Relating juvenile migration timing and survival to adulthood in two species of threatened Pacific salmon (*Oncorhynchus* spp.)

Mark D. Scheuerell*[1], Richard W. Zabel[1] and Benjamin P. Sandford[2]

[1]*National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, WA 98112, USA; and* [2]*National Marine Fisheries Service, Northwest Fisheries Science Center, Pasco Research Station, Pasco, WA 99301, USA*

Summary

1. Migration timing in animals has important effects on life-history transitions. Human activities can alter migration timing of animals, and understanding the effects of such disruptions remains an important goal for applied ecology. Anadromous Pacific salmon (*Oncorhynchus* spp.) inhabit fresh water as juveniles before migrating to the ocean where they gain > 90% of their biomass before returning to fresh water as adults to reproduce. Although construction of dams has delayed juvenile migration for many populations, we currently lack a synthesis of patterns in migration timing and how they relate to subsequent survival to adulthood for Pacific salmon, especially for at-risk populations.

2. We studied two groups of Pacific salmon from the Columbia River basin in the northwestern United States currently listed under the U.S. Endangered Species Act. We examined how the proportion of juveniles surviving to return as adults varied with year of migration, date of arrival in the estuary, water temperature and coastal ocean upwelling using data from over 40 000 individually tagged Chinook salmon *Oncorhynchus tshawytscha* and steelhead *Oncorhynchus mykiss*.

3. In general, models with *year*, *day* and *day*^{2} had much better support from the data than those with *temperature* and *upwelling*. For Chinook salmon, we also found a residual effect of temperature after controlling for day, but the effect was small for steelhead.

4. For both species, juveniles migrating from early to mid-May survived 4–50 times greater than those migrating in mid-June. As expected, however, the estimated peak in survival varied among years, presumably reflecting interannual variation in the nearshore physical environment and trophic dynamics that affect salmon during the critical juvenile life stage.

5. *Synthesis and applications.* Our results indicate a possible management objective would be to speed arrival to the estuary by increasing springtime river flows. These findings also provide some insight into the mechanisms underlying seasonal differences in survival patterns, but additional studies are needed to better resolve the issue. Future changes to river flow and water temperature associated with climate change and human activities may further alter migration timing, and thus this phenomenon deserves further attention.

Key-words: Chinook, dams, migration, *Oncorhynchus mykiss, Oncorhynchus tshawytscha,* steelhead, survival, temperature, timing

Introduction

The timing of migration is often a key life-history trait for migratory species (Baker 1978). Migration timing determines the degree of spatio-temporal overlap with important resources and the magnitude of ecological interactions, which may prove critical to future survival or reproduction (i.e. 'match/mismatch hypothesis' *sensu* Cushing 1990). Accordingly, individuals are thought to time their migration to optimize fitness, subject to constraints. For example, blue wildebeest *Connochaetes taurinus* Burchell 1823 presumably time their annual migrations to minimize competition for seasonally available food and water, and to swamp predators

*Correspondence author. E-mail: mark.scheuerell@noaa.gov

during the calving season (Boone, Thirgood & Hopcraft 2006). Male great reed warblers *Acrocephalus arundinaceus* Linneaus 1758 that leave their wintering grounds and migrate earlier can occupy breeding territories sooner, leading to higher reproductive success (Hasselquist 1998). Consequently, anthropogenic disturbances that disrupt migration timing, such as climate change or artificial barriers, can have negative fitness consequences on populations (Durant *et al.* 2007; Waples *et al.* 2008), potentially leading to increased risk of extinction for threatened populations.

Anadromous Pacific salmon (*Oncorhynchus* spp.) are renowned for their extensive migration from fresh water, where they rear as juveniles, to the northern Pacific Ocean, where they obtain > 90% of their biomass before returning to spawn in fresh water as mature adults (Quinn 2005). Juveniles are believed to synchronize their seaward migration to maximize growth and survival in the ocean (Pearcy 1992). This transition from juvenile to adult is typically viewed as a population 'critical period' because survival during the first year at sea is very low and highly variable (Quinn 2005). Although year-to-year variability in juvenile-to-adult survival appears related to ocean conditions during the period of ocean entry (Scheuerell & Williams 2005; Zabel *et al.* 2006), within-year patterns of juvenile-to-adult survival and the mechanisms that determine these patterns remain largely unknown.

