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LARVAL THERMAL TOLERANCE OF KELLET'S WHELK (*KELLETIA KELLETII*) AS A WINDOW INTO THE RESILIENCE OF A WILD SHELLFISHERY TO MARINE HEATWAVES

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ABSTRACT Marine heatwave (MHW) events are emerging as dominant and disruptive extreme disturbance events on the Pacific coast. These events are expected to have significant impacts on shellfish species and aquaculture operations. In general, thermal stress induced by MHW events has been documented to have impacts on the productivity and biodiversity of coastal marine ecosystems in California. Yet, there is limited understanding on how thermal stress will affect economically important shellfish species, especially at vulnerable early life stages. This study assessed the effect of high temperature stress that resembled recent local MHW conditions on the larval stages of the Kellet's whelk, *Kelletia kelletii*, an emerging seafood species from California temperate reefs. Adult whelks were collected at temperate reef sites in the Santa Barbara Channel, and larvae were sourced from egg capsules laid by adult whelks in the laboratory. Thermotolerance trials were determined for two stages of *K. kelletii* larvae: encapsulated veligers and veligers that had emerged from the capsules as hatchlings. During the trials, larvae were scored for two metrics: (1) mortality and (2) developmental abnormality. After exposure of larvae to a range of temperatures (15°C–37°C) in acute thermotolerance trials (1 h), the mortality of veligers and hatchlings occurred at similar temperatures. In contrast, temperatures that induced developmental abnormalities for both encapsulated veligers and hatchlings were lower than temperatures that caused mortality. And further, temperatures that induced abnormal development were different for the two stages. These results provide some of the first insights on effects of environmentally relevant MHW temperatures on larval forms of the Kellet's whelk, and suggest the potential decline of populations *in situ* in response to continued stress from local MHW events.

KEY WORDS: Kellet's whelk, *Kelletia kelletii*, larval development, thermal tolerance, LT_{50}, ocean warming, marine heatwaves, Santa Barbara Channel

INTRODUCTION

Marine heatwave (MHW) events, defined as prolonged periods of anomalously high seawater temperatures (Hobday et al. 2016), have emerged as influential, and disruptive, climate-change driven disturbances in coastal oceans, threatening marine biodiversity worldwide (Oliver et al. 2021). As physical phenomenon, MHW events are extreme disturbance events in coastal marine ecosystems and have impacted marine invertebrate communities (Smale et al. 2019). In coastal California, impacts of a major MHW in 2014 to 2016 included major declines in the kelp canopy biodiversity, high mortality of abalone (Cavanaugh et al. 2019, Rogers-Bennett & Catton 2019, Seuront et al. 2019), and altered biogeographic ranges of marine invertebrates (Sanford et al. 2019). Recent modeling efforts suggest that MHW events will intensify in frequency and intensity in the future (Oliver et al. 2021) with estimates that MHW events will become annual events under "business-as-usual" emission scenarios (IPCC 2019). The marine research community has noted that there is a gap in knowledge regarding plasticity, resilience, and the thermal tolerance of key marine species (Oliver et al. 2019). The goal of this study was to examine the thermal tolerance of early stages of an emerging shellfish fisheries species, a benthic gastropod, the Kellet's whelk (*Kelletia kelletii*, Forbes, 1850), a species that has already experienced MHW events across its biogeographic range.

In addition to impacts on coastal marine ecosystems, the continued occurrence of MHW events pose a threat to aquaculture and fisheries (Wernberg et al. 2013). Significant impacts of these extreme thermal stress events on aquaculture have been reported. For example, in Hawai'i, during the 2009 to 2010 El Niño Modoki, a period of high temperature was linked to mortality events in economically and culturally important fishponds (McCoy et al. 2017). Likewise, on the Western Australian coast, a 2010 to 2012 MHW event resulted in high mortality of abalone as well as major reductions in recruitment of scallops, prawns, and swimmer crabs (Caputi et al. 2016). In the western Atlantic, large mortality events of mussels have also been reported after extreme heat events (Seuront et al. 2019). Taken together, these observations indicate that MHW events have caused disruptions in aquaculture practices worldwide, and that a diversity of shellfish species are vulnerable via reduced recruitment and direct mortality in response to extreme thermal stress.

