

Responses of ichthyoplankton assemblages to the recent marine heatwave and previous climate fluctuations in several Northeast Pacific marine ecosystems

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Abstract

The effects of climate warming on ecosystem dynamics are widespread throughout the world's oceans. In the Northeast Pacific, large-scale climate patterns such as the El Niño/Southern Oscillation and Pacific Decadal Oscillation, and recently unprecedented warm ocean conditions from 2014 to 2016, referred to as a marine heatwave (MHW), resulted in large-scale ecosystem changes. Larval fishes quickly respond to environmental variability and are sensitive indicators of ecosystem change. Categorizing ichthyoplankton dynamics across marine ecosystem in the Northeast Pacific can help elucidate the magnitude of assemblage shifts, and whether responses are synchronous or alternatively governed by local responses to regional oceanographic conditions. We analyzed time-series data of ichthyoplankton abundances from four ecoregions in the Northeast Pacific ranging from subarctic to subtropical: the Gulf of Alaska (1981–2017), British Columbia (2001–2017), Oregon (1998–2017), and the southern California Current (1981–2017). We assessed the impact of the recent (2014–2016) MHW and how ichthyoplankton assemblages responded to past major climate perturbations since 1981 in these ecosystems. Our results indicate that the MHW caused widespread changes in the ichthyoplankton fauna along the coast of the Northeast Pacific Ocean, but impacts differed between marine ecosystems. For example, abundances for most dominant taxa were at all-time lows since the beginning of sampling in the Gulf of Alaska and British Columbia, while in Oregon and the southern California Current species richness increased as did abundances of species associated with warmer waters. Lastly, species associated with cold waters also increased in abundances close to shore in southern California during the MHW, a pattern that was distinctly different from previous El Niño events. We also found several large-scale, synchronized ichthyoplankton assemblage composition shifts during past major climate events. Current climate projections suggest that MHWs will become more intense and thus our findings can help project future changes in larval dynamics, allowing for improved ecosystem management decisions.

KEYWORDS

California Current, climate change, fish larvae, Gulf of Alaska, ichthyoplankton, marine heat wave, Pacific Ocean

1 | INTRODUCTION

The effects of climate warming on ecosystem dynamics are widespread throughout the world's oceans. Elevated temperatures alter oceanographic conditions which can influence the growth, survival, and distribution of species (Free et al., 2019; Pinsky et al., 2013), alter the availability of prey resources (Beaugrand & Kirby, 2018), and ultimately impact the structure and function of marine food webs (Pecl et al., 2017; Poloczanska et al., 2016). In the Northeast Pacific, large-scale changes in climate associated with the El Niño/Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) have caused several historical large-scale ecosystem shifts with direct impacts on individual species (Koslow et al., 2017; Lilly & Ohman, 2018), assemblage structure (Peabody et al., 2018), and ecosystem production (Hare & Mantua, 2000; Levin & Möllmann, 2015).

Recently, unprecedented warm ocean conditions from 2014 to 2016, also referred to as a marine heatwave (MHW, Bond et al., 2015; Di Lorenzo & Mantua, 2016), caused extensive changes to the physical and biological oceanographic conditions in the Northeast Pacific. This MHW started with the appearance of a large body of anomalously warm offshore water in the central North Pacific Ocean due to relaxed winter mixing (Bond et al., 2015) that appeared in coastal waters of the Northeast Pacific during 2014. This was followed by a strong El Niño event during 2015–2016 impacting much of the Northeast Pacific (Di Lorenzo & Mantua, 2016). Combined, these anomalous conditions can be classified as a severe MHW, which lasted ~710 days (almost three times as long as the next longest recorded MHW worldwide; Hobday et al., 2018), and was the warmest 3-year period on record (since 1920) in the California Current (Jacox et al., 2018). The MHW caused widespread changes to the food webs at all trophic levels, from phytoplankton (Peña et al., 2018) to fishes, seabirds, and marine mammals (Brodeur et al., 2019; Jones et al., 2018; Piatt et al., 2020; Yang et al., 2019). Impacts appeared in the form of low abundances of several normally abundant invertebrate and fish taxa (Brodeur et al., 2019), changed spatial distributions and phenology (Auth et al., 2018; Sanford et al., 2019), which contributed to poor prey condition (von Biela et al., 2019), and reduced survival (Jones et al., 2018; Piatt et al., 2020). Yet, due to differences in functional and life-history traits (Sunday et al., 2015), responses were not ubiquitous and several species instead flourished during this period (Cavole et al., 2016; Thompson, 2018).

Variation in the abundance of larval fishes reflects a combination of changing adult spawning stock biomass and cumulative mortality experienced up until the time of sampling (Hsieh et al., 2005; Koslow et al., 2011; Llopiz et al., 2014). In addition, while, adult and juvenile marine fishes occupy a myriad of habitats

(e.g., mesopelagic, neustonic, benthic), larvae from almost all species reside in the upper 100 m of the water column and therefore sampling larvae provides important ecological insights into fish community dynamics as a whole. Larval fish abundance, spatial distribution, and phenology respond quickly to environmental variability (Asch, 2015; Auth et al., 2018; Goldstein et al., 2018; Koslow et al., 2017), and commonly larvae have narrower thermal tolerances than larger individuals (Pörtner & Peck, 2010). Larval stages are thus commonly more sensitive to climatic fluctuations, making them valuable as indicators of changes occurring in the ecosystem (Boeing & Duffy-Anderson, 2008; Brodeur et al., 2008). However, even similar taxa or species within the same assemblage can show diverse responses to environmental perturbations (Doyle et al., 2019; McClatchie et al., 2018; Morley et al., 2017). Understanding how ichthyoplankton assemblages respond to climatic variation can provide insight into food web processes, changes to adult populations and may also indicate failed recruitment (Bailey & Houde, 1989), though for many species a clear link between early-life history and recruitment seldom exists (Lowerre-Barbieri et al., 2016).

The Gulf of Alaska and California Current ecosystems have experienced dramatic shifts in the ichthyoplankton assemblages in recent decades (Brodeur et al., 2008; Koslow et al., 2017; Marshall et al., 2019). In the California Current, the assemblage structure of both adult and larval fishes has exhibited substantial changes in abundance (Koslow et al., 2017), including a rapid, long-lasting increase in warm-water mesopelagic species beginning in 1976 (Peabody et al., 2018), and massive boom and bust cycles of northern anchovy (*Engraulis mordax*) and Pacific sardine (*Sardinops sagax*; Thompson, et al., 2019). Moreover, shifting distributions (McClatchie et al., 2018) and earlier or protracted spawning phenology in the California Current (Asch, 2015; Auth et al., 2018) were documented for several, but not all, species. Off the coast of British Columbia, changes in sea surface temperature (SST) and zooplankton biomass appear significantly related to the spatiotemporal distributions of Pacific herring (*Clupea harengus*; Godefroid et al., 2019). In the Gulf of Alaska, species such as walleye pollock (*Gadus chalcogrammus*), Pacific cod (*Gadus macrocephalus*), and northern rock sole (*Lepidopsetta polyxystra*) commonly decline during warm ocean conditions, whereas rockfishes (*Sebastes* spp.) and southern rock sole (*Lepidopsetta bilineata*) show opposite patterns and tend to co-occur in higher abundances (Doyle & Mier, 2016).