Many populations of Pacific salmon throughout the northwestern United States have declined precipitously over the past century because of anthropogenic activities (Ruckelshaus *et al.* 2002). In many cases, construction of hydropower dams has altered water flow and temperature, and shifted the migration timing of juvenile salmon (Zabel & Williams 2002; Williams 2008). Although most mainstream dams allow for both juvenile and adult passage around them, these structures have transformed free-flowing rivers into a series of large reservoirs, and the altered hydrological regime has major implications for migratory behaviour (Waples *et al.* 2008). For example, Raymond (1979) estimated that it now takes approximately 2 weeks longer for juvenile salmon to migrate downstream through the Snake and Columbia Rivers. Directional shifts because of increased migration times under altered flow regimes could further jeopardize at-risk populations even though closely related populations vary considerably in the timing of their seaward migrations within and among populations (Achord, Zabel & Sandford 2007). Thus, understanding how juvenile migration timing relates to survival to adulthood will not only provide an indication of how dams have impacted salmon populations, but can also produce valuable information for recovery strategies.

We studied how juvenile migration timing affects subsequent survival to adulthood for two species of Pacific salmon: Chinook salmon *Oncorhynchus tshawytscha* Walbaum 1792 and steelhead *Oncorhynchus mykiss* Walbaum 1792. We focused our analyses at the level of an 'evolutionary significant unit' (ESU, Waples 1991), defined as a population of salmon that (1) is reproductively isolated from other conspecific populations, and (2) represents an important component in the evolutionary legacy of the species. The two ESU we examined are from the Snake River, the largest tributary of the Columbia River (Fig. 1). Both ESU are listed as 'threatened' under the United States Endangered Species Act. We analysed information from over 40,000 individually tagged salmon on the exact time when the fish entered the Columbia River estuary and whether they successfully returned as adults.

Materials and methods

STUDY SPECIES AND DATA

Juveniles from the first ESU, Snake River spring/summer Chinook salmon, migrate to the ocean after rearing in fresh water for approxi-

Fig. 1. Map of the Columbia and Snake Rivers indicating the locations of various hydroelectric dams (dark symbols) along the migratory pathway for salmon. Individual fish were detected at Bonneville Dam as juveniles on their downstream migration and at Lower Granite Dam as returning adults. The uppermost dam shown is Hell's Canyon, which prohibits returning adults from migrating any further upstream. The current portion of the Snake River basin accessible to salmon is shown in grey.

mately 1 year. Chinook salmon return to their natal streams to spawn after spending 1–4 years foraging and maturing in the northeast Pacific Ocean, after which they die. Individuals from the second ESU, Snake River steelhead, migrate to sea after 1–4 years in freshwater and mature after 1–2 years before returning to spawn. Steelhead are iteroparous and may spawn again.

We used data from passive integrated transponder (PIT) tags (Prentice, Flagg & McCutcheon 1990) to estimate differences in juvenile-to-adult survival within and among years. Each tag has a distinct identification code that allows researchers to track information on individual fish, such as the date and location of tagging. Juvenile salmon were captured, anesthetized, and a PIT tag (∼12 mm long) was inserted into the abdominal cavity with a hypodermic needle, where it remained for life. Following tagging, detectors in juvenile bypass systems at hydropower dams along the Snake and Columbia Rivers (Fig. 1) identified juveniles during their downstream migration; detectors in adult fish ladders at dams recorded the surviving individuals as they swam upstream toward their spawning grounds. The combined juvenile and adult detections of individual fish thus provided information on juvenile migration timing and an index of ocean survival. All PIT-tag data are publicly available from the Pacific States Marine Fisheries Commission (http://www.ptagis.org).

