Putting the Pacific marine heatwave into perspective: The response of larval fish off southern California to unprecedented warming in 2014–2016 relative to the previous 65 years

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Abstract

The 2014-2016 Northeast Pacific Marine Heatwave (MHW) induced the warmest 3-year period on record in the California Current Ecosystem. We tested whether larval fish assemblage structure, phenology and diversity dynamics were comparable to past warming events from 1951-2013. First, we hypothesized, based on past observations of biological effect of warming, that mesopelagic species with southern distributions relative to southern California and Pacific sardine *Sardinops sagax* (a coastal pelagic species) would increase during the MHW while northern mesopelagics and northern anchovy *Engraulis mordax* (coastal pelagic) abundances would decline. Similar to past warming, southern mesopelagics increased and northern mesopelagics decreased. Unexpectedly, however, a common southern mesopelagic, Mexican lampfish *Triphoturus mexicanus*, was approximately three times more abundant than the previous annual high. Further, whereas sardine abundance did not increase, larval anchovy abundance rose to near-record highs in summer 2016. Second, we hypothesized that fishes would spawn earlier during the MHW. Fishes did not spawn in an earlier season within a year, but five of six southern mesopelagic taxa spawned earlier than typical within winter and spring. Third, we predicted that species richness would increase moderately due to an influx of southern and exodus of northern species. Richness, however, was very high in all seasons and the highest ever during the summer as multiple species with primarily southern distributions were recorded spawning for the first time in southern California. The richness of northern species was also unexpectedly high during the MHW. Northern species likely persisted in the study area because in addition to the warm water, pockets of cold water were consistently present. If, as predicted, conditions similar to the MHW become more common as oceans warm, this unique and largely unexpected combination of fishes may reflect future biological conditions.

Key words: Ichthyoplankton; California Current Ecosystem; Ecosystem indicator; Ecosystem modelling; Fisheries management; Ecosystem-based management

1. Introduction

Evidence of climate change is currently being observed worldwide (IPPC, 2018), and it is predicted that the pace of modification will increase in the near future (Golledge et al., 2019; Mahlstein, Daniel, & Solomon, 2013). Marine heatwaves (MHWs), periods of elevated sea surface temperatures lasting days to months (Hobday et al., 2016), are one consequence of warming oceans (Jacox, Alexander, Bograd, & Scott, 2020). It is forecast that novel conditions such as record sea surface temperatures will occur more frequently and that conditions similar to recent MHWs will become more common (Frölicher, Fischer, & Gruber, 2018; Oliver et al., 2018). Marine heatwaves hold the potential to restructure ecosystems and affect ecosystem services (Smale et al., 2019), and it is therefore important to assess the impacts of recent MHWs on marine life to get a sense of potential future ecosystem state. Here, we compare how the larval fish assemblage responded to a large Marine Heatwave off southern California in 2014-2016 relative to 1951-2013.

Biological impacts of MHWs are recorded throughout the world. For example, a MHW in 2016 induced unprecedented coral bleaching on the Great Barrier Reef, Australia (Hughes et al., 2017). Further, a MHW off southwest Australia in 2011 caused an ecosystem shift as habitat-forming seaweeds greatly decreased and the ecosystem became relatively depauperate (Wernberg et al., 2016). In southeast Australia, a MHW in 2015/2016 caused outbreaks of disease in shellfish and mortality in mollusks (E. C. J. Oliver et al., 2017). In the Mediterranean, MHWs in 2003 and 2006 caused extensive seagrass mortality and thus decreased the density of a species that supports many marine species (Marba & Duarte, 2010). Given that MHWs can induce large changes to ecosystems, evaluating biological effects of MHW is important for fisheries and ecosystem management in a changing world (Caputi et al., 2016; Karp et al., 2019; Miller et al., 2014).

Despite large-scale increases in temperature under climate change and during MHWs, it is possible that physical conditions can vary at fine spatial scales. For example, localized cold water, thermal refuges buffer streams against broad warming (Isaak et al., 2016; Torgersen, Price, Li, & McIntosh, 1999). In the California Current Ecosystem (CCE) and other eastern boundary currents worldwide, increased upwelling that infuses, cold, salty, nutrient-rich water was predicted (Bakun, 1990), and then observed (Sydeman et al., 2014), under climate change due to increasing thermal gradients between land and sea. Furthermore, the presence of cold, fresh, oxygen and nutrient rich water associated with the equatorward-flowing California Current was detected off central California during the MHW in the CCE (Schroeder et al., 2019). Both the cold, fresh and cold, salty waters compressed towards shore off California during the MHW (Santora et al., 2020; Zaba & Rudnick, 2016; Zaba, Rudnick, Cornuelle, Gopalakrishnan, & Mazloff, 2020). Heterogeneity in water mass composition under climate change, therefore, has the potential to offset to some degree the impact of warming on biological assemblages.

Warming events are common in the California Current Ecosystem (CCE), and 225 MHWs, as defined by Hobday et al. (2016), occurred between 1982 (when satellite sea surface temperature recording began) and 2019 (Thompson et al., 2019). The 2014-2016 event, however, was the largest in size and longest in duration (Jacox et al., 2018), and dwarfed previous MHWs in the

CCE (figure 14 in A.R. Thompson et al. 2019). This MHW began with anomalously high sea level pressure followed by elevated sea surface temperature (SST) in the Gulf of Alaska in the boreal winter of 2013-2014 (Bond, Cronin, Freeland, & Mantua, 2015). The warm surface waters eventually spread to the coastal and southern regions of the CCE by mid-2014 (Bond et al., 2015). SST remained highly elevated through mid-2015 when a strong El Niño developed, resulting in high water temperatures both at the surface and at depth (Di Lorenzo & Mantua, 2016; Jacox et al., 2016). Anomalously warm waters persisted through mid-2016. Overall, mean annual sea surface temperature (SST) in 2015 was the highest since records began in 1920 (1.7°C SST anomaly), and mean SST from 2014-16 was the uppermost over any consecutive three-year periods (1.3°C anomaly) (Jacox et al., 2018). In addition to rising SST, salinity was significantly elevated throughout much of the CCE as a saline water mass advected shoreward between 2013 and 2019 (Ren & Rudnick, 2021). Despite the predominantly warm conditions, there were relatively small areas where the ocean was anomalously cool due to the presence of upwelled (cold and salty) and/or subarctic California Current (cold and fresh) waters (Schroeder et al., 2019; Zaba et al., 2020). Given that MHWs are predicted to increases in the future, evaluating biological responses to the 2014-2016 MHW may provide a glimpse of the make-up of the ecosystem in years to come.

The unprecedented physical oceanographic anomalies associated with the CCE 2014-2016 MHW induced biological changes at multiple trophic levels (Cavole et al., 2016). For example, there was a large increase in harmful algal blooms (McCabe et al., 2016; Ryan et al., 2017); decreased primary production (Kahru, Jacox, & Ohman, 2018; Morrow et al., 2018); and abrupt changes in phytoplankton (Du & Peterson, 2018), zooplankton (Brodeur, Auth, & Phillips, 2019; Peterson et al., 2017), pelagic invertebrate (Brodeur et al., 2019; Van Noord & Dorval, 2017), ichthyoplankton (Auth, Daly, Brodeur, & Fisher, 2018; Nielsen et al., 2021), and recently recruited fish (Basilio, Searcy, & Thompson, 2017; Santora et al., 2017; Schroeder et al., 2019) assemblages. At higher trophic levels, top predators displayed emaciated body condition and/or increased mortality (Laake, Lowry, DeLong, Melin, & Carretta, 2018; S. McClatchie et al., 2016; Piatt et al., 2020; Robinson, Thayer, Sydeman, & Weise, 2018)). In addition to impacting the CCE, the MHW greatly affected the Gulf of Alaska as larval abundances of most fishes were very low (Nielsen et al., 2021), the body size of a key forage fish, Pacific sand lance *Ammodytes personatus* was much reduced relative to recent cool years (von Biela et al., 2019), and adult abundance of ecologically and commercially important Pacific cod *Gadus microcephalus* plummeted immediately following the MHW (Barbeaux, Holsman, & Zador, 2020). Although these studies help elucidate biological changes during the 2014-2016 MHW, it is difficult to evaluate the degree to which these occurrences were unusual because the temporal duration of analyzed time-series ranged only from 2-32 years prior to 2016. To put the 2014-2016 event in better perspective, we compared larval fish assemblages during the CCE MHW to those dating back to 1951 using data from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. We specifically addressed whether 2014-2016 was different from the past in terms of 1) assemblage structure, 2) phenology (the timing of spawning) and 3) species diversity.

