Indigenous sea gardens can buffer impacts of contemporary heatwaves

by

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Abstract

While societies around the world are grappling with the challenge of maintaining productive food systems that are resilient to climatic disturbances, Indigenous communities have been adapting to climatic shifts for millennia. Here, we investigated if ancestral clam gardens, intertidal rock wall terraces built by Indigenous peoples throughout the Holocene, can mediate the impacts of contemporary heatwaves. During a simulated heatwave, we found that clam garden sediments were on average 5.4 °C cooler than non-walled beach sediments at 5cm depth and spent 1.26 times more hours above the optimal temperature threshold for clam growth. By keeping sediments cooler for longer, a clam garden encompassed clams that had an 11-fold lower expression of toll-like receptor 1, a gene associated with bacterial infection. These results suggest that clam gardens can alter clam physiology at a sub cellular level. By keeping clams cooler and safer to eat than non-walled beaches, this study highlights the important role clam gardens across the coast of the Pacific Northwest can and will continue to play in maintaining Indigenous food security and sovereignty in light of ongoing climate change.

Keywords: Climate Change; Food Sovereignty; Indigenous Mariculture; Heatwaves; Clam Gardens

To the Hul’q’umi’num and SENĆOŦEN speaking peoples whose ancestors made these rock walls and to the future generations who will harvest from these places.

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Finally, I am thankful for my family, for their love, support, and patience and for my husband Dylan, for his unwavering care.

Author positionality

My given name is Emily Rose Spencer. I am of European ancestry, specifically English, German, Russian, and Polish. My families on both sides settled in Australia in the mid 19th century before moving to Turtle Island in the mid 20th century. My parents grew up in Coast Salish territory. I was born and raised on Anishinaabe and Kanien'kéha territories, it was there I first fostered my connection to the land and water, and I am so grateful for that. I now live on the territories of the Hul'q'umi'num, SENĆOŦEN, and lək̓ʷəŋən speaking peoples. I am immensely grateful for the knowledge holders who have taught me so generously and for the lessons I've learned from the land. I would also like to acknowledge the Nations on whose territories Simon Fraser University resides, the səl̓ilw̓ətaʔɬ (Tsleil-Waututh), kʷikʷəƛ̓əm (Kwikwetlem), Sḵwx̱wú7mesh Úxwumixw (Squamish) and xʷməθkʷəy̓əm (Musqueam) Nations. Huy ch q'u / HÍSW̱ḴE (Thank you).

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Introduction

Maintaining food systems around the world's oceans that are both productive and resilient to the impacts of extreme climactic events has become a global priority as heatwaves increase in intensity and duration (Thornton *et al.*, 2014; Oliver *et al.*, 2018; Gaupp, 2020; Settee and Shukla, 2020). Moreover, calls to center equity in ocean policies and decolonize ocean science are increasing (Ignace *et al.*, 2023; Salomon *et al.*, 2023; Spalding *et al.*, 2023). At this nexus, there is a need to better protect the health and access to traditional ocean-based foods to support Indigenous food sovereignty (Armstrong-buisseret, 2022; Soma *et al.*, 2022). While Indigenous food systems have responded to extreme climate events for millennia spurring the development of governance systems and adaptive management practices that have long supported social-ecological resilience (Powys Whyte, 2016; Toniello *et al.*, 2019), it remains unknown if these ancestral innovations, now disrupted by colonial laws (Simpson, 2004), are resilient to the magnitude and pace of human-induced climate change we face today. Here, in collaboration with nine coastal Salish Nations in western Canada, we co-designed an experiment to test the degree to which a recently revitalized ancestral food system can buffer the impacts of extreme marine heat events.

Heat stress is a major structuring force in intertidal communities (Hochachka and Somero, 2002; Harley, 2011), the occurrence of which is projected to rise with the increased frequency of heatwaves, such as the unprecedented heatwave that engulfed the Pacific Northwest in 2021, killing billions of marine invertebrates within a period of 5 to 7 days (White *et al.*, 2023). In nearshore ecosystems, marine invertebrates live near the extent of their thermal tolerances and have a limited ability to buffer temperatures beyond that range (Harley, 2008). When temperatures rise, the energetic demands of an animal increases (Kleiber, 1972), necessitating the redirection of resources away from non-essential functions, such as growth, reproduction, and immune response, towards the production of heat shock proteins that help an animal tolerate stressful temperatures (Wendling and Wegner, 2013; Brownlee, 2022). While these physiological impacts of extreme heat are impacting populations of marine invertebrates, external factors such as disease can cause additional stress.

Recent increases in disease outbreaks among marine invertebrates have been linked to rising ocean temperatures and heatwaves (Burge *et al.*, 2014). It is well-established that disease dynamics depend on the interactions between environmental variables, pathogens, and hosts (Burge *et al.*, 2014). By increasing air and water temperatures, heatwaves can speed up bacterial growth, increasing pathogen concentration in their hosts (Wendling and Wegner, 2013; Burge *et al.*, 2014; Go *et al.*, 2017; Green *et al.*, 2019; Ndraha, Wong and Hsiao, 2020). Simultaneously, the host immune response may be downregulated to respond to heat stress, rendering an animal more susceptible to disease (Wendling and Wegner, 2013). Across a population, the impacts of extreme heat events have resulted in mass marine mortality events caused by the additive effects of both heat stress and increased pathogen growth (Wendling and Wegner, 2013; Go *et al.*, 2017; Green *et al.*, 2019). While these mass mortality events constitute ecological disasters that can propagate through social-ecological systems with profound impacts on human well-being (Rogers-Bennett and Catton, 2019; Hamilton *et al.*, 2021), it has been suggested that ancestral mariculture innovations hold promise as technologies that could buffer climate extremes (Slater 2018, Lepofsky and Salomon 2023, Salomon et al 2023).

Across the Pacific northwest coast of North America, there has been a resurgence in the restoration, use, and tenure of clam gardens[1] (H-GINPR, 2016; Olsen, 2019; Augustine *et al.*, 2022; Augustine, Stocks and Slade, 2023), an ancestral Indigenous mariculture technology shown to stabilize local water temperatures (Salter 2018). Clam gardens are intertidal rock wall terraces built by people since the late Holocene, and were continually used, adapted, and maintained prior to the incursion of colonial law and dispossession of Indigenous land (Toniello *et al.*, 2019). Despite reduced stewardship over recent generations, clam gardens today can double the growth rates of clams and encompass 2 to 4 times more clam biomass than non-walled beaches (Groesbeck *et al.*, 2014). By reducing the slope of intertidal clam habitat, clam gardens expand the optimal intertidal height for culturally salient butter and littleneck clams. It has been shown that this reduction in slope increases seawater retention,

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[1] The preferred English term of Hul'q'umi'num and SENĆOŦEN speakers in the Southern Gulf Islands is "sea garden" given the teaching that these places are designed to cultivate many intertidal marine species in addition to clams (Augustine, Stocks and Slade, 2023). We use this term and 'clam garden' to maintain the connection with previous academic publications on these ancestral features.

moderating the temperature experienced by clams (Salter, 2018). Growth conditions are further ameliorated through management practices including the addition of crushed shells to sediments (Lepofsky *et al.*, 2015; H-GINPR, 2016). It has remained unknown, however, if clam gardens, and their shell-rich sediments, could reduce the level of heat stress experienced by clams, particularly during heatwaves.

In collaboration with nine Hul’q’umi’num and W̱SÁNEĆ coast Salish Nations and Parks Canada, we sought to understand how clam garden revitalization affects the physiological response of clams to climate-induced heat stress. Specifically, we asked, 1) how does temperature vary across clam habitat on a clam garden and an unmodified non-walled clam beach? 2) to what extent can clam gardens and their shell-rich sediments buffer the impacts of heatwaves on clams? We addressed these questions by simulating a marine heat wave and transplanting clams across a revitalized clam garden and nonwalled beach. We predicted that the reduced slope of the clam garden and increased seawater retention would keep sediment temperatures cooler across the extent of clam habitat on a clam garden compared to a non-walled clam beach thereby reducing the expression of genes associated with heat stress and disease in clams.

Methods

Study Area

To understand the extent to which clam gardens and their shell-rich sediments mediate the effects of extreme heat events on clams, we conducted temperature surveys and a heatwave experiment at two different paired clam garden and non-walled beach sites in the Southern Gulf Islands on the southwest coast of British Columbia, Canada. Fifteen Indigenous Nations, collectively self-referred to as ‘Coast Salish’, have ancestral ties to this archipelago (Augustine, Stocks and Slade, 2023) as evidenced by over 60 ancient clam gardens and many more clam harvesting beaches in this region alone (H-GINPR, 2016). Despite the longstanding and ongoing relationships between Coast Salish peoples and clams, ongoing impacts of colonization, including climate change, have disrupted those relationships that maintain productive beaches. To improve the health of clam beaches and to revive ancestral practices of maintaining these beaches, nine Coast Salish Nations (Cowichan Tribes, Halalt, Lyackson, Penelakut, Stz’uminus, Tsartlip, Pauquachin, Tseycum, and Tsawout) and Parks Canada are experimentally restoring two clam gardens and two non-walled beaches in this area (See webpage). We compared intertidal temperature profiles over 30 days in May 2022 at a clam garden (Russel Island) and non-walled clam beach (Saturna Island) and experimentally manipulated temperature and sediment characteristics at a clam garden and non-walled beach on Salt Spring Island (Figure 1).

Consent and Research Co-Design

We were given permission from members of Hul’q’umi’num and SENĆOŦEN speaking Coast Salish Nations to conduct research on their *Stuqnets* (rock walls; Hul’q’umi’num)*/KOINAS* (clam place; SENĆOŦEN). Our research questions were co-developed with members from these nations with whom we continue to engage with to interpret and share our findings. Further, all stages of our research have been closely guided by two knowledge holders and advisors from the Hul’q’umi’num-speaking nations: Ala̱ga̱mił Nicole Norris and Kenneth Thomas.

