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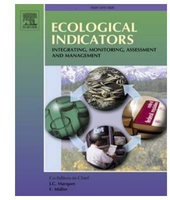

Shifting signals: Correlations among freshwater, marine and climatic indices often investigated in Pacific salmon studies

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ABSTRACT

The common practice of incorporating environmental indices into population models has greatly advanced our understanding of ecological systems. Unfortunately, we are increasingly seeing published correlations between population indicators and environmental indices breaking down when tested with new data. Examining how the correlations among indices change over time could help explain underlying causal mechanisms, which ultimately strengthen the basis for prediction of population indicators. For migratory animals such as anadromous salmon (*Oncorhynchus* spp.), the habitat conditions they experience can affect their lifetime fitness and population viability. We analyzed 43 freshwater, marine, and climate indices associated with 72 river sites and five coastal ecoregions inhabited by Chinook and coho salmon (*O. tshawytscha* and *O. kisutch*) in the western USA. Utilizing long time series (ranging from 32 to 124 years), we examined spatial and temporal patterns in correlations through hierarchical clustering across sites and non-stationarity across time. Individual river sites clustered into two Northwest and one Southwest groups. Northwest sites generally showed stronger correlations between freshwater and climate indices, while Southwest sites showed stronger correlations within freshwater or within marine/climate indices. For a closer examination at shorter periods, we parsed the time series into 10-year windows and showed how pairwise correlations changed over time with spring–summer Pacific Decadal Oscillation index in the Northwest and with spring flow in the Southwest. Stronger correlations across multiple indices tended to occur when large-scale climatic events (e.g., Oceanic Niño and Pacific Decadal Oscillation indices) were in-phase, and phase transitions (e.g., from positive to negative) occurred in the same 10-year window. In a third analysis, we assessed how well indices provided unique vs. confounding/complex information and had consistent vs. varying relationships based on the mean and variance of 10-year correlations. Across index types, the variance in correlations tended to be lowest in marine vs. climate indices, higher among freshwater indices, and highest for freshwater vs. marine/climate indices. Yet, the mean strength of correlations for freshwater vs. marine/climate indices was still comparable to those among freshwater ones. Overall, identifying time periods when correlations tend to change will help interpret historical and projected population indicators. Spatial trends in the strength of correlations also indicate that the level of confounding effects among indices can differ regionally. We emphasize the importance of knowing the strength and variability of correlations among indices, and their representativeness of ecological processes in the context of combined phases of multiple climatic indices.

1. Introduction

In migratory species, elucidating which environmental factors constrain biological processes can be challenging because of strong and potentially changing correlations among indices within and across habitats (Mueter et al., 2005; Pierce et al., 2008; Faaborg et al., 2010). Many environmental indices are correlated through climatic, physical and hydrogeographic processes (Leathers et al., 1991; McCabe and Dettinger, 1999; Wang et al., 2014), while others are due more to chance and are thus statistical artifacts. Understanding functional relationships

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is important for assessing impacts of climate change and management actions to mitigate stressful environmental conditions (NMFS, 2014). Clarifying the correlation structure among environmental indices on their own, which is the focus of the current study, can help to assess our power to detect actual forcing factors and therefore help other studies correctly project ecological responses or population indicators under alternative environmental conditions. Identifying time periods when correlations tend to change is particularly important for improving retrospective and projection analyses.

In addition, understanding the correlation structure among environmental indices across habitats is important because of biological carryover effects that occur across life stages (Hettinger et al., 2012; O'Connor et al., 2014). The habitat conditions in one life stage influence an organism's biological condition, which often affects survival or behavior in the next life stage. Carryover effects include physical condition, physiological state, behavior and ultimately survival. Furthermore, similar mechanisms with cumulative effects can result when organisms experience similar conditions repeatedly across habitats (e.g., temperature effects; Healey, 2011; Martins et al., 2012). If environmental conditions across life stages are correlated, we might not be able to differentiate the impacts of environmental factors in different life stages, despite management interest in doing so. To assess our power to differentiate forcing factors, we first need to characterize the correlation structure of environmental indices, including time steps lagged appropriately for the migratory animal.

For anadromous fishes, studying the correlation structure among their potential indices would help guide studies on mechanistic linkages between environmental conditions and their population indicators. Pacific salmon (*Oncorhynchus* spp.; e.g., Redfish Lake sockeye salmon [*O. nerka*] and Yukon River Chinook salmon) migrate thousands of kilometers through diverse habitats across freshwater and marine environments (Willson and Halupka, 1995; Quinn, 2018). Although marine indices have been found to strongly correlate with salmon responses (Mueter et al., 2005; Burke et al., 2013; Wells et al., 2016), much variation in salmon population dynamics can also be explained by freshwater indices (Greene et al., 2005; Crozier and Zabel, 2006). Furthermore, these freshwater indices can exert direct effects within a life stage and indirect effects in subsequent life stages through influences on growth rates and phenology (Crozier et al., 2008). Thus, carefully selecting which environmental indices to examine across life stages in freshwater and marine habitats can be a nontrivial but vital practice in studying organisms with complex life histories.

An important part in understanding the correlation structure among environmental indices encountered by anadromous salmon is the spatiotemporal scale of their migrations. Relationships between different indices of climate variability that occur over long distances of thousands of kilometers, a phenomenon termed teleconnection, are thus important to consider. Some recent advances in understanding climatic teleconnections between the atmosphere and ocean and across ocean-to-freshwater environments are reviewed by Di Lorenzo et al. (2013) and Sagarika et al. (2015). However, a comprehensive suite of environmental indices and the spatiotemporal scales relevant to a migratory species are often not fully considered in biological studies. Even as these studies reflect important understanding in the correlation structure among freshwater, marine and climate indices (i.e., within and between these types), climatologists and ecologists generally consider a select number of environmental indices across broad landscapes. An examination of patterns among multiple freshwater and marine indices in the context of teleconnections would help researchers choose which indices to test against salmon population indicators at multiple spatial scales; it could help determine which inferences made are likely to be stable over time and which may require interpretation of results related to confounding factors.

To be more strategic in selecting and interpreting indices tested against migratory animal population indicators, it is necessary to better understand the correlations among freshwater, marine, and climate indices. We illustrate how the correlation structure can differ across space and time on the west coast of the contiguous United States of America. First, we examined correlations between pairs of long, multidecadal time series of environmental indices associated with 72 river sites, and determined Northwest and Southwest regional patterns. Second, to clarify when correlations change, we parsed the time series to 10-year time windows. To demonstrate how large-scale marine/climate indices can influence specific populations far away, we compared patterns in the two most interior river sites with anadromous fish populations in the contiguous western USA, lower Salmon River and the Sacramento River. These sites also have among the longest time series, which allowed the best assessment of changing correlations over time. We focused on interior sites to contrast with previous studies looking at coastal sites that are expected to be highly correlated with marine conditions simply because of their proximity (Lawson et al., 2004). Third, to generalize our guidance on which indices are reliably distinct over time, we summarized the mean and variance of 10-year correlations by index type and spatial scale. Because most time series of animal population indicators are relatively short and most studies include a small number of indicators, exploring how correlation structure among environmental indices change across short time frames through the entire time series could provide context for interpreting recent trends in ecosystems (e.g. latest 5-year trends in Harvey et al., 2017). Our study aims to help scientists and decision makers avoid mistaking a direct effect for a confounded index and projecting into the future when the correlation they discovered is likely to change.

2. Methods

2.1. Data

We examined 72 river sites where Chinook and coho salmon spawn, rear, or migrate (StreamNet, www.streamnet.org) that had at least 30 years of freshwater environmental data (see Table S1 in Supplementary Material for metadata). In the marine environment, we delineated five coastal ecoregions that fit within the ecoregions of the California Current System determined by Spalding et al. (2007). These ecoregions represent areas where salmon first enter the ocean after their juvenile downstream migration. We included marine indices that encompass both the initial conditions salmon encounter near their ocean entry point (regional), and across their entire marine stage (large). We grouped 43 environmental indices into four categories based on index type and spatial scale: local freshwater/land ("FW_{local}"; Table 1), regional freshwater/land ("$FW_{regional}$"), regional coastal marine ("$M_{regional}$"), and large-scale marine and climate ("MC_{large}").

In the freshwater environment, we examined 19 indices (see Table 1a for descriptions and references). For FW_{local} indices, we examined seasonal maximum air temperatures from the Parameter-elevation Relationships on Independent Slopes Model (Daly et al., 2008). We also tested seven indices of river flow. The flow time series ranged from 32 years (water years 1984–2015, Beaver Creek, Oregon), to 124 years (water years 1892–2015, Sacramento River, California), and averaged 85 $\pm$ SD 22 years (median of 87 years) across the 72 sites. The $FW_{regional}$ indices were represented by seasonal mean air temperature and Palmer Hydrological Drought Index for the Northwest and Southwest regions. The designation of regions in the current study are based on the Northwest (Washington, Oregon and Idaho, USA) and West (California and Nevada, USA) regions defined by Karl and Koss (1984). We used air temperature because many sites did not have long (>30 years) time series of stream temperature data.

The 14 $M_{regional}$ indices were seasonal means of sea surface temperature (SST) and indices related to coastal upwelling (see Table 1b for descriptions and references). The long-term SST data set at coarse spatial resolution ($2^{\circ} \times 2^{\circ}$) was the Extended Reconstructed Sea Surface Temperature v3b. The SST data at finer spatial resolution ($<0.05^{\circ} \times 0.05^{\circ}$) but shorter time series were remotely sensed satellite data from

Table 1a
Freshwater indices.

Spatial scale	Index category	Index descriptions	Index names	Years
Local (river site); "FW_{local}"	Maximum air temperature	Seasonal means of monthly maximum air temperature from the Parameter-elevation Relationships on Independent Slopes Model (PRISM; Daly et al., 2008) [1]	Max. temperature (Win., Spr., Sum., Aut.; JFM, AMJ, JAS, OND)	1895–2015
	River flow	Calculated from daily discharge observations from U.S. Geological Survey's National Water Information System [2] (Table S1): seasonal means in a calendar year; and 1-day minimum, 1-day maximum, and coefficient of variation of daily flow in a water year	River flow (Win., Spr., Sum., Aut.; JFM, AMJ, JAS, OND); Min. flow, WY (Oct–Sept); Max. flow, WY;CV of flow, WY	Various years spanning 1895–2015
Regional; "$FW_{regional}$"	Mean air temperature	Seasonal means of monthly indices from National Climate Data Center (NCDC) [3]	Mean temperature (Win., Spr., Sum., Aut.; JFM, AMJ, JAS, OND)	1895–2015
	Drought	Seasonal means of monthly Palmer Hydrological Drought Index (PHDI) from NCDC [4]	Drought Index (Win., Spr., Sum., Aut.; JFM, AMJ, JAS, OND)	1895–2015

[1] www.prism.oregonstate.edu, accessed 2016/12/13.
[2] http://waterdata.usgs.gov/nwis/, accessed 2017/01/03.
[3] http://www7.ncdc.noaa.gov/CDO/cdo, accessed 2017/04/20.
[4] http://www7.ncdc.noaa.gov/CDO/cdo, accessed 2017/04/20.

