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Santa Barbara

Marine heatwaves impact reproductive success in

Strongylocentrotus purpuratus

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

by

Adriane Michelle McDonald

Committee in charge:

Professor Gretchen Hofmann, Chair

Professor Halley Froehlich

Professor Nick Nidzieko

Professor Karen Chan, University of Washington

December 2025

The dissertation of Adriane Michelle McDonald is approved.

Halley Froehlich, Ph.D.

Nick Nidzieko, Ph.D.

Karen Chan, Ph.D., University of Washington

Gretchen Hofmann, Ph.D., Committee Chair

December 2025

Marine heatwaves impact reproductive success
in *Strongylocentrotus purpuratus*

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by

Adriane Michelle McDonald

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VITA OF ADRIANE MICHELLE MCDONALD

December 2025

EDUCATION

2019 – present **University of California Santa Barbara (UCSB), Santa Barbara, CA**
Ph.D. Candidate in Ecology, Evolution, and Marine Biology (EEMB)
Advisor: Professor Gretchen Hofmann
Expected Graduation Date: December 2025

2015 – 2019 **Spelman College, Atlanta, GA**
B.S. in Biology, *Magna Cum Laude*, Ethel Waddell Githii Honors
Program

FELLOWSHIPS & AWARDS

2025 UCSB EEMB Block Grant

2024 National Science Foundation INTERN – Supplemental Grant
Collaborative Organization: Marine Mammal and Sea Turtle Division,
Southeast Fisheries Science Center, National Oceanic and Atmospheric
Administration (NOAA)

2023 Long-term Ecological Research (LTER) Program Graduate Writing
Fellowship

2021 Schmidt Family Foundation Research Accelerator Award

2021 National Science Foundation (NSF) Graduate Research Fellowship
Program

2021 Center for Diverse Leadership in Science Early-Career Fellowship

2019 Associated Students Coastal Fund Minor Research Grant

2019 University of California – Historically Black Colleges and Universities
Initiative Graduate Fellowship

PUBLICATIONS

Chan, K. Y. K., Kui, L., **McDonald, A. M.**, Ritger, A. L., & Hofmann, G. E. (2024).
Coastal marine heatwaves in the Santa Barbara Channel: decadal trends and
ecological implications. *Frontiers in Marine Science*, 11.
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<https://lternet.edu/stories/land-and-water-cover/>

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[doi:10.3389/fmars.2023.1212781](https://doi.org/10.3389/fmars.2023.1212781)

Aluru, N., Krick, K. S., **McDonald, A. M.** Karchner, S. I. (2020) Developmental Exposure to PCB153 (2,2',4,4',5,5'-Hexachlorobiphenyl) Alters Circadian Rhythms and the Expression of Clock and Metabolic Genes, *Toxicological Sciences*, 173(1), 41–52. [doi:10.1093/toxsci/kfz217](https://doi.org/10.1093/toxsci/kfz217)

PRESENTATIONS

McDonald, A.M., Hofmann, G.E. (2024) Impacts of Marine Heatwaves on a Primary Driver of Northeast Pacific Kelp Forest Recovery and Decline (*S. purpuratus*). The Diversity Project Summer Symposium; 2024 August 17; Los Angeles, California.

^T **McDonald, A. M.**, Hofmann, G. E. (2023) Investigating Impacts Of Marine Heatwaves On A Primary Driver Of Kelp Forest Recovery And Decline: *Strongylocentrotus purpuratus*. Western Society of Naturalists Meeting; 2023 November 11; Monterey, California.

^T **McDonald, A. M.**, (2020) What We Know: California Aquaculture and Environmental Stressors. Western Society of Naturalists Meeting; 2020 November 7; Virtual.

^T **McDonald, A. M.**, Aluru, N., Krick, K. S.Karchner, S. I. (2020) Developmental Exposure to PCB153 (2,2',4,4',5,5'- Hexachlorobiphenyl) Alters Circadian Rhythms and the Expression of Clock and Metabolic Genes. Ocean Sciences Meeting; 2020 February 17; San Diego, California.

McDonald, A. M., Aluru, N., Krick, K. S.Karchner, S. I. (2020) Developmental Exposure to PCB153 (2,2',4,4',5,5'- Hexachlorobiphenyl) Alters Circadian Rhythms and the Expression of Clock and Metabolic Genes. WHOI Summer Undergraduate Research Forum; 2018 August 8; Woods Hole, Massachusetts.

McDonald A. M., Tekle Y. (2019) Vestigial genes? Examining the Presence of Genes Encoding for Radial Spoke and Central Pair in Non- flagellate Amoebas. Spelman College Research Day; 2019 April 25; Atlanta, Georgia. **Award: First Place**

McDonald A. M., Wang D. (2018). Analyzing Promoter 5' Deletions on InvINH1 during Seed Development. Spelman College Research Day; 2018 April 20; Atlanta, Georgia.

McDonald A. M., Wang D. (2018). Analyzing Promoter 5' Deletions on InvINH1 during Seed Development. Annual Biomedical Research Conference for Minority Students; 2018 November 15; Indianapolis, Indiana.

^T **McDonald A. M.,** Bideau S., Gasca M. (2017) Urchins Are Important Herbivores and Mediate Positive Effects of Sediment on Algal Turfs. University of California, Los Angeles Summer Research Symposium; 2017 August 18; Los Angeles, California

McDonald A. M., Bideau S., Gasca M. (2017) Urchins Are Important Herbivores and Mediate Positive Effects of Sediment on Algal Turfs. Ocean Sciences Meeting; 2018 February 14; Portland, Oregon.

McDonald A., Lawrence A., Williams A. The Effect of Germline Mutations on the MSH2 Gene in Hereditary Nonpolyposis Colorectal Cancer. Spelman College Research Day; 2017 April 21; Atlanta, GA.

PROFESSIONAL EXPERIENCE

Summer 2024 **Graduate Student Researcher,** Marine Science Institute, Santa Barbara Coastal Long-term Ecological Research (SBC LTER), UCSB
P.I.: Robert Miller, Ph.D.

Summer 2020 **Graduate Student Researcher,** Marine Science Institute, SBC LTER, UCSB
P.I.: Robert Miller, Ph.D.

2017 – 2019 **Undergraduate Researcher,** Department of Biology, Spelman College
P.I.: Professor Dongfang Wang

Summer 2018 **Summer Student Research Fellow,** Department of Biology, Woods Hole Oceanographic Institution
P.I.: Neel Aluru, Ph.D.

Summer 2017 **Undergraduate Researcher,** Department of Ecology and Evolutionary Biology, UC Los Angeles
P.I.: Professor Paul Barber and Professor Peggy Fong

TEACHING EXPERIENCE

Spring 2024 **Teaching Assistant,** EEMB116: Invertebrate Zoology, EEMB Department, UCSB, Santa Barbara, CA

Spring 2023 **Head Teaching Assistant,** EEMB2LL: Introductory Biology Lab, EEMB Department, UCSB, Santa Barbara, CA

Winter 2022 **Teaching Assistant, MCDB1LL:** Introductory Biology Lab,
Molecular, Cellular, and Developmental Biology Department, UCSB,
Santa Barbara, CA

MENTORSHIP & LEADERSHIP

Summer 2024 Graduate Student Mentor, Academic Research Consortium, Graduate
Division, UCSB, Santa Barbara, CA

Summer 2024 Graduate Student Mentor, Field-based Undergraduate Engagement
through Research, Teaching, and Education (FUERTE), UCSB,
Santa Barbara, CA

2023 – 2024 Graduate Student Symposium Committee Member, Ecology,
Evolution, and Marine Biology Department, UC Santa Barbara

2023 – 2024 Graduate Student Assistant, Office of Black Student Development,
UCSB, Santa Barbara, CA

Summer 2023 Graduate Student Mentor, Academic Research Consortium, Graduate
Division, UCSB, Santa Barbara, CA

Summer 2023 Graduate Student Mentor, FUERTE, UCSB, Santa Barbara, CA

Summer 2022 Lead Mentor for Global Change Biology Research Experience for
Undergraduates Program, EEMB Department, UC Santa Barbara

OUTREACH & SCIENCE COMMUNICATION

2023 – 2024 Graduate Student Symposium Planning Committee, EEMB
Department

2023 Black Gaucho Family Weekend Planning Committee, UCSB, Santa
Barbara, CA

2022 – 2023 LTER Graduate Student Writer, Long-term Ecological Research
Program (LTER) Network Office

HONORS AND PROFESSIONAL AFFILIATIONS

Black Women in Ecology, Evolution, and Marine Science Member
Black in Marine Science Member
Association for the Sciences of Limnology and Oceanography
Phi Beta Kappa Honor Society
Beta Beta Beta National Biology Honor Society

CERTIFICATIONS & TRAININGS

2021	Introduction to R for Bioinformatics – UC Davis Bioinformatics Core, Online
2021	Science Storytelling for Impact, Schmidt Family Foundation
2017	AAUS Scientific Diver

ABSTRACT

Marine heatwaves impact reproductive success in *Strongylocentrotus purpuratus*

by

Adriane Michelle McDonald

Marine heatwaves (MHWs) are persisting and increasing in frequency and duration, and they are occurring with greater severity than in past decades. MHWs are a widespread occurrence, and events can span thousands of miles. As anthropogenic climate change worsens, we will be experiencing more intense marine heatwave events, so investigation into their biological impacts is necessary. My research focus was centered on the impacts of marine heatwaves, on the purple sea urchin, *Strongylocentrotus purpuratus*. *S. purpuratus* is an important sedentary herbivore in Santa Barbara Coastal kelp forests. Previous research identifies transgenerational plasticity in urchins, where the environment of the adults impacted the phenotype of offspring. Specifically, maternal and paternal provisioning in eggs and offspring assist with successful fertilization and offspring physiology. In my dissertation, I had three aims: 1) investigate how exposure to fluctuating MHWs during gametogenesis in adults impacts egg quality and fertilization success, 2) utilize SBC LTER data to investigate MHW patterns and how they correlate with *S. purpuratus* abundance, size, and larval settlement, and 3) probe for local adaptation between populations of *S. purpuratus* across their biogeographic distributions along the California Current Large Marine Ecosystem. In my first aim, I discovered that exposure to MHW conditions during gametogenesis led to larger eggs with greater protein content. If adults are exposed to adverse conditions during gametogenesis, they may provision greater biomolecules in eggs to help with

growth and development. In my second aim, I discovered decreases in urchin abundance over time and an impact of urchin abundance on kelp detritus. This is consistent with the phase shift from healthy kelp forests to urchin barrens that we have seen during periods of ecological stress. In my third aim, I discovered egg and gonad differences in urchins from Mohawk reef, the southernmost site. Eggs were smaller, but gonad weight was greater in Mohawk urchins. This suggests the potential for local adaptation, but further research is necessary, such as a common garden experiment, to further investigate population level differences. Overall, marine heatwaves are occurring regularly and can cause adverse organismal impacts, but tolerance mechanisms may allow organisms to survive or thrive in future climate scenarios.

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I. Introduction

Statement of problem

MHWs are defined as periods of anomalously warm surface seawater temperatures, events that last for at least five days. Anomalously warm water temperatures are defined as temperatures beyond the 90th percentile based on a 30-year historical baseline period (Hobday et al. 2016). Evidence shows that the number of MHW events and total MHW days have been increasing over the years with models predicting that MHWs will only continue to become more frequent due to global climate change (Frölicher et al. 2018). Already we see that since 1982, frequency of MHWs has doubled.

Ecologically, these temperature events have been shown to impact coastal marine ecosystems worldwide (Oliver et al. 2021, Wernberg et al. 2013), altering community structure and function (Smith et al. 2023). In 2013, a MHW persisting for ~2 years formed off the northeast Pacific coast spanning from Alaska down to Baja California. This MHW, commonly known as “the Blob,” caused horizontal and vertical range shifts in fish (Li et al. 2019) and invertebrates (Cavole et al. 2016). In addition, major changes in biodiversity were observed (Michaud et al. 2022, McPherson et al. 2021, Suryan et al. 2021, Sanford et al. 2019, Rogers-Bennett and Catton 2019), and Shanks et al. 2019). Because MHWs are now a recurrent Northeast Pacific phenomenon (Xu et al. 2021) and climate change impacts the severity of MHWs, potential negative ecological impacts of MHWs are a critical research need, especially regarding ecosystem services and socioeconomic issues (Smith et al. 2021).

In our local area, the coastal region of Santa Barbara Channel, data has shown that MHWs have been persistent for almost a decade (Figure 1). In addition to “the Blob” in

2013, 2018 was another major year with multiple MHW events, although not as intense as years when the Blob occurred (see Table 1 and Figure 1). However, overall frequency of when MHWs occur has increased since 2013, impacting the potential ability of marine ecosystems to recover. The presence of these anomalous events has the potential to completely restructure marine ecosystems by causing deleterious impacts to foundational species present in the Santa Barbara Channel such as *Macrocystis pyrifera* (Giant kelp) (Smale et al 2019, Cavanaugh et al. 2019). MHWs in the northeast Pacific have also caused biomass decrease and shifts in biogeography of fish stocks (Cheung and Frölicher 2020, Yang et al. 2019, Leising et al. 2015) and pelagic microzooplankton (Brodeur et al. 2019).

	MHW events	Total days	Average length of MHW	Average Intensity
<i>2015 surface</i>	8	238	~30 days	2.9567
<i>2015 bottom</i>	7	243	~35 days	2.8367
<i>2018 surface</i>	6	82	~14 days	2.2120
<i>2018 bottom</i>	5	76	~15 days	2.4113

Table 1. MHW data from two years with persistent MHW events. Intensity is calculated by subtracting the climatological mean temperature from the recorded temperature on that day.

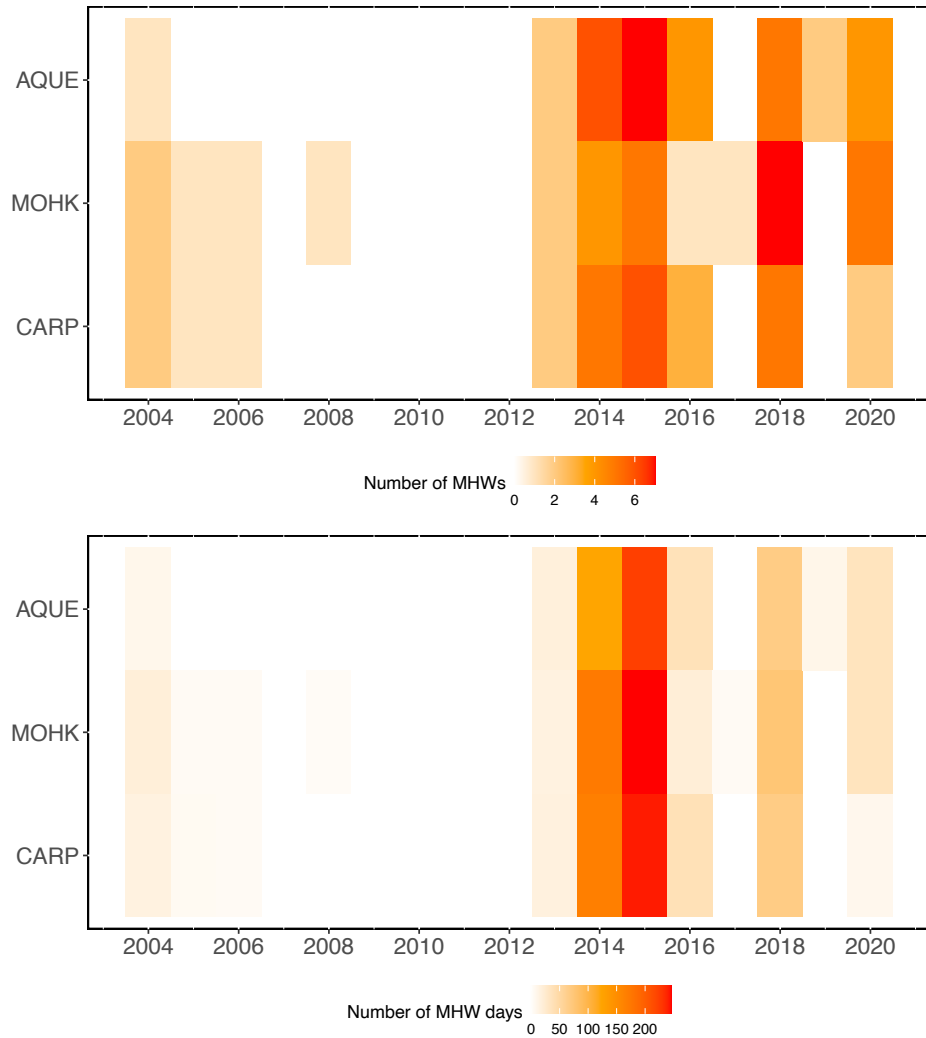


Figure 1. Heat maps showing A) the number of MHW events and B) total MHW days at three core study sites of the Santa Barbara Coastal Long Term Ecological Research program (SBC LTER) from 2004 to 2020, as illustrated by the x-axis. On the y-axes, abbreviations are site names for Arroyo Quemado (AQUE), Mohawk Reef (MOHK), and Carpinteria Reef (CARP). Warmer colors indicate more MHW events (A) and more MHW days (B). Data were sourced from the SBC LTER data catalog (Reed and Miller 2022). Plot courtesy of Dr. Li Kui.

Kelp forests and MHWs: the study system

Existing data shows an increase in frequency of MHW events in the SBC, which led to my interest in looking at MHWs in productive kelp forest ecosystems in the temperate Pacific. The Northeast Pacific is one of the most productive marine ecosystems, providing habitat and food resources to many organisms as well as many

other ecosystem services. Previous work illustrates the vulnerability of kelp forests to MHWs (Pfister et al. 2017, Smale et al. 2019, Smale 2019, Suryan et al. 2021) and indicates that regime shifts known as “tropicalization” may occur that prevents recovery of kelp forests (Wernberg et al. 2016). In fact, the historically resilient and robust northern California kelp forests transitioned to an altered ecosystem state with low productivity (McPherson et al. 2021) and large sea urchin barrens (Rogers-Bennett and Catton 2019). In Southern California, mean sessile invertebrate cover declined during “the Blob”; although elevated temperatures may not be the sole reason for this loss (Michaud et al. 2022). At an even more southern kelp forest ecosystem, there were significant declines of *M. pyrifera* and significant changes in overall kelp forest community structure, such as declines in fish and invertebrate species after the MHWs of 2014-2017 (Arafeh-Dalmau et al. 2019). Overall, more southern regions of the Pacific region appear to be more sensitive to climatic changes (Beas-Luna, et al. 2020 and Hammond and Hofmann 2010) though northern regions are also susceptible to detrimental phase shifts that impact kelp forest community structure in the Eastern Pacific.

Changing kelp forest community dynamics in the face of environmental change led me to select the purple sea urchin, *S. purpuratus*, as my study organism. Urchins are an important benthic invertebrate in kelp forests that can be impacted by climate stressors, such as elevated temperature, due to their limited mobility and pelagic larval stage. During the 2015 MHW, there was a decline in sea urchin biomass in the SBC (Reed et al. 2016) and abundance declined at more southern sites in response to the same 2014-2016 MHW in the California Current System. Other studies have shown that northern sea urchin populations have increased in abundance during and post-MHW,

creating urchin barrens (McPherson et al. 2021). These barrens may be due to increased settlement of sea urchins even in the face of elevated temperature (Hernandez et al. 2010), which suggests that the projected increase of MHW events in the future may only further contribute to more of a shift from a healthy balanced kelp forest ecosystem to large urchin barrens, especially as urchins are able to survive starved and poorly nourished for years (Dolinar 2021). The difference in urchin abundance between southern and northern areas may be due to the regional difference in MHW temperature dynamics where Southern populations of urchins may already be living at their temperature range edge and unable to adapt to a higher temperature in contrast to Northern populations.

In addition to overall changes in population dynamics, *S. purpuratus* show cellular and whole organism level responses to MHWs. Female purple sea urchins have been identified to develop larger eggs when they experience elevated temperature during gametogenesis (Suckling et al. 2015). When exposed to MHW temperatures, male *S. purpuratus* sperm have diminished performance (Leach et al. 2021) which may negatively impact overall fertilization success. In other urchin species, exposure to elevated temperature also negatively impacted normal development success and fertilization success (Byrne et al. 2009). Documented impacts on elevated temperature on various life history stages of *S. purpuratus* provide information on how urchins may fare as MHW events increase in intensity and frequency; however, MHW dynamics are extremely variable, so my dissertation will contribute to this field of research. Specifically, I focused on analyzing how different MHW dynamics are within the Santa Barbara Channel region and how that translates to urchin and kelp abundance. Additionally, further exploring MHW impacts during important life history events and in

different populations will provide essential information on biogeographical and phenological impacts, which may be useful for ecosystem management strategies.

Objective

The main goal of my dissertation research is to examine marine heatwave (MHW) events and their impact on larval development and fertilization success of a sessile benthic marine invertebrate native to coastal kelp forests, the purple sea urchin, *Stronglyocentrotus purpuratus*. This work will be primarily conducted in the Santa Barbara Channel (SBC) region, part of the southern California Current System. The purple sea urchin is an ideal study organism due to their ecological significance in kelp forests (Pearse 2006), and the significant history the species has as a model organism in developmental biology, including their quick developmental timeline and ease of handling in a laboratory setting. The questions that frame my dissertation are:

- (1) when and where are MHW's occurring and how do these patterns correlate with *S. purpuratus* adult abundance and larval settlement as well as *M. pyrifera* abundance,
- (2) how does exposure to fluctuating MHWs during gametogenesis in adults impact egg quality and fertilization success, and
- (3) are there population level differences in *S. purpuratus* across their biogeographic distributions along the California Current Large Marine Ecosystem?

Generally, my hypotheses are:

- (1) There is an increase of MHW frequency and intensity over time, and that will be associated with subsequent increases in urchin abundance and size and decreases in *M. pyrifera*,
- (2) Exposure to fluctuating MHWs during gametogenesis will lead to greater provisioning of energy biomolecules to eggs and offspring, enabling progeny to be better suited to fare well in adverse environmental conditions during development,
- (3) If *S. purpuratus* are closer to their southernmost range edge, there will be greater gonadosomatic indices, greater thermal tolerance during fertilization, and increased maternal provisioning of biomolecules compared to their more northern counterparts.

Overall, my work is contextualized by MHWs as high environmental temperature events that have become common in our region and identified to impact members of the kelp forest benthic marine invertebrate community.

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II. Marine heatwave impacts on *S. purpuratus* egg and offspring quality

Introduction

Anthropogenic climate change is causing the exacerbation of natural disasters, such as extreme temperature, hurricanes, and droughts, globally (IPCC 2012). Extreme temperature anomalies in the ocean, known as marine heatwaves (MHWs), are extreme disturbance events that are increasing in frequency, duration, and intensity (Capotondi et al. 2024, Oliver et al. 2018). MHWs are identified when the sea surface temperature exceeds that of the 90th historical baseline for at least 5 consecutive days, although thermal anomalies can last for fewer days (Hobday 2018). MHWs have altered community structure and function worldwide (Smith et al. 2023) and impacts of MHWs are still being quantified. There are many different patterns of MHWs that can exist in the environment. Prolonged MHWs may last for months or years while fluctuating marine heatwaves may only last for a week at a time with periods of temperature recovery in between. Investigating various MHW patterns in different ecosystems and among different taxa is essential to properly assess potential impacts globally.

My study system of interest, the Santa Barbara Channel, is a very productive, biodiverse marine ecosystem characterized partially by rocky reefs with acres of kelp forests of *Macrocystis pyrifera*, a foundational species and dominant source of primary production. In the Santa Barbara Channel, MHW patterns have varied. This region has experienced prolonged MHW stress via an extreme event in 2014-2015 (Di Lorenzo and Mantua 2016), fluctuating MHWs in 2018, and persistent bottom marine heatwaves (Chan et al. 2024) (Figure 1). Spatial variability of foundational species, such as giant kelp, are of particular concern with the increase in MHW events (Cavanaugh et al. 2019

e, Filbee-Dexter et al. 2020, McPherson et al. 2021, Smale et al 2019, Tait et al. 2021) with evidence of environmental shifts impacting primary productivity of northern California kelp forests. Studies have shown that kelp forests may be vulnerable to MHWs (Pfister et al. 2017, Smale et al. 2019, Smale 2019, Suryan et al. 2021) and may experience regime shifts known as “tropicalization” that prevent recovery (Wernberg et al. 2016, McPherson et al. 2021). In response to the 2014-2015 MHW, a phase shift from a robust kelp forest to large sea urchin barrens occurred in Northern California (Rogers-Bennett and Catton 2019). Evidence has also indicated that grazing pressure may increase under elevated temperature due to increased physiological demand of herbivorous organisms, such as sea urchins and fish (Johnson et al. 2011, Verges et al 2014, Bennett et al. 2015b). Overall, extreme MHW events have caused major changes in biodiversity (Michaud et al. 2022, McPherson et al. 2021, Suryan et al. 2021, Sanford et al. 2019, Rogers-Bennett, Catton 2019, Li et al. 2019, Cavole et al. 2016) and biomass decreases of fish stocks (Cheung and Frölicher 2020, Yang et al. 2019, Leising et al. 2015) and pelagic zooplankton (Brodeur et al. 2019.), though in contrast, abundance of kelp in the Santa Barbara Channel region was not as severely impacted as in other regions (Reed et al. 2016) such as Australia that have experienced significant warm water anomalies starting in 2011 (Wernberg 2021). It is clear that MHWs may impacts organisms and regions differently, so it is vital to continue to study their impacts to assess how kelp forests and the organisms that relay on them may fare in response to future MHWs.

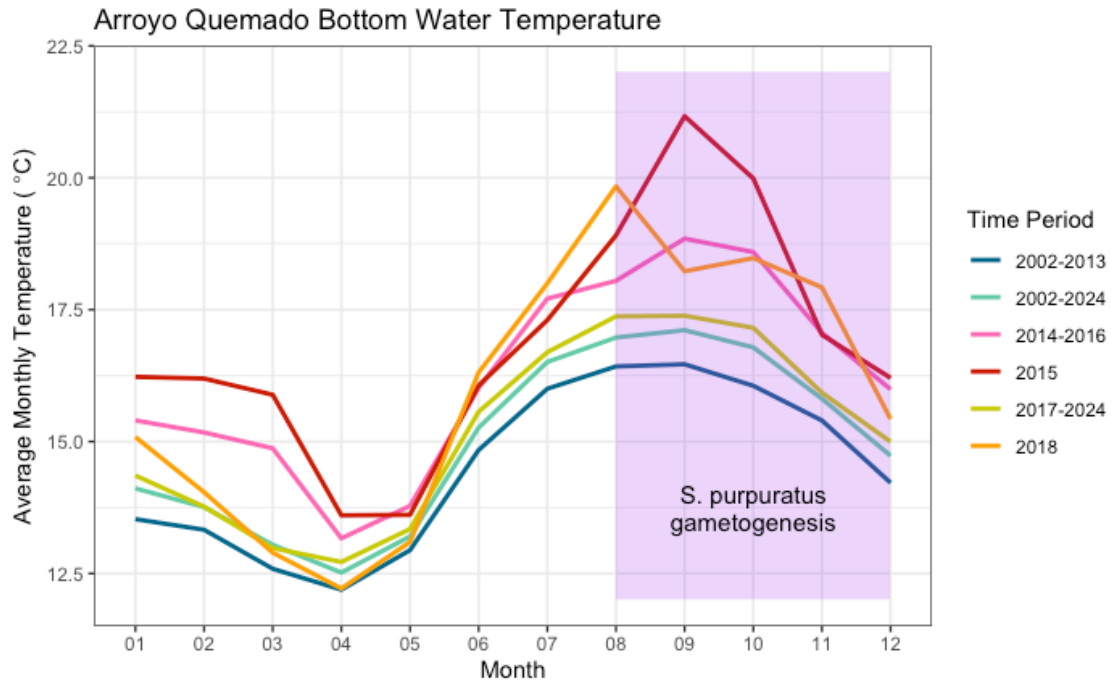


Figure 2. Average monthly temperature at Arroyo Quemado (34.46774988, -120.11905), a Santa Barbara Coastal Longterm Ecological Research (SBC LTER) Site, at a depth range of 5.4 m to 10.7 m. Temperatures were collected from August 2002 to July 2024 by two submersible temperature loggers (Tidbit, Onset Computer Corporation). Temperatures were recorded every 15 minutes. Each line corresponds to a particular time period. The dark blue line represents the time period of 2002-2013, before ‘the Blob’ formed in the Northeast Pacific region. The yellow line represents 2017-2024, which is after ‘the Blob.’ The pink line corresponds to the years 2014-2016, ‘the Blob’ years. The red line represents the average monthly temperature for 2015, a peak year for ‘the Blob.’ The orange line represents the average monthly temperature for 2018, a marine heatwave year considered to be less severe than ‘the Blob,’ with more fluctuating MHWs.

Strongylocentrotus purpuratus, the purple sea urchin, is a dominant herbivorous, benthic, sessile organism in kelp forest ecosystems of the California coast. In the Santa Barbara Channel, they are a key part of kelp forest food webs, relying on *Macrocystis pyrifera* for food and being a food source for sea stars, sheephead fish, and sea otters. *S. purpuratus* is also commonly used as a model organism because of their rapid development, ease of culturing, and transparent embryos. In the context of climate change, their pelagic embryos, broadcast spawning, and sessile nature create an opportunity to assess their susceptibility to changes in environmental conditions such as

temperature, ocean acidification, and other stressors. Additionally, the *S. purpuratus* gametogenesis period correlates with a time in the environment where MHWs are common (July – December) in the Santa Barbara Channel and due to the presence of bottom MHWs (Chan et al. 2024) and limited movement, they may be unable to find refuge from these temperature events. Existing studies demonstrate increased mortality and depletion of energy reserves in a subtidal gastropod at a temperature below its thermal tolerance in response to MHW temperatures (Leung et al. (2017). In sea urchins, MHWs caused lasting physiological impacts (Minuti et al. 2021) even after return to ambient conditions. As MHWs in the SBC coincide with *S. purpuratus* gametogenesis, exploring potential mechanisms of resilience in adults and their offspring through maternal provisioning will contribute to further understanding of MHW impacts.

