Decadal-scale changes in body size along a thermal gradient are consistent with the temperature-size rule: a case study using intertidal snails

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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.

Predictions

1. Snail size is inversely related to temperature. That is, we expected size declines over time, assuming sea and/or air temperatures have increased during same period [@Barry1995]. We expected the 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 coincide with the areas of greatest warming (e.g., due to metabolic effects of warming 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)

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.

Results

Decadal-scale changes in snail body size

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

Modnames	K	Delta_AIC	ModelLik	AICWt	Cum.Wt
Era x Species x Tidal height	14	0.000	1.000	0.976	0.976
All three 2-way intx	12	7.385	0.025	0.024	1.000
Era x Tidal height	6	29.176	0.000	0.000	1.000
Era x Species	8	94.572	0.000	0.000	1.000
Era	4	237.400	0.000	0.000	1.000
Species x Tidal height	8	1065.652	0.000	0.000	1.000
Species	5	1078.808	0.000	0.000	1.000
Null model	3	1084.847	0.000	0.000	1.000
Tidal height	4	1086.817	0.000	0.000	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 *L. keenae*. We can inspect this further by plotting the mean snail size as a function of era and tidal height (Fig. 2).

The temporal increase in size for *L. keenae* was consistent with the prediction that extreme warm 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 on the exposed face in this zone (zone D).

Short-term intertidal temperature measurements

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 *L. keenae*, we placed a logger each in a crevice and the exposed face for each sampling area (A-D; Fig. 3).

In general, habitat temperature increased with tidal height, except for the two highest zones for *L. keenae* (Fig. 4). 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

In summary, we can reject the hypothesis that body size increase observed in the highest intertidal site was due to exceptionally warm temperatures. We can provide a spatial test of this hypothesis by using the present day dataset, which was sampled with greater spatial resolution (i.e., larger numbers of replicates per sampling area). Each replicate (n = 90) was assigned to the nearest temperature logger (n = 17) with the most similar

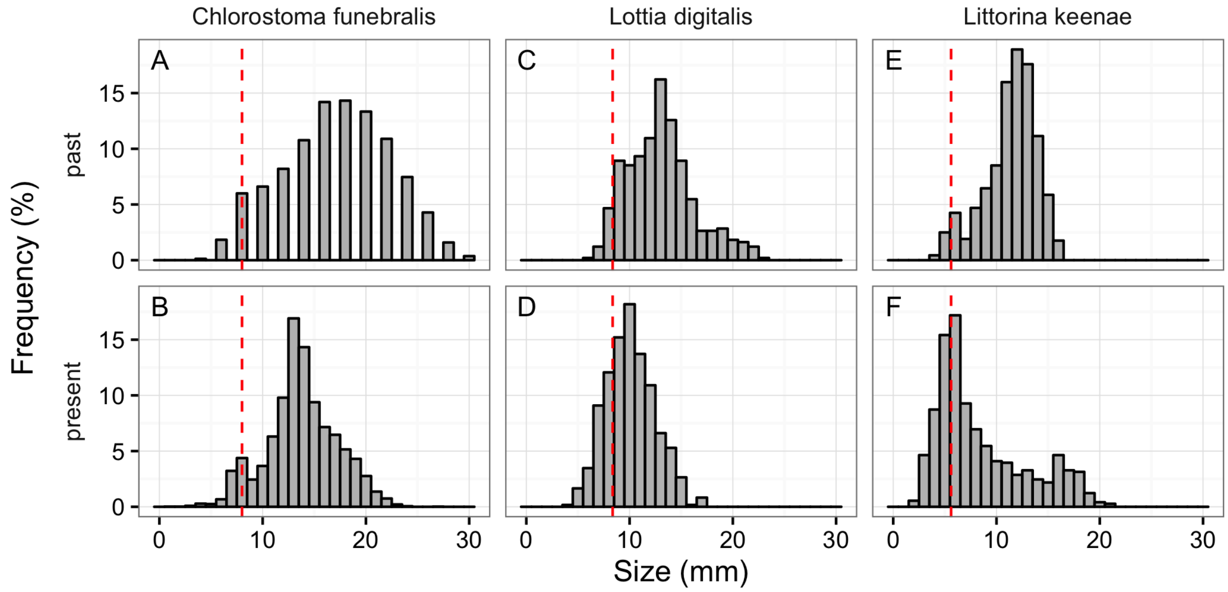

Figure 1: Size frequency distributions of three intertidal snails. The dashed red line indicates the 5th percentile of size for each species in the past. Only snails larger than this threshold were included for all statistical tests and summary calculations. We did this to ensure a conservative test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