Pathfinder and Multi-scale Ultra-high Resolution satellites. We also examined six coastal upwelling/downwelling indices that can indicate the phenology and magnitude of bottom-up ecological processes (Bograd et al., 2009).

The MC_{large} indices were the Oceanic Niño Index in the Niño 3.4 region, Aleutian Low Pressure Index, Pacific Decadal Oscillation index, and North Pacific Gyre Oscillation index (see Table 1b for descriptions and references). We compared Niño 3.4 and PDO indices with freshwater and coastal marine conditions to look for signs of teleconnections within a year Y and even stemming from the previous year Y–1. The spatiotemporal range of the correlations could indicate different mechanisms of pre-conditioning the habitat before the salmon arrive.

Because autocorrelation in time series can inflate correlations between indices, a common practice is to prewhiten data by demeaning, detrending and removing autocorrelation (Bayazit and Önöz, 2007). However, our goal was not to assign mechanistic relationships among indices; rather, it was to elucidate apparent relationships that would influence interpretation of biological responses or population indicators. Thus, we were more interested in apparent correlations than a pattern of residuals. Even so, we explored correlations with prewhitened data, in addition to the raw data, in case it affected our conclusions. We found similar patterns to those from the raw data and even cases of strengthened correlations after prewhitening (e.g., Figs. S1 and S2 in Supplementary Material). Results presented in the rest of this paper are from analyses of the raw data as acquired from data sources, and not additionally prewhitened.

2.2. Analyses

2.2.1. Long time series: regional, averaged correlation structure

To determine which sites had similar patterns of correlations among environmental indices, we applied a hierarchical cluster analysis with the function hclust (R Core Team, 2019). The distance metric entered in the analysis was essentially the complement of the correlation between two sites' among-index correlations (i.e., 1– R). More specifically, we used a vector (Z_i) for each site i of correlation coefficients following a Fisher Z-transformation:

$z = \frac{1}{2} ln\left(\frac{1+r}{1-r}\right) = tanh^{-1} r$ (Fisher, 1915). This transformation changes r correlation coefficients, bounded by –1 and 1, to z correlation coefficients that have a normal distribution. This transformation allows the variance to be approximately constant for all values of z, instead of getting smaller as the r correlation coefficient gets closer to –1 or 1 (see Fig. S3 in Supplementary Material). A vector Z_i was determined for 11 FW_{local} indices paired to all 43 indices (i.e., 407 separate between-index correlations). We then determined the correlation ($R_{i,j}$) between vectors Z_i and Z_j for different sites i and j. The distance measures ($D_{i,j}$) between sites were calculated as 1 – $R_{i,j}$. Thus, the hierarchical cluster analysis was performed using all 43 freshwater and marine indices; but it excluded comparisons among regional freshwater, marine, and climate indices that would have been repeated among many or all sites (i.e., not all 903 between-index correlations possible among 43 indices). The optimal number of partitioned clusters was determined using the criterion of Calinski and Harabasz (1974) with the function cascadeKM (Oksanen et al., 2019), based on the function kmeans (R Core Team, 2019).

For each cluster of sites, we averaged correlation coefficients, r, across sites and plotted them in a correlation matrix. As a guide, we break down the correlation matrix to submatrices by index type with detailed descriptions of hypothesized patterns and references (Box S1 in Supplementary Material) that can be compared to our study results.

We chose to examine correlations directly in this paper, rather than with other dimension-reduction or time-series-specific statistical methods to keep the results as intuitive as possible, and to reveal any dynamics that would affect real organisms (such as temporal autocorrelation). For example, dynamic factor analysis (Zuur et al., 2003) is amenable to examining trends in non-stationary data. But it is limited in its ability to examine changing correlations because it assumes constant loadings through time. Alternatively, a factor stochastic volatility model (Kastner et al., 2017), which is more often applied in the financial econometrics field than ecology, can assess changing correlations among indices. However, the number of indices we are testing in the current study represent a variety of processes across space. A factor stochastic volatility model would be better suited for a local study with fewer processes at stake. To achieve our heuristic aims, we chose to apply the more common and direct comparison of simple correlations.

2.2.2. Short time series: Changing correlations

We parsed the time series into consecutive 10-year windows so we could visualize when, by how much, and in what direction, correlations among indices changed over time. We chose a 10-year window because many salmon time series are approximately one to two decades long. Relatively few monitoring programs started decades ago, and maintaining funding for such programs is difficult.

We looked for periods when changes in correlations occurred across sites. We limited our analysis to pairwise comparisons of the full suite of local freshwater indices with a single large-scale or regional index because our previous step had already shown strong correlation among the MC_{large} indices. Furthermore, upwelling indices and satellite SST time series were too short for this analysis. For the Northwest, we chose to examine the spring–summer PDO as our representative MC_{large} index because of its association with other indices, its influence on salmon, and its long time series (Mantua et al. 1997, Burke et al. 2013, Peterson et al. 2014). For the Southwest, we chose to examine spring mean flow for similar reasons. Its association with other indices has been studied by Wang et al. (2014) and is related to regime shifts between dry and wet

Table 1b
Marine and climate indices.

Spatial scale	Index category	Index descriptions	Index names	Years
Ecoregional; "$M_{regional}$"	Sea surface temperature	Seasonal means of Extended Reconstructed Sea Surface Temperature V3b[5]	ERSST (Win., Spr., Sum., Aut.; DJF, MAM, JJA, SON)	1854–2015
	Sea surface temperature	Seasonal means of sea surface temperature, Pathfinder[6] and Multi-scale Ultra-high Resolution[7] satellite data	Satellite SST (Win., Spr., Sum., Aut.; JFM, AMJ, JAS, OND)	1982–2015
	Coastal upwelling/ downwelling	Indices were spring transition index (STI), end and length of upwelling season (END and LUSI), total upwelling magnitude (TUMI), and total downwelling magnitude (TDMI), and the North Pacific High pre-conditioning Cumulative Upwelling Index (pCUI)[8] at four different Pacific Fisheries Environmental Laboratory stations (39°N, 125°W; 42°N, 125°W; 45°N, 125°W; and 48°N, 125°W)	Upwelling/ downwelling indices (STI, END, LUSI, TUMI, TDMI, pCUI)	1967–2015
Large-scale; "MC_{large}"	Niño-3.4	Oceanic Niño Index in Niño 3.4 region[9]; means from Jan–Jun and Jul–Dec means in years $Y-1$ and Y	Niño 3.4 (Win–Spr [Jan–Jun], Y-1; Sum–Aut [Jul–Dec], Y-1; Win–Spr; Sum–Aut)	1870–2015
	Aleutian Low Pressure Index	Index[10] of the Aleutian Low pressure system from Dec, $Y-1$ through Mar, Y in the north Pacific, calculated as the mean area (km^2) with sea level pressure ≤ 100.5 kPa and expressed as an anomaly from the 1950–1997 mean.	ALPI (Win.; Nov–Mar)	1900–2015
	Pacific Decadal Oscillation Index	Index of sea surface temperature pattern in the North Pacific[11]; means from months Apr–Sep and Oct–Mar in years Y and $Y-1$)	PDO (Spr–Sum [Apr–Sep], Y-1; Aut–Win [Oct–Mar], Y-1; Spr–Sum; Aut–Win)	1900–2015
	North Pacific Gyre Oscillation Index	North Pacific Gyre Oscillation Index[12]; (Dec-Mar mean in years Y and Y-1)	NPGO (Win.; Dec-Mar)	1950–2015

[5] Smith et al. (2008), in which ERSST v3b does not include satellite data compared to ERSST v3; data from http://cci-reanalyzer.org/reanalysis/monthly_tseries/, accessed 2017/01/03.
[6] Kilpatrick et al. (2001); SST, Pathfinder Ver 5.0, Day and Night, Global, Science Quality, Monthly Composite, 1982–2009, dataset name "erdPHsstamday" from http://coastwatch.pfeg.noaa.gov/erddap/index.html, accessed 2015/02/03.
[7] Chin et al. (2017); Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 0.01°, Monthly, 2003–2015; dataset name "jplMURSST41mday" from http://coastwatch.pfeg.noaa.gov/erddap/index.html, accessed 2016/12/30.
[8] calculated following Bograd et al. (2009) and Schroeder et al. (2013), with data from http://www.pfeg.noaa.gov/products/PFELData/upwell/daily/, accessed 2017/05/09.
[9] Peterson et al. (2014); https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Nino34/, acccessed 2017/01/04.
[10] (Wallace and Gutzler, 1981; Trenberth and Hurrell, 1994); data from http://www.beringclimate.noaa.gov/data/ index.php, accessed 2017/01/04.
[11] Mantua et al. (1997); data from research.jisao.washington.edu/pdo/, accessed 2017/01/04.
[12] Di Lorenzo et al. (2008); data from http://www.o3d.org/npgo/, accessed 2017/01/04.

conditions driven by teleconnections.

To demonstrate that these relationships can occur over vast distances, we showed detailed results for two interior locations: lower Salmon River, Idaho in the interior Northwest, and Sacramento River at Red Bluff Diversion Dam, California in the interior Southwest. In these case studies, the bivariate correlation coefficients for 10-year windows are represented in the bubble plots. For each bivariate comparison, we report the mean and variance of the 10-year correlation coefficients, as well as the first-order autocorrelation (function arima; R Core Team, 2019) and correlation coefficients for the complete time series. The site level is where most biologists conduct work related to their target population, and thus these results exemplify the most tangible indices in our study.

2.2.3. Strength and variability in correlations by index type

In this section, we compared the mean and variability of correlations among FW_{local}, $FW_{regional}$, $M_{regional}$ and MC_{large} index types. Across the 10-year windows, we categorized the z correlation coefficients among indices as low vs. high mean and low vs. high variance (Table 2). Indices that have both low mean (|mean z correlation coefficient| < 0.4) and low variance in z correlation coefficient ($\sigma^2 < 0.15$) provide unique information and thus would be favorable candidate predictors. Indices with consistently lower levels of correlation would cause fewer multicollinearity issues in modeling (Møller and Jennions, 2002; Dormann et al., 2013). There would be a lower risk of missing mechanistic relationships because of confounding effects. Indices that have at least moderate correlation (|mean z correlation coefficient| > 0.4) and low variance in z correlation coefficient ($\sigma^2 < 0.15$) represent pairs in which collinearity may be an issue and we would interpret results more cautiously. When indices are correlated, there may be another index that truly represents the underlying causal mechanism. Although, when we consider the perspective of the fish, both environmental indices (e.g., river temperature and flow) may actually be experienced in manners

Table 2
Interpretation of categories of low/high mean of z correlation coefficients and low/high variance (σ^2) of z correlation coefficients across the 10-year moving window times series of environmental indices. Low correlation is defined as $|\text{mean } z| < 0.4$ and high correlation is defined as having $|\text{mean } z| > 0.4$. Low variance of z is $\sigma^2 < 0.15$ and high variance of z is $\sigma^2 > 0.15$.

