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Continuing Long-Term Shifts in Larval Fish Phenology in the Southern California Current Ecosystem Are Matched by Rapid Advances in the North

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ABSTRACT

Changing environmental conditions are leading to shifts in the timing of seasonal events globally. In the ocean, environmental cues affecting larval fish (ichthyoplankton) abundance may not be synchronized with factors optimizing larval and juvenile survival, making the study of ichthyoplankton phenology in the context of a changing environment critical. In the southern California Current Ecosystem (CCE), a major eastern boundary current upwelling system, significant long-term shifts in larval fish phenology have been previously observed. To assess the stability of these estimates and extend them to the northern CCE, we evaluated multidecadal trends in ichthyoplankton abundance for 57 species from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) and 25 species from the Newport Hydrographic Line (NH Line). We show that on average, larval fish phenology in the southern CCE has continued to advance with an estimated rate of -0.18 ± 0.05 day year⁻¹ from 1951 to 2022, while phenology in the northern CCE has advanced at a rate of -0.48 ± 0.26 day year⁻¹ from 1996 to 2023. Thirty-nine percent of species showed significant advancing phenology, 12% exhibited delayed phenology, and 49% showed no long-term linear change. A comparison analysis showed that species in these groups had similar rates of change between the two locations for the 1997-2017 period. Phenological shifts in the southern CCE tracked changes in the phenology of upper ocean temperature, zooplankton, and upwelling. These variables poorly explained shifts in the northern CCE, where short-term effects of the El Niño-Southern Oscillation and the 2014-2016 marine heatwave on ichthyoplankton phenology were observed for some species. This research highlights regional variability and continuing phenological shifts in one of the world's most productive marine ecosystems.

1 | Introduction

Phenology is the study of seasonality of recurring biological or ecological events. Changes in phenology have been shown to be one symptom of anthropogenic climate change (Cohen et al. 2018; Iler et al. 2021; Inouye 2022). Terrestrial spring events have significantly advanced, with an estimated global rate of change of -0.28 dayyear⁻¹ (Parmesan 2007). In the ocean, spring phenology has advanced -0.44 dayyear⁻¹ on average, with phenological shifts observed for molluscs, phytoplankton, zooplankton, teleosts, benthic invertebrates, and marine reptiles (Poloczanska et al. 2013; Cooley et al. 2022). Some studies

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show that rates of advance tend to be faster at lower trophic levels across both terrestrial and aquatic systems (Thackeray et al. 2016), yet others find no trophic asynchronies (Loughnan et al. 2024). While the form and magnitude of species' phenological responses to climate change vary considerably, phenology in marine systems tends to be more sensitive to changes in the environment than in terrestrial systems (Edwards and Richardson 2004; Poloczanska et al. 2013), having significant implications for fisheries and ecosystem-based management (Chittenden et al. 2010; Peer and Miller 2014; Olmos et al. 2023).

Marine fish species vary in the frequency and seasonal timing of reproduction across their life cycle. The timing and duration of reproductive stages are often affected by a combination of environmental and endogenous cues (Lam 1983; Bromage et al. 2001), making fish spawning phenology sensitive to changing environmental conditions. Environmental cues that can regulate spawning phenology includepermissive factors which allow proper reproductive development in spawning adults, such as nutritional status (Bromage et al. 2001); controlling factors which time this development, such as temperature-mediated egg maturation rates; proximate factors which synchronize adult reproductive development to seasonality in the environment, such as increasing day length (photoperiod) and temperature triggering development in spring-summer spawners (Pankhurst and Porter 2003); and evolutionary factors which affect the survival of the young, such as larval prey availability and currents which can cause egg or larval dispersal away from areas that facilitate survival (Lam 1983; Slesinger et al. 2021). For a given fish population or species, spawning seasonality may vary temporally with climate-induced changes in these environmental cues, spatially with shifts in latitude or depth, or demographically with shifts in the size and age structure of the adult spawning stock (Lowerre-Barbieri et al. 2011).

The early life history of most fishes includes a pelagic larval stage, during which time they feed in the upper layers (~100m) of the water column where they can be collected via net tows (Moser 1996). Changing environmental conditions have led to observed shifts in the timing of larval fish (ichthyoplankton) abundances over recent decades. Edwards and Richardson (2004) estimated a temperature-mediated advance of -27 days over their 45-year time series, roughly -0.6 day year⁻¹, for meroplankton including ichthyoplankton in the central North Sea. A meta-analysis by Poloczanska et al. (2013) estimated global phenological advancement for larval bony fishes at -1.12 ± 0.17 day year⁻¹. Off the southeastern coast of the United States, recent research has identified persistent advances in the timing of larval estuarine ingress related to increasing water temperatures, with an average community shift of -0.88 day year⁻¹ (Thaxton et al. 2020).

Eastern boundary current upwelling systems (EBUSs) have disproportionately high productivity due to nutrient influx from seasonal coastal upwelling (Pauly and Christensen 1995), leading these regions to contribute ~20% of global marine fisheries catch (Chavez and Messié 2009). The importance of EBUSs to fisheries and ecosystem services highlights the need for continued evaluation of climate change impacts on these regions (Bograd et al. 2023). The California Current Ecosystem (CCE) is one of four major EBUSs globally, supporting mean primary productivity of $0.99 \text{ g Cm}^{-2} \text{ day}^{-1}$ (Carr 2001). In the CCE, climate change is leading to shifting environmental conditions, including increased

upper-ocean temperatures (Di Lorenzo et al. 2005; Rasmussen et al. 2020), ocean acidification (Osborne et al. 2020), reduced midwater oxygen (Koslow et al. 2011), and regionally variable shifts in coastal upwelling (Bograd et al. 2009). Observed biological impacts include changes in the timing and duration of phytoplankton blooms (Foukal and Thomas 2014) and reduced abundances of cool-water fishes (Koslow et al. 2011; Siegelman et al. 2018). Furthermore, models predict that by the end of the century, 90%– 100% of the CCE will be experiencing a novel local climate (Smith et al. 2022). Of interest is how ichthyoplankton phenology across the CCE has changed and may continue to change in relation to this evolving environment.