To address the gap in knowledge on thermotolerances of economically important species, this study assessed the impact of temperatures typical of a MHW on larval development of the Kellet's whelk, a large fished gastropod native to the kelp forests of the Santa Barbara Channel. Notably, this region of the California Current System has experienced one of the longest and most intense MHW events on record (Oliver et al. 2021), and thus, MHW temperature exposures are ecologically relevant for Kellet's whelks in the present-day. Although few studies have examined thermal tolerance across temperatures that reflect recent or future MHW conditions (Oliver et al. 2019), emerging studies of this nature are documenting deleterious

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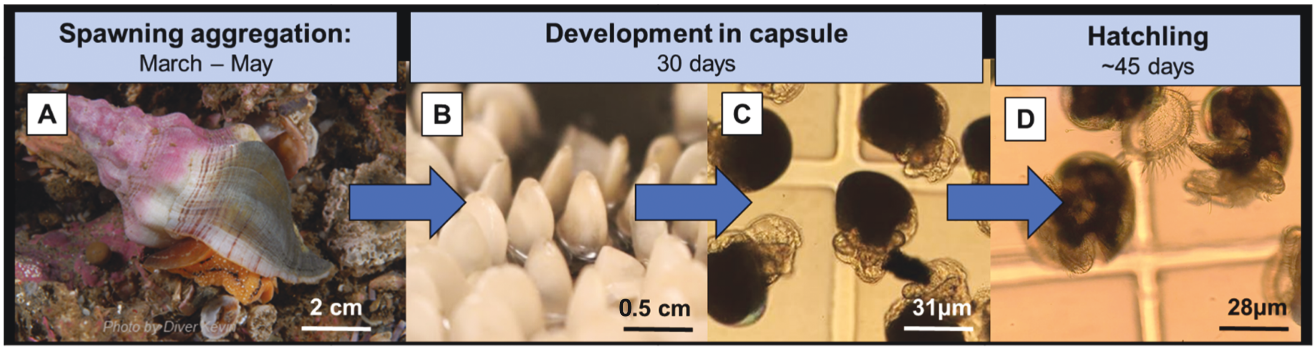

Figure 1. The life cycle of the Kellet's whelk: (A) after spring spawning aggregations, adult females deposit egg capsules on rocky substrate in the kelp forest. Larvae will undergo (B, C) development within the capsule as encapsulated veligers for 4–7 weeks before (D) hatched veligers ("hatchlings" or "planktonic veligers") are released into the water column. Photo credit, Panel B: Dr. Terence Leach.

impacts on marine metazoans. For example, a recent study on sea bream, an aquaculture finfish, found that larval fish experienced physiological stress at MHW temperatures (Balbuena-Pecino et al. 2019).

Among kelp forest benthic scavengers, the Kellet's whelk is an ideal shellfish species to study with regard to impacts of MHW events on a fisheries species. Representative of a new and expanding fishery in coastal California (California Department of Fish and Wildlife 2019), whelks are highly abundant and are easily maintained in the laboratory as adults and as larvae. While the Kellet's whelk has been caught recreationally and as bycatch in commercial crab fisheries since 1979, little is known about the whelk's biology. Found from 2 to 70 m deep and distributed from central California to Baja California, Mexico, the Kellet's whelk has been reported to be expanding its geographical range northward into Monterey Bay, CA (Zacherl et al. 2003).

Whelks are long-lived and have separate sexes that reproduce annually via internal fertilization. Whelks can store sperm for an undetermined time (possibly up to a year). Females lay masses of egg capsules on benthic substrate (between March and July), and development of encapsulated embryos occurs over a 4–6 week period when veligers emerge as hatched veligers (also known as hatchlings) (Fig. 1). From an environmental perspective, many life stages of the Kellet's whelk would experience MHW temperatures in nature, with early development in capsules, hatching, and adult gametogenesis occurring at a time of recorded past MHW events in the Santa Barbara Channel. With life history characteristics (e.g., slow growth, and externally developing encapsulated larvae) that make whelks especially vulnerable as an underregulated fishery, stress from MHW events add an additional unknown climate change-related stress to the fishery. For adaptive management, it is essential to gain more knowledge on the thermal sensitivity of early stage whelks to facilitate the inclusion of climate change-related disturbances such as MHW events in fisheries assessments.