For Chinook salmon, we used PIT-tag data from juvenile migration years 1998–2000 and 2002–2003 and subsequent adult return years 1999–2007. For steelhead, we used data from juvenile migration years 1999–2000 and 2002–2003 and subsequent adult return years 2000–2005. We omitted migration year 2001 for both species because of very low adult returns (only seven Chinook and one steelhead). We assigned migration dates to juveniles based on their detection date at Bonneville Dam (BON), the lowermost dam along their migration pathway (Fig. 1). For adults, however, we measured their detection (i.e. survival) at Lower Granite Dam (LGR), the uppermost dam, because the adult detection equipment at BON was only partially operational until 2002. We saw no need to adjust our samples for possible temporal differences in detection probabilities for either juveniles or adults because (1) our pool of juveniles was already based only on fish that had been detected at BON and (2) adult detection efficiency at LGR is consistently estimated at 100% (D. Marsh, NOAA Fisheries Service, Seattle, WA, USA, personal communication). The data on within-year migration timing for juveniles were restricted to 1 May to 20 June because of very low numbers of fish migrating before or after those dates. Based on these criteria, our dataset consisted of 26 687 juvenile and 594 returning adult Chinook and 14 593 juvenile and 349 returning adult steelhead.

We know that survival varies among the many populations comprising each ESU and that factors such as fish size also play a role (Zabel & Williams 2002). However, including information on all of these additional factors would reduce our sample size to such an extent that it would be difficult, if not impossible, to obtain reliable estimates of their effects. Therefore, we characterize the relationship between juvenile-to-adult survival and migration timing at a broad scale, with the goal of directing future research toward understanding the specific mechanisms underlying the relationships.

We did, however, undertake a qualitative examination of whether seasonal changes in smolt 'origin' or length might play a role in explaining the patterns we observed by plotting the number of smolts detected at BON by day, grouped according to the sub-basin where they were captured, tagged and released, and then examining a daily time series of mean length of smolts that were tagged in the subbasin with the largest sample size (Hydrological Unit Code 17060107; Fig. S1, Supporting Information). We did so to avoid comparing fish that were tagged days, weeks, or even months apart, often in

disparate locations, because we had no way to evaluate differences in growth rates between the time of tagging and the time they were detected at BON. Our analysis failed to reveal any obvious patterns in location or body size that might relate to the seasonal changes in smolt-to-adult survival that we observed (Figs S2–S5, Supporting Information).

STATISTICAL ANALYSES

Because the data were based on individually PIT-tagged fish, we treated each individual fish as the unit of comparison in our survival analyses (i.e. a Bernoulli trial). We used logistic regression (Hosmer & Lemeshow 2000) to determine relationships between the probability of returning as an adult and a suite of predictor variables, with individuals assigned a value of 1 if they returned as an adult or 0 if they did not return and were presumed dead. We tested for under- or over-dispersion, but found no evidence for it (i.e. dispersion ranged from 0·97 to 1·01 across all models and both species, and none were significantly different from 1).

We considered the following explanatory variables: year, day of arrival below BON, river temperature at BON and the daily Coastal Upwelling Index (CUI) from 45N 125W (http://www.pfeg.noaa.gov). We treated year as a categorical, fixed effect and allowed for possible interactions between year and the other covariates. We also included a quadratic term for each of the covariates so that its effect would not be strictly increasing or decreasing.

The CUI is an index of current strength (i.e. volume of water upwelled per unit of coastline) and is used as an indicator of nearshore ocean conditions important to salmon (see Scheuerell & Williams 2005). The mechanisms by which upwelling might influence salmon survival via bottom-up processes probably operate on time scales of days to perhaps weeks. Daily upwelling indices are significantly autocorrelated at time lags of 2–7 days across all years, so we felt that matching the exact date of upwelling was not critical. We chose the upwelling index for the same day because our intention was to describe temporal patterns of within-year survival probabilities.

We were also interested in the joint effects of day and water temperature because they are two important environmental cues for migration (Quinn 2005), but these variables are highly correlated during the time of year considered here (Pearson's $r = 0·965$ across all years) and that would have created problems with respect to underlying assumptions of the regression model. Therefore, we first regressed temperature on day and then used the model residuals as an indicator of the additional effect of temperature after controlling for day because fish might tend to migrate earlier than average in a year that was particularly warm for the given time of year (or conversely, migrate later if it was unseasonably cold). We did not consider models that included the joint effects of day and CUI or the temperature–day residuals and CUI. Thus, we ultimately tested a set of 26 models for each species (Table 1).

