Testing the generality of the temperature-size rule in space and time: a case study using intertidal snails

Robin Elahi

August 11, 2016

Introduction

In this study we used a comparative-historical approach to test the hypothesis that reductions in body size, consistent with climate warming, have occurred over a period of 5–7 decades. Moreover, we examined the consistency of change across a suite of species that span a range of environmental variability. Specifically, we examine changes in the size-frequency distributions of three gastropods inhabiting a gradient of thermal stress in the rocky intertidal between 1947-1963 and 2014-2015.

Methods

To test the hypothesis that consistent shifts in animal body size occurred over decadal time-scales, we studied three species of intertidal gastropods (*Chlorostoma funebralis*, *Lottia digitalis*, *Littorina keenae*) at Hopkins Marine Station, Pacific Grove, CA, USA. We chose these species because (1) historical size-frequency data were available, (2) they comprise a single phylogenetic and functional group (grazing gastropods), and (3) the benthic intertidal community at Hopkins Marine Station has exhibited a fingerprint of change consistent with climate warming [@Barry1995]. Moreover, these three species span a gradient of thermal stress in the rocky intertidal zone, permitting a preliminary investigation of the hypothesis that environmental variability influences temperature-size shifts [@Gardner2011]. We quantified the thermal variability experienced by each species in the sampling areas using a short-term (8 weeks) deployment of temperature loggers. The historical shifts in body size were interpreted in the context of long-term (50 years) environmental records.

Predictions

1. Snail size is inversely related to temperature. That is, I expect size declines over time, assuming sea and/or air temperatures have increased during same period [@Barry1995]. Expect opposite pattern if temperatures have decreased, or no pattern if temperatures have not changed.

   a. Prediction: snails are smaller now than 50 years ago
   b. Test: Size ~ Era

2. Change in snail size is mediated by tidal height. Climate warming is expected to be manifested as increases in temperature variability, as well as increases in mean temperature. Temperature variability typically increases with tidal height.

   a. Prediction: An increase in extreme temperatures in the higher intertidal selects for larger individuals because larger snails are less susceptible to dessication mortality [@Gardner2011]
   b. Alternative: Temporal reductions in body size are largest in the high intertidal (e.g., due to metabolic effects without a compensatory increase in consumption)
   c. Test 1: Size ~ Era x Species x Tidal height
   d. Test 2: Temperature ~ Species x Tidal height (tests the assumption that temperature increases with tidal height, and that this response is consistent across species)

Results (outline)

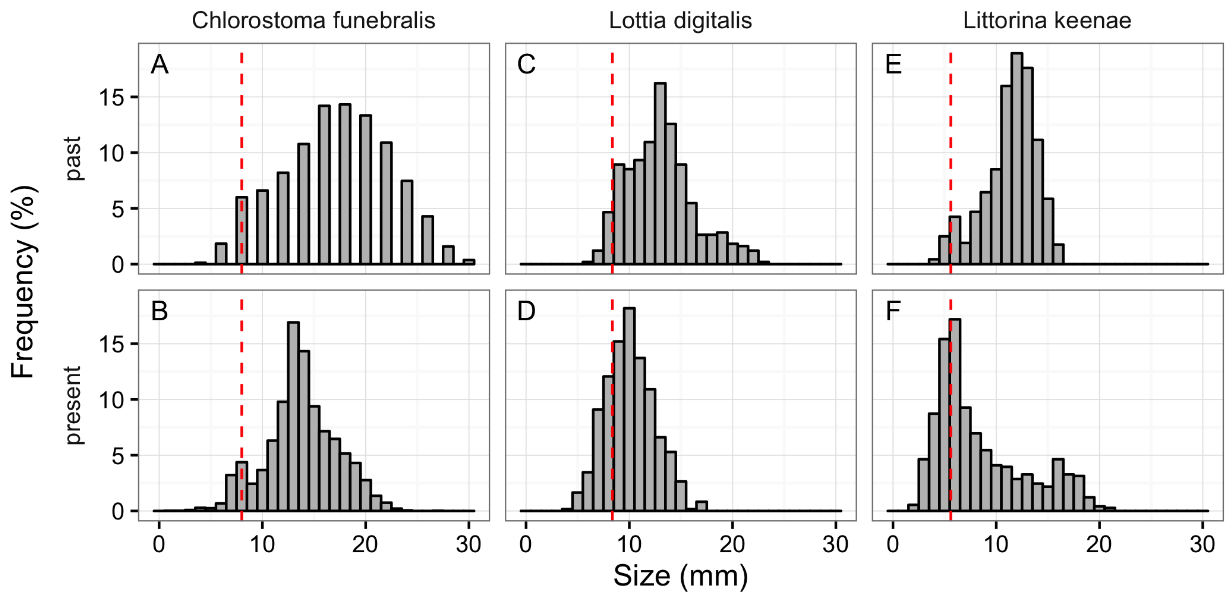

Figure 1: Figure 1. Size frequency distributions of three intertidal snails. The dashed red line indicates the 5th percentile of size for each species in the past. Only snails larger than this threshold were included for all statistical tests and summary calculations. I did this to ensure a conservative test of declining body size; that is, it is possible that the previous investigators sampled the smallest individuals less carefully than we did.

We used a linear mixed-effects model (nlme package) to test the hypothesis that snail size frequency distributions differed between era (past vs present), and that this variation was mediated by tidal height. We treated sampling areas as random intercepts in the model.