Major climate oscillations cause changes in physical and biological oceanographic conditions, which, in turn, influence local larval dynamics (Boeing & Duffy-Anderson, 2008; Peabody et al., 2018). However, the recent MHW differed from past warming (Lilly & Ohman, 2018) as seen by the first records of several

warm-water zooplankton species (Peterson et al., 2017), and the highest ever concentrations of winter-spawned (January–March) Pacific hake (*Merluccius productus*), Pacific sardine, and northern anchovy larvae off Oregon (these species are normally summer spawning species in this region; Auth et al., 2018). This could indicate that the impact and prolonged extent of the MHW on fish assemblages was different and potentially more severe compared to past warming events.

Few efforts have compared ichthyoplankton dynamics across several large marine ecosystems throughout the Northeast Pacific. However, such cross-ecosystem analyses could elucidate the magnitude and scale of potential shifts in fish assemblages. The timing of larval assemblage responses to major climate oscillations could be synchronous across different ecoregions or alternatively show substantial local adaptations to regional oceanographic processes within each ecoregion (Thompson et al., 2014). For example, ENSO events commonly originate in the tropics and can have lagged influences further north (Di Lorenzo & Ohman, 2013), which can result in quasi-synchronous assemblage shifts (Beaugrand et al., 2015), while PDO oscillations have been linked to inverse production regimes between the Gulf of Alaska and California Current ecosystems (Hare et al., 1999). There is currently no cross-ecosystem assessment of the effects of the recent MHW on fish larval dynamics. It would be informative to know if the MHW resulted in unique patterns or whether changes of similar magnitude have occurred in the past (e.g., during strong ENSO events), as well as whether the impacts differed among large marine ecosystems. Given expected future climate warming and potential occurrence of warming events similar to the recent MHW (Frölicher et al., 2018), such analyses will provide an important first look at the potential structure of future ichthyoplankton assemblages along the Northeast Pacific Shelf.

Ecological time-series provide valuable data for assessing how natural systems are perturbed by environmental changes (Edwards et al., 2010). Here, we analyze time-series of ichthyoplankton abundances from four adjacent ecoregions ranging from subarctic to subtropical large marine ecosystems: the Gulf of Alaska (1981–2017), British Columbia (2001–2017), Oregon (1998–2017), and southern California Current (1981–2017). First, we assess the impact of the recent MHW in 2014–2016 on ichthyoplankton assemblages. Second, we assess if there are synchronized or divergent responses among ichthyoplankton assemblages across all four regions over time. We pose the following hypotheses:

- The impact of the MHW on ichthyoplankton abundances, species richness, and presence of warm-water and cold-water species was pronounced and widespread across all ecoregions.
- Due to the length and magnitude of the MHW, the ichthyoplankton assemblage responses were different compared to past warm events.
- Ichthyoplankton assemblages have responded synchronously to past large-scale climatic variation.

2 | MATERIALS AND METHODS

2.1 | Data sources

We analyzed long-term larval data from four ecoregions, which we refer to as western Gulf of Alaska, British Columbia, Oregon, and southern California Current (Figure 1). Though the latter three sampling programs all occur in the California Current, we refer to these by the location names to avoid confusion. Sampling procedures for each region are described below and summarized in Table S1.

In the western Gulf of Alaska, the National Oceanic and Atmospheric Administration (NOAA) Alaska Fisheries Science Center (AFSC) has conducted ichthyoplankton surveys annually from 1981 to 2011, and biennially in odd years from 2013 to 2017. Pre-flexion and flexion stage larvae were collected using a 60 cm diameter bongo net with either a 333 or 505 μm mesh size, or in a few cases from a 1 m^2 Tucker trawl equipped with 505 μm mesh. Previous studies have shown comparable catch rates among these mesh sizes and gears (Boeing & Duffy-Anderson, 2008; Shima & Bailey, 1994). Oblique tows extend from the surface to 10 m off bottom or 200 m, whichever is shallower (Dougherty et al., 2010). Flowmeters in each

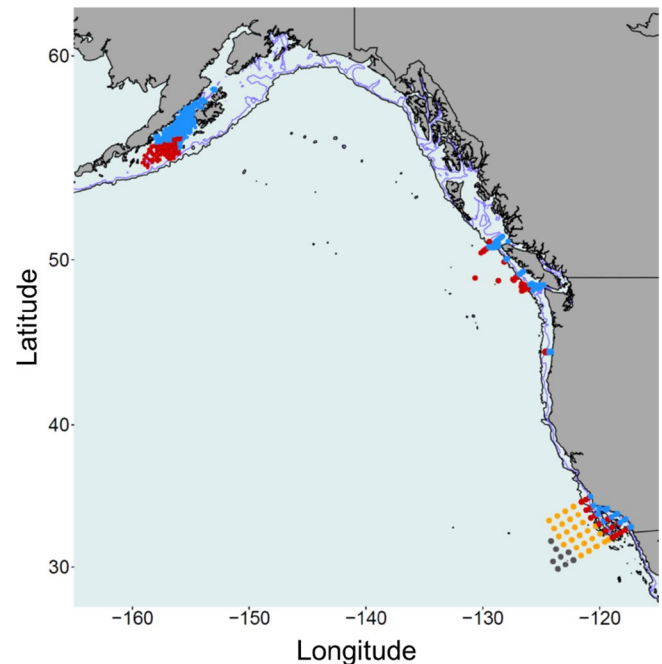


FIGURE 1 Overview of the ichthyoplankton data grouped according to the spatial clustering prior to the time-series analyses across the Northeast Pacific Ocean starting in the north, from the Gulf of Alaska (1981–2017), with data from the southern (red) and Shelikof (blue) areas, British Columbia (2001–2017), offshore (red) and inshore (blue) areas, Oregon (1998–2017), offshore (red) and inshore (blue) areas, to the southern California Current (1981–2017), inshore (blue), nearshore (red), midshore (yellow), and offshore (gray) areas. Blue (200 m) and black (1,000 m) lines denote bathymetry contours [Colour figure can be viewed at wileyonlinelibrary.com]

net were used to estimate the volume of water filtered, allowing quantification of larval catch per unit effort. Samples were stored in 5% formalin and then identified to the lowest taxonomic level (commonly species, but in some cases genus) at the Plankton Sorting and Identification Center in Szczecin, Poland. Additionally, taxonomy was verified by AFSC experts (Matarese et al., 2003).

Ichthyoplankton from the southern continental shelf of British Columbia (off the coast of Vancouver Island) have been consistently sampled by Fisheries and Oceans Canada (DFO) since 2001. Ichthyoplankton sampling in this region has been focused on surveys in late-spring (usually May) at 30–50 stations along the west coast of Vancouver Island. Standard sampling protocols used either a 58 cm diameter bongo frame fitted with black 253 μm mesh nets or a 56 cm diameter bongo frame with black 236 μm mesh nets. A flowmeter was placed in the mouth of one side of the bongo frame to estimate the volume of water filtered. In earlier years, some surveys used a single net SCOR frame with a diameter of 56 cm and a net with 335 μm mesh. Tow profiles were typically vertical hauls from 250 m or 10 m above bottom to the surface. Occasional oblique net tows were also conducted. Samples were preserved in 10% formalin and all ichthyoplankton were identified to the lowest possible taxonomic level in the DFO laboratory at the Institute of Ocean Sciences, Sidney, BC. Larval fish identified as pre-flexion and flexion stages were used for our analyses (see Mackas et al., 2001, for further details on the sampling program in British Columbia).

