

Coherent population dynamics associated with sockeye salmon juvenile life history strategies

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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.

Résumé : S'il est généralement reconnu que la diversité est importante pour le maintien de la stabilité des métapopulations, les caractéristiques écologiques qui mènent à une dynamique synchrone au sein de groupes de populations demeurent souvent mal comprises. Nous avons utilisé l'analyse des facteurs dynamiques avec contraintes pour examiner les motifs de covariance de la productivité entre 16 unités de conservation (UC) de saumons sockeyes (*Oncorhynchus nerka*) du fleuve Fraser. Nous avons plus particulièrement vérifié s'il y a covariance entre des tendances cohérentes de la productivité et cinq attributs écologiques distincts, à savoir : les caractéristiques physiques du lac de séjour, les interventions de gestion à grande échelle, la similitude génétique, la phénologie de la migration des adultes et les caractères migratoires des juvéniles. Le modèle le mieux coté comptait deux tendances basées sur les caractéristiques du lac de séjour et les caractères migratoires des juvéniles. Une tendance représentait la dynamique d'UC élevées dans des lacs de séjour avant l'entrée en mer et caractérisées par des migrations marines relativement rapides. La seconde comprenait une UC de type marin, de la rivière Harrison, qui entre dans le milieu marin sans élevage dans un lac de séjour et migre plus lentement. La réaction uniforme des UC de type lacustre ainsi que le cycle biologique singulier de l'UC de la rivière Harrison donnent à penser que les tendances cohérentes sont structurées par des caractères qui présentent une covariance avec le type de cycle biologique général, plutôt qu'avec des caractéristiques à échelle fine. Nous documentons en outre une variabilité temporelle considérable de la force de la dynamique synchrone entre les UC du fleuve Fraser. Un plus grand synchronisme ces dernières années indiquerait que l'importance de facteurs régionaux communs pourrait avoir augmenté par rapport à celle de processus locaux. [Traduit par la Rédaction]

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 fresh water (river- or sea-type salmon) to those that rear in fresh water for months or

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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 (*Oncorhynchus 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 fresh water (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. 2002a; Malick et al. 2017), and many populations in the southern portion of the species range declined from the mid-1990s 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: (i) freshwater rearing habitat, (ii) management interventions, (iii) genetic similarity, (iv) adult migration phenology, and (v) 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; Liebold 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, 1993; Fleming and Gross 1990), 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 (*Oncorhynchus tshawytscha*) 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 (EStu) and early summer (ES runs), which can increase energy expenditure during upstream migrations (Macdonald 2000; Grant et al. 2011). During the summer (S) and late (L) runs, high water temperatures can also increase the difficulty 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 (Blackburn 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 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

Table 1. Fraser River sockeye salmon conservation units and a subset of their component spawning populations retained for the analyses performed in this study.

Conservation unit	Spawning population(s)	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-L	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 (minority early summer)	Spawning 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

Note: 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 the online Supplementary analyses¹. 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).

the following spring. The majority of juvenile sockeye salmon migrate to nearby nursery lakes, where they rear for 1 or 2 years. Juvenile sockeye salmon then migrate downstream to the ocean where they mature before completing their return migration 2–3 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 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 (>25 000 from 1950 to 2003; >75 000 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).

