# Depth-dependent temperature variability in the Southern California bight with implications for the cold-water gorgonian octocoral *Adelogorgia phyllosclera*

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ABSTRACT

Cold-water corals are highly sensitive to changes in water temperature, as it is an important determinant of their distribution. In recent years, several heatwave events have occurred in multiple marine ecosystems, including the northeast Pacific Ocean. However, the effects of elevated ocean temperatures on cold-water corals are largely unknown. Determining the upper thermal limits of cold-water octocorals is an important first step in identifying if warm-water events pose a potential threat. Temperature data were obtained from loggers placed in the Channel Islands National Marine Sanctuary (CINMS) at 20, 50, 100, and 200 m prior to the 2015–2016 El Niño Southern Oscillation (ENSO) event and used to characterize warm-water anomalies. Live colonies of the common gorgonian octocoral, *Adelogorgia phyllosclera*, were collected from the CINMS using a remotely operated vehicle (ROV) and transported to laboratory aquaria where they were maintained. A laboratory study was conducted to investigate the upper thermal limit of *A. phyllosclera* during a series of temperature assays using coenenchyme health scores, polyp activity, and estimated survival. Results of *in-situ* temperature analyses indicated that warm-water anomalies occurred frequently at 50 and 100 m, with most of these anomalies occurring during strong ENSO months. Based on the laboratory temperature assays, the upper thermal limit of *A. phyllosclera* was estimated to be 20 °C, with a time to effect of 96 hours. During the 2015–2016 ENSO event, this upper thermal limit was exceeded (21.1 °C) by warm-water anomalies at 20 m that lasted up to 14.1 hours, and approached (18.3 °C) by warm-water anomalies at 50 m that lasted up to 52.7 hours. Projections for future warm-water events suggest that the upper thermal limit of *A. phyllosclera* and other cold-water corals will likely be reached more frequently in the coming years. Thus, understanding the responses of cold-water corals to thermal stress will help predict the resilience of these species to future ocean warming.

## 1. Introduction

The term *cold-water coral* is generally used as a synonym for *deep-sea coral*. These are effectively different terminologies to describe similar ecosystems, but *cold-water coral* does not restrict the definition of these organisms to depths > 200 m since some of these *deep-sea corals* have been documented as shallow as 50 m in the fjords of Norway (Rogers, 1999). Cold-water coral ecosystems provide complex, heterogeneous habitats that promote benthic biodiversity (Freiwald et al., 2009; Henry and Roberts, 2007). Gorgonian octocorals are the most diverse group of corals with over 3000 described species, 75% of which are found in waters deeper than 50 m (Cairns, 2007). Octocorals can form dense

fields of large, tree-like structures called 'coral gardens' (Freiwald et al., 2004; Stone, 2006) that can provide shelter, feeding areas, and nurseries for many commercially important fish species (Krieger and Wing, 2002; Mortensen and Buhl-Mortensen, 2005). Cold-water gorgonian octocorals in deep and mesophotic reefs are part of some of the most vulnerable marine communities since they are easily disturbed by bottom-trawling (Freiwald et al., 2004; Watling and Norse, 1998) and oil and gas exploration (Etnoyer et al., 2016; DeLeo et al., 2016; Frometa et al., 2017; Girard and Fisher, 2018). Due to extremely slow growth rates, it may take decades to centuries for cold-water corals to recover from disturbances (Fisher et al., 2014).

In recent years, warm-water anomalies during marine heatwaves

have severely impacted marine ecosystems (Oliver et al., 2018). These warm-water events have increased the incidence of large-scale shallow-water coral mortality events (Hughes et al., 2018; Heron et al., 2016; Sánchez et al., 2014; Turley, 1999) and may pose a threat to cold-water corals. Such anomalies are increasingly detected in subsurface waters (Torrents et al., 2008; Zaba and Rudnick, 2016; Guihen et al., 2012), which is a concern for cold-water corals, since water temperature is a critical determinant in their distribution (Roberts et al., 2006). Cold-water corals may have similar heat stress responses as shallow water corals including the production of heat shock proteins and the expression of stress genes (Downs et al., 2000), changes in metabolic demand (Lesser, 1997), reduced energy stores (Ezzat et al., 2013), and reduced reproductive output (Michalek-Wagner and Willis, 2001).

Short-term climatic events, such as El Niño Southern Oscillation (ENSO), have been linked to marine heatwave variability (Oliver et al., 2018) and provide an opportunity to assess the threat of warm-water anomalies to cold-water octocorals. In the Eastern Tropical Pacific Ocean, mass bleaching of shallow-water corals has already been linked to marine heatwaves during ENSO events (Glynn et al., 2001). ENSO-related marine heatwaves (Oliver et al., 2018) have also resulted in mass mortality of marine invertebrates (Garrabou et al., 2009) and cold-water (12–25 °C) habitat forming species like kelp forests off California (Wernberg et al., 2013; Smale and Wernberg, 2013). These marine heatwave events have been increasing in frequency and intensity off California (Oliver et al., 2018), demonstrating the importance of determining the responses of marine species to these events.

One of the most advanced metrics to measure thermal anomalies in marine ecosystems is the Degree Heating Week (DHW) product used to monitor and predict bleaching and mortality of shallow-water and mesophotic corals (Eakin et al., 2010; Liu et al., 2014; Hobday et al., 2016; Safaie et al., 2018). This product relies on long-term, satellite-based sea surface temperature (SST) data to monitor the duration and intensity of warm-water anomalies above a local mean summer threshold temperature (Strong et al., 1997). The DHW model was based on the thermal stress response of shallow-water coral species, which may compromise its application to species that have narrow physiological limits, such as many cold-water corals (Roberts et al., 2006).