Asch (2015) analyzed an assemblage of 43 larval fish species from 1951 to 2008 obtained from the California Cooperative Oceanic Fisheries Investigations (CalCOFI), a long-term ocean observing program in the southern CCE. Asch (2015) found that on average, larval fishes in the southern CCE were appearing earlier in the year at a rate of -0.12 dayyear⁻¹, associated with shifts in the phenology of sea surface temperature, mesozooplankton, and upwelling. While >10 years of additional CalCOFI data are available, little further work has been initiated on long-term phenological change in this region. Thompson et al. (2022) showed that most mesopelagic fishes spawned earlier within a season during the 2014-16 marine heatwave off southern California. Recent short-term phenological shifts in larval abundances have also been observed in the northern CCE. Auth et al. (2018) analyzed several larval fish species of the northern CCE during the 2014-16 marine heatwave, finding abnormally high abundances of summer-spawning northern anchovy (Engraulis mordax) and Pacific sardine (Sardinops sagax) during the anomalously warm winter. These short-term changes in ichthyoplankton seasonality in the northern CCE were similar to species responses that have been observed during past El Niño events (Brodeur et al. 1985; Auth et al. 2015). However, long-term assemblage-wide phenological trends in the northern CCE have not been assessed.

Here, we report findings from a phenological analysis of an updated CalCOFI ichthyoplankton dataset with 57 species from 1951 to 2022 in following with the methods of Asch (2015). We then extended this work to analyze long-term trends in ichthyoplankton phenology in the northern CCE, using observational data from 1996 to 2023 from the Newport Hydrographic Line (NH Line) off the coast of central Oregon. Our study objectives were to determine if: (i) the broad phenological trends in the southern CCE identified in Asch (2015) still hold with a larger fish assemblage and an additional decade of data; (ii) ichthyoplankton phenology in the northern CCE is also changing over time; (iii) environmental variability explains variability in northern CCE ichthyoplankton phenology; and (iv) trends in ichthyoplankton phenology in the northern CCE are similar to those in the southern CCE.

2 | Materials and Methods

2.1 | Observational Data

In the southern CCE, CalCOFI cruises regularly sample 66 stations along six transect lines between San Diego, CA, and Avila, CA, that extend 700km offshore (Figure 1). Ichthyoplankton were sampled using bongo nets (71-cm diameter, 505-m mesh)



FIGURE 1 | Location of CalCOFI and NH Line sampling stations, marked in red, against bathymetry (colorbar). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

obliquely towed to 210-m depth. Samples were sorted and identified to the lowest taxonomic resolution possible, and counts were multiplied by a standard haul factor and presented as larval density in numbers per 10 m^2 . For further details on CalCOFI sample collection and processing, see Kramer et al. (1972). Here, we used a CalCOFI dataset of larval density from 1951 to 2022 (Chen et al. 2024). We kept only those species with abundance data in at least five decades, resulting in 57 species for analysis (Table S1). Of those, 32 species were in common with the assemblage analyzed in Asch (2015).

The NH Line is a single transect in the northern CCE off the coast of Newport, OR (44.65°N), with seven core stations out to 25nmi from shore and 13 outlying stations out to 200nmi from shore. Core station sampling on the NH Line has occurred biweekly to monthly since 1996, resulting in a shorter but higher temporally resolved dataset compared to CalCOFI. Ichthyoplankton were sampled with a double oblique bongo net (60-cm diameter, 335-m mesh) or a 1-m ring net (during 1996-2000) towed to 30-42m depth, then sorted, identified to the lowest taxonomic resolution possible, and reported as average density in numbers per m³. Further details on NH Line sample collection and processing are described in Auth et al. (2018) and Brodeur et al. (2008). We used the NH Line dataset of larval density from 1996 to 2023, keeping stations with \geq 80 samples and \geq 20 years of data (stations 1 and 5 through 45; Figure 1). These thresholds were chosen as they reflected a breakpoint in station sampling frequency. We then retained only species with at least 14 years (≥ 50%) of data, resulting in 25 species for analysis (Table S1; Chen et al. 2024).

2.2 | Estimating Phenological Shifts

To examine long-term phenological trends and account for variations in sampling effort over time, ichthyoplankton abundance data were averaged decadally for CalCOFI and over 3-year periods for the NH Line. Data analysis closely followed the study methodology outlined in Asch (2015), with any changes summarized here.

Central tendency (CT) is the center of gravity of the mean monthly abundance curve, used as a conservative indicator of the timing of seasonal peak abundance (Ji et al. 2010). For each dataset, CTs of larval abundances were calculated for each species and the overall assemblage using the equation:

$$CT = \sum_{i=1}^{12} (m_i * a_i) \div \sum_{i=1}^{12} a_i,$$

where m_i is the month of the year, and a_i is the average larval abundance in that month for a given period (Edwards and Richardson 2004; Figure S1). No species displayed distinct bimodality, eliminating the need to split them into multiple phenophases for this calculation. For those species classified as 'fall-winter spawners' based on the sum of larval abundance being higher in October to March compared to April to September, years were shifted so that i=1 would refer to a month prior to their seasonal rise in abundance, allowing us to better capture any directional trend from 1 year to the next. For all fall-winter CalCOFI species and most fall-winter NH Line species, m_1 was July and m_{12} was the following June; for two NH Line species (eared blacksmelt [Lipolagus ochotensis] and rex sole [Glyptocephalus zachirus]), m_1 was October and m_{12} was the following September. Central tendency anomalies (CTas) were calculated relative to the mean CT of the decades or 3-year periods, and values were multiplied by 30.44 to generate anomalies in days.

To evaluate assemblage-wide changes in CT, CTas for each dataset were regressed against time. The slope of this linear regression was used as an estimate for overall phenological trend. Pearson correlations of CTa against time were then calculated for each individual species. In following with the methods of Asch (2015), we categorized species into three broad groups on the basis of the correlations, aiming to isolate species showing advancing phenology, those showing delaying phenology, and those with no long-term linear change. In Asch (2015), a conservative threshold of |r| = 0.50 was used, whereby species with $r \ge 0.50$ were categorized as having delaying phenology, those with $r \leq -0.50$ had advancing phenology, and those with -0.50 < r < 0.50 were described as having no long-term linear change. Adopting this threshold here for the extended CalCOFI dataset resulted in a 'no linear change' group that continued to show significant trends towards advancing phenology. This likely reflects an increase in the power of statistical analyses to detect significant changes due to the addition of data from a greater number of years. Instead, we used a threshold of |r| = 0.33, which would split the range of Pearson's r into three

equal parts and was sufficient to produce the intended groupings. For each group, CTa was regressed against time to evaluate the direction, magnitude, and significance of phenological change.