Off the central Oregon coast, ichthyoplankton samples were collected from five stations spaced ~ 9 km apart along the Newport Hydrographic line (NH; N 44.65°, W 124.10–124.65°). Sampling was conducted in winter approximately every 2 weeks between January and beginning of April in 1998–2017. Due to inclement weather or equipment malfunctions, all stations were not sampled during all surveys. Sampling was conducted primarily at night using either a 1 m diameter ring net with 333 μm mesh or a 60 cm diameter bongo net with 200 μm mesh (333 μm after 2005). A depth recorder and flowmeter were placed in the net during each tow to determine tow depth and volume of water filtered. Each net was fished as a double oblique tow within the upper ~ 30 m of the water column at a retrieval rate of ~ 30 m/min and a ship speed of 0.5–0.8 m/s. Ichthyoplankton samples were preserved at sea in a 10% buffered formalin seawater solution. In the laboratory, fish larvae from each sample were sorted, counted, and identified to the lowest taxonomic level possible using a dissecting microscope. Sampling protocols are further described in Auth et al. (2018) and Brodeur et al. (2008).

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has been monitoring larval fish assemblages continuously off the coast of California from 1951 to the present. Although sampling methodology, as well as spatial and temporal sampling intensity, has varied through time (Thompson et al., 2017), we focus here on 66 “core” stations that have been consistently sampled during spring cruises, and restrict our focus to data from 1981 to 2017. That allowed direct comparison to the time-series from the other adjacent ecosystems, which was the main focus of our analyses. Thus, previous known assemblage shifts which have occurred

between 1951 and 1980 (Peabody et al., 2018) are not assessed in the current analysis. The stations are located along six lines that run perpendicular to the coast from just north of the US/Mexico border to approximately Pismo Beach, California (Figure 1). At each station, oblique tows using a 71 cm diameter bongo with 505 μm mesh nets equipped with a flowmeter were deployed to 210 m (or within 20 m of the bottom at shallow stations) and towed to the surface. Plankton from the starboard net were preserved at sea in 5% tris-buffered formalin. In the laboratory, larval fishes were sorted and identified to the lowest possible level of taxonomic resolution. All individual larvae were identified to species except for those that could not be differentiated based on morphology (Thompson et al., 2017). Larval counts were divided by the proportion of the sample that was sorted (samples with very high species volumes were partially sorted) following standard CalCOFI protocols (Kramer et al., 1972).

For all ecoregions, catches are reported as individuals per 10 m². To obtain consistent temporal coverage and minimize bias due to differences in larval development among years, we used data sampled within consistent time periods within each region and included taxa identified to the species and genus level. In the Gulf of Alaska, samples collected between day-of-the-year (DOY) 135 (May 14) and 160 (June 8) were used. In the British Columbia region, the best spatiotemporal coverage was between DOY 119 (April 29) and 181 (June 30). For the Oregon sampling, data were restricted to samples between DOY 22 (January 22) and 93 (April 3). For California (CalCOFI), we similarly focused on spring data from March and April. Because these winter and spring data were collected with different methods in each region, and samples covered different depths and spatiotemporal periods, quantitative abundance estimates are comparable within a region, while cross-ecosystem comparisons were restricted to trends and time-series dynamics.

To determine if changes in Northeast Pacific ichthyoplankton assemblage dynamics are related to variable ocean conditions, we collated regional climate datasets for the four study regions. As a proxy for the regional climate, SST (Figure 2a) from the NCAR/NCEP reanalysis project for the core areas of the Gulf of Alaska (N 55.0–56.0°, W 154.0–155.0°), British Columbia (N 48.5–49.5°, W 127.5–128.5°), Oregon (N 44–45°, W 125.0–125.5°), and southern California Current (N 32–33°, W 120.0–122.0°) were acquired from <https://www.esrl.noaa.gov/psd/cgi-bin/data/timeseries/timeseries1.pl>. Monthly data from January to April were averaged to represent annual winter-spring SSTs for each region. We focused on winter and spring temperatures since the ichthyoplankton were collected in winter and spring. In addition, the Oceanic Niño Index (ONI; Figure 2b), which characterizes El Niño and La Niña events, was acquired from https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. Using the ONI index, we categorized ENSO events based on the 3-month average of December–January–February. ENSO events were considered strong if anomalies exceeded 1 (El Niño) or were below -1 (La Niña; Santoso et al., 2017). ENSO anomalies commonly peak during winter period. For the purpose of our analyses and the timing of our sampling considered, we consistently refer to an ENSO event as associated

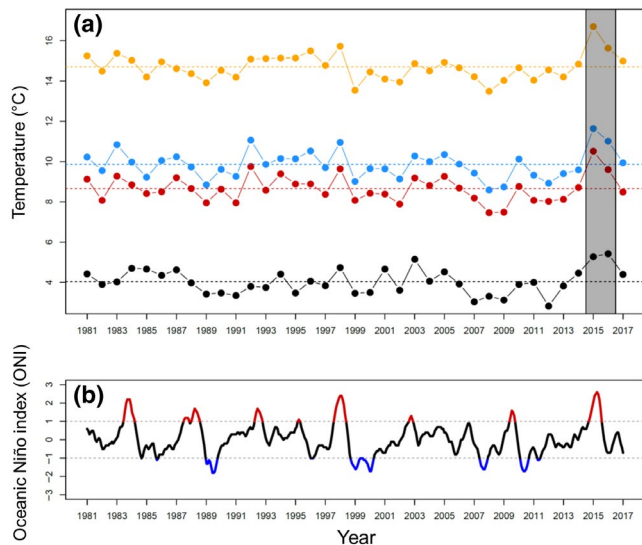


FIGURE 2 Long-term trends in (a) mean January–April sea surface temperature, from the Gulf of Alaska (black), British Columbia (red), Oregon (blue), and southern California Current (yellow), (b) the ONI index. Dotted lines in (b) denote average temperature for each region for the period 1981–2017. Gray shaded area demarcates the marine heatwave reference period (2015–2016). Dotted lines in (b) denote threshold of 1 anomaly used to denote “strong” ENSO events, with El Niño shown in red and La Niña periods shown in blue [Colour figure can be viewed at wileyonlinelibrary.com]

with the latter year. In other words, the El Niño event measured in December–January–February of 1997–1998 is referred to as a 1998 event when comparing to the ichthyoplankton larval dynamics.

2.2 | Data standardization

To standardize spatial coverage of the surveys, each observation was associated with a spatial grid cell of 25×25 km for the Gulf of Alaska, British Columbia, and southern California regions. Only grid cells that had data for at least half the years of the total time-series were included. Within each grid, mean values were calculated for that specific grid cell for each species/genus for each year. A spatial clustering approach was then used to identify spatial areas within each region that shared the most similar ichthyoplankton communities. The purpose of the spatial clustering analysis was to identify areas that had similar species compositions within each region. For example, offshore regions commonly have distinctly different species composition compared to coastal areas. Bray–Curtis dissimilarities were calculated from $\log_e + 1$ -transformed data, and then spatial clusters were estimated using a flexible beta of -0.25 (Lance & Williams, 1967). This approach was not used for the Oregon region where fewer stations were sampled; instead, data were grouped into time-series representing “inshore” (stations NH 5 and NH 10) and “offshore” (stations NH 15, NH 20, and NH 25) based on distance from the coast (station designations represent number of nautical miles from the coast). Time-series were then constructed as annual means from each separate cluster

for the different regions. Unbiased means of larval abundances were used as we found no substantial differences between unbiased mean values, delta means, and spatially weighted Voronoi corrected mean values. The final larval dataset for the comparative analyses included two time-series from the Gulf of Alaska region (southern region, Shelikof Strait), two from British Columbia (inshore, offshore), two from Oregon (inshore, offshore), and four from California (inshore, nearshore, midshore, and offshore; Figure 1). Names are semantic and used here to denote the boundaries between regions identified by the spatial clustering and are not directly comparable among different ecosystems. Cluster breaks generally aligned with oceanographic features such as currents and upwelling, though such processes are dynamic features that vary in time.

