Temperature spikes and marine heatwaves trigger rapid larval development in *Pisaster ochraceus* (Echinodermata: Asteroidea)

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Abstract

In the North Pacific, marine heatwaves (MHWs) have been increasing in intensity, frequency, and duration, and have resulted in large ecological shifts in the rocky intertidal. The sea star *Pisaster ochraceus,* a keystone species in the rocky intertidal, has seen declines of up to 90% associated with MHWs. This study focused on the effect of MHWs and temperature "spikes" on the larval stage of *P. ochraceus*. Larvae were reared in control ambient (CA) temperatures of 11.0-16.0°C, constant control (CC) temperatures 11.0-11.7 (±1°C), and MHW temperatures that rose to a maximum of 20°C (±1°C) over a 12-day period and remained high for 40 days before returning to ambient conditions. Morphological measurements and development of larvae from each treatment were obtained once a week. Linear regression and PCA analysis were conducted to summarize and visualize the morphological data. Linear regression revealed strong correlations between total length and total width and stronger correlations between total length and preoral process length for CA and MHW treatments. PCA showed that at 15 days post fertilization (dpf) and 22 dpf, the morphological space occupied by MHW larvae differed significantly from both control treatments, while the two control groups (CA and CC) were similar. By 29 dpf, the morphological space occupied by larvae in all three treatments diverged significantly. The separation of CC larvae in morphological space from CA larvae was evident. Spicule formation and the appearance of brachiolar arms and adhesive disk appeared much earlier for MHW larvae than for larvae in the control treatments (CA and CC). This study shows that both MHWs and temperature spikes can trigger rapid larval growth and development, potentially impacting settlement through their effects on the development of critical juvenile structures.

Introduction

Marine heatwaves (MHWs) are generally defined as a span of five days or more where sea surface temperature anomalies exceed the seasonally varying 90th percentile (Hobday et al. 2016). MHWs can trigger mass mortality events in foundation species, such as reef building corals and kelp forests, leading to a decrease in biodiversity and regime shifts in marine ecosystems such as the rocky intertidal (Smale et al. 2019, Meunier et al. 2024). Scientists have continuously proved that MHWs have been increasing in frequency, intensity, and duration globally, and the days of believing these events were once in every 100 or 50 years are long over. For instance, it has been found that when comparing MHW frequency between the time frames 1982-1998 and 2000-2016, MHW frequency in the global ocean increased 82% (Oliver et al., 2018, Barkhordarian et al. 2022).

On trend with global predictions, MHWs in the North Pacific have been increasing in intensity, frequency, and duration. From 2014-2016, the MHW later known as “The Blob”, devastated the Northern Pacific leading to significant declines in commercially important fish species and wrecking kelp communities (Joyce et al., 2022, Michaud et al., 2022). Then, from 2019-2021, another significant MHW occurred, leaving concerns that recovery from previous biodiversity loss may be unlikely (Wernberg et al. 2025). Located off the North Pacific Ocean lies the Salish Sea, a semi-enclosed estuary influenced by both freshwater and oceanic inputs. The Fraser River delivers significant amounts of freshwater to the system, with input increasing during the spring and summer due to snow and ice melt driven by seasonal increase in temperature

(Cameron, 1996). Simultaneously, ocean water enters the Salish Sea from the south through the Strait of Juan de Fuca and the north through the Strait of Georgia. Although the Salish Sea is currently relatively cool, it is expected to warm as the inflow temperature of seawater from the Pacific Ocean is expected to rise by approximately 3.5°C by 2095, influenced by MHWs (Khangoankar et al., 2019).

Organisms living in the Salish Sea are connected to the Pacific by two straits. They are therefore directly impacted by MHW events that occur on the outer coasts and the fallout that comes with these events, such as mass mortality events and regime shifts as previously mentioned. One species, the Ochre sea star *Pisaster ochraceus*, plays a large role in these regime shifts, as they are a keystone species in the rocky intertidal of the North American Pacific coast (Paine 1966). This species has a diet favoring mussels (*Mytilus californianus*), and when *P. Ochraceus* are not present these bivalves can take over the ecosystem due to release from predation. In 2014, a Sea Star Wasting Disease (SSWD) outbreak led to a decrease in density of *P. ochraceus* from 59-84% and saw biomass decrease from 60-90%. Additionally, mottled stars (*Evasterias troschelii*) became dominant following SSWD's onset as formerly dominant *P. ochraceus* declined, potentially due to decrease in competition (Kay et al. 2019). Additionally, anomalously warm temperatures influence the prevalence and severity of marine infectious diseases, with studies linking temperature to SSWD morbidity (Harvell et al., 2019). In the Salish Sea, warmer temperatures were associated with higher SSWD prevalence in *P. ochraceus* in the field, and faster disease progression and mortality in laboratories experiments (Eisenlord et al., 2016), highlighting the relationship between temperature and SSWD and their combined effects on adult *P. ochraceus.*

Despite the prevalence of studies on how sustained high temperatures linked to MHWs impact the adult stage of *P. ochraceus*, little has been done to investigate MHWs and their impacts on the larval stage, even though they might be the link to understanding the recovery of these species. Echinoderm larvae are relatively sensitive to warming, making this life stage a potential developmental bottleneck that could hinder successful recruitment into populations (Lang et al. 2023).