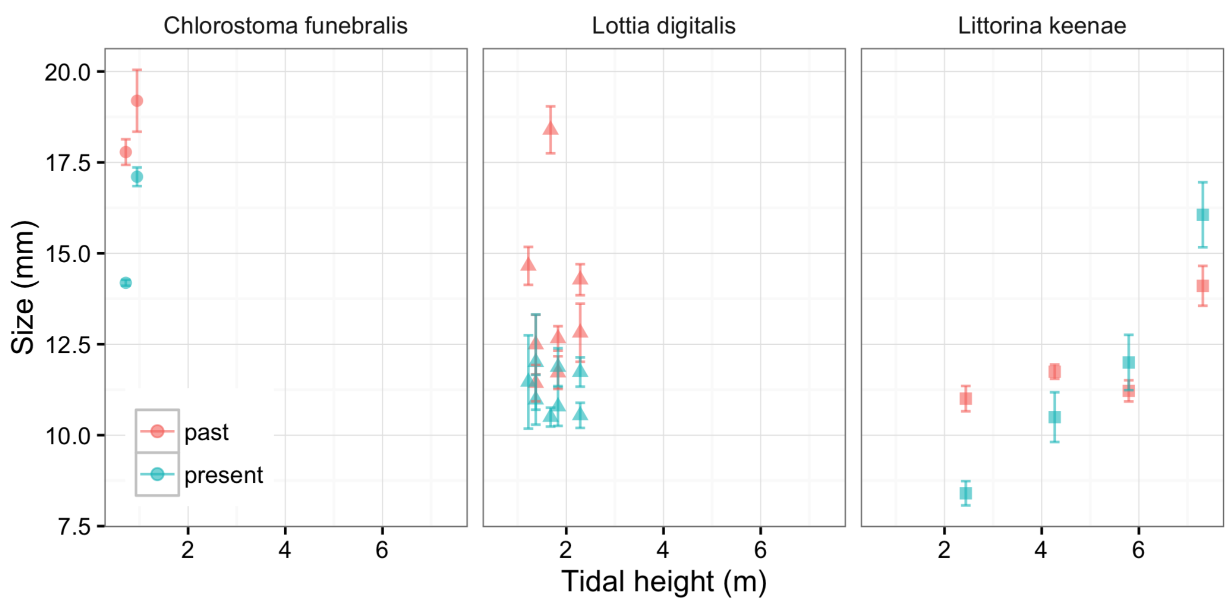

Figure 2: Snail body size (mean +- CI) as a function of tidal height and species. In general, mean body size has declined. However, *L. keenae* has actually increased in mean body size in the high intertidal.