We ranked all candidate models according to the Akaike Information Criterion (AIC) and used Akaike weights (w) to determine the relative support for each model (Burnham & Anderson 2002). The value of w for any model i is

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{R} \exp(-0.5\Delta_r)}, \qquad \text{eqn 1}$$

where Δ_i is the difference in AIC between model i and the overall best model among the R candidates (i.e. that with the lowest AIC). Next, for each species, we used ws to compute the relative importance of each variable on a scale of 1–0. The relative impor-

Table 1. Relative performance of the candidate models for predicting juvenile-to-adult survival of Chinook salmon and steelhead

Chinook			Steelhead		
Model	ΔAIC	w	Model	ΔAIC	w
$Y + D + D^2 + R$	0·0	0·670	$Y + D + D^2 + Y{*}D$	0·0	0·460
$Y + D + D^2 + Y{*}D + R$	3·9	0·093	$Y + D + D^2 + Y{*}D + R$	1·5	0·222
$Y + D + D^2 + R + Y{*}R$	4·1	0·086	$Y + T + T^2 + Y{*}T$	3·1	0·095
$Y + D + D^2$	5·1	0·052	$Y + D + Y{*}D$	4·8	0·043
$Y + D + D^2 + Y{*}D + R + + Y{*}R$	5·4	0·046	$Y + T + Y{*}T$	5·4	0·030
$Y + D + D^2 + Y{*}D$	6·3	0·029	$Y + T + T^2$	5·4	0·030
$Y + D + Y{*}D + R + Y{*}R$	8·4	0·010	$Y + D + D^2$	5·9	0·024
$Y + D + R$	9·4	0·006	$Y + D$	6·0	0·023
$Y + D + R + Y{*}R$	11·0	0·003	$Y + D + Y{*}D + R$	6·7	0·016
$Y + D$	12·0	0·002	$Y + D + D^2 + Y{*}D + R + Y{*}R$	6·8	0·016
$Y + D + Y{*}D + R$	12·2	0·001	$Y + D + D^2 + R$	6·9	0·015
$Y + D + Y{*}D$	13·0	0·001	$Y + D + R$	7·5	0·011
$Y + T + T^2 + Y{*}T$	16·9	0·000	$Y + T$	8·6	0·006
$Y + T + T^2$	18·7	0·000	$Y + D + R + Y{*}R$	9·9	0·003
$Y + T + Y{*}T$	23·9	0·000	$Y + D + D^2 + R + Y{*}R$	10·0	0·003
$Y + T$	25·7	0·000	$Y + D + Y{*}D + R + Y{*}R$	10·8	0·002
$Y + U + U^2$	46·5	0·000	Y	21·9	0·000
$Y + U + U^2 + Y{*}U$	46·6	0·000	$Y + R$	23·8	0·000
Y	47·0	0·000	$Y + U$	23·9	0·000
$Y + R$	47·3	0·000	$Y + U + U^2$	25·1	0·000
$Y + U$	47·8	0·000	$Y + U + Y{*}U$	25·9	0·000
$Y + U + Y{*}U$	50·1	0·000	$Y + U + U^2 + Y{*}U$	27·8	0·000
D	223·3	0·000	D	35·7	0·000
T	235·0	0·000	T	59·2	0·000
U	284·6	0·000	U	84·7	0·000
Reference	298·6	0·000	Reference	96·8	0·000

The regression variables are year (Y), day (D), day^2 (D^2), river temperature (T), coastal upwelling (U) and the residuals from the temperature–day regression (R). Interactions between year and the covariates are denoted by an (*). The Reference model contains only a constant and all other models include a constant by default. ΔAIC is the difference in AIC between the top-ranked model (shown in bold) and the model in question. AIC weights (w) give relative support for any particular model.

tance for variable j was the sum of w_j across all the models where variable j occurs (Burnham & Anderson 2002). We used model averaging (Burnham & Anderson 2002) to derive a broad scale perspective of temporal changes in survival that was not conditional on any particular model because the model estimated to be the 'best' can vary from data set to data set (e.g. across years and between species). We used the Akaike weights to weight the parameters from each model (Burnham & Anderson 2002), such that the model averaged estimate for a given parameter, say β, was

$$\hat{\bar{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i. \qquad \text{eqn 2}$$

