Title

Understanding Relationships Between Human and Marine Communities via Experimentation, Long-Term Data and Education

Author

Clare, Xochitl Seancia

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Understanding Relationships Between Human and Marine Communities via Experimentation, Long-Term Data and Education

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Ecology, Evolution & Marine Biology

by

Xochitl S. Clare

Committee in charge:

Professor Gretchen Hofmann, Chair

Professor Deron Burkepile

Professor Halley Froelich

Professor Linda Adler-Kassner

June 2023

The dissertation of Xochitl S. Clare is approved by

Deron Burkepile

Halley Froelich

Linda Adler-Kassner

Gretchen Hofmann, Committee Chair

June 2023

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As a mentor and educator, I had enriching opportunities to work alongside many students. I thank my mentees for their enthusiasm towards marine science (Paul Huang, Samantha Chen, Eva Juengling Bean, Lauren Jennings, Tasi LeDonne). It was also my honor to mentor visiting students, Kyaralind Vasquez-Liriano and Will DeJesus, participants of the UCSB Ocean Change Biology Research Experiences for Undergraduates (REU) program.

My education and outreach programming I developed for my dissertation at the UCSB Research Experience & Education Facility (REEF) would not have been possible without the collaborative spirit and guidance of REEF Director Scott Simon who facilitated my many relationships with Santa Barbara community educators and students. Specifically, I am honored to have been able to direct three years of stellar REEFlections cohorts during the 2019, 2020, and 2022 years of the symposium (2019 REEFlections Cohort: Tasi LeDonne, Nelson Beltran, Iris Chan, Anshika Bagla, Arielle Martinka, Jeffrey Childs; 2020 REEFlections Cohort: Ally Aplin, Kim Krotine, Nelson Beltran, and Kyler Plouffe; 2022 REEFlections Cohort: Madigan Boborci, Fern CapittiFenton, Paul Huang, Lauren Jennings, Parker Malhotra**,** Zoe Manalo, Chloe Jenniches, Lex Rosenberg). REEFlections would not have been possible without the time and dedication of REEFlections student event organizers during the 2019, 2020, and 2022 years of the symposium (2019 REEFlections Organizers: Tasi LeDonne; 2020 REEFlections Organizers: Iris Chan, Lilly Witonsky; 2022, REEFlections Organizers: Andie Van Horn, Josie Spiegelman). I would also like to acknowledge the time and support of the REEFlections research mentors who supported their students in participating in the symposia I directed. I also share gratitude for the students who participated in interviews for the portions of my dissertation research on REEFlections.

I am also grateful for many mentors, collaborators in publication, and colleagues and over the course of my dissertation, within and outside of UCSB. I thank the following persons for their intellectual engagement, bright insight, career counsel, and encouragement: Paul Teall, Kim Selkoe, Crow White, Danielle Zacherl, Li Kui, Jann Vendetti, Casey Richart, Gina Contolini, Stephen Miller, Daniel Costa, Jen Maresh, Dimitri Deheyn, Yulianna Ortega, Carlos Mireles, Anthony Shiao, Eric Palkovacs, Dan Reed, Robert Miller, Irwin Appel, Risa

Brainin, Robby Nadler, Ian Kellett, Chris Jenkins, De'Marcus Robinson, and Javier Read De Alaniz.

Without the ability to afford swimming lessons, or marine science summer camps that I spent most of my life far away from the ocean prior to attending college. Since then, over the course of my experience at UCSB, I developed strong dive mentors and relationships, excelled in my aquatic development: I have learned to swim, obtained my Open Water, Rescue, and American Academy of Underwater Sciences Scientific Diving Certifications over the six years I attended UCSB. This would not have been possible without the time, patience, and warmth of my dive mentors at UCSB and Santa Barbara Aquatics (Eric Hessel, Clint Nelson, Andrew Bolling, and Jed Grundy) for helping me embark on my underwater journey by assisting me with finding gear, lessons, and aquatic support. I am now proud to serve as a dive ambassador, physically breaking barriers as a BIPOC (Black, Indigenous, and People of Color) marine scientist. I am dedicated to carry my aquatic lessons-learned forward, in making individuals of all backgrounds feel welcome to partake in the ocean discovery needed to help understand our changing planet.

As a Latina African American with Central American and Caribbean heritage with a background of financial hardship, a am grateful for a plethora of UCSB community members that supported me in ensuring I was able to receive the support and aid to combat a variety of barriers along my higher education journey (Arica Lubin and Ryan Sims. Associate Director, Academic Counselor).

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Finally, I thank my immigrant single mother, Valencia Sin-Clare, who kept my aquatic dreams afloat through bright books and media at an early age—balancing each scientific lesson at home, with an artistic one. I am proud to represent a multicultural first-generation background and thank all those who have continued to nurture my passions in marine science, art, and education to help build the marine biologist and performing artist I am today.

VITA OF XOCHITL S. CLARE
June 2023

EDUCATION

2017 - 2023	**University of California, Santa Barbara (UCSB)** Doctor of Philosophy in Ecology, Evolution & Marine Biology (EEMB) Dissertation Advisor: Professor Gretchen Hofmann
2012 - 2017	**University of California, Santa Cruz (UCSC)** Bachelor of Science in Marine Biology Bachelor of Arts in Theater Arts

FELLOWSHIPS & AWARDS

2020 - present	Washington Research Foundation Postdoctoral Fellowship (2023-2026) BioOne Ambassador Award; Nominated By The National Shellfisheries Association (2023) Smith Conservation Research Fellowship Program Honorable Mention (2023) National Science Foundation Graduate Research Fellowship Program (NSF-GRFP) (2020 - 2023) UC President's Pre-Professoriate Fellowship (2022 - 2023) Reef Check Kelp Forest Monitoring Training: 2022 SCUBA Diversity Scholarship UCSB Hansma Fellowship Award (2020)
2018 - 2019	UCSB EEMB Graduate Department Residual Funds (Spring 2018) Ford Foundation Fellowships Honorable Mention (2018) UCSB Bridge to the Doctorate (BD) Fellowship (2017 - Summer 2020) UCSB EEMB Graduate Fellowship (Summer 2017 - 2018) Carl Storm Underrepresented Minority (CSURM) Fellowship for 2018 Predator-Prey Interactions GRC ($600)
2017	Association for the Sciences of Limnology and Oceanography Multicultural Program (ASLOMP) Award ($2000) UCSC Kresge & Porter College Collaborative Student Project Award: *Rethinking Natural History* ($1000) UCSC Kenneth and Ann Thimann Scholarship (2017)

UCSC Dean’s Undergraduate Research Award for Senior Thesis: *Energy Densities of Forage Fish from the Mesopelagic Zone of the North Pacific Ocean and Its Implications for a High-Level Marine Predator, the Northern Elephant* Seal (2017)

PROFESSIONAL EXPERIENCE

Research

2017 - present **University of Washington, School of Aquatic and Fishery Sciences, Padilla-Gamiño Lab: Postdoctoral Researcher;** *Connecting academic and local non-governmental organizations to mitigate anthropogenic stressors in tropical marine protected areas*

University of California, Santa Barbara, Santa Barbara Coastal Long Term Ecological Research Project, Hofmann Lab: Doctoral Researcher; *Investigating climate change stressors (ocean acidification and warming) on feeding ecology, reproduction, and early life stages of the Kellet’s whelk*

Smithsonian Tropical Research Institute, Collin Lab: Visiting Researcher (2023);
Investigating the impact of fluctuating marine heatwave treatments on adult and larval tropical urchins

2016 - 2017 **Scripps Institute of Oceanography (SIO), University of California, San Diego, Deheyn Lab: Visiting Researcher (2016);**
Ocean Acidification (OA) Affects the Nervous System in Marine Invertebrates—The Case of a Luminous Brittlestar

2014 - 2016 **UCSC Institute of Marine Sciences (IMS): Joseph M. Long Marine Laboratory (LML)**

Palkovacs Lab: Intern; *Local Adaptation in a Shell-drilling Predator*, Dog-whelk Sea Snail Ocean Acidification Experiment (2015 - 2017)

Costa Lab: Intern; *Elephant Seal Prey-Energy Library* (2014 - 2016)

Mentoring

2021 - present **University of California, Santa Barbara**

Research Mentor; UCSB Ocean Global Change Biology Research Experience for Undergraduates (REU), Project: *TurnUp2.0: Exploring Marine Heatwave Impacts on Early Development & Larval Thermotolerance in K. kelletii Larvae in Santa Barbara, California* (2022)

Curriculum Designer for Mentor Training; Field-based Undergraduate Engagement through Research, Teaching, and Education (FUERTE)

Graduate Student Mentor; McNair Scholars Program

2020 **Writing Consultant;** NSF-GRFP Application Reviewer

Mentoring

2018 **Research Mentor;** UCSB Ocean Global Change Biology Research Experience for Undergraduates (REU), Project: *Feeding Behavior in Warming Seas* (2018)

Mentor & Seminar Leader; University of California Leadership Excellence through Advanced Degrees (UC LEADS) Graduate Student Super-Mentor & Professional Development Seminar Series Leader (*Designing Your Poster, Presenting Your Work*) (2018)

Teaching

2018 - 2020 **Teaching Assistant & Reader;** Introduction to Biology Lab, Ecology of Infectious Disease

PUBLICATIONS

2023 **Clare, X.S.,** Kui. L., Hofmann, G.E., *Thermotolerance of a wild shellfish fishery under fluctuating marine heatwave conditions*, Journal of Shellfish Research (Submission planned for Fall 2022)

Clare, X.S., Adler-Kassner, L., *REEFlections: Exploring undergraduate experiences in navigating virtual science communication,* Journal of Diversity in Higher Education (Submission planned for Fall 2022)

2022 **Clare, X.S.,** Dillon Whited et al., *Length-weight relationship of the kelp forest gastropod and emerging fisheries species Kellet's whelk, Kelletia kelletii,* Journal of Shellfish Research (Submitted)

Clare, X.S., Hofmann, G.E., Kui. L., *Larval thermal tolerance as a window into the resilience of a wild shellfish fishery to marine heatwaves,* Journal of Shellfish Research

GRANTS IN SUPPORT OF RESEARCH

2020 - 2021	Restore America’s Estuaries Scholarship for 2020 National Coastal & Estuarine Virtual Summit ($100) Conchologists of America Academic Grant ($1,700)
2019	UCSB Associated Students Coastal Fund ($13,279) *Funds to support the construction of a tank system for marine heatwave research*
2018	UCSB EEMB Graduate Department Residual Funds ($1,300)

PROFESSIONAL ACTIVITIES

Internships & Special Training

2022 - present	**OceanX Young Explorers Program (2023):** Led film and media segments on ocean warming experiments, aboard the *OceanXplorer* **Coastal Media Project (2022):** UCSB Department of Film and Media Studies & Carsey-Wolf Center, Executive Producer; *Beyond Access*, a film on the importance of equitable access to nature in Santa Barbara **Stanford University Postdoctoral Recruitment Initiative in Sciences and Medicine (PRISM) Program (2022)** **American Academy of Underwater Sciences (AAUS):** UCSB Scientific Diving Program (2018 - present)

Workshops & Symposia

2020 - 2022	**Workshop Leader; 2022 LTER All Scientists' Meeting** Guillen, M., Hofmann, G.E., **Clare, X.S.,** *A tool kit to support inclusive mentoring practices*: Led a workshop for graduate students and postdocs to hone field and lab based mentoring skills

Founder & Director; UCSB Research Experience & Education Facility (REEF), *REEFlections*, 2020 - 2022 REEF Undergraduate Research Symposium, Symposium (Virtual and In-Person)

2017 - 2019 **Session Leader; SACNAS Graduate Chapter & Bridge to the Doctorate Fellows,** *Being Your Authentic Self in Graduate School: Community, Advocacy, and Resilience: Excelling Together.* Society for Advancement of Chicanos/Hispanics and Native Americans in Science (SACNAS)

Founder & Director; UCSB Research Experience & Education Facility (REEF), *REEFlections*, 2019 REEF Undergraduate Research Symposium, Symposium

Conference Presentations

2020 - 2022 **Clare, X.S.,** Hofmann, G.E. *Thermotolerance of a wild shellfish fishery under fluctuating marine heatwave conditions.* 2022 Western Society of Naturalists, Oral Presentation

Santa Barbara Coastal Long Term Ecological Research Group. *Benthic community and organismal responses to disturbance in Santa Barbara Channel kelp forests.* 2022 LTER All Scientists' Meeting, Poster Presentation

2020 - 2022 **Clare, X.S.,** Hofmann, G.E. *Turning Up the Heat: Examining the effects of parental temperature environments on the quality of progeny in a fished marine invertebrate.* 2021 Western Society of Naturalists, Virtual Oral Presentation

Clare, X.S., *REEFlections Testimonios: Exploring undergraduate experiences in navigating virtual scientific storytelling*. 2021 Ecological Society of America Annual Meeting, Virtual Oral Presentation

Clare, X.S., Hofmann, G.E. *Snails on the menu?: Using long-term ecological data to contextualize performance of a California kelp forest predator and emerging fishery* *species, Kelletia kelletii.* 2020 Western Society of Naturalists, Virtual Oral Presentation

Clare, X.S., Hofmann, G.E. *Snails on the menu?: Using long-term ecological data to contextualize performance of a California kelp forest predator and emerging fishery species, Kelletia kelletii.* 2020 Gulf & Caribbean Fisheries Institute 73rd Annual Meeting, Virtual Oral Presentation

2017 - 2019 **SACNAS Graduate Chapter & Bridge to the Doctorate Fellows,** *Being Your Authentic Self in Graduate School: Community, Advocacy, and Resilience: Excelling Together*. Society for Advancement of Chicanos/Hispanics and Native Americans in Science (SACNAS), Session Leader

Founder & Director; UCSB Research Experience & Education Facility (REEF), *REEFlections*, 2019 REEF Undergraduate Research Symposium, Symposium

Clare, X.S., Hofmann, G.E. *Snails on the menu?: Using long-term ecological data to contextualize performance of a California kelp forest predator and emerging fishery species, Kelletia kelletii.* 2019 World Congress of Malacology, Oral Presentation

Clare, X.S., Hofmann, G.E. *Snails on the menu? Investigating ocean acidification impacts on kelp forest predator, K. kelletii.* Long Term Ecological Research All Scientists Meeting, Poster Presentation

Clare, X.S., Hofmann, G.E. *Snails on the menu? Investigating ocean acidification impacts on kelp forest predator, K. kelletii.* UC Davis, Bodega Marine Laboratory Meeting, Oral Presentation

Conference Presentations

2015 - 2017

Clare, X.S., Hofmann, G.E. *Arms race in the Anthropocene: How will juvenile sea hare inking defenses fare in the future?* Gordon Research Conference (GRC) on Predator-Prey Interactions, Poster Presentation

Clare, X.S., Deheyn, D.D. *Ocean Acidification Affects the Nervous System in Marine Organisms—The Case of a Luminous Invertebrate*. Association for the Sciences of Limnology and Oceanography (ASLO) Aquatic Sciences Meeting, Poster Presentation

Clare, X.S., Deheyn, D.D. *Ocean Acidification Affects the Nervous System in Marine Organisms—The Case of a Luminous Invertebrate*. Western Society of Naturalists, Poster Presentation

Clare, X.S., Maresh, J.L., Goetsch, C., Costa, D.P. *Elephant Seal Prey-Energy Library*. California Alliance for Minority Participation (CAMP) Statewide Symposium, Poster Presentation

Film, Media & Spotlights

2022 - present

Podcast Guest; *"Intersectionality & Graduate School"* Grad School Femtoring Podcast (2022)

Podcast Guest; *"Intersectional Marine Biology"* Greenhouse Sass (2022)

Guest Host; *"Chocolate Baby Storytime"* Guest Marine Biologist (2022)**,** Healing Justice Santa Barbara

2021 - 2022

Sound; *"Ghosts on the Horizon"* (2021)**,** GreenScreen Environmental Media Production, UCSB Department of Film and Media Studies & Carsey-Wolf Center

Professional Association of Diving Instructors (PADI) AmbassaDiver; Women's Dive Day Organizer, Panels (Diversity & Inclusion in Scuba Diving, International Day of Women & Girls in Science), Instagram & Blog

UCSB Santa Barbara Coastal Long Term Ecological Research Outreach (Vimeo, TikTok, Instagram)

2019 - 2020 **Black in Marine Science Week;** Social Media Organizer & Instagram Takeover

Los Padres ForestWatch; Latinx Conservation Week Live Chat

UCSB Graduate Division Spotlight; *GradStories*

Girls that Scuba, Girls that Freedive; Instagram Feature

2019 - 2020 **Sirene Project;** Website Profile, Instagram Feature

USCB Coastal Fund; Grantee Website and Facebook Feature

2018 - 2019 **Women Doing Science;** Instagram Takeover

UCSB Graduate Division Spotlights; Pamphlets & Booklets, Department flyers, Instagram Takeover: *A Day in the Life Of*, USCB Campus Banners, UCSB Home Page Feature: *Voices*

Women in Ocean Science; Instagram Profile

Santa Barbara Museum of Natural History; Instagram Profile

SERVICE

Invited Lectures

2021 - present **Speaker;** *"Outdoor Liberation Speaker Series"*, Latino Outdoors, The North Face, VF Corporation, Panel (2022)

Plenary Speaker; *Generations*. 2022 LTER All Scientists' Meeting, Panel

Speaker; *"Agua Es Vida"*, Latino Conservation Week, Latino Outdoors, Virtual Panel (2022)

Speaker; *"Graduate Studies"*, UCSC Younger Lagoon Reserve Internship Program, Virtual Panel

2019 – 2020 **Speaker;** *"Green Careers: Graduate Studies"*, UCSC Career Center, Virtual Panel (2020)

Speaker; *"Graduate School for Environmental Professions"*, UCSB Making Adventures Possible for all Students (MAPAS), Virtual Panel

Invited Lecturer; UCSC Center to Advance Mentored, Inquiry-Based Opportunities (CAMINO), Virtual Seminar

Invited Lecturer; UCSC Doris Duke Conservation Scholars Program, Virtual Seminar

Commencement Speaker; UCSC STEM Diversity Program Virtual Commencement Ceremony

Academic & Departmental

2021 - present **Graduate Student Mentor;** UCSB Field-based Undergraduate Engagement through Research, Teaching, and Education (FUERTE), Panels & Seminars

Seminars; "*Turning Up the Heat: Climate Science in Action"*, Outreach Santa Barbara County (K-12), UCSB REEF Virtual Seminars

2019 - 2020 **Speaker; "***All-Gaucho Reunion",* UCSB Research Experience & Education Facility, Virtual Seminar

Seminar Speaker; UCSB *"Thriving, Not Surviving: Navigating Higher Education as a First-Generation College Student"* Virtual Program, in collaboration with the UCSB McNair Program, Opening New Doors to Accelerate Success (ONDAS) Student Center, Transfer Student Center (TSC), and Education Opportunity Program (EOP)

Public Service & Outreach

2018-2019 **Field Work Volunteer;** BIOMA Sea Turtle Research Conservation Program, Ostional Wildlife Refuge, Costa Rica

Presenter; World Oceans Day, Santa Barbara Museum of Natural History, Sea Center

STEAM (Science, Technology, Engineering, Art, and Mathematics

2018 - 2019	**Producer, Director;** *STEAMy Improv Workshops* for UCSB Ecology of Infectious Disease (EEMB 40) course sections in collaboration with UCSB EEMB, Theater & Dance, Center for Innovative Teaching, Research (CITRAL) Departments
2017	**Producer, Director;** UCSC Educational Performance Production: *Rethinking Natural History: Bridging understanding of the natural world through performance art*

ABSTRACT

Understanding Relationships Between Human and Marine Communities via Experimentation, Long-Term Data and Education

by

Xochitl S. Clare

Marine heatwave (MHW) events defined as prolonged periods of anomalously high seawater temperatures have emerged as influential and disruptive climate-change driven disturbances in coastal oceans, threatening marine biodiversity worldwide. As a physical phenomenon, MHW events are extreme disturbance events in coastal marine ecosystems and have impacted marine invertebrate communities. In coastal California, impacts of a major MHW in 2014 to 2016 included major declines in the kelp canopy biodiversity, high mortality of abalone, and altered biogeographic ranges of marine invertebrates. Recent modeling efforts suggest that MHW events will intensify in frequency and intensity in the future, with estimates that MHW events will become annual events under “business as-usual” emission scenarios. In this light, my dissertation at the University of California, Santa Barbara (UCSB) in the Hofmann Lab examined adult and early stages of an emerging shellfish fisheries species, a benthic gastropod, the Kellet’s whelk (*Kelletia kelletii*) in the ecological context of MHWs.

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Chapter 1: Introduction

Understanding marine heatwaves

Marine heatwave (MHW) events defined as prolonged periods of anomalously high sea surface temperatures (SST) (Hobday et al., 2016) have emerged as influential, and disruptive, climate-change driven disturbances in coastal oceans, threatening marine biodiversity worldwide (E. C. J. 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, Reed, Bell, Castorani, & Beas-Luna, 2019; Rogers-Bennett & Catton, 2019; Seuront, Nicastro, Zardi, & Goberville, 2019), and altered biogeographic ranges of marine invertebrates (E Sanford, Sones, Garcia-Reyes, Goddard, & Largier, 2019). Recent modeling efforts suggest that MHW events will intensify in frequency and intensity in the future (E. C. J. Oliver et al., 2021) with estimates that MHW events will become annual events under "business as-usual" emission scenarios (Pörtner, 2022). **In this light, my dissertation at the University of California, Santa Barbara (UCSB) in the Hofmann Lab examined adult and early stages of an emerging shellfish fisheries species, a benthic gastropod, the Kellet's whelk (*Kelletia kelletii*, Forbes, 1850) in the ecological context of MHWs.**

Implications for fisheries in the face of MHWs

In addition to impacts on coastal marine ecosystems, the continued occurrence of MHW events pose a threat to aquaculture and fisheries (Smith et al., 2021; T. 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 wild caught shellfish species are vulnerable via reduced recruitment and direct mortality in response to extreme thermal stress. The marine research community has noted that there is a gap in knowledge regarding plasticity, resilience, and the thermal tolerance of key marine species (E. Oliver, 2019).

Assessing MHWs impacts in the Santa Barbara Channel

The California kelp forest represents one of our planet's most dynamic ecosystems with natural resources that support commercial and small-scale fisheries alike. However, ecosystem resources the kelp forests provide are at risk due to MHWs. As an example, 2013–2014 MHW in the Northeast Pacific, nicknamed "the Blob" stretched from the coast of Alaska to Baja California and persisted through the end of 2015 (Cavole et al., 2016). This MHW resulted in biogeographical species range shifts (Cavole et al., 2016), mass strandings of megafauna, and closures of economically important fisheries. As a result of MHWs that have threatened the stability of kelp forest ecosystems, work from the UCSB Santa Barbara Coastal Long-Term Ecological Research (SBC-LTER) Project has (1) helped quantify the impacts of MHWs on community structure in the Santa Barbara Channel, (2) understand the ecosystems shifts that occur as a result of MHWs and (3) cultivated a detailed record of extreme temperature events in the Santa Barbara Channel. This effort supports the work of ocean change biology on important fisheries species, such as the work in my dissertation. Data from the SBC-LTER was used to contextualize the ocean warming work in my dissertation.

Bottom MHWs

While we have conventionally understood MHWs in reference to anomalous SSTs, we are now expanding our knowledge on the spatial scope and vertical distribution of MHWs, and investigating the occurrence of bottom MHWs (BMHWs). Recently, oceanographers have observed extreme ocean warming at depth, with the vertical distribution of the anomalous ocean temperatures reaching to the benthos. These benthic anomalous ocean warming events, BMHWs, have been observed globally (D. Amaya et al., 2023), and have been linked to coral bleaching events at sites in French Polynesia in recent studies (Wyatt et al., 2023). In this light, relying solely on understandings of MHWs that are based on sea surface satellite data does not allow for a complete understanding of local temperature dynamics in order to predict how marine ecosystems will respond to climate warming. Oceanographers have identified that we must integrate our understanding across ocean space to mitigate the impacts of MHWs (Starko et al., 2022). Addressing this need, in my dissertation, I was able to identify BMHWs at SBC-LTER study sites in the Santa Barbara Channel and designed experiments that are ecologically relevant to the thermal environment in situ for adult benthic invertebrates (SBC-LTER).

Oceanographic forecasting of MHWs for ecosystem management

Past ecosystem management efforts have been limited by our capacity to predict and prepare for MHW events. Although MHWs have been recorded around the globe, since we have suffered from a limited ability to predict MHWs, the majority of climate action to mediate the impact of MHWs has been retroactive. Globally, the documented socioeconomic impacts of MHWs have been significant (Smith et al., 2021). For example, in the Northeast Pacific region, commercial and recreational fisheries were closed after the catastrophic "Blob" event, where both the MHW caused harmful algal blooms that resulted in unsafe shellfish sales. Economic losses in 2016 were estimated at $48 million (Holland, 2020). The Dungeness crab fishery from Washington to California was closed for 2015–2016 season after the impacts on the fishery were observed (Holland, 2020). Moving forward, being able to forecast MHWs will allow communities to be proactive for extreme MHW events allowing businesses to better prepare for climate event market shocks linked to our marine resources (Jacox et al., 2022). Along with building tools to track MHWs, recent studies have now developed the ability forecast marine heatwaves. A recent MHW forecasting study uses thirty years of retrospective forecasts to develop MHW predictions 1 to 12 months in advance (Hannah, 2021). Using both oceanographic and climate change biology approaches, MHW trackers and forecasting serves as a tool for community management in the Santa Barbara Channel.

Study system

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. As a new and expanding wild fishery in coastal California (CDFW, 2020), whelks are highly abundant and are easily

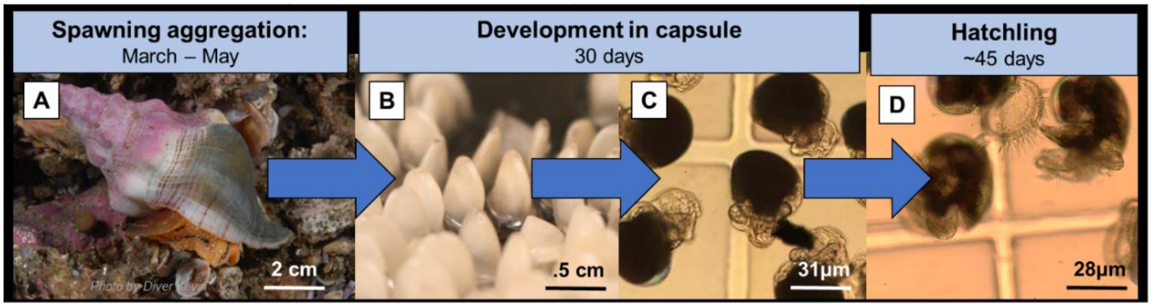


Figure 1. The life cycle of Kellet's whelk: (a) After spring spawning aggregations, adult females deposit egg capsules on rocky substrate in the kelp forest. Larvae will undergo (b, c) development within the capsule as encapsulated veligers for 4-7 weeks before (d) hatched veligers ("hatchlings" or "planktonic veligers") are released into the water column.

maintained in the laboratory as adults and as larvae. Found from 2 to 70 m deep and distributed from central California to Baja, the Kellet's whelk has been reported to be expanding its geographical range northward into Monterey Bay, CA (D. Zacherl, S. Gaines, & S. Lonhart, 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) (Figure 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. There is no doubt that whelk populations that have faced an increase in fishing pressure over the past five years have also endured repeated MHWs in the Santa Barbara Channel.