The CCE is one of the best-studied marine ecosystems in the world, and we thus have the capacity to evaluate if the 2014-2016 MHW induced biological anomalies comparable to past warming events. Based on observations of the impacts of warming events on fish larvae in the CCE (Auth et al., 2018; Nielsen et al., 2021) and around the world (Catalan, Rubin, Navarro, & Prieto, 2006; Keane & Neira, 2008), we developed specific hypotheses regarding responses of assemblage structure, phenology and richness to the MHW. First, taxa that have similar spatial distributions and/or adult habitat often respond similarly to changes in oceanographic conditions (Hsieh, Kim, Watson, Di Lorenzo, & Sugihara, 2009; Thompson, Watson, McClatchie, & Weber, 2012). Based on past larval fish research in the CCE (Moser et al., 2001), we predicted whether abundances of all relatively common taxa would increase or decrease during the MHW. In particular, our first hypothesis was that *the ichthyoplankton assemblage would be dominated by mesopelagic species with southern distributions relative to southern California (Hsieh et al., 2009)*. In addition, analysis of sardine and anchovy population dynamics throughout the Pacific Ocean between approximately 1950 and 2000 indicated that sardine increase under warm and anchovy under cold conditions (Chavez, Ryan, Lluch-Cota, & Niquen, 2003). We thus hypothesized *that abundances of Pacific sardine Sardinops sagax (hereafter sardine) would increase while northern anchovy Engraulis mordax (anchovy) would decrease or remain low during the MHW*. Second, fishes in the CCE (Asch, 2015) and elsewhere in the world (Lombardo, Buckel, Hain, Griffith, & White, 2020) have spawned earlier in the year during warm ocean conditions. Our second hypothesis was that *fish would spawn both earlier within a season and in earlier seasons (i.e., in winter rather than spring) during the MHW (Asch, 2015)*. Our third hypothesis was that *species richness would increase moderately during the MHW relative to years with cooler waters* because species richness tends to be higher in warmer waters (Miller, Hayashi, Song, & Wiens, 2018). However, reduction of cold-water species may temper increases in species richness. Relatedly, past (Hubbs, 1948; Hubbs & Schultz, 1929; Lea & Rosenblatt, 2000) and current (Walker et al., 2020) warming events induced an influx of extremely rare, tropical species into the waters off southern California. Our fourth hypothesis was *that larvae of rare, tropical species would increase while larvae of rare, northern species would be absent off southern California during the MHW*.

2. Materials and Methods

CalCOFI has been collecting depth-integrated plankton samples quarterly from the same 66 stations since 1951 (Fig. 1) using obliquely towed nets (505- μm mesh, 333 μm mesh on the cod end). Net contents were preserved at sea in a sodium borate-buffered 5% formalin solution (Kramer, Kalin, Stevens, Thrailkill, & Zweifel, 1972; P. Smith, 1974; P. E. Smith & Richardson, 1977). All larval fishes were then sorted, identified and archived at the Ichthyoplankton Ecology Lab at the Southwest Fisheries Science Center in La Jolla, CA. Raw larval abundances were divided by the percent of the sample that was sorted (samples with very thick zooplankton were split using a Folsum Plankton Splitter) and multiplied by a standard haul factor that accounted for the depth of a tow and the filtered volume of water (Kramer et al., 1972). We ultimately expressed abundances as the number of larvae under a circle of water with an area of 10 m^2. Although CalCOFI now collects samples in winter, spring, summer and fall, historical collections were often sparser in fall than other seasons; we thus focused on winter, spring and summer. We excluded winter 2014 because the research vessel broke down during that cruise and most of the stations were not sampled.

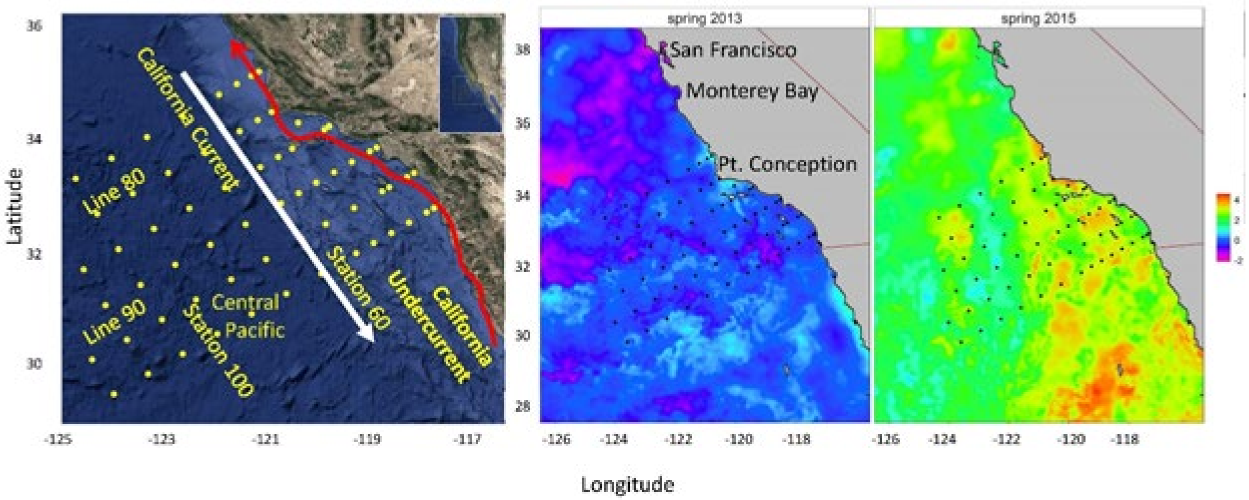


Figure 1. Left. Location of the 66 "core" CalCOFI stations off southern California and major water masses. The California Current flows from the north into southern California while the California Undercurrent flow at depth from the south. Central Pacific water is generally offshore and to the south of southern California and moves on and off the continental shelf in response to environmental forcing. Upwelled water is not shown but is typically close to shorelines. Middle. Satellite-derived sea surface monthly sea surface temperature anomalies centered on March 16, 2013 and Right. March 16, 2015.

Two major methodological sampling changes occurred during the 65-year period analyzed in this study (Thompson, McClatchie, Weber, Watson, & Lennert-Cody, 2017). First, the depth to which nets sunk changed from 140 m to 210 m in 1969. Second, bongo nets (two joined hoops) replaced single-ring nets in 1978. Four larval fish taxa were caught more efficiently during the day by bongo than ring nets, and we adjusted abundance estimates for these fishes in 1971-1977 following Thompson et al. (2017). The influence of changing tow depth on abundance estimates of larval fishes is unknown. However, zooplankton abundance are directly comparable between 1951-1969 and 1978-2016 (Ohman & Smith, 1995), and we therefore did not adjust larval fish abundance estimates from the earliest and current periods.

Our capacity to identify larvae to species has improved since 1951, and we can currently identify almost all species based on morphology. The most notable exceptions are rockfishes (genus *Sebastes*) where we can morphologically distinguish only Aurora rockfihs *S. aurora,* Splitnose rockfish *S. diploproa,* Chilipepper rockfish *S. goodei,* Shortbelly rockfish *S. jordani,* Cowcod rockfish *S. levis,* Mexican rockfish *S. macdonaldi* and Bocaccio rockfish *S. paucispinis*; the remainder were grouped as rockfishes *Sebastes* spp. Genetic barcoding of rockfish larvae collected in 2005 identified 30 species within the *Sebastes* spp. group and found that shortbelly and squarespot *S. hopkinsi* were numerically dominant (Thompson, Hyde, Watson, Chen, & Guo, 2016). We are working back chronologically to identify archived specimens to current standards, and samples from 1961-present are at present resolved to current standards. Prior to

1961, we grouped several more taxa to genus or family: bristlemouths Gonostomatidae (primarily Showy Bristlemouth *Cyclothone signata* with fewer Benttooth Bristlemouth *C. acclinidens* and *Diplophos* spp.), Lightfishes *Vinciguerria* spp. (almost all Panama Lightfish *Vinciguerria lucetia*), Lampfish in the genus *Nannobrachium* (mostly Broadfin Lampfish *N. ritteri* with fewer Pinpoint Lampfish *N. regalis*), and Sanddabs *Citharichthys* spp. (mostly Pacific Sanddab *C. sordidus* and Speckled Sanddab *C. stigmaeus* at approximately equal abundances). In the analyses (see below), we used the full data set with fishes at coarser taxonomic resolution (1951-2016) to evaluate major changes in assemblage composition and phenology and the shorter set (1961-2016) with all taxa identified to current standards to examine diversity dynamics.

Analysis

Oceanography

To illuminate ocean temperature conditions during and prior to the MHW we first used the R package rerddapXtracto (Mendelssohn, 2021) to obtain monthly satellite sea surface temperature anomalies data from the Jet Propulsion Laboratory's Multi-scale Ultra-high Resolution merged, multi-sensor analysis product. CalCOFI regularly samples oceanographic conditions at each station at 14 depths (e.g., 10 m, 20 m…) between the surface and 500 m with a Sea-Bird Electronics 911plus V2 Conductivity Temperature Depth instrument. To examine subsurface conditions, we calculated depth-specific temperature anomalies for stations between 2014 and 2016 relative to mean temperature at the same stations, depth and season between 1951 and 2013. To visualize temperature anomalies during the MHW, we created interpolation plots based on depth and CalCOFI station (each sampling location is assigned a station and line number; station number increases with distance from shore, and line number decreases with latitute) from lines 80 and 90 (Fig. 1, left panel) using the package kriging (Olmedo, 2014).

