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Marine heat waves, climate change, and failed spawning by coastal invertebrates

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Abstract

To investigate the timing and intensity of winter spawning by coastal invertebrates, we enumerated embryos in plankton samples collected in daily time series from January to March of 2014 (79 d), 2015 (73 d), and 2016 (74 d). Samples were collected near the mouth of the Coos Bay estuary in Oregon. We enumerated several hundred different morphologically distinct types of embryos and larvae representing at least five phyla. Forty-three embryo types were abundant enough (abundance > 500 over the time series) to enable statistical analysis. Twenty of these types were identified using genetic barcoding of which there were four nemerteans, four gastropods, four chitons, five polychaetes, and two echinoderms. In winter 2014, hydrographic conditions were similar to average historical values. Conditions in 2015 and 2016 were characterized by marine heat waves (MHWs). In 2015, the "warm blob"—anomalously warm water in the Northeastern Pacific—affected conditions and in 2016, there was a strong El Niño. In 2015 and 2016, winter spawning intensity was orders of magnitude lower than in 2014 and many taxa failed to spawn (11 and 24 in 2015 and 2016, respectively); spawning appears to have been adversely impacted by the MHWs. The MHW of 2015 has been attributed to anthropogenic global climate change while the 2016 El Niño may have been strengthened by climate change. The frequency, intensity, and duration of MHW are projected to increase dramatically with global warming, which may adversely affect reproduction and recruitment by numerous marine taxa.

With the increasing atmospheric concentration of CO_2, the average temperature of the atmosphere is increasing. Associated with climate change is an increase in the frequency, intensity, and duration of heat waves on land (Rahmstorf and Coumou 2012). Climate change is also causing heat waves within the ocean, marine heat waves (MHWs), defined as "discrete prolonged anomalously warm water events" (Frolicher et al. 2018). MHWs have recently occurred in the Mediterranean, off western Australia, in the northwest Atlantic and in the northeast Pacific (Frolicher and Laufkotter 2018). Models of climate change suggest that the frequency, intensity, and duration of MHWs will increase (Rahmstorf and Coumou 2012). The impact of these MHWs on organisms has been diverse and often extreme (Frolicher and Laufkotter 2018; Harvell et al. 2019). How MHWs affect the vulnerable early life history stages of marine invertebrates is not known.

A variety of coastal gastropods (e.g., abalone, limpets, and trochid snails) spawn during periods of large surface waves usually associated with downwelling conditions (e.g., onshore transport of ocean surface waters) as indicated by higher sea surface temperatures and lower salinities (Sasaki and Sheperd 1995; Shanks 1997; Onitsuka et al. 2010). Large waves may export embryos rapidly out of the surf zone decreasing their exposure to benthic predators and strong turbulence (Shanks 1997; Gyory and Pineda 2011). They would be transported into the coastal ocean during a period of onshore surface flows, which may maintain larvae close to shore and future settlement sites (Shanks 1997). Preliminary data from Oregon suggested that many intertidal and shallow subtidal invertebrates might spawn during large wave events associated with downwelling (Emlet 2006). To test this hypothesis, we collected daily plankton samples from which we enumerated embryos. Given the stage of development (one to several cells), the embryos were likely hours old and indicative of a recent spawning event. Our 3-yr study of winter spawning by coastal invertebrates in the northeast Pacific sampled during a year that was hydrographically "normal" and during 2 yr with hydrographic conditions characterized by MHW. During these MHW, abundances of spawned embryos from a broad range of benthic organisms were dramatically lower than in the normal year.

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Additional Supporting Information may be found in the online version of this article.

Methods

Samples were obtained by pumping water at high tide from the end of the Oregon Institute of Marine Biology pier (43.349653°N, 124.329768°W) (Fig. 1). The pump intake was 1–2 m below the surface at high tide and the pier is 1.7 km from the mouth of the estuary and the coastal ocean; on every high tide, the water at the end of the pier is predominately from the coastal ocean (Roegner and Shanks 2001).

We used a diaphragm pump (AMT Model 335E-K6, 2 hp electric motor) located 4–5 m above sea level. The pump was attached to a rigid, PVC intake pipe (7.5 cm diameter and 33 m long). The intake opening was strapped to a pier piling and was fitted with a strainer to keep out material > 1–2 cm. The intake line was dry when no pumping was occurring, hence, there were no filter feeders in the line that might have consumed plankton as the water was being pumped. The outflow from the pump ran through a flexible, noncollapsible hose (10 cm diameter and 3 m long) that filled a plankton tower and flowed through a partially submerged plankton net (Fig. 2). The pump was connected to a timer that was set daily to begin pumping a half hour or less before the next predawn or daytime high tide.