To test the thermal tolerance of early stage *Kelletia kelletii*, laboratory experiments that tested acute tolerance of temperature were designed using temperature observations from the Santa Barbara Coastal Long Term Ecological Research (SBC-LTER) program (Fig. 2) (Reed & Miller 2022). These data documented the MHW event of 2014 to 2016, and also show MHW events that occurred in 2019 (Fig. 2). The most recent warming event, the Northeast Pacific Marine Heatwave of 2019 (also known as NEP 19) surpassed 2014 to 2016 levels of warming (Amaya et al. 2020). Using these temperature observations to frame contemporary MHW stress, larval *K. kelletii* spawned from parents from temperate reef sites in the Santa Barbara Channel, were tested across a 15°C–37°C temperature range and scored for mortality and degrees of normal development. These temperatures are a common temperature range to assess larval marine invertebrate thermal tolerances (Zippay & Hofmann 2010). Overall, the findings of this study indicate that temperatures that are typical of present-day MHW events altered developmental success in larval staged Kellet's whelk, indicating that MHW events could impact future populations of this ecologically and economically important shellfish species.

MATERIALS AND METHODS

Specimen Collection and Husbandry

Adult Kellet's whelk were hand-collected in summer 2018 via SCUBA from benthic kelp forest reef sites in the Santa Barbara

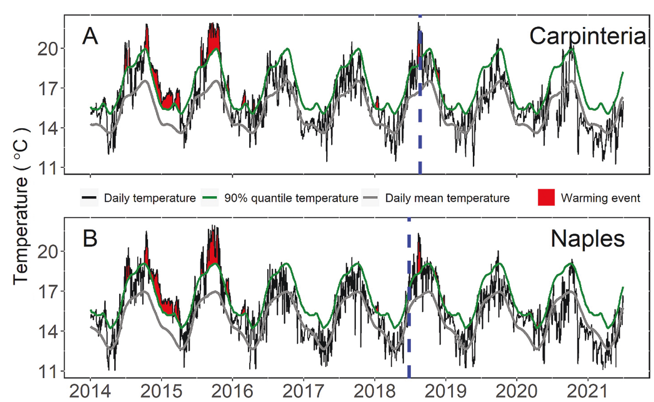

Figure 2. Time series of benthic temperature data from January 2014 to July 2021 at adult whelk kelp forest collection sites, Carpinteria Reef and Naples Reef, Santa Barbara Channel, CA USA. Daily mean temperature data is indicated by the gray line whereas the 90th percentile is indicated by the green line. The benthic temperature data for this study captures the "Blob" (MHW temperatures from 2014 to 2016) as well as more recent MHW temperature anomalies (2018 to 2019) shown in red. Using oceanographic data from the Santa Barbara Coastal Long Term Ecological Research (SBC-LTER) program, the MHW patterns are plotted with the methods described by Schlegel and Smith (2018). The blue dashed line indicates the dates when the adult whelks were collected in the field.

Channel region. Whelks collected from Naples Reef, CA USA (34° 25.335′ N, 119° 57.122′ W) were at a depth of 12.5 m; and whelks collected from Carpinteria Reef, CA USA (34° 23.467′ N, 119° 32.648′ W) were at a depth of 9.1 m. Adult specimens were collected under California Scientific Collection permits (SC-1223 to G. E. H., and SC-11964 to Dr. Robert Miller as the permit to the Santa Barbara Coastal LTER). Immediately following collection, adult whelks were transported in coolers to aquaria facilities at the Marine Science Institute of the University of California, Santa Barbara (UCSB) where they were maintained in flow-through sea water tanks through their summer reproductive season (March–July 2019). During this acclimation period, whelks from each site were held in separate tanks (14 whelks per tank) and were fed once weekly. The light–dark cycle was not strictly controlled and was that of natural daylight conditions within the seawater workroom.

Kellet's Whelk Development and Sampling Protocol

For the thermal tolerance trials (described below), egg capsules and larvae from the capsules were pooled from females from the two collection sites. During the capsule deposition stage (April–July 2019), male and female whelks were housed in the same tanks during mating and oviposition at approximately 15°C, an average ambient temperature. All egg capsules were maintained at a 12:12 light–dark schedule, and from each clutch, capsules were randomly selected. To evaluate thermal tolerances of larvae in their final week within the egg capsule, and during their first days as swimming larvae, larvae were sampled from capsules at two distinct stages for thermal tolerance trials: (1) encapsulated veligers and (2) hatchlings. These two stages are defined via their relationship to the capsule, and the stage of larval development. From a developmental perspective, early stage *Kelletia kelletii* undergo development with a period of intracapsular development (30–35 days) to planktonic development after release from the capsule (approximately 5.5–9 weeks), and finally to benthic settlement. Over the course of intracapsular development, *K. kelletii* transition from embryos, to trochophores, to the encapsulated veliger prior to emerging from egg capsules as a hatched veliger. It is unknown if *K. kelletii* produces nurse embryos within egg capsules. A single whelk can lay a minimum of 100 egg capsules each year, with each capsule housing up to 1,200 larvae. The transitions whelk larvae undergo within their capsule and during hatching may be highly predictive of larval condition, swimming ability, and settlement success. Hereafter, larvae in the encapsulated veliger stage will simply be referred to as "veligers" and "hatched veligers", those that have naturally emerged from the capsule, will be referred to as "hatchlings."

