Title: Quantifying changes in fish population stability using statistical early warnings of regime shifts

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Open data and code: This research is based on publicly available data cited in the manuscript text. Derived data products are available via the Environmental Data Initiative repository: `https://doi.org/10.6073/pasta/aa552e1f82f95a33c2ea657e3c0706e4`. Derived data products and code reproducing these results are available on Zenodo: `https://doi.org/10.5281/zenodo.14907908`.

Abstract

Ecological conservation and management benefits from tools that can foresee impending problems, or those in early stages. Statistical early warnings of regime shifts, which can identify generic changes in system behavior associated with stability loss and potential abrupt changes to a new, distinct state, are theoretically well grounded and have been successfully applied in real-world settings. However, early warning indicators have seldom been applied to empirical animal population data. We quantified early warning metrics in 29 fishes using > 4 decades of monitoring data from the San Francisco Estuary and Sacramento-San Joaquin river system to develop an index describing the magnitude of evidence of population stability loss and potential regime shifts, relative to other studied species. Spatial synchrony increased in over twice as many species as it decreased, but temporal variance and lag-1 autocorrelation showed no tendency to have increased across species species. A composite early warning indicator (EWI) index developed from these metrics identified higher-risk species (e.g., white croaker, tule perch) from lower-risk ones (e.g., northern anchovy, fathead minnow). The composite index was uncorrelated with long-term abundance trends or whether the species is native or non-native. We also developed an index of confidence in the composite EWI score; considering both the EWI score and confidence index simultaneously suggests possible responses for research and management. For high EWI score, high confidence species may be candidates for targeted research and interventions, while high EWI score, low confidence species may be candidates for enhanced monitoring to better constrain population dynamics. Despite concerns about attributing changes in EWI metrics to regime shifts in short time series, there appears to be value in applying generic EWIs to population time series of animals with generation times ≥ 1 year, and approaches like ours may be valuable when little is known about organism life history, and when applying a consistent protocol can facilitate comparison across many species.

Introduction

Species conservation and ecosystem management are resource limited, motivating creative ways to identify priorities for enhanced monitoring, management interventions, and scientific study. Prioritization schemes that can foresee impending problems, or those in early stages, can be especially valuable (Dietze et al., 2018; Scheffer et al., 2009), in part because interventions at these incipient stages tend to be less costly and more effective (Ellis et al., 2011; Mandel et al., 2010). Statistical early warnings of regime shifts quantify changes in the dynamics of a system that are associated with abrupt changes between system states (Kéfi et al., 2014; Dakos et al., 2008; Scheffer et al., 2009). Here, a regime shift is defined as an abrupt change to a new, distinct state–such as a shift from a clear-water to an algal bloom state in a lake–which is assumed to correspond to a shift from one dynamical basin of attraction to another. Early warning indicators include measures of variance, autocorrelation, and other distributional properties (Scheffer et al., 2009; Dakos et al., 2012; Kéfi et al., 2014; Seekell et al., 2011). Despite a robust body of theory on early warning indicators (EWIs; e.g., Scheffer et al., 2009; Kéfi et al., 2014; Dakos et al., 2012) and successful applications in anticipating regime shifts in real-world ecosystems (e.g., Pace et al., 2017; Wilkinson et al., 2018), EWIs have scarcely been applied to animal population data to evaluate potential regime shifts in population dynamics.

Well-developed theory on the stability of complex systems and regime shifts proposes that regime shifts may be preceded by general changes in system dynamics, including increased variance and autocorrelation (Dakos et al., 2012; Kéfi et al., 2014; Buelo et al., 2018; Nolting and Abbott, 2016; Patterson et al., 2021; Scheffer et al., 2009). The intuition behind these dynamical changes is often illustrated using a so-called "ball and cup diagram" representing a system's stability landscape (see, e.g., Figure 1 of Scheffer et al., 2009). A ball representing the system state sits in a depression in the stability landscape, representing an attractor. Modest perturbations (e.g., environmental variation) nudge the ball away from its attractor, causing the ball's position in the stability landscape to vary. As the system's stability erodes, an equivalent perturbation moves

the ball further from the attractor (i.e., increased variance). The ball also moves more slowly back toward the attractor, causing measurements of the system at successive times to become more similar to the previous one (i.e., increased autocorrelation). For spatially extended systems, increases in spatial variance and autocorrelation may also accompany loss of resilience as a regime shift is approached (Scheffer et al., 2009; Kéfi et al., 2014; Buelo et al., 2018). When a regime shift takes place, some perturbation 'kicks' the ball into a different basin of attraction. Empirical research in a range of settings has successfully applied EWIs to the prediction of regime shifts, even developing functioning regime shift alarm systems (Carpenter et al., 2011; Wilkinson et al., 2018) and demonstrating that early intervention triggered by an EWI-based alarm system can reverse an ecosystem regime shift (Pace et al., 2017).

To date, natural populations of animals are largely unexplored from the perspective of EWIs, and differences between animal populations and other applications of EWIs should make us cautious. One important difference is that many successful applications of EWIs in real-world systems feature much higher data density (e.g., hourly) on organisms like phytoplankton with rapid growth and generation times. By contrast, populations of animals that have generation times ≥ 1 year are often censused only once per year, and variation in higher-frequency (e.g., monthly) measurements may likely confound demographic change with organism phenology or behavior. As a result, it may take many decades to accumulate analogous data. With fewer observations and lower sampling resolution, we might expect EWI metrics to have greater sampling variation, and for shorter lags (in terms of number of observations) between changes in EWI metrics and a regime shift. Despite this, many of the same statistics used as EWIs (e.g., measures of temporal variance) are *also* ubiquitous metrics of stability in ecology (Donohue et al., 2016; Kéfi et al., 2014; Wang and Loreau, 2014; Schindler et al., 2015). Thus, it stands to reason that there is value to applying EWI metrics to animal population time series to investigate changes in population stability, even if specific connections to regime shifts are imprecise. Additionally, while the field has often been concerned about catastrophic regime shifts, EWIs can indicate more subtle

changes in regime (Kéfi et al., 2013); and while EWIs agnostic to the direction of change in the focal variable, whether an increase or decrease in the focal variable is harmful is context-dependent. For example, we may be concerned about population crashes (decreases) in native species, but about population booms (increases) in non-native ones.

We quantified temporal change in regime shift early warning indicator statistics (EWIs) in a suite of 31 fish species in central California, USA by leveraging long-term monitoring studies in the San Francisco Bay Estuary and Sacramento-San Joaquin river system spanning more than four decades. We developed a composite relative index of change in EWI/stability metrics and asked whether values of this index were associated with long-term population trends or native/non-native status. Additionally, we developed a confidence metric that takes into account differences among species in data quality and agreement across spatial units and metrics. Considering these two axes, composite EWI score and certainty, can facilitate prioritization of research and management action. For example, studying or (if known) managing drivers of population change could be logical steps for high EWI score/high confidence species, whereas improving monitoring may be needed for high EWI score/low confidence taxa.

Methods

Study system

The San Francisco Estuary and Sacramento and San Joaquin river systems form a large estuary and inland delta draining the Central Valley of California, USA. A region with a large human population and intensive agriculture, the system's geomorphology, hydrology, and biota are heavily altered by human activities. Dams and water diversions have altered the magnitude and timing of downstream flows (Hanak, 2011; Yarnell et al., 2015), and water control structures have restricted access to spawning and rearing habitats (Hanak, 2011; Moyle, 2002). Climate warming and changes in flows have jointly altered water temperature (Brown et al., 2013; Willis et al., 2021). Invasions of numerous aquatic organisms have altered habitat quality, primary production, and trophic and competitive interactions (Moyle, 2002; Moyle et al., 2011). Several

fish populations, especially those of native anadromous fishes, are in steep decline (Moyle et al., 2011), including including delta smelt, winter and spring run Chinook salmon (*Oncorhynchus tshawytscha*) and southern distinct population segment green sturgeon (*Acipenser medirostris*), each of which receive protections under state and federal Endangered Species Acts. Additionally, longfin smelt (*Spirinchus thaleichthys*) has undergone major population declines (Tobias et al., 2023) and is listed under the California and Federal Endangered Species Acts; and white sturgeon (*A. transmontanus*) became a formal candidate for listing under the California Endangered Species Act in 2024. These concerns and others have motivated multiple long-running, multi-location monitoring studies that can be leveraged to study the dynamics of target and non-target taxa (Stompe et al., 2020; Tempel et al., 2021; Colombano et al., 2022). However, many fish species remain understudied, leading to uncertainties concerning their population dynamics and responses to changing environmental conditions.

Data

We analyzed a suite of long-term fish monitoring data in Central California for potential early warnings of regime shifts. (Bashevkin et al., 2024) compiled data from 10 monitoring studies; we selected data from 3 studies (Table 1), focusing on those that have operated the longest and over the broadest geography, and conducted sampling in fall months (September-December). We used data spanning 1980 to 2023 because effort measures (e.g., sample volume) began becoming widely available in the selected monitoring studies in 1980. We combined fall fish sampling with determinations of age-0 maximum lengths thresholds based on expert knowledge and length-frequency analyses (Walter et al. *in review*) to quantify fall age-0 fish catch per unit effort (CPUE), except in cases where this was inconsistent with aspects of species life history, as detailed here. For white sturgeon, we used a threshold of 1000 mm, corresponding to an age of approximately 10 years; white sturgeon begin reaching reproductive maturity at $\approx 10-15$ years of age (Blackburn et al., 2019).

