ba water concentrations in coastal waters and within the Central Valley and collected additional samples from coastal areas and tributaries, including the Cosumnes, Mokelumne, Calaveras, Stanislaus, and San Joaquin Rivers (Fig. 1, Table A1 in Appendix 1). The purpose of this data collection effort was to provide an estimate of the variation in freshwater Sr:Ca and Ba:Ca observed in the Central Valley and determine if there were freshwater systems with elevated Sr:Ca that could confound interpretation of migratory history based on adult otoliths. Water samples were collected and processed as described above. Samples of known concentration (NIST 1643e) were introduced throughout the run to estimate accuracy: measured concentrations were within 2.5, 1.8, and 2.6% of reported values for Ca, Sr, and Ba, respectively (n = 3). Precision was estimated with repeated measurements of the same sample (NIST 1643e) and varied by <3.2% for all 3 elements (n = 3).

The relationships between water Sr:Ca and Ba:Ca and salinity (0 to 32) were predicted based on end member water concentrations similar to those observed in the Delta region, which is the downstream extent of freshwater in the Central Valley, and coastal waters. For our model, we assumed conservative mixing behavior for Ca, Sr, and Ba. However, it is important to note that Ba often displays non-conservative mixing with regions of Ba release, due to desorption and resuspension, between salinities of 1 and 15 (Coffey et al. 1997). Therefore, our Ba:Ca model represents a minimum estimate for water Ba:Ca at low salinities. It is likely that at low salinities Ba:Ca ratios often exceed values predicted based on conservative mixing, particularly during periods of high freshwater discharge (Coffey et al. 1997, Colbert & McManus 2005).

Back-calculation of juvenile size. The reconstruction of individual length at specific habitat transitions, such as freshwater emigration, based on otolith measurements requires an accurate back-calculation model. Therefore, we confirmed that otolith size provides a robust predictor of fall Chinook salmon size during the first year of life by collecting juveniles from several locations and brood years to quantify the relationship between fish and otolith size (Table 2). We measured juvenile FL (0.5 mm) prior to preservation, removed sagittal otoliths, and measured otolith width (OW, to the nearest µm) along the dorsal–ventral growth axis at the widest point. There were no significant differences in OW between left and right sagittae (n = 50, $p > 0.40$), and preliminary analysis indicated that OW was a better predictor of fish length than otolith length. All otolith distances were measured using a Leica® stereoscope and Image Pro Plus®. A linear regression analysis of FL and OW was completed for all juveniles.

Application to Central Valley fall Chinook salmon. Adult Chinook salmon were collected during the Ore-

Table 2. *Oncorhynchus tshawytscha*. Source, year of collection, and size range of juvenile Chinook salmon used to develop the relationship between otolith and fish size. n: number of juveniles included for each category; CV: Central Valley; OR; Oregon

Source	Year of collection	Fork length (mm)	n
Mokelumne River hatchery, CV	2008	40–48	7
Umpqua River hatchery, OR	2007	40–94	15
Trask River hatchery, OR	2007	43–88	8
Merced River hatchery, CV	2008	51–83	11
Rogue River hatchery, OR	2007	63–80	9
Coastal ocean, southern OR	2006–2007	84–125	52
Coastal ocean, off Columbia River	1999, 2000, 2002, 2006	98–166	21

gon ocean troll fishery in 2006. Biological data, including FL (cm), a tissue sample for genetic analysis, and several scales were collected from 2567 individuals. Otoliths were collected from a subset of those adults (n = 395). The region of origin for each individual was determined using a microsatellite DNA baseline, the Genetic Analysis of Pacific Salmonids, which identifies Central Valley fall Chinook salmon with a reported mean accuracy of 94.5% (Seeb et al. 2007). Fifty-nine percent of the fish were identified as Central Valley fall Chinook salmon. Only otoliths from fish identified as Central Valley fall Chinook salmon with >90% posterior probability of assignment were included in remaining analyses (n = 100). Scales were used to determine individual age and, hence, year of emigration. Individual age was determined by counting winter annuli on scales. Each scale was read by 2 observers, and disagreements were resolved during a joint third reading. Scales from other Central Valley adult Chinook salmon of known age were available and included to provide a test of ageing accuracy (n = 31): for these individuals, age was known due to the presence of coded wire tags (CWTs) (Jefferts et al. 1963).

Adult otoliths (n = 100) were prepared as described in 'Materials and methods', 'Otolith incorporation of Sr and Ba in juvenile Chinook salmon', except that 52% were prepared as transverse and 48% as sagittal sections. We visually inspected all sections for proper orientation and exposure of the core primordia to ensure that data were collected along the same dorsal–ventral axis on all samples. For 9 individuals, we prepared one otolith as a transverse section and one as a sagittal section to compare the back-calculated size estimates generated with the 2 preparations. Otolith ^{43}Ca, ^{86}Sr, and ^{138}Ba data were collected along transects that intersected the core region (Fig. 3) using methods similar to those described above. Limits of detection (ppm) were calculated as 3 SD of background measurements: Ca = 0.09, Sr = 0.09, and Ba = 0.007. The mean %RSDs for NIST 612 glass during data collection were ^{43}Ca = 3.0, ^{86}Sr = 4.4, and ^{138}Ba = 4.2%. External estimates of accuracy based on USGS MACS-2 were within 3 and 2% of known values for Sr:Ca and Ba:Ca, respectively.