2.3 | Analyses of MHW larval assemblage dynamics

First, we assessed how the MHW impacted the ichthyoplankton assemblages. To do so, we contrasted total larval abundance (expressed as number of individuals per 10 m^2) and species richness (number of species observed) estimates during the MHW years to all other sampled years for each region. We considered 2015 and 2016 as the MHW years (which include the El Niño event in 2015/16) and thus the period where the ichthyoplankton would primarily reflect impacts from the MHW. It is acknowledged that the MHW started in 2014 in the North Pacific, however given that our ichthyoplankton collections were done during winter and spring, impacts of the MHW may not yet have been present in the 2014 data throughout the ecoregions, particularly in the south. Species richness estimates were first corrected for sampling effort using rarefaction curves since sampling extent and effort varied among years within the areas (as defined by the spatial cluster analyses), following recommendations in Gotelli and Colwell (2001). Rarefaction curve corrections allowed for the corrected species richness comparison among years within an area, but not across areas or regions, and also did not represent total species coverage (i.e., 100% species richness within an ecosystem). Based on the rarefaction curves, species richness was then computed from the average sample sizes (i.e., the spatial grid points used to calculate annual spring averages) across all years. The average sample sizes were 58 and 33 in the Gulf of Alaska Shelikof and southern regions (Figure 1), respectively. For the British Columbia regions, annual sample sizes were 10 for the offshore and 21 for the inshore data. In the Oregon inshore region, the sample size was 6, while for California, the mean sample sizes were 14, 16, 24, and 8 for the inshore, nearshore, midshore, and offshore areas, respectively. Years that had fewer samples than half the mean sample size number were considered uncertain and were excluded. For the Oregon offshore region, too few samples were available to calculate robust species richness curves, and since species richness appeared correlated with sample sizes, species richness estimates were not considered from this region.

In addition, we assessed the total abundance of warm-water and cold-water affinity species during the MHW as indicators of changes

to the ichthyoplankton fauna in each region (species list in Table S2). Estimates of warm-water and cold-water larval abundances were z-scored and standardized for comparisons. Warm-water and cold-water affinity species followed previous established categorizations based on responses to ocean temperatures (e.g., Brodeur et al., 2008; Doyle & Mier, 2016; Hsieh et al., 2005; Table S2), though it is acknowledged that some species have fairly large geographic ranges.

2.4 | Cluster analyses

Next, we used two types of two-way clustering approaches (i.e., unconstrained and chronological) to assess changes in ichthyoplankton assemblages for each ecoregion. For the cluster analyses, we used the 30 most abundant species and only included species that were present two or more years. This resulted in a lower number of species included for the British Columbia inshore (20), offshore (13), and Oregon offshore (26) regions. Unconstrained two-way clustering groups similar years based on their ichthyoplankton assemblage dynamics. The purpose of the two-way clustering was to assess the potential rarity of the ichthyoplankton assemblage compositions during the MHW (i.e., the years 2015 and 2016) compared to previous years, and compare the assemblage compositions in the year 2017 following the MHW. In other words, did the ichthyoplankton assemblages return to non-heatwave conditions after the MHW had subsided? If the years 2015 and 2016 aligned in different clusters, we referred to 2015 as the MHW year, since 2015 was the main period of the MHW (Hobday et al., 2018) and also was the only MHW year sampled in the Gulf of Alaska. The unconstrained two-way cluster analyses were performed using Ward's minimum variance method on $\log_e + 1$ -transformed data. We visually examined each year cluster and identified deep obvious breaks as indication of clear assemblage differences and then determined which years fell within the cluster that contained 2015.

The chronological clustering approach constrains the years to a chronological order and, thus, can be used to identify temporal assemblage shifts over time (Morse et al., 2017; Peabody et al., 2018; Perretti et al., 2017). The chronological clustering technique allowed us to assess to what extent changes to the ichthyoplankton assemblages have occurred in the past, and determine if and when potential shifts have occurred at similar times along the entire coast. Because large-scale climatic shifts in the physical environment may originate in one area and take months before impacts on the fauna in other ecosystems are detectable, we considered coast wide assemblage shifts to be events occurring in either a single year or quasi-synchronized across two adjacent years. Chronological clustering conducts hierarchical clustering of a distance matrix, where clusters are constrained by sample time (in our case year). We used the *coniss* agglomeration method (Grimm, 1987) when running the chronological clusters. Because our time-series were relatively short, common statistics such as broken stick (Bennett, 1996; Morse et al., 2017) or multivariate regression trees (De'ath, 2002; Perretti et al., 2017) often fail to statistically

characterize assemblage shifts. To categorize assemblage shifts, we therefore visually identified years where deep transitions occurred from the chronological clusters following methods as described by Thompson, et al. (2019). Data were $\log_e + 1$ -transformed and the analyses performed on Bray–Curtis dissimilarity matrices. All statistical analyses and plotting were conducted in R (R Core Team, 2018) using R-packages *cluster* (Maechler et al., 2018), *rioja* (Juggins, 2019), *gplots* (Warnes et al., 2016), *dendextend* (Galili et al., 2015), and *ggplot2* (Wickham, 2016).

3 | RESULTS

In all ecoregions winter-early spring (January–April) SSTs were elevated during the MHW and higher than previous warm years such as in 1998, 2005, and 2010 (Figure 2a). The year 2015 was the warmest in the time-series for the British Columbia, Oregon, and southern California Current regions. In the Gulf of Alaska, only spring temperature in 2016 was slightly warmer than 2015. The defined threshold of ± 1 anomaly showed that El Niño events occurred during 1982–1983, 1986–1987, 1987–1988, 1991–1992, 1994–1995, 1997–1998, 2002–2003, 2009–2010, and 2015–2016. La Niña events were present during 1988–1989, 1995–1996, 1998–1999, 1999–2000, 2007–2008, 2010–2011, and 2011–2012 (Figure 2b).

The ichthyoplankton data during the MHW showed highly anomalous patterns in most regions, but not in consistent ways. Total larval fish abundances in 2015 were very low in both Gulf of Alaska areas (south, Shelikof Strait) and in both the British Columbia inshore and offshore areas (Figure 3a). In the Gulf of Alaska, low abundances in 2015 were evident in seven of the 10 most the common and dominant species, such as *G. chalcogrammus*, *G. macrocephalus*, *H. elassodon*, while only *Sebastes* spp. and *S. leucopsarus* were present in higher abundances (Figure S1). In British Columbia, larval abundances of *Sebastes* spp. and *S. leucoparus* were low, while species such as *R. jordani* and *P. thompsoni* were higher than average in both regions. For the Oregon inshore and offshore regions, total larval abundances in 2015 and 2016 reached the highest levels ever measured (Figure 3a) due mainly to record-high numbers of northern anchovy and Pacific sardine larvae (Figure S1). In addition *Chitharichthys* spp. and *G. zachirus* were very high, while *Ammodytes* spp. were very low. Total larval abundances in Southern California showed average values during the MHW compared to other years and were similar between 2015 and 2016. Common species of northern anchovy and sardines were below average, while *Sebastes* spp. were above average in the nearshore and inshore regions. Offshore abundances of *Vinciguerria* spp. were the third highest observed during the time period while Pacific sardines again showed low abundances. Most other species in the offshore and midshore regions were close to average.