Table 1: Table 1. Model selection results for linear mixed effects models testing the fixed effects of era, species, and tidal height on snail body size

Modnames	K	AIC	Delta_AIC	ModelLik	AICWt	LL	Cum.Wt
Era x Species x Tidal height	14	40542.24	0.000	1.000	0.976	-20257.12	0.976
All three 2-way intx	12	40549.62	7.385	0.025	0.024	-20262.81	1.000
Era x Tidal height	6	40571.42	29.176	0.000	0.000	-20279.71	1.000
Era x Species	8	40636.81	94.572	0.000	0.000	-20310.41	1.000
Era	4	40779.64	237.400	0.000	0.000	-20385.82	1.000
Species x Tidal height	8	41607.89	1065.652	0.000	0.000	-20795.95	1.000
Species	5	41621.05	1078.808	0.000	0.000	-20805.52	1.000
Null model	3	41627.09	1084.847	0.000	0.000	-20810.54	1.000
Tidal height	4	41629.06	1086.817	0.000	0.000	-20810.53	1.000

The model selection results suggest a strong interaction between all three predictors. In general, the peaks of the size frequency distributions have shifted to the left for all three species (Fig. 1), and thus mean snail body size is xx% smaller now than it was xx years ago. However, the 3-way interaction appears to be driven by increases in the maximum size of Littorina keenae. We can inspect this further by plotting the mean snail size as a function of era and tidal height:

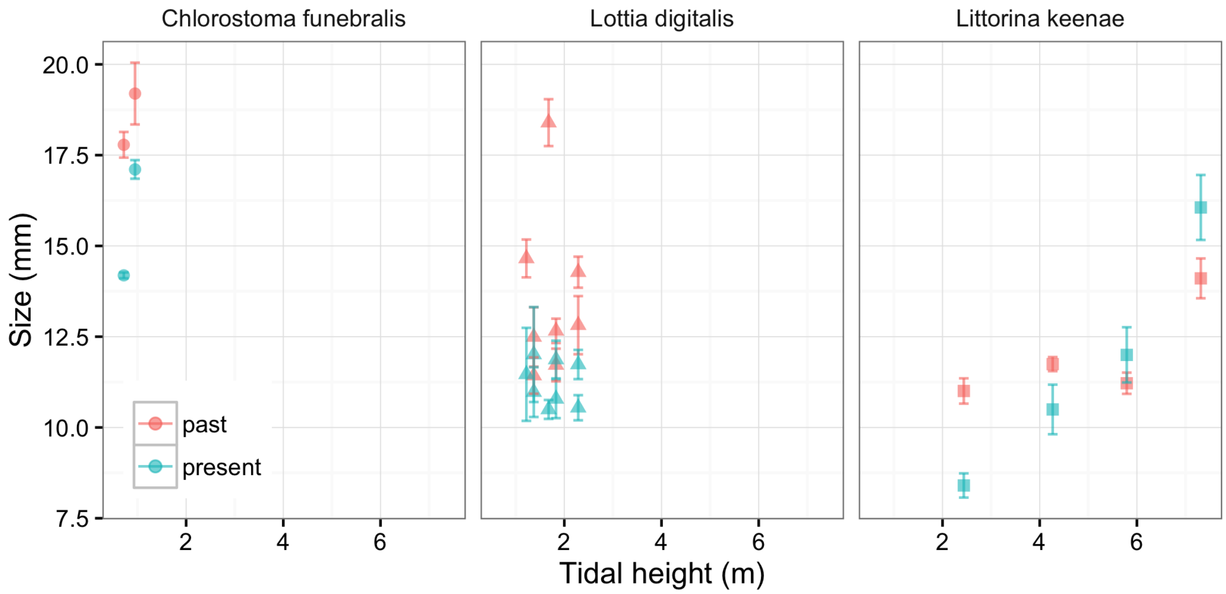

Figure 2: Figure 2. Snail body size (mean +- CI) as a function of tidal height and species. In general, mean body size has declined. However, Littorina keenae has actually increased in mean body size in the high intertidal.

The temporal increase in size for Littorina keenae was consistent with the prediction that extreme temperatures select for larger snails. Notably, all of the snails at the highest intertidal location were concentrated in a single crevice, suggesting that abiotic conditions (e.g., temperature, wind, dessication risk) were considerably more stressful in this zone (zone D).

To test the assumption that temperature means and variability increased with tidal height, we deployed temperature loggers in locations that spanned the tidal range of each sampling area. For Littorina keenae, we placed a logger each in a crevice and the exposed face for each sampling area (A-D).

In general, habitat temperature increased with tidal height, except for the two highest zones for Littorina keenae. We hypothesize that these higher zones displayed lower than expected temperatures because:

1. The lower projected area results in lower radiative heating of the rock
2. The white projected area, due to bird guano, results in reflection of solar radiation
3. The high elevation, relative to the surrounding intertidal habitat, facilitates cooling through evaporation due to boundary layer effects

Next, I replotted the mean body sizes of Littorina keenae as a function of habitat temperature. For habitat temperature, I only used the data from loggers deployed on rock faces, except for zone D (the highest zone), for which I used the logger data from the rock crevice. This is because in the lower zones (A-C), snails were collected primarily from the rock face, whereas for the high zone (D), snails were collected exclusively from the single large crevice. I use maximum temperature because this displayed the largest variation across tidal heights (Fig. 4), and arguably, is the most biological relevant metric of temperature for intertidal snails (xxx).