We then combined otolith Sr:Ca and Ba:Ca data and structural analysis to determine individual length at freshwater emigration. For each individual, the OW at the time of freshwater emigration was determined by the initial and abrupt increase in otolith Sr:Ca, which indicates exit from freshwater, prior to stabilizing at brackish/ocean values (Fig. 3). This transition was verified by the occurrence of low or declining otolith Ba:Ca at the same time as the abrupt increase in otolith Sr:Ca. Threshold values for otolith Me:Ca during freshwater, brackish, and marine residence were determined based on our relationships between (1) otolith and water Me:Ca (see 'Results', 'Otolith incorporation of Sr and Ba in juvenile Chinook salmon') and (2) water Me:Ca and salinity (see 'Results', 'Spatial patterns in water chemistry'). Individual FL (mm) at freshwater emigration was estimated using the measurements of OW based on otolith Sr:Ca and Ba:Ca and the linear relationship between FL and OW developed for juvenile fall Chinook salmon (see 'Results', 'Back-calculation of juvenile size'). Confidence intervals (95% CI) for back-calculated size predictions were generated using standard methods ($\hat{Y}_i \pm t_{0.05(2)} \times s_{\hat{Y}i}$; Zar 1999).

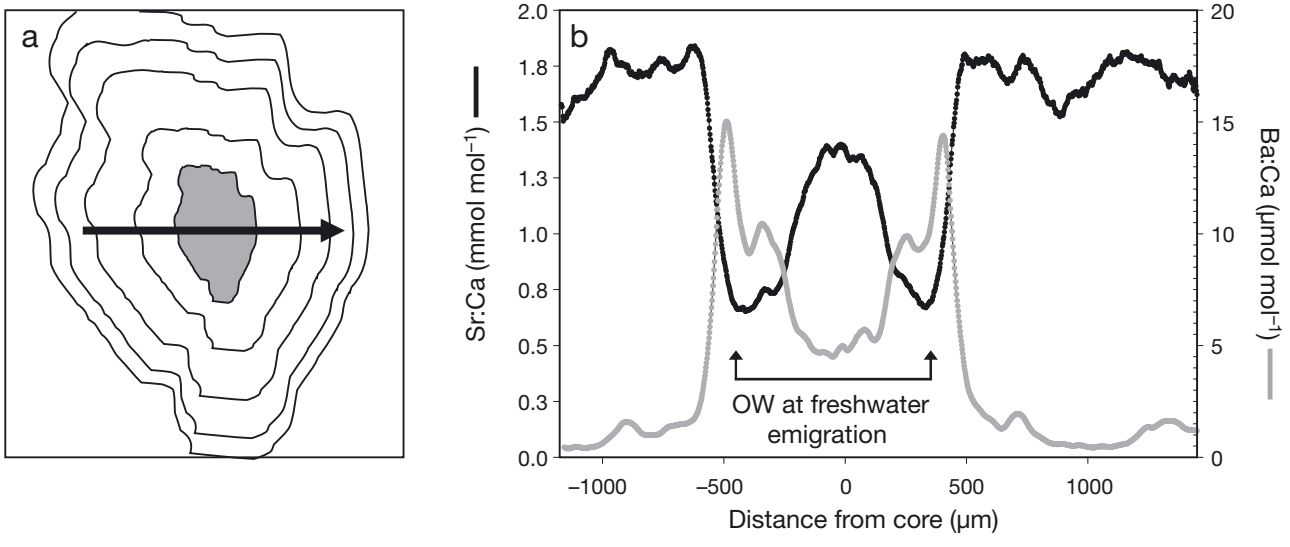

Fig. 3. *Oncorhynchus tshawytscha*. (a) Schematic of a sagittal section of an adult fall Chinook salmon otolith. Laser path for elemental analysis is identified. The core, which represents the egg and early juvenile life history, is shaded. (b) Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}) across the otolith. Measurement of otolith width (OW) at freshwater emigration is identified

Production of juvenile fall Chinook salmon. We would need comprehensive data on the relative abundance of the phenotypes present in natural and hatchery juvenile production in 2003 and 2004 to estimate survival rates for each phenotype based on our adult sample. However, there are no estimates for total natural production in the Central Valley basin. Therefore, we used data available from in-stream rotary screw traps to describe the size and relative abundance of naturally produced juveniles. We compiled daily information on size and number of individuals collected in traps on the lower Sacramento, Feather, Mokelumne, and Stanislaus Rivers (Fig. 1). The data from these 4 traps combined represent the size and relative abundance of >70% of the natural production (Yoshiyama et al. 2000). All of these traps, except for the lower Sacramento River trap, are placed at river locations selected to maximize collection of naturally spawned emigrants. State hatcheries transport their production to estuarine waters for release so they would not be collected in-river. The only federal hatchery in the basin, i.e. the Coleman National Fish Hatchery on Battle Creek, releases juveniles in-stream and they could be collected in the lower Sacramento River trap. Additionally, estimates of total natural production upstream of a trap were available for the Feather and Mokelumne Rivers as well as a fifth trap on lower Battle Creek (Fig. 1). Trap data were obtained from the Bay Delta and Tributaries Project (http://bdat.ca.gov/) and R. Vincik, California Department of Fish and Game. For hatchery production, comprehensive data on the number and size of juveniles released in 2003 and 2004 are available from the Regional Mark Information System (www.rmpc.org/). Therefore, we compiled information on hatchery production from the 5 Central Valley hatcheries: the Coleman National Fish Hatchery and 4 state-run hatcheries, including the Nimbus, Feather River, Mokelumne River, and Merced River hatcheries. Release information is reported as fish lb^{-1}; therefore, Piper et al. (1982) was used to convert mass to FL. We used the data collected from traps and hatchery records to generate (1) daily mean size estimates and cumulative percent frequencies for emigrants, and (2) size-frequency distributions for in-stream and hatchery production in 2003 and 2004 for comparison with our adult reconstructions of size at freshwater emigration.

