Response of juvenile Chinook salmon to managed flow: lessons learned from a population at the southern extent of their range in North America

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Abstract Fourteen years (1996–2009) of juvenile Chinook salmon, *Oncorhynchus tschawytscha* (Walbaum), migration data on the regulated Stanislaus River, California, USA were used to evaluate how survival, migration strategy and fish size respond to flow regime, temperature and spawner density. An information theoretic approach was used to select the best approximating models for each of four demographic metrics. Greater cumulative discharge and variance in discharge during the migration period resulted in higher survival indices and a larger proportion of juveniles migrating as pre-smolts. The size of pre-smolt migrants was positively associated with spawner density, whereas smolt migrant size was negatively associated with temperature and positively associated with discharge. Monte Carlo techniques indicated high certainty in relationships between flow and survival, but relationships with juvenile size were less certain and additional research is needed to elucidate causal relationships. Flow is an integral part of the habitat template many aquatic species are adapted to, and mismatches between flow and life history traits can reduce the success of migration and the diversity of migratory life history strategies. The analyses presented here can be used to assist in the development of flow schedules to support the persistence of salmon in the Stanislaus River and provide implications for populations in other regulated rivers with limited and variable water supply.

K E Y W O R D S :   California, life history, Monte Carlo, river regulation, screw trap, survival.

Introduction

Pacific salmon, *Oncorhynchus* spp., stock abundances exhibit large temporal fluctuations that, in part, are determined by co-varying environmental parameters that characterise regional climatic conditions. This is not surprising given the profound effect freshwater flow has upon the physical, chemical and biological processes in streams, estuaries and associated coastal waters (Albright 1983; Junk *et al.* 1989; Wilcock *et al.* 1996). The freshwater hydrograph influences water temperature and quality, creation and maintenance of channel complexity, seasonal activation of floodplain habitats, regulation of primary productivity and stimulation of migration in aquatic species (Dingle 1996; Poff *et al.* 1997; Ahearn *et al.* 2006). Particulate organic and inorganic matter, as well as juvenile salmon, are carried seaward by freshwater flow and incorporated into coastal marine food chains. In turn, conditions within coastal waters influence the health, survival and reproductive success of adult salmon returning to natal streams, causing a biological feedback on long-term health and success of salmon stocks (Mantua *et al.* 1997; Greene *et al.* 2005).

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Salmon streams throughout the northern hemisphere have undergone dramatic and long-term anthropogenic changes including damming, mining, levee construction, hydropower generation and floodplain disconnection. Such effects have altered hydrologic, sediment and temperature regimes and impacted the native flora and fauna of these systems (Merritt & Cooper 2000; Trush *et al.* 2000; Vinson 2001). The associated decline of salmon populations that support valuable commercial and recreational fisheries has triggered efforts to design flow regimes for regulated rivers that provide conditions suitable to support self-sustaining populations. Yet, there remains a lack of information regarding the responses of different salmon life stages to specific environmental variables that can be used to inform flow strategies. Given the demands for large-scale water regulation and diversion within lotic ecosystems, effective resource management requires an understanding of how environmental conditions affect salmon (i.e. quantity, quality and migration strategy) during the freshwater portion of a given population's life cycle (Hoekstra *et al.* 2007; Nislow & Armstrong 2012).

It was hypothesised that juvenile salmon would demonstrate demographic responses to inter-annual variation in flow magnitude, flow variance and temperature. This hypothesis was tested by modeling how independent variables affected the proportion of juveniles transitioning from rearing to migration using an index of survival, the life stage when migration out of the natal stream was initiated and fish size. For this effort, 14 years of juvenile Chinook salmon migration data were collected at two locations on the Stanislaus River, California, USA, a highly regulated stream with an extant population of naturally reproducing Chinook salmon, *Oncorhynchus tschawytscha* (Walbaum). The monitoring sites included the downstream extent of identified Chinook salmon spawning habitat that was used to estimate fry abundance and the downstream extent of rearing used to estimate the abundance of Chinook salmon emigrating out of the natal stream. These analyses provide resource managers with essential information that can be used to better inform flow management for Chinook salmon in the Stanislaus River and provide implications for relationships between environmental drivers and Chinook salmon ecology in other regulated rivers.

Methods

Study site

The Stanislaus River drains approximately 2400 km^2 from the western slope of the central Sierra Nevada Mountains to its confluence with the San Joaquin River.

The watershed has a Mediterranean climate with dry summers, and approximately 90% of the annual precipitation occurs between November and April. Historically, relatively low-magnitude flow pulses occurred from late autumn until early spring in response to rainfall in the lower watershed followed by a snow melt-driven pulse from spring through early summer. In the 20th century, more than 40 dams were constructed on the Stanislaus River for flood protection, power generation, irrigation and municipal water supply. Collectively, these dams have the capacity to store 240% of the average annual runoff in the catchment and have reduced the amount of habitat available to Chinook salmon by 53% (Yoshiyama *et al.* 2001). Goodwin Dam (GDW), located at river kilometre (rkm) 94, is currently the upstream migration barrier to adult Chinook salmon and demarks the upstream end of the lower Stanislaus River (Fig. 1). Most fall-run Chinook salmon spawning in the lower Stanislaus River (LSR) occurs in the 29-km reach below GDW (from GDW to ~rkm 66); however, spawning has been observed as far downstream as rkm 53.1.

New Melones Dam, completed in 1979, impounds a reservoir that accounts for approximately 85% of the total storage capacity in the system and is the primary instrument of flow regulation in conjunction with GDW that serves as a re-regulating facility for the larger reservoir. In the years since New Melones Dam operation began, the LSR (below GWD) has changed from a dynamic river system, characterised by depositional and scour features, to a relatively static and entrenched system (Kondolf & Batalla 2005). Annual mean daily discharge has been reduced from 48 to 23 m^3 s^{-1} with mean 30-day maximum discharge reduced from 137 to 38 m^3 s^{-1} (Brown & Bauer 2009). Vegetation encroachment into the active channel, as well as urban and agricultural development, has altered the natural river channel-floodplain connection and has led to the coarsening of bed material, particularly within spawning habitat between Goodwin Dam and Honolulu Bar (Fig. 1).