Although records show that whelk catch rates experienced a large increase in 1993, management of the whelk fishery is still developing. Whelk can be harvested by hand and via rock crab or lobster traps with proper licensing and permitting during the open season for commercial harvest. For the state of California, commercial harvest starts July 1st to once the harvest reaches the total allowable catch for Kellet's whelk (100,000 lbs per person), or through the first Wednesday after the 15th of March (lobster season harvest closure).

Recreational harvest of whelk is permitted outside of protected areas. While catch bag limits for the whelk have been established (35 individuals), like many harvested invertebrate species, there is no formal stock assessment. Most concerning, both recreational and commercial harvest of whelk are not regulated by minimum individual size limits. Kellet's whelk life history characteristics (e.g., slow growth, and externally developing larvae) make whelks especially vulnerable to a underregulated fishery. As MHWs are increasing in intensity, it is essential to gain more knowledge on the implementation of regulations that can best pair with the whelk's biology.

For my study region, between the two actively fished and economically important shelled gastropods in this California kelp forest ecosystem—red abalone and Kellet's whelk—there is little information on thermal tolerance of their early vulnerable stages (Zippay & Hofmann, 2010). While our understanding of the thermal tolerances of shelled gastropods in the Santa Barbara Channel is limited, it may be that that slow moving, temperate reef organisms are more vulnerable to thermal stress due to their limited ability to escape warming events (Leung, Connell, & Russell, 2017). Further, it is possible that long lived organisms with shorter generation times, such as red abalone and Kellet's whelk that can live up to ten and twenty years, respectively, may possess lower adaptive capacity to environmental change.

Education and outreach

To address the challenges that climate change will bring to on our marine ecosystems, we need increased engagement, and contributions from individuals from many backgrounds, experiences, and areas of expertise. Traditional science education approaches often fail to value the integration of student identities in STEM education settings. Educational tools and programming I developed for my dissertation utilized narrative to bridge my findings with the scientific community and the broader public. My educational tools engaged the public and highlighted student perspectives and backgrounds into discussion on global change biology topics. Specifically, I collaborated with the UCSB Research Experience & Education Facility, the campus aquarium, maintained by UCSB undergraduates, who host education programs for general public visitors. I worked with the REEF to establish (1) an education intervention, REEFlections, an undergraduate science communication symposium and (2) established an experiment display ("science in action") temperature manipulation system and outreach program at the REEF. I founded and directed for REEFlections for three years (2019, 2020, and 2022) and conducted an assessment on student participants in the 2020 REEFlections cohort for my dissertation. In order to determine whether or not my outreach and education intervention reached inclusivity goals for the program, I examined student interview transcripts for areas where students reported experiencing a sense of belonging (SOB) as a result of participating in STEM research and REEFlections-related activities. To establish "science in action" outreach programming I developed in collaboration with the REEF and Coastal Fund (UCSB Coastal Fund Grant Number: FALL 19-09), my experiments outlined in subsequent chapters (Chapter 3 and 4) were staged at the UCSB REEF. I initiated the establishment of an experiment display temperature manipulation system to showcase climate “science-in-action” by engaging a wider suite of persons than typically involved in the process of scientific discovery in global change biology research at UCSB. For two of the experiments in my dissertation (Chapter 3 and 4), I recruited undergraduate research assistants from a broad range of STEM and non-STEM disciplines to assist with my research and education program development. I trained students to research and education assistants for the display and guided them in using scientific storytelling to engage the public with my research.

Dissertation summary

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 ecology. For my dissertation I conducted organismal biology investigations using physiology and larval biology techniques. I conducted lab experiments on adult and early stages of *K. kelletii* to uncover characteristics of a small-scale molluscan fishery species in the face of environmental variability. My dissertation work represents the most recently published exploration of Kellet’s whelk development and larval staging (Clare, Kui, & Hofmann, 2022). I also consulted long term ecological research (LTER) datasets to contextualize my larval experimental findings.

In summary, with projects centered on the on the response of an emerging fishery species to MHWs, my dissertation is comprised of these three elements of research: (a) organismal biology, (b) long-term ecological data analysis, and (c) educational programming. I employed these three elements to achieve the following aims (Figure 2):

Specific Aims:

1. Develop eco-physiology methodology to investigate the effects of marine heatwave temperatures on *K. kelletii* progeny

2. Conduct laboratory acclimations of adult *K. kelletii* to investigate the impacts of adult reproduction and larval development on larval thermotolerance
3. Use narrative-based learning as a tool for STEM outreach & education

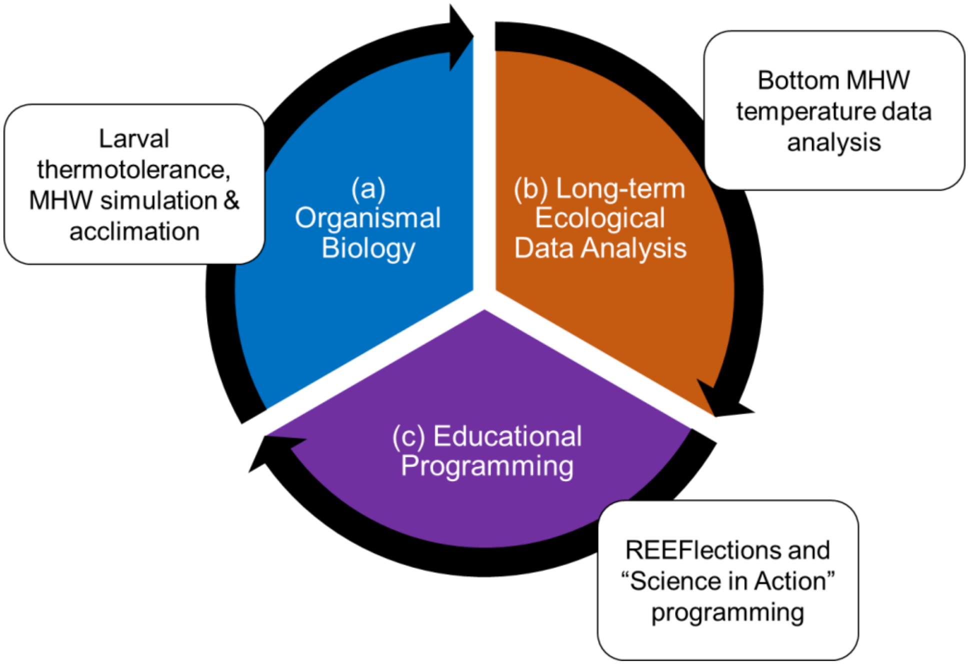


Figure 2. Schematic diagram of three elements of my dissertation research. The figure displays the three elements of my dissertation research: (a) organismal biology, (b) long-term ecological data analysis, and (c) educational programming, and how they relate to the research projects outlined in the subsequent chapters of my dissertation.

Chapter 2: Eco-physiology methodology for investigating the effects of marine heatwave temperatures on *K. kelletii* progeny

INTRODUCTION

In this chapter, **I examined the thermal tolerance of vulnerable early developmental stages** for the Kellet's whelk. The goal of this work was to **assess how early stage *K. kelletii* respond to environmental temperatures that have occurred in the Santa Barbara Channel during past MHW events** (Figure 3). Specifically, MHWs in the region have usually started in summer and would range into late fall/early winter with temperatures increasing 1-6 °C above seasonal averages.

Thermal stress induced by MHWs has been documented to have impacts on the productivity of coastal ecosystems around the globe. Due to the loses driven by MHWs (e.g., economic, social, and cultural), MHWs have stirred concern among practitioners in aquaculture and as well as managers of wild fisheries. While similar studies on shellfish fisheries species also report MHWs as a threat (Leung et al., 2017), surprisingly, little data can be found regarding thermal tolerances of shellfish fishery species.

There have been select studies on thermal tolerances of early stage benthic marine invertebrates (Pecorino, Lamare, Barker, & Byrne, 2013; Woolsey, Keith, Byrne, Schmidt-Roach, & Baird, 2015), including studies on ecologically and economically important kelp forest species such as the giant red sea urchins (Wong & Hofmann, 2020) and in estuarine species such as the Olympia oyster (Bible, Evans, & Sanford, 2020). Among the few studies on larval thermotolerance of shellfish species, there are even fewer studies that assess tolerance, sensitivity, and resilience of early stage shellfish that are explicitly conducted in a MHW context. Specifically, where thermal tolerance is interrogated across a range of temperatures that reflect present day to MHW conditions, to future MHW conditions—which are predicted to increase in intensity (E. Oliver, 2019).

Even within the same habitat, different gastropod species are able to adjust physiological traits to accommodate acute thermal stress (Leung et al., 2017). However, the varied levels of robustness or sensitivity to MHWs is unknown for critical early life stages for many marine invertebrates in the kelp forest—especially gastropod shellfish species. Therefore, since some marine gastropods show localized resilience to warmer temperatures (Somero, 2010), further thermal tolerance trials are necessary to determine levels of thermal resilience for economically important gastropod shellfish species. Addressing this need, the goals of the study in this chapter were to answer the following research question: How do early stage *K.*

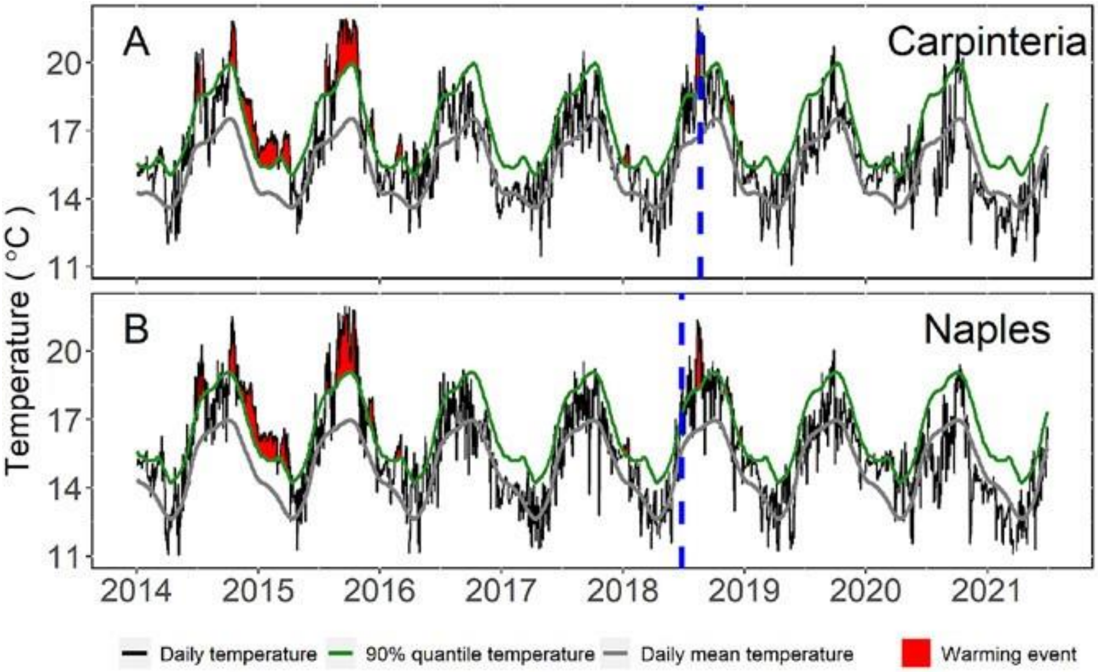
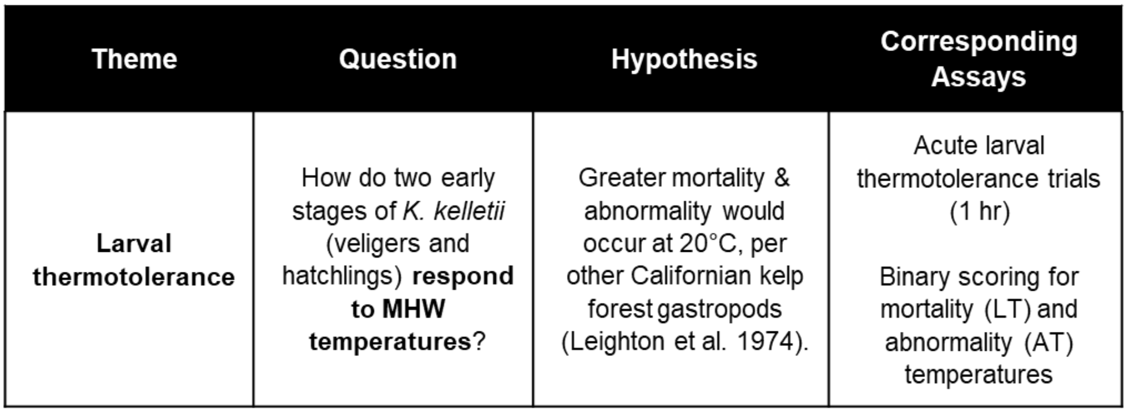


Figure 3. Time series of benthic temperature data from January 2014 to July 2021 at adult whelk kelp forest collection sites, Carpinteria Reef and Naples Reef, Santa Barbara Channel, CA USA. Daily mean temperature data is indicated by the gray line whereas the 90th percentile is indicated by the green 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.

kelletii respond to environmental temperatures that have occurred in the Santa Barbara Channel during past MHW events in acute thermal tolerance trials? I addressed this question by testing the following hypothesis that earlier stages of development would show greater levels of thermal tolerance, as has been shown in other California kelp forest gastropod species (Leighton, 1974) (Table 1).



Theme	Question	Hypothesis	Corresponding Assays
Larval thermotolerance	How do two early stages of *K. kelletii* (veligers and hatchlings) **respond to MHW temperatures**?	Greater mortality & abnormality would occur at 20°C, per other Californian kelp forest gastropods (Leighton et al. 1974).	Acute larval thermotolerance trials (1 hr) Binary scoring for mortality (LT) and abnormality (AT) temperatures

Table 1. Hypotheses and assays for the study described in Chapter 2 of my dissertation. The goals of the study in this chapter were to answer the research question listed above via the listed hypothesis. Corresponding assays for the hypothesis and research question are outlined in this table.

MATERIALS & METHODS

Specimens 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 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 wk), 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 wk 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 a 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 wk of development, capsules were randomly sampled from laid 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 fresh 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 chemosensory signaling between patches of hatching capsules (Miner, Donovan, & Andrews, 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 fresh 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 handheld 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 wk. 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 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

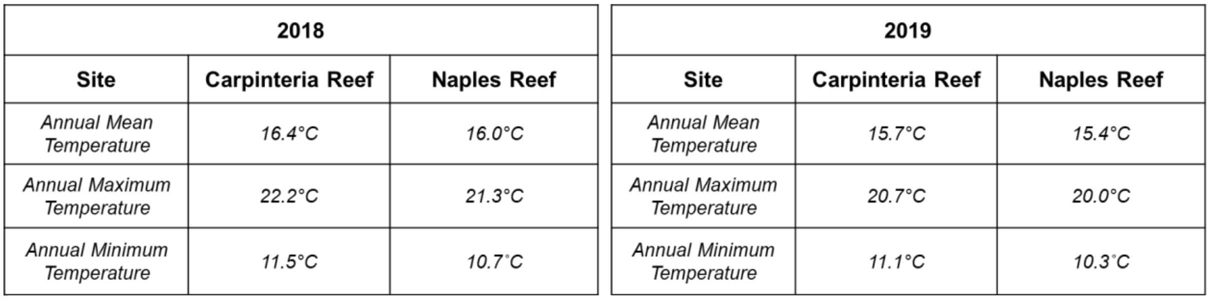
At the end of the thermal tolerance trial, vials of larvae were removed from the heat block and control vials of larvae were removed from the cold room. Thermal tolerance was measured using two metrics: (1) percent mortality and (2) degrees of developmental abnormality. Lethal temperatures (LTs) were 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 petridish. Prior to being pipetted into a slide for scoring, veligers were gently swirled in fresh seawater in the dissection petridish 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, were used to record larval abnormality in thermal tolerance trials. Both the LT_{50} and AT_{50} (median 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, as 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, Machler, Bolker, & Walker, 2015), MASS (Ripley, 2013), and base packages in R (version 3.5). Significance tests (p-values, degrees of freedom, and z-scores) were conducted to determine whether or not there was a statistically significant relationship between mortality and abnormality and the response variable, temperature, in the model.

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 (SBC-LTER 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



2018		
Site	**Carpinteria Reef**	**Naples Reef**
Annual Mean Temperature	*16.4°C*	*16.0°C*
Annual Maximum Temperature	*22.2°C*	*21.3°C*
Annual Minimum Temperature	*11.5°C*	*10.7˚C*

2019		
Site	**Carpinteria Reef**	**Naples Reef**
Annual Mean Temperature	*15.7°C*	*15.4°C*
Annual Maximum Temperature	*20.7°C*	*20.0°C*
Annual Minimum Temperature	*11.1°C*	*10.3˚C*

Table 2a and b. Annual mean, minimum and maximum benthic temperatures from the SBC-LTER study sites: Carpinteria and Naples Reef, CA, USA from 2018 to 2019.

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 (SBC-LTER 2022). An ocean heatwave analysis was performed using a heatwave R package (Schlegel, 2018). The daily mean temperature (Figure 3) was calculated using daily data from 2000 to 2021 for Carpinteria Reef and from 2012 to 2021 for Naples Reef. The 90th percentile temperature threshold was used to detect warming events (Figure 3).

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

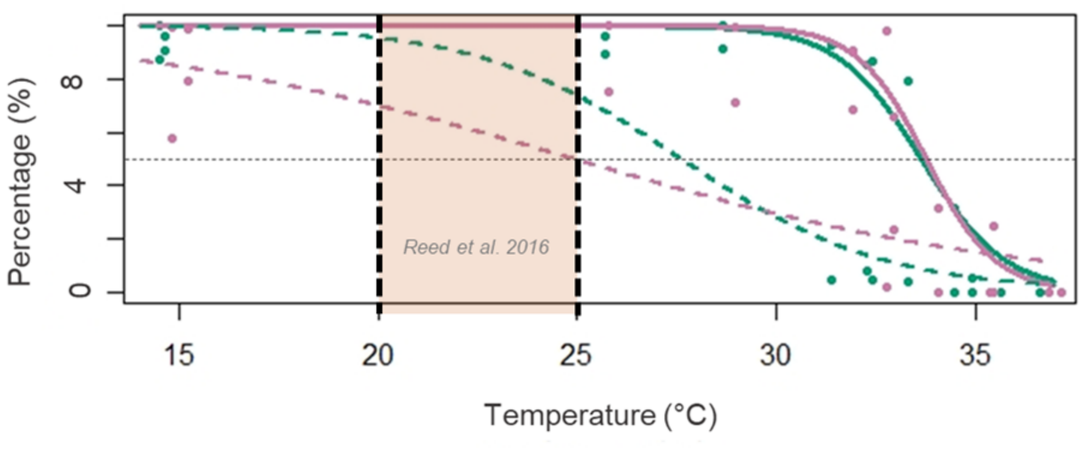
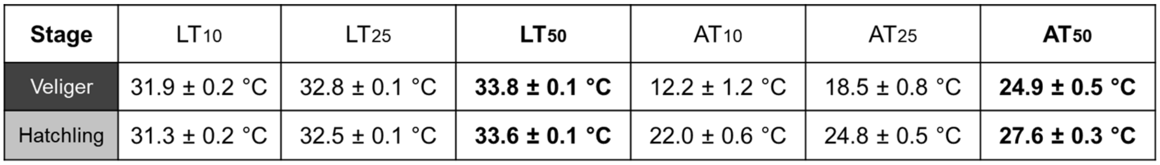


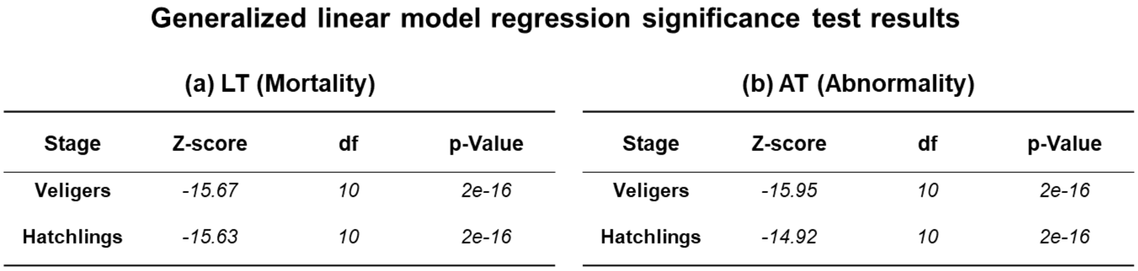
Figure 4. Thermal tolerance shown as percent mortality (LT_{50}; solid curves) and percent abnormality (AT_{50}; dashed curves) for *Kelletia kelletii* encapsulated veligers and hatchlings following 1 h temperature exposures. The black dashed line indicates where half of the larvae experienced 50% mortality (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.

at similar temperatures and (2) significant levels of developmental abnormality were induced at lower temperatures than temperatures that caused mortality. Significance testing on the relationship between mortality and abnormality and the response variable, temperature, in the generalized linear model used for this study can be found in Table 4. 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).



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**

Table 3. 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. All values are given as a mean ± standard error.



Generalized linear model regression significance test results

(a) LT (Mortality)

Stage	Z-score	df	p-Value
Veligers	*-15.67*	*10*	*2e-16*
Hatchlings	*-15.63*	*10*	*2e-16*

(b) AT (Abnormality)

Stage	Z-score	df	p-Value
Veligers	*-15.95*	*10*	*2e-16*
Hatchlings	*-14.92*	*10*	*2e-16*

Table 4a and b. Lethal temperature (LT) and abnormality temperature (AT) generalized linear model significance test results. This study finds that the output from generalized linear mixed-effects model analyzing the effect of larval temperature treatments on (a) LT and (b) AT values of *K. kelletii*, thermotolerance are significantly in fit the scoring data. The values used for this model and significance testing were generated from mortality and abnormality scoring. The degrees of freedom for the residual deviance are also reported in these tables.

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 3, Figure 4). 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 3, Figure 4). 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 3, Figure 4).

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 3). In addition, temperatures that induced abnormal development were lower than those that induced larval mortality (Table 3, Figure 4). 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 3, Figure 4). 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 3). 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 (T. 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 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 K. 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 *K. 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 with thermotolerances found in similar gastropod shellfish species in the SBC, 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 3, Figure 4). 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 3, Figure 4).

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 MHW temperatures 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 have 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. Whereas “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 (CDFW, 2020).

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 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 industry 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.

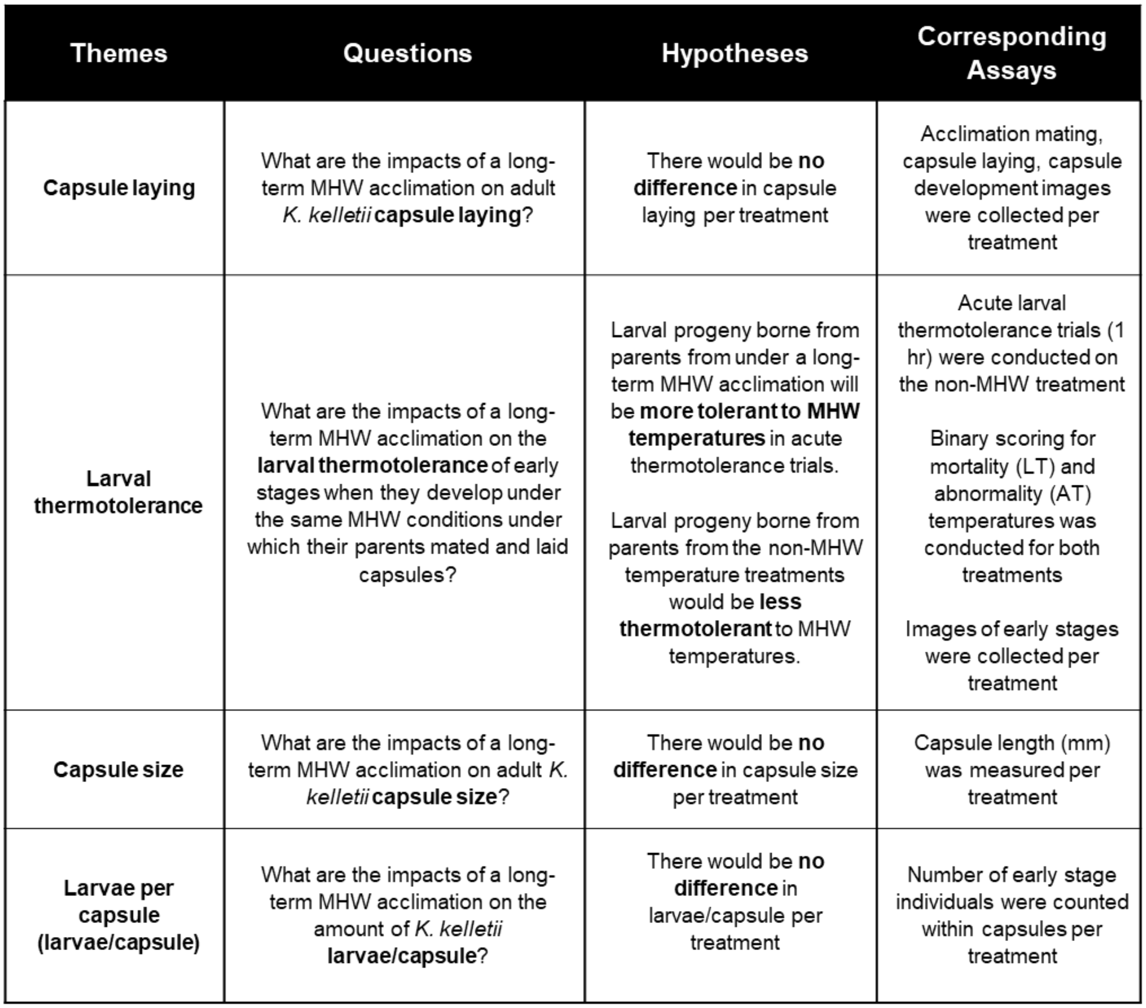
Chapter 3: Impacts of a long-term MHW acclimation on reproduction, early stage development and acute thermal stress *K. kelletii*

INTRODUCTION

As described in Chapter 1, there are knowledge gaps regarding how MHWs impact life history and early stages of many benthic marine invertebrates (E. Oliver et al., 2018; T. Wernberg et al., 2013). In general, MHWs will have varied impact on organisms depending on how MHW thermal stress aligns with important reproduction and life history events (Leach, BuyanUrt, & Hofmann, 2021). One of the gaps in ecological studies on MHWs and marine invertebrates are that experiments are often not contextualized with actual data from the environment. For example, a recent review on eco-physiology studies reports that larval thermotolerance (acute thermal stress) studies on early stage invertebrates do not incorporate environmental data, quantitative and qualitative developmental metrics side-by-side (Jacox et al., 2022). This is a common limitation for many researchers who do not have research projects with embedded environmental monitoring such as the SBC LTER.