RESULTS

Otolith incorporation of Sr and Ba in juvenile Chinook salmon

For Sr:Ca, data were available across a range of temperatures (4.9 to 15.3°C), salinities (0 to 33), and water Sr:Ca ratios (1.5 to 8.6 mmol mol^{-1}) (Table 1). Otolith Sr:Ca increased curvilinearly as water Sr:Ca increased, and a polynomial regression provided the best fit to the data (Fig. 4a). For Ba:Ca, data were available across a range of temperatures (8.8 to 15.3°C), salinities (0 to 32), and water Ba:Ca ratios (5 to 1600 µmol mol^{-1}) (Table 1). Otolith Ba:Ca also increased as water Ba:Ca increased, although in a linear manner; therefore, a linear model was used to describe the relationship (Fig. 4b). It appears that otolith Ba:Ca may have reached a plateau of ~11 µmol mol^{-1} at water Ba:Ca ratios of ~1100 µmol mol^{-1}; however, data from fish reared at higher levels of Ba:Ca would be needed to draw any firm conclusions. It is important to note

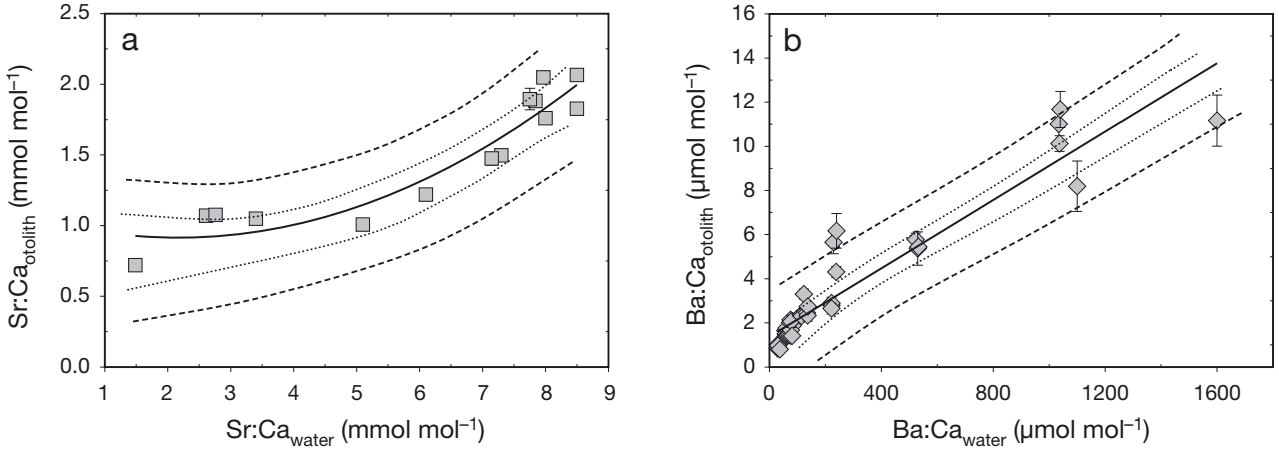

Fig. 4. *Oncorhynchus tshawytscha*. Relationships between otolith and water Sr:Ca and Ba:Ca. (a) Mean (±1 SE) otolith Sr:Ca versus water Sr:Ca (mmol mol^{-1}). Curve (solid line) was fit by following relationship: $y = 0.027$ (±0.011 SE) $x^2 - 0.118$ (±0.121 SE) $x + 1.043$ (±0.266 SE) ($p < 0.001$, $r^2 = 0.89$, n = 14). (b) Mean (±1 SE) otolith Ba:Ca versus water Ba:Ca (µmol mol^{-1}). Curve (solid line) was fit by the following relationship: $y = 0.008$ (±0.0004 SE) $x + 1.37$ (±0.207 SE) ($p < 0.001$, $r^2 = 0.89$, n = 38). Estimates for the 95% confidence (dotted line) and prediction (dashed line) intervals are included

that although there were positive relationships between otolith and water Me:Ca ratios, the rate of incorporation declined as water Me:Ca increased. For example, at water Ba:Ca > 1000 µmol mol^{-1}, <1% was incorporated into otoliths, whereas at water Ba:Ca = 5 µmol mol^{-1}, 32% was incorporated into otoliths.

Spatial patterns in water chemistry

Observed freshwater Me:Ca within the Central Valley ranged from 2.41 to 5.48 mmol mol^{-1} for Sr:Ca and from 141 to 1679 µmol mol^{-1} for Ba:Ca (Table A1). Observed ocean Me:Ca averaged (±SD) 8.55 ± 0.33 mmol mol^{-1} for Sr:Ca and 5.03 ± 1.08 µmol mol^{-1} for Ba:Ca. We used the empirically derived relationships between otolith and water Me:Ca (Fig. 4) to predict otolith Me:Ca ratios for juvenile Chinook salmon from the Central Valley (Table A1). We then compared predictions with observed otolith Me:Ca values, which were generated by averaging across ~100 µm of each adult otolith during presumptive freshwater and marine residence (n = 99). Note that one otolith was removed from analysis (see 'Results', 'Application to Central Valley fall Chinook salmon').

