



# Population diversity in salmon: linkages among response, genetic and life history diversity

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Response diversity and asynchrony are important for stability and resilience of meta-populations, however little is known about the mechanisms that might drive such processes. In salmon populations, response diversity and asynchrony have been linked to the stability of their meta-populations and the fisheries that integrate across them. We examined how population diversity influenced response diversity and asynchrony in 42 populations of Chinook salmon from the Fraser River, British Columbia. We examined diversity in the survival responses to large-scale ocean climate variables for populations that differed in life history. Different life-histories responded differently to ocean environmental conditions. For instance, an increase of offshore temperature was associated with decreased survival for a population with ocean rearing juveniles but increased survival for a population with stream rearing juveniles. In a second analysis, we examined asynchrony in abundance between populations, which we then correlated with life history, spatial, and genetic diversity. Populations that were more genetically distant had the most different population dynamics. Collectively, these results suggest that fine-scale population diversity can contribute to the asynchrony and response diversity that underpins the stability of fisheries or metapopulation dynamics, and emphasize the need to manage and conserve this scale of population diversity.

Response diversity to environmental variability can increase the resilience and stability of systems (Elmqvist et al. 2003). Response diversity is when populations or species respond differently to environmental conditions leading to asynchrony in dynamics (Elmqvist et al. 2003). This asynchrony among populations or species can increase the stability of the aggregate through statistical averaging, also termed a portfolio effect (Doak et al. 1998, Tilman et al. 1998). Foundational studies have explored theoretical relationships between diversity and stability in communities (Doak et al. 1998, Tilman et al. 1998, Yachi and Loreau 1999) with empirical examples focused primarily on plant communities (Tilman et al. 2006) but more recently include bird (Karp et al. 2011), coral reef fish (Thibaut et al. 2012) and salmon fisheries (Schindler et al. 2010). While the consequences of diversity on stability have become a major theme in ecology and conservation, relatively little is known about the specific mechanisms that lead to the asynchrony, that ultimately underpins diversity–stability relationships (Loreau and Behera 1999, Thibaut and Connolly 2012). In particular, understanding the underpinnings of response diversity can enable the linkage of management and conservation decisions to the stability of communities and populations and their ecosystem services (Mori et al. 2012).

Understanding the patterns and drivers of synchrony among populations has been a focus of population ecologists for decades (Liebhold et al. 2004). In general, more distant populations tend to be more asynchronous (Ranta et al. 1997, Peterman et al. 1998, Post and Forchhammer 2002), potentially driven by differences in environmental forcing (i.e. Moran effect) (Moran 1953), dispersal among populations (Ranta et al. 1995) or trophic interactions with other synchronized species (Bjørnstad and Bascompte 2001). Alternatively, intrinsic characteristics of populations could influence how they respond to perturbations, thereby contributing to patterns of synchrony. For instance, different local adaptations or life-history strategies could influence how populations respond to different environmental conditions (Crozier and Zabel 2006). Thus, there remains a need to examine linkages among extrinsic (i.e. distance) versus intrinsic population properties and asynchrony. Furthermore, the majority of studies of population asynchrony do not examine the potential climate driver of population dynamics, thereby decreasing predictive capacity and leaving a potential disconnect between studies of synchrony and studies of response diversity.

Pacific salmon provide an excellent opportunity to examine the role of genetic and life history diversity in among population asynchrony because of the great diversity among populations in close proximity. Research on Pacific salmon *Oncorhynchus* spp. has highlighted relationships between population diversity and asynchrony. Schindler et al. (2010)

showed that the portfolio effect is responsible for a 2-fold increase in catch stability of sockeye salmon *O. nerka* from Bristol Bay, Alaska. This portfolio effect occurs because of asynchrony among populations in this system; even nearby populations are relatively asynchronous in their abundances and productivity (Rogers and Schindler 2008), presumably influenced by differential responses to local environmental conditions such as rearing lake temperatures (Rogers and Schindler 2011). In addition, Crozier and Zabel (2006) found that juvenile survival in populations of Chinook salmon in the Columbia River basin responded differently to environmental forcing; in some populations survival was related to temperatures, while in other populations survival was related to low fall stream flows. Spatial variation in juvenile survival within a metapopulation can reduce inter-annual changes in juvenile recruitment (Thorson et al. 2014). Generally, fine-scale differences in the dynamics of Pacific salmon populations are thought to be linked to both variation in watershed features, such as geology, that filters large-scale climate signals producing local environmental variation, as well as local adaptations, such as life histories, leading to different responses to environmental conditions (Schindler et al. 2008). This response diversity can be integrated into ecological processes such as predation by wildlife (Schindler et al. 2013) and meta-population dynamics (Schtickzelle and Quinn 2007), as well as fisheries (Schindler et al. 2010), stabilizing such processes. Although there is evidence for how watershed location and characteristics influence response diversity, there is little evidence that directly relates variation in life history or the underlying genetic variation among populations to response diversity and asynchrony in Pacific salmon populations (but see Moore et al. (2014)).

Population diversity of Pacific salmon has been dramatically altered by human activities in some parts of their range. At the most basic level, there are now fewer populations of salmon than in the past (Gustafson et al. 2007). In the US approximately 29% of populations have been extirpated, and this loss has been especially pronounced for populations with longer freshwater migrations (Gustafson et al. 2007). In addition to population loss, elements of population diversity (i.e. habitat, life history and genetic variation) have also been greatly reduced, mainly due to dams, hatchery production, and habitat alteration (Waples et al. 2009). Impacts of hatcheries and dams can degrade genetic structure (Pearse et al. 2010) and life history diversity (Waples et al. 2007) of populations, homogenizing populations and potentially homogenizing responses to environmental change. Evidence from disturbed populations showed that dams and hatchery production might lead to synchronization of populations over time, which can weaken portfolio effects and increase risk of extinction (Moore et al. 2010, Carlson and Satterthwaite 2011). Understanding how population diversity drives response diversity and asynchronous dynamics in large intact watersheds with relatively few dams and little hatchery influence could help identify the appropriate scales for management and aid the conservation of stability for salmon meta-populations and their fisheries (Anderson et al. 2013).

Studies that explore beyond the patterns of diversity–stability and seek to identify the processes that underpin response diversity are needed to better understand how

management and environmental change might impact the stability of groups of populations (Loreau and Behera 1999, Thibaut and Connolly 2012). Here, we examined how different aspects of population diversity mediate response diversity and asynchrony in Chinook salmon *O. tshawytscha*. We first explored the hypothesis that population survival responds differently to the marine environment. We compared responses in marine survival to large-scale climate forcing of five populations that differ in life history. Then we investigated how asynchrony among 41 populations is mediated by three aspects of population diversity: life history, genetics, and spatial diversity in breeding and juvenile habitat.