The unconditional variance estimator for the same model averaged parameter is then given by

$$\widehat{\text{var}}\left(\hat{\bar{\beta}}\right) = \left[\sum_{i=1}^{R} w_i \sqrt{\widehat{\text{var}}\left(\hat{\beta}_i | g_i\right) + \left(\hat{\beta}_i - \hat{\bar{\beta}}\right)^2} \right]^2, \qquad \text{eqn 3}$$

where $\hat{\bar{\beta}}$ is the model-averaged estimate from eqn 2 and $\widehat{\text{var}}\left(\hat{\beta}_i | g_i\right)$ is the variance in $\hat{\beta}_i$ conditional on model g_i. We constructed 95% confidence intervals around the model-averaged mean response assuming the logit-transformed variable was normally distributed. The variance on which the confidence interval

was based was calculated using a formula analogous to eqn 3, replacing β with the response variable (i.e. smolt-to-adult survival). Computed confidence intervals were then back-transformed onto the interval (0,1). We conducted all statistical analyses using the R programming language (http://www.r-project.org).

Results

The proportion of juvenile salmon surviving to adulthood was nonlinearly related to their timing of seaward migration (Figs 2 and 3). For both species, the data provided strong support for models with terms for *year*, *day* and *day*^{2}. In addition, the *day–temperature* residual term was an important factor for Chinook, but not nearly so for steelhead (Tables 1–2). On the other hand, the *year × day* interaction term had relatively large weight for steelhead whereas it had little influence for Chinook (Table 2). Furthermore, although the main effects of *temperature* and *temperature*^{2} were of some importance for steelhead, they had no measurable effect for Chinook.

Estimated survival of Chinook was generally highest for juveniles migrating in early to mid-May and then decreased across the remainder of the migration season (Fig. 2). Year-class survival estimates (i.e. total number of returning adults
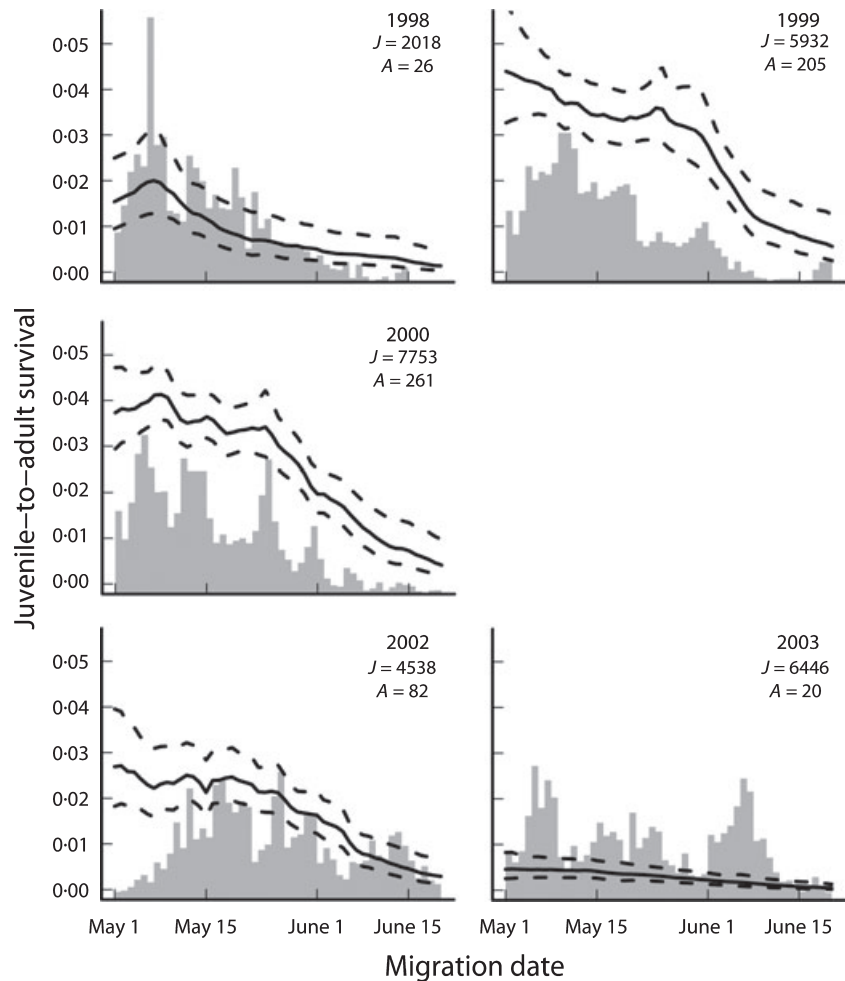
Fig. 2. Model-averaged proportion of Chinook juveniles surviving to adulthood versus migration date (solid line) for migration years 1998–2000 and 2002–2003. Dashed lines denote the 95% confidence interval about the mean response. The total number of migrating juveniles (J) and subsequent number of surviving adults (A) is shown for each year-class. The histogram (grey shading) displays the proportion of juveniles included in this study that migrated on each day (note: *y*-axis for histogram equals twice that for survival [i.e. scale = 0–0·1]).