Studies on other echinoderms, for example, the sea urchin *Evechinus Chloroticus* show that early development is negatively affected by an increase in seawater temperature (Delorme & Sewell 2013). Elevated temperatures also impact the rate of larval development of the sea star *Echinaster (Othilia) brasiliensis*, as embryos reared in seawater at 27°C and 31°C developed more quickly than those reared in seawater at 20°C (Contins et al. 2025). This establishes that rising seawater temperatures could significantly disrupt the developmental timeline of this species, which has implications for other echinoderms. These studies suggest that high temperatures could reduce larval survival and impair recruitment, potentially leading to distributional shifts. However, it is possible that accelerated growth and development at high temperatures could be advantageous to planktotrophic larvae, as they could settle more rapidly and thus escape high planktonic predation.

Previous research conducted on *P. ochraceus* larvae reared in control ambient, water pumped in from the San Juan Channel without any temperature manipulation, and MHW conditions showed that, initially, larvae reared in the MHW treatment grew and developed at a more accelerated rate compared to those in the control ambient conditions. However, by the end of the experiment, the growth and development of the larvae in the control ambient and MHW treatments had converged (Baetsle & George 2024). Research conducted on adult *P. ochraceus* suggests that fluctuating temperature regimes may provide energetic advantages. Adult individuals that experienced episodic temperature fluctuations (9-12°C) had the greatest growth rates because they had high ingestion rates during warmer phases but enjoyed reduced metabolic costs during colder phases (Sanford 2002). Given the evidence from these studies, it is reasonable to hypothesize that temperature fluctuations or "spikes" may impact *P. ochraceus* larval growth and development.

Since there is limited research on ocean warming effects on *P. ochraceus* larvae, this study aims to fill this gap by assessing the effects of prolonged MHWs and temperature spikes on *P. ochraceus* larval growth and development. Larvae exposed to MHW conditions throughout development will be compared with those reared under constant and ambient seawater temperatures. We hypothesized that in the presence of abundant food, larvae subjected to a MHW treatment will develop faster compared to those in the ambient control followed by those in the constant control. Furthermore, we predict that the larval growth trajectories of the ambient control and MHW treatments will converge, due to accelerated growth during naturally occurring MHWs and temperature spikes, while the constant control and MHW treatments will not.

Methods and Materials

Collection and Experimental Setup

In early June *P. ochraceus* adults were collected at the Friday Harbor laboratory, San Juan Islands near the weather station at Cantilever Point (N 48° 32’ 46.065097” W 123° 0’ 28.341992”). To induce spawning, adults were injected with 2-2.5ml 100 micromolar 1-methyladenine. Two females and one male spawned. Eggs and sperm were collected using a 3ml plastic pipette and placed into respective beakers. The eggs were fertilized and examined for fertilization success after 5 minutes. Fertilization success was 100%. Embryos were divided among 15 1-gallon jars filled with 0.45µm filtered sea water and placed in three water tables. Each sea water table represented a treatment (control ambient (CA), constant control (CC) and a marine heatwave treatment (MHW)) with five replicate jars per treatment. Water circulation in the CA and MHW water tables (each measured 104.5cm x 104.5cm x 14.5cm) came directly from the San Juan channel while circulation of sea water in the CC tank (128cm x 59cm x 26.5cm) was closed and maintained with a JBJ Accela Pro pump connected to an Arctica titanium chiller DBA 150 throughout the experiment. In addition, insulation material surrounded the entire tank. These experimental conditions kept the temperature in the CC treatment at 11.0-11.7℃ (±1℃). No experimental temperature manipulation was done for the sea water temperature in the CA treatment. The temperature in the CA treatment tank varied between 11.0℃ and 16.0℃ due to temperature spikes that occurred in the San Juan Channel in June and a 5-day MHW in July. For the MHW treatment, temperatures initially varied from 12.1 to 12.4°C reflecting the temperature of sea water from the San Juan Channel. Three days post fertilization, temperatures were gradually increased from