We focused on fall age-0 CPUE for two primary reasons: 1) the sampling gears used in these

Monitoring study	First year	Months	Method	Regions sampled
SFBS	1980	All	Midwater trawl, otter trawl	Central, Confluence, San Pablo, South Bay, Suisun
DJFMP	1976	All	Beach seine, midwater trawl	Central, Confluence, North Delta, San Pablo Bay, South Delta, Suisun, Sacramento River, San Joaquin River
FMWT	1967	Sep-Dec	Midwater trawl	Central, Confluence, Napa River, North Delta, San Pablo Bay, South Delta, Suisun

Table 1: Attributes of monitoring studies contributing data to this study. SFBS = San Francisco Bay Study. DJFMP = Delta Juvenile Fish Monitoring Program. FMWT = Fall Midwater Trawl Survey.

monitoring programs primarily select for small-bodied fishes, so excluding larger size classes, which are caught less reliably, reduces noise arising from sampling variation; 2) most studied species spawn in spring to early summer and must persist through relatively poor (e.g., low flow, supraoptimal water temperatures, low dissolved oxygen) conditions during summer and early fall before the wet season begins—as a result, fall age-0 abundances provide an index of recruitment. Point observations were aggregated by region-sampling method combinations and to an annual time step by averaging. Some sampling methods (e.g., midwater trawl) are used by multiple monitoring programs, with some differences in detailed sampling protocols, but preliminary analyses and earlier research (Walter et al. *in review*) showed good agreement between samples using the same method, but greater variability between methods. The different sampling methods

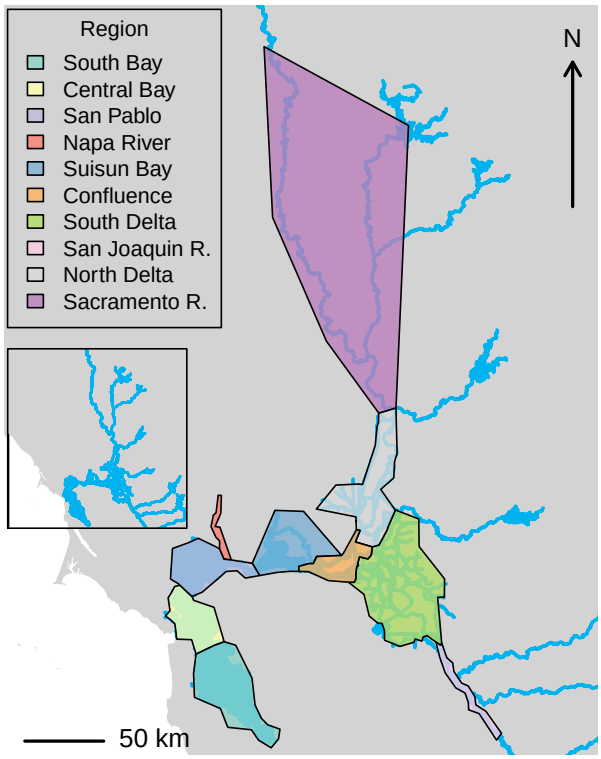

Figure 1: Map of study area and and analysis regions.

contributing to this study (midwater trawl, beach seine) sample different habitats (pelagic, benthic, and littoral, respectively), and monitoring locations span different regions with characteristic environmental conditions and fish communities (Figure 1) so we considered each region-sampling method combination a spatial unit. All fishing gears have selectivity biases related to fish size and portion of the water column sampled (Zale et al., 2012; Mitchell et al., 2017), making it difficult to simply combine catch information across surveys. We collated data on 39 candidate species, focusing on a subset of relatively commonly sampled and relatively abundant species, as well as those identified by wildlife and natural resource agency partners as species of interest, though some species were later discarded for having insufficient data for our analyses, resulting in a total of 29 species (Table S1).

Analyses

We focused on three early warning indicator (EWI) statistics: the temporal coefficient of variation (CV), the lag-1 temporal autocorrelation, and spatial synchrony. The temporal CV and lag-1 temporal autocorrelation were computed for each region-gear type combination in moving temporal windows so that we could quantify temporal trends in each. The moving window width was 5 years. As a robustness check, we also computed results using a window width of 7 years. EWI statistics were not computed in windows having > 1 year of missing data. Spatial synchrony was calculated using the same moving temporal windows by taking the mean of Pearson rank correlations between all pairs of spatial units having > 1 year of missing data during the window. Windows in which < 3 spatial units lacked sufficient data were ignored. We also considered unreliable and discarded EWI statistic measures that were more than than 3.5 standard deviations above or below the mean.

Temporal trends in EWI statistics for each species-by-spatial unit combination (temporal CV, lag-1 autocorrelation) or each species (spatial synchrony) were computed using ordinary least squares (OLS) linear regression. Although temporal autocorrelation is a concern for evaluating statistical significance when present, OLS regression provides unbiased estimates of regression parameters even for correlated data, and in this study we did not seek to determine whether trends were statistically significant. To ignore potentially spurious trends supported by few data points, we computed EWI trends only when there were at least 5 EWI measurements spanning no fewer than 10 years. EWI trends were represented by their t-statistic, i.e., the regression parameter describing the linear relationship between the EWI statistic and year divided by its standard error. Thus, we give the largest values to high-magnitude (increasing or decreasing) trends that also have high precision in their estimates (i.e., low variability around the trend). Assigning higher weight to more precisely estimated trends helps to reflect uncertainty that can arise from measurement error or stochasticity. Due to differences in true population size and sampling efficiency, we expected uncertainty to differ among species.

We developed an index describing the relative evidence of EWIs for each species by scaling and aggregating the spatial synchrony, temporal CV, and temporal autocorrelation components as follows. As spatial synchrony is already a single value for each species, it was simply rescaled on an interval from 0 (minimum relative risk) to 1 (highest relative risk). Because the temporal CV and temporal autocorrelation components were computed by spatial unit, we first aggregated among spatial units by averaging, and then rescaled to the 0-1 interval. A combined risk index was computed by averaging across the aggregated and rescaled component indices, and again rescaling to the 0-1 interval. Our aggregation and rescaling procedures effectively assign equal weight to all spatial units and component EWI metrics.

To investigate whether the EWI score was associated with long-term fish population trends, we examined the Pearson correlation between EWI scores and fish population trends. Fish population trends were quantitatively estimated using mixed effects linear regression with the natural logarithm of CPUE as the response variable, year as a fixed effect, and spatial unit as a random effect on the intercept. Linear mixed effects models were fit using the 'lme4' R package (Bates et al., 2015). To investigate whether the EWI score was associated with native/non-native status, we used analysis of variance in the 'stats' R package (R Core Team, 2024).

We also developed an index describing confidence in the relative risk index that takes into account agreement across EWI statistics, invariability among spatial units, and the number of sampling units contributing to the EWI metrics. We assumed that the species for which we could make the most confident assessment were those for which the EWI statistic trends agreed on their sign, for which variability among spatial units in EWI trends is lowest, and for which the EWI estimates were derived from a large number of samples. The confidence score had four components: the base-10 logarithm of total number of sampling events in which a species was detected (i.e., non-zero catch); -1 times the standard deviation (SD) of lag-1 autocorrelation trends (t-values); -1 times the SD of temporal CV trends (t-values), and the number of EWI trends components having the same sign. The SDs of lag-1 autocorrelation trends and temporal CV

trends were multiplied by -1 so that larger values would correspond to less variability across spatial units. As above, for the lag-1 autocorrelation trends and the temporal CV trends, t-values for distinct spatial units were averaged to yield one representative metric for each species. Also similar to above, the confidence score components were first rescaled to the 0-1 interval, the components were averaged to produce a combined metric, and this combined metric was again rescaled to the 0-1 interval so that 1 corresponds to the species with the highest confidence score and 0 to the species with the lowest.

Results

Inspection of select EWI time series provides examples in which EWI statistics increased or were elevated corresponding with apparent fish population regime shifts (Figure 2). Delta smelt and striped bass are two species known to have exhibited concerning abundance declines across the study area over recent decades (Moyle et al., 2016; Colombano et al., 2022). Delta smelt, an endangered species, saw its abundances in South the delta confluence region decline substantially, particularly after $\approx$ 2000; over that same period, the lag-1 temporal autocorrelation also increased (Figure 2a). Striped bass, a long-established non-native game fish, was sampled at higher abundances in the delta confluence during the first $\approx$ 10 years of the time series but was uncommon thereafter; the temporal CV was elevated at the beginning of the time series, declining substantially around the time of population collapse (Figure 2b). Because of a known population collapse in striped bass (Stevens et al., 1985), this pattern was interpreted as being already elevated in the earliest years of our time series because of stability loss and potential regime shifts realized early in the 1980-2023 study period. Mississippi silverside is an invasive forage fish introduced to California in 1967 that has quickly expanded its range (Cook Jr and Moore, 1970; Mahardja et al., 2016); its spatial synchrony rose quickly as population abundances began to increase and has subsequently declined, possibly signaling a transition to a new, high-density population regime (Figure 2c).