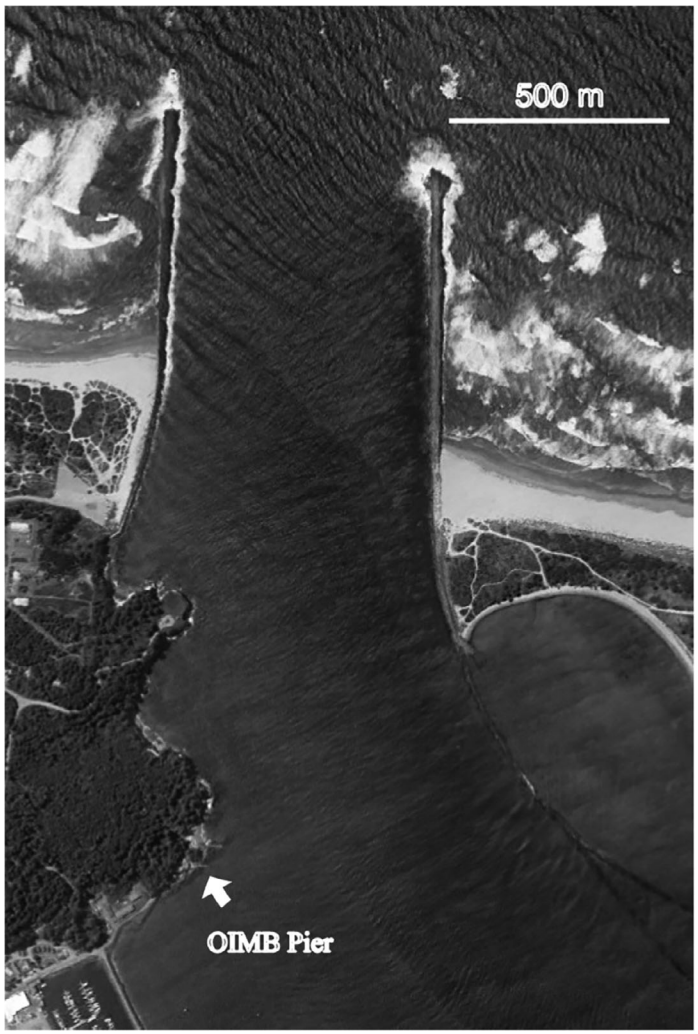

Fig. 1. Location of the OIMB pier sample site relative to the mouth of the Coos Bay estuary. A zooplankton sample was collected daily during the winters of 2014, 2015, and 2016 with a pump system on the pier with sample collection occurring during the first daytime high tide. The pier is located 1.7 km from the open ocean. Peak rising tide currents at the bay mouth range from 0.7 to 1.4 m s^{-1}; hence, it takes from 20 to 40 min during a rising tide for water from the mouth of the bay to transit to the OIMB pier. On a rising tide, ocean water arrives at the pier approximately 2–3 h prior to high tide. Image modified from Google Earth.

Seawater coming from the pump filled the outer region of two concentric cylinders. Water from the outer cylinder flowed into an inner cylinder (30 cm diameter) that held a plankton net (125 μm mesh) that was partially submerged in an outflow tank (Fig. 2). Plankton retained by the net was concentrated into a 3.8-liter plastic cod end jar attached to the bottom of the net and suspended in the outflow tank. This design was chosen to minimize damage to zooplankton during the collection interval.

Pumping duration was from 15 to 60 min with lower pumping times during periods when detritus was in high abundance. Flow rate was determined by measuring the time it took for the pump system to fill a 20-liter bucket. This measurement was taken three times every few days during each time series; flow rates were about 0.2 m^3 min^{-1}. For each sample, approximately 3–12 m^3 of water was filtered through the plankton net. Samples were generally removed from the net within an hour of sampling and taken to the laboratory where samples were sorted and counted live.

In the laboratory, samples were transferred to beakers of seawater, which, to minimize stress on the zooplankton and embryos, were set in constant temperature water baths (~ 10°C) to maintain a temperature similar to that of the ocean. The volume of water in the beakers was determined by weight. After vigorous mixing of the sample, a Stempel pipette was used to remove an aliquot, which was inspected under a dissecting microscope. Sample analysis continued until approximately 20% of the sample had been inspected. Counts of abundant taxa continued until we had enumerated 200 individuals at which point we stopped their enumeration and continued enumerating less abundant taxa (Venrick 1978). All meroplankton and embryos were enumerated. When possible, meroplankters were identified to the lowest taxonomic level using Shanks (2001). Larvae and embryos, which we could not identify, were removed from the sample, photographed, and frozen for later analysis by genetic barcoding. The photographs were used to generate a photographic guide and in which distinct morphological types were given provisional coded names. Photographs of embryos relevant to this article are presented in Supporting Information Section A. Sample processing was labor-intensive and each year we employed 6–9 undergraduate interns and several graduate students to carry out the work. Because of the large number of different types of larvae and embryos encountered (> 300), sample