Fall-run Chinook salmon freshwater life stages and timing

Similar to many anadromous salmonids, California Central Valley fall-run Chinook salmon exhibit distinct life stages that occur during specific time periods (Merz *et al.* 2013). In general, adults migrate from the Pacific Ocean to natal streams between August and December and spawning is initiated shortly after (peak from early October to late November). Chinook salmon require relatively cool, clear, flowing streams with appropriate substrate for successful spawning (Zeug *et al.* 2013), incubation and emergence (Tappel & Bjornn 1983).
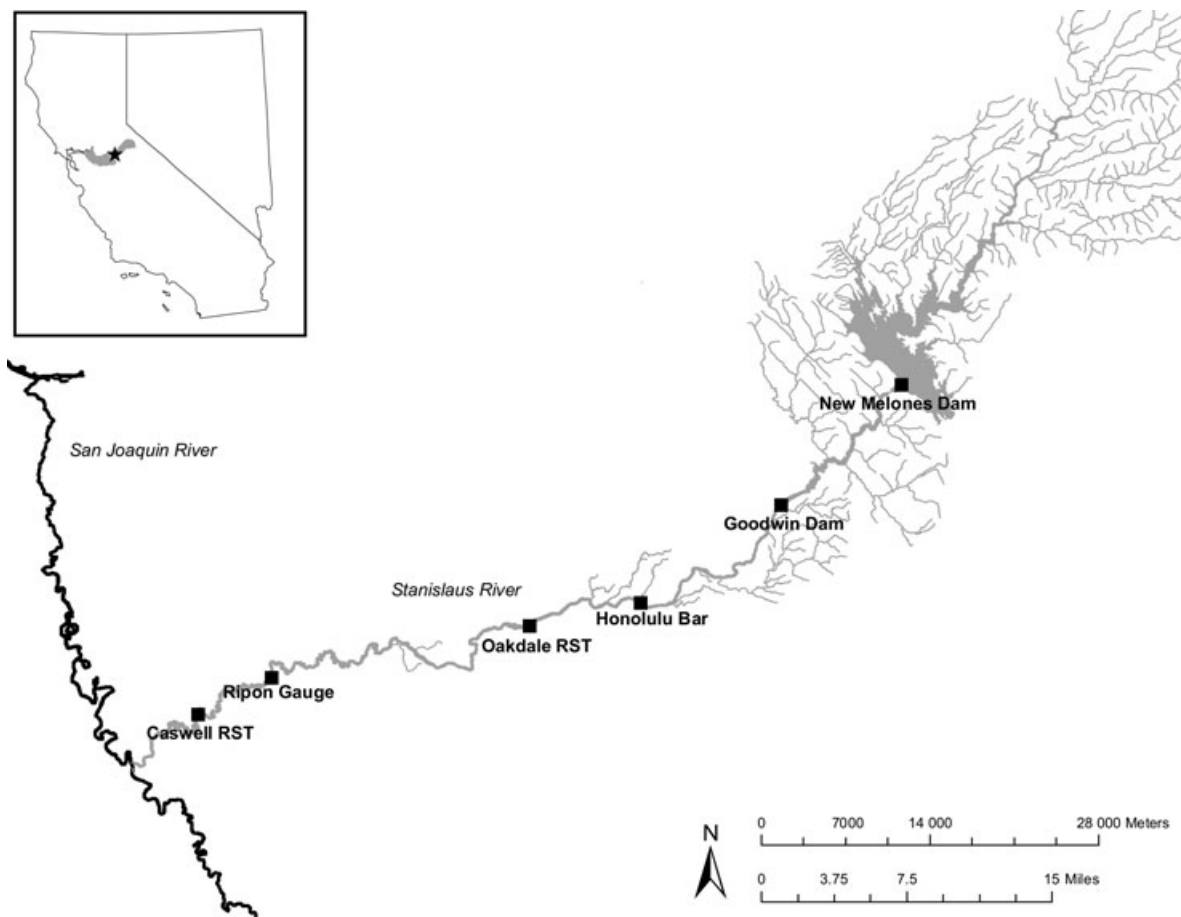
Figure 1. Location of the lower Stanislaus River, California and the location of rotary screw traps (RST) and other relevant features within the study area.

Incubation typically occurs from October through March, and emigration occurs from late December to early July.

Environmental variables

A suite of variables was measured to characterise LSR hydrologic and temperature regimes during the study period (Table 1). To facilitate comparisons of environmental conditions across years, a uniform range of days for each year was created to represent the juvenile rearing and emigration period. The beginning of the period was calculated as the day that 2.5% of cumulative juvenile Chinook salmon catch was observed for each year and averaged across years (mean = day of the year 17). The end date was calculated as the day that 97.5% of cumulative catch was observed for each year and averaged across years (mean = day of the year 147). These start and endpoints were assumed to represent conditions the majority of juveniles experienced as they reared and migrated downstream through the LSR.

Hydrologic variables included in the analysis were cumulative discharge during the rearing period and variance in discharge during the rearing period. Mean daily flow was obtained from the United States Geological Survey stream gauge on the Stanislaus River located near Ripon, CA (Fig. 1) and converted to total daily flow (m^3 day^{-1}). To calculate cumulative flow, total daily flow was summed for the rearing period (130 days) each year (Table 1). Variance in flow was calculated as the sample variance of the total daily flow (m^3 day^{-1}) during the 130-day rearing period. Flow variation provides a mechanism for habitat creation and activation (e.g. bar formation, floodplain inundation) and has been identified as a trigger for fish migration and overall changes in metabolism (Raymond 1968; Hvidsten *et al.* 1995; Baker & Morhardt 2001).

Table 1. Environmental variables and estimates of Chinook salmon spawner abundance in the Stanislaus River during 1996–2009

Year	Cumulative discharge $\times 10^8$ (m^3)	Discharge variance $\times 10^9$ (m^3)	Degree days	Spawner abundance
1996	6.12	6.02	1602	168
1997	10.66	6.39	1838	5588
1998	8.07	5.33	1489	3087
1999	7.02	4.61	1533	4349
2000	4.78	3.75	1710	8498
2001	2.22	1.01	1767	7033
2002	2.23	0.52	1696	7787
2003	2.02	0.29	1773	5902
2004	1.68	0.41	1847	4015
2005	1.89	1.05	1849	1427
2006	11.02	8.90	1449	1923
2007	3.27	0.56	1659	443
2008	2.34	0.83	1639	865
2009	1.62	0.47	1737	595

Degree-days were used to represent the overall water temperatures that juvenile Chinook salmon were exposed to during the rearing period each year. Temperature data were obtained from the United States Geological Survey gauge on the Stanislaus River located near Ripon, CA (11303000). Degree-days were calculated by summing the mean temperature for each day during the juvenile rearing period. The use of degree-days for calculating the temperature-dependent development of poikilotherms is widely accepted as a basis for building phenology and population dynamics models (Taylor & McPhail 1985; Roltsch *et al.* 1999), and accumulated thermal units (analogous to degree-days) have been shown to initiate physiological changes linked to outmigration behavior of juvenile Chinook salmon (Sykes & Shrimpton 2010).