We focus in the main text on aggregated and relativized metrics, as the central goal of this

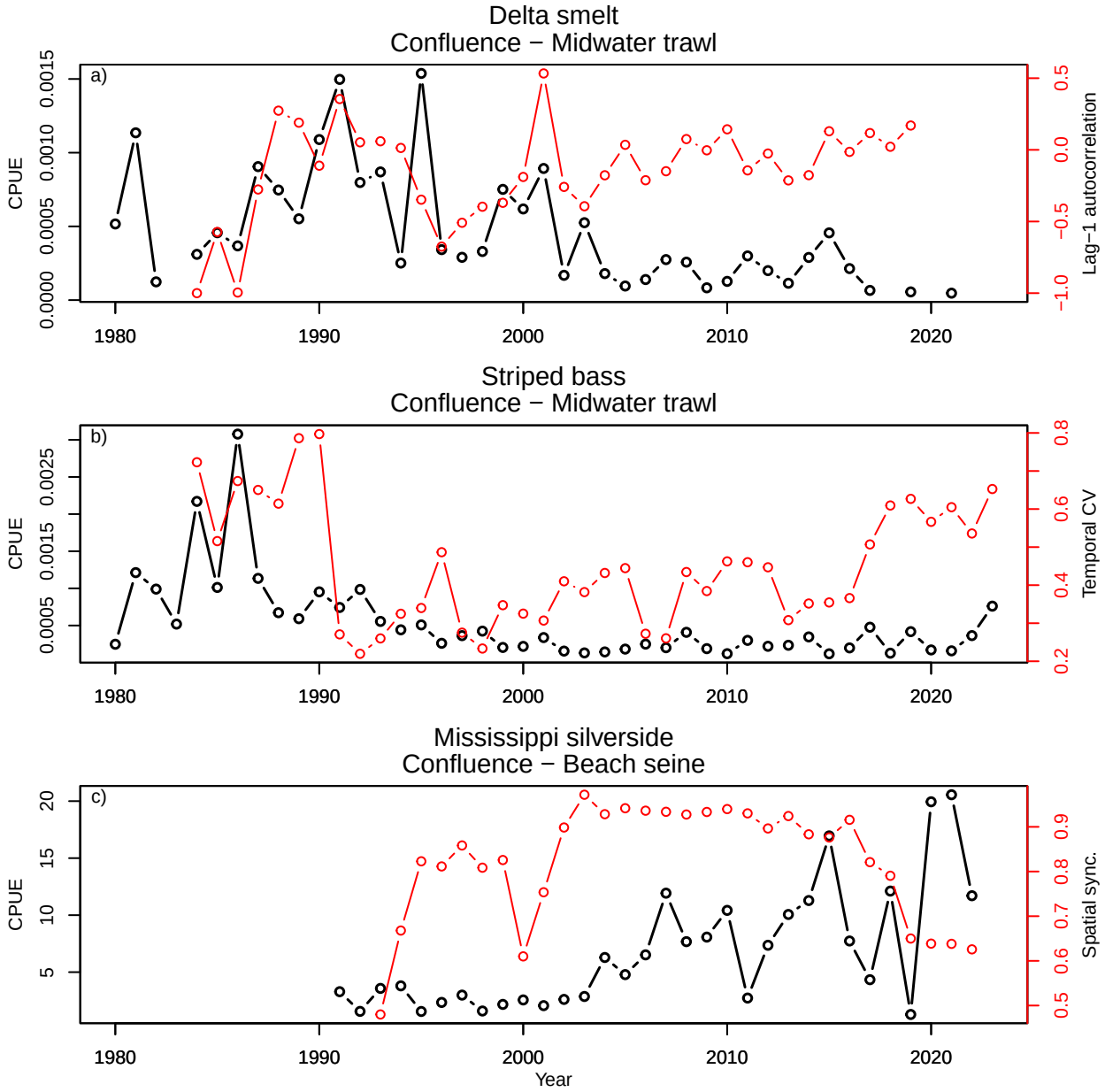

Figure 2: Selected examples of fish population time series (black) and EWI statistics (red). The scale of CPUE differs by sampling method because of different effort measures.

study was to develop a relative index of change in EWIs/stability at the species level for our study region; trends in the component metrics for individual species-spatial unit combinations are shown in Supplementary Material Figures S.1-S.3. For context, we provide a brief summary here. The median t-value for trends in temporal CV, across all species and spatial units, was -0.08. After aggregating (averaging) by species, the median t-value was -0.34. The median t-value for trends in lag-1 autocorrelation, across all species and spatial units, was -0.20. After aggregating (averaging) by species, the median t-value was -0.11. The median t-value for trends in spatial synchrony across all species was 1.01; although there was a slight tendency for temporal variance and autocorrelation to have decreased over time, there was a larger-magnitude tendency for spatial synchrony to have increased in more species than it declined.

Composite relative EWI scores varied among fishes (Figure 3). Species with the highest EWI scores, corresponding to the greatest loss of population stability compared to the set of studied species, include white croaker, bay pipefish, and tule perch. Species with the lowest risk included northern anchovy, white catfish, and fathead minnow. Species' EWI score components (i.e., EWI metric trend t-statistics, averaged by species and rescaled) were modestly negatively correlated to weakly positively correlated with each other. The Pearson correlation between the spatial synchrony and temporal CV components was -0.04; the Pearson correlation between the trends in spatial synchrony and in lag-1 autocorrelation was 0.32; and the Pearson correlation between the trends in temporal CV and lag-1 autocorrelation was -0.26. EWI scores were uncorrelated with long-term abundance trends (Pearson correlation = 0.11, $p = 0.58$). EWI scores also did not differ between native and non-native species ($F = 0.55$; $df = 1, 27$; $p = 0.47$).

Relative confidence also varied substantially among fishes (Figure 4). Fishes with the highest relative confidence included American shad and northern anchovy; fishes with the lowest confidence included bay pipefish, Pacific pompano, and channel catfish.

Considering the relative EWI and confidence scores together facilitates categorization of species with, for example, relatively high EWI score and high confidence versus relatively high

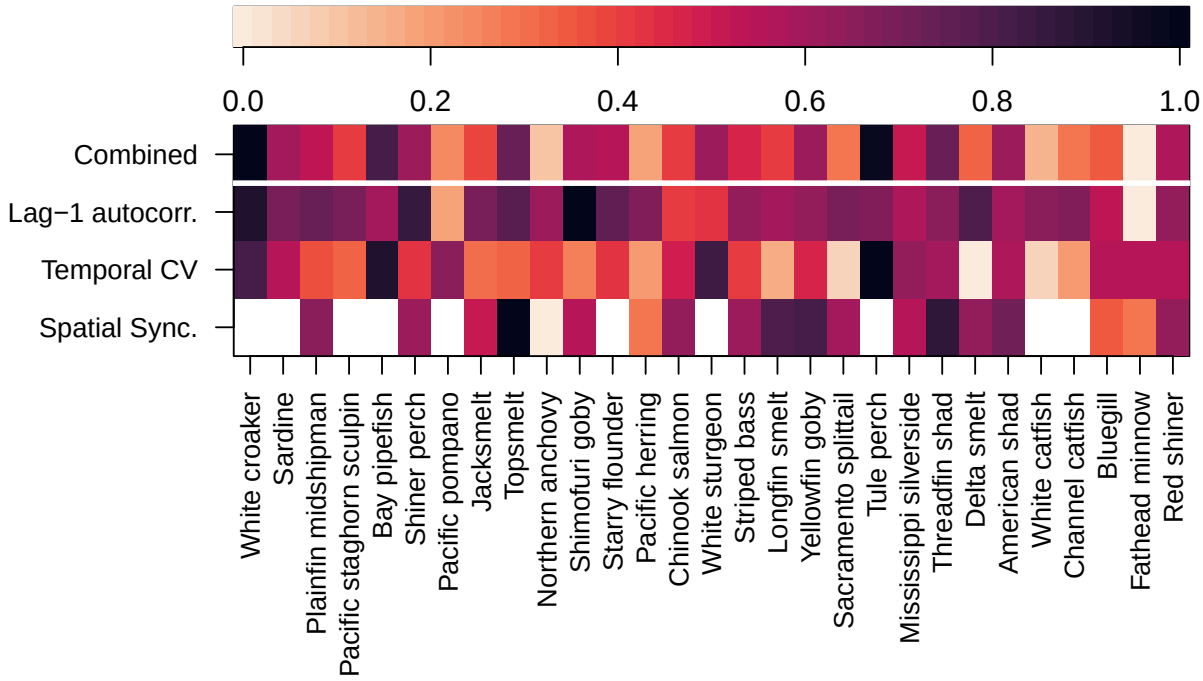

Figure 3: Relative risk of fish population regime shifts based on EWI statistics. The lower 3 rows show relative risk from three component metrics developed by rescaling long-term trends (t-values) to the 0-1 interval. The top row shows the combined (averaged) statistic. Note that several species were not consistently observed in ≥ 3 regions and so the spatial synchrony component was not included.

EWI score but low confidence. The species' EWI and confidence scores were not correlated (Pearson correlation = -0.005, p = 0.98).