## Material and methods

### Study system

We studied population diversity in a total of 42 populations of Chinook salmon in the Fraser River in British Columbia, Canada (Fig. 1 and Supplementary material Appendix 2, Table A1). The Fraser River is one of the largest salmon producing watersheds in the world, draining approximately 240 000 km<sup>2</sup> (Déry et al. 2012). It is also one of the largest watersheds in the world that is undammed on its mainstem (Nilsson et al. 2005). The adult Chinook salmon of this watershed are targeted by economically and culturally important fisheries, including commercial, recreational and First Nations fisheries. These fisheries generally target in-river migrating adult Chinook salmon and thus integrate across multiple populations and may differentially impact certain populations and life histories. Response diversity of Chinook salmon populations could be important to the stability and resilience of the greater Fraser River Chinook salmon meta-population as well as the fisheries that integrate across them (Moore et al. 2015).

Within the Fraser River watershed, Chinook salmon exhibit substantial variation in spawning location, genetics, and life-history among populations. First, they use spatially diverse habitats. For instance, Chinook salmon populations in this study range from lower in the Fraser watershed to 1375 km upstream. Second, Chinook salmon return to spawn in their natal streams, which over time leads to local adaptation and genetic isolation among populations within large watersheds such as the Fraser River (Taylor 1991, Olsen et al. 2010). Previous work studying protein and microsatellite variation in Chinook salmon populations has identified geographical and life-history based genetic divergence among populations within the Fraser River (Beacham et al. 2003). Third, Chinook salmon exhibit one of the most complex and diverse life histories of Pacific salmon (Quinn 2005). A common difference among populations is return timing to freshwater; populations may return to freshwater from March to October and can be broadly categorized as spring, early summer, mid-summer, late summer or fall migrants (Parken et al. 2008). Populations are also often categorized as either subyearling- or yearling. Subyearling Chinook salmon only spend days to a few months rearing in freshwater after emerging from their incubation gravel before migrating to the ocean. Yearling Chinook salmon typically spend one year

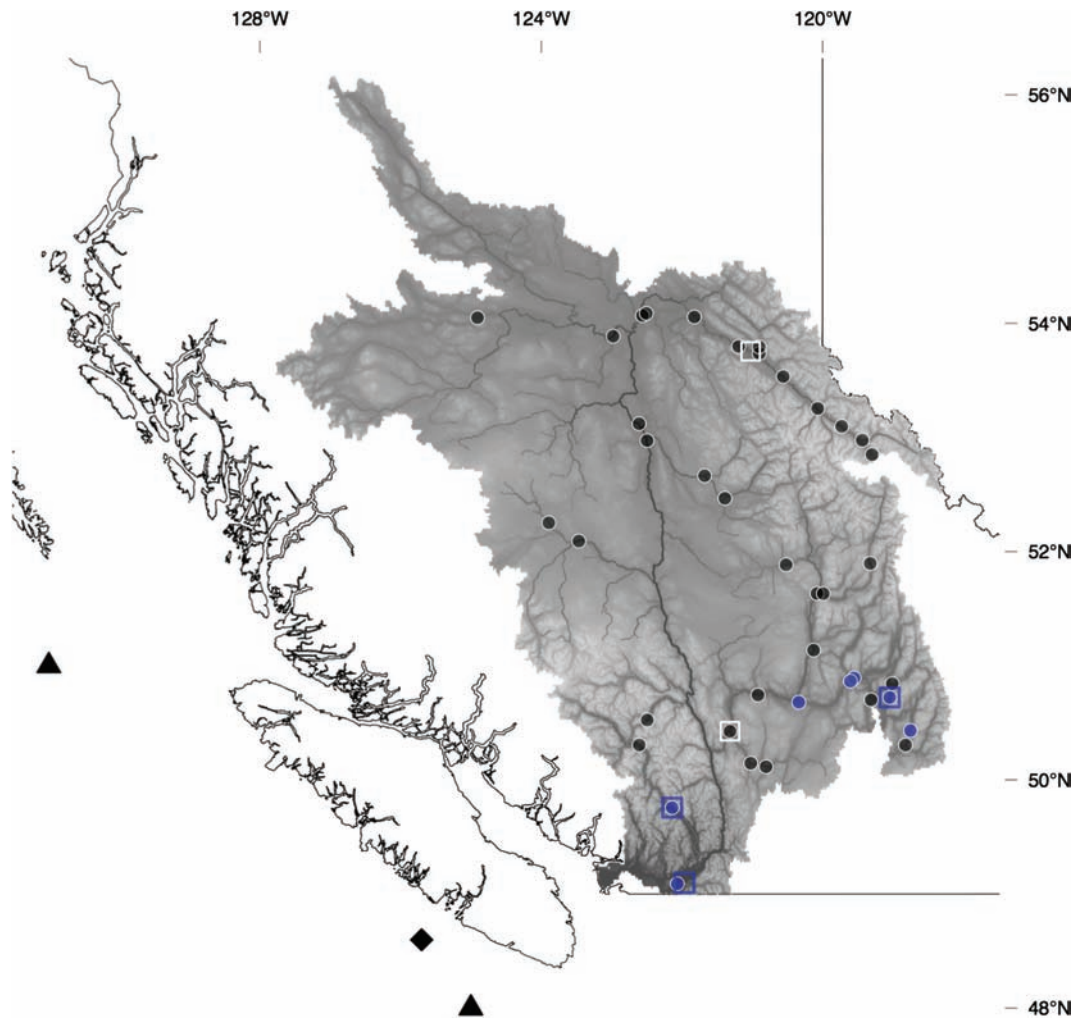


Figure 1. Map of Fraser Chinook populations and locations where climate data were measured. Open white squares are yearling hatchery populations, open blue squares are subyearling hatchery populations, black circles are yearling wild populations, and open blue circles are wild subyearling populations. Solid triangles are locations where Coastal Upwelling Indices are measured and the solid diamond is where sea surface temperature is measured.

in freshwater before migrating to sea (Rich 1925, Sharma and Quinn 2012). This categorization encompasses a number of other differences, including size at smoltification, reproductive investment, size and age-at-maturity, and proximity of spawning stream to the ocean (Groot and Margolis 1991). We examined how these different elements of population diversity were associated with response diversity.