Predictions for otolith Sr:Ca during freshwater residence ranged from 0.91 (±0.17 95% CI) to 1.20 (±0.09 95% CI) mmol mol^{-1} (Table A1). The majority (85/99) of otolith Sr:Ca observations during presumed freshwater residence fell within the predicted 95% CI (0.75 to 1.29 mmol mol^{-1}). Thirteen fish displayed otolith Sr:Ca lower than predicted (i.e. 0.62 to 0.74 mmol mol^{-1}) and one fish displayed otolith Sr:Ca higher than predicted (1.31 mmol mol^{-1}). Our predictions for otolith Ba:Ca during freshwater residence ranged from 2.47 (±0.35 95% CI) to 14.30 (±0.88 95% CI) µmol mol^{-1} (Table A1). The majority (83/99) of observations of otolith Ba:Ca during presumed freshwater residence also fell within the predicted 95% CI (2.12 to 15.18 µmol mol^{-1}). Two fish displayed otolith Ba:Ca lower than predicted (i.e. 1.78 to 2.10 µmol mol^{-1}) and 14 fish displayed otolith Ba:Ca higher than predicted (15.40 to 32.28 µmol mol^{-1}). For otolith Me:Ca during ocean residence, observed values tended to be lower than predicted. Observed otolith Sr:Ca during ocean residence ranged from 1.50 to 2.20 mmol mol^{-1} and 44% of the observations fell with the predicted range (2.01 ± 0.13 95% CI); the remaining observations were all less than predicted. Observed otolith Ba:Ca during ocean residence ranged from 0.35 to 1.31 µmol mol^{-1} and 12% of the observations fell with the predicted range (1.40 ± 0.40 95% CI); the remaining observations were all less than predicted. There was no overlap in the mean otolith Me:Ca ratios observed during presumed freshwater and marine residence.

We generated predictions for water Sr:Ca and Ba:Ca from salinities of 0 to 32 based on end member water Me:Ca values similar to those observed in the Delta region and coastal waters (Fig. 5). Based on predicted and observed values, residence in freshwater (with Sr:Ca < 7 mmol mol^{-1} and Ba:Ca > 80 µmol mol^{-1}) would result in otolith signatures distinct from residence in marine waters (with Sr:Ca > 7.0 mmol mol^{-1} and Ba:Ca < 80 µmol mol^{-1}; Fig. 5, Table A1). Given the predicted water Me:Ca ratios within the Central Valley, otolith Me:Ca ratios would not be distinct at salinities >3 for Sr:Ca and >6 for Ba:Ca. (Fig. 5). However, as noted, Ba release commonly occurs in low salinity waters. If localized enrichment of Ba occurs in low salinity waters and results in Ba:Ca > 80 µmol mol^{-1} while Sr:Ca remains greater than freshwater values (>7.0 mmol mol^{-1}), otolith signatures of fish residing in those waters would be distinct from freshwater or marine signatures. Based on these predictions and observations, otolith Sr:Ca < 1.5 mmol mol^{-1} with Ba:Ca > 2 µmol mol^{-1} indicates freshwater residence, otolith Sr:Ca ≥ 1.5 mmol mol^{-1} with Ba:Ca > 2 µmol mol^{-1} indicates brackish residence, and otolith Sr:Ca ≥ 1.5 mmol mol^{-1} with Ba:Ca < 2 µmol mol^{-1} indicates brackish/ocean residence.

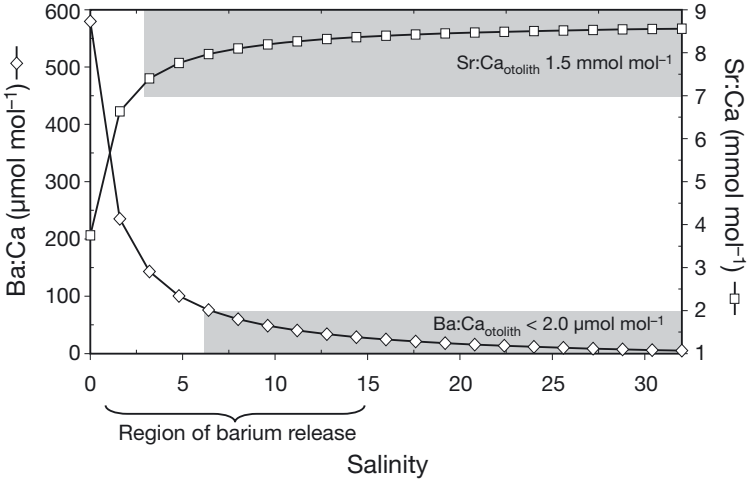

Fig. 5. Predicted relationship between water Ba:Ca and Sr:Ca and salinity. Freshwater values (salinity = 0) are within the range observed in the Central Valley Delta region. Shaded boxes indicate the water Me:Ca and salinities at which there would be minimal variation in otolith Me:Ca. Predicted values for otolith Ba:Ca and Sr:Ca at those water Me:Ca ratios and salinities are included in shaded boxes. Predictions were based on observed relationship between otolith and water Me:Ca, measured water Me:Ca, and the assumption of conservative mixing behavior

Back-calculation of juvenile size

For juveniles, FL (mm) was positively and linearly related to OW (µm) ($r^2 = 0.93$, n = 123, $p < 0.001$). Therefore, we used the following relationship to estimate FL based on OW:

$$FL = 0.060\ (\pm 0.002\ SE) \times OW + 6.91\ (\pm 2.19\ SE) \quad (1)$$

Fish were grouped into 10 mm bins based on back-calculated size at freshwater emigration.