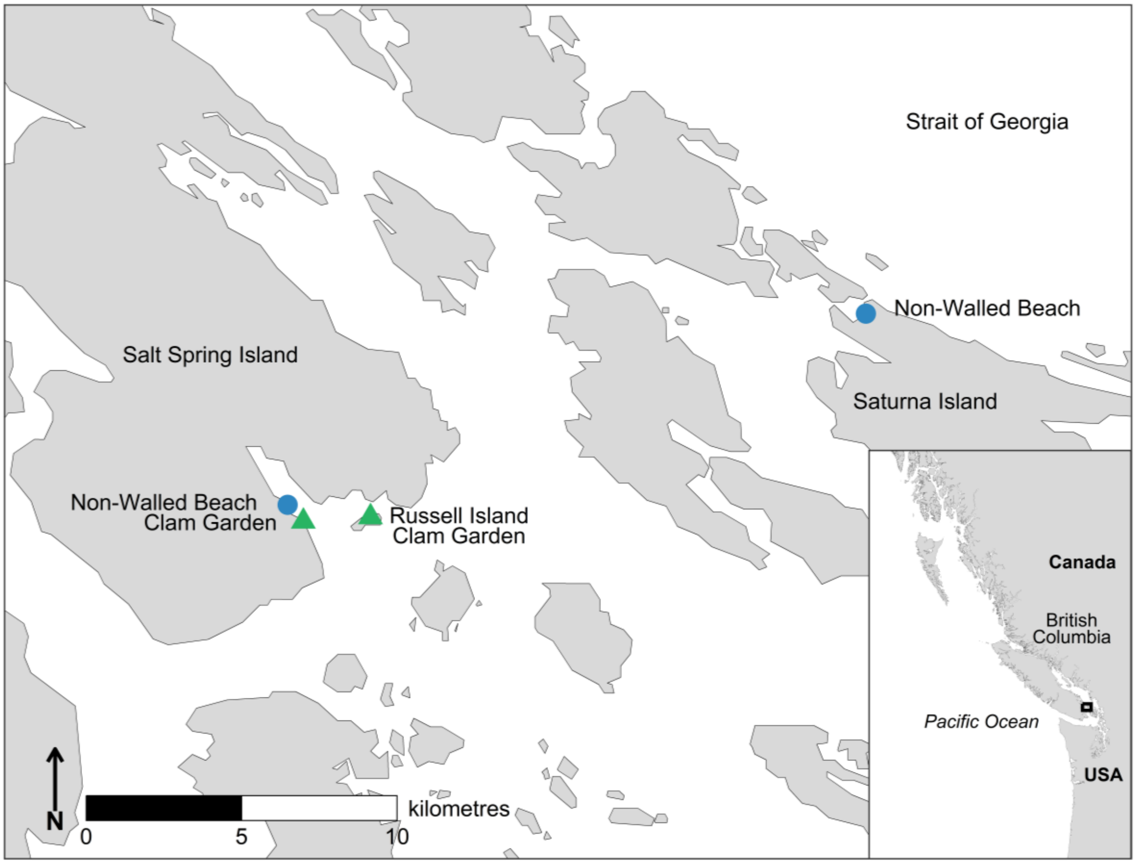

Figure 1. **The study area is within Coast Salish Territory, located in the Southern Gulf Islands, British Columbia, Canada. Russell Island clam garden and Saturna Island non-walled beach are the temperature survey sites and Salt Spring Island clam garden and non-walled beach are the heatwave experiment sites.**

Beach Temperature Maps

To quantify how subsurface sediment temperatures vary across a clam garden and non-walled beach at low tide, we recorded sediment temperatures at multiple locations across intertidal clam habitat at one clam garden (Russell Island) and one non-walled beach (Saturna Island) from May 18 – June 18, 2022. At each site, we deployed twenty-two temperature loggers (HOBO MX 2201, Onset, Bourne, MA) across the “low”, “mid”, and “high” intertidal zones of each beach. Due to the variation in slope between clam gardens and non-walled beaches, the specific tidal height of these zones varied between sites (see Groesbeck et al. 2014). At the clam garden, the lower extent of clam habitat tidal height was determined by the rock wall. The presence of clams determined the lower extent of clam habitat on the non-walled beach and the upper extent of clam habitat on both beaches. The clam garden has a North facing aspect, while the non-walled beach is West facing, however both sites likely experience the same amount of sun exposure because there is no shade on clam habitat at either site. Temperature loggers were placed below surface sediments at 10 cm depth to measure the temperature experienced by native harvestable clams like butter and littleneck clams. Measurements were recorded every two minutes. From these data, we estimated temperature maximum, minimum, standard deviation, and the number of hours above 15 °C for the study period. Maximum temperatures coincided with low tides and the minimum temperatures likely represented water temperature as they coincided with high tides. Lastly, temperature interpolation maps of the summary statistics were created for each site based on the spatial coordinates of each temperature logger.

Heatwave Experiment

To understand if, and to what extent, clam gardens and their shell-rich sediments buffer the impacts of extreme heat events on clams, we simulated a heatwave of similar magnitude and duration as the 2021 heatwave that affected the Pacific Northwest Coast.

At each site, we established 20 experimental 50 cm x 50 cm x 20 cm plots at 1.15 m above chart datum across a 100 m of beach. We chose this tidal height because it represents the upper extent of clam habitat on both beaches where clams are exposed to air temperatures for the longest period of time. To account for spatial variability within sites, plots were divided into 5 experimental blocks of 4 (n=20 per beach), where treatments (with and without heat n=10 plots, and with and without shell hash n=10 plots) were fully crossed (Figure 2).

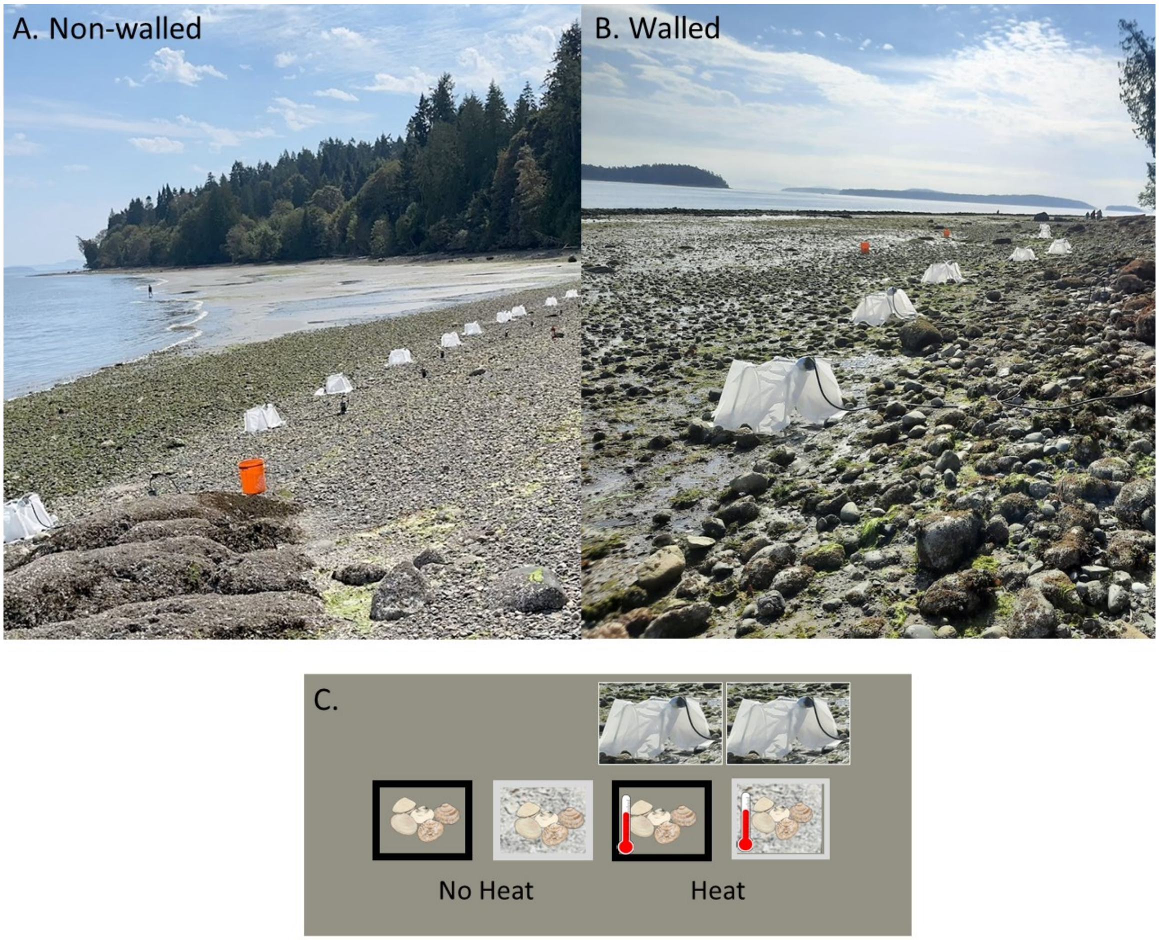

Figure 2. **To simulate a heatwave, 20 experimental plots were created across (A) a non-walled beach and (B) clam garden at 1.15m above chart datum. (C) The plots were divided into blocks of 4, where treatments (shell enriched (grey) or not (black) and heated or unheated) were fully crossed. Sediment temperature and littleneck clam physiology were measured at each plot.**

To simulate a heatwave, we constructed mini heat tents using portable infrared propane heaters (Martin® Tulsa, Oklahoma, USA) which we attached to metal frames covered in flame-resistant plastic, inspired by Hoos and Harley (Hoos and Harley, 2021). Heaters, pointed at the ground, hung ~0.5 m above the sediment and heated an area of ~0.5 m^2. The tents were designed to keep localized temperatures elevated and avoid heat dissipation due to wind. Heat tents were set up at each site as soon as the plots were exposed at low tide and dismantled before the tides rose to the plots. During the experimental period, heat tents maintained air temperatures between 35 – 50 °C.

To test the potential cooling effect of shell hash, we added shell fragments to 10 plots with and without heat. Fragments of barnacle and clamshell were collected from the upper intertidal zone of the beaches with permission from the local Nations. Shell was sieved to a size of 6.35 mm (0.25 inches), and mixed with natural sediments to mimic the conditions at clam gardens (Salter, 2018). This sediment mixture was used to fill the entire volume of the plot and was supplemented daily throughout the experiment to maintain a strong treatment effect. The sediments of the plots that did not receive a shell addition were similarly disturbed to control for the disturbance of digging.

Two weeks prior to the heatwave experiment, we transplanted 3 – 4 adult littleneck clams into each of our experimental plots. The clams originated from the same source population at a non-walled clam beach within 15 km of the experimental site. To avoid predators, the clams were enclosed in a galvanized steel mesh cage of 24 cm x 24 cm x 12 cm with a mesh size of 12.7 mm (0.5 inches), allowing the animals to feed and move as normal. To avoid density dependence, we rehomed any ambient non-experimentally transplanted clams found in the plots while they were being dug.

We recorded sediment temperatures in each plot throughout the experiment with n=3 HOBO MX, Pendant, or Tidbit v2 temperature loggers per plot (Onset, Bourne, MA). In each plot, we measured temperature at the sediment surface, and at 5- and 10-centimetres depth. Temperatures were recorded each minute during the experimental period and the data were summarized over the five-day experimental period as 1) maximum temperature reached while the heaters were on, and 2) number of hours that sediment temperatures were above 18 °C, the extent of optimal littleneck clam thermal range for growth.

Clam Gene Expression

Following the 5-day heatwave treatment, transplanted littlenecks were removed from the sediments one block at a time, immediately dissected, and stored on dry ice to preserve their gene expression. Samples were then stored at -80 °C in the laboratory.

Total RNA was extracted from ~1 cm * 50 mm sections of the gill tissue using the Monarch® Total RNA Miniprep Kit Protocol (New England Biolabs, MA, USA). Tissue samples were homogenized in RNA lysis buffer solution and briefly vortexed before being transferred to a removal column for RNA purification. Genomic DNA was removed using RNA wash buffer, DNase I Reaction Buffer, and RNA priming buffer. To ensure that equal amounts of RNA were used for analyses, RNA concentrations were measured by absorbance using the Eppendorf Spectrophotometer (Germany) and the samples were diluted to 50ng/µL RNA. Single-strand cDNA was synthesized using the iScript Select cDNA Synthesis Kit™ (Bio-Rad, Canada) and random primers.