The California coast, including the Southern California Bight (SCB), experiences seasonal upwelling which induces abnormally cool conditions (typically between 8 and 14 °C) at shallow depths (20–200 m; Chavez et al., 2002), and supports a rich diversity of cold-water corals. However, the SCB is also a region where warm-water anomalies may pose a threat to these sensitive taxa (Whitmire et al., 2017). Sea surface temperature anomalies have previously been observed along the Southern California coast in concurrence with the 1982–83 (Fiedler et al., 1986), 1991–92 (Lynn et al., 1995), 1997–98 (Bograd and Lynn, 2003) ENSO events. However, recent warm-water anomalies in the SCB during 2014 and 2015 were detected as deep as 50 m and were predicted to continue and potentially become even more extreme during the strong ENSO event forecasted for the winter of 2015–2016 (Zaba and Rudnick, 2016). Additionally, gorgonian densities off Anacapa Island, CA have declined from 2005 to 2014 (Etnoyer et al., 2015), accompanied by increased observations of dead gorgonians in the central California region during remotely operated vehicle (ROV) surveys in the fall of 2016 (California Department of Fish and Wildlife, Marine Region, 2017). The dead gorgonians comprised ~ 23% of all the octocorals observed in the surveys from Soquel Canyon to Point Buchon (California Department of Fish and Wildlife, Marine Region, 2017). The cause of the gorgonian mortalities remains unknown; however, one hypothesis suggested was that the mortality events were related to warm-water anomalies occurring in the region.

Although the impacts of climate change on shallow-water and mesophotic corals have been investigated extensively, the effects on cold-water corals are largely unknown. The research that has examined the effects of climate change on cold-water corals mostly has focused on ocean acidification (Lunden et al., 2013; Gómez et al., 2018). Effects of

ocean warming on cold-water corals might be less apparent because bleaching would not occur as it does for shallow-water corals due to the lack of photosynthetic symbiotic algae, zooxanthellae. Therefore, other metrics must be used to identify the influence of thermal stress on cold-water corals.

Understanding the sensitivity of cold-water octocorals to warming oceans is of pressing concern as warm-water anomalies have been documented in regions where cold-water octocorals may occur (Zaba and Rudnick, 2016), and are expected to increase in frequency and duration under continued ocean warming (Oliver et al., 2018). However, there is little baseline information on the intensity and duration of these anomalies, or of how cold-water octocorals may be affected.

The objectives of this study were to: (1) characterize warm-water anomalies in the SCB at depths cold-water octocorals are known to occur (20–200 m) in a historical and contemporary context, and (2) examine the thermal limits of the cold-water octocoral, *Adelogorgia phyllosclera*, using live colonies maintained in cold-water aquaria for short-term temperature assays that monitored survivorship, health scores, and polyp activity. *Adelogorgia phyllosclera* (Bayer, 1958) is an azooxanthellate gorgonian octocoral endemic to the SCB (Fig. 1) found primarily in cold waters between 50 and 100 m (Salgado et al., 2018; Fig. 2). Specifically, we tested the hypotheses that warm-water anomalies occurred in the 20–200 m depth range during the 2015–2016 ENSO event, and that these anomalies exceeded the upper thermal limit of *A. phyllosclera*.

## 2. Methods

### 2.1. Defining the warm-water anomaly threshold

The California Cooperative Fisheries Investigations (CalCOFI) program has collected hydrographic data at 75 stations in the Southern California Bight in 1949. Since 1985, quarterly conductivity, temperature, and depth (CTD) casts have been conducted, whereas prior to 1985 casts occurred monthly or as little as once annually with missing data in some years. Temperatures were measured using bathythermographs, bucket thermometers, or paired protected reversing thermometers until 1994, after which a Sea-Bird Electronics, Inc. 911 + CTD instrument was used. Water temperature data from the 1949–2016 CalCOFI data reports were used to understand the historical context for warming events (http://new.data.calcofi.org/index.php/publications/calcofi-data-reports). Measurements at 20, 50, 100 and 200 m were compiled using data from three CalCOFI sampling stations with latitudes and longitudes closest to temperature loggers deployed at 20, 50, 100, and 200 m near Anacapa Island, CA in 2015 (Table 1). Because these stations were not sampled consistently by CalCOFI, several stations were used to compile data for each depth. When a sampling station was no longer used by CalCOFI, another station with coordinates similar to the temperature loggers deployed in 2015 was selected.