As a robustness check, we also computed results using a window width of 7 years; the EWI scores and confidence metrics were largely similar regardless of window width (Figures S.4-S.8). As for the results with a window width of 5 years, the species EWI and confidence scores were not significantly correlated (Pearson correlation = 0.17, p = 0.37). However, there were modest changes to how species were categorized into quadrants of the EWI score-confidence plot (Figure S.9). For example, delta smelt, chinook salmon, and striped bass were in quadrant I (high risk, high confidence) when using a window width of 7 years. These differences were present despite strong numerical similarities between the scores computed with 5 versus 7 years, highlighting

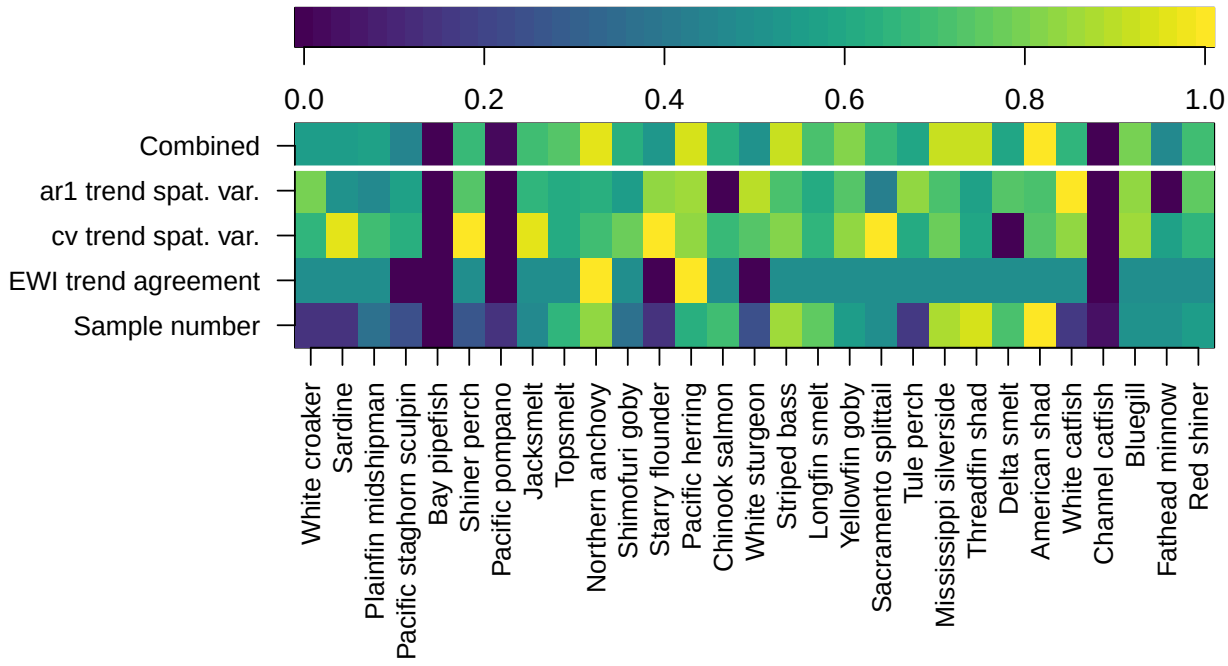

Figure 4: Relative confidence in EWI-based risk assessment. We considered confidence in the EWI score to be highest when the metrics were based on a large number of samples, when the direction of trends in EWI metrics agreed, and when there was less spatial variability in the trends in lag-1 autocorrelation and temporal cv. Note that for the purposes of this metric, the spatial variability in EWI trends have been rescaled so that 1 corresponds to the lowest variability (highest confidence) and 0 corresponds to the greatest variability (lowest confidence).

limitations of discrete categorization based on simple thresholds.

Discussion

Directional trends in metrics of stability that also serve as statistical early warnings of regime shifts varied widely among fishes in central California, USA, highlighting species exhibiting loss of stability potentially heralding a nearing regime shift (e.g., white croaker, tule perch, Pacific lamprey), as well as others that may have gained population stability over the study period (e.g., northern anchovy, fathead minnow). Across species, there was no systematic tendency for temporal variance or autocorrelation to have increased, but spatial synchrony increased on average. Composite EWI scores, which took into account changes in all three EWI metrics, were unrelated to long-term population trends or to whether the species is native or non-native. Despite

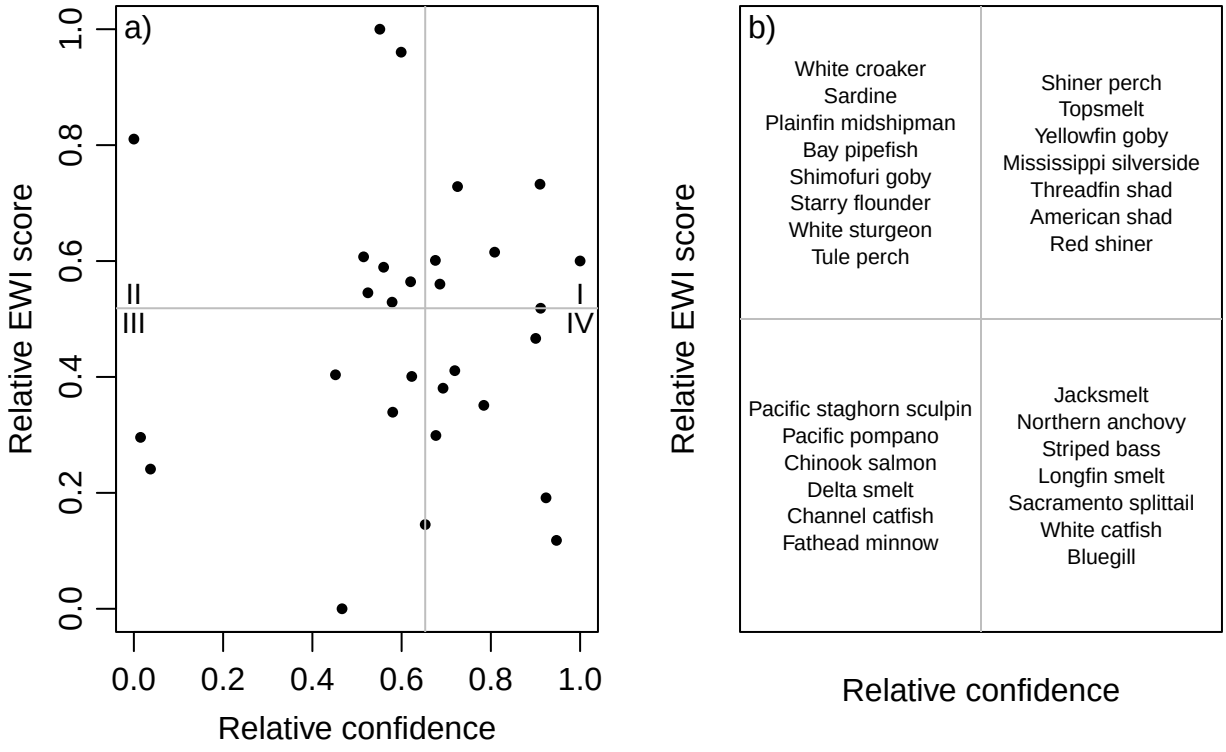

Figure 5: Relative EWI score versus confidence. a) scatterplot of index values; b) names of species in each quadrant of the scatterplot, where quadrant boundaries are defined by the median of each axis.

this, the potential for population regime shifts in declining native species like white sturgeon should be highly concerning for conservation and fishery management, as well as in non-native species like Mississippi silverside that may transition to a new, high-density regime. Additionally, the lack of correlation between long-term population trends and EWI scores corroborates that EWI measures provide information on stability that is largely orthogonal to long-term abundance trends, as expected. In other words, measures of stability can provide an additional dimension of information to support decision-making in conservation and natural resource management.

In synthesizing across 29 species using data from multiple monitoring programs, we encountered varying degrees of uncertainty. A primary way we sought to take this into account was to develop a metric of certainty that took into account agreement across spatial units and EWI metrics, as well as how more data generally leads to greater precision and a higher signal-to-noise

ratio. Simultaneous consideration of the composite EWI scores and the certainty metric can aid decision-making. We propose that the quadrants of Figure 5 can be translated into general recommendations for research and management, though we emphasize that other sources of information should also be used to identify at-risk species and to prioritize research and management efforts. This analysis supports that those in quadrant 1 (high risk, high confidence) be investigated for drivers of population dynamics, to determine whether changes to environmental conditions are having negative consequences, and to ascertain possible population management strategies. Those in quadrant II (high risk, low confidence) should be candidates for additional monitoring to help constrain population variability and temporal dynamics. Those in quadrant III (low risk, low confidence) are also candidates for strengthened monitoring, but may be of lower priority than those in the quadrant II. Those in quadrant IV (low risk, high confidence) would not be prioritized for additional monitoring or research based on these criteria, but may still be high priority based on different criteria.

Although we found no systematic association between long-term population trends and the EWI score, we found it notable that four species whose populations have been described as having collapsed (striped bass, Chinook salmon, delta smelt, longfin smelt) had relatively low EWI scores, often with relatively high confidence (Figure 5). While it's not fully known whether the severe and rapid declines of these species precisely fulfill the dynamical assumptions underpinning theory on EWIs, they seem reasonably described as regime shifts in the broad sense. Why, then, in our study have they scored relatively low for evidence of EWIs and loss of stability? A likely explanation is timing: the roots of these population collapses generally began prior to the beginning of our study in 1980 and had already manifest by the middle of the study period. For example, historical surveys suggest that prior to 1980, the first year of this study, delta smelt abundances were markedly higher on average than after (Moyle et al., 2016). In other studies of early warnings of regime shifts, early warning indicators often returned toward normal following the regime shift (Buelo et al., 2018, 2022), so we do not expect EWIs to remain elevated

throughout the time series if the population in in a new, low-density regime. Since a primary goal of our approach was to identify species showing current evidence of loss of stability and potential for regime shifts, not to describe regime shifts in the distant past, we consider this characteristic of our results a feature, not a bug. However, this characteristic highlights the importance of temporal frame for understanding ecological trends (Bahlai et al., 2021; Wilkinson et al., 2020).