Target genes were identified based on *a priori* hypotheses about the physiological impacts of heatwaves on clams and previous research (Raap *et al.*, 2022). Primer pairs were designed based on the transcriptome data for littleneck clams (Raap *et al.*, 2022) and were validated by performing a dilution series with cDNA and calculating their amplification efficiency (Ea) as described by Pfaffl (2001). Genes of interest included the *Heat-shock protein (hsp) 70* and *Von Willebrand factor type D domain (vwd),* both of which are involved in the heat response and *Toll-like receptor 1 (tlr1),* which is involved in the immune response. Housekeeping genes included *Actin 2* and *Elongation Factor* which were not differentially expressed in the previous study on littleneck clams (Raap *et al.*, 2022) (Table 1). Quantitative real-time PCR (qRT-PCR) of the tissue samples was performed in duplicates using the iQ SYBR green supermix kit (Bio-Rad).

Table 1. Genes used for the RT-PCR of littleneck clams (*Protothaca staminea).* Genes involved in immune response (*Toll-like receptor 1, TLR1)* and heat response (*Heat-shock protein, HSP70*; and *Von Willebrand factor type D domain, VWD)* as well as the housekeeping genes (*Actin 2;* and *Elongation Factor, EF)*. Amplification efficiency (Ea) is given for eachtarget gene.

Gene	Ea
TLR1	2.56
HSP70	2.60
VWD	2.30
Actin 2	2.21
Elongation Factor	1.95

Statistical Analyses

We took an information theoretic approach to determine the strength of evidence for the effect of each treatment on sediment temperature and clam gene expression. We selected model structures that best described our experimental design and *a priori* hypotheses based on previous research spanning ecological and ethnographic reports and Hul'q'umi'num knowledge. The error distributions for our models were chosen based on the distribution of the data and informed by Bolker (2007) and Dunn and Smyth (2005).

Beach Temperature Maps

We used general and generalized linear models to assess the fixed effects of beach status (clam garden or non-walled beach) and intertidal zone (low, middle, and high nested within site) on subsurface sediment maximum temperature, standard deviation of temperature, and number of hours temperature was above 15 °C. We used a Gaussian likelihood for maximum temperature as this variable is continuous and could be positive or negative, and a Tweedie likelihood and log link function for the standard deviation of temperature and the number of hours above 15 °C because these variables were positive only, and continuous data, where zero values are possible. Our models were constructed with the 'glmmTMB' package in R (Brooks *et al.*, 2017). We ran model diagnostics using the 'DHARMa' package in R to check model assumptions, test for over- and under-dispersion, homogeneity of variance, outliers, and verify the model fit (Hartig and Lohse, 2022). Note that the Levene test for homogeneity of variance was significant for the maximum temperature model, revealing that variances were not equal across the two beaches. The 'marginaleffects' package in R was used to summarize the model effects as predictions and comparisons with standard error (Arel-Bundock, 2023).

We used Empirical Bayesian Kriging Regression Prediction (EBKRP) to create interpolation maps and visualize how maximum temperature and the standard deviation of temperature varied across a clam garden and a non-walled beach. Using ArcGIS Pro™, we modeled the spatial autocorrelation of temperatures on the beaches with semivariogram models and interpolated the temperatures between the sampling locations to create a continuous map surface. We chose a Bayesian modeling approach to account for the error introduced by estimating the underlying semivariogram, increasing the accuracy of the standard errors of the prediction compared to other Kriging models (Pilz and Spöck, 2008; Krivoruchko and Gribov, 2019; Gribov and Krivoruchko, 2020; Kirvoruchko, 2021). Further, EBKRP is a frequently used and robust method to work with temperature data, especially when there are underlying trends through space (Gribov and Krivoruchko, 2020; Njoku *et al.*, 2023).

To account for the influence of tidal height on temperature, we used digital elevation models (DEM) of each site set to a resolution of 1 m^2 as a predictor in our model. The strength of the relationship between the DEMs and temperature metrics (as reported in the R^2 value) was used to set the influence of the DEM data for each model. We used the K-Bessel semivariogram model structure which can accommodate the broadest range of data sets with the greatest reliability (Johnston *et al.*, 2001). We increased the spatial resolution of the output map to match the high spatial variability of subsurface sediment temperature by limiting the sample locations used to inform the model estimate of a given cell to the nearest 7 – 10 locations (or up to 12 sample locations if they were all within 20 – 30 m of the cell).

Heatwave Experiment

We used general and generalized linear mixed effects models to assess the direct effects of beach status (clam garden or non-walled beach), heat (heated or unheated), and shell hash (enriched or not) on sediment temperature and the mediating effect of being on clam garden during a heatwave by including the interaction of beach status and heat. The model included the random effect of block nested within the site. We included a shell treatment in the experimental design because it was of interest to our collaborators and because we hypothesized the light colour of the shell may reduce the temperatures the clams experienced. We did not however, include interaction terms with shell and beach status and shell and heat in our model because we did not expect a significant effect of shell enrichment on sediment temperature. To see the model results with the full set of interactions, see Appendix G.

To test for the effects of beach status, heat, and shell addition on maximum sediment temperature at the surface, 5 cm, and 10 cm below the surface, we used a Gaussian likelihood because the data was continuous and could have positive or negative values. We used a gamma likelihood to model the number of hours above 18

°C as these data were continuous and positive only. At 10 cm below the surface, the Tweedie likelihood was chosen because data were continuous, positive, and could have zero values. Again, we used the ‘glmmTMB’ package in R to construct our models and used the ‘DHARMa’ package in R to verify the model assumptions, model fit, and to check the residuals (Brien and Brooks, 2021; Hartig and Lohse, 2022). The Levene test for homogeneity of variance was positive for the maximum temperature models at the surface and 5 cm depth, showing that the variances were not equal across the two beaches. All other model assumptions, however, were met. One outlier was removed from the surface data for the number of hours over 18 °C because it was over 5 standard deviations below the mean and likely reflective of a technical failure. We maintained 19 observations from the clam garden and 20 observations from the non-walled beach for this portion of the analysis. Two outliers were removed from the 5 cm and 10 cm data for the number of hours over 18 °C because they were 2 – 4 standard deviations below the mean, and were from the same block, likely indicative of spatial heterogeneity, i.e., a groundwater source. The removal of these two outliers did not affect the balance of the design as one was from a heatwave plot and the other from an ambient temperature plot, and we maintained 18 observations at the clam garden and 20 at the non-walled beach. The ‘marginaleffects’ package in R was used to summarize the model effects as predictions and comparisons with standard error (Arel-Bundock, 2023).

To evaluate the qRT-PCR data, we used the ‘MCMC.qpcr’ package in R (Matz, 2015) and followed the methods described by Matz, Wright, and Scott (2013). This Bayesian method uses a Markov Chain Monte Carlo algorithm to estimate the effects of all the experimental factors on the expression of each gene. The model has a single response variable, the transcript count. The transcript count’s rate is modeled on a log-linear scale using a generalized linear mixed model and a Poisson error distribution. This method is robust against the impacts of small sample size and noise introduced by low-abundance target genes (Matz, Wright and Scott, 2013). This Bayesian approach accounts for variability in the housekeeping genes, as the prior is set according to the gene’s stability. A value of 1 for gene stability would indicate that the genes are perfectly stable. We increased the value from the recommended 1.2 to 1.3 because we saw higher than normal coefficients of variation for the housekeeping genes (9.4% and 8.1% for *Actin 2* and *Elongation factor* respectively, Appendix A.1).

We constructed a model of transcription count based on our hypotheses of the system, such that ln(rate) ~ gene + gene:Heatwave + gene:Beach Status + gene:Heatwave: BeachStatus + gene:Shell + [gene:block] + [sample]. The random effect of the sample (clam) accounts for the variation in the quantity of cDNA amongst samples (Matz, Wright and Scott, 2013). The count data is presented as a fold change compared to a control, in this case, the non-walled beach unheated treatment, and without shell enrichment. Model convergence, fit, and homogeneity were verified, and met the model assumptions, although we did observe heteroscedasticity across the range of genes and treatments.

Assumptions and limitations

Sites designated as clam gardens or non-walled beaches differ in characteristics other than the presence of a rock wall and their slope. Although we aimed to control for wave exposure and aspect in our site selection, no two beaches are ever the same and may differ in temperature for reasons other than the presence or absence of a clam garden. For instance, performing the temperature surveys at sites most useful for the Nations leading the restoration activities meant selecting one site in the outer Gulf Islands (Winter Cove on Saturna Island), with a slightly greater tidal amplitude (4.2 m over 4 years) than Russell Island (3.8 m over 4 years) and somewhat different oceanographic influences. These factors may have also influenced sediment temperature on the beach. Another limitation is that our simulation of a heatwave was imperfect, as we did not increase water temperature, which did rise during the 2021 heatwave (Hilborn, Hannah and Lu, 2023). For this reason, our heatwave simulation should be considered conservative. Furthermore, it has not been confirmed that this *Heat shock protein 70* and *Von Willebrand type D domain* do in fact respond to heat in the littleneck clams. *Hsp 70* is commonly used to measure thermal stress in intertidal animals (Tomanek and Somero, 2000; Helmuth and Hofmann, 2001); however, verification of its role in littlenecks is suggested as some heat shock proteins are induced by other environmental factors including heavy metals, hypoxia, hyperoxia, and ultraviolet light (Hochachka and Somero, 2002; Fabbri, Valbonesi and Franzellitti, 2008) and, while *vwd* has been associated with heat stress in oyster, its role has not been confirmed in littleneck clams (Buckley and Rast, 2015; Prado-Alvarez et al., 2009).

Results

Beach Temperature Maps

As predicted, from May – June 2022 the clam garden sediment at 10 cm depth experienced lower and more stable maximum temperatures than the non-walled beach (Figures 3, 4 A & B, Appendix D.1 & D.2). On average, the maximum temperature was 4.5 °C ± 0.5 °C (SE) cooler on the clam garden than on the non-walled beach (Figure 3). Moreover, the maximum temperature varied less across the shallow sloped clam garden than across the steeper non-walled beach (1.4 °C ± 0.9 °C (SE) and 3.3°C ± 0.8 °C (SE), respectively, Figures 3, 4 A & B). The highest maximum temperatures were recorded at the top of the non-walled beach where tidal elevation was higher relative to the top of clam habitat on the clam garden (Figures 3, 4 B). Even on the lowest extent of intertidal clam habitat in the non-walled beach, temperature was on average 1.24 times warmer than across the entire clam garden. The clam garden had 81.5% more area within the optimal thermal range (12 – 18 °C) (Bernard, 1983) for clam growth than the non-walled beach, where the predicted maximum temperature exceeded this range on 95% of the beach surface (Figure 4 C & D).

