Coherent population dynamics associated with sockeye salmon juvenile life history strategies

Freshwater, C., Burke, B., Scheuerell, M., Grant, S., Trudel, M., & Juanes, F.

2018

The final publication is available at:
https://doi.org/10.1139/cjfas-2017-0251

Citation for this paper:

Freshwater, C., Burke, B., Scheuerell, M., Grant, S., Trudel, M., & Juanes, F. (2018). Coherent population dynamics associated with sockeye salmon juvenile life history strategies. *Canadian Journal of Fisheries and Aquatic Sciences,* 75(8). https://doi.org/10.1139/cjfas-2017-0251

Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Coherent population dynamics associated with sockeye salmon juvenile life history strategies

Journal:	*Canadian Journal of Fisheries and Aquatic Sciences*
Manuscript ID	cjfas-2017-0251.R2
Manuscript Type:	Article
Date Submitted by the Author:	20-Oct-2017
Complete List of Authors:	Freshwater, Cameron; University of Victoria, Biology Burke, Brian; National Marine Fisheries Service, Northwest Fisheries Science Center, Scheuerell, Mark; National Marine Fisheries Service - NOAA Grant, Sue; Fisheries and Oceans Canada Trudel, Marc; Department of Fisheries and Oceans, Juanes, Francis; University of Victoria, Department of Biology
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	dynamic factor analysis, LIFE HISTORY < General, MIGRATION < General, POPULATION DYNAMICS < General, synchrony

Coherent population dynamics associated with sockeye salmon juvenile life history strategies

Running header: Ecological drivers of coherent dynamics

Cameron Freshwater[1*], Brian J. Burke[2], Mark D. Scheuerell[2], Sue C.H. Grant[3], Marc Trudel[1,4,+], and Francis Juanes[1]

[1]Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5, Canada

[2]NOAA Fisheries, Northwest Fisheries Science Center, Seattle, Washington, 98112, USA

[3]Fisheries and Oceans Canada, Delta, British Columbia, V3M 6A2, Canada

[4]Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia, V9T 6N7, Canada

[+]Present address: Fisheries and Oceans Canada, St. Andrews Biological Station, St. Andrews, New Brunswick, E5B 2L9, Canada

Corresponding author:

Cameron Freshwater; Department of Biology, University of Victoria, Victoria, British Columbia, V8W 3N5, Canada; camfresh@uvic.ca

ABSTRACT

Although the importance of diversity to maintaining metapopulation stability is widely recognized, the ecological characteristics that lead to synchronous dynamics within population aggregates are often unclear. We used a constrained dynamic factor analysis to explore patterns of covariance in productivity among 16 Fraser River sockeye salmon (*Oncorhynchus nerka*) conservation units (CUs). Specifically, we tested whether coherent trends in productivity covaried with five distinct ecological attributes: physical characteristics of nursery lakes, large-scale management interventions, genetic similarity, adult migration phenology, or juvenile migratory traits. The top-ranked model had two trends based on nursery lake characteristics and juvenile migratory traits. One trend represented the dynamics of CUs that rear in nursery lakes prior to ocean entry and undergo relatively rapid marine migrations. The second included a sea-type CU, Harrison River, which enters the marine environment without rearing in a nursery lake and migrates more slowly. The uniform response of lake-type CUs, as well as Harrison River CU's unique life history, suggests that coherent trends are structured by traits that covary with broad life history type, rather than fine scale characteristics. Furthermore, we document substantial temporal variability in the strength of synchronous dynamics among Fraser River CUs. Greater synchrony in recent years suggests that the importance of shared regional drivers, relative to local processes, may have increased.

Keywords: dynamic factor analysis, life history, migration, population dynamics, synchrony

INTRODUCTION

Diversity tends to stabilize systems across ecological scales (McCann 2000). For example, asynchronous dynamics among multiple subpopulations can reduce the temporal variability of metapopulations (Schindler et al. 2010). As a result, metapopulation stability can be increased by conserving a sufficient number of component subpopulations (Anderson et al. 2015). In certain instances, however, population aggregates can be more efficiently stabilized by preserving components with distinct ecological characteristics with the goal of maximizing functional diversity (Mori et al. 2013; Anderson et al. 2015).

Unfortunately, identifying specific mechanisms that lead to asynchronous dynamics is difficult, particularly for highly migratory species such as anadromous Pacific salmon (*Oncorhynchus* spp.) that interact with diverse ecosystems. One approach to understanding patterns of synchrony within salmon metapopulations is to focus on coarse life-history characteristics that are correlated with growth or survival. For example, Pacific salmon populations are commonly composed of multiple age classes. Age-at-maturity can reflect broad differences in life-history variation that range from fish that spend no time rearing as juveniles in freshwater (river- or sea-type salmon), to those that rear in freshwater for months or years prior to migrating to the ocean (lake-type salmon) (Groot and Margolis 1991). Individuals within a given age cohort generally exhibit similar productivity because survival rates vary interannually in both freshwater and marine ecosystems (Schindler et al. 2010). Ultimately this interannual variability can result in heterogeneous age structures stabilizing metapopulation dynamics (Schindler et al. 2010; Moore et al. 2014).

Many Pacific salmon metapopulations, however, do not exhibit substantial variation in age structure or life-history strategy. For example, the Fraser River sockeye salmon (*O. nerka*) metapopulation is abundant (range: 1-13 million spawners annually; DFO 2016), consisting of hundreds of spawning populations aggregated into 24 conservation units (CUs) (Grant et al. 2011). Despite this apparent richness, the metapopulation exhibits relatively little variation in age of maturity. The majority of Fraser River individuals return after two winters in freshwater (one as eggs in the gravel and one as juveniles in a rearing lake) and two winters in the northeast Pacific Ocean (Burgner 1991; but see Holt and Peterman 2004). The Harrison River CU is an exception to this pattern, with individuals migrating to sea shortly after emerging from gravel and maturing after 2-3 years in the ocean.

Sockeye salmon productivity (recruits per spawner) is correlated at regional scales (e.g. throughout British Columbia and Washington; Mueter *et al*. 2002, Malick *et al*. 2017) and many populations in the southern portion of the species range declined from the mid-1990’s to 2009 (Peterman and Dorner 2012). Yet productivity has not varied uniformly across populations during this period (Grant et al. 2011; Peterman and Dorner 2012; Ye et al. 2015). We suggest ecological processes occurring at finer scales may drive variation in productivity unexplained by regional environmental forcing. Here we focus on five distinct mechanisms that may underpin patterns of covariance in productivity among Fraser River sockeye salmon CUs: 1) freshwater rearing habitat, 2) management interventions, 3) genetic similarity, 4) adult migration phenology, and 5) juvenile marine migration characteristics.

First, a range of environmental factors during freshwater residence can influence salmon reproductive success or survival, and may result in populations with similar habitats exhibiting shared trends in productivity. For example, interannual variation in conditions such as river flow, water temperature, or dissolved oxygen can influence spawner success (Connor and Pflug 2004; Crossin et al. 2008), egg or juvenile survival (McNeil 1966; Crozier and Zabel 2006), and growth (Clarke et al. 1981; Beacham and Murray 1985). Since these conditions can vary across freshwater habitats, covariance between populations may be spatially correlated (i.e. the Moran effect; Moran 1953, Liebhold et al. 2004). Furthermore, the intrinsic carrying capacity of nursery lakes is linked to physical characteristics such as depth, latitude, and elevation (Shortreed et al. 2001). Thus, covariance in productivity may be particularly strong among populations that rear in similar nursery habitats and increase with spatial proximity.

Second, anthropogenic interventions to alter freshwater spawning or rearing habitat may buffer populations from natural variability and result in divergent trends in productivity. Although hydropower development and hatchery impacts are less widespread in the Fraser River than many other North American watersheds, several CUs have been disproportionately influenced by large-scale management actions. The Anderson-Seton, Nadina-Francois, and Harrison (Upstream) CUs contain spawning channels developed between 1966 and 1973, which may stabilize freshwater productivity, relative to natural populations, from environmental stochasticity (Grant et al. 2011). Similarly, the Chilko Lake CU contained a spawning channel (1988-2003) and received large-scale fertilization treatments in the late 1980s and early 1990s that may have increased the growth of fry and spawner abundance (Bradford et al. 2000, Maxwell et al. 2006; but see Akenhead et al. 2016). Finally, the dynamics of the Pitt River CU may have been influenced by hatchery practices (Peterman and Dorner 2012).

Third, covariance in productivity among populations may be correlated with life history characteristics. Traits such as fecundity and egg size (Beacham and Murray 1985; Fleming and Gross 1990; Beacham and Murray 1993), thermal tolerance (Eliason et al. 2011), and body size

(Beacham and Murray 1987; Beacham et al. 2014b) vary widely among salmon populations and are typically heritable (Taylor 1991; Carlson and Seamons 2008). Although detailed life history data are unavailable for many populations, genetic similarity between CUs may serve as a proxy and effectively predict patterns of covariance in productivity. Indeed, trends in abundance among Fraser River Chinook salmon (*O. tshawystcha*) populations are more strongly correlated with genetic relatedness than spatial proximity, age structure, or nursery habitat (Braun et al. 2016).