Hypothesis 1: Mesopelagic species with southern distributions and Pacific sardine dominated the ichthyoplankton assemblage

Assemblage Dynamics

We classified each taxa based on its spatial distribution relative to southern California and adult habitat affinity following Hsieh et al. (2005). We relied on expert knowledge (coauthor William Watson and the website Global Biodiversity Information Facility gbif.org) to make habitat and geographic assignments for the fishes not included in Hsieh et al. (2005). Notably, although Pacific Hake *Merluccius productus* (hake) associate with the continental slope in spring and are considered a groundfish by the Pacific Fisheries Management Council (PFMC 2019), we classify hake as a coastal pelagic because adults typically reside in pelagic habitats at depths of 50 – 150 m and vertically migrate to the surface at night (Hamel et al., 2015).

We evaluated how ichthyoplankton assemblage structure in 2014-2016 differed from prior years dating back to 1951. All analyses and plots were created using R 3.6.3 (R_Core_Team, 2020). We calculated log means of abundance for each common taxon (> 200 individuals under 10 m^2 throughout the time series; Table 1) in a year and season. We then performed separate nonmetric multidimensional (nmds) analyses within winters, springs, and summers to visualize assemblage composition in MHW years relative to previous years using the vegan package (Oksanen et al., 2019). Next, we evaluated which years significantly clustered together based on assemblage composition using a modified version of pvclust (Suzuk, Terada, & Shimodaira, 2019) that allowed us to set method.dist = "bray–curtis" and method.hclust = "ward" (github, 2019).

We further illustrated taxa dynamics by creating time-series plots of means of each taxa analyzed in the nmds analysis. We also predicted abundance dynamics (increase, decrease, no change) for all relatively common taxa based on changes in abundance association with prior warming events (Chavez et al., 2003; Hsieh et al., 2009; Moser et al., 2001). We characterized abundance as increased (decreased) if abundance ranking was in the top (bottom) five during the MHW relative to all years in a season when the taxa typically spawns. For example, Mexican lampfish almost never spawn in southern California during the winter, so we only evaluated rankings in spring and summer. All figures were created using ggplot2 (Wickham, 2016).

Hypothesis 2: Fish spawned earlier within a season and in earlier seasons during the MHW

Phenology
We tested whether the timing of spawning (phenology) changed during the MHW. To determine if phenology changed between seasons we calculated mean ichthyoplankton abundance for each year and season. We then determined the fraction of total mean abundance in each season. If spawning was earlier in the year during the MHW, then, for example, the proportion of spawning would have increased in the winter and decreased in the summer. We plotted the proportion of spawn against year for each taxon and season and used t-tests to compare proportions before and during the MHW in each season.

To determine if spawning was earlier within a season during the MHW, we calculated anomalies of mean ichthyoplankton abundance during 2014-2016 relative to 1951-2013 on each day of the year when sampling occurred from 2014-2016. We then used a general linear model to regress abundance anomaly against day. A significant, negative (positive) slope indicated that spawning occurred earlier (later) within a season during the MHW.

Hypothesis 3: Species richness increased moderately during the MHW

Species richness
We calculated the mean number of species in each year and season. To determine which types of species drove overall species richness, we examined diversity dynamics for groups of species with similar spatial centers of abundance and adult habitat affinity. We considered centers of abundance to be north, central, of south of southern California, and differentiated between species with pelagic versus benthic adult habitats. We plotted patterns of richness against year for all species combined and for each habitat by distribution category in each season.

Hypothesis 4: Rare, tropical species increased while rare, northern species were absent during the MHW.

Rare species
We recorded all taxa that appeared for the first, second or third times in southern California in a given season in 2014-2016. We described the spatial center of distribution, adult habitat, and

most common spawning season of these species to evaluate if there were systematic traits that characterized the very rare species in CalCOFI samples between 2014 and 2016.

3. Results

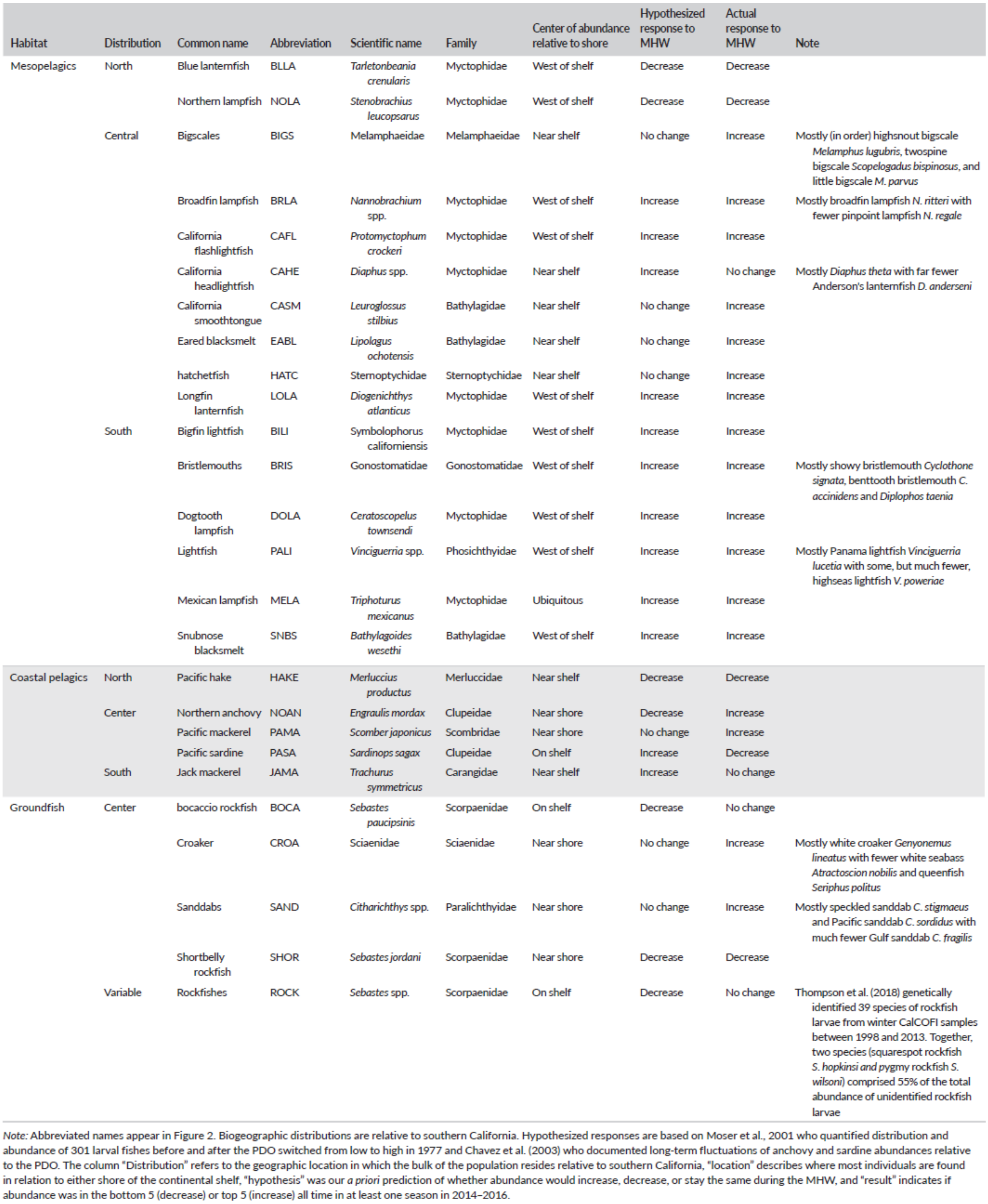
Species descriptions
Twenty-six taxa were common enough for analysis of overall ichthyoplankton assemblage dynamics. Sixteen of the twenty-six reside in mesopelagic habitats. Of the mesopelagic taxa, two have northern, eight central and six southern distributions relative to southern California (table 1). Of the five coastal pelagic species, the distribution centers of hake is north, anchovy, sardine and Pacific mackerel *Scomber japonicas* are centered on, and jack mackerel south of southern California (table 1). Southern California is the center of the distribution of most of the common groundfishes. Among the unidentified rockfishes, most are either north or centered on southern California, although a small number of species are more common off Baja California (Love, Yoklavich, & Thorsteinson, 2002).

Oceanography
Sea surface temperature changed dramatically prior to the onset of versus during the MHW (Fig. 1). In spring, 2013, for example, SST was either average or below average within and around the CalCOFI grid. By contrast, SST was mostly above average in spring 2015, and there were no obvious areas where SST was below average (Fig. 1). From a subsurface perspective, however, there were consistently pockets of cooler than average water during the MHW (Fig. 2, Fig. S1). For example, in each MHW spring, water temperature was at or below average in a narrow region close to shore. In addition, anomalously cool water was persistent at depths between approximately 100 and 150 m near station 70 (Fig. 2, S1), which is near the continental shelf break (Fig. 1).

Hypothesis 1: Southern mesopelagics and sardine will increase while northern mesopelagics and anchovy will decrease during the MHW

Assemblage Dynamics
Our predictions that southern mesopelagics would increase and northern mesopelagics decrease during the MHW were correct, but the notion that sardine would rise and anchovy fall was completely wrong. In each season, nmds axis 1 values for MHW years were positive and defined by high abundances of central and/or southern mesopelagic fishes such as bristlemouths, Mexican lampfish, Panama lightfishes, dogtooth lampfish, hatchetfish, and bigfin lightfish (Fig. 3a,b,c). The MHW years contrasted strongly from years defined largely by species such as northern lampfish, blue lanternfish, California smoothtongue, shortbelly rockfish or hake (Fig. 3a,b,c).