We conducted two complementary analyses using different datasets and approaches. 1) Marine survival: we quantified how (ocean) climate conditions impact the marine survival of five indicator populations. This analysis estimated the response diversity of populations to several key ocean climate variables. 2) Population diversity and asynchrony: we examined how population diversity influenced asynchrony of population dynamics among 41 populations, which include all except one population that did not meet our data criteria (details below), used in the previous analyses. This dataset included information on three aspects of population diversity: life history, genetics, and spawning location. Asynchrony differs from traditional response diversity in that it provides no direct link to changes in large-scale forc-

ing variables such as changes in environmental conditions; however, it arguably serves as a proxy for response diversity to unknown and unmeasured large-scale variability. These two datasets are complementary because they capture different ecological scales and types of population diversity. Below we overview these two sets of data and analyses.

### Marine survival

We quantified variability in marine survival by estimating population-specific coefficients for the effects of ocean conditions on survival of different Chinook salmon populations. This analysis focused on marine survival estimates derived from coded-wire tag recovery data from five indicator/hatchery streams with time series ranging from 16 to 25-yr (Supplementary material Appendix 2, Fig. A6). We also used information on large-scale ocean climate conditions that these Chinook salmon populations experience in the first year at sea. We focused this analysis on life-history diversity; the five populations represent all but one of the major life his-

tories found in Fraser Chinook (Table 1 and Supplementary material Appendix 2, Table A1). The Chilliwack population was established from translocation and is genetically very similar to the Harrison River fall population; therefore the two indicator populations are likely to exhibit strong covariance in survival (Supplementary material Appendix 2, Fig. A7).

### Coded-wire tags and marine survival index

We used estimates of marine survival for the five Fraser River indicator populations from 1981 to 2009, although there were fewer years for some indicator populations due to discontinued monitoring and changes in funding (Supplementary material Appendix 2, Fig. A6a). This index of marine survival is reconstructed using the coded-wire tag recoveries and represents the marine survival of a population after 2-yr in the ocean; estimates are independent of freshwater survival. This is a relative measure of hatchery survival in the absence of fishing. Coded-wire tags are placed in the snout of hatchery fish just before they are released as smolts. These tags contain information about their release location and date and the adipose fin is clipped as a visual cue the fish is tagged. Fish with coded wire tags are recovered in fisheries and when they return to spawn. Marine survival is calculated as the sum of fishing mortalities (recovered tags and estimated incidental mortality) and spawner abundance divided by the total number of tagged fish released in a brood year. There are a number of assumptions with these estimates of survival and are outlined in PSC (1988). Briefly, estimates of marine survival track the number of tags recovered from ocean and terminal fisheries, natural mortality, and abundance on spawning grounds for a given cohort. These estimates are currently used as the management standard for populations managed under the Pacific Salmon Commission (Sharma et al. 2013).

### Marine climate data

We compiled data on climate variables that have previously been shown to impact salmon. Sea surface temperature (SST) is used as a proxy for the biological conditions in the marine environment (Mueter et al. 2002) and has been linked to the productivity of marine zooplankton communities (Francis et al. 2012). Reconstructed monthly mean SST time series for 48.6°N and 125.7°W were obtained from NOAA and are available at (<www.esrl.noaa.gov/psd/>) (Fig. 1 and Supplementary material Appendix 2, A6b). The Pacific Decadal Oscillation (PDO) is an ocean scale index that integrates sea surface temperature anomalies across the North Pacific. Time series of monthly PDO values were compiled from the Univ. of Washington and are available at <http://research.jisao.washington.edu/pdo/PDO.latest>

(Supplementary material Appendix 2, Fig. A6c). The Pacific Coastal Upwelling Index (CUI) is a measure of the degree of upwelling at specific locations along the west coast of North America. Upwelling occurs when the surface waters are displaced (through wind stress and or the rotation of the earth). This nutrient rich water stimulates plankton production and can enhance fish growth and survival (Scheuerell and Williams 2005). We compiled CUI data for two locations (48°N, 125°W and 51°N, 131°W) (Fig. 1 and Supplementary material Appendix 2, A6d), which are available at (<www.pfel.noaa.gov/products/PFEL/modeled/indices/PFELindices.html>) that overlap the distributions of juvenile Chinook salmon from the Fraser River during their first year of life at sea (Tucker et al. 2011).

For all marine climate variables, we lagged the variables by 1–2 yr from the brood year such that fish from the 2000 brood year with subyearling (migrates to the ocean in its first year) and yearling (migrates to the ocean in its second year) life histories would be compared to climate variables in 2001 and 2002 respectively. We used monthly values for climate variables beginning in March of their first year at sea to February of their second year at sea.

### Analyses

We examined the hypothesis that relationships between marine survival and climate variables differ among populations. We used linear models to relate climate variables to marine survival and included an interaction between climate and population. Models describing marine survival are as follows:

$$S_i = \alpha + \phi P_i + \gamma C + \delta(P_i \cdot C) + \epsilon \quad (1)$$

Where  $S$  is the marine survival of population  $i$ ,  $\alpha$  is the intercept,  $\phi$  is the main effect of population  $i$ ,  $\gamma$  is the effect of a monthly climate variable ( $C$  – SST, CUI at 48°N, CUI at 51°N, and PDO for months between March in their first year at sea and February in their second year at sea),  $\delta$  is the interaction between the population  $i$  and a climate variable, and  $\epsilon$  is the residual error. A significant interaction suggests difference among populations in the response of marine survival to climate. Each climate variable was related to marine survival data (years of marine survival data range – 16–25). Models were visually inspected for normality of residuals, heteroscedasticity and independence of residuals (Zuur et al. 2010).

### Population diversity and asynchrony

Our second set of analyses focused on asynchrony and population diversity for a larger dataset, based on time

Table 1. Life history diversity for Fraser Chinook salmon populations. Life history traits are the dominant traits for populations, variation within populations in some traits is common (e.g. location of juvenile rearing in the first year).

Juvenile rearing location (yr 1)	Return timing	Years in freshwater	Age at maturity	Estimated number of wild populations	Number of hatchery populations	Life history code
Stream	Spring	2	4	6	1	Spring 4 <sub>2</sub>
Stream	Spring	2	5	31	1	Spring 5 <sub>2</sub>
Ocean	Summer	1	4	5	1	Summer 4 <sub>1</sub>
Stream	Summer	2	5	11	0	Summer 5 <sub>2</sub>
Ocean	Fall	1	4	2	2	Fall 4 <sub>1</sub>

series of adult abundance on their spawning grounds for 41 populations (1982–2006). Spawning adults were counted annually by Fisheries and Oceans, stock assessment personnel, or partner groups. Abundances are estimated using one of three methods: 1) visual surveys (aerial or stream walks); 2) mark recapture studies; or 3) fences or fishways. From visual counts, estimates of annual abundance are calculated using an expansion factor. Details about how specific populations are enumerated and how abundance estimates are calculated can be found in (PSC 2003, Sharma et al. 2013). For our analyses of asynchrony we examined correlations between time series of abundance. We also calculated spawner-to-spawner ratios from these abundance estimates, which are the spawners at time  $t$  that gave rise to spawners at time  $t + x$ ,  $x$  is the dominant age at maturity for the population. We note that these abundance data may be subject to observation error and influenced by both natural and fisheries mortality. Thus, differential harvest rates, management interventions, density dependence, and natural mortality could all be contributing to this index of population abundance. We also acknowledge that age at maturity may also vary among years. For this analysis, we focus on three aspects of population diversity: 1) life history, 2) genetics, and 3) spatial diversity.