This figure supports the hypothesis that maximum temperature mediated the direction of size change in Littorina keenae. That is, up to a mean maximum temperature of 28C, snails increased in size. Beyond this threshold, snails decreased in size. Across all three species, the reductions in body size tended to be largest in the sampling areas that exhibited the highest maximum habitat temperatures.

The present day dataset was sampled with greater spatial resolution (i.e., larger numbers of replicates per sampling area), and thus was used to provide a more robust spatial test of the temperature-size rule. Each

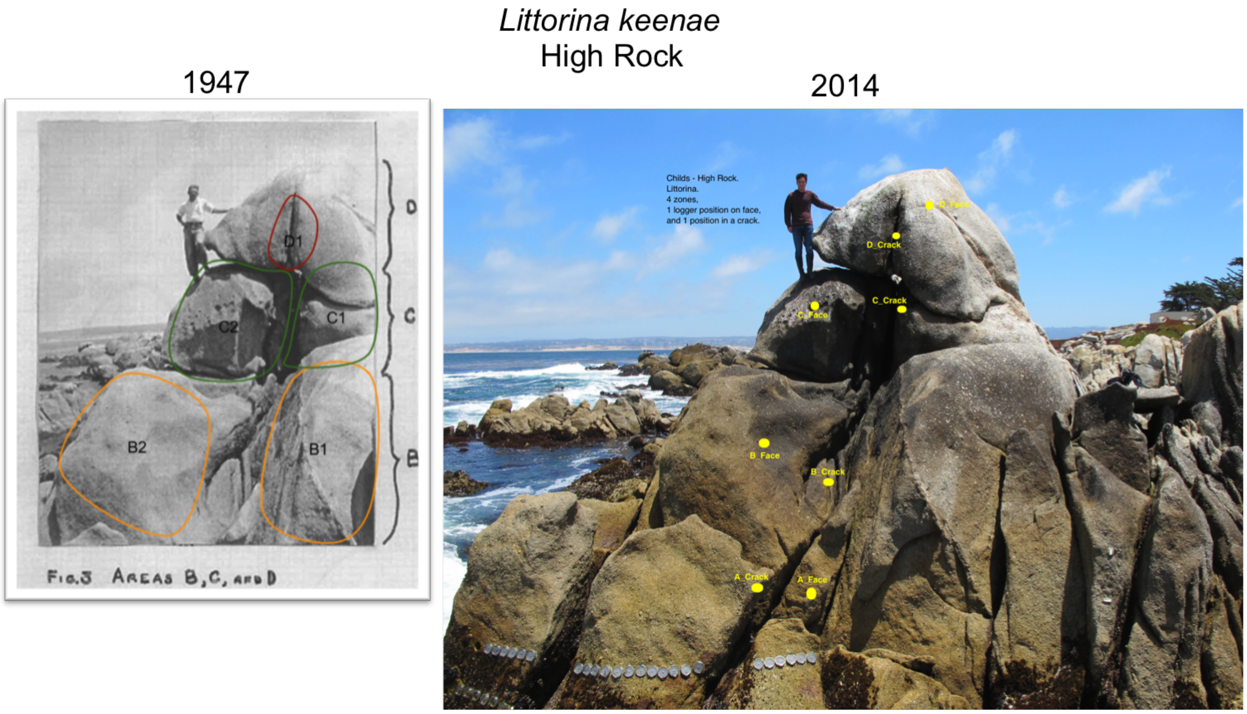

Figure 3: Figure 3. Comparison of the sampling areas (A-D) for Littorina keenae, on High Rock, at Cabrillo Point in Pacific Grove, California. In the 1947 photo, the colored lines represent areas that were resampled in 2014 within three of the four original zones sampled by Childs (A-D). In the 2014 photo, the yellow points indicate the locations of temperature loggers. The sampling areas span approximately 6m (2-8m above MLLW)

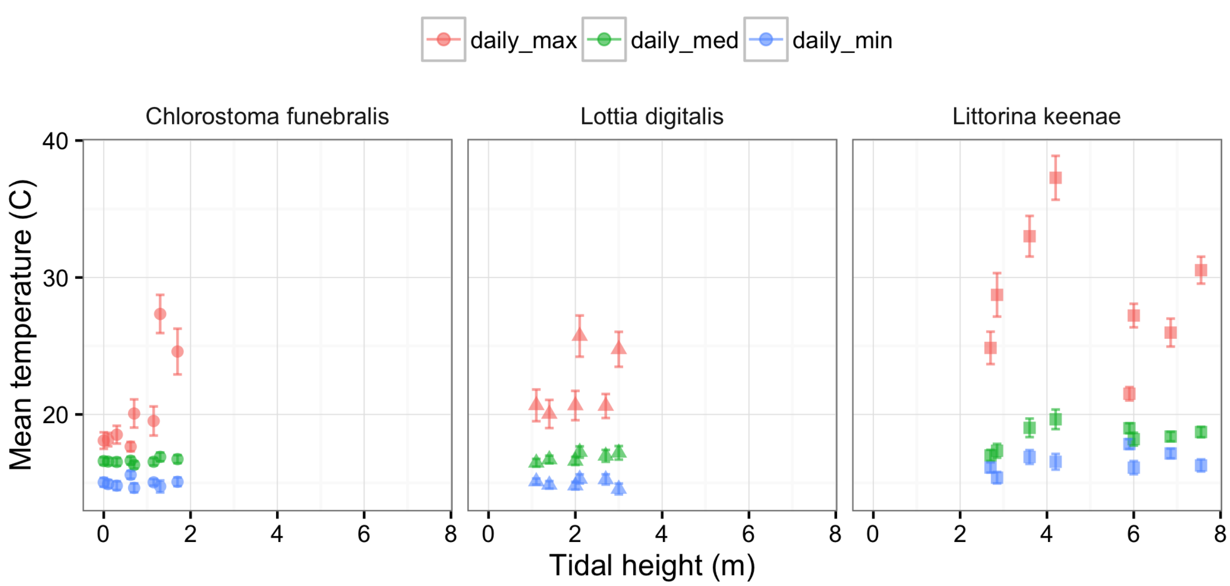

Figure 4: Figure 4. Habitat temperatures (mean +- CI of daily maximum, median, and minimum) as a function of tidal height and species.