While there was no tendency across species for temporal variance and autocorrelation to have increased through time (i.e., median t-statistics near zero), more than twice as many species exhibited increases in spatial synchrony (13) as decreases (6). In addition to its role as a generic EWI, spatially synchronous metapopulations are thought to be more prone to extinction (Heino et al., 1997), and spatial synchrony is closely related to the stability of total region-wide abundances because the synchronous components of local fluctuations reinforce each other in the regional total, whereas the asynchronous ones tend to cancel out (Anderson et al., 2021). Note that we quantified changes in temporal variance in local spatial units, not in region-wide totals, so these findings are not in conflict. This finding contributes to an emerging consensus that spatial synchrony in biotic variables (e.g., population size, carbon assimilation) has recently risen in many systems, likely as a result of climate change (Reuman et al., 2024; Hansen et al., 2020).

Above, we asserted that applying EWIs to annual-interval animal population time series was valuable, particularly considering that change in EWIs corresponds to change in stability even if a tipping point is not near, but that caution was warranted. Selected examples documented change in EWIs that were consistent with apparent regime shifts, such as marked population declines (Figure 2), offering some support. However, rarely did we detect unambiguous increases in the EWIs that were unambiguously *prior to* some apparent state change; the most prominent of these was for Mississippi silverside, where spatial synchrony rose markedly prior to apparent population booms in multiple spatial units (e.g., Figure 2c). Considering this evidence, it seems that EWI metrics may be unable to consistently and reliably provide early warnings when time series are short. Future studies might quantify how time series length and moving window width

affect the reliability of EWIs using appropriately realistic simulation models. We remain cautiously optimistic about the value of using generic statistical indicators of stability and regime shifts to animal population time series. They are simple empirical tools that provide information on a dimension of population health beyond long-term trends in mean abundance. While expectations concerning their behavior were first explored through simple theoretical models, the statistics themselves assume little about the dynamics of the underlying system; alternatives like population viability analysis (PVA; Morris and Doak, 2002) make projections that may be more sensitive to underlying model assumptions and structures, though we are not aware of research directly addressing this question. Other methods for reconstructing the stability of empirical (Carpenter et al., 2022) and modeled (Nolting and Abbott, 2016) populations can yield much more detailed and sophisticated insights, but are correspondingly more data hungry and reliant on model assumptions, limiting their potential applications. Approaches like ours could be especially valuable in cases where little is known about organism life history to aid in model design, or when applying a simple and consistent protocol can facilitate comparison across many species.

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Supplementary Information to: Quantifying changes in fish population stability using statistical early warnings of regime shifts

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Species	**Habitat**	**Family**	**Native**
White croaker *Genyonemus lineatus*	Marine, Benthopelagic	Sciaenidae	Yes
Sardine *Sardinops sagax*	Marine, Pelagic	Alosidae	Yes
Plainfin midshipman *Porichthys notatus*	Marine, brackish, Demersal	Batrachoididae	Yes
Pacific staghorn sculpin *Leptocottus armatus*	Marine, brackish Demersal	Cottidae	Yes
Bay pipefish *Syngnathus leptorhynchus*	Marine, brackish, Demersal	Syngnathidae	Yes
Shiner perch *Cymatogaster aggregata*	Marine, brackish Benthopelagic	Embiotocidae	Yes
Pacific pompano *Peprilus simillimus*	Marine, brackish Benthopelagic	Stromateidae	Yes
Jacksmelt *Atherinopsis californiensis*	Marine, brackish Pelagic	Atherinopsidae	Yes
Topsmelt *Atherinops affinis*	Marine, brackish, Pelagic	Atherinopsidae	Yes
Northern anchovy *Engraulis mordax*	Marine, brackish Pelagic	Engraulidae	Yes
Shimofuri goby *Tridentiger bifasciatus*	Marine, brackish, Demersal	Oxudercidae	No
Starry flounder *Platilichthys stellatus*	Marine, brackish, fresh, Demersal	Pleuronectidae	Yes

Pacific herring *Clupea pallasii*	Marine, brackish Benthopelagic	Clupeidae	Yes
Chinook salmon *Oncorhynchus tshawytscha*	Marine, brackish, fresh, Benthopelagic	Salmonidae	Yes
White sturgeon *Acipenser transmontanus*	Marine, brackish, fresh, Demersal	Acipenseridae	Yes
Striped bass *Morone saxatilis*	Marine, brackish, fresh, Benthopelagic	Moronidae	No
Longfin smelt *Spirinchus thaleichthys*	Marine, brackish, fresh Benthopelagic	Osmeridae	Yes
Yellowfin goby *Acanthogobius flavimanus*	Brackish, Demersal	Oxudercidae	No
Sacramento splittail *Pogonichthys macrolepidotus*	Brackish, freshwater, Benthopelagic	Cyprinidae	Yes
Tule perch *Hysterocarpus traskii*	Brackish, freshwater, Benthopelagic	Embiotocidae	Yes
Mississippi silverside *Menidia audens*	Brackish, fresh, Pelagic	Atherinidae	No
Threadfin shad *Dorosoma petenense*	Brackish, freshwater, Pelagic	Dorosomatidae	No
Delta smelt *Hypomesus transpacificus*	Brackish, freshwater, Pelagic	Osmeridae	Yes
American shad *Alosa sapidissima*	Brackish, freshwater, Pelagic	Alosidae	No
White catfish *Ameiurus catus*	Freshwater Demersal	Ictaluridae	No
Channel catfish *Ictalurus punctatus*	Freshwater, Demersal	Ictaluridae	No
Bluegill *Lepomis macrochirus*	Freshwater, Benthopelagic	Centarchidae	No
Fathead minnow *Pimephales promelas*	Freshwater, Demersal	Cyprinidae	No
Red shiner *Cyprinella lutrensis*	Freshwater, Benthopelagic	Cyprinidae	No

Table S.1: Attributes of fish species used in this study. Information is from Fishbase and expert knowledge.

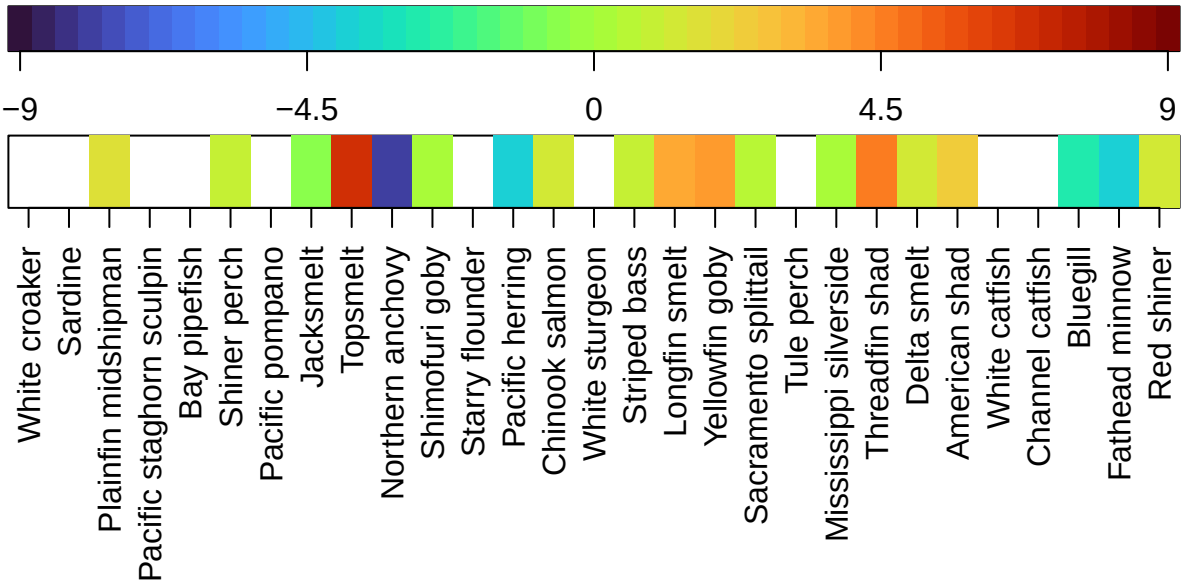

Figure S.1: Temporal trends (t-values) in spatial synchrony of fall age-0 CPUE by species. Blank cells indicate that insufficient data were available to compute the trend in spatial CV, e.g., because the species was not consistently caught by multiple region-gear type combinations.