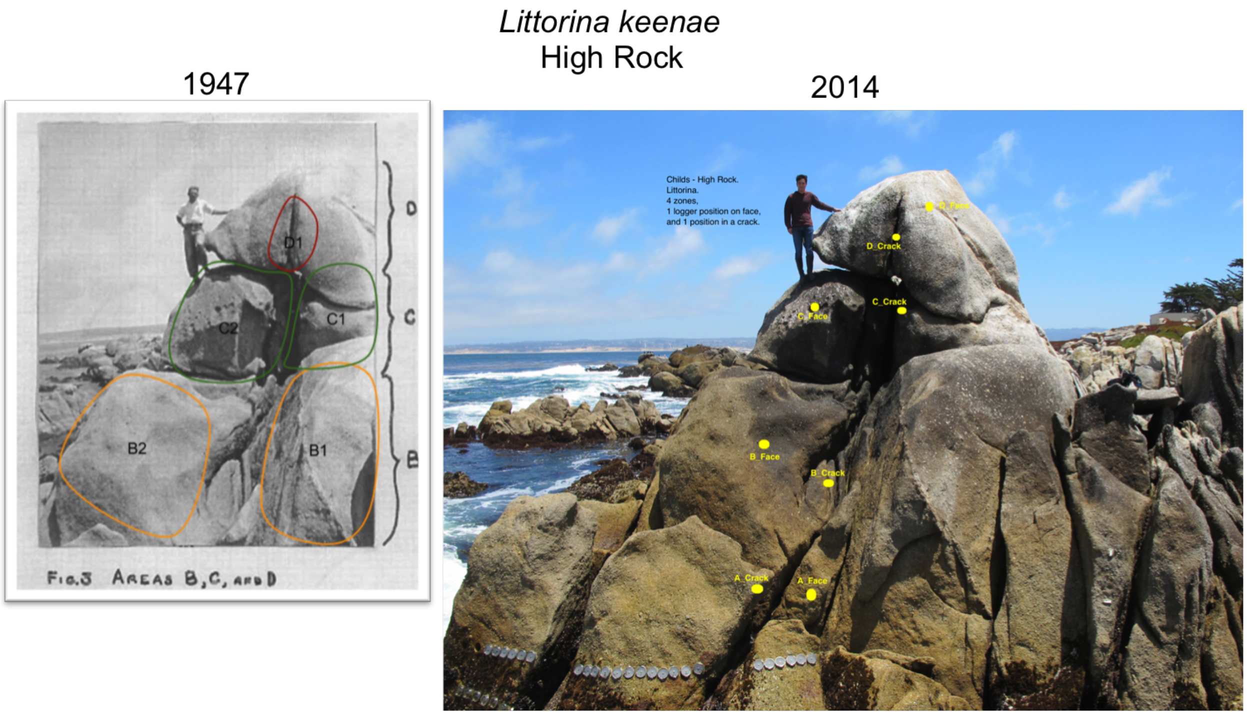

Figure 3: Comparison of the sampling areas (A-D) for Littorina keenae, on High Rock, at Cabrillo Point in Pacific Grove, California. In the 1947 photo, the colored lines represent areas that were resampled in 2014 within three of the four original zones sampled by Childs (A-D). In the 2014 photo, the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

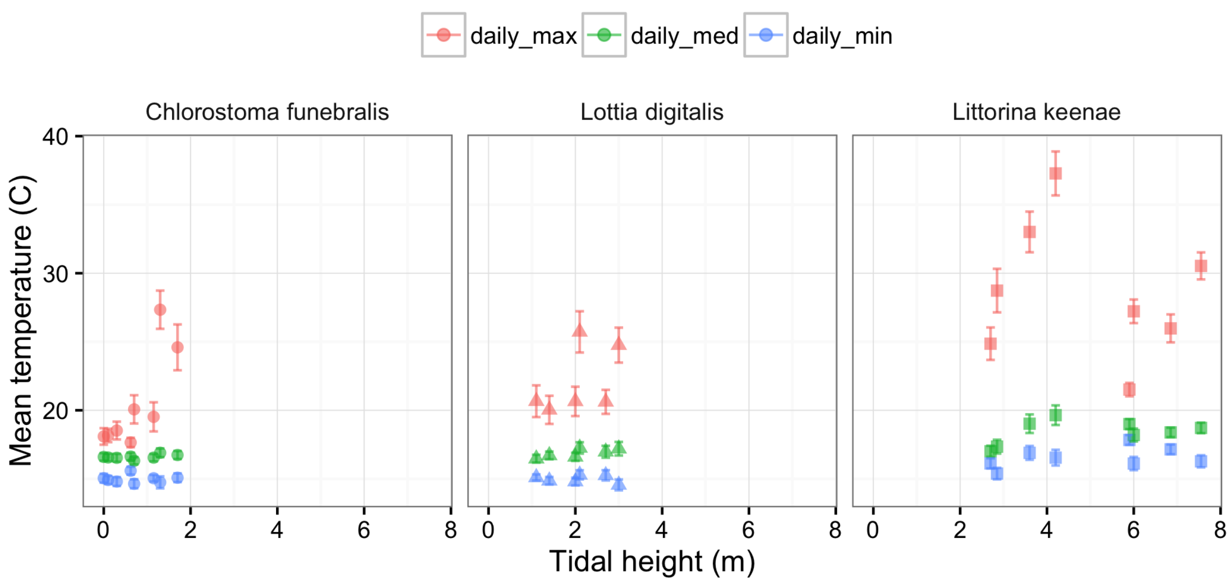

Figure 4: Habitat temperatures (mean +- CI of daily maximum, median, and minimum) as a function of tidal height and species.

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.