### **Life history diversity**

Fraser Chinook populations are typically categorized into 5 dominant life history strategies (spring 4<sub>2</sub>, spring 5<sub>2</sub>, summer 4<sub>1</sub>, summer 5<sub>2</sub>, and fall 4<sub>1</sub>, see Table 1 for additional details), where a spring 4<sub>2</sub> population would return to freshwater to spawn during the spring months, the majority of fish would be in their fourth year and would have spent two years in freshwater. We used return timing to freshwater (May, June, July, August and September) (Parken et al. 2008), age-at-maturity (4 or 5 yr), and freshwater residency (1 or 2 yr) (Table 1 and Supplementary material Appendix 2, Table A1). There is some variation in age at maturity within populations, usually less than 20% of the populations return either one year early or later than the dominant age (PSC 2003). We constructed two dissimilarity matrices made up of: 1) all life history variables including freshwater residency (1 or 2 yr), ocean residency (2 or 3 yr), age at maturity (4 or 5 yr), adult return timing month (May, June, July, August or September) (Parken et al. 2008) and 2) just freshwater residency (1 or 2 yr) using the Gower's index (Borcard et al. 2011). These matrices describe the difference in life-histories between pairs of populations.

### **Genetic diversity**

Tissue samples collected from 41 populations of Chinook salmon in the Fraser River were analyzed for 15 microsatellite loci (Supplementary material Appendix 2, Table A2). Allelic frequencies were used to calculate genetic distances among populations. For genetic distance we calculated Weir and Cockerham's (1984) approximation of  $F_{ST}$  using the program TREEFIT (Kalinowski 2009). Descriptive statistics for the genetic analysis can be found in Supplementary material Appendix 2, Table A2 and A3.

### **Spatial diversity**

Distance between populations was measured as the Euclidean and river distance between the stream mouths of

two populations using ArcGIS 10.1. Euclidean distance is likely to be related to similarity in freshwater climate conditions, whereas river distance is probably more representative of the connectivity between populations. These two distance metrics are correlated ( $r = 0.68$ ), but diverge especially at larger distances (Supplementary material Appendix 2, Fig. A8). We present results for river network distance here and for Euclidean distance in the supplementary information (Supplementary material Appendix 2, Fig. A9). We also examined the isolation by distance to better understand the underlying driver of genetic diversity by relating geographic and genetic distance (Meirmans 2012).

### **Analyses**

We described patterns of covariation in population dynamics using pair-wise Pearson's correlations in spawner abundance and spawner-to-spawner ratios for 41 populations, which estimates the degree of linear correlation between two populations. Only populations with fewer than four missing years of spawner abundance data (1982–2006) were used. The magnitude and direction of correlations coefficients (i.e.  $r$  values) were used as measures of asynchrony between two populations. While the Pearson's correlation coefficient is the simplest and most commonly recognized metric of synchrony (Liebhold et al. 2004), it may not be robust to non-linear relationships. Simple correlations also are unable to detect changes in the strength of correlations between populations through time. To address these potential issues, we explored two other non-linear synchrony metrics and applied a moving window approach to our time series (Supplementary material Appendix 1).

We examined four potential mechanisms that could drive asynchrony: 1) stream network distance between populations, 2) the genetic distance between populations, 3) life history similarity of all traits, and 4) similarity in freshwater residency (subyearling vs yearling). Support for each hypothetical mechanism was evaluated using the Mantel  $r$  ( $r_M$ ) and  $p$ -value (significance –  $p < 0.05$ ) from Mantel tests using the *ecodist* package (Goslee and Urban 2007) in R statistical software (R Core Team), which test for correlations between two matrices (Borcard et al. 2011). The  $r_M$  for the Partial Mantel represents the correlation between the first explanatory variable with the response after accounting for the second explanatory variable.

## **Results**

### **Marine response diversity**

There was large variation in marine survival index within and among populations (Supplementary material Appendix 2, Fig. A6a). For example, survival ranged from 1.7 to 30% for Chilliwack whereas Lower Shuswap fish varied from 0.7 to 6.6%. Populations also showed varying patterns of covariance in ocean survival with correlations ( $r$ ) between populations ranging from  $-0.3$ – $0.9$  (Supplementary material Appendix 2, Fig. A7). Marine climate variables were highly variable across the 30-yr time series (Supplementary material Appendix 2, Fig. A6b–d).

Chinook salmon populations responded differently to climate variables and this appeared to be mediated by life histories. For example, subyearling and yearling populations exhibited opposite correlations to SST from March through to October (Fig. 2A), with March SST showing significant population by SST interaction term (Table 2). Specifically, yearling populations experienced higher survival when SSTs were warmer whereas subyearling populations experienced higher survival when temperatures were cooler (Fig. 3). Although, the interaction between population and SST was only significant for March ( $p < 0.01$ ), the direction of the effect is consistent when compared between the two life histories, (Fig. 2A; Table 2). For example, between March and