In winter, the two MHW years (2014 was not available) clustered significantly together (Fig. 3a, S2 top). In spring, 2015 and 2016 fell on the same branch but were not significantly similar. 2014 also did not significantly cluster with another year but was on a different branch from 2015 and 2016 (Fig. 3b, S2 middle). In summer, all MHW years were on the same branch and 2015 and 2016 were significantly similar to one another (Fig. 3c, S2 bottom).



Habitat	Distribution	Common name	Abbreviation	Scientific name	Family	Center of abundance relative to shore	Hypothesized response to MHW	Actual response to MHW	Note
Mesopelagics	North	Blue lanternfish	BLLA	*Tarletonbeania crenularis*	Myctophidae	West of shelf	Decrease	Decrease	
		Northern lampfish	NOLA	*Stenobrachius leucopsarus*	Myctophidae	West of shelf	Decrease	Decrease	
	Central	Bigscales	BIGS	Melamphaeidae	Melamphaeidae	Near shelf	No change	Increase	Mostly (in order) highsnout bigscale *Melamphus lugubris*, twospine bigscale *Scopelogadus bispinosus*, and little bigscale *M. parvus*
		Broadfin lampfish	BRLA	*Nannobrachium* spp.	Myctophidae	West of shelf	Increase	Increase	Mostly broadfin lampfish *N. ritteri* with fewer pinpoint lampfish *N. regale*
		California flashlightfish	CAFL	*Protomyctophum crockeri*	Myctophidae	West of shelf	Increase	Increase	
		California headlightfish	CAHE	*Diaphus* spp.	Myctophidae	Near shelf	Increase	No change	Mostly *Diaphus theta* with far fewer Anderson's lanternfish *D. anderseni*
		California smoothtongue	CASM	*Leuroglossus stilbius*	Bathylagidae	Near shelf	No change	Increase	
		Eared blacksmelt	EABL	*Lipolagus ochotensis*	Bathylagidae	Near shelf	No change	Increase	
		hatchetfish	HATC	Sternoptychidae	Sternoptychidae	Near shelf	No change	Increase	
		Longfin lanternfish	LOLA	*Diogenichthys atlanticus*	Myctophidae	West of shelf	Increase	Increase	
	South	Bigfin lightfish	BILI	Symbolophorus californiensis	Myctophidae	West of shelf	Increase	Increase	
		Bristlemouths	BRIS	Gonostomatidae	Gonostomatidae	West of shelf	Increase	Increase	Mostly showy bristlemouth *Cyclothone signata*, benttooth bristlemouth *C. accinidens* and *Diplophos taenia*
		Dogtooth lampfish	DOLA	*Ceratoscopelus townsendi*	Myctophidae	West of shelf	Increase	Increase	
		Lightfish	PALI	*Vinciguerria* spp.	Phosichthyidae	West of shelf	Increase	Increase	Mostly Panama lightfish *Vinciguerria lucetia* with some, but much fewer, highseas lightfish *V. poweriae*
		Mexican lampfish	MELA	*Triphoturus mexicanus*	Myctophidae	Ubiquitous	Increase	Increase	
		Snubnose blacksmelt	SNBS	*Bathylagoides wesethi*	Bathylagidae	West of shelf	Increase	Increase	
Coastal pelagics	North	Pacific hake	HAKE	*Merluccius productus*	Merluccidae	Near shelf	Decrease	Decrease	
	Center	Northern anchovy	NOAN	*Engraulis mordax*	Clupeidae	Near shore	Decrease	Increase	
		Pacific mackerel	PAMA	*Scomber japonicus*	Scombridae	Near shore	No change	Increase	
		Pacific sardine	PASA	*Sardinops sagax*	Clupeidae	On shelf	Increase	Decrease	
	South	Jack mackerel	JAMA	*Trachurus symmetricus*	Carangidae	Near shelf	Increase	No change	
Groundfish	Center	bocaccio rockfish	BOCA	*Sebastes paucipsinis*	Scorpaenidae	On shelf	Decrease	No change	
		Croaker	CROA	Sciaenidae	Sciaenidae	Near shore	No change	Increase	Mostly white croaker *Genyonemus lineatus* with fewer white seabass *Atractoscion nobilis* and queenfish *Seriphus politus*
		Sanddabs	SAND	*Citharichthys* spp.	Paralichthyidae	Near shore	No change	Increase	Mostly speckled sanddab *C. stigmaeus* and Pacific sanddab *C. sordidus* with much fewer Gulf sanddab *C. fragilis*
		Shortbelly rockfish	SHOR	*Sebastes jordani*	Scorpaenidae	Near shore	Decrease	Decrease	
	Variable	Rockfishes	ROCK	*Sebastes* spp.	Scorpaenidae	On shelf	Decrease	No change	Thompson et al. (2018) genetically identified 39 species of rockfish larvae from winter CalCOFI samples between 1998 and 2013. Together, two species (squarespot rockfish *S. hopkinsi and* pygmy rockfish *S. wilsoni*) comprised 55% of the total abundance of unidentified rockfish larvae

Note: Abbreviated names appear in Figure 2. Biogeographic distributions are relative to southern California. Hypothesized responses are based on Moser et al., 2001 who quantified distribution and abundance of 301 larval fishes before and after the PDO switched from low to high in 1977 and Chavez et al. (2003) who documented long-term fluctuations of anchovy and sardine abundances relative to the PDO. The column "Distribution" refers to the geographic location in which the bulk of the population resides relative to southern California, "location" describes where most individuals are found in relation to either shore of the continental shelf, "hypothesis" was our *a priori* prediction of whether abundance would increase, decrease, or stay the same during the MHW, and "result" indicates if abundance was in the bottom 5 (decrease) or top 5 (increase) all time in at least one season in 2014–2016.

Figure 2. Common Taxa used in nmds and phenology analyses.

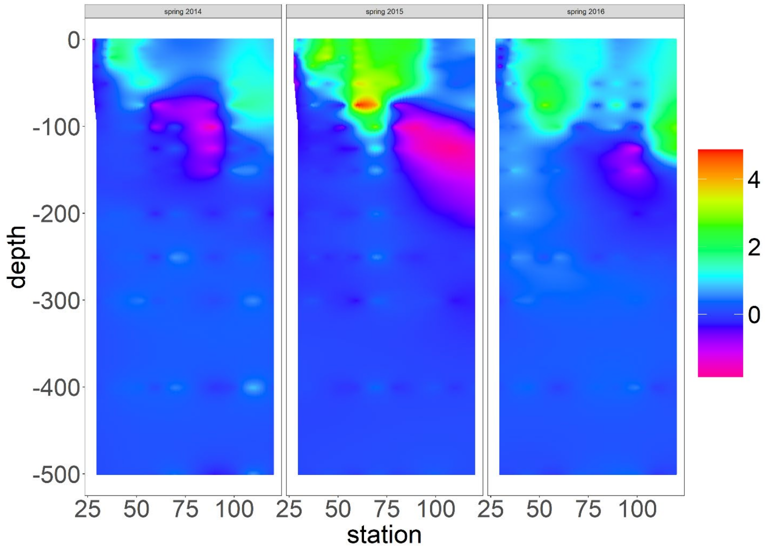


Figure 3. Interpolated temperature anomalies based on CTD samples in spring 2014, 2015 and 2016 on CalCOFI line 90. CalCOFI stations are on the x-axis with lower values depicting stations closer to shore. Additional temperature profile anomalies are in Supplemental Figures S1A and S1B.

Adult habitat helped explain whether taxa responded to the MHW in a manner similar to past warming events. Mesopelagic taxa dynamics met *a priori* expectations better than coastal pelagics or groundfishes (table 1, Fig. S3a). As expected, larval abundances of both northern, mesopelagic species, northern lampfish (Fig. 4) and blue lampfish, were in the bottom five all time abundance in at least one season during the MHW and spring 2015 was one of only five springs completely lacking blue lampfish. Conversely, seven of eight mesopelagic taxa with distributions centered on southern California increased (e.g., California flashlight fish; Fig. 4) even though only four of the eight increased during past warming events (table 1, Fig. S3b). Abundances of all southern mesopelagics were in the top five in one or more seasons during the MHW. In particular, spring 2015 bristlemouth, spring 2015 Mexican lampfish, summer 2014, 2015, and 2016 Mexican lampfish (Fig. 4), winter 2016 Panama lightfish, and winter 2016 snubnose blacksmelt abundances all had seasonal high abundances (table 1, Fig. S3c). Mexican lampfish were especially abundant during the MHW years as mean abundance was 3.1, 3.4, and 1.7 times higher than the previous high in 2014, 2015, and 2016, respectively (Fig. 4, S3c).

Dynamics of coastal pelagic species differed greatly from expectations (table 1, Fig. S3d). Sardine abundance decreased, with 2016 being the first year since 1984 when no sardine larvae were captured in spring, while anchovy increased to the point that 2016 had the fifth highest abundance of larval anchovy in summer and the highest since 1969 (Fig. 4). In contrast to expectations, Pacific mackerel abundance increased while jack mackerel did not change during the MHW. Hake was the only coastal pelagic taxa that met expectations; it had the third lowest spring abundance on record in 2014 (Fig. S3d).