Veliger Sampling

Larvae developed within capsules and were monitored in ambient seawater tanks until the veliger stage was reached. After 4 weeks of intracapsular larval development, single capsules of veligers were separated from egg clusters to be used in thermal tolerance trials. Individual capsules were sampled randomly across and within egg clusters. In the final step of veliger sampling, single egg capsules of veligers were individually deposited into 20 ml vials to be used for thermal tolerance trials. Veligers from a random sampling of clutches from both sites were used to evaluate thermal tolerances.

Hatchling Sampling

As larvae within capsules neared 5–6 weeks of development, capsules were randomly sampled from capsule clusters and were placed in mesh bins to allow larvae to swim free from capsules and hatch naturally. Mesh bins allowed for a small amount of flowing seawater in between daily water changes during the hatchling holding period (1–3 days). Larvae in whelk species have been noticed to emerge simultaneously in capsule clusters via chemo-sensory signaling between patches of hatching capsules (Miner et al. 2010). Therefore, randomly sampled capsule clusters were kept together in mesh bins and sampled for thermotolerance trials on a single day when it appeared that the majority of capsules were hatched. Like veliger thermotolerance trial sampling, hatchlings were pooled across sites and females for thermotolerance trials. Hatchling sampling was done by transferring larvae from plastic beakers as they hatched, into larger sampling bins, and finally into large glass beakers to achieve desired larval concentrations. After pouring hatchlings from plastic beakers into a midsized bin, egg capsules were washed over the bin to maximize collection of emerging hatchlings. By gently siphoning water from a submerged mesh, excess water was removed from the bins to achieve 150–250 ml concentration of hatchlings in the final larger sampling beakers. In the final step of hatchling sampling, 5 ml concentrations of hatchlings were deposited into 20 ml vials for thermal tolerance trials. Each temperature treatment vial contained approximately 200 hatchlings in seawater. Hatchlings from a random sampling of clutches from both sites were used to evaluate thermal tolerances.

Thermal Tolerance Trials

Thermal tolerance of *Kelletia kelletii* larvae was measured for both encapsulated veligers and hatchlings using constant, acute temperature exposures. Water baths were attached at each end of an aluminum heat block to establish a temperature gradient for each set of trials. Temperatures were recorded using an OMEGA hand-held digital thermometer equipped with a wire thermocouple (Thermolyne PM 20,700/Series 1218). Due to differences in development timing between veligers and hatchlings, thermal tolerance trials were held over the course of approximately 2 weeks. Larvae of both stages were exposed to 12 temperatures that ranged from approximately 15°C to 37°C for 1 h; temperatures along the heat gradient were: approximately 14.8°C, 15.2°C, 25.8°C, 29.0°C, 32.0°C, 32.8°C, 33.0°C, 34.1°C, 35.4°C, 35.5°C, 36.9°C, 37.2°C. Vials of larvae were haphazardly arranged across the heat block such that larvae were exposed to each of the 12 treatment temperatures. Larvae were held in control temperature treatment vials at approximately 14.8°C–15.2°C in a cold room at the start of each 1 h trial. All larvae were scored, photographed, and measured within 1–2 h after the 1 h thermal tolerance trial was complete.

Scoring for LT and AT Trials

At the end of the thermal tolerance trial, vials of larvae were removed from the heat block and control vials of larvae were removed from the cold room. Thermal tolerance was measured using two metrics: (1) percent mortality and (2) degrees of developmental abnormality. Lethal temperatures (LTs) were assessed using standard methods for calculating LT thresholds. Abnormality temperatures (ATs) were assessed by examining abnormalities of the general body morphology as indices of structural abnormalities (e.g., velum, shell composition). Percent mortality and abnormality were determined via binary scoring. To determine percent mortality, 100 larvae from each vial were scored as either alive or dead based on the presence or absence of ciliary movement (swimming behavior) viewed under a light microscope. Veligers were maintained within their capsules in vials for all thermal tolerance trials. Once the trial was complete, veligers were forcibly removed from their capsules to be evaluated for scoring. To observe veliger swimming behavior, capsules were dissected, and veligers were released in a petri-dish. Prior to being pipetted into a rafter slide for scoring, veligers were gently swirled in fresh seawater in the dissection petri-dish to let them swim free from their capsular jelly. Hatchlings were simply pipetted to rafter slides for scoring. Percent of larval abnormality was determined by screening for irregular movement, sporadic swimming behavior, or significant damage to important body structures.