These research challenges are especially true for studies on long-lived organisms with long pelagic early stage durations like *K. kelletii*. Long-lived "non-model" organisms like *K. kelletii* tend to have life history traits that are difficult to observe in the laboratory, making much of our insight on the impacts of environmental change biased by studies that focus on model species (Richards et al., 2017). *K. kelletii*, however, is an ideal species to examine early stages development since they produce a large numbers of capsules that contain hundreds of embryos laid in controlled laboratory settings. This presents an opportunity to conduct long-term laboratory based MHW experiments on early stage *K. kelletii* since early stage development occurs over a period of months that has aligned with the timing of MHWs in the Santa Barbara Channel (Reed et al., 2016).

Chapter 3 describes the results of an experiment where adult whelks were acclimated in the laboratory to MHW conditions, and allowed to lay egg capsules over the course of the acclimation. This study examines the impacts of thermal stress associated with MHW events on Kellet's whelk's reproductive biology and early development (Table 5).



Themes	Questions	Hypotheses	Corresponding Assays
Capsule laying	What are the impacts of a long-term MHW acclimation on adult *K. kelletii* **capsule laying**?	There would be **no difference** in capsule laying per treatment	Acclimation mating, capsule laying, capsule development images were collected per treatment
Larval thermotolerance	What are the impacts of a long-term MHW acclimation on the **larval thermotolerance** of early stages when they develop under the same MHW conditions under which their parents mated and laid capsules?	Larval progeny borne from parents from under a long-term MHW acclimation will be **more tolerant to MHW temperatures** in acute thermotolerance trials. Larval progeny borne from parents from the non-MHW temperature treatments would be **less thermotolerant** to MHW temperatures.	Acute larval thermotolerance trials (1 hr) were conducted on the non-MHW treatment Binary scoring for mortality (LT) and abnormality (AT) temperatures was conducted for both treatments Images of early stages were collected per treatment
Capsule size	What are the impacts of a long-term MHW acclimation on adult *K. kelletii* **capsule size**?	There would be **no difference** in capsule size per treatment	Capsule length (mm) was measured per treatment
Larvae per capsule (larvae/capsule)	What are the impacts of a long-term MHW acclimation on the amount of *K. kelletii* **larvae/capsule**?	There would be **no difference** in larvae/capsule per treatment	Number of early stage individuals were counted within capsules per treatment

Table 5. Hypotheses and assays for the study described in Chapter 3 of my dissertation. The goals of the study in this chapter were to answer the research questions listed above by testing the listed hypotheses. Corresponding assays for each hypothesis and research question are outlined in this table.

To design this experiment, I used temperature data from the SBC-LTER database and acclimated adults to temperatures that matched the 20˚C average temperature of the 2014-16 “Blob” MHW, and a Non-MHW temperature that represented the average ambient seawater temperature in the Santa Barbara Channel (15˚C) (SBC-LTER). In this portion of my dissertation research, I reached my goals to assess the impacts of MHW temperatures on adult reproductive traits (e.g., timing of capsule laying) and on early development stages, with the exception of conducting acute thermal stress trials on the MHW treatment egg capsules. Adult whelks in the MHW treatment did not lay enough capsules that were in a suitable condition to be assessed in for acute thermal stress. For the early stages I was able to collect, I assessed general characteristics of development along with acute thermal stress of three encapsulated stages: embryos, trochophores, veligers, and a fourth stage, hatchlings that have emerged from the capsule by that later stage in development.

MATERIALS & METHODS

Specimens collection and husbandry

Adult Kellet’s whelks were hand-collected in Spring 2021 via SCUBA from Carpinteria Reef, California, USA, a benthic kelp forest reef site in the Santa Barbara Channel (34˚ 23.487’ N, 119˚ 32.517’ W). Adult whelks were collected at a depth of 8 m using California Scientific Collection permits (SC-1223 to G.E. Hofmann, and SC-11964 to Dr. Robert Miller as the permit to the Santa Barbara Coastal LTER). Immediately following collection, adult whelks were placed in coolers and transported to UCSB aquaria facilities where they were maintained in flow-through seawater tanks through their summer reproductive season of March to July 2021. A light-dark cycle was set by natural daylight conditions within the aquaria facility. Over the course of the acclimation, adult whelks were weighed, measured and fed twice weekly ad libitum.

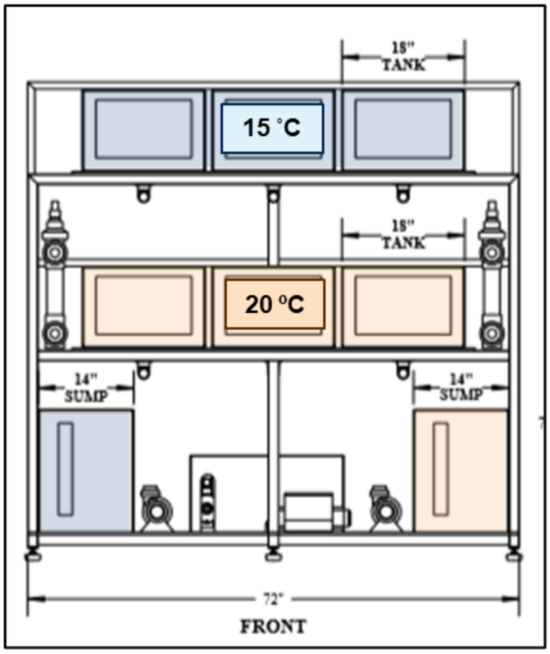


Figure 5. Diagram of the temperature-controlled aquarium system used for the MHW experiment. The system consisted of three 18 gallon tanks per temperature treatment (15˚C and 20˚C). A semi-open flow-through connected to external circulating fresh seawater. A sump was used to maintain treatment temperature and water circulation to supplement the water in each treatment.

Environmental temperature data

Temperatures chosen for the MHW acclimation experiment were based on environmental data at the whelk collection site, Carpinteria Reef. Temperature data were collected as a part of ongoing research activities of the SBC-LTER (SBC-LTER). Temperature data were collected using Onset HOBO TidbiT 5000 temperature loggers (MX2204) deployed on the benthos where adult *K. kelletii* were collected, and where egg masses are deposited by adults whelks. Two data loggers at each site were programmed to record temperatures every 15 minutes. Sensors were deployed at a depth of approximately 7 m and were retrieved biannually. These temperature data are publicly available in the Environmental Data Initiative repository (SBC-LTER, 2022).

Adult acclimation and capsule laying conditions

Adult whelks were acclimated to a Non-MHW treatment ambient temperature of 15˚C and MHW treatment of 20˚C in 18 gal aquarium tanks. Using a temperature-controlled flow-through seawater system (Figure 5), aquaria were maintained at these temperatures during whelk mating, reproduction, capsule laying and early stage development. Three treatment tanks were used per temperature treatment and five adult whelks were held in each tank.

Developmental timeline and capsule observations

For this experiment, I assessed characteristics of early stages of *K. kelletii*. The developmental biology of *K. kelletii* is relatively under-studied, and has been only recently described by other researchers (Vendetti, 2020). In brief, over the course of four-weeks of intracapsular development, *K. kelletii* transition from embryo, to trochophore, to the encapsulated veliger prior to emerging from egg capsules as a excapsulated veligers, also referred to as a hatchlings (Clare et al., 2022; Vendetti, 2020). A single whelk can lay a minimum of one hundred egg capsules each year, with each capsule containing up to 1,200 larvae (CDFW, 2020; Rosenthal, 1970; Vendetti, 2020; Wilson, 2017). Whelk mating pairs were documented as they formed via photo and written observations. Temperature and photo data were analyzed to develop developmental timelines per treatment. The developmental timeline was constructed from marking the first incident of developmental “markers” such as capsule laying (oviposition) and developmental stages (e.g., trochophore, veliger, hatchling) for each overall treatment. To test the significance of developmental timeline data, I conducted a two-tailed nested ANOVA without replication to determine if the difference between the number of days to oviposition significantly differed between temperature treatments per tank.

To determine the effects of long-term MHWs on the developmental biology of *K. kelletii*, egg capsules were sampled from experimental tanks as they were laid in both the Non-MHW and MHW treatment. This strategy allowed for all stages of development to be monitored as the early stages in the capsules progressed to each developmental stage. For capsules from each treatment, I measured: (1) capsule height, (2) number of early stages/capsule, and (3) the tolerance of early stages to acute thermal stress. For traits 1-3 above, capsule height and numbers of early stage individuals per capsule were counted for capsules from each treatment according to methods described in (Vendetti, 2020). Egg capsule height was determined for a random sample of 79 capsules from each treatment, measuring from the base of the capsule to the escape aperture. Capsule width and thickness were not measured. A two tailed z-test was conducted to determine whether or not there was a significant difference in capsule height between treatments. For staging and counting of the early stages, individuals were excapsulated by hand (with forceps and dissecting scissors). To determine the number of early stage individuals, a random sample of 12 egg capsules from each treatment was used to estimate early stage individuals per capsule. The subset of egg capsules used to determine the weekly stage status of larvae within capsules were also used for the acute thermal stress trials. A two tailed t-test was conducted to determine whether or not there was a significant difference in number of early stages/capsule between treatments.

Protocol for scoring stage progression in capsules

Capsules that were laid by adults in the MHW treatment or Non-MHW treatment were maintained in the same temperature treatment tanks as parent whelks for the duration of the capsule development and hatching. Capsules were examined and scored for the number of different stages present within capsules. This scoring step was performed for 52 capsules from the MHW treatment adults and 83 capsules from the Non-MHW treatment adults. Under ambient conditions, early stage individuals typically develop over the course of 4-7 weeks for *K. kelletii* (CDFW, 2020; Vendetti, 2020). In general, each of the four weeks of development contain one of the four major stages of development: embryo, trochophore, veliger, and hatchling (Vendetti, 2020; Wilson, 2017). While a majority of individuals in an egg capsule transition to each major stage per week, it is typical for a small proportion of individuals within a capsule to still be transitioning or “stalled” (undeveloped or developmentally arrested) in an earlier developmental stage (Vendetti, 2020).

To determine whether or not a major portion of larvae had reached the time-appropriate stage of development each week, the stage “status” of a subset of capsules was recorded. To determine the stage status of a capsule, 50 individuals per capsule were scored to determine the capsule stage classification. Most of the capsules sampled presented multiple stage scoring possibilities, with the. Multiple stages scores per capsule meant that if a capsule included individuals of multiple early stages, each of those individual’s stages were scored separately for that capsule. For example, if a capsule contained veligers and trochophores; for each of those two stages observed, both of those stages were recorded as a stage class observed in that capsule. These findings are descriptive and were not analyzed via significance tests.

Acute thermal tolerance trials and scoring for effects of MHW acclimation

Early development stages (trochophore, veligers, and hatchlings) were evaluated via acute thermal stress trials as they were removed from the acclimation treatment. For the acute thermal stress trials, 50 individuals were scored for each of the three stages: trochophores, veligers, and hatchlings. While thermal tolerance trials were not conducted on MHW treatment individuals, a random sampling of early stage individuals from egg clutches from both treatments were used to evaluate thermal stress on early stage individuals laid by MHW temperature acclimated adults, that underwent development in the MHW treatment. Non-MHW treatment early stage individuals were sampled according to methods for acute thermal stress trials in Chapter 2. The sampling for each developmental stage for this study is as follows:

Trochophore and veliger sampling: Larvae developed within capsules and were monitored in ambient seawater tanks until the trochophore veliger stages were reached. Single capsules of early stage individuals 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 capsule sampling, single egg capsules containing early stage individuals were individually deposited into a 20 ml vials to be used for thermal tolerance trials. Trochophores and veligers from a random sampling of clutches from each treatment tank were used to evaluate thermal tolerances.

Hatchling sampling: As larvae within capsules neared the end of their intracapsular development, capsules were randomly sampled from laid capsule clusters and were placed in mesh bins inside temperature treatment tanks to allow larvae to swim free from capsules and hatch naturally. Mesh bins allowed for a small for of fresh flowing seawater to move through the mesh during the hatching period (1–3 days). Hatching 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. 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 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 fresh seawater. Like trochophore and veliger thermotolerance trial sampling, hatchlings were pooled across treatment tanks and females for thermotolerance trials.

<u>Thermal tolerance trials:</u> Thermal tolerance of *K. kelletii* larvae from this study was measured for encapsulated trochophores and veligers, and free-swimming hatchlings using constant, acute temperature exposures (1 hr). Non-MHW larvae were exposed to nine temperatures that ranged from approximately 14.8°C to 37.2°C for 1 h; temperatures along the heat gradient were: approximately 13.3, 25.2, 27.0, 28.9, 29.5, 30.7, 32.1, 33.4, 35.8 °C according to acute thermal stress trial methods described in Chapter 2). Thermotolerance trial methods for this study were as follows: 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 handheld digital thermometer equipped with a wire thermocouple (Thermolyne PM 20,700/Series 1218). Due to differences in development

timing between trochophores, veligers, and hatchlings, thermal tolerance trials were held over the course of approximately two weeks. Vials of larvae were haphazardly arranged across the heat block such that larvae were of the nine treatment temperatures. Larvae were held in control temperature treatment vials at approximately 13.2 - 13.5°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 mortality and abnormality: Scoring for mortality and abnormality of early stages for both treatments was determined via the percentages of the following categories: alive, dead, normal and abnormal. To score developmental abnormality and mortality for MHW treatment larvae, 50 individuals were scored for two stages: trochophores and veligers.

Median lethal temperatures (LTs) and abnormality temperatures (ATs) were determined for larval thermotolerance trials. Scoring for LT and AT values for this experiment were as follows: At the end of thermal tolerance trials, vials of larvae were removed from the heat block and control vials of larvae were removed from the cold room. LTs were assessed using standard methods for calculating LT thresholds. ATs were assessed by examining abnormalities of the general body morphology as indices of structural abnormalities (e.g., velum, shell composition, degraded cell membranes). A generalized linear model was used to test larval thermal tolerances of trochophores, veligers and hatchlings 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 (Ripley, 2013), and base packages in R (version 3.5). Significance tests and z-scores were calculated to determine whether or not there was a statistically significant relationship between mortality and abnormality and the response variable, temperature, in the model.

Percent mortality and abnormality were determined via binary scoring. 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. Trochophores and veligers were maintained within their capsules in vials for all thermal tolerance trials. Once the trial was complete, trochophores and veligers were forcibly removed from their capsules to be evaluated for scoring. To observe trochophore and veliger movement and swimming behavior, capsules were dissected, and larvae were released in a petridish. Prior to being pipetted into a slide for scoring, larvae were gently swirled in fresh seawater in the dissection petridish to let them move freely from their capsular jelly. Hatchlings were simply pipetted to rafter slides for scoring. Percent of larval abnormality was determined by screening for irregular movement. Thereafter, early stage individuals were photographed (n = 50 individuals per capsule) under bright field DIC illumination at 10× on a compound microscope (Olympus BX50) with attached digital camera (Motic Images) using Motic Images Plus (version 3.0). A two proportion z-test was conducted for each stage to determine whether differences between the proportions of mortality and abnormality proportions between treatment tanks were significant.

RESULTS

The main findings of this study were that (1) adult whelks acclimated to MHW conditions laid capsules later than the Non-MHW acclimated whelks, (2) embryos in the MHW treatment progressed to each stage faster as compared to the embryos that developed in capsules maintained at the Non-MHW temperature treatment, (3) the Non-MHW treatment larvae progressed to each developmental stage over a longer timeframe than is typically observed for *K. kelletii*, and (4) egg capsule and body condition of early stages that developed in MHW conditions had higher degrees of developmental abnormalities compared to larvae that developed at cooler, Non-MHW conditions. Since MHW treatment adults laid capsules of lower structural quality, size and amount, this resulted in an inability to challenge MHW treatment early stages in acute thermal stress trials following the acclimation period. Instead, early stage individuals from capsules that developed in the MHW treatment were scored for their mortality and abnormality as a result of being laid in capsules that developed under MHW acclimation temperatures.

Developmental timeline and capsule observations

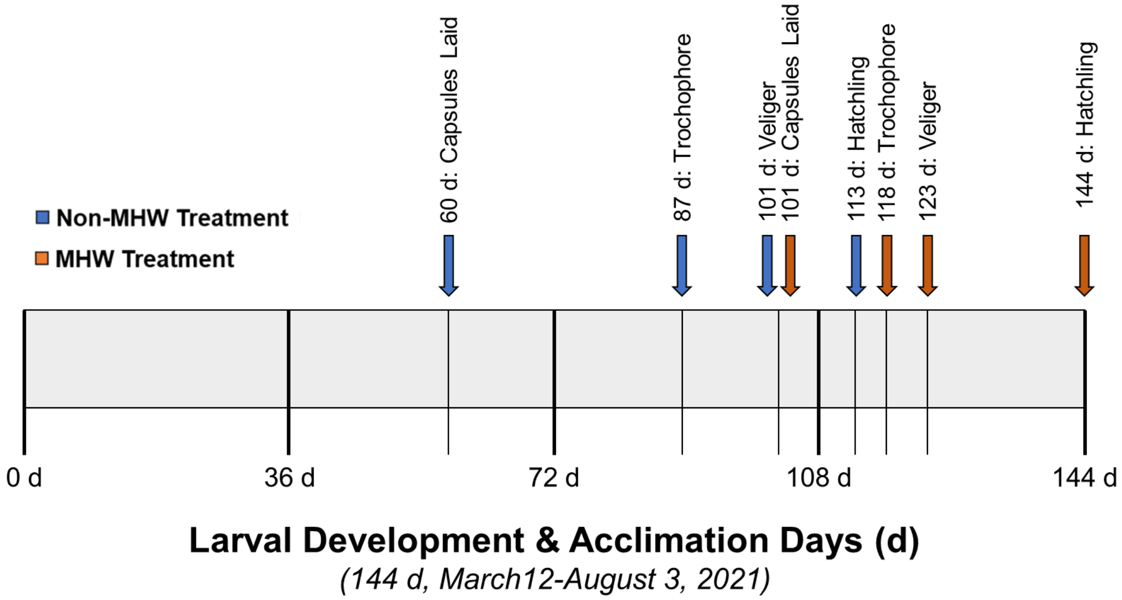


Figure 6. Timing of capsule laying and development timeline over the course of the 144 d acclimation (March 12 – August 3, 2021). The Non-MHW treatment larvae developed over a timeframe of 53 d (May 11-July 3, 2021). MHW treatment larvae developed over a timeframe of 43 d (June 21-July 13, 2021).

Adult whelks were acclimated at the two temperature treatments of 15°C and 20°C for 144 d (March 12 to August 3, 2021) (Figure 6). The first major observation was that there was a difference in the timing of capsule laying. The 15°C Non-MHW acclimated adults produced capsules 28.5% earlier than adults in the 20°C MHW treatment. Specifically, egg capsules were laid by 60 d (May 11, 2021) and 101 d (June 21, 2021) of the acclimation for the Non-MHW and MHW treatments, respectively.

In terms of the developmental timeline, early stage development in the Non-MHW (15°C) treatment occurred over a 53 d timeframe (May 11-July 3, 2021). The MHW treatment early stages developed faster over the course of 43 days (June 21-July 13, 2021), approximately 19% faster than the Non-MHW development rate. The early stage development of the Non-MHW and MHW treatment larvae are described in both days after capsule laying (oviposition) and days of the acclimation (Figure 6). While observed differences in developmental timelines between the temperature treatments are clear, differences observed in the oviposition dates per each treatment tank were not statistically significant via a two-tailed nested ANOVA test (Table 6a and 6b).

(a) Day of acclimation (d) at which oviposition occurred per treatment tank

Treatment Tank	Non-MHW	MHW
Tank 1	*101*	*101*
Tank 2	*60*	*109*
Tank 3	*61*	*109*

(b) Developmental analysis

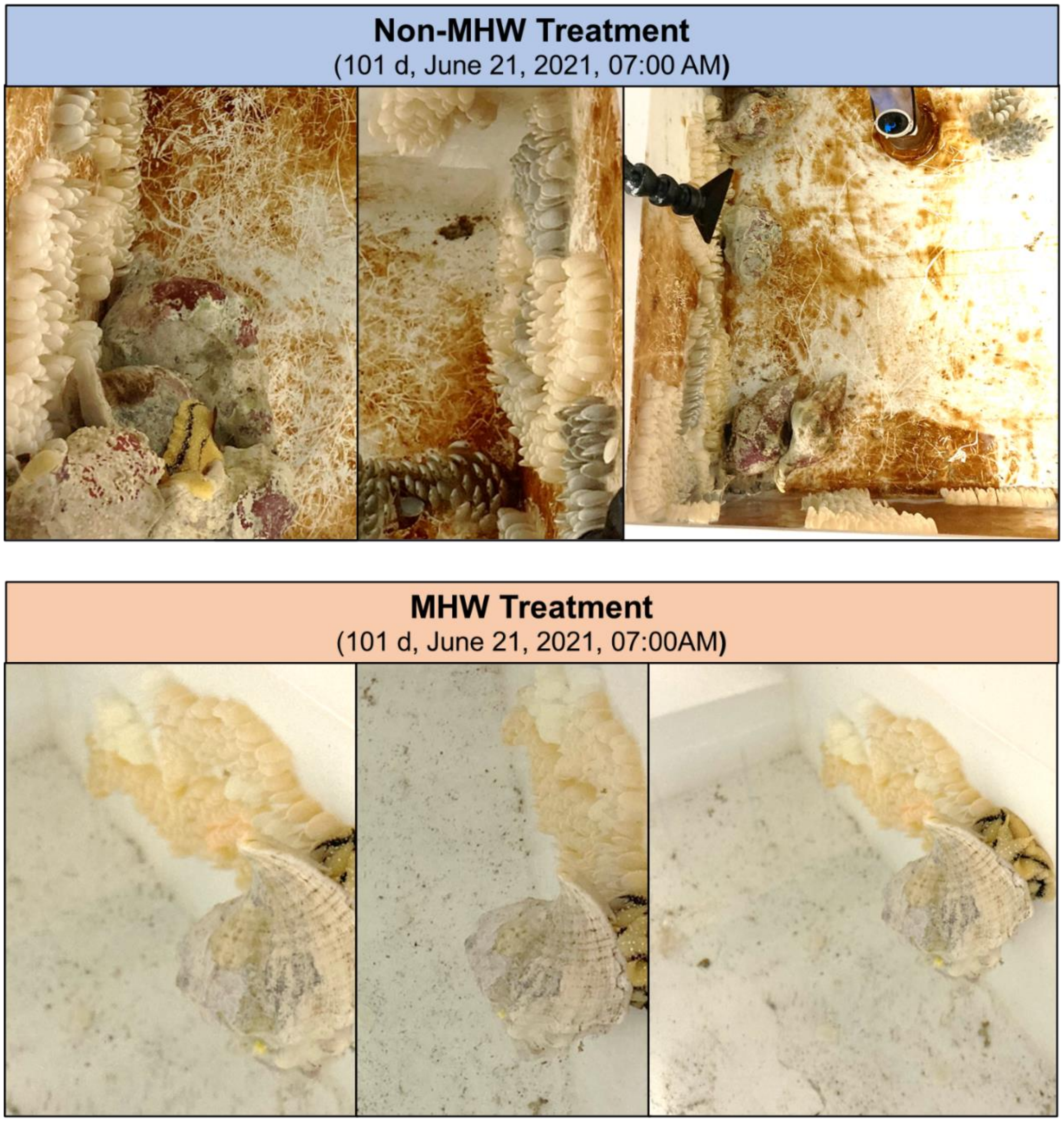
Nested ANOVA: Two-Tailed Without Replication

Treatment	Non-MHW	MHW
Variance	*547*	*21.33333*
n (Treatment tanks)	*3*	*3*
F-Value	*4*	
p-Value	*0.18*	

Table 6a. Day of acclimation at which oviposition (capsule laying) occurred per treatment tank and Table 6b. Two-tailed nested ANOVA on oviposition (capsule laying) dates per treatment tank. 6a. Showcases the day of the acclimation at which oviposition occurred per treatment tank. 6b. Displays the results from a two tailed nested ANOVA that was conducted to determine whether there was a significant difference in days at which oviposition occurred per treatment tank between the Non-MHW and MHW treatments. The p-value found was greater than the significance level of 0.05, which confirmed that the differences observed in the oviposition dates per each treatment were not statistically significant.

Capsule height and larvae per capsule

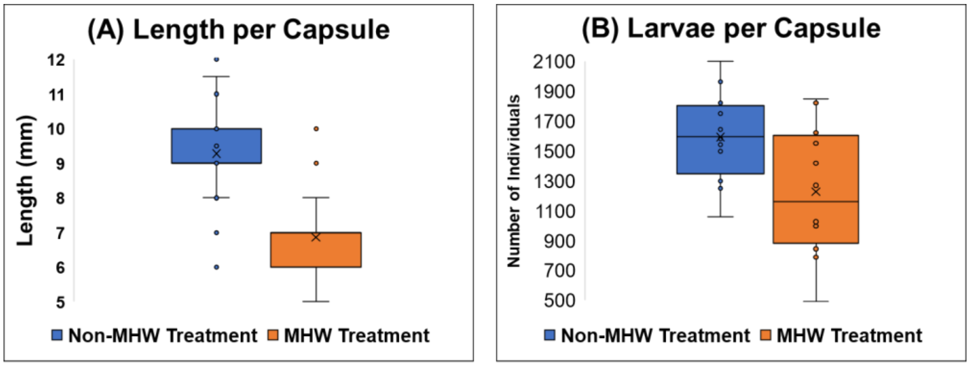
Overall, capsule characteristics varied between the acclimation treatments. This variation was observed in (1) capsule morphology, (2) numbers of early stage individuals/capsule, and (3) the general condition of encapsulated individuals. For the gross morphology of capsules, Non-MHW treatment capsules were lingulate and smooth whereas MHW treatment capsules were short, contained clumps of undeveloped larvae and cloudy, thin, runny, capsule jelly (Figure 7). The overall size of capsules was also different between treatments. Here, Non-MHW and MHW treatment capsules averaged 9.3 mm and 6.7 mm in height, respectively, from their base to escape aperture (n = 79 capsules per treatment). The average number of early stage individuals per capsule were 1,591 and 1,226 individuals per capsule (n = 12 capsules per treatment) for Non-MHW and MHW treatments, respectively. Approximately 20-30 individuals were lost in dissection while counting the number of larvae per capsule. The mean, minimum, and maximum capsule heights and early stage individuals per capsule were determined and are displayed in Table 7a and b, Figure 8a and b. The p-value found in both height and larvae/capsule analyses were less than the significance level of 0.05, which confirms that the differences observed in the length of each capsule and number of larvae per capsule per each treatment were statistically significant (Table 8 a and b).


Non-MHW Treatment
(101 d, June 21, 2021, 07:00 AM)

MHW Treatment
(101 d, June 21, 2021, 07:00AM)

Photos by Xochitl Clare, Eva Juengling Bean, and Paul Huang

Figure 7. Images of capsules laid by adult *K. kelletii* in the two experimental treatments. This figure shows representative masses of egg capsules as laid by adults in the treatment on 101 d of the long-term acclimation. At 101 d of the acclimation, the Non-MHW treatment larvae had reached the veliger stage, shown in grey capsules, (top). The first set of capsules were also laid in the MHW treatment on 101 d (bottom).