Fourth, populations with similar spawning migration phenologies (i.e. run timings) may exhibit common trends in productivity due to shared exposure to adverse environmental conditions. Higher discharge generally occurs during earlier migrating runs (Early Stuart and Early Summer Run), which can increase energy expenditure during upstream migrations (Macdonald 2000; Grant et al. 2011). During the Summer and Late Runs, high water temperatures can also increase the difficult of spawning migrations (Cooke et al. 2004; Crossin et al. 2008). Although estimates of recruitment are corrected for losses due to prespawn mortality, difficult migratory conditions may result in negative legacy effects on subsequent generations (DFO 2014). Furthermore, run timing may serve as a proxy for offshore distributions. Fraser River sockeye salmon typically migrate into the river after holding nearshore for a relatively short period (Burgner 1991; Grant et al. 2011). Thus, differences in run timing suggest populations differ in either their offshore distribution or the timing of their return migration (Blackbourn 1987). Indeed, early migrants from the Takla-Trembleur-EStu CU are more likely to migrate through Juan de Fuca Strait than later run timings (DFO 2016a). Variation in spatial distribution, phenology, or migration route may influence growth or survival via differential exposure to competition, prey resources, or predators.

Finally, the migratory patterns of juvenile sockeye salmon may covary with trends in population productivity. The mortality of Pacific salmon is high during early marine residence (Parker 1968; Healey 1982) and may strongly influence recruitment (Pearcy 1992). Generally, Fraser River sockeye salmon enter the marine ecosystem in the Strait of Georgia, migrate north along the continental shelf, and move offshore into the Gulf of Alaska by late autumn (Tucker et al. 2009). However, there is evidence that migratory phenology, both out of the Fraser River and along the continental shelf, can vary among CUs (Tucker et al. 2009; Beacham et al. 2014a; Neville et al. 2016), and may be correlated with body size (Beacham et al. 2014b). Furthermore, differences in early marine migratory characteristics may have cumulative effects on later life stages (Freshwater et al. 2016a). If CUs exhibit similar migratory phenologies, spatial distributions, and physical condition, they may also experience similar rates of survival.

Here we examine 16 Fraser River sockeye salmon CUs over a 38-year period to identify coherent trends in productivity and to determine whether covariance in productivity was correlated with freshwater rearing habitat, different management actions, genetic relatedness, adult run timing, or early marine migration characteristics.

METHODS

Sockeye Salmon

Sockeye salmon is an anadromous, semelparous fish distributed throughout the North Pacific. Adults return to natal rivers and lakes in summer and autumn to spawn and juveniles emerge the following spring. The majority of juvenile sockeye salmon migrate to nearby nursery lakes, where they rear for one or two years. Juvenile sockeye salmon then migrate downstream to the ocean where they mature before completing their return migration two to three years later. Canada's most abundant sockeye salmon run returns to the Fraser River in southern British Columbia. These populations initially enter and rear for several weeks to months in the Strait of Georgia before migrating along the continental shelf to mature in the Gulf of Alaska (Burgner 1991; Tucker et al. 2009).

Sea-type (also referred to as river-type) sockeye salmon exhibit an alternative life history strategy. These individuals do not rear in freshwater lakes, but instead migrate directly downstream after emergence and rear for several months in tidal sloughs, then enter the ocean proper relatively late in the summer (Healey 1980; Birtwell et al. 1987; Beamish et al. 2016). Relative to lake-type juveniles, sea-type individuals also migrate away from nearshore areas late in the year and may use alternative migratory routes (Tucker et al. 2009; Beacham et al. 2014a; Beamish et al. 2016). Although relatively rare, a number of sockeye salmon populations are dominated by sea-type individuals (Gustafson and Winans 1999), including the Harrison River conservation unit (CU) included in our analysis (Healey 1978; Beamish et al. 2016).

Data Sources

We used estimates of spawner abundance and recruitment (age-specific catch plus escapement minus an adjustment for mortality during upstream migration; Grant et al. 2011) for 16 CUs throughout the Fraser River watershed. CUs are functionally equivalent to evolutionary significant units of Pacific salmon in the United States (Waples 1995) and consist of population assemblages that share a common life history strategy, run timing, genetic history, and freshwater nursery habitat (Holtby and Ciruna 2007). Techniques for estimating escapement in the Fraser River have varied by CU and year and include a combination of higher precision fence and mark recapture methods, and lower precision visual surveys; in more recent years, high precision sonar methods have also been used in particular systems. Generally, there are two broad categories of survey precision, with higher precision techniques employed for CUs in years when escapements are expected to be relatively large (>25K from 1950-2003; >75K from 2003 to present) and lower precision techniques used otherwise (Grant et al. 2011). Catch is estimated in marine and freshwater fisheries for each stock (approximately equivalent to a CU) and age class. Escapement is also organized by age from spawning ground samples. Methods for estimating Fraser River sockeye salmon catch and escapement are reviewed in detail in Grant et al. (2011).

We focused our analysis on 16 Fraser River CUs with long, continuous time series of escapement and age-specific recruitment (Table 1). In one case, we used a single population (Seymour River) as a proxy for its CU (Shuswap-ES) because the other major population had a relatively short time series. Our analysis included data for brood years from 1973-2010. We excluded prior data because several CUs were supplemented with spawning channels after 1973 (Grant et al. 2011). Fraser River sockeye salmon typically mature between ages 3 and 5. As a result, 2010 is the most recent brood year for which complete age-specific recruit data were available and the last year included in our analysis.

Table 1. Fraser River sockeye salmon conservation units and a subset of their component spawning populations retained for the analyses performed in this study. Genetic groupings are based on allele frequency data published in Beacham et al. (2006) and Holtby and Ciruna (2007). Genetic groups are arranged alphabetically beginning with the most divergent group, i.e. Group A is least similar to the rest of the watershed. Bolded CUs had time series extending to 1948 and were included in supplementary analyses. The subset of spawning populations presented here

corresponds to those described in Beacham et al. (2006); a full summary of the spawning populations that form each CU are presented in Grant et al. (2011).

Conservation Unit	Spawning Populations	Genetic Group	Run Timing	Management Intervention
Harrison (Upstream)	Weaver	A	Late	Spawning channel
Harrison River	Harrison River	A	Late	NA
Lillooet-Harrison	Birkenhead	A	Late	NA
Pitt	Pitt	A	Early Summer	Hatchery
Seton	Portage	B	Late	NA
Seymour (proxy for Shuswap-ES)	Seymour (Scotch also contributes to Shuswap-ES)	B	Early Summer	NA
Shuswap-Late	Adams River (Lower and Upper), Shuswap (Lower, Middle, and Upper), Eagle, Little River, Cayenne, Little River	B	Late	NA
Anderson-Seton	Gates	C	Early Summer	Spawning channel
Chilko	Chilko (South and Main)	D	Summer	Spawning

			(minority Early Summer)	channel and fertilization
Kamloops	North Thompson, Raft	D	Early Summer	NA
North Barriere	Fennell	D	Early Summer	NA
Quesnel	Horsefly (Upper, Lower, and Middle), Mitchell, McKinley, Roaring River, Wasko Creek, Blue Lead	D	Summer	NA
Francois-Fraser	Stellako	E	Summer	NA
Nadina-Francois	Nadina	E	Early Summer	Spawning channel
Takla-Trembleur	Dust, Forfar, Gluskie, Hudson Bay, Blackwater, Porter Creek	E	Early Stuart	NA
Takla-Trembleur-Stuart	Pinchi Creek, Kuzkwa Creek, Middle River, Tachie	E	Summer	NA

We estimated productivity ($\log_e$ recruits per spawner) using total recruits (i.e. the sum of 2.1, 2.2 and 2.3 returns for a given brood year, except for Harrison River fish where 1.1, 1.2 and 1.3 age classes dominate) and an estimate of effective female spawners, which better accounts for interannual differences in sex ratios and pre-spawn mortality. Effective female spawners are the product of female escapement estimate and spawner success, which is based on the egg proportions in female carcasses observed on the spawning grounds.

Ecological Covariates

Pacific salmon have complex life histories and interact with a range of distinct environments that may shape their population dynamics. We accounted for this diversity by constructing models that explicitly tested whether freshwater rearing habitat, management interventions, genetic similarity, adult migration phenology, or juvenile marine migratory traits best predicted shared trends in productivity. These ecological covariates are described in detail below.

Freshwater Rearing Habitat

The 16 CUs incorporated in this analysis rear in 20 nursery lakes (Fig. 1). Each CU may rear in a single or multiple nursery lakes, with the CU's name typically reflecting the lake(s) where rearing occurs, as well as run timing. For example, individuals from the Francois-Fraser S CU are summer-run fish that rear in Francois and Fraser lakes. However, one CU, Shuswap-L, may rear in Adams, Mabel, Mara, or Little Shuswap lakes, as well as Shuswap Lake (Grant et al. 2011). Given that comprehensive monitoring of lake ecosystems is lacking (e.g., limnology, predator-prey dynamics), we focused our analysis on characteristics that are readily available and likely to influence juvenile rearing conditions, but do not exhibit strong temporal variability. For each nursery lake we included spatial location (latitude and longitude), elevation, surface area, and mean depth from Shortreed et al. (2001). Values that were unavailable in that document were retrieved from the BC Ministry of Environment bathymetry database (http://a100.gov.bc.ca/pub/fidq/viewBathymetricMaps.do). As a proxy for the difficulty of freshwater migration, we also included an estimate of the in-river distance from each lake's mouth to the Fraser River estuary using topographic maps (when a CU rears in multiple lakes we used the mouth of the lowest elevation lake to estimate migration distance). These data are summarized in Table S1. When fry from a CU rear in multiple nursery lakes we used mean values for all characteristics, except for surface area, which we summed. To identify CUs with similar locations, elevation, surface area, migration distance, and mean depth, we calculated a dissimilarity matrix from Euclidean distances and used UPGMA (unweighted pair group method with arithmetic mean) hierarchical clustering to group CUs (Borcard et al. 2011). Cluster analyses were completed with the *vegan* package using R 3.2.2 (R Core Team 2017).