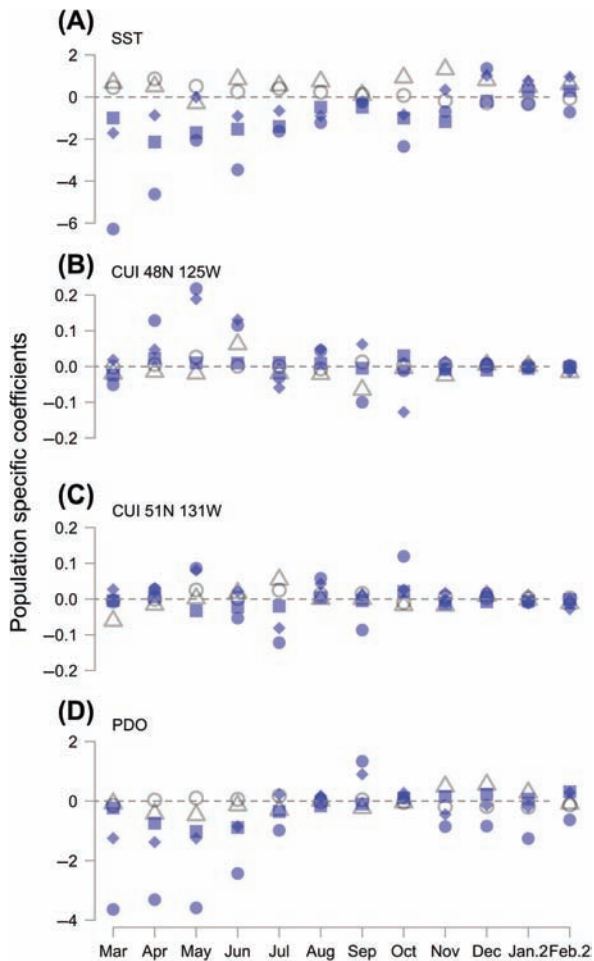


Figure 2. Plots of population-specific coefficients from linear regression models that relate (A) sea surface temperature (SST), (B) Coastal Upwelling Index (CUI 48°N, 125°W), (C) Coastal Upwelling Index (CUI 51°N, 131°W), and (D) Pacific Decadal Oscillation (PDO) to marine survival. Marine survival is based on coded-wire tag recoveries and is the survival of individuals in a population from when they are released to their return to freshwater after accounting for fishing mortality. Only one climate metric was included in each model and population specific coefficients (slopes) are derived from an interaction term between population and climate. Symbols represent populations (closed blue squares are Lower Shuswap River, closed blue diamonds are Harrison River, closed blue diamonds are Chilliwack River, open grey circles are Dome Creek, and open grey triangles are Nicola Creek,) and life history (subyearling – solid blue or yearling – open grey). The significance of interactions are found in Table 2.

Table 2. Summary of p-values for interaction terms in models relating percent marine survival to sea surface temperature, Pacific Decadal Oscillation, Coastal Upwelling Index at 48°N and 51°N from March in the first year of ocean entry to February in the following year. Significant interactions are in bold.  $R^2$  values are for the whole model.

Month	SST		CUI at 48N		CUI at 51N		PDO	
	p-value	R <sup>2</sup>	p-value	R <sup>2</sup>	p-value	R <sup>2</sup>	p-value	R <sup>2</sup>
March	<b>0.003</b>	<b>0.50</b>	0.773	0.39	0.704	0.38	0.136	0.44
April	0.229	0.42	0.498	0.40	0.914	0.38	0.444	0.42
May	0.658	0.40	0.070	0.49	0.855	0.38	0.179	0.45
June	0.187	0.43	0.583	0.42	0.796	0.38	0.442	0.42
July	0.789	0.39	0.953	0.38	0.264	0.41	0.909	0.38
August	0.673	0.39	0.867	0.38	0.962	0.38	0.999	0.37
September	0.993	0.37	0.903	0.38	<b>0.795</b>	0.38	0.736	0.39
October	0.804	0.38	0.603	0.39	<b>0.050</b>	<b>0.45</b>	0.999	0.37
November	0.921	0.38	0.817	0.38	0.883	0.38	0.884	0.38
December	0.968	0.38	0.940	0.38	0.956	0.38	0.907	0.38
January	0.991	0.37	0.996	0.37	0.972	0.38	0.863	0.38
February	0.943	0.38	0.902	0.38	0.875	0.39	0.981	0.37

October 15 out of 16 coefficients describing the effect of SST on survival for yearling populations are positive and 23 out of 24 are negative for subyearling populations (Fig. 2A).

Populations showed variable responses to Coastal Upwelling Index measured at 48°N. There were no significant interactions between the CUI measured at 48°N and population (Table 2). During the spring months (April–June) survival was highest in years of higher coastal upwelling for the two subyearling populations (Harrison and Chilliwack) that are in the ocean during this time but the responses were insignificant and weak for yearling populations (Fig. 2B). Associations between survival and Coastal Upwelling Index measured at 51°N were highly variable but we observed opposite relationships in October for yearling and subyearling populations (Fig. 2C); the interaction between population and CUI measured at 51°N was significant ( $p = 0.05$ ). Subyearling populations show consistently negative relationship with PDO during spring (March–June) but no consistent pattern was observed for yearling populations (Fig. 2D).

### Population diversity and asynchrony

On average Chinook populations displayed relatively asynchronous dynamics as indicated by the low average correlations between the spawner abundance of populations through time and spawner-to-spawner ratios (correlation for spawner abundance mean and SD:  $r = 0.17 \pm 0.30$ ; correlation for spawner-to-spawner mean and SD:  $r = 0.21 \pm 0.28$ ). However, correlations for individual population pairs varied dramatically from  $-0.74$  to  $0.88$  for spawner abundance and from  $-0.42$  to  $0.94$  for spawner-to-spawner ratios.

Asynchrony between populations was strongly related to genetic differentiation. Specifically, the more genetically distant two populations were, the more asynchronous their changes in abundance through time (Fig. 4B; spawner abundance:  $r_M = -0.31$ ,  $p$ -value  $< 0.01$ ; spawner-to-spawner:  $r_M = -0.34$ ,  $p$ -value  $< 0.01$ ). These correlations are independent of life history. For example, the strength of the relationships ( $r_M$ ) are similar among genetic differentia-