2.3 | Evaluating Relationships Between Phenological Shifts, Ecological Traits, and Environmental Variability

To examine potential patterns and influences on phenology, relationships between ichthyoplankton CTa and species ecological characteristics, local oceanic variables, and basin-scale climate oscillations were assessed. Asch (2015) analyzed nine ecological traits, some of which were originally defined by Hsieh et al. (2005): taxonomic order, adult habitat, cross-shore distribution, biogeographic affinity, fishing status, adult trophic level, month of maximum larval abundance, frequency of larval occurrence, and amplitude of the mean seasonal cycle. For each trait, group variation in phenological trend was visualized with boxplots or scatterplots (Figures S2–S4). Data exploration indicated that fishing status, trophic level, frequency of occurrence, and amplitude of the mean seasonal cycle had no clear effect on phenological trends (Figure S4), so these covariates were dropped from our analysis. Principal components analysis (PCA) was applied to determine major modes of variability among the remaining five ecological traits. Species clustering together in the PCA ordination plots were grouped, and their CTa was regressed against time.

The local oceanic variables assessed included: epipelagic temperature (T), zooplankton biomass, and coastal upwelling. Asch (2015) constrained T to temperatures measured at precisely 0-m depth; however, because this does not reflect the whole vertical space typically occupied by larval fishes (Moser and Smith 1993), we averaged CalCOFI T over the upper 100 m. Similarly, upper 100mT from the seven core stations was obtained from the NH Line hydrographic database. Zooplankton biomass was used to broadly evaluate phenological matchmismatch. Zooplankton displacement volume (ZDV) was obtained from the CalCOFI database. Gelatinous organisms >5mL biovolume were removed. NH Line zooplankton sampling records the biomass of two major copepod groups at the 5 and 25 nmi stations: a northern, lipid-rich, cold-water assemblage and a southern, lipid-poor, warm-water assemblage (Hooff and Peterson 2006; Fisher et al. 2015). Positive values of the monthly Bakun coastal upwelling index (BCUI) were evaluated at the positions nearest to each sampling location: 33° N, 119° W for CalCOFI and 45°N, 125°W for NH Line (National Oceanic and Atmospheric Administration 2024a; Schwing et al. 1996). While several new upwelling indices have been developed since Asch (2015), the original Bakun index is the only one with temporal coverage extending back to 1951 (Jacox et al. 2018). Combinations of local oceanic variables were included in candidate general linear models of ichthyoplankton phenology using the stats::lm function in R. If the Durbin-Watson test showed significant autocorrelation, an AR(1) term was added. Model selection was based on Akaike's information criterion corrected for small sample size (AICc) using the AICcmodavg::aictab R function.

Effects of the El Niño-Southern Oscillation (ENSO) on ichthyoplankton phenology were examined. Monthly ENSO phases were characterized from the Oceanic Niño Index (National Oceanic and Atmospheric Administration 2024b) using the threshold of five consecutive seasons at ±0.5°C to define El Niño/La Niña events, with intervening periods classified as neutral. Asch (2015) also assessed the effects of the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO). However, recent studies have identified nonstationarity in the relationships between these indices and environmental conditions (Litzow et al. 2018; Litzow et al. 2020a; Litzow et al. 2020b; Werb and Rudnick 2023), so we did not conduct PDO or NPGO analyses. Larval abundance data were aggregated into bins according to ENSO phase, and CT and CTa were then calculated. ANOVAs were performed comparing fish phenology during different ENSO phases. If the ANOVA assumptions of normality and homoscedasticity were violated, Kruskal-Wallis tests were performed instead. Any significant effects were further examined post hoc (Tukey's HSD or Dunn's test).

2.4 | Comparison Tests

While decadal averaging was necessary to assess the full CalCOFI time series and maintain comparability with Asch (2015), CalCOFI sampling frequency was sufficient to analyze data in 3-year periods from 1997 to 2017. NH Line data were filtered for this time frame to allow a broad comparison between the two locations over these two decades. For each location, species' CTa, correlations between CTa and time, phenology groups, and estimated phenological trends were calculated with the same methods as the full analyses above. Trends of CalCOFI and NH Line phenology groups were compared with t-tests, and the frequency of species falling into different phenology change groups was compared with a chi-squared test.

To evaluate any effects from using a different dataset (modified methodology and inclusion of more species) from Asch (2015), the current study's CalCOFI dataset was also examined over the Asch (2015) time period of 1951–2008, and estimated phenological trends were compared with Asch (2015). The results of this study's full CalCOFI analysis were then also compared with those of Asch (2015), accounting for both the modified methodology and an additional decade of data. Trends of phenology change groups in the two studies were compared with *t*-tests, and the frequencies of species falling into different phenology groups were compared with a chi-squared test.

All data analysis and visualizations were performed using R version 4.3.1 (R Core Team 2023), and additional considerations for bias correction are described in the supplement.

3 | Results

3.1 | Trends in Ichthyoplankton Central Tendency

Mean CT of both the CalCOFI total assemblage and the NH Line total assemblage showed slight decreasing trends over time, indicating that fish larvae in both regions are appearing



FIGURE 2 | Mean central tendency anomaly (CTa) over time for ichthyoplankton assemblage and species groups. Left column: CalCOFI; Right column: NH Line. Panels show phenology of the overall assemblage (a, b), species shifting earlier (c, d), species with no long-term linear change (e, f), and species shifting later (g, h). Axes ticks indicate the start of the year. Bars show ±1 standard error. In some cases, bars are too small to be visible due to small standard errors. Note that y-axes limits vary by row.

earlier in the year than previously observed (Figure 2a,b). A linear regression of central tendency anomalies against year suggested that larval fishes in the CalCOFI assemblage have on average advanced their phenology by -0.18 ± 0.05 day year⁻¹, or -12.88 days since the time series began in the 1950s (F=11.77, df=379, p < 0.001). Meanwhile, NH Line ichthyoplankton have advanced by -0.48 ± 0.26 day year⁻¹, or -12.85 days since observations began in 1996 (F=3.33, df=218, p=0.07).