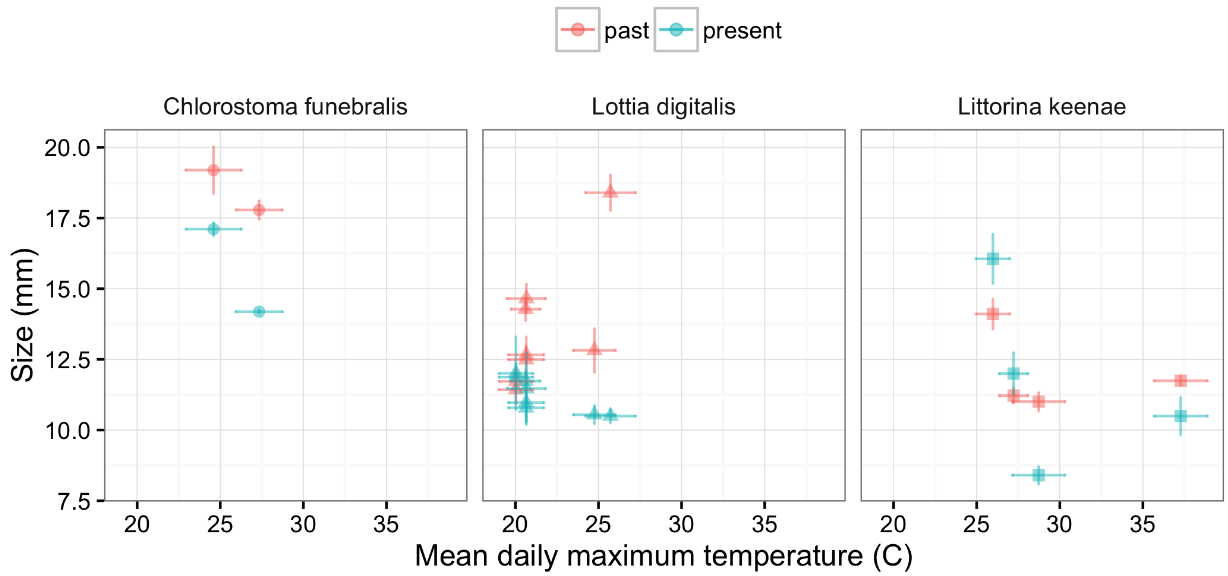

Figure 5: Figure 5. Body size (mean +- CI) plotted as a function of maximum habitat temperature (mean +- CI of daily maximum) as a function of era and tidal height for all three species

replicate (n = 90) was assigned to the nearest temperature logger (n = 17) with the most similar tidal height. We used another linear mixed effects model to test the effects of mean temperature (daily maximum, daily median, daily minimum) on body size. Sampling units were treated as random intercepts in the model.

Snail body size correlated negatively with daily maximum temperature, and thus we can reject the hypothesis that extreme temperatures select for larger snail body size at our study site. Body size did not correlate strongly with daily median temperatures (except for Chlorostoma funebralis), but was correlated positively with daily minimum temperature. Together, these results suggest that body size is maximized at intermediate temperatures, at least for Chlorostoma and Littorina. Indeed, a quadratic regression better fits the relationship between size and median temperature.

Therefore, we suggest that the observed increases in Littorina body size in the higher intertidal zones (but relatively cool temperatures) may be due to beneficial increases in temperature.

Our results thus far have demonstrated:

1. Declines in snail body size over five decades
2. Largest declines were observed in present day areas associated with high maximum temperatures
3. Present day snail body sizes are correlated negatively with maximum habitat temperatures

Together, our results would be consistent with the 'third universal prediction' of body size decline with climate warming IF maximum habitat temperatures have increased during the course of our study. Of course, we do not have long-term temperature records for the sampling areas in the study. Instead, we will examine long-term temperature records of sea surface temperatures collected daily at Hopkins Marine Station, and records of air temperature from an inland weather station.

We tested for temperature trends using regression with correlated errors.