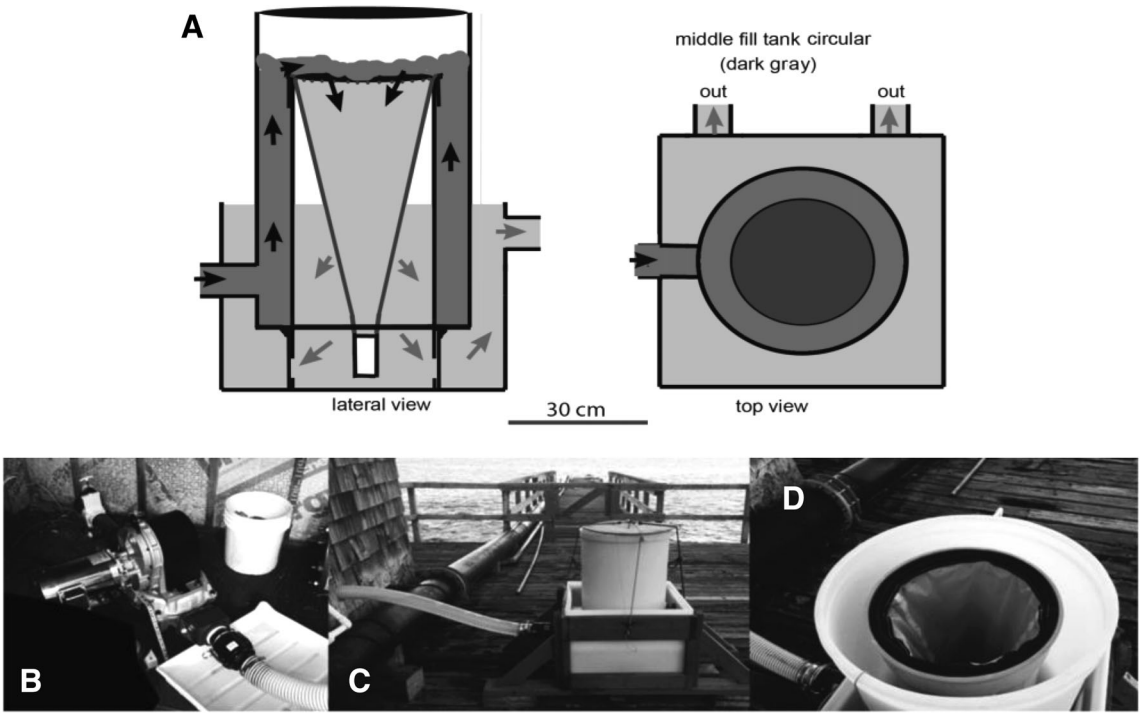

Fig. 2. (**A**) Schematic diagram of pump net tower. The plankton net (dark gray, 125 μm) was suspended in a seawater-filled tank. Water from the pump entered at the top of the net, passed through the net into a large box, and then exited out the side of the box. The lower end of the net and cod end remained submerged. (**B**) Photograph of the diaphragm pump system. (**C**) Side view of the pump net tower on the OIMB dock and (**D**) top view of the net suspended in the pump net tower.

processing proceeded slowly. The students used laptop computers on which the photographic guide was displayed to aid in the identification.

Individual embryos, larvae, or holoplankters that had been photographed and frozen were barcoded with Sanger sequencing methods. DNA was extracted, and partial sequences of cytochrome c oxidase (COI) or 16S mitochondrial genes were amplified using the protocols described in Hiebert et al. (2013). Briefly, DNA was obtained from individual specimens with a Chelex extraction method (InstaGene, BioRad). We used "universal" primers: 16SArL [5′ CGCCTGTTTATCAAAAACAT 3′] and 16S BrH [5′ CCGGTCTGAACTCAGATCACGT 3′] (Palumbi et al. 1991) for 16S rDNA; LCO 1490 [5′GGTCAACAAATCATAAAGATATTGG 3′] and HCO 2198 [5′ TAAACTTCAGGGTGACCAAAAAATCA 3′] (Folmer et al. 1994). We also used "redesigned" COI primers described by Geller et al (2013), and for echinoderms COI primers described by Ward et al (2008), Heimeier et al (2010), and Hoareau and Boissin (2010). Polymerase chain reaction (PCR) thermocycling was carried out with 4–8 μL of undiluted template DNA as follows: 95°C for 2 min; 35 cycles of 95°C for 40 s, 45–55°C (45–52°C for COI, 45–52°C for 16S) for 40 s, and 72°C for 1 min; and a 2 min final extension at 72°C. PCR products were purified using Wizard SV Gel and PCR Cleanup kit (Promega) and sent to Sequetech (Mountain View, CA) to sequence in both forward and reverse directions. Sequences were read, trimmed, and assembled in Geneious v. 7 0.1.7 (Biomatters) and then compared to sequences in GenBank (NIH) or to sequences of known adult specimens collected at OIMB and sequenced by the Emlet and Maslakova laboratories. Assignment of species specific identity to planktonic specimens is based on 98+% sequence match for COI and 99+% for 16S, but caution is warranted due to incomplete knowledge of sequence variability within species and due to the potential for misidentification of material in the GenBank database.

We compared the daily and annual abundance of embryos to a variety of time series of physical conditions. In 2014 and 2015, temperature was measured with an Onset® tidbit temperature logger placed within the seawater-filled box with the zooplankton net. The logger sampled every 10 min, but only data from the period when the pump was operating and filling the box with seawater were used to calculate the average daily seawater temperature. In 2016, temperature in the seawater-filled box was measured with a handheld sensor at the time the zooplankton sample was retrieved. Salinity was determined from a handheld probe (Oakton Salt 6+®). Hourly wave height data from the NOAA Port Orford, Oregon (#46015) wave buoy located approximately 75 km south of Coos Bay were used to calculate daily averages.

Ocean conditions varied dramatically over the 3 yr. Conditions in 2014 appeared normal while conditions in 2015 and 2016 appeared to be indicative of MHWs. To test this hypothesis, we compared our data to historical values of sea surface temperature and also salinity collected daily from the OIMB pier (1968–1996) and wave data from the Port Orford NOAA buoy

(2003–2013). Frequency distributions of historical and annual hydrographic data (e.g., wave height, seawater temperature, and salinity) were statistically compared with Kolmogorov-Smirnov (KS) tests with a Bonferroni correction applied to take into account the multiple comparisons (critical $p < 0.002$).

We assume that the data from abundant taxa are less affected by random sampling errors than are data from taxa that were not abundant or rare. Because of this concern, we limited the analysis to abundant taxa, which we define as embryo phenotypes in which the sum of the daily concentrations (number caught per day scaled by the volume of water filtered, i.e., $\#/m^3$) over the time series was > 500 individuals during at least one winter.