		Mean	
		Low (<0.4)	High (>0.4)
Variance	High (>0.15)	***Category B. Noisy information, low correlation:*** same as Category A, but careful interpretation recommended because of occasional high correlation	***Category D. Noisy information, high correlation:*** same as Category C, but careful interpretation recommended because of occasional low correlation
	Low (<0.15)	***Category A. Unique information:*** both indices can be tested and distinguished in linear models, with less risk of confounding effects	***Category C. Confounding and complex effects:*** each index can be separately tested, but caution is needed in conclusions; indirect effects may arise due to unknown true mechanisms; complex effects may arise because both indices are experienced by fish

that influence their responses. Finally, indices that have high variance in z correlation coefficient ($\sigma^2 > 0.15$) may indicate spurious relationships and also require more careful interpretation.

3. Results

3.1. Long time series: regional, averaged correlation structure

The correlation structure of the 43 indices from each site clustered into broad Northwest and Southwest regions (Fig. 1). The occurrence of colored and white spaces in the correlation matrix (Fig. 2) shows that many correlations exist among the indices, but that not all indices are correlated to each other. These correlations, which are averaged across sites within each NW/SW cluster, revealed some distinguishing patterns. For the NW1 sites, there were strong correlations between freshwater and marine/climate indices (submatrices E and F; upper triangle in Fig. 2). For the NW2 sites, there was a lack of correlations between flow and other indices that are present for NW1 sites (lower portion of submatrices A, E and F; Fig. S4 in Supplementary Material). For SW sites, there were correlations among freshwater indices and correlations among marine and climate ones (submatrices A, B and D; lower triangle in Fig. 2). There were also some correlations between flow and $M_{regional}$ indices (submatrix F; Fig. 2) that are not apparent in the NW sites. Overall, our results showed that temperature-related freshwater indices were closely correlated with large-scale marine/climate indices in the Northwest, whereas flow-related indices were closely correlated with marine indices in the Southwest. These patterns are generally consistent with existing theories of underlying climatic and physical processes across long distances as described in greater detail in Box S1 in the Supplementary Material.

The number of cases in which $|r| \geq 0.3$ (i.e., colored in Fig. 2), or $|r| \geq 0.5$, differed between the NW1 and SW sites and by index type. The mean correlations across NW1 sites generally showed a larger number of and stronger correlations between freshwater and marine/climate indices than in SW sites (respectively, 44 vs. 28 index pairs with $|r| \geq 0.3$; and 6 vs. 0 index pairs with $|r| \geq 0.5$; Fig. 2, submatrices E and F). The opposite pattern existed among marine and climate indices (Northwest and Southwest respectively, 67 vs. 87 index pairs with $|r| \geq 0.3$; and 36 vs. 49 index pairs with $|r| \geq 0.5$; Fig. 2, submatrices B and D). We describe these correlations in greater detail (Box S2 in Supplementary Material) for each lettered submatrix of Fig. 2 and compare to predicted patterns (Box S1 in Supplementary Material).

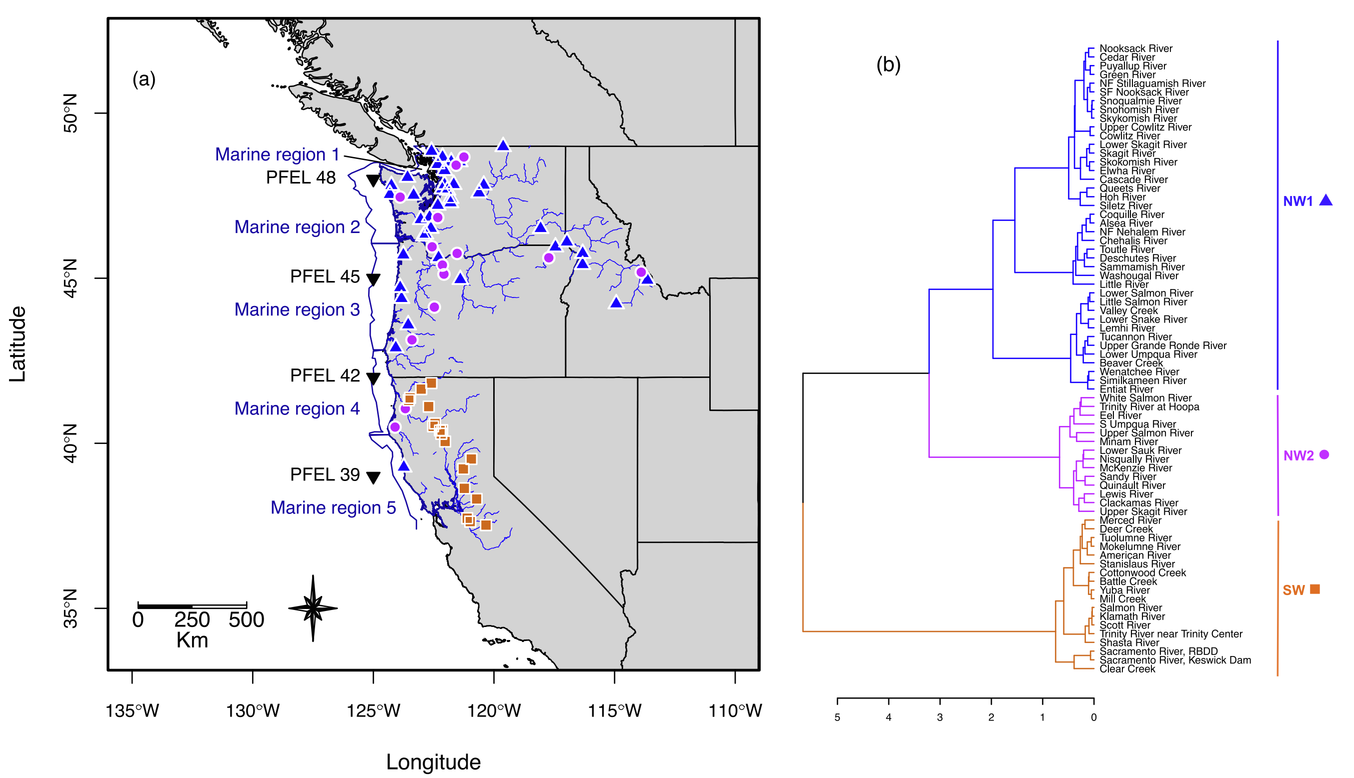

Fig. 1. Map of sites in the freshwater environment and coastal ocean ecoregions of the California Current Ecosystem. A hierarchical cluster analysis was run on a distance metric representing correlations of each local freshwater index against all 43 environmental indices. Sites grouped into three clusters are represented by cool colors in the Northwest (blue triangle, NW1; purple circle, NW2) and a warm color in the Southwest (orange square; SW).

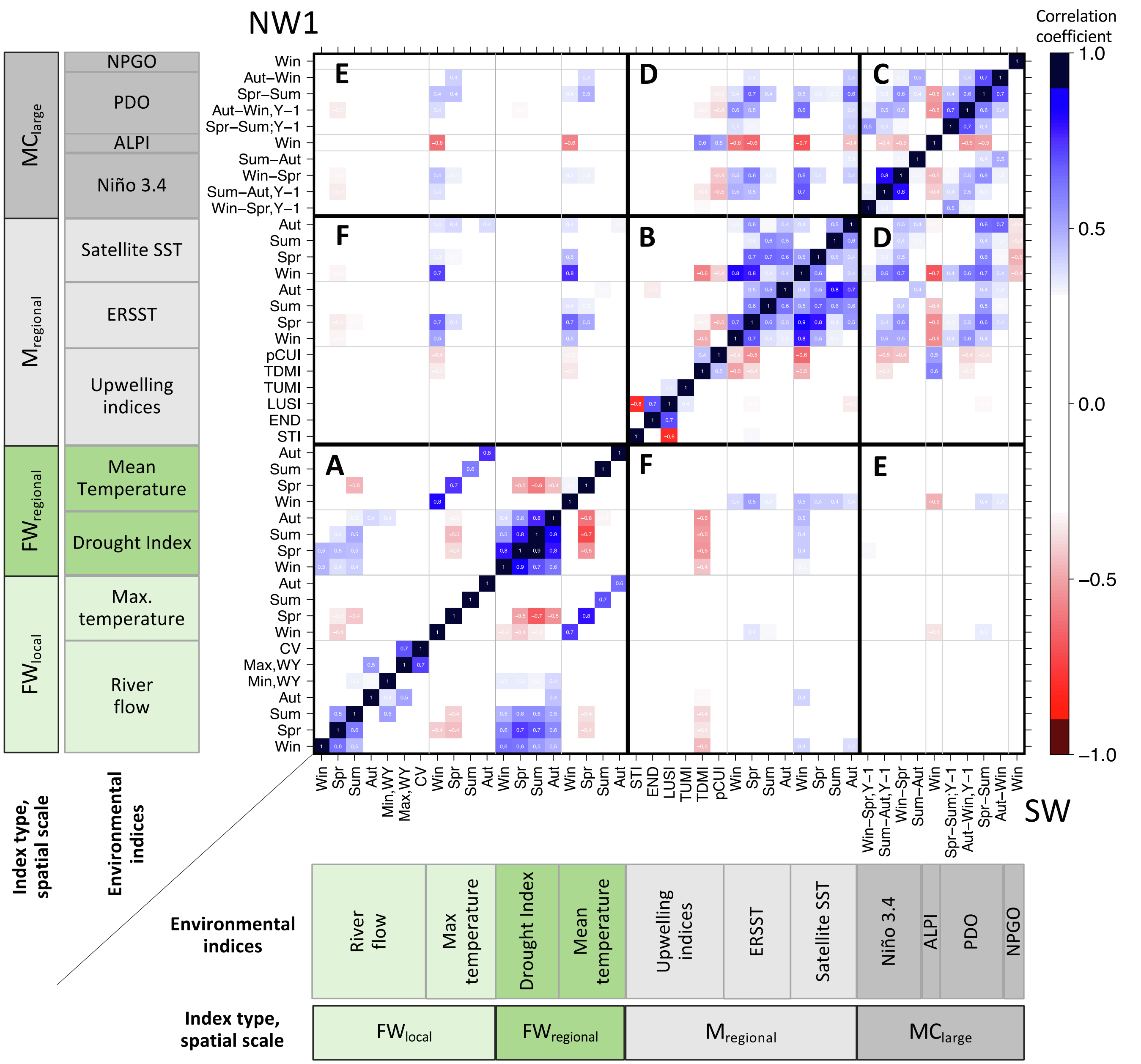

Fig. 2. Correlation matrix of freshwater, marine, and climate indices, representing mean correlations across sites by NW1 (upper triangle) and SW (lower triangle) cluster of sites. For a comparison between NW1 and NW2 clusters, see Figure S4 in Supplementary Material. Correlation coefficients of colored squares legible if viewed digitally and zoomed in.