In addition to the three physical parameters described above, the number of adult spawners was acquired for each study year. These data were used to account for potential density-dependent effects on the demographic metrics. Spawner numbers were estimated by annual carcass surveys performed by the California Department of Fish and Wildlife and obtained from their 'Grand Tab' data base file available at https://nrm.dfg.ca.gov/FileHandler.ashx?documentversionid=33911XXX.

Fish sampling

Rotary screw traps (2.4-m diameter cone; manufactured by E.G. Solutions, Corvallis, OR, USA), were operated at two locations from 1996 to 2009 to index survival between the traps and estimate the size and life stage of juvenile Chinook salmon emigrating from the system. Rotary screw traps (RSTs) are commonly used in the

Pacific Northwest to monitor impacts of river management (e.g. habitat restoration, flow manipulation, dam management) on wild stocks (Volkhardt *et al.* 2007; Merz *et al.* 2013). Rotary screw traps are potentially powerful tools for validating assumptions regarding the effects of watershed restoration programs and land-use policies on fish populations (Solazzi *et al.* 2000; Johnson *et al.* 2005). These traps can also be used to assess survival between life stages, such as egg-to-smolt survival or parr-to-smolt overwinter survival (Solazzi *et al.* 2000; Johnson *et al.* 2005) and the effects of environmental parameters on migration timing and development (Sykes *et al.* 2009; Sykes & Shrimpton 2010).

The upstream RST was located at Oakdale (rkm 64.3; Fig. 1), which is immediately downstream from the majority of spawning habitat (hereafter referred to as the upstream trap). The upstream trap was assumed to provide a measure of juvenile Chinook salmon production from the spawning reach (Merz *et al.* 2013). The Caswell trap located at the lower extent of LSR rearing habitat (rkm 12.9) approximately 9 km from the San Joaquin River confluence (hereafter referred to as the downstream trap) was used to provide an estimate of out-migrating juveniles. Therefore, the lower trap provides a measure of size and survival of juvenile Chinook salmon exposed to the rearing reach just before exiting the LSR. Trap operations and configurations did not change among years at the upstream site where a single trap was operated. At the downstream site, two traps were operated in tandem for years 1996–2008; however, due to low flow and changes to site channel conditions, the trapping operation was relocated approximately 50 m downstream in 2009 to a site that would only accommodate a single trap.

Operation of LSR RSTs generally followed guidelines outlined in standard protocols [CAMP (Comprehensive Assessment & Monitoring Program] 1997; Volkhardt *et al.* 2007). Traps were deployed each year between mid-December and mid-January, and sampling was terminated when at least seven consecutive days of trapping resulted in zero catch. This typically occurred in June or July near the end of the Central Valley fall-run Chinook salmon emigration (Williams 2006). Traps were checked daily or multiple times per day depending on debris load. Trap cones were raised on days when sampling did not occur due to excess debris or dangerous conditions.

All Chinook salmon <200 mm fork length (FL) and not demonstrating secondary sexual characteristics (e.g. releasing milt, spawning coloration) were designated as juveniles. Chinook salmon in the LSR are considered 'ocean type' because they primarily emigrate from the system prior to their first winter and typically before July

(Clarke *et al.* 1994). However, there are at least two distinct migration strategies. Juveniles may emigrate from the LSR in winter or early spring prior to smoltification (fry and parr) and rear in the estuary or possibly other non-natal waters prior to ocean entry, or they may rear in the LSR and leave as smolts later in the spring (Limm & Marchetti 2009; Merz *et al.* 2013). To examine factors influencing interannual variation in out-migration strategy, juvenile Chinook salmon were sub-classified as pre-smolt and smolt life stages. Although specific life-stage designations (i.e. fry, parr or smolt) based on morphological characteristics were made in the field, there was considerable variability in the characteristics used to differentiate the life stages, depending on the year and personnel conducting the sampling. Therefore, a piecewise linear regression model for each year of data was used to provide a more objective temporal split between pre-smolt- and smolt-dominated migration periods. These models are commonly used to identify thresholds, or 'breakpoints', where the slope of a regression line changes (Betts *et al.* 2007; Muggeo 2008). First, fish lengths were plotted by date for each year and trap location to provide a visual representation of the pattern of change in fish size. Next, the segmented statistical package in R, which uses initial estimates of breakpoint(s) to iteratively fit a standard linear model to the data, was used to generate an estimated annual breakpoint value (Muggeo 2008). This value corresponded to a day for each year and was considered the 'smolt date' whereby all fish captured up to and including the smolt date were categorized as pre-smolts and all fish captured after the smolt date were categorised as smolts, regardless of previous life stage designation.

To derive accurate abundance estimates at each trap, it was first necessary to estimate RST efficiency for each site. Mark-recapture trials with juvenile Chinook salmon were performed to estimate trap efficiency at both sites. Experimental mark-recapture groups of both hatchery and natural-origin juveniles were used to estimate trap efficiencies at the upstream ($n = 185$) and downstream ($n = 247$) traps. Release group sizes ranged from 17 to 6737 depending on the availability of fish for the trial and were performed during periods of flow change and throughout the migration period to capture the range of efficiency variability. Fish were dye-marked using a photonic marking gun (MadaJet A1000, Carlstadt, NJ, USA) with dye on the caudal or anal fin. Releases occurred approximately 430 m upstream of the traps from the north bank at a narrow, deep area of the river. Fish releases occurred approximately 1 h after dark in small groups (5–10 individuals) to encourage mixing with natural (unmarked) Chinook salmon in the river, reduce schooling and mimic pulses in natural catch during nighttime migration. Marked fish were transported in a non-motorised boat and released across the channel at various points away from the bank. Traps were processed starting 1 h after completing release activities. Additional recaptures were recorded with the subsequent catch. To avoid pseudoreplication in efficiency analyses, data were pooled when multiple releases occurred on the same date. The maximum number of days post release that marked fish were collected ranged from 5 to 17 at the downstream trap and from 9 to 39 at the upstream trap.