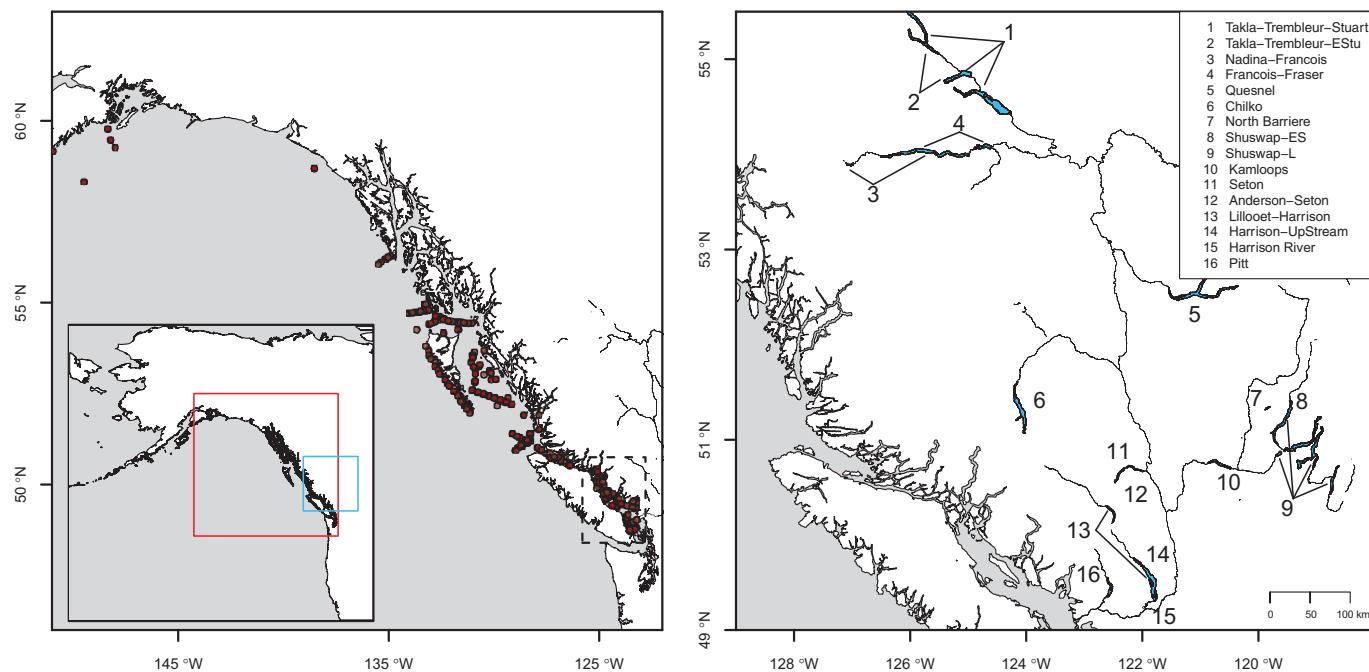
We focused our analysis on 16 Fraser River CUs with long, continuous time series of escapement and age-specific recruitment (Table 1). In one case, we used a single population (Seymour River) as a proxy for its CU (Shuswap-ES) because the other major population had a relatively short time series. Our analysis included data for brood years from 1973 to 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.

We estimated productivity (\log_e recruits (R) per spawner (S)) 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 prespawn 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

Fig. 1. Catch locations of juvenile sockeye salmon during marine sampling surveys (circles, left panel). 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).



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, migra-

tion 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).

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).