Exposure to elevated temperature during gametogenesis impacts offspring physiology and success, where adult urchins may invest nutrients in their eggs to prepare offspring for survival in adverse conditions. Prior studies have described these cellular and whole organism level responses of *S. purpuratus* to MHWs. Female urchins have been identified to develop larger eggs when they experience elevated temperature during gametogenesis (Chamorro et al. 2023, Suckling et al. 2015). When exposed to MHW temperatures, male urchins produce sperm with diminished performance (Leach et al. 2021) which may negatively impact overall fertilization success. In other urchin species, exposure to elevated temperature also negatively impacted normal development success and fertilization success (Byrne et al. 2009). Gonadal growth, development, and spawning has been identified to occur earlier in cooler water temperatures, potentially suggesting that stressful conditions, such as elevated temperature, stall successful

gametogenesis and spawning (Basch and Tegner 2007). These clear impacts suggest a need to provide additional analyses on the specific mechanisms urchins and other broadcast-spawning sessile invertebrates may utilize for resilience.

Food availability to support energy needs is an important factor for organismal resilience in response to, or in preparation for, adverse environmental conditions. Energy reserves are often depleted when organisms are exposed to stressful conditions, such as temperature. Studies on adults in MHW studies have shown that exposure to a rapid increase to anomalously high temperatures caused significant physiological demands. MHWs caused significant declines in reproductive rates, increases in metabolically driven food demands, nonadaptive metabolic depression, and mortality (Chandrapavan et al. 2019, Wild et al. 2019, Hemraj 2020, Piatt et al. 2020, Minuti et al. 2021) in marine organisms. Transgenerational impacts such as maternal provisioning in eggs or offspring physiology is also a consequence of MHW exposure in adults.

For early stages of benthic invertebrates, there is limited information about the plasticity and resistance capacity when facing new temperature regimes. As with adults, the lack of sufficient reserves in early life history stages of organisms can cause impacts on body size, growth rate, and tolerance thresholds (Mendt and Gosselin 2021, Mendt and Gosselin 2022). Some studies have shown that there may be an immune response to support tolerance of high temperatures (Wilkins et al. 2024). Energetically, increased provisioning of biochemicals in eggs allow early stages to fare better during development in potentially detrimental oceanographic environments. Proteins, lipids, and carbohydrates are primary biochemical constituents that contribute to growth and efficiency of marine invertebrates as surplus energy storages (Jaeckle 1995, Holland and

Gabbott 1971, Wourms 1987). In early stages, they provide major energetic and structural elements for larval development (Moran and McAlister 2009). These energy reserves allow quick metabolic responses for elevated energy demands due to increased stress (Sokolova et al. 2012), though they have limited capacity. Energy reserves are fundamental to an organism's health and fitness in response to stress; however, environmental stress can affect the energy balance of an organism due to its need to maintain homeostasis in stressful conditions

To further understand the impact of MHWs during phenological events (e.g., the timing of gametogenesis) and specifically the role of adult thermal history on energy reserves in eggs and the physiology of offspring, I conducted laboratory acclimations of *S. purpuratus* to temperatures typical of marine heatwave events during gametogenesis. Eggs from acclimated *S. purpuratus* were collected and embryos were cultured to probe for differences in the biochemical composition of eggs and offspring from adults with MHW vs. non-MHW thermal histories. Here, I tested the hypotheses that: exposure to short-term fluctuating marine heatwaves during gametogenesis will 1) increase the survival and performance of offspring in the form of increased body size, biochemical constituents, and thermal tolerance, and 2) increase maternal provisioning of biochemical constituents in eggs.

As the climate changes and detrimental environmental conditions persist, the ability of organisms to adapt to their external environment is a research priority. Phenotypic plasticity, the ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions (Pigliucci et al. 2006), is one method that organisms can use to adapt to adverse conditions. Transgenerational plasticity, the

phenomenon that plasticity can arise in offspring in response to the environmental conditions their parents experience, is a form of phenotypic plasticity that can be achieved through maternal or paternal provisioning. Transgenerational plasticity has been identified in early stages of *S. purpuratus*. Differences in conditions experienced by mothers had an impact on gene methylation in the offspring of *S. purpuratus* (Strader et al. 2019). Paternal effects on fertilization have also been observed where sperm performance diminished when fathers are exposed to a MHW temperature during gametogenesis (Leach et al. 2021). Although, when parents are exposed and able to thrive in less-than-optimal environmental conditions, their offspring have been identified to be better suited to thrive in those same conditions (Chang et al. 2021, Ross et al. 2016, Shama et al. 2014). Additionally, studies have shown that southern populations of purple urchins may be able to withstand a completely different thermal regime than northern populations (Schoville et al. 2012). Populations from cooler environments may have a lower thermal tolerance, where their capacity for stronger plasticity is greater than those from warmer environments that may be near their thermal limit (Sasaki et al. 2019).

This research contributes to existing work on climate change stressor impacts on the egg quality and offspring success of MHW-acclimated *S. purpuratus*. The focus of this study is on maternal provisioning of urchins experiencing fluctuating MHWs, which are likely to increase in future climate change scenarios. In this chapter, I acclimated SBC *S. purpuratus* adults to MHW temperatures mimicking fluctuating MHW patterns that were seen previously in 2018. I used temperature loggers throughout the acclimation in a flow-through seawater system to collect the specific temperature conditions experienced by adults. To describe the influence of MHWs during gametogenesis on adults, I assessed

mortality, gonadosomatic indices, and egg quality. I then used eggs and sperm from acclimated adults to create cultures of *S. purpuratus* and raise them to gastrula and prism larvae. These two stages were selected as gastrulation is an important bottleneck for larval survival and the prism stage is when they are forming their tripartite gut and is the stage right before they begin to feed on their own. Larvae were used for thermal tolerance trials to assess LT₅₀ values, biochemical content, and oxidative stress through protein carbonylation and respirometry on prism larvae.

Methods

Animal Collection and Acclimation

Ninety urchins were collected subtidally on SCUBA at Arroyo Quemada, CA, a long-term study site for the Santa Barbara Coastal LTER (34.46774988, -120.11905). Adult urchins were returned to the laboratory and maintained in flow-through seawater tables for approximately one week at ambient temperature (~15°C) prior to being placed in MHW acclimation treatments. Throughout the initial acclimation period they were fed giant kelp blades (*Macrocystis pyrifera*) ad libitum and were monitored for any disease or premature spawning. The presence of disease was identified by spine loss, lesions on tests, and lack of tube feet adhesion.

To determine how exposure to multiple MHWs during gametogenesis influences fertilization and offspring performance, sets (n = 40 for each) of adult urchins were acclimated to one of two treatments (1) the control, non-MHW treatment at 15°C or (2) a MHW treatment where the dynamics of temperature change matched the timing of MHW events (Figure 2). The experiment was conducted from October to December of 2022 for

10 weeks. This time-period coincides with historically reported *S. purpuratus* gametogenesis in Santa Barbara populations (G. Hofmann, pers.comm.). Each acclimation treatment consisted of four 10-gallon replicate tanks, each containing 10 adult urchins, held in a seawater table, acting as a water bath, to maintain temperature. Seawater was supplied to treatment tanks via a dripper irrigation system with a flow rate of 16 L/hr. The temperature of the seawater table was controlled using DeltaStar Tank System driven by In-Line Water Chillers (Model DS-5, Aqua Logic, Inc., San Diego, CA, USA). Temperature of each tank was monitored daily using a 1 Channel RTD IP67 Waterproof Temperature Meter (Omega Engineering). HOBO 64K Pendant Temperature Data Loggers (Onset Computer Corporation) were placed in each seawater table to collect temperature data at 5-minute intervals during adult acclimation and embryo culturing. Submersible Water Pumps, 3500L/H, 100W (KEDSUM) were placed in each treatment tank to maintain water mixing. Urchins in each tank were fed seven fronds of *M. pyrifera* once a week and inspected daily. Any urchins that showed signs of disease (loss of spines, reduced spine mobility, black spots, reduced ability to attach) or death were immediately removed.

Adult Gonadosomatic Index

To characterize the influence of MHW temperatures on gametogenesis, I measured gonadosomatic index (GSI) for a set of adults from each of the acclimation treatments. GSI was measured post-acclimation on the same day as another set of urchins were spawned to create embryo cultures (detailed below). Un-spawned adults from the MHW acclimation treatment (n = 17) and non-MHW treatment (n = 26) were weighed on

a scale to the nearest 0.001g and measured with a digital caliper to the nearest 0.01mm. Gonads were dissected from individual urchins, and weighed on a digital scale to the nearest 0.001g. GSI was calculated using the formula: Wet Gonad Weight/Total Wet Weight x 100. The final values represent the relative mass of the gonads to the overall body weight as a percentage.

Urchin Spawning and Fertilization

In tandem with GSI sampling, remaining urchins were induced to spawn by injecting 0.53M KCl into the celom (Strathman 1987). Sperm was collected by pipetting around the area of the gonophores, then collected via pipette and stored dry in 1.5 mL tubes on ice until activation through seawater dilution. Eggs were collected by inverting spawning females on a 250 mL beaker containing UV sterilized 0.35 micron filtered seawater. Egg quality was assessed through visual checks of consistently sized round eggs using a compound microscope. Sperm quality was checked by diluting an aliquot with FSW, thus activating the sperm, and examining for mobility using a compound microscope. Eggs were counted under a compound microscope in five 5 uL aliquots to collect information on total egg counts per female. Test fertilizations were conducted for each male and female cross by adding diluted activated sperm to egg water aliquots and marking for percent of fertilized eggs after 5 minutes of contact. To limit natural genetic diversity, I used the best performing male's sperm (good motility and greater than 95% fertilization via visual tests) from the test fertilizations to fertilize two separate pools of eggs from healthy females from the MHW acclimated condition (n=3) and control condition (n=3). Beakers containing pooled eggs were gently mixed to simulate natural

wave movement while diluted sperm in seawater (at approx. 10^5 cells per mL) from the chosen male from the control treatment was added in small increments to avoid polyspermy. Once each of the pooled eggs reached 95% fertilization, embryos were deposited in 12 L larval culturing containers for rearing.

Embryos were raised at 15°C as the focus of this experiment was to explore the impact that MHWs may have on offspring from MHW-impacted and non-MHW-impacted parents. MHWs are more common during the gametogenic period of purple sea urchins (Chan et al. 2024) and less likely to occur during and directly after spawning. Two offspring treatments were identified as: CC and HC where the first letter indicates the parental acclimation and the second letter indicates the developmental temperature. Culturing containers were set up as indicated in Chamorro et al. 2023. Each container was stocked with 130,000 embryos. Seawater temperature in each container was monitored daily using 1 Channel RTD IP67 Waterproof Temperature Meter (Omega Engineering).

Embryo Sampling

Embryo sampling was conducted at the gastrula and early prism stage of development. Embryos were identified as reaching each stage by distinguishing developmental characteristics described in Strathmann (1987) from water samples taken from culturing containers. Gastrulae were characterized as the embryo displaying ingression of the primary mesenchyme cells at the vegetal plate. Prism larvae were characterized by having the full tripartite archenteron and growth of the body rods.

Gastrulae were sampled at ~29 hours post fertilization (hpf) and prism larvae were sampled at ~48 hpf.

Gastrulae were sampled by draining 6 L of the 12 L culturing buckets through a 60 μ m mesh strainer. Embryos were concentrated into a 15 mL Eppendorf tube and four 5 μ L aliquots were counted to calculate the total count of embryos in each tube. 2000 gastrulae per tube were frozen in cryovial tubes for future biochemical analyses and 1000 gastrulae per 1.5 mL Eppendorf tube were preserved in 2% formalin in FSW for morphometric analysis.

Morphology of eggs

To assess maternal provisioning in females that have been acclimated in different environments, egg area and average diameter were measured. 1000 eggs from each contributing female were preserved in 1.5 mL eppendorf tubes in 2% formalin in FSW for morphometric analysis promptly after spawning. Pictures were taken of 50 eggs per female using a compound microscope at 4x with Moticam Live Resolution microscope camera (Motic). Egg diameter and area of 35 eggs per female were measured using Image J software. The average of 3 measured diameters and 2D area of each egg was used for analysis.

Biochemical composition of eggs

2,000 eggs per female were deposited in a 1.5 mL cryovial, centrifuged to remove seawater, and then flash frozen in liquid nitrogen and stored at -80C until lipid or protein analysis was performed. Total lipid was extracted using methods described in Chamorro

et al (2023), a method based on Sewell (2005). The concentrated eggs from each sample were suspended in 250 μ L of Milli-Q water and sonicated at 2 amps for a total of 45s at 15s intervals (Fisher Scientific Sonic Dismembrator 500). Each homogenized sample was then transferred to a 5mL glass V-vial (Wheaton) and combined with 125 μ L of chloroform (HPLC grade) and 250 μ L of methanol (HPLC grade). Samples were shaken vigorously and then centrifuged at 2,680 RCF for 5min at 4°C (Beckman Coulter Allegra™ 21R Centrifuge). Using a pulled Pasteur pipette the aqueous and chloroform layers were transferred to a clean V-vial; chloroform and water were then added to the final volume ratio of 4:3:2 of water:chloroform:methanol. Samples were then hand shaken and centrifuged again at 2,680 RCF for 5min at 4°C. After centrifuging, the chloroform layer was carefully transferred to a clean glass vial. All samples were flushed with N₂ and stored at -20°C prior to analysis.

Total lipid was quantified spectrophotometrically using modified methods based on Marsh and Weinstein (1966). Briefly, samples were placed under a flow of N₂ to allow chloroform to evaporate. Once dried, 500 μ L of sulfuric acid (ACS grade) was added to each sample, covered with aluminum foil, and dried in a furnace at 200°C for 15min. Samples were allowed to cool for 10 minutes prior to the addition of 2.5 mL of deionized water to each vial. Samples were allowed to cool for an additional 10 minutes, mixed, and then absorbance of each sample was measured on a spectrophotometer at 375nm. A standard curve of a known mass of lipid within a range of 25-175 μ g was also prepared and run in parallel with each batch of samples ($R^2 = 0.98-0.99$). The lipid profile used to generate the standard curve consisted of major lipid classes found in *S. purpuratus* eggs which were previously reported in Wong et al. (2019); specifically, the

standard was comprised of 51% triacylglycerol (Glyceryl tripalmitate, Sigma-Aldrich, Catalog No. T5888), 38% phospholipid (L- α -Phosphatidylcholine, Sigma-Aldrich, Catalog No. P3556), and 11% sterol (Cholesterol, Sigma-Aldrich, Catalog No. C8667).

Eggs used for protein quantification were prepared using the same freezing process as described for lipid quantification. Three tubes from each contributing female were used to quantify total protein concentration. Protein was extracted from 2,000 eggs from each female using methods described in Chamorro et al. (2023). Briefly, 100 μ L of homogenization buffer (20mM Tris-HCl, (pH 7.6); 130mM NaCl; 5mM EDTA) with 1% Triton-X and 1% Protease Inhibitor Cocktail was added to each sample of concentrated eggs and sonicated on ice for 20s. Samples were then shaken (Thermolyne M71735 Slow Speed Roto Mix) on ice for 20 minutes, followed by centrifugation at 14,000 RPM for 20 minutes (Eppendorf 5415C Centrifuge). The supernatant was transferred to a 1.5mL microcentrifuge tube and stored at -20°C until analysis. Total protein content was quantified using the Pierce™ BCA Protein Assay Kit following manufacturer's instructions. The standard curve was generated using bovine serum albumin ($R^2 = 0.99$).

Protein carbonyl content was determined in eggs with the remaining frozen samples using the Sigma Aldrich Carbonyl Assay Kit (MAK486) following manufacturer's instructions. Briefly, a 250 uM Carbonyl Standard was prepared from a 50 mM Carbonyl Standard and purified water. 100 uL of the standards: 0uM Carbonyl, 75 uM Carbonyl, 150 uM Carbonyl, and 250 uM Carbonyl, and the samples were transferred to separate wells of a clear 96-well plate. 100 uL of reagent were added to each well and mixed briefly by tapping. The plate was incubated for 30 minutes at room temperature and optical density was measured at 375 nm.

Morphology of gastrulae

To assess maternal environment impacts on offspring, I assessed embryo size such as outlined with eggs in the prior sections. 1000 embryos from each contributing culture bucket were preserved in 1.5 mL Eppendorf tubes in 2% formalin in FSW for morphometric analysis promptly after sampling. Gastrula diameter and area were measured using Image J. Gastrula diameter was measured from where the vegetal plate invaginates across to the apical plate side and 2-dimensional area of the whole embryo was measured. Measurements of 35 embryos from each culturing bucket were collected.

Biochemical composition of embryos

2,000 embryos from each culturing bucket were deposited in a 1.5 mL cryovial, centrifuged to remove seawater, and then flash frozen in liquid nitrogen and stored at -80°C until total protein and protein carbonyl analysis was performed.

Three tubes from each culturing bucket for either gastrula or prism stage embryos were used to quantify total protein concentration. Protein was extracted from 2,000 embryos from each culturing bucket developmental stage using methods described in Chamorro et al. (2023). Briefly, 100µL of homogenization buffer (20mM Tris-HCl, (pH 7.6); 130mM NaCl; 5mM EDTA) with 1% Triton-X and 1% Protease Inhibitor Cocktail was added to each sample of concentrated eggs and sonicated on ice for 20s. Samples were then shaken (Thermolyne M71735 Slow Speed Roto Mix) on ice for 20 minutes, followed by centrifugation at 14,000 RPM for 20 minutes (Eppendorf 5415C Centrifuge). The supernatant was transferred to a 1.5mL microcentrifuge tube and stored at -20°C until analysis. Total protein content was quantified using the Pierce™ BCA Protein

Assay Kit following manufacturer's instructions. The standard curve was generated using bovine serum albumin ($R^2 = 0.99$).

Three tubes from each culturing bucket for either gastrula or prism stage embryos were used to quantify protein carbonyl content. Proteins were homogenized using the same protocol as outlined above for the BCA protein assay. The supernatant was transferred to a 1.5mL microcentrifuge tube and stored at -20°C until analysis. Protein carbonyl content was quantified using the Sigma Aldrich Carbonyl Assay Kit following manufacturer's instructions. The standard curve was generated using a 250 uM Carbonyl Standard.

Prism respirometry

To further examine oxidative stress in embryo offspring from females experiencing different thermal environments, oxygen consumption rates were measured for the prism stage following Marsh and Manahan (1999), with modifications. For each culturing bucket ($n = 6$ cultures), embryos were placed into five glass respirometry chamber vials (684-795 uL) at a range of concentrations (100, 200, 300, 400, 500, 600 individuals per vial). The embryos from both treatments were incubated at 15°C FSW. One blank vial per each replicate per treatment was filled with FSW to account for possible background respiration. Oxygen concentrations were measured following a 7-hour incubation of all vials. After incubation, the seawater was transferred using a gas-tight syringe (Hamilton Company, USA) to an optode containing a fiber-optic oxygen meter (Micro TX3; PreSens, Germany) that had been previously calibrated using sodium

sulfite and FSW. The rate of oxygen consumption per individual (pmol O₂/h/individual) was calculated from a generated standard curve.

Thermal tolerance and developmental success of embryos

To assess if maternal conditions resulted in physiological differences in offspring, I measured thermal tolerance by quantifying survival after acute temperature exposure. Thermal tolerance was measured for both gastrula and prism stage embryos. For each stage and treatment, embryos across replicate culturing buckets were pooled together to obtain approximately 12,000 embryos per treatment. Embryos were divided equally among ten 20-mL vials so that each vial contained approximately 1000 embryos in 5 mL of FSW. Two water baths attached to the opposing ends of an aluminum heat block created a temperature gradient spanning from ~17°C to ~32°C. The vials were randomly distributed so that gastrula embryos from each treatment were exposed to various temperatures (17.2°C, 18.2°C, 19.6°C, 21.2°C, 22.6°C, 24.2°C, 26.1°C, 28.3°C, 30.6°C, 32.6°C) for 1 hour. Prism embryos were exposed to the following temperatures due to natural variations in the heat block: 17.6°C, 18.5°C, 19.6°C, 20.7°C, 21.6°C, 23.6°C, 25.0°C, 26.75°C, 28.4°C, 30.5°C. I confirmed that each temperature contained a vial from each treatment. Temperatures were recorded using a 1 Channel RTD IP67 Waterproof Temperature Meter (Omega Engineering). Following the acute temperature exposure, 100 embryos per vial were immediately scored as either alive or dead based on the presence or absence of ciliary movement when viewed under a compound microscope. Vials were placed in a 12°C cold room during the duration of scoring to halt further mortality.

To assess the impact of acute temperature stress on the developmental progression of embryos, vials were set up for gastrula-stage embryos as described above for thermal tolerance assay, with the same temperature regime. Instead of scoring immediately, vials were held in a 12°C cold room for ~20 hours, with two water changes in between, to allow for progression to the next developmental stage, prism. Identification of the prism stage was characterized by tripartite gut formation and spicule growth. Embryos were scored for survival, abnormal development, and successful development to the prism stage.

Statistical analysis

All statistical analyses were conducted in R Studio (Version 2025.05.0+496). Adult survival data was generated using the Kaplan-Meier method and analyzed using a log-rank test. To quantify size-dependent variation in reproductive investment (gonadosomatic indices), I modeled the relationship between gonad mass and body mass using log-log allometric scaling. This type II regression assumes both variables contain measurement error and are biologically linked. Model residuals were used as an index of size-adjusted gonad investment, with positive residuals indicating larger gonads than expected for a given body size and negative residuals indicating reduced gonad investment. A linear mixed-effect model was used to analyze maternal thermal acclimation on lipid, protein, protein carbonylation, and size data in eggs and gastrula and prism larvae. Maternal acclimation treatment was set as a fixed effect while each individual mother was set as a random effect in egg analyses. In larval analyses, culture bucket was set as a random effect. Respirometry data was analyzed with a t-test

comparing the respiration rate of prism larvae from either females experiencing MHW conditions or control conditions. For the thermal tolerance trials and developmental success trials, the impact of maternal acclimation temperature on survivorship and successful development was analyzed using a generalized linear mixed effect model (lme4 package). The LT50 value was calculated using a regression for each maternal treatment. To analyze fertilization success in urchins experiencing two different temperatures during oogenesis, I conducted a linear model with temperature and acclimation treatment as fixed effects.

Results

Adults

Adult *S. purpuratus* were successfully maintained at either a non-MHW (15°C) or MHW treatment temperature condition (fluctuating MHW events at 20°C) (Figure 2) during their gametogenic period. Urchins in the MHW treatment were exposed to two serial MHW events lasting 18 and 17 days, respectively. There was some mortality of adult urchins during the acclimation period for both treatments; however, adults in the MHW treatment experienced significantly greater mortality throughout the acclimation while mortality in the control, cool water temperature was limited to the first few days (Figure 3). In addition, there was a pattern to the mortality events in the MHW treatment. Specifically, mortality in the MHW treatment was greater during time periods of temperature ramp down post-MHW event. The first recovery period, when temperature began to ramp down after the first simulated MHW, resulted in a decrease of the survival probability to 80%. By the end of the 70-day acclimation period, the survival probability for MHW-acclimated urchins decreased to 50% while the survival probability for urchins from the control treatment remained at approximately 98% (p -value < 0.001) (Figure 3).

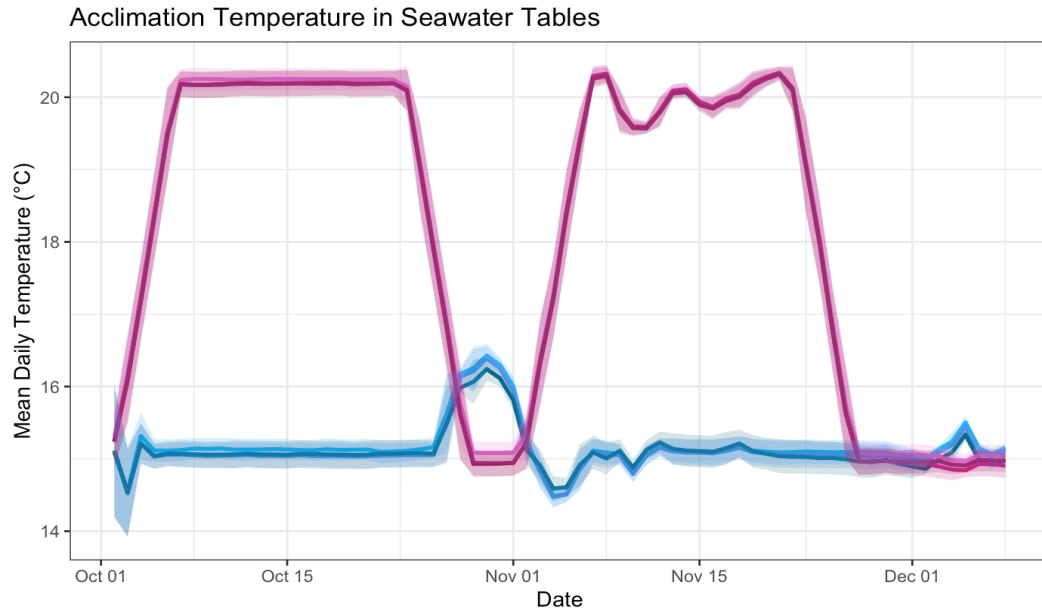


Figure 2. Average daily temperature experienced by adult urchins during acclimation. Temperatures were collected every 15 minutes by 6 submersible temperature loggers from October 1st, 2022 to December 12th, 2022. A logger was placed at either the right, center, or left of the seawater table acclimation for each treatment. Each treatment had three temperature loggers throughout the acclimation period. Mean daily seawater temperature in degrees Celsius is shown over time for the control (blue) and MHW (pink) urchin acclimation. Solid lines represent daily mean temperatures for each table, and shaded ribbons indicate $\pm$ standard deviation around the daily mean.

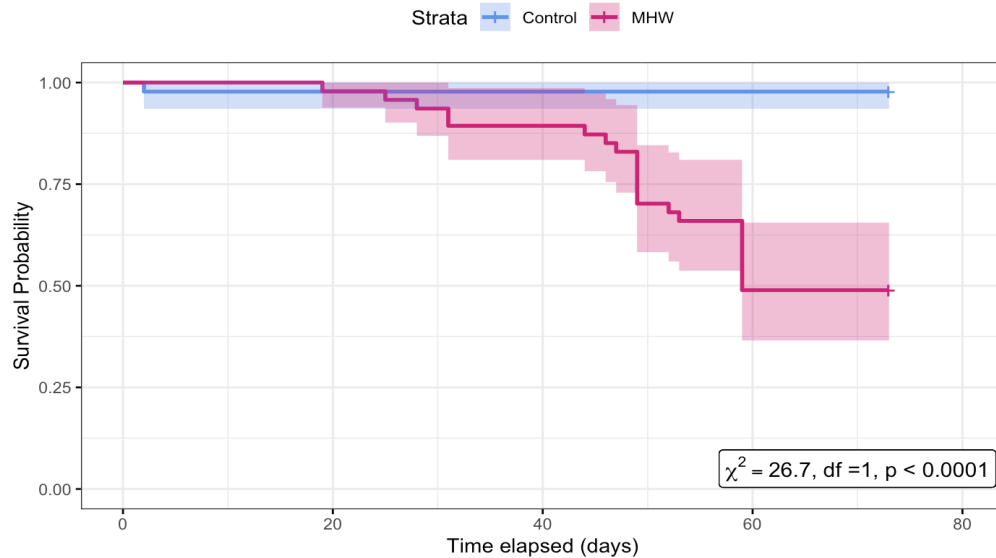


Figure 3. Survival probability in *S. purpuratus* adults during acclimation. Adult urchins were acclimatized to either a control (15°C) or fluctuating MHW temperature regime (2 MHW events lasting 2 weeks each) from October to mid-December. The blue line represents the survival probability of the urchins experiencing the control seawater condition over the course of the acclimation period using the Kaplan-Meier survival method. The pink line represents the survival probability of the urchins exposed to the MHW temperature regime.

GSI as an adult trait showed no difference between adults following acclimation to non-MHW and MHW temperatures. The mean GSI percentage, normalized to body weight, in the non-MHW group trended higher at 2.103% while the mean in the MHW group was 1.784% (p -value = 0.4491) (Figure 4). Lastly, I observed a trend where MHW acclimated adults had greater variability in GSI amongst individuals. (Figure 4). GSI values of MHW acclimated urchins ranged from 0% - 6.75%. GSI values of urchins from the control treatment ranged from 0% - 3.58%. Residuals of GSI log-transformed gonad mass were similar across treatments (Figure 4B).



A. _____



B.

Figure 4. Allometric scaling of gonad mass with body size and size-adjusted gonad investment in *Strongylocentrotus purpuratus*. (A) Relationship between log body mass and log gonad mass for individuals from each Treatment (pink = MHW, blue = CONTROL). Lines show fitted allometric regressions from a linear model including an interaction between log body mass and treatment; the slope of each line represents the allometric scaling exponent b . (B) Size-adjusted gonad investment, expressed as residuals from the allometric model in panel (A), plotted by treatment. Positive residuals indicate individuals with larger gonads than expected for their body size, whereas negative residuals indicate reduced gonad investment. Boxes show the interquartile range, horizontal lines indicate medians, and points represent individual urchins.

Traits of Eggs

When examining the characteristics of eggs from the two acclimation groups, we found that egg size and biochemical composition varied with temperature treatments. Specifically, there was overwhelming evidence that egg diameters differ between adult acclimation treatments ($W = 4905$, $p\text{-value} < 0.001$). Eggs from MHW-acclimated females were approximately $2.2\ \mu\text{m}$ larger in average diameter (effect size = 0.446, magnitude = moderate). Average egg diameter from MHW and non-MHW acclimated female urchins was $82.44\ \mu\text{m}$ and $79.53\ \mu\text{m}$, respectively (Figure 5a.). Egg area followed

similar trends as there were significant differences between treatments (p -value < 0.001) with a moderate effect size. Eggs from MHW-acclimated females were on average 277.195 μm^2 larger than eggs from the control treatment. The 2D area from MHW and non-MHW acclimated female urchins was 5345.979 μm^2 and 4974.972 μm^2 , respectively (Figure 5b.)