Data analysis

Logistic regression was used to develop a predictive model of daily trap efficiencies. The dependent variable in these models was the binomial probability of capture. Independent variables included flow (log transformed), temperature, turbidity, fork length at release and year. A model was fit with an intercept (β_0), and then each explanatory variable was entered one at a time. The variable with the greatest explanatory power was then included in the model, and the remaining variables were again entered one at a time. The procedure was terminated when none of the remaining variables had a statistically significant effect on capture at $\alpha = 0.05$. The final model for the upstream trap included flow (negative relationship) and a year effect. The final model for the downstream trap included significant negative relationships with flow and fish fork length and a year effect.

Daily catch of migrating juvenile Chinook salmon for each trap was estimated as:

$$\hat{n} = \frac{c}{\hat{q}}$$

where c is the number of Chinook salmon captured each day and q is the estimated trap efficiency for that day from the logistic model. Error estimates for daily catch were calculated using the methods described in Appendix 1. During some years, there were periods when traps were not fished. A weighted average of all observed counts for the 5 days before and 5 days after the missing value were used to estimate a missing value of daily count (c) within a sampling period. The weights were equal to 1 through 5, where daily values that were 1 day before and after the missing day were weighted as 5, values that were two days before and after the missing day were weighted as 4, and so on. Annual catch estimates were generated by summing daily catch and error estimates (Fig. 2).

Three variables were estimated to describe the demographics of the juvenile Chinook salmon cohort in each
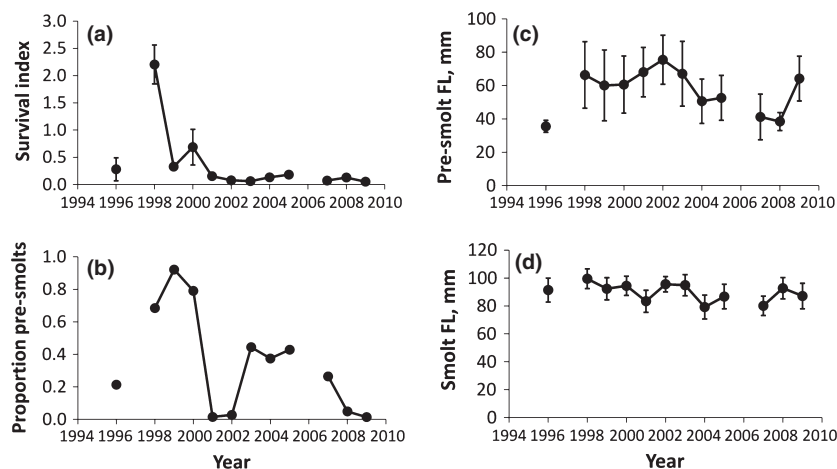
Figure 2. Demographic metrics (mean ± SD) of the Stanislaus River juvenile Chinook salmon population during 1996–2009. (a) Survival index. (b) Proportion of migrants classified as pre-smolts. (c) Mean fork length (FL) of pre-smolt migrants. (d) Mean FL of smolt migrants.

year. First, annual catch estimates at each trap were used to index survival between the two traps:

$$S_i = \frac{\widehat{P_D}}{\widehat{P_U}}$$

where S_i is the index of survival, $\widehat{P_D}$ is the estimated catch at the downstream trap and $\widehat{P_U}$ is the estimated catch at the upstream trap (Fig. 2). Second, migration strategy was estimated as the proportion of all juveniles that migrated out of the system as pre-smolts in each year. Third, the fork length of juvenile emigrants was estimated in each study year. Fish length was separated by pre-smolts and smolts because portions of the population migrate at each stage. Migration strategy and fish length were modeled using only data from the downstream trap because this location captured fish that were actively migrating out of the system.

Prior to modeling the demographic metrics, a correlation analysis was performed on predictor variables to identify potential sources of multicollinearity. Correlations between all predictors were high (>0.70); thus, the full suite of predictor variables could not be included in the same statistical model without unacceptable variance inflation. Instead, four models were constructed (one for each demographic metric), and the strength of each predictor was evaluated using an information-theoretic approach.

For each of the four demographic metrics, the assumption of normality was tested with a Shapiro–Wilk test and auto correlation was tested with cross-correlation coefficients. When a parameter was identified as non-normal, an appropriate transformation was applied and the assumption of normality was retested. Four linear models were constructed for each demographic metric (16 total models) where the independent variables were: (1) cumu-

lative discharge; (2) discharge variance; (3) degree days and (4) spawner abundance. Akaike's information criterion corrected for small sample size (AIC_c) was used to evaluate the weight of evidence for each predictor. The difference in AIC_c values between each candidate model and the best model was calculated (ΔAIC_c), and models with a value <2 were considered to have similar support in the data (Burnham & Anderson 2002). Model weights (AIC_c W) also were calculated. These values are interpreted as the probability of each model being the 'best' of the four evaluated. The R^2 values of models with ΔAIC_c values <2 were used to evaluate overall model fit.

Finally, because estimates rather than observations were used as response variables in the linear models, Monte Carlo methods were used to reduce uncertainty in model estimates. One hundred re-samples of each response variable were performed for each year using a distribution informed by the sample mean and associated error. Abundance at each trap (used to calculate the survival index) was described by a negative binomial distribution, whereas a normal distribution was used for pre-smolt and smolt size. A predictor was considered to have good support in the data if the 95% confidence interval of its coefficient did not include zero.

Results

Survival

Indices for survival between the two traps ranged from 5% in 2009 to >200% in 1998 (Fig. 2). Fewer trap efficiency trials may have led to the survival index over 200% in 1998. As one of the survival estimates was >100%, the data were scaled so that the value for 1998 was 100% and the values for all other years were

adjusted accordingly prior to use in statistical models. Following $\log_{10}$ transformation, the data were found to be normal ($W = 0.909$, $P = 0.209$) and no autocorrelation was detected ($r = 0.36$, $P = 0.338$). Model selection based on ΔAIC_c values revealed that cumulative discharge and discharge variance had similar support for predicting survival, whereas degree days and the number of spawners were relatively poor predictors (Table 2). Both models had good overall fit to the data with R^2 values of 0.68 and 0.67 for cumulative discharge and discharge variance, respectively (Fig. 3). The coefficient in both models was positive indicating that survival increased as cumulative discharge and discharge variance increased (Table 3). The Monte Carlo exercise revealed that 94% of models that included cumulative discharge and 89% of models that included discharge variance had coefficients with confidence intervals that did not include zero suggesting low uncertainty for these relationships.