Water temperature data for each depth layer were pooled and a water anomaly metric was calculated as the historical mean of all months with data available from 1949 to 2016 ($\overline{x}^H$) plus two standard deviations (2SD). The $\overline{x}^H$ values at each depth were compared using a Kruskal–Wallis test and post-hoc Wilcoxon pairwise comparisons with a Bonferroni-type adjustment. The anomaly threshold of the historical mean plus two standard deviations was employed in lieu of other methods such as HotSpots (i.e., derived from subtracting the Mean Monthly Maximum (MMM) from SST values) or Degree Heating Weeks (DHW) models, which were developed and verified based on the thermal stress response of shallow-water corals (Liu et al., 2014). The HotSpots and DHW models require SST values to be 1 °C above the MMM (Liu et al., 2014). The MMMs were calculated for 20, 50, 100, and 200 m using the CalCOFI data from 1948 to 2016 to compare the MMM method with the 2SD method that was adopted here. The anomaly threshold of 2SD above the historical mean for each depth (Table S1) was more conservative and comparable to the MMM
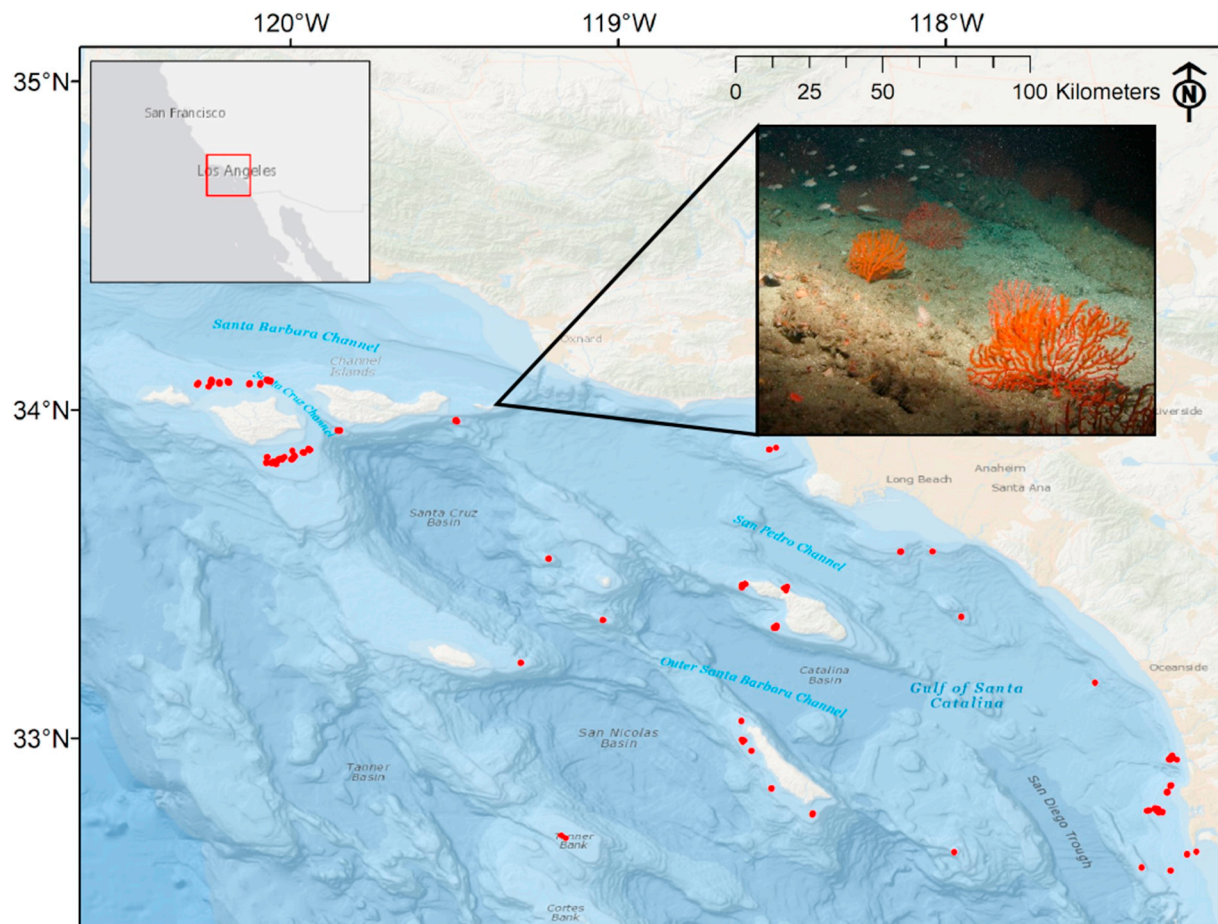
**Fig. 1.** Map of *Adelogorgia phyllosclera* occurrences in the Southern California Bight with an *in situ* photograph of *A. phyllosclera* in the CINMS. Photo credit: Marine Applied Research and Exploration (MARE) ROV team. Map courtesy: Robert McGuinn, NOAA Deep-Sea Coral Research and Technology Program.

anomaly threshold with less than a 10% difference between the MMM and 2SD thresholds (Table S1).

### 2.2. Characterizing warm-water anomalies during the 2015–2016 ENSO event

*In situ* water temperature data were obtained from temperature loggers deployed to 20, 50, 100 and 200 m at the AI-1 site on the north side of Anacapa Island located in the Channel Islands National Marine Sanctuary (CINMS) in November 2015 by the RV *Shearwater* (Table 2, Caldow et al., 2015). In July 2016, the temperature loggers were retrieved by the ROVs *Beagle* and *Hercules* (Etnoyer et al., 2017). While deployed, the loggers measured water temperature every 5 min, with a precision of 0.02 °C. For each *in situ* data logger depth, all water temperatures that exceeded the appropriate warm-water anomaly threshold (Table 3) were flagged. In addition to calculating the percent occurrence of anomaly events, the repetitive nature of *in situ* sampling also enabled characterization of anomaly duration, which was calculated as the time elapsed between each unbroken series of flagged temperature readings.

### 2.3. Sample collection and husbandry

In 2015 and 2016, 20 live *A. phyllosclera* samples were collected at 80–90 m using the ROVs *Beagle* and *Hercules* aboard the ships RV Shearwater (Etnoyer et al., 2017) and EV Nautilus (Raineault et al., 2017). Whole colonies were kept in 3.78 L plastic containers in a refrigerator on the ship, with daily water changes (~20–30%) using ambient surface water chilled to the *in situ* temperature at depth (10 °C).

The colonies were shipped in the plastic containers to the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Coastal Ocean Science (NCCOS) laboratory in Charleston, SC. Upon receipt, corals were slowly acclimated to artificial seawater in a laboratory environment [deionized water with artificial sea salts (Instant Ocean); 34.5 psu; 10 °C] over 48 h while residing in shipping canisters.

After acclimation, whole colonies were transferred to a 568 L closed-system aquarium composed of a 492 L holding tank, small sump, and protein skimmer (Frometa et al., 2017). Water quality was maintained through partial (20%) water changes every 2 weeks so that nutrients did not exceed predetermined thresholds ($NH_3$ = 0.00 mg L$^{-1}$; $NO_2^-$ = 0.00 mg L$^{-1}$; $PO_4^{3-}$ = 0.30 mg L$^{-1}$) to prevent microbial growth. Corals were fed *ad libitum* with a pipette containing 100 mL of artificial seawater with a combination of 10 mL of Marine Snow® (Two Little Fishies, Inc., Miami Gardens, FL) and 5 squares of frozen Coral Gumbo™ (Hikari Sales USA, Hayward, CA). Colonies were maintained for a period of 9 months with no noticeable decline in condition (i.e.

**Table 1**
Number of different CalCOFI sampling stations used to compile each temperature station data set and the mean distance (weighted by the number of sampling stations) to the temperature loggers deployed near Anacapa Island, CA in 2015.