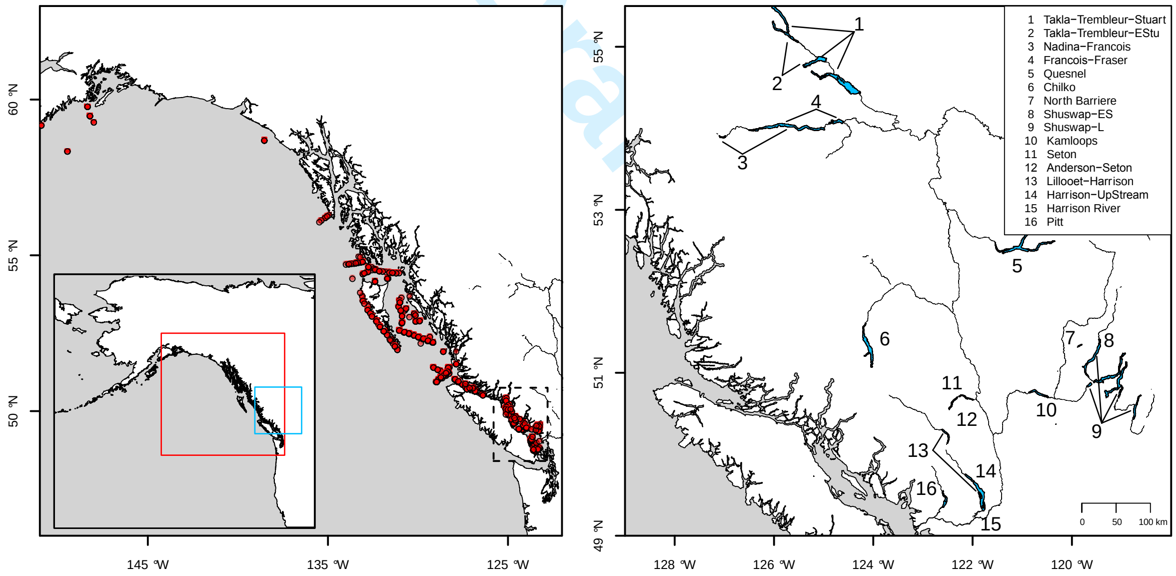

Figure 1. Catch locations of juvenile sockeye salmon during marine sampling surveys (red filled circles on left). The Strait of Georgia is outlined by a dashed polygon. On right, location of nursery lakes used by Fraser River conservation units included in this study: 1) Takla-Trembleur-Stuart-S, 2) Takla-Trembleur-EStu, 3) Nadina-Francois-ES, 4) Francois-Fraser-S, 5)

Quesnel-S, 6) Chilko-S, 7) North Barriere-ES, 8) Shuswap-ES, 9) Shuswap-L, 10) Kamloops-ES, 11) Seton-L, 12) Anderson-Seton-ES, 13) Lillooet-Harrison-L, 14) Harrison (UpStream)-L, 15) Harrison River-L, 16) Pitt-ES. Figure created using the *maps* package (Becker et al. 2016) in R 3.2.2 (R Core Team 2017).

We identified Harrison River as an out-group (i.e. the CU least similar to all others) *a priori* to the cluster analysis, because juveniles from this CU migrate directly to the marine environment after emergence and therefore could not be assigned to a nursery lake. With the exception of Harrison River, CUs generally clustered by position in the watershed (i.e. upper, middle, or lower) (Fig. 2).

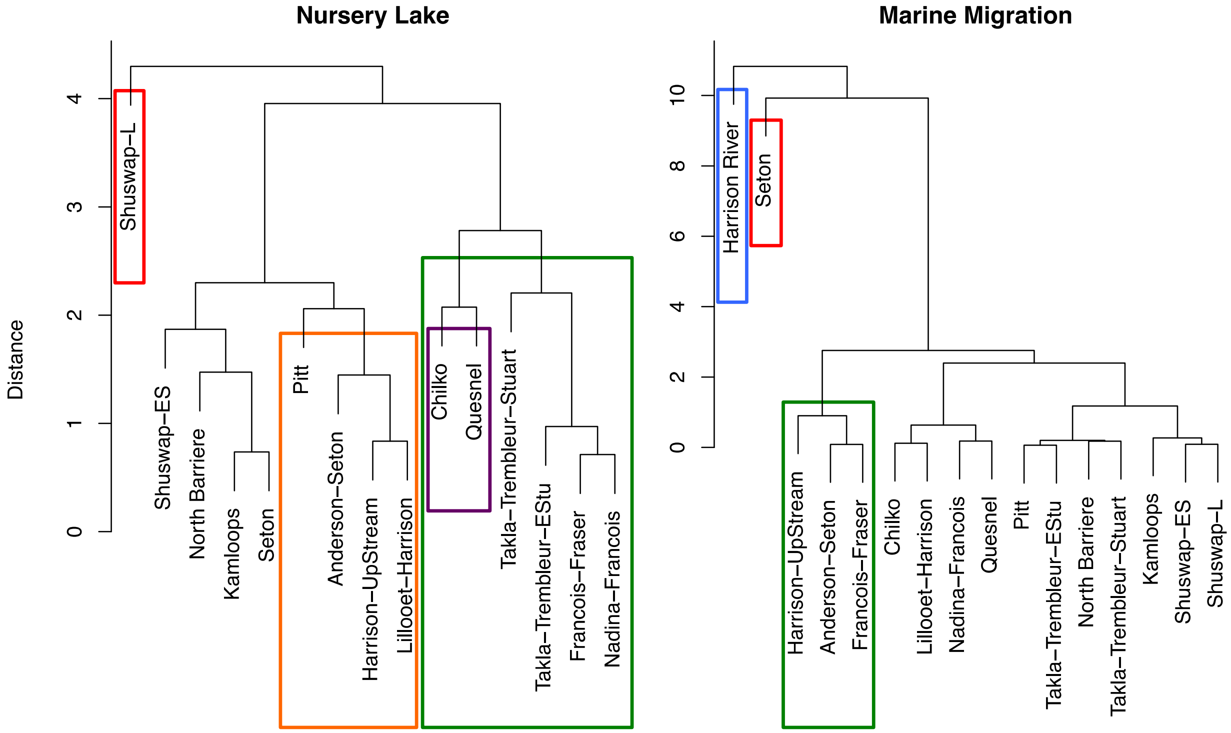

Figure 2. UPGMA cluster diagrams for nursery lake (left) and marine migration (right) characteristics. Colored boxes represent the order in which groups of CUs were assigned unique trends: blue first, followed by red, green, purple and orange. Note that the sea-type Harrison River CU is not included on the left because it does not rear in a nursery lake and was classified as an out-group *a priori*.

Management Intervention

As noted above, five Fraser River CUs have experienced substantial management actions intended to increase and stabilize productivity. We identified the CUs with spawning channels

(Anderson-Seton-ES, Nadina-Francois-ES, and Harrison (U/S)-L) as an outgroup due to the long history of these impacts and evidence that they have increased productivity (Grant et al. 2011). The Pitt-ES (hatchery influence) and Chilko-S (whole lake fertilization and spawning channel) CUs were assigned to third and fourth groups, respectively, because the duration of these interventions was shorter and their impact less certain (Bradford et al. 2000; Peterman and Dorner 2012; Akenhead et al. 2016).

Genetic Similarity

The genetic structure of sockeye salmon throughout the North Pacific has been extensively examined and the more abundant spawning populations within Fraser River CUs can be readily identified using microsatellites (Beacham et al. 2005) or single nucleotide polymorphisms (Beacham et al. 2010). Previously published data grouped closely related populations into CUs (Beacham et al. 2006; Holtby and Ciruna 2007), as well as CUs into clusters (Holtby and Ciruna 2007), using allele frequencies and Weir and Cockerham's (1984) genetic differentiation index. Allele frequencies were estimated at 14 microsatellite loci; detailed methods and population specific sample sizes can be found in Beacham et al. (2005). In Table 1 we present the subset of spawning populations that contribute to each CU and are referenced in Beacham et al. (2006), as well as groupings of closely related CUs that are identified in Holtby and Ciruna (2007).

Run Timing

Fraser River CUs are assigned to one of four run-timing groups based on their return migration phenology. Early Stuart individuals typically return to the lower Fraser River from late-June to late-July, early summer from mid-July to mid-August, summer from mid-July to

September, and late-run from late-July to mid-October (Grant et al. 2011); however, there can be considerable overlap among run timing groups. Since CUs are already assigned to a specific run, we did not complete a cluster analysis for this covariate, however our subsequent analyses did require CUs to be ranked in terms of their similarity to one another. *A priori* we identified the Early Stuart run as the most basal out-group since it contains only one CU, has the strongest evidence for a unique offshore phenology or distribution, and can experience elevated levels of en route mortality when Fraser River flows are high (Grant et al. 2011; DFO 2016a). We classified late-run CUs as the next most basal out-group due to evidence that several late-run CUs have experienced anomalously high prespawn mortality in recent years (Cooke et al. 2004).

Marine Migration

We collected juvenile sockeye salmon during summer and autumn research surveys, which are designed to estimate the abundance, distribution, and condition of juvenile Pacific salmon during their early marine residence. Summer sampling along the continental shelf (i.e. west coast of Vancouver Island north to the Alaskan border) generally takes place in June (Tucker et al. 2009; Beacham et al. 2014a), while sampling in the Strait of Georgia occurs in late June and early July (Preikshot et al. 2012; Beamish et al. 2016). Fish are collected via a mid-water trawl deployed from CCGS W.E. Ricker or a chartered vessel from set survey locations (details of sampling methods in Beamish et al. 2000 and Sweeting et al. 2003; Fig. 1). Beginning in 1996 for continental shelf surveys and 2008 for Strait of Georgia surveys, a subset of fish were assigned to spawning populations using the coastwide genetic stock identification techniques described above (Table S2; details in Beacham et al. 2014a).