3.2. *Short time series: Changing correlations*

We delved deeper into the correlative structure by parsing the time series into 10-year windows. We observed correlations that spanned periods of strongly negative, strongly positive, and weak correlations (for example Fig. 3, and Fig. S5, in Supplementary Material). The changes in climate indices that are in-phase in one direction to in-phase in the other direction (i.e., both negative to both positive, or both positive to both negative; Fig. 3) are important types of in-phase transitions to keep in mind when interpreting correlations among indices.

Across sites, we observed periods of stronger mean correlations of spring–summer PDO with all other indices (Fig. 4). Stronger periods of correlations were also observed between spring flow and all other indices (Fig. 5). Northwest sites generally showed stronger correlations with spring–summer PDO than Southwest sites (Fig. 4). The 10-year windows showing stronger correlations across sites tended to match the windows when both Niño 3.4 and PDO indices were in-phase positively and negatively at separate points within a 10-year window (Fig. 3). In contrast, periods of stronger correlations between the mean spring flow and other indices were more apparent across sites in the Southwest than Northwest (Fig. 5). The stronger relationships with the PDO index in the Northwest and with flow in the Southwest support our findings in the long time series analysis (Fig. 2).

In the case study with lower Salmon River, the mean spring–summer PDO showed stronger trends of correlations with other indices in the following 10-year windows: 1925–34, 1975–84 (marine and climate only), 1995–2004, and 2005–14 (Fig. 6). The 1925–34 window showed that the mean spring–summer PDO was more correlated with ALPI, SST, air temperature, drought, and flow indices than other time windows. In contrast, the 1975–84 window had a linear trend in the mean spring–summer PDO over time, and there were generally higher correlations between the PDO index and various marine and climate indices. The

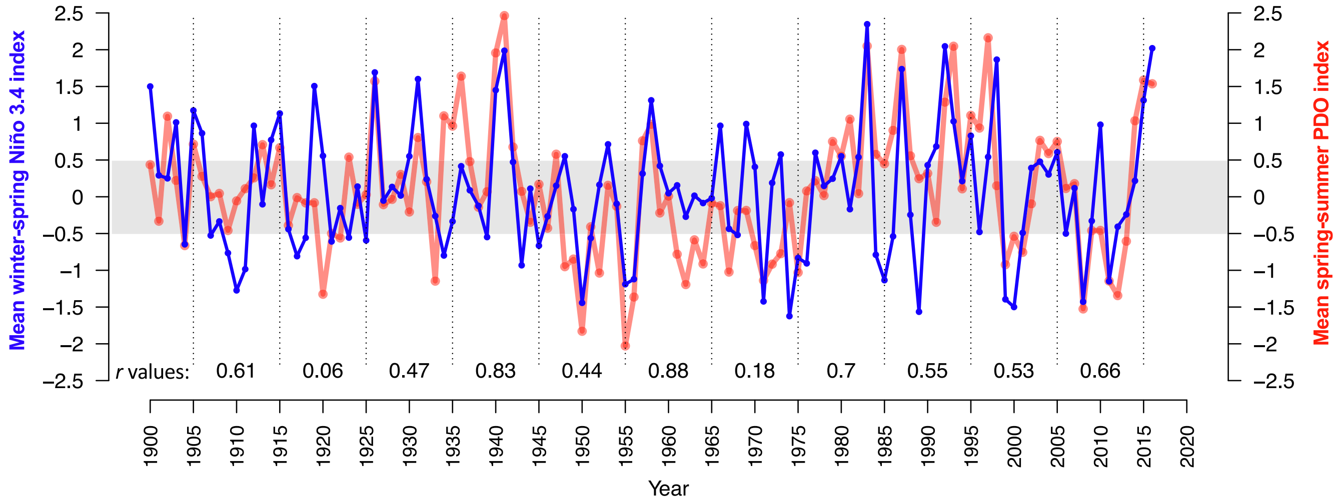

Fig. 3. Correlation coefficients for Niño 3.4 and PDO indices across 10-year windows (separated by vertical lines). Area of neutral values for PDO and Niño 3.4 indices is represented by the gray shading. The indices are in-phase positively when their values are > 0.5 and are in-phase negatively when their values are < −0.5.

1995–2004 and 2005–14 windows showed that stronger correlations were with flow, temperature, and SST indices. Notably, the correlations with flow and temperature indices changed from positive to negative in these last two decades. Another notable change is that the mean spring–summer PDO index was strongly correlated with upwelling indices in 1975–84 and 1985–94 windows, but then was correlated with NPGO in 1995–2004 and 2005–14 windows. Even in a site-specific case study, we are seeing many trends of changing correlations across 10-year windows.

We note that some site-specific differences can occur. The 1955–64 window showed stronger correlations across many Northwest sites, but not in the lower Salmon River (Fig. 4). Strong correlations associated with the lower Salmon River occurred in 1925–34, 1995–2004, and 2005–14 (Fig. 6), which correspond to many other Northwest sites (Fig. 4).

For the Sacramento River, the local mean spring flow was more strongly correlated with other indices of flow, drought, and maximum air temperature indices, than with marine and climate indices (Fig. 7). Thus, this local freshwater index was more representative of other freshwater indices than marine and climate indices. The periods when spring mean flow was more strongly correlated with other freshwater indices were 1915–24, 1925–34, 1975–84, 1995–2004, and 2005–14 windows. The periods of higher correlations with spring mean flow in the Sacramento River (Fig. 7) were similar to patterns across sites (Fig. 5).

Some pairs of indices in the Sacramento River showed correlations that changed between negative and positive values across the 10-year windows (Fig. 7). Examples include correlations of mean spring flow with fall maximum temperature, LUSI and END upwelling indices, and spring–summer ERSST indices. In contrast, the TDMI upwelling index was consistently negative, and we see this negative correlation in the long time series correlation matrix (Fig. 2).

3.3. Strength and variability in correlations by index type

The temporal trends (i.e. correlations with year) showed weaker correlations than those among index types (Fig. 8a). The z correlation coefficients were close to 0, averaging between –0.25 and 0.25 and having relatively high variances centering around 0.07 and 0.2. These results show that ten-year windows are too short to detect linear trends of climate change, but are expressions of climate-related decadal oscillations.

In contrast, $M_{regional}$ and MC_{large} indices generally had the strongest mean z correlation coefficients, with some>0.75 (equivalent to $r > 0.64$) in absolute value (Fig. 8c). This result matches the strong r values we observed in the correlation matrix with long time series (Fig. 2). It also matches the correlations across 10-year windows with spring–summer PDO (Fig. 6).

The variances of z differed among index types. Many $M_{regional}$ and MC_{large} index pairs had low variances with $\sigma^2 < 0.1$ (Fig. 8c); but some also had high variances, a number of which had among the highest ($\sigma^2 \approx 0.3$). Among FW_{local} and $FW_{regional}$ indices (Fig. 8b), few index pairs had $\sigma^2 < 0.05$. The variance of z was generally greater between (Fig. 8d) than within index types (Fig. 8bc). Yet, the z correlation coefficients of FW_{local} and $FW_{regional}$ vs. $M_{regional}$ and MC_{large} indices (Fig. 8d) were comparable and generally greater than those of FW_{local} and $FW_{regional}$ indices (Fig. 8b).

Index pairs across the categories of low/high mean vs. low/high variance of z correlation coefficients (Table 2) occurred at similar proportions across the Northwest and Southwest (Fig. 9). Most cases of index pairs were of low correlations across all index types (categories A and B, Table 2). Few cases of high mean and high variance of z correlation coefficients (category D, Table 2) occurred, and were generally for correlations among MC_{large} and $M_{regional}$ indices. A small proportion of cases of low but variable z correlation coefficients (category B, Table 2) occurred among MC_{large} indices. Generally, MC_{large} indices were either consistently correlated (high z, category C) or not (low z; category A). There were greater proportions of cases of high mean and low variance of z correlation coefficients (category C, Table 2) for large-scale indices (Fig. 9a) than for local-scale indices (Fig. 9b).

Some differences still occurred between the two regions. The Southwest showed a greater proportion of cases with high correlations among MC_{large}, $M_{regional}$, and $FW_{regional}$ indices (Fig. 9a) and between FW_{local} and $M_{regional}$ indices (Fig. 9b). In contrast, the Northwest proportionally showed more cases of high and consistent z correlation coefficients between FW_{local} and MC_{large} indices (Fig. 9b). These results are consistent with the teleconnection-related correlations in the Northwest and the coastal-marine-related relationships in the Southwest we observed in the correlation matrix (Fig. 2) and across 10-year windows (Figs. 4 and 5). Furthermore, the NW2 sites showed low proportions of Categories C and D (high mean of z correlations) between FW_{local} and other index types (Fig. 9b). This result also corresponds to the lack of correlations between flow and other FW_{local}, $FW_{regional}$, $M_{regional}$ and MC_{large} indices observed in the NW2 sites (Fig. S4 in Supplementary Material).