Application to Central Valley fall Chinook salmon

Adult Chinook salmon ranged in size from 66 to 102 cm FL at capture, and their scales displayed 2 or 3 winter annuli except for one fish with 4 winter annuli. As the fish with 4 annuli was the only individual that emigrated in 2002, it was removed from the analysis. Therefore, all individuals included hereafter emigrated in 2003 (n = 49) or 2004 (n = 50). All the 31 known-age, CWT-fish were correctly aged (= 100% accuracy). There was no systematic difference in back-calculated size estimates (paired *t*-test, df = 9, p = 0.46) between transverse and sagittal sections and the mean difference in back-calculated size was <5%.

Overall, estimated length at freshwater emigration ranged from 33 to 104 mm FL. The error (95% CI) associated with individual back-calculations ranged from 2.3 to 10.7% and averaged 3.0%. Parr-sized individuals comprised the largest emigrant group in both 2003 and 2004 (mean ± SD across years = 47.5 ± 0.8%), followed by smolts (32.4 ± 6.2%), and fry (20.1 ± 5.4%; Fig. 6a). For 18 individuals, the transition from fresh to marine waters included a period during which otolith Sr:Ca was >1.5 mmol mol^{-1} and Ba:Ca was >2 µmol mol^{-1}, which is predicted to represent residence in brackish waters. Of the 18 individuals with this brackish otolith signature, 11 were fry, 6 were parr, and 1 was a smolt.

Juvenile production

Over 36 million fall Chinook salmon were released from state and federal hatcheries in 2003 and more than 27 million were released in 2004 (Fig. 6b). The majority of juveniles were released as smolts (54 to 65%), followed by parr (35 to 45%), with less than 2% released as fry. The majority of juveniles (>75%) collected in traps within the Sacramento River basin emigrated as fry in both 2003 and 2004 (Fig. 6c,d). Although some juveniles from the federal hatchery could be collected in the lower Sacramento River trap, the observed size distribution of fish collected in that trap indicates that the catch consisted of primarily natural production (Fig. 6b versus Fig. 6d). Juveniles from the Mokelumne and Stanislaus Rivers displayed more even distributions of emigrant size classes (Fig. 6e,f).

Given the low proportion of hatchery fish released at fry sizes (<2%), there is a high likelihood that the fry emigrants observed in the adult samples represent natural production. Additionally, there was greater natural production (3×) above the Feather River trap in 2004 than 2003, which resulted in more fry-sized emigrants (Fig. 6c). Similarly, the mean estimate of total natural production upstream of a trap on lower Battle Creek was greater (2.8×) in 2004 than in 2003 (581 677 and 206 266 juveniles in 2004 and 2003, respectively), and those catches comprised predominantly individuals <40 mm FL (i.e. >90%). Given that the Feather River and Battle Creek are estimated to contribute nearly 50% of the total production in the Central Valley (Yoshiyama et al. 2000), it appears that fry production was greater in 2004 than in 2003. Despite this apparent interannual variation in production, fry emigrants made up an average of 20% of the adult sample in both years (Fig. 6a), which indicates potentially greater fry survival in 2003 than 2004. Furthermore, our data indicate that parr emigrants represent a greater proportion of the adult sample than the juvenile emigrant population (Fig. 6a versus Fig. 6b–f), potentially a result of in-river growth of fry emigrants or greater rates of survival for parr emigrants.

DISCUSSION

Quantifying the extent of phenotypic variation in juvenile migratory behavior is the initial step in understanding if, and how, such variation contributes to the resilience of managed populations. Examining the role of phenotypic variation in managed populations is an important component of effective conservation. This is particularly true within the highly modified Central Valley, where freshwater flows are often re-allocated during smolt emigration to improve survival under the assumption that smolts contribute disproportionately to the adult population (Brandes & McLain 2001, Williams 2001). Additionally, studies examining survival of juveniles during migration through the riverine and Delta regions of the Central Valley focus on individuals >75 mm FL, a result of using telemetry methods that require relatively large individuals (i.e. >140 mm) (Perry et al. 2010) or focusing on hatchery fish (Kimmerer 2008). In the present study, the relative proportions of the juvenile migratory phenotypes present within adult samples were similar across both years, and there was no clear evidence that smolt-sized emigrants contributed disproportionately to the adult