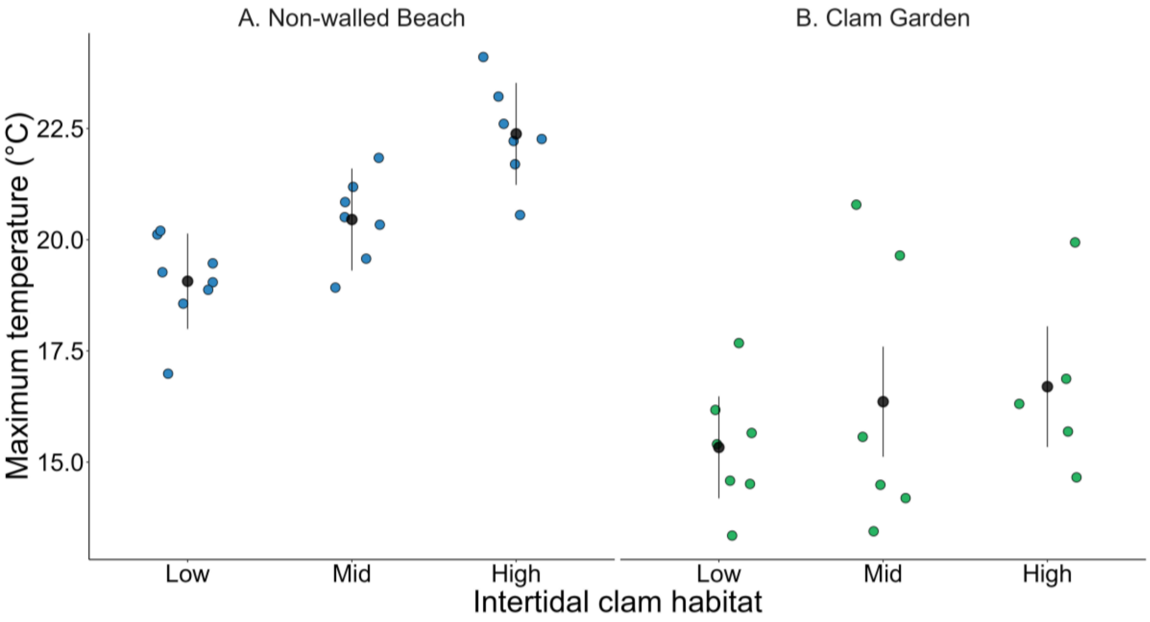

Figure 3. **Maximum temperature 10 cm below beach surface recorded across intertidal clam habitat within (A) a non-walled beach and (B) a clam garden from May 18 – June 18, 2022. Empirical temperatures are shown for the clam garden (green) and non-walled beach (blue). Model predictions and 95% confidence intervals in black.**

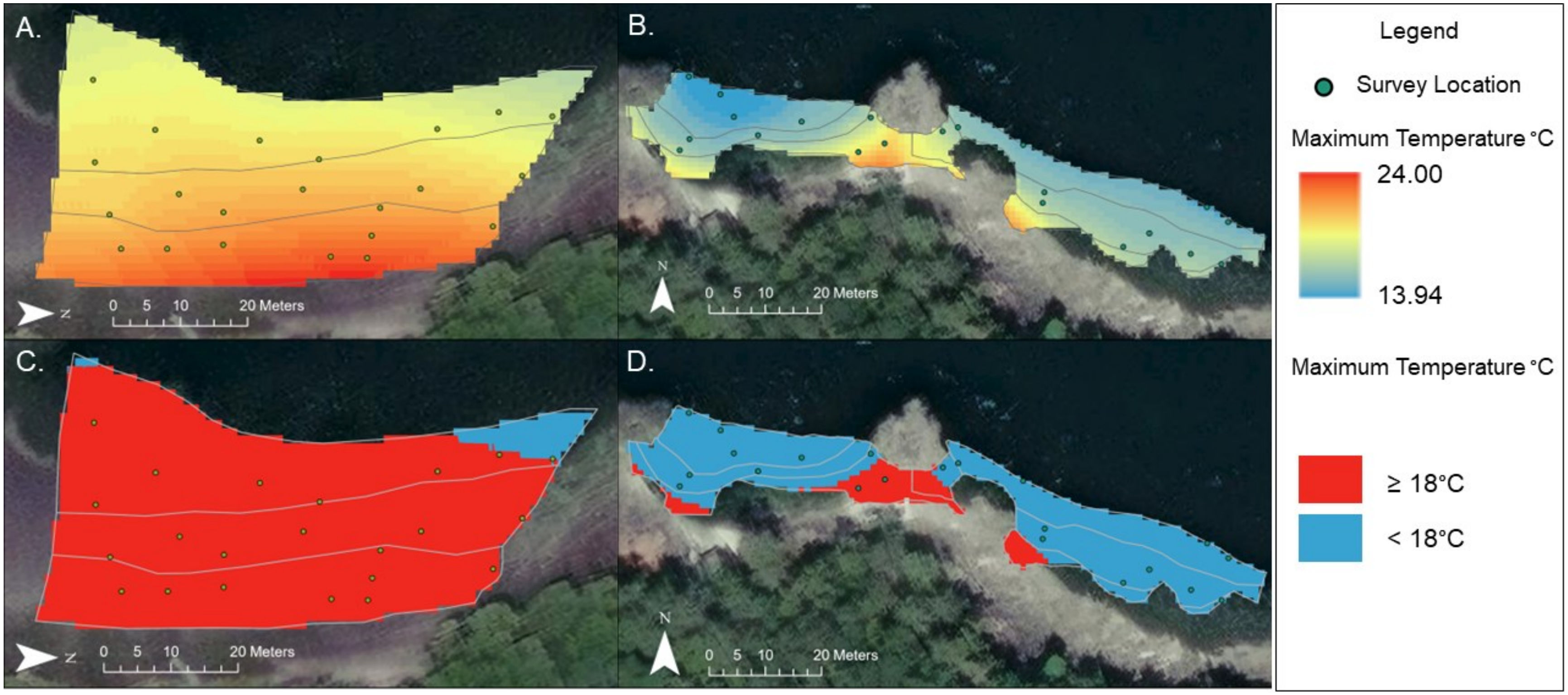

Figure 4. Predicted maximum temperatures in May and June 2022 , 10 cm below the beach surface at two sites; (A) a non-walled beach and (B) a clam garden in the Southern Gulf Islands, BC, Canada. Area where maximum predicted temperatures are ≥ 18 °C (red) and < 18 °C (blue) on (C) a non-walled beach and (D) a clam garden. The grey lines represent the spatial extent of clam habitat divided into low, mid, and high intertidal zones specific to each site.

Compared to the non-walled beach, clam habitat on the cooler clam garden spent on average 10.9 times fewer hours from May to June 2022 at temperatures over 15 °C, the temperature threshold that favors the growth of bacterial pathogen *V. parahaemolyticus,* (37.2 ± 3.45 (SE), and 3.4 ± 0.86 (SE) hours respectively, Figure 5). At the top of clam habitat, the non-walled beach spent on average 13.05 times more time above this thermal threshold than the clam garden.

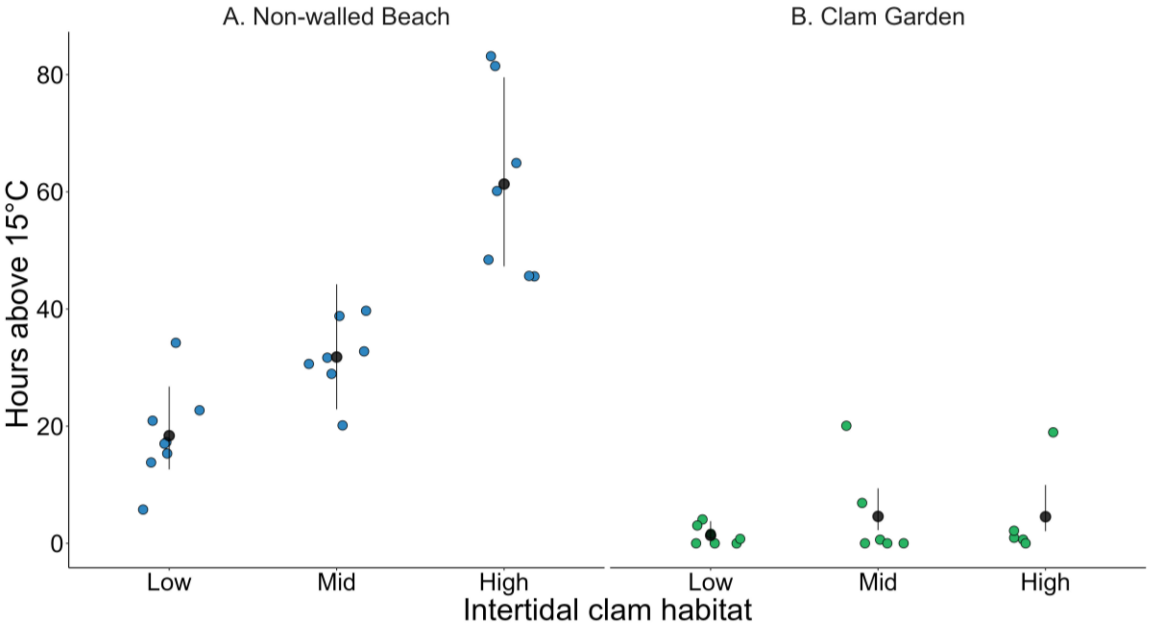

Figure 5. **Hours beach temperature at 10 cm depth was over 15 °C across intertidal clam habitat within (A) a non-walled beach and (B) a clam garden from May 18 – June 18, 2022. Empirical temperatures are shown for the clam garden (green) and non-walled beach (blue). Model predictions and 95% confidence intervals in black.**

Heatwave simulation

Maximum temperatures

The simulated heatwave increased maximum sediment temperatures at all depths and had the greatest magnitude of effect at the beach surface (Figure 6, Appendix E.1). Heated plots increased the average maximum beach surface temperature from 32.9 °C ± 1.16 °C (SE) to 48.2 °C ± 1.23 °C (SE), an increase of 15.22 °C ± 1.9 °C (SE) (Figure 6 A & B). At 5 cm below the surface, the clam garden was cooler than the non-walled beach, both in the unheated and heated plots. In the absence of a simulated head wave, the clam garden had a direct cooling effect on subsurface temperatures at 5 cm depth where sediments were ~1.18 times cooler than non-walled beaches (Figure 6 D, F). During a heat wave, the effect of the clam garden led to additional cooling at 5 cm depth. In the presence of a heatwave, the clam garden was on average 1.24 times lower (5.4 °C cooler) than non-walled beach, although both beaches warmed. Further, at 5 cm depth, the heatwave increased maximum temperatures on the non-walled beach by an average of 4.71 °C ± 0.81 °C (SE), while the temperatures on the clam garden only rose by an average of 2.88 °C ± 0.81 °C (SE) (Figure 6 C & D). We did not detect a clam garden effect at the beach surface, whether plots were heated or not. At the surface, shell addition had a slight cooling effect of 3.33 °C ± 1.90 °C (SE), although this effect was imprecise (Figure 6 A & B). The effect of the shell was minimal at 5 and 10 cm depth, although trending to be cooler (Figure 6 C & D, Appendix E.1).