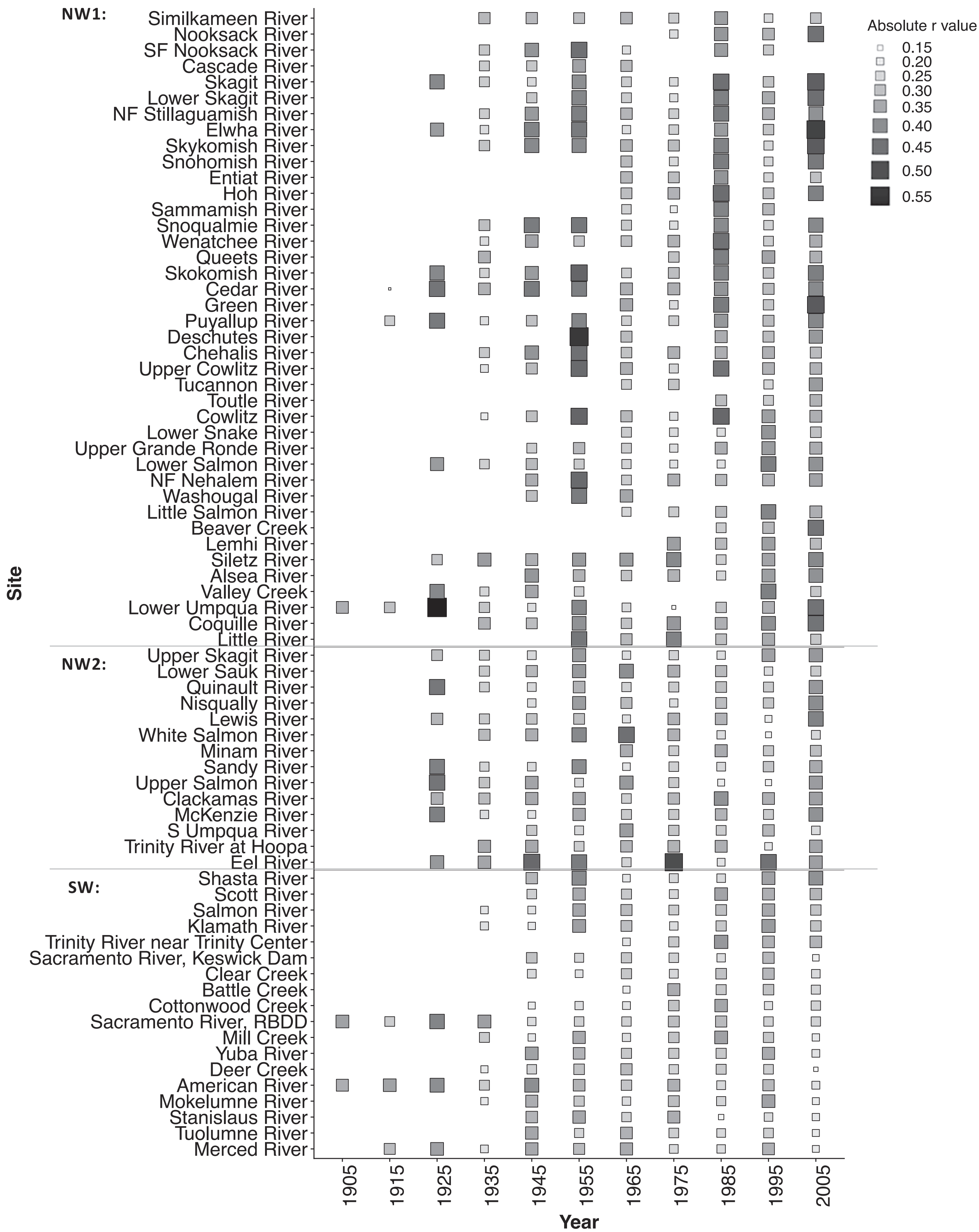

Fig. 4. Mean absolute values of correlation coefficients across pairs of indices for each site and each 10-year window of data, labelled with the starting year. Pairs of indices are between the spring–summer PDO index and local freshwater indices.

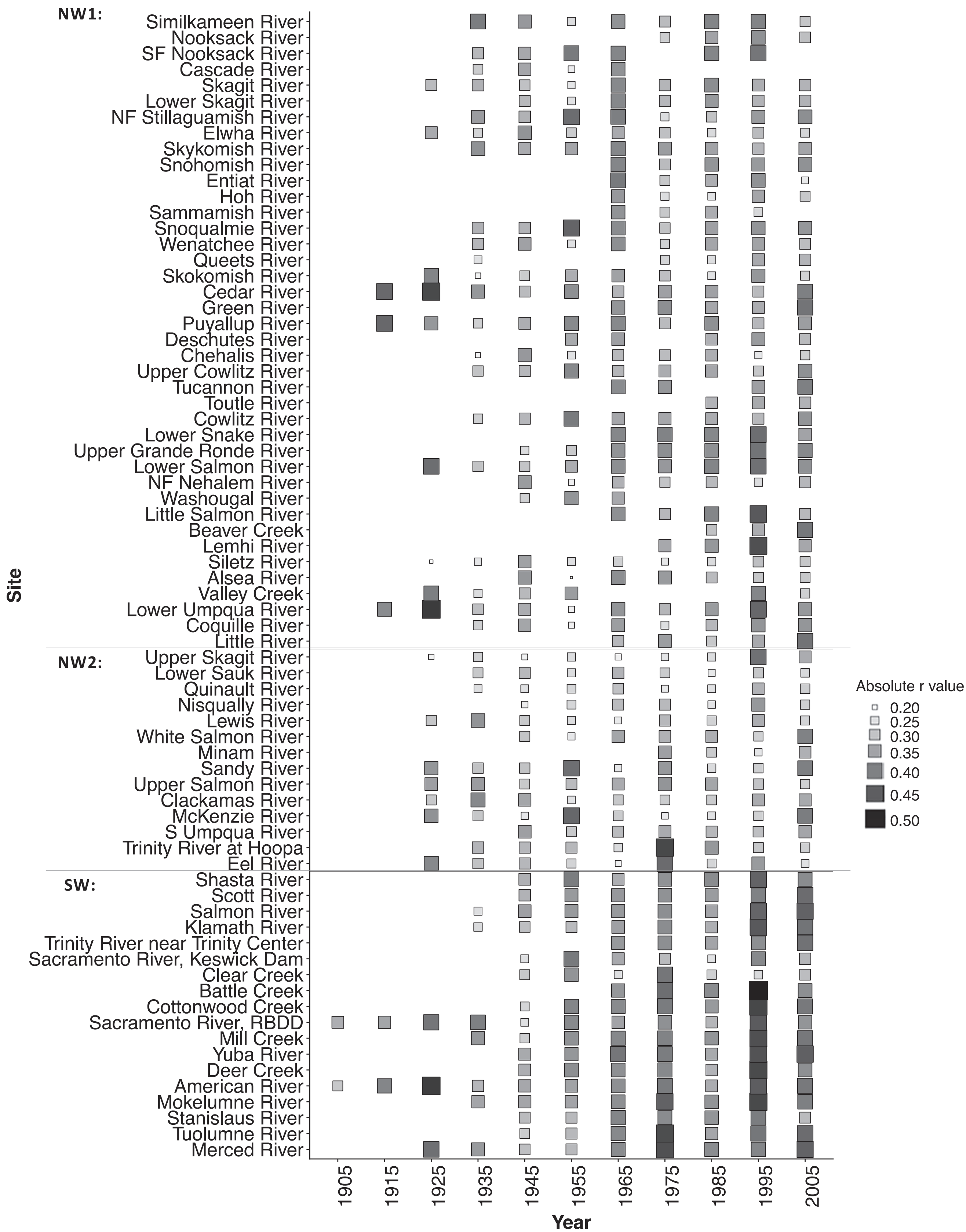

Fig. 5. Mean absolute values of correlation coefficients across pairs of indices for each site and each 10-year window of data. Pairs of indices are of the mean spring monthly river flows against the local freshwater indices, regional ERSST, and large-scale climate indices.

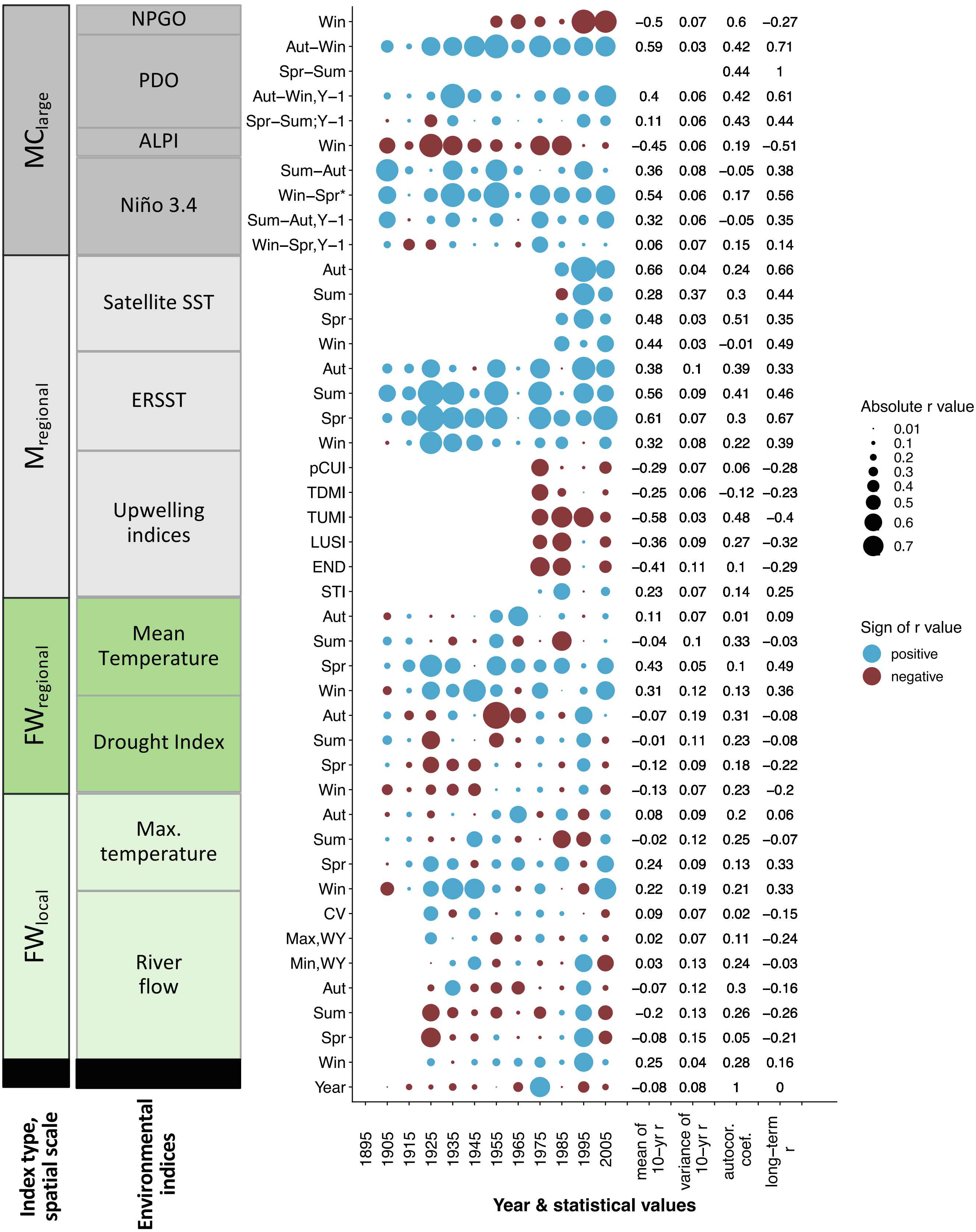

Fig. 6. Bubble plot representing correlation coefficients across 10-year windows (labelled with starting year) of all environmental indices examined in current study against the mean spring–summer PDO index for the lower Salmon River. First-order autocorrelation coefficients and long-term *r* correlation coefficients are reported for whole time series for descriptive purposes. *The winter-spring Niño 3.4 index above shows correlation coefficients with spring-summer PDO that correspond to those in Fig. 3.