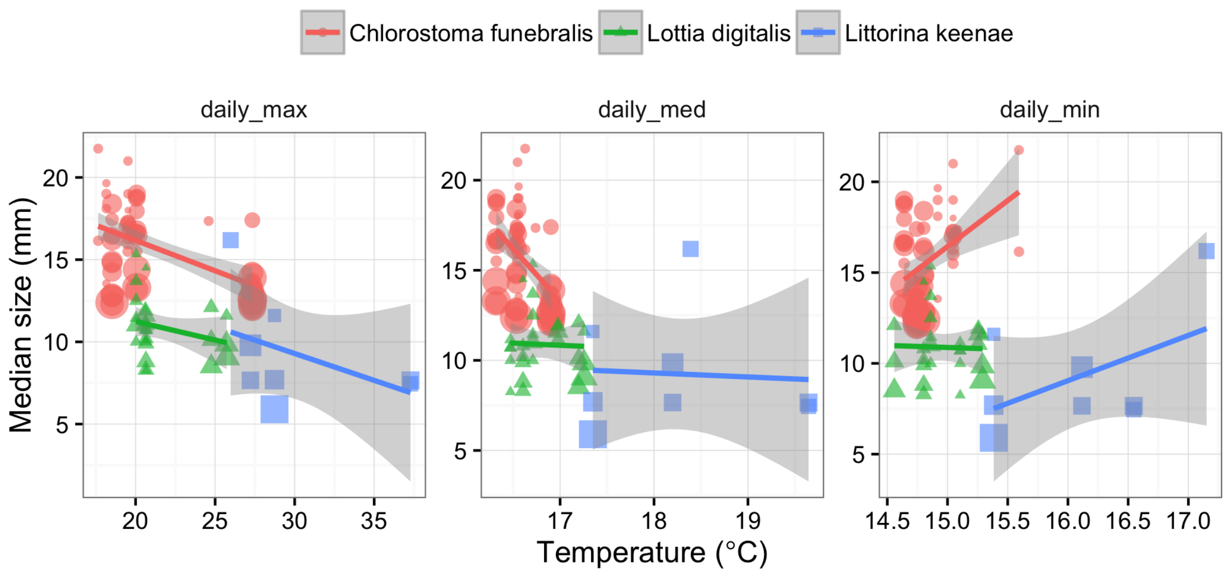

Figure 5: Body size (median of each replicate) plotted as a function of habitat temperature (mean +- CI of daily maximum, median, minimum) for all three species. The size of points is proportional to the number of snails in each replicate

Snail body size correlated negatively with daily maximum temperature (Fig. 5), mirroring the temporal pattern of body size reduction. Body size did not correlate strongly with daily median temperatures (except for *C. funebralis*), but was correlated positively with daily minimum temperature. Together, these results suggest that body size is maximized at intermediate temperatures, at least for *C. funebralis* and *L. keenae*. Indeed, a quadratic regression better fit the relationship between size and median temperature (Fig. 6). Therefore, one mechanism for the observed increases in Littorina body size in the higher intertidal zones (but relatively cool temperatures) may be due to beneficial increases in temperature over the past six decades.

13-year hindcasts of limpet body temperature

To provide a longer thermal context for the short-term temperature measurements, we used a heat budget model to hindcast the body temperatures of a limpet (*Lottia gigantea*) from August 1 1999 to July 31 2013. The model estimated a limpet body temperature every 10 minutes for each of the intertidal locations we deployed temperature loggers.

With regard to the model parameters, the following settings were used:

- A brown-shelled *L. gigantea* was modeled. The shell length of the snail is 35.4 mm.
- We measured the orientation of the substratum (compass direction and slope above horizontal) for each logger position, each with an associated shore height
- The model was run with 0 wave swash (worst case scenario, leading to hotter temperature due to less wave splash), so that a given shore height would only be submerged when the tide + significant wave height summed up to a value above the given shore level