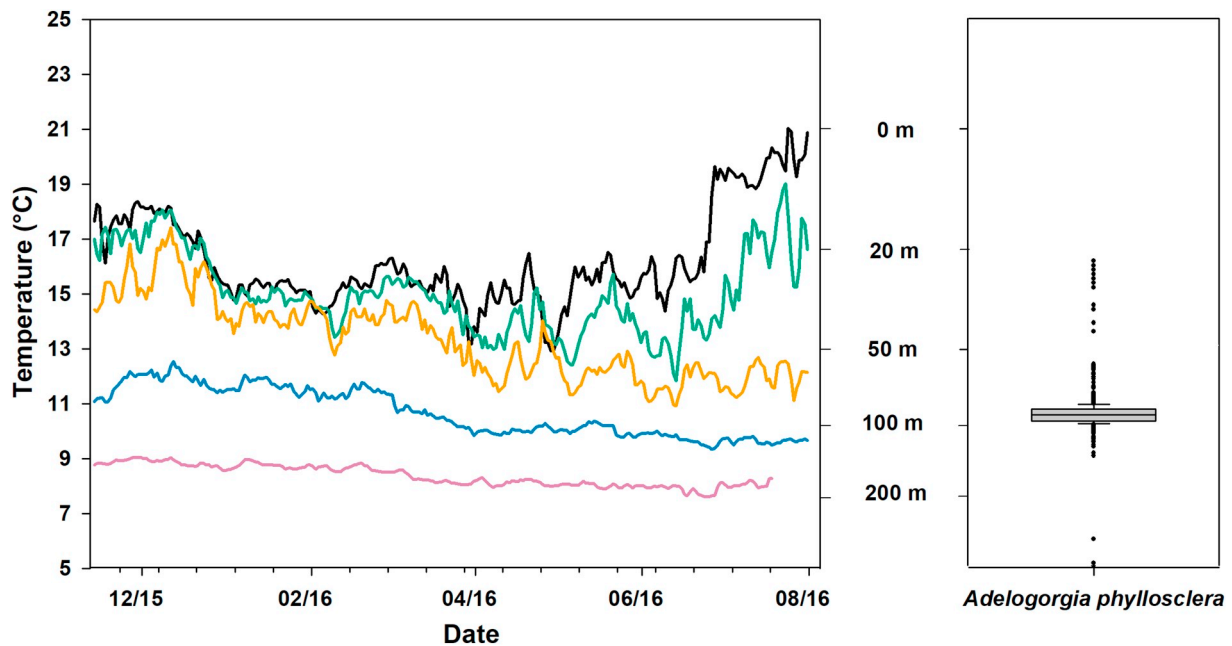| Temperature station | Number of sampling stations used | Weighted mean distance from temperature loggers (km) ± SE |
|---|---|---|
| 1 | 25 | 48.7 ± 11.2 |
| 2 | 28 | 102.9 ± 6.7 |
| 3 | 6 | 150.3 ± 6.0 |

**Fig. 2.** Time series plot of daily sea surface temperature (SST; *black*) obtained from the National Buoy Data Center (NBDC) Station 46,217 and mean daily temperatures at 20 (*green*), 50 (*orange*), 100 (*blue*), and 200 (*pink*) m from temperature loggers deployed in the Channel Islands National Marine Sanctuary off the coast of Anacapa Island, CA from November 13, 2015 to July 31, 2016 (Etnoyer et al., 2017). The depth at which temperatures were recorded is indicated by *color* and by the *y-axis* of boxplot showing the depth distribution of *A. phyllosclera* (n = 4132) from NOAA Deep-Sea Coral Research and Technology Program. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

coenenchyme necrosis and loss of tissue).

### 2.4. Fragmentation and temperature assays

Whole *A. phyllosclera* colonies were cut into smaller fragments of about 40–60 polyps and attached with cyanoacrylate glue to small glass pegs with a hole drilled in the center. Fragments were replaced into the main holding tank for 7 days to recover from the fragmenting process. After the recovery period, fragments were placed in 1 L glass beakers (one fragment per beaker) containing 1 L of freshly made seawater (34.5 psu) and covered with aluminium foil to minimize evaporation. The fragments were kept upright by attaching the glass pegs to a small plastic grid at the bottom of the beaker. Three temperature assays were conducted:

1. Shock: fragments were immediately placed into beakers pre-set to each thermal set-point and held in incubators for 96 h
2. Fast acclimation: fragments were acclimated to set-point by $1\,°C\,h^{-1}$ from 10 °C and then held at each thermal set point for 96 h
3. Slow acclimation: fragments were placed in an incubator at 10 °C and increased by $1\,°C\,day^{-1}$

The shock and fast acclimation assays consisted of five temperature treatments (e.g., thermal set-points): 5, 10 (control), 15, 20, and 25 °C. The slow acclimation assay had no pre-determined thermal set-point but was conducted to determine the thermal limit under gradually increased temperatures ($1\,°C\,day^{-1}$) until complete mortality of all

fragments was observed. Thermal set-points and rates of increase corresponded to those observed in the *in situ* temperature data from the loggers deployed in the CINMS.

Beakers were kept in incubators (a separate incubator for each temperature treatment) in the dark with aeration. Each temperature treatment consisted of six replicates (fragments) from six distinct colonies. The slow acclimation assay was designed using two replicate incubators, each with six coral fragments (n = 12). Water quality (temperature, salinity, and pH) were monitored daily and 50% water changes were made every 48 h. Corals were fed daily by pipette with a combination of Coral Gumbo™ and Marine Snow® after all uneaten food from the previous day had been removed to prevent fouling of the water.