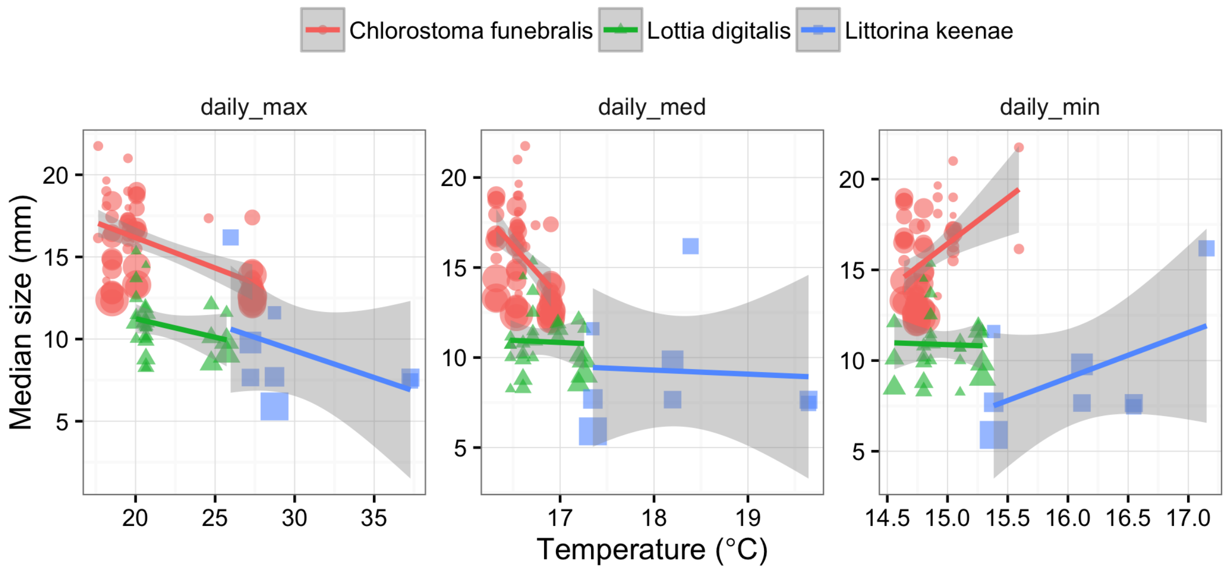

Figure 6: Figure 6. Body size (median of each replicate) plotted as a function of habitat temperature (mean +- CI of daily maximum, median, minimum) for all three species. The size of points is proportional to the number of snails in each replicate

Table 2: Table 2. Summary of linear regressions testing temperature trends for each species

species	metric	slope	std_error	p_value	duration_yrs	change_temp_C
Chlorostoma funebralis	max_C	0.0099538	0.0053359	0.0670100	62	0.617
Chlorostoma funebralis	med_C	0.0045468	0.0047765	0.3449655	62	0.282
Chlorostoma funebralis	min_C	0.0021733	0.0041332	0.6009495	62	0.135
Lottia digitalis	max_C	0.0086016	0.0041492	0.0416481	76	0.654
Lottia digitalis	med_C	0.0042283	0.0039819	0.2917415	76	0.321
Lottia digitalis	min_C	0.0005415	0.0036989	0.8839989	76	0.041
Littorina keenae	max_C	0.0068836	0.0036816	0.0653681	78	0.537
Littorina keenae	med_C	0.0033335	0.0034277	0.3338815	78	0.260
Littorina keenae	min_C	0.0007527	0.0031678	0.8128102	78	0.059

Only maximum temperature displayed a positive trend over time for each species ($P = 0.04 - 0.07$). Annual median and minimum temperatures did not change over time. When the estimated rate (degrees per year) was multiplied by the duration of the regression, the change in estimated maximum temperature ranged from 0.54 - 0.65 C. We used this value to calculate the change in median size (mm) per degree C.

For comparison, we estimated the slope of the relationship between present day size and maximum habitat temperature (Figure 6).