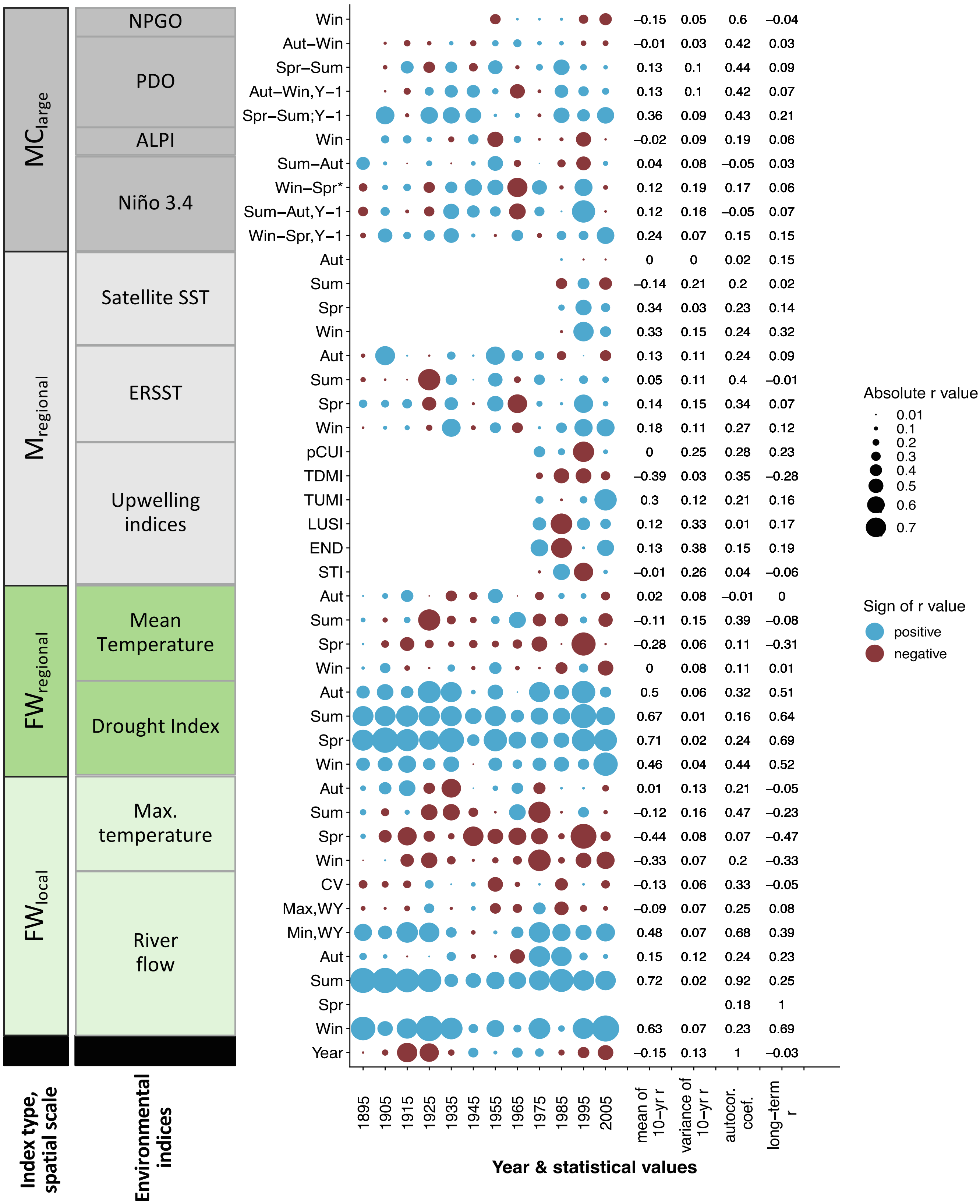

Fig. 7. Bubble plot representing correlation coefficients across 10-year windows of all environmental indices examined in current study against mean spring mean flow for Sacramento River at Red Bluff Diversion Dam. First-order autocorrelation coefficients and long-term *r* correlation coefficients are reported for whole time series for descriptive purposes.

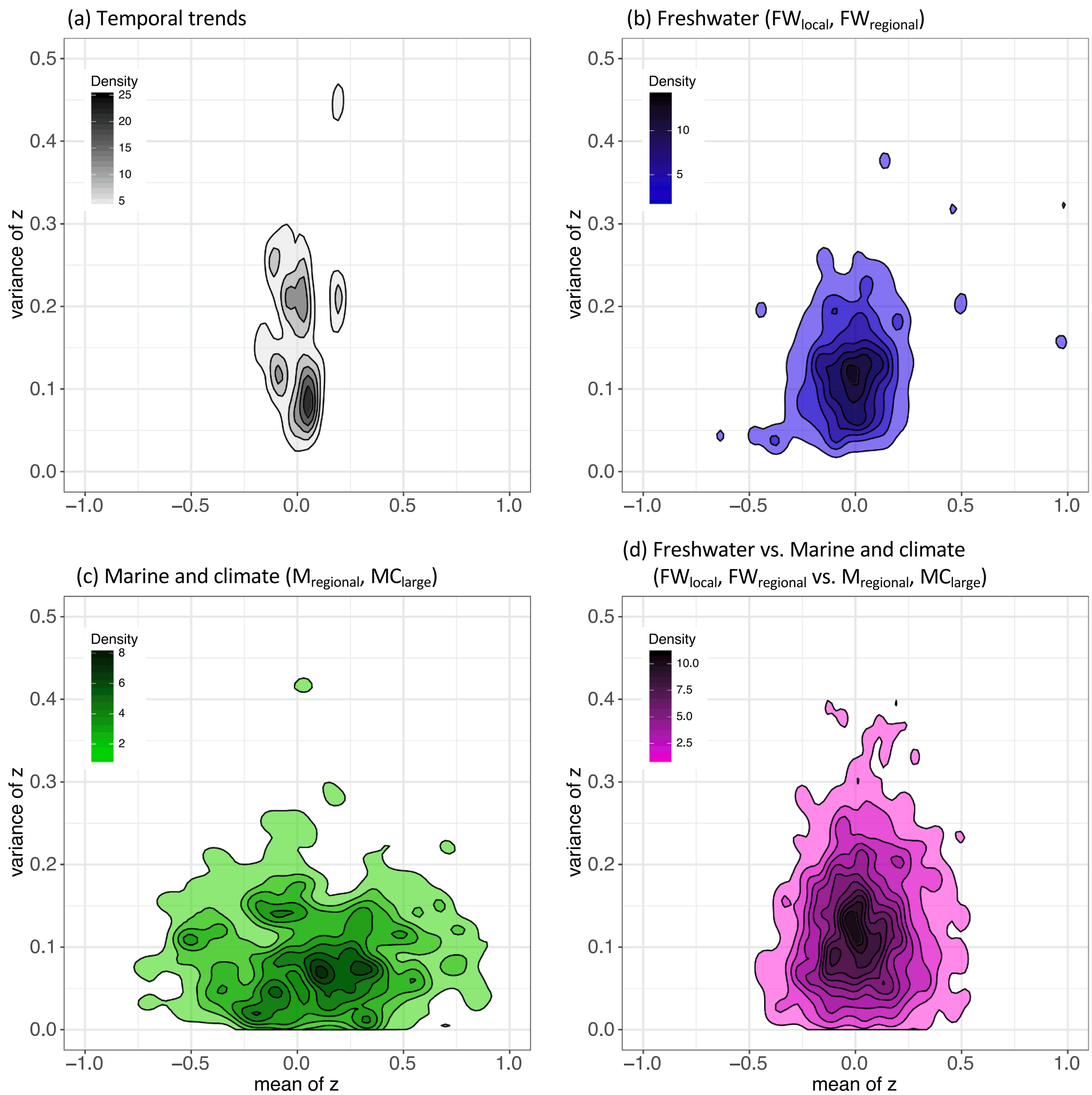

Fig. 8. Variance and mean of z (Fisher Z-transformation of *r* correlation coefficient) across the 10-year windows of data by environmental index types for all bivariate comparisons of the 44 indices (including year as an index) at all 72 sites. See Figures S6 and S7 in Supplementary Material, for correlations untransformed and for correlations using prewhitened data, respectively.

4. Discussion

The study of environmental indices in relation to migratory animal population indicators intersects multiple climatological and ecological perspectives. This aggregate set of processes can be challenging to account for in statistical models. Nonetheless, understanding the general patterns in correlations among freshwater, marine, and climate indices through time can help guide the choices we make when selecting specific indices to test against salmon population indicators and in interpreting results (Fig. 10). Our study showed that the correlation structure differed regionally (Fig. 10a), at certain periods of time (Fig. 10b), and by index type (Fig. 10ab).

We begin our discussion with two perspectives of how to interpret correlations across habitats and life stages. These perspectives can be important as we consider regional patterns of teleconnections, identify periods of stronger correlations, and become cognizant of the implications elicited by non-stationarity. A detailed account of correlations among freshwater, marine, and climate indices is particularly important in anadromous fishes. We thus delve into these details and then finish by discussing our study in context of improved data quality in the future.

4.1. Teleconnections and cross-life-stage effects

We can interpret the correlations among environmental indices in two different ways. In one perspective, the correlations represent how teleconnections setup the conditions that migratory salmon experience across habitats. In the other, the correlations represent the carryover (or cross-life-stage) and cumulative (or repeated) biological effects. Both perspectives can co-exist. Still, a salient difference is that the former is climate-centric and can represent multiple local conditions, while the latter is fish-centric and emphasizes biological effects.

The most prominent signs of teleconnections that we detected in our study were from the large-scale climate indices of Niño 3.4, ALPI and PDO. They were generally correlated with sea surface temperatures, total downwelling magnitude index and pre-conditioning coastal upwelling index. These large-scale indices influence the coastal conditions when Chinook and coho salmon migrate to sea in spring and summer. These large-scale indices also correlate with winter air temperature and