Statistical Analysis of LT_{50} and AT_{50} Data

The LT_{50}, the LT at which 50% of larvae died (median mortality), was used as a measure of mortality in the thermal tolerance trials. LT_{50} values are a standard metric used to assess temperature sensitivity (Bilyk & DeVries 2011). In addition, the AT_{50}, where 50% of larvae showed abnormal development or behavior, was used to record larval abnormality in thermal tolerance trials. Both the LT_{50} and AT_{50} (median mortality and abnormality) were determined for veligers and hatchlings. LT_{10} and LT_{25} as well as AT_{10} and AT_{25} values (temperatures at which 10% or 25% of larval mortality or abnormality occurs) were also calculated, because smaller increments of mortality or signs of abnormality might have biological significance (Collin & Chan 2016). A generalized linear model was used to test larval thermal tolerances in both stages across temperature treatments. Temperature treatments were set as fixed continuous factors in the model. LT and AT values were calculated using a logistic regression for each temperature treatment. Statistical analyses for thermal tolerance were performed using the lme4 (Bates et al. 2015), MASS (Venables & Ripley 2002), and base packages in R (version 3.5).

Environmental Temperature Data

Temperatures used in thermotolerance trials were collected at the two study sites: Carpinteria Reef and Naples Reef, as a part of ongoing research activities of the SBC-LTER (Reed & Miller 2022). Temperature data were collected via Onset HOBO TidbiT v2 temperature loggers deployed on the kelp forest benthos where adult *Kelletia kelletii* were collected, and where egg masses are laid by the adults. Two data loggers at each site were programed to record every 30 min with recording times offset by 15 min. Sensors were deployed at a depth of approximately 7 m and were retrieved biannually. Data are published in the Environmental Data Initiative repository (Reed & Miller 2022). An ocean heatwave analysis was performed using a heatwave R package (Schlegel & Smit 2018). The daily mean temperature (Fig. 2) was calculated using daily data from 2000 to 2021 for Carpinteria Reef and from 2012 to 2021 for Naples Reef. The 90^{th} percentile temperature threshold was used to detect warming events (Fig. 2).

RESULTS

General Observations

Thermal tolerance trials were conducted on two early life history stages: an intracapsular stage, the veliger, and the extracapsular free-swimming larval stage, the hatchling. In general, there were two observations that applied to both stages: (1) mortality for both stages occurred at similar temperatures and (2) significant levels of developmental abnormality were induced at lower temperatures than temperatures that caused mortality. In addition, developmental abnormality was observed at distinctly different temperatures for the two stages. Shell size of veligers and hatchlings were around 31 and 28.14 mm, respectively (this was determined by examining a small subset of larvae: $n = 4$ veligers, $n = 13$ hatchlings). Analysis of morphometric data did not reveal a body size-correlated response to thermal stress (data not shown).

Assessment of Mortality (LT)

There were no major differences in thermal tolerances found when comparing temperature sensitivity between developmental stages using standard analyses of lethal thresholds (Table 1, Fig. 3). Specifically, the LT_{10}, LT_{25}, and LT_{50} values were 31.9°C, 32.8°C, 33.8°C for veligers, and 31.3°C, 32.5°C, 33.6°C for hatchlings (Table 1, Fig. 3). Across the range of temperature exposure (15°C–37°C), LT_{10}, LT_{25}, and LT_{50} values for both veligers and hatchlings showed a very similar gradual increase in mortality until exposure temperatures reached approximately 32°C where a rapid increase in mortality was observed (Table 1, Fig. 3).

Assessment of Developmental Abnormality (AT)

In contrast to temperature-induced mortality, degrees of developmental abnormality differed between the two larval stages. Here, AT_{10}, AT_{25}, and AT_{50} all differed by larval stage

TABLE 1.

Lethal temperature (LT_{10}, LT_{25}, LT_{50}) and abnormality temperature (AT_{10}, AT_{25}, AT_{50}) values for each temperature treatment for each larval stage.