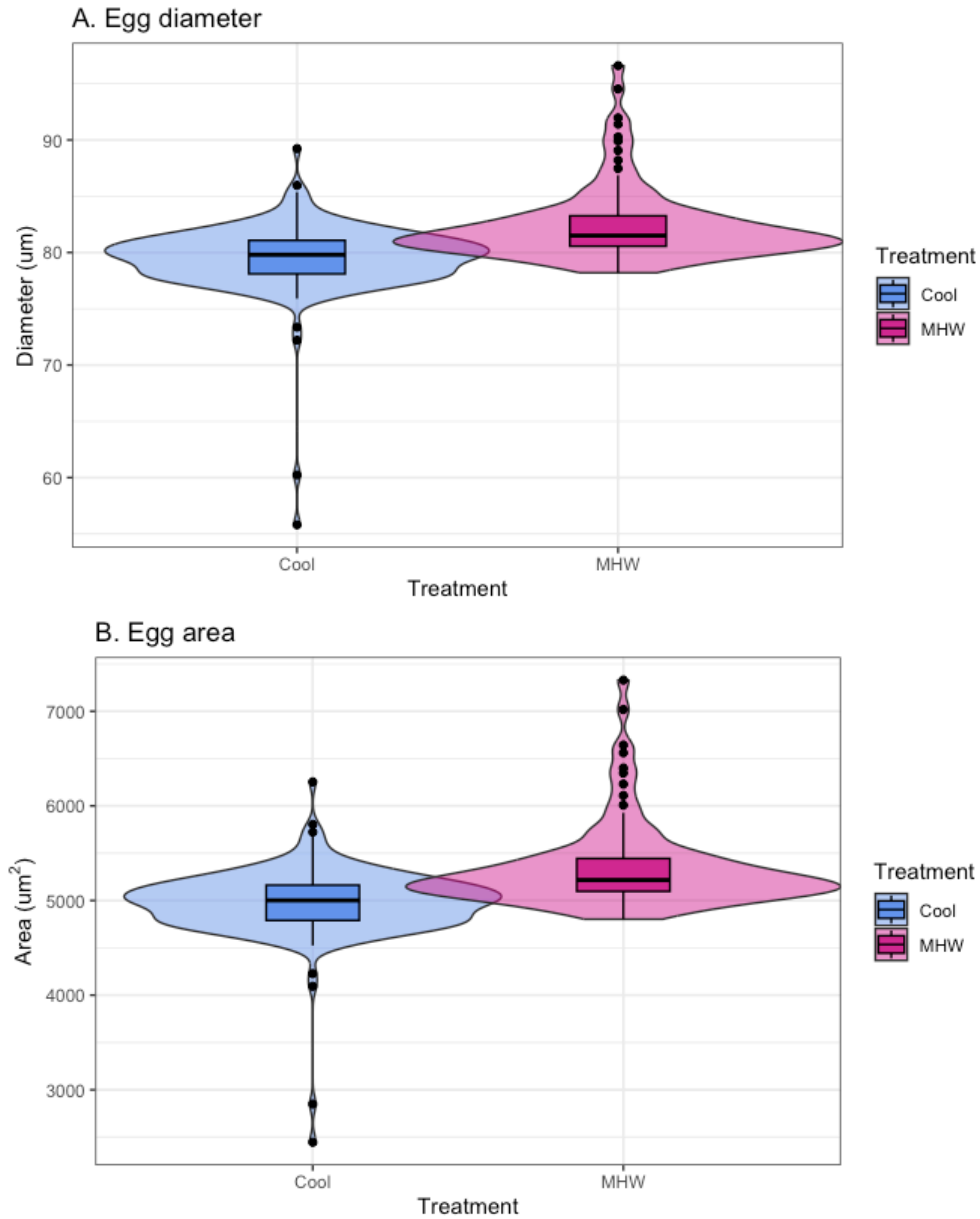


Figure 5. Morphometric analysis of *S. purpuratus* eggs. (A) Distribution of egg diameter(μm) for *Strongylocentrotus purpuratus* females exposed to from the Cool (control, blue) and MHW acclimation treatment (pink) (p -value < 0.001) temperature treatments. Violin plots show the full distribution of egg diameters, with embedded boxplots indicating the median, interquartile range, and 1.5x IQR whiskers; points represent individual egg measurements. (B) Distribution of egg area (μm^2) for *Strongylocentrotus purpuratus* females exposed to from the Cool (control, blue) and MHW acclimation treatment (pink) (p -value < 0.001) temperature treatments. Violin plots show the full distribution of egg area, with embedded boxplots indicating the median, interquartile range, and 1.5x IQR whiskers; points represent individual egg measurements.

Biochemical reserves were enhanced in eggs from females with a thermal history of MHW temperatures, but total lipid content was not statistically significant. The biochemical composition of eggs was impacted by maternal acclimation during the 10-week acclimation period that coincided with the timing of oogenesis in nature but was more impacted by differences between females (random-effect SD = 0.592). Both lipid content and protein concentrations for eggs from MHW-acclimated females were significantly greater than in eggs from non-MHW acclimated females. A linear mixed-effects model with female ID as a random effect indicated that egg lipid content did not differ significantly between treatments (Estimate $\pm$ SE = 0.71 ± 0.43 ng/egg, $t = 1.64$, $df = 7$, $p = 0.146$) (Figure 6b.). Eggs from MHW treatment females had 0.710 ng/egg more total lipid content with the mean value in the control and MHW treatments at 3.150 ng/egg and 3.860 ng/egg, respectively (Figure 6b.). Protein concentration in eggs from MHW-acclimated females was significantly greater (p -value = 0.02, $W = 22.5$, moderate effect size) than that in eggs from non-MHW acclimated females. There was an average of 18.021 ng/egg in eggs from MHW-acclimated females and 15.932 ng/egg in the non-MHW group (Figure 6a.).

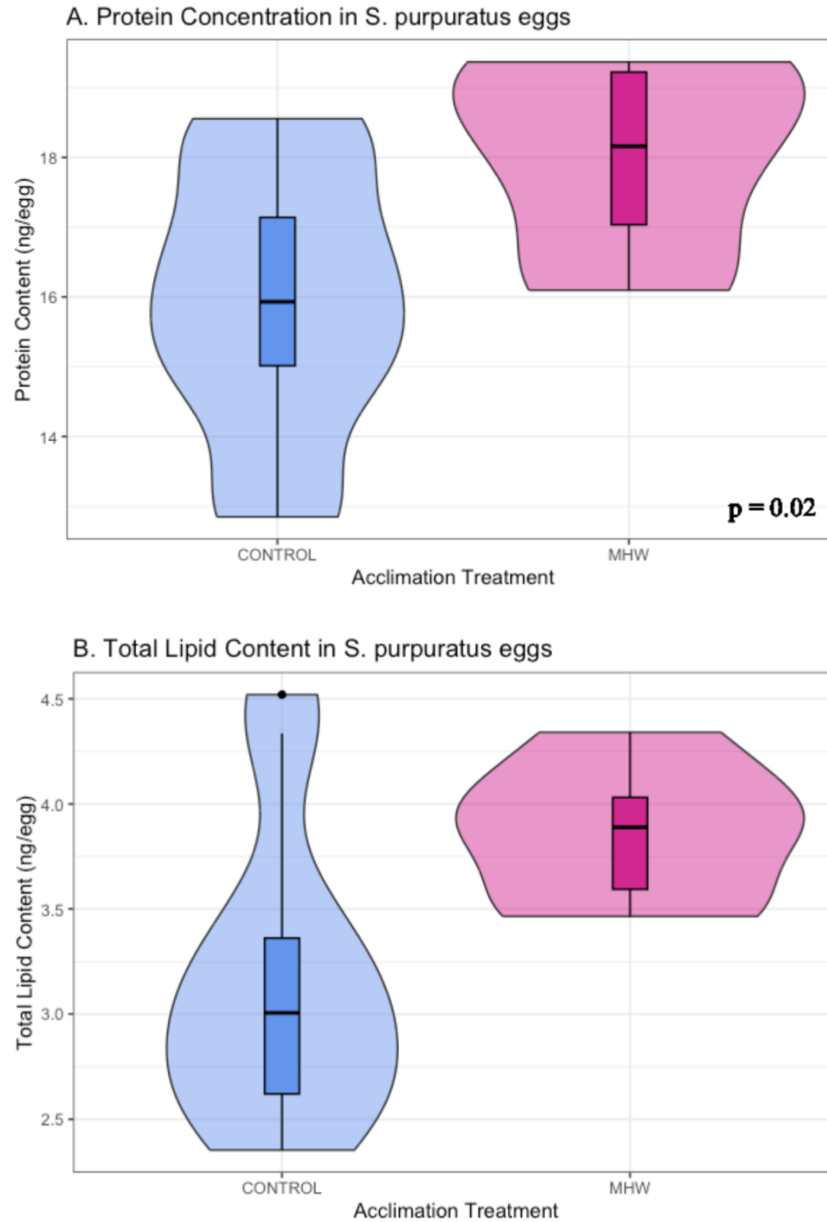


Figure 6. *S. purpuratus* egg biomolecule content. A) **Effects of thermal acclimation on protein content of *Strongylocentrotus purpuratus* eggs.** Protein concentration (ng/egg) is shown for eggs produced by females acclimated to control and marine heatwave (MHW) temperature treatments. Violin plots depict the distribution of protein concentrations, with embedded boxplots indicated the median, interquartile range, and 1.5x IQR whiskers. Eggs from MHW-acclimated females exhibited significantly higher protein content than those from control females ($p = 0.02$). (B) **Effects of thermal acclimation on lipid content of *Strongylocentrotus purpuratus* eggs.** Lipid content (ng/egg) is shown for eggs produced by females acclimated to control and marine heatwave (MHW) temperature treatments. Violin plots depict the distribution of lipid content, with embedded boxplots indicated the median, interquartile range, and 1.5x IQR whiskers. Linear mixed effect models were used with female as a random effect.

Eggs did not demonstrate protein carbonylation differences in response to maternal temperature (p -value = 0.4734), though protein carbonyl content in MHW female eggs trended higher. The mean protein carbonyl concentration in eggs from MHW females was 226.8929 and the mean in eggs from control females was 184.7738 nmol/mL (Figure 7). Again, there was greater variation in values from MHW-acclimated females compared to the females from the control. The range of protein carbonyl content in MHW females was 169.46 – 322.25 nmol/mL while the range in control females was 164.25 – 207.11 nmol/mL. Additionally, protein carbonyl content in eggs was greater for both acclimation treatments in nmol/mL than the embryo stages.

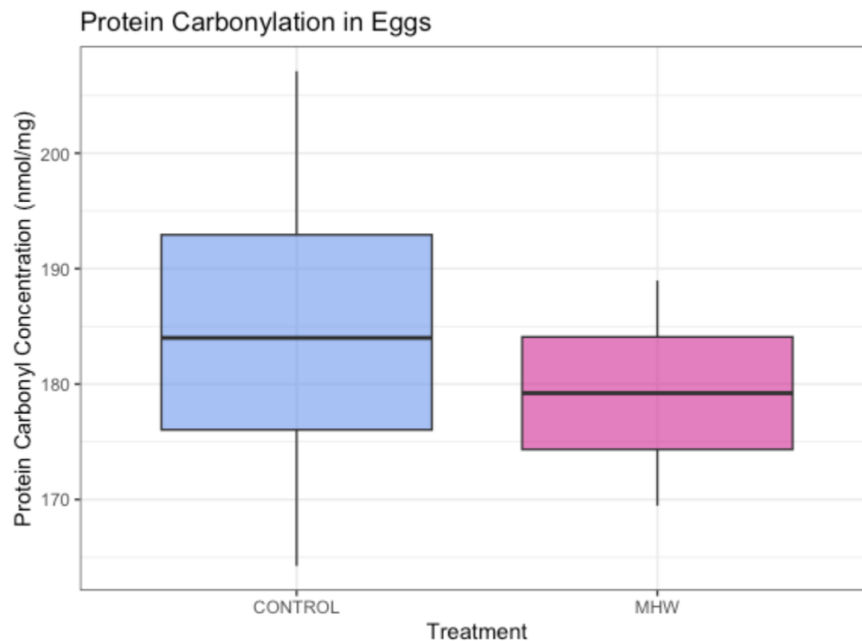


Figure 7. Protein carbonylation in *Strongylocentrotus purpuratus* eggs under thermal acclimation treatments. Protein carbonyl concentration (nmol mg⁻¹ protein), a marker of oxidative protein damage, is shown for eggs produced by females acclimated to control (blue) and marine heatwave (pink) (MHW) temperature treatments. Boxplots display the median, interquartile range, and 1.5× IQR whiskers. This figure compares levels of oxidative protein modification between treatments following thermal exposure.

Traits of Larvae

As a biochemical indicator of protein damage and oxidative stress, I measured levels of protein carbonylation in gastrulae and prism-stage larvae raised from the spawning of females from the two temperature treatments. I found two non-statistically significant trends: early stages from the MHW treatment had greater levels of protein carbonylation as compared to early stages from the non-MHW females. Second, there was a stage difference with levels increasing with developmental stage when comparing gastrula and prism (Figure 8).

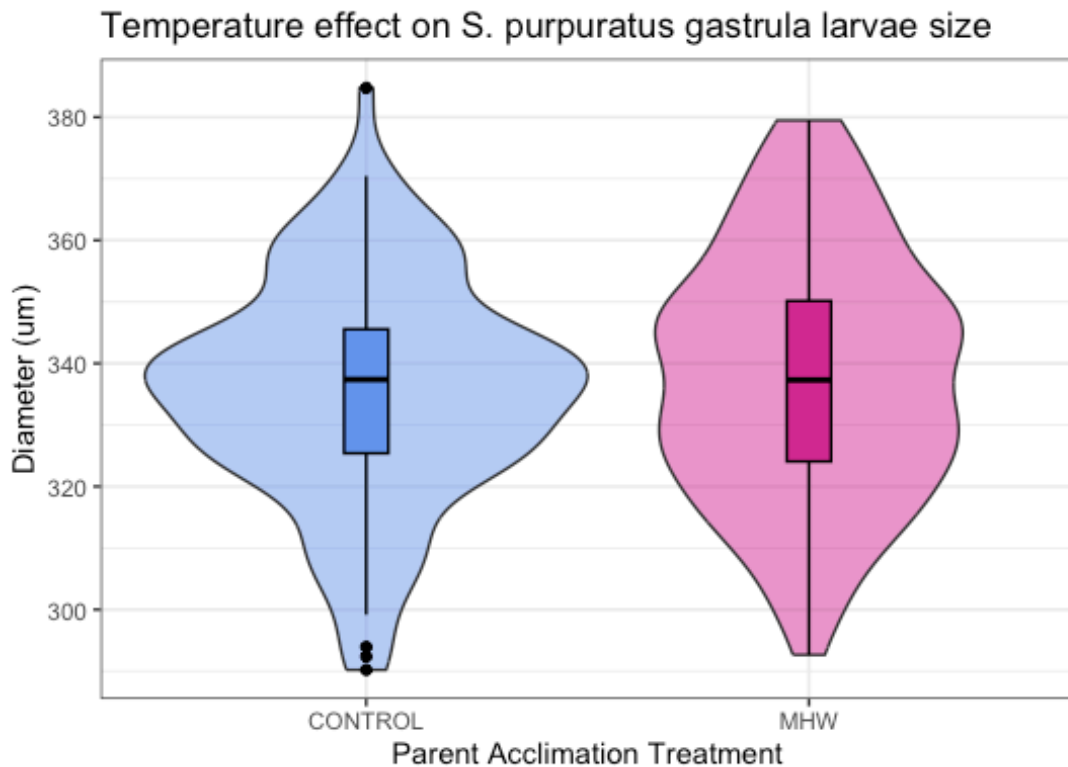


Figure 8. Effects of parental thermal acclimation on gastrula larval size in *Strongylocentrotus purpuratus*. Diameter (µm) of gastrula-stage larvae produced by adults acclimated to control (blue) and marine heatwave (pink) (MHW) temperature treatments. Violin plots depict the distribution of larval diameters, with embedded boxplots showing the median, interquartile range, and 1.5× IQR whiskers; points represent individual larval measurements. This figure illustrates treatment-level differences in early larval size associated with parental thermal history. p -value > 0.05.

The average protein carbonyl content in control treatment gastrula embryos was 68.714 nmol/mg and the average in MHW treatment gastrula was 86.357 nmol/mg (p -value: 0.083), a difference of 17.643 nmol/mg. There was a similar trend in protein carbonyl content between prism embryos from the MHW treatment and control treatment with a difference of 11.666 nmol/mg (Figure 9). Specifically, the average protein carbonyl content for MHW prism embryos was 91.857 and the average for the control prism embryos was 80.191 nmol/mg (p -value: 0.095). Lastly, there was an increase in the protein carbonyl content between developmental stages in both treatments. The protein carbonyl content in control embryos increased by 11.476 nmol/mg between the gastrula and prism stage (p -value: 0.0323). There was a slight increase of 5.500 nmol/mg in protein carbonyl content in MHW embryos from the development of gastrula to the prism stage (p -value = 0.5789).

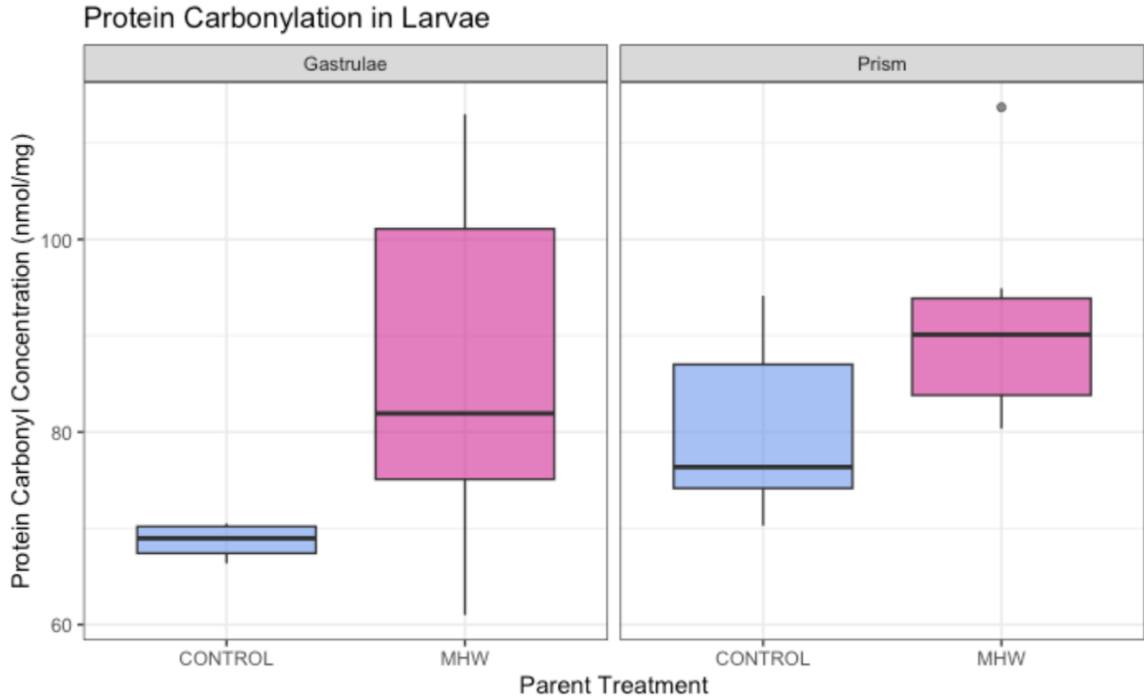


Figure 9. Protein carbonylation in *Strongylocentrotus purpuratus* larvae under thermal acclimation treatments. Protein carbonyl concentration (nmol mg⁻¹ protein), a marker of oxidative protein damage, is shown for larvae produced by females acclimated to control (blue) and marine heatwave (pink) (MHW) temperature treatments. On the left is protein carbonylation at the gastrula stage and on the right is the prism stage. Boxplots display the median, interquartile range, and 1.5× IQR whiskers. This figure compares levels of oxidative protein modification between treatments following parental thermal exposure.

To further understand the protein dynamics in the developing sea urchins, I measured total protein content in gastrula and prism-stages and found total protein concentration trended higher in embryos from MHW-acclimated females, though not significant. The mean protein concentration in the control gastrula population was 584.472 while the mean in the MHW gastrula population was 594.580 (p -value: 0.586). The mean protein concentration in the control prism population was 265.756 while the mean in the MHW prism population was 292.644 (p -value: 0.097) (Figure 10). In both treatments, protein content was impacted by life stage. Earlier stages had greater protein content on average per larvae than prism-stage larvae (p -value < 0.001) (Figure 10).

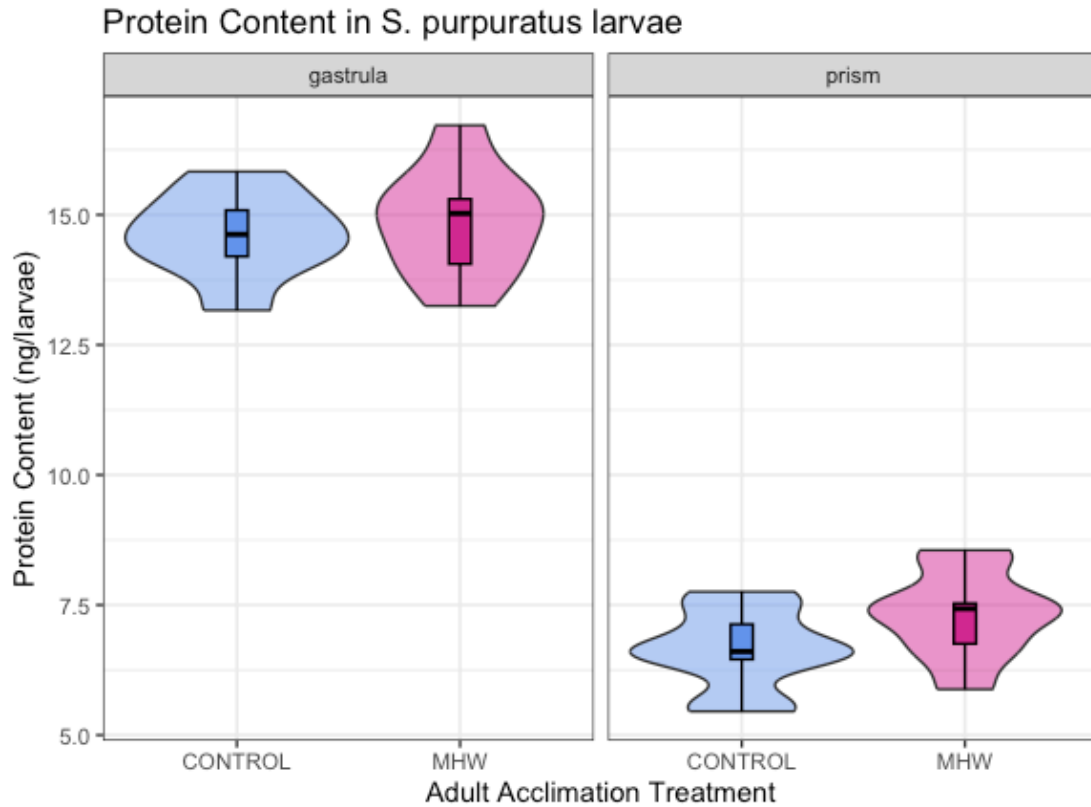


Figure 10. *S. purpuratus* larvae protein content. A) **Effects of thermal acclimation on protein content of *Strongylocentrotus purpuratus* gastrulae.** Protein concentration (ng/larvae) is shown for larvae produced by females acclimated to control or marine heatwave (MHW) temperature treatments. Violin plots depict the distribution of protein concentrations, with embedded boxplots indicated the median, interquartile range, and 1.5x IQR whiskers. (B) **Effects of thermal acclimation on protein content of *Strongylocentrotus purpuratus* prism larvae.** Protein concentration (ng/larvae) is shown for larvae produced by females acclimated to control and marine heatwave (MHW) temperature treatments. Violin plots depict the distribution of lipid content, with embedded boxplots indicated the median, interquartile range, and 1.5x IQR whiskers. Linear mixed effect models were used with female as a random effect.

There was no significant difference in the metabolic rates of prism-stage larval offspring from females in the control treatment and MHW treatment (Figure 11). The mean respiration rate in larvae from the control treatment was 9.744 pmolO₂/hr/individual while the mean in larvae from the MHW treatment was 12.192 pmolO₂/hr/individual (Figure 10).

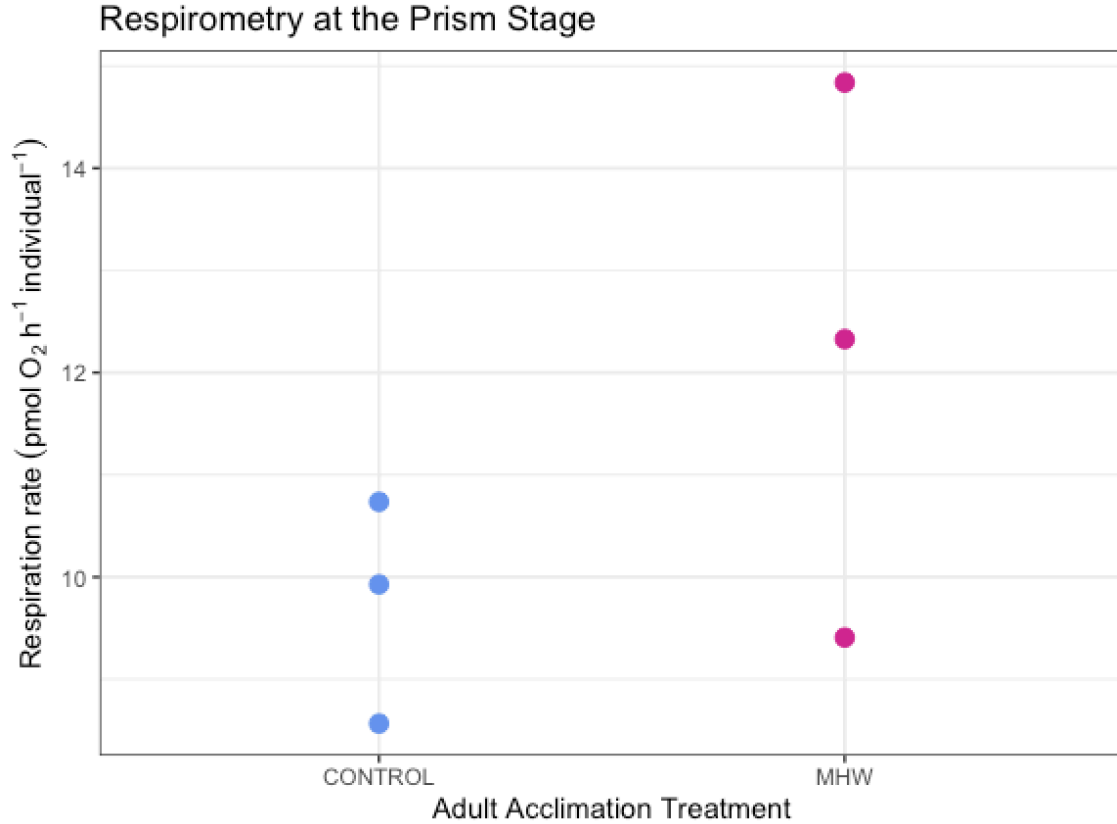


Figure 11. Respiration rate (pmol O₂h⁻¹/individual) for *S. purpuratus* prism larvae under different adult acclimation treatments. Oxygen consumption was measured using glass respirometry chamber vials (n = 6) that contained a range of individual embryos (100-600) per vial. Points represent measurements of oxygen consumption (pmol O₂ h⁻¹ individual⁻¹) from offspring produced by adults held under control conditions or MHW conditions. Each point represents larvae from 6 different larval culturing buckets (CC1, CC2, CC3, HC1, HC2, HC3) All respiration measurements were performed at 15°C. $p > 0.05$.

The embryos coming from females acclimated to a MHW temperature regime had a higher LT₅₀ during the gastrula stage by 0.70°C. The LT₅₀ of prism-stage embryos had an opposite trend where embryos from females acclimated to the control temperature had a higher LT₅₀ than the embryos from MHW-acclimated females, a slight difference of 0.005°C. Overall, LT₅₀ values of embryos scored for survival post-thermal tolerance trials ranged from 26.765°C to 27.918°C, a little over 1 degree difference between the lowest and highest LT₅₀ values. When assessing the ability of gastrula-staged embryos to progress to the next developmental stage, embryos from MHW-acclimated females had a

higher LT_{50} , where the value is indicative of 50% of embryos successfully developing to the next stage, prism, after experiencing a 1-hour heat shock. The embryos from MHW-acclimated females had higher LT_{50} values at 22.313°C compared to the 22.190°C of control embryos (Figure 11).

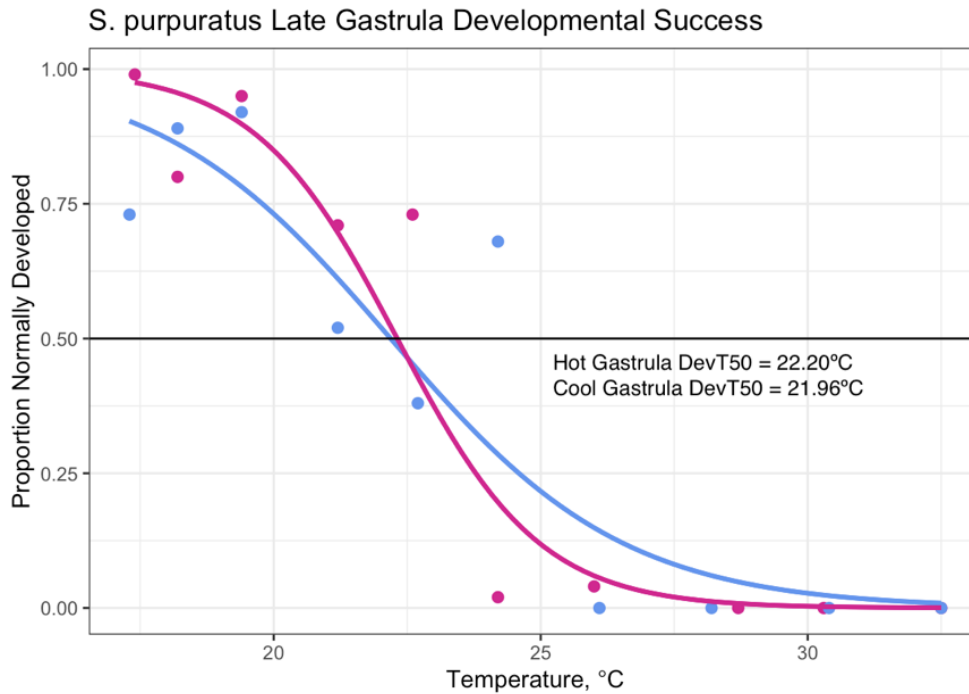


Figure 10. Temperature-dependent developmental success of *S. purpuratus* embryos at the gastrula stage. Points show the observed proportion of embryos developing normally across experimental temperatures for MHW (pink) and cool/control (blue) adult acclimation treatments. Solid curves represent fitted logistic dose-response models describing the decline in normal development with increasing temperature. The horizontal line indicates 50% normal development ($DevT_{50}$). Estimated values were 22.20°C for the MHW treatment and 21.96°C for the control treatment, indicating thermal sensitivity of late gastrula development across treatments.