In the southern CCE, groups of species displayed advances, delays, or no change in phenology. In the CalCOFI assemblage, 27 species (47%) showed significant advancing phenology (F=68.78, df=180, p<0.001, Figure 2c), shifting at a rate of -0.57 ± 0.05 dayyear⁻¹ (mean ±SE; range: -0.21 to -1.30 dayyear⁻¹). Fished species in this group included: chub mackerel (*Scomber japonicus*), cabezon (*Scorpaenichthys marmoratus*), and Pacific hake (*Merluccius productus*). Nine CalCOFI species (16%) showed significant delaying phenology (F=32.04, df=56, p<0.001, Figure 2g), shifting at a rate of 0.65±0.07 dayyear⁻¹ (range: 0.44 to 1.07 dayyear⁻¹). Fished species with delaying phenology included: butterfish (*Peprilus simillimus*), Pacific barracuda (*Sphyraena argentea*), and California flounder (*Paralichthys californicus*). The remaining 21

species (37%) were classified as having no long-term linear change (F=0.33, df=139, p=0.57, Figure 2e). Fished species in this group included: northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sagax*), and Pacific jack mackerel (*Trachurus symmetricus*). Additionally, some taxa in this group displayed a marked decrease in CT in the 1970s, which appeared to drive the assemblage dip in CT in that decade.

Similarly, species in the northern CCE also exhibited advances, delays, or no change in phenology. In the NH Line assemblage, 5 species (20%) showed significant advancing phenology (F = 16.29, df = 40, p < 0.001, Figure 2d). Their average change in CT was -3.05 ± 0.79 day year⁻¹ (range: -1.29 to -5.92 day year⁻¹). Fished species in this group were Dover sole (Microstomus pacificus) and butter sole (Isopsetta isolepis). One NH Line species (4%), Pacific staghorn sculpin (Leptocottus armatus), showed delaying phenology (F = 5.08, df = 6, p = 0.07, Figure 2h), shifting at a rate of $2.36 \text{ day year}^{-1}$. The remaining 19 species (76%) showed no long-term linear change (F=0.02, df=168, p=0.90, Figure 2f). Fished species in this group included northern anchovy (Engraulis mordax), lingcod (Ophiodon elongatus), and starry flounder (Platichthys stellatus). This group showed a sharp increase in CT in 2012-14, at the start of the period including the marine heatwave known as 'the Blob,' which appeared to drive the assemblage increase in CT for that period. A chi-squared test examining whether the frequency of species falling into the advancing, delaying, and no-change groups was the same between the CalCOFI and NH Line assemblages was significant ($\chi^2 = 10.78$, df = 2, p < 0.005), indicating that the overall distribution of species falling into each category changed regionally when assessed over the full time periods.

3.2 | Patterns Between CTa and Ecological Traits

PCA of the CalCOFI assemblage revealed three clusters of species sharing similar traits, with the first two principal components (PCs) accounting for 49.5% of the variance in this dataset. One cluster was associated with positive loadings on PC1. Common traits among these 25 species were the orders Pleuronectiformes and Perciformes/Scorpaenoidei, coastal distribution, demersal habitat, and cool-water association (Figure 3a,c,e). Members of this group showed advancing phenology at a rate of $-0.17 \text{ day year}^{-1}$ (*F* = 3.90, df = 164, p = 0.05, Figure S6e). A second group of species had primarily negative loadings on PC1 and positive loadings on PC2. These nine species clustered less closely together, but common traits included the order Scombriformes, widespread coastal-oceanic distribution, epipelagic habitat, and a later month of maximum larval abundance (Figure 3a,c,e). These species did not show a significant phenological trend (F=0.36, df=60, p=0.55, Figure S6a). A third cluster of species was associated with primarily negative loadings on both PC1 and PC2. Common traits in these 22 species included the orders Myctophiformes, Stomiiformes, and Argentiniformes, and mesopelagic habitat with oceanic distribution (Figure 3a,c,e). This group had advancing phenology of $-0.25 \text{ day year}^{-1}$ (*F*=9.40, df=151, *p* < 0.01, Figure **S6c**).

The first two PCs accounted for 71.5% of the variance in the NH Line dataset. With sampling generally occurring closer



FIGURE 3 | Results of PCA on ichthyoplankton assemblages. Left column: CalCOFI; Right column: NH Line. Panels (a, b) show species ordination with markers proportional to the magnitude of phenological trend and colored by the direction of trend (black=negative, white=positive). Remaining panels show correlations between ecological traits and PC1 and PC2, with traits being taxonomic orders (c, d); adult habitat, cross-oceanic distribution, biogeographical affinity, and month of maximum larval abundance (e, f).

to shore and at shallower depths, the NH Line assemblage was predictably dominated by demersal, coastal species. Groups of species with similar ecological traits showed less variability in their phenological trends compared to CalCOFI groups (Figure 3a,b). The largest cluster of 20 species was associated with primarily negative loadings on PC1, with common traits including the orders Pleuronectiformes and Perciformes/Cottoidei, coastal distribution, and demersal habitat (Figure 3b,d,f). This group showed advancing phenology of $-0.79 \text{ day year}^{-1}$ (*F*=4.21, df=174, *p*<0.05, Figure S6f). Another cluster of four species had positive loadings on both PC1 and PC2. Common traits in this group were the order Myctophiformes, mesopelagic habitat, oceanic distribution, and a later month of maximum larval abundance (Figure 3b,d,f). This group did not show a significant phenological trend (F = 0.006, df = 33, p = 0.94, Figure S6d). Species in this group showed particularly low, negative CTa in the first 3 years period, but trended from positive to negative CTa during the rest of the time series (Figure S6d). When the first 3 years were excluded from the analysis, their rate of advance was significant at $-1.31 \text{ day year}^{-1}$ (*F* = 6.41, df = 30, *p* < 0.05). The remaining species, northern anchovy (Engraulis mordax),



FIGURE 4 | Phenology of environmental variables over time. Bars show ± 1 standard error. In some cases, bars are too small to be visible due to small standard errors.

was the only epipelagic, coastal-oceanic species represented in the dataset. It showed positive loading on PC1 and negative loading on PC2 (Figure 3b,d,f), and did not have a significant long-term trend in phenology (F=0.03, df=7, p=0.87, Figure S6b).