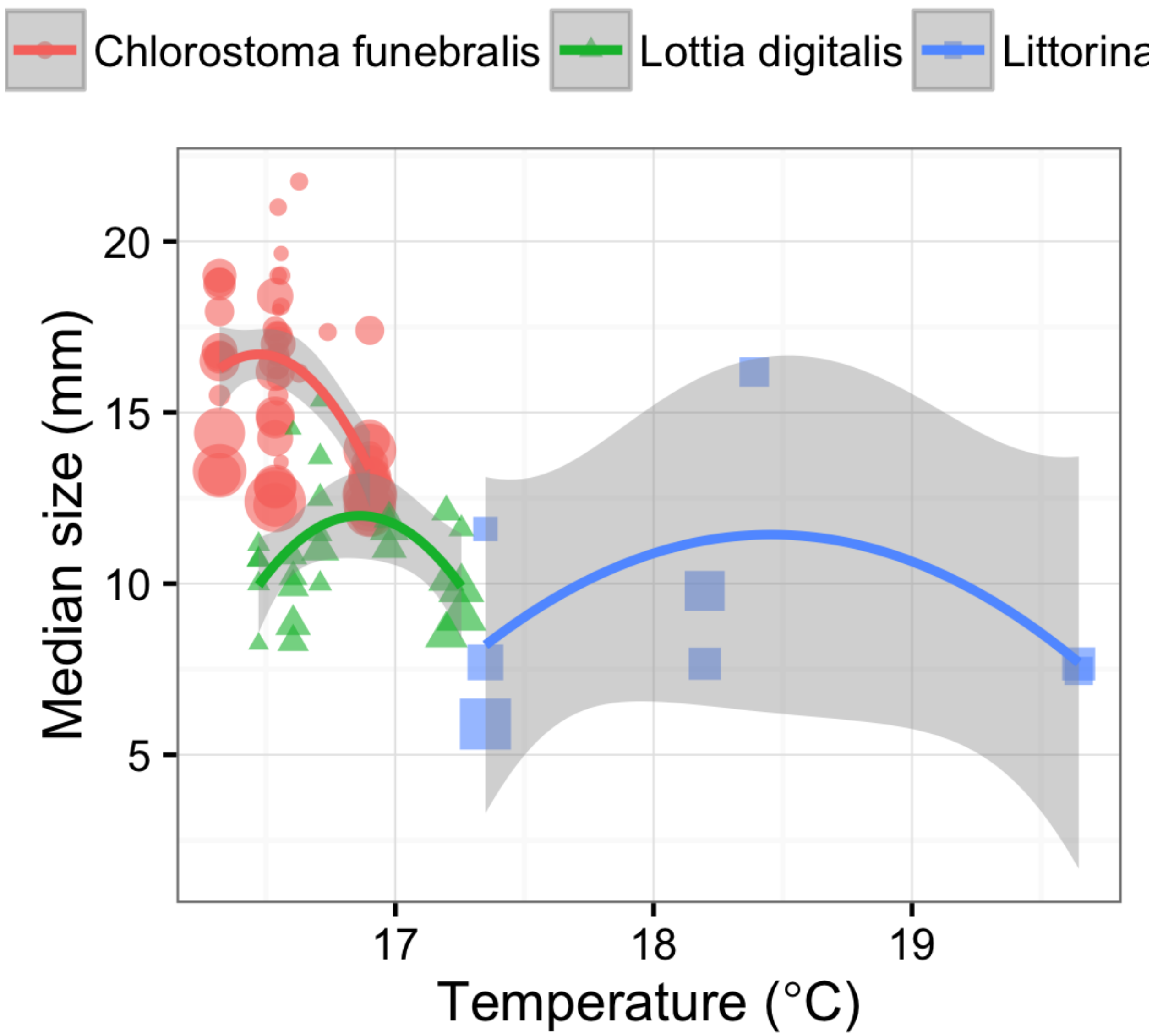

Figure 6: Body size (median of each replicate) plotted as a function of median habitat temperature (mean +- CI) for all three species. The size of points is proportional to the number of snails in each replicate

- The model likely overpredicts body temperature for the three species in our study because:
    1. The model limpet (*L. gigantea*) was larger than the limpet in our study (*L. digitalis*), and larger than the other two snails
    2. The surface area of the attachment point of limpets (i.e., the foot) is relatively larger than the feet of *C. funebralis* and *L. keenae*, and thus conductive heat transfer is lower for these latter species
    3. *L. keenae* can reduce its body temperature by glueing itself to the substratum and retracting its foot [Miller reference]
    4. *C. funebralis* often lives within algal turfs which provide shade and moisture

We summarised the model output (predicted temperature at 10-minute intervals) as follows:

1. Get daily maximum, median, and minimum
2. For each month, calculate the mean daily maximum, median, minimum
3. For each year, retrieve the maximum monthly mean, median monthly mean, and minimum monthly mean

The hindcast results were surprising because maximum body temperatures increased with shore height only for *C. funebralis* (Figure 7). These snails live on horizonal substrata, which heat up faster than nearby vertical surfaces (which harbored the other two species in our study). Moreover, the predicted temperatures were lower than the observed temperatures (Figure 4).