Management intervention

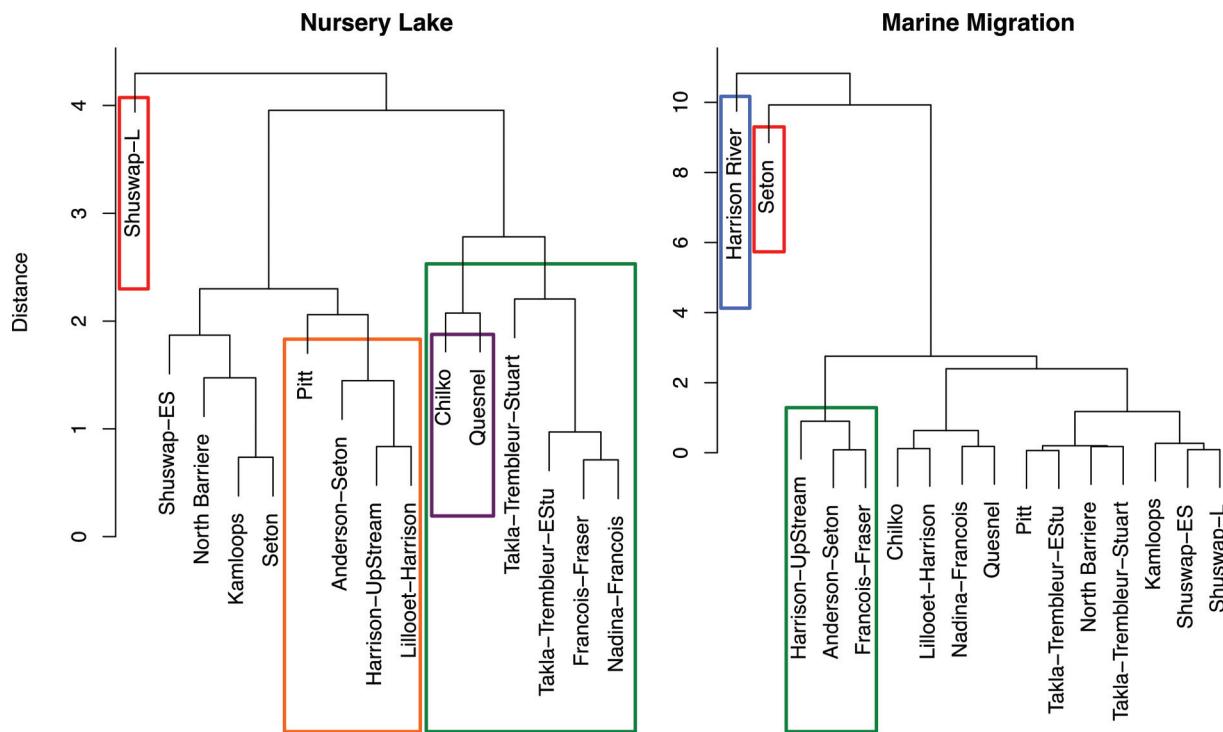
As noted above, five Fraser River CUs have experienced substantial management actions intended to increase and stabilize productivity. We identified the CUs with spawning channels (Anderson-Seton-ES, Nadina-Francois-ES, and Harrison (Upstream)-L) as an outgroup due to the long history of these impacts 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.

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0251>.

Fig. 2. UPGMA (unweighted pair group method with arithmetic mean) cluster diagrams for nursery lake (left) and marine migration (right) characteristics. Colored boxes represent the order in which groups of conservation units (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. [Colour online.]



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 midwater 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 S2¹; 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 S2¹). 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. Because of 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 S2¹). Conversely, Harrison Lake (Upstream), Anderson-Seton, and Francois-Fraser individuals were larger, with the majority cap-

tured outside of the Strait of Georgia during summer surveys (Fig. S1; Table S2¹). 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 :

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

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

$$Y_t = \alpha_t + \beta S_t + v_t, \quad \text{where } v_t \sim MVN(\mathbf{0}, \Sigma_{R_p})$$

$$\alpha_t = \alpha_{t-1} + w_t, \quad \text{where } w_t \sim MVN(\mathbf{0}, \Sigma_\alpha)$$

and Y_t is a column of CU-specific estimates of $\log_e(R_i/S_i)$. 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 ($\alpha_{i,t}$), 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 $\mathbf{0}$ and variance-covariance matrix R . Thus, the multivariate Ricker model in the DFA framework becomes

$$Y_t = Z\alpha_t + \beta S_t + a + v_t, \quad \text{where } v_t \sim MVN(\mathbf{0}, \Sigma_{R_p})$$

$$\alpha_t = \alpha_{t-1} + w_t, \quad \text{where } w_t \sim MVN(\mathbf{0}, \Sigma_\alpha)$$

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 Σ_R included two estimated parameters down the diagonal and zeros elsewhere.

To ensure that the model is identifiable, we set the variance-covariance matrix Σ_α to the identity matrix I with ones along the diagonal and zeros elsewhere. Finally, we modeled the initial vector of productivities as random effects with a mean of zero and the initial state vector (α_0) set to a mean of zero and a diagonal variance-covariance matrix with large variance (here equal to 10):

$$\alpha_0 \sim MVN(\mathbf{0}, 10)$$

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).