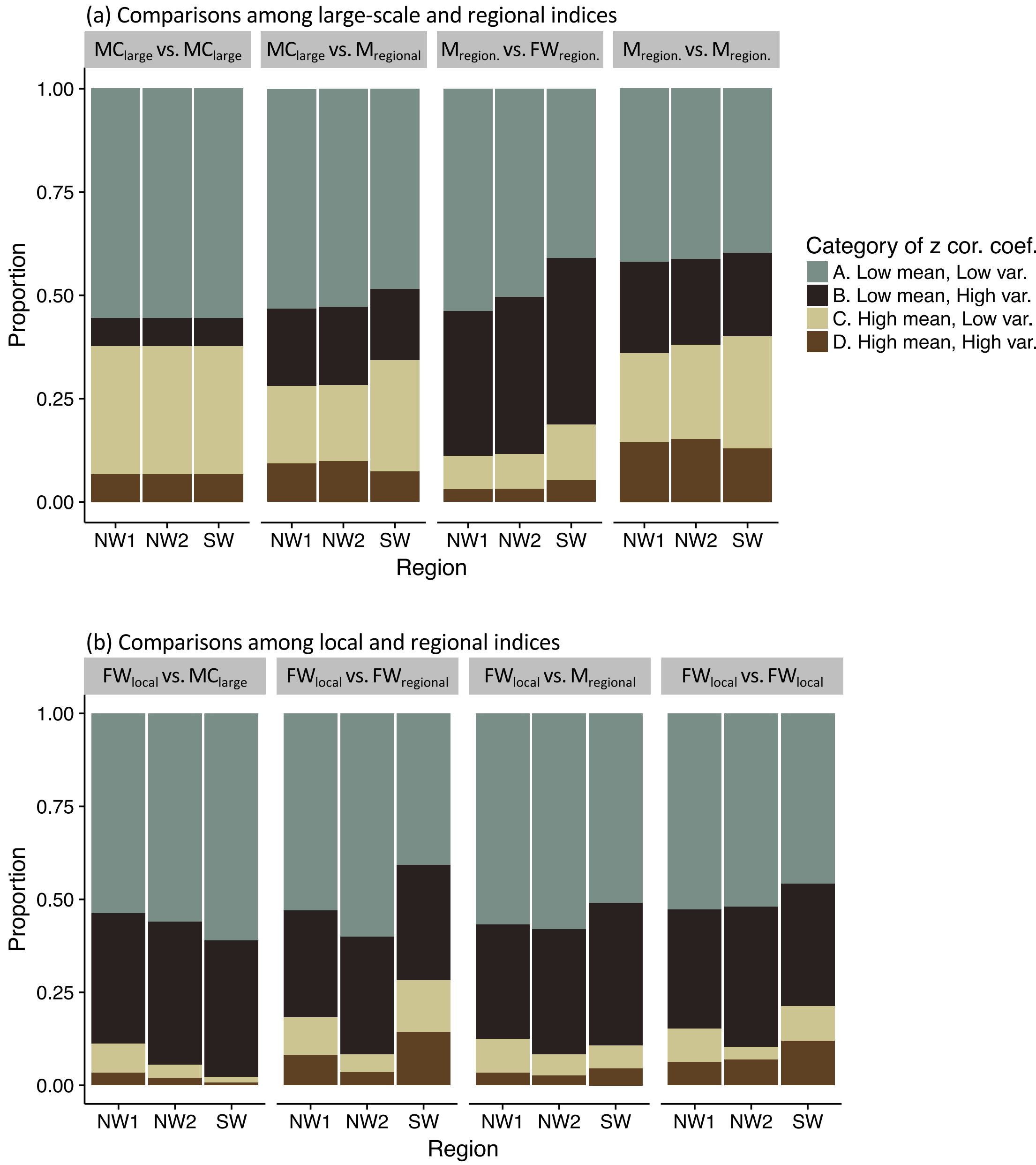

Fig. 9. Proportion of cases of index type comparisons in categories of high and low mean z and variance of z (see Table 2) across all sites within each of the NW1, NW2, and SW clusters of sites for (a) large-scale indices and (b) local-scale indices. Index types are: MC_{large} = climate, large-scale; $M_{regional}$ = marine, regional coast; $FW_{regional}$ = freshwater, regional-scale; FW_{local} = freshwater, local-scale.

spring flow in the freshwater environment. Thus, one large-scale index that exerts teleconnections to local conditions could be a good predictor of salmon responses through a large number of specific mechanisms.

In the second perspective, a biological emphasis is placed on carry-over and cumulative effects. The habitats salmon pass through sequentially are connected through physical processes, so fish can experience similar conditions across life stages. Correlations existed among winter-spring temperatures, spring-summer flows, and spring-summer sea surface temperatures. Thus, from the juvenile rearing habitat, through the downstream-migrating fish habitat, and into the early ocean environment, salmon experience similar conditions that may have compounding effects. Given the potential importance of cumulative effects, even if each of their single effects is small, these may have implications on predetermined high bars of variance explained between single environmental indices and population indicators (e.g., $R^2 > 0.5$ in stock assessments; Møller and Jennions, 2002; Satterthwaite et al., 2019). Factors with less variance explained in any one of the life stages can still be important when considered cumulatively and as a whole across multiple life stages.

This leads to questions of how we can explicitly characterize carry-over and cumulative effects and the appropriate lagging of indices. Given a particular research study, the spatial and temporal scales of the population indicator investigated can be used to infer the appropriate scales of environmental indices. We note that in our current study, we did not examine salmon population indicators. Even so, we found that correlations among indices lagged only a season or two were greater than those lagged a year. Thus, correlated seasonal indices will be important to consider when setting up analyses and interpreting results. For example, increased river temperatures near critical thresholds can strongly affect successful spawning by adults, incubation of salmon eggs, and development of juveniles (Beechie et al., 2013; Martin et al., 2017). Similarly, cross-seasonal warm conditions in both freshwater and

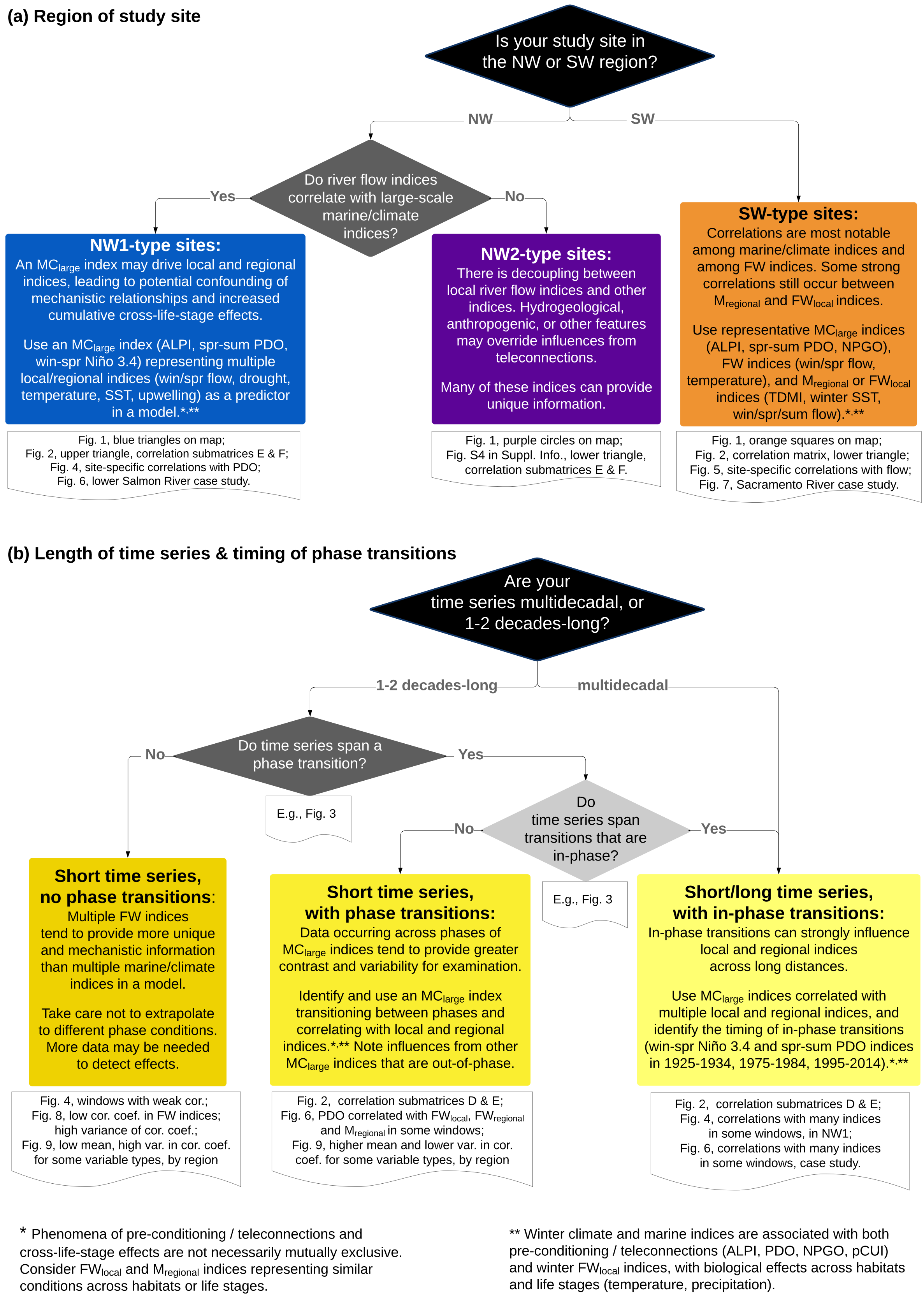

Fig. 10. Decision tree for choosing freshwater, marine, and climate indices as predictors to examine further for migratory species responses. The two main decisions are based on (a) region of study site and (b) length of time series and timing of phase transitions. MC_{large} = climate, large-scale; $M_{regional}$ = marine, regional coast; $FW_{regional}$ = freshwater, regional-scale; FW_{local} = freshwater, local-scale.

marine systems can result in a warm winter for eggs, warm and low flow conditions in the spring and summer for fry and parr, and low food resources from spring through fall for smolts entering the ocean. Other migratory species may experience similar stresses across life stages.

In particular, correlations with wintertime conditions can relate to both teleconnections and cross-life-stage biological effects. Our study findings support the importance of wintertime as a season linked to teleconnections and environmental conditions (Hamlet and Lettenmaier, 1999; Di Lorenzo et al., 2013; Tamaddun et al., 2017) that juvenile Chinook and coho salmon experience. The winter season indices of ALPI, PDO, NPGO, and pre-conditioning coastal upwelling index (Di Lorenzo et al., 2013; Schroeder et al., 2013; Heyer et al., 2017) setup conditions that the fishes experience in winter through summer as they rear in freshwater and migrate to marine environments. Winter temperatures and precipitation are also conditions salmon experience that correlate with other conditions in subsequent life stages, such as spring and summer flow and sea surface temperature indices. These environmental conditions can influence their growth, migration timing and survival in the freshwater and marine environments (Beer and Anderson, 2013; Munsch et al., 2019).

Determining whether the indices represent pre-conditioning processes and/or biological effects across life stages is important. This could change our expectations of how well large-scale and local indices predict salmon population indicators depending on whether indices maintain similar correlations in the future. If the indices are correlated and unchanging, we might be looking in the wrong place for mechanistic links. That is, they might still predict population responses, but the mechanistic basis might be mis-identified and mitigative actions would be ineffective. Furthermore, our choices and interpretations of indices will depend on how the correlations among indices are expected to change by region, site, length of time series, and specific years.

4.2. Spatial and temporal patterns of correlations

The major spatial patterns relevant to the correlations among environmental indices in our study appeared at the regional scale (i.e., Northwest/Southwest; Fig. 10a). These regional scales span approximately 600–1000 km, and likely represent teleconnections that include relationships between the El Niño-Southern Oscillation (ENSO) index and air temperature, precipitation, and floods (Ward et al., 2014; Heyer et al., 2017). Our study showed overall stronger correlations of winter and spring air temperature and river flow with marine/climate indices in the Northwest than the Southwest. In the Southwest, we did not detect strong correlations of flow and drought with climate indices. Freshwater-related indices do correlate with coastal conditions (Sagarika et al., 2015; Heyer et al., 2017), which we observed even in our case study of Sacramento River at Red Bluff Diversion Dam. Moreover, any clustering nested within these two regions did not appear to be driven at the scale of ocean polygons. Other studies have detected correlations among population-specific salmon survival in the marine environment that correspond to a smaller spatial scale of 350–450 km (Kilduff et al., 2014). We did detect two clusters of sites nested within the Northwest region, which appeared to be driven by relationships with local freshwater indices. Largely, the correlative patterns among the indices in our current study spanned Northwest/Southwest regions.