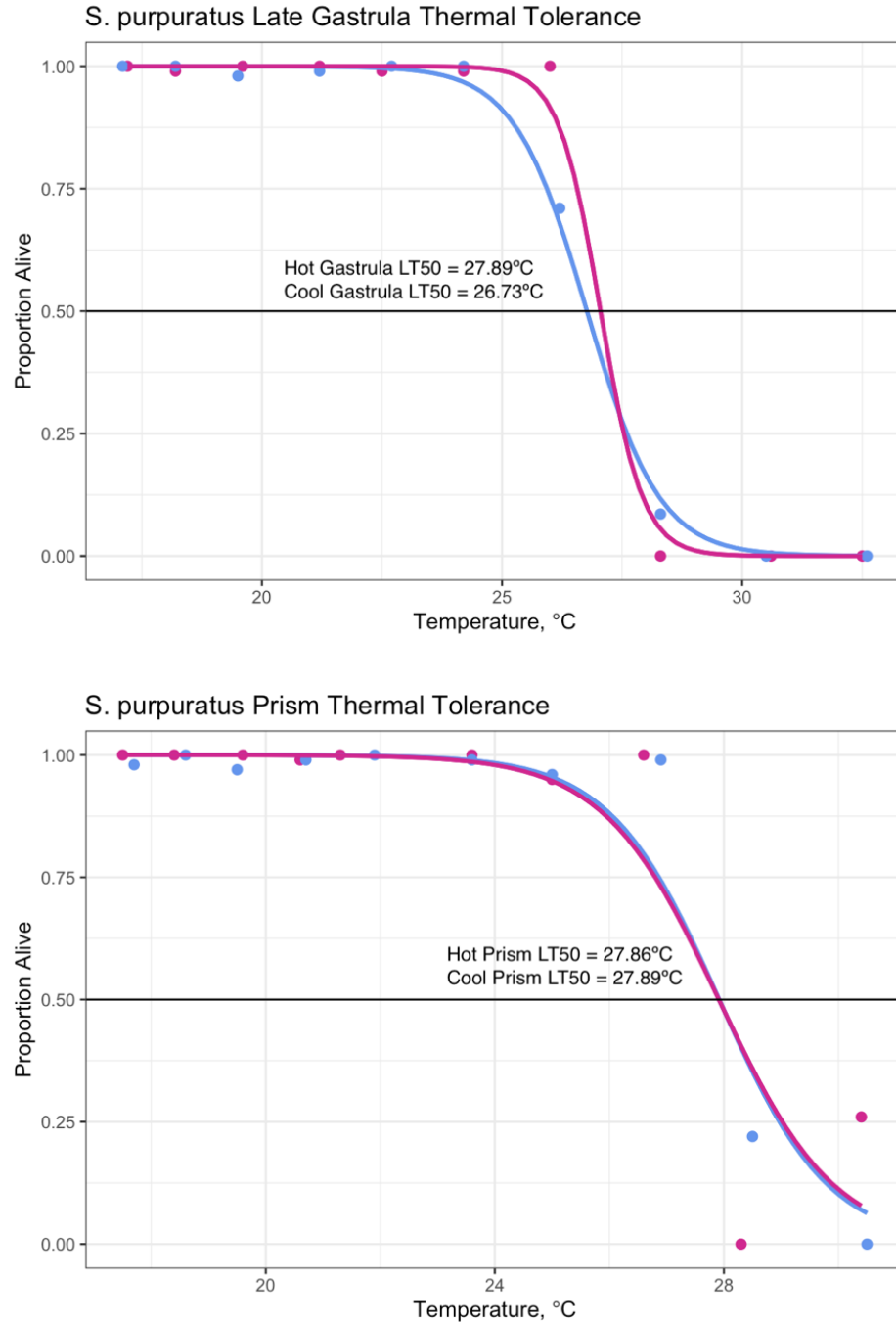


Figure 11. Thermal tolerance for *S. purpuratus* embryos. (A. Gastrulae, B. Prism embryos) Points show the observed proportion of embryos surviving across experimental temperatures for MHW (pink) and cool/control (blue) adult acclimation treatments. 100 embryos per each developmental stage per vial were scored alive or dead. Proportions alive were calculated for each temperature exposure in the heat block and the temperature at which 50% of embryos died was identified per treatment per vial, LT₅₀. Solid curves represent fitted logistic dose-response models describing the decline in survivorship with increasing temperature. The horizontal line indicates 50% mortality (LT₅₀). Estimated values were 27.89°C for the MHW treatment gastrulae, 26.73°C for control gastrulae, 27.86°C for the MHW treatment prism larvae, and, 27.89°C for control prism larvae.

Discussion

General Observations

MHWs are causing detrimental impacts to ecosystems globally and there have been many studies on the current and future impacts on marine ecosystems and specific populations of marine species (Mills et al. 2013, Cavole et al. 2016, Wernberg et al. 2016, Oliver et al. 2017, Jones et al. 2018, Smale et al. 2019, Filbee-Dexter et al. 2020). In addition to the temperature anomalies, MHWs may also interact with other existing environmental stressors, such as hypoxia and ocean acidification, to impact ocean health and sustainability (Rogers-Bennett and Catton, 2019, Polazzo et al. 2022). Because of the natural variability of MHWs, there still is a lot more to learn about these extreme temperature events, for example, how and when they impact marine species. These elevated temperature events may last for as little as 5 days but may still negatively influence ecosystem health if their timing coincides with important phenological time periods. In this case, MHWs occurring during gametogenesis of urchins may signal for greater maternal provisioning to allow offspring to succeed in adverse environmental conditions.

In this study, I found that when exposed to fluctuating marine heatwave temperatures, adult urchins were unable to adapt, and mortality was greater in comparison to their counterparts that acclimated in a stable temperature environment commonly seen in non-MHW conditions. Though mortality was greater in MHW-acclimated urchins, there was no difference in the GSI in urchins from different treatments. Interestingly, the GSI in MHW-acclimated urchins had more variable values.

In eggs, there was no difference in size between the two treatments, though past studies indicate clear size differences due to maternal temperature where females acclimated to higher temperature conditions generate larger eggs. Egg size in MHW females trended larger in my study, though not significantly (Figure 5). Though size was statistically similar, the biochemical content in eggs exhibited greater change between the two treatments. Protein and lipid content in eggs from MHW acclimated females was greater. Protein and lipid content is used for many organisms as energy reserves in response to stress. Elevated heat stress during gametogenesis may probe females to provision greater nutrients to eggs to prepare for successful fertilization and offspring health and survival in potentially adverse environments.

I also measured protein carbonylation as an indirect biochemical indicator of severe oxidative damage and degradation of cellular proteins (Dalle-Donne et al. 2003, Dalle-Donne et al. 2007, Akagawa 2020). Proteins are involved in many physiological processes during development (Chandramouli et al. 2014) and irreversible modifications could have lasting detrimental effects (Dalle-Donne et al. 2006). Particularly, measuring carbonylation of proteins allows us to assess cellular damage induced by reactive oxygen species (ROS). In *S. purpuratus*, protein carbonyl content in embryos showed interesting results. When gastrulae developed to prism larvae, the protein carbonyl content increased significantly. I did not see the same results in larvae from MHW-acclimated females. Instead, I saw a very slight increase in the average and greater variation between samples. In another marine invertebrate, *Penaeus monodon*, oxidation status of the proteome was reorganized in response to pesticide exposure (Dorts et al. 2009). McDonagh et al. 2005 shows higher levels of protein carbonylation in tissues from invertebrate, *Mytilus edulis*,

from a more polluted site. However, in response to heat stress, differences in protein carbonylation profiles did not lead to distinct changes in *Mytilus* congeners (Dowd and Somero 2023). In a study evaluating heat stress impacts on protein carbonyl levels, no change was detected in cells when tested immediately after heat stress. When tested after a 3-hour recovery period, decrease in protein carbonyls of senescent cells were detected (Bozaykut et al. 2013). In this study, I observed an increase in protein carbonyl content in older, prism-stage embryos in the control condition (Figure 8). Overall, additional analyses on the patterns of protein carbonylation in embryos in response to environmental stress of adult *S. purpuratus* would allow us to further understand the role of maternal effects on protein activity and oxidative stress during development.

Response of Adult Urchins to Acclimation

I found a differential response of adults to thermal acclimation during their gametogenesis. Urchins in the MHW treatment experienced great mortality. Interestingly, mortality tended to increase during periods of thermal recovery, as consistent with previous MHW studies (Minuti et al. 2021). Mortality of *S. purpuratus* during the recovery period between MHWs suggests a lack of stress coping mechanism and/or sustained physiological damage that occurred during the heat stress. Different MHW patterns may impact adult survival variably. Long-term, persistent MHWs may allow urchins to fully acclimate with limited mortality as adults (Chamorro et al. 2023). The rapid onset and offset of MHWs over the course of a week may make it harder for urchins to acclimate to abrupt changes in temperature. In sea turtles, cold-stunning events are common where turtle mortality occurs due to rapidly decreasing ocean temperatures

and the lack of movement to warmer waters (Schwartz 1978, Witherington and Ehrhart 1989, Still et al. 2002, 2005). In another species of urchins, *Sterechinus neumayeri*, shorter-term acclimations to altered conditions showed evidence of limited ability to acclimate to increased temperature (Suckling et al. 2014). Organismal responses to MHWs are variable depending on the magnitude of the temperature change. When within the scope of natural temperature variability, organisms may increase physiological responses to enhance coping strategies in relation to stress. However, more severe thermal stress or rapid increases or decreases in temperature, may cause more detrimental impacts in benthic, sessile marine invertebrates.

In many cases where adult female urchins are exposed to adverse biotic or abiotic conditions, they will put greater effort into reproductive output. The results of the gonad index work are consistent with this idea where I did not observe a marked decrease in gonadosomatic indexes even in the presence of extreme elevated temperatures. Additionally, I did find a greater range of GSI values in the females acclimated to MHW conditions in comparison to those in our control.

S. purpuratus gonad size peaks in December, the time of our laboratory spawning, and is the lowest in June (Booolootian 1966, Pearse 1981, Pearse & Cameron 1991, Ebert et al. 2012). Gametogenesis of sea urchins responds to photoperiod and gamete maturation increases under accelerated photoperiods (Ishii et al. 2022). Past studies have also shown that gametogenesis is independent of temperature and other environmental signals (Pearse & Cameron 1991). Interestingly, in *S. purpuratus* southern range-edges (Baja California), urchins have had some of the highest reproductive outputs (Lester et al. 2007). One study showed increased gonad index in years with warmer thermal

environments; however, this could be due to other environmental variables such as increased food abundance (Bennett and Giese 1955). In fish, exposure to elevated temperature led to reduced GSI (Im et al. 2016, Dorts et al. 2012). In other studies, gonad index in urchins was impacted by the interaction of temperature and diet (Azad et al. 2011), where a moderated temperature led to optimized gonad production compared to elevated temperature conditions. Food availability was consistent in both conditions in my study and there were no differences in the GSI. Further investigating the interactions of food choice, quality, and changing environmental conditions on GSI would be a next step in determining what influences gonad index. Previous studies have already shown that a combination of temperature, algal food quality and faster water flows positively impacts gonadal growth, development, and spawning while intertidal sites with higher temperatures, less availability of drift algae, and higher population density had greater gonad production (Basch and Tegner 2007). Previous studies have expressed that reproductive output in *S. purpuratus* can be influenced by a combination of factors (Lester et al 2007); however, the single stressor of MHWs did not show significant effects in this study.

Maternal provisioning of eggs

Maternal provisioning is dynamic and varies between species, populations, ecosystems, and specific conditions experienced during gametogenesis. In some cases, maternal exposure to adverse conditions, such as temperature or predators, resulted in offspring better suited to survive in those conditions through provisioning of biochemical constituents, larger size, or development of defensive physical features such as horns, for

example (Gilbert 1967, Kreuger and Dodson 1981, and Stemberger and Gilbert 1987).

The reliance on endogenous energy reserves in early embryonic development in conjunction with the necessary growth during development may influence the ability of early stages to respond to adverse environmental conditions, such as elevated temperature, and lead to low plasticity of embryos in comparison to later feeding stages (Pottier et al. 2022). In sea urchins, the formation of the tripartite gut occurs as pluteus larvae approximately 48 hpf; therefore, they are relying on endogenous energy reserves for development and survival prior.

Maternal provisioning is a mechanism in which adults can provision nutrients and biochemical constituents through eggs for offspring development. Females naturally provision; however, certain external stimuli may influence greater provisioning. Moran et al. 2013 found that planktotrophs have a scaling factor significantly less than 1 when plotting egg energy versus egg size. This demonstrates a trend toward lower energy density with larger eggs. When *S. purpuratus* have been exposed to a simulated prolonged MHW event, they generated larger eggs with more protein and lipid content in comparison to their counterparts experiencing lower temperatures (Chamorro et al. 2023). Biochemical composition, protein and lipid content, were quantified to identify differences in maternal provisioning in eggs from females experiencing different gametogenic temperature environments. In this study, results were consistent with past research and biochemical constituents in eggs were greater in adults acclimated to MHW conditions. Average egg size was larger in diameter and area in MHW-acclimated females, though not significantly so I did not find that egg size correlated to biochemical composition. It is possible that the recovery periods between these shorter-term simulated

MHW temperature anomalies provided a sense of refuge. Temperature refuge may halt the signal for greater maternal provisioning. Additionally, energy reserves and not egg size may be a better indicator for evidence of maternal provisioning as other studies have seen differential energy reserves and with no clear differences in size in echinoderms (Gagliano and McCormick 2007, McAlister and Moran 2012). Greater amounts of biochemical constituents may be present in larger eggs; however, that is not always the case. Therefore, egg size should not be used as a reliable sole indicator for maternal provisioning.

Proper development of marine invertebrate larvae is supported by egg nutrients from maternal reserves especially prior to becoming feeding larvae. Lipids in particular are important for pre-feeding larvae (Villinski et al. 2007, Meyer et al. 2007, Prowse, Sewell, and Byrne et al. 2007). I focused on the lipid content in eggs of acclimated females because lipids serve as the major energy source for echinoderm eggs (Jaeckle 1995). Lipids are the primary metabolic energy reserve in most marine organisms (Holland 1978), thus making them essential for early development. Proteins are important as maternal reserves for larval development as they help construct the larval body (Moran and Manahan 2003). Both total lipid content and protein content was elevated in eggs from MHW-acclimated females, suggesting that the thermal stress experienced by the adult females led to greater investment in their eggs. Greater investment in eggs can increase performance and growth during embryonic development. Though maternal provisioning is a mechanism that can lead to offspring health in response to global change, there's evidence that suggests that parental conditioning is not an overarching solution in all marine invertebrates (Byrne et al. 2020). The timing of conditioning,

however, is an important factor to consider as conditioning in gametogenesis has produced beneficial outcomes for offspring (Parker et al. 2012, Karelitz et al., 2019). When adults and offspring environments differed, parental conditioning was maladaptive and offspring were more sensitive (Byrne et al. 2017). Variability in natural ocean environments are vast, so it is difficult to replicate environmental conditions in the lab to identify specific impacts that are occurring in the wild.

Response of early stages

In this study I measured three performance traits of the progeny from the differentially acclimated females: (1) thermal tolerance, (2) respirometry measures, and 3) an assessment of oxidative stress to proteins by measure levels of protein carbonyl groups.

LT50 values differed in prism and gastrula larvae that were from females that experienced different acclimation treatments. LT50 values were greatest from offspring that came from MHW parental treatments. This is consistent with past thermal tolerance studies in our lab. Chamorro et al. identified a 0.3°C difference between embryos from females experiencing MHW temperatures compared to control temperatures. However, in Leach and Hofmann, sire experiencing higher thermal temperatures yielded offspring with slightly lower LT50 values (0.5°C difference). When parental treatments were similar and developmental temperatures differed, offspring experiencing warm temperature treatments had higher LT50 values. In this study, adult urchins were acclimated for a shorter period – 28 days. These thermal tolerance studies being conducted on *S. purpuratus* have led to identification of very high LT50 values. *S. purpuratus* has a wide

range and is known to be tolerant to adverse environmental conditions. Their high tolerance could be explained by the climate extremes hypothesis, which suggests that organisms with high temperature variability evolve wider thermal tolerance ranges (Addo-Bediako et al. 2000).

There was no difference in respiration rate in the different populations of prism-stage larvae; however, there was higher protein carbonyl content in gastrula and prism embryos from MHW-acclimated females. Protein carbonyl content is a widely used marker and the most general indicator for oxidative stress. It is used to assess protein oxidation, which can be brought on by the modification of a protein induced by reactive oxygen species (ROS). One copepod study found that protein carbonylation was higher in females subjected to variable salinity compared to the control (Martinez et al. 2020). Higher levels in protein carbonylation in both marine and terrestrial organisms (*Mytilus edulis*, *Eobania vermiculata* and *Symphodus melops*) were found from chemically polluted sites (McDonagh et al. 2005, Almroth et al. 2008, Itziou et al. 2010). Overall, there are few studies describing the protein carbonyl content of marine invertebrates and how it impacts organismal physiology.

Protein carbonylation levels may be indicative of aging in animals. Though some studies indicate no effect of age on protein carbonyl content (Ivanina et al. 2008), in this study there was a significant difference in protein carbonyl content in gastrula and prism embryos. Though I saw elevated protein carbonyl levels in later stages of *S. purpuratus* embryos and in *S. purpuratus* embryos from females experiencing MHW stress, there was no difference in the measured metabolic rate of prism embryos (Figure 9). Additionally, in both total protein content and protein carbonyl content, I saw decreases

in larvae developing from gastrula to prism (Figure 9 and 10). Changes in lipid and protein in embryos in *S. purpuratus* are seen in a previous study indicating decreases in both once embryos reach 2 days old (Shilling and Manahan 1990). Urchins do not develop their tripartite gut that is necessary for feeding until ~72 hpf. The lack of the ability to feed along with the metabolic energy needed for development may lead to complete depletion of energy reserves. These energy reserves are important for meeting metabolic demand; therefore, the rate of depletion is an important factor in offspring health. There has been increased study of MHWs and their impacts in recent years. To provide a more comprehensive view of MHWs, future laboratory studies assessing MHW impacts on marine ecosystems. Marine ecosystems are highly variable and dynamic. Laboratory experiments in global change biology have been better contextualized by long-term monitoring, which allows us to mimic what is happening out in nature.

Conclusion

There are mixed results in the larval physiology of embryos from adult *S. purpuratus* that experienced heat stress. Though phenotypic differences such as morphology may not be significant between eggs and embryos from different parents in our treatments, I saw differences in their biochemical content that may impact growth or likelihood of survival in response to elevated temperature stress. During the intense MHW year of 2015 in the Northeast Pacific region, the average temperature in the month of September was 21.17°C. This is the middle of *S. purpuratus* gametogenesis, therefore, the temperatures experienced during this lab experiment have occurred in nature and may occur with future MHWs.

This chapter suggests that adult urchins were unable to adjust to abrupt temperature changes, as seen in the high mortality rates during the simulated recovery periods with water temperatures reflecting ambient conditions. In addition to adult urchin mortality, MHW periods may impact maternal provisioning of biochemical constituents in female urchins but not egg size. The provisioning of lipids and proteins to eggs will be beneficial to early offspring health and survival. Though this study did not look at how adverse conditions during offspring development impacts their survival, past studies showed that offspring from females that experienced adverse environmental conditions had greater tolerance to elevated temperature.

This thesis chapter contributes to existing research addressing MHW impacts on the fecundity of *S. purpuratus* and marine invertebrates, broadly. In order to gain a broader understanding of MHW dynamics on early stages of *S. purpuratus*, I focused on how larval settlement of urchins is impacted by MHW patterns historically, using Santa Barbara Coastal LTER datasets. I will address this in my next chapter.

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III. Marine heatwave event patterns and the impacts on the larval abundance and biomass of *Strongylocentrotus purpuratus* Santa Barbara Channel populations

Introduction

Marine heatwaves (MHWs) have influenced foundation and keystone species globally. These impacts cause cascading impacts to communities, food webs and ecosystem functioning. In the Northeast Pacific region, we have seen these consequences in the form of species shifts, fish stock declines, smaller phytoplankton size, and mass strandings (Cavole et al. 2016, Yang et al. 2019, Cheung and Frölicher 2020, Wyatt et al. 2022). Seagrass and macroalgae abundance also showed decreases by > 40% following MHW events, with declines in macrophytes observed with increasing MHW intensity (Smith et al. 2024). A model investigating the potential impacts of MHWs on seagrass resilience, found that significant impacts are expected with longer durations causing greater decline, reduced resilience, higher extinction risk, and prolonged recovery (Hatum et al 2024). The Northeast Pacific region is characterized by the presence of *M. pyrifera*, Giant kelp, as a food source, shelter, and important nutrient cyclers. Through the absorption of CO₂, kelp forests help to mitigate climate change, thus the decrease in macroalgae due to MHWs is a detrimental consequence and may get worse as MHWs get more frequent if kelp forests are unable to recover.

Over the past few decades, studies on the impacts of MHWs have increased globally. Abiotic aspects of MHWs have been well-studied and understanding of MHW traits has broadened (Joyce et al 2024). Understanding different patterns of MHWs is an essential part of figuring out how coastal ecosystems may be impacted in the future. Beyond

location and depth, there are many other MHW metrics that contribute to the impacts on marine ecosystem health such as duration, frequency, depth, and intensity. Evidence indicates that MHWs have the potential to impact a variety of coastal marine ecosystems in the Pacific. From 2013-2015 “the Blob” formed off the northeast Pacific coast, causing horizontal and vertical range shifts in marine organisms, including benthic invertebrates (Michaud et al. 2022, Rogers-Bennett and Catton 2019, Sanford et al. 2019, Reed et al. 2016, Cavole et al. 2016). Additionally, MHWs are a recurrent Northeast Pacific phenomenon (Xu et al. 2021) and due to climate change, increased severity of MHW impacts is likely.

Along with species-level impacts, MHWs differentially impact life history stages. The important kelp forest organism, *S. purpuratus*, is a relatively stationary species that spends time as adults at the benthos. Sessile taxa are more affected by MHWs than highly mobile and planktonic taxa due to their inability to respond quickly through migration in the face of rapidly changing conditions. As MHWs are known to occur at the benthos as well as the surface in the SBC region, adult urchins are susceptible to adverse environmental conditions that may be caused by MHWs. In my region of interest, MHWs commonly occur during *S. purpuratus* gametogenesis, late Summer – early Fall. When urchins experience heat stress during gametogenesis it leads to diminished sperm performance and greater maternal provisioning of proteins and lipids in eggs (Leach et al. 2021, Chamorro et al. 2024). Though MHWs do not commonly occur during *S. purpuratus* early development (Winter), impacts are still felt due to parental provisioning. Heat stress has been associated with increase in abnormal development, mortality, and lasting impacts on reproduction and immune response (Gibson et al. 2011, Shanks et al.

2020, and Minuti et al. 2021). In similar low-mobile invertebrates that broadcast spawn and have pelagic larvae, the exposure to MHW events also causes adverse impacts on reproduction and recruitment (Shanks et al. 2020). Evidence of decreased abundance of abalone, scallops, and prawns through mortality and recruitment reduction has also been detected in response to a MHW event (Caputi et al. 2016). In the lab, *Carinus maenas*, European shore crab, were exposed to varying MHWs that ultimately caused severe detrimental impacts on their survival, development duration, and dry mass. This along with other studies emphasize the importance of heatwave timing relative to the life cycle (Deschamps et al 2025). As MHWs are common in the Northeast Pacific region during months where *S. purpuratus* are undergoing gametogenesis, there may be patterns between MHW events and larval settlement. In this chapter, I hypothesized that if study sites have intense MHW years, then larval settlement will be lower than non-MHW years and less intense MHW years.

Thermal anomalies occur differently with latitude as well as depth. In the Northeast Pacific region, MHWs have been identified all along the coast from the Gulf of Alaska (Rallu De Malibran 2024) to Baja California. Many studies have expressed how MHWs contribute to significant declines in kelp forest health (Filbee-Dexter and Wernberg 2018, Straub et al. 2019, Thomsen et al. 2019, Smale 2020). These declines also directly and indirectly impact overall marine ecosystem health and productivity. In Baja California, MHWs have been shown to alter Giant kelp community dynamics in the way of fewer individuals and fewer fronds on individuals (Arafteh-Dalmau 2019). Though adverse impacts due to MHWs are identified, Giant kelp resilience to MHWs is spatially different with the Santa Barbara coastal region having more resistance when being compared to

Baja California region (Cavanaugh et al. 2019). In this chapter, I investigate MHW patterns using long-term datasets collected by the Santa Barbara Coastal Long-term Ecological Research Program (SBC LTER). In addition to temperature data, I use *S. purpuratus* larval settlement and adult abundance data as well as *M. pyrifera* abundance data to further investigate how MHWs influence kelp forest dynamics in the Santa Barbara Channel and if there is evidence for MHW refuge for *M. pyrifera*. Sea surface temperature datasets are essential for understanding natural climate variabilities and upper ocean conditions. Benthic environments support many flora and fauna, such as *S. purpuratus* and other mobile-limited invertebrates; however, long-term sea surface temperature data are more readily available via public datasets than benthic temperature. Lack of bottom temperature long-term datasets limit the ability to assess trends in temperature at a similar scale to sea-surface temperature datasets, though it may still grant us an opportunity to assess patterns of elevated temperature and temperature anomalies.

MHWs have impacted the biodiversity of the kelp forest community in the Santa Barbara Channel. During the 2015 MHW, there was a decline in adult sea urchin biomass in the SBC (Reed et al. 2016) and abundance declined at more southern sites in the California Current System in response to the same 2014-2016 MHW. Other studies have shown that sea urchins from more Northern populations have increased abundance during and post-MHW, creating urchin barrens (McPherson et al. 2021). The difference in abundance between sites may be due to the regional difference in MHW temperature dynamics where Southern populations of urchins may already be living at their temperature range edge and unable to adapt to a higher temperature in contrast to

Northern populations. Nevertheless, the presence of these anomalous events has the potential to completely restructure marine ecosystems by causing deleterious impacts to foundational species present in the SBC such as *Macrocystis pyrifera* (Giant kelp) (Smale et al 2019). Understanding the pattern of MHWs as well as how the biomass, abundance, and larval settlement of *S. purpuratus* may vary with these temperature events will show us how sentinel species may play a part in this restructuring. Studies by SBC LTER investigators have shown that sea urchin recruitment does vary on the coast (Okamoto et al. 2020) and I plan to use these types of data to explore more closely recruitment patterns and how they correlate to MHW events in the Santa Barbara Channel. Larval environments are an important factor in determining offspring success. Lab studies indicated larger and more thermally tolerant *S. purpuratus* larvae when exposed to elevated temperatures during development (Leach and Hofmann 2023).

This chapter focuses on a crucial physical property of the ocean that influences sea water density, oxygen content, ocean currents, and marine habitats. As MHWs are happening in an important time in sea urchin gametogenesis, larval development, and larval settlement, I used existing SBC LTER data to look at how MHW events have correlate with and have impacted these life history events. In more southern invertebrate species from warm-temperate environments, there have been ranges shifting more northward even in sessile invertebrates such as urchins (Lonhart et al. 2019). As northern species of *S. purpuratus* can fare better during MHWs, larval settlement may change latitudinal for more favorable conditions. I used multiple SBC LTER databases to illustrate the patterns of MHWs, and further, to correlate MHW events to changes in the adult and larval populations of purple urchins as well as giant kelp abundance and size at

core study sites. I hypothesized that as MHW events have become more common and intense over time, kelp forest abundance decreases and purple urchin populations for all stages increase in size.

Methods

Study Sites

To measure temperature dynamics within the Santa Barbara Channel where *S. purpuratus* are found in abundance, data was analyzed from five sites: Alegria Reef (ALE: 34.46085, -120.28998), Arroyo Quemado Reef (AQE: 34.46495, -120.11965), Carpinteria Reef (CARP: 34.39015, -119.5399), and Mohawk Reef (MKO: 34.39323, -119.73012), and Naples Reef (NAP: 34.42388, -119.95032). These sites were selected because they are areas where we know MHWs occur and have corresponding biological datasets with *S. purpuratus* larval settlement and recruitment data.

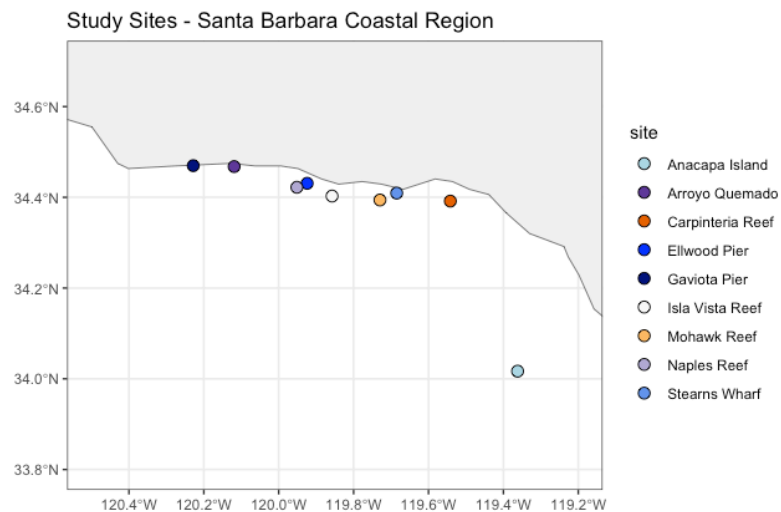


Figure 1. Study Sites used for analyses. Each point corresponds to a SBC LTER site. Navy = Gaviota Pier (34.46978, -120.22821), Dark blue = Ellwood Pier (34.43085, -119.92408), Sky blue = Stearns Wharf (34.40934, -119.68493), light blue = Anacapa Island (34.01681, -119.3621), Dark purple = Arroyo Quemado (34.4677499, -120.11905), light purple = Naples Reef (34.4221216, -119.95154), white = Isla Vista Reef (34.402783, -119.85755), yellow = Mohawk Reef (34.3940708, -119.72957), orange = Carpinteria Reef (34.3916319, -119.54169).