The impact of the MHW was also less predictable on larval abundances of groundfishes than mesopelagics (table 1, Fig. S3e). On the one hand, whereas we hypothesized that croakers and sanddabs would not change during the MHW, spring sanddab abundance was the second highest on record in 2014, summer sanddab abundance was the second and third highest in 2014 and 2015 (Fig. 4), and croaker abundance was the third highest ever in 2016. On the other hand, we expected that rockfishes and bocaccio rockfish would decrease, but abundances of both taxa were close to average in 2014-2016. Shortbelly rockfish was the only groundfish that conformed to expectation; it was absent for only the second time in 65 years in spring 2015.

Hypothesis 2: Species will spawn early in a season and early in the year during the MHW

Phenology

There was no strong indication that species systematically spawned earlier in the year during the MHW (table S1, Fig. S4, top). Of the mesopelagic taxa, northern lampfish spawned significantly less in winter and more in spring (opposite to our expectation). Among central mesopelagics, California smoothtongue spawned more in summer than usual (also opposite to the prediction) while longfin lanternfish spawning increased in winter. Bigfin lightfish and snubnose blacksmelt increased spawning in winter, but were the only southern mesopelagic taxa that changed during the MHW. None of the coastal pelagic nor groundfish species changed inter-season spawning patterns. Given the large number of comparisons, there was no systematic tendency fishes to spawn in earlier seasons (e.g., winter versus spring) during the MHW.

There was evidence that species spawned earlier within a season during the MHW than among seasons. In particular, five (bristlemouths, dogtooth lampfish, lightfishes, Mexican lampfish, snubnose blacksmelt) of six southern mesopelagics (table S2, Fig. S5a) spawned earlier within at least one season during the MHW (only bigfin lightfish did not change). In addition, three (lampfish in the genus *Nanobrachium*, hatchetfishes, longfin lanternfish) of eight central mesopelagics spawned earlier within at least one season. Northern mesopelagics, however, did not spawn earlier within a season, and northern lampfish actually spawned later in winter than average during the MHW. There was no systematic trend in timing of within season spawning for coastal pelagics as hake spawned later in winter while jack mackerel earlier in winter (Fig. S5b). Similarly, groundfishes did not exhibit a consistent tendency to spawn earlier (or later) as only croaker spawned later in winter and this pattern was driven by one day late in the season (Fig. S5c).

Hypothesis 3: A moderate increase in species richness

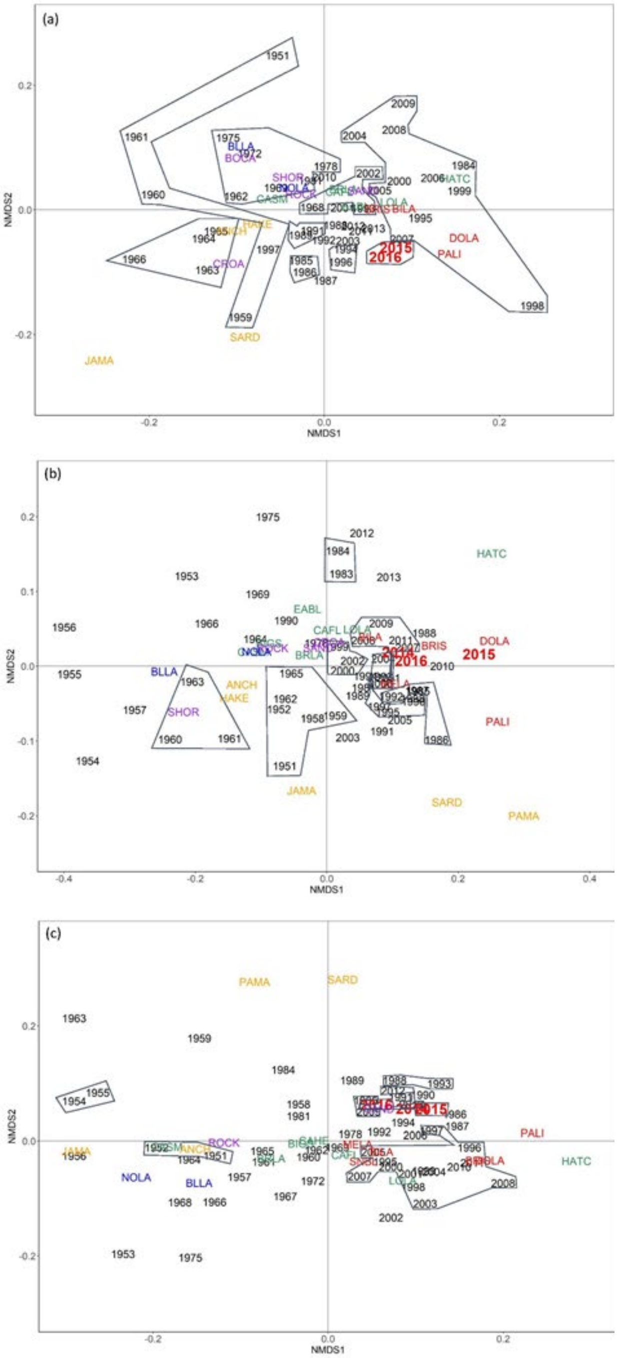


Figure 4. NMDS plots depicting assemblage dynamics in (a) winter, (b) spring and (c) summer from 1951 to 2016. Polygons delineate years that significantly clustered together (see Figure S1). The MHW years, 2014–2016 are in red in larger, bold font than previous years. Species are color-coded based on habitat and biogeographic affiliation as follows: blue = mesopelagic, north; green = mesopelagic, center; red = mesopelagic, south; orang = coastal pelagic; purple = groundfish. Stress = 0.18, 0.13, and 0.13 for winter, spring, and summer, respectively.

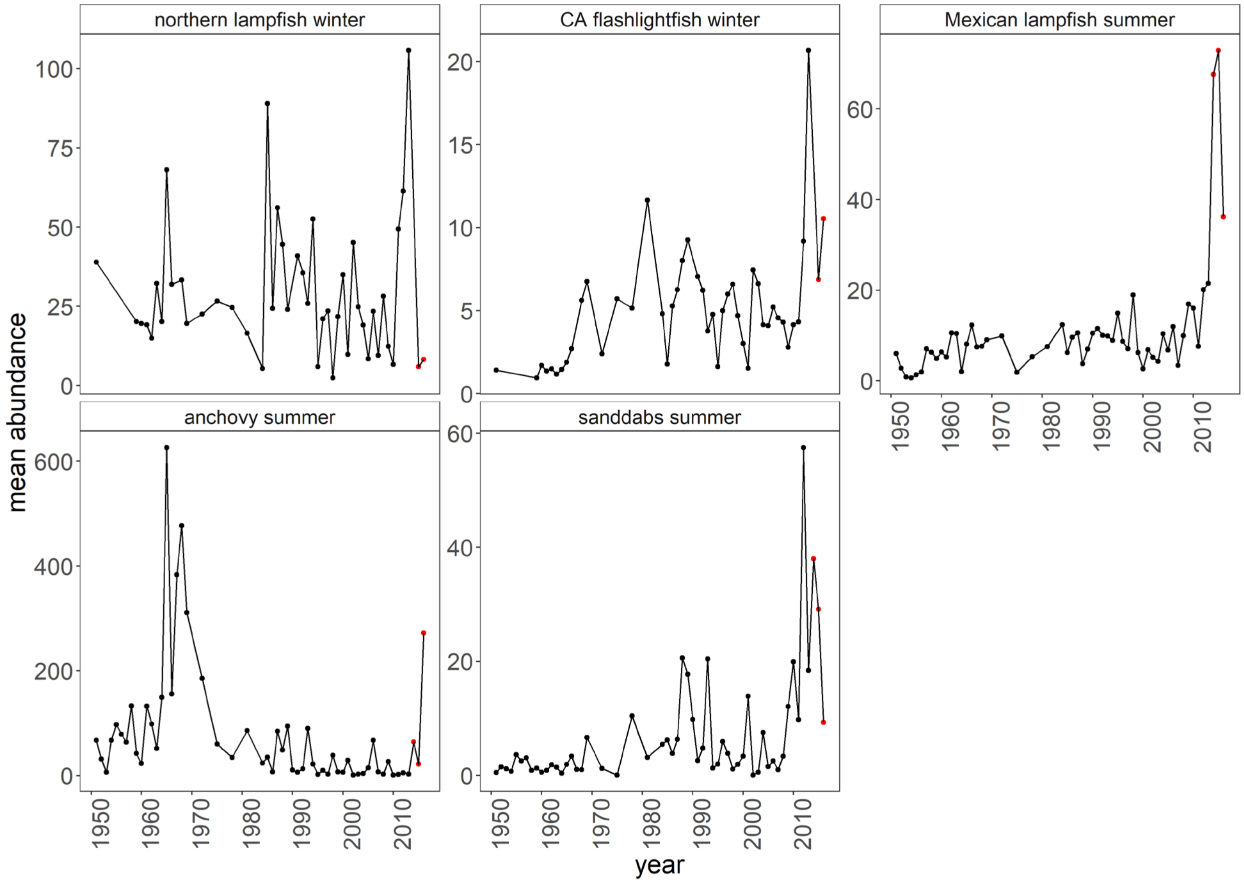


Figure 5. Mean abundances of representative taxa from each habitat-distribution grouping in a given season: northern mesopelagic (northern lampfish), central mesopelagic (California flashlightfish), southern mesopelagic (Mexican lampfish), coastal pelagic (anchovy) and groundfish (sanddabs). Mean abundance of all species from each season is shown in Figure S3

Species Richness

We expected a moderate increase in species richness but observed a large increase. Overall ichthyoplankton species richness was very high during the MHW. In winter, 2015 and 2016 were among the top seven years from 1961-2016 (Fig. 5). The third highest number of species in spring occurred in 2015, and 2014 and 2016 were well above average. Summer 2014 had the highest number of species in the history of CalCOFI for any season, 2015 was the second highest summer, and 2016 the fourth highest summer.