(A) Length per Capsule		
Treatment	Non-MHW	MHW
Mean	*9.28481*	*6.860759*
Median	*9*	*7*
1st Quartile	*9*	*6*
3rd Quartile	*10*	*7*
Min	*6*	*5*
Max	*12*	*10*

(B) Larvae per Capsule		
Treatment	Non-MHW	MHW
Mean	*1591.8*	*1226.2*
Median	*1593*	*1160*
1st Quartile	*1346.5*	*881.25*
3rd Quartile	*1801*	*1603.5*
Min	*1060*	*491*
Max	*2098*	*1844*

Table 7a and b, Figure 8a and b. Capsule height and larvae per capsule for each treatment. Figures 7a and b display the measured (A) Length per capsule and amount of (B) Larvae per capsule. The tables 3a and b below the figures display the mean, median, 1st, 3rd, quartiles, minimum and maximum values per each set of data.

Capsule height

z-Test: Two Sample for Means

Treatment	*Non-MHW*	*MHW*
Mean	*9.28*	*6.860759*
Known Variance	*1.05*	*1.031245*
n (capsules)	*79*	*79*
Z-score	*14.91684*	
p-Value	*0*	

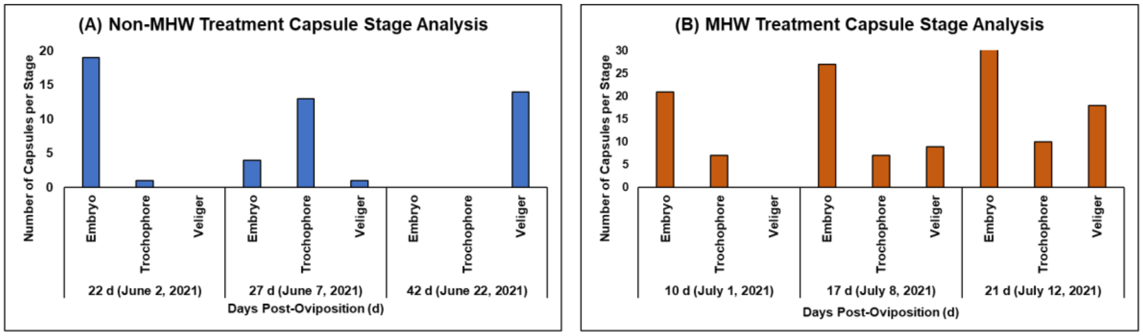
Larvae per capsule

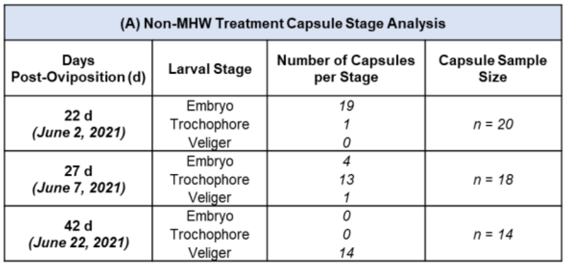
Two-Tailed t-Test: Two-Sample Assuming Unequal Variances

Treatment	*Non-MHW*	*MHW*
Mean	*1591.75*	*1226.17*
Variance	*88174.57*	*185111.80*
n (capsules)	*12*	*12*
df	*20*	
t Stat	*2.42*	
p-Value	*0.03*	

Table 8a. Two tailed z-test results for capsule height data and Table 8b. Two tailed t-test results for the number of larvae per capsule. A two tailed t-test was conducted to determine whether there was a significant difference in the number of larvae per capsule between the Non-MHW and MHW treatments. A two tailed z-test was conducted to determine whether there was a significant difference in capsule height between the Non-MHW and MHW treatments. The p-value found in both analyses were less than the significance level of 0.05, which confirms that the differences observed in the length of each capsule and number of larvae per capsule per each treatment are statistically significant.

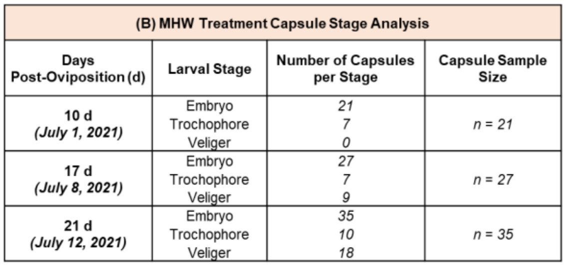
Effects on progression of development





(A) Non-MHW Treatment Capsule Stage Analysis

Days Post-Oviposition (d)	Larval Stage	Number of Capsules per Stage	Capsule Sample Size
22 d ***(June 2, 2021)***	Embryo Trochophore Veliger	*19* *1* *0*	*n = 20*
27 d ***(June 7, 2021)***	Embryo Trochophore Veliger	*4* *13* *1*	*n = 18*
42 d ***(June 22, 2021)***	Embryo Trochophore Veliger	*0* *0* *14*	*n = 14*



(B) MHW Treatment Capsule Stage Analysis

Days Post-Oviposition (d)	Larval Stage	Number of Capsules per Stage	Capsule Sample Size
10 d ***(July 1, 2021)***	Embryo Trochophore Veliger	*21* *7* *0*	*n = 21*
17 d ***(July 8, 2021)***	Embryo Trochophore Veliger	*27* *7* *9*	*n = 27*
21 d ***(July 12, 2021)***	Embryo Trochophore Veliger	*35* *10* *18*	*n = 35*

Figure 9a and b, Table 9a and b. Early stages observed each sampling week per treatment. The figures and tables show the stage classifications of larvae within egg capsules relative to days post-oviposition for each treatment. For the Non-MHW treatment, a majority of egg capsules sampled contained larvae that reached distinct stages by the sampling date: larvae within capsules reached embryo, trochophore, and veliger, stages by 22, 27, and 42 d post-oviposition, respectively. For the MHW treatment, stalled (undeveloped) larvae of all stages were present in all capsules. MHW treatment capsules contained substantial number of stalled embryos for each sampling date.

There was a difference in the Non-MHW treatment and the MHW treatment, when scoring early stages for progression through development and for normal development. For the Non-MHW treatment, 19 egg capsules (out of n = 20 capsules), 13 egg capsules (out of n = 18 capsules), and 14 egg capsules (out of n = 14 capsules) contained individuals that reached the embryo, trochophore, and veliger, stages by 22, 27, and 42 d post-oviposition, respectively.

For the MHW treatment, several stages of stalled (undeveloped or arrested and transitioning) individuals were present in a capsule at a time. For each of the sampling days, of MHW treatment capsules, each set of capsules contained large number of stalled embryos. On 10 d, 17 d, and 21 d post-oviposition, 21 egg capsules (out of n = 21 capsules), 27 egg

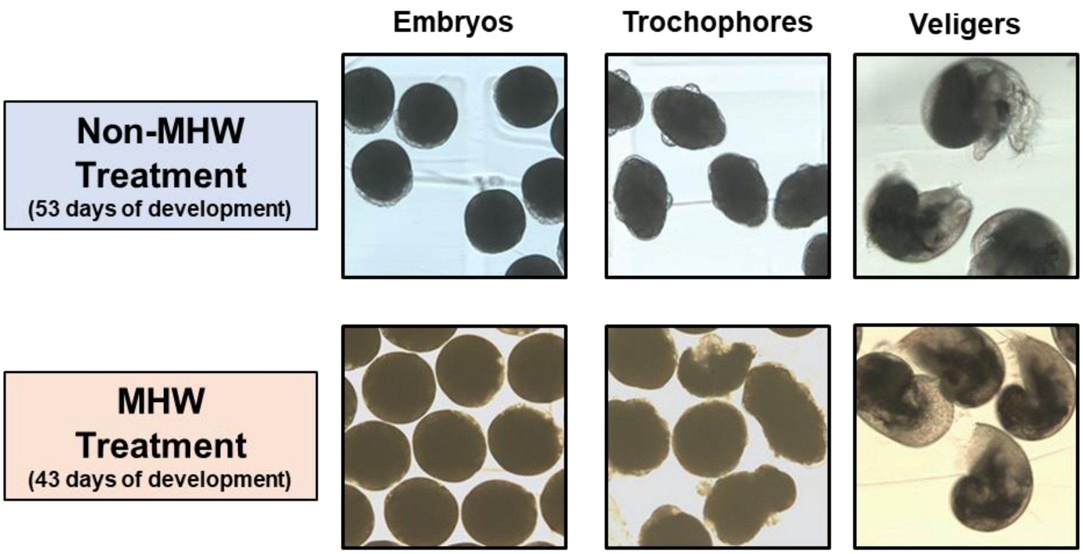


Figure by Paul Huang and Xochitl Clare
Photos by Xochitl Clare, Eva Juengling Bean, and Paul Huang

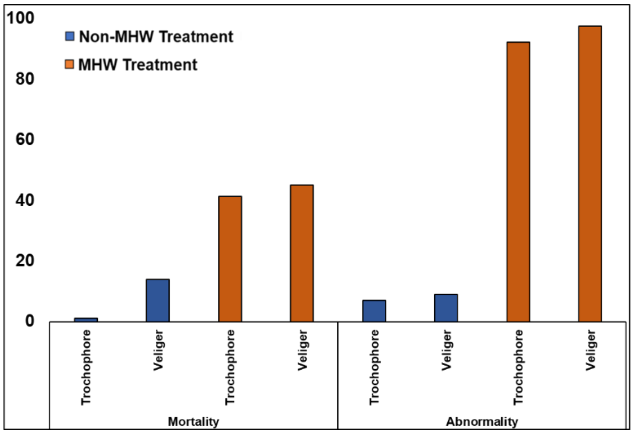
Figure 10. Images of early stage *K. kelletii* from the two experimental treatments. Images of representative early stage individuals at three early stages (embryos, trochophores and veligers) are shown in the panels above. The early stages shown all developed in the respective treatments: Non-MHW treatment (top) and the MHW treatment (below) at 15˚C and 20˚C respectively.

capsules (out of n = 27 capsules), and 35 egg capsules (out of n = 35 capsules) contained embryos, respectively. The number of capsules classified per stage are listed in Figure 9 a and b, Table 9 a and b.

Trochophores developed by 27 d post-oviposition and by 87 d of the acclimation. At 41 d post-oviposition and 101 d of the acclimation, veligers were present. After 53 d post-oviposition and 113 d of the acclimation, hatchlings emerged from capsules. MHW treatment egg capsules were laid by 101 d (June 21, 2021) of the temperature acclimation. Trochophores developed by 17 d post-oviposition and by 118 d of the acclimation. At 22 d post-oviposition and 123 d of the acclimation, veligers were present. After 43 d post-oviposition and 144 d of the acclimation, hatchlings emerged from capsules. Images of representative early stage individuals for each treatment are displayed in Figure 10.

Mortality and abnormality scoring of early stage individuals

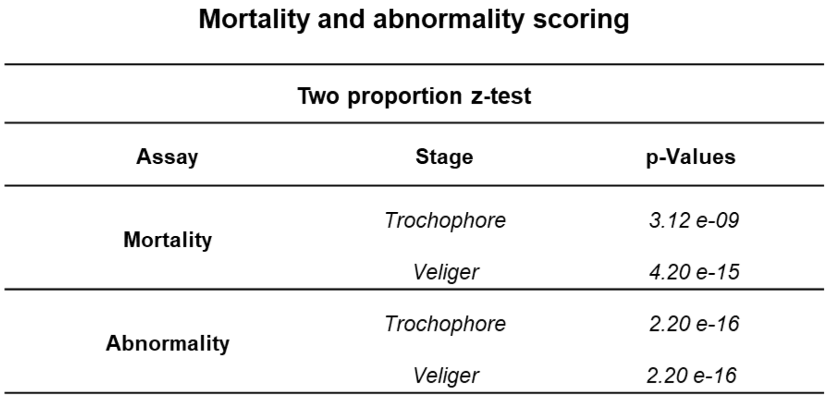
In order to track how MHW exposure might affect thermal tolerance in early stage whelks, I compared mortality and degrees of developmental abnormality in early stages in the Non-MHW and MHW treatments. There was, however, an imbalance in the dataset created by the loss of viable embryos in the capsules from the MHW treatment. Adult whelks from the MHW treatment laid capsules of lower structural quality, size and amount and MHW capsules could not be properly sampled for acute thermal stress. Contrastingly, larvae and egg capsules from the Non-MHW treatment reached distinct stages and showed normal body condition (Clare et al., 2022; Vendetti, 2020; Wilson, 2017) (Figure 11). Thus, the assessment of the MHW and Non-MHW progeny was as follows: The mortality and developmental abnormality of Non-MHW larvae was scored from larvae that were collected to be used as controls for acute thermal stress trials, and early stages from the MHW treatment were scored for mortality and abnormality without undergoing a thermal stress trial. In the latter case, the long period over which development occurred in the 20°C



Thermal Stress Assessment	Treatment	Stage *n = capsules*	Percentage (%)
Mortality	*Non-MHW*	*Trochophore* *n = 2*	*1.0*
		Veliger *n = 2*	*14.0*
	MHW	*Trochophore* *n = 24*	*41.3*
		Veliger *n = 23*	*45.0*
Abnormality	*Non-MHW*	*Trochophore* *n = 2*	*7.0*
		Veliger *n = 2*	*9.0*
	MHW	*Trochophore* *n = 24*	*92.1*
		Veliger *n = 23*	*97.4*

Figure 11. Average percent mortality and abnormality for larvae from both treatments. Individuals (n = 50) were scored per capsule to determine the average percentage of mortality and abnormality per treatment. For trochophores, n = 2 non-MHW treatment capsules n = 24 and MHW treatment capsules. For veligers, n = 2 non-MHW treatment capsules and n = 23 MHW treatment capsules were analyzed. The same subset of capsules in each treatment were scored for both mortality and abnormality.

acclimation tanks had a significantly negative impact on the success of those early stage individuals (Table 10).



Mortality and abnormality scoring

Two proportion z-test		
Assay	**Stage**	**p-Values**
Mortality	*Trochophore*	*3.12 e-09*
	Veliger	*4.20 e-15*
Abnormality	*Trochophore*	*2.20 e-16*
	Veliger	*2.20 e-16*

Table 10. Two proportion z-test for mortality and abnormality scoring. A two proportion z-test was used to test the significance of differences between observed mortality and abnormality percentages between non-MHW treatments and MHW treatments for two stages of Kellet's whelk larvae: trochophores and veligers. All of the p-values from significance testing yielded values less than alpha = 0.05. Thereby the differences found between mortality and abnormality percentages for each stage and treatment in this study were significant.

Specifically, for the Non-MHW treatment, 14% and 9% of trochophores (n = 2 capsules) experienced mortality and abnormality, respectively. MHW treatment trochophores and veligers experienced similar levels of mortality and abnormality after the acclimation period. For MHW treatment, 45.04% and 97.4% of trochophores (n = 24 capsules) experienced mortality and abnormality, respectively. For the Non-MHW treatment, 1% and 7% of veligers (n = 2 capsules) experienced mortality and abnormality, respectively. For the MHW treatment, veligers (n = 23 capsules) experienced 41.27% and 92.1% mortality and abnormality, respectively (Figure 11).

DISCUSSION

The goal of this part of my dissertation was to assess impacts of a long-term MHW acclimation on the adult *K. kelletii* behavior of capsule laying, and on the condition of early stages when progeny develop under the same conditions under which the adults laid capsules.

The most important findings of the study were: (1) the number of early stage individuals per capsule was influenced by temperatures during mating and rearing, with higher temperatures producing significantly lower numbers of offspring per capsule, (2) the rate of development under MHW temperatures (20˚C) was faster than the rate of development observed for embryos of the Non-MHW treatment (15˚C), (3) early stage individuals that developed under MHW conditions showed arrested development within capsules, and (4) greater levels of mortality and abnormality was observed when embryos developed under MHW conditions, of such a great amount, that it was not possible to use the MHW individuals in one of the assays, the acute thermal stress trials.

Notably, many of the general observations of *K. kelletii* adult reproduction and early stage development reported here are consistent with those documented elsewhere (MacGinitie, 1949; Morris, 1980; K. N. Rodriguez, 2017; Romero, Gallardo, & Bellolio, 2004; Rosenthal, 1970; Vendetti, 2020; Wilson, 2017; D Zacherl et al., 2003). For example, the length of the Non-MHW treatment early stage development period and the condition of capsules in the Non-MHW treatment observed in this study are consistent with past studies on *K. kelletii* life history. Below, I discuss the findings of this study and conclude by contextualizing experimental results in the context of MHW events in the Santa Barbara Channel.

Observations about capsules

One of the major observations of this study was that capsule traits varied between those laid in the MHW treatment (20˚C) as compared to the Non-MHW treatment (15˚C). Observations on oviposition in the Non-MHW treatment of this study align with what has been observed in similar conditions (15˚C) for whelks. Adult whelks in the Non-MHW treatment in this study began oviposition in May, similar to the timeframe when whelks in the Santa Barbara Channel have been observed to begin oviposition. *K. kelletii* oviposition has been determined to occur earlier for whelks in southern California (April to May) (CDFW, 2020; Cumberland, 1995) and occurs later for whelks in central California (May to July) (CDFW, 2020). These observations have also been confirmed by a recent study (Vendetti, 2020) where oviposition in Santa Barbara collected whelks was observed from July-August.

Many studies have examined the influence of environmental stress on fecundity and egg laying (Gage, 1995; Marshall, Bolton, & Keough, 2003; Olofsson, Ripa, & Jonzen, 2009). Bet hedging theory, with respect to reproduction under climate change scenarios has been recently examined in organisms across a wide range of aquatic and terrestrial study systems. To test hypotheses on physiological costs of egg capsule quality of capsules laid by *K. kelletii* adults under a long-term MHW acclimation, this study examined the size and quality of egg capsules. The condition, average number of early stage individuals/capsule, and capsule size served as metrics and/or proxies to estimate differential metabolic costs of the adult whelks producing capsules at different temperatures.

There were observable differences in capsule shape when comparing capsule condition between the two treatments. Specifically, the Non-MHW treatment capsules were lingulate and smooth, as capsules have been typically described under ambient conditions in previous studies (Vendetti, 2020), whereas capsules from the MHW treatment were mishappen, thin, and easily ruptured during the sampling process.

K. kelletii egg capsule height ranges between 6-9 mm (CDFW, 2020; Vendetti, 2020) under ambient conditions. The average Non-MHW treatment capsule height recorded in this study (9.3 mm) was at the higher range of height typically observed for *K. kelletii* egg capsules. The average MHW treatment capsule height recorded in this study (6.7 mm) was at the lower range of height typically observed for *K. kelletii* egg capsules.

Under ambient conditions, it is known that early stage size is inversely related to egg capsule size, with smaller capsules containing larger larvae for *K. kelletii* (CDFW, 2020; Vendetti, 2020). It is also known that the height of egg capsule, and number of egg capsules laid is directly correlated to the size of the egg laying female, with larger females laying more capsules of greater height and smaller sized larvae under ambient conditions for *K. kelletii* (CDFW, 2020; Vendetti, 2020). Past metabolic studies on marine invertebrates have shown that larger early stage size does not always correlate with better performance (Marshall et al., 2003). Aside from the findings reported here, other studies have not yet examined the relationship between capsule size, early stage individuals/capsule number and early stage body condition as a result of result of being laid in capsules that developed under MHW acclimation temperatures. Studies have also not yet examined the correlation between larger early stage size to better performance in *K. kelletii*. More observations on reproductive strategies are essential for building a population level understanding of important shellfish species like *K. kelletii* under climate change scenarios.

There was also a difference in the number of early stages/capsule with 1,591 individuals/capsule and 1,226 individuals/capsule (n = 12 capsules per treatment) observed for Non-MHW and MHW treatments, respectively. The average number of early stage individuals/capsule in the Non-MHW treatment was 23% greater than the average number of early stage individuals/capsule observed in the MHW treatment. Past studies report that *K. kelletii* egg capsules contain 400-1200 larvae per capsule (CDFW, 2020; Vendetti, 2020).

This study also found that the average early stage individuals/capsule recorded for both the Non-MHW and MHW treatments was greater than what has been reported in previous studies. Overall, the findings in this study suggest that adult *K. kelletii* under a long-term MHW acclimation produce smaller capsules with a lower average number of progeny/capsule.

A diverse range of reproductive strategies occur in marine animals that place embryos in external vessels for development (gelatinous masses, tough capsules, pelagic masses) (Miner et al., 2010). As marine organisms face greater adaptation pressures in oncoming ocean warming, it is essential to further understand how parental reproductive strategies affect the success of progeny. Future studies that aim to understand the impact of thermal stress on bet-hedging strategies in *K. kelletii* should not only analyze capsule height and number of early stage individuals/capsule, but should also examine capsule width and early stage body size under thermal stress. A greater understanding of adult whelk metabolic capacity under ambient and MHW conditions (protein and lipid analysis) in future studies would help describe the range of capsule quality whelks can produce under thermal stress.

Rate of development

This comparative study found that the rate of development of early stages varied as a function of the adult thermal history via their acclimation temperatures. Specifically, MHW treatment individuals had a faster overall development period as compared to non- MHW treatment individuals. Specifically, the MHW treatment larvae developed over a period of 43 days as compared to 53 days for the Non-MHW treatment. The faster rate of development at 20˚C versus 15˚C is not unexpected since temperature increases biological rate processes. In addition, in nature, these data suggest that progeny from *K. kelletii* that reproduce during MHWs may hatch sooner than expected in comparison to non-MHW years.

Another observation was that the rate development of early stage progeny from whelks I used from the Santa Barbara Channel differed from those that have been reported in the literature. Studies have reported 30-34 d (at 14.5-17.5 ºC) as the time needed for early stage *K. kelletii* to progress through development to hatching (CDFW, 2020; Rosenthal, 1970; D. Zacherl, S. D. Gaines, & S. I. Lonhart, 2003). However, the longer development timeframe of Non-MHW treatment reported in my study aligns with the longer period before excapsulation found in (Vendetti, 2020) of 39-55 d (at 13-16 ºC). Overall, populations of *K. kelletii* may vary in their development traits via local adaptation (Hofmann et al., 2014; E. Sanford & Worth, 2010). Overall, differences from reports in the literature on developmental timing may be due to population differences, and the fact that past observations on developmental timing were made decades ago, with enough time to have had local adaption alter the timing of *K. kelletii* reproduction and early stage development in the warming Santa Barbara Channel.

Progression of development

Larvae in the Non-MHW treatment reached the trochophore, veliger, and hatchling stages 24, 21, and 53 d post-oviposition. Larvae in the MHW treatment reached the trochophore, veliger, and hatchling stages 17, 22, and 43 d post-oviposition. While oviposition occurred later in the MHW treatment, larvae reached each main developmental stage about 10-19 d earlier than the Non-MHW treatment. The development timeframes of both treatments in this acclimation experiment have not been previously reported in other studies.

This finding of an increased rate of early stage development under warmer temperatures in this study is supported by past observations in marine invertebrates (Kuo & Sanford, 2009). For example, a recent study on the Atlantic purple sea urchin (*A. punctulata*) observed faster egg fertilization and early development cleavage rates under MHW conditions in comparison to ambient conditions (Bojorquez & Feehan, 2021). Environmental conditions (e.g., temperature, predation) that cause hatchling plasticity can have population-level consequences for a species. As an example, hatching early for some Treefrog species likely comes at a cost. Treefrog juveniles that hatch early enter their aquatic environment at a smaller size and are more susceptible to predation (Kuo & Sanford, 2009; Miner et al., 2010; Warkentin, 1995). Future experimentation is needed to address how accelerated or delayed timing of development and hatching can impact juvenile *K. kelletii*.

Effects of temperature on the progression of normal development

Overall, early stage individuals in the MHW treatment showed stalled or arrested development in comparison to the Non-MHW treatment. For the Non-MHW treatment, a majority of egg capsules sampled contained larvae that reached distinct stages at a predicted time after capsule laying. Specifically, for the individuals within the Non-MHW treatment, progeny within capsules reached embryo, trochophore, and veliger, stages by 22, 27, and 42 d post-oviposition, respectively. For the MHW treatment, stalled (undeveloped) larvae of all stages were present in all capsules, where each capsule contained a greater number of stalled embryos for each sampling date than in the Non-MHW treatment (Figure 9 a and b, Table 9 a and b).

A previous study on early stage *K. kelletii* observed that under ambient conditions (13-16˚C), approximately 2.5% - 38% of individuals in capsules did not match the developmental stage of the majority of individuals for each major period of development (Vendetti, 2020). This aligns with past observations on gastropod and buccinid development where egg capsules usually contain a mixture of developed and undeveloped individuals (typically embryos) where individuals may derive nourishment from their yolk, intracapsular albumen (capsule jelly), or by ingesting nurse eggs or siblings within their capsule (Vendetti, 2020). For example, in both *Crepidula dilatata* and *Nucella crassilabrum* nutritive embryos constitute over 90% of the individuals deposited in each capsule (Gonzalez & Gallardo, 1999).

However, past observations confirm that *K. kelletii* do not consume undeveloped eggs (siblings or nurse eggs), but likely use internal egg stores and capsule jelly as a food source while developing inside capsules (Vendetti, 2020). In other words, undeveloped individuals in *K. kelletii* capsules are not intended to serve as food sources, but are in fact stalled individuals. Thus, the larger number of undeveloped individuals in the MHW treatment capsules can likely be attributed to the effects of the MHW acclimation on increased arrested development.

Mortality and abnormality scoring of early stage individuals

Results of this study highlighted differences in mortality and developmental abnormality when comparing early stages from the Non-MHW and MHW treatments. These findings will be discussed in the context of mortality and abnormality scoring of early stage individuals that were laid in capsules that developed under MHW acclimation temperatures.

Whelks from the MHW treatment laid capsules that could not be properly sampled for acute thermal stress trials due to the fact that they were small, misshapen and often leaking capsule jelly. Instead, larvae from the MHW treatment were scored using the same protocol that was used to score the Non-MHW treatment larvae after acute thermal tolerance trials. Binary scoring of developmental abnormality and mortality showed that larvae in capsules that were laid under MHW conditions experienced greater numbers of mortality and abnormality than individuals in the Non-MHW treatment.

For the MHW treatment, the percentages of average mortality and average abnormality were similar between stages (trochophores and veligers), where trochophores experienced only 3.77% more average mortality and 5.3% more average abnormality than veligers. Overall, MHW treatment larvae experienced a greater number of abnormality than mortality (Figure 11). In other words, although more than half of the larvae survived the long-term acclimation (Figure 11), 92.1-97.4% of individuals experienced developmental abnormality. Specifically, average abnormality is 50.83-52.36% greater than the average mortality experiences by both trochophores and veligers (Figure 11).

These results imply that all progeny that developed in the MHW treatment experienced the same number of mortality and abnormality regardless of stage. Unlike acute thermal tolerance results, where later stages are more vulnerable to acute stress, this study finds that when progeny are laid and develop under prolonged MHW conditions, larval stage does not influence thermal tolerance.

Conclusion and summary

Overall, this study demonstrated that MHW temperatures have impacts on *K. kelletii* early life history by (1) accelerating the rate of early stage development within egg capsules, but (2) also reducing the quality and number of progeny in an egg capsule. These data suggest that over prolonged time, more MHWs in the coming years could alter the harvest and population of *K. kelletii* in situ. Since source populations of adults used in this experiment had recently experienced a MHW in the Santa Barbara Channel (the Blob and NEP 2019), it is likely that the regularity of MHWs has influenced the thermotolerance and development rates of early stage *K. kelletii* via local adaptation (Jacox et al., 2022; Reed et al., 2016).