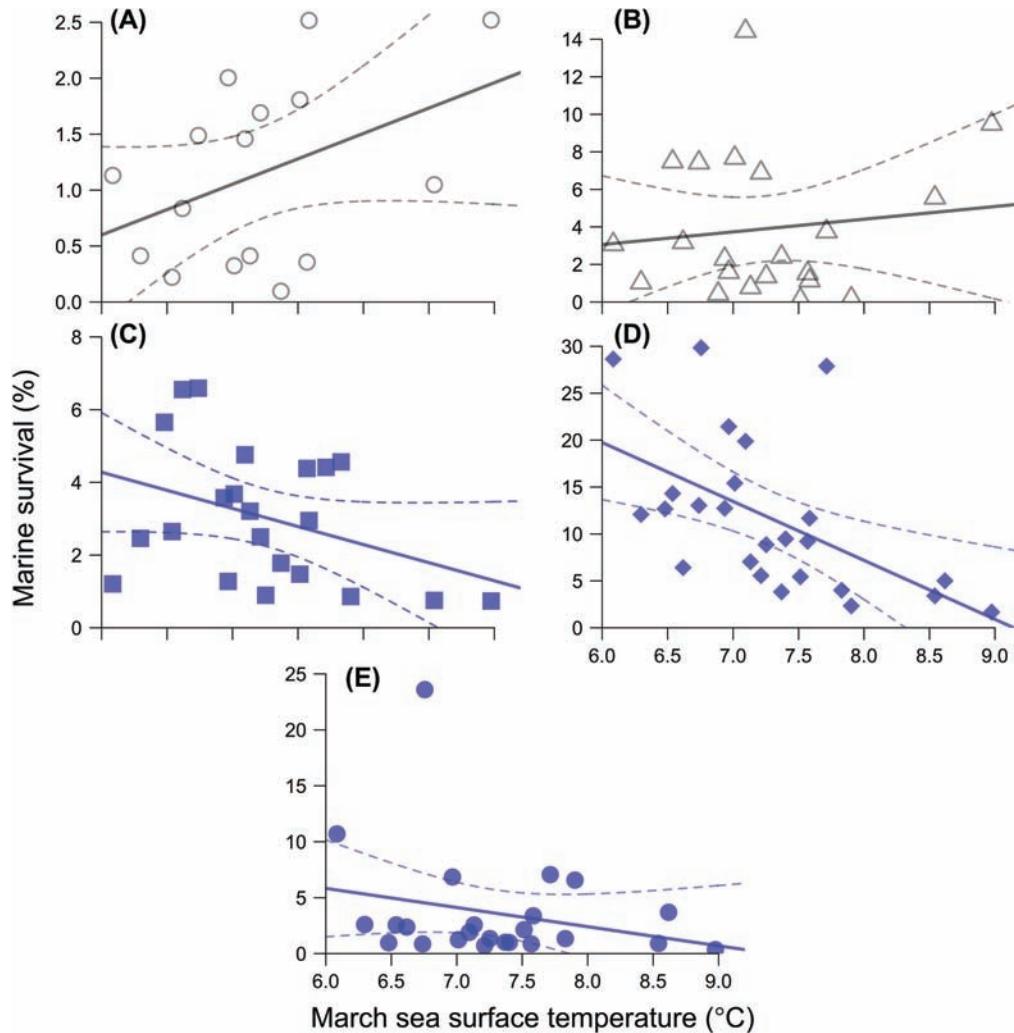


Figure 3. Plots of the relationships between marine survival and March sea surface temperatures for (A) Dome Creek (spring 5<sub>2</sub>), (B) Nicola Creek (spring 4<sub>2</sub>), (C) Lower Shuswap River (summer 4<sub>1</sub>), (D) Chilliwack River (fall 4<sub>1</sub>), (E) Harrison River (fall 4<sub>1</sub>). These results for March sea surface temperature represent the strongest evidence for response diversity out of the broader suite of climatic analyses (Fig. 2 and Table 2). Solid lines represent the mean slope and hashed lines are the 95% confidence bounds from linear models. Grey plots are yearling and blue plots are subyearling populations. Symbols are same as in Fig. 3.

tion models with and without life history diversity (spawner-to-spawner ratio: genetic diversity  $r_M = -0.34$ ; genetic diversity + life history  $r_M = -0.34$ ; genetic diversity + juvenile residency  $r_M = -0.36$ ) (Table 3B). In the Partial Mantel models the  $r_M$  values refer to the correlation between genetic differentiation and asynchrony after accounting for the second explanatory variable; they are not correlation coefficients for the whole model. Life history also explained variation in asynchrony (spawner abundance: life history distance  $r_M = -0.34$ ,  $p$ -value  $< 0.01$ ; spawner-to-spawner ratio: life history distance  $r_M = -0.18$ ,  $p$ -value  $< 0.05$ ) (Table 3, Fig. 4C). Moreover, freshwater residency (subyearling vs yearling) was also correlated with asynchrony (spawner abundance  $r_M = -0.41$ ,  $p$ -value  $< 0.01$ ; spawner-to-spawner ratio: life history + genetic differentiation  $r_M = -0.27$ ; juvenile residency + genetic differentiation  $r_M = -0.39$ ; spawner-to-spawner ratio: life history + genetic

differentiation  $r_M = -0.09$ ; juvenile residency + genetic differentiation  $r_M = -0.14$ ) (Table 3). While there was some evidence that network distance influences asynchrony among populations (spawner abundance  $r_M = -0.13$ ,  $p$ -value  $< 0.05$ ; spawner-to-spawner ratio  $r_M = -0.04$ ,  $p$ -value  $> 0.05$ ) it was much weaker than the relationships with genetic distance and life history distance (Table 3). Even nearby populations that are within 50 km exhibited a broad range in correlations of population dynamics, from  $-0.21$  to  $0.7$  (Fig. 4A), highlighting the fine spatial scale of asynchrony. Network distance was also related to genetic distance suggesting that isolation by distance is present in Fraser River Chinook (Supplementary material Appendix 2, Fig. A10).

### Other metrics of asynchrony

We examined patterns of asynchrony with methods to explore possibilities for non-linearity and non-stationarity (Supplementary material Appendix 1). To examine non-