Coral fragments for the shock and fast acclimation temperature

**Table 3**
Historical mean temperatures ($\overline{x}^H$) and anomaly thresholds ($\overline{x}^H + 2SD$) for 20, 50, 100, and 200 m calculated using the CalCOFI data from 1949 to 2016 with percent of observations from the CINMS temperature loggers exceeding the $\overline{x}^H$ and $\overline{x}^H + 2SD$ during the 2015–2016 ENSO event.

| Depth (m) | Historical Mean Temperature | % of logger observations > $\overline{x}^H$ | Anomaly Threshold ($\overline{x}^H + 2SD$) | % of logger observations > $\overline{x}^H + 2SD$ |
|---|---|---|---|---|
| 20 | 15.0 °C | 45.0 | 16.9 °C | 17.0 |
| 50 | 12.2 °C | 70.5 | 13.7 °C | 41.5 |
| 100 | 10.2 °C | 57.0 | 11.0 °C | 38.5 |
| 200 | 8.7 °C | 24.8 | 9.7 °C | 0.0 |

**Table 2**
Deployment and recovery details of temperature loggers with latitude and longitude. Latitude and longitude are in decimal degrees.

| Depth (m) | Deployment date | Recovery date | Temperature logger brand | Latitude | Longitude | Deployment method |
|---|---|---|---|---|---|---|
| 20 | 11/12/2015 | 8/2/2016 | Hobo | 34.017 | −119.441 | Shipside |
| 50 | 11/12/2015 | 8/2/2016 | Hobo | 34.021 | −119.447 | Shipside |
| 100 | 8/4/2015 | 8/2/2016 | Star-Oddi | 34.964 | −119.485 | ROV |
| 200 | 3/14/2015 | 7/18/2016 | Star-Oddi | 33.959 | −119.475 | Shipside |

assays were photographed and health (details below) was assessed at 0, 24, 48, 72, and 96 h. During the slow acclimation assay, coral fragments were photographed and health was assessed every 24 h until complete mortality. Health scores for *A. phyllosclera* were developed based on the methods of DeLeo et al. (2016) and Frometa et al. (2017) and modified to exclude polyp activity as that was assessed separately. Health scores were assigned to each fragment based primarily on the percentage of discoloured tissue (changing from red/orange to black).

Health scores were assigned as follows:

5: 100% tissue-covered skeleton with no discoloration of coenenchyme.

4: Between 75% - 100% tissue-covered skeleton, minimal tissue discoloration (< 50%).

3: Between 75% - 100% tissue-covered skeleton, majority tissue discoloured (> 50%).

2: ~50% tissue-covered skeleton with remaining tissue discoloration to black.

1: < 50% tissue-covered skeleton with any remaining tissue discoloured.

0: Fragment is entirely bare skeleton.

For the shock and fast acclimation assays, polyp activity was also estimated from the same photographs as coenenchyme health scores using the method of (Torrents et al., 2008; Fig. 3). For each coral fragment the percentage of three expansion states of the polyps was recorded: tentacles of polyp totally expanded (State 1), tentacles of polyp emerging from the gastric cavity without an expanded state (State 2) and totally retracted polyp tentacles (State 3). Using these data, the percentage of polyp activity per fragment (Torrents et al., 2008) was calculated from the formula:

$$(State\ 1 \times 1) + (State\ 2 \times 0.5) + (State\ 3 \times 0).$$

### 2.5. Survival and polyp activity analysis

Health scores and polyp activity percentages were averaged for replicate coral fragments for each temperature treatment and plotted over time to investigate health and polyp activity decline. Differences within the treatments at the 96 h end-point were tested using a non-parametric
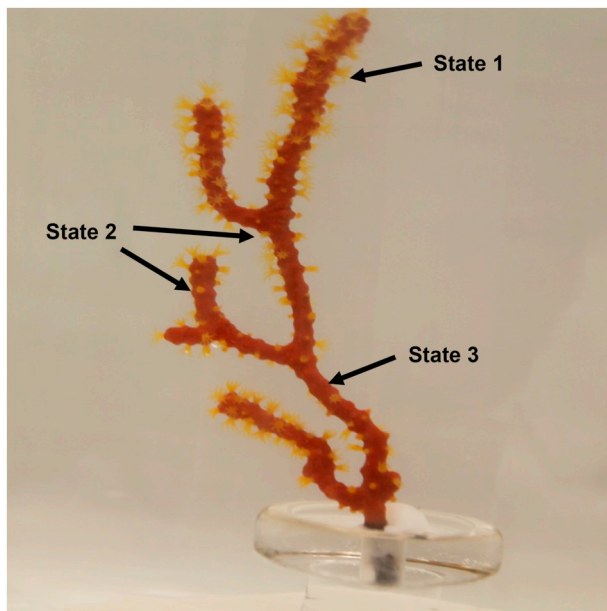


**Fig. 3.** Picture of the three polyp states on *A. phyllosclera* as defined in Torrents et al. (2008). Polyps that were fully or mostly extended were defined as State 1, polyps that were partially retracted were defined as State 2, and polyps that were fully retracted were defined as State 3.

Kruskal–Wallis test, and if applicable, post-hoc Wilcoxon pair-wise comparisons were performed.

A Kaplan–Meier (K–M) survival analysis was performed for the shock and fast acclimation temperature assays. Fragments declining to a health status of 3 or below were marked as an "event," whereas remaining data were censored in this analysis (DeLeo et al., 2016). A log-rank test was used to evaluate significant differences among the temperature treatments for each assay where ($\alpha$ = 0.05). If significant, a pairwise log-rank test evaluated differences between temperature treatments. Because the probability of mortality increased as temperature increased during the slow acclimation assay, an accelerated failure model with a Weibull distribution was used to determine the mean time-to-event (death). The mean time-to-event was then used to infer between what temperatures death occurred.

## 3. Results

### 3.1. Defining the warm-water anomaly threshold

The historical mean temperatures ($\overline{x}^H$) at 20, 50, 100 and 200 m ranged from 15.0 °C at 20 m depth to 8.7 °C at 200 m depth (Table 3). The historical mean temperatures were significantly different from each other (Kruskal–Wallis, $p < .0001$) where mean temperatures and the anomaly thresholds decreased with depth (Table 3). Historical temperature variation decreased with depth, and correspondingly the difference between the means and anomaly thresholds decreased from 20 to 100 m (Table 3). However, there was a slight (0.2 °C) increase in the difference between the mean and anomaly threshold from 100 to 200 m (Table 3).