Chapter 4: Larval thermotolerance of *K. kelletii* under a short-term MHW simulation

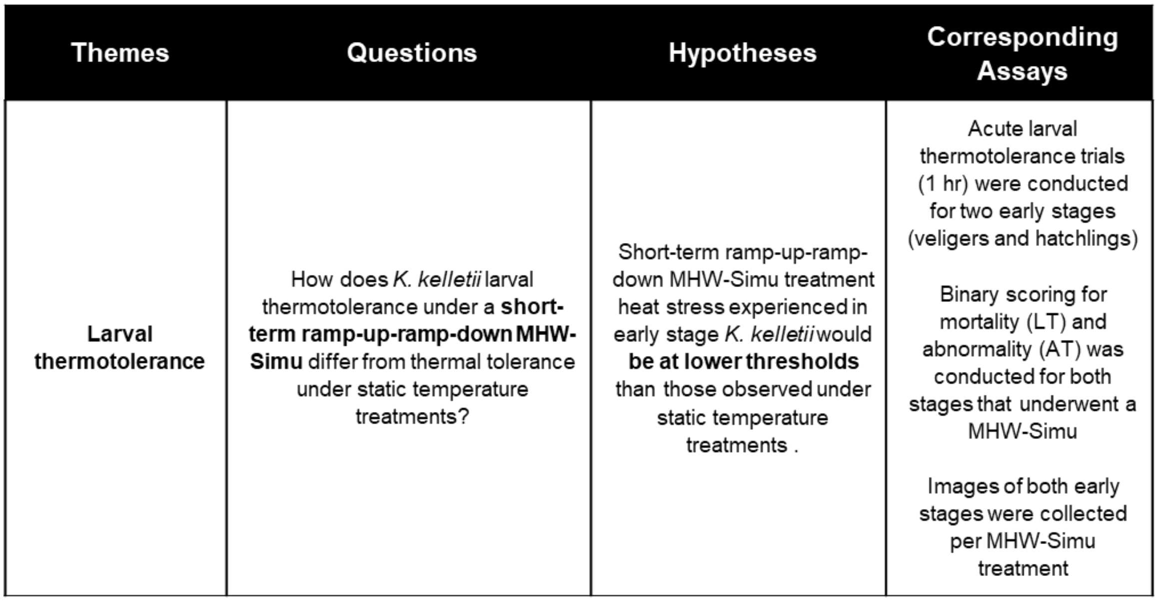
INTRODUCTION

Background

As described in Chapter 1, MHWs can vary in duration from a minimum of 5 days (d) to prolonged periods of time (e.g., weeks to months) such as was observed with the Blob in 2014-2016. In the past seven years, eco-physiology studies have investigated the impact on long-term MHW stress on subsequent generations of marine invertebrates in a larval biology context (Clare et al., 2022; Leach et al., 2021; Minuti, Byrne, Campbell, Hemraj, & Russell, 2022)(Chamorro et al., 2023; Unpub.). While my work in Chapter 3 explored the impacts of a prolonged MHW event on *K. kelletii* larval development, this chapter addresses the impact of shorter MHWs, a pattern that has routinely been documented in the Santa Barbara Channel since 2018 (Chan et al., 2023; In Preparation.)

The rationale for this study was that MHW experiment treatments using static temperatures do not fully capture the full range of the dynamic temperature conditions faced by benthic marine organisms in nature during MHWs. Several studies on marine invertebrates have shown improved organism performance under fluctuating temperature treatments that more accurately represent the abiotic habitat of key species (Arlauskas, Derobert, & Collin, 2022; Pilditch & Grant, 1999; Rodgers, Cocherell, Nguyen, Todgham, & Fangue, 2018; E. Sanford, 1999). Overall, in order to support management and predicting the biological consequences of MHWs, it is essential to design experiments that assess realistic periods of thermal stress that align with current ecological conditions.

To do this, I conducted a **MHW simulation (MHW-Simu) of a short MHW cycle of 14 days (d) where temperatures were ramped up to MHW levels and then back down to ambient conditions in order to mimic ocean temperatures of one MHW event that might be encountered during larval development of *K. kelletii* in-situ.** In this experiment, I mimicked the manner in which MHWs occur in the Santa Barbara Channel and then maintained an extreme temperature exposure for 7 d; thus, the simulated MHW event by definition lasted 7 d, a common time frame for MHWs in the Santa Barbara Channel (G. E. Hofmann, personal communication). In addition, the temperatures used here were from benthic loggers and thus the experiment examined the effect of thermal stress on the benthos, or a bottom MHW (D. J. Amaya, Jacox, M. G., Alexander, M. A., Scott, J. D., Deser, C., Capotondi, A., & Phillips, A. S., 2023). This study conducted a qualitative and quantitative examination of early stage survivorship, body condition, and tolerance of acute thermal stress in response to the MHW-Simu. Data presented are from assessments on two early stages: veligers and hatchlings. The goals of this MHW-Simu study on the whelk larvae answers the following question: How does larval development and thermotolerance under a short-term ramp-up-ramp-down MHW-Simu differ from thermal tolerance under static temperature treatments? I addressed this question by testing the following hypothesis that heat stress



Themes	Questions	Hypotheses	Corresponding Assays
Larval thermotolerance	How does *K. kelletii* larval thermotolerance under a **short-term ramp-up-ramp-down MHW-Simu** differ from thermal tolerance under static temperature treatments?	Short-term ramp-up-ramp-down MHW-Simu treatment heat stress experienced in early stage *K. kelletii* would **be at lower thresholds** than those observed under static temperature treatments .	Acute larval thermotolerance trials (1 hr) were conducted for two early stages (veligers and hatchlings) Binary scoring for mortality (LT) and abnormality (AT) was conducted for both stages that underwent a MHW-Simu Images of both early stages were collected per MHW-Simu treatment

Table 11. Hypothesis and assays for the study described in Chapter 4 of my dissertation. The goals of the study in this chapter were to answer the research question listed above via the listed hypothesis. Corresponding assays for the hypothesis and research question are outlined in this table.

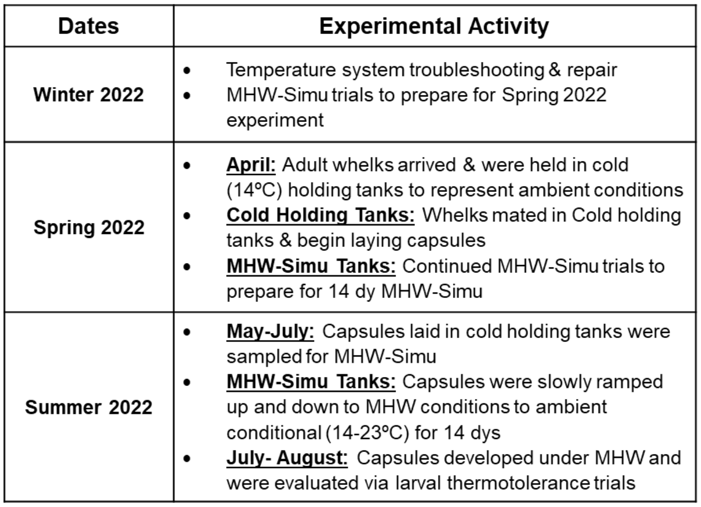
under a short-term ramp-up-ramp-down MHW-Simu treatment would be at lower thresholds than those observed in past static temperature treatments (figure 11).

This study did not involve any formal hypothesis testing. While I only report observed results in this chapter, the research in this chapter lays the methodological groundwork to be able to test additional hypotheses on this question in future studies. With the support of future experimentation, this study also establishes the foundation to use environmental data to explore impacts of fluctuating short-term MHWs for larval whelks.

MATERIALS & METHODS

Experimental rationale

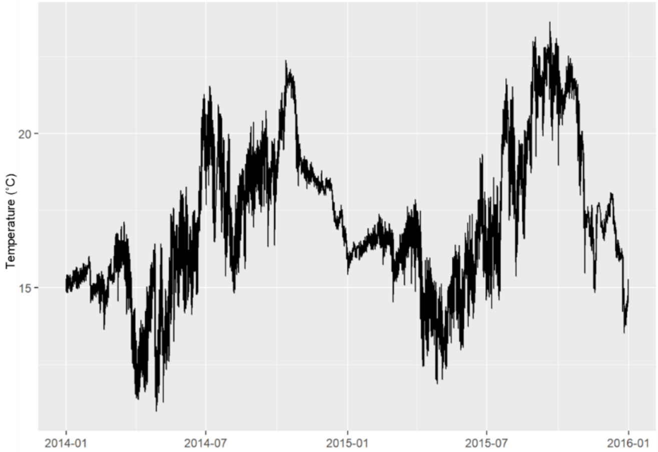
As described in Chapter 1, the research in this chapter was intended to gain insight on best practices for conducting each phase of MHW experimentation on larval *K. kelletii*. The methodology for the experimental phases that make up this work were previously established in the form of standalone experiments described in Chapters 2 and 3 (Table 12).

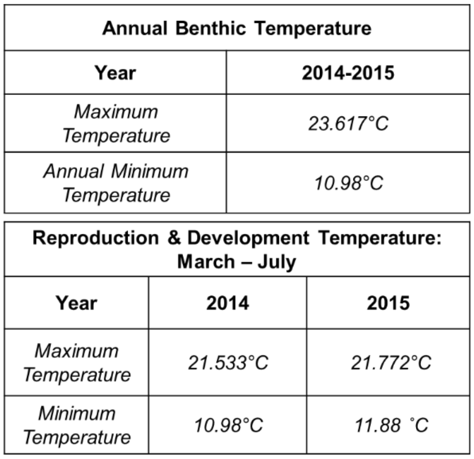


Dates	Experimental Activity
Winter 2022	- Temperature system troubleshooting & repair - MHW-Simu trials to prepare for Spring 2022 experiment
Spring 2022	- **April:** Adult whelks arrived & were held in cold (14ºC) holding tanks to represent ambient conditions - **Cold Holding Tanks:** Whelks mated in Cold holding tanks & begin laying capsules - **MHW-Simu Tanks:** Continued MHW-Simu trials to prepare for 14 dy MHW-Simu
Summer 2022	- **May-July:** Capsules laid in cold holding tanks were sampled for MHW-Simu - **MHW-Simu Tanks:** Capsules were slowly ramped up and down to MHW conditions to ambient conditional (14-23ºC) for 14 dys - **July- August:** Capsules developed under MHW and were evaluated via larval thermotolerance trials

Table 12. Experimental design and timeline. Iterative timeline of experimental activies for the MHW-Simu from Winter-Summer 2022.

Environmental temperature data





Annual Benthic Temperature	
Year	**2014-2015**
Maximum Temperature	*23.617°C*
Annual Minimum Temperature	*10.98°C*

Reproduction & Development Temperature: March – July		
Year	**2014**	**2015**
Maximum Temperature	*21.533°C*	*21.772°C*
Minimum Temperature	*10.98°C*	*11.88 ˚C*

Figure 12. Benthic temperature for (a) Annual periods and (b) *K. kelletii* reproduction and development periods between 2014-2015. Annual minimum and maximum benthic temperatures from the SBC-LTER benthic study sites: Carpinteria Reef, CA, USA during the whelk reproductive and larval development period March-July for 2014 and 2015.

Temperature data used create the MHW-Simu are from environmental data collected at the whelk collection site, Carpinteria Reef, as a part of ongoing research activities of the SBC-LTER (SBC-LTER). Temperature data were collected via Onset HOBO TidbiT v2 temperature loggers deployed on the kelp forest benthos where adult *K. kelletii* were collected, and where egg masses are laid by the adults. Two data loggers at each site were programmed 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 (SBC-LTER). The daily mean temperature was calculated using daily data from 2000 to 2021 for Carpinteria Reef and from 2014 to 2015 for Naples Reef. The maximum temperatures and minimum temperatures, respectively for that period were: 23.617 ºC and 10.98 ºC (Figure 12). This environmental data analysis was used to set the ramp-up-ramp-down temperatures for the MHW-Simu.

Specimens collection and husbandry

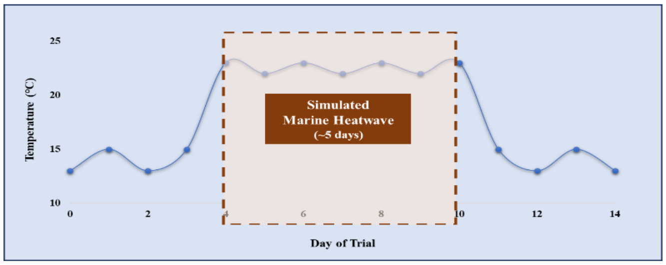


Figure 13. MHW-Simu goal temperatures. A conceptual diagram for the ramping up and down of temperatures for the MHW-Simu (14ºC to 23ºC to 14ºC).

Adult Kellet's whelks were hand collected in Spring 2022 (April 5, 2022) via SCUBA from benthic kelp forest reef sites in the Santa Barbara Channel region at a depth of 7.9 m from Carpinteria Reef, CA, USA. Whelks were collected under California Scientific Collection permits and transported to the UCSB Marine Science Institute as described in Chapters 2 and 3.

Adult whelks were held in three separate cold "holding" tanks held at 14 ºC (8 whelks per tank). Adult whelks were housed for 117 d (April 27- August 22, 2022) in the cold holding tanks as adults mated. Whelks were monitored and maintained in REEF system tanks as described in Chapters 2 and 3.

Developmental timeline

Capsules were laid in the cold holding tanks on 14 d period of the experiment (May 11, 2022). Subsets of capsules began to reach the veliger and hatchling stage on 41 d and 62 d (June 7, 2022) and 62 (June 28, 2022) of the experiment for each respective stage. The larvae and capsules that were laid in the Cold tanks were used for the MHW Simu.

MHW-Simu

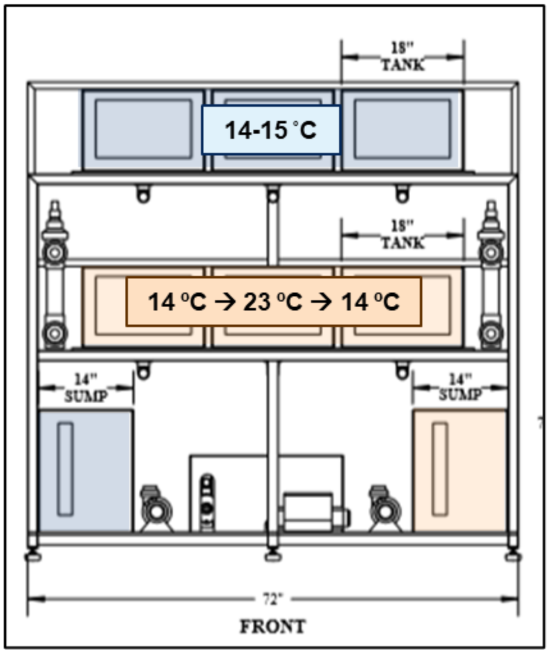
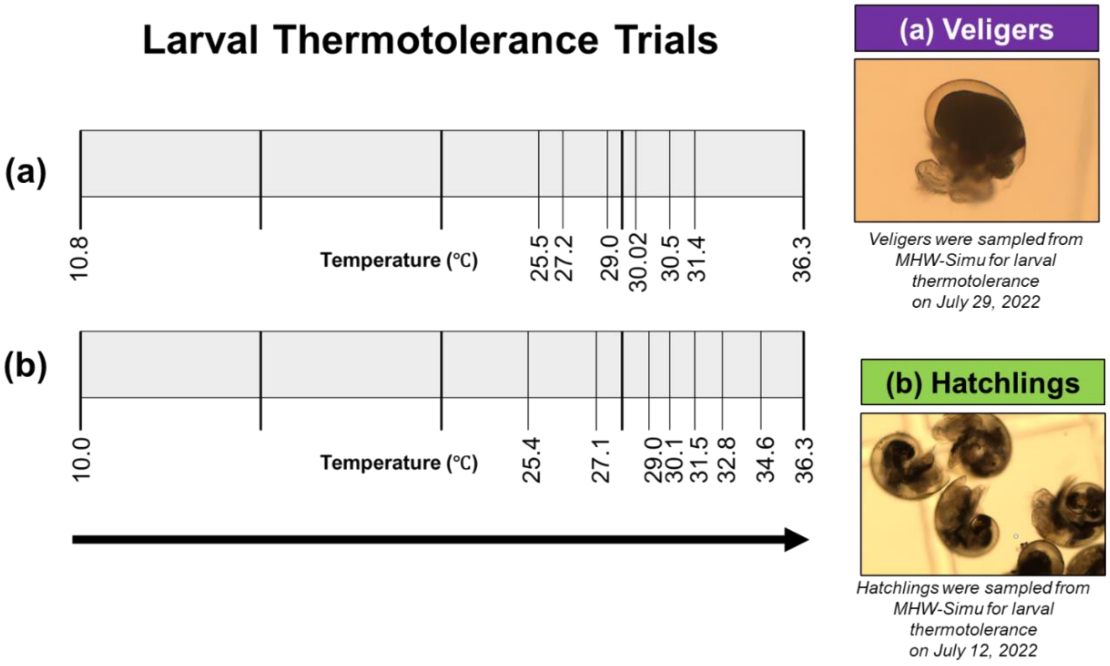


Figure 14. Temperature treatments for MHW-Simu in temperature manipulation system. The diagram above shows treatment temperatures used to rear larvae under 14-15 ºC and then for the following MHW-Simu (14ºC, to 23ºC back to 14ºC) whelks prior to evaluating their progeny via thermotolerance

As capsules were laid by adults that mated in cold holding tanks (14 ºC), capsules that were sampled from each stage endured 14 d ramp-up-ramp-down MHW Simu period (Figure 13). Temperatures were manually ramped up and down via the same temperature manipulation system used in Chapter 3 (Figure 14). Temperatures were gradually set to ramp up from 14 ºC to 23 ºC and back down to 14 ºC over the course of 14 d period. Once temperatures were set to 23 ºC, they were set at 23 ºC for a 7 d MHW simulated period before being set to ramp back down to 14 ºC. For the veliger MHW-Simu trial, temperature data were collected via Onset HOBO TidbiT v2 temperature loggers in experimental tanks. Temperature loggers in each tank were programmed to record temperatures every fifteen minutes. For the hatchling MHW-Simu trial, temperature data were recorded manually via a laser thermometer gun twice daily. Larvae were sampled from cold holding tanks, randomized, and held in mesh bins in MHW-Simu for each 14 d period (according to sampling described in Chapters 2-3). The MHW-Simu trials were staged from 79 - 92 d (July 15-July 28,2022) and 62 - 75 d (June 28 – July 11, 2022) of the experiment for veligers and hatchlings, respectively.

Larval thermotolerance trials and scoring



Veligers were sampled from MHW-Simu for larval thermotolerance on July 29, 2022

Hatchlings were sampled from MHW-Simu for larval thermotolerance on July 12, 2022

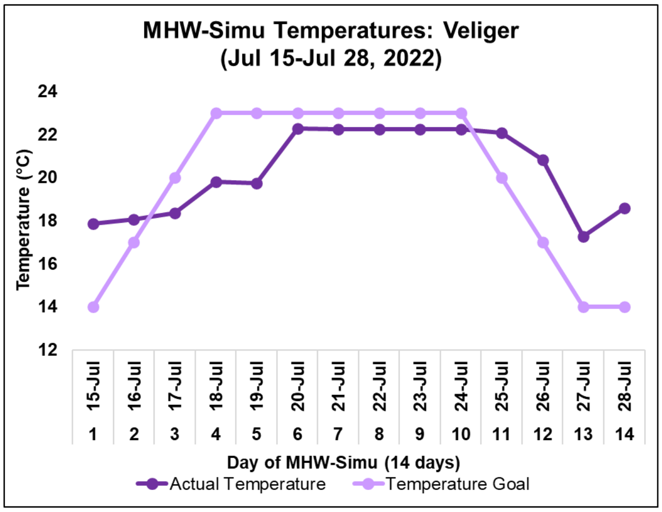
Figure 15. Larval thermotolerance trial acute treatment temperatures. This diagram shows actual thermotolerance temperatures used for larvae that had experienced the MHW-Simu trials. Thermotolerance trials occurred on 93 d and 76 d for veligers and hatchlings, respectively. The photographs display (a) veligers and (b) hatchlings that were sampled from MHW-Simu trials and were used in thermotolerance trials.

Once MHW-Simu period was over for veligers and hatchlings, larvae were tested in acute thermal tolerance trials and scoring as described in Chapters 2. Acute thermal stress trials occurred on 93 d and 76 d (July 29, 2022 and July 12, 2022) and for veligers and hatchlings, respectively. Since whelks lay capsules in staggered order, I ran a trial on capsules that appeared to be nearing the hatchling stage first. Following running hatchlings through the MHW-Simu and thermotolerance trials, I conducted a MHW-Simu and thermotolerance trial on the veligers. Due to experimental constraints, a control subset of larvae (a subset that did not experience a MHW-Simu) were not run through a larval thermotolerance trial. The larval thermotolerance results from this experiment were intended to be compared to the LT and AT findings of in Chapter 2 and 3 (Clare et al., 2022). Findings from these thermotolerance trials will contribute to help develop methodology for future MHW-Simu manipulations on *K. kelletii*.

Hatchlings were sampled for acute thermal stress trials by transferring larvae from mesh bins into larger sampling bins, and finally into large glass beakers to achieve desired larval concentrations as described in Chapters 2-3. Encapsulated veligers were removed from the MHW-Simu trial and randomized into vials for acute thermal tolerance trials using methods described in Chapters 2-3. Larvae of both stages were exposed to nine temperatures that ranged from ~10 to ~ 37°C (Figure 15). Larvae were held in control temperature treatment vials at ~10 – 10.8°C in a cold room at the start of each 1 h trial. The nine treatment temperatures for hatchling thermotolerance trials were: 10, 24.5, 27.1, 29, 30.1, 31.5, 32.8, 34.6, and 36.3°C. The nine treatment temperatures for veliger thermotolerance trials were: 10.8, 25.5, 27.2, 29, 30.2, 30.5, 31.4, and 36.3°C. Thereafter, early stage individuals were photographed (n = 50 individuals per capsule) under bright field DIC illumination at 10× on a compound microscope (Olympus BX50) with attached digital camera (Motic Images) using Motic Images Plus (version 3.0).

RESULTS

The overall observations with respect to the MHW-Simu I executed were that (1) the actual temperatures for each separate MHW-Simu trial reached the same average maximum temperature of 22.1-22.3 ºC and (2) ranged from being 0.32 ºC - 0.49 ºC warmer than the MHW-Simu goal temperatures over the 14 d overall. The main larval thermotolerance findings of this study were that larvae that underwent a 14 d MHW-Simu period and acute thermotolerance trials (1) experienced varied amounts of survivorship, but (2) consistently experienced large amounts of abnormality across all temperature treatments.



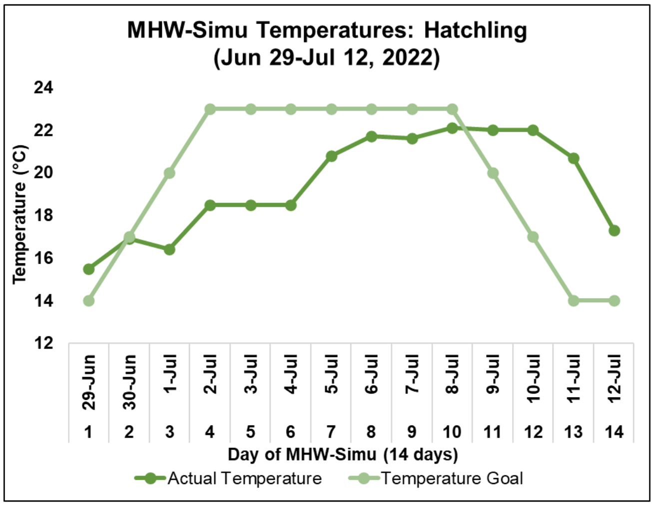
Veliger			
Day	Date	Temperature Goal (°C)	Actual Temperature (°C)
1	15-Jul	*14*	*17.85031*
2	16-Jul	*17*	*18.06908*
3	17-Jul	*20*	*18.3644*
4	18-Jul	*23*	*19.79678*
5	19-Jul	*23*	*19.73718*
6	20-Jul	*23*	*22.2697*
7	21-Jul	*23*	*22.25173*
8	22-Jul	*23*	*22.25373*
9	23-Jul	*23*	*22.25276*
10	24-Jul	*23*	*22.24676*
11	25-Jul	*20*	*22.0895*
12	26-Jul	*17*	*20.82868*
13	27-Jul	*14*	*17.27657*
14	28-Jul	*14*	*18.59905*

Figure 16. MHW-Simu trial goal and actual temperatures for veligers. This figure displays the temperature data for the veliger MHW-Simu trial (July 15 – July 28, 2022). Temperature data were collected via temperature loggers in experimental tanks that were programmed to record temperatures every 15 minutes. The table and graph values represent daily average temperatures during the veliger MHW-Simu trial.

MHW-Simu trials for veligers and hatchlings

The maximum average temperature reached by the veliger MHW-Simu trial was 22.3 ºC on the 6 d (July 20, 2022) of the 14 d ramp-up-ramp-down period. The minimum average temperature reached was 17 ºC on 13 d (July 27, 2022) of the 14 d ramp-up-ramp-down period (Figure 16). For 4 -10 d, which represented the peak MHW-Simu days (July 18 - July 24, 2022), the actual temperatures were 1.46 ºC warmer than the temperature goal on average. On average, the actual temperatures were 0.49 ºC warmer than the temperature goal for all 14 d period of simulation overall.

The maximum average temperature reached by the hatchling MHW-Simu trial was 22.1 ºC on 10 d (July 8, 2022) of the 14 d ramp-up-ramp-down period (Figure 17). The minimum average temperature reached was 15.5 ºC on the 1 d (June 29, 2022) of the 14 d



Hatchling			
Day	Date	Temperature Goal (°C)	Actual Temperature (°C)
1	29-Jun	*14*	*15.5*
2	30-Jun	*17*	*16.9*
3	1-Jul	*20*	*16.4*
4	2-Jul	*23*	*18.5*
5	3-Jul	*23*	*18.5*
6	4-Jul	*23*	*18.5*
7	5-Jul	*23*	*20.8*
8	6-Jul	*23*	*21.7*
9	7-Jul	*23*	*21.6*
10	8-Jul	*23*	*22.1*
11	9-Jul	*20*	*22*
12	10-Jul	*17*	*22*
13	11-Jul	*14*	*20.7*
14	12-Jul	*14*	*17.3*

Figure 17. MHW-Simu trial goal and actual temperatures for hatchlings. This figure displays the temperature data for the hatchling MHW-Simu trial (June 29 – July 12, 2022). For the hatchling MHW-Simu trial, temperature data were recorded manually via a laser thermometer gun twice daily. These data are not data averages.

ramp-up-ramp-down period. For 4-10 d, which represented the peak MHW-Simu days (July 2 - July 8, 2022), the actual temperatures were 2.76 ºC cooler than the temperature goal on average. On average, the actual temperatures were 0.32 ºC cooler than the temperature goal for all 14 d period of simulation overall.