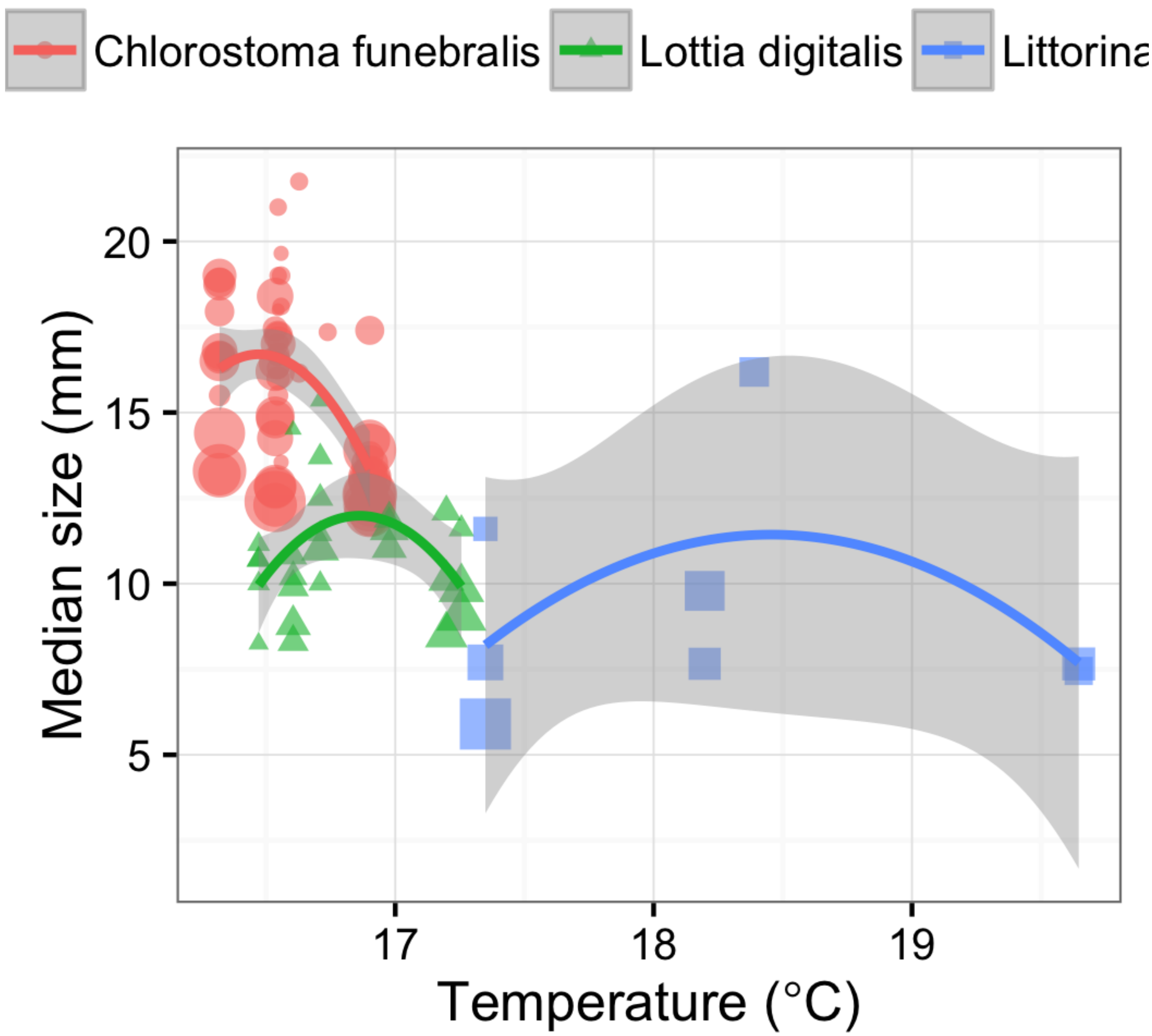

Figure 7: Figure 7. Body size (median of each replicate) plotted as a function of median habitat temperature (mean +- CI) for all three species. The size of points is proportional to the number of snails in each replicate

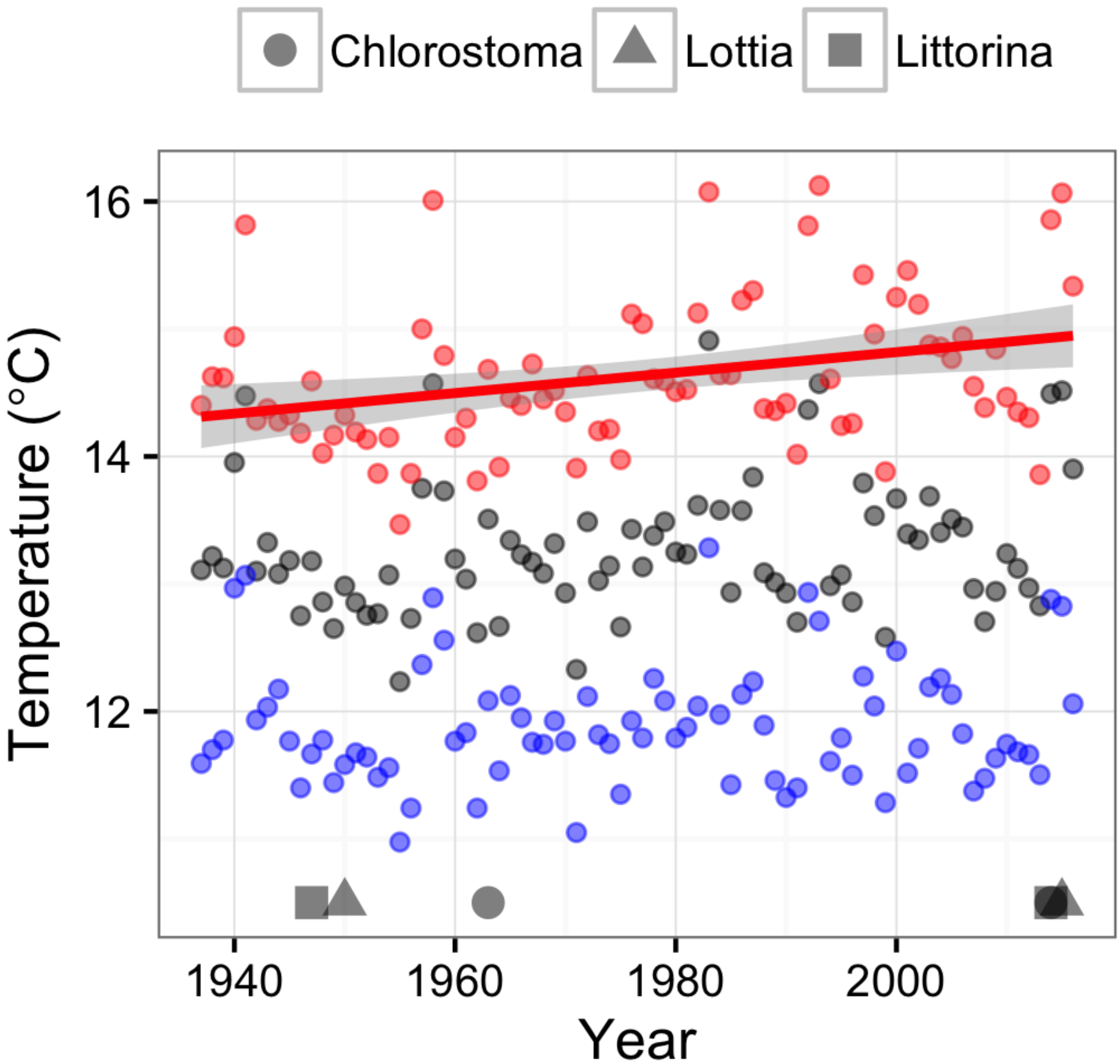

Figure 8: Figure 8. Sea surface temperatures at Hopkins Marine Station. Each point represent the monthly mean of each year. Red, black, and blue points represent maximum, median, and minimum values. Gray symbols next to the x-axis represent the years during which snails were sampled