Results

During the three winters (January–March 2014, 2015, and 2016), ocean conditions (temperature, salinity, and wave height) varied dramatically (Figs. 3, 4). The characteristics of the ocean in 2014 appeared "normal" with respect to historical data. Conditions were neutral for both La Niña and El Niño (CCIEA Team 2015). The observed distributions of daily temperature, salinity, and wave height were not significantly different from historical values (Table 1 and Fig. 4) (Huyer 1977). Beginning in winter 2013/2014, there was anomalous warming of a large area in the Northeastern Pacific and Gulf of Alaska. This MHW was christened the "warm blob" (Bond et al. 2015). Water from the "warm blob" moved onto the continental shelf in September 2014 (Peterson and Robert 2015), well after our winter 2014 sampling, and bathed the shore during our winter 2015 sampling (Bond et al. 2015; Peterson et al. 2017; Oliver et al. 2018). Our sampling in winter 2016 occurred during the strong 2015/2016 El Niño (Newman et al. 2018), another MHW. The distribution of seawater temperatures at the OIMB pier for the 2015 and 2016 winters was significantly warmer (~ 1.5–2°C higher) than both historical and 2014 values (Fig. 4). The distributions of salinities in both of these years were significantly lower than both historical and 2014 values (Fig. 4). In addition, salinity values in 2016 were significantly lower than in 2015 (Fig. 4). These results are consistent with observations made at other locations on the Oregon coast (Peterson et al. 2017). In 2015, surface wave heights were significantly lower than those observed historically and in 2014 and 2016 (Fig. 3). In 2016,

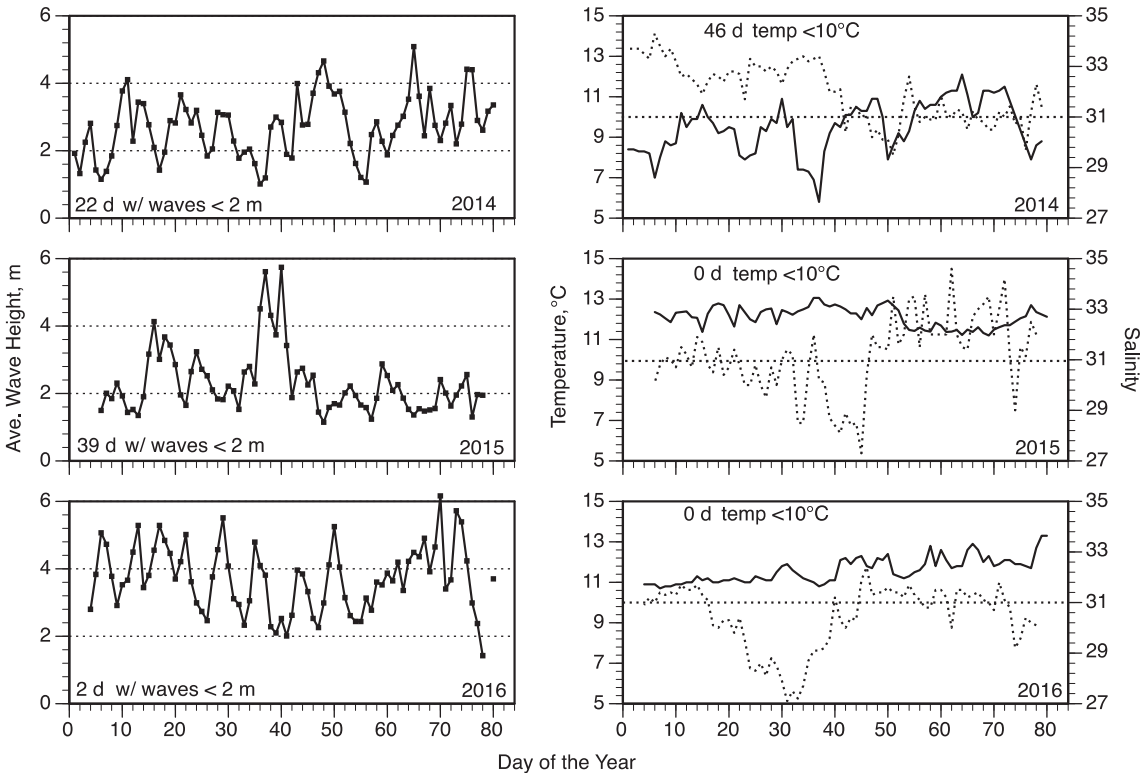

Fig. 3. Hydrographic conditions during the three winter time series. Average daily wave height varied from < 2 m to 6 m during 2014 and 2015, but during the strong El Niño of 2016/2017 wave heights dipped below 2 m on only 2 d and were > 5 m on 9 d. The range in temperature (solid line) and salinity (dotted line) in 2014 was not different from historical values; temperature ranged from 6°C to 11°C and salinity from 31 to 34. The "warm blob" in 2015, a period of anomalously warm water in the Northeast Pacific, and the 2016/2017 El Niño, dramatically altered conditions. In 2015, temperature never dropped below 11°C and the low temperature in 2016 was only 10.7°C. In 2015, salinity ranged from a low of ~ 27 during a period of high rainfall and downwelling favorable winds to > 34 during upwelling favorable winds. In 2016, salinity remained low during the entire time series (27–32) perhaps due to persistent downwelling favorable winds.