Larval thermotolerance trials and scoring

Veliger		
Temperature (°C)	Survivorship (%)	Normality (%)
10.8	*36*	*0*
25.5	*34*	*0*
27.2	*100*	*0*
29	*98*	*0*
30.2	*0*	*0*
30.5	*100*	*0*
31.4	*86*	*0*
36.3	*0*	*0*

Hatchling		
Temperature (°C)	Survivorship (%)	Normality (%)
10	*97*	*1*
24.5	*92*	*6*
27.1	*48*	*10*
29	*36*	*2*
30.1	*78*	*18*
31.5	*98*	*0*
32.8	*66*	*0*
34.6	*0*	*0*
36.3	*100*	*0*

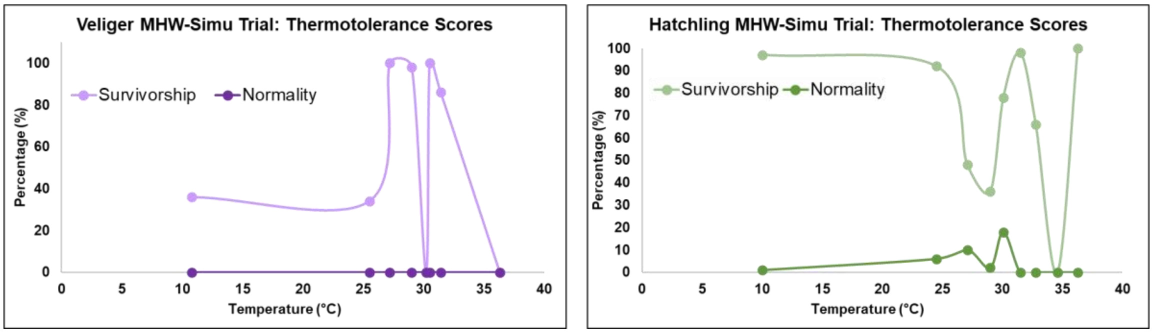
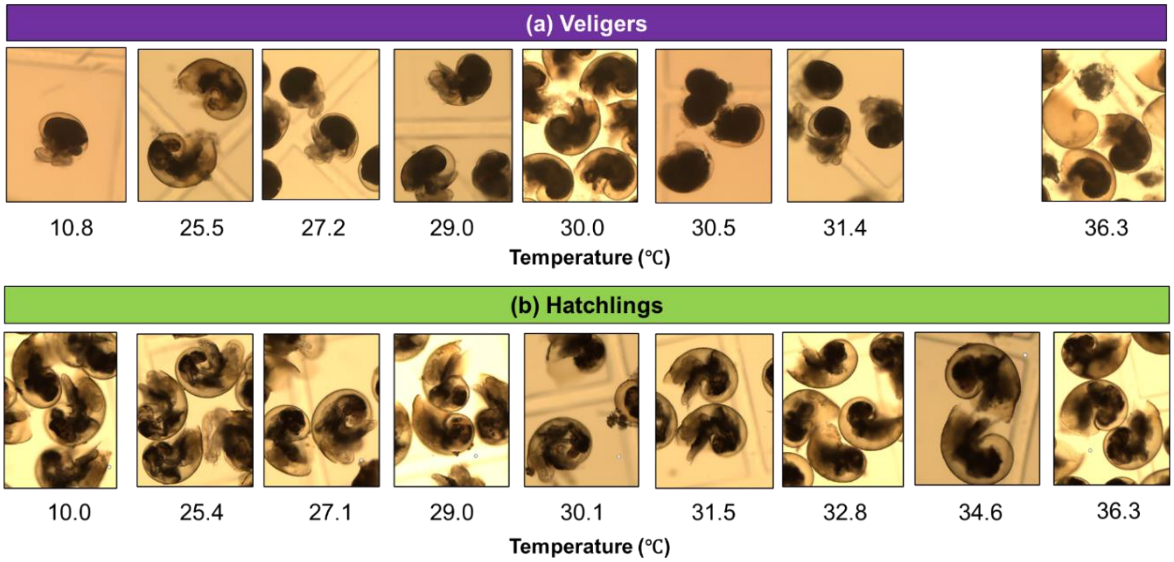


Figure 18. Larval thermotolerance trial results for veligers and hatchlings. This figure shows the scoring results from the larval thermotolerance trials for both stages (veligers and hatchlings) as they underwent a 1hr acute heat trial as described in Chapters 2 and 3.

LT and AT binary scores could not be analyzed via generalized linear model and a logistic regression. Therefore, LT and AT larval thermotolerance values could not be calculated for veligers and hatchlings. Instead, here I report actual survivorship (mortality) and normality scores (Figure 18) alongside qualitative observations on the larvae (Figure 19).

Binary scoring of developmental survivorship (mortality) and normality for larvae that underwent the 14 d MHW-Simu period and acute thermotolerance trials are as follows: For veligers, 0% of individuals were scored as normal, and there were a wide range of survivorship scores across all the thermotolerance treatment temperatures (Figure 18 and 19). For hatchlings, there was an average of 7.4% of individuals scored as normal, and there were a wide range of survivorship scores across all the thermotolerance treatment temperatures (Figure 18 and 19).


(a) Veligers

(b) Hatchlings

Figure 19. Images of early stage individuals after the 1 h acute thermal tolerance trial. Representative images are shown for veligers (a) and hatchlings (b) following a 1 h exposure to the temperatures listed below each image. Prior to the trial, capsules were removed from the MHW-Simu tanks and early stage individuals were excapsulated. The first image per stage (far left) represents individuals that were exposed to 10.0 – 10.8 ºC control temperatures after being removed from the MHW-Simu treatment. Excapsulated veligers were exposed to seven acute thermal tolerance treatment temperatures (25.5 – 36.3 ºC) and the older hatchling stage was exposed to eight acute temperatures (25.4 – 36.3 ºC). Images were taken on a Olympus BX50 scope at 10× magnification.

DISCUSSION

The goal of this part of my dissertation was to assess impacts of a short-term MHW on the larval thermotolerance of *K. kelletii* in two larval stages, veligers and hatchlings. The most important findings of the study were that both stages (1) displayed varied amounts of survivorship, and (2) large amounts of abnormality after experiencing the 7 d MHW and acute thermal stress trials. Below, I discuss the findings of this study and conclude by contextualizing experimental results in MHW environmental data and previous findings in Chapter 2 and 3.

MHW-Simu and environmental temperatures

While MHW-Simu trials, did not reach the exact temperature goal of maintaining 23 ºC for the intended 7 d MHW event (Day 4 – 10 of the experiment), the maximum temperatures of each trial were, 22.1 - 22.3 ºC, only a 0.7 - 0.9 ºC difference than the MHW goal temperature, 23 ºC. SBC-LTER environmental data shows that MHWs during Fall 2014-15 ("Blob" MHW) exceeded 23 ºC. The average maximum temperatures of for both MHW-Simu trials (Figure 16 and 17) still fall into ±1 ºC of the 23 ºC MHW temperatures reached during past Fall MHWs in the Santa Barbara Channel (SBC-LTER).

Additionally the actual MHW-Simu temperatures reached, temporally align with temperatures that fit into the ecological context of when the experiment occurred Spring-Summer. Specifically, Summer-Spring (March – July) ocean temperatures in 2014 and 2015 in the Santa Barbara Channel were 21.5 ºC and 21.8 ºC for each respective year. Overall, the MHW-Simu trials in this study reflected temporally aligned peak temperatures *K. kelletii* would experience in the Santa Barbara Channel (Reed et al., 2016; SBC-LTER). Further, the temperatures reported here are benthic temperatures, and SBC-LTER data suggest that there are regularly "bottom" MHWs (BMHWs) in the kelp forests region (SBC-LTER). The observation of BMHWs has been reported for other regions of the global oceans (D. J. Amaya, Jacox, M. G., Alexander, M. A., Scott, J. D., Deser, C., Capotondi, A., & Phillips, A. S., 2023), and have been linked to coral bleaching (Wyatt et al., 2023).

Larval thermotolerance

Larvae of both stages consistently showed overwhelming developmental abnormality across all acute temperature treatments in larval thermotolerance trials. Hatchlings showed slightly greater levels of normality than veligers under acute thermal stress, however only by

7.4%. The varied levels of survivorship (mortality) observed for both stages cannot be explained by the data presented here. Control temperatures (10 ºC and 10.8 ºC) used for each stage do not represent ambient temperatures (10.8 ºC) or control temperatures used for past *K. kelletii* larval thermotolerance trials (Chapter 2 and 3). It is possible, that low levels of survivorship for veligers under the control temperature (10.8 ºC) could be attributed to the fact that larvae tend to appear dead and less mobile under cooler temperatures (Clare observation; 2021). However, the effect of cooler temperatures on mortality and abnormality of *K. kelletii* veligers remains to be confirmed by additional experimentation.

Recommendations for future experimentation

In closing, I will discuss recommendations for future experimentation as it relates to larval thermotolerance trials and simulating MHWs.

<u>MHW-Simu:</u> Future MHW-Simu experimentation on *K. kelletii* should ensure that MHW-Simus are staged during time periods that mimic past periods when MHWs frequently occur in the Santa Barbara Channel. Additionally, future acclimations on *K. kelletii* adults and larvae should also be staged for longer periods, from gametogenesis, to oviposition, to larval excapsulation to learn more about the reproductive strategy system in *K. kelletii* . As we develop a greater understanding of the impact of BMHWs (D. J. Amaya, Jacox, M. G., Alexander, M. A., Scott, J. D., Deser, C., Capotondi, A., & Phillips, A. S., 2023; Starko et al., 2022), it will be essential for future studies to use bottom environmental temperatures to contextualize MHW-Simu manipulations.

<u>Larval thermotolerance:</u> As mentioned previously, due to experimental constraints, a control subset of larvae (a subset that did not experience a MHW-Simu) were not run through a larval thermotolerance trial. Future experimentation will benefit by incorporate a greater

suite of controls and manipulations using larvae that (1) do not undergo a MHW-Simu or thermotolerance trials, (2) undergo larval thermotolerance trials, (3) undergo a MHW-Simu and (4) undergo a MHW-Simu or thermotolerance trials (Figure 20). While the larval thermotolerance survivorship scoring data was highly variable per acute temperature treatment, to determine any trends that can emerge from larval thermotolerance trials on individuals after a MHW-Simu, future experimentation should average several replicates of larval data. Scoring additional replicates of larvae for thermotolerance that have also undergone MHW-Simu trials may reveal any outliers or stage specific responses to both trials. While it still may not be possible to calculate LT and AT values for larval thermotolerance via a linear model and logistic regression for larvae under the experiment design in this study, there may be qualitative aspects of thermal tolerance that can be uncovered by examining a wider range of treatment temperatures Although larval thermotolerance trials in Chapter 3 focused on a range of experimental temperatures that

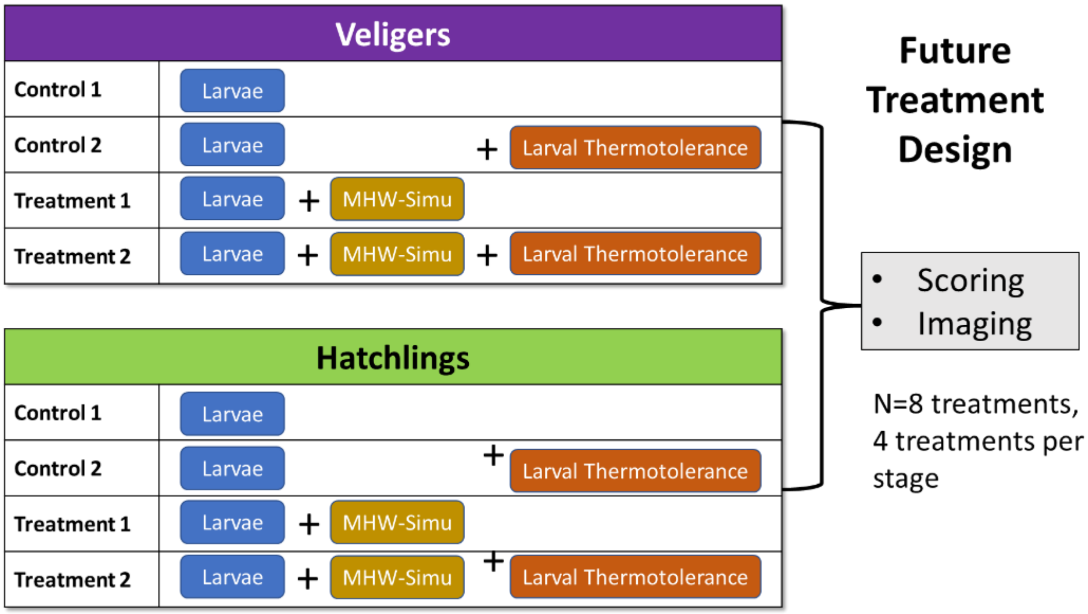


Figure 20. Future experimentation recommendations for a short-term MHW-Simu on *K. kelletii* veligers and hatchlings. These figure shows a conceptual treatment design for future MHW-Simu experimentation for both stages (veligers and hatchlings). Future iterations of this work should include 8 treatments (4 treatments per stage).

were shown to appropriately assess *K. kelletii* thermotolerance (see Chapter 2 and Chapter 3) (Clare et al., 2022), for future experimentation involving short-term MHW-Simus, it would be beneficial to challenge larvae to a wider range of temperatures, especially temperatures that can represent ambient temperatures (e.g., 10 - 22 ºC) to gain any qualitative insight on the effects of a short-term MHW-Simu on larval thermotolerance.

Chapter 5: REEFlections: Understanding sense of belonging in undergraduate research virtual science communication

INTRODUCTION

Background

This portion of my dissertation focuses on a preliminary examination of an active learning undergraduate education intervention I designed to use **dialogue and reflection to boost sense of belonging (SOB)** for UCSB Research Experience & Education Facility (REEF) undergraduates as they navigate entering marine science fields. I accomplished this via establishing **an undergraduate science communication (scientific storytelling) research symposium, REEFlections, which I staged annually for three years (2019-2022) in collaboration with the REEF.**

Belonging—has been long established as a critical human need for well-being and social adjustment (St-Amand, 2017; Strayhorn, 2018; Vaccaro & Newman, 2016). It has also been shown by teachers and researchers that a sense of belonging (SOB) is associated with academic motivation, success, and persistence in higher education (T. M. Freeman, Anderman, & Jensen, 2007; Hausmann, Schofield, & Woods, 2007; Hoffman, 2002; Vaccaro & Newman, 2016). Building education programs that sustain students' SOB is essential to retain students in STEM fields. Addressing this need, **this preliminary study focuses on interviews with three REEF undergraduates who participated in 2020 REEFlections, where I analyzed student interviews to evaluate the ways students report SOB through participating in REEFlections.**

Intervention rationale

Student fears of being devalued (not-belonging) based on identity, have been shown to undermine student performance in STEM (Miyake et al., 2010). Underrepresented minority (URM) students in higher education also commonly report not feeling welcome into STEM disciplines (S. L. Rodriguez & Blaney, 2021). Early career stage interventions have been shown to increase immediate and long-term student performance and motivation to pursue STEM (London, Rosenthal, Levy, & Lobel, 2011). Thus, to increase diversity, equity, and inclusion (DEI) in STEM fields**,** carefully crafted combinations **of** narrative-based active learning interventions must be implemented at “gateway” stages in higher-education (S. Freeman et al., 2014; London et al., 2011; Norris, Guilbert, Smith, Hakimelahi, & Phillips, 2005).

A science communication symposium, like REEFlections, is a narrative-based active learning activity that offers students the opportunity to disseminate their findings while applying knowledge of their past experiences in STEM. In ecological and environmental sciences, students need a suite of experiences to advance in careers in environmental and ecological science. These experiences include: coursework, individual discovery (research), and dissemination, where students share their scientific findings within and outside their communities in their own voice (Murrow, 1951; Tanner, 2012). Dissemination allows for “meaning making” (sensu (Ignelzi, 2000)), a critical aspect of building SOB in an early career individual (London et al., 2011). While symposia and scientific meetings are the traditional ways undergraduates begin to gain experience in dissemination by having discipline specific dialogue with experts in their field, due to departmental resource constraints, student involvement in undergraduate research does not always guarantee an opportunity to participate in symposia and scientific meetings. Additionally, campuses often do not often have sufficient funds for professional development resources that support undergraduate researchers in attending symposia and scientific meetings (e.g., presentation and networking workshops) (Petrella, 2008). Being underprepared to professionally participate in symposia and scientific meetings can amplify the feeling of not-belonging for the small percentage of students who may have the opportunity to participate in symposia or scientific meetings, deterring students from STEM fields altogether (Petrella, 2008).

The REEF provides a platform that develops strong educators, science communicators and researchers. As a result, a portion of REEF students are experienced in both science communication (scientific storytelling), and in navigating a research environment. A subset of undergraduates at the REEF serve as both public educators (K-12) at the REEF aquarium facilities and undergraduate researchers in research groups on campus. By employing scientific storytelling skills to disseminate marine science, REEF students increase public inclusion in marine science while simultaneously developing SOB in marine science. The aptitude towards leadership in science education and communication so strongly displayed by REEF undergraduates is much needed in future leaders in STEM fields and academic environments.

Individuals like REEF students with “soft-skill” strengths, are historically overlooked and do not feel welcome to participate in STEM research environments, where “hard skills” are traditionally rewarded over “soft skillsets (Balcar, 2016; de Campos, 2020; Karimi, 2021). This indirect devaluation of students with strong “soft skills” (Balcar, 2016; de Campos, 2020; Karimi, 2021), can lead to a decrease of SOB in students that identify with having a strong “soft” skillset. To honor the simultaneous undergraduate research and student led-science communication by a subset of REEF students, I developed REEFlections as an opportunity for REEF undergraduate researchers to be affirmed by their community. The program I developed challenges students, already comfortable public speaking to employ their science communication skillsets in disseminating high level research in an accessible way that honors their personal narrative.

Research framework

There were three preliminary framing pieces that were the foundation for establishing REEFlections and examining 2020 REEFlections student interviews in this exploration. The framing pieces were:

(a) Staging a narrative-based active learning symposium as metacognitive activity
(b) Sense of belonging (SOB)
(c) Optimal distinctiveness theory (ODT)

In the following sections, I will discuss the specific ways these preliminary framing pieces were incorporated into the program structure of REEFlections (2019-2022).

<u>(a) Staging a narrative-based active learning symposium as metacognitive activity:</u> Narrative-based active learning activities took the form of scientific storytelling in establishing REEFlections programming (2019-2022). By using narrative (dialogue) as a part of scientific storytelling I designed the program to allow for student validation and academic affirmation for participants (LopezLeiva, Roberts-Harris, & von Toll, 2016). An emphasis on student interaction makes narrative-based active learning activities, such as storytelling successful in developing inclusive environments that increase SOB (Benmayor, 2012; Bernal, Burciaga, & Carmona, 2012; Espino, Vega, Rendon, Ranero, & Muniz, 2012). For these reasons, narrative-based active learning interventions in STEM have been shown as a

promising tool to increase SOB by closing DEI achievement gaps (Cohen, Garcia, Purdie-Vaughns, Apfel, & Brzustoski, 2009). In this light, REEFlections moved beyond the outcomes of traditional STEM symposiums because it was organized and executed to liken a performance event. For example, undergraduate organizers were introduced to backwards timeline event planning and participants were required to attend dress rehearsals, “cue-to-cue”, and “tech” rehearsals. Finally, in all years of REEFlections, participants received performance-style direction to “take the stage” and share their lived-experience in their respective research journeys. Fashioning the research talks as personable-style presentations made room for the symposium to be a metacognitive activity, where participants were encouraged not to simply bring their research, but themselves to the program (Benmayor, 2012; Bernal et al., 2012; Espino et al., 2012).

(b) SOB: The definitions of SOB described here were used to evaluate student interview data from 2020 REEFlections (Table 13). The components of SOB have been defined as including: (1) Positive Relationships (Goodenow, 1993; Hagerty, 1992; St-Amand, 2017; Williams & Downing, 1998), (2) Perceived Value (Waller, 2020), (3) Social Support (St-Amand, 2017; Strayhorn, 2018) and (4) Harmonization (Hagerty, 1992; Hunt, 1990; Maslow, 1962; St-Amand, 2017). (1) Positive Relationships were the foundation of the REEFlections program. In each year of REEFlections, undergraduates deepened relationships with REEF peers and research mentors. Presenters openly provided each other constructive feedback, resulting in a sense of unification as all members of the REEFlections cohort (or “cast”) worked together on behalf of the “production”. A critical aspect of developing one’s own identity in a discipline is being able to have (2) Perceived Value of one’s independent work. As a part of REEFlections, students constructively recalled the various ways their research brought value to the research groups they were a part of. (3) Social Support was also in the fabric of REEFlections. For example, the built-in expedited timeline (11 - 30 days) of organizing and rehearsing towards presenting in REEFlections, drove organizers, participants, and their mentors to work closely, intimately and emerge as a cohort. Further, in REEFlections, REEF students and their peers were supported by their community as they reached a significant professional developmental milestone by presenting in REEFlections. Each student experienced (4) Harmonization, as they were self-motivated to apply to participate in REEFlections as an extracurricular activity.

<u>(c) Optimal Distinctiveness Theory:</u> Finally, I proponed that students experienced (5) Affirmation of Past Skills and Character Traits, as SOB component of REEFlections. While not traditionally listed as a component of SOB, Optimal Distinctiveness Theory (ODT) suggests that a feeling of SOB includes a balance of harmonization (sameness) and a perceived value of distinctiveness (uniqueness) (Berger, Rosenholtz, & Zelditch, 1980; Brewer, 1991; Taifel, 1986; Waller, 2020). Specifically, REEFlections, allowed participants backward and forward on how their uniqueness shaped them in the present moment, contributing to SOB (Brewer, 1991; Waller, 2020) (Table 13).

Preliminary study overview

The coronavirus disease 2019 (COVID-19) dominated 2020 and brought highly unusual circumstances (e.g., remote learning) during a time also consumed with social unrest (e.g., George Floyd protest movement, May 26, 2020) that escalated just five days before the 2020 REEFlections symposium (May 31, 2020) (Howard, 2022). Given these academic performance barriers, the 2020 REEFlections students, organizers, and mentors persevered under rigorous working timelines and difficult conditions. Despite the many challenges brought on by this period, as the 2020 REEFlections Director, I was able to foster an environment that supported SOB for 2020 REEFlections students.

To investigate 2020 REEFlections students experiences further, for this chapter, I used student interview data to do a preliminary exploration on interviews with three undergraduates who participated in 2020 REEFlections. I analyzed interviews to determine which components of SOB were most shared by student participants after participating in a virtual 2020 REEFlections, during an especially challenging time in our world. In summary, the goals of this preliminary study in this chapter were to answer the following research question: **Which components of SOB were most mentioned in 2020 REEFlections student interviews as they reflected on their experiences in STEM and participation in REEFlections?**

This preliminary exploration did not involve any formal hypothesis testing. However, I expected the 2020 REEFlections program would cause **students to reflect more greatly on the affirmation of their past skills or character traits as a REEFlections participant in interviews**. REEF students involved in REEFlections already display exemplary leadership skills ("soft skills"), such as public speaking, peer mentoring, and a wide-ranging understanding of marine science. REEF students' participation in REEFlections simply brings together these strengths in a more traditional academic context, a symposium. Therefore, I expected that as a result of participating in REEFlections, student interviews would reveal that students showed a newfound confidence on the body of STEM skills they had been building all along.

MATERIALS & METHODS

Program organizers

The REEFlections program organizer team was comprised of myself, the REEFlections Director, a REEF student Co-Director, program advisor, and publicist. I, the founder of REEFlections served as the Director of 2020 REEFlections. Entering this role, I had in-person and virtual experience mentoring REEF students (2018-2020). As the Director of 2020 REEFlections, I also had experience collaborating with the REEF in prior academic years of my Ph.D. where I served as a graduate student research mentor to REEF students.

The REEF facility Program Coordinator typically serves as the student Co-Director for the REEFlections. The 2020 REEFlections Co-Director had experience as a student speaker in the inaugural cohort of REEFlections in 2019. The Co-Director of REEFlections typically serves as a liaison between myself, the REEFlections Director, all participants, and the REEF Director. Thereby, Co-Director and I worked closely execute program logistics for email communications. The REEF Director advised our programming decisions, was instrumental in recruitment, and establishing the tone for the event at organizational meetings. The REEF facility student publicists are typically recruited to serve as REEFlections program organizers to increase public engagement with the REEFlections online media promotion (email invitations, reminders, and social media). The publicist for 2020 REEFlections, had experience serving as a publicity team member for the REEF.

Participant recruitment and program timeline

Student recruitment for 2020 REEFlections began Winter 2019. To be eligible for REEFlections, students had to have been involved in a research lab, worked at the REEF, and had received confirmation that their research mentors would support their involvement in REEFlections. Students must have been able to attend the virtual symposium to be selected for the program. Finally, both student and mentor participants to must have agreed to attend rehearsal meetings with program organizers to participate in REEFlections.

Three rounds of participant recruitment were facilitated by myself, REEF student staff and the REEF Director. The first round of recruitment involved emailing call to REEF students where interested students were asked to submit an email indicating interest in participating in REEFlections. In the second round of recruitment, the REEF Director individually sought out qualified candidates (in-person, via email, and thought REEF staff). From both rounds of recruitment, four students were selected to move onto the final stage of the recruitment process. At this stage, students were asked to share a few sentences on their research, identify their research group, names and contact information of their project mentors via an online form.

In keeping with the framing piece, SOB, it was essential to establish modes of social support for REEFlections participants via mentorship. Once student participants were chosen, I surveyed student’s research mentors via an email questionnaire on their ability to support their students in their participation in the REEFlections by mentoring students in developing presentation materials, attend REEFlections and rehearsal sessions. Mentors for REEFlections could range from on campus roles can range from Principal Investigators, to graduate students, researchers, to postdoctoral fellows within the campus community. In order to remain sensitive to challenges that were brought to all participants due to COVID-19, prior to confirming mentor pairs, I sent an email survey to gage mentors’ availability to support their students given their current circumstances. Additional time was taken to review mentor responses so the programs organizers could prepared to provide alternate support (another mentor or co-mentor) to a student participants. The email questionnaire outlined the ways mentors would need to be able to support their mentee in the days leading up to the symposium by: guiding their student in selecting presentation content, arranging this content into a presentation, and reviewing their student's final presentation product. Finally, we also sent out email surveys to ensure that each student's PI was aware of their mentee's involvement in REEFlections and that mentors were able to attend some portion of the symposium. All research mentors identified by applicants indicated that they were fully available to support their mentee.

Due to the sudden onset of needing to accommodate the COVID-19 pandemic timeline adjustments listed above, REEFlections was postponed as program organizers and I established remote working strategies for communicating with displaced REEF students and research mentors that were involved in the REEFlections recruitment process. The participation of students and their research mentors was confirmed eleven days away from the original symposium date.

While mentor support and encouragement were shown to be critical for participant success in the previous iteration of REEFlections, to support student's research mentors, guest mentors (REEFlections alumni and graduate students in affiliated disciplines) were recruited to serve as an "expert panel" for student rehearsals. Expert panelists (REEFlections alumni and graduate students in affiliated disciplines) were opportunistically recruited over the course of 3-5 days via email based on availability to participate in two Zoom rehearsal nights. Over nine experts volunteered to attend each student rehearsal allowing for a large number of expert volunteers to provide panel feedback on both rehearsal nights. The expert panel was an intentional way the program supported student's mentors by providing alternate support for REEFlections students during the pandemic. This allowed the program to be more mindful of the varied capacity mentors had to support their students under COVID-19 circumstances.