High richness in winter was driven by above-average occurrence of southern pelagic, central pelagic, northern pelagic and southern benthic species (Fig. 5). In spring, the number of northern benthic, central pelagic, northern pelagic and southern benthic species tended to be high. In summer, all species groups were above average during the MHW with southern pelagic and central pelagic contributing the most species.

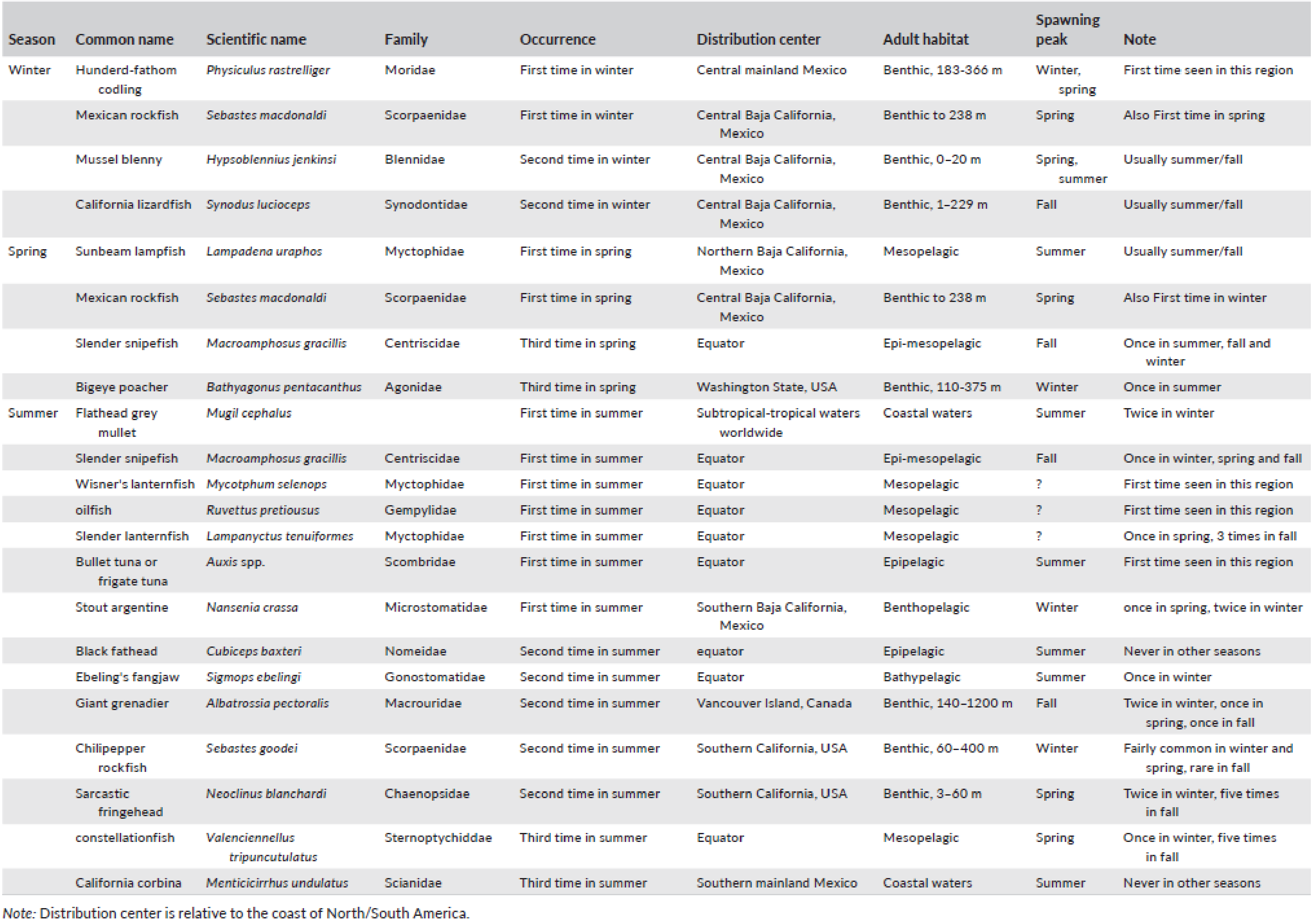
Hypothesis 4: Rare, tropical species will increase while rare, northern species will be absent

Rare species
This hypothesis was partially met. Larvae from four species with ranges well south of southern California, hundred-fathom codling *Physiculus rastrelliger*, Wisner's lanternfish *Myctophum selenops*, the oilfish *Ruvettus pretiosus* and frigate tuna *Auxis* spp., were collected for the first time in CalCOFI's history during the MHW (table 2). Of the species observed for the first, second or third time in a particular season, the distributions of almost all are centered south of southern California, sometimes even as far south as at the equator (table 2). However, two of the rare species, bigeye poacher *Bathyagonus pentacanthus* and giant grenadier *Albatrossia pectoralis,* are more common north of the sampling region.

4. Discussion

The response of larval fishes in the CCE to the 2014-2016 MHW were nuanced and not entirely predictable based on observations from past warming events in this region. First, we hypothesized that abundances of southern mesopelagic taxa and sardine would increase while anchovy would decrease. Southern mesopelagics did increase, but Mexican lampfish far exceeded previous highs. In addition, not only did sardine remain low, anchovy increased greatly during the MHW. Second, we hypothesized that species would spawn earlier within a season and in early seasons but while five of six southern mesopelagics spawned earlier within winter or spring no other species systematically spawned earlier in a year and there was no evidence that any species spawned in an earlier season. Third, we expected a moderate increase in species richness but observed record high richness as both southern and northern species were present. Therefore, although some aspects of the larval assemblage were similar to previous warm (strong El Niño) years, the abundances and types of fishes stood out in 2014-2016.

Figure 6. Dynamics of species richness per year in winter, spring and summer from 1961 to 2016 for all species combined (upper left) and groups of species with various distributions relative to southern California (e.g., north) and habitat affinities (e.g., pelagic) [Colour figure can be viewed at wileyonlinelibrary.com]



Season	Common name	Scientific name	Family	Occurrence	Distribution center	Adult habitat	Spawning peak	Note
Winter	Hunderd-fathom codling	*Physiculus rastrelliger*	Moridae	First time in winter	Central mainland Mexico	Benthic, 183-366 m	Winter, spring	First time seen in this region
	Mexican rockfish	*Sebastes macdonaldi*	Scorpaenidae	First time in winter	Central Baja California, Mexico	Benthic to 238 m	Spring	Also First time in spring
	Mussel blenny	*Hypsoblennius jenkinsi*	Blennidae	Second time in winter	Central Baja California, Mexico	Benthic, 0–20 m	Spring, summer	Usually summer/fall
	California lizardfish	*Synodus lucioceps*	Synodontidae	Second time in winter	Central Baja California, Mexico	Benthic, 1–229 m	Fall	Usually summer/fall
Spring	Sunbeam lampfish	*Lampadena uraphos*	Myctophidae	First time in spring	Northern Baja California, Mexico	Mesopelagic	Summer	Usually summer/fall
	Mexican rockfish	*Sebastes macdonaldi*	Scorpaenidae	First time in spring	Central Baja California, Mexico	Benthic to 238 m	Spring	Also First time in winter
	Slender snipefish	*Macroamphosus gracillis*	Centriscidae	Third time in spring	Equator	Epi-mesopelagic	Fall	Once in summer, fall and winter
	Bigeye poacher	*Bathyagonus pentacanthus*	Agonidae	Third time in spring	Washington State, USA	Benthic, 110-375 m	Winter	Once in summer
Summer	Flathead grey mullet	*Mugil cephalus*		First time in summer	Subtropical-tropical waters worldwide	Coastal waters	Summer	Twice in winter
	Slender snipefish	*Macroamphosus gracillis*	Centriscidae	First time in summer	Equator	Epi-mesopelagic	Fall	Once in winter, spring and fall
	Wisner's lanternfish	*Mycotphum selenops*	Myctophidae	First time in summer	Equator	Mesopelagic	?	First time seen in this region
	oilfish	*Ruvettus pretiousus*	Gempylidae	First time in summer	Equator	Mesopelagic	?	First time seen in this region
	Slender lanternfish	*Lampanyctus tenuiformes*	Myctophidae	First time in summer	Equator	Mesopelagic	?	Once in spring, 3 times in fall
	Bullet tuna or frigate tuna	*Auxis* spp.	Scombridae	First time in summer	Equator	Epipelagic	Summer	First time seen in this region
	Stout argentine	*Nansenia crassa*	Microstomatidae	First time in summer	Southern Baja California, Mexico	Benthopelagic	Winter	once in spring, twice in winter
	Black fathead	*Cubiceps baxteri*	Nomeidae	Second time in summer	equator	Epipelagic	Summer	Never in other seasons
	Ebeling's fangjaw	*Sigmops ebelingi*	Gonostomatidae	Second time in summer	Equator	Bathypelagic	Summer	Once in winter
	Giant grenadier	*Albatrossia pectoralis*	Macrouridae	Second time in summer	Vancouver Island, Canada	Benthic, 140–1200 m	Fall	Twice in winter, once in spring, once in fall
	Chilipepper rockfish	*Sebastes goodei*	Scorpaenidae	Second time in summer	Southern California, USA	Benthic, 60–400 m	Winter	Fairly common in winter and spring, rare in fall
	Sarcastic fringehead	*Neoclinus blanchardi*	Chaenopsidae	Second time in summer	Southern California, USA	Benthic, 3–60 m	Spring	Twice in winter, five times in fall
	constellationfish	*Valenciennellus tripuncutulatus*	Sternoptychiddae	Third time in summer	Equator	Mesopelagic	Spring	Once in winter, five times in fall
	California corbina	*Menticicirrhus undulatus*	Scianidae	Third time in summer	Southern mainland Mexico	Coastal waters	Summer	Never in other seasons