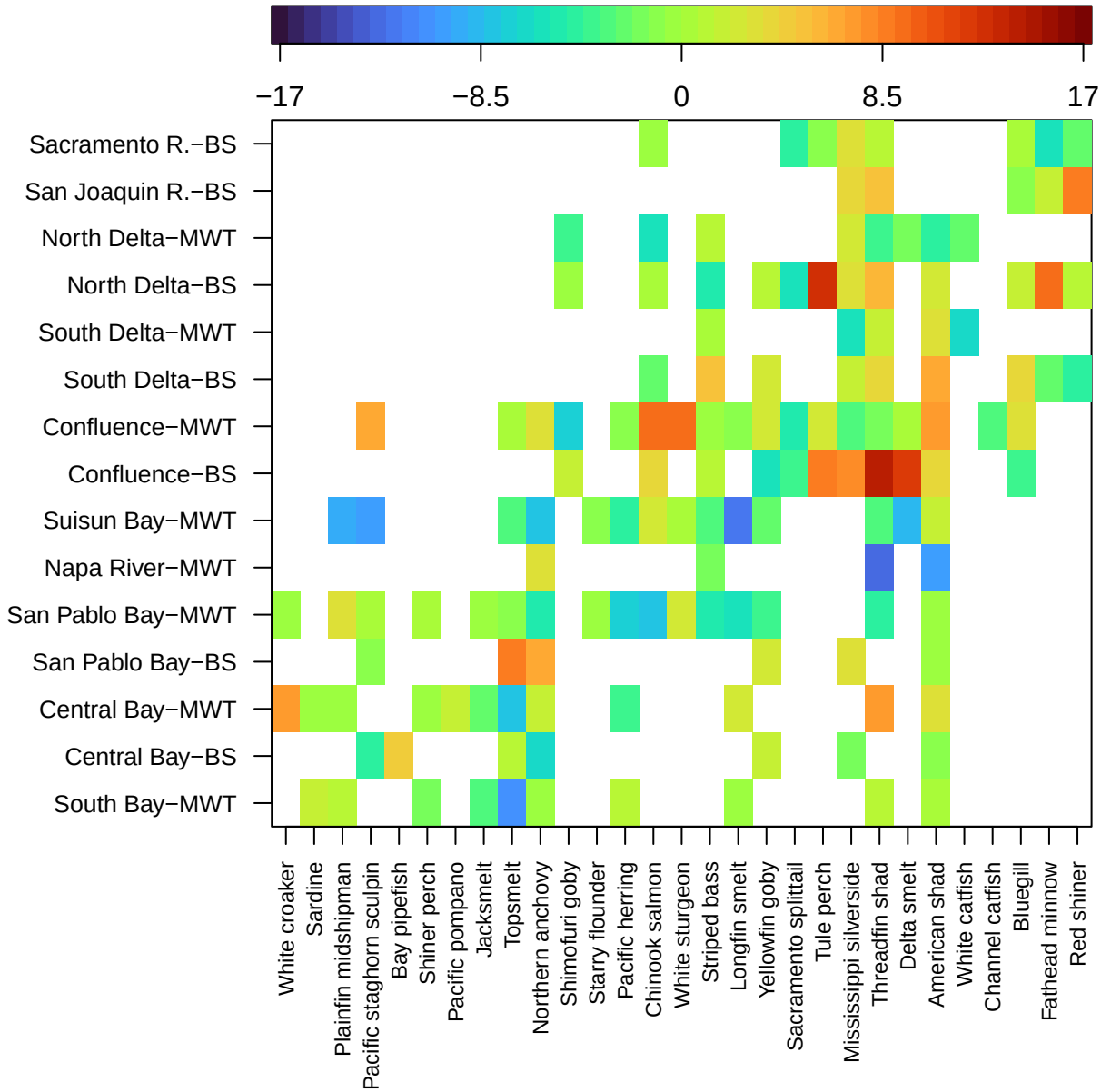

Figure S.2: Temporal trends (t-values) in the temporal coefficient of variation (CV) of fall age-0 CPUE by species and region-gear type combination. Blank cells indicate that insufficient data were available to compute the trend in temporal CV.

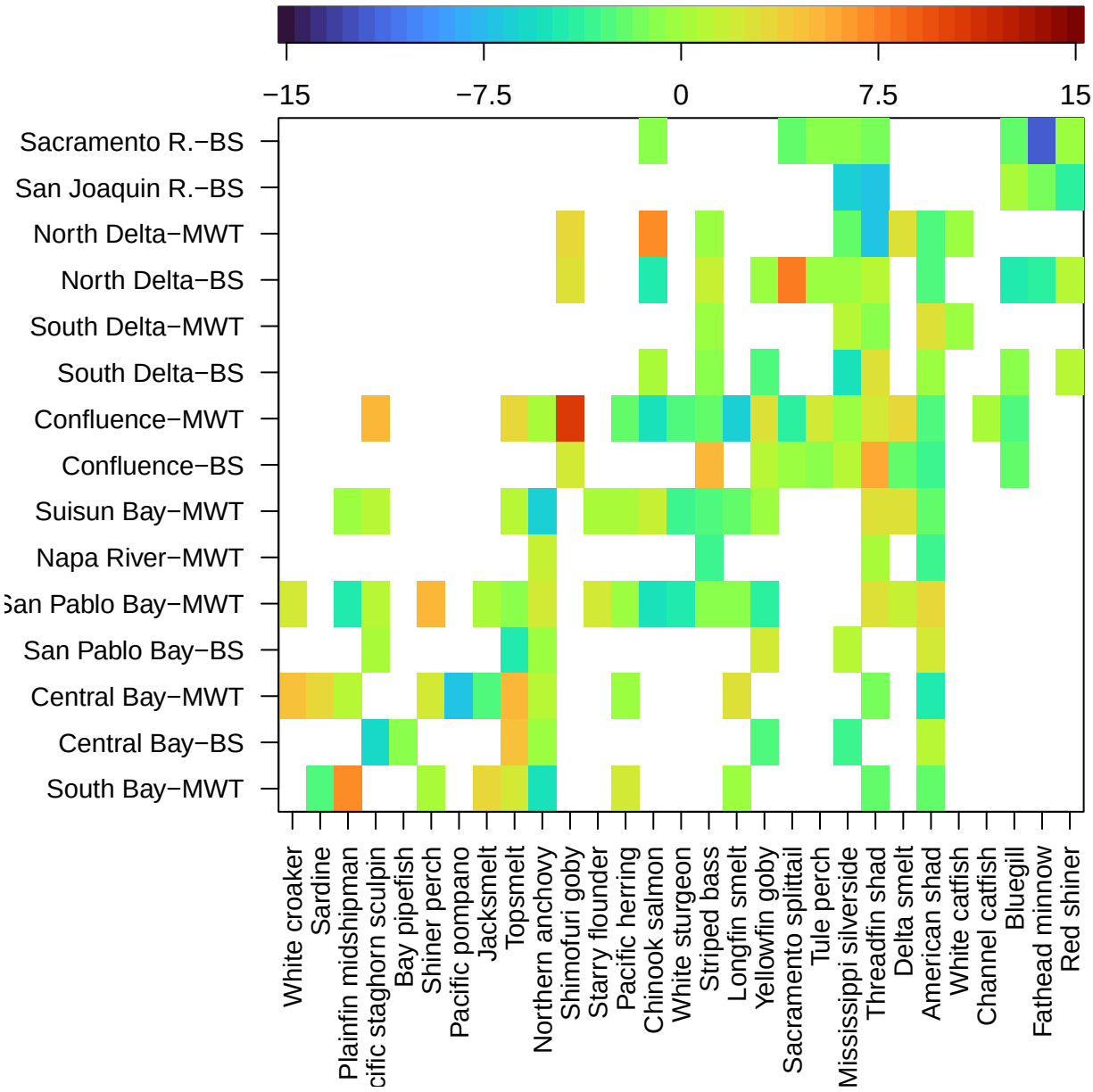

Figure S.3: Temporal trends (t-values) in the lag-1 temporal autocorrelation of fall age-0 CPUE by species and region-gear type combination. Blank cells indicate that insufficient data were available to compute the trend in lag-1 autocorrelation.

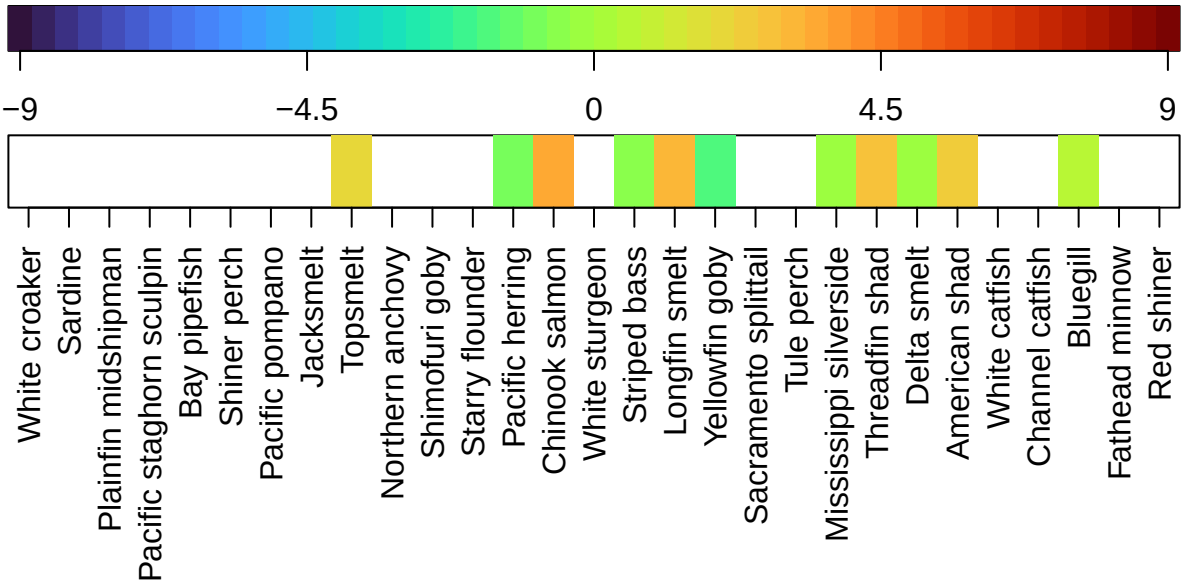

Figure S.4: Temporal trends (t-values) in spatial synchrony of fall age-0 CPUE by species using a 7-year window width. Blank cells indicate that insufficient data were available to compute the trend in spatial CV, e.g., because the species was not consistently caught by multiple region-gear type combinations.