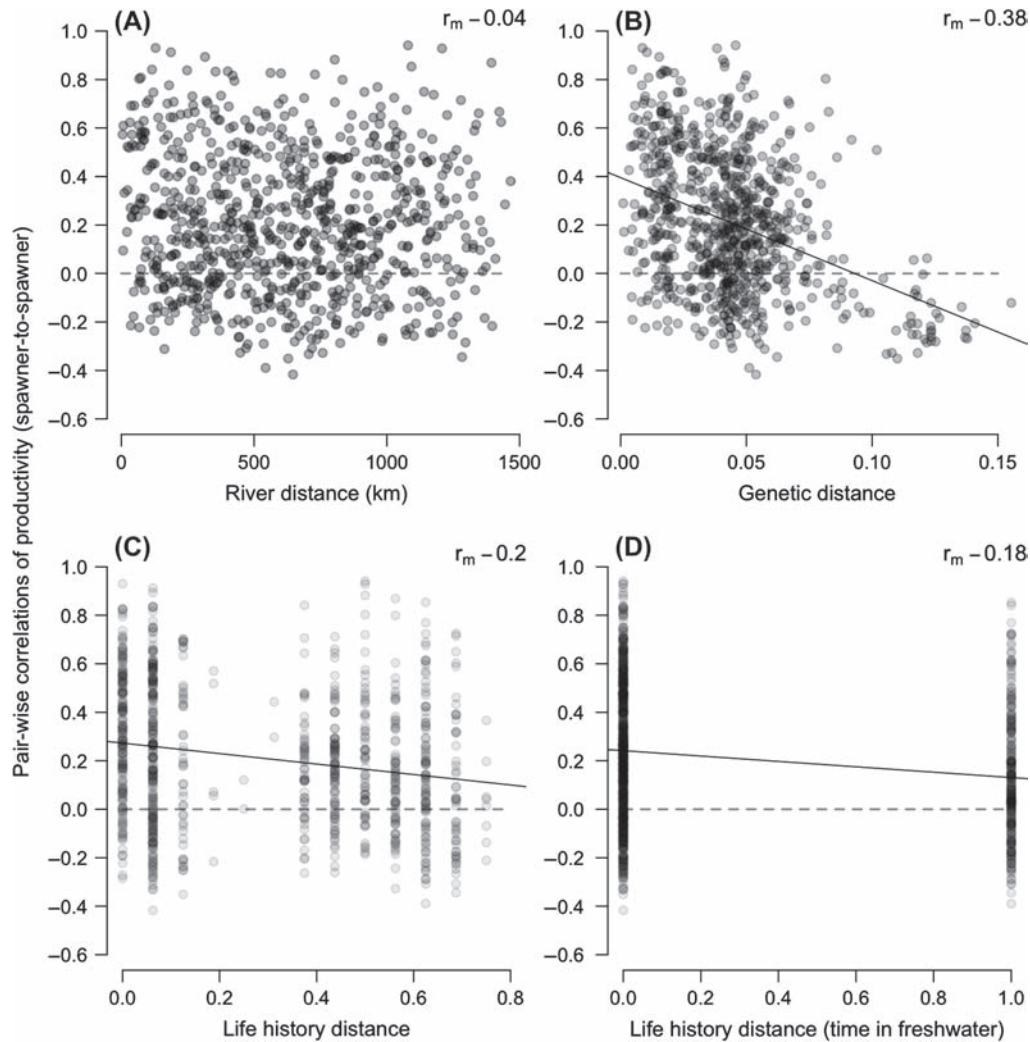


Figure 4. Plots showing how (A) river network distance, (B) genetic distance, and two life history distance metrics, (C) all life history traits and (D) juvenile freshwater residency relate to pair-wise correlations of spawner-to-spawner ratios. Life-history distance indicates whether pairs of populations have the same (distance=1) or dissimilar life histories (distance=0). The correlation between pair-wise correlations and predictor variables is presented using Mantel's  $r_M$  and lines are from linear regression models and only for visual representation of the trend.

linearity, we quantified concordance in minima and maxima (concurrency) and phase synchrony (Gouhier and Guichard 2014). Life history differences among populations was negatively linked to concurrency, but other aspects of populations were not significantly related to concurrency. Furthermore, we found no relationships with the phase synchrony metric. To examine non-stationarity, we used a moving window analysis to examine how correlation coefficients among population shifted through time. While the average correlation coefficient did change through time (Supplementary material Appendix 1, Fig. A2 and A3), relationships between asynchrony and populations characteristics such as genetic and life-history differences remained qualitatively similar to the analyses of the full dataset (Supplementary material Appendix 1, Fig. A4 and A5). More details about these analyses can be found in Supplementary material Appendix 1.

## Discussion

Previous theoretical and empirical work has illustrated that response diversity can lead to asynchrony in abundance among populations and ultimately increase the stability (Anderson et al. 2015) and resilience of metapopulations and fisheries that integrate over population diversity (Elmqvist et al. 2003, Schindler et al. 2010, Moore et al. 2015). We found variable responses of marine survival to sea surface temperature and coastal upwelling in Chinook salmon populations during their first year at sea. Although only a few strong relationships were observed of the many explored, consistent patterns suggest these relationships may be mediated by life history. In a second analysis, we revealed that the more asynchronous populations were more genetically distinct and exhibited larger differences in life history traits. Taken together, these results illustrate response diversity in Chinook salmon to climatic variability and illuminate



Table 3. Summary of Mantel and Partial Mantel tests explaining asynchrony between populations in their a) spawner abundance and b) spawner-to-spawner ratio. For Partial Mantel analyses, models are directly relating variable A to asynchrony while accounting for (variable B). Correlation coefficients are represented by  $r_M$  values (similar to the Pearson's correlation coefficient) and p-values are for one-tailed tests.

Response	Analysis	Model	$r_M$	p-value
a) Spawner abundance	Mantel	Genetic	-0.31	0.002
		Life history	-0.34	0.001
		Residency	-0.41	0.001
		River distance	-0.13	0.012
	Partial Mantel	Genetic (Life history)	-0.22	0.019
		Genetic (Residency)	-0.28	0.003
		Genetic (River distance)	-0.28	0.002
		Life history (Genetics)	-0.27	0.003
		Life history (Residency)	-0.04	0.211
		Life history (River distance)	-0.33	0.002
		Residency (Genetic)	-0.39	0.002
		Residency (Life history)	-0.24	0.003
		Residency (River distance)	-0.39	0.001
		River distance (Genetic)	-0.03	0.246
		River distance (Life history)	-0.10	0.032
		River distance (Residency)	-0.12	0.016
b) Spawner-to-spawner	Mantel	Genetic	-0.34	0.001
		Life history	-0.18	0.047
		Residency	-0.18	0.035
		River distance	-0.04	0.230
	Partial Mantel	Genetic (Life history)	-0.34	0.001
		Genetic (Residency)	-0.36	0.001
		Genetic (River distance)	-0.39	0.001
		Life history (Genetics)	-0.09	0.157
		Life history (Residency)	-0.09	0.150
		Life history (River distance)	-0.20	0.031
		Residency (Genetic)	-0.14	0.060
		Residency (Life history)	-0.04	0.334
		Residency (River distance)	-0.18	0.054
		River distance (Genetic)	0.10	0.042
		River distance (Life history)	-0.02	0.402
		River distance (Residency)	-0.03	0.289

some of the aspects of population diversity that underpin such responses.

### Marine response diversity

Chinook salmon populations with different life-histories responded oppositely to increased sea surface temperatures experienced in their first year at sea. Subyearling populations had lower survival with warmer sea surface temperature, whereas yearling populations had higher survival with warmer sea surface temperature. Specifically, according to our analyses, an increase in temperature of 1°C (around the mean) was associated with an estimated 71% (CI<sub>95%</sub>: 52–113) decrease in survival for an subyearling population and an estimated 19% (CI<sub>95%</sub>: 12–47) increase in survival for a yearling population (Fig. 3A and B, respectively). Sea surface temperature (SST) is a proxy for biological conditions in the marine environment and is generally thought to be negatively correlated with survival for Pacific salmon species in southern British Columbia (Mueter et al. 2002, Sharma et al. 2013), however there are exceptions (e.g. chum salmon (Mueter et al. 2002)). A more plausible explanation is that SST serves as a proxy for freshwater conditions or northern offshore ocean conditions that coincide with the

migration patterns of yearling populations (Tucker et al. 2011). Regardless of ultimate mechanisms, our results suggest that populations with different life histories relate differently to ocean temperature.