Table 2. Relative importance of the regression variables used in the survival analyses

Variable	Chinook	Steelhead
Year (Y)	1·000	1·000
Day (D)	1·000	0·837
Day squared (D^2)	0·977	0·739
Temperature (*T*)	0·000	0·163
Temperature squared (T^2)	0·000	0·126
Upwelling (U)	0·000	0·000
Upwelling squared (U^2)	0·000	0·000
Residuals (R)	0·916	0·288
Year × day (Y × D)	0·151	0·759
Year × temperature (Y × T)	0·000	0·126
Year × upwelling (Y × U)	0·000	0·000
Year × residuals (Y × R)	0·152	0·025

Variable weights were based on model weights given in Tables 1 and 2 and measure the overall strength of evidence for each predictor variable on a scale from 0 to 1.

divided by total number of juveniles) ranged more than tenfold among years, from a high of 0·035 in 1999 to a low of 0·0031 in 2003. The model-averaged estimate of the mean proportion of surviving adults was not a smooth function over time for Chinook because of the residual effect of temperature after controlling for day (Fig. 2).

Within-season patterns in survival for steelhead differed from those for Chinook (Fig. 3). In all years except 1999, survival for steelhead was much higher in early- to mid-May than June. In 1999, estimated survival peaked during late May. The highest overall year-class survival for both Chinook and steelhead occurred in 2000 and the lowest in 2003. Unlike Chinook, however, the model-averaged estimate of the mean proportion of surviving adults for steelhead was a much smoother function of time because of the relative unimportance of the residual effect of temperature after controlling for day (Fig. 3).

The environmental predictor variables did not improve model fit much for either species, especially compared with the time indices (Tables 1–2). In simpler models, water temperature had explanatory power similar to day of arrival, presumably because of the high correlation between the two (Pearson's *r* = 0·965 across all years). For both species, however, coastal upwelling had a much less measurable effect on survival than day, temperature, or the residuals from the temperature-day regression.

Discussion

We demonstrated that migration timing plays a major role in determining juvenile-to-adult survival for Chinook salmon and steelhead, with early migrating individuals typically
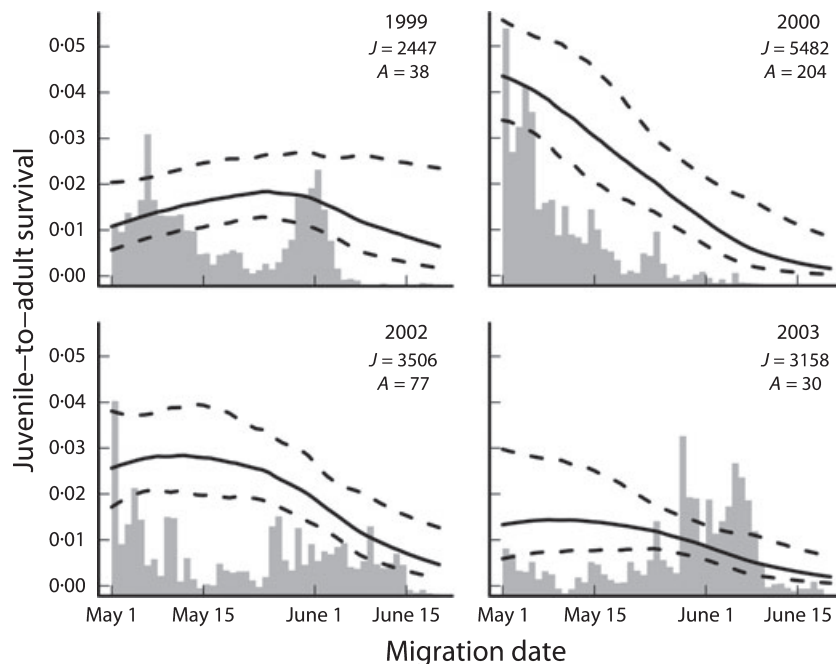
Fig. 3. Model-averaged proportion of steelhead juveniles surviving to adulthood versus migration date (solid line) for migration years 1999–2000 and 2002–2003. Dashed lines denote the 95% confidence interval about the mean response. The total number of migrating juveniles (J) and subsequent number of surviving adults (A) is shown for each year-class. The histogram (grey shading) displays the proportion of juveniles included in this study that migrated on each day [note: *y*-axis for histogram equals twice that for survival (i.e. scale = 0–0·1)].