Migration strategy

The proportion of juvenile Chinook salmon that migrated as pre-smolts ranged from >0.92 in 1999 to 0.01 in 2001 and 2009 with a mean of 0.35 (SD = 0.32). Autocorrelation was not detected in the data ($r = 0.54$, $P = 0.136$), and the assumption of normality was met ($W = 0.905$, $P = 0.183$). Cumulative discharge was the best predictor of migration strategy, and discharge variance also had support in the data. However, the ΔAIC_c value of 2.11 for discharge variance was >2.00 that was the cutoff for assuming a similar level of support as the best fit model. (Table 2). Overall fit was good for models of cumulative discharge and dis-

Table 2. Results of the model selection exercise for juvenile Chinook salmon demographic metrics (response variable). Models for each response variable are listed in order from the most to least likely

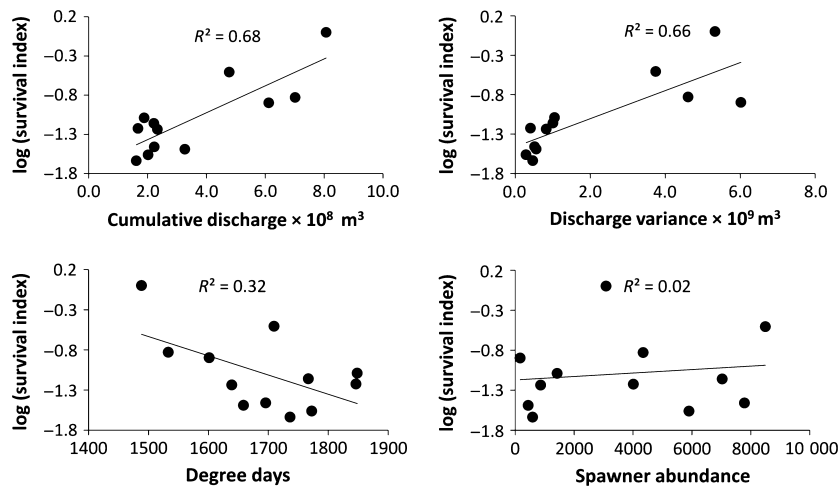| Response variable	Predictor	AIC_c	ΔAIC_c	AIC_c W
Survival index	Cumulative discharge	8.75	0.00	0.58
	Discharge variance	9.42	0.67	0.41
	Degree days	17.83	9.08	<0.01
	Spawner abundance	22.32	13.57	<0.01
Proportion of	Cumulative discharge	5.73	0.00	0.68
pre-smolt	Discharge variance	7.84	2.11	0.24
migrants	Degree days	11.09	5.36	0.05
	Spawner abundance	11.94	6.21	0.03
Pre-smolt size	Spawner abundance	−21.81	0.00	0.96
	Discharge variance	−13.53	8.28	0.02
	Degree days	−13.38	8.43	0.01
	Cumulative discharge	−13.25	8.56	0.01
Smolt size	Degree days	−47.03	0.00	0.42
	Cumulative discharge	−46.17	0.86	0.27
	Discharge variance	−45.89	1.14	0.24
	Spawner abundance	−43.47	3.56	0.07

charge variance with R^2 values of 0.43 and 0.33 respectively (Fig. 4). Similar to the survival models, the coefficients for both independent variables was positive indicating that more Chinook salmon juveniles migrated as pre-smolts when cumulative discharge and discharge variance were higher (Table 3). Monte Carlo estimates could not be generated for the migration strategy data because life stage-specific information was not consistently available from the efficiency tests to generate error estimates that could inform a distribution. All statistical analyses were performed with the program R (R Development Core Team 2012)

Pre-smolt migrant size

Juvenile Chinook salmon that emigrated as pre-smolts averaged 63.5 mm FL across all years with the smallest and largest pre-smolt emigrants observed in 1996 and 2002 (35.5 and 75.4 mm respectively). The data were normal following $\log_{10}$ transformation ($W = 0.901$, $P = 0.163$), and autocorrelation was not significant ($r = 0.49$, $P = 0.182$). Spawner abundance was the only variable that accounted for size variation in pre-smolt migrants among years (Table 2). The R^2 value for this model was 0.51 indicating the model was a good fit to the data (Fig. 5). The size of pre-smolt migrants was greater in years with higher spawner abundance (Table 3). Models from the Monte Carlo exercise revealed only moderate certainty for the relationship with spawner density. Forty six percent of models yielded a coefficient with a confidence interval that did not include zero.

Smolt migrant size

Fork lengths of juveniles that emigrated as smolts averaged 86.8 mm across all years. The smallest smolt emigrants were observed in 2007 (80.1 mm) and the largest in 1998 (99.5 mm). Autocorrelation was not significant ($r = -0.170$, $P = 0.653$), and the logarithm-transformed data met the assumption of normality ($W = 0.933$, $P = 0.416$). Model selection indicated that three models were similarly supported predictors of smolt size (Table 2). The best model included degree days as the independent variable and competing models included cumulative discharge and discharge variance. All three competing models had moderately good fit with R^2 values of 0.31, 0.27 and 0.25 for degree days, cumulative discharge and discharge variance, respectively (Fig. 6). The coefficient for degree days was negative, whereas the coefficients for cumulative discharge and discharge variance were positive. The Monte Carlo exercise suggested high uncertainty in these relationships with ≤13% of models for any of the three predictors having

Figure 3. Relationships between the juvenile Chinook salmon survival index and four predictor variables.