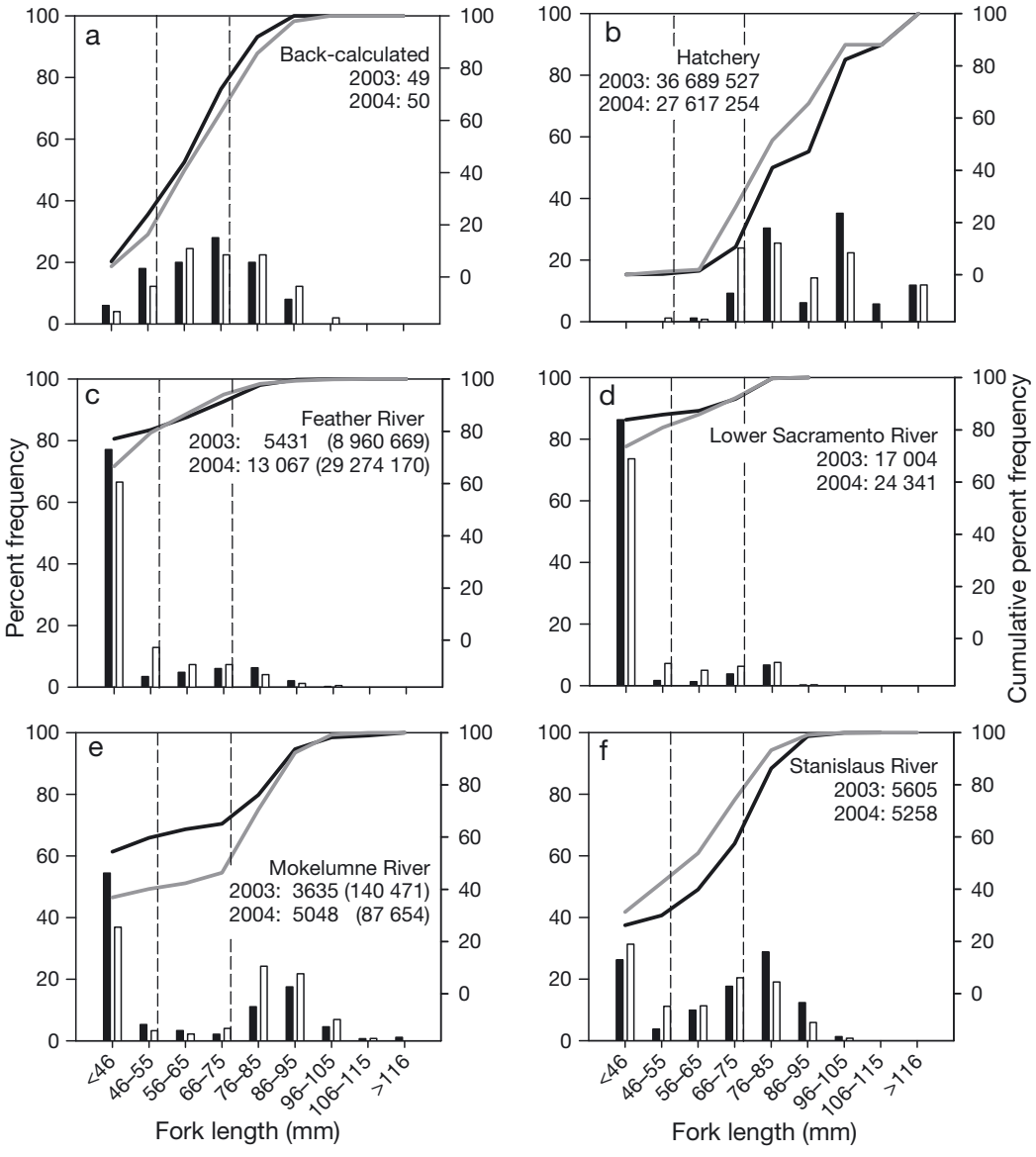

Fig. 6. *Oncorhynchus tshawytscha*. Size (fork length, mm) frequency distributions (bars) and cumulative percent frequency of occurrence (solid lines) for Central Valley fall Chinook salmon emigrants. (a) Back-calculated size at freshwater emigration for adult fall Central Valley Chinook salmon as determined based on otolith structure and chemistry. (b) Size of hatchery-produced Chinook salmon upon release. (c–f) Size of primarily naturally produced Chinook salmon collected in rotary screw traps: (c) Feather, (d) Lower Sacramento, (e) Mokelumne, and (f) Stanislaus Rivers. The numbers of fish used to generate each distribution are included. For the Feather and Mokelumne River traps, estimates for the total number of individuals produced upstream of the trap are included (95% CI: Feather River in 2003 = 7 158 975 to 13 851 505 and in 2004 = 20 186 009 to 37 851 505; Mokelumne River in 2003 = 95 974 to 310 357 and in 2004 = 67 068 to 134 898). Size designations for fry (≤55 mm FL), parr (56 to 75 mm FL), and smolt (>75 mm FL) are indicated by dashed lines. Filled bars and black lines represent 2003 emigrants and open bars and grey lines represent 2004 emigrants

population. Furthermore, similar proportions of juvenile migratory phenotypes were observed in both years despite the fact that natural production was apparently lower in 2003 than 2004, which likely resulted in fewer fry emigrants. Although the relative survival of distinct migratory phenotypes appears to vary across years, these 3 phenotypes likely consistently contribute to adult production. The adult Central Valley fall Chinook salmon used in the present study were collected within the Oregon salmon troll fishery. Central Valley fall Chinook salmon have been captured consistently in the Oregon troll fishery (Weitkamp 2010); however, additional information on the juvenile migratory phenotypes represented in additional samples of Central Valley adult fall Chinook salmon, including those collected from other fishery locations and on spawning grounds, is needed to evaluate the consistency of the observed patterns.