13°C to 20.0°C, by decreasing the flow of sea water from the San Juan channel into the tank and adding three heating rods over 11 days (see Table 1). The temperature was then maintained at 20°C (±1°C) for 40 days followed by a rapid decrease to ambient temperature conditions in three days. These experimental conditions simulated a MHW with a slow onset and a rapid decline rate (see Hobday et al. 2016). Water pumps were used to maintain an even distribution of temperature within each tank. Temperatures were monitored using INKBIRD sensors and recorded by HOBO TidbiT MX 2203 Temperature 400' Data Loggers placed in each tank. Continuous water movement in each jar was maintained using a stirring system developed by Strathmann (1987). Swinging paddles placed in each jar were used for food distribution and oxygenation. Twice a week the paddles were rotated within and between the jars of the three treatments (after rinsing in RO water) and once a week the jars in the MHW and CA treatments were switched between sea tables to avoid pseudoreplication. Every two days, larvae were fed a mixed diet of *Rhodomonas* spp and *Dunaliella tertiolecta,* with increased concentrations over time, from 2000 cells/ml to a maximum of 8000 cells/ml, to match larval growth and development. Water changes were made once a week by siphoning about 80% of the sea water from each jar and replacing it with fresh 0.45µm filtered sea water.

Table 1. Slow onset rate of a simulated marine heatwave during growth and development of two-day-old embryos to 13-day-old bipinnariae in the MHW treatment.

Larval age	Temperature (°C)
2	12.2
3	13
4	15
5	14.9
6	17
7	18
8	18
9	18.1
10	19
11	19
12	19
13	19.5

Sampling and Measurements

Ten to fifteen larval samples per jar for a total of approximately 50 to 60 larvae per treatment were photographed once a week through a light compound trinocular Nikon eclipse *ci* microscope fitted with a Hayear camera and associated software. When the larvae were 36 days post fertilization (dpf), and too big, we switched to a light compound BH2 Olympus trinocular microscope fitted with a 2x lens. Growth and developmental stages were assessed once a week; total length (TL), total width (TW), stomach length (SL), stomach width (SW), preoral process length (PrePL), postoral process length (PostPL), and posterolateral arm length (PLA) when present were measured in microns (Table 2, Figure 1). Measurements were made using ImageJ. The fusion of the coelomic pouches, appearance of spicules, and brachiolar arms were use to assess how rapidly larvae were developing towards metamorphosis (Figure 3).

Table 2. Explanations for morphological measurements measured (see Sampling and Measurements section for full variable names).

TL + TW	Associated with both growth and development, shorter and wider larvae are associated with being less advanced while longer and narrower larvae are associated with being more advanced
SL +SW	Associated with both growth and development, rounder stomachs are associated with less advanced larvae while narrower and longer are associated with more advanced larvae
PrePL	Associated with development of settlement structures (e.g. brachiolar arms and adhesive disc)
PostPL	Associated with the development of juvenile structures (spicule formation, etc.)
PLA	Important for swimming and orienting in the water column, appear around 16-19 days (Pia et al. 2012, George and Strathmann 2019)

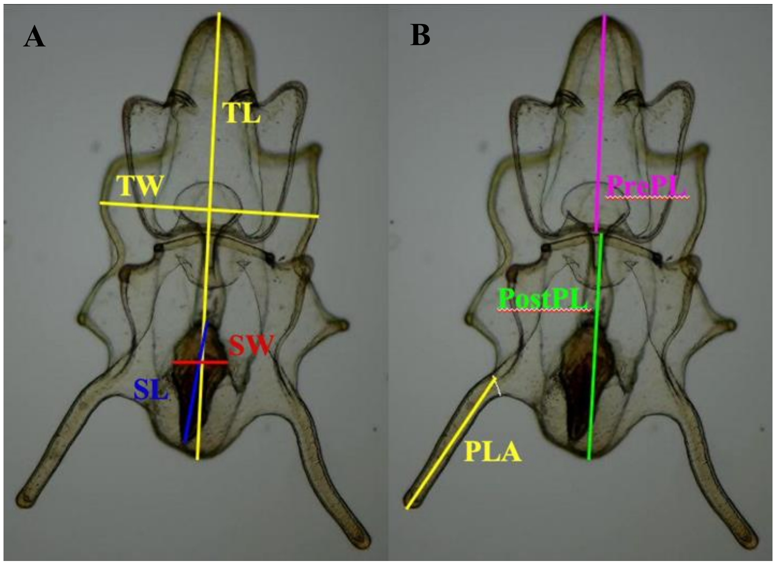

Figure 2. Graphic depiction of the seven morphological variables measured **A.** variables TL, TW, SL, SW **B.** PrePL, PostPL, PLA (see Sampling and Measurements section for full variable names).

