

Seasonality in Lake Champlain Copepod Thermal Limits

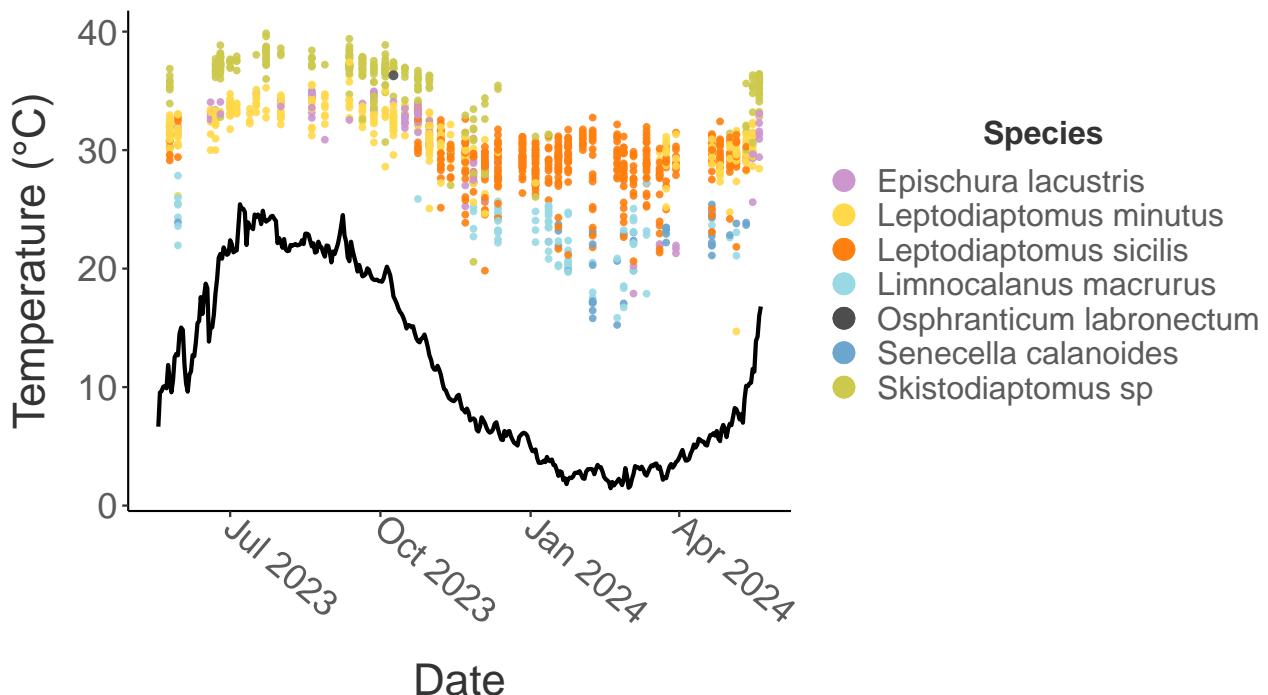
2025-09-13

Copepod Collection

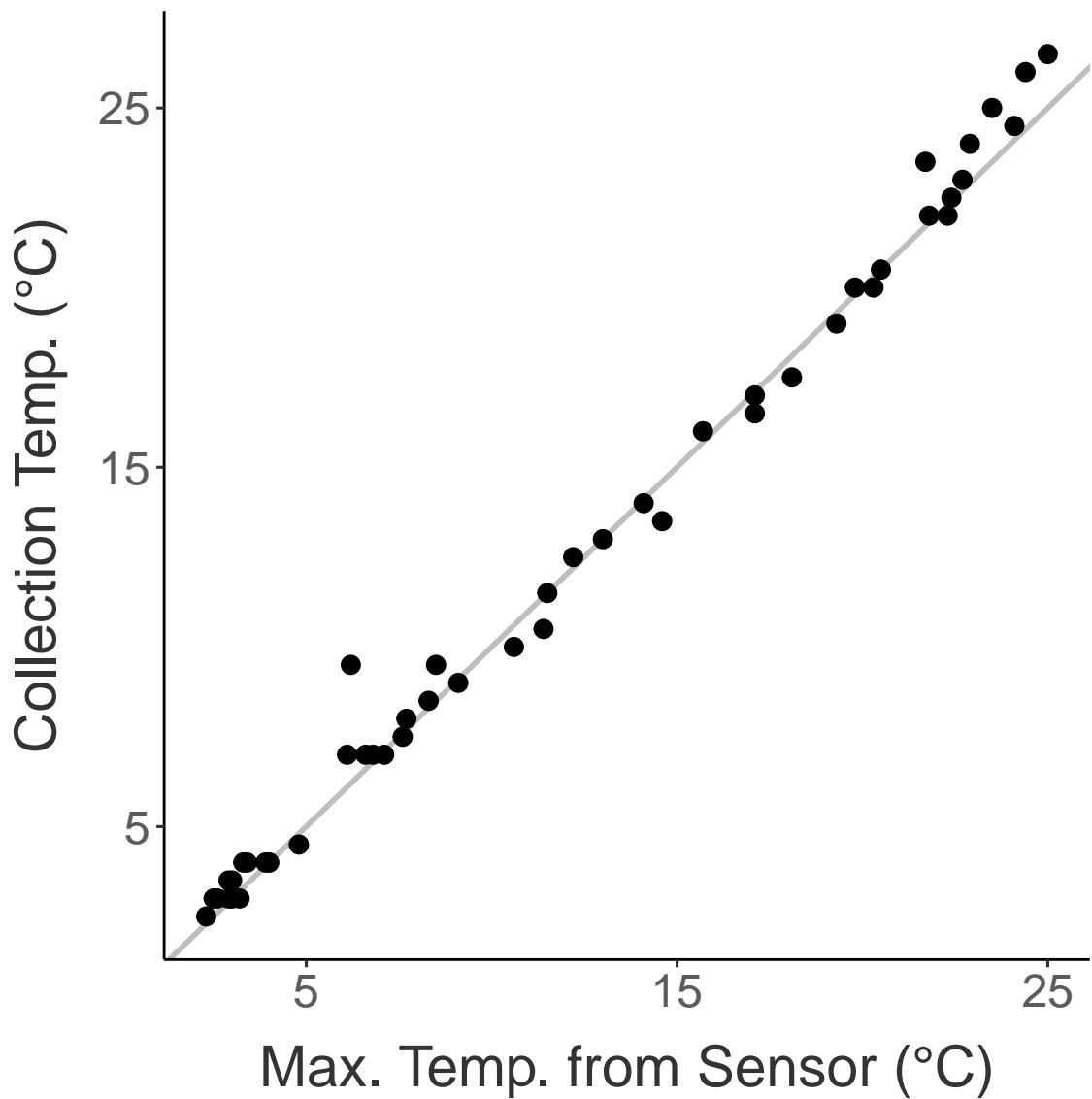
Copepods were collected at approximately weekly intervals from Lake Champlain (Burlington Fishing Pier). Plankton was collected from the top 3 meters using a 250 um mesh net.

Collections began in late May 2023. Several gaps are present, but collections have continued at roughly weekly intervals since then. Copepods from 48 collections were used to make a total of 1312 thermal limit measurements. Over this time period, collection temperatures ranged from 2.5 to 26.5°C.