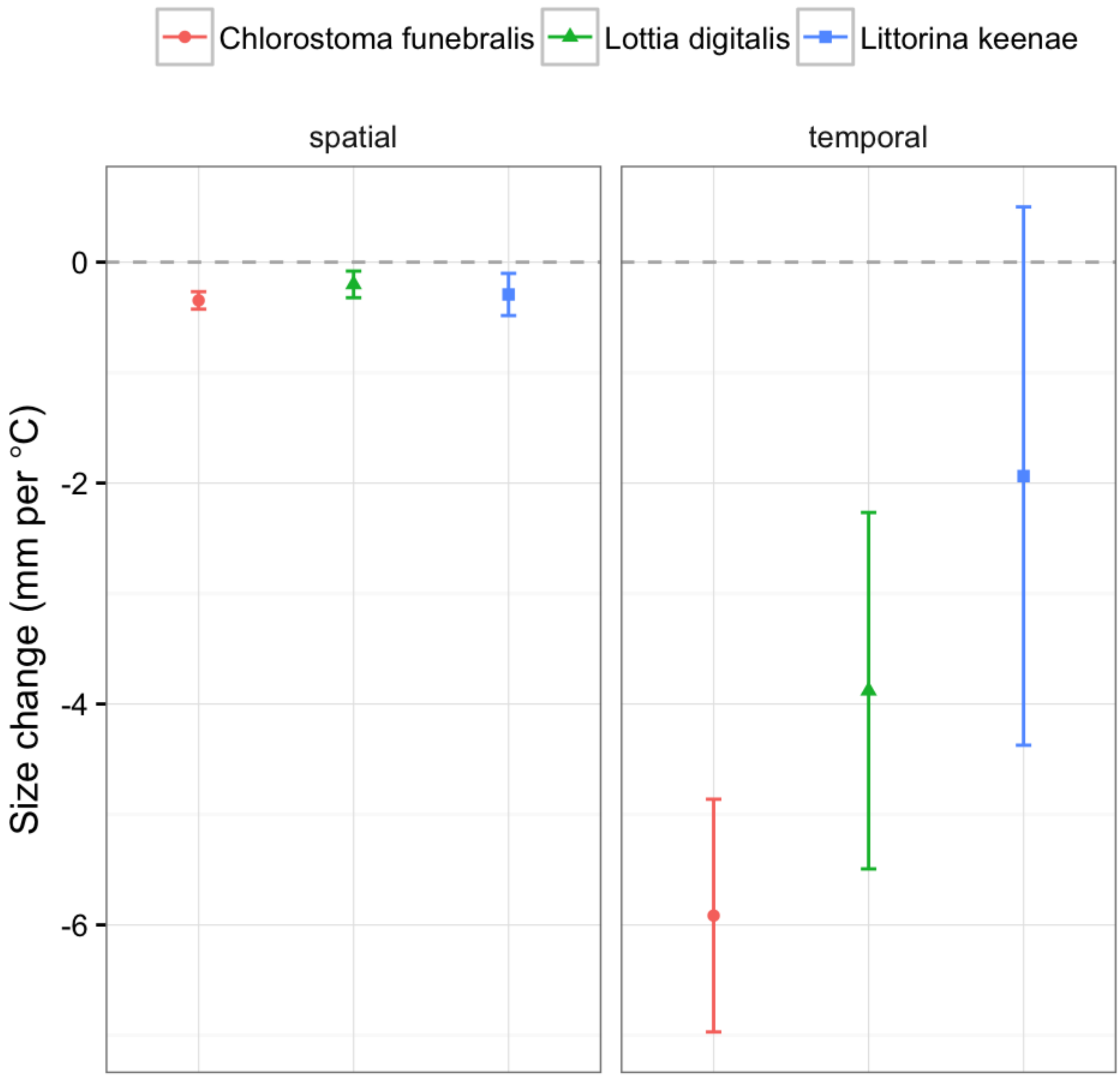

Figure 9. Spatial and temporal estimates of size change per degree C. Spatial estimates were based on mixed effects models for each species (size ~ mean daily maximum temperature). Temporal estimates were estimated as change in median size between eras (for each sampling area), divided by change in temperature estimated from the linear regression between maximum temperatures (Fig. 8).

To provide some aerial temperature context for these intertidal snails, I retrieved long-term air temperature records from NCDC station # 5795, Monterey. Although these data are several (xx) km inland from the rocky intertidal study sites in Pacific Grove, these are the best available time-series to my knowledge.

The data available were daily maximum, minimum, and observed temperature at a given time. I analyzed it similarly to the HMS seawater data. Briefly, I calculated the monthly maximum, median, and minimum values of daily maximum, minimum, and observed values. These monthly values were then averaged, and used in regression analyses (accounting for temporal autocorrelation, as above).