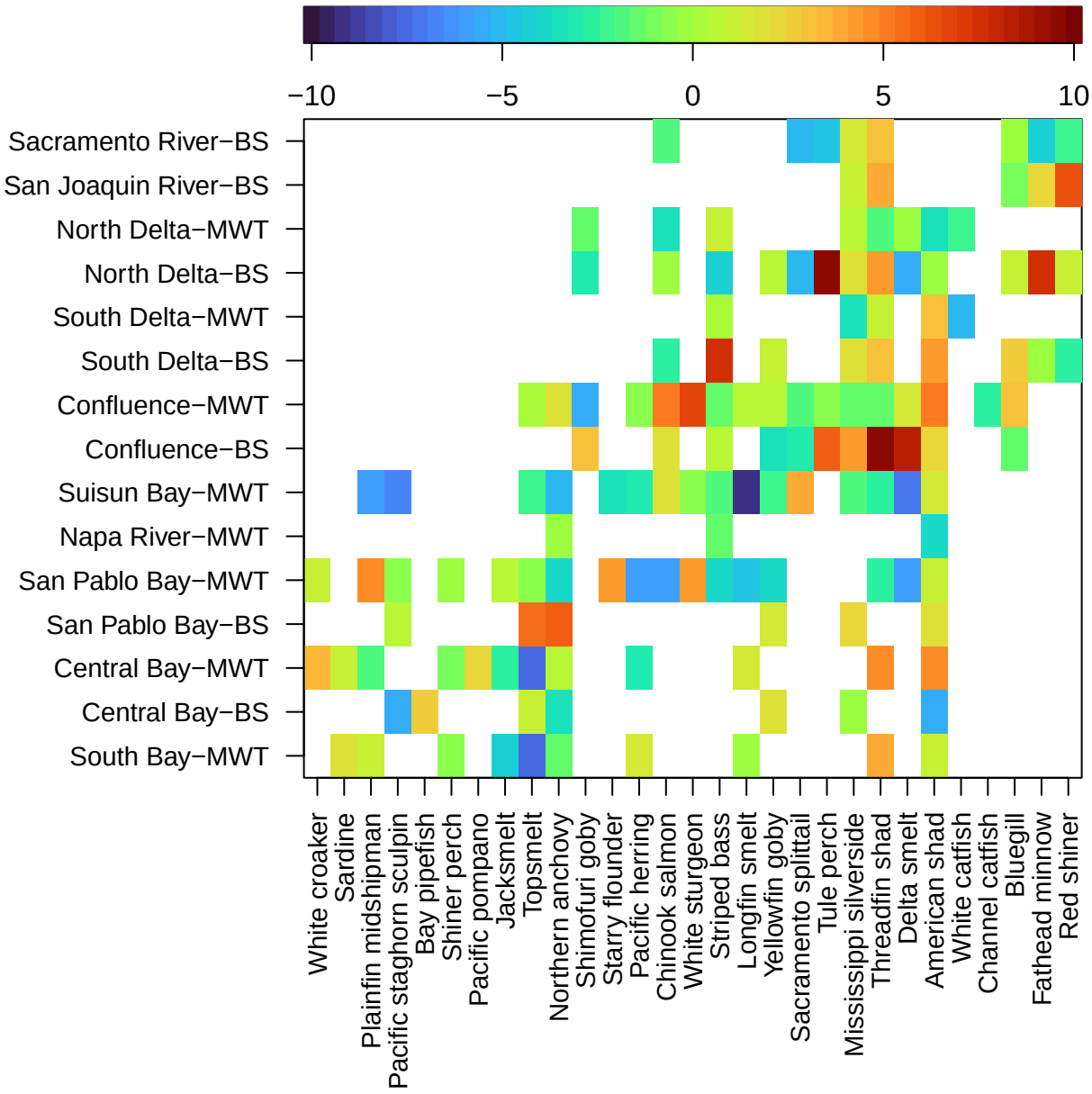

Figure S.5: Temporal trends (t-values) in the temporal coefficient of variation (CV) of fall age-0 CPUE by species and region-gear type combination using a 7-year window width. Blank cells indicate that insufficient data were available to compute the trend in temporal CV.

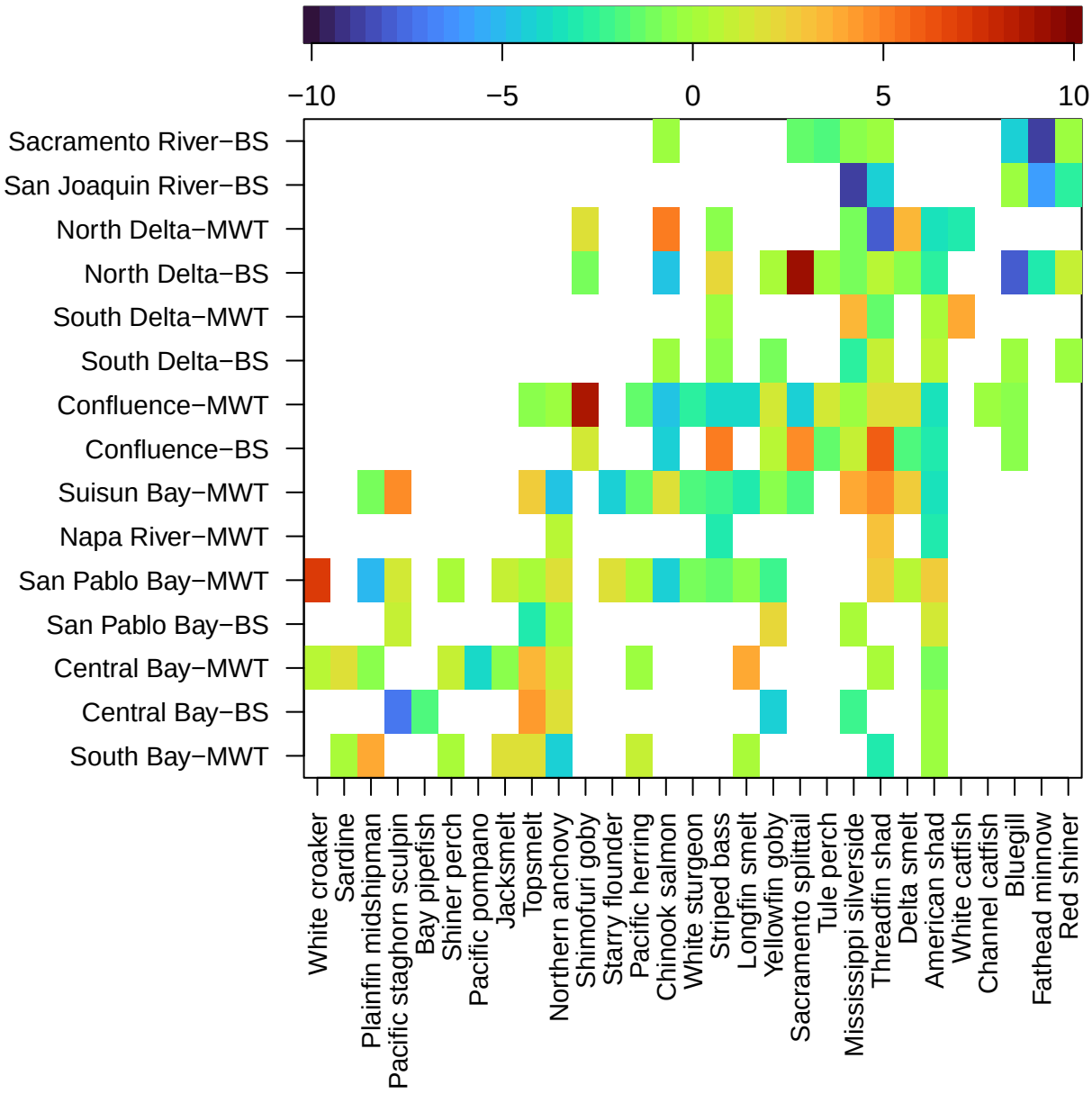

Figure S.6: Temporal trends (t-values) in the lag-1 temporal autocorrelation of fall age-0 CPUE by species and region-gear type combination using a 7-year window width. Blank cells indicate that insufficient data were available to compute the trend in lag-1 autocorrelation.