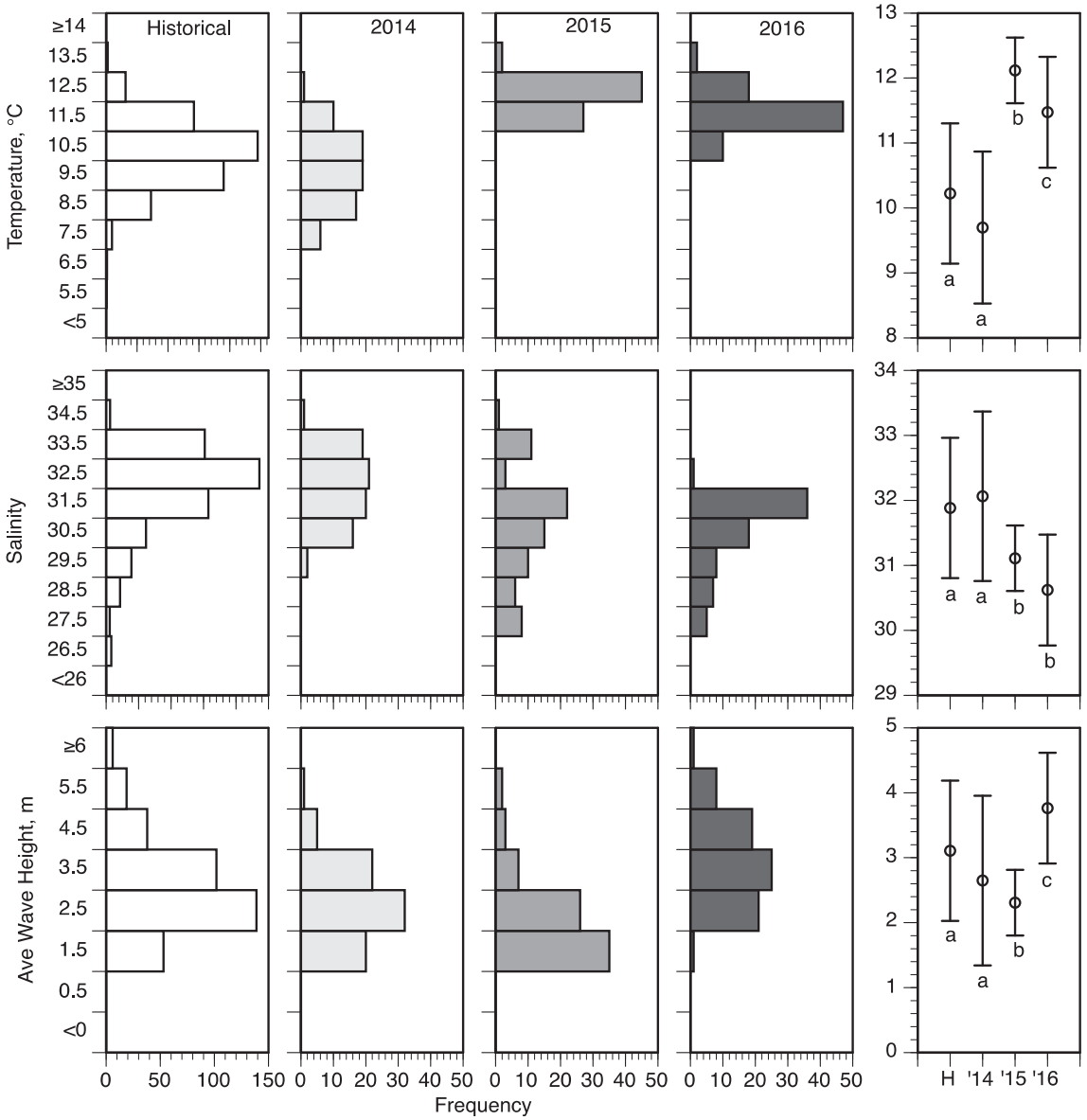

Fig. 4. Daily hydrographic data from the winters of 2014 (light gray bars), 2015 (medium gray bars), and 2016 (dark gray bars) compared to historical values (open bars) of temperature and salinity sampled at the OIMB pier (1968–1996) and wave data from the NOAA Port Orford buoy (2003–2013). Frequency histograms and plots of average (± SD) daily sea surface temperature (top row), salinity (middle row), and wave height (bottom row). In the plots of average values, subscript letters below each SD bar indicate which distributions were similar and different as indicated by Kolmogorov-Smirnov tests. See Table 1 for statistical results.

surface wave heights were significantly higher than historical values and those in 2014 and 2015 (Fig. 4). Indeed, in 2016, there were only 2 d during the 74-d time series when average daily surface wave height was < 2 m (Fig. 3).