We used stock-identified catch data from these surveys to estimate variation in two metrics related to early marine migration phenology among sockeye salmon CUs. First, we calculated mean fork length within each CU since juvenile sockeye salmon migratory rate (Freshwater et al. 2016b) and catch distribution (Tucker et al. 2009; Beacham et al. 2014b) are correlated with body size. Second, we calculated the proportion of the total catch of a given CU that occurred outside the Strait of Georgia (Table S2). Since Fraser River sockeye salmon enter and rear in the Strait of Georgia before migrating north along the continental shelf, this proportion serves as a proxy for differences in entry timing or duration of nearshore residence. Due to small sample sizes for certain CUs, we estimated mean body size and spatial distribution data across all sampling years.

We next calculated a dissimilarity matrix based on Mahalanobis distances (to account for correlations between size and capture location) and grouped CUs with UPGMA hierarchical clustering. Broadly, CUs fell into one of three groups based on early marine migratory traits (Fig. 2). Harrison River individuals were generally small and captured exclusively in the Strait of Georgia (Fig. S1; Table S2). Conversely, Harrison Lake (Upstream), Anderson-Seton, and Francois-Fraser individuals were larger, with the majority captured outside of the Strait of Georgia during summer surveys (Fig. S1; Table S2). The remaining CUs were intermediate in these traits and clustered together.

Analyses

Relationships between multivariate time series and explanatory variables are often examined with Mantel tests, which determine whether two or more matrices are significantly correlated with one another. Mantel tests are ideal for testing for significant relationships between variables representing measures of distance (e.g. genetic or spatial data; Borcard and Legendre 2012); however, they fail to account for the temporal autocorrelation that is present in time series data. As an alternative, we used dynamic factor analysis (DFA), which is a dimension reduction technique that can be used to identify and model common trends in nonstationary, multivariate time series (Zuur et al. 2003).

We modeled productivity for each CU *i* in brood year *t* with a Ricker model, which included a time-varying estimate of productivity ($\alpha_{i,t}$) and density-dependent effects within a given CU. For each CU *i*:

$$\log_{\mathrm{e}}\left(\frac{R_{i,t}}{S_{i,t}}\right) = \alpha_{i,t} + \beta_i S_{i,t} + v_{i,t},$$

where $S_{i,t}$ is the number of effective female spawners in year *t*, $R_{i,t}$ is the number of recruits produced by $S_{i,t}$, β_i is the density dependent effect, and $v_{i,t}$ is a residual error assumed to be normally distributed with 0 mean and variance σ_{R_P}. Following Peterman et al. (2003), we modeled $\alpha_{i,t}$ as a first-order Markov process, whereby

$$\alpha_{i,t} = \alpha_{i,t-1} + w_{i,t},$$

and $w_{i,t}$ is a process error assumed to be normally distributed with 0 mean and variance σ_α. Together these two equations form a state-space model, which we can write in matrix form, such that

$$\mathbf{Y_t} = \boldsymbol{\alpha}_\mathbf{t} + \boldsymbol{\beta}\mathbf{S_t} + \mathbf{v}_t, \text{where } \mathbf{v}_t \sim \mathrm{MVN}(0, \boldsymbol{\Sigma}_{\mathrm{R}_P})$$

$$\boldsymbol{\alpha}_\mathbf{t} = \boldsymbol{\alpha}_{\mathrm{t}-1} + \mathbf{w}_\mathrm{t}, \text{where } \mathbf{w}_t \sim \mathrm{MVN}(0, \boldsymbol{\Sigma}_{\boldsymbol{\alpha}})$$

and $\mathbf{Y_t}$ is a column of CU-specific estimates of $\log_e\left(\frac{R_i}{S_i}\right)$. However, rather than assume year-specific productivities $\alpha_{i,t}$ differed for each CU *i*, we instead set some of them equal depending on the *a priori* groupings discussed above. Specifically, we compared the performance of multiple, constrained DFA model structures that tested the hypothesis that CUs with similar traits exhibit shared, distinct trends in productivity through time (details below).

In DFA, the observed data are modeled as linear combinations of one or multiple latent "trends", each of which can be modeled as a random walk (Zuur et al. 2003). We incorporated the standard Ricker model into this framework by modeling **Y** as a linear combination of a limited number of common temporal patterns ($\boldsymbol{\alpha}_{i,t}$), loadings on those shared productivities (**Z**), offsets (**a**) representing CU-specific deviations from mean productivity, and observation errors (**v**) distributed as multivariate and normal with a mean of **0** and variance-covariance matrix **R.** Thus, the multivariate Ricker model in the DFA framework becomes

$$\mathbf{Y_t} = \mathbf{Z}\boldsymbol{\alpha}_t + \boldsymbol{\beta}\mathbf{S}_t + \mathbf{a} + \mathbf{v}_t, \text{where } \mathbf{v}_t \sim \text{MVN}(0, \boldsymbol{\Sigma}_{\text{R}_P})$$

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \mathbf{w}_t, \text{where } \mathbf{w}_t \sim \text{MVN}(0, \boldsymbol{\Sigma}_\alpha)$$

We assumed that the variances of the observation errors **R** were related to survey effort and that there was no covariance. Therefore we estimated one variance parameter for each of the two categories of survey precision *P* (i.e. CUs with typically low or high abundance; Grant et al. 2011) so that $\boldsymbol{\Sigma}_\text{R}$ included two estimated parameters down the diagonal and zeros elsewhere.

To ensure that the model is identifiable, we set the variance-covariance matrix $\boldsymbol{\Sigma}_{\boldsymbol{\alpha}}$ to the identity matrix **I** with 1's along the diagonal and 0's elsewhere. Finally, we modeled the initial vector of productivities as random effects with a mean of zero and the initial state vector ($\boldsymbol{\alpha}_0$) set to a mean of zero and a diagonal variance-covariance matrix with large variance (here equal to 10)

$$\boldsymbol{\alpha}_0 \sim \mathrm{MVN}(0, 10)$$

We estimated the parameters and states for different DFA models with the *MARSS* package (Holmes et al. 2014) using R 3.2.2 (R Core Team 2017).

As the DFA model structure is flexible and there were many possible model forms, we specifically set up a multi-model comparison procedure to test among competing hypotheses. For each covariate type (nursery lake, genetic, run timing, or marine migratory characteristics), this procedure began with a null model that estimated a single common trend among all CUs. Against this null model, we compared a model containing one additional trend, representing the most basal out-group identified *a priori* or in a given cluster analysis (see previous section for details). This group represents the CUs whose nursery lake, management intervention, genetic, run timing, or marine migratory characteristics are most divergent from the watershed average.. We repeated this process, estimating up to six nursery lake, four management intervention, five genetics, four run timing, and four marine migration trends (Table S3).

A single factor loading Z was estimated for all the CUs sharing a common trend (similarly, if only one CU was in an assigned group it received its own trend). We repeated the model identification process across each covariate matrix (i.e. nursery lake, management intervention, genetic, run timing, and marine migration), including the null. We then compared the support for each model within the data using AICc. We note that because the Harrison River CU was both assigned as an out-group *a priori* in the nursery lake models and identified as an out-group in the marine migration cluster analysis, the two-trend models for these ecological covariates are structurally identical. Thus, we consider a model that assigns a unique trend only to the Harrison River CU to describe broad patterns in life history (i.e. sea-type vs. lake-type), rather than differences in lake or migratory traits alone. In total we compared 18 distinct models.

The approach presented here is different than that of most published DFA studies (e.g., Malick and Cox 2016, Jorgensen et al. 2016, Ohlberger et al. 2016), which typically estimate population-specific loadings across multiple trends, then use the combination of loadings and trends to evaluate relationships among populations *post hoc*. By assigning groupings *a priori* and preventing loadings from varying within a group, we constrained the models so that variation among time series was predominantly described by trend assignment (as opposed to loadings). As a result, these models are less suitable for unstructured exploratory analyses or predicting future dynamics, but are more ideal for testing specific hypotheses about patterns of covariance among time series.

After examining potential drivers of covariance in productivity, we explored how synchrony in productivity among Fraser River CUs has changed through time. We calculated rolling, 10-year estimates of system synchrony (φ) using the index presented in Loreau and de Mazancourt (2008), which varies between 0 (asynchrony) and 1 (total synchrony), and where:

$$\varphi = \frac{\Sigma_{ij}\sigma_n^r(i,j)}{(\Sigma_i\sigma_{xi})^2} = \frac{\sigma_n^c}{(\Sigma_i\sigma_{xi})^2}$$

Here, *i* and *j* represent individual CUs, σ_n^r is the covariance in productivity ($\log_e$(R/S)) between CUs *i* and *j* and σ_n^c is a scalar indicating the variance of total community productivity for a complex of *n* CUs. We estimated synchrony using the *synchrony* package in R (Gouhier and Guichard 2014).

Finally, we conducted three sensitivity analyses. First, we repeated the DFA while excluding two CUs that had relatively small sample sizes in marine sampling surveys. Second, we repeated the DFA and estimated synchrony within a subset of 10 CUs with time series dating to 1948. Third, we repeated both analyses using an alternative index of productivity. Previous analyses indicate certain Fraser River CUs may exhibit delayed density dependence (Grant et al. 2011; Peterman and Dorner 2012). To account for these effects, we estimated common trends and changes in synchrony using residuals from stationary Larkin models for CUs with evidence of delayed density dependence or stationary Ricker models for those that did not. The results of all three analyses were consistent with those presented here and are provided as a supplement.