### 3.2. Characterizing warm-water anomalies during the 2015–2016 ENSO Event

Analysis of *in situ* temperature logger data from the 2015–2016 ENSO event indicated that there was a higher percent of recorded temperatures above the anomaly threshold at 50 and 100 m in comparison to 20 and 200 m (Table 3). Likewise, there were a greater number of anomaly events at 50 (206 events) and 100 m (609 events) than there were at 20 (73 events) and 200 m (0 events; Table 3; Fig. 4). During these anomaly events, temperatures reached almost 6 °C above $\overline{x}^H$ at 25 and 50 m, which was 20% higher than the anomaly threshold for 20 m and 33% higher than the anomaly threshold for 50 m (Table 4). Most of these anomaly events came about quickly and lasted 1.5–3 h. However, some anomaly events persisted for several consecutive days, particularly at 50 and 100 m (Table 4).

Temporal differences in warm-water anomaly events were observed according to depth. Anomaly events at 20 m were only observed during July 2016 (Fig. 4). Anomaly events at 50 and 100 m were observed mostly from November 2015 to February 2016, with the longest of these events lasting between 50 and 60 h (Table 4; Fig. 4).

### 3.3. Temperature assays

For the shock temperature assay, declines in health scores for fragments exposed to 25 °C were observed at 24 h and persisted until 96 h (Fig. 5A). Health deterioration was also observed for fragments exposed to 20 °C beginning at 48 h and continuing through 96 h. A Kruskal–Wallis test revealed significant differences ($p < .05$) in the health scores of fragments at 96 h with pairwise comparisons revealing significant differences in the health scores of fragments exposed to 20 and 25 °C compared to the control (10 °C). Although mean polyp activity was highly variable, there were significant differences at 96 h for fragments exposed to 25 °C (Kruskal–Wallis, $p < .05$; Fig. 5B). Significant differences were detected among K–M survival estimates between temperature set-points ($p < .0001$; Fig. S1). However, pairwise comparisons using a log-rank test revealed that this difference was only
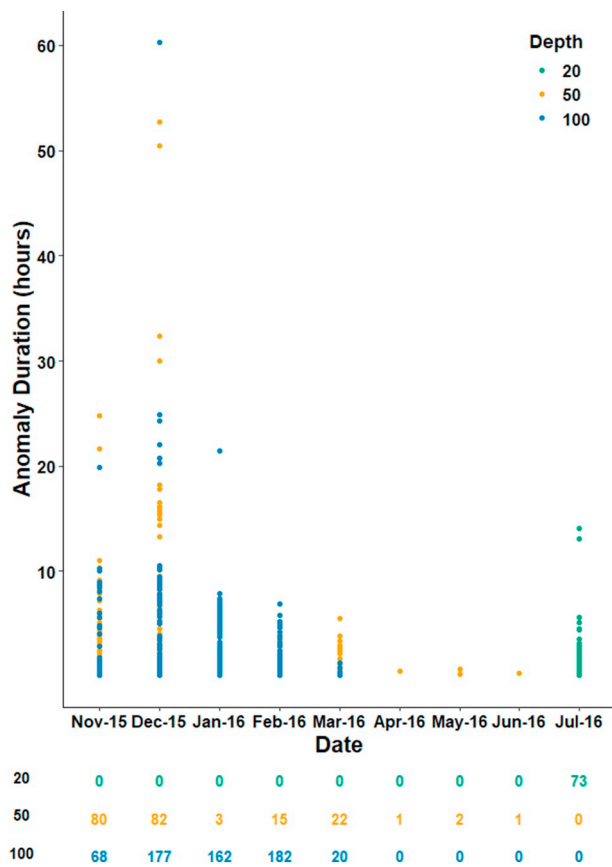
**Fig. 4.** A bar plot of warm-water anomaly (calculated as 2 standard deviations above the mean historical temperature) durations in values of hours by month. Anomalies were calculated from data loggers placed at 20, 50, and 100 m around Anacapa Island, CA from November 2015 to July 2016 (Etnoyer et al., 2017). No anomalies were detected at 200 m. Numbers underneath the bar plot indicate the number of anomalies that occurred during that month.

**Table 4**

Warm-water anomaly characteristics from the CINMS temperature loggers placed at 20, 50, 100, and 200 m from November 2015–July 2016.

| Depth (m) | Number of anomaly events | Anomaly event mean duration (h) | Anomaly event maximum duration (h) | Anomaly event maximum temperature (°C) |
|---|---|---|---|---|
| 20 | 73 | 1.5 | 14.1 | 21.1 |
| 50 | 206 | 3.8 | 52.7 | 18.3 |
| 100 | 609 | 1.8 | 60.3 | 13.8 |
| 200 | 0 | – | – | – |

for fragments exposed to 25 °C ($p < .05$; Table 5) where the mean survival estimate dropped below 50% at 72 h and complete mortality of all fragments occurred at 96 h (Table 6; Fig. S1).

A significant difference in health scores of fragments between temperature treatments was observed during the fast acclimation assay (Kruskal–Wallis, $p < .05$; Fig. 5C). Pairwise comparisons revealed that significant differences in health score were only observed for fragments exposed to 20 and 25 °C ($p < .05$). Again, mean polyp activity was extremely variable throughout the experiment (Fig. 5D) and significant differences from the control (10 °C) at 96 h were only observed for fragments exposed to 25 °C (Kruskal–Wallis, $p < .05$). Significant differences were detected among K–M survival estimates between temperature set-points ($p < .0001$; Fig. S2). Pairwise comparisons using a log-rank test revealed that this difference characterized only those fragments exposed to 25 °C (Table 5). The mean survival estimate for 25 °C dropped below 50% at 48 h and complete mortality for all

fragments occurred at 72 h (Table 6; Fig. S2). The mean survival estimate for 20 °C also reached 50% survival at 96 h; however, this survival curve was not significantly different ($p < .05$) from the control.

When coral fragments were exposed to temperatures increased by 1 °C day$^{-1}$ during the slow acclimation assay, mean survival dropped below 50% at 120 h (15 °C) and complete mortality of all fragments was observed at 144 h (16 °C). The accelerated failure model indicated that the time-to-event (death) when coral fragments were exposed to a temperature increase of 1 °C day$^{-1}$ was at 134.5 h which falls between 15 and 16 °C (Fig. S3).