experiencing much higher survival than later migrating ones. This study represents one of the most extensive efforts to describe this type of relationship in a natural population. This type of study will be increasingly important as more and more species are subjected to anthropogenic impacts (e.g. climate change) that disrupt their phenology (e.g. Parmesan 2006).

An important outcome is the possibility of tailoring management programmes to maximize survival. Based on the results described here, one focus of the management of Snake and Columbia River salmon populations would be to increase their downstream migration rate so that they arrive in the estuary earlier. This can be achieved by increasing river flow from storage reservoirs or increasing the amount of water spilled over the dams, which allows individuals to pass the dams more quickly (Zabel *et al.* 2008).

MIGRATION TIMING OF JUVENILE SALMON

Juvenile salmon rely on endogenous (e.g. hormone concentrations and body size) and environmental (e.g. photoperiod, temperature and food supply) cues for initiating seaward migration (Beckman *et al.* 2000). Larger Chinook salmon juveniles tend to initiate seaward migration earlier (Zabel & Achord 2004), and also survive better than smaller fish (Zabel & Williams 2002; Zabel & Achord 2004), suggesting a balance between early migration timing and attaining a large enough size to assure survival through adulthood. Furthermore, the various populations from the Snake River composing the aggregate ESU we analysed actually show considerable variation in their respective juvenile migration timing (Achord *et al.*

2007), a possible cause and consequence of so-called salmon 'biocomplexity' (*sensu* Hilborn *et al.* 2003). Unfortunately, low numbers of returning adults precluded us from examining how both migration timing and fish size relate to intra-annual differences in survival.

Water temperature also has important effects on salmon migration, growth and survival (Quinn 2005). In our case, however, river temperature by itself was not as good a predictor of survival as migration date. On the other hand, we did find considerable support for models that included a residual effect of temperature after controlling for day, especially for Chinook. The strength of coastal upwelling currents affects water temperature, nutrient supply and the structure of the nearshore food web, and has been linked to juvenile-to-adult survival of Pacific salmon (Scheuerell & Williams 2005). We failed to find much support from the data for an effect of upwelling, however, perhaps because of an inability to match daily upwelling indices with survival over such short time scales. That is, we would expect a time lag between upwelling and survival if upwelling affected salmon survival through its indirect effects on primary and secondary productivity. Attempting to match the appropriate lag in upwelling with survival was simply beyond the scope of this study, but would be an interesting avenue of future research.

Salmon populations often show density dependence with respect to growth and survival during both the freshwater (Achord, Levin & Zabel 2003; Einum, Sundt-Hansen & Nislow 2006; Ward *et al.* 2007) and marine (Ruggerone *et al.* 2003; Ruggerone & Goetz 2004) phases of their life cycle. When comparing plots of our survival estimates to the number of juveniles

migrating on any given day (Figs 2 and 3), one might consider that survival tends to be higher on days when more fish are migrating. It is certainly an interesting question, but unfortunately, the histograms of juvenile migrants only reflect the fish used in our study and not the entire population of juvenile salmon migrating on any given day. That is, we only considered wild fish of the same species that migrated in-river. In addition to those we analysed, there are also large numbers of hatchery-reared salmon, salmon that were transported downstream in barges, and other ESU and species of salmon (e.g. coho *Oncorhynchus kisutch* Walbaum, sockeye *Oncorhynchus nerka* Walbaum). It was beyond the scope of this paper to consider all of the other potential factors associated with fish density.