Stronger 10-year correlations among freshwater, marine, and climate indices tended to occur when PDO and ENSO indices were in-phase (Fig. 10b). The correlations across indices were particularly apparent when they were positively in-phase at one time and negatively in-phase at another time within the same 10-year window (Figs. 3–7). Thus, strong teleconnections that drive physical processes in a similar direction and with sufficient contrast of conditions within the time series appear to be needed for correlations across multiple environmental indices. Combined effects of PDO and ENSO, when they are in-phase or out-of-phase, have also been observed globally across the dry-wet scale of precipitation (Wang et al., 2014).

We did not always observe these same trends of higher correlations during the positive and negative in-phase occurrences (e.g. not observed in the 1985–1994 or 1995–2004 windows for some sites; Fig. 4), although this may be an artefact of when the 10-year windows were set. In additional analyses, when we shifted the beginning of the time windows by 5 years, we still found higher correlations matching periods of positive and negative in-phase occurrences (data not shown). Thus, statistical limitations given the length of the time series and when the data were collected can play an important role on conclusions.

In the marine environment, exceptions to higher correlations when climate indices are in-phase may also be due to local conditions such as local wind forcing. Fiedler and Mantua (2017) observed times of mismatches between sea surface temperature anomalies in the California Current System and the Niño-3.4 region. In the California Current System, local forcing can dominate in its northern extent, while remote forcing can be more important in its southern extent (Frischknecht et al., 2015).

It is important to note that there are many interwoven processes in the atmosphere and our predictions of environmental conditions cannot always depend on a few teleconnections. Other teleconnections such as the Pacific North American (PNA), West Pacific (WP) patterns, North-Atlantic Oscillation (NAO), and Eastern Atlantic (EA) exist; and the multiplicity of their influences can obscure any effects generally expected on ENSO patterns (Wise et al. 2015). The PNA can drive patterns of temperature and precipitation (Leathers et al., 1991). In a positive phase of the PNA, there is an enhanced Pacific Ocean jet and meridional flow that can propel dry west regional patterns, while its negative phase forces wetter conditions. A high subtropical phase of the Western Pacific can bring wet conditions into California, and its low subtropical phase can produce wet conditions in northern Rockies. Also, the North-Atlantic Oscillation can shape the patterns of snowmelt (Myoung et al., 2017). Thus, other teleconnections can weaken or strengthen correlations among environmental indices even when ENSO and PDO indices are in-phase.

4.3. Correlations among index types

4.3.1. Freshwater indices

In our study, the correlations among freshwater indices were generally weaker than those among marine and climate ones, and were thus capturing non-redundant information. Flow in particular had the potential of differentiating between a larger number of hypotheses than is possible in the marine environment. This seems to be the case even if we used a small number of flow indices compared to the hundreds available for hydrologic classification (Olden et al., 2012).

A few reoccurring correlations across sites were still detected in our study: winter or spring temperature with spring or summer flow; 1-day minimum flow with summer flow; 1-day maximum flow with fall flow; and coefficient of variation of flow with 1-d maximum flow. But as climate change progresses and affects the hydrologic timing of freshets and the variability of discharge, the correlations among specific flow indices are expected to change and in turn affect fish populations (Déry et al., 2012; Ward et al., 2015). As freshwater time series get longer, and as the climate continues to change, it will be important to identify and understand relationships among indices when selecting which ones to test against animal population indicators.

4.3.2. Marine and climate indices

Strong correlations occurred among marine/climate indices, likely because of ocean-atmospheric processes and strong local physical connections in ocean circulation. In our study, a number of the upwelling indices correlated with wintertime climate indices of ALPI and NPGO, but also with PDO and Niño 3.4 indices in other seasons. In the winter season, we also observed that coastal upwelling indices tended to be most strongly correlated with sea surface temperature indices. The correlations we detected likely reflect complex processes involving large-scale and local forcing. For example, in a separate study, a principal components analysis of monthly upwelling indices revealed winter and summer as dominant seasonal modes that respectively matched multi-decadal processes and high-frequency variability; these seasonal modes were associated with indices of growth and reproduction of different fish and bird species in the California Current Ecosystem (Black et al., 2011).

Longer-term changes in the phenology of coastal marine conditions can also occur. Years with El Niño conditions showed delayed and weak upwelling in the central California Current Ecosystem, while La Niña years showed the opposite (Bograd et al., 2009; Jacox et al., 2015). Also, there were later and shorter upwelling seasons (generally March through August) in northern stations compared to southern stations in the California Current Ecosystem.

In the last few decades, a fundamental change in correlation among some marine and climate indices occurred that involve PDO and NPGO indices (Sydeman et al., 2013; Litzow et al., 2018). Similar to these other studies, we detected a change from the 1985–94 to the 1995–2004 windows: the spring–summer PDO index was correlated to upwelling indices, but then changed to be correlated with NPGO. In relation to salmon survival, strong associations with upwelling were found in these earlier decades (Logerwell et al., 2003; Scheuerell and Williams, 2005), but stronger associations with NPGO were found in more recent decades (Kilduff et al., 2015). It is important to interpret relationships of salmon responses given the changing correlations among environmental indices because their variances are changing over time. In our study, the correlation between spring–summer PDO and the total upwelling magnitude along Washington coast stayed strong through the 1995–2004 window, but many of the other upwelling indices had nearly zero correlation (Fig. 6). The PDO index is in itself not a biological index that directly affects salmon responses; rather, it was correlated to biological and ecological processes such as metabolic rates, prey availability and predation risk historically (Mantua et al., 1997; Peterson et al., 2014). The PDO index could thus be regarded as a latent variable of ecological processes in these earlier decades. Increased importance of other indices to salmon, such as the NPGO index, may signal fundamental changes in relationships among marine and climate indices (Litzow et al., 2018). Changing relationships among the conditions that constitute climate indices are gaining greater awareness, especially in the context of indices that are primarily statistical or that are representative of environmental conditions driving ecological patterns (Litzow et al., 2020).

4.3.3. Freshwater vs. Marine and climate indices

In addition to the NW1 regional pattern driven by correlations between large-scale climate indices and local conditions, we found a divergence of the NW2 cluster of sites. The divergence was driven largely by the presence/absence of correlations between flow and other indices, and we suggest three explanations. First, dams can drastically alter river flows, and may have been involved in patterns at nine of the 14 sites in NW2. The sites with altered flow regulation at dams included the Upper Skagit River site downstream of Ross Dam, the McKenzie River site downstream of multiple dams on the river and its tributaries, the White Salmon River site downstream of Condit Dam until its removal in 2011, and the Trinity River site downstream of Trinity and Lewiston dams. Second, local patterns with finer-scale processes than those of teleconnections could relate to varied hydrogeology. The spatial heterogeneity within the Intermountain West (i.e., between the Cascade Range/Sierra Nevada and the Rocky Mountains) is characterized by diverse terrains and varied topography that can influence the expression of climatic processes occurring in the atmosphere and at the surface (Wise et al., 2015; Heyer et al., 2017). Particular small-scale controls on precipitation patterns include elevation and aspect. High-elevation sites tend to have more precipitation, while aspect influences the incoming direction of the air and hence precipitation. Thus, the large-scale ocean and atmospheric processes on climate in the region are further influenced by variations at the small scale. For example, weaker correlations between ENSO (or SST in the Niño 3.4 region) and precipitation in the Snake River Basin has been observed (Heyer et al., 2017). Although our case study of the lower Salmon River showed correlations between freshwater and marine/climate indices, these correlations were not apparent for the upper Salmon River site. Third, at the dam-free sites, noisy data may relate to processes we did not examine explicitly. For example, the south Umpqua River and the lower Sauk River had mean 10-year correlations between seasonal mean flows and spring–summer PDO nearing zero with variances > 0.2. Overall, even if we did not identify why there was a lack of correlation between freshwater and marine/climate indices, determining whether or not such correlations exist has implications on how they can be interpreted as indices of salmon responses.

4.3.4. As data quality improves

Determining which ecological processes are important to survival at different life stages and how they can be represented with existing data remains a challenge. Undoubtedly, we expect more and better quality environmental data to become available over time (e.g., improvements on remotely sensed satellite data and extended reconstructed sea surface temperature data). Yet, ecologists will still need to decide which indices best represent the ecological processes and which of these among the correlated ones to test against migratory animal population indicators. We could examine all indices of interest through separate models and then combine the predictions through techniques such as model averaging; however, there are limitations rooted in such statistical techniques (Banner and Higgs, 2017). Grounding our analyses with an understanding of biological and ecological processes will provide the needed realism.

As a case in point worth noting, our result of more unique information in freshwater than marine and climate indices does not necessarily equate proportionally to its importance. This result may reflect our limited knowledge of where salmon occur in the coastal and open ocean compared to the myriad of known freshwater habitats and microhabitats (Hurst, 2007). It may also be because of greater synchronization of physical processes in the ocean compared to those of rivers in a complex topography. Either way, it is important to at least uncover the correlation structure among indices to provide context on which ones may be unique or interchangeable for hypothesis testing.

4.4. Conclusion

Our paper provides an entryway to a wider perspective on the interrelatedness of freshwater, marine, and climate conditions. An understanding of these relationships will help investigators choose and use indices of migratory animal population indicators. One important relationship is how teleconnections explain Northwest/Southwest regional patterns of correlations among environmental indices (Fig. 10a). In the Northwest, large-scale marine/climate indices can summarize multiple local indices of temperature and flow. In the Southwest, the correlations that occur among marine/climate indices, among flow indices, and between coastal marine and flow indices are important to consider. Whether to select indices that are correlated or not for further investigation with animal responses will be an important decision. The context of a climate-centric (e.g., pre-conditioning of environment) and organism-centric (e.g., cross-life-stage effects) perspectives will be notable in decisions of which indices to select and how to interpret their potential influences on animal responses.

The more subtle nuances within clusters of sites and across diverse sites could be better understood by superimposing influences from multiple teleconnections (e.g., from Niño 3.4 and PDO indices), in-phase vs. out-of-phase phenomena, local hydrogeologic processes, and anthropogenic practices (Fig. 10b). Even within just the marine-climate correlations, understanding their changing relationships can be important to environmentally-based stock assessment of marine fish, such as groundfish and herring recruitment (Litzow and Mueter, 2014; Litzow et al., 2014). The frequent changes in correlations underscore the importance of long-term data sets and continued monitoring across habitats of migratory animals. Time series in ecology are often assumed to have a constant mean and variance for analysis. However, changes in correlations among multiple indices occur over time. Identifying periods of higher and weaker correlations will be important in making inferences regarding salmon population indicators across climate phases (i.e., periods when relevant climate indices are in-phase or out-of-phase, and their direction of change). As the climate continues to change, it becomes more evident that maintaining a mindset encompassing static processes limits our abilities to explain patterns among environmental indices. This recognition in the context of multiple climatic teleconnections will help foster the development and utility of more resilient methodological approaches that account for changing correlations.

CRediT authorship contribution statement

Jennifer L. Gosselin: Conceptualization, Methodology, Data curation, Formal analysis, Investigation, Visualization, Writing - original draft, Writing - review & editing. **Lisa G. Crozier:** Conceptualization, Funding acquisition, Methodology, Writing - review & editing, Project administration. **Brian J. Burke:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary materials

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107167.

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