Among the hundreds of embryo phenotypes (~ 247) enumerated, 43 (five phyla) had total abundances of > 500 individuals during at least one winter; this analysis focuses on these more abundant embryos. Of the taxa identified by genetic barcoding (20), there were four nemerteans, four gastropods, four chitons, five polychaetes, and two echinoderms. In winter 2014, we observed six spawning events when embryos from multiple taxa (9–22 embryo phenotypes per event) were abundant for one to several days (time series of four representative taxa in Fig. 5). During spawning events, embryo concentrations were on the order of 10^4–10^5 m^{-3} and between events these embryos were absent or nearly so. As was seen in previous research (Shanks 1997), spawning events tended to occur when waves were large, seawater temperature was rising, and salinity was falling (unpublished data)—conditions indicative of a storm coupled with downwelling. Spawning pulses were fewer and smaller in 2015 and 2016 (Fig. 5); the number of embryo phenotypes observed during

Table 1. Results of Kolmogorov-Smirnov test (test statistic *D*, probability *p*) comparing the distributions of daily seawater temperature, salinity, and wave height between historical data and those collected in 2014, 2015, and 2016. Historical values of temperature and salinity were sampled at the OIMB pier (1968–1996) and wave data are from the NOAA Port Orford buoy (2003–2013). df in all tests is greater than 70. To take into account the multiple statistical comparisons, a Bonferroni correction was applied (critical $p < 0.002$).

Year	Temperature	Salinity	Wave height
2014 vs. historical	0.139, 0.171 NS	0.222, 0.002 NS	0.170, 0.052 NS
2015 vs. historical	0.823, < 0.0001	0.488, < 0.0001	0.400, < 0.0001
2016 vs. historical	0.578, < 0.0001	0.547, < 0.0001	0.306, < 0.0001
2014 vs. 2015	0.944, < 0.0001	0.342, < 0.0001	0.233, < 0.001
2014 vs. 2016	0.658, < 0.0001	0.370, < 0.0001	0.436, < 0.0001
2015 vs. 2016	0.432, < 0.0001	0.181, 0.161 NS	0.609, <0.0001

NS not significant at the critical p.

an event was much lower (3–5 embryo phenotypes per event), the strength of the spawning events as indicated by the daily concentrations of embryos was much weaker (maximum 10–100 m^{-3}). Out of the 43 taxa, 38 (88%) were more abundant in 2014 than in 2015 or 2016 (Fig. 6). Ignoring taxa that were absent in a given year, on average the more abundant taxa in 2014 were 47 (range 1.1–518) and 763 (range 4.4–4153) times more abundant than in 2015 and 2016, respectively. In 2015 and 2016, 11 and 24 (26% and 56%), respectively, of these 43 taxa were absent or occurred at total abundances < 10 during the entire time series. By our measures, spawning (as inferred from embryo abundance) by these 43 coastal invertebrates in winter 2015 and 2016 when compared to 2014 ranged from a complete failure to vastly reduced output. Consistent with our observations, during the 2015 and 2016, MHWs in the Southern California Bight, fecundity, and larval production of barnacles were also significantly reduced (Pineda et al. 2018).

Discussion

There are a variety of potential reasons why embryo abundances were drastically lower in 2015 and 2016. Massive die offs of marine invertebrates and algae have been observed during some MHWs (Wernberg et al. 2016; Harvell et al. 2019). Loss of an adult population would, obviously, lead to spawning failure. We did not observe any mass die offs during either 2015 or 2016 and, given the diversity of intertidal organisms that spawned in 2014 and not in 2015 and 2016, a die off event of the necessary magnitude would have been obvious. Some organisms spawn in response to increased phytoplankton abundance