3.3 | Relationships Between CTa and the Environment

We examined relationships between ichthyoplankton phenology and the phenology of local environmental variables: epipelagic temperature, zooplankton abundance, and coastal upwelling. A linear regression between CalCOFI temperature CTa and time indicated that temperatures are warming 26.6 days earlier in the year compared to the 1950s, advancing at a rate of 0.37 ± 0.14 day year⁻¹ (mean ± SE; F=6.85, df=5, p < 0.05, Figure 4a). There was no significant long-term trend for coastal upwelling at 33° N, 119° W (Figure 4c) nor for CalCOFI mesozooplankton displacement volume (Figure 4e).

At the NH Line, CTa of epipelagic temperature was highest in the period 2012–14 going into the 2014–16 marine heatwave, reflecting warmer temperatures later in the year than usual. This variable did not show a significant linear trend (Figure 4b). CTa of the positive Bakun upwelling index at 45°N, 125°W showed a significant decreasing trend (F=7.12, df=7, p<0.05),

indicating that upwelling near the NH Line is occurring progressively earlier at a rate of 0.64 ± 0.24 day year⁻¹ (Figure 4d). Upwelling phenology was fairly stable in this area up to 2012 and then showed an accelerated trend towards starting earlier in the year. The southern copepod assemblage remained fairly stable throughout the time series, except for a large shift from negative CTa in 2009-12 to positive in 2012-15. The northern copepod assemblage exhibited decreasing CTa (advancing phenology) from 1996 to 2014. While temperature, upwelling, and southern copepods showed peaks in CTa in 2012-2014, northern copepods only showed this increase in CTa in 2015-17, potentially reflecting a delayed response to the marine heatwave among these species. However, there was no significant longterm trend for either copepod group (Figure 4f). When comparing the two regions of the CCE, the NH Line generally exhibited larger interannual and decadal fluctuations in phenology across all environmental variables compared to CalCOFI.

Combinations of the three local environmental variables were included in candidate linear models of larval fish phenology. Most categories had multiple plausible models with delta AICc < 2.00 (Table S2). For CalCOFI species shifting earlier, the best-fit model (lowest AICc) indicated that ichthyoplankton phenology for this group was positively related to the phenology of temperature and zooplankton, and negatively related to the phenology of upwelling (Table 1). These species would appear earlier in times when temperature warmed and mesozooplankton abundance increased earlier in the year, and when coastal upwelling increased later in the year. For CalCOFI species shifting later, the most parsimonious model only included a negative effect of temperature, indicating that these species appeared later in years when warming was earlier (Table 1). For CalCOFI species having no long-term linear trend, CTa was positively related to mesozooplankton CTa (Table 1), suggesting environmental influences on larval fish interannual variability without a long-term trend.

For NH Line species shifting earlier or later over time, the null model had the lowest AICc (Table S2). The model with the

TABLE 1		Most	plausible	linear	models	(lowest	AICc)	relating
phenology of	of e	enviror	nmental v	ariables	with C	alCOFI i	chthyop	plankton
phenology.								

	CalCOFI Ichthyoplankton CTa				
	Phenology change group				
		No linear			
	Earlier	change	Later		
Temperature CTa	0.799***		-1.075***		
Zooplankton CTa	0.302***	0.361***			
Upwelling CTa	-2.002***				
Intercept	0.239	-0.046	-1.156		
Observations	182	141	58		
R^2	0.202	0.052	0.256		
Adjusted R ²	0.189	0.045	0.242		

Note: Durbin–Watson tests showed no significant autocorrelation. ***p < 0.01.

second-lowest AICc included a positive relationship with the phenology of northern copepods, although this was not statistically significant (Table 2). The no linear-change group showed positive relationships with the phenology of northern and southern copepods, displaying the influence of environmental variability on their phenology even though there was not a long-term linear trend (Table 2). Temperature only appeared in the alternative models for the no linear-change group (Table S2), showing no significant effect on advancing or delaying species.

In addition to local environmental variables, relationships with basin-scale ENSO conditions were assessed. If ENSO conditions had strong effects on the phenology of larval fishes in addition to long-term trends, ichthyoplankton phenology during these events would be expected to be significantly different from phenology in other phases. No phenology change group in the CalCOFI assemblage showed any significant difference in CTa in relation to ENSO phase (Figure 5a). NH Line species with no long-term change trended towards earlier phenology during El Niño events compared to neutral conditions, while advancing and delaying species showed no significant effects (Figure 5b).

3.4 | CalCOFI And NH Line Comparison

The two study regions were broadly compared from 1997 to 2017 with data averaged over 3-year periods (Figures S7–S8). In this analysis, the assemblage trend in phenology for CalCOFI was not significant (F=2.7, df=382, p=0.10), but groups of species continued to show significant linear trends. Twenty-two species (39%) shifted earlier at a rate of -2.46 ± 0.31 day year⁻¹ (F=62.22, df=144, p<0.001), and 11 species (19%) shifted later at 3.18±0.66 day year⁻¹ (F=23.10, df=71, p<0.001). The remaining 24 species (42%) showed no long-term linear change (F=0.40, df=163, p=0.53). Similarly, at the NH Line, the

TABLE 2Image: Most plausible linear models (lowest AICc) relating thephenology of environmental variables with NH Line ichthyoplanktonphenology.

	NH Line Ichthyoplankton CTa				
	Phenology change group				
	Earlier	No linear change	Later		
Northern Copepod CTa	0.629	0.356**	1.274*		
Southern Copepod CTa		0.788***			
Intercept	-0.671	0.068	0.551		
Observations	42	170	8		
R^2	0.039	0.074	0.471		
Adjusted R^2	0.015	0.063	0.383		

Note: For species with earlier phenology, the second most parsimonious model is shown because the most parsimonious model based on the AICc was the null model. Durbin–Watson tests showed no significant autocorrelation. *p < 0.1.