Stage	LT_{10}	LT_{25}	LT_{50}	AT_{10}	AT_{25}	AT_{50}
Veliger	31.9 ± 0.2°C	32.8 ± 0.1°C	33.8 ± 0.1°C	12.2 ± 1.2°C	18.5 ± 0.8°C	24.9 ± 0.5°C
Hatchling	31.3 ± 0.2°C	32.5 ± 0.1°C	33.6 ± 0.1°C	22.0 ± 0.6°C	24.8 ± 0.5°C	27.6 ± 0.3°C

All values are given as an M ± SE.

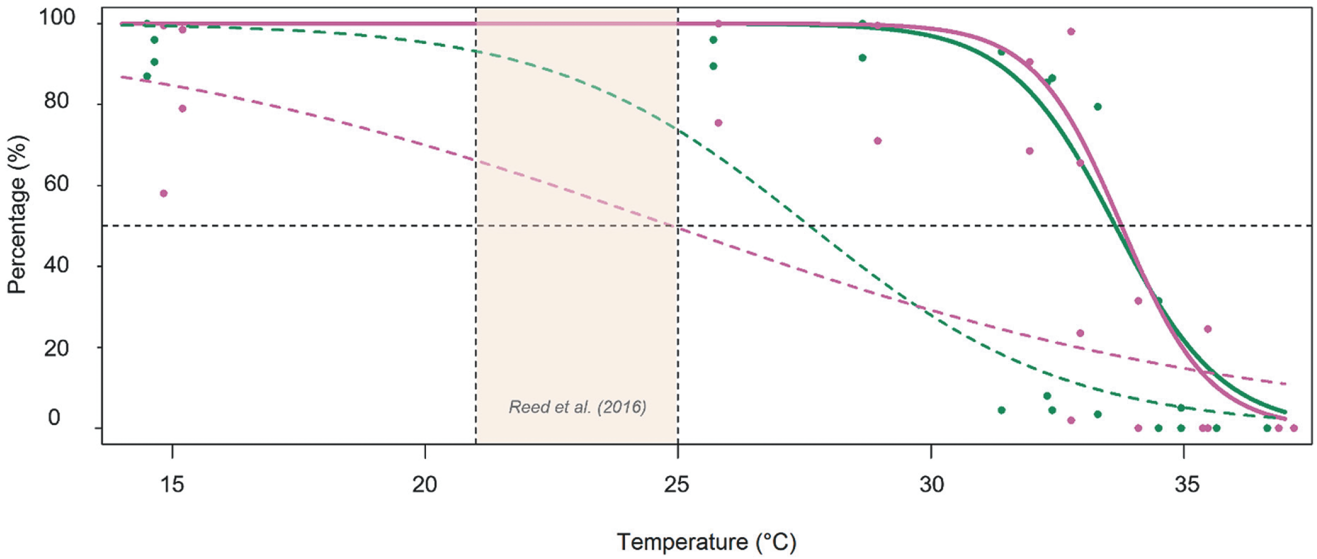

Figure 3. Thermal tolerance shown as percent mortality (LT_{50}; solid curves) and percent abnormality (AT_{50}; dashed curves) for *Kelletia kelletii* encapsulated veligers and hatchlings following 1 h temperature exposures. The black dashed line indicates where half of the larvae experienced 50% mortality (LT_{50}). Points are plotted as percent survivorship and abnormality with the lines showing the logistic regression for each temperature treatment. Larvae used in thermal tolerance trials were sampled in the laboratory from broods of adult females from Carpinteria and Naples Reef. 2015 MHW temperatures by Reed et al. (2016) intersect with 50% normality for veliger stage larvae.

(Table 1). In addition, temperatures that induced abnormal development were lower than those that induced larval mortality (Table 1, Fig. 3). The percentage of abnormality observed in hatchlings indicated by AT_{10} and AT_{25} trial values showed incremental increases in signs of abnormality at 22.0°C, 24.8°C before reaching 50% abnormality (AT_{50}) at 27.6°C. In contrast, the encapsulated veligers experienced temperature-induced abnormality at AT_{10} and AT_{25} temperatures of 12.2°C and 18.5°C, which increased to 50% abnormality (AT_{50}) at 24.9°C, a temperature that was approximately 2.5 degrees cooler than the AT_{50} observed for hatchlings (Table 1, Fig. 3). The range of temperatures that induced considerable levels of larval stress spanned over 15 degrees (20°C–35°C), in contrast to the 10 degree range (25°C–35°C) of temperatures that induced larval mortality (Table 1). Overall, developmental abnormality was observed at much lower, and over a wider range of temperatures, than larval mortality.