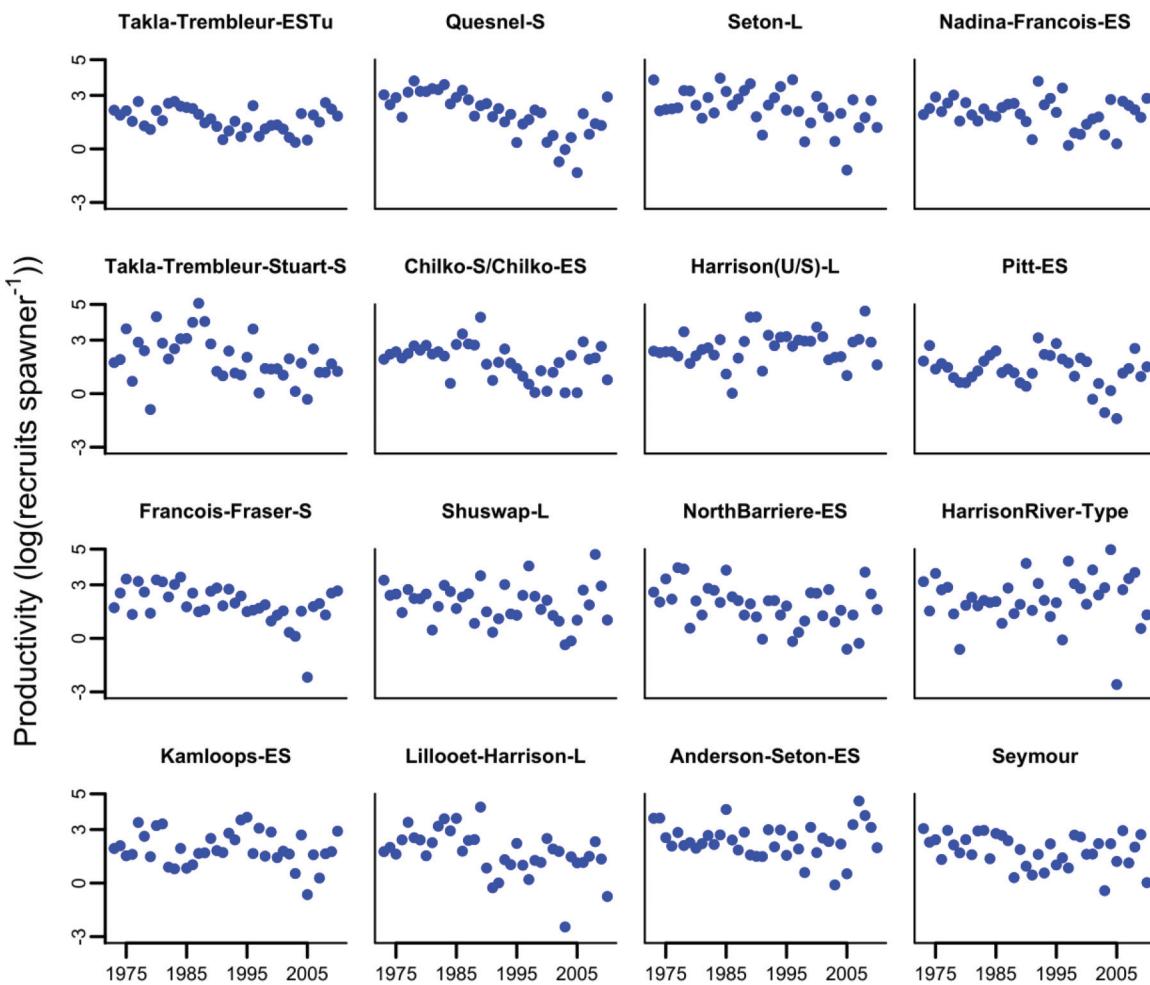
As the DFA model structure is flexible and there were many possible model forms, we specifically set up a multimodel comparison procedure to test among competing hypotheses. For each covariate type (nursery lake, genetic, run timing, or marine migratory characteristics), this procedure began with a null 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 S3¹).