**p<0.1.

****p<0.01.



FIGURE 5 | Phenology of (a) CalCOFI and (b) NH Line ichthyoplankton groups during ENSO conditions. Different letters show significant differences (p < 0.05).

assemblage phenological trend from 1997 to 2017 was not significant (F=2.07, df=169, p=0.15). Nine NH Line species (36%) showed advancing phenology at a rate of -3.02 ± 0.71 day year⁻¹ (F=17.92, df=58, p<0.001), and 6 species (24%) delayed at 1.63±0.53 day year⁻¹ (F=9.351, df=39, p<0.01), while 10 species (40%) showed no linear change (F=0.26, df=68, p=0.61). T-tests comparing rates of change between CalCOFI and NH Line species were insignificant for both species shifting earlier (t=0.38, df=20.98, p=0.71) and species shifting later (t=1.80, df=12.06, p=0.10), showing that group phenological trends were statistically similar. A chi-squared test comparing the frequencies of species falling into the earlier, later, and no change groups was insignificant (χ^2 =0.23, df=2, p=0.89), indicating that this frequency was similar between the two regions.

3.5 | Current Study and Asch (2015) Comparison

To check the effect of using a different CalCOFI dataset (i.e., additional species and slightly different methods) from Asch (2015), we analyzed our CalCOFI dataset over the

Asch (2015) time period of 1951–2008. In this analysis, the CalCOFI assemblage used in the current manuscript showed advancing phenology at a rate of -0.14 ± 0.07 dayyear⁻¹ (*F*=4.309, df=322, *p*<0.05). A t-test comparing the mean assemblage trends between this restricted CalCOFI dataset and the Asch (2015) dataset was not significant (t=-0.55, df=103.28, *p*=0.58), indicating that the rate of phenological advance did not change with the inclusion of more species and modified methodology.

The results of this study's full CalCOFI analysis, accounting for the additional species and modified methods as well as the extension of the period analyzed, were then compared with those of Asch (2015). A t-test comparing the mean assemblage trends between the two studies was not significant (t=0.09, df=105.44, p=0.93), indicating that the estimated rates of phenological change were similar. In addition, t-tests comparing group rates of change were not statistically significant for species shifting earlier (t=0.29, df=40.44, p=0.78) nor for species shifting later (t=1.27, df=13.71, p=0.23), indicating that the species falling into these groups advanced or delayed in phenology at similar rates. Finally, a chi-squared test comparing the frequency of species falling into each phenology change group was not significant ($\chi^2 = 0.05$, df = 2, p = 0.98), suggesting that these frequencies were similar between the two studies.

4 | Discussion

4.1 | Long-Term Trends in Ichthyoplankton Phenology

Ichthyoplankton phenology is changing for the majority of species in the CCE. Despite some effects of short-term events (such as the 2014–16 marine heatwave) and interannual climate oscillations, significant long-term trends in phenology were observed in 63% of CalCOFI species and 24% of NH Line species in this study. The inclusion of more species and an additional decade of data led to estimated phenological trends in the southern CCE that are consistent with the results of Asch (2015), highlighting the robustness of their findings. The overall advancing trends observed in Asch (2015) are continuing, with an updated central estimate of -0.18 ± 0.05 day year⁻¹. Differences between the two studies were observed in the linear models, relation to ENSO, and individual species' trends, which are discussed further below.

Despite the shorter timeframe and less statistical power to detect change compared to CalCOFI, some long-term phenological trends are also becoming apparent at the NH Line. Over the full time series, the phenology of the NH Line assemblage has advanced faster than the CalCOFI assemblage at a rate of -0.48 ± 0.26 day year⁻¹. Only one species was categorized as shifting later at the NH Line. One similarity between the two regions was that the majority of species either shifted earlier or showed no linear change, while a relatively small number of species shifted later. In addition, at both sampling locations, mesopelagic-oceanic and demersal-coastal species showed phenological advances, with mesopelagic-oceanic species advancing the most. Our finding that ichthyoplankton phenology in the northern CCE has shifted at a faster rate than in the southern CCE appeared consistent with previous research showing stronger phenological advances at higher latitudes (Parmesan 2007; Post et al. 2018). However, when both locations were compared from 1997 to 2017 with data averaged over 3-year periods, CalCOFI and NH Line results were very similar. While analyses over a longer time period were necessary to observe assemblage-wide changes at both locations, groups of species from 1997 to 2017 continued to show significant advancing or delaying phenological trends, and these trends were statistically similar between the northern and southern CCE. In other words, broad phenological changes at the NH Line matched changes at CalCOFI, highlighting rapid shifts in the northern CCE that have not been previously observed.

4.2 | Hypothesized Mechanisms of Phenological Change

Thirty-nine percent of species in this study showed significant advancing phenology. For advancing species in the CalCOFI assemblage, the most favorable model linking ichthyoplankton and environmental variables indicated a positive relationship with the phenology of temperature, whereby larvae appeared earlier when warming occurred earlier. This finding is consistent with Asch (2015) and previous research on the relationship between temperature and reproductive phenology. Temperature acts as a controlling factor on fish spawning through affecting the maturation rate of eggs relative to the ovulation cycle (Bromage et al. 2001). Higher temperatures speed up reproductive development through the increasing of metabolic rates (Lowerre-Barbieri et al. 2011), generally resulting in the earlier appearance of larvae. Temperature also acts as a proximate cue, with warming stimulating gonadal development in spring-summer spawners and cooling stimulating development in fall spawners, synchronizing spawning with increasing prey availability (Pankhurst and Munday 2011; Pankhurst and Porter 2003). The best-fit model for CalCOFI advancing species also suggested a positive relationship with mesozooplankton abundance, indicating synchrony with prey availability, and a negative relationship with coastal upwelling. While a positive relationship with zooplankton was also observed by Asch (2015), that study did not observe a negative relationship with upwelling. Larvae in our study appeared earlier in years when upwelling in the CalCOFI survey area was delayed. This negative relationship could reflect the fact that upwelling influences offshore transport of passively drifting larvae, which could adversely affect coastal species that use nearshore juvenile habitats.

Mesopelagic species showed the fastest rates of advance compared to epipelagic and demersal species (Figure S6). Most mesopelagic fishes reside in the Central Pacific and Pacific Equatorial water masses. These water masses become more voluminous in the CalCOFI survey area during warming events (Moser et al. 1987). Prior to 1976, common mesopelagic taxa, such as Mexican lampfish (Triphoturus mexicanus) and Panama lightfish (Vinciguerria lucetia), were rarely found in the core CalCOFI area in winter and spring. Abundances abruptly increased subsequent to the change from a cool to a warm regime around 1976 as warmer water impinged on the sampling area earlier in the year (Moser et al. 2001; Hsieh et al. 2009). Another step change towards increasingly warm conditions occurred in 2014. The abundance of warm-water-associated mesopelagic species spiked during this period (Thompson et al. 2022). Elevated abundances in winter/spring have persisted through at least 2023 as conditions have mostly remained warm (Thompson et al. 2024). Thus, transport of warm water masses earlier in the year may be a significant driver of the early appearance of these species in plankton samples.