Salmon populations may have adapted their timing of juvenile migration to exploit optimal foraging conditions and avoid predators in the estuary and nearshore ocean (Pearcy 1992). Our study was not designed to identify specific mechanisms responsible for the patterns in survival that we observed, but we can offer some possible explanations. Recently, Emmett, Krutzikowsky & Bentley (2006) reported on the abundance and distribution of predatory (e.g. Pacific hake *Merluccius productus* Ayres 1855) and forage (e.g. Pacific herring *Clupea pallasi* Valenciennes 1847) fishes in the Columbia River plume and nearshore environment during spring and early summer 1998–2003. Rarely did they capture any predatory fish before 14 May, but catches increased after this date and peaked in late June and early July – essentially the inverse of our estimates of salmon survival. Forage fish, which may act as competitors for food or alternate prey for predators, did not show as consistent a pattern in density as for predatory fish (Emmett *et al.* 2006). Colonial seabirds nesting in the lower estuary also prey heavily upon juvenile salmon during their seaward migration, with consumption about one-third higher in June than in May (Roby *et al.* 2003).

A large majority of the world's rivers have been impounded, negatively affecting the dispersal and migration of aquatic organisms (Nilsson *et al.* 2005). The Columbia River basin is no exception – over 200 hydroelectric and multipurpose dams exist there currently (Payne *et al.* 2004). Their collective effect on basin hydrology has altered migratory timing of juvenile Pacific salmon. Our results show that earlier migrants currently survive at much higher proportions than later migrants, suggesting that overall juvenile-to-adult survival may have been higher previous to development of the hydropower system.

Climate change will impose additional stress on rivers impounded by dams compared with free-flowing rivers that can respond via dynamic interactions between the streambed, floodplain and riparian zone (Palmer *et al.* 2008). In the Columbia River basin, projected shifts in stream flow and increased water temperature are expected to limit suitable rearing habitat, increase metabolic demand, increase predation risk and lower overall survival for juvenile salmon (Crozier, Zabel & Hamlett 2008b). Climate change also poses a special set of problems for organisms like salmon whose life-history transitions coincide with the phenology of the larger community because of uncertainty in the degree of match or mismatch between predator requirements and resource availability

(Durant *et al.* 2007). Already, climate change has uncoupled trophic interactions for zooplankton (Winder & Schindler 2004) and migrating ungulates (Post & Forchhammer 2008). Depending on the degree to which juvenile salmon use stream temperature as a cue to initiate migration, warmer temperatures in the future may shift migration earlier, potentially improving their survival to adulthood if the patterns that we found continue to hold. The ocean also responds to changes in climate, however, with large effects on juvenile-to-adult survival (Logerwell *et al.* 2003; Scheuerell & Williams 2005). Therefore, if salmon rely more heavily on a signal unrelated to climate change (e.g. day length) or freshwater migration cues do not match changes in the marine environment, juveniles could face an increasing spatio-temporal mismatch with their prey resources, or greater overlap with predators.

Timing of juvenile migration in salmonids is heritable (Taylor 1990) and, therefore, we may expect to see Pacific salmon populations respond to anthropogenic changes by shifting their migration timing. Already, juvenile salmon appear to be responding plastically by migrating earlier in warmer years (Achord *et al.* 2007). However, the relative contribution of genetic differences versus phenotypic plasticity remains unknown. Furthermore, any expected evolutionary shift will be subject to trade-offs among correlated traits, such as growth rate, and other evolutionary constraints (Crozier *et al.* 2008a). These may limit the ability of salmon populations to 'track' changes in optimal conditions, and may ultimately determine whether these threatened populations can recover. Clearly, we must consider the effects of human activities on the response of salmon populations to changes in their juvenile migration timing.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. Map of the anadromous portion of the Snake River basin showing individual sub-basins.

Fig. S2. Number of Chinook smolts emigrating on a given day, grouped by the sub-basin in which they were captured, tagged, and released.

Fig. S3. Number of steelhead smolts emigrating on a given day, grouped by the sub-basin in which they were captured, tagged, and released.

Fig. S4. Time series of mean length of Chinook smolts captured, tagged, and released in subbasin 17060107.

Fig. S5. Time series of mean length of steelhead smolts captured, tagged, and released in subbasin 17060107.

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