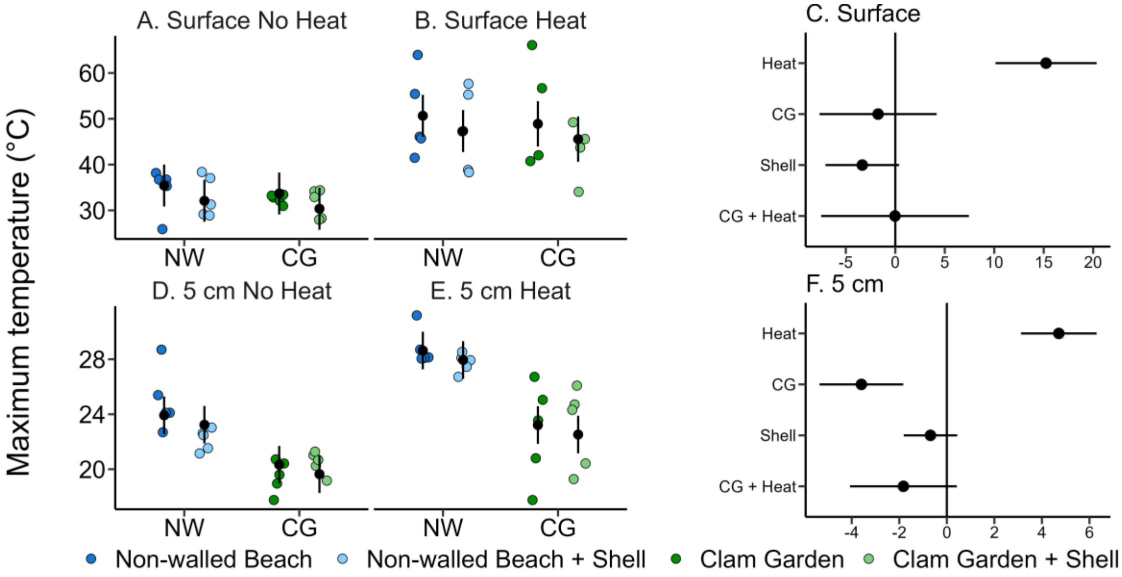

Figure 6. **Maximum beach temperature recorded at surface (top) in (A) no heat and (B) heat treatments, with (C) model coefficients, and at 5 cm depth (bottom) in (D) no heat and (E) heat treatments, with (F) model coefficients. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.**

Hours above optimal temperatures for clam growth

Despite the same duration of the heatwave simulation, clam garden plots stayed cooler for longer, spending less time above 18 °C over the five-day period than the non-walled beach (Figure 7, Appendix F.1). The strongest magnitude of the clam garden effect was observed at 10 cm below the sediment, where on average clam garden plots spent ~1.52 fewer hours above the thermal threshold than the non-walled beach (Figure 7 C & D). When averaged across both beach types, we did not detect a strong effect of the heat treatment on the number of hours above 18 °C at any depth (Figure 7 B & D, Appendix F.1). However, when looking at the effect of the heatwave simulation on the clam garden, we saw that at 5 and 10 cm depths, the heatwave treatment extended the length of time temperatures were greater than 18 °C (Figure 7 C & D, Appendix F.1). Yet, even in the presence of heat, the clam garden still spent 1.16- and 1.26-times fewer hours above the 18 °C thermal threshold at 5 cm and 10 cm depth respectively (Figure 7 C, Appendix F.1).

The shell treatment did not have a strong effect on the hours above 18 °C at the surface, although it trended towards fewer hours spent above 18 °C (Figure 7 B). Contrary to our predictions, the magnitude of the effect of the shell increased with depth, and at 10 cm depth, shell plots spent 3.49 ± 1.69 (SE) fewer hours above the thermal threshold compared to plots that were not enriched with shell (Figure 7 C & D).

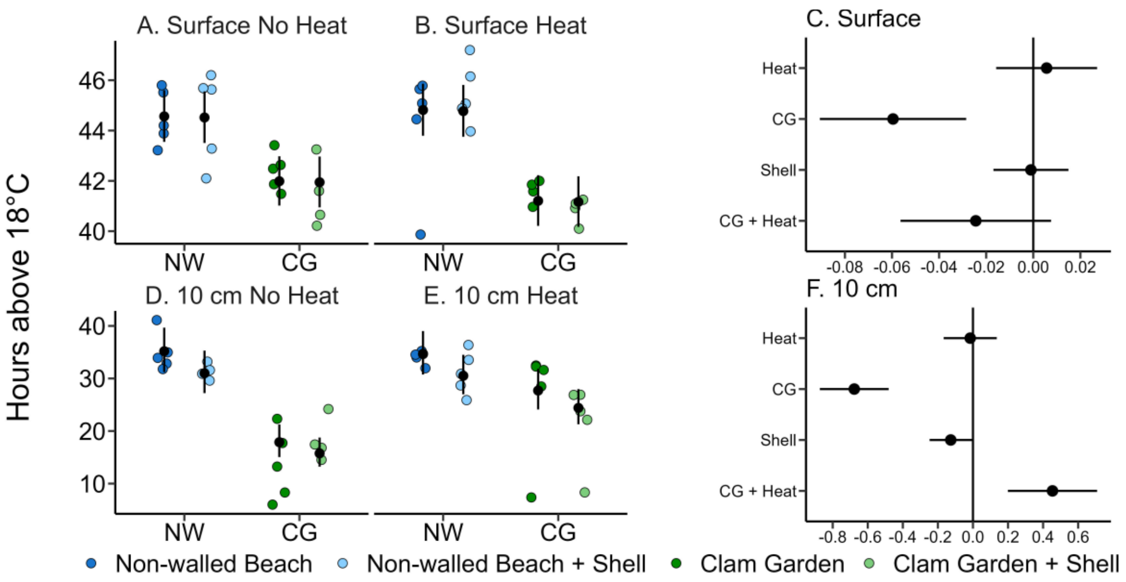

Figure 7. Hours beach temperature was above 18 °C at surface (top) in (A) no heat and (B) heat treatments, with (C) model coefficients, and at 10 cm depth (bottom) in (D) no heat and (E) heat treatments, with (F) model coefficients. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.

Clam Ecophysiology

Littleneck clams from unheated clam garden plots had a ~11-fold downregulation of *toll-like receptor 1 (tlr1)* compared to unheated clams in non-walled beaches where no sediment was manipulated (Figure 8 A). When heat was added to the non-walled beach, there was a 1.6-fold upregulation of the *tlr1* gene (Figure 8 B). When the heat was added to the clam garden, there was an ~11-fold upregulation of *tlr1,* increasing the mean response to similar values of the unheated non-walled beach with no sediment manipulation (Figure 8 B). Furthermore, there is increased variability in *tlr1* gene expression on clams in a clam garden (Figure 8 B). We observed that across all treatments, shell hash additions tended to show a downregulation of the *tlr1*; however, their credible intervals overlapped with the plots where sediments were not manipulated suggesting a weak effect of shell on the expression of *tlr1* (Figure 8 A & B).

Expression of the heat response genes (*Von Willebrand factor type D domain (vwd)* and *heat-shock protein (hsp) 70)* in littleneck clams from the cool clam garden was similar to, albeit more variable than the control group (a ~ 1.5-fold downregulation and ~1.5-fold upregulation respectively) (Figure 8 A & B). In the absence of heat, the shell treatment had no strong effect on littleneck gene expression at either site (a 0.2- and -0.2-fold change in *vwd*, and -0.4- and -1.3-fold change in *hsp* at the clam garden and non-walled beach respectively). On the non-walled beach, where we added heat and clams were hotter for longer, their expression of *vwd* and *hsp* was upregulated by ~ 0.5-, 1.2-fold respectively (Figure 8 B). When the clams in the clam garden were heated, their expression of *vwd* and *hsp* was more variable than the controls, although with similar means (Figure 8 B). Again, in the heated plots, there was no strong effect of shell on littleneck clam gene expression, with similar means to the plots with unmodified sediments.

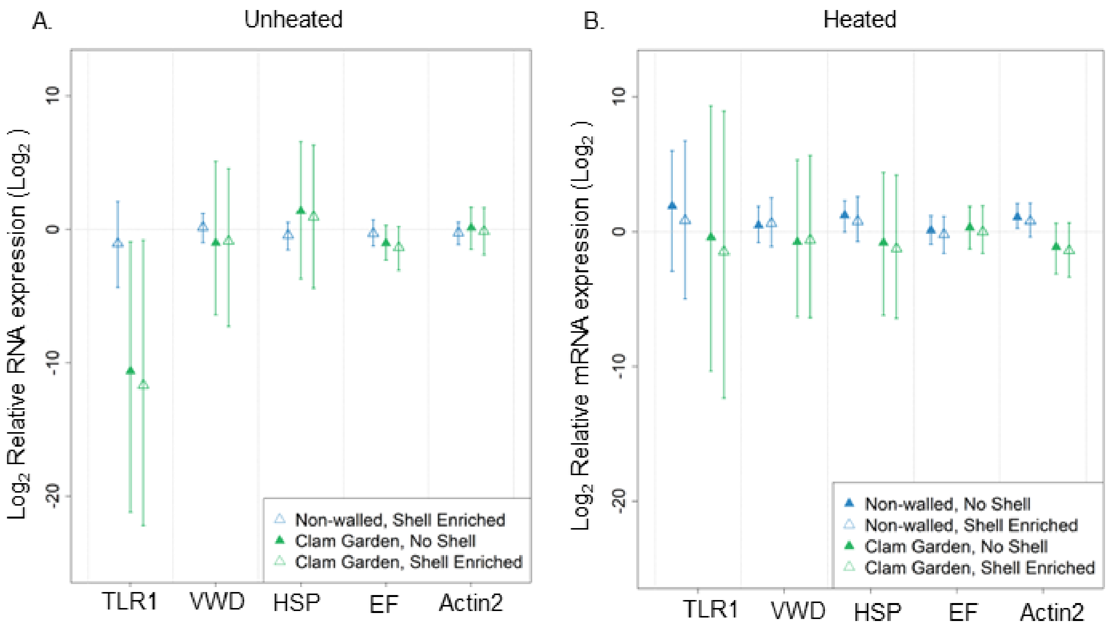

Figure 8. **Relative expression of target gene to control (i.e. the non-walled beach unheated and no shell enrichment) in littleneck clams. Effects of being on a non-walled beach (blue), a clam garden (green), and in shell hash (open triangles) in (A) ambient conditions (B) and in a simulated heatwave. The points are posterior means, and the lines represent 95% credible intervals. The genes include immune response (toll-like receptor 1, tlr1), heat response (Von Willebrand Doman type D,VWD; and Heat shock protein 70, HSP) and housekeeping genes (Elongation factor, EF; and Actin 2).**

Discussion

As climactic disturbances threaten global food security, opportunities for climate solutions involve learning from, engaging with, and shifting power to Indigenous Nations who have a long history of adapting their food systems in the face of extreme climatic events. Here, we show that clam gardens, a recently revitalized Indigenous maricultural innovation, can buffer the impacts of heatwaves on clams. In ambient conditions, a clam garden experienced lower temperatures in the summer, maintaining more optimal temperatures for clam growth (Figures 3 & 4). During an experimentally imposed heatwave, we found that a clam garden reduced the magnitude and duration of extremely high temperatures experienced by clams (Figures 6 & 7). By keeping sediments cooler, clams in the unheated clam garden exhibited less of an immune response to bacterial infection (Figure 8), suggesting that under ambient conditions, clam gardens can buffer bacterial loads in clams, infections of which can cause mass mortality events in shellfish and public health concerns. Finally, we found little evidence to suggest that adult clams experienced heat stress during our experiment (Figure 8), demonstrating their resilience to heatwaves. Although the magnitude of these cooling effects may vary across clam gardens, our results are generalizable given the consistency by which multiple clam gardens within multiple regions of the Northeastern Pacific coast effect intertidal slope, sea water flow, and sediment temperature (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016; Salter, 2018). Overall, our findings provide evidence that clam garden revitalization is a solution to food sovereignty concerns in light of increasing heatwaves, and highlights the essential role of Indigenous science, knowledge holders, and stewards in ocean policy and governance today.