## 4. Discussion

The purpose of this study was to determine if warm-water anomalies occurred at depths where cold-water corals occur; and, if so, assess the threat of thermal stress during extreme climatic events, specifically the 2015–2016 ENSO event. The 50–100 m depth range had historical mean temperatures between 10 °C and 12 °C. The 50–100 m depth range was also associated with the highest percentage of observations above the 2SD anomaly threshold (Table 3) and greatest number of anomalies (Table 4) that persisted for longer periods of time in comparison to 20 and 200 m. These results indicate that warm-water anomalies are not restricted to the upper 50 m of the water column as previously suggested (Zaba and Rudnick, 2016) and that organisms inhabiting 50–100 m might be exposed to more warm-water events than those living at 20 or 200 m.

This study also demonstrated that the cold-water gorgonian octocoral, *Adelogorgia phyllosclera*, is sensitive to high temperature exposures. The shock and fast acclimation temperature assays indicated that exposure to 25 °C resulted in decreased coral health, polyp activity, and survival (Fig. 5; Table 6). Interestingly, the time at which fragments reached 50% survival occurred 24 h earlier in the fast acclimation experiment compared to the shock experiment, possibly due to effects from the additional 15 h of acclimation time undergone by fragments in the 25 °C treatment of the fast acclimation experiment. These temperature assays also revealed a significant decline in health scores at 20 °C (Fig. 5A, C). Significant declines in polyp activity and overall survival were not observed at 20 °C, likely reflecting the high variability among the small number of replicates (Fig. 5B, D). The slow acclimation temperature assay indicated that complete mortality occurred at a time corresponding to temperatures between 15 and 16 °C, which is much lower than the shock and fast acclimation assays. Although there is some variation in the upper thermal limit of *A. phyllosclera* based on the results of the shock and fast acclimation assays relative to those of the slow acclimation assay, these findings indicated that the upper thermal limit for *A. phyllosclera* lies near 20 °C. Temperatures at 20 m reached above this estimated upper thermal limit during the 2015–2016 ENSO event (Table 4). Although *A. phyllosclera* occurs mostly between 50 and 100 m, there have been observations between 20 and 50 m (Fig. 2) indicating that individuals of this species were likely exposed to the estimated upper thermal limit estimated in this study.

The thermal limit estimated for *A. phyllosclera* is lower in comparison to those of temperate/ mesophotic gorgonians in the Mediterranean Sea, also determined through thermal exposure experiments. Those studies found the upper thermal limits of *Corallium rubrum* to be 24–25 °C (Torrents et al., 2008) and *Eunicella singularis* to be 26–28 °C (Ezzat et al., 2013). However, these upper thermal limits were lower when corals were exposed for longer periods of time (Torrents et al., 2008), which is consistent with the present findings where the upper thermal limit of the slow acclimation assay was lower than the shock or fast acclimation assay. Also, the endpoint used to assess thermal stress can affect where the upper thermal threshold is set for corals. For example, the thermal limit can be can be identified sooner when sensitive, sublethal endpoints such as protein concentration, lipid concentration, and respiration are used rather than mortality (Brooke
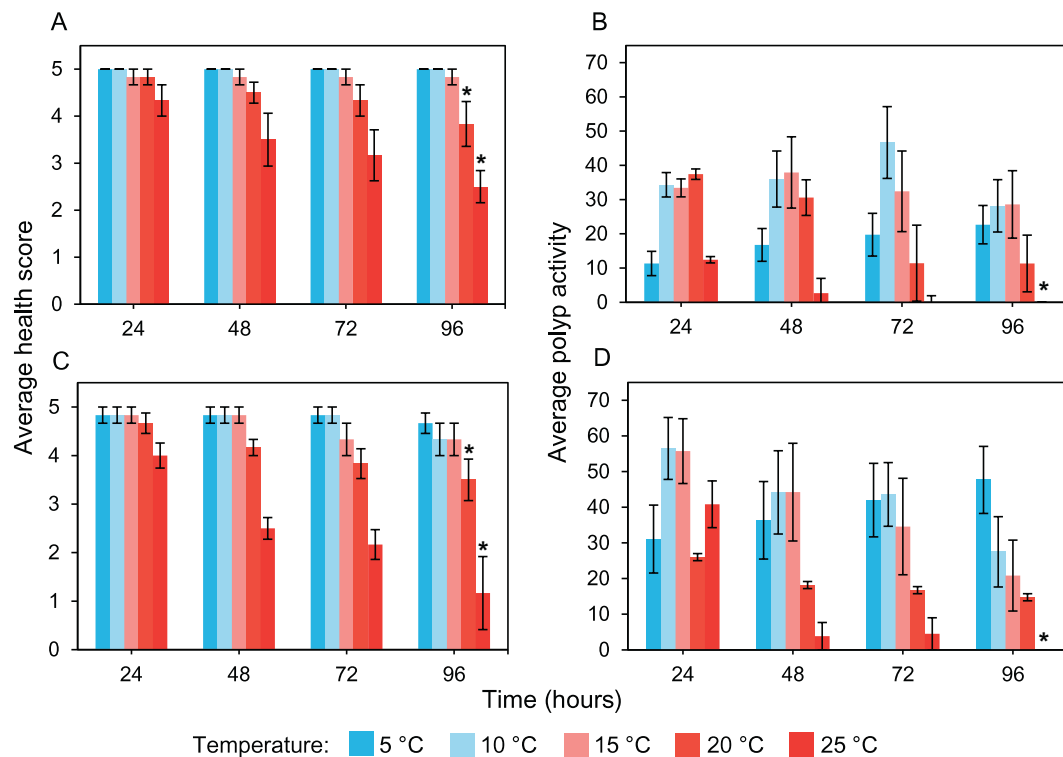
**Fig. 5.** A plot showing mean health scores (A) and mean percent polyp activity (B) for the shock assay and mean health scores (C) and mean percent polyp activity (D) for the fast acclimation assay with bars representing SE. A score of 5 indicates 'healthy' and a score of 1 indicates 'unhealthy' or 'near mortality'. Polyp activity is measured as a percent where a polyp activity of 0 indicates that all polyps were completely retracted and a polyp activity of 100 indicates that all polyps were completely extended. *Asterisks* indicate statistical significance ($p < .05$) in post-hoc pairwise comparisons.