Corrected species richness estimates were also anomalous in several of the regions during the MHW. In the southern California Current system, corrected species richness was among the highest in 2015 and 2016, particularly in the inshore, nearshore, and midshore regions (Figure 3b). In Oregon, corrected species richness

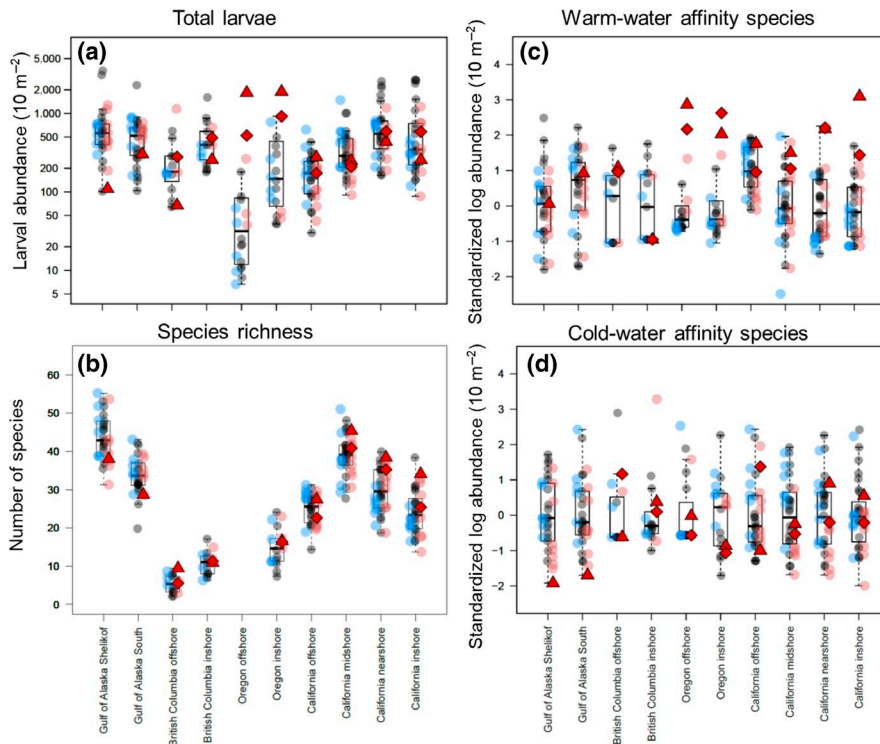


FIGURE 3 Comparison of marine heatwave anomalies for 2015 (red triangle) and 2016 (red diamond), with past El Niño years shown in red, average years in black, and La Niña years in blue. Data shown are (a) total larval abundances, (b) sample-corrected species richness, and standardized (z-scored) log abundances of (c) warm-water and (d) cold-water assemblages (warm-water and cold-water species shown in Table S2). Note that in (a) y-axis is log transformed. Boxes indicate the 25th and 75th percentiles [Colour figure can be viewed at wileyonlinelibrary.com]

was average during the MHW. For British Columbia, the inshore area had average species richness while richness in the offshore area was high. In the Gulf of Alaska, corrected species richness in both the south and Shelikof areas were among the lowest observed (Figure 3b).

Standardized abundances of warm-water affinity species were at an all-time high in Oregon during the MHW in 2015 and 2016 (Figure 3c), driven by northern anchovies and Pacific sardines. Similarly, in the inshore and nearshore southern California Current, standardized abundances of warm-water affinity species reached their highest levels in 2015 and third highest in 2016. In the mid-shore and offshore areas, abundances in 2015 were sixth and fourth highest, respectively, out of the 35 years sampled, while values for 2016 were still high but slightly lower than 2015. In British Columbia, warm-water abundance values for 2015 and 2016 were high in the offshore areas, but low in the inshore area (Figure 3c). In the Gulf of Alaska, standardized abundance values of warm-water taxa were among the highest in the southern area in 2015, but below average in the Shelikof Strait. Abundances of cold-water affinity taxa in 2015 was overall among the lowest ever observed in most of the regions (Figure 3d). Exceptions were in inshore British Columbia, and in the inshore and nearshore region of southern California. The latter results in the southern California current were unlike previous warm years and unlike the 2016 El Niño year, and could reflect that the relatively high upwelling close to shore observed during the MHW resulted in adequate conditions for cold-water larvae. Combined our analyses suggest that larval patterns in 2015 during the MHW were unusual, but the responses were different among ecoregion. Our analyses also showed that values in both 2015 and 2016 were commonly but not always distinct from the other years for a given area,

supporting the multi-year impact of the MHW. There were no samples in 2016 for the Gulf of Alaska areas due to biennial sampling.

Summaries of the unconstrained two-way cluster analyses revealed that the impact of the MHW on the ichthyoplankton assemblage composition was evident in 2015 and 2016, but that by 2017 it had largely subsided in the examined ecoregions (Figure 4a). An example of an individual two-way cluster plot for the Gulf of Alaska Shelikof region is shown in Figure 4b, while all other individual two-way cluster analyses plots are available in the Supporting Information (Figure S2). Overall, the larval assemblages in 2015 were similar to those in 2016 (red ovals, Figure 4a), except for British Columbia and the inshore California area where 2014 was in the same cluster as 2015 but not 2016 (gray ovals, Figure 4a). In contrast, there were few similarities between 2015 and 2017 indicating that the impact of the MHW in 2015 and 2016 on the ichthyoplankton fauna had subsided by 2017. Combined, our analyses indicate that the impact of the MHW on the ichthyoplankton fauna was widely visible in 2015 and 2016 across all systems.

The second purpose of the two-way cluster analyses was to assess how unusual the ichthyoplankton composition was during the MHW compared to previous years. The ichthyoplankton assemblage compositions during the MHW were different from almost all past years (<2014; Figure 4a) except for the Gulf of Alaska region. In the southern California Current (California) regions, only three previous years (not the same for each region) appeared similar to the MHW cluster. In the Oregon region (1998–2017), one (offshore) and zero (inshore) previous years were associated with the cluster that included the MHW years (Figure 4a). In British Columbia, albeit the shortest time-series (2001–2017), zero (offshore) and three (inshore) previous years appeared similar to 2015. For British Columbia, 2015