S. purpuratus SBC-LTER long-term dataset

S. purpuratus abundance data has been collected annually by surveying six 1m² quadrats at 8 meter intervals along 40 meter transects and recording the number of individuals. SBC LTER divers estimated average size for the purpose of estimating its biomass (Reed and Miller 2022). Density of urchins has also been collected along 40 meter transects by measuring at least 50 individual *S. purpuratus*. Size is the test diameter measured to the nearest 0.5 cm using calipers (Reed and Miller 2022). Lastly, *S. purpuratus* settlement is measured as the number of individuals found on 85 cm² wood-backed brushes with polypropylene bristles. Brushes are deployed in two-week intervals and data have been collected since 1990 (Schroeter et al. 2022).

Temperature SBC LTER long-term dataset

Santa Barbara Channel temperature data was collected from near-shore oceanographic moorings deployed at sites maintained by SBC LTER. The temperature datasets are: Moored CTD and ADCP data from Alegria Reef Mooring, 1999-2021; Moored CTD and ADCP data from Arroyo Quemado Reef Mooring, 2004-2024; Moored CTD and ADCP data from Naples Reef Mooring, 2001-2024; Moored CTD and ADCP data from Mohawk Reef Mooring, 2005-2024; Moored CTD and ADCP data from Carpinteria Reef Mooring, 2001-2024. Moorings were deployed at 8-20 meters deep and collected data every 20 minutes (Washburn et al. 2025).

S. purpuratus Larval Settlement SBC-LTER long-term dataset

To analyze larval settlement data, I utilized another SBC LTER long-term dataset. To collect larval settlement data, SBC LTER researchers deployed two pairs of wood-backed brushes of 85 cm² with polypropylene bristles in the following SBC LTER sites: Anacapa Island, Ellwood Pier, Gaviota Pier, Stearns Wharf, Scripps Pier, Ocean Beach Pier, and Point Cabrillo from 1990 to present. Brushes were deployed in 2-week intervals beginning in 1990. Once collected after their 2-week deployment, samples are examined in a Petri dish under a microscope using the protocol described in Schroeter 2017. For my thesis work, the sites I focused on were Anacapa Island, Ellwood Pier, Gaviota Pier, and Stearns Wharf as the only sites in the Santa Barbara Coastal region.

Macrocystis pyrifera detritus biomass

Macroalgal detritus biomass was measured at five SBC LTER reefs: AQE, CARP, Isla Vista Reef (34.40283, -119.85755), MHK, and NAP. Sites were selected because they historically supported giant kelp. Six 1 m² quadrats were positioned by divers along each transect (1 40 m x 2 m transect per site). Divers collected all algal detritus within each six 1 m² quadrat along a transect. Detritus was brought back to a laboratory to be sorted, dried, and then weighed (Reed and Miller 2025).

S. purpuratus adult abundance

The data used for analysis of urchin density is the long-term dataset managed by the SBC-LTER that encompasses various reef biota, macroalgal detrital accumulation, substrate type, and seafloor irradiance. Data was collected at five reefs: ARQ, CAR,

IVEE, MHK, and NAP. The depth range at these reefs is 5.8 m to 8.9 m. At these sites, divers surveyed six 1 m² quadrats positioned at 8-meter intervals along each 40-meter transect. The number of individuals for species of reef invertebrates and macroalgae were recorded. The areas were searched within each quadrat without disrupting the bottom substrate or displacing organisms.

Statistical analyses

All statistical analyses were conducted in R Studio (Version 2025.05.0+496). Sea surface temperature time series were analyzed for each site (ARQ, NAP, MKO, CAR) using the *heatwaveR* pipeline to identify MHW events and their characteristics (i.e. intensity, duration). For each site, temperature record was converted to a climatology object using baseline period 2005-03-25 to 2024-09-27. Discrete MHW events were detected, and event metrics were aggregated into time blocks. Using a generalized linear model with a Poisson error distribution and log link, I tested for temporal trends and site differences in heatwave duration and heatwave max intensity. To investigate the relationship between kelp detritus wet weight and urchin abundance, a generalized linear mixed-effects model fit with *glmmTMB* was used. Kelp detritus wet weight was a continuous fixed effect while site was a categorical fixed effect, and year was a random effect. To account for overdispersion, I modeled count using a negative binomial distribution. Model coefficients were estimated on the log scale. To investigate the relationship between kelp detritus wet weight and urchin size, I used a linear mixed-effects model. Kelp wet weight was a continuous fixed effect, site was a categorical fixed effect, and year was a random effect. Urchin size and count was analyzed using a linear

mixed-effect model with year as a continuous fixed effect to detect temporal trends and site as random effects. I also analyzed urchin size and count using a linear mixed-effect model with site as a fixed effect to detect site differences and year as a random effect. Lastly, to investigate effects of temperature and time on larval settlement, settlement count was log transformed and then analyzed using a multiple linear regression model with sea surface temperature, year, site, and month as fixed effects. Data were log transformed to improve normality and stabilize variance. Sea surface temperature was included as a continuous predictor. To account for long-term trends and seasonality, year and month were included as fixed effects. Site was also included as a fixed effect to look at spatial differences.

Results

MHW Analysis Using SBC LTER Long-Term Temperature Datasets

In all sites of interest for temperature analysis, MHW event frequency has increased since 2013, the onset of the Northeast Pacific MHW deemed ‘the Blob’ (Figure 1). In all sites, there have been MHW events every year since 2013 excluding 2021. At the Arroyo Quemado site, there were 316 total MHW days in 2013 and 2014 combined. In all other years, there have been 235 total MHW days, including the MHW year of 2018 where there were 85 MHW days. MHW event count for SBC LTER sites of interest ranged from 32 to 40. The southernmost site of interest, Carpinteria (34.39015, -119.5399), had the most total MHW events even though there were two years without MHW events. Carpinteria reef also had the most intense MHW event of 5.68 lasting for 17 days in August 2018. Max intensity is defined as the max temperature anomaly above

a long-term average, a measure of severity. Mean intensity is the average over the entire duration of the MHW.

Max Intensity of MHW events Occuring in SBC LTER SITES

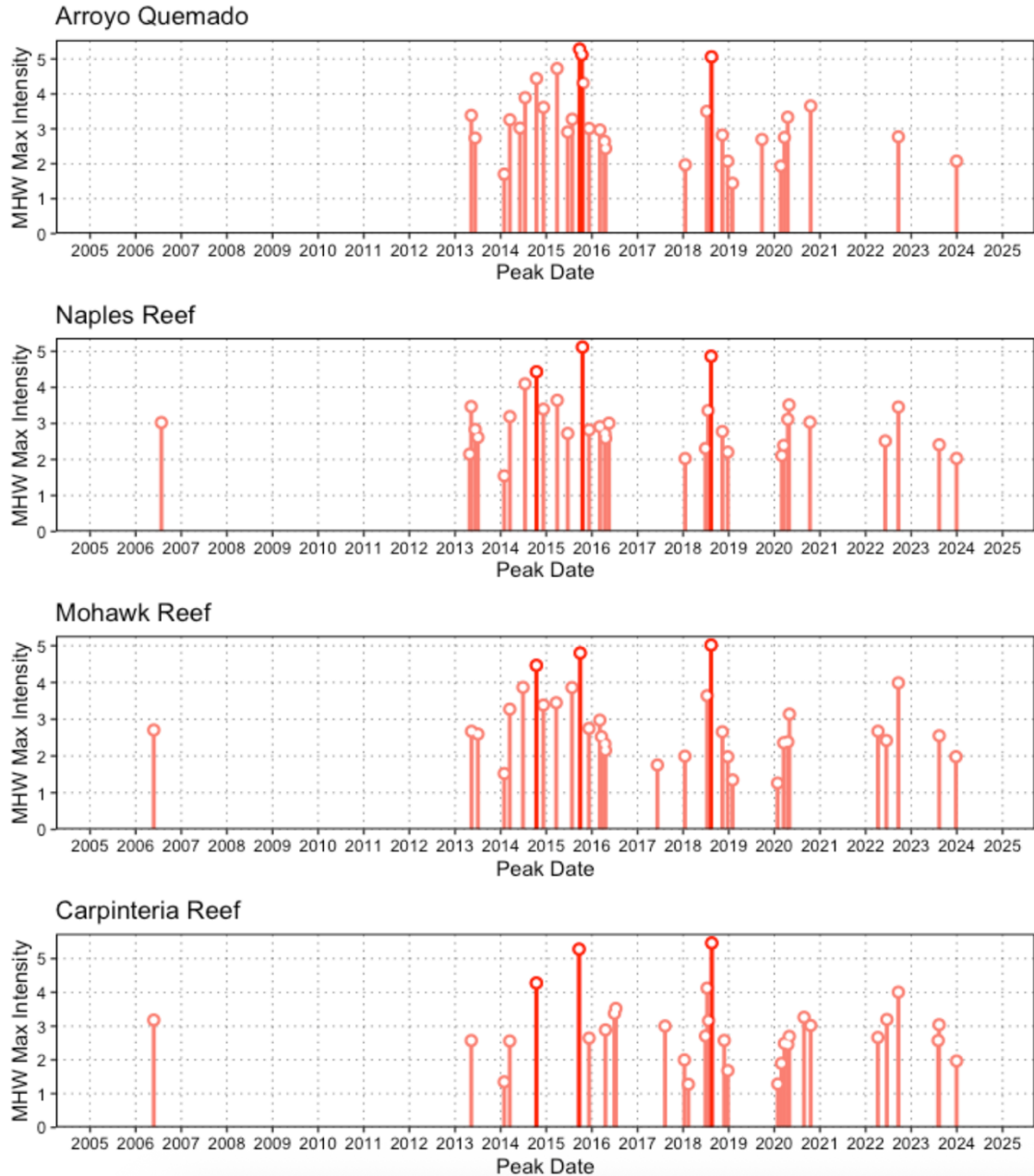


Figure 2. Lollipop plots of MHW Max Intensity at SBC LTER Sites. Graphs of sites are listed in order from northernmost site to southernmost site (Arroyo Quemado, Naples Reef, Mohawk Reef, Carpinteria Reef). Temperature data spans the timeframe 2005-2025. Each lollipop corresponds to a MHW event and is plotted by their max intensity. Intensity refers to the degree of the anomaly. Max intensity is the highest degree of the anomaly for the MHW event.

A Poisson GLM was used to predict total MHW days using year and SBC LTER site. Results from the model indicated that total MHW days tends to decrease over time (Figure 3). Sites Arroyo Quemado, Carpinteria Reef, and Naples Reef were all similar in their counts, but Mohawk reef had significantly fewer MHW days. Max intensity of MHW events was also significant, with little variability among sites. Results from linear mixed model showed a small, but significant downward trend in maximum intensity over time. Mean intensity followed a similar trend with time, though not significant.

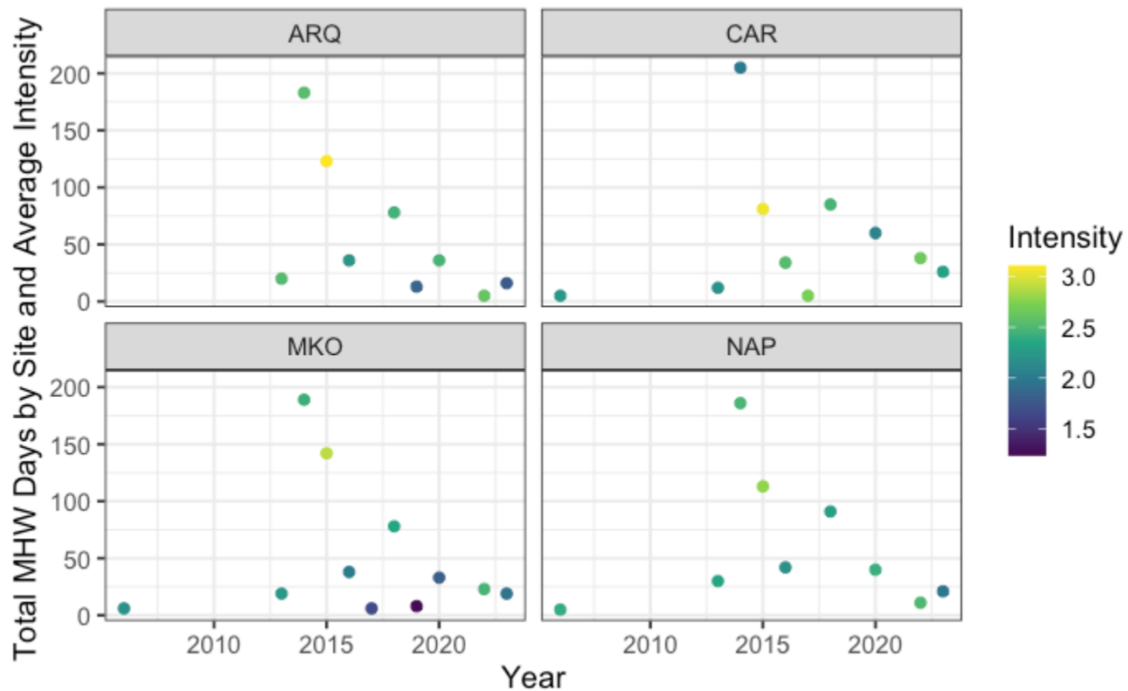


Figure 3. Total annual MHW days from 2008-2022 across four sites (ARQ, CAR, MKO, NAP) from a GLM using Poisson regression. ARQ = Arroyo Quemado, CAR = Carpinteria, MKO = Mohawk Reef, and NAP = Naples Reef. Points show observed values for each year. The average intensity of the MHW events for each year and site are indicated by the color of the points. Yellow indicates higher intensity and dark purple refers to lower intensity.

*Analysis of Adult *S. purpuratus* Abundance and Size with Time and Site*

There were significant differences in average urchin abundance by year (p -value < 0.001). The abundance of *S. purpuratus* in Arroyo Quemado, Carpinteria, and Naples

peaked at the onset of MHW years. Abundance at Arroyo Quemado and Carpinteria peaked at the start of the 2014 ‘blob’ year while abundance at Naples peaked at the onset of 2018, another MHW year with fluctuating MHWs (Figure 4). The average abundance of adult urchins before ‘the Blob’ was greater than the average abundance of adult urchins after ‘the Blob’ even though abundance peaked during MHW years (Table 2). Analysis of average *S. purpuratus* abundance between years using site as a random effect showed significant differences. There were significantly more urchins on average in 2013 than years 2016 (p -value: 0.0151), 2019 (p -value: 0.0239), 2023 (p -value: 0.0580), and 2025 (p -value: 0.0182). Total urchin counts also exhibited a significant relationship between years (Figure 5). In 2011, 2012, and 2013, urchin abundance was significantly greater than other years.

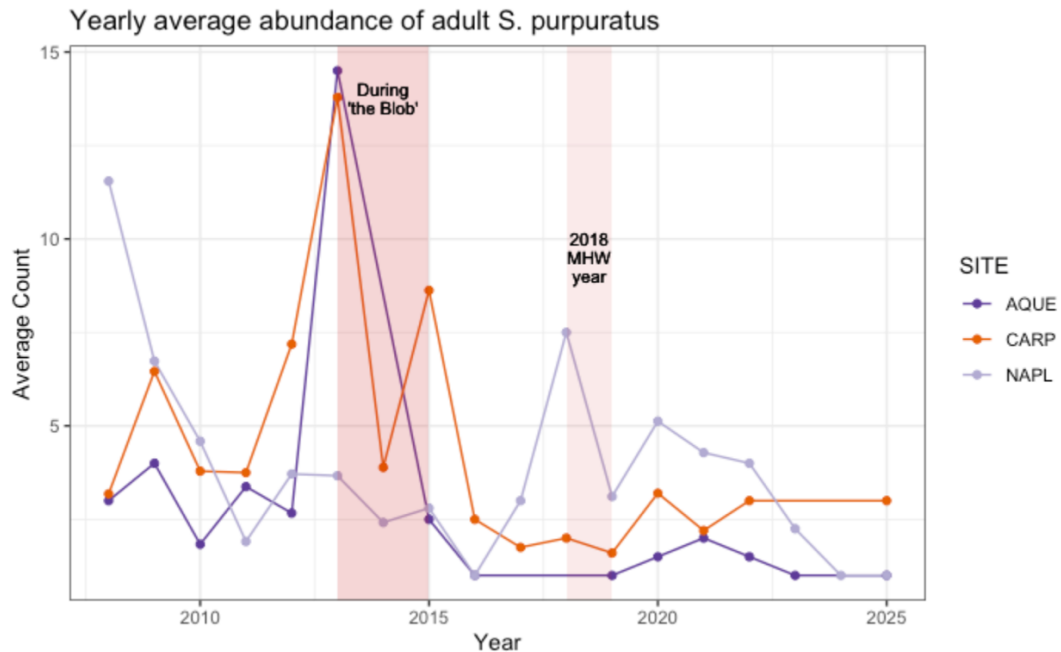


Figure 4. Time series of abundance of adult *S. purpuratus*. Average yearly count of adult *S. purpuratus* at three different SBC LTER sites: Arroyo Quemado Reef (red), Carpinteria Reef (green), and Naples Reef (blue). The darker red shaded region indicates the time of ‘the Blob’ MHW. The lighter red shaded region indicates the time of the 2018 MHW year.

Pre-MHW, 2008-2012				MHW years, 2012-2015				Post-MHW, 2015-2025			
Site	Mean	Max	Minimum	Site	Mean	Max	Minimum	Site	Mean	Max	Minimum
AQUE	2.975000	4.000000	1.833333	AQUE	8.500000	14.500000	2.500000	AQUE	1.285714	2.0	1.0
CARP	4.873425	7.18750	3.181818	CARP	8.766534	13.785714	3.888889	CARP	2.406250	3.2	1.6
NAPL	5.698513	11.54762	1.909091	NAPL	2.961111	3.666667	2.416667	NAPL	3.227183	7.5	1.0

Table 1. Average count for adult *S. purpuratus*. The average count for adult *S. purpuratus* separated in three different time periods: pre-MHW, ‘the Blob’, and post-MHW. All three sites are listed for all time periods. Mean, max count, and minimum count are calculated for each time period of interest.

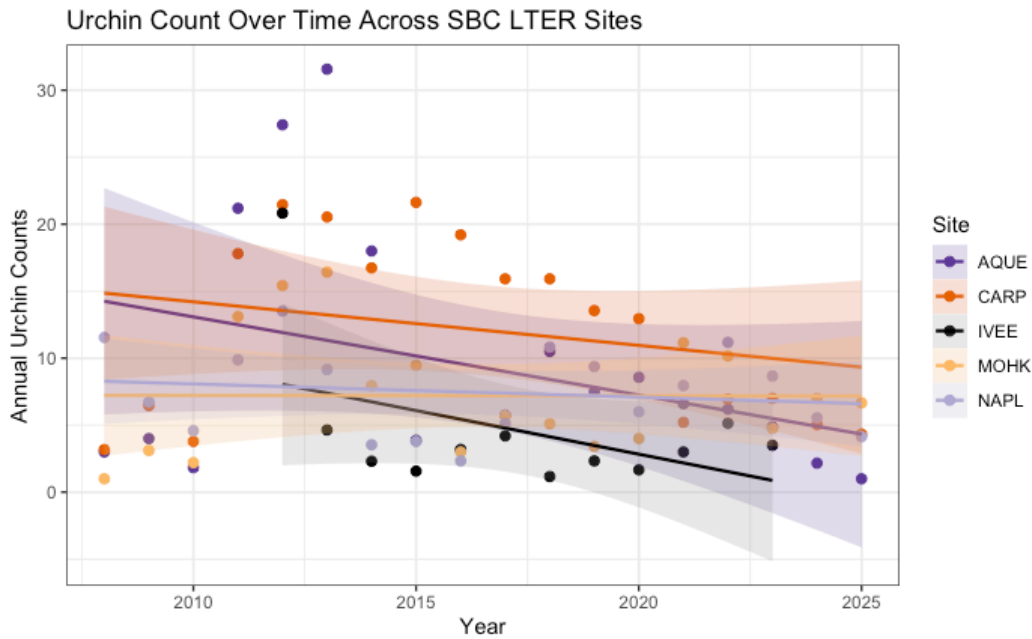


Figure 5. Interannual trends in adult sea urchin counts across Santa Barbara Channel sites. Annual adult *Strongylocentrotus purpuratus* counts is shown by year for each site (AQUE, NAPL, IVEE, MOHK, and CARP). Points represent annual counts, and solid lines show site-specific linear trends with 95% confidence intervals. Statistical inference is based on a negative binomial generalized linear mixed model (log link) including year as a categorical fixed effect and site as a random intercept ($n = 84$ observations across 5 sites).

Urchin counts were also significantly different between sites. Carpinteria Reef and Naples Reef, the southernmost and northernmost sites respectively, had significantly more urchins than other sites (p -value < 0.001) (Figure 6).

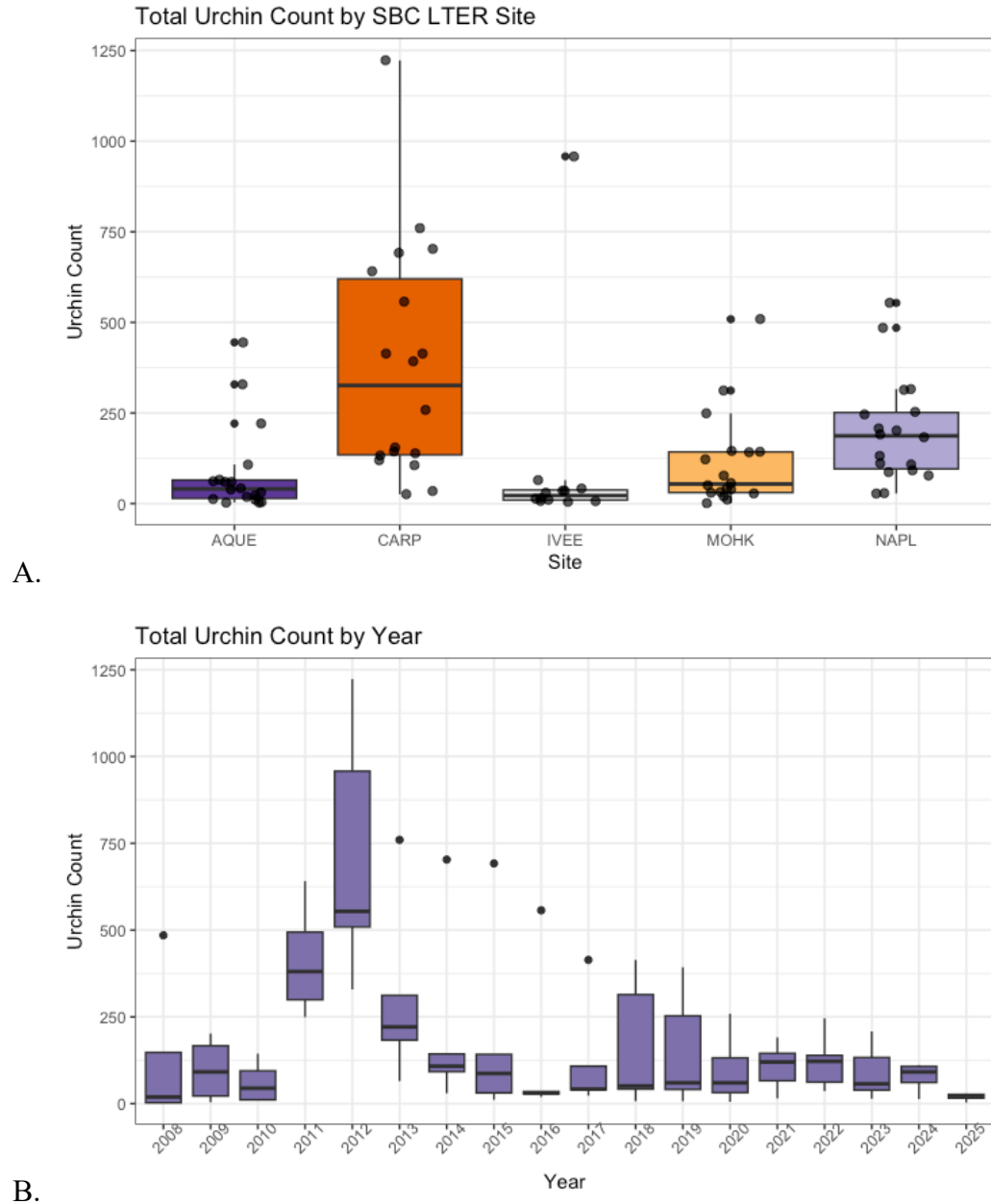
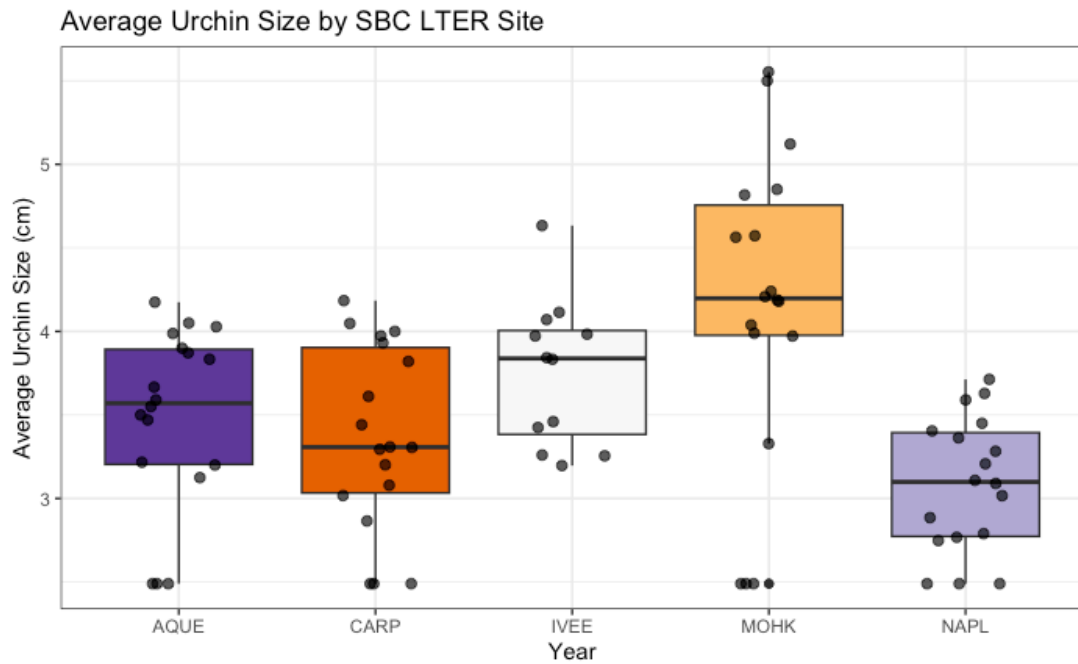


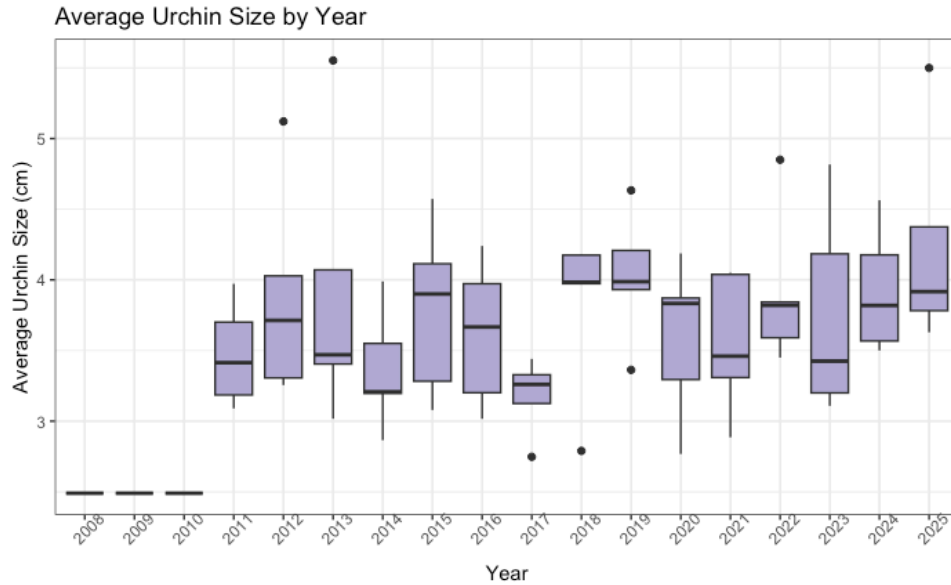
Figure 6. Total *S. purpuratus* counts across SBC LTER sites and over time. (A) Annual *S. purpuratus* counts across SBC LTER sites. Colors were aligned by site with purple = AQUE, orange = CARP, white = IVEE, yellow = MOHK, and light purple = NAPL. Boxplots show the distribution of urchin counts at each site, with points representing annual urchin counts. **(B) Annual variation in total *S. purpuratus* counts across survey years (2008-2025).** Boxplots show the median, interquartile range, and full range of observations, with points representing outliers.

Site also had a significant relationship with urchin size. Mohawk Reef and Naples Reef yielded urchins with significantly different size averages (Figure 7). A linear mixed

model identified that on average, urchins from Mohawk Reef were larger than those from all other sites. In contrast, urchins from Naples Reef were significantly smaller than those from all other sites, except Carpinteria Reef. Analysis of the impact of time on urchin size highlighted an overall increase in average size (cm) since 2010. Tukey post-hoc comparisons showed no differences among the early years (2008-2010), but the following years (2012-2025) had significantly higher average urchin size relative to earlier years ($p < 0.001$) (Figure 8).



A.



B.

Figure 7. (A) Average *S. purpuratus* size (cm) across SBC LTER sites. Colors were aligned by site with purple = AQUE, orange = CARP, white = IVEE, yellow = MOHK, and light purple = NAPL. Boxplots show the distribution of urchin size at each site, with points representing average by year. (B) **Annual variation in total *S. purpuratus* size across survey years (2008-2025).** Boxplots show the median, interquartile range, and full range of observations, with points representing outliers.