**Table 5**
Pairwise comparisons of K–M survival estimates using Mantel–Cox log-rank analysis. The event was a decline in health rating to 3 or below.

| Log-rank | Temperature treatment (°C) | 5 | 10 | 15 | 20 |
|---|---|---|---|---|---|
| Shock | 10 | 1.000 | – | – | – |
| | 15 | 1.000 | 1.000 | – | – |
| | 20 | 0.198 | 0.198 | 0.198 | – |
| | 25 | **0.003** | **0.003** | **0.003** | **0.034** |
| Fast acclimation | 10 | 1.000 | – | – | – |
| | 15 | 1.000 | 1.000 | – | – |
| | 20 | 0.198 | 0.198 | 0.198 | – |
| | 25 | **0.003** | **0.003** | **0.003** | **0.034** |

Bolded values indicate significant difference ($p < .05$).

et al., 2013).

With evidence that warm-water events are increasingly threatening coral reef ecosystems, there has been interest and controversy surrounding the 'deep reef refugia hypothesis' (Glynn, 1996; Riegl and Piller, 2003; Kahng et al., 2014; Rocha et al., 2018; Smith et al., 2016), which postulates that deep reefs are protected from disturbances that affect shallow reefs, particularly thermal stress events. One of the key assumptions of this hypothesis is that the deep water in which these corals inhabit (50–100 m) is less variable than shallow water and therefore less prone to anomalies. In this study, *in situ* temperature variability decreased with depth (Fig. 2), but there were more warm-water anomalies observed at 50 and 100 m than at 20 m (Fig. 4). These warm-water anomalies observed at 50 and 100 m occurred mostly between November 2015 and February 2016, whereas warm-water anomalies at the surface and at 20 m occurred exclusively during July 2016 (Fig. 4), indicating that the seasonal timing of deep-water anomalies was different than the seasonal timing of surface and shallow-water anomalies. The temporal pattern observed from the temperature logger data (Fig. 4) supports that these warm-water

anomalies observed at 50 and 100 m may be related to ENSO events as they coincide with peak ENSO months (November–January). However, this study covers only one ENSO event and more observations throughout several ENSO events are needed to support this relationship. These findings contradict the assumption that deep water is less prone to anomalies than shallow water in the Southern California Bight region. Furthermore, the findings also suggest that the cold-water corals are as vulnerable to climate change as shallow-water corals (Pey et al., 2011) if not more so, because they are likely adapted and acclimatized to environments characterized by little variability in temperature (Delibrias and Taviani, 1985; Rogers, 1999). Further investigations into the thermotolerance and depth distribution of important species are still needed to understand the potential effects of thermal stress on cold-water corals.

Impacts of warm-water events on marine ecosystems and species can last beyond the event itself (Oliver et al., 2018), making it important to assess other sublethal effects (cellular and physiological) of thermal stress on cold-water octocorals. Furthermore, cold-water octocorals can exhibit reduced metabolic rates, in comparison to shallow water corals, that might delay their cellular and physiological stress responses (Ferrier-Pagès et al., 2009). In the current study, the upper thermal limit estimated for *A. phyllosclera* (~20 °C) was rarely exceeded from November 2015 to July 2016, making it unlikely that thermal stress was the direct source of gorgonian mortalities observed in the central California region (California Department of Fish and Wildlife, Marine Region, 2017). Nonetheless, indirect and sublethal effects of thermal stress could have contributed to the mortalities. Few studies have considered the cellular and physiological responses of gorgonians to thermal stress (Ezzat et al., 2013; Brooke et al., 2013; Ferrier-Pagès et al., 2009). Detailed investigations are needed to improve our understanding of the thermal limits of cold-water octocorals, particularly those aimed at identifying differences in the thermal stress response between cold-water corals and their shallow-water and mesophotic

**Table 6**

The Kaplan–Meier survival estimates calculated at 96 h for the shock and fast acclimation temperature assays.

| Temperature (°C) | Survival estimate | SE | 95% confidence interval | |
|---|---|---|---|---|
| | | | Lower | Upper |
| Shock | | | | |
| 5 | 1.00 | – | – | – |
| 10 | 1.00 | – | – | – |
| 15 | 1.00 | – | – | – |
| 20 | 0.67 | 0.19 | 0.38 | 1.00 |
| 25 | 0.00 | – | – | – |
| Fast acclimation | | | | |
| 5 | 1.00 | – | – | – |
| 10 | 0.83 | 0.15 | 0.58 | 1.00 |
| 15 | 0.83 | 0.15 | 0.58 | 1.00 |
| 20 | 0.50 | 0.20 | 0.23 | 1.00 |
| 25 | 0.00 | – | – | – |

For temperature treatments where there was complete survival or complete mortality, standard error (SE) and 95% confidence intervals could not be calculated, and indicated by '–'.

counterparts, such as vulnerability to disease, changes in reproduction, and metabolic demand.

## 5. Conclusions

The primary aim of this study was to experimentally assess whether cold-water octocorals may be sensitive to warm-water anomalies such as those that occurred during the 2015–2016 ENSO event. Warming ocean temperatures corresponding to the strong ENSO event were hypothesized to be a threat to deep-water gorgonian octocorals in the SCB. In this case, the upper thermal limit of *A. phyllosclera* determined in this study was briefly exceeded at 20 m in the course of a warm-water anomaly that lasted up to 14.1 hours during the 2015–2016 ENSO event. The projections for future warm-water events (Oliver et al., 2018) suggest that the upper thermal limit of *A. phyllosclera* will likely be reached or exceeded more frequently in the coming years. Thus, it is important to continue monitoring and examining the effects of thermal stress on these organisms linked to the functioning and health of this ecosystem.

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