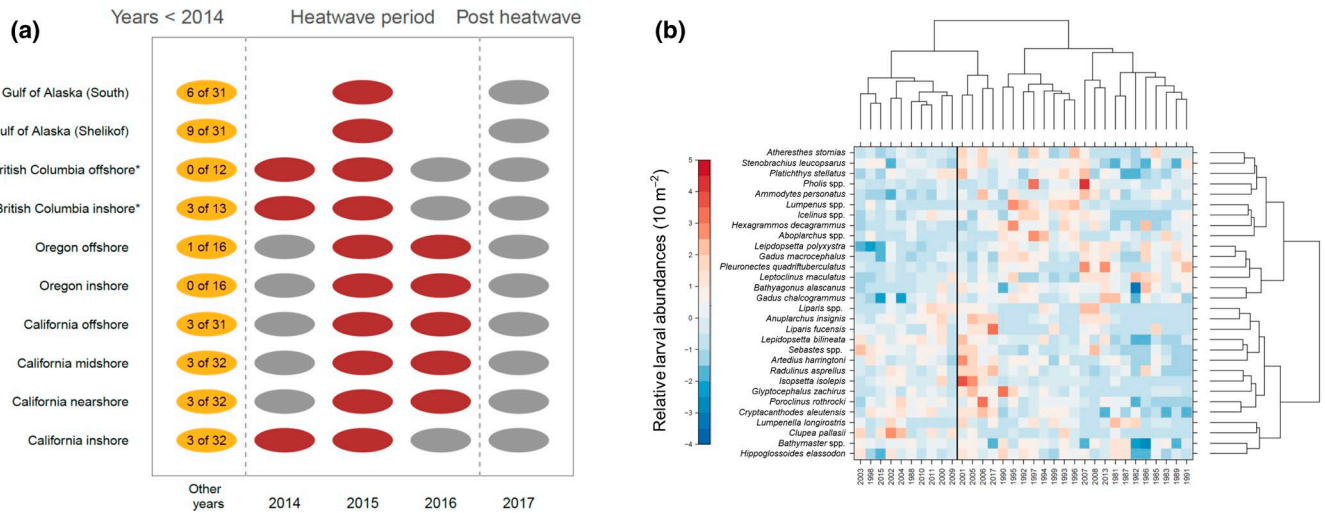


FIGURE 4 (a) Summary of two-way cluster analyses, showing years with similar larval fish assemblages to the marine heatwave (MHW) reference year 2015. For consistency, 2015 was used as the reference year for the MHW, though the MHW was a multiyear event during 2014–2016. Numbers in yellow ovals denote years associated with the MHW cluster relative to total years analyzed for each cluster for years prior to 2014. Red ovals denote years aligned in the same cluster as 2015, while gray ovals denote years that associated with a different cluster than the MHW cluster. *Sampling effort in British Columbia offshore was at times relatively low and thus species composition should be treated with caution. (b) An example of a two-way cluster analysis from the Gulf of Alaska Shelikof region showing which years aligned in the same cluster as 2015 (black vertical line denote the MHW cluster break) and thus indicate similar ichthyoplankton assemblages. See Supporting Information for all other sub-region two-way cluster analyses [Colour figure can be viewed at wileyonlinelibrary.com]

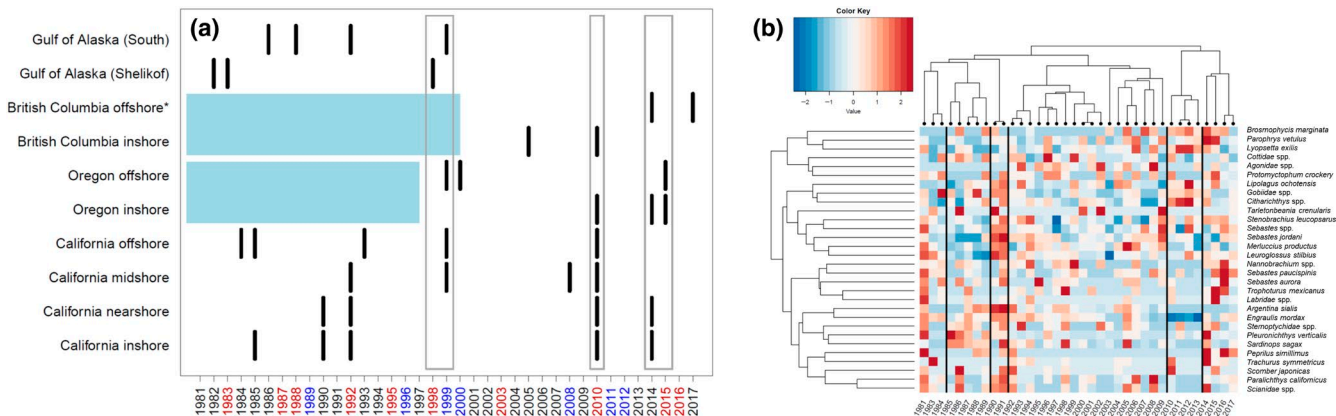


FIGURE 5 (a) Overview of community shifts (black lines) identified using chronological cluster analyses across the Northeastern Pacific Ocean. Gray boxes denote times of common community shifts. Blue shaded areas denote time periods prior to sampling for the British Columbia and Oregon regions. Note that the years 2012, 2014, and 2016 are missing for the Gulf of Alaska. Years are color coded to depict El Niño (red), average (black), and La Niña (blue) events. *Species composition in BC offshore was relatively low and data should be treated with caution. (b) An example of an individual chronological two-way cluster analysis for the inshore California Current region, showing community shifts (vertical black lines) for the years 1985, 1990, 1992, 2010, and 2014. See Supporting Information for all other sub-region chronological cluster analyses [Colour figure can be viewed at wileyonlinelibrary.com]

and 2016 did not cluster together; instead 2014 and 2015 clustered together. In the Gulf of Alaska (no data available for 2014 or 2016), nine (Shelikof) and six (south) other years aligned in the same cluster as 2015, indicating that the larval assemblage composition in the Gulf of Alaska was not very unusual during the MHW, despite the low mean values observed for most common species (Figure 3a). These findings suggest that ichthyoplankton assemblage compositions were different, except for in the Gulf of Alaska, during the 2015–2016 MHW compared to previous observations.

The chronological cluster analyses revealed large-scale concurrent shifts in the Gulf of Alaska, Oregon, and California in 1998–1999. In 2010 and 2014–2015, concurrent shifts were apparent for British Columbia, Oregon, and California (Figure 5a). A smaller assemblage shift was present in the Gulf of Alaska data during 2015 (Figure S3); however, it was not large enough to be considered a deep break. Individual chronological cluster plot for the inshore California Current region is shown in Figure 5b, and all other cluster plots are presented in the Supporting Information (Figure S3). In

addition, assemblage shifts appeared around 1992 for California and the Gulf of Alaska (note: no data from Oregon and British Columbia). These coast-wide shifts in the ichthyoplankton assemblages, which may be quasi-synchronous in that they occurred in adjacent years, all occurred around the time of major climatic phase shifts as shown by the ONI index (Figure 2b). The years 1998 and 2010 were both strong El Niño events followed by climatic transition to La Niña conditions while 2014–2016 was the MHW period.

4 | DISCUSSION

4.1 | Impact of the MHW

As hypothesized, the MHW caused widespread changes in the ichthyoplankton fauna along the coast of the Northeast Pacific Ocean, similar to what has been observed for many marine species in other ecosystems (Poloczanska et al., 2016; Smale et al., 2019). For the majority of the common ichthyoplankton taxa in the Gulf of Alaska and British Columbia, abundances were at or near all-time lows during the MHW. In Oregon and southern California Current, the primary impacts of the MHW were seen in the form of increased species richness and generally high abundances of species that are commonly associated with warmer waters (Auth et al., 2018; Hsieh et al., 2005). A similar pattern of changes in species dynamics was observed during the MHW for zooplankton and micronekton in Oregon (Brodeur et al., 2019; Peterson et al., 2017) and the southern California Current (Lilly & Ohman, 2018; Sakuma et al., 2016). Off the Oregon coast anomalously high larval abundances, primarily northern anchovy, Pacific sardine, and Pacific hake were observed during the MHW: three species whose larvae have seldom been collected in this area during winter (Auth et al., 2018). Our findings of high species richness and increased warm-water affinity species in the California Current, and very low total larval abundances in British Columbia and the Gulf of Alaska indicate that ichthyoplankton assemblages responded markedly to the MHW but also very differently among the ecoregions.