Table 3. Coefficients and standard errors (in parentheses) for each predictor variable in linear models describing the four demographic metrics of juvenile Chinook salmon

| Response variable	Cumulative discharge	Discharge variance	Degree days	Spawner abundance
Survival index	7.05×10^{-5} (1.52×10^{-5})	7.33×10^{-6} (1.64×10^{-6})	-0.002 (0.001)	2.16×10^{-5} (4.89×10^{-5})
Proportion of pre-smolt migrants	3.74×10^{-5} (1.34×10^{-5})	3.42×10^{-6} (1.54×10^{-6})	-0.001 (0.001)	2.48×10^{-5} (3.17×10^{-5})
Pre-smolt size	-1.28^{-6} (6.07×10^{-6})	-3.34×10^{-7} (6.32×10^{-7})	0.0001 (0.0002)	2.52×10^{-5} (7.78×10^{-6})
Smolt size	2.91×10^{-6} (1.54×10^{-6})	2.96×10^{-7} (1.64×10^{-7})	-1.57×10^{-4} (7.32×10^{-5})	2.87×10^{-6} (3.15×10^{-6})
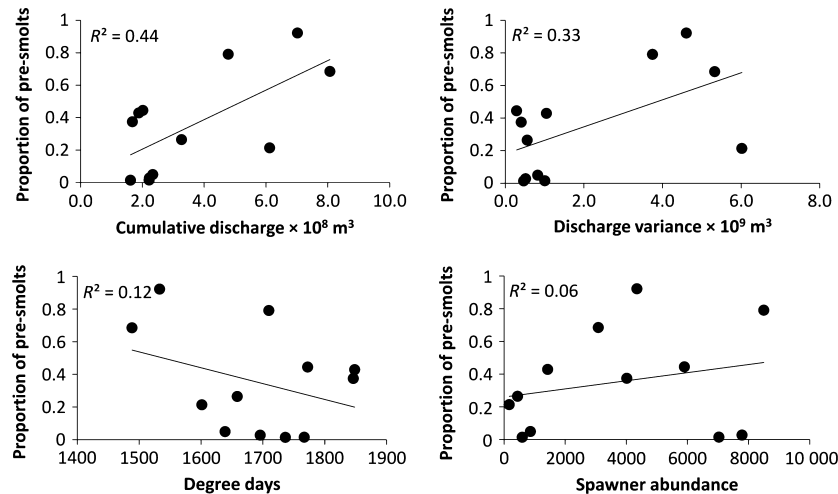
Figure 4. Relationships between the proportion of pre-smolt Chinook salmon migrants and four predictor variables.

coefficients with confidence intervals that did not include zero.

Discussion

The influence of flow regimes on the health of aquatic ecosystems has been widely recognised (Poff *et al.* 1997; Bunn & Arthington 2002). However, few studies have evaluated the demographic response of fish populations to flow regimes over multiple generations (Souchon *et al.* 2008). Analysis of 14 years of RST data on the LSR indicated that hydrology was a significant driver of several demographic characteristics of a Chinook salmon population. A strong positive response in survival, the
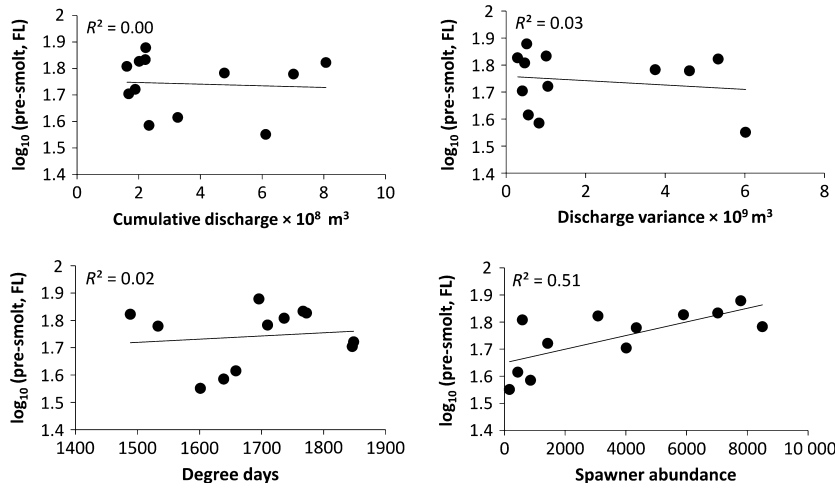
Figure 5. Relationships between the fork length (FL) of pre-smolt Chinook salmon migrants and four predictor variables.
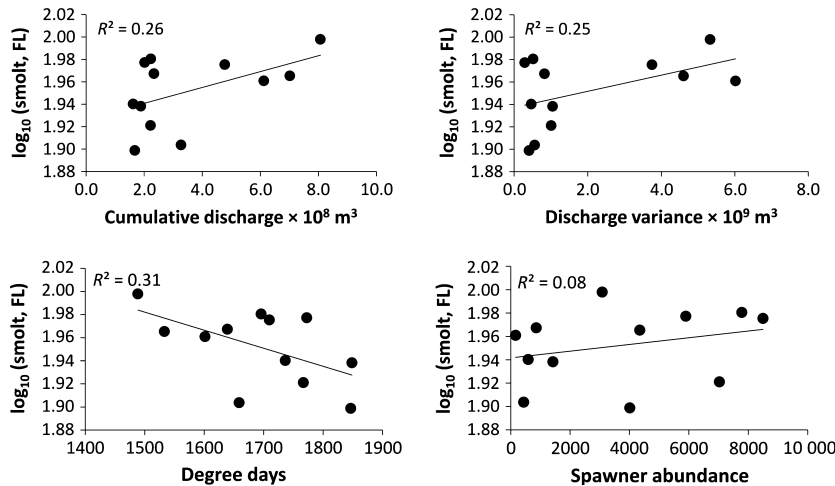

Figure 6. Relationships between the fork length (FL) of smolt Chinook salmon migrants and four predictor variables.

proportion of pre-smolt migrants and the size of smolts were observed when cumulative flow and flow variance were greater. Together, these data suggest that periods of high discharge in combination with high discharge variance are important for successful emigration as well as migrant size and the maintenance of diverse migration strategies.

Survival of migrating juveniles was higher when both cumulative discharge and discharge variance were greater. In a review of flow effects on salmonids, Nislow and Armstrong (2012) reported that reduced flow during the early emigration period was associated with lower growth and survival. Flow pulses provide fish access to seasonal habitats such as floodplains and side channels where food resources are often more abundant and predator densities lower (Junk *et al.* 1989; Bellmore *et al.* 2013). Chinook salmon rearing on California floodplains have been found to grow significantly

faster than fish in the main channel (Sommer *et al.* 2001; Jeffres *et al.* 2008). Since the construction of New Melones Dam, the LSR has become increasingly incised resulting in greater disconnection from its floodplain because greater flows are now required for floodplain inundation (Kondolf *et al.* 2001). A lack of access to off-channel habitats in years with low discharge and discharge variance may partially explain why low survival indices were observed. Higher velocities within the main channel may also reduce exposure time of migrating juveniles to predation within a specific stream reach (Cavallo *et al.* 2013). While turbidity data were not available, increased turbidity during high flow events might also influence behavior and success of emigrating juveniles (Gregory & Levings 1998), and this should be investigated further.