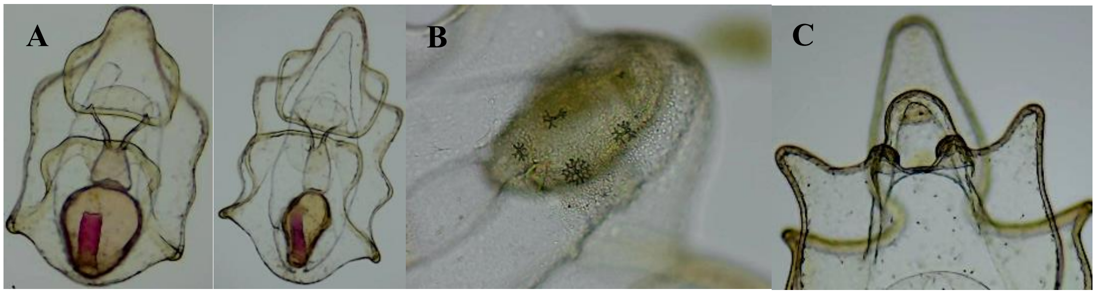

Figure 3. A. The left image shows a CA bipinnaria with coelomic pouches separate and the right image shows a MHW bipinnaria with coelomic pouches fused. B. Appearance of spicules around the stomach region in the posterior region of a MHW larva C. Development of brachiolar arms in the anterior region of a MHW larva.

Data Analysis

All statistical analyses were conducted with R through Rstudio. To determine whether 8 and 15-day old larvae differed in total length among the three treatments, a two-way ANOVA with Treatment (CA, CC and MHW) and larval age (8dpf, 15dpf) as fixed factors was run for unequal sample sizes with type 3 sums of squares using the lm function in r with the car package. The interaction between Treatment and larval age was included; 374 larvae were used in the analysis. When differences were significant the Tukey HSD test was used to discern which treatments differed. Similar tests were run to determine whether posterolateral arm length differed among 22- 29- and 36 dpf larvae. Due to extremely low sample sizes for the CC and CA treatments, 15-day old larvae were excluded from this analysis; 473 larvae were used in this analysis.

We used linear regression to compare growth rates of TL vs. TW, TL vs. SL etc. To summarize and visualize all measured variables PCA analysis was conducted using packages FactoMineR for the analysis and factoextra for the visualization. Permutational Multivariate Analysis of Variance (PERMANOVA), a test that is not restricted by the general assumptions of an ANOVA; and extended to accommodate heterogeneity of within group dispersions; was used to look for differences in the treatment means (CA, CC and MHW) and PERMDISP a test for homogeneity of dispersions was used to determine differences in the distribution of larvae around their means. This latter test addressed the question as to whether the within-treatment dispersion is similar among the three treatments (Anderson 2017). All data were conducted using packages vegan. The pairwiseAdonis package was used to determine which treatments differed from each other.

Results

The interaction term was significant. Tukey HSD test revealed that total larval length did not differ between CA and CC larvae 8 and 15dpf, (8dpf: p=0.9806, n=140; 15dpf: p=0.9222, n=117; respectively, Table 3). Total larval length of 8 and 15dpf MHW larvae differed significantly from CA larvae (8dpf: p=0.0000, n=133; 15dpf: p=0.0000, n=113) and CC larvae (8dpf: p =0.0005, n =113; 15dpf: p=0.0000, CC n=114, Tukey HSD, Table 3). Between 8dpf and 15dpf, the mean total lengths for CA and CC doubled (Table 3). However, during the same time frame, the mean total lengths for the MHW larvae, almost tripled. Eight and 15dpf, CA and CC larvae were comparatively more like each other in size at temperatures between 11 and 12°C than MHW larvae that were currently at a temperature of 18-20°C.

Table 3. Mean Total Length (TL) ± standard deviation in microns for 8 and 15-days post fertilization (dpf) larvae of the sea star *Pisaster ochraceus* from Control Ambient, CA; Control Constant, CC; and Marine heatwave (MHW) treatments. n is the total number of larvae measured.

Treatment	8 dpf		15 dpf	
CC	334 ±80.7	n=71	621.8 ±80.5	n=58
CA	318.2 ±87.9	n=69	645.8 ±101.4	n=59
MHW	430.6 ±164.0	n=62	1117.4 ±227.3	n=55

Linear regression between TL and TW for 15, 22, and 29 dpf bipinnariae revealed a strong positive correlation across all three treatments (CA, R=0.95; CC, R=0.96; MHW, R=0.92; Figure 4). Linear regression between the TL and PrePL 15, 22, and 29 dpf bipinnariae revealed a stronger positive correlation for CA and MHW (R= 0.98, R=0.99 respectively) than for CC (R=0.83, Figure 5).