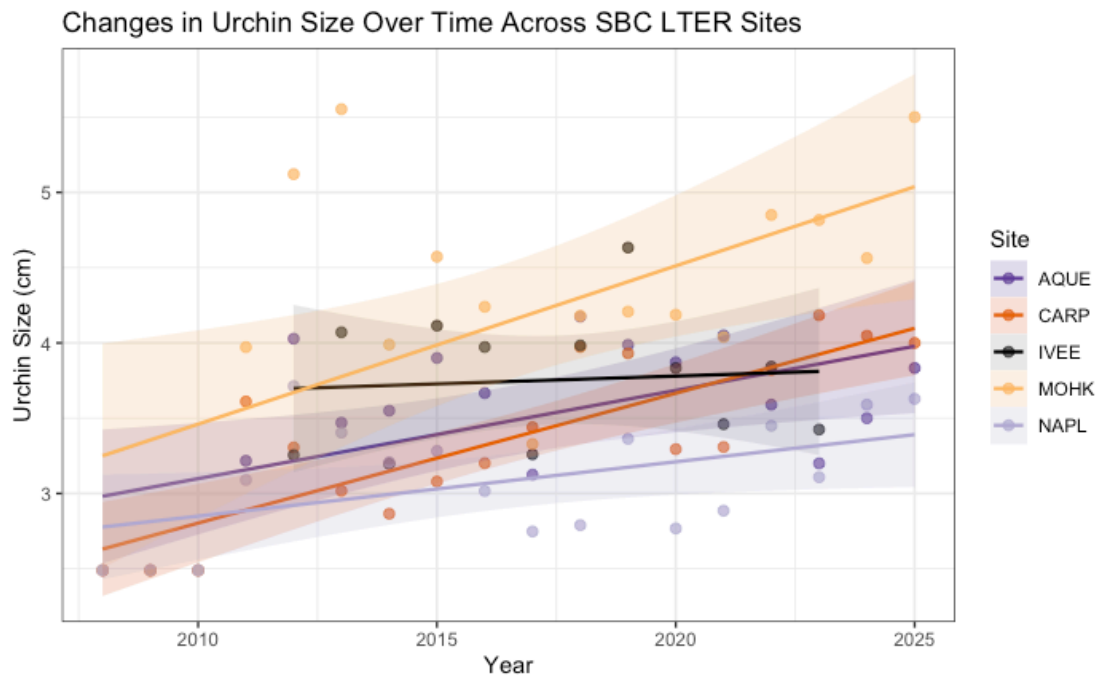


Figure 8. Interannual trends in adult sea urchin size across Santa Barbara Channel sites. Average adult *Strongylocentrotus purpuratus* size (cm) is shown by year for each site (AQUE, NAPL, IVEE, MOHK, and CARP). Points represent annual mean size estimates, and solid lines show site-specific linear trends with 95% confidence intervals. Statistical inference is based on a linear mixed effects model of size through time. ($\beta = 0.050 \pm 0.005$ SE, $p < 0.001$).

Analysis of Adult S. purpuratus Abundance and M. pyrifera Detritus

After accounting for differences among sites and years, higher kelp biomass was associated with fewer urchins (Figure 9, 10). A negative binomial GLM showed significance between urchin abundance and kelp biomass (p -value < 0.001). Analysis indicated that per kg of *M. pyrifera*, we would see a 20% reduction of *S. purpuratus*. All sites showed significance between urchin abundance and kelp detritus weight at all sites except Mohawk Reef. Though urchin abundance declines where kelp biomass is high, the average size of individuals showed no significant difference. Urchin size was analyzed using a linear mixed-effect model with site and year as random effects. Though not a statistically significant relationship, the correlation coefficient indicated that urchins are smaller when kelp biomass is high (Correlation: -0.078).

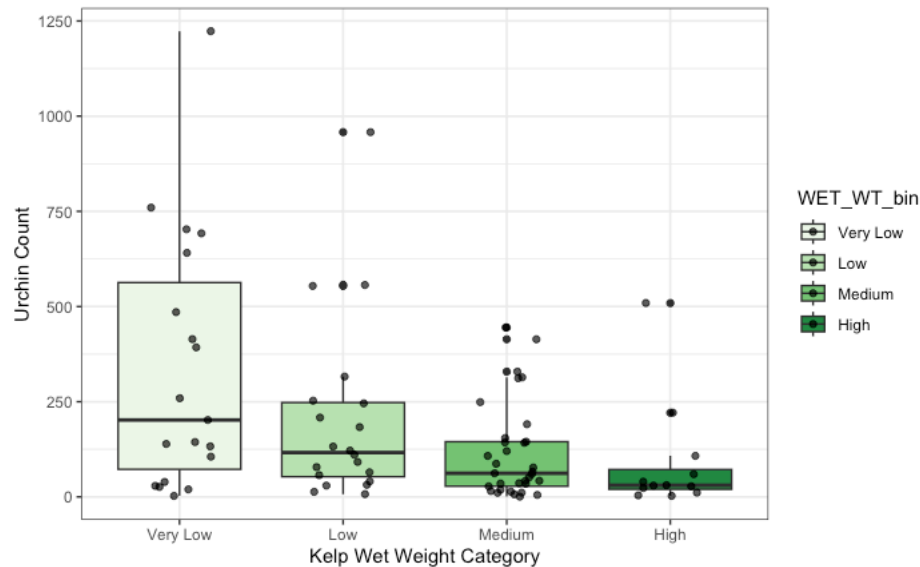


Figure 9. Relationship between kelp detritus wet weight and urchin abundance. Boxplots show urchin count distributions across sites with very low, low, medium, high, and very high detritus wet weight. Detritus wet weight was log transformed to reduce skewness. Very low refers to kelp wet weight that was between 0 and 3, low = 3, 5, medium = 5-7, high = 7-10 on a log scale.

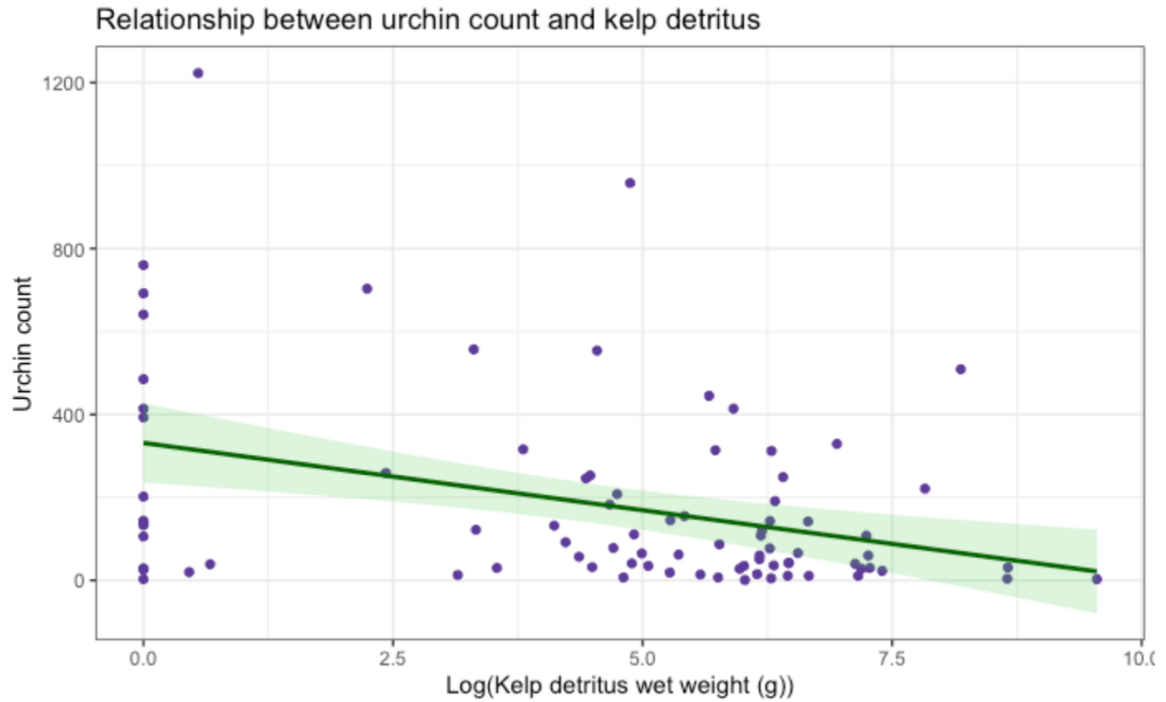


Figure 10. Relationship between giant kelp detritus wet weight and sea urchin abundance. Observed sea urchins counts are plotted against log-transformed *M. pyrifera* detritus wet weight (g). Points represent individual observations. The solid line shows model-predicted urchin counts across the range of detritus availability, and the shaded ribbon represents 95% confidence intervals around the fitted relationship.

Average detritus weight has been consistently low since 2016, with increases at Arroyo Quemado in 2013, 2015, and 2020. After 2016, the detritus wet weight did not exceed 5g for all remaining years for all sites. Detritus at Arroyo Quemado was greatest of all sites in 2015. In fact, compared to all sites, Arroyo Quemado has significantly greater average *M. pyrifera* detritus wet weight. In 2025, wet weight of detritus was at its lowest of all sites (Figure 11). With site as a random effect, average detritus wet weight was significantly different in 2008 compared to the years 2010, 2011, 2012, 2018, 2019, 2022, 2023, 2024, and 2025 (p -value < 0.05). Overall across sites, there was a sharp decline of *M. pyrifera* detritus after 2008 that persisted through 2025.

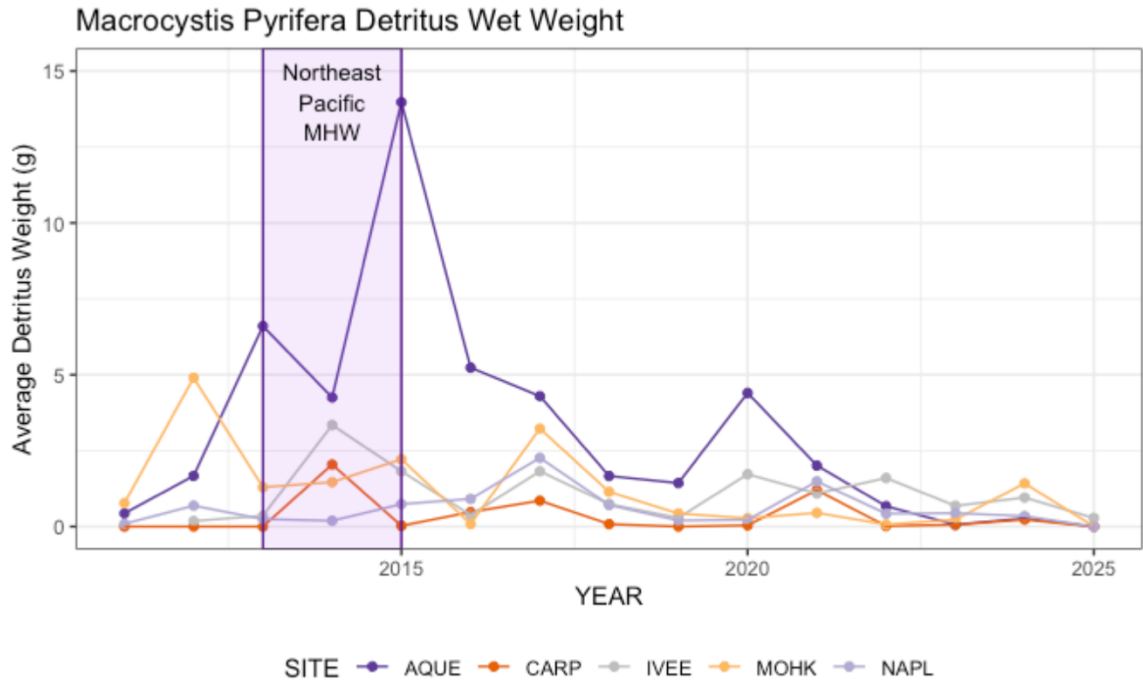


Figure 11. Interannual variation in *M. pyrifera* detritus wet weight across SBC LTER sites from 2008-2025. Mean wet weight of *M. pyrifera* (g) is shown by year for five sites (AQUE, CARP, IVEE, MOHK, and NAPL). Points represent annual detritus wet weight at each site and lines connect values to years to illustrate temporal trends. The shaded region denotes the Northeast Pacific marine heatwave (2014-2016), ‘the Blob’. Detritus availability varied markedly among sites and years, with pronounced site-specific responses during and following ‘the Blob’ period.

Drivers of S. purpuratus Larval Settlement

I identified 3 drivers of sea urchin larval settlement: temperature, season, and long-term trend. Analysis of *S. purpuratus* larval settlement identified a long-term declining trend since 2010 (p -value < 0.001) (Figure 12). Temperature was also shown to significantly affect settlement (p -value < 0.001) (Figure 13), as larval settlement drops at higher temperatures. Strong seasonality of settlement was also identified, with it peaking in April and May (Figure 12B).

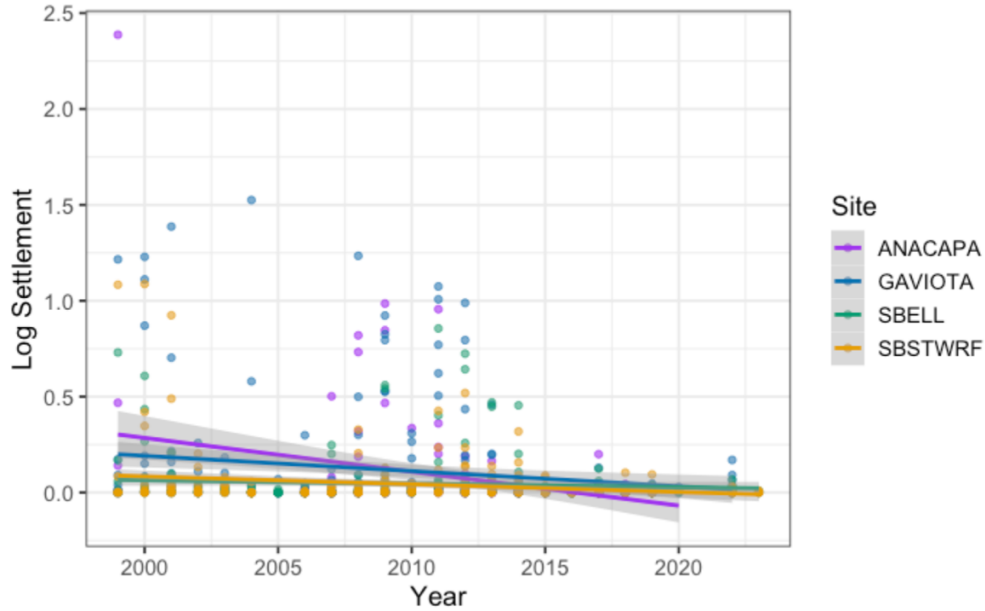


Figure 12. Temporal trends in sea urchin settlement over time across sites. Larval settlement was log transformed to account for skewed data. Larval settlement is shown as a function of time across four sites (Gaviota, SBSTWRF, SBELL, and Anacapa). Colored points refer to individual settlement observations colored by site: purple = Anacapa, blue = Gaviota, green = SBELL/Ellwood, and yellow = SBSTWRF/Stearns Wharf. Solid lines show site-specific linear fits with 95% confidence intervals. ($\beta = -0.0057 \pm 0.0011$ SE, $p < 0.001$).

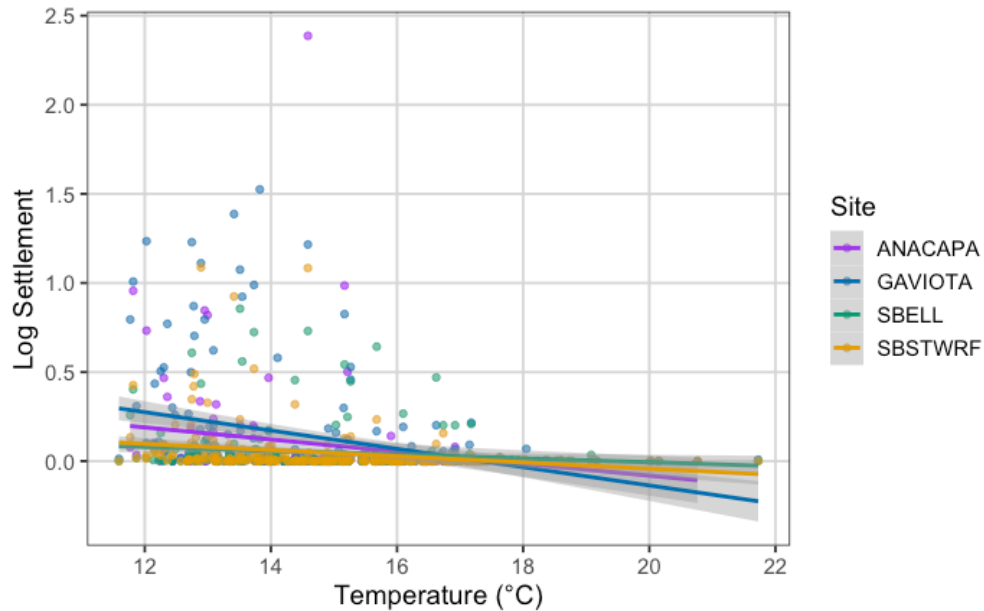


Figure 13. Relationship between temperature and larval settlement across sites. Larval settlement was log transformed to account for skewed data. Larval settlement is shown as a function of in situ temperature in degrees Celsius across found sites (Gaviota, SBSTWRF, SBELL, and Anacapa). Colored points refer to individual settlement observations colored by site: purple = Anacapa, blue = Gaviota, green = SBELL/Ellwood, and yellow = SBSTWRF/Stearns Wharf. Solid lines show site-specific linear fits with 95% confidence intervals. ($\beta = 0.013 \pm 0.0067$ SE, $p = 0.051$).

Discussion

The Santa Barbara Channel (SBC) kelp forest ecosystem is biologically rich and ecologically significant. Giant kelp, *M. pyrifera*, is the foundation of the kelp forests and serves as a major part of the species rich food web (Morton et al. 2021) and provides community structure that promotes diversity and stability (Lamy et al. 2020, Kushner et al. 2013). Many invertebrates, such as echinoderms and crustaceans, compose kelp forest communities, but the composition can shift based on factors like time and temperature (Michaud et al. 2022). Impacts of urchin grazing on kelp and the ability of healthy kelp forest ecosystems to transition to urchin barrens is well known and has been of interest for decades (Tegner and Dayton 2000, Ebeling 1985, Dean et al. 1984, Hagen 1983, Schiel 1982, Mann 1977, Vadas 1977, Lawrence 1975). More recent studies have further explored the dynamics within kelp forest ecosystems and have shown that severe declines of kelp are associated with multiple stressors, such as El Niño events, sedimentation, and coastal development (Foster and Schiel 2010). MHWs as an environmental stressor, have impacted community structure of kelp forest ecosystems by facilitating poleward redistribution of marine species (Lonhart et al. 2019). As the number of MHW events, their duration, and intensity are increasing over time and their occurrence is year-round (Chan et al. 2024), my goal for this chapter was to probe for patterns between temperature, kelp, and urchins in the SBC region.

In this chapter, I analyzed long-term SBC LTER datasets to further explore dynamics between kelp, urchins, and temperature. I hypothesized that there would be an increase in MHW intensity over time as well as total MHW days, consistent with many other studies (Oliver et al. 2018, Oliver et al. 2019, Frölicher et al. 2018). I also expect

MHW presence to be associated with a decrease in *S. purpuratus* larval settlement as temperature and other environmental conditions has been shown to influence settlement in other invertebrates and species with planktonic larvae (Raventos et al. 2021, Bergenius et al. 2005, Nozawa and Harrison 2000). In years when MHWs frequently occurred, I hypothesized that there would be decreases in adult *S. purpuratus* size as higher temperatures has led to greater growth and gonad production in tropical urchin, *Lytechinus variegatus* (Watts et al. 2011), growth in green sea urchin, *Strongylocentrotus droebachiensis* (Siikavuopio et al. 2012), and growth in red sea urchin, *Mesocentrotus franciscanus*, but at their larval stage (Wong and Hofmann 2020). Lastly, I expected kelp detritus to decline with urchin abundance and during MHW years. Ocean warming has shown to enhance feeding in urchins (Azad et al. 2011) and cause tissue degradation (Bunting et al. 2024, Castro et al. 2024). Overall, analyses revealed downward trends of MHW metrics and larval settlement over time, overall increase in average size of purple sea urchins, and an inverse relationship between kelp detritus and urchin abundance.

Marine heatwaves occurring annually since ‘the Blob’

Marine heatwaves in the SBC region have been occurring regularly and subsurface MHWs contribute to the potential for long-lived MHWs (Chan et al. 2024, Song et al. 2023). ‘the Blob’ was a major MHW event that persisted at a large-scale. Though MHWs have been occurring regularly, temperature anomalies in years post-Blob, like in 2019-2020, were of shorter duration and at smaller spatial scales (Ross 2021). In fact, because of different MHW dynamics during the years of 2019-2020 when ‘the Blob 2.0’ occurred, prolonged marine ecosystem damage is unlikely to be similar to ‘the Blob’

level impacts (Amaya et al. 2020). Results from my analyses showed that though MHWs are occurring annually in the SBC, but MHW events have not been as intense as ‘the Blob’ years and have been fluctuating, lasting on average ~18 days in 2018. In 2013 and 2014, there were 316 MHW days, but in all other years, there have been 235 total MHW days. Notably, ‘the Blob’ coincided with El Niño, a positive phase of El Niño-Southern Oscillation (ENSO) and a climate phenomenon associated with a rise in global temperatures and linked to MHWs (Hobday et al. 2023, Capotondi et al. 2022, Di Lorenzo and Mantua 2016, Philander 1983). El Niño influence on ocean conditions is prominent and enhances MHW occurrences in the eastern Pacific Ocean (Gregory et al. 2024, Holbrook et al. 2019). This link between El Niño and MHWs describes the decrease in intensity and MHW days since ‘the Blob’ years. Importantly, projections suggest more frequent multi-year El Niño events under future anthropogenic forcing (Ding et al. 2022). As detrimental ecological impacts of El Niño and MHWs have been identified on kelp populations in the Northeast Pacific region (Spiecker and Menge 2022), long-lasting negative ecological impacts in our region may continue to have significant impacts when El Niño and MHWs occur simultaneously. The negative phase of ENSO, La Niña, shows connections with MHWs as well. During La Niña periods, the number of MHW days nearly halves (Holbrook et al. 2019), which may provide a thermal refuge for marine organisms with shorter and less intense MHWs. In the 2020s, La Niña was a notable triple-dip event, persisting from 2021 through 2023. This is consistent with the lack of identified MHWs in 2021 across sites in my analysis. The time refuge from MHW events, is noticeable in this region and may have allowed for maintenance of adult *S. purpuratus*

Increase in urchin size, but not abundance, over time

Many studies have assessed urchin size in relation to feeding and environmental stressors during early stages (Pearce et al. 2004). The purple sea urchin is a common model organism for developmental biology, but due to its long-life span as an adult, it is difficult to measure changes in size in lab experiments. Using long-term SBC LTER datasets, I was able to identify an overall increase in urchin size since 2010, but no time influence on urchin abundance. Urchin abundance did differ between sites, with the northernmost and southernmost site with significantly more urchins. This is consistent with a previous study that identified little variability in abundance at a large spatial scale (between regions), and greatest variability at the smallest spatial scale (between sites) (Jenkinson 2020). Another study showed that growth patterns in sea urchin, *Centrostephanus rodgersii*, did not vary across the climate-forced extended range (Ling et al. 2009). In 2011, intertidal and subtidal populations of *S. purpuratus* were decimated over a large region, in Northern California (Jurgens et al. 2015). In Japan, temperature was one of the major factors influencing dynamics of urchin abundance (Ohgaki et al. 2019)

*Urchin abundance links with *M. pyrifera* detritus*

Kelp provides essential services to a wide range of marine life. Kelp forests are shelters (Miller et al. 2018, Holbrook et al. 1990), food sources (Koenigs et al. 2015), coastal protectors (Elsmore et al. 2024), and carbon sinks (Filbee-Dexter et al. 2023, Filbee-Dexter et al. 2020). Kelp also has significant impacts on seawater chemistry and productivity (Pfister et al. 2019). In this chapter, I focused on the relationship of Giant

kelp (*M. pyrifera*) detritus on urchin abundance and size. Kelp is an abundant and productive macroalgae on rocky coasts (Billot et al. 2003), but 80% of kelp production is lost as detritus. Kelp detritus is one of the greatest food sources and comes from the erosion of blades, breakage of fronds, or dislodgement of algae (Krumhansl and Scheibling 2012). Higher rates in detritus and declines in nutritional quality and degradation have been linked to temperature increases; however, reduction in kelp biomass led to declines in detrital production long-term (Frontier et al. 2022, Lowman et al. 2021, Krumhansl et al. 2014).

In my analysis, I found higher kelp detritus biomass connected to low urchin abundance but there was no effect on urchin size. In fact, per kg of *M. pyrifera* wet weight, we would expect to see a 20% reduction of urchin abundance. Results are consistent with studies suggesting that unchecked urchin grazing decimates kelp forests and can create urchin barrens (Miller et al. 2023, Williams et al. 2021). Sea urchins feed on drift algae and attached kelp (Randell et al. 2025), but through this consumption they become important mediators of kelp detritus by capturing drift kelp and making it available to suspension feeders (Yorke et al. 2019) that may utilize macroalgal detritus as a food source (Duggins and Eckman 1997). However, unchecked urchin abundance may impact growth rates of benthic suspension feeders as urchin barrens led to decreases in growth rates compared to areas with kelp forests (Duggins et al. 1989). Other studies showed impacts of detritus and kelp biomass on sessile invertebrates. In limpets, decreases in kelp detritus resulted in increased mortality in limpets (Bustamante et al. 1995). Kelp biomass had a strong positive effect on the abundance of benthic sessile invertebrates: clams, worms, tunicates, and sea cucumbers (Miller et al. 2015). In urchin,

S. droebachiensis, there were decreases in growth rate and gonad size and an increase in abundance as time increases since the disappearance of kelp in the region (Lang and Mann 1976). Sea urchin grazing during and after climate events like El Niño resulted in reductions of kelp stock and productivity (Tegner and Dayton 1991). Though urchin grazing is voracious, the presence of urchin predators (i.e. Spiny lobsters) mediates the impacts of grazing on *M. pyrifera* (Jenkinson et al. 2020). Kelp abundance is also inversely correlated with the Pacific Decadal Oscillation and Oceanic Nino Index, where cooler seawater temperatures were associated with greater abundance (Pfister et al. 2017). The relationship between urchins, kelp, and temperature is dynamic and further investigation would contribute to untangling the future direct and indirect impacts of climate change in kelp forest ecosystems.

Strong seasonality and temperature effect in S. purpuratus larval settlement

Lastly, *S. purpuratus* larval abundance peaked during April/May, which correlates with their spawning patterns and pelagic life cycle. *S. purpuratus* historically spawn from December-February and have a pelagic, free-swimming larval stage lasting on average 20-86 days (Strathmann 1978, Strathman 1987). As pelagic larvae, they are more susceptible to changes in environmental conditions such as elevated temperature stemming from MHW events (Pandori and Sorte 2018, Pandori and Sorte 2021). Though they are vulnerable during their pelagic stage, MHWs are less likely to occur in Spring in the Northern hemisphere. However, MHW presence is likely to occur during *S. purpuratus* gametogenesis and transgenerational effects have shown that adverse environmental conditions during this life stage impacts early stages of the purple urchin

(Chamorro et al. 2023, Leach et al. 2023, Strader et al. 2019, Wong et al. 2019) and among other urchin species (Karelitz et al. 2019, Marceta et al. 2022). My analyses showed a long-term declining trend in urchin settlement since 2010 and a significant effect of temperature on settlement. At higher temperatures, larval settlement drops. This is consistent with Miller and Emlet 1997 that observed low settlement rates in *S. purpuratus* during warm water events. In tropical urchin, *Diadema antillarum*, settlement was found to be high during years with elevated temperature (Hernandez et al 2010). Overall, there are many factors that could be influencing the larval settlement patterns. MHWs and elevated temperature may adversely impact spawning (Shanks et al. 2019), increase feeding demand for invertebrates and fish that consume pelagic larvae (Piatt et al. 2020), reduce sperm performance (Leach et al. 2021), lead to decrease in normality during larval development (Contins et al. 2025, Sánchez-Ovando et al. 2023), and accelerate early development (Bojorquez and Feehan 2021), shifting when settlement occurs.

Conclusion

Understanding MHWs and their current and projected impacts is essential to develop strategies to protect marine ecosystems globally. The impacts of MHWs on kelp forest ecosystems is well studied, with many studies quantifying the impacts that ‘the Blob,’ a large-scale MHW persisting for years, had on shifts in kelp, invertebrate, and fish abundance (Liang et al. 2024, Michaud et al. 2022, Starko et al. 2022, Arafeh-Dalmau et al. 2019, Smale 2019). This showed the persistence of MHW events through years,

though ‘the Blob’ years led to MHW events that were very intense because of the co-occurring El Niño.

Intense MHWs like the Blob have long-lasting impacts on marine ecosystem biodiversity, affecting sensitive species. Biodiversity can stabilize ecosystems in the face of environmental change, but differing species’ resilience to MHWs and other environmental stressors can lead to destabilization (Ives and Carpenter 2007, Rogers-Bennett and Catton 2019, Loreau 2021, McPherson et al. 2021). In mobile invertebrates and algae, increase in the diversity-stability relationship strength is seen during and after a MHW, where ecosystem stability increases at a greater rate with diversity (Liang et al. 2024). In the same study, no change was seen for sessile invertebrates. As our climate continues to change, investigating phase shifts, range shifts, and further ecological impacts in kelp forest ecosystems is necessary to inform kelp restoration efforts, monitor the status of kelp forests, and to sustain biodiverse communities. In my next chapter, I will explore the impact of parental origin on egg quality of *S. purpuratus* to probe for potential local adaptation to temperature in purple sea urchins.

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IV. The effects of parental origin on the fertilization success and maternal provisioning of *S. purpuratus*

Introduction

The differential effects of MHWs on marine ecosystems are well studied with observations ranging from the ecological to societal impacts (Wernberg et al. 2025, Capotondi et al. 2024, Smith et al. 2023). Organismally, the thermal stress from MHWs has been shown to impact species differently depending on life stage (Deschamps et al. 2025, Giménez and Torres 2025, Gall et al. 2021, Sorte et al 2010), native vs. non-native (Castro et al. 2021, Sorte et al. 2010), natural environmental variability (Starko et al. 2024, Guibourd de Luzinais et al. 2024), and existing synergistic stressors (Guerrero-Meseguer et al. 2020). As the climate continues to change globally, it is necessary to continue to consider the population variation to climate change in predictive models and manipulative mesocosm experiments. Evidence shows that variability in thermal history even over small spatial scales may influence the ability of species to adapt to climate change (Rangel and Sorte 2022). Adverse environmental conditions may lead to physiological adaptation, epigenetic changes, behavior changes such as range shifts, and increased mortality rates. Many taxa can adapt to thermal changes; however, rapid warming is challenging for even highly mobile animals (Devictor et al 2012). In addition to mobility, other characteristics have been shown to influence the organismal response to MHWs. Life stage is an important consideration with sessile marine invertebrates as many are broadcast spawners and have pelagic larvae that are more susceptible to environmental changes.