At the NH Line, no plausible models for advancing species included a relationship with the phenology of temperature, and these species were best described with a null model. In Asch (2015), advancing CalCOFI species trended towards advancing phenology during El Niño events, but it was not observed here for either the northern or southern CCE, suggesting that the long-term trend signal is now more influential than interannual shifts in ENSO conditions. Different types of El Niño events may also lead to different phenological responses, potentially contributing to this change. Fisher et al. (2015) showed that copepod biomass in the northern CCE responded differently to El Niño events depending on their magnitude, duration, and type (classical Eastern Pacific vs. Central Pacific El Niño Modoki). El Niño Modoki events have increased in intensity and frequency in recent decades (Lee and McPhaden 2010) and have been associated with lagged shifts in local temperature and copepod community composition relative to Eastern Pacific events (Fisher et al. 2015).

Twelve percent of species in this study showed significant delaying phenology. For delaying species in the CalCOFI assemblage, the most favorable model indicated a negative relationship with the phenology of temperature, whereby larvae appeared later when warming occurred earlier. While elevated temperatures early in the year are known to delay reproduction in fall-spawning species (Pankhurst and Munday 2011), only one species in this group (smalleye squaretail [Tetragonurus cuvieri]) was identified as a fall spawner, with the majority of group members spawning primarily in the summer. Species with peak abundance in late summer may resemble patterns typically seen for fall spawners. In Asch (2015), this group also had a positive relationship with the phenology of coastal upwelling, which was hypothesized to result from preferential spawning during low-upwelling conditions to increase larval retention in coastaldemersal species. Five of nine delaying CalCOFI species in this analysis were categorized as coastal-demersal (Table S1), but this relationship with the phenology of upwelling was not significant. Delaying species on the NH Line were best described with a null model. Their second-best fit model showed a positive relationship with northern copepod phenology, suggesting some synchrony with prey availability for this group, but had no clear relationship with temperature or coastal upwelling.

Forty-nine percent of species in this study showed no long-term linear change over their respective time series. Several of the species in this group were characterized by serial, multiple-batch spawning, such as northern anchovy (CalCOFI and NH Line), Pacific sardine (CalCOFI), and Pacific jack mackerel (CalCOFI). These species spawn multiple times throughout an extended spawning season (McEvoy and McEvoy 1992; Hernandez-Vazquez 1994; Moser 1996), such that their phenology of larval occurrence may not be as closely linked to the phenology of physical environmental variables. Phenology for species in this group may also be mediated by external cues with high temporal variability, resulting in a lack of a long-term trend. The amount of variance explained by linear models for species with no longterm linear change was improved through the inclusion of mesozooplankton phenology (CalCOFI) and copepod phenology (NH Line), both of which showed interdecadal fluctuations without significant linear trends. Other factors not showing a long-term trend, such as endogenous cues, photoperiod, and basin-scale climate oscillations, may also play dominant roles for some of these species. At the NH Line, species with no long-term change advanced in phenology during El Niño events. Several species in this category also showed delayed phenology in the period 2012-2014 leading into the MHW. This may have resulted from 2014 temperatures staying warm abnormally late in the year, potentially extending the spawning season for some species, such as was found for northern anchovy in Auth et al. (2018). Cooley et al. (2022) and additional references therein showed that 19% of meroplankton (including larval fishes) showed no significant phenological or distributional response to long-term climate

change. Poloczanska et al. (2013) suggested possible reasons for a lack of phenology change, including insufficient data, evolutionary adaptation, and complex interactions between multiple environmental drivers.

4.3 | Northern CCE Versus Southern CCE

Differences in the influence of environmental variables on ichthyoplankton phenology were apparent between the two locations. Phenological shifts at the NH Line were not as well explained by the environmental variables included in the linear models compared to changes in the CalCOFI time series, particularly for advancing species. Our results suggest that at the NH Line, upwelling is occurring significantly earlier in the year, while temperature and zooplankton are not showing significant long-term change in phenology. However, upwelling only appeared in the second best-fit model describing species with no long-term linear change. While all species groups showed potential relationships with copepod phenology, none included upper-ocean temperature. Temperature is generally a stronger proximate cue for spawning at lower latitudes, with photoperiod increasing in importance at higher latitudes (Pankhurst and Porter 2003). Since the phenology of temperature and photoperiod has not changed over this time period, an interaction between the two is unlikely to explain the rate of phenological advance observed at the NH Line, and other proximate cues may be more influential in the region. Environmental variability along the NH Line includes freshwater input from the Columbia River and coastal streams (Huyer et al. 2007). Freshwater input has been shown to be an important spawning cue for some species (Pankhurst and Porter 2003), and seasonal abundances of forage fishes near the Columbia River plume have been linked to variability in river flow (Kaltenberg et al. 2010). Auth (2011) noted a significant link between Columbia River outflow and larval abundance of Engraulis mordax, Lyopsetta exilis, and Sebastes species with varying time lags. Hooff and Peterson (2006) found that changes in the NH Line copepod community were more strongly tied to source water variability and lagged remote basin-scale forcing than local oceanic variables. Examination of these alternative factors may yield improved explanations of changing NH Line ichthyoplankton phenology.

Many species that are adapted to a wide latitudinal range exhibit variations in their reproductive strategies and phenology over that range (Neuheimer and MacKenzie 2014; Slesinger et al. 2021; de Araujo Ferreira and Neuheimer 2024), including differences in the relative importance of different spawning cues (Ward et al. 2003) as well as in thermal tolerance limits affecting spawning time and early life survival (McKenzie et al. 2020). In this study, several species that were common between the CalCOFI and NH Line assemblages showed strong differences in their trends at each location. For example, slender sole (Lyopsetta exilis) was categorized as having no long-term linear change in the CalCOFI assemblage (r = 0.07), but showed significant advancing phenology at the NH Line (r=-0.39), -2.86 day year⁻¹). Similarly, blue lanternfish (*Tarletonbeania* crenularis) had no long-term linear change in the NH Line assemblage (r=-0.07), but showed advancing phenology at CalCOFI (r = -0.55, -0.40 dayyear⁻¹). Other species, such as northern anchovy (Engraulis mordax) and English sole (*Parophrys vetulus*), were classified as belonging to the same phenology groups across both regions of the CCE. While some variability may be attributed to differences in sampling methodology and time series metrics at each location, these results underscore the importance of regional assessments rather than generalizing phenological trends across the CCE.