Clam garden resilience to heatwaves

The clam garden was most effective at buffering the maximum temperature of the simulated heatwave at 5 cm depth (Figure 6 D, E & F). While the beach surface of both sites reached nearly 50 °C under the heatwave simulation, matching temperatures recorded during the 2021 heatwave in British Columbia (White *et al.*, 2023), at 5 cm below the surface, clam garden sediment was 1.23 times cooler than the non-walled beach (Figure 6 E), due to increased seawater retention of the clam terrace. Recently recruited juvenile clams live in the top few centimeters of beach sediments where they are exposed to extreme air temperatures, making them vulnerable to heat-induced mortality (Dethier *et al.*, 2019). Post-settlement mortality is common in juvenile clams and can profoundly influence population dynamics (Keough and Downes, 1982; Hunt and Scheibling, 1997; Munroe, 2016). Our findings suggest that clam gardens, by buffering temperatures in juvenile clam habitat, may reduce the thermal stress experienced by clams and improve their growth and survival at this critical life stage, potentially explaining why Jackey et al. (2016) observed higher survival of juvenile clams (0.5 – 2mm) on clam gardens.

Our results demonstrate that being in a clam garden alters the ecophysiology of clams (Figure 8). This is consistent with a study by Raap *et al.* (2022) who found lower levels of heat stress genes, *Heat shock protein 70 (hsp),* and *Von Willebrand factor type D domain (vwd),* in clams from clam gardens compared to nonwalled beaches, both under typical summer air temperatures. Unlike that study, we observed similar albeit more variable levels of *hsp* and *vwd* between adult clams from the clam garden and the non-walled beach both with and without our heat wave simulation (Figure 8). The discrepancies in our findings are likely because we studied transplanted adult clams exposed to differential thermal conditions over 5 days whilst Raap et al. (2022) studied locally recruited juveniles that had experienced site-specific thermal conditions over their lifetimes. Compared to adult clams, juvenile clams are likely to experience more thermal stress living near the sediment surface (Dethier *et al.*, 2019). Further, they may have lower levels of heat stress in a clam garden as indicated by our temperature findings. The production of heat shock proteins is energetically costly, and over repeated thermal stress, energy reserves may become diminished in an individual clam, leading to reduced growth rates (Brownlee 2022; Li et al. 2007; Wendling and Wegner 2013). The lower levels of heat stress observed by Raap et al. (2022) and our findings, may provide a mechanism explaining why juvenile clams grow faster in clam gardens (Groesbeck *et al.*, 2014).

Although we predicted that clams would have an upregulation of *hsp* and *vwd* during the heatwave simulation caused by thermal stress, we found little evidence in support of this hypothesis (Figure 8), likely because adult clams, being buried deep (12 cm) in sediment, were buffered from high surface temperatures and desiccation stress, only experiencing temperatures a few degrees above normal. These results are supported by a previous study showing that razor clams buried at 15 cm depth are able to withstand temperatures of 10 – 15 °C above normal (Zhang, Storey and Dong, 2020). Because they do not live close to their thermal limits, clams likely have a broad thermal range over which they can have adaptive responses (such as the heat stress response) to rising temperatures, meaning they are expected to be less affected by climate change than other bivalves in the high intertidal living close to their thermal maximum (Tomanek, 2010). Further evidence modeling future fisheries projections given the Intergovernmental Panel on Climate Change scenarios shows that clams are expected to be some of the most resilient marine fisheries on the Pacific Northwest Coast (Weatherdon *et al.*, 2016). Our findings further suggest that clam gardens act as a climate solution, by cultivating species that are resilient to warming temperatures.

Our data are unique in demonstrating that a clam garden, by keeping sediments cool under ambient conditions, reduced the genetic response of clams to bacterial pathogens by 11-fold compared to the non-walled beach as measured by the expression of the *toll-like receptor 1 (tlr1)* gene (Figure 8A). Meanwhile, under the simulated heatwave, the clam garden exhibited similar levels of *tlr1* to the non-walled beach (Figure 8B), suggesting that during the heatwave, temperatures on the heated clam garden rose to levels that encouraged bacterial growth that the clams responded to.*Tlr1* are pattern recognition receptors that help immune cells recognize pathogens, including the bacteria *Vibrio parahaemolyticus* known to cause the mass mortality of shellfish and public health concerns (Go *et al.*, 2017; Green *et al.*, 2019; Ndraha, Wong and Hsiao, 2020). Warming waters improve the growth of bacterial pathogens, with the growth of *V. parahaemolyticus* favored at temperatures over 15 °C, and optimal at 35-37 °C (Ndraha, Wong and Hsiao, 2020). Our survey data show that a clam garden spent 13 times less time over this thermal threshold for *V. parahaemolyticus* growth (Figure 5), suggesting that a reduction in subsurface sediment temperatures is the mechanism by which clams on clam gardens have reduced bacterial infection. Another non-mutually exclusive hypothesis is that clams, by experiencing fewer physiological stressors in the clam gardens (Raap *et al.*, 2022; Cruz Coto *et al.*, 2023), are healthier and better able to fight bacterial infection than clams on non-walled beaches. In either case, our findings suggest there are positive health implications to eating clams from a clam garden, and we suggest future studies investigate the bacterial communities and loads varying between clam gardens and non-walled beaches.

Temperature surveys revealed that a clam garden was cooler during the summer (Figures 3 & 4) and had 81% more area within the optimal thermal range for native butter and littleneck clams than a non-walled beach (Figure 4 C & D). Clams need stable temperatures to grow, and temperatures between 12 – 18 °C are preferred for the growth of littleneck and butter clams (Bernard, 1983), influencing their distribution in the intertidal zone. By altering beach slope and creating a terrace at the optimal intertidal height for native clams to grow, clam gardens extend the area of optimal clam habitat and enhance growing conditions (Groesbeck *et al.*, 2014; Salter, 2018), including extending the area of optimal temperatures as illustrated in our findings. We observed that the maximum temperature of the beach mirrors the slope of the beaches, with temperatures on the flatter clam garden being more stable and lower across the extent of clam habitat, while temperatures were hotter and at higher tidal elevations on the steeper non-walled beach (Figure 3). The patterns we observed are consistent with a study from replicate clam gardens and non-walled beaches surveyed just north of our study area on Quadra Island, Canada which found that the moderated temperatures on a clam garden drove higher biomass, densities, and growth rates of clams, potentially due to decreased heat stress (Salter, 2018). Further, by extending the habitat within the optimal growth conditions for the native harvestable clams, clam gardens may reduce the likelihood of invasions from the more thermally tolerant varnish clam (Siegrist, 2010) and thus maintain populations of culturally important species into the warming future.

Experimental evidence suggests that enriching beach sediments with crushed shells may buffer the duration of extreme temperatures during heatwaves, with the greatest effect observed at 10 cm below the sediments (Figure 7 F). By creating more interstitial space, the crushed shells likely increased the flow of water through the sediments (Thompson, 1995), cooling subsurface sediments given the high heat capacity of seawater. Returning shells to the beach is an Indigenous management practice (Lepofsky *et al.*, 2015; H-GINPR, 2016; Olsen, 2019) widely recognized to benefit clams by providing structure for settling larvae, calcium carbonate for shell growth, protection from predators, and increased water flow (Thompson, 1995; Green *et al.*, 2013; Waldbusser *et al.*, 2015; H-GINPR, 2016; Greiner *et al.*, 2018; Salter, 2018; Olsen, 2019). As illustrated by our findings, this management practice also facilitates cooler summertime subsurface sediment temperatures. Shell hash additions have the potential to buffer multiple climactic stressors (Greiner *et al.*, 2018; Doyle and Bendell, 2022), including extreme temperatures. Our findings reinforce the knowledge engrained in Indigenous management practices and the important role that the revitalization of these practices is playing in cultivating resilient food systems.

Climate change, food systems, and Indigenous food sovereignty

Our results suggest that clam gardens can be resilient to the impacts of extreme heat events. By maintaining cool sediment temperatures during periods of extremely hot ambient air temperature, clam gardens are more likely to maintain productive populations of native clams as our climate warms compared with unmodified clam beaches. Further, by reducing bacterial growth inside clams, clam gardens may reduce the incidence of disease, therefore increasing opportunities for safe harvest. Both mechanisms promote food security and food sovereignty. These findings are particularly important to the food sovereignty of the Indigenous Nations whose ancestors built these structures. The revitalization of clam gardens through the transmission of knowledge surrounding these stewardship and harvest practices is reconciling the relationships between people, the ocean, and with non-human kin, improving equity in ocean spaces. Through acts of resurgence, many Indigenous Nations are revitalizing their ancestral food and governance systems, innovating climate solutions that support productive populations of foods (Corntassel and Hardbarger, 2019; Joseph and Turner, 2020; Settee and Shukla, 2020).

Extreme weather events caused by climate change are expected to exacerbate food insecurities, perpetuating food injustices (Zeuli *et al.*, 2018; Settee and Shukla, 2020). Currently, there is a lack of attention to and acknowledgment of traditional and wild foods in food system planning (Soma *et al.*, 2022), undermining Indigenous food justice. Further, access to these culturally important foods is strongly affected by governance systems (Bennett *et al.*, 2018; Settee and Shukla, 2020). There is a need to ensure diversity in the representation of voices, perspectives, and leadership in food system planning and climate adaptation strategies (Sbicca, 2012; Soma *et al.*, 2022). Fortunately, there are current opportunities to improve equity in food systems whilst resources are being directed toward food system transformations to improve resilience to climactic disturbance (Mehrabi *et al.*, 2022).

We showcase that Indigenous Nations are well-positioned to develop locally relevant climate solutions. Opportunities to move forward with these equitable and practical climate solutions include adopting governance approaches that shift power to Indigenous stewardship. Current colonial institutions can support Indigenous stewardship by facilitating access to land and territory, providing funding, and adopting pluralism in worldviews, governance, and legal systems (Norgaard, 1989; Corntassel, 2012, 2018; Armitage *et al.*, 2019; M'sɨt No'kmaq *et al.*, 2021; Salomon *et al.*, 2023). In light of rapid climate change and growing inequity in ocean governance (Spalding *et al.*, 2023), now is the time to leverage both contemporary and Indigenous governance and ways of knowing to find equitable solutions to maintain food sovereignty and ocean health in the future.

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Appendix A.