RESULTS

Despite variation across an array of ecological traits, CUs throughout the Fraser River exhibited largely coherent changes in productivity (Fig. 3). Models that estimated one to three productivity trends among all Fraser River CUs typically outperformed models with a larger number of trends (Table 2; Table S3), suggesting groups of CUs with distinct ecological characteristics are generally not responding asynchronously to one another. The most parsimonious model estimated two trends that were assigned based on nursery lake and marine migration traits (Table 2), i.e. a life history type model. The null model, which included one trend shared among all CUs, was the next most highly ranked, though its performance was considerably worse. Models that assigned trends based on management intervention, genetic similarity, or run timing, regardless of the number of trends, performed more poorly (Table S3). The top ranked model remained the same when we repeated our analysis but a) excluded CUs with low sample sizes during marine surveys, b) included only CUs with time series extending back to 1948, and c) modeled alternative estimates of productivity (Table S4, S5).

The top-ranked model was constrained to estimate one trend for all CUs that rear for at least one year in nursery lakes and migrate relatively quickly out of the Strait at large body size. It assigned a separate trend to the single sea-type CU included here, which also contains smaller and slower moving marine migrants. The first trend, which applied to 15 of the 16 CUs in the analysis, was characterized by relatively stable dynamics until the mid-1980s when a marked decline began (Fig. 4). The decline in productivity persisted for over a decade, reaching its lowest point in the mid-2000s. Between 2006 and 2010 the productivity of lake-type CUs returned to the long-term mean. Conversely, the productivity of the Harrison River CU (the only sea-type CU in this analysis) was stable until the mid-1990s, after which its productivity steadily increased (Fig. 4). The trends estimated by the top-ranked model were similar when the analysis was restricted to CUs with longer time series and when alternative productivity indices were used (Online Supplement; Figs S2-S3).

Table 2. Top ranked models from dynamic factor analysis with trends assigned to CUs based on four groups of ecological covariates. The full suite of models is presented in Table S3.

Ecological Covariate	Number of Trends	Log-likelihood	Number of Parameters	ΔAICc	AIC Weight
Migration/ Nursery Lake	2	-783.48	35	0	0.959
Null	1	-787.77	34	6.33	0.040

Nursery Lake	3	-789.50	36	14.29	<0.001
Migration	3	-792.89	36	21.07	<0.001
Genetics	2	-796.28	35	25.60	<0.001

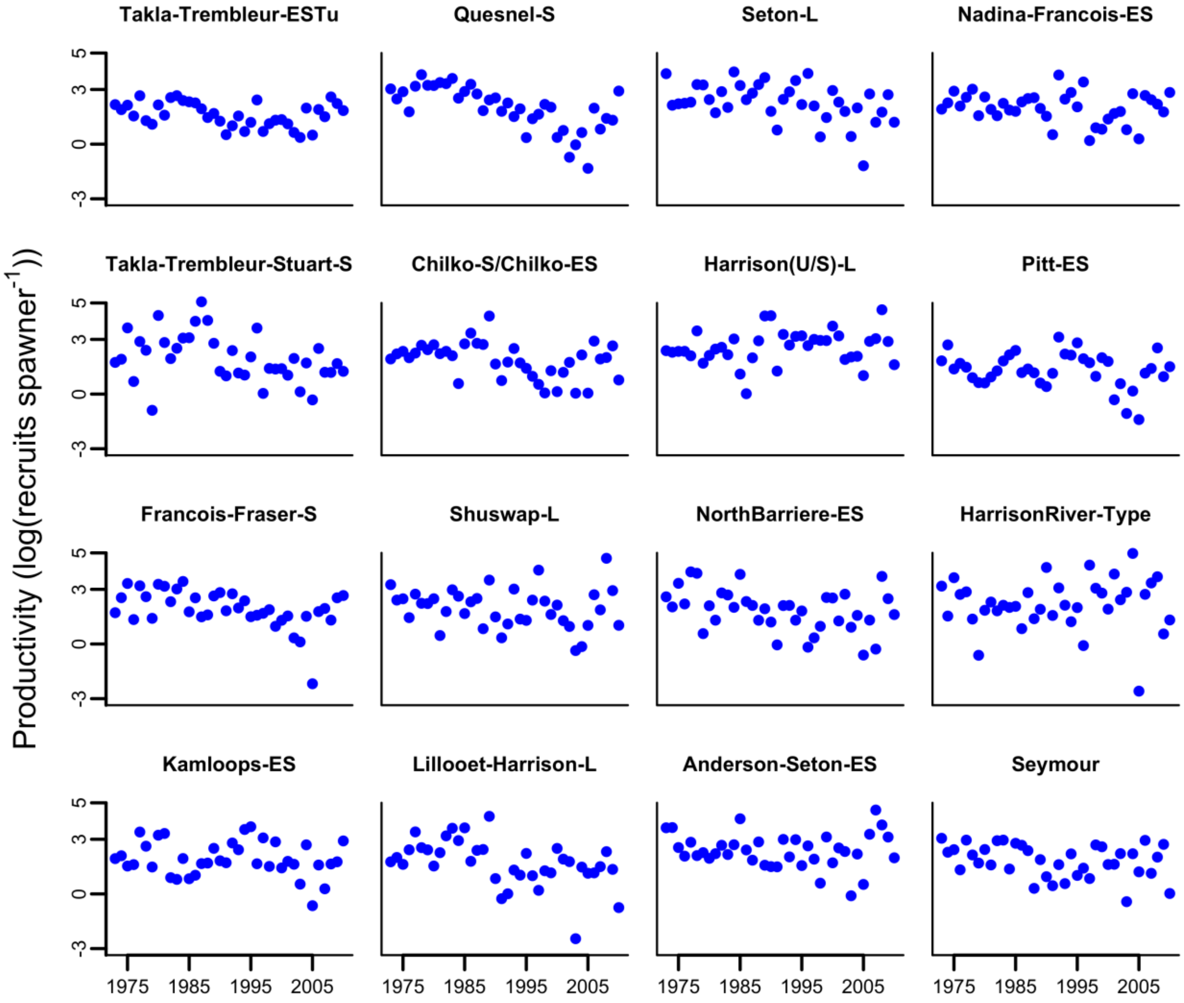

Figure 3. Time series of productivity for Fraser River sockeye salmon CUs.

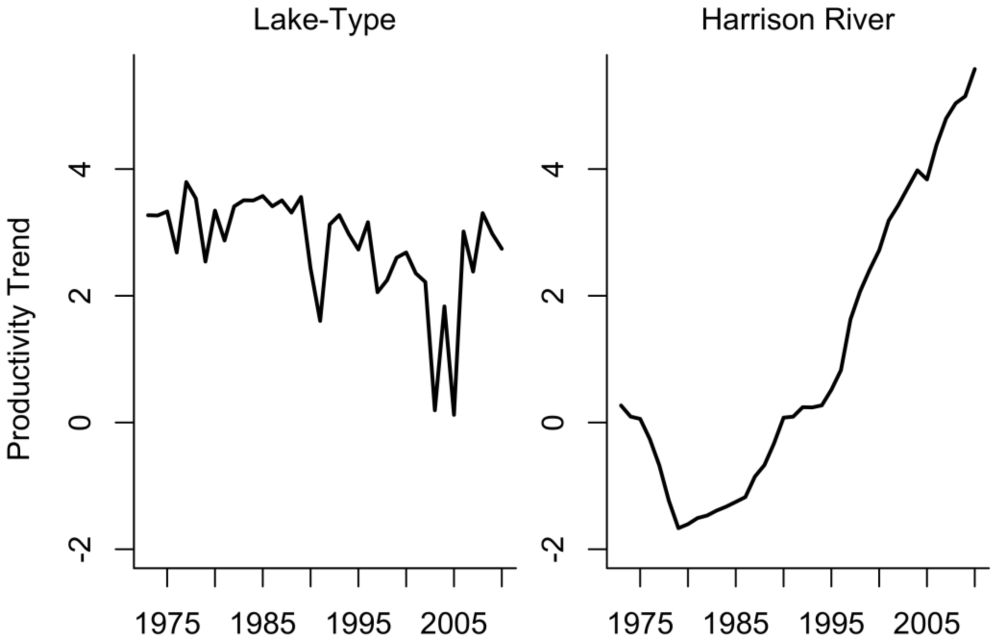

Figure 4. Trends in productivity estimated from top-ranked DFA for 15 lake-type sockeye salmon CUs (left) and the sea-type Harrison River CU (right).

Since the 1980s, productivity among Fraser River CUs has become more synchronized. The largest increases occurred in the early 2000s when productivity was uniformly low (Fig. 5). However, the 11 CUs with longer time series exhibited similarly high levels of synchrony through the 1960s (Fig. 5), suggesting that current levels of synchrony, though high, may not be unprecedented. Removing the Harrison River CU from the analysis resulted in moderately greater trends in synchrony (Fig. 5). Increases in synchrony through time were also evident with alternative estimates of productivity (Fig. S4).