4.2 | How unusual were the effects of the MHW?

Our second hypothesis, that the MHW resulted in unusual and large changes to the ichthyoplankton assemblages compared to previous events, was partly supported. Record high temperatures were visible during the MHW in all ecosystems, and the unconstrained two-way cluster analyses showed that 2015 and 2016 had similar assemblage composition, indicating the multi-year impact of the MHW on larval assemblages. It is important to note that the MHW transitioned from an event where near-surface water temperatures were elevated in 2014–2015 (i.e., the “blob”) into a strong El Niño in late 2015 (Sanford et al., 2019). For British Columbia, Oregon, and California, the assemblage composition during the MHW appeared distinct, as only a few of the previous years clustered with the MHW

period. In addition, the earlier shift observed in British Columbia may reflect the influence from elevated surface water temperatures in the Alaska and British Columbia coastal regions occurring already in spring and summer of 2014 (Bond et al., 2015). In contrast, the ichthyoplankton assemblage in the Gulf of Alaska during 2015 (2016 not sampled) appeared similar to several previous years. For the Gulf of Alaska, this resemblance between years was present despite the fact that abundances were at all-time lows for many dominant taxa in the Gulf of Alaska in the Shelikof region, suggesting that while overall abundance was affected, species' presences were not unusual. The differences among assemblage responses in the different regions suggest that warming from the MHW influenced larval dynamics in different ways. However, our findings also suggest that while temperatures anomalies during the MHW were extreme compared to the past, the resultant ichthyoplankton responses were more nuanced and complex.

Nonetheless, substantial changes to the ichthyoplankton assemblages due to the MHW did occur in each ecoregion. However, it is important to recognize the different impacts that warming temperatures may have in these distinct systems, and consequently, how they structure larval assemblages and eventually food-web linkages. In addition, the impact from the warm event during 2014–2015 and the following El Niño may also have impacted the biota differently. Temperature anomalies at depth were markedly different among regions with differential effects on species (Li et al., 2019). Responses of fishes to temperature variation differ among species, and it appears that shallow water species showed more pronounced distributional shifts compared to deep water species during the MHW (Li et al., 2019). Changing temperatures which influence adults can also shift larval phenologies (Asch, 2015; Auth et al., 2018; Rogers & Dougherty, 2019), which can alter predator–prey dynamics by decoupling spatial and temporal overlap (Asch et al., 2019), as well as adult movement patterns and their spawning outputs (Sundby & Nakken, 2008). Enhanced temperatures also directly influence individual metabolic rates and thus larval growth, survival, and prey availability (Moyano et al., 2017). Changing temperatures also reflect changing oceanographic processes such as onshore transport, which can result in pronounced shifts between inshore and offshore larval assemblages (Koslow et al., 2013; McClatchie et al., 2018). Such processes can alter the strength of stratification between the surface and deeper waters, reducing the flux of nutrients and primary production. In the California Current, warmer temperatures can reflect altered oceanographic patterns, and typically the magnitude of upwelling that provides cold and nutrient-rich water to the coastal region (Peterson et al., 2017). During the MHW, relaxed upwelling and onshore transport caused high influxes of warm-water species such as northern anchovy, Pacific sardine, and Pacific hake that are only very rarely seen at these latitudes in winter and spring in Oregon (Auth et al., 2018). These changes in oceanographic conditions during the warm period also lowered primary production in much of the northern California Current system (Morrow et al., 2018; Whitney, 2015), though carbon export and zooplankton grazing were less affected (Morrow et al., 2018). However, within the California Current, larval

fish responses to warming between the north and south are not necessarily congruent (Thompson et al., 2014). Oceanographic conditions were very unusual in California (approximately N 35°–N 41°) with highly anomalous warm water just offshore abutting anomalously cold water against the shoreline (Fewings & Brown, 2019). In fact, this cold-water intrusion close to shore likely explains the relatively high abundances of cold-water affinity species observed in the two southern California Current regions closest to the coast during 2015. Midwater trawls targeting juvenile and adult fishes during the MHW also detected a unique fish assemblage, as southern mesopelagic species were very abundant in the relatively warm water just offshore while coastal species that depend on cold, nutrient-rich water were very abundant close to shore (Sakuma et al., 2016).

Although temperature is a major forcing factor, other factors also influence assemblage structure. Koslow et al. (2011) have suggested that the influence of midwater oxygen levels also structures mesopelagic larvae distributions. However, oxygen levels generally remained high during the MHW and thus appear unlikely to have caused the changes in larval communities observed in this period. Pacific Subarctic Upper Water that is transported south by the California Current is a major source of oxygenated water in the California current ecosystem (Bograd et al., 2019). Typically, the California Current is suppressed during warm, El Niño conditions in the California current ecosystem (Bograd et al., 2019). From 2014 to 2016, however, the California Current shifted closer to shore during the MHW (Zaba et al., 2020), resulting in the influx of cool, oxygenated waters into much of the southern portion of the study system (Schroeder et al., 2019). Overall, this combination of warm offshore and cold nearshore water off California resulted in very high overall species richness during the MHW (Santora et al., 2017), which is consistent with our results of record high warm-water species and relatively high presence of cold-water affinity ichthyoplankton throughout the California Current ecosystems. In southern California, warm-water affinity fish taxa enter the CalCOFI area from two primary sources during warming periods (Moser & Smith, 1993). First, an assemblage comprised primarily of mesopelagic species associated with central Pacific water often impinge upon the shelf and approach shore during El Niño events, and then recede under La Niña conditions (Moser & Smith, 1993; Thompson et al., 2012). Second, warm-water species can enter the southern California Bight nearshore with the California Undercurrent (McClatchie, 2014). It appears that increased flow of the California Undercurrent greatly affected the ichthyoplankton assemblage in southern California during the MHW as the abundance of warm-water species reached record levels in the California inshore and nearshore regions during the MHW (Thompson, et al., 2019), and this influx coincided with increased presence of Pacific Equatorial-influenced water in the inshore southern California region (McClatchie et al., 2018).