Organisms with a pelagic embryonic stage have historically been thought of as not exhibiting much local adaptation, but a recent review shows that 66% of marine invertebrates with a planktonic dispersal exhibit or are suspected to exhibit local adaptation (Sanford and Kelly 2011). Additionally, adaptive divergence occurs at a variety of spatial scales, some regional and some with finer spatial scales as small as meters (Sanford and Kelly 2011). As I am interested in contributing to the continued research on impacts of environmental conditions on early pelagic stages of marine invertebrates, I used *S. purpuratus* as my model organism. As *S. purpuratus* has a wide range from Baja California to Alaska, I aimed to assess potential population differences throughout their range and at different life history stages. For my study, I collected adult purple urchins from 3 sites on the US west coast (CCLME) ranging from Fogarty Creek, Oregon on the north (FC), Bodega Marine Reserve (BMR) and a reef site near Santa Barbara, Mohawk Reef (MKO) in the south.

Geographic variation within species in nature is expected (Grosberg and Cunningham 2001). Along the East Pacific Coast there is a significant environmental variation from Washington to Central California. This region is characterized by common coastal upwelling plumes that contribute to variation in water temperature, pH, and nutrients over a variety of spatial scales (Sanford and Kelly 2011). Upwelling is persistent and can play a role in generating spatial variation in invertebrates with larval planktonic stages (Menge 2000) which may contribute to bottom-up influences in rocky intertidal ecosystems. In northern California, substantial changes in geographic distributions and abundances were reported in response to the 2014-2016 marine heatwaves (Sanford et al. 2019). Between central California and the Baja California Peninsula, there were range expansions,

reappearances, increases, and other species responses to warm water anomalies (Lonhart et al. 2019).

Although planktonic larval stages have been thought of as a way of species dispersal, studies have identified a smaller larval dispersal pattern of 10-100 km for marine invertebrates (Palumbi 2004), suggesting high local larvae retention where larvae recruit closer and more abundantly to natal populations than previously believed. Larval retention is likely to be common along upwelling coasts (Morgan et al 2018 and Morgan et al 2009), including my study area. When larvae remain close to their natal population instead of dispersing to other populations, low connectivity levels can be a consequence. In fact, connectivity levels have been identified to be lower than predicted. Marshall et al. 2010 indicates phenotype-environment mismatches as a factor in reducing population connectivity in species with sessile adult stages where the scale of dispersal exceeds the scale of environmental heterogeneity. My study organism, *S. purpuratus*, has been found to have significant genetic subdivision over short geographic distances along the Western Coast of the United States (Edmands et al. 1996). This supports the potential of local adaptation in *S. purpuratus*, which may contribute to differences in maternal provisioning in eggs.

The ability of organisms to adapt to their external environment is an important mechanism for survival in despite of detrimental conditions as the climate changes. Geographic variation in the environment of marine organisms can impact a variety of biochemical and physiological processes that can lead to local adaptation within the same species in various habitats. Environmental conditions have been shown to play a large part in the traits and tolerance of many marine organisms, where southern populations

with warmer thermal environments may be able to withstand a completely different thermal regime than northern populations (Schoville et al. 2012). Studies have also shown that although populations from cooler thermal environments may have a lower thermal tolerance, their capacity for stronger plasticity is greater than those from warmer environments that may be near their thermal limit (Sasaki et al. 2019).

Evidence of local adaptation in *S. purpuratus* has primarily been found along the California Current Large Marine Ecosystem (CCLME), a 3,000 km expanse of the coast that has been identified as a pH mosaic (Kelly et al. 2013, Pespeni et al. 2013, Evans et al. 2017, Chan et al. 2017). Study sites used in this chapter span approximately 1,500 km of the CCLME. In my region of interest, a past study demonstrates the potential for local adaptation in *S. purpuratus*. *S. purpuratus* offspring from sites with more variable pH levels were less sensitive to acidification (Hofmann et al. 2014). Evidence for local adaptation to pH in *S. purpuratus* guides my interest in investigating potential for local adaptation in response to differing thermal environments and exposure to MHWs. One study identifies narrower *hsp70* expression in early-stage individuals from *S. purpuratus*' Southern range edge, suggesting that organisms may be more stressed and living at their upper thermal limit (Hammond and Hofmann 2010). There is a surprising knowledge gap surrounding local adaptation in the ecologically important purple sea urchin, though we see transgenerational effects when adult sea urchins are acclimated to specific environmental conditions, such as low pH or elevated temperature (Wong et al. 2018, Minuti et al. 2022, Chamorro et al. 2023). Because of known geographic variation in physical ocean processes and the continued presence of MHWs, I investigated the

physiological and biochemical differences in the eggs of regionally different populations of *S. purpuratus*.

Methods

Urchin Collection

Urchins (n = 40) were collected from each field site (Figure 1) after their gametogenesis and before spawning to be assessed for fertilization success and egg quality. Urchins were collected in each site at time of peak gravidity. The three sites were: Mohawk Reef (34.39407, -119.72957) in Central California, Bodega Marine Reserve in Northern California (38.31613, -123.0705), and Fogarty Creek in Oregon (44.8395, -124.0498). Urchins were immediately transferred to the lab for data collection.

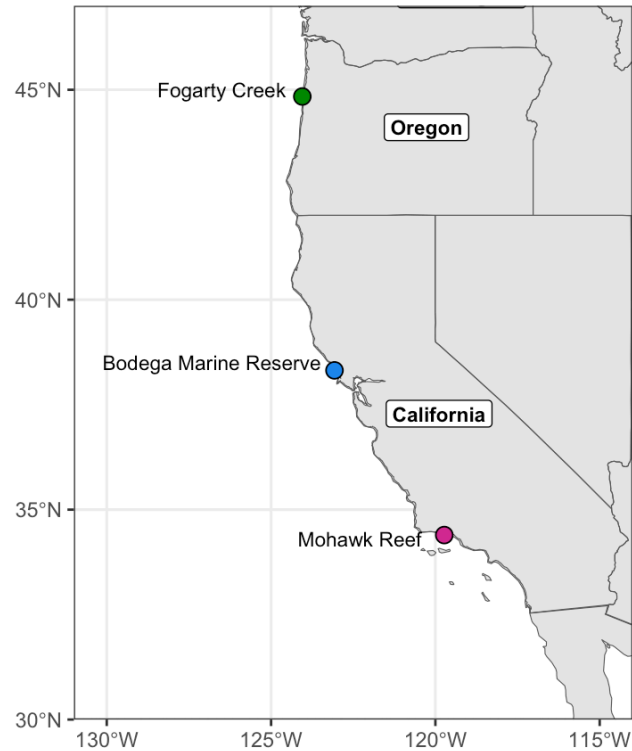


Figure 1. Map of study sites used for Chapter 3 analyses. Green: Fogarty Creek (44.8395, -124.0498), Blue: Bodega Marine Reserve (38.31613, -123.0705), and Pink: Mohawk Reef (34.39407, -119.72957)

Gonadosomatic Indices

Gonadosomatic Index (GSI) in adult urchins from each site (n = 10 per site) was immediately assessed once urchins were transferred to the lab. Urchins were first weighed on a scale to the nearest 0.01g and measured using a digital caliper to the nearest

0.01 mm. Once initial measurements were recorded, urchins were cracked open using dissecting scissors and gonads were removed, placed in a tray and weighed to the nearest 0.01 g. GSI was calculated for each urchin measured using the following formula:

$$\text{GSI} = \text{Gonad Weight} / \text{Total Body Weight} \times 100$$

Fertilization Success

Fertilization success assays were conducted by spawning urchins, fertilizing eggs in vials located in a heat block and then scoring for successful fertilization at a range of temperatures. Pooled eggs and sperm at a concentration of 1:100 from each site was collected and fertilized in scintillation vials acclimated to a range of temperatures (10.2°C, 13.5 °C, 19.4 °C, 24.1 °C) (Figure 2). Fertilization was allowed to proceed for 30 seconds of contact time, and then 1mL of 0.55M KCl was added to inhibit further fertilization. Fertilization success for 100 eggs per vial was scored using the following qualifications:

- i. Unsuccessful fertilization event – no fertilization membrane present
- ii. Abnormal fertilization event – tight fertilization membrane or abnormal cell cleavage present
- iii. Successful fertilization event – smooth, raised fertilization membrane with normal cleavage present.

Preserved sperm samples were counted using a Hemocytometer to obtain precise sperm concentrations per vial. Methods are adapted from Fertilization Success Trail Protocol, Leach 2022.

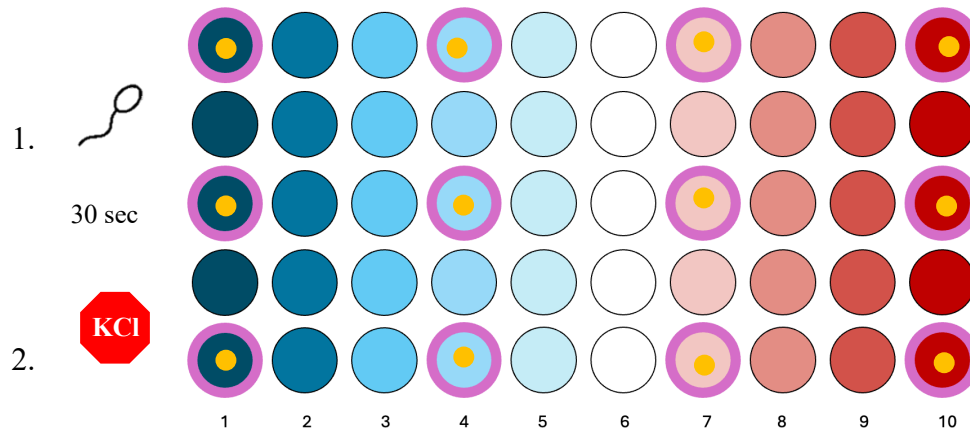


Figure 2. Experimental design for fertilization success assay. Urchins were spawned and eggs were collected in filtered seawater then pooled together. Approximately 1,000 eggs were placed in each pink circle which corresponds to different temperatures. The orange circle represents urchin eggs ($n=1000$). The dark blue circles in column 1 were the coldest temperatures and the dark red circles in column 10 were the hottest temperatures. As column numbers increased, temperature increased by approximately $1.5^{\circ}\text{C} - 1^{\circ}\text{C}$ temperature increase. Once all eggs were placed in vials in the heat block, sperm at a concentration of 1:100 was added to each vial for 30 seconds of contact. KCl was added after sperm exposure to halt fertilization for scoring.

Egg morphometrics

Samples of 1000 eggs for each site were collected and preserved in 2% formalin in FSW. 35 eggs per female were photographed for morphometric analysis using a compound microscope (Olympus BX50) at 10x objective with an attached digital camera (Motic 10 MP and Motic Image Plus software). Images were measured for diameter and total area using ImageJ (National Institutes of Health, USA) and calibrated using a stage micrometer.

Biochemical composition of eggs

Lipid and protein content were determined using the same methods as described in Chapter 2. Samples of eggs ($n = 2000$) from each female were collected in 1.5mL Eppendorf tubes then frozen in liquid nitrogen to be stored at -80°C for assays.

Samples for protein analysis were prepared using a homogenization buffer consisting of 20mM Tris-HCl (pH 7.6), 130 mM NaCl, 5mM EDTA, 1% Triton-X and 1% Protease Inhibitor Cocktail. 100uL of buffer was added to each sample and sonicated for 20 seconds (Fisher Scientific Sonic Dismembrator 500). Samples were shaken on ice for 15 minutes (Thermolyne M71735 Slow Speed Roto Mix) then centrifuged at 16,000 RCF for 20 minutes. Supernatant was transferred to a microcentrifuge tube and stored at -20°C. 20 uL of each protein homogenates were then used in a BCA Protein Assay Kit following manufacturer's instructions to calculate protein concentration in each sample.

Total lipids were extracted using methods described in Wong et al. 2019 and details are described in Chapter 2. Frozen egg samples were suspended in 250 uL of Milli-Q water and sonicated at 2 amps for 3 15s intervals. Samples were then transferred to 5mL glass V-vials and combined with 125 uL of HPLC grade chloroform and 250 uL of HPLC methanol. Samples were capped, vigorously shaken, and then centrifuged at 2,680 RCF at 4°C for 5 minutes (Beckman Coulter Allegra 21R Centrifuge). The chloroform and aqueous layers were transferred to a different clean V-vial using a pulled Pasteur pipette. Chloroform and Milli-Q water were added to acquire a final volume ratio of 4:3:2 of water:chloroform:methanol. Samples were capped and vigorously shaken and centrifuged again at the same settings. The chloroform layer (bottom) was transferred to a clean glass vial and flushed with Nitrogen gas and stored with parafilm on top at -20°C prior to quantification.

Lipid quantification used methods based on Marsh and Weinstein and is described in Chamorro et al. 2023.

Statistical analyses

All statistical analyses were conducted in R Studio (Version 2025.05.0+496). To quantify size-dependent variation in reproductive investment (gonadosomatic indices) between sites, I modeled the relationship between gonad mass and body mass using log–log allometric scaling. This type II regression assumes both variables contain measurement error and are biologically linked. Model residuals were used as an index of size-adjusted gonad investment, with positive residuals indicating larger gonads than expected for a given body size and negative residuals indicating reduced gonad investment. A linear mixed-effect model was used to analyze site differences on lipid, protein, and size data in eggs. Site was set as a fixed effect while each individual mother was set as a random effect in analyses. To analyze fertilization success in urchins from MKO and BMR, I conducted a linear mixed-effect model with replicate as a random effect and temperature and site as fixed effects.

Results

Gonadosomatic Indices

Urchins from Mohawk Reef (MKO) had a significantly higher GSI, the ratio between the gonad weight and total weight, than Fogarty Creek (FC) and Bodega Marine Reserve (BMR). Analyses also revealed that MKO urchins allocated proportionally more energy reserves to gonads than those from other sites. GSI of adult urchins from the three sites ranged from 16.69 to 0.61. The mean GSI value for all sites were 9.75 +/- 1.19 at MKO 4.14 +/- 0.38 at Bodega Marine Reserve BMR, and 1.95 +/- 0.22 at FC. When

adjusted for size, the means were 2.46 ± 0.23 , 1.53 ± 0.10 , and 1.38 ± 0.13 for MKO, BMR, and FC, respectively.

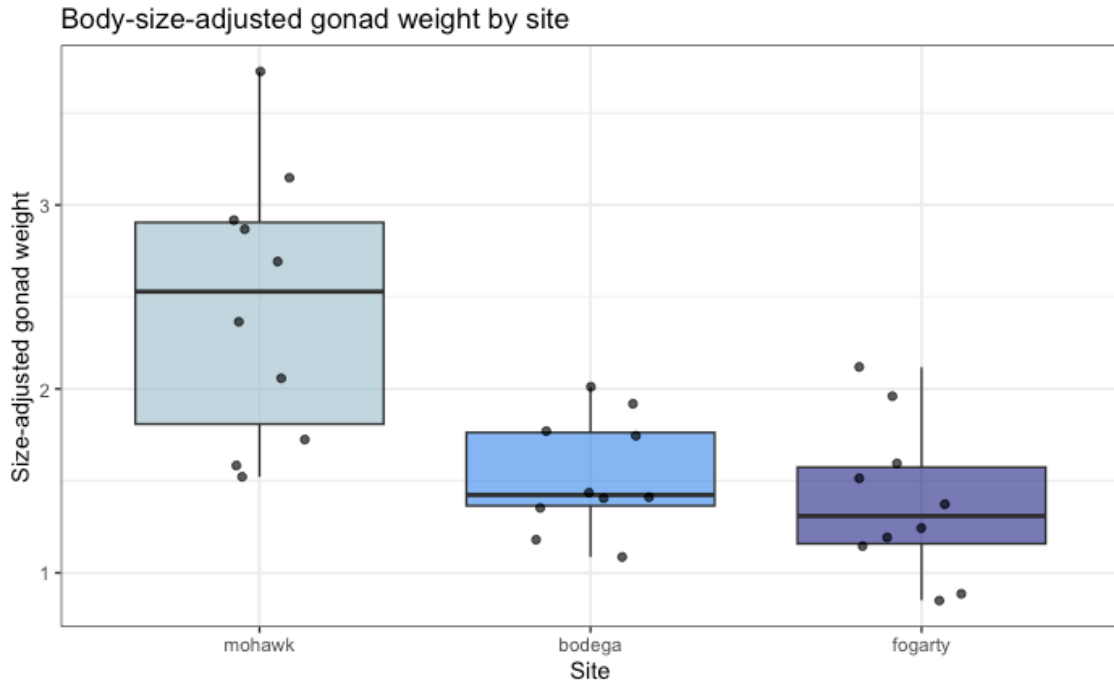


Figure 3. Body-size-adjusted gonad weight by site. Box plot of gonad weight adjusted by size of urchins in three sites: Bodega Marine Reserve (Blue), Fogarty Creek (Navy), and Mohawk Reef (Light blue). Individual points represent individual urchins from each site. Boxplots indicating the median, interquartile range, and 1.5x IQR whiskers; points represent individual urchin measurements.

Allometric regression of $\log(\text{gonad weight})$ vs.
 $\log(\text{body weight})$ by site

Parameter estimates (mean $\pm$ SE)

site	Intercept	Slope
bodega	$0.185 \pm 0.646^*$	$1.16 \pm 0.36^*$
fogarty	$0.061 \pm 0.805^{**}$	$1.52 \pm 0.4^{**}$
mohawk	$0.109 \pm 0.567^{**}$	$1.62 \pm 0.3^{***}$

Table 1. Summary table of allometric regression to examine how gonad size scales with body size. Sites are listed in alphabetical order. The relationship between variables is represented by the equation:

$$\text{Gonad weight} = \exp(\text{Intercept}) * (\text{Body weight})^{\text{slope}}.$$

Allometric scaling was used for further analysis to describe how gonad weight scaled with size differences of the adult urchins. Gonad mass does not always scale linearly with body mass, so an allometric equation was used to compare gonad development independent of body size (Ebert et al. 2011). Significant site differences were present in the allometric relationship between gonad weight and body weight. Here, gonad weight had a positive relationship with body weight, however at different rates for each site (Fig 3). All sites exhibited positive allometry as the scaling exponents (*b*) were 1.62 at MKO, 1.16 at BMR, and 1.52 at FC. Regression equations were:

$$\text{Mohawk Reef: Gonad Weight} = 0.109 * \text{Body Weight}^{1.62}$$

$$\text{Bodega Marine Reserve: Gonad Weight} = 0.185 * \text{Body Weight}^{1.16}$$

$$\text{Fogarty Creek: Gonad Weight} = 0.061 * \text{Body Weight}^{1.52}$$

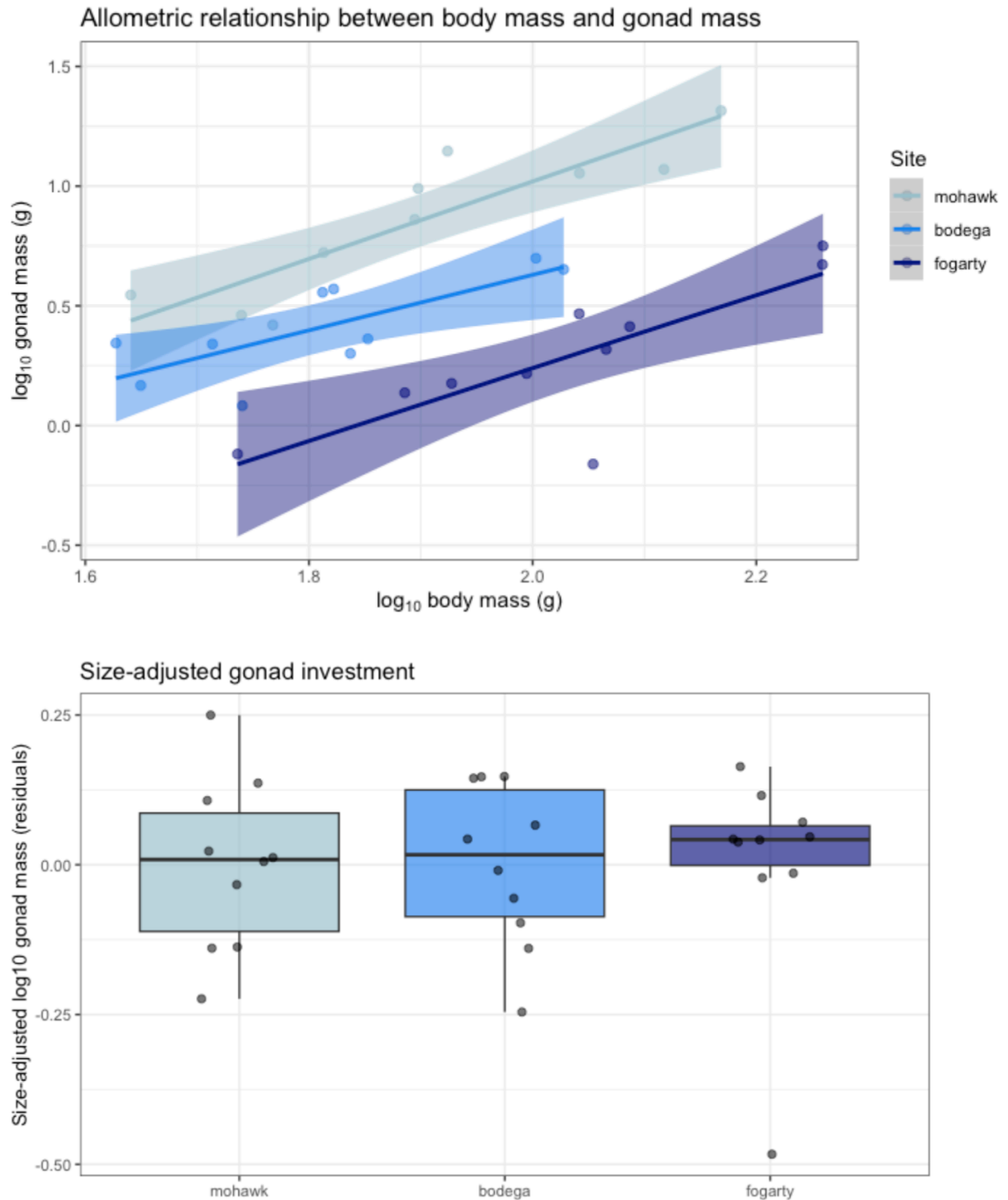


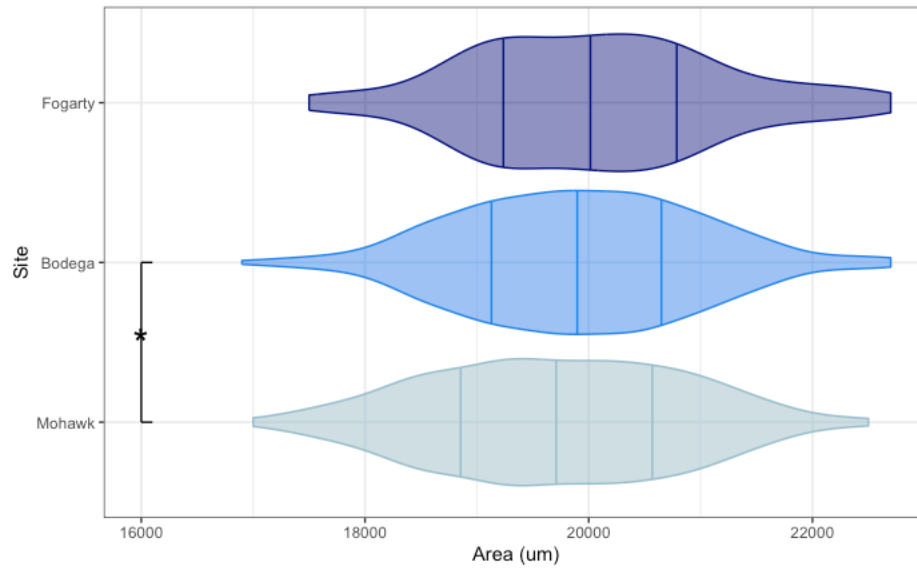
Figure 4. Allometric scaling of gonad mass with body size and size-adjusted gonad investment in *Strongylocentrotus purpuratus* from sites across Northeast Pacific region.

(A) Relationship between log body mass and log gonad mass for individuals from each site (light blue = MKO, blue = BMR, navy = FC). Lines show fitted allometric regressions from a linear model including an interaction between log body mass and site; the slope of each line represents the allometric scaling exponent b . (B) Size-adjusted gonad investment, expressed as residuals from the allometric model in panel (A), plotted by site. Positive residuals indicate individuals with larger gonads than expected for their body size, whereas negative residuals indicate reduced gonad investment. Boxes show the interquartile range, horizontal lines indicate medians, and points represent individual urchins.

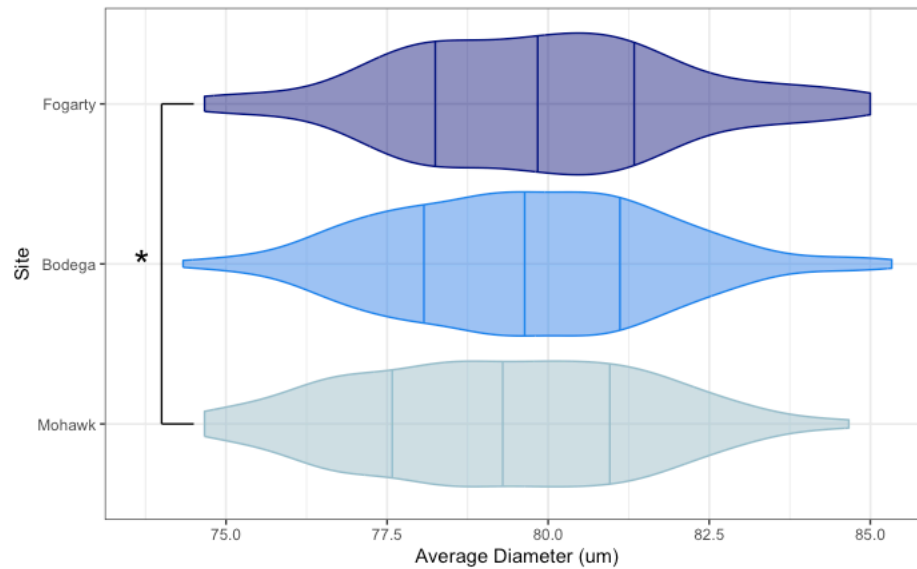
Differences in egg morphometrics by site

In general, morphometric analysis revealed significant differences between MKO and FC egg diameter and between MKO and BMR egg area. MKO had a smaller average diameter ($p < 0.05$), but a larger average area than FC though non-significant (Figure 5). Compared to BMR, MKO had a larger average area ($p < 0.05$), but a smaller average diameter though non-significant.

Egg size for eggs collected from females from all three sites was determined by total area and average diameter as described in Chapter 2. There were 315 eggs measured from BMR (from 9 females), 210 (from 6 females) measured from Mohawk Reef, and 105 (from 3 females) measured from Fogarty Creek. Urchins from Fogarty Creek yielded the largest mean egg size overall (Fig 5). Though average diameter of eggs from Mohawk Reef was smaller than those from Bodega Marine Reserve, area was larger. The standard deviation of the average area of eggs from Mohawk Reef was about double that of the standard deviations from other sites. An ANOVA was performed for both diameter and area in which both were significant. To determine significance between pairs of groups, a Tukey HSD was conducted to compare the difference between all pairs of group means. Average egg diameter between those from Mohawk Reef and Bodega Marine Reserve were significant (p -value: 0.03). Average area between eggs from Mohawk Reef and Bodega Marine Reserve was also significant (p -value: 0.007). Eggs from BMR females were significantly larger in diameter than eggs from Mohawk Reef females, but smaller in total area.



A.



B.

Figure 5. Violin plots of average area (A) and diameter (B) of eggs from 3 sites: Mohawk Reef (pink), Fogarty Creek (Green), and Bodega Marine Reserve (Blue). The 3 lines in each violin represent the 25th quartile, mean (50th quartile), and 75th quartile of the area or diameter for each site. Significance (p -value < 0.05) was found between Mohawk Reef and Bodega Marine Reserve for both area and diameter (p -value: 0.007) for area and 0.03 for diameter.

Summary of Egg Size by Site

Site	N	Mean Diameter	SD - Diameter	Mean Area	SD - Area	Median Diameter	Median Area
Bodega	315	0.07960	0.00235	0.00540	0.00028	0.07967	0.00539
Fogarty	105	0.07994	0.00229	0.00547	0.00026	0.08000	0.00544
Mohawk	210	0.07918	0.00227	0.00546	0.00048	0.07933	0.00549

Table 2. Summary statistics of *Strongylocentrotus purpuratus* egg size by site. The table reports sample size (N), mean and median egg diameter (mm), and mean and median egg area for embryos collected from Bodega, Fogarty, and Mohawk, along with associated standard deviations.

Biochemical energy molecules in eggs

In analyzing biochemical energy, there were no significant differences in energy molecules across the sites. The protein concentration of urchins from all sites was highly variable among samples. Highest protein concentration was found in FC urchin eggs at 10.678 ng/egg and lowest concentration was in BMR urchin eggs at 9.274 ng/egg (Figure 7). Lipid content data had less variance, but MKO had the largest spread of raw data. Here, FC had the highest average lipid content at 4.4042 ng/egg +/- 0.158 and BMR had the lowest lipid content at 2.741 ng/egg +/- 0.264 (Figure 6).