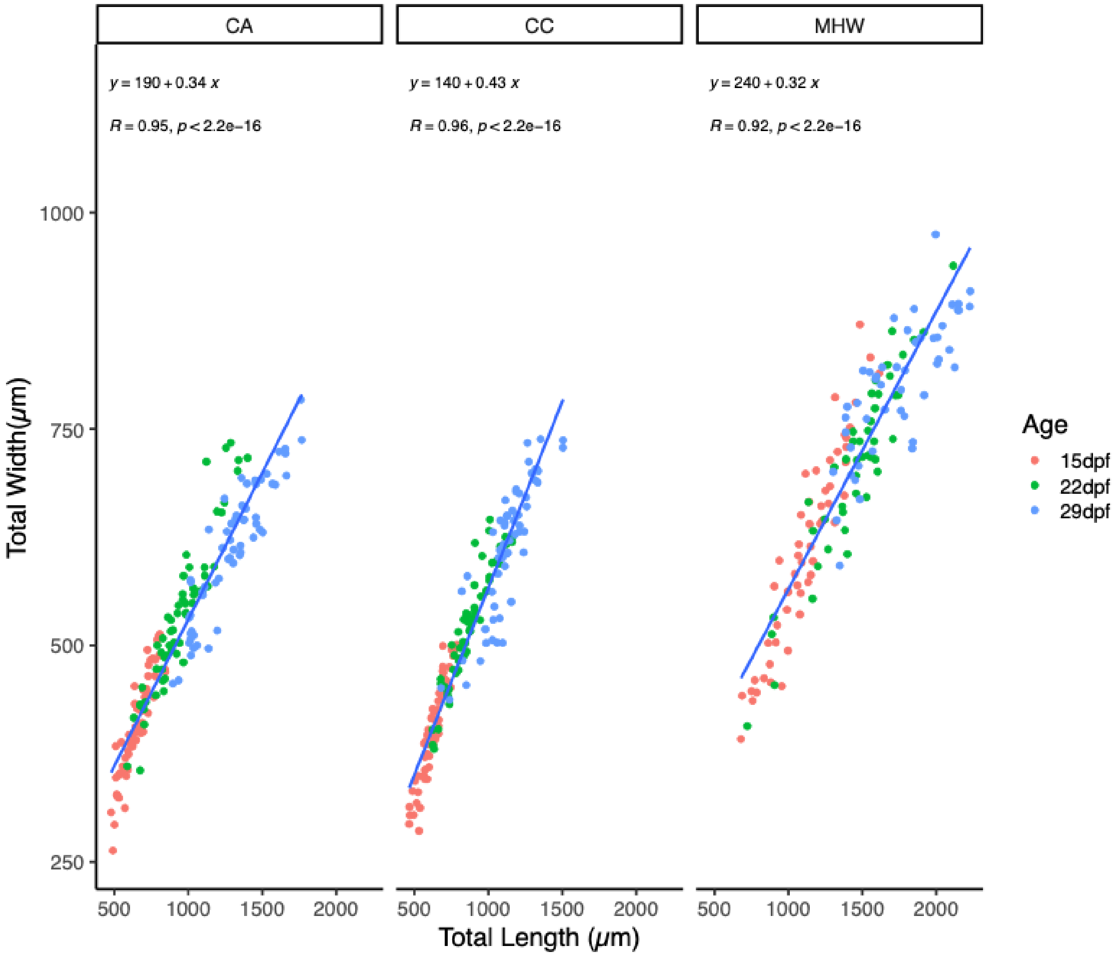

Figure 4. Linear regression of Total Length (TL) and Total Width (TW) measured in microns for 15-, 22-, and 29-day old larvae of the sea star *Pisaster ochraceus* kept in Control Ambient, CA; Control Constant, CC; and Marine heatwave (MHW) treatments. CA treatment R=0.95, CC treatment R=0.96, MHW R=0.92.