Although estuaries are known to provide rearing habitat for Chinook salmon (Reimers 1973, Healey 1991, Simenstad et al. 1982, Bottom et al. 2005, Volk et al. 2010), research in San Francisco Bay indicates that juvenile Chinook salmon may derive less benefit from estuarine residence than more northerly populations (MacFarlane & Norton 2002). During the 1997 emigration, juvenile Chinook salmon (68 to 110 mm FL) resided in the estuary for an average of 40 d and grew relatively slowly (mean = 0.18 mm d^{-1}) (MacFarlane & Norton 2002). Overall, their mean condition declined as they migrated through San Francisco Bay until they reached adjacent coastal waters where their growth rates accelerated (MacFarlane & Norton 2002). These observations led to the supposition that 'the ecological and evolutionary propensity of emigrating juveniles to conform to a strong ocean-type life history, with little estuarine dependency and a hastened ocean entry, may be another unique attribute of Central Valley Chinook salmon' (MacFarlane & Norton 2002, p. 255). However, MacFarlane & Norton (2002) estimated growth based on change in mean size, which may be biased by size-dependent emigration and may in fact underestimate actual growth. Additionally, smaller fish, which may display different patterns of growth and residence, may have been under-represented in their mid-water trawl collections. The relative importance of estuarine rearing may vary across years with different environmental conditions. In the present study, a substantial proportion of the fish (40%) entered brackish waters at sizes <65 mm FL. Extended estuarine residence may be important for smaller fall Chinook salmon emigrants in the Central Valley.

Hatchery fish account for an estimated 17 to 90% of the total adult fall Chinook salmon production in the Central Valley (Kjelson et al. 1982, Yoshiyama et al. 1998, Yoshiyama et al. 2000, Barnett-Johnson et al. 2007). The relatively large range in estimates of hatchery contribution is due, in part, to challenges associated with accurately identifying hatchery fish and interannual variation in the hatchery contribution. However, given that most hatchery fish are released at sizes >55 mm FL, it is likely that fry-sized emigrants observed in the present study represent natural production. Additional information on the origin of individual fish (hatchery versus naturally spawned) may be obtained through more detailed structural (Barnett-Johnson et al. 2007) or chemical (^{34}S:^{32}S, Weber et al. 2002) otolith analyses. Given the error rates associated with the identification of hatchery fish using structural analysis (~10%) and the instrumentation required for sulfur analysis (Weber et al. 2002), we did not incorporate either in the present study. Nonetheless, although fry-sized emigrants are consistently observed in lower rivers and estuaries (Collins 1892, Rich 1920, Reimers 1973), they remain a minor consideration in the Central Valley's water and salmon management practices (Brandes & McLain 2001, Williams 2001). It is plausible that fry emigrants comprise a migratory contingent, i.e. a subpopulation aggregate that share common migratory pathways and thus experience differential survival compared with other contingents (Hjort 1914, Clark 1968, Secor 1999).

Theoretically, the presence of diverse juvenile migratory contingents provides resilience for a population that confronts varying environmental conditions (Thorpe et al. 1998, Secor 1999, Waples et al. 2009). However, as noted earlier, empirical evidence for the survival of distinct migratory variants within the Central Valley has been difficult to acquire. Survival estimates based on comparisons between juvenile and adult abundance are problematic because they are confounded by large variations in sampling efficiency. Tagging studies have been initiated in several Central Valley river systems to quantify the relative contribution of juvenile migratory phenotypes to adult populations. However, low production of naturally spawned juveniles, low recapture rates, and the 3 to 5 yr required to examine adult returns have prevented robust conclusions using this methodology. Analysis of the structural variation in scales has been used on a limited basis to provide information on the relative contribution of migratory phenotypes (Reimers 1973). However, these studies require extensive baseline development and are highly subjective; they are best suited to differentiating between individuals that emigrate from freshwater in their first year of life (sub-yearlings) or in their second year of life (yearlings), rather than among size classes within the sub-yearling life history. Approaches similar to ours can be applied to other diadromous species, at finer spatial scales (e.g. within rivers), and over a period of several years to further examine how successful juvenile migratory behaviors vary under different environmental conditions without the need to recapture individuals.

Our results indicate that a combined marker approach (otolith Sr:Ca and Ba:Ca) holds promise for improving reconstructions of migratory history, but there are several factors to consider. For example, we observed that otolith Ba:Ca provided a slightly greater ability to differentiate residence in low salinity waters than otolith Sr:Ca in this species. However, by combining these 2 tracers, we were able to identify a pattern indicative of residence in brackish waters (i.e. otolith Sr:Ca > 1.5 mmol mol^{-1} and Ba:Ca > 2 µmol mol^{-1}). More detailed examination of the temporal and spatial variation in water Sr:Ca and Ba:Ca throughout San Francisco Bay and Delta during emigration may allow for more precise spatial determination of habitat use. Overall, the ability to reconstruct individual salinity history within a system largely depends on the freshwater Me:Ca values. Similar otolith chemical analyses

in systems with greater freshwater Ba:Ca (>600 µmol mol^{-1}) and/or lower Sr:Ca (<4 mmol mol^{-1}) than the lower reaches of the Central Valley should provide additional salinity resolution (i.e. Volk et al. 2010).