Note: Distribution center is relative to the coast of North/South America.

Figure 7. Species collected for either the first, second, or third time since 1961. Distribution center is relative to the coast of North/South America.

Assemblage Structure

To shed light on how fishes might respond to future warming, it is important to discern the mechanisms driving population dynamics of fishes. At a base level, redistribution and/or an increase/decrease of overall population size can drive changes in assemblage structure within spatially confined regions such as southern California. Here, it is likely that both factors contributed to the observed dynamics.

Redistribution likely affected the abundances of pelagic taxa in southern California during the MHW. Physical oceanography is highly dynamic off central and southern California (Fig. 1) as Central Pacific (CP; warm, moderately saline), California Undercurrent (CU; warm, saline; also called Equatorial Pacific water), California Current (CC; cold, fresh), and upwelled (cold, saline) water bodies converge in the CalCOFI region (Checkley & Barth, 2009; S McClatchie, 2014), and distinct fish assemblages can associate with each water mass (Hsieh et al., 2009; H G Moser & Smith, 1993; H G Moser, Smith, & Eber, 1987). There was an unusual combination of each of these water masses during the MHW that likely contributed to the novel larval assemblage (Zaba et al., 2020). Southern California warmed rapidly in 2014-2015 and CP waters moved closer to shore. Many of the southern, mesopelagic taxa reside within the CP water mass (H G Moser et al., 1987), and this likely contributed to the rise in abundance of these species in 2014. In addition, CC water was displaced inshore by the warm water mass (Zaba & Rudnick, 2016), which may have brought some northern species into southern California. In mid-2015, the eastern Pacific entered a positive ENSO phase (Fiedler & Mantua, 2017), and CP/CU water contributions increased significantly and extended deeper than the period between 2014 to mid-2015 (Bograd, Schroeder, & Jacox, 2019). It is probable that the anomalously high abundances of Mexican lampfish and Panama lightfish in the southeast were a result of fish movement into southern California with the CU, while elevated abundances of several mesopelagics in the southwest were related to incursion of CP water during the MHW. Despite the increased CU signature at depth during El Niño years, in the upper portion of the water column, CC waters actually increased during this period (Bograd et al. 2019). In contrast to a typical El Niño where the SCB experiences a combination of decreased upwelling and poleward advection of warmer water (Bograd et al. 2019), 2015/2016 had both above average upwelling (Frischknecht, Münnich, & Gruber, 2017) and incursion of CC water (Schroeder et al., 2019). However, residual warm water from 2014, coinciding with large El Niño-driven increases in warm water beginning in 2015 (in 2015, the greatest temperature anomalies were at ~200m while the largest temperature anomalies were in the upper 50 m in 2014), likely resulted in the continuation of the MHW through late 2016 (Jacox et al., 2016; Zaba et al., 2020). The unusual combination of CU, CP, CC, and upwelled waters likely contributed to the unique southern California fish assemblage during the MHW.

Overall changes in population sizes also affected assemblage structure during the MHW. While population sizes of many species declined during the MHW due to low food resources (Cavole et al., 2016; Galvez, Pardo, & Elorriaga-Verplancken, 2020; Jones et al., 2018), environmental conditions seemed to be conducive for large increases in some economically and ecologically important species. Multiple rockfishes had record or near record-high recruitment from 2013-2016 (Schroeder et al., 2019). Although conditions were predominantly warm during this period, much of the region where rockfishes spawn in central California was impacted by cool, low salinity, high oxygen CC water, and there was a significant correlation between rockfish recruitment and the prevalence of CC water between 1982 and 2016 (Schroeder et al., 2018). The 2016 increase in larval anchovy also reflected an overall increase in population size. Anchovy recruitment was very high in 2015 (Thompson et al. 2018). By summer 2016, the 2015 recruits were reproductively mature and hence anchovy larval abundance was extremely high. In 2019, overall anchovy abundance was probably higher than at any point subsequent to the 1960s (Thompson et al., 2019). Changes in overall population size also must have driven increased abundance of benthic taxa in southern California such as sanddabs and croakers, but the actual causes that induced these rare increases are opaque. More research is needed to fully understand the relative contribution of population movement versus change in population size on assemblage dynamics during MHWs.

In addition to our findings, there is ample evidence of changes to biological assemblages in the CCE during the MHW. Cavole et al. (2016) reviewed biological dynamics through 2015 and documented mass strandings, distribution and abundance shifts and documented unusual occurrences of phytoplankton, zooplankton, fish, birds and/or marine mammals throughout the CCS. Within the plankton assemblage, recent studies documented low phytoplankton biomass and increased cyanobacteria just north of the CCE near the Salish Sea (Pena, Nemcek, & Robert, 2019), low phytoplankton biomass off California (Jacox et al., 2016; Kahru et al., 2018) and decreasing phytoplankton biomass off Baja California (Gomez-Ocampo, Gaxiola-Castro, Burazo, & Beier, 2018). Zooplankton assemblages also changed throughout the CCE as species off Baja California (Lavaniegos, Jimenez-Herrera, & Ambriz-Arreola, 2019) and Oregon (Thompson et al., 2019) transitioned from relatively large, northern species to smaller southern species, the mean body size of Northern Pacific krill *Euphausia pacifica* ((Thompson et al., 2019) decreased off northern California, and gelatinous species became much more prevalent in the northern (Brodeur et al., 2019) and central (Thompson et al., 2019) CCE. Finally, there were unprecedented changes to larval fish assemblages throughout the CCS. In the northern California Current, total larval abundances during winter were at record highs, driven by unusually high spawning of species such as anchovy, sardine and hake (Auth et al., 2018). In the Gulf of Alaska, larval fish assemblages changed significantly in the eastern but not western region (Goldstein, Duffy-Anderson, Matarese, & Stockhausen, 2019). Taken together, our and other studies off the west coast of North America demonstrate that the biology of the whole region was very different than average during the MHW.

Worldwide, large-scale changes to biological assemblages has also occurred during MHWs. In Australia, for example, marine heatwaves induced for the first time recorded bleaching of corals in the northwest although corals in the more temperate southwest were not affected (Le Nohaic et al., 2017) or even increased (Tuckett, de Bettignies, Fromont, & Wernberg, 2017). Whereas corals increased in southwest Australia, seagrass incurred a large decrease as a result of a MHW (Strydom et al., 2020). Indeed, kelp assemblages changed in multiple locations around the world as a result of warming over the past decade (Straub et al., 2019) as canopy forming kelp tended to decrease (Beas-Luna et al., 2020; Filbee-Dexter et al., 2020; McPherson et al., 2021) and turf-forming seaweeds increase (Straub et al., 2019). The unprecedented environmental conditions during the past decade induced myriad changes to ecosystems both in the CCE and across the world. If conditions similar to recent MHWs increase in frequency in the future as expected (Jacox et al. 2020), then biological conditions observed in oceans worldwide may also become more common.

Despite large-scale warming during the 2014-2016 MHW in the CCE, pockets of cold water were consistently present throughout the region. It is possible that these locations served as cold-water refugia and mitigated components of the ecosystem against broad-scale warming. For example, recruitment of rockfishes off California correlated positively with cold water from 1983-2016, and recruitment was exceedingly high before (2013) and during (2014-2016) the MHW (Schroeder et al., 2019). Detailed oceanographic analysis indicated that cold water was prevalent in adult rockfish habitats during the MHW (Schroeder et al., 2019). Although further investigation needs to be conducted, it is possible that the cold-water regions were associated with high anchovy recruitment in 2015 (Thompson et al., 2019). In addition to the CCE, cold-water refugia is critical for persistence of species in, for example, stream ecosystems. Despite rising temperatures, cold water associated species such as bull trout (*Salvelinus confluentus*), cutthroat trout (*Oncorhynchus clarkii bouvierii)* and westslope cutthroat trout (*Oncorhynchus clarkii lewisii*) persist in montane streams in the northwestern United States due to cold-water refugia (Isaak et al., 2016). If similar locations with cold water continue to be associated with future MHW in the CCE, then this may buffer species that are intolerant to warm conditions.