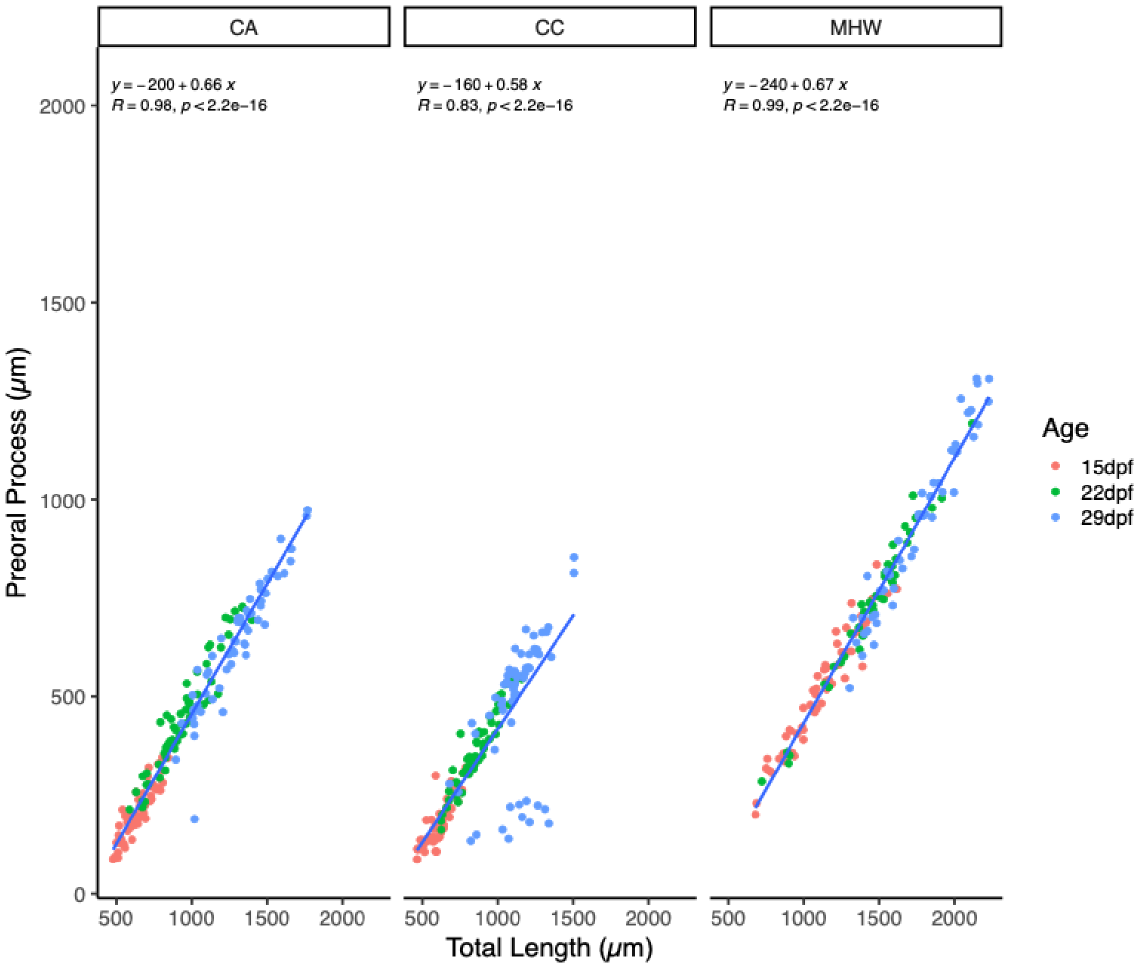

Figure 5. Linear regression of Total Length and Preoral Process Length (PrePL) measured in microns for 15-, 22-, and 29-day old larvae of the sea star *Pisaster ochraceus* kept in control ambient, CA; Control Constant, CC; and Marine heatwave (MHW) treatments. CA treatment R=0.98, CC treatment R=0.83, MHW R=0.99.

For 15 dpf larvae PC1 and PC2 explained 85.5% of the variability (Figure 6A). At 15 dpf PERMANOVA revealed that there were no significant differences between the two control treatments (CA and CC), but both controls differed significantly from the MHW treatment (Table 4). PERMDISP analysis revealed a significant difference between MHW and CC, but not between CC and CA. The difference between CA and

MHW (p = 0.06) was borderline. When larvae were 22 dpf PC1 and PC2 explained 85.8% of the variability (Figure 6B). At 22 dpf, the larvae in CA and CC treatments remained statistically similar, and the MHW treatment continued to differ significantly from both control groups (Table 4). There were no significant differences in dispersion across treatments, indicating similar levels of morphological variation. PCA from 29 dpf larvae had a PC1 and PC2 explain 81.4% of the variability in the data (Figure 6C). Twenty-nine days post fertilization, larvae in all treatments were significantly different from each other (Figure 6D, Table 4).