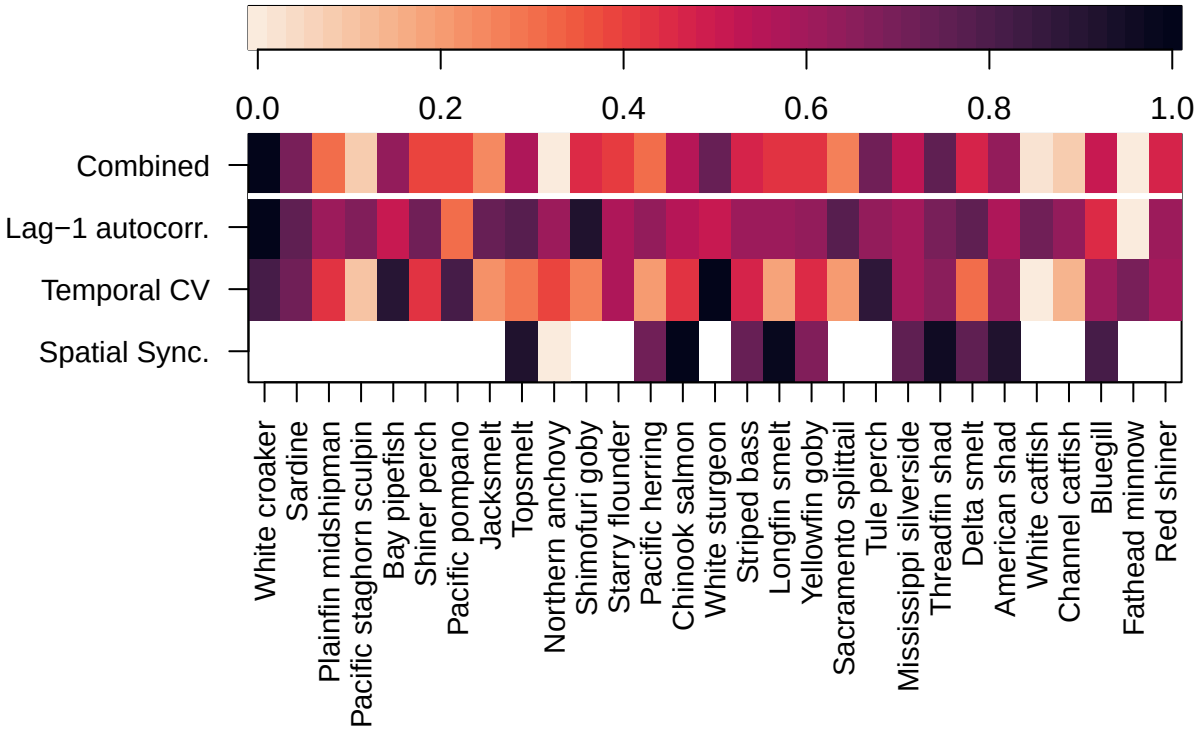

Figure S.7: Relative risk of fish population regime shifts based on EWI statistics using a window width of 7 years. The lower 3 rows show relative risk from three component metrics developed by rescaling long-term trends (t-values) to the 0-1 interval. The top row shows the combined (averaged) statistic. Note that several species were not consistently observed in ≥ 3 regions and so the spatial synchrony component was not included.

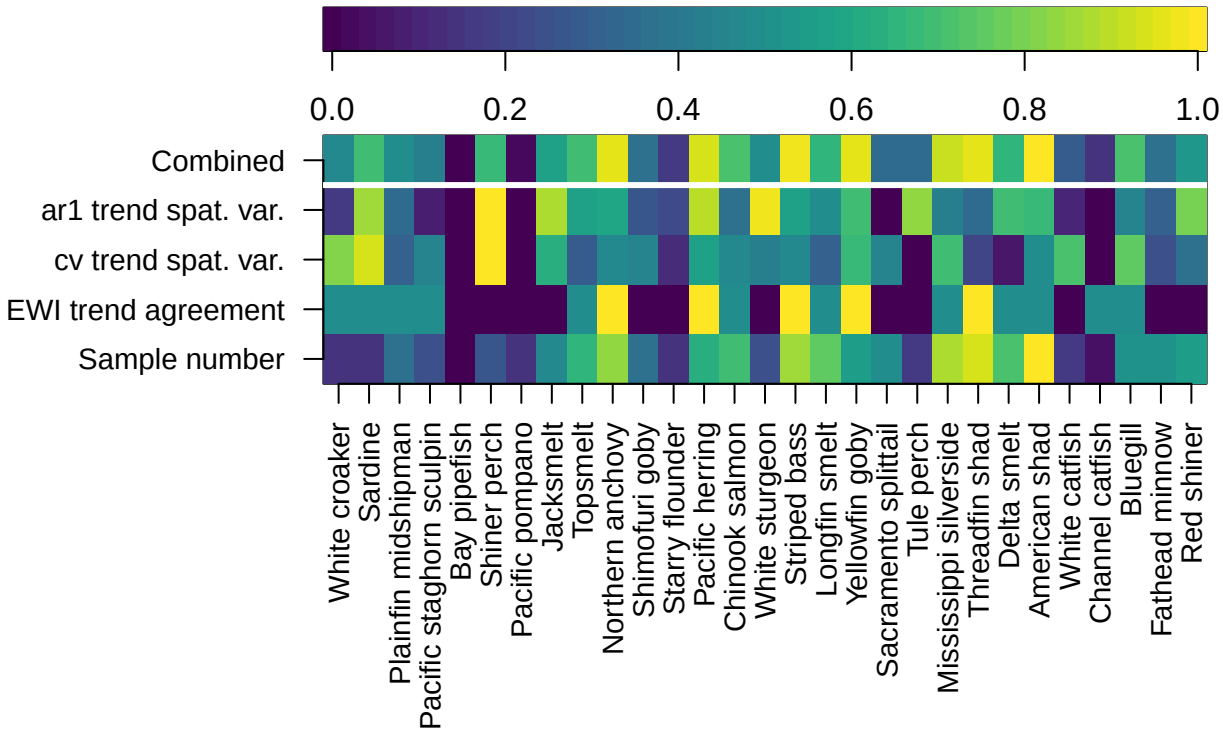

Figure S.8: Relative confidence in EWI-based risk assessment using a 7-year window width. We considered confidence in the EWI score to be highest when the metrics were based on a large number of samples, when the direction of trends in EWI metrics agreed, and when there was less spatial variability in the trends in lag-1 autocorrelation and temporal cv. Note that for the purposes of this metric, the spatial variability in EWI trends have been rescaled so that 1 corresponds to the lowest variability (highest confidence) and 0 corresponds to the greatest variability (lowest confidence).

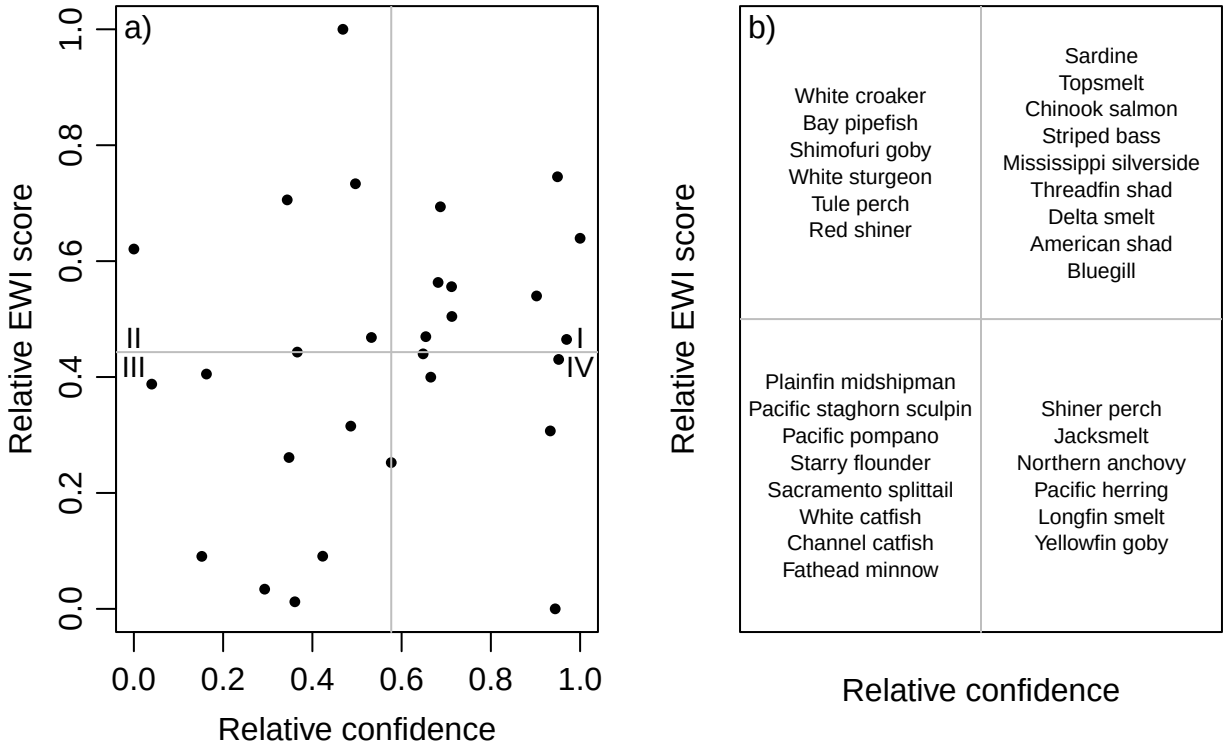

Figure S.9: Relative EWI score versus confidence using a 7-year window width. a) scatterplot of index values; b) names of species in each quadrant of the scatterplot, where quadrant boundaries are defined by the median of each axis.