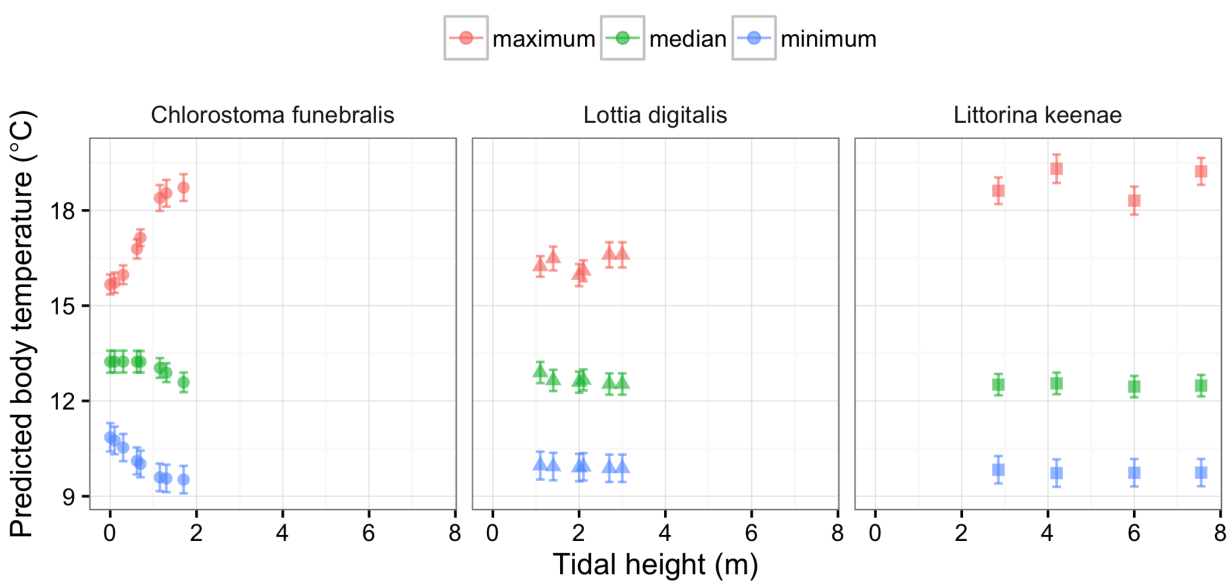

Figure 7: Predicted body temperatures (mean +- CI of annual maximum, median, and minimum) for an intertidal limpet as a function of tidal height and species.

These particular microsites are generally either low on the shore, or on north or northwest-facing rocks that recieve very little direct sunlight. The overall hottest site only reached a maximum temperature of 25.5 C, even though it was 7.55 m above MLLW. That site faces southwest, so it would primarily get sun in the later afternoon, rarely the hottest time of day at HMS.

Long-term temperature trends

Our results are 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.

Sea surface temperature

We tested for temperature trends using regression with correlated errors. Only maximum temperature displayed a positive trend over time for each species (Table 2, Fig. 8). Annual median and minimum temperatures did not change over time.

Table 2: Summary of linear regressions testing surface seawater 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

Air temperature

To provide an aerial temperature context for these intertidal snails, we 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 our knowledge.

The data available were daily maximum, minimum, and observed temperature at a given time. We analyzed it similarly to the HMS seawater data. Briefly, we calculated the monthly median 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: Summary of linear regressions testing air temperature trends in Monterey, California

climate_var	slope	std_error	p_value	duration_yrs	change_temp_C
air_max	-0.0214249	0.0097155	0.0310372	66	-1.414
air_min	0.0018587	0.0100873	0.8543918	66	0.123
air_obs	-0.0028729	0.0118156	0.8087490	60	-0.172

The only significant temporal trends were for daily maximum temperatures, which actually decreased over time (Fig. 9).