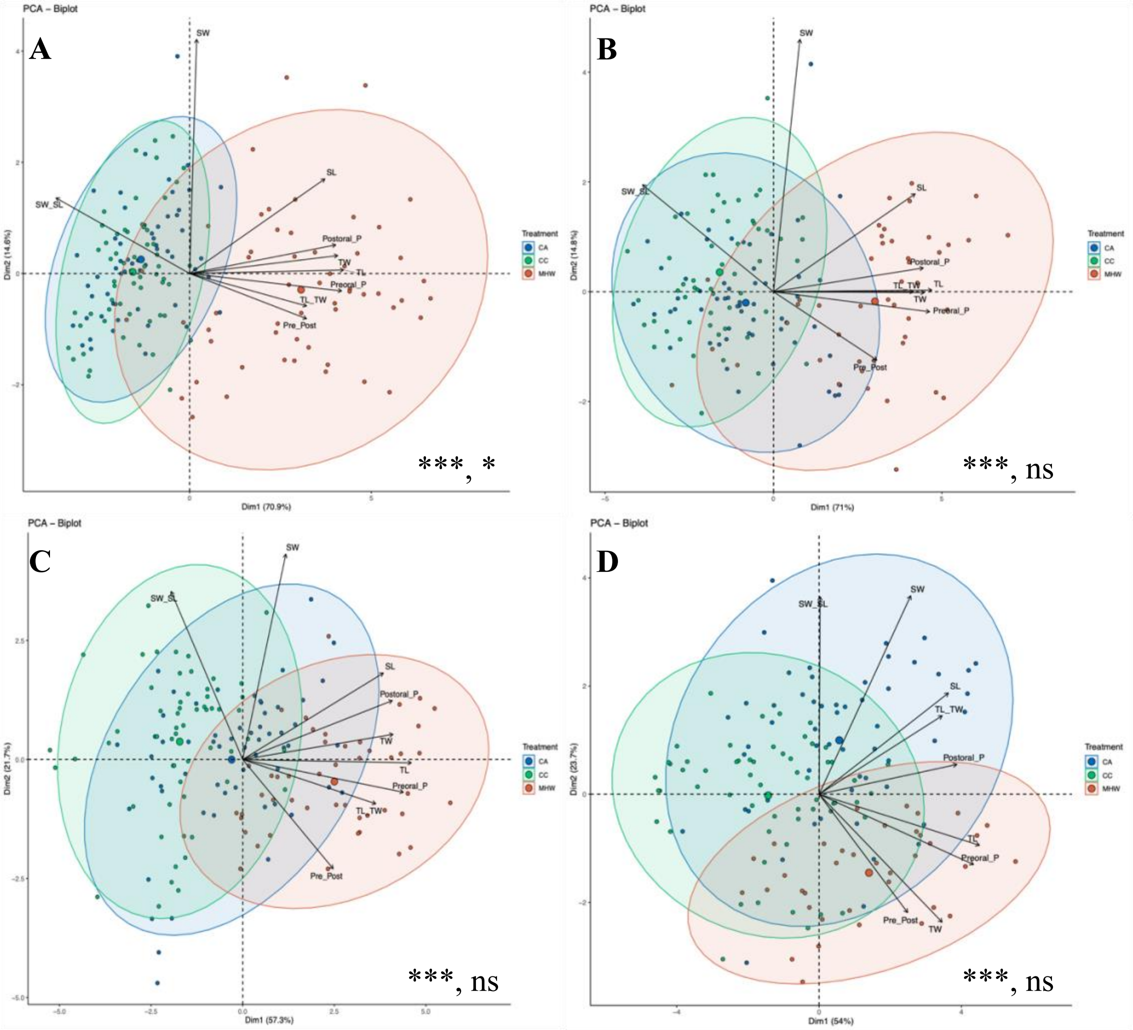

Figure 6. Principal Component (PC) analysis for larvae of the sea star *Pisaster ochraceus* from Control Ambient, CA; Control Constant, CC; and Marine heatwave (MHW) treatments. The percent contribution of each PC is displayed, for **A.** 15 days post fertilization **B.** 22 days post fertilization **C.** 29 days post fertilization **D.** 36 days post fertilization. The vectors direction and length represent the contribution of the 6 variables (TL, TW, SL, SW, PrePL, PostPL) and 3 ratios (SW/SL, TL/TW, PrePL/PostPL). Abbreviations are spelled out in the section on sampling and measurements. Asterisks refer to significance of the statistical tests conducted (PERMANOVA, PERMDISP) (see Table 4).

Table 4. F and p values from PERMANOVA and PERMDISP for *Pisaster ochraceus* larvae from 3 treatments (Control Ambient (CA), Constant Control (CC), and Marine heatwave (MHW)). Number of observations in parentheses.

Larval Age	PERMANOVA	PERMDISP
15 dpf	F=86.163, p=0.001 ***(170)	F=4.384, p=0.03 *
22 dpf	F=60.056, p=0.001 ***(157)	ns (F=0.783, p=0.49)
29 dpf	F=44.161, p=0.001 ***(164)	ns ((F=0.859, p=0.41)
36 dpf	F=27.852, p=0.001 *** (149)	ns (F=0.577, p=0.48)

ns = non-significant. '***' 0.001 '**' 0.01 '*' 0.05.

From 15 to 36dpf, the three treatments showed different patterns in mean PLA length. At 22dpf, the three treatments did not differ from each other in mean PLA length (CA-CC: p=0.9995, n=81; MHW-CC: p=0.1977, n= 75; MHW-CA: p=0.2911 n=102, 2-way ANOVA for unequal sample sizes, Table 5). At 29dpf, MHW larvae had significantly longer PLAs than CA and CC larvae (CA: p=0.0091, n=107; CC: p=0.0000, n=105), while PLA length of CA and CC larvae did not differ significantly (p=0.4450, n=116). At 36dpf, all treatments became significantly different from each other (CA-CC: p=0.0025, n=116; MHW-CC: p=0.0000, n=104; MHW-CA: p=0.0000, n=106). At and after 29dpf, MHW larvae had the longest PLAs and demonstrated pronounced growth, with individuals advancing more quickly and reaching the highest values by the end of the experiment, although this treatment had the greatest variability (Table 5).

In addition to the earlier appearance of PLAs in MHW larvae, spicule formation, the appearance of brachiolar arms and adhesive disk also appeared much earlier for these larvae as opposed to larvae in the control treatments (CA and CC).