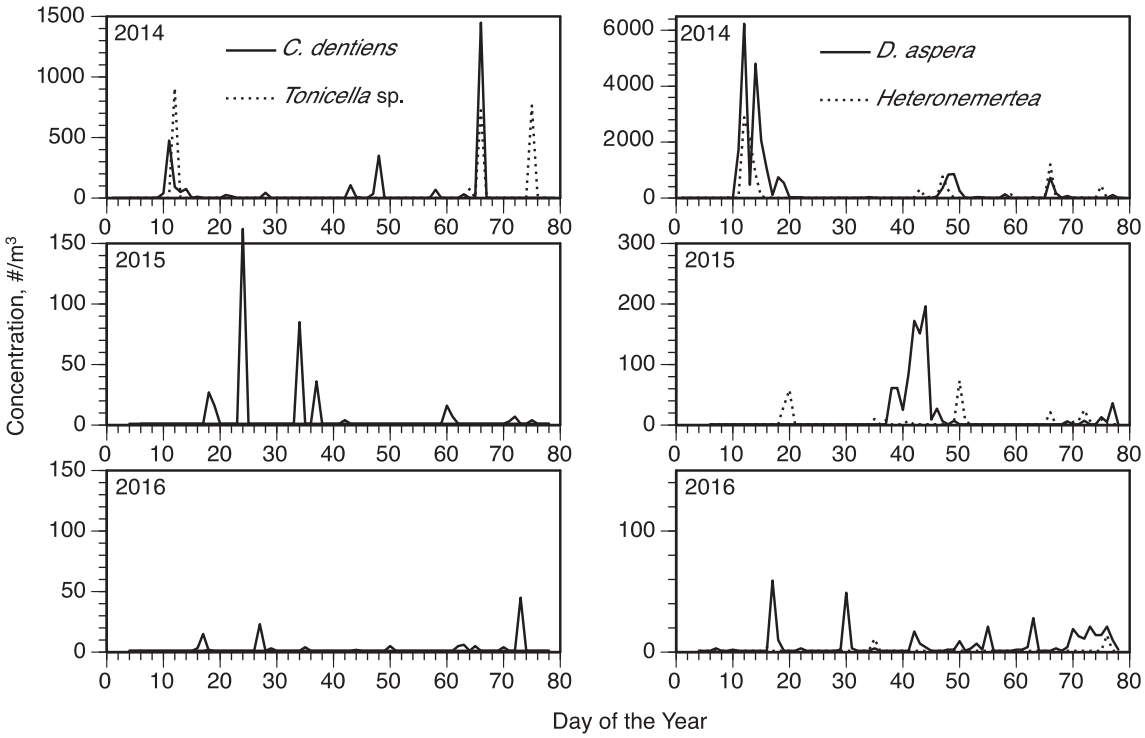

Fig. 5. The daily concentrations (#/m^3) of embryos in plankton samples for four representative taxa during winter 2014, 2015, and 2016. Note that the Y-axis scales for 2015 and 2016 are 10–40 times smaller than in 2014 figures. The concentrations of embryos from two chiton taxa, *Cyanoplax dentiens* (solid line) and *Tonicella* sp. (dashed line), are presented on the left and for a gastropod and nemertean, *Diodora aspera* (solid line) and Heteronemertea (dashed line), on the right. The total abundances of embryos over the time series in 2014, 2015, and 2016 were: *C. dentiens* 2851, 356, and 107; *Tonicella* sp. 2487, 0, and 2; *D. aspera* 21,427, 851, and 341; Heteronemertea 9292, 258, and 28, respectively.

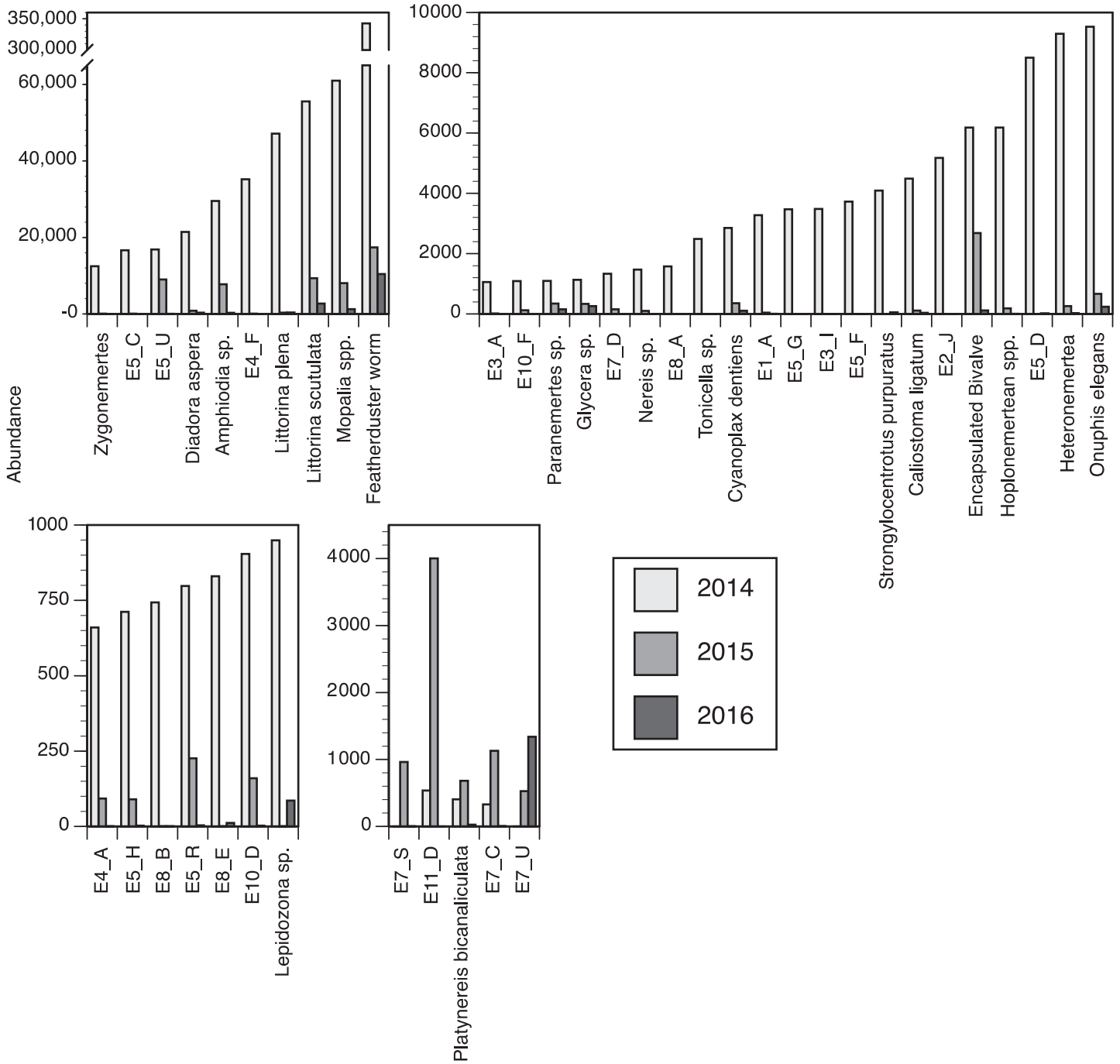

Fig. 6. Total abundance of embryos collected from daily plankton samples during the winter 2014, 2015, and 2016. Note the change in scale between figures. The comparison is limited to taxa with abundances > 500 during at least 1 yr (43 taxa). Embryos of named-taxa were identified by genetic bar coding, otherwise an embryo phenotype was given a provisional name (embryos are illustrated in Supporting Information Section A). Thirty-eight taxa (90%) were most abundant in 2014, 3 (7%) in 2015, and only 1 (2%) in 2016. Of the taxa that were abundant in 2014, 11 of these taxa were absent or at abundances < 10 in 2015 and 24 in 2016.