Environmental Temperature Data

To support the experimental design of the study and provide insight into temperature conditions in the Santa Barbara Channel, HOBO temperature loggers were deployed at study sites where *Kelletia kelletii* are found. The annual mean, maximum, and minimum temperatures for 2018 were: 16.4°C, 22.2°C, and 11.5°C at Carpinteria Reef and 16.0°C, 21.3°C, and 10.7°C Naples Reef, respectively. The annual mean, maximum, and minimum temperatures at for 2019 were: 15.7°C, 20.7°C, and 11.1°C at Carpinteria Reef and 15.4°C, 20.0°C, and 10.3°C Naples Reef, respectively (Table 2).

DISCUSSION

Overview

An increase in the frequency and intensity of MHW events is anticipated to impact many economically important marine organisms (Wernberg et al. 2013). Limited knowledge of the thermal tolerances of these species to extreme thermal stress events constrains the ability to predict the biological and economic consequences of MHW events on species such as *Kelletia kelletii* and other temperate wild fishery species. To address this knowledge gap, this study tested the tolerance of two early life stages of *K. kelletii* to temperatures that were observed during MHW events that had already occurred in their biogeographic

TABLE 2.

Annual mean, minimum, and maximum benthic temperatures from the SBC-LTER study sites: Carpinteria and Naples Reef, CA USA from 2018 to 2019.

2018			2019		
Site	Carpinteria Reef	Naples Reef	Site	Carpinteria Reef	Naples Reef
Annual mean temperature	16.5°C	16.0°C	Annual mean temperature	15.7°C	15.3°C
Annual maximum temperature	22.2°C	21.3°C	Annual maximum temperature	20.7°C	20.0°C
Annual minimum temperature	11.5°C	10.7°C	Annual minimum temperature	11.1°C	10.3°C

range on the central coast of California. This study resulted in two salient findings: (1) developmental abnormalities in larvae were observed at lower temperatures than temperatures that induced mortality and (2) the temperatures where developmental abnormality was observed (AT_{50}) occurred at environmental temperatures recorded during past and for expected MHW events in the future. Below these findings are discussed in terms of the larval biology of the Kellet's whelk, and with regard to the impacts of future MHW events on this emerging fishery species.

Larval Biology and the Thermotolerance of Kelletia kelletii *Early Life History Stages*

Thermal lethal thresholds (LT_{50} values) for Kellet's whelk veligers and hatchlings found in this study (33.8°C and 33.6°C, respectively) are values that are quite high and not representative of environmental temperatures that *Kelletia kelletii* early stages would experience during development *in situ*. This is not unusual as many other studies have demonstrated that LT_{50}s are "off the ecological map" in temperature range (Bilyk & DeVries 2011, Collin & Chan 2016). In this study, when the two larval forms were scored for developmental success, significant developmental abnormalities were observed in both stages at temperatures that are within present-day MHW ranges. These results suggest that MHW events could have a deleterious impact on the success of larval stages in the field. There were differences between the two stages that were assessed. Specifically, whereas larval mortality for both encapsulated veligers and hatchlings occurred at similar temperatures, developmental abnormality was observed at distinctly different temperatures for veligers and hatchlings, with veligers displaying greater sensitivity to high temperature.

Kellet's whelks have higher larval thermotolerances in comparison to thermotolerances found in similar gastropod shellfish species in the Santa Barbara Channel, such as the red abalone (*Haliotis rufescens*, Swainson, 1822), another shellfish species that shares habitat with the Kellet's whelk. The LT_{50} of red abalone was approximately 32°C in the late-veliger stage (Zippay & Hofmann 2010). The LT_{50} data in this study indicated that Kellet's whelk veligers found in this study are about 1.8°C greater than that of red abalone veligers. Such comparisons and further thermotolerance studies will help illuminate the impacts of MHW temperatures on other gastropod fisheries species in the future. Specifically, the LT_{10}, LT_{25}, and LT_{50} values were 31.9°C, 32.8°C, 33.8°C for veligers, and 31.3°C, 32.5°C, 33.6°C for hatchlings (Table 1, Fig. 3). Across the range of temperature exposure (15°C–37°C), LT_{10}, LT_{25}, and LT_{50} values for both veligers and hatchlings showed a very similar gradual increase in mortality until exposure temperatures reached approximately 32°C where a rapid increase in mortality was observed (Table 1, Fig. 3).