By contrast, the Gulf of Alaska is not a wind-driven upwelling ecosystem where changing temperatures directly reflect movement of distinct water masses (Stabeno et al., 2016). The Gulf of Alaska is generally considered a downwelling system, though the Alaska

Stream, Alaska Coastal Current, and tidal currents intersects islands, topography, and bathymetry to create regional upwelling areas. Thus, rather than influxes of southern taxa and high species richness, the main effect of the MHW on the Gulf of Alaska ichthyoplankton appeared to be very low abundances of many common taxa in the Shelikof region. During 2015, water temperatures were elevated throughout the water column in the Shelikof region from surface to bottom (Yang et al., 2019), and since many of the eggs and larvae occupy deeper waters (Matarese et al., 2003), this may have caused particularly unfavorable conditions for survival and growth. For instance, the hatch success of Pacific cod eggs, which are demersal, is highly dependent on temperature and likely declined as a result of the pronounced warming during the MHW (Laurel & Rogers, 2020). In addition, the availability of larval fish prey, such as zooplankton, was low during the MHW (Kimmel & Duffy-Anderson, 2020). Combined, these studies suggest that in the Gulf of Alaska Shelikof region the low abundances for most major taxa could be due to poor survival (Laurel & Rogers, 2020) as well as changes in spawning phenology (Rogers & Dougherty, 2019) of some taxa. In the southern Gulf of Alaska region, abundances were only slightly below average while warm-water affinity species were among the highest observed since 1981. This could indicate that this region experienced some influxes of more warm-water species from offshore areas during the MHW. Similar processes may also have occurred in the British Columbia offshore region, as seen with the high species richness and relatively high abundance of warm-water affinity species, although this is currently under further investigation.

Assemblage resilience is contingent on whether species assemblages are persistently altered or return to average conditions after a cessation of a climatic perturbation. Analyses of large-scale shifts in ichthyoplankton dynamics should help identify potential changes between ecosystems states (Levin & Möllmann, 2015), even if depicting a full ecosystem regime shift require multi-trophic level data (Beaugrand et al., 2015; Levin & Möllmann, 2015). While fully elucidating if a lasting shift occurred during the MHW likely requires several additional years of larval observations, our results from the unconstrained clustering contrasting the conditions during the MHW with larval samples from 2017 provide an important first look. In all the regions, the ichthyoplankton assemblage composition in 2017 was similar to years before the MHW, but appeared different from those during the MHW, though results were less pronounced in the Gulf of Alaska. This indicates that the ichthyoplankton assemblages returned to more normal pre-heatwave states in 2017. Although we did not have ichthyoplankton data from the Gulf of Alaska in 2016, given that the temperatures were as warm as 2015 (Yang et al., 2019), it is plausible to speculate that the ichthyoplankton fauna in the Gulf of Alaska still resembled MHW conditions in 2016. Despite the unprecedented warm conditions during the 2014–2016 MHW, our analyses indicated that the ichthyoplankton communities showed resilience to major environmental perturbations. Similar to other analysis across multi-trophic levels (Litzow et al., 2020), our findings indicate that the larval assemblages assessed in these large marine ecosystems did not permanently shift to a new stable state

following the MHW. Additional post-event sampling will be needed to confirm this, however the likely occurrences of new MHW events may also make it difficult to distinguish whether any future changes are the result of a single event or accumulated effects from multiple climate events.

4.3 | Synchronized long-term shifts across regions

Our analyses of the long-term ichthyoplankton dynamics using constrained clustering showed several synchronized ecosystem-wide composition shifts. Some shifts occurred in adjacent years and can be considered quasi-synchronized. It is not surprising that there are some regional differences in the exact timing of these major shifts, as has also been observed elsewhere (Beaugrand et al., 2015). Furthermore, large-scale climatic shifts in the physical environment may originate in one area and take months before impacts on the fauna in other ecosystems are detectable (Di Lorenzo & Mantua, 2016). Nonetheless, the chronological cluster analyses revealed clear temporal shifts in the ecoregions from California to the Gulf of Alaska in the years 1998–1999 (British Columbia not sampled), 2010, and 2014–2015 (except Gulf of Alaska). An additional shift was also visible in 1992 (an El Niño event) in the two longer time-series (i.e., the Gulf of Alaska and southern California Current). The timing of these shifts also concurs with previously documented shifts in the ichthyoplankton fauna during past El Niño events, in both the California Current (Auth et al., 2015) and Gulf of Alaska (Bailey & Picquelle, 2002; Boeing & Duffy-Anderson, 2008). Thompson et al. (2014) noted that El Niño events appear to cause larger impacts on assemblages than La Niña events in the California Current. Our analyses showed that while assemblage shifts appear to primarily occur during El Niño events, wide-scale changes also seemed to occur during periods of pronounced phase shifts (i.e., transition between El Niño and La Niña phases), such as in 1998–1999 and 2010.

Chronological cluster analysis characterizes strong shifts of alternative phases over time (Peabody et al., 2018; Perretti et al., 2017). Consequently, this method is suitable for identifying abrupt changes in assemblage structure while these analyses will not capture gradual changes that are perhaps due to slower, long-term ecosystem changes. In addition, the technique is not always capable of depicting shifts at the beginning or ends of time-series. The method failed to detect a shift in the Gulf of Alaska areas during the MHW in 2015 despite the very low abundances of the majority of the most common taxa. A smaller shift was visible in the cluster analyses, but not to the extent that it could be identified as a true assemblage shift. Yet, it is clear that major changes to abundances of most of the common species occurred in this ecosystem during the MHW. Thus, the lack of a clearly identified shift is more likely a limitation of the chronological clustering method in failing to detect a breakpoint for the Gulf of Alaska in the years 2013, 2015, and 2017, which were all highly variable and different from one another in terms of their larval compositions.

5 | FUTURE PERSPECTIVES

Understanding how atmospheric and oceanographic changes influence larval fish assemblages can give key insights into the response of ecosystems to climate variability. As a component of the lower trophic community, larval fish assemblages respond rapidly to bottom-up forcing (Boeing & Duffy-Anderson, 2008), and can be important sentinels of impending future responses by mid- and upper-trophic levels, which can lag physical changes by several years (Walsh et al., 2015). In addition, the presence of fish larvae is indicative of spawning, which may be harbingers of potential climate-mediated range shifts and colonization of new habitat by itinerant adult species. Finally, climate-mediated changes in phenology and magnitude of spawning, with both positive and negative species-specific responses (Cavole et al., 2016), can be detected from studies of larval fish variability (Asch, 2015). Our analyses, covering major ecosystems from the Gulf of Alaska to Southern California, showed that previous warm events clearly affected ichthyoplankton assemblage dynamics, likely through changed larval mortalities and/or distributional shifts. Such shifts can have major impacts on recruitment dynamics, as seen for walleye pollock and Pacific cod in the Gulf of Alaska, as well as Pacific sardine and northern anchovy in the California Current region (Checkley et al., 2017). It has also been estimated that the effects of MHW on production of important fishery species in the Northeast Pacific were substantially greater than those estimated using predicted global warming trends alone (Cheung & Frölicher, 2020).

Layered on top of long-term warming trends (Frölicher et al., 2018), current climate projections suggest that MHWs will become more intense under global warming (Oliver et al., 2018). Indeed, in 2019, ocean temperatures in the Northeast Pacific were again much warmer than average during the summer and fall (Amaya et al., 2020). Preliminary larval observations from the Gulf of Alaska and British Columbia for 2019 appear consistent with many of the patterns shown in our analyses for 2014–2016 as abundances of many common species were again low. Also, the presence of normally rare southern Pacific hake and protracted seasonal spawning of northern anchovy were observed again off Oregon during winter of 2019. In southern California, offshore warm-water affinity mesopelagic species were again at near record high abundances in 2019 and similar to the 2014–2016 MHW. Such large and sudden climate perturbations have been shown to cause whole-scale ecosystem shifts known as regime shifts, including in the California Current and Gulf of Alaska in the past (Hare & Mantua, 2000). What were once highly unusual thermal conditions are likely to become more common with long-term climate warming and may result in novel shifts in marine ecosystems.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

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

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