Program assignments and activities

Participant (student and mentor) preparation was done according to the methods I used to bridge student and mentor participation in the first iteration of REEFlections in 2019. Expectations for participation were reviewed in a Zoom slideshow orientation for participants I led alongside the REEF Director and program organizers. As I did in the 2019 REEFlections expectation orientation, I encouraged research mentors to be involved in assisting speakers with developing presentation materials and guiding their mentees in presenting their research during the orientation. Over the course of the program I provided a suite of science communication assignments and activities to prepare participants for the symposium. Students also participated in remote science communication meetings with myself, the REEF Director, research mentors and guest mentors (REEFlections alumni and graduate students in affiliated disciplines). All program preparation was held remotely over Zoom.

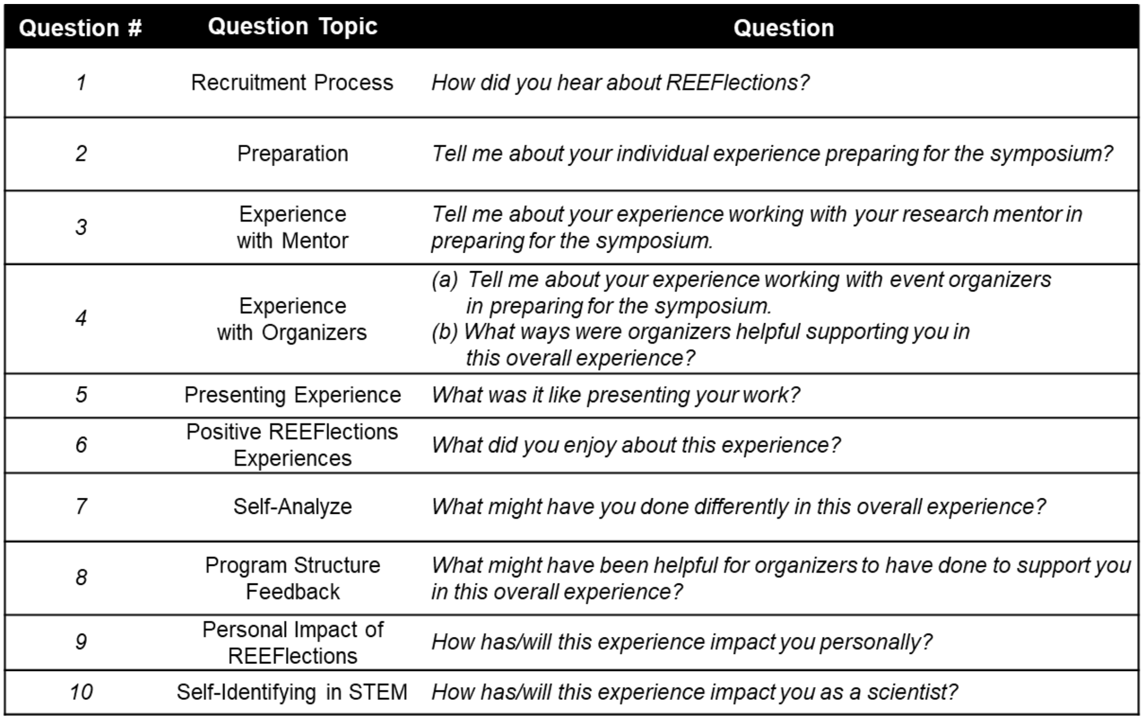
Similar to 2019 REEFlections, 2020 REEFlections students were allowed to use PowerPoint slides and were asked to create a presentation with traditional research talk components: project title, background, research questions, methodology, results, and acknowledgements). In keeping with the framing piece to stage a narrative-based active learning symposium as metacognitive activity, I challenged speakers to move beyond the Zoom presentation slide format in using dialogue that was interactive and engaged audiences on their research journey (e.g., polls, monologue, and imagery). Final presentations were expected to be in a “flash talk” format (3 – 7 mins).

Prior to the symposium student sessions with the recruited expert panelists (REEFlections alumni and graduate students in affiliated disciplines) was a critical component of the 2020 REEFlections program. In keeping with the framing piece to propose that optimal distinctiveness theory (ODT) played a role in components of perceived SOB (e.g., “Affirmation of Past Skills and Character Traits”) in this preliminary examination, I designed the REEFlections preparation process as a “rehearsal”. REEF students are well-experienced in rehearsing their aquarium programs (e.g., storytelling structure, audience engagement) prior to “performing” for the public. To affirm REEFlections students’ past experiences in rehearsing presentations, similar to 2019 REEFlections, for 2020 REEFlections, the expert panel provided feedback on student presentations during two nights of rehearsals. Experts provided feedback via live Google Sheet scorecards that protected student’s private feedback from being seen by other students. The expert panel was asked to provide live feedback verbally over Zoom to ensure students could clearly understand their written feedback on the live Google Sheet scorecards. Expert panelists were informed of the shortened program timeline and other aspects of stress students were working under. Experts were also instructed to provide both positive and negative constructive feedback in the student’s final days before “taking the stage”. I instructed students to be prepared to improvise and expect technical difficulties as our campus was only recently navigating hosting events over Zoom.

Virtual symposium

The 2020 REEFlections symposium was held virtually on a Friday evening on May 31, 2020, via Zoom. The event began with opening statements by myself, the REEF Director, and the REEFlections Co-Director (15 min). This was followed by student presentations (30 mins) and closing statements (15 min). Mentors introduced speakers (1 min) prior to each student presentations. Prior to the start of the event, I informed audiences of the shortened program timeline COVID-19 related challenges students overcame in preparing for the symposium. Immediately after the event, participants were invited to a Zoom celebration (20 min) to congratulate participants and organizers on their work on the symposium. 2020 REEFlections had a minimum of 99 attendees over the course of the Zoom event.

Interview methodology



Question #	Question Topic	Question
1	Recruitment Process	*How did you hear about REEFlections?*
2	Preparation	*Tell me about your individual experience preparing for the symposium?*
3	Experience with Mentor	*Tell me about your experience working with your research mentor in preparing for the symposium.*
4	Experience with Organizers	*(a) Tell me about your experience working with event organizers in preparing for the symposium.* *(b) What ways were organizers helpful supporting you in this overall experience?*
5	Presenting Experience	*What was it like presenting your work?*
6	Positive REEFlections Experiences	*What did you enjoy about this experience?*
7	Self-Analyze	*What might have you done differently in this overall experience?*
8	Program Structure Feedback	*What might have been helpful for organizers to have done to support you in this overall experience?*
9	Personal Impact of REEFlections	*How has/will this experience impact you personally?*
10	Self-Identifying in STEM	*How has/will this experience impact you as a scientist?*

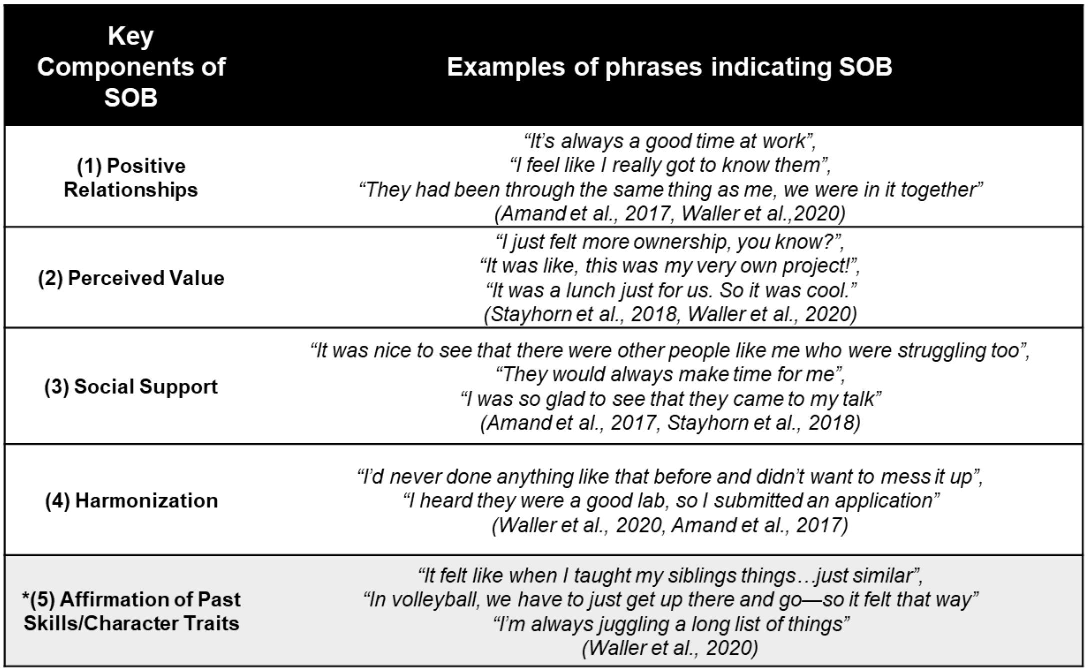
Table 14. Interview questions organized by question topic. The table shows list of guiding questions used for student interviews organized by question number and topic.

This research sought to investigate which components of SOB were most mentioned in 2020 REEFlections student interviews as they reflected on their experiences in STEM and participation in REEFlections. This preliminary study focuses on three semi-structured interviews with student speakers that participated in 2020 REEFlections (Table 14). I contacted all student speaker participants via email five days after the symposium to participate in a virtual one-one-one talk-back, a "DebREEFing" (20-30 mins). The REEFlections Co-Director assisted me in coordinating emails to schedule student interviews. "DebREEFing" interview dates overlapped with our campus' first iteration of virtual final exams. Three out of the four students I interviewed consented to have their transcript data incorporated in this preliminary study. I collected all interview data over the course of six days after requesting interview time with students. Students were informed that our Zoom meetings were recorded and would not be shared without their permission. I also prompted students to notify me via email any stage after the interview if they were not comfortable having their transcripts used in this preliminary study. In emails requesting interview time with students, I openly shared my desire to learn more about their journey and perspective on their experiences in the program. Students were informed during and prior to interviews that our meeting would be conversational and open-ended. In keeping with the first framing piece of staging a narrative-based active learning symposium as metacognitive activity, I established the interview as a metacognitive activity. I did this by sharing my perspective on the importance of reflection on one's accomplishments in light of the social unrest and COVID-19-related events during the time of the interviews. I used a list of guiding questions (Table 14), as well as follow-up questions that arose over the course of the interviews that were self-reflective. (See supplementary materials for additional information on human subject protocol for this preliminary study).

Coding transcripts

All procedures for this work was approved by the University of California, Santa Barbara Institutional Review Board (IRB) for human subjects research (Protocol Number: 36-21-0218). The university's IRB ensures compliance with all federal and state regulation subjects. Student interviews were transcribed and analyzed using emergent themes to identify instances where student experiences indicated SOB. Transcript responses from the same list of interview questions was used to generate each a dataset of instances where student experiences indicated SOB). I consulted Johnny Saldaña's Coding Manual for Qualitative Research for best practices for coding qualitative interview data collected (Saldaña, 2015). Coding methods I used for this preliminary study also modeled techniques in similar assessment studies for higher-education interventions (Ghaffar, Khairallah, & Salloum, 2020; Hashimoto-Martell, McNeill, & Hoffman, 2012). Transcripts were de-identified for coding and data analysis to protect student. Student re-identification for this preliminary study were numerical identification: Student 1, Student 2, and Student 3. In the first round of coding, student interview transcripts were color-coded to identify broad codes. This first round of coding was also used to identify areas of the transcripts where students reflected on their REEFlections experience for each interview question. The final coding scheme (Table 15) emerged from the analysis of the interview data, coming from identified themes, topics and subthemes. Most of the interview questions allowed for several coding options. For example, if a student included several ideas in their responses, I coded separately each of those ideas, concepts or topics for each subcode category. I, the primary researcher was the interpreter of all transcripts. Prior to the final round of coding for student experiences and SOB, I reviewed all coding categories, and finalized rubrics. Subcategories of code were generated for unstructured interview questions and responses. Unstructured portions of the interview transcripts were also coded using emergent themes and broad categories. The length of unstructured interview questions and responses was observed via qualitative coding notes for additional interview insights.

I used the afore defined SOB framework (Table 13) to explore the following question about 2020 REEFlections: **“Which components of SOB were most mentioned in 2020 REEFlections student interviews as they reflected on their experiences in STEM and participation in REEFlections?”**. ‘Student mentions’ of SOB were elicited via the 10 questions in Table 14. To determine the aspects of REEFlections where student’s experiences indicated a perception of SOB, each student mention of experiences that contained



Key Components of SOB	Examples of phrases indicating SOB
(1) Positive Relationships	*“It’s always a good time at work”, “I feel like I really got to know them”, “They had been through the same thing as me, we were in it together” (Amand et al., 2017, Waller et al.,2020)*
(2) Perceived Value	*“I just felt more ownership, you know?”, “It was like, this was my very own project!”, “It was a lunch just for us. So it was cool.” (Stayhorn et al., 2018, Waller et al., 2020)*
(3) Social Support	*“It was nice to see that there were other people like me who were struggling too”, “They would always make time for me”, “I was so glad to see that they came to my talk” (Amand et al., 2017, Stayhorn et al., 2018)*
(4) Harmonization	*“I’d never done anything like that before and didn’t want to mess it up”, “I heard they were a good lab, so I submitted an application” (Waller et al., 2020, Amand et al., 2017)*
***(5) Affirmation of Past Skills/Character Traits**	*“It felt like when I taught my siblings things…just similar”, “In volleyball, we have to just get up there and go—so it felt that way” “I’m always juggling a long list of things” (Waller et al., 2020)*

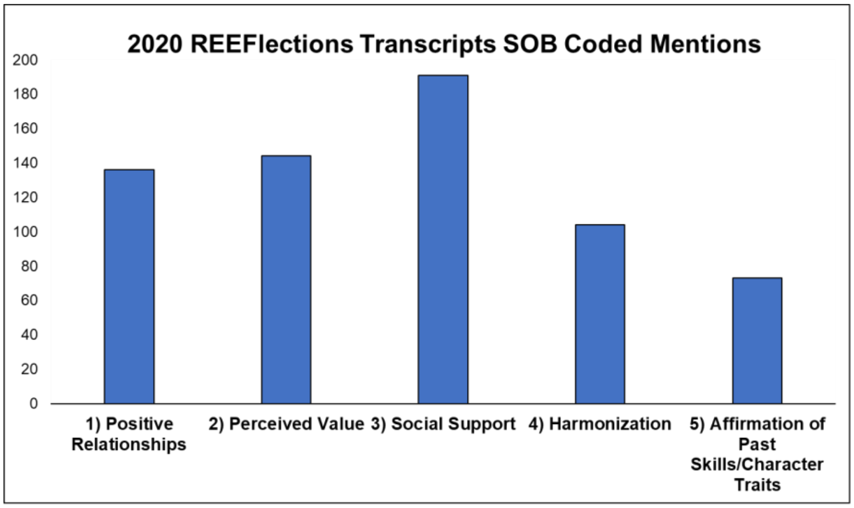
Table 15. SOB scoring rubric for each component of SOB for the preliminary study. This table shows the guiding example phrases that were used to subcode for each of the five key components of SOB. The guiding example phrases for coding were both quotes paraphrased from transcripts and quotes from SOB literature.

components of SOB was counted per interview question per student. The term ‘SOB coded mentions’ will be used hereafter to refer to phrases or sentences (lines of transcripts) that were coded as falling under the definition of SOB for this preliminary study. The key components of SOB identified by this preliminary exploration were used as a coding rubric to score transcripts for SOB. The five key components of SOB that were coded were: (1) Positive Relationships, (2) Perceived Value, (3) Social Support, (4) Harmonization, (5) Affirmation of Past Skills/Character Traits (Table 13). A list of example phrases was generated to guide to the SOB coding process. The guiding example phrases for coding were both quotes paraphrased from transcripts and quotes from SOB literature. The guiding example phrases that were used to subcode for SOB were listed in the rubric (Table 15). In the final data analysis, the sum of mentions of SOB coded phrases in transcripts were pooled per question and analyzed using the question topic categories (Table 14) to calculate the average number of SOB coded student mentions per question topic. During the interview with Student 1, when discussing Question 9 (“How has/will this experience impact you personally?”) (Table 14), Student 1 referred to a thank you letter they wrote to organizers as their response to that question. Thus, for scoring that question, Student 1’s letter transcript was used as data for the SOB dataset. SOB coded mentions were also analyzed per each student per overall question topic category (Table 14) in the final data analysis.

RESULTS

In the following sections I will discuss observations on findings from the overall research questions in this preliminary exploration. The main finding of this preliminary study was that Social Support received the greatest number of SOB coded student mentions in transcripts among the five categories of SOB. When SOB coded student mentions were analyzed per student per question, the greatest number of SOB coded student mentions were when discussing their experience with their mentor (Figure 22).

SOB coded mentions

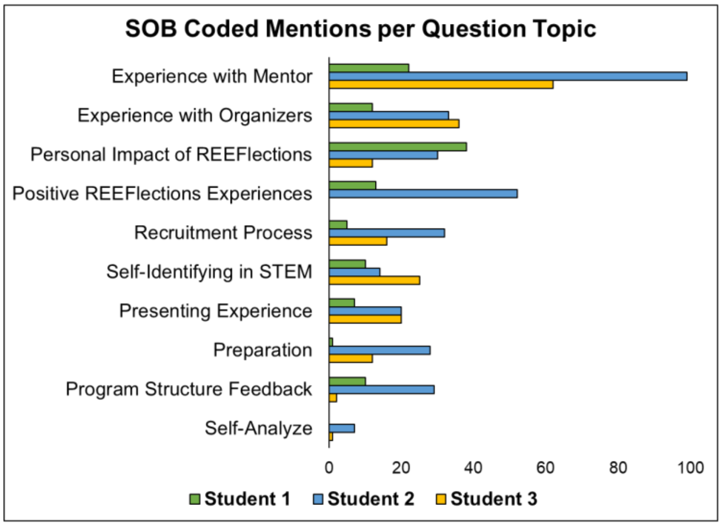


SOB Category	Score
1) Positive Relationships	*136*
2) Perceived Value	*144*
3) Social Support	*191*
4) Harmonization	*104*
5) Affirmation of Past Skills/Character Traits	*73*

Figure 21. 2020 REEFlections Student SOB coded mentions. This figures shows the number of SOB coded mentions per transcript that were pooled for all students in this preliminary study.

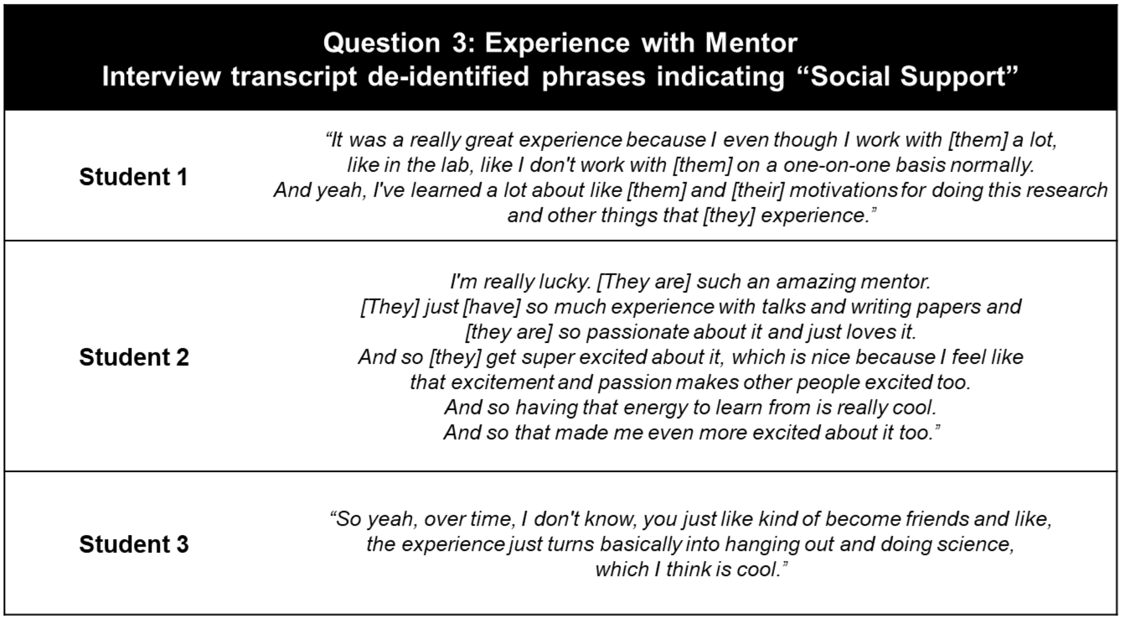
The number of SOB coded mentions per transcript of the 30 min interviews (n = 3 students) pooled for all students in this preliminary study were as follows for each category of SOB in decreasing order: there were 191 SOB coded mentions of Social Support, 144 SOB coded mentions of Perceived Value, 136 SOB coded mentions of Positive Relationships, 104 SOB coded mentions of Harmonization, and 73 SOB coded mentions of Affirmation of Past Skills/Character Traits (Figure 21). The three SOB categories with the greatest number of SOB coded mentions in transcript data were for the following categories (in decreasing order): Social Support, Perceived Value and Positive Relationships. Social Support received the greatest number of SOB coded mentions, 28-25% greater than the other two top categories (Perceived Value and Positive Relationships). Meanwhile, the amount of SOB coded mentions of Perceived Value and Positive Relationships categories differed only by 6%. This may suggest that there were high aspects of Social Support in the 2020 REEFlections program that contributed to SOB for participants overall.

In order to further understand the amount of SOB coded mentions for each question topic per student, I also analyzed SOB coded mentions for each overall question category (Figure 22) in transcripts for the final data analysis. Here, the number of SOB coded mentions by each student are reported by question topic (Figure 22). The average number of SOB coded mentionss for each question are shown in Figure 22. The questions that resulted in student responses with the greatest number of SOB coded mentions were for the following question categories (in decreasing order): Experience with Mentor, Experience with Organizers, and Personal Impact of REEFlections. The number of SOB coded mentions were



Question Topic	Number of SOB Coded Mentions Student 1	Student 2	Student 3	Average number of mentions
Experience with Mentor	*22*	*99*	*62*	***61***
Experience with Organizers	*12*	*33*	*36*	***27***
Personal Impact of REEFlections	*38*	*30*	*12*	***27***
Positive REEFlections Experiences	*13*	*52*	*0*	***23***
Recruitment Process	*5*	*32*	*16*	***18***
Self-Identifying in STEM	*10*	*14*	*25*	***16***
Presenting Experience	*7*	*20*	*20*	***15***
Preparation	*1*	*28*	*12*	***14***
Program Structure Feedback	*10*	*29*	*2*	***14***
Self-Analyze	*0*	*7*	*1*	***3***

Figure 22. SOB coded mentions per question topic. This figure shows the number SOB coded mentions for each overall question category per student as well as the averages of SOB coded mentions per question category.



Question 3: Experience with Mentor Interview transcript de-identified phrases indicating “Social Support”	
Student 1	*“It was a really great experience because I even though I work with [them] a lot, like in the lab, like I don't work with [them] on a one-on-one basis normally. And yeah, I've learned a lot about like [them] and [their] motivations for doing this research and other things that [they] experience.”*
Student 2	*I'm really lucky. [They are] such an amazing mentor. [They] just [have] so much experience with talks and writing papers and [they are] so passionate about it and just loves it. And so [they] get super excited about it, which is nice because I feel like that excitement and passion makes other people excited too. And so having that energy to learn from is really cool. And so that made me even more excited about it too.”*
Student 3	*“So yeah, over time, I don't know, you just like kind of become friends and like, the experience just turns basically into hanging out and doing science, which I think is cool.”*

Table 16. Transcript phrases indicating “social support”. This table shows a quote per student from responses to the Experience with Mentor question (Question 3) that were also coded for “Social Support”.

greatest when discussing the topic: Experience with Mentor (Question 3, “Tell me about your experience working with your research mentor in preparing for the symposium”). Codes from transcript data indicated that the Experience with Mentor question topic received the highest average number of SOB coded mentions, 56% greater than the SOB coded mentions of the other two top categories (Experience with Organizers and Personal Impact of REEFlections). Meanwhile, the number of SOB coded mentions of the Experience with Organizers and Personal Impact of REEFlections categories had the same average number of SOB coded mentions (Figure 22). ”).

Overall, this preliminary study found Social Support received the greatest number of SOB coded student mentions in transcripts among the five categories of SOB, and that the Experience with Mentor question topic received the highest average number of SOB coded mentions. To better understand the overlapping nature of these two results, a quote per student from responses to the Experience with Mentor question (Question 3) that were also coded for Social Support are presented in Table 16. Considering the SOB scoring in this preliminary exploration overall, these quotes further display that student's development of SOB was centralized on Social Support and experiences with research mentors according to interview responses from this preliminary study.

DISCUSSION

The goal of this part of my dissertation was to determine which aspects of SOB were most reported in student experiences via interviews with 2020 REEFlections participants. The most important findings of this preliminary study were that Social Support was the most frequently reported aspect of SOB in student interview responses on 2020 REEFlections-related experiences. Below, I discuss the findings of this preliminary study and conclude by contextualizing coding results in the context of our current understanding in building SOB in STEM higher education. In the following sections I also contextualize my preliminary findings in the scope of the framing pieces of this work: (a) staging a narrative-based active learning symposium as metacognitive activity, establishing a (b) sense of belonging (SOB) and, (c) proposing that optimal distinctiveness theory (ODT) played a role in components of perceived SOB (e.g., "Affirmation of Past Skills and Character Traits") in this preliminary examination.

This preliminary study finds that perceived Social Support was the most mentioned aspect of SOB in student interviews as students reflected on their perceived experiences in STEM and REEFlections. Additionally, via further examination, students SOB coded mentions occurred most often when discussing the topic: "Experience with Mentor" (Question 3, "Tell me about your experience working with your research mentor in preparing for the symposium"). In combination, these two results indicate that students perceived that social support, specifically, from research mentors helped build SOB for student participants in 2020 REEFlections. While students perceived to have received social support from their peers, they also perceived a deepening of their relationships with research mentors as they worked closely with them under an expedited timeline for the symposium (Figure 22).

In keeping with the SOB framing piece of this preliminary study, the findings on the importance of perceived social support confirm findings of past studies that show that social support is a critical element in establishing SOB in educational setting (Xu, Solanki, McPartlan, & Sato, 2018). Quotes from responses to the Experience with Mentor question (Question 3) that were also coded as Social Support presented in Table 16 suggest that student's perception of stronger social connections with their mentor via their experience in REEFlections, boosted their enthusiasm for STEM related activities within and outside the REEFlections. Similarly, past studies have shown that perceiving that one has a social support network, boosts confidence and endurance when faced with possible barriers to success in educational settings (London et al., 2011).

For example, a focus group study on Aboriginal urban at-risk youth social support in school environments found that social support was vital to fostering SOB. Social support was essential for Aboriginal urban at-risk youth to be able to establish trust in their school environments in order to for youth to be more open to academic assistance (Richmond & Smith, 2012). A study on STEM intervention programs (SIPs) for Latino male undergraduates in engineering at a public university in California also had similar findings on a greater SOB for students due to social support elements in the SIP (Abrica, 2022) Participants in SIPs emphasized that because of a more holistic social support structure, students felt they were not “alone” in their classes, and eventually felt a SOB (Abrica, 2022).