The proportion of Chinook salmon juveniles migrating as pre-smolts also responded positively to higher

cumulative discharge and discharge variance, supporting diversity in migration strategies (greater proportion of smolt migrants during lower discharge conditions, greater proportion of pre-smolt migrants during higher discharge conditions). It is unknown if LSR pre-smolt or smolt migrants survive better to later life stages; however, pre-smolt migrants from the Central Valley do survive and return as adults to spawn (Miller *et al.* 2010). The maintenance of multiple migration strategies can improve the persistence of salmon populations by spreading risk over space and time (Schindler *et al.* 2010). Reduction or elimination of the pre-smolt migration strategy by reducing cumulative discharge and discharge variance could have serious consequences for the LSR Chinook salmon population as risks associated with migration are increasingly concentrated into a relatively short time period (Carlson & Satterthwaite 2011).

The number of adult spawners was the only well supported predictor of pre-smolt size. Previous studies have found that marine-derived nutrients from spawner carcasses are incorporated into stream food webs that support juvenile salmon (Cederholm *et al.* 1999; Reimchen *et al.* 2002). Thus, increased spawner density may have increased productivity of invertebrate prey exploited by juvenile salmon or direct nutrient uptake from decomposing carcasses (Bilby *et al.* 1996). Alternatively, favorable ocean conditions that result in greater spawner returns may allow females to produce higher quality eggs that result in larger juveniles (Brooks *et al.* 1997; Heinimaa & Heinimaa 2004). However, caution should be used when interpreting this relationship. Negative density dependence may occur when spawner density exceeds the range observed during the years of this study. Thus, the relationship may not be linear across the range of potential spawner returns. Monte Carlo resamples of the data suggested there was only moderate certainty in this relationship. Additionally, both survival and the proportion of pre-smolt migrants could have stronger relationships with spawner density at levels above those observed during this study. The effects of quantity and quality of adult spawners on LSR juvenile offspring should also be evaluated further.

Juvenile size and water temperature at the time of Chinook salmon emigration can have a significant effect on ocean survival (Zeug & Cavallo 2013). Our results indicated that smolt size at emigration from the LSR had the strongest relationship with degree days. The Stanislaus River is located near the southern range limit of Chinook salmon spawning where temperatures can frequently exceed the optimum for the species (Myrick & Cech 2004; Williams 2006). Fish are strongly influenced by water temperature, which affects body temperature, growth rate, food consumption, food con-

version and other physiological functions (Houlihan *et al.* 1993; Azevedo *et al.* 1998). The negative relationship between smolt size and temperature suggests that temperatures may get high enough to impede growth in certain years. Monte Carlo resamples indicated high uncertainty in all relationships with smolt size. However, the negative effects of altered flow regimes can be exacerbated by temperatures outside of the optimum for juvenile salmonids (Nislow & Armstrong 2012), and further investigation of this issue in the LSR is warranted.

Despite strong relationships between hydrology and early Chinook salmon ontogeny and survival within the LSR, several considerations should be recognised when interpreting these results. Although RSTs are a tool frequently used to monitor migratory fishes (primarily salmon), they only provide indirect evidence of survival in relation to environmental conditions. More direct evidence can be obtained with techniques such as biotelemetry; however, long term data sets obtained with these technologies are not yet available for analysis, nor does such technology presently lend itself to earlier stages of salmon (i.e. fry-sized fish). Additionally, RSTs may be limited during periods of high flows when debris loads compromise trap operations and field personnel safety. This could mean that RSTs underestimate the number of juvenile salmon emigrating during these periods. It is likely that this aspect of RSTs contributed to the 1998 results when a greater number of Chinook salmon was estimated at the downstream trap. Finally, information theoretic methods can only select the best models from a candidate set. There may be predictors not examined here that better explain the data (e.g. predation rate) but were not available for analysis. If data on other potential predictors are available in the future, their fit can be evaluated against the predictors examined here. Regardless of these issues, RSTs provide robust, long-term monitoring data sets that are required to evaluate population-level responses to changes in flow regime (Souchon *et al.* 2008; Poff & Zimmerman 2010), and model selection identified several strong relationships between juvenile Chinook salmon and flow regime.

Pacific salmon life history diversity differs significantly across streams with different hydrologic regimes (Beechie *et al.* 2006). Conservation of such diversity is a critical element of recovery efforts, and preserving and restoring life history diversity depends in part on environmental factors affecting their expression (Schindler *et al.* 2010). This study found significant responses from juvenile Chinook salmon demography to variation in the LSR hydrologic regime. Although many methods have been used to establish sufficient flows for fish (Jowett 1997), strategies that mimic aspects of the natural flow regime are more likely to be successful (Richter *et al.*

1997). Flow regimes are an integral part of the habitat template to which aquatic species are adapted (Townsend & Hildrew 1994; Lytle & Poff 2004), and mismatches between flow and species life history traits (e.g. migration strategy) can create bottlenecks for population persistence (Schiemer *et al.* 2003). Reduced flow variance and cumulative flow were associated with reduced survival and the proportion of pre-smolt migrants. Although the volume of water released in regulated streams is paramount to fisheries management, stream flows during biologically important times of the year appear equally important (Kiernan *et al.* 2012). Together, these data suggest that cumulative discharge, discharge variance and water temperature are important environmental drivers, and they all should be included in the development of regulated flows to support the persistence of Chinook salmon populations and diverse life history strategies. While this study focused on a single Pacific salmon race in a highly regulated system, the analyses demonstrated here can be employed wherever migratory species and environmental parameters are adequately monitored.