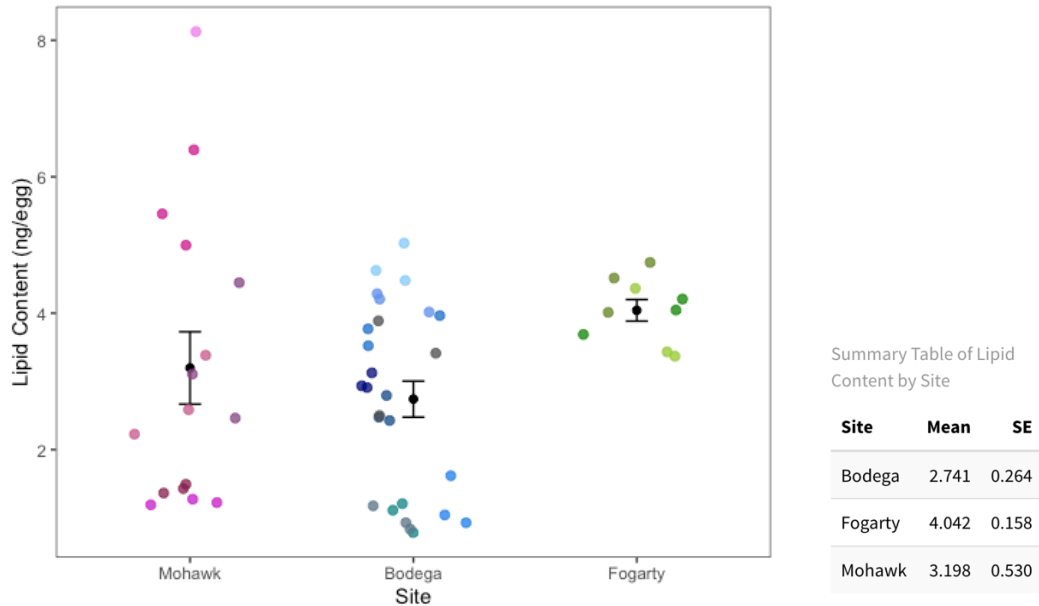


Figure 6. Total lipid content (ng/egg) for each site. Each replicate (3) for each individual graphed by site: Pinks: Mohawk Reef (n = 6), Blues: Bodega Marine Reserve (n = 9), and Greens: Fogarty Creek (n = 3). Means are indicated by the black dot for each site with standard error represented by the error bars. Specific summary statistics are located within the table.

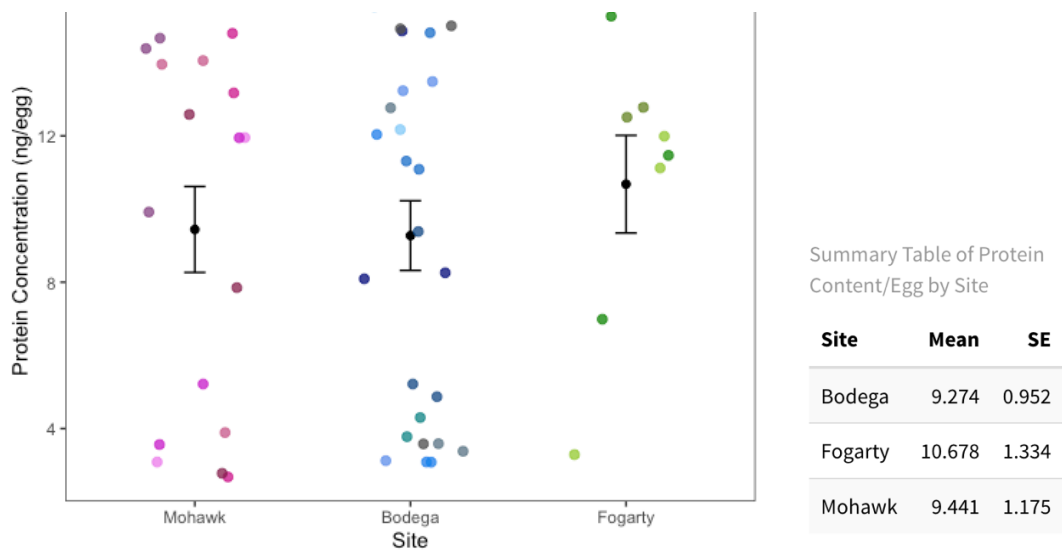


Figure 7. Protein concentration (ng/egg) for each site. Each replicate (3) for each individual graphed by site: Blues: Bodega Marine Reserve (n = 9), Greens: Fogarty Creek (n = 3), and Pinks: Mohawk Reef (n = 6). Means are indicated by the black dot for each site with standard error represented by the error bars. Specific summary statistics for each site are located within the table.

Fertilization success

Fertilization success varied as a function of location; however, I was unable to test FC due to a deficit of eggs. Testing fertilization success at different temperatures (low, medium, high) in Mohawk and BMR urchins resulted in sites reacting similarly to the effects of temperature. A GLMM showed some variance among individual female replicates: 0.02669 and little variation between replicates (sd: 0.1634). Additionally, analysis showed differences in the likelihood of abnormality where embryos from Mohawk adults are 85% less likely to be abnormal than urchins from BMR ($p = 0.003$) (Figure 8).

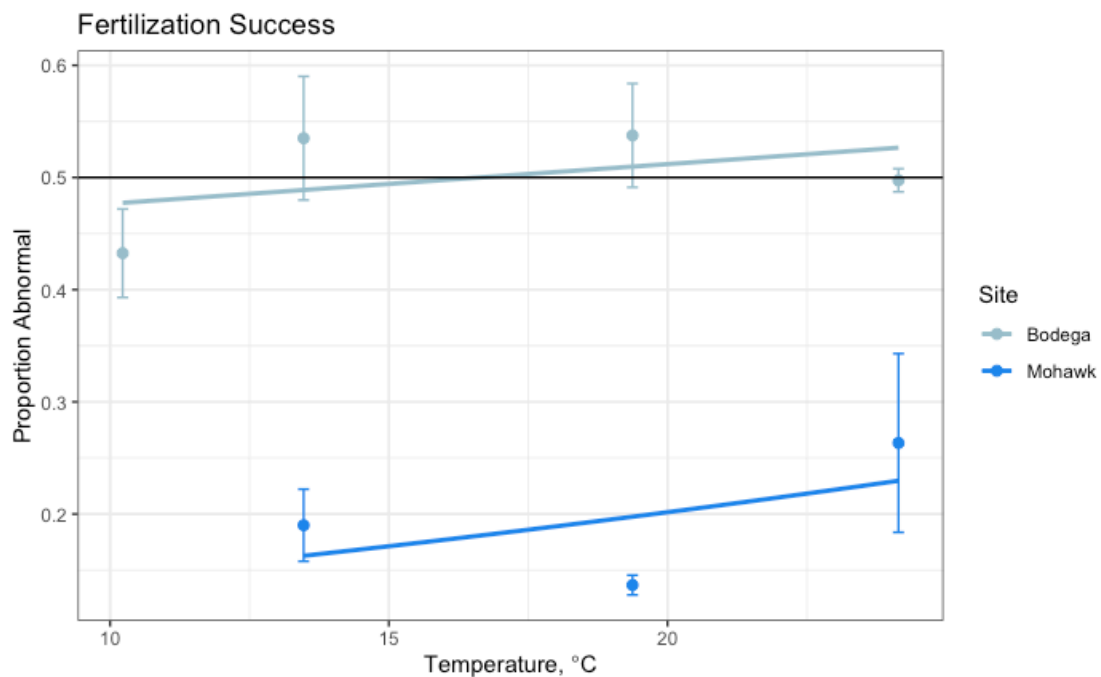


Figure 8. Temperature effects on abnormal fertilization of *S. purpuratus* across sites. Points represent observed proportions of abnormal zygotes, fertilized eggs at each experimental temperature for Bodega (blue) and Mohawk (light blue). Solid lines show fitted linear relationships between temperature and the proportion of abnormal fertilization for each site. The horizontal line denotes 50% abnormal fertilization. Across the temperature range, urchins from Bodega exhibited consistently higher proportions of abnormal fertilization.

Discussion

The goal of this chapter was to probe for potential local adaptation by testing for differences in fertilization success, GSI, and biochemical properties of eggs of three different sites along the Northeast Pacific region. I predicted that urchins from MKO, the southernmost site, would have the greatest GSI, egg size and biochemical energy molecules. Results from previous studies suggests more stressed organisms at their upper thermal limit (Hammond and Hofmann 2010, Pörtner 2001). As MKO is not near the range edge of *S. purpuratus*, I expected physiological parameters to be near normal levels. In many taxa, offspring phenotype can be influenced by parental environment (Marshall et al. 2008, Herman and Sultan 2011, and Agrawal et al. 1999), which is referred to as transgenerational plasticity and can include provisioning of non-genetic factors. In *S. purpuratus*, transgenerational plasticity studies have shown impacts of maternal environment on DNA methylation of offspring (Strader et al. 2019)

Generally, adult *S. purpuratus* from the southern-most site MKO had greatest GSI and the least abnormality during fertilization, but maternal provisioning of biochemical energy molecules was similar between all sites. Many recent local adaptation studies focus on the effects of CO₂-driven ocean acidification, showing the capacity for rapid evolutionary change under high pCO₂ (Kelly et al. 2013, Pespeni et al. 2013, Petak et al. 2023). *S. purpuratus* local adaptation studies have primarily focused on pH due to the episodic upwelling that characterizes the CCLME. In other marine invertebrates, evidence of intraspecific population variation to heat stress suggest adaptation to local environmental differences in an invertebrate with planktonic larval dispersal with extensive gene flow (Gleason and Burton 2013). As transgenerational plasticity has been

present in *S. purpuratus* through various studies (Chamorro et al. 2023), the potential for local adaptation is an important exploration as the climate continues to change and cause the increase of extreme weather events like MHWs. Though *S. purpuratus* experiences high gene flow (Palumbi 1994), there is evidence that local adaptation may be present (Sanford and Kelly 2011, Bernatchez 2016) and the goal of this chapter was to expand on the evidence of phenotypic differences between *S. purpuratus* populations from three different sites across ~1,500 km strives to contribute to growing evidence on the phenotypic differences between *S. purpuratus* populations.

Gonadosomatic indices increased in southern-most site

Historically, there is evidence of high interpopulation variation in urchin gonad index (Pearse and Cameron 1991, Lozano et al 1995, Basch and Tegner 2007) and seasonal enlargement and shrinkage of the gonads (Lawrence et al. 1965). Food availability also impacts gonads in urchins with enriched *M. pyrifera* led to increased gonad weight (Cuesta-Gomez and Sanchez-Saavedra 2014). Relatedly, in urchin barrens, sea urchin reproductive capacity was lower, suggesting that in environments with limited macroalgae, there is a shift in energy allocation (Smith and Garcia 2021). When investigating GSI, all three sites had a positive allometric relationship, which shows that as body size increase so does gonad size but in a non-linear fashion. In fact, analysis showed that all sites' gonads would increase at a rate of > 1 as their mass increases. In Connor 1972, gonad size increases rapidly in central Oregon intertidal populations relative to body size. MKO, the southernmost site, had the highest average GSI and the highest allometric scaling exponent. The allometric relationship is used to

understand how reproductive investment, gonad mass, scales with overall body size. Similarly, in other studies, test diameter had a direct impact on body weight and body weight had a direct impact on gonadal wet weight in urchins (Yang et al. 2010, Zhang et al 2010). As MKO had the highest allometric scaling exponent, b , gonad size increases at a faster rate relative to a change in body size when compared to the two other sites: BMR and FC.

Increased gonad growth with warmer temperature conditions is well documented in previously published studies. When manipulating temperature in the lab, there were decreased gamete percentages and increased gonadal apoptosis when urchins are exposed to elevated temperatures (Johnstone et al 2019). Additionally, another study shows high wet weight and test diameter growth rates at 22C and unfavorable rearing results at temperatures beyond, suggesting temperature capacity limits (Santos et al. 2020) Elevated temperature could drastically impact reproductive output in sea urchins as physiological parameters are impacted at extreme temperatures (Delorme and Sewell 2016). Information on gonad quantity is useful as they are essential for producing gametes, which then are needed for reproduction and development, but analysis on eggs from females of these same urchin populations can also show population differences on gonad quality. Sea urchin gonads comprise of considerable amounts of proteins, lipids, and carbohydrates (Arafa et al. 2012) which led me to investigate protein and lipid content in their gametes.

Biochemical content and size of eggs across sites were similar

Differences in maternal provisioning of biochemical molecules, proteins and lipids, were absent. At all sites, there was a wide range of total lipid and protein content despite MKO urchins having the highest GSI. Proteins and lipids are essential biomolecules that are important components for growth. There are many reports of the importance of protein during planktotrophic development in marine invertebrates (Jaekle 1995, Prowse et al. 2008). The presence of similar total egg protein among sites in my study corroborates the importance of yolk protein across populations of *S. purpuratus*. Additionally, there is evidence of ancestral lipid maternal provisioning in tropical sea urchin species to sustain larvae through early development (Prowse et al. 2009, Byrne et al. 2008). These essential biomolecules were not statistically different between populations, but evidence of protein and lipid differences in transgenerational studies suggest the capacity of females to allocate biomolecules to eggs in response to stressful environmental conditions.

Egg size was also similar between sites and there was no clear pattern as there were significant differences between the average area of eggs from MKO and BMR; however, diameter was larger in FC urchin eggs compared to those from MKO. Previous studies have linked elevated temperature with larger eggs, which is demonstrated in this study with the southern-most site having the largest egg area on average. However, the northern-most site, Fogarty Creek, had urchins with a larger mean diameter than both more southern sites. In many different organisms, larger body sizes are expected with increase in latitude, Bergmann's rule. Bergmann's rule is when animals in higher latitude regions tend to be bigger than those in lower-latitude areas. Temperature-size rules

explain this in marine organisms, where organisms grow larger in colder waters. Larger eggs provides sperm with a larger target and can influence fertilization success in populations, as fertilization success is primarily determined by the rate of physical collisions between sperm and eggs. Additionally, eggs increase in size as they mature, so differences in egg size could be attributed to urchins being in different gametogenic periods at the time of collection. A past study showed how larger egg size led to greater plasticity of larval feeding structures (McAlister 2007). Knowing that MHWs have occurred during *S. purpuratus* gametogenesis and they continue to occur widely along the entirety of the Pacific Coast this chapter provides vital biological information on how differing physical ocean environments may impact kelp forest ecosystem dynamics and *S. purpuratus* larval dynamics in the future. As egg compositions and egg size do not always directly correlate (McAlister and Moran 2012), morphometrics of eggs was another trait I included in analyses.

Elevated temperature led to decreased fertilization success

Urchins from MKO are more likely to not have abnormal fertilized eggs at all temperatures measured compared to urchins from BMR. Even at more normal temperatures, urchins from BMR had a significantly greater proportion of abnormal fertilization. For both sites overall, temperature did not have a large impact on abnormality, but as temperature increased so did the proportion of abnormality. In other echinoderms, temperatures are also shown to reduce fertilization success and normal early cleavage (Pereira et al. 2020, Rupp 1973). In previous studies, sperm performance decreased in urchins experiencing MHW temperatures during gametogenesis (Leach et

al. 2021). Suboptimal temperatures led to reduction of fertilization success and increased abnormality of larvae in two oyster species (Parker et al. 2010). In corals, increase in temperature negatively impacted fertilization success as it required an increase of sperm concentration to obtain 50% fertilization (Albright and Mason 2013). Though successful fertilization can still occur under elevated temperature with increase in sperm concentration, higher temperatures also led to greater developmental abnormality during embryogenesis (Bassim et al. 2002). In fish species, higher temperature led to decreased motile sperm (Mehlis and Bakker 2014) and increased proportion of unfertilized and abnormal eggs as well as deformed embryos (Cingi et al. 2010). Overall, many studies show that elevated temperature negatively impacts fertilization success in the form of decreased sperm performance and greater abnormality. Results from fertilization success assays conducted in this chapter are consistent with previous studies as abnormality increases with temperature in both MKO and BMR urchins.

Conclusion

Rapid global change for physical and chemical oceanic properties has consequences for the climate, society, economy, and ecosystems (IPCC, 2019). Temperature has been increasing, which can lead to stronger storm systems, rising sea levels, and individual organismal impacts. Though negative consequences have been occurring and are likely to get worse, there are some organisms that may benefit from or be less impacted by changing oceanic conditions such as temperature. Many studies have identified *S. purpuratus* to be a potential “winner” in climate change scenarios. *S. purpuratus* grow larger in warmer waters and can survive in a starved state for long

periods of time. *S. purpuratus* have limited mobility, but their range extends from Baja California to Alaska showcasing tolerance to temperature. Range shifts of adults are unlikely because of their limited movement; however, range shifts may be present in the form of increased larval settlement in specific areas due to oceanic conditions that are favorable for embryos.

Investigating biogeographical differences in gametogenesis of *S. purpuratus* led to results that suggest adult origin differentially impacts gametogenesis through factors such as gonad production and fertilization success. Maternal provisioning of biomolecules was similar across populations and highly variable. Overall, population differences were most seen in MKO urchins, the southernmost population. This supports past studies as many demonstrate sensitivity of species close to their southernmost range edge. During and after MHWs, urchin populations are robust especially in more northern areas. In Oregon, purple sea urchin populations rapidly increased in 2014 after being primarily absent in the area. *S. purpuratus* densities becoming very high by 2019, after an intense 2018 MHW year, shows tolerance of adult urchins to temperature changes in the region (Groth 2023, Rogers-Bennett et al. 2024, Rogers-Bennett and Catton 2019). The shift between robust kelp beds and urchin barrens is considered a discontinuous phase shift, where the kelp beds may not reestablish until urchin grazing intensity decreases well below the threshold that triggered the initial shift (Filbee-Dexter and Scheibling 2014). However, urchin presence is not synonymous with health and many urchins were identified as “zombie urchins” that are able to survive while experiencing prolonged food deprivation (McCue 2010) because of endogenous reserves, such as lipids and proteins. In red sea urchin, *Mesocentrotus franciscanus*, there was a tradeoff between reproduction

and survival and urchins from barrens at substantially lower energy reserves, lower gonadal mass, and reductions in resting metabolic rate compared to kelp forest urchins (Spindel et al. 2021). In sea urchin, *Centrostephanus rodgersii*, smaller body size and slower growth were seen in urchins from a barren habitat compared to macroalgal beds (Ling et al. 2009 and Ling and Johnson 2009). Sensitivity of *S. purpuratus* to temperature at their southern-range edge and physiological impacts of formed urchin barrens in their northern range, suggests that urchins are likely to be broadly impacted by global change in the future. Though *S. purpuratus* have limited mobility, range shifts can be seen through the decrease of abundance of southern species and increase of larval settlement and survival in Northern regions. Kelp forests are extremely productive ecosystems, but the shift to urchin barrens dramatically reduces this productivity. Understanding the potential for urchin barrens to occur in productive kelp forests in the face of MHWs is necessary to prepare for subsequent consequences due to climate change in the future.

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V. Conclusion

Increasing climate change impacts and their compounding effects underline the need for climate adaptation globally. From 2000 to 2020, there were over 4,600 documented climate-related disasters that impacted over 3.3 billion people (Donatti et al. 2024). Climate models project ocean warming to be widespread by the end of the century and overall warming exacerbates duration, frequency, and intensity of extreme SST events, like MHWs (Capotondi et al. 2024, Oliver et al. 2018). The longest MHW on record, ‘the Blob,’ occurred in the northeast Pacific from 2014 to 2016 and caused major ecosystem impacts. Overall, MHW impacts are experienced at the individual, population, and community levels. Organismal responses to MHWs vary with event characteristics (i.e. intensity) and among populations and individuals based on life history and local adaptation to their region. Research indicates that latitudinal distributions of marine species conform closely with their thermal tolerance (Sunday et al. 2012) and such, MHW impacts may intensify toward the warm-range edge of a species’ distribution (Smith et al. 2024). The projected increase of intensity, duration, and frequency of MHWs as well as the knowledge that impacts can be variable due to life history stage, population differences, and varying MHW characteristics framed my dissertation focus.

Regional warming variability is influencing physical and ecological ocean changes

Internal climate variability in the North Pacific has historically been led by the Pacific Decadal Oscillation (PDO). Briefly, PDO is a long-term climate pattern of SST anomalies in the north Pacific Ocean (NOAA 2025). Recent analyses show that beyond 2013, basin-wide warming overwhelms SST changes of the PDO, though PDO has not

changed in strength or spatial patterns (Cluett et al. 2025). This shift reveals a divergence from what is expected of regional temperature anomalies. Ocean warming along with regional variability produces physical and ecological changes in this region. Ecosystem degradation caused by extreme regional warming can be seen through species shifts, mass mortality, and changes in productivity (Chaudhary et al. 2021, Hastings et al. 2020, Proud et al. 2017, Sorte et al. 2010, Hughes et al. 2018, Cheung et al. 2012). The increase in frequency of severe marine heatwaves with ecosystem-wide impacts has led to various MHW studies investigating patterns as well as organismal impacts.

MHWs are causing detrimental organismal impacts globally

Severe marine heatwaves are impacting marine ecosystems globally. In tropical reef systems, coral bleaching is occurring more frequently and the interval between bleaching is becoming too short for full recovery, even thermal refugia is on the path to disappearing (Hoegh-Guldberg et al. 2013, Heron et al. 2016, Hughes et al. 2018, van Hooidonk et al. 2013). A review indicates global climate change has led to an increase in introduced species and shifts in species' ranges that have the potential to threaten global biodiversity and community structure and function (Chaudhary et al. 2021, Hastings et al. 2020, Sorte et al. 2010). In Western Australia, MHWs have caused scallop fishery collapse, mortality of abalone, and decline in western king prawn recruitment. Recovery of these invertebrate populations are impacted by the species sensitivity, range, and spatial overlap of the MHWs and species distribution (Caputi et al. 2019). In Oregon, MHWs affected winter spawning intensity of coastal invertebrates (Shanks et al. 2019). Stage-specific MHW impacts were highlighted in European shore crab, *Carinus maenas*,

and overall larval performance was lower during intense MHWs (Deschamps et al. 2025). Specifics-specific MHW impacts have also been identified, with some species benefitting from MHWs (Mauricieri et al. 2025, Wong et al. 2026). Responses to MHWs also vary with latitude in invertebrate species (Smale et al. 2017). These MHW studies have underlined the importance for MHW studies that take in account the various MHW dynamics, community structure, and species functions. Though MHW studies have been steadily increasing, there is still much to consider as we continue to assess how MHWs will impact ocean ecosystems in the future.

From this body of research, three main takeaways are discussed below:

Fluctuating short-term MHWs creates a temperature refuge that influences maternal provisioning in *S. purpuratus* eggs

MHWs are extremely dynamic climate events. They vary in duration, frequency, intensity, and magnitude, making them difficult to replicate in laboratory experiments. Many MHW studies focus on long-lasting MHWs, such as ‘the Blob,’ however, MHWs may last for as few as 5 days. In the Santa Barbara Coastal region, the 2018 MHW year had an average of 6 MHW events on the surface lasting ~14 days each. Fluctuating MHWs may be beneficial for benthic organisms as tolerance to MHWs is exhibited in organisms in highly variable thermal habitats (Schubert 2021). Many studies indicate that exposure to highly variable environments can facilitate acclimation to future environmental stress (Johnson et al. 2021, Hilker et al. 2016). The focus of Chapter II was to investigate whether fluctuating MHWs can facilitate possible tolerance to environmental stress via maternal provisioning in the purple sea urchin. This study

contributes to the existing literature that identifies increased phenotypic plasticity in organisms from more heterogeneous environments (Vargas et al. 2017, Miller et al. 2020). Many lab experiments investigating transgenerational plasticity have used stable elevated temperatures (Chamorro et al. 2023), but my goal was to assess the potential for increased plasticity in urchins by mimicking varying MHW temperatures.

In Chapter II, I exposed urchins to MHW temperature patterns based off SBC LTER temperature patterns from 2018 during their gametogenesis, a time-period that coincides with when MHW are likely to occur in our region. To assess whether differences in MHW patterns have differential impacts on *S. purpuratus* egg quality and maternal provisioning, I conducted biochemical and physiological assays on acclimated eggs and subsequent offspring. Exposure to fluctuating MHWs led to significant mortality in adult urchins, though there were no differences in the gonadosomatic indices from the surviving populations. Evidence of maternal provisioning in eggs was confirmed as protein concentration and total lipid content trended greater in MHW-acclimated urchins. The increase in biomolecule content in MHW urchins did not extend to morphometric analyses as there was no difference in egg size. In addition, MHW-exposure during gametogenesis led to greater LT_{50} values in gastrula for survival and developmental normality.

Maternal provisioning is a process in which a mother provides offspring with resources during development and is a significant factor in offspring survival and development. As MHWs are expected to become more frequent and continue to be detrimental at an ecosystem-level and individual-level, it is necessary to explore when and how females provision nutrients in response to their environment.

MHW presence in the Santa Barbara Coastal region create ecological winners and losers

MHWs are a detrimental stressor impacting ecosystems globally; however, not all species will be impacted negatively (Fredston et al. 2023). As MHWs are complex, their changing dynamics may influence ecosystems differently depending on the intensity, duration, magnitude, and any synergistic stressors experienced by species. Species most vulnerable from MHWs are those with narrow species ranges, limited mobility, and close to their temperature limit (Wernberg et al. 2025). In the Santa Barbara Coastal region, we have seen impacts on the foundational flora and fauna species. Overall, sessile invertebrate cover and species richness during ‘the Blob’ declined, but not all responded equally, and some species were resistant to change (Michaud et al. 2022). Additionally, species “winners” in MHW conditions may cause subsequent impacts in ecosystems. For example, after ‘the Blob,’ the increases in urchin species prevent kelp from recovering in the SBC region (Maucieri 2025). This highlights the importance of understanding species-specific responses to MHWs and other environmental stressors.

To monitor MHW presence and ecosystem impacts, long-term datasets are essential. The Santa Barbara Coastal Long-term Ecological Research Program includes a collaborative team of scientists that develop and maintain long-term experiments to provide information on ecosystem change. For Chapter III, I used SBC LTER datasets to assess MHW patterns, *M. pyrifera* abundance, and *S. purpuratus* abundance in the SBC region. I hypothesized that as MHWs have become more present in this region over time, *S. purpuratus* abundance would increase while *M. pyrifera* abundance and *S. purpuratus* larval settlement would decrease and fail to recover.

Results from Chapter III revealed that MHWs have been occurring consistently in the SBC region since ‘the Blob.’ At all sites, 2021 was the one year without MHWs. Abundance of adult *S. purpuratus* peaked at the onset of ‘the Blob’ in 2 sites and peaked at the onset of the 2018 MHW year in the third site (Naples Reef). At all sites, abundance has not recovered post-peak, though there were significantly more urchins in the northernmost and southernmost sites. We see a similar pattern in *M. pyrifera* detritus wet weight where peak was during ‘the Blob’ in 2015 and has not recovered since. Higher kelp detritus biomass was associated with fewer urchins and had no impact on urchin size. In another study, macroalgal abundance increased during and after MHWs and there was no change in sessile invertebrates in rocky intertidal habitats. However, abundance of an herbivorous mollusk decreased during and after a MHW (Ishida et al. 2023). In *S. purpuratus* larval settlement, there were no clear patterns related to MHW presence. There has been an overall long-term declining trend in settlement since 2010. Okamoto et al. 2020 found similar results with urchin settlement responding negatively to elevated temperature.

MHWs are an extremely dynamic climate-related stressor that impact marine ecosystems and species at a population and individual level. As a foundational species, *M. pyrifera*’s variable responses to MHWs provide vital information on what regions primarily characterized by kelp may be particularly vulnerable to acute elevated temperature stress in the future. *S. purpuratus* are more resilient to temperature stress and can adjust to temperature changes at a cellular level. *S. purpuratus* are voracious herbivores, so understanding the dynamics of two important kelp forest species and how

MHWs impact their abundance is directly related to kelp forest health, resilience, and recovery.

Adult origin differentially impacts gametogenesis and successful fertilization

As previously mentioned, MHWs are extremely dynamic and responses to this stressor may vary even within species. Research indicates that populations originating from more variable and warmer thermal environments tend to be less susceptible to warming (Miller et al. 2019). Significant local-scale variation in thermal responses highlights the importance of understanding potential response differences within and between species populations. In kelp, we have seen variable recovery across space post-MHW event. Kelp from Baja California showed high recovery while kelp from the Monterey Peninsula exhibited a slow decline and patchy recovery (Bell et al. 2023). During a MHW event, there was a large and immediate impact on *M. pyrifera* near its southern-range edge, but impacts were delayed in their central region and more resilient in their northern region (Cavanaugh et al. 2019). However, other studies showed variation in Oregon kelp species responses where population dynamics were strongly influenced by regional environmental processes (Spiecker and Menge 2022). In invertebrates, lower local ocean temperatures and greater kelp cover supported more invertebrate communities during a MHW event (Maucieri 2025). After MHW events, decreases in fish and invertebrate species were determined in regions near their warm distribution limit (Arafeh-Dalmau et al. 2019). Warm-affinity species increased in these areas suggesting MHW presence can facilitate the establishment of tropical and invasive species.

In Chapter IV, I explored the potential for local adaptation in my study organism, *S. purpuratus*. Marine species with pelagically-dispersed larvae are not always broadly dispersed and may experience strong selective pressures to maintain local differences (Sotka 2005). *S. purpuratus* is distributed widely along the east Pacific coast and have shown local adaptation driven by a mosaic of pH conditions (Kelly et al. 2013, Garrett et al. 2020, Petak et al. 2023). There is evidence of differential thermal tolerance in urchins across their biogeographic range, showcasing differences in *hsp70* expression in urchins closer to their southern range (Hammond and Hofmann 2010). In addition to latitudinal differences, depth also has been indicated to influence sea urchins during their reproduction (Basch and Tegner 2007). Previous research led me to select 3 sites along *S. purpuratus* range: Mohawk Reef in Central California, Bodega Marine Reserve in Northern California, and Fogarty Creek in Oregon. I collected urchins from each site to analyze egg morphometrics, biochemical content, and fertilization success. I hypothesized that urchins from more Northern sites would have greater GSI values, smaller eggs, and less biomolecule content in eggs. Results showed little differences between egg size and protein and lipid content at all sites. GSI values in urchins from MKO were largest and analyses indicated that their gonads grow with their test size at a greater rate compared to the two more northern sites. Fertilization success, the proportion of normal embryos at a range of temperatures, was also greatest in MKO urchins at all temperatures. For all sites, fertilization success decreased with increases in temperature.

Overall, Chapter IV contributes to the literature assessing biogeographical differences in *S. purpuratus* reproduction. As MHWs have occurred and will continue to occur

during *S. purpuratus* gametogenesis, assessing the impacts on urchins from different origins is a necessary metric to evaluate how population dynamics may shift in the future.

Future Directions

MHWs are projected to increase in frequency, duration, and intensity in the future due to climate change and species responses to MHW events are variable. MHWs are particularly impactful during important life-history stages, like gametogenesis, spawning, embryo development, and larval settlement. As an excellent model organism, *S. purpuratus* is well-studied. Future research directions may analyze whether plasticity in offspring may extend to further development to juvenile and adult stages. Including more sites to continue to probe for local adaptation to temperature would provide better understanding on population differences in *S. purpuratus*. The purple sea urchin is an important herbivore in kelp forest ecosystems and the noted impacts of MHWs on a cellular level should continue to be a priority.

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