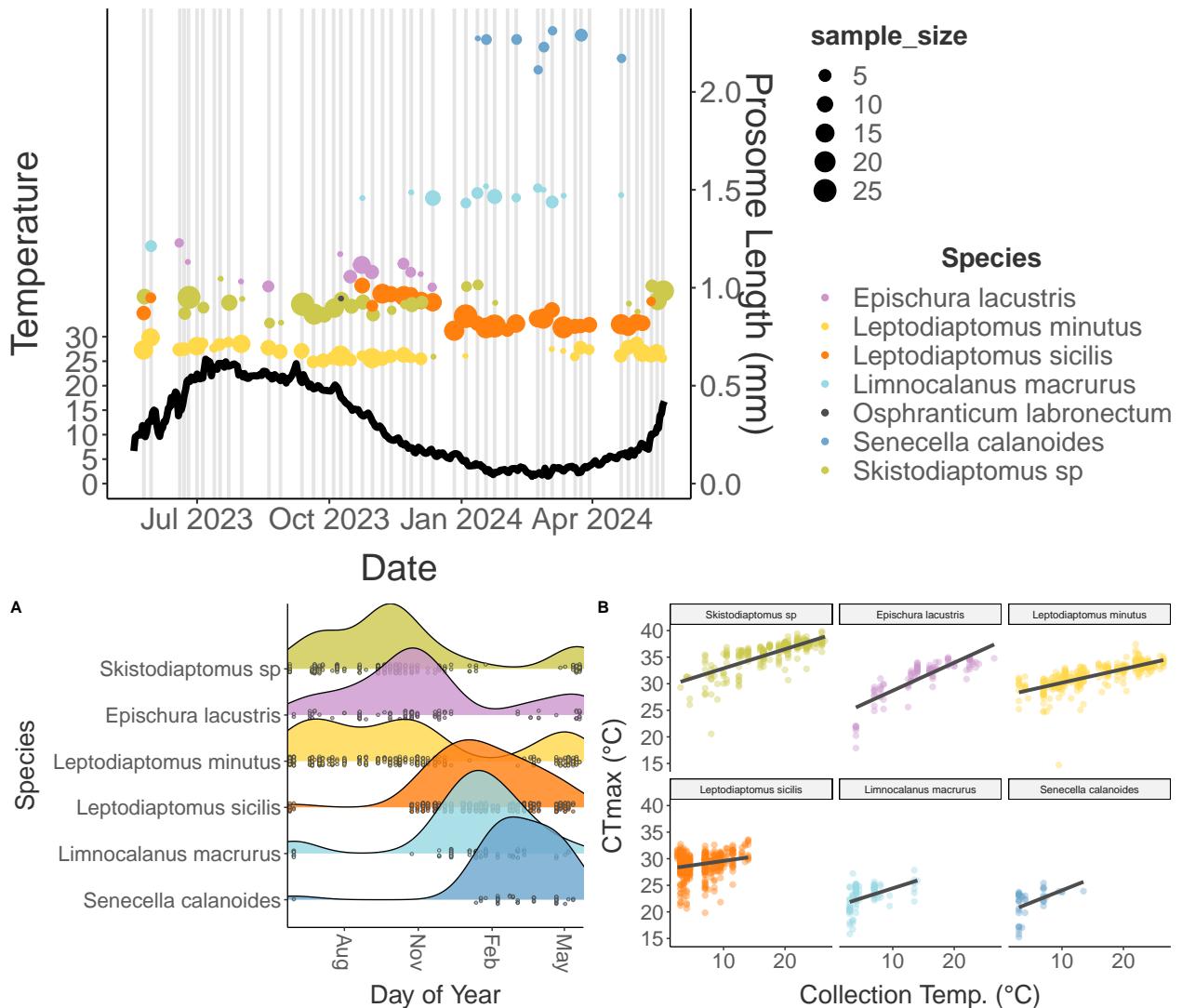
There is substantial variation in thermal limits across the species collected. There is also some degree of variation within the species, with thermal limits increasing slightly during the summer.



Temperatures observed at the time of collection closely resembled the maximum daily temperature from the temperature sensor data. Maximum temperature was used as a proxy instead of mean temperature as collections were usually made during afternoons or early evenings, just following the warmest part of the day.