Acknowledgments

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Appendix (1) The following describes the methods used to estimate the variance and confidence intervals for total annual juvenile Chinook salmon catch. It begins with a description of the variance of a given daily catch estimate ($\hat{n}$), and then extends the formulas to the total annual catch. As noted in the methods, daily catch was estimated by:

$$\hat{n} = \frac{c}{\hat{q}}, \qquad (1)$$

where c was the observed daily count of trapped juveniles and $\hat{q}$ was the estimated trap efficiency for that day. To simplify notation, $\hat{q}$ is expressed in terms of the daily 'expansion factor' denoted e, where:

$$\hat{e} = \frac{1}{\hat{q}}. \qquad (2)$$

Thus, the daily catch estimate ($\hat{n}$) can be expressed as the following product:

$$\hat{n} = \hat{e}c. \qquad (3)$$

There are two sources of variability in $\hat{n}$. First, there is error associated with the estimation of trap efficiency via logistic regression, which will be expressed as error in $\hat{e}$. Second, there is sampling error associated with the

daily count (c), which is assumed to be a binomial variable. An estimate of the variance of $\hat{n}$ is given by Goodman (1960):

$$\hat{\sigma}^2\{\hat{n}\} = \hat{e}^2.\hat{\sigma}^2\{c\} + c^2.\hat{\sigma}^2\{\hat{e}\} - \hat{\sigma}^2\{\hat{e}\}.\hat{\sigma}^2\{c\} \qquad (4)$$

To obtain a variance estimate for $\hat{e}$, it is fist expressed in terms of the back-transformation of the logit function (see equation (4)). Substituting equation 2 into equation 4 and rearranging yields:

$$\hat{e} = 1 + \exp[-(\hat{\beta}_0 + \hat{\beta}_1 x)] = 1 + \exp(-\hat{y}), \qquad (5)$$

where $\hat{y}$ is the logit transform of the estimated trap efficiency $\hat{q}$ (see equation (3)). Given that the distribution of $\hat{y}$ is approximately normal, $\hat{e}$ is assumed to be log-normally distributed with an estimator of variance given by Gelman *et al.* (1995, p. 478):

$$\hat{\sigma}^2\{\hat{e}\} = \exp(-2\hat{y}) * \exp(\hat{\sigma}^2\{\hat{y}\}) * [\exp(\hat{\sigma}^2\{\hat{y}\}) - 1] \quad (6)$$

The variance of $\hat{y}$, which is a prediction from a linear regression, can be expressed in matrix notation as (Neter *et al.* 1990, p. 215):

$$\hat{\sigma}^2\{\hat{y}\} = \mathbf{X}'\mathbf{s}^2\{\mathbf{b}\}\mathbf{X}, \qquad (7)$$

where $\mathbf{X}$ is a vector containing the daily values of the explanatory variables, $\mathbf{X}'$ denotes the transpose of $\mathbf{X}$, and $\mathbf{s}^2\{\mathbf{b}\}$ denotes the scaled estimate of the variance-covariance matrix for the logistic regression coefficients ($\hat{\beta}$). Specifically,

$$\mathbf{X} = \begin{bmatrix} 1 \\ x \end{bmatrix}, \mathbf{X}' = [1 \ \ x], \mathbf{s}^2\{\mathbf{b}\} = \hat{\phi}\begin{bmatrix} \hat{\sigma}^2\{\hat{\beta}_0\} & \hat{\sigma}\{\hat{\beta}_0, \hat{\beta}_1\} \\ \hat{\sigma}\{\hat{\beta}_0, \hat{\beta}_1\} & \hat{\sigma}^2\{\hat{\beta}_1\} \end{bmatrix}.$$
$$(8)$$

Here, x is the daily value of log(flow). Note that the variance-covariance matrix for the logistic regression coefficients is multiplied (i.e. scaled) by the estimated dispersion parameter ($\hat{\phi}$) to account for extra-binomial variation. Equation 6 through equation 8 define the variance estimate for $\hat{e}$ required in equation 4. Also required in equation 4 is the variance of c, the observed daily count of trapped juveniles. Assuming that c follows a binomial distribution conditional on daily catch (n) and trap efficiency (q) (i.e. $c \sim \text{Bin}(n, q)$), the theoretical variance for c would equal $nq(1-q)$. However, a more reasonable and conservative approach is to assume that c is subject to the same extra-binomial variation estimated for the trap-efficiency tests. Extra-binomial variation

would be expected due to unaccounted for factors affecting trap efficiency or characteristics of fish behavior, such as schooling. Thus, the variance of c is estimated as:

$$\hat{\sigma}^2 c = \hat{\phi}\hat{n}\hat{q}(1 - \hat{q}) \qquad (9)$$

.

Equations A4 through A9 define the variance estimate for a given daily catch estimate ($\hat{n}$) given the estimated trap efficiency ($\hat{q}$) and trap count (c) for that day. The estimated total catch (N) of juveniles across days ($i = 1, 2, 3, \ldots, k$) of the sampling season is the sum:

$$\hat{N} = \sum_{i=1}^{k} \hat{n}_i, \qquad (10)$$

with associated variance (Mood *et al.* 1974, p. 179)

$$\hat{\sigma}^2\{\hat{N}\} = \sum_{i=1}^{k} \hat{\sigma}^2\{\hat{n}_i\} + 2\sum_{i=1}^{k-1}\sum_{j>i}^{k} \hat{\sigma}\{\hat{n}_i, \hat{n}_j\}. \qquad (11)$$

The left side of equation 11 is sum of the variances of the daily catch estimates as defined by equation 4. The right side denotes the sum of the covariances among all pairs of daily catch estimates. These covariances arise from the fact that all daily catch estimates are based on predictions of q derived from the same logistic regression. Following from equations 3 and 5, the covariance of any two catch estimates can be approximated as follows:

$$\hat{\sigma}\{\hat{n}_i, \hat{n}_j\} = (c_i\hat{e}_i) * (c_j\hat{e}_j) * (\mathbf{X}'\mathbf{s}^2\{\mathbf{b}\}\mathbf{X}), \qquad (12)$$

where

$$\mathbf{X} = \begin{bmatrix} 1 & x_i \\ 1 & x_j \end{bmatrix}, \mathbf{X}' = \begin{bmatrix} 1 & 1 \\ x_i & x_j \end{bmatrix}. \qquad (13)$$

Again, $\mathbf{s}^2\{\mathbf{b}\}$ denotes the scaled variance-covariance matrix for the logistic coefficients as in equation 8.

Approximate 95% confidence intervals for $\hat{N}$ assuming log normally distributed error is given by:

$$95\%LCI\{\hat{N}\} = \frac{\hat{N}}{c}, \text{ and } 95\%UCI\{\hat{N}\} = \hat{N} * c, \qquad (14)$$

where

$$c = \exp(Z_{\alpha/2}) * \sqrt{\log_e(1 + (\hat{\sigma}\{\hat{N}\}/\hat{N})^2)} \qquad (15)$$