4.4 | Fisheries Management, Limitations, and Future Research

Visser and Both (2005) argued the need for a yardstick against which observed phenological trends should be compared to interpret whether these responses to environmental change are 'sufficient' to limit adverse population effects. Larval fish phenology is often discussed in the context of its relationship to recruitment success through the match-mismatch hypothesis (Cushing 1990), using the phenology of prey availability as the comparative yardstick. Differential sensitivity to environmental cues across trophic levels can result in asynchrony between seasonal predator and prey populations (Edwards and Richardson 2004), potentially leading to year-class failures (Durant et al. 2007).

This study attempted to broadly assess trophic-level matchmismatch through the inclusion of mesozooplankton phenology in our linear models. As noted in Asch (2015), CalCOFI ZDV is an aggregate measure of the abundance of numerous species that do not distinguish prey quality; however, it is assumed to broadly represent the availability of prey for larval fishes. The phenology of CalCOFI advancing species was positively related to mesozooplankton phenology. While mesozooplankton themselves showed no significant long-term change in their phenology, their CTa has been lower (indicating advances) in recent decades. Species with no long-term linear change were also positively related to mesozooplankton phenology in the CalCOFI best-fit model. CalCOFI delaying species showed no relationship with mesozooplankton, suggesting that these species may be most at risk of phenological mismatch. Meanwhile, at the NH Line, species with no long-term linear change were positively related to copepod phenology. Advancing and delaying species also showed a positive relationship with copepod phenology in their second-best models, although this relationship was not significant for advancing species. Northern and southern copepod biomasses on the NH Line are often used as indicators of ecosystem health and the relative contribution of different water masses and allow some estimation of prey quality. Though they may not fully represent larval fish prey, the lack of a strong relationship with copepod phenology for advancing species suggests a potential disconnect with an important environmental variable. In cooler regions, there is a narrower optimal window for spawning as a result of increased environmental seasonality reducing the length of the growing season (Conover 1990, 1992; Lowerre-Barbieri et al. 2011; Slesinger et al. 2021). Therefore, the consequences of mistiming reproduction may be more severe at higher latitudes, with increased likelihoods of experiencing phenological mismatches. This may be one concern, particularly for those NH Line species which are rapidly advancing their phenology out of sync with local environmental variability. Conversely, no-change and delayed species' higher synchrony with prey might indicate a resilience to trophic mismatches.

Multiple factors can affect the timing of seasonal events, and it is important to consider different pathways and alternative causes for observed phenological changes (see e.g., Tillotson et al. 2021). Untangling specific mechanisms of changing larval fish phenology and their relative contributions remains challenging. For instance, linear models relating environmental variability to ichthyoplankton phenology at the NH Line explained little variance. The addition of variables mentioned previously, such as freshwater input, may improve these results. The magnitude of variables may have more effect than their phenology for some species, or effects could have time lags. Potential interactions between variables leading to non-linear changes in phenology should also be explored. The demographic structure of adult populations has also been shown to be a significant predictor of spawning time (Lowerre-Barbieri et al. 2011), in some cases being equally as important as water temperature (Carscadden et al. 1997; Rogers and Dougherty 2019). While these alternative factors were beyond the scope of our current study, their potential effects should be taken into account in future work. In this study, we did not distinguish between inshore versus offshore samples, nor did we take into account spatiotemporal shifts in source water masses, which may change the timing that spawning adults and larval fishes appear in the sampling area. Exploring these factors will be an important next step to distinguish between phenological shifts in spawning versus changing spatiotemporal distributions.

This study focused on exploring broad, assemblage-wide trends with data averaged over multiple years. Individual species categorized as showing particularly strong correlations between CTa and time (e.g., medusafish [*Icichthys lockingtoni*], CalCOFI, r=-0.94), as well as those species with particularly fast estimated rates of change (e.g., padded sculpin [*Artedius fenestralis*], NH Line, $-5.92 \text{ day year}^{-1}$), may benefit from more focused future research to increase the accuracy of estimated trends and explore more specific environmental drivers, such as those mentioned above. Finally, future studies may explore whether these observed long-term shifts in ichthyoplankton phenology are associated with changes in recruitment success, particularly for species identified to be at risk of trophic-level mismatches and for fished species of commercial interest.

5 | Conclusion

Larval fish phenology is changing throughout the CCE. On average, fishes are appearing earlier in the year, with southern CCE ichthyoplankton continuing to advance at previously observed rates, and northern CCE ichthyoplankton advancing at a similarly fast rate over the past two decades. These long-term changes can be partially attributed to variability in the phenology of upper ocean temperature, zooplankton abundance, and coastal upwelling. Shifts in ichthyoplankton phenology over time may lead to trophic-level mismatches for those species whose rates and directions of change are not synchronized with their prey.

Author Contributions

Kathryn S. Chen: formal analysis, software, visualization, writing – original draft, writing – review and editing. Colleen M. Petrik:

conceptualization, funding acquisition, methodology, project administration, writing – original draft, writing – review and editing. **Rebecca G. Asch:** conceptualization, methodology, writing – review and editing. **Andrew R. Thompson:** data curation, writing – review and editing. **Toby D. Auth:** data curation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the results of this study are publicly available on Zenodo at https://doi.org/10.5281/zenodo.15014303. Ichthyoplankton, mesozooplankton, and temperature data were obtained from California Cooperative Oceanic Fisheries Investigations (CalCOFI) at https://calcofi.org/data/. The Bakun upwelling index data were obtained from the Environmental Research Division of the US National Oceanic and Atmospheric Administration at https://ocean view.pfeg.noaa.gov/products/upwelling/dnld. The Oceanic Niño Index v5 used to characterize the El Niño-Southern Oscillation were obtained from the Climate Prediction Center of the US National Oceanic and Atmospheric Administration at https://origin.cpc.ncep.noaa.gov/produ cts/analysis_monitoring/ensostuff/ONI_v5.php.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.