Stability of housekeeping genes for qPCR

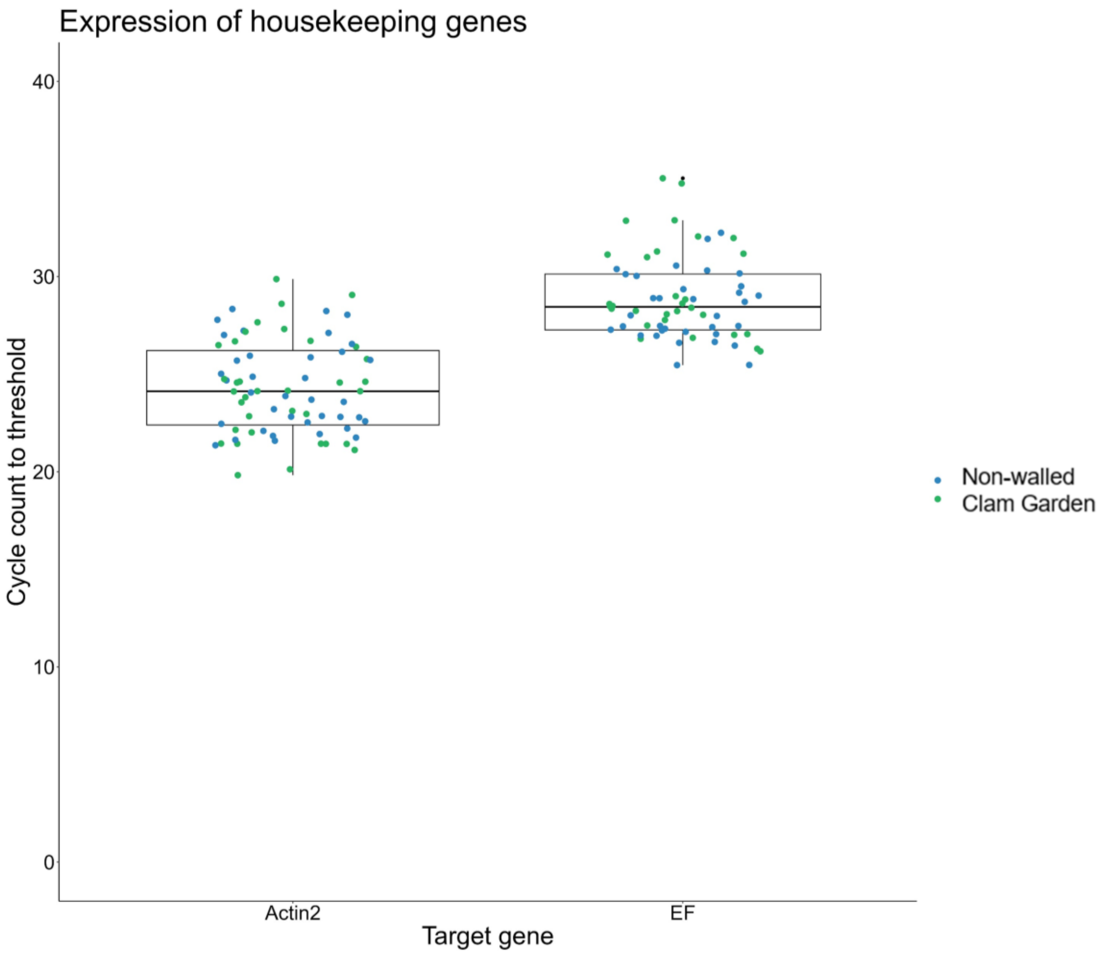

Figure A.1. **Expression of housekeeping genes Actin 2 and Elongation Factor (EF) in littleneck clams on a non-walled beach (blue) and a clam garden (green).**

Appendix B.

Minimum temperature of beach temperature survey

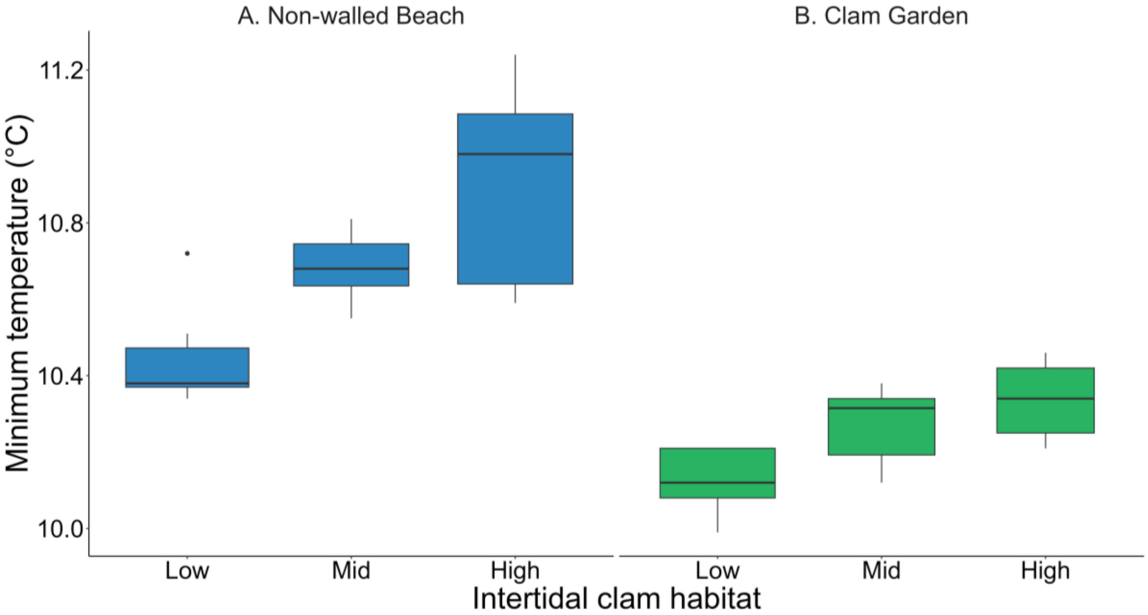

Figure B.1. Minimum temperature 10 cm below beach surface recorded across intertidal clam habitat within (A) a non-walled beach and (B) aclam garden from May 18 – June 18, 2022.

Appendix C.

Error estimate from maximum temperature map

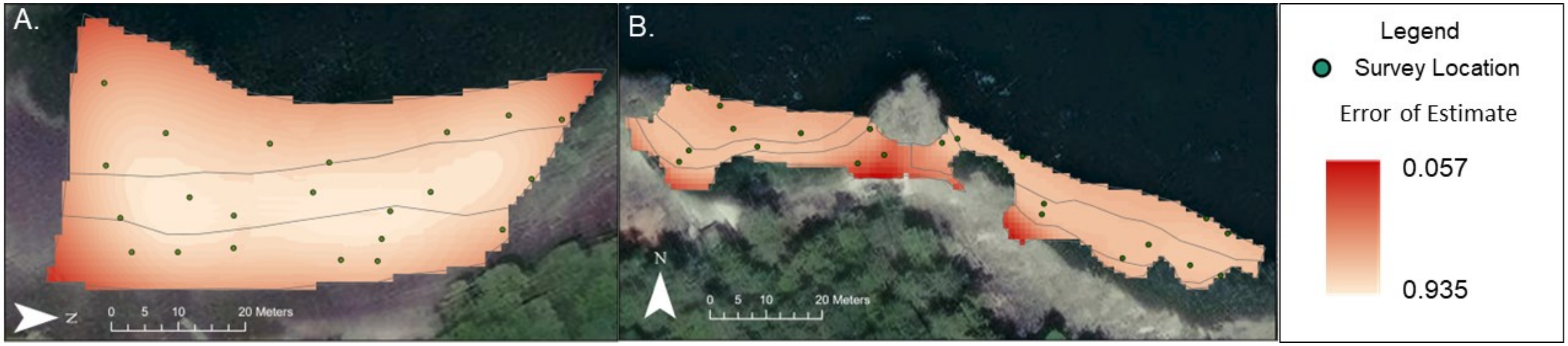

Figure C.1. Error of predicted maximum temperature estimates 10cm below beach surface at two sites in May and June 2022 at (A) a non-walled beach and (B) a clam garden in the Southern Gulf Islands, BC, Canada. The grey lines represent the spatial extent of clam habitat divided into low, mid, and high intertidal zones specific to each site.

Appendix D.

Standard deviation of beach temperature survey

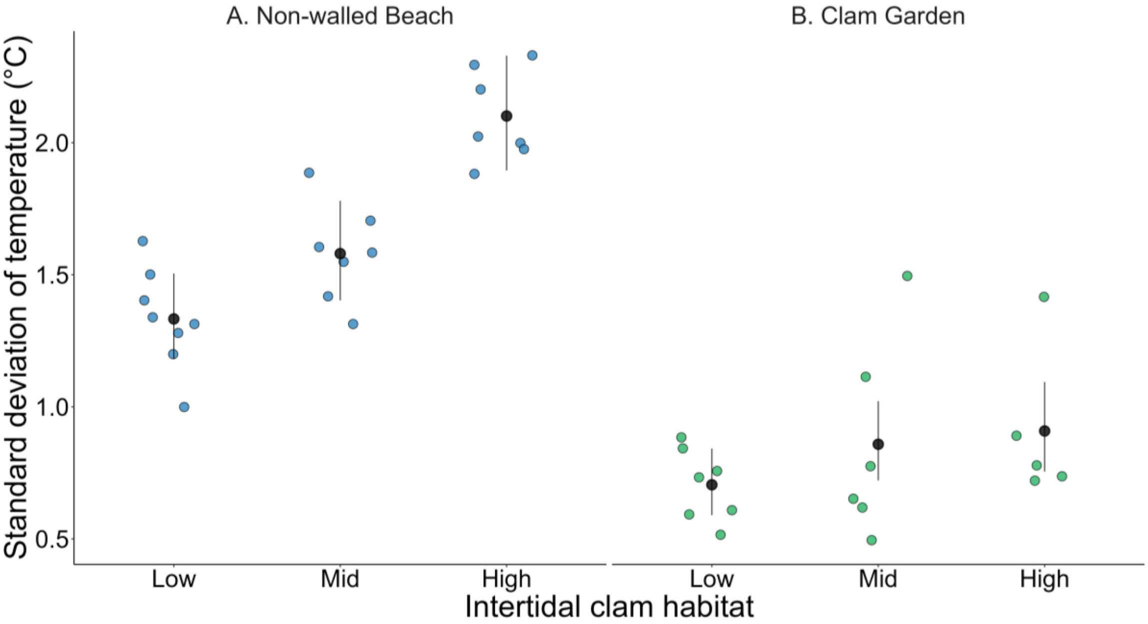

Figure D.1. Standard deviation of temperature 10 cm below beach surface recorded across intertidal clam habitat within (A) a non-walled beach and (B) a clam garden from May 18 – June 18, 2022. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.