Conclusions

Our results support the 'third universal prediction' that climate warming is associated with body size declines in intertidal snails. Sampling areas lowest in the intertidal were associated with the largest declines in body

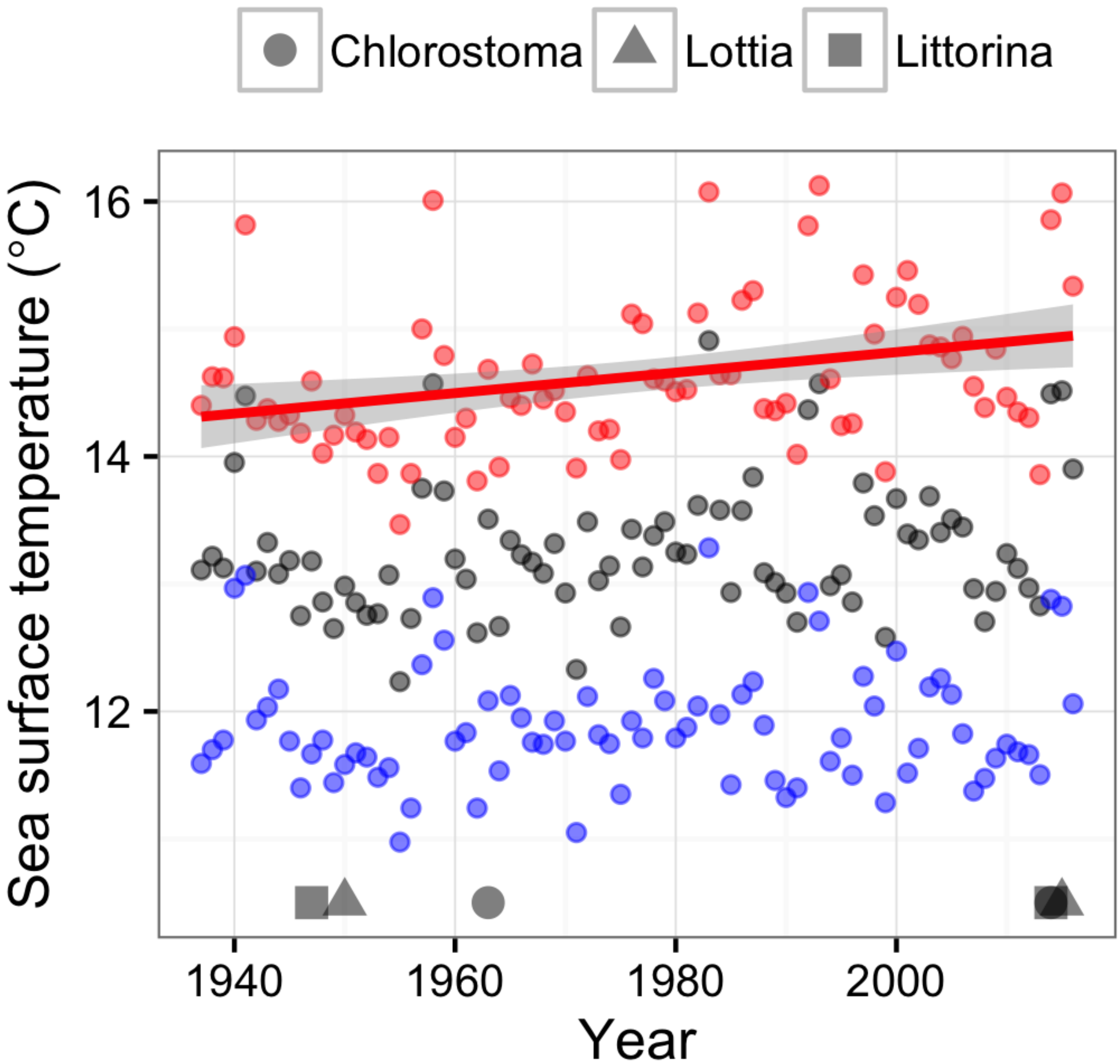

Figure 8: Sea surface temperatures at Hopkins Marine Station. Each point represents the monthly mean of each year. Red, black, and blue points represent maximum, median, and minimum values. Gray symbols next to the x-axis represent the years during which snails were sampled