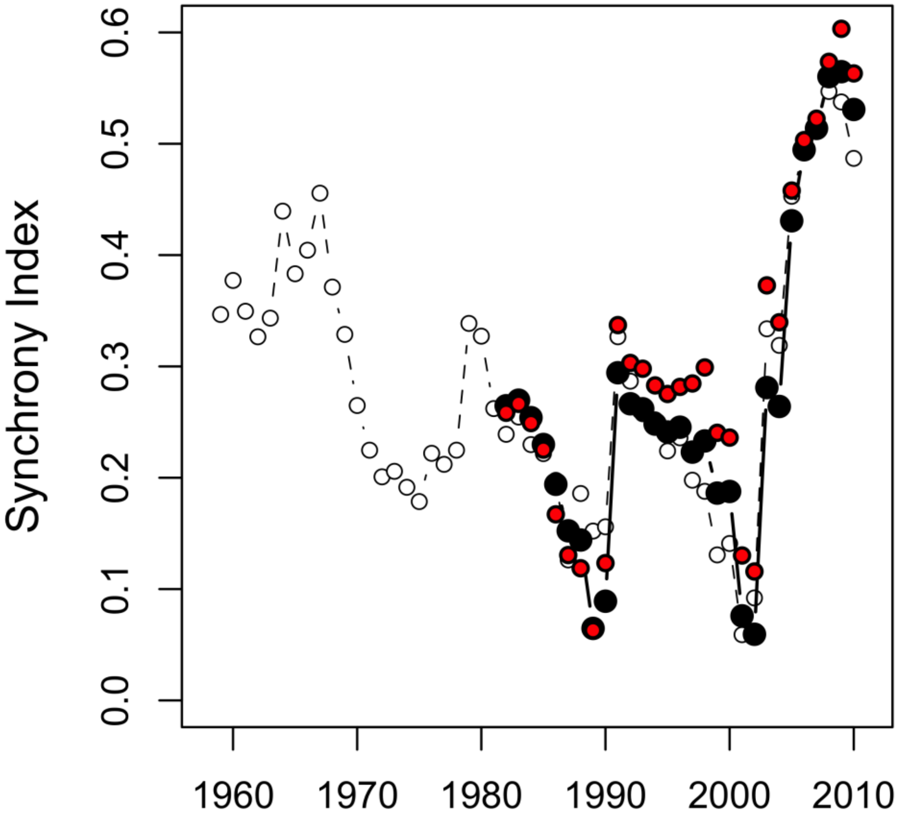

Figure 5. 10-year moving window estimates of synchrony in productivity ($\log_e$(recruits spawner^{-1})) among Fraser River sockeye salmon CUs. Filled symbols with solid lines represent the 15 CUs with time series extending to 1973 and that were included in primary analyses; open symbols with dashed lines represent 10 CUs with productivity time series extending to 1948; red symbols represent the primary analysis CUs excluding Harrison River productivity data.

DISCUSSION

Fraser River sockeye salmon CUs exhibit variation in nursery lake attributes, management interventions, genetic similarity, adult migration timing, and juvenile marine migration traits. Yet we found little evidence that subgroups sharing these traits exhibited greater productivity covariance with one another than they did with the Fraser River watershed as a whole. Our top ranked model assigned a shared trend to 15 of 16 CUs, which exhibited stable dynamics for several decades before declining precipitously in the late 1980s – a pattern consistent with previous observations (Grant et al. 2011; Peterman and Dorner 2012). This decline in productivity was followed by a recovery to the long-term average between 2005 and 2010. Conversely, Harrison River, the only CU assigned an alternative productivity trend, did not exhibit a decline, but rather its productivity has steadily increased through 2010 (Grant et al. 2011; Peterman and Dorner 2012). Harrison River, a sea-type population, does not rear in a nursery lake and migrates through the nearshore more slowly than other CUs in the watershed (Beacham et al. 2014a; Beamish et al. 2016). Therefore it was assigned as an outgroup in both the nursery lake and marine migration model sets, confounding a clear test of either trait as the principal driver of coherent dynamics. As a result, broad life history type appears to be the most parsimonious ecological covariate for productivity.

Lake-type populations may exhibit coherent dynamics due to regional environmental drivers moderating the quality of freshwater nursery habitats. Changes in flow regime, ice out date, or temperature can influence the productivity of salmon populations via freshwater survival (Connor and Pflug 2004; Crossin et al. 2008; Rogers and Schindler 2011). Low smolt survival during nursery lake residence is an obvious mechanism that could lead to strong declines in lake-type CUs, which would not be observed in Harrison River. However, drivers of freshwater productivity frequently appear to be moderated by local differences in physical habitat characteristics, resulting in effects that vary at small scales (Crozier and Zabel 2006; Rogers and Schindler 2011; Braun and Reynolds 2014). Furthermore, freshwater survival for Chilko sockeye salmon, the only Fraser River CUs with long-term, stage specific-survival data, has been above average in the past decade (DFO 2016b), even though its productivity declined through 2005 (Peterman and Dorner 2012). Furthermore, if regional drivers were strongly influencing freshwater productivity, we might expect CUs that received management interventions, which have the explicit goal of increasing freshwater growth or survival, to exhibit divergent dynamics (although the efficacy of some of these programs is equivocal; e.g., Akenhead et al. 2016).

Synchronous dynamics may instead be more closely associated with events that occur during marine residence, when many Fraser River CUs rear in sympatry. Pacific salmon productivity can track basin-scale environmental variation (Mueter et al. 2002b; Kilduff et al. 2015), which may be correlated with changes in predation risk, foraging conditions, or competition during marine residence. Survival in Pacific salmon often appears to be particularly poor shortly after ocean entry (Parker 1968; Healey 1978) and this early marine mortality may regulate productivity (Pearcy 1992). If mortality during marine residence is variable in space or time, CUs with similar early marine characteristics may exhibit similar patterns in productivity. Harrison River's unique early marine life history lends support to this hypothesis. As previously noted, Harrison River juveniles enter the Strait of Georgia at a small size, remain there until relatively late in the year, and may experience differential marine survival as a result (Healey 1980; Beamish et al. 2016).

Unfortunately Harrison River individuals exhibit a suite of unique marine characteristics that prevent the identification of a single mechanism likely to drive differential survival. First, Harrison River juveniles rear for several weeks in the Fraser River estuary before migrating to Howe Sound in late June or early July (Healey 1980; Birtwell et al. 1987; Beamish et al. 2016). Catches of other Fraser River CUs in both these regions are low and most juveniles appear to disperse towards the Gulf Islands or north towards Johnstone Strait immediately after marine entry in early May (Healey 1980; Preikshot et al. 2012; Neville et al. 2013). Rearing in tidal sloughs or Howe Sound may lead to greater survival for Harrison River fish if predators are cued to target large pulses of juveniles outmigrating in early summer (Furey et al. 2016). A later ocean entry phenology may also increase the availability of prey to Harrison River juveniles because zooplankton biomass typically peaks in the Strait of Georgia in July and August (Mackas et al. 2013). Second, while the majority of Fraser River sockeye salmon migrate through Johnstone Strait, a substantial proportion of Harrison River juveniles appear to utilize a southern migratory corridor through Juan de Fuca Strait, then migrate up the west coast of Vancouver Island (Tucker et al. 2009; Beacham et al. 2014a; Beamish et al. 2016). Since Johnstone Strait appears to be a region of poor growth and high-energy expenditure (Ferriss et al. 2014; McKinnell et al. 2014; Journey et al. *in press*), some fraction of Harrison River fish may experience lower mortality by avoiding this corridor.

Alternatively, processes occurring after individuals have migrated out of the Strait of Georgia may predominantly regulate variation in the marine survival of sockeye salmon, for example overwinter mortality (Farley et al. 2011), competitive interactions (Ruggerone and Connors 2015), or physical oceanographic processes (Malick et al. 2017). While most Fraser River CUs appear to migrate off the continental shelf near Alaska before their first ocean winter, out of several hundred Harrison River fish sampled, only two have been collected north of Johnstone Strait in any season (Beacham et al. 2014a). Therefore, Harrison River's divergent productivity may be associated with a unique offshore ecology. Unfortunately knowledge of sockeye salmon distributions as they mature is limited because offshore surveys are rare and relatively few individuals have been sampled since genetic stock identification techniques were widely adopted.

Although the dominant trend across Fraser River sockeye salmon CUs was characterized by a recent return to average levels of productivity, the long-term status of the metapopulation remains uncertain. We were unable to incorporate the most recent productivity data (i.e. spawners that returned in 2016) because age-specific estimates of abundance were not yet available; however preliminary data suggest that the productivity of summer-run CUs has declined for the 2015 and 2016 returns. Furthermore, our results suggest that the productivity of Fraser River CUs has become increasingly synchronized. Greater synchrony is particularly concerning given that we found little evidence of functional diversity (as indicated by productivity trends) among CUs, which could act to buffer the system as a whole from poor rearing conditions.

What may have weakened the Fraser River portfolio effect is less clear. Greater synchrony among Pacific salmon populations is often attributed to hydropower development and hatchery propagation, which can result in reduced phenotypic diversity and homogeneous responses to shared stressors (Moore et al. 2010; Carlson and Satterthwaite 2011; Satterthwaite and Carlson 2015). Although anthropogenic disturbances are present on the Fraser River (e.g. forestry, agriculture, water use), hatchery and hydropower influences are limited (Nelitz et al. 2011). Nevertheless the Fraser River synchrony estimates we present here are broadly equivalent to those of Central Valley fall-run Chinook salmon, a stock aggregate that has been strongly impacted by anthropogenic development (Satterthwaite and Carlson 2015).

It is possible that the Fraser River meta-population is intrinsically more susceptible to synchronizing effects. As previously noted, asynchronous dynamics are commonly observed within relatively small spatial areas. For example, sockeye salmon population dynamics in western Alaska are strongly correlated within nursery lakes and between life history types (Rogers and Schindler 2008; Griffiths et al. 2014b). Relative to these Alaskan systems, the Fraser River has relatively little age class diversity (Burgner 1991), which may increase the likelihood of coherent dynamics. Supporting this hypothesis, western Alaska's salmon portfolios are considerably more stable than those in the Fraser River and other southern regions (Griffiths et al. 2014a). Additionally large-scale environmental drivers may have strengthened divergent patterns between Alaskan and British Columbia populations in recent years. Relative to sockeye salmon populations at the southern end of the species range, northern populations tend to exhibit opposite trends in productivity (Mueter et al. 2002a; Peterman and Dorner 2012) and are more weakly associated with large scale environmental drivers (Malick et al. 2017). As a result, northern populations may currently be in a regime where freshwater processes at fine spatial scales are the principal driver of variation in productivity, while local processes in the south are obscured by relatively uniform poor marine survival.