Consequences for Fisheries

Impacts of MHW events on important marine invertebrate fisheries and the coastal marine ecosystems appear to be wide-ranging, from disease outbreaks in farmed stock, to mortality in wild stock (Smale et al. 2019). Recent studies have shown MHW events can influence long- and short-term population-level success via deleterious effects on spawning, reproduction, and recruitment of marine invertebrates leading to ongoing challenges in managing invertebrate fishery species. For example, a study from Coos Bay estuary in Oregon that investigated winter spawning by coastal invertebrates in larval plankton samples (representing at least five phyla including gastropods) found that during the winters of 2015 to 2016, after the Northeastern Pacific MHW (also known as "the Blob"), many invertebrate taxa failed to spawn (Shanks et al. 2020). In this same light, although a laboratory-based study, the data presented here clearly illustrate the potential effects of MHWs events on immediate reproduction in a single season for Kellet's whelk.

As an example of lasting effects on invertebrate fisheries, 7 y after the 2011 Western Australian dramatic MHW event, only parts of the marine ecosystem are starting to show signs of recovery. As result of the 2011 MHW, scallop fisheries experienced a 3–5 y closure, Roe's abalone (*Haliotis roei*, Gray, 1826), a locally important molluscan fishery species to the region, also suffered extreme mortality and has not recovered because spawning populations have sharply declined (Caputi et al. 2016). Such population-level impacts of MHW events will affect management decisions for fished invertebrate species. While "closed versus open seasons" are helpful as a management tool when ocean temperatures follow historical seasonal trends—the irregularity of MHW events show the importance of adapting new approaches to fishing behavior and management that reflect the increasingly unpredictable nature of the environment. Management that incorporates the impact of extreme disturbance events such as MHW events could allow for agile responses to the health of larval, juvenile, and reproducing populations that support invertebrate fisheries (Caputi et al. 2016).

The impacts of local MHW events on the Kellet's whelk have yet to be incorporated into a management strategy. The majority of whelks are commercially harvested at three ports in California (Santa Barbara, San Diego, and Terminal Island), with most of whelk landings emerging from the Santa Barbara Channel. Despite a growing consumer interest and an increase in active participants in the fishery, the latest harvest reports show a decline in landings—from 191,177 pounds, during the peak of the fishery in 2006, to 79,754 pounds in 2018. Some of the lowest annual harvests in recent years overlap with the 2014 to 2016 MHW in the Santa Barbara Channel. It is to be determined via additional surveys as to whether the decline in landings is due to a decrease in fishing pressure, extreme ocean temperatures, or perhaps a decrease in whelk populations (California Department of Fish and Wildlife 2019).

Whereas *Kelletia kelletii* are often included in many ecological surveys by research programs working on the California coast (e.g., Partnership for Interdisciplinary Studies of Coastal Oceans), few studies have analyzed seasonal population dynamics of whelks to complement seasonal harvesting regulation development. Further, for such a historically abundant kelp forest species, few experiments on larval ecophysiology, developmental studies, or culturing techniques have been published, a status that is not uncommon for a marine invertebrate fishery species. Overall, this study attempts to fill some of these gaps in knowledge by presenting one of the first observations on early stage *K. kelletii* with respect to a climate change threat, extreme temperatures during MHW events.

Summary

This study revealed that *Kelletia kelletii* larvae exhibited significant abnormalities at present-day MHW temperatures, an observation that suggests this shellfish species is vulnerable to environmental stress created by MHW events. To increase understanding of the vulnerability of this fisheries species, future research on parental effects, transgenerational plasticity, and the general adaptive capacity of whelks is important. Future physiological studies would benefit from focusing on metrics such as respirometry and feeding rates, of adults and larvae to help predict how access to food would influence the thermotolerance of this species in the field. As an example of this work, a study on *Turbo militaris*, a large harvested Australian turbinid snail, evaluated the influence of MHW temperatures on nutritional properties of body tissue and immune health (Mamo et al. 2019). Additional physiological studies such as these described will help small- and large-scale shellfish industries mitigate climate change threats.

Overall, larval physiology and studies that highlight the adaptive capacity of fisheries species allow us to examine the resilience of economically important species in their first window of life to ensure their continued role in ecosystem services that support human society. Preliminary findings from this study on *Kelletia kelletii* can be applied to building a stronger sense of the biology of an emerging shellfish species during a life stage most vulnerable to a warming sea and simultaneously provide insight to a growing shellfish fishery.

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