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 AIC_c . 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 versus 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

$$\varphi = \frac{\sum_{ij} \sigma_n^c(i,j)}{\left(\sum_i \sigma_{xi} \right)^2} = \frac{\sigma_n^c}{\left(\sum_i \sigma_{xi} \right)^2}$$

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

Here, i and j represent individual CUs, σ_{ij}^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 Supplementary material¹.

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 S3¹), suggesting groups of CUs with distinct ecological characteristics are generally not responding asynchronously to one another. The most parsimonious

Table 2. Top-ranked models from dynamic factor analysis with trends assigned to CUs based on four groups of ecological covariates.

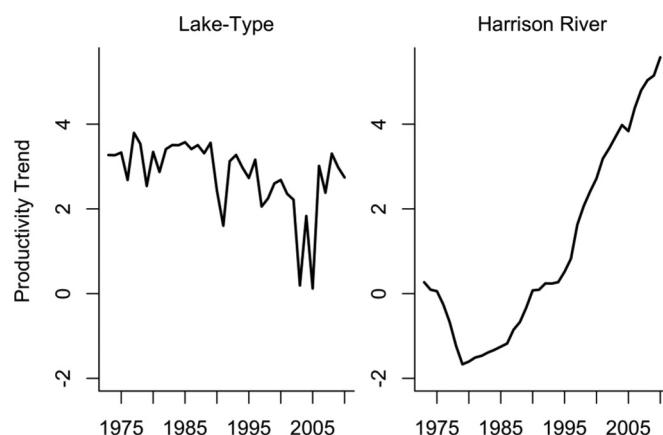
Ecological covariate	No. of trends	Log-likelihood	No. of parameters	ΔAIC_c	AIC weight
Migration or nursery lake	2	-783.48	35	0	0.959
Null	1	-787.77	34	6.33	0.040
Nursery lake	3	-789.50	36	14.29	<0.001
Migration	3	-792.89	36	21.07	<0.001
Genetics	2	-796.28	35	25.60	<0.001

Note: The full suite of models is presented in Table S3¹.

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 S3¹). 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 (Tables S4, S5¹).

The top-ranked model was constrained to estimate one trend for all CUs that rear for at least 1 year in nursery lakes and migrate relatively quickly out of the Strait of Georgia at large body size. It

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



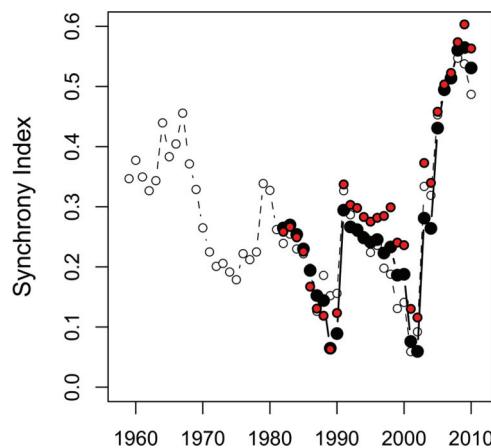
assigned a separate trend to the single sea-type CU included here, which also contains smaller and slower moving marine migrants. The first trend, which applied to 15 of the 16 CUs in the analysis, was characterized by relatively stable dynamics until the mid-1980s when a marked decline began (Fig. 4). 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 (refer to online Supplement; Figs. S2–S3¹).

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. S4¹).

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 outlier in both the nursery lake and marine migration model sets, confounding a clear test of either trait as the principal driver of coherent dynam-

Fig. 5. 10-year moving window estimates of synchrony in productivity ($\log_e(\text{recruits/spawner})$) among Fraser River sockeye salmon CUs. Black 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. [Colour online.]



ics. 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 CU 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. 2018), 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 metapopulation 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 understand variability better 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.

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