Regardless of what has led to high levels of synchrony, current productivity patterns suggest little opportunity to efficiently optimize returns on the Fraser River sockeye salmon portfolio. If populations within an aggregate contain distinct functional responses to environmental stochasticity, long-term productivity can be maximized by explicitly conserving a range of phenotypes (Anderson et al. 2015). In the case of Fraser River sockeye salmon we did not detect evidence that ecological diversity was associated with divergent patterns of productivity in recent years (with the exception of Harrison River). Therefore, it is unclear what axis of phenotypic diversity managers should conserve to ensure metapopulation persistence. In such a scenario, the most precautionary approach is to minimize risk by sustaining the largest number of population groups feasible (Anderson et al. 2015).

We observed broadly coherent trends among sockeye salmon CUs, providing additional evidence that regional environmental drivers likely moderate Pacific salmon productivity via changes in survival or growth. To better understand variability among Fraser River sockeye salmon populations, future research should seek to identify drivers of productivity that are constrained to disproportionately influence lake-type populations and could plausibly increase synchrony among populations. An improved understanding of fine-scale differences in marine distribution among populations may be particularly valuable.

Acknowledgements

We greatly appreciate the efforts of the many Pacific Salmon Commission and DFO biologists who generated and contributed the time series data used in this analysis. We also thank the crew of the CCGS W. E. Ricker, who assisted with the collection of fish samples at sea. Eric R. Buhle provided valuable feedback on modeling approaches and comments from two anonymous reviewers greatly improved this manuscript. Funding was provided by an NSERC PGS-D3 Scholarship, a Montalbano Scholar’s Fellowship, the Liber Ero Foundation, and an NSERC Discovery Grant. All applicable national guidelines for the care and use of animals were followed.

Literature Cited

Akenhead, S., Irvine, J., Hyatt, K., Johnson, S., Michielsens, C., and Grant, S. 2016. Habitat manipulations confound the interpretation of sockeye salmon recruitment patterns at Chilko Lake, British Columbia. NPAFC Bull. **6**(1): 391-414.

Anderson, S.C., Moore, J.W., McClure, M.M., Dulvy, N.K., and Cooper, A.B. 2015. Portfolio conservation of metapopulations under climate change. Ecol. Appl. **25**(2): 559-572.

Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014a. Stock-specific migration pathways of juvenile Sockeye Salmon in British Columbia waters and in the Gulf of Alaska. Trans. Am. Fish. Soc. **143**(6): 1386-1403.

Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H., and Trudel, M. 2014b. Stock-specific size of juvenile Sockeye Salmon in British Columbia waters and the Gulf of Alaska. Trans. Am. Fish. Soc. **143**(4): 876-888.

Beacham, T.D., Candy, J.R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Deng, L., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2005. Estimation of stock composition and individual identification of Sockeye Salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. Trans. Am. Fish. Soc. **134**(5): 1124-1146.

Beacham, T.D., McIntosh, B., MacConnachie, C., Miller, K.M., Withler, R.E., and Varnavskaya, N. 2006. Pacific Rim population structure of sockeye salmon as determined from microsatellite analysis. Trans. Am. Fish. Soc. **135**(1): 174-187.

Beacham, T.D., McIntosh, B., and Wallace, C. 2010. A comparison of stock and individual identification for sockeye salmon (*Oncorhynchus nerka*) in British Columbia provided by microsatellites and single nucleotide polymorphisms. Can. J. Fish. Aquat. Sci. **67**(8): 1274-1290.

Beacham, T.D., and Murray, C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. **42**: 1755-1765.

Beacham, T.D., and Murray, C.B. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. **44**: 244-261.

Beacham, T.D., and Murray, C.B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). J. Fish Biol. **42**(4): 485-508.

Beamish, R.J., McCaughran, D., King, J.R., Sweeting, R.M., and McFarlane, G.A. 2000. Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. N. Am. J. Fish. Manage. **20**: 369-375.

Beamish, R.J., Neville, C.M., Sweeting, R.M., Beacham, T.D., Wade, J., and Li, L. 2016. Early ocean life history of Harrison River sockeye salmon and their contribution to the biodiversity of sockeye salmon in the Fraser River, British Columbia, Canada. Trans. Am. Fish. Soc. **145**(2): 348-362.

Becker, R.A., Wilks, A.R., Brownrigg, R., Minka, T.P., and Deckmyn, A. 2016. maps: Draw Geographical Maps. R Package version 3.1.1.

Birtwell, I.K., Nassichuk, M.D., and Buene, H. 1987. Underyearling sockeye salmon (*Oncorhynchus nerka*) in the estuary of the Fraser River. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis and C.C. Wood. Canadian Special Publication of Fisheries and Aquatic Sciences. pp. 25-35.

Blackbourn, D.J. 1987. Sea surface temperature and pre-season prediction of return timing in Fraser River sockeye salmon. *In* Sockeye Salmon (*Oncorhynchus nerka*) Population Biology and

Future Management. *Edited by* H.D. Smith, S.L. Margolis and C.C. Wood. Canadian Special Publication of Fisheries and Aquatic Sciences, Ottawa, Canada. pp. 296-306.

Borcard, D., Gillet, F., and Legendre, P. 2011. Numerical ecology with R. Springer, New York, NY.

Borcard, D., and Legendre, P. 2012. Is the Mantel correlogram powerful enough to be useful in ecological analysis? A simulation study. Ecology **93**(6): 1473-1481.

Bradford, M.J., Pyper, B.J., and Shortreed, K.S. 2000. Biological responses of sockeye salmon to the fertilization of Chilko Lake, a large lake in the interior of British Columbia. N. Am. J. Fish. Manage. **20**(3): 661-671.

Braun, D.C., Moore, J.W., Candy, J., and Bailey, R.E. 2016. Population diversity in salmon: linkages among response, genetic and life history diversity. Ecography **39**(3): 317-328.

Braun, D.C., and Reynolds, J.D. 2014. Life history and environmental influences on population dynamics in sockeye salmon. Can. J. Fish. Aquat. Sci. **71**(8): 1198-1208.

Burgner, R.L. 1991. Life history of Sockeye Salmon (*Oncorhynchus nerka*). *In* Pacific Salmon Life Histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C.

Carlson, S.M., and Satterthwaite, W.H. 2011. Weakened portfolio effect in a collapsed salmon population complex. Can. J. Fish. Aquat. Sci. **68**(9): 1579-1589.

Carlson, S.M., and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evolutionary Applications **1**: 222-238.

Clarke, W.C., Shelbourn, J.E., and Brett, J.R. 1981. Effect of artificial photoperiod cycles, temperature, and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), Chinook (*O. tshawytscha*), and sockeye (*O. nerka*) salmon. Aquaculture **22**: 105-116.

Connor, E.J., and Pflug, D.E. 2004. Changes in the distribution and density of pink, chum, and Chinook salmon spawning in the upper Skagit River in response to flow management measures. N. Am. J. Fish. Manage. **24**: 835-852.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R.M., Macdonald, J.S., Patterson, D.A., Healey, M.C., and van der Kraak, G. 2004. Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. Fish. Res. **29**(2): 22-33.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., and Farrell, A.P. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. **86**(2): 127-140.

Crozier, L., and Zabel, R.W. 2006. Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. J. Anim. Ecol. **75**(5): 1100-1109.

DFO. 2014. Supplement to the pre-season return forecasts for Fraser River Sockeye Salmon in 2014. DFO CSAS Sci. Resp. **2014/041**.

DFO. 2016a. Run timing and diversion rate models for Fraser River sockeye. DFO Canadian Science Advisory Secretariaty Science Response.

DFO. 2016b. Supplement to the pre-season run size forecasts for Fraser River Sockeye Salmon (*Oncorhynchus nerka*) in 2016. DFO CSAS Sci. Resp. **2016/047**.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., and Farrell, A.P. 2011. Differences in thermal tolerance among sockeye salmon populations. Science **332**(6025): 109-112.

Farley, E.V., Starovoytov, A., Naydenko, S., Heintz, R., Trudel, M., Guthrie, C., Eisner, L., and Guyon, J.R. 2011. Implications of a warming eastern Bering Sea for Bristol Bay Sockeye Salmon. ICES J. Mar. Sci. **68**(6): 1138-1146.

Ferriss, B.E., Trudel, M., and Beckman, B.R. 2014. Regional and inter-annual trends in marine growth of juvenile salmon in coastal pelagic ecosystems of British Columbia, Canada. Mar. Ecol. Prog. Ser. **503**: 247-261.

Fleming, I.A., and Gross, M.R. 1990. Latitudinal clines: a trade-off between egg number and size in Pacific salmon. Ecology **71**(1): 1-11.

Freshwater, C., Trudel, M., Beacham, T.D., Godbout, L., Neville, C.-E., Tucker, S., and Juanes, F. 2016a. Disentangling individual- and population-scale processes within a latitudinal size-gradient in Sockeye Salmon. Can. J. Fish. Aquat. Sci. **73**: 1190-1201.

Freshwater, C., Trudel, M., Beacham, T.D., Godbout, L., Neville, C.-E., Tucker, S., and Juanes, F. 2016b. Divergent migratory behaviours associated with body size and ocean entry phenology in juvenile sockeye salmon. Can. J. Fish. Aquat. Sci. **73**(1723-1732).