In keeping with staging a narrative-based active learning symposium as metacognitive activity as a framing piece of this study, this preliminary exploration shows how the components of active learning and social support in REEFlections, provide infrastructure for establishing student perceptions of SOB. The unique combination of skills displayed by REEF students (having both research and science communication experience) inspired the initiation of REEFlections. While these skills are somewhat specific to REEF students and lend to greater ease in staging an narrative based active learning intervention, we must not overlook the aptitude of all students to engage in STEM narrative based in this capacity. Narrative based active learning activities like scientific storytelling empower the voices of early career individuals in STEM (S. Freeman et al., 2014; Norris et al., 2005), at a critical step of scientific growth (London et al., 2011) and should be accessible to students of all backgrounds and skillsets.

This preliminary study did not find that optimal distinctiveness theory (ODT) played a major role in components of perceived SOB in this preliminary examination (e.g., “Affirmation of Past Skills and Character Traits”). However, evidence for student perceptions of “Affirmation of Past Skills and Character Traits” could be further investigated via more coding categories or additional interview questions that target this aspect of SOB directly in future examinations of this framing piece.

In summary, as suggested by these preliminary findings, programs like REEFlections urge students to be more passionate leaders in marine science by increasing student perceptions of SOB. Therefore, more assessments of narrative based STEM interventions must be executed to further investigate the ways in which programs like REEFlections can continue to foster student SOB in higher education.

Recommendation for future SOB active learning intervention assessments

In closing, I will discuss recommendations for future assessments of SOB active learning interventions. Future active learning intervention assessments with more quantitative measurements of SOB will benefit from assessing multiple treatment groups. For example, EarSketch, a STEM intervention, used active learning approaches to connect a diverse cohort of students to coding via exercises by using culturally significant artforms (popular music) involving remixing of popular music where intervention treatment groups showed significantly greater gains in “intention to persist” and greater gains in motivation towards STEM coursework (Siva, Im, McKlin, Freeman, & Magerko, 2018). This preliminary exploration benefitted from the ability to compare student perception of the program and any subsequent SOB by having clearly separate treatment groups. While treatment groups would be difficult to establish within REEFlections program structure, the small cohort size and annual nature of REEFlections allows for cross cohort comparisons and short participant follow-up assessment surveys to establish quasi-treatments per cohort of REEFlections.

For future active learning intervention assessments with more qualitative measurements of SOB, studies will benefit from multiple rounds of transcript coding using blind interpreters. Specifically, grouping and regrouping codes and themes into categories and sub-categories may allow for a greater understanding of what patterns exist around SOB coded responses with respect to interview questions. Quantitative assessment approaches may advocate for a larger sample sizes of transcript data to gain a better understanding of student perceived SOB, yet qualitative approaches to assessing a small cohort intervention, like REEFlections, have also shown opportunity for more nuanced analyses of SOB, using individual phrases as samples onto themselves (Benmayor, 2012; Bernal et al., 2012; Espino et al., 2012).

Chapter 6: Conclusion

Extreme ocean warming, observed as ocean temperature anomalies or marine heatwaves (MHWs), are becoming a more persistent threat to coastal ecosystems (Benthuysen, Oliver, Chen, & Wernberg, 2020; Donovan et al., 2021; Hobday et al., 2016; E. C. J. Oliver et al., 2021). While our capacity to predict MHWs is growing (Benthuysen et al., 2020; Jacox et al., 2022), predictions about how marine populations will respond to thermal stress are still developing for many invertebrate fisheries species. It is clear that some marine species have an adaptive capacity to MHWs (Caputi et al., 2016; E. Sanford & Worth, 2010), however, more explorations on life histories of economically important invertebrate species are needed to protect ocean resources (Caputi et al., 2016). Early life history stages have been shown to be a potential window of resilience or vulnerability population level impacts of ocean warming (Hammond & Hofmann, 2010; Zippay & Hofmann, 2010). Overall, more experimentation on early life history and reproduction in response to MHWs has been highlighted as a fisheries management need (CDFW, 2020).

Ecosystem management can serve as an arm of public action to support climate change biology (Caputi et al., 2016; CDFW, 2020; Lester et al., 2018; White, Halpern, & Kappel, 2012). In order for the public and to advocate for environmental issues, such as the impact of marine heatwaves on coastal resources (e.g., fisheries), marine science practitioners must find more personable ways to engage the public and early career individuals (e.g., undergraduates) in marine science. Meeting these needs, the two main areas of my dissertation research were in understanding the (1) thermal tolerance of early stage marine invertebrates and (2) increasing undergraduate and public access to marine science.

Thermal tolerance of early stage marine invertebrates

My global change biology research addressed the impact of thermal stress on the performance of early stage individuals under climate change stressors, specifically, MHWs. Further, I was interested in the environmental context of physiological impacts of MHWs. In comparison to sea surface MHWs, bottom marine heatwaves (BMHWs) are an emerging area of study (D. Amaya et al., 2023; Starko et al., 2022; Wyatt et al., 2023) (Chan et al., 2023; In Preparation), especially as it pertains to marine invertebrate taxa. The timing of MHWs that occur in benthic habitats may play a crucial role in shaping the ability for early stage individuals to reach subsequent life history stages. Addressing these concerns, my dissertation explored how the parental temperature environment influenced offspring development and physiological performance of early life history stages in an emerging benthic shellfish species in the Santa Barbara Channel, the Kellet's whelk, *Kelletia kelletii*.

My dissertation research was contextualized by MHW events in the Santa Barbara Channel (2014-2018), that have been shown to have had negative impacts on kelp forest ecosystems (Cavanaugh et al., 2019; Michaud, Reed, & Miller, 2022; Reed et al., 2016; Smale et al., 2019; T. Wernberg et al., 2013; T. Wernberg, Smale, D. A., Frölicher, T. L., & Smith, A. J., 2021). SBC-LTER MHW bottom temperatures were analyzed as an abiotic factor that could have influenced early development in *K. kelletii* (SBC-LTER). The three main research questions of my experimental work were:

1. How do early stage *K. kelletii* respond to environmental temperatures that have occurred in the Santa Barbara Channel during past MHW events? (Chapter 2)
2. What are the impacts of a long-term MHW acclimation on the adult *K. kelletii* behavior of capsule laying, and on the condition of early stages when progeny

develop under the same MHW conditions under which the adults laid capsules? (Chapter 3)

3. How does larval development and thermotolerance under a shorter term simulated MHW differ from thermal tolerance under static temperature treatments? (Chapter 4)

To address these questions I developed eco-physiology methodology to investigate the effects of MHW temperatures on *K. kelletii* progeny (Chapter 2), and conducted MHW laboratory acclimations (long and short-term) on adult and early stage *K. kelletii* to investigate the impacts of MHWs on adult reproduction and larval development on thermal tolerance (Chapter 3 and 4). The above research questions were addressed over three dissertation chapters within this dissertation (Chapters 2-4). The three main outcomes of this research are outlined and discussed below.

Impacts of MHWs on reproduction and early stage development

My initial investigations on mortality and abnormality of early stage *K. kelletii* after acute thermal tolerance trials showed that temperatures where developmental abnormality was observed occurred at environmental temperatures that have been recorded during past and recent MHW events (Chapter 2; (Clare et al., 2022)). This experiment was essential as it set the foundation for understanding thermal tolerance in *K. kelletii*. Thereafter, I assessed impacts of a long-term MHW acclimation (144 d) on adult *K. kelletii* capsule laying and the thermal tolerance of early stages (Chapter 3). It was clear that a long-term MHW acclimation influenced capsule size, the number of early stage individuals per capsule, and increased the rate of early stage intracapsular development. In one of the more dramatic outcomes in Chapter 3, the impact of the long term MHW acclimation was so severe that it was not possible to conduct acute thermotolerance trials on the larvae that were contained in the capsules laid by adults laid in in the MHW treatment. While no thermotolerance data (LT and AT) were obtained in this study, this experiment provided greater insight into the differences in rate of development for *K. kelletii* developing under MHW conditions. My final experiment in my dissertation assessed impacts of a short-term MHW simulation (MHW-Simu) on the larval thermotolerance of *K. kelletii* (Chapter 4). Early stage individuals showed varied degrees of survivorship, and high levels of abnormality after experiencing the short-term MHW (7 d) and acute thermal stress trials. The limitations of the experiment in Chapter 4 were that the findings could not be supported by comparison to control thermotolerance data on "non-MHW-Simu" treatment individuals. Nevertheless, this experiment was a useful exploration of how to use a more realistic temperature context to assess thermal stress in early stage *K. kelletii*.

Recommendations for future experimentation

The varied nature of the methods of each experiment in my dissertation make it difficult to compare results between experiments. Additionally, due to the nature of how Kellet's whelks laid capsule clusters (50-100 capsules) per day made it challenging to examine larvae prior to the start of thermotolerance and MHW simulation trials. As an example, specific larvae were not examined before being placed in the thermotolerance and experimental tanks for trochophore and veligers since that would involve compromising (opening and damaging) the capsules larvae were developing in. Future manipulations should consider using consistent sampling and development observation methods across several years of experimentation to better facilitate comparison between experiments.

Other recommendations for future *K. kelletii* MHW experimentation include: multi-generational, population-level, and physiological investigations that involve both lab and field work. Like other marine invertebrates, shellfish species the Kellet's whelk could possibly provision their progeny to be more resilient to oncoming MHW thermal stress via transgenerational plasticity, (TGP) (Leach et al., 2021; Wong & Hofmann, 2020). Future work may consider conducting a TGP assessments in the lab and in the field to provide greater ecological context to the lab-based findings on larval thermotolerance in this dissertation. Considering the biogeographical range shift *K. kelletii* have undergone (D Zacherl et al., 2003), local adaptation and TGP are very likely to be present among *K. kelletii* populations along the Pacific coast. However, this has yet to be confirmed via experimentation. Future work may consider evaluating local adaption and TGP via biochemical or molecular means (e.g., via protein heat shock protein and lipid analyses), in reproducing females and early stage individuals. These analyses have been shown to be helpful in determining aspects of thermotolerance and heat stress in other shellfish species (Strader et al., 2020) (Chamorro et al., 2023; Unpub.).

Recommendations for K. kelletii fisheries population modeling with respect to MHWs

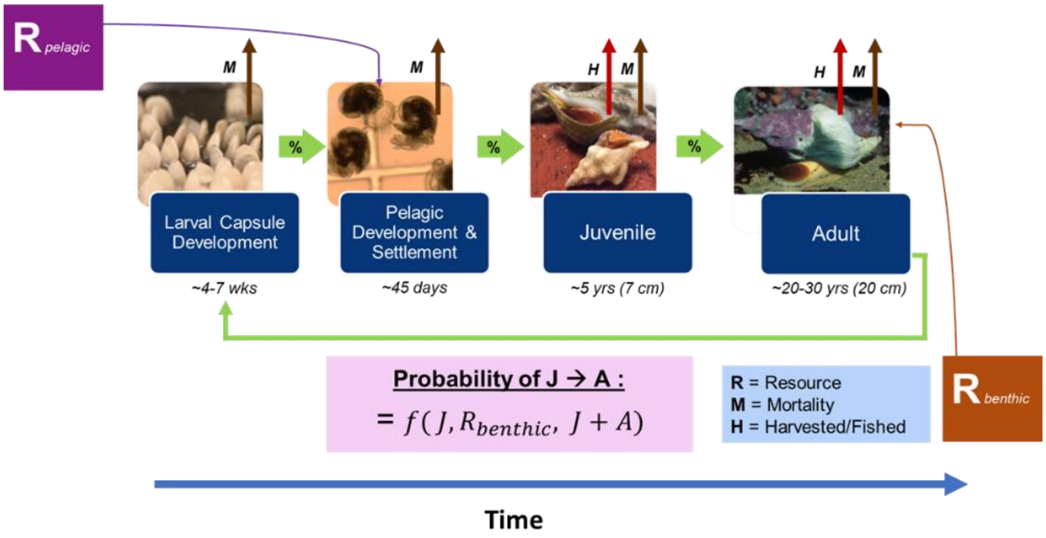


Figure 23. Conceptual framework for a stage-based matrix model of *K. kelletii*.

Predictive modeling of fished populations and MHWs can serve to support fisheries and ecosystems under MHW stress in a variety of ways. Conservation biology and ecosystem management have long used stage-based matrix models that have been shown to be incredibly useful for species like the Kellet's whelk that are not well-represented via traditional ecological surveys (Chen & Liao, 2004; Fujiwara & Caswell, 2001). Recent studies on the impacts of MHWs on West Coast fisheries have determined that enhanced monitoring and modeling of fished species will help provide early warnings of oncoming impacts as well as a stronger mechanistic understanding of fished populations (Free et al., 2023). Specifically, long-term datasets, such as that of the SBC-LTER, combined with experimental findings, such as that of my dissertation, can be used to develop models that support decisions made by management agencies and fishing communities in determining the status of fisheries with respect to MHWs. Eco-physiological life history studies on the effects of MHWs on a fished marine invertebrate (Chapter 2 and 3), can be used to develop mathematical tools to understand population level changes in response to environmental perturbations (Simas, Ribeiro, & Ferreira, 2001). As an example, my dissertation findings could be incorporated into a life stage model (see conceptual population model Figure 23) where vital rates are placed in the context of the whole life cycle of an organism and can be classified into several approaches depending on whether time and stage are continuous or discrete variables (Fujiwara & Caswell, 2001). Life history traits from my dissertation on the development of *K. kelletii* could be used to develop a population projection matrix (Leslie matrix) to calculate what the population will be from time *t* to time *t+1* (Figure 23) (Chen & Liao, 2004).

Variable	Parameter
Growth	
G	Growth rate per stage
Survival	
Ma	Mortality at stage *a*
Reproduction	
Fa	Fecundity at stage *a*
	Sex ratio: Proportion of mature females at stage *a*
	Effective reproductive ratio at stage *a*
EPR	Eggs per recruit
Fishing Pressure	
k	Catchability slope constant
H*rec*	Recreational harvest
E*rec*	Recreational harvest effort
H*comm*	Commercial harvest
E*comm*	Commercial harvest effort

Table 17. Conceptual parameters for a stage-based matrix model of *K. kelletii*.

However, proposing a model for a data limited fishery with respect to MHWs is a task not met without challenge. Due to the fact that populations respond to climate change induced environmental variability, such as MHWs, in a variety of ways at different life stages, population models for invertebrate fisheries often rely on parameter estimates. Invertebrate fisheries, such as *K. kelletii*, are often data poor fisheries with limited information on life cycle traits of to use to infer how a stock or population is performing. Ecological surveys used to model data limited invertebrate fishery populations are often non-targeted surveys (not fishery based) and tend not to sample the full population of the fished species to support fisheries life-stage models. Therefore, to design population models for *K. kelletii* management, future models would benefit from creating model parameters based on a synthesis of literature on similar species (Table 17).

Similar steps have been taken for other invertebrate species, such as the Dungeness crab, where only sparce data were available (Washington Department of Fish and Wildlife legal catch records of 1996–2013) to develop range estimates of vital rate values for the organism. As an example, in order to build a model that analyzed the effect of hypoxia on the data limited Dungeness crab fishery in Hood Canal, Washington, parameter value assumptions were developed to model a general sense of effects of harvest and hypoxia at each "age-step" of the population (Froehlich, Essington, & McDonald, 2017). A preliminary model with "courser" time steps, such as life stage (versus age) of *K. kelletii*, would greatly aid in *K. kelletii* management efforts and could serve as a strong step forward in determining how a data limited invertebrate fishery population, such as *K. kelletii* will be affected by MHWs. A preliminary model of this nature would also be useful in setting management recommendations, harvesting periods and catch size limits for the whelk.

Additionally, a formal stock assessment would assist in providing foundation for modeling general population trends of *K. kelletii* with respect to MHWs, wherein data on boating hours, fishing gear deployment duration, estimates of fishing effort and landings data would be data needed to determine a catch per unit index. These metrics, alongside life history traits, would serve as a proxy of drivers of change in *K. kelletii* harvested populations with respect to MHWs.

Recommendations for K. kelletii fisheries and management with respect to MHWs

The most salient management considerations that have emerged from my dissertation research are that (1) phenology with respect to the life cycle and (2) MHW forecasting are essential aspects of managing the Kellet's whelk emerging fishery. As we grow in our capacity to understand organismal responses to environmental phenomenon, we increase our ability to utilize (1) phenology, the timing of life cycle events at the population level to determine how economically important populations will respond to MHWs. Phenology, often focusing on climate change effects, has become increasingly relevant to conservation and management (Ettinger, Chamberlain, & Wolkovich, 2022). My findings show that Kellet's whelk adults that experience MHW temperatures lay few and low-quality capsules with unsuccessful development of embryos (Chapter 2 and 3). These findings indicate that management strategies should include (2) embracing MHW forecasting that support the whelk fishery and identify potential thermal refuges (Jacox et al., 2022). In the following section, I will discuss means by which to address the aforementioned management concerns below.

Kellet's whelk are predominantly harvested as a bycatch (incidental) species in the California spiny lobster (*Panulirus interruptus*) and crab fisheries. In the California spiny lobster fishery, Kellet's whelk and lobster are 90% of the individual animals caught by number (CDFW, 2020). Mixed fisheries, or "multi-species fisheries" require management that differs from single-species fisheries, in considering dual impacts of fisheries per species. With these features of the fishery, it is important that management considerations for the Kellet's whelk should pair with biological considerations of both species under MHWs.

As an example, in comparing the thermal tolerances for both early stage *K. kelletii* and *P. interruptus*, it was found that the upper limit of development for *P. interruptus* is 21.5 °C (Serfling & Ford, 1975; Velazquez, 2003). Similar to *K. kelletii*, embryonic development and larval hatching of *P. interruptus* coincides with seasonal ocean warming (Velazquez, 2003). However, *P. interruptus* in the California Current Large Marine Ecosystem have been shown to have greater recruitment during warmer years as the result of an analysis of long-term oceanographic trends between 1951 and 2008 (Koslow, Rogers-Bennett, & Neilson, 2012). Here, larval survival and recruitment were positively associated with warm ocean conditions throughout the Pacific west coast fishery (Koslow et al., 2012). In contrast, this same study found that a positive relationship with survivorship and recruitment was not consistent with Baja fished populations during that same timeframe (Koslow et al., 2012).

These findings are consistent with other studies, the findings of my dissertation are similar to the data for spiny lobster, where an impact of MHW temperatures on Kellet's whelk development is observed, yet overall trends and patterns remain to be unclear without further investigation. Studies that have found an impact of increased temperature on reproduction and development on larval California spiny lobster recommend the use of flexible management where opening and closing dates of harvest can account for population performance unpredictability under MHWs (Velazquez, 2003). More studies are finding that there is a response, but patterns in responses are unclear, so we should be prepared for flexible management.

Considering my dissertation findings, I would recommend that similar strategies be taken for managing the Kellet's whelk. While adaptive management may be logistically challenging to coordinate with many constituents, studies find that promoting engagement and public collaboration enhances the adaptive capacity of fishing communities long-term (Free et al., 2023). Increased costs to adaptive management approaches have been mitigated by utilizing partnerships, incentives, and affordable technological advancements (e.g., digital platforms for fishers) (Villasenor-Derbez, Amador-Castro, Hernandez-Velasco, Torre, & Fulton, 2022), that can make monitoring and management more inclusive.

Altogether the findings of my dissertation research affirm past and recent studies on the negative impacts of MHW on early stage shellfish species. Future experimentation on acclimations will allow a greater understanding of how organismal thermal limits will influence reproduction and the thermal tolerance of *K. kelletii* progeny as it pertains to the future of the emerging fishery.

Increasing undergraduate and public access to marine science

As we turn the corner into a pivotal decade for our planet, our society needs environmentally minded individuals and communicators than can educate the public on the importance of the environmental research process. In recent years, research groups have prioritized outreach as a part of their research programs (Nadkarni & Stasch, 2013), however many outreach initiatives arise out of “good-will” (Petrella, 2008), but do not have the capacity to build programming based on established pedagogical approaches that increase inclusivity in STEM. To combat challenges with engaging students and the public with STEM, I developed two platforms for outreach and education as a part of my dissertation that are grounded in the literature on narrative-based active learning.

First in this area, to address challenges with increasing diversity, equity, and inclusion (DEI) and student sense of belonging (SOB) in STEM higher education, I explored the levels of student SOB in an education intervention I developed. The intervention I developed was a symposium that showcased science communication of undergraduate research called “REEFlections”, which focused on using narrative-based active learning to increase SOB for UCSB students at the UCSB Research Experience & Education Facility (REEF) facility. Secondly, the “Science in Action” temperature system and outreach program I developed was a means to conduct MHW research while engaging the public and REEF undergraduates in marine science.

REEFlections: I was the director for REEFlections for three years (2019, 2020, and 2022) and conducted an assessment on student participants in the 2020 REEFlections cohort for my dissertation. 2020 REEFlections was a unique year for the symposium as it was virtual, occurred in the midst of the global COVID-19 pandemic, and violent social unrest. Student interviews showed that even during an exceptionally challenging time, students sought new skills, employed past skills (in science communication and their research topic), rehearsed/practiced, and sought to have better time management in order to navigate REEFlections assignments and activities. Most importantly, my findings indicate that “Social Support” was the most frequently reported aspect of SOB in 2020 REEFlections-related student experiences.

My dissertation research on REEFlections emphasizes the importance of narrative-based active learning activities in establishing a more welcoming environment in STEM. It is clear that social support in the form of peer and mentor interaction in my REEFlections intervention was successful in developing inclusive environments that supported student performance. Another component of active learning unique to my REEFlections program was narrative and dialogue. Since it is not possible to represent aspects of all student’s experiences (e.g., gender, sexual orientation, cultural background) in an education program, narrative-based active learning allows for the integration of culturally diverse and personally relevant connections to STEM in small ways. This helps demonstrate to students that diverse perspectives are valued in the classroom. For example, EarSketch, a STEAM-based active learning intervention for computer science increased SOB by using popular music to enable students to express their personal narrative in their course work (Siva et al., 2018). Models on inclusive education assert that unidirectional instruction isolates and alienates students in underrepresented minority groups (Dewsbury, 2017; Freire, 1986). Student investment and retention of STEM concepts is elevated when dialoguing is used as a tool to create equity between instructors and students (Benmayor, 2012; Bernal et al., 2012; Espino et al., 2012; LopezLeiva et al., 2016). For students that feel marginalized in their own campus communities, and further marginalized in new academic environments, interactive active learning programs provide moments of dialogue that allow for student's experiences to be validated in the classroom (S. Freeman et al., 2014; Norris et al., 2005). These learning environment gains serve to benefit students of all backgrounds in feeling more welcome in STEM. The intervention I designed was proactive about utilizing findings and practices from a wider range of fields to establish the intervention's pedagogical foundation, such as that of: Social, Cognitive, and Psychological Sciences (SOB theory)—and more daringly, Humanities and Arts (e.g., science communication).

"Science in Action" temperature manipulation system and outreach program: The MHW acclimation and simulation experiments for my dissertation research (Chapter 3 and 4) were staged in the temperature manipulation experiment display system I initiated at the REEF. The temperature manipulation experiment display system served as a public facing "science in action" experimental platform to service both the climate change biology and the outreach portions of my dissertation. This collaboration was also initiated as a platform to facilitate the involvement of REEF undergraduates in marine science research on campus. The experiment-display now serves as a long-standing platform for research and outreach at the REEF and for future marine science graduate students at UCSB. In this section, I will discuss some of the outreach gains and experimental challenges involved in this “science in action” REEF collaboration for the MHW acclimation and simulation experiments in my dissertation.

The outreach and education programs staged from the experiment display spanned two campus working phases of COVID-19: severe workplace safety concerns for COVID-19 (Chapter 3, 2021) and relaxed safety concerns for COVID-19 (Chapter 4, 2022). In both phases, I was successful in engaging K-12 students in my experiment-display research (virtually and in-person). I mentored a team of REEF undergraduate research assistants (2019-2022) to participate virtual and in-person science communication with the public via the display by modeling presentations myself from which project personnel were able to develop their own “real-time” presentations.

The combined events of students returning to campus and participating in my research was a phenomenal way to initiate a “new normal” scenario for returning and incoming student cohorts during COVID-19. Student research assistants were onboarded virtually, and as COVID-19 safety restrictions began to relax, additional REEF undergraduates were onboarded in-person. Assessing student skill and ability to partake in undergraduate research was one of the challenges of remote mentoring, onboarding and recruitment. Thus, there was also a limited capacity for training undergraduate researchers. This resulted in project assistants having varying levels of familiarity with the larval biology methods needed to collect project data. Further, a limited student availability and funds for student time in both projects (Chapter 3 and 4) resulted relying on project personnel who could only be recruited to work on a voluntary basis or for limited hours. Despite these challenges, the temperature manipulation system and animal husbandry was maintained by REEF student employees with mixed levels of aquaria experience (intermediate to expert).

This “science in action” collaboration by nature, was intended to unveil the organic aspects of marine science research to public (K-12) audiences. Future collaborations of this nature, between research and outreach groups, will benefit from better coordination of space use. As an example, campus visitor presentation programming often occurred in simultaneous experimental spaces. The larvae for the experiment in Chapter 4 were scored in a REEF trailer at the REEF facility. While working in the REEF trailer supported scientific goals (to be in closer proximity to working with larvae), since the REEF trailer is also an education space, it was often difficult to balance the co-use of the space with ongoing REEF activities. Nevertheless, conducting the experiment in the REEF trailer allowed both REEF undergraduates and visiting students an opportunity to witness “science in action”.

Outreach programs catered towards supporting undergraduate research can enhance the research effort and can contribute to the broader impacts of the research at hand (Jordan, 2012; Shirk et al., 2012). However, like most education and research collaborations, the research collaboration I initiated at the REEF involved a suite of research-to-outreach tradeoffs. These findings align with past studies on the tradeoffs experienced in citizen science research-to-outreach initiatives. Studies on citizen science outreach programs find that similar tensions can emerge between scientific goals (acquiring data) and educational goals (engaging students and the public), even when missions are well aligned between programs and organizations (Sickler, 2014). As an example, a study on ecological citizen science outreach identifies that research-to-outreach programs often experience tradeoffs between data quality, protection, transparency, and trust. Specifically, data quality can vary by volunteer experience (e.g., prior knowledge and training) (Anhalt-Depies, Stenglein, Zuckerberg, Townsend, & Rissman, 2019; Lewandowski & Specht, 2015). Based on past research-to-outreach studies and my dissertation findings, I recommend that research-to-outreach projects anticipate these tradeoffs, develop practices to address tradeoffs, and regularly reassess protocols and procedures. Assessments of ingroup protocols and procedures should involve feedback from participants to ensure that all participants are aware of the agreed methods for data collection (Anhalt-Depies et al., 2019; Lewandowski & Specht, 2015).

My dissertation findings on the value of the my “science in action” research-to-outreach program are also supported by past studies. Despite the identified tensions that arise in research-to-outreach collaborations, it is largely agreed that the tradeoff cost of integration of scientific value and public science experiences creates important compelling discourse on scientific issues for scientists and non-scientists (Sickler, 2014). Similarly, I found in my dissertation work that the cost of engaging non-scientist research assistants (undergraduate researchers) and public audiences (K-12, and the general public) did not outweigh the benefits of this collaboration. Namely, during a time where there were high levels of uncertainty around public safety (with respect to COVID-19 and social unrest), the research-to-outreach collaborations I facilitated at the REEF allowed for fast-pace critical thinking on how to circumvent research challenges while guiding the oncoming generations of STEM in climate change biology.

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