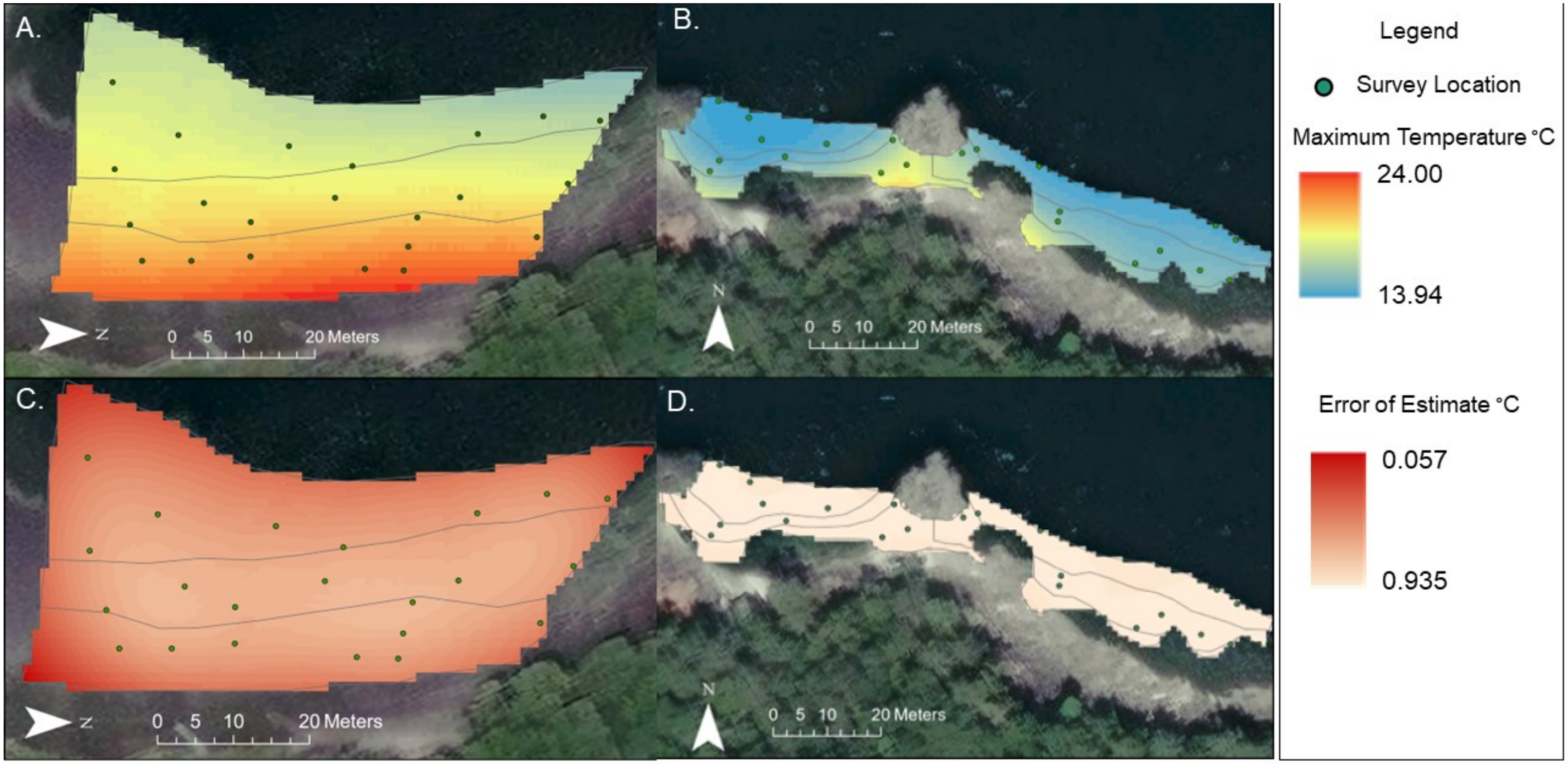

Figure D.2. Predicted standard deviation of temperatures 10cm below beach surface at two sites in May and June 2022 at (A) a non-walled beach and (B) a clam garden in the Southern Gulf Islands, BC, Canada. Error of prediction estimate on (C) a non-walled beach and (D) a clam garden. The grey lines represent the spatial extent of clam habitat divided into low, mid, and high intertidal zones specific to each site.

Appendix E.

Maximum temperature recorded at 10cm depth during experiment

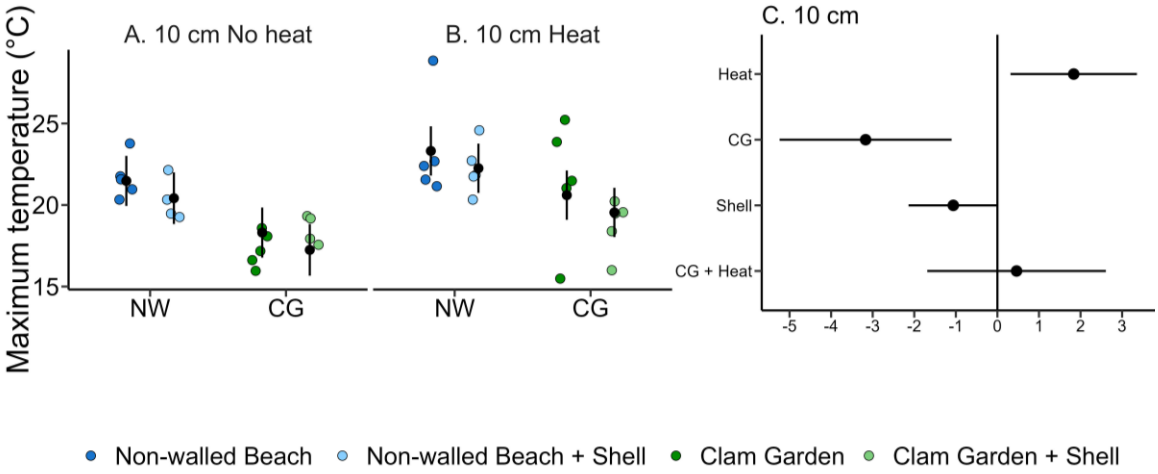

Figure E.1. **Maximum beach temperature recorded at 10cm depth in (A) no heat and (B) heat treatment with (C) model coefficients for the effect of each treatment. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.**

Appendix F.

Hours above 18°C recorded at 5cm depth during experiment

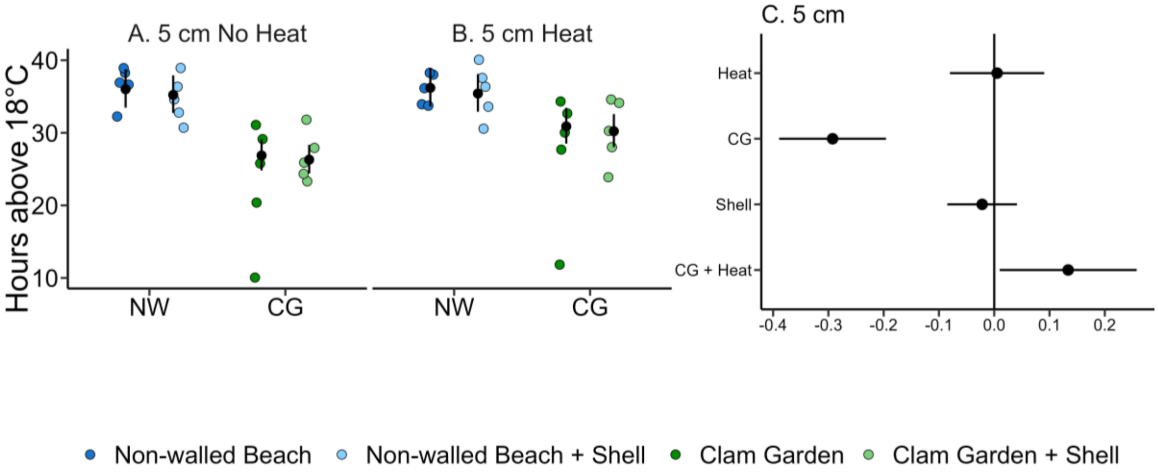

Figure F.1. Hours temperature was above 18°C at 5 cm depth in (A) no heat and (B) heat treatment with (C) model coefficients for the effect of each treatment. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.

Appendix G.

Experimental temperature data modeled with full interaction term

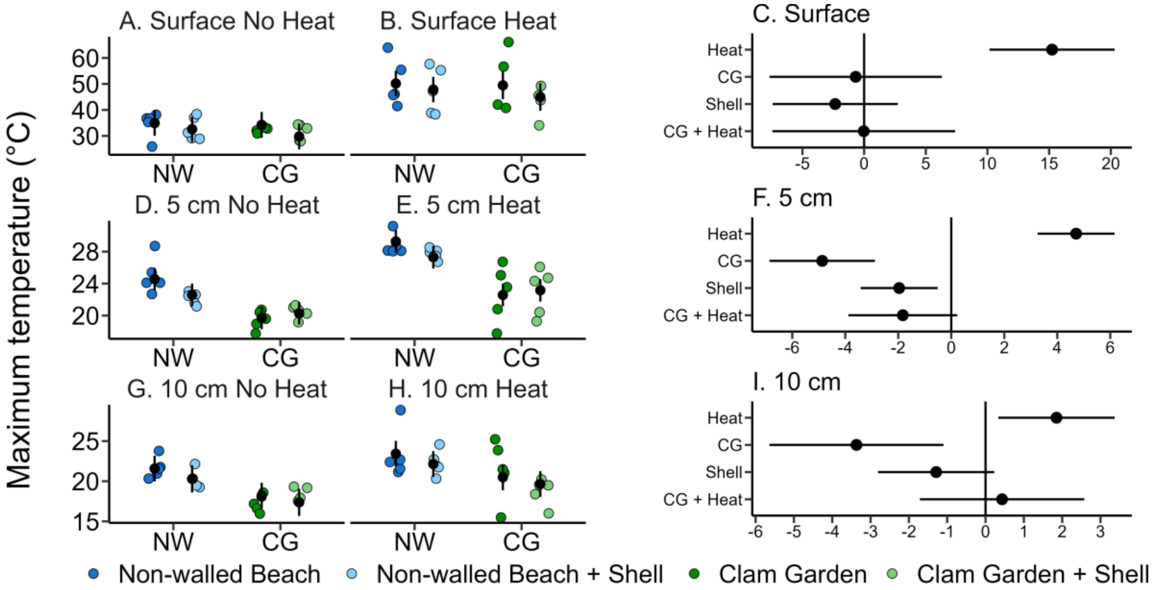

Figure G.1. **Maximum beach temperature recorded at surface (top) in (A) no heat and (B) heat treatments with (C) model coefficients, at 5 cm depth (middle) with (D) no heat and (E) heat treatments with (F) model coefficients, and at 10 cm depth (bottom) in (G) no heat and (H) heat treatments, with (I) model coefficients. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.**

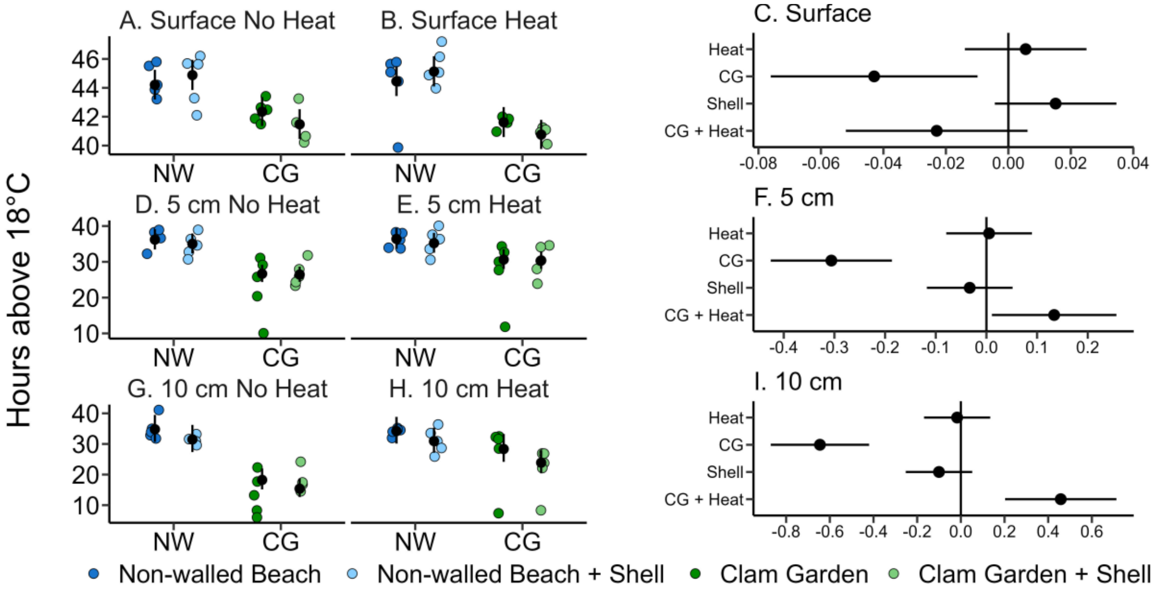

Figure G.2. **Hours beach temperature was over 18°C at surface (top) in (A) no heat and (B) heat treatments with (C) model coefficients, at 5 cm depth (middle) with (D) no heat and (E) heat treatments with (F) model coefficients, and at 10 cm depth (bottom) in (G) no heat and (H) heat treatments, with (I) model coefficients. Empirical temperatures are shown for the non-walled beach (blue) and clam garden (green). Model predictions and 95% confidence intervals in black.**