Table 5. Mean Posterolateral Arm lengths ± standard deviations in microns for larvae of the sea star *Pisaster ochraceus* from Control Ambient, CA; Control Constant, CC; and Marine heatwave (MHW) treatments. NA indicate Posterolateral Arm lengths were not yet developed. n is the total number of larvae measured.

Treatment	15 dpf		22 dpf		29 dpf		36 dpf	
CC	NA	n=58	58.4 ±33.1	n=59	239.5 ±175.9	n=60	426.1 ±216.3	n=59
CA	NA	n=59	122.4 ±88.3	n=55	338.3 ±143.7	n=59	750.4 ±347.8	n=58
MHW	115.6 ±85.8	n=55	329.9 ±259	n=55	634.0 ±639.3	n=58	955.7 ±823.8	n=47

Discussion

This study aimed to both investigate the effects of temperature spikes and clarify the effects of short, natural, and prolonged MHWs on *P. ochraceus* larval growth and development. This was done by comparing larvae exposed to constant high temperatures associated with heatwave conditions throughout their development with those reared under constant and ambient seawater temperature conditions. Ambient conditions were defined as the naturally occurring temperature fluctuations that were simultaneously occurring in the San Juan Channel. Our hypothesis was that larvae reared under MHW and ambient conditions would converge in growth and development whereas those reared in MHW and constant control conditions would not converge. At 36dpf, there was not sufficient evidence to support the hypothesis that ambient and MHW larvae had converged or would converge. However, the encroachment of CA larvae into the morphological space of the MHW larvae, from 15dpf-36dpf, serves as evidence that they were becoming morphologically similar over time. Our hypothesis that MHW and constant control larvae would not converge was supported and was illustrated by the fact that the morphological space occupied by CC and MHW larvae remained significantly different for the duration of the experiment.

Initially, CA and CC larvae did not differ significantly in total lengths 8dpf and 15dpf, and for all morphological variables visualized in PCAs. However, differences between CA and CC larvae became apparent as temperatures rose during a temperature spike followed by a natural MHW that started when larvae were 28 days old. This may have accounted for the observed separation in the morphological space occupied by CA and CC larvae 29 and 36dpf. This evidence illustrates how temperature spikes and MHWs can rapidly affect the growth of *P. ochraceus* larvae. From this we conclude that larvae reared in conditions where temperature spikes are present will experience accelerated growth and development compared to those raised under constant temperature conditions.

During the late bipinnaria stage (16-23dpf), PLA buds appear and elongate (Pia et al. 2012), making them useful developmental markers. At 15dpf, MHW larvae (at 20°C) had mean PLA lengths of 115.6 microns—appearing one day earlier than expected—while CA and CC larvae (at 11-12°C) had very few measurable PLAs. Between 29dpf and 36dpf, CA larvae experienced temperature spikes and a MHW, and at 36dpf CA larvae's mean PLA length differed significantly from those of CC larvae. PLA length more than doubled for 36dpf CA larvae. These results demonstrate that elevated temperatures accelerate *P. ochraceus* larval development under both constant MHW conditions and sporadic temperature spikes when food is abundant.

Metabolic rate increases in ectotherms in reaction to high temperatures and *P. ochraceus* larvae are known to consume algal particles at higher rates when reared in higher temperatures (Schulte et al. 2015, George et al. 2021). In this study, larvae were reared with abundant food in all treatments, however this is not always the case in the wild. If larvae are subjected to temperature spikes or MHWs in the wild when food is scarce, this may create a stressful environment because their elevated metabolic rates would demand more food than would be available. Additionally, the effects of MHWs on the preferred algal food sources, including *Rhodomonas spp* and *Dunaliella tertiolecta,* of *P. ochraceus* larvae are unclear, especially if MHWs and increased temperatures impact the nutrients in these food sources. This raises the question of how decreased food availability and quality would impact the growth and development of *P. ochraceus* larvae. As seawater temperatures in the Salish Sea are expected to rise, diatom concentrations are predicted to decrease by 14% while dinoflagellate concentrations could more than double (Khangaonkar et al. 2019), potentially shifting algal communities toward warm-water species and impacting food sources for *P. ochraceus* larvae.

It has been shown that increased temperatures may lead to a decrease in echinoderm settlement, and therefore as ocean temperatures continue to increase, the amount of echinoderm larvae that successfully settle may decrease (Doll et al. 2022). *P. ochraceus* is a keystone species in the rocky intertidal area with an essential role in the food web as a predator of California mussels (Paine 1966). A decrease in the settlement of *P. ochraceus* larvae would mean a further decrease in the adult population, as larvae would fail to settle and mature. It is thus necessary to further explore how MHWs and temperature spikes impact *P. ochraceus* growth, development, and survival to settlement, as this has large implications for their recovery as a species.

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