For most populations of Chinook salmon, it is unclear how much variation in juvenile migratory behavior exists, how fluid that variation is, and whether survival varies among individuals with distinct migratory behaviors. Furthermore, it is not known if or how habitat modifications (such as the construction of dikes, levees, and bypass channels), freshwater discharge, harvest, and artificial propagation affect the relative proportion and survival of juvenile emigrants (but see Kimmerer 2008, Perry et al. 2010). As Healey (2009) notes, management strategies that enhance a dominant tactic (smolt-sized emigrants in this case) could reduce life-history diversity and result in a loss of population resilience. However, there is evidence that management practices can also result in the development of novel migratory phenotypes (i.e. a reservoir-rearing life history) (Connor et al. 2005). Lindley et al. (2009) indicate that hatchery production has reduced variation in juvenile size, condition, and migration timing in Central Valley fall Chinook salmon; they suggest that increased life-history diversity could reduce variability in adult production. The contribution of 3 juvenile migratory phenotypes to the Central Valley adult population indicates that a conservative management approach would focus on maintenance of life-history variation rather than the promotion of a particular phenotype.

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Appendix 1. Additional data on water and otolith chemistry

Table A1. Water Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}) and predictions for Chinook salmon otolith Sr:Ca (mmol mol^{-1}) and Ba:Ca (µmol mol^{-1}). Data from Weber (2002) were collected monthly from October 1997 to September 1999; data from C. E. Zimmerman (unpubl. data) were collected in March, July, and November in 2003–2005; National Stream Quality Accounting Network (NASQAN; http://water.usgs.gov/nasqan/) data were collected approximately monthly from 1973–1995 (n = 46); and samples were collected in February 2008 for the present study. Predicted otolith Me:Ca ratios were based on observed otolith and water Me:Ca ratios (see 'Results' for details). For water Me:Ca, Weber (2002) = median values; all others = mean values ± SD. For predicted otolith Me:Ca, 95% CI are presented in parentheses. nd: no data available

Location	Water Sr:Ca (mmol mol^{-1})	Water Ba:Ca (µmol mol^{-1})	Predicted otolith Sr:Ca (mmol mol^{-1})	Predicted otolith Ba:Ca (µmol mol^{-1})	Source
Sacramento River	2.41	408	0.91 (0.17)	4.51 (0.36)	Weber (2002)
Upper Sacramento River	3.00 (0.75)	nd	0.93 (0.15)	nd	C. E. Zimmerman (unpubl. data)
Battle Creek	3.99	417	1.00 (0.12)	4.58 (0.37)	Weber (2002)
Mill Creek	3.42	288	0.95 (0.13)	3.59 (0.34)	Weber (2002)
Deer Creek	3.47	709	0.96 (0.13)	6.83 (0.53)	Weber (2002)
Upper Deer Creek	3.66 (0.75)	nd	0.97 (0.13)	nd	C. E. Zimmerman (unpubl. data)
Butte Creek	2.76	141	0.92 (0.15)	2.47 (0.35)	Weber (2002)
Feather River	3.07	440	0.93 (0.14)	4.76 (0.38)	Weber (2002)
Feather River Hatchery	3.18	446	0.94 (0.14)	4.81 (0.38)	Weber (2002)
American River	3.41	584	0.95 (0.13)	5.87 (0.45)	Weber (2002)
American River Hatchery	3.61	618	0.96 (0.13)	6.13 (0.47)	Weber (2002)
Upper Yuba River	2.89 (0.38)	nd	0.93 (0.15)	nd	C. E. Zimmerman (unpubl. data)
Northern Delta	3.94	595	0.99 (0.12)	5.95 (0.45)	Weber (2002)
Southern Delta	5.36	514	1.18 (0.09)	5.33 (0.41)	Weber (2002)
Mokelumne River	4.92	1140	1.11 (0.10)	10.15 (0.86)	Weber (2002)
Mokelumne River Hatchery	5.15	1168	1.14 (0.10)	10.37 (0.88)	Weber (2002)
Tuolumne River	3.75	708	0.98 (0.13)	6.82 (0.53)	Weber (2002)
Tuolumne River	3.96 (0.97)	nd	0.99 (0.12)	nd	C. E. Zimmerman (unpubl. data)
Merced River	3.21	1606	0.94 (0.14)	13.74 (1.25)	Weber (2002)
Upper Merced River	4.03 (0.57)	nd	1.00 (0.12)	nd	C. E. Zimmerman (unpubl. data)
Merced River Hatchery	3.32	1679	0.95 (0.14)	14.30 (1.31)	Weber (2002)
Upper Calaveras River	3.16 (0.55)	nd	0.94 (0.14)	nd	C. E. Zimmerman (unpubl. data)
Upper Stanislaus River	4.51 (0.39)	nd	1.05 (0.11)	nd	C. E. Zimmerman (unpubl. data)
San Joaquin River at Vernalis	5.30 (0.08)	425 (5)	1.17 (0.10)	4.64 (0.37)	NASQAN
Lower Cosumnes River	3.54 (0.08)	747 (61)	0.96 (0.13)	7.12 (0.55)	Present study
Lower Mokelumne River	5.37 (0.06)	1622 (6)	1.18 (0.10)	13.86 (1.26)	Present study
Lower Calaveras River	2.56 (0.10)	524 (144)	0.92 (0.16)	5.40 (0.41)	Present study
Stanislaus River	4.10 (0.12)	698 (52)	1.01 (0.12)	6.74 (0.52)	Present study
Lower San Joaquin River	5.48 (0.04)	468 (8)	1.20 (0.10)	4.97 (0.39)	Present study
Coastal ocean	8.55 (0.33)	5.03 (1.08)	1.98 (0.13)	1.41 (0.40)	Present study

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