(Himmelman 1975), but, during winter, phytoplankton concentrations are at an annual minimum.

The warmer seawater during the MHWs may have prevented or slowed normal gametogenesis such that, come winter, ripe gametes were not available for spawning. Falling temperatures in the fall initiates gametogenesis in a variety of temperate chiton and worm taxa (Himmelman 1978; Lawrence and Soame 2004); sea surface temperatures did not drop in the fall of 2015 during the warm blob or in 2016 during the El Niño (Peterson et al. 2017). In some abalone species, sperm production stops at

higher temperatures (Rogers-Bennett et al. 2010). In the urchin *Strongylocentrotus purpuratus*, higher temperatures (> 17°C) for even short periods (10 d) prevent spawning (Cochran and Engelmann 1975). Embryo development in *Cancer magister*, the Dungeness crab, is compromised at > 12°C and fails entirely at temperatures > 16°C (Wild 1983). In 2014, 2015, and 2016 time series, seawater temperatures were ≥ 12°C on 0 d, 61 d, and 25 d, respectively. Alternately, organisms may have been ready to spawn, but during the MHWs the ocean conditions needed to trigger concerted mass spawning never occurred. Comparison of embryo abundances in 2015 and 2016 to those in 2014 did not show temporal shifts in embryo abundances suggesting that the timing of spawning was not altered by the higher temperatures. We did not expect to see such large decreases in reproductive output and did not collect the necessary data to test any of these hypotheses.

El Niños, even strong El Niños such as the one in 2015/2016, are natural occurrences. During the 2016 El Niño, however, in the Niño 4 region of the central equatorial Pacific, sea surface temperatures were exceptionally high (Newman et al. 2018). These high temperatures were unprecedented and while they could have occurred naturally, models suggest that this was unlikely and the high temperatures were likely an effect of anthropogenic climate change (Newman et al. 2018). The warm blob was almost certainly a consequence of anthropogenic climate change (Oliver et al. 2018). Modeling suggests that the intensity and duration of the blob were ≥ 7.3 times more likely to have occurred under the altered conditions than natural. Under natural conditions, the return time for such an anomalous MHW is estimated as only 1 in 120 yr, but under anthropogenic climate change the return time drops to just 1 in 5 yr (Bond et al. 2015; Oliver et al. 2018). Consistent with this prediction, a second warm blob started to form in the Northeast Pacific in fall 2018, but the generating weather conditions subsided (C. Mass, Univ. of Washington, pers. comm.). In fall 2019 yet another warm blob has formed (https://www.fisheries.noaa.gov/feature-story/new-marine-heatwave-emerges-west-coast-resembles-blob). The warm blob MHW was caused by a persistent high-pressure ridge that deflected storms away from the Northeast Pacific preventing typical seasonal deep mixing of the water column with concomitant cooling of the surface waters (Peterson et al. 2017). The high-pressure ridge was generated by a persistent and slowly moving meander in the Jet Stream. Due to the decreasing temperature difference between the Artic and temperate zones caused by climate change, the Jet Stream is producing much larger and often slowly moving meanders and this phenomenon is one of the major causes of extreme weather events both on land and in the ocean (Mann et al. 2018). We sampled during two MHWs, both of which were influenced by anthropogenic climate change.

MHWs have been observed to cause mass mortality of marine animals and plants and alter the geographic range of a diversity of organisms (Frolicher and Laufkotter 2018; Harvell et al. 2019). The biological impacts of MHW have perturbed fisheries causing modifications of fishing practices and harvest, led to closures of fisheries, and price collapses (Frolicher et al. 2018). The negative impacts of MHW on embryo abundance (and by inference spawning) have not previously been reported. It is clearly very difficult to observe spawning failure by marine invertebrates; that we were able to relate our observations to oceanic conditions was due to intensive sampling across a period of changing ocean conditions. While mass mortality of a species during a MHW is a dramatic and obvious impact (Frolicher and Laufkotter 2018; Harvell et al. 2019), the failure to spawn during a MHW is a much more subtle impact but the ultimate effect may be similar, the decline, or local extinction of populations. This may be particularly true for semelparous organisms in which case a single MHW could devastate and perhaps extirpate a local population. For short-lived species, a similar impact may occur from repeated MHW as we observed with significantly reduced embryo production in both the 2015 and 2016 MHW. Given the extremely high mortality during pelagic larval development and benthic recruitment (> 95% at each life history stages) (Rumrill 1990; Gosselin and Qian 1997), even moderate reductions in reproductive output could lead to failure of cohorts recruiting into adult populations. This additional strain on populations could cause them to be less resilient to the other impacts of climate change on marine communities.

Due to climate change, MHWs are becoming more common, larger, and hotter (Frolicher et al. 2018). For example, between 1982 and 2016, the observed number of MHW days worldwide has doubled (Frolicher et al. 2018) and this trend is projected to continue into the future. Models suggest that with global warming of 1.5–3.5°C, there will be an additional 16- to 41-fold increase, respectively, in the number of MHW days with concomitant increases in both the extent and severity of the MHW. Given the severity of the biological impacts observed during recent MHW, they may become one of the dominant drivers of climate-related change in marine communities. Substantial reductions in embryo production among intertidal and subtidal benthic marine species that we have documented here could drastically impact benthic populations and food webs in coastal ecosystems.

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Conflict of Interest

None declared.

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