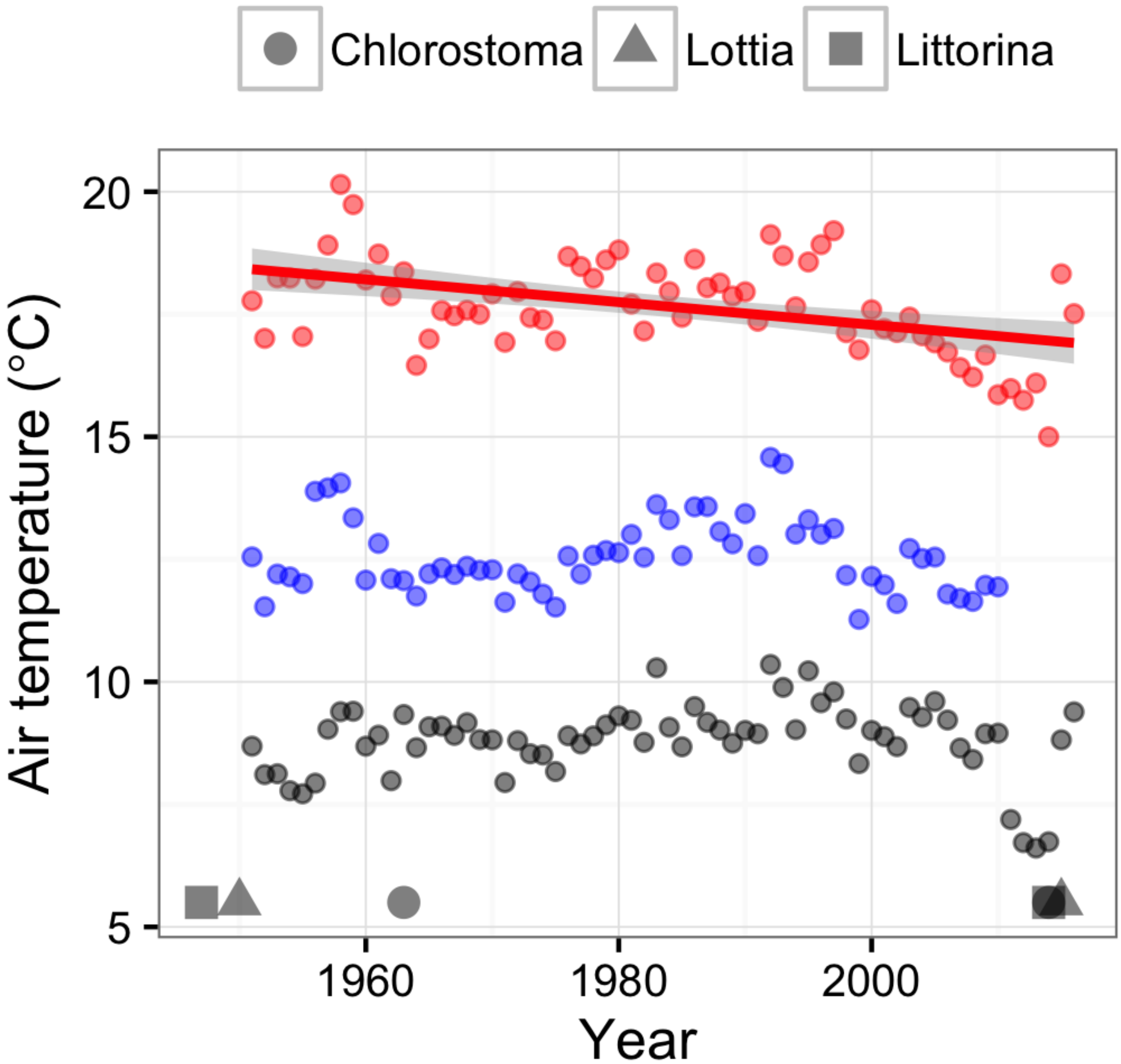

Figure 9: Air temperatures at the Monterey weather station. Each point represents the mean of median monthly temperatures for each year. Red, black, and blue points represent maximum, observed, and minimum temperature measurements (original data were daily estimates). Gray symbols next to the x-axis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

size, and the sign of body size change reversed for *L. keenae* in the highest intertidal area.

Our results suggest a temperature-related hypothesis for the variation in body size change along the thermal gradient. Long-term seawater warming (maximum temperatures) but aerial cooling (maximum temperatures) was observed in the region. Therefore, the observed declines in body size in the low intertidal but observed increases in body size in the high intertidal were consistent with the temperature-size rule (i.e., 'hotter is smaller').

Of course, we will have to list alternative hypotheses because our results are necessarily observational.

Next steps

1. Correlate Hopkins weather station data to the Monterey weather data?
    - I have the weather station data from Chris Patton, but I should probably use the air temperatures that went into the heat budget models
2. Estimate duration of time that each tidal height is submerged?
3. Include density of snails as covariate in models?