Furey, N.B., Hinch, S.G., Mesa, M.G., and Beauchamp, D.A. 2016. Piscivorous fish exhibit temperature-influenced binge feeding during an annual prey pulse. J. Anim. Ecol. **85**(5): 1307-1317.

Gouhier, T.C., and Guichard, F. 2014. Synchrony: quantifying variability in space and time. Methods Ecol. Evol. **5**(6): 524-533.

Grant, S.C.H., MacDonald, B.L., Cone, T.E., Holt, C.A., Cass, A., Porszt, E.J., Hume, J.M.B., and Pon, L.B. 2011. Evaluation of uncertainty in Fraser Sockeye (*Oncorhynchus nerka*) wild salmon policy status using abundance and trends in abundance metrics. Candian Science Advisory Secretariat Research Document **2011/087**.

Griffiths, J.R., Schindler, D.E., Armstrong, J.B., Scheuerell, M.D., Whited, D.C., Clark, R.A., Hilborn, R., Holt, C.A., Lindley, S.T., Stanford, J.A., and Volk, E.C. 2014a. Performance of salmon fishery portfolios across western North America. J. Appl. Ecol. **51**(6): 1554-1563.

Griffiths, J.R., Schindler, D.E., Ruggerone, G.T., and Bumgarner, J.D. 2014b. Climate variation is filtered differently among lakes to influence growth of juvenile sockeye salmon in an Alaskan watershed. Oikos **123**(6): 687-698.

Groot, C., and Margolis, L. 1991. Pacific Salmon Life Histories. University of British Columbia Press, Vancouver, B.C.

Gustafson, R.G., and Winans, G.A. 1999. Distribution and population genetic structure of river- and sea-type sockeye salmon in western North America. Ecol. Freshwat. Fish **8**: 181-193.

Healey, M.C. 1978. The distribution, abundance, and feeding habits of juvenile Pacific salmon in Georgia Strait British Columbia. Fisheries and Marine Service Technical Report 788.

Healey, M.C. 1980. The distribution and residency of juvenile Pacific salmon in the Strait of Georgia, British Columbia, in relation to foraging success. Proceedings of the North Pacific Aquaculture Symposium **82**: 61-69.

Healey, M.C. 1982. Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. Can. J. Fish. Aquat. Sci. **39**: 952-957.

Holmes, E.E., Ward, E.J., and Scheuerell, M.D. 2014. Analysis of multivariate time-series using the MARSS package.

Holt, C.A., and Peterman, R.M. 2004. Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. Can. J. Fish. Aquat. Sci. **61**: 2455-2470.

Holtby, L.B., and Ciruna, K.A. 2007. Conservation units for Pacific salmon under the Wild Salmon Policy. CSAS Res. Doc. **2007/070**: 358 p.

Journey, M., Trudel, M., Young, G., and Beckman, B.R. *in press*. Testing the trophic gauntlet hypothesis: physiological measures of juvenile salmon growth in Johnstone and Queen Charlotte Straits. Fish. Oceanogr.

Kilduff, D.P., Di Lorenzo, E., Botsford, L.W., and Teo, S.L. 2015. Changing central Pacific El Ninos reduce stability of North American salmon survival rates. Proceedings of the National Academy of Sciences.

Liebhold, A., Koenig, W.D., and Bjørnstad, O.N. 2004. Spatial synchrony in population dynamics. Annu. Rev. Ecol., Evol. Syst. **35**: 467-490.

Macdonald, J.S. 2000. Mortality during the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*): a study of the effect of ocean and river environmental conditions in 1997. Can. Tech. Rep. Fish. Aquat. Sci. **2315**: 120 p.

Mackas, D., Galbraith, M., Faust, D., Masson, D., Young, K., Shaw, W., Romaine, S., Trudel, M., Dower, J., Campbell, R., Sastri, A., Bornhold Pechter, E.A., Pakhomov, E., and El-Sabaawi, R. 2013. Zooplankton time series from the Strait of Georgia: Results from year-round sampling at deep water locations, 1990–2010. Prog. Oceanogr. **115**: 129-159.

Malick, M.J., Cox, S.P., Mueter, F.J., Dorner, B., and Peterman, R.M. 2017. Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. Fish. Oceanogr. **26**(3): 268-281.

McCann, K.S. 2000. The diversity-stability debate. Nature **405**: 228-233.

McKinnell, S., Curchitser, E., Groot, K., Kaeriyama, M., and Trudel, M. 2014. Oceanic and atmospheric extremes motivate a new hypothesis for variable marine survival of Fraser River Sockeye Salmon. Fish. Oceanogr. **23**(4): 322-341.

McNeil, W.J. 1966. Effect of the spawning bed environment on reproduction of pink and chum salmon. Fish. Bull. **65**(2): 495-523.

Moore, J.W., McClure, M., Rogers, L.A., and Schindler, D.E. 2010. Synchronization and portfolio performance of threatened salmon. Conserv. Lett. **3**(5): 340-348.

Moore, J.W., Yeakel, J.D., Peard, D., Lough, J., and Beere, M. 2014. Life-history diversity and its importance to population stability and persistence of a migratory fish: steelhead in two large North American watersheds. J. Anim. Ecol. **83**: 1035-1046.

Moran, P.P. 1953. The statistical analysis of the Canadian lynx cycle. Aust. J. Zool. **1**(3): 291-298.

Mori, A.S., Furukawa, T., and Sasaki, T. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biological Reviews **88**(2): 349-364.

Mueter, F.J., Peterman, R.M., and Pyper, B.J. 2002a. Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. Can. J. Fish. Aquat. Sci. **59**(3): 456-463.

Mueter, F.J., Ware, D.M., and Peterman, Randall M. 2002b. Spatial correlation patterns in coastal environmental variables and survival rates of salmon in the north-east Pacific Ocean. Fish. Oceanogr. **11**(4): 205-218.

Nelitz, M., Porter, M., Parkinson, E., Wieckowski, K., Marmorek, D., Bryan, K., Hall, A., and Abraham, D. 2011. Evaluating the status of Fraser River sockeye salmon and role of freshwater ecology in their decline. Cohen Commission Technical Report 3: 222 p.

Neville, C.-E., Johnson, S., Beacham, T., Whitehouse, T., Tadey, J., and Trudel, M. 2016. Initial estimates from an integrated study examining the residence period and migration timing of juvenile sockeye salmon from the Fraser River through coastal waters of British Columbia. NPAFC Bull. **6**(1): 45-60.

Neville, C.-E.M., Trudel, M., Beamish, R.J., and Johnson, S.C. 2013. The early marine distribution of juvenile Sockeye Salmon produced from the extreme low return in 2009 and the extreme high return in 2010. NPAFC Tech. Rep. **9**: 65-68.

Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, Central British Columbia. J. Fish. Res. Board. Can. **25**(4): 757-794.

Pearcy, W.G. 1992. Ocean ecology of North Pacific salmonids University of Washington Press, Seattle, WA.

Peterman, Randall M., and Dorner, B. 2012. A widespread decrease in productivity of Sockeye Salmon (*Oncorhynchus nerka*) populations in western North America. Can. J. Fish. Aquat. Sci. **69**(8): 1255-1260.

Peterman, R.M., Pyper, B.J., and MacGregor, B.W. 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. **60**(7): 809-824.

Preikshot, D., Beamish, R.J., Sweeting, R.M., Neville, C.M., and Beacham, T.D. 2012. The residence time of juvenile Fraser River Sockeye Salmon in the Strait of Georgia. Mar. Coast. Fish. **4**(1): 438-449.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rogers, L.A., and Schindler, D.E. 2008. Asynchrony in population dynamics of sockeye salmon in southwest Alaska. Oikos **117**(10): 1578-1586.

Rogers, L.A., and Schindler, D.E. 2011. Scale and the detection of climatic influences on the productivity of salmon populations. Global Change Biol. **17**(8): 2546-2558.

Ruggerone, G.T., and Connors, B.M. 2015. Productivity and life history of sockeye salmon in relation to competition with pink and sockeye salmon in the North Pacific Ocean. Can. J. Fish. Aquat. Sci. **72**(6): 818-833.

Satterthwaite, W.H., and Carlson, S.M. 2015. Weakening portfolio effect strength in a hatchery-supplemented Chinook salmon population complex. Can. J. Fish. Aquat. Sci. **72**(12): 1860-1875.

Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**(7298): 609-612.

Shortreed, K.S., Morton, K.F., Malange, K., and Hume, J.M.B. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected B.C. nursery lakes. Canadian Science Advisory Secretariat.

Sweeting, R.M., Beamish, R.J., Noakes, D.J., and Neville, C.M. 2003. Replacement of wild coho salmon by hatchery-reared coho salmon in the Strait of Georgia over the past three decades. N. Am. J. Fish. Manage. **23**(2): 492-502.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture **98**: 185-207.

Tucker, S., Trudel, M., Welch, D.W., Candy, J.R., Morris, J.F.T., Thiess, M.E., Wallace, C., Teel, D.J., Crawford, W., Farley, E.V., and Beacham, T.D. 2009. Seasonal stock-specific migrations of juvenile Sockeye Salmon along the west coast of North America: implications for growth. Trans. Am. Fish. Soc. **138**(6): 1458-1480.

Waples, R. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. Am. Fish. Soc. Symp. **17**: 8-27.

Ye, H., Beamish, R.J., Glaser, S.M., Grant, S.C., Hsieh, C.H., Richards, L.J., Schnute, J.T., and Sugihara, G. 2015. Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. Proceedings of the National Academy of Science **112**(13): E1569-E1576.

Zuur, A.F., Tuck, I.D., and Bailey, N. 2003. Dynamic factor analysis to estimate common trends in fisheries time series. Can. J. Fish. Aquat. Sci. **60**(5): 542-552.