We also found that both subyearling and yearling populations experienced higher survival associated with coastal upwelling but responses differed to the location and timing of upwelling. In subyearling populations, survival was highest for large upwelling events during May and June around the southern tip of Vancouver Island (48°N, 125°W). This effect was greatest for the Harrison and Chilliwack populations, which are in the ocean during this time whereas the effect was smaller for the Lower Shuswap population, which doesn't enter the marine environment until July. For yearling populations we found the same positive relationship but for coastal upwelling measured during July off the northern tip of Vancouver Island (51°N, 131°W). These differences in responses are likely a reflection of their different migration behaviour. Subyearling populations spend more time in the coastal environment and migrate much slower, spending most of their first year in southern BC waters and are only found north of Vancouver Island into their second year at sea, whereas yearling populations generally migrate much faster, spending their first summer in southern BC and are found north of Vancouver Island by the

fall (Tucker et al. 2011, Sharma and Quinn 2012). Although we cautiously interpret the results from this set of analyses, relationships that define response diversity are needed to transform portfolio management of meta-populations from a theoretical exercise (Anderson et al. 2013) to a more predictive management tool (Mori et al. 2012).

### Population diversity and asynchrony

We found that population asynchrony is related to various metrics of diversity, and most strongly to genetic differentiation. Populations that were genetically distant ( $F_{ST} \geq 0.09$ ) demonstrated asynchronous dynamics with mean correlations ( $r$ ) of  $-0.16$ . In contrast, populations that were genetically similar ( $F_{ST} \leq 0.09$ ) were more synchronous with mean correlations of  $0.23$  (Fig. 4). We found similar results for life history; populations that exhibited similar life histories were more synchronous. Our results are supported by Thorson et al. (2014), which examine synchrony in juvenile survival among 15 populations, all with the same juvenile life histories (i.e. yearling) and similar adult life histories. They reported relatively high levels of synchrony (average Pearson's correlation of  $0.59$ ) compared to the asynchrony (average Pearson's correlation of  $0.18$ ) we found across a diversity of juvenile and adult life histories. Our analyses suggest that the influence of life history on asynchrony is largely due to differences in freshwater residency (i.e. subyearling vs yearling). After accounting for variation in life history, the partial correlation between genetic differentiation and spawner-to-spawner ratio was  $0.34$ , which suggests that the variables are related to independent variation in spawner-to-spawner ratio. This relationship between genetic diversity and life history is complex and it is suspected that salmon have undergone parallel evolution and are subject to population level polymorphism triggered by environmental cues (Moran et al. 2013). In addition, the microsatellite markers used in this study are non-encoding, therefore they are thought to reflect levels of gene flow between populations and not genes under selection which might track genetic-based life history characters more closely. Distance among pairs of populations was not a strong predictor of differences among population dynamics, in contrast to previous studies (Rogers and Schindler 2008). The result that genetic diversity and life history were correlated with asynchrony indicates that fine-scale local adaptations and life-histories are directly or indirectly linked to asynchronous dynamics.

We acknowledge that genetic differentiation could be a proxy for unmeasured fine-scale variation in life history traits. We used broad categories for our life history traits, which may miss finer scale differences in life histories. For example, populations are described by their run timing (spring, early summer, mid summer, late summer, fall) (Parken et al. 2008) but populations in a single run timing group may have slightly different run timings or migration pathways that render them more or less susceptible to fisheries (Beacham et al. 2003). Thus, fine scale diversity likely mediates the exposure and tolerance to unmeasured environmental- and anthropogenic-forcing of Chinook salmon populations, thereby controlling population asynchrony.

Such asynchrony enables positive relationships between diversity and stability (Doak et al. 1998). A large body of work has demonstrated that communities with higher species diversity are more stable (reviewed by Cardinale et al. (2012)). However, few examples show the effects of genetic diversity among populations on stability (Cardinale et al. 2012). While the need to conserve genetic diversity is well recognized, few studies have linked genetic diversity to population metrics that may indicate the productivity and persistence of populations (Hughes et al. 2008) (but see (Hughes 2004, Cadotte et al. 2012)). One rare example is that of Hughes (2004), who found that high intra-specific genetic diversity of seagrass *Zostera marina* increased resistance to disturbance and recover faster after being disturbed. Such fine-scale diversity is likely being lost much more rapidly than species diversity (Hughes et al. 1997), likely compromising the stability and resilience of meta-populations (Anderson et al. 2015).

Salmon management is increasingly striving to conserve and manage for population diversity. Genetic differentiation among salmon populations is thought to reflect their post-glacial colonization history as well as local adaptations, which has evolved over hundreds if not thousands of years (Teel et al. 2000). Chinook salmon populations that spawn closer to each other are generally more similar genetically (i.e. isolated by distance) within the Fraser River (Supplementary material Appendix 2, Fig. A10) and throughout the species range (Moran et al. 2013). While we found that genetic differences among populations and life history diversity are correlated with asynchrony and response diversity, human impacts on salmon populations, including dams (McClure et al. 2008a), hatcheries and fishing (McClure et al. 2008b), continue to erode biological diversity in salmon populations (Waples et al. 2009). For example, the dynamics of populations impacted by dams and hatcheries are becoming increasingly synchronous (Moore et al. 2010, Carlson and Satterthwaite 2011). In addition, Pearse et al. (2010) show that genetic diversity of California steelhead *O. mykiss* has decreased over the past century due to genetic swamping from hatcheries. The direct loss of populations from dams by blocking access to freshwater habitats have led to substantial changes in genetic diversity (McClure et al. 2008a). The development of Conservation Units (Canada) (Canada 2005) and Evolutionary Significant Units (United States) (Waples 1991) for salmon management acknowledges the importance of managing for population diversity. For example, criteria for viable salmonid populations now consider the number and spatial extent of populations in ESUs (McElhany et al. 2000). However, salmon populations are often lumped into broad groups for management decisions; for example, Fraser River Chinook salmon are lumped into four geographical stock complexes and three in-migration timing groups (DFO 1999). In contrast, management of Fraser sockeye salmon is moving towards integrating fine-scale diversity, management is moving away from the four major run timing groups to 18, which are more representative of the population diversity in the watershed. Yet, broad scales of management are still being applied to species in some regions and are missing the finer scales of population diversity that apparently provide the foundation for asynchrony among populations within salmon meta-populations and fisheries, which may lead to

stability and resilience (Schindler et al. 2010, Moore et al. 2015). Our results emphasize that the scale at which population diversity is managed needs to be carefully considered so as to preserve the diversity that increases stability and resilience. Conservation of genetic and life history diversity will provide biological insurance against environmental change.

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Supplementary material (Appendix ECOG-01102 at <[www.ecography.org/readers/appendix](http://www.ecography.org/readers/appendix)>). Appendix 1–2.