The unusual composition of fishes in the CCE during the MHW had strong but nuanced implications to other components of the ecosystem. Changes in fish abundance and species composition in southern California resonated with marine predators during the MHW. For example, female California sea lion *Zalophus californianus* in southern California were largely malnourished between 2011 and 2015 (Thompson et al., 2019). While underfed adult females do not typically die of starvation, they produce less milk such that pups are underweight, grow slowly, and often starve to death (Melin et al., 2010). Lactation condition in sea lions depends greatly on the species of consumed prey, and condition improves when diets are rich in sardine and/or anchovy (S. McClatchie et al., 2016). The influx of anchovy into the CCE during the MHW provided adult females with high-caloric prey, and pup weight and growth rate were above average from 2016-2018. Not all predators benefited from the rise in anchovy. Among shore birds on Southeast Farallon Island, fledgling productivity in recent years depended on whether young were capable of consuming anchovy. Chick survival in 2019 was high for Brandt's cormorant *Phalacrocorax penicillatus*, a species that feeds chicks partially digested regurgitate, but historically low for common murre *Uria aalge* that provides whole prey items to chicks as chicks were unable to consume adult anchovy (Thompson et al., 2019). Again, predator responses to the effects of the MHW were not uniform and were species-specific.

Phenology

Altered phenology under climate change has the potential to induce ecosystem change, and we expected to observe a widespread trend towards spawning earlier in the year and earlier within a season during the MHW. This expectation was based on Asch (2015) who found a trend for earlier spawning in 18 of 43 species between 1951 and 2008. Because zooplankton phenology did not change during this period, she discussed the potential for increased larval mortality under climate change if spawning did not overlap with zooplankton prey productivity (Asch, 2015; Cushing, 1975). Subsequent to Asch (2015), incidents of altered phenology have been documented in phytoplankton (Chivers, Edwards, & Hays, 2020; Salgado-Hernanz, Racault, Font-Munoz, & Basterretxea, 2019), crustaceans (Emond, Sainte-Marie, & B?ty, 2020), and fish (Lombardo et al., 2020) in various locations around the world. Within the CCE, anchovy was very abundant during the winter off Oregon even though it had never been observed to spawn in this season, and sardine and hake were much more abundant than normal in winter of the MHW (Auth et al., 2018). Our phonological results were less dramatic than Auth et al. (2018) as there was no evidence that fishes systematically spawned in an earlier season during the MHW relative to 1951-2013. We did find that the majority of southern mesopelagic taxa, as well as jack mackerel, were more abundant earlier in either winter or spring than normal during the MHW. This result largely aligns with Asch (2015) as 10 of the 18 species with significantly earlier spawning in her study were mesopelagics and jack mackerel. It is difficult, however, to conclude that earlier appearance of mesopelagic or jack mackerel larvae in the CalCOFI region is indicative of overall earlier spawning in the whole population. The CalCOFI area covers only a small fraction of the spatial distribution of these species and each are associated with particular water masses that impinge onto the sampling area (Moser & Smith, 1993; Moser et al., 1987). It is thus possible that the early appearance of larvae is a function of earlier impingement of preferred habitat onto CalCOFI rather than earlier spawning of the entire population. In addition, concern that warming will lead to recruitment failure due to match-mismatch or redistribution did not play out for several economically important stocks in southern California during the MHW as recruitment of anchovy, most rockfishes, and sanddabs was very high even when the ocean was unprecedentedly warm (Jacox et al., 2018; Thompson et al., 2019). Our overall results suggest that altered phonology did not play a large role on the dynamics of the larvae fish assemblage off southern California during the MHW.

Diversity

We expected that larval fish species richness would rise slightly, but observed that richness in southern California was the highest ever recorded during the MHW. Augmented richness was most likely partially driven by an influx of warm water species from the south. Indeed, richness was elevated for most species with southern ranges relative to southern California. However, richness of species with northern distributions was also average or high throughout the MHW, and the coupled richness of both northern and southern species probably contributed to the overall record high species richness. It is likely that the pockets of cold water facilitated the presence of cold-water species despite the overall warm conditions from 2014-2016.

Elevated species richness during the MHW was not unique to the CalCOFI region but extended further north. The number of forage fish and groundfish species present off the Northern Californian coast increased substantially during the MHW (Santora et al., 2017). Off the coast of Oregon, increases in species richness was also observed for larval fish, copepods, dinoflagellates and diatoms attributed to an influx of southern species (Auth et al., 2018; Peterson et al., 2017). Such observations of regional increases in species richness during warming have also been observed in other parts of the world (Hiddink & ter Hofstede, 2008; Morson, Grothues, & Able, 2019; ter Hofstede, Hiddink, & Rijnsdorp, 2010).

The processes that drove up ichthyoplankton species richness were multifaceted during the 2014-2016 MHW event. Nevertheless, extended periods of intense heating, especially when in combination with other environmental stressors, could have the capacity to alter marine community composition. Species diversity is in decline globally, but regionally it is often found to be stable or increasing over longer time scales due to expansion of habitat boundaries, and retention of new species offsetting extinction events of local species (Batt, Morley, Selden, Tingley, & Pinsky, 2017; Sax & Gaines, 2003). Many fishes and their planktonic larval stages, with a high capacity for dispersal, respond quickly to climate driven extensions of suitable habitat, although species with a narrow range of distributions and tolerances are at risk of local extinction (Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Sunday et al., 2015). Thus, MHWs have the potential to accelerate invasions and extinctions in the CCE and on regional scales elsewhere. With expected increases in ocean temperature and variability (Jacox et al., 2020), MHWs could push assemblage changes further and faster than long-term warming trends alone (Hobday et al., 2016; Wernberg et al., 2013). If, however, the MHWs are consistently associated with cold water, then impacts of warm water could, to some extent, be offset. Observation of future MHW will inform whether cold pockets regularly accompany broad-scale warming and refine expectations of species diversity dynamics in the CCE.

Rare species

In addition to finding record-high species richness, there was an abundance of extremely rare species during the 2014-2016 MHW. El Niño warming events in the CCE have long been associated with an influx of rare southern fish species (Hubbs, 1948; Lea & Rosenblatt, 2000; Walker et al., 2020). The MHW of 2014-2016 seemed to differ from past warm water events, however, as larvae of both southern and northern origin were detected, perhaps due to the unique combination of water masses present at the beginning of the MHW (Zaba et al., 2020). In contrast to our efforts, most previous reports of anomalous fishes in southern California focused on adults. Detecting larval fishes may be more challenging than adults because while adults may be present, individuals may not actually be spawning outside of their normal range. In addition, adult observations can be made through many more sampling sources than larvae. Recently, Walker et al. (2020) used a combination of reporting methods including commercial and recreational fishing, SCUBA photography clubs, and public reporting of uncommon fish sightings to compile a list of 28 unique, anomalous fish families identified in the SCB between 2014 and 2016. Our ichthyoplankton-based efforts identified 17 unique families of larval fishes, with only two overlapping species. Together, these efforts identified 43 unique, anomalous, fish families present in the SCB during the 2014-2016 MHW, a large increase from the 29 anomalous families recorded during the 1997-1998 El Nino warm period (Lea and Rosenblatt 2000). However, as discussed in Walker et al. (2020), this increase could potentially be due to the widespread prevalence of cameras and smartphones during 2014-2016 as compared to the late 1990's, instead of simply a greater influx of southern species. Our ichthyoplankton-based results, however, demonstrate that the presence of rare species was not merely due to augmented sampling.

5. Conclusion

Models predict that ocean conditions similar to the current MHW will increase in the future (Alexander et al., 2018; Frölicher et al., 2018; Oliver et al., 2018). Indeed, another strong MHW, second in size and longevity only to the 2014-2016 event, formed in the eastern Pacific in 2019 (Thompson et al., 2019). We found that larvae of many mesopelagic species and overall larval fish diversity were at all-time highs during the 2014-2016 MHW. Whereas increased abundance of larval mesopelagics during warming has been observed during past warming events in the CCE (Auth et al., 2018; Hsieh et al., 2005; Sakuma et al., 2016; Thompson et al., 2012), we also found that larval abundance of anchovy increased greatly toward the tail end of the MHW. The combination of high abundances of anchovy and subtropical mesopelagic taxa had never occurred in the 70-year CalCOFI time series (Thompson et al., 2019), and illustrates the unique nature of biological conditions in the CCE during the large MHW of 2014-2016. This strange brew also highlights that biological responses to MHW may not be predictable based on past observations and that the diversity of water masses likely moderated the biological response to the overall extreme warmth of 2014-2016. It is thus important to continue monitoring changes to marine ecosystems and resolve precise mechanisms driving population and community dynamics during these interesting times.

6. Acknowledgements

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7. Author Contributions. Not applicable

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