Table 3: Table 3. Summary of linear regressions testing air temperature trends in Monterey, California

climate_var	metric	slope	std_error	p_value	duration_yrs	change_temp_C
air_max	maximum	-0.0190276	0.0110438	0.0897300	66	-1.256
air_max	mean	-0.0191699	0.0093359	0.0441303	66	-1.265
air_max	median	-0.0214249	0.0097155	0.0310372	66	-1.414
air_max	minimum	-0.0128014	0.0083627	0.1307557	66	-0.845
air_min	maximum	0.0064645	0.0086894	0.4596258	66	0.427
air_min	mean	0.0023151	0.0102570	0.8221448	66	0.153
air_min	median	0.0018587	0.0100873	0.8543918	66	0.123
air_min	minimum	-0.0084774	0.0137850	0.5407505	66	-0.560
air_obs	maximum	0.0040535	0.0109393	0.7123231	60	0.243
air_obs	mean	-0.0012084	0.0110741	0.9134853	60	-0.073
air_obs	median	-0.0028729	0.0118156	0.8087490	60	-0.172
air_obs	minimum	0.0052342	0.0105075	0.6202682	60	0.314
precip	maximum	-0.0239452	0.0297469	0.4238215	66	-1.580
precip	mean	-0.0015774	0.0040491	0.6981454	66	-0.104
precip	median	0.0000891	0.0007098	0.9004625	66	0.006
precip	minimum	-0.0000953	0.0000348	0.0079271	66	-0.006

The only significant temporal trends were for daily maximum temperatures, which actually decreased over time (Figure 10).

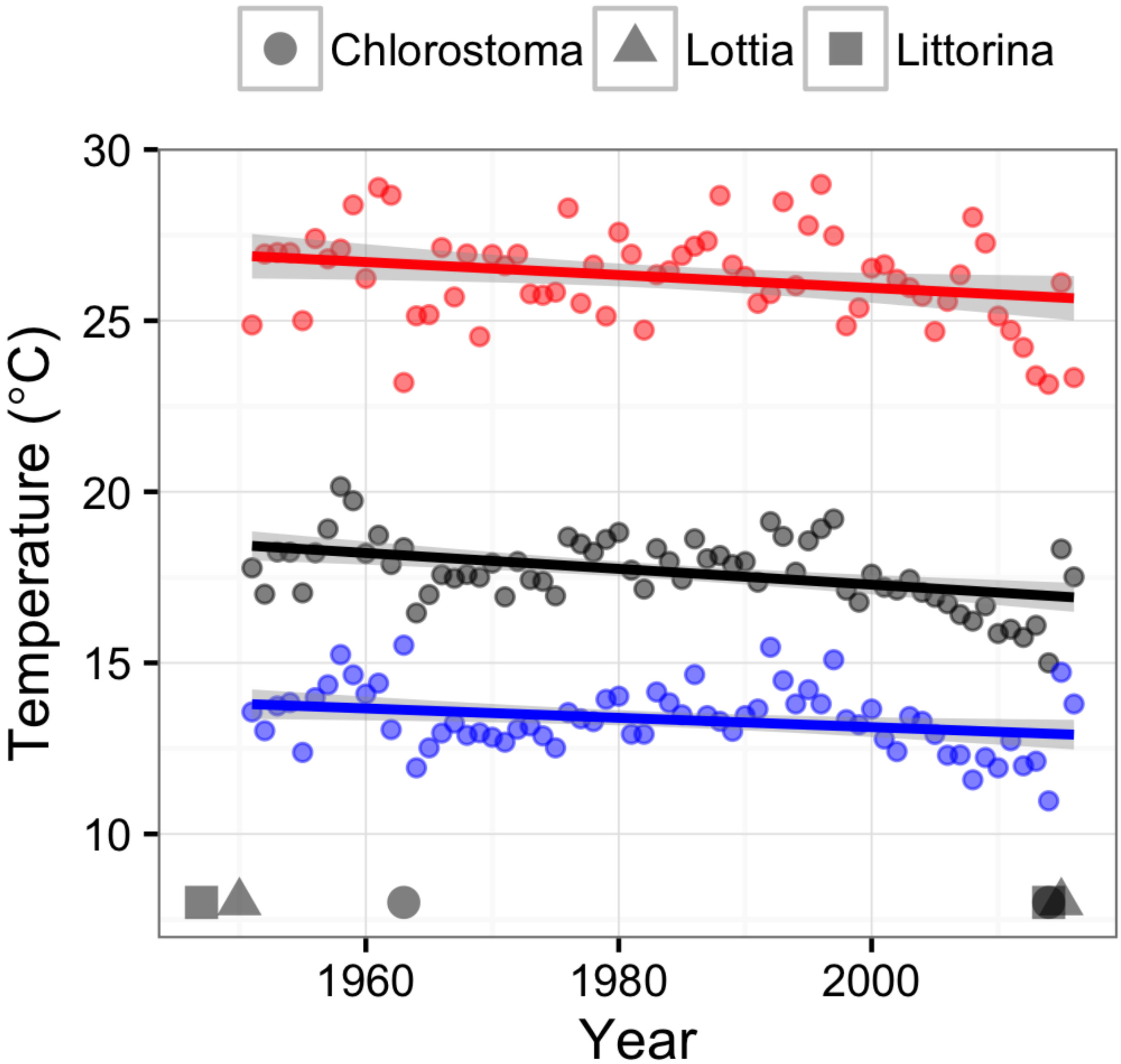

Figure 9: Figure 10. Maximum air temperatures at the Monterey weather station. Each point represent the mean of monthly temperatures for each year. Red, black, and blue points represent maximum, median, and minimum values estimated for each month (original data were daily estimates). Gray symbols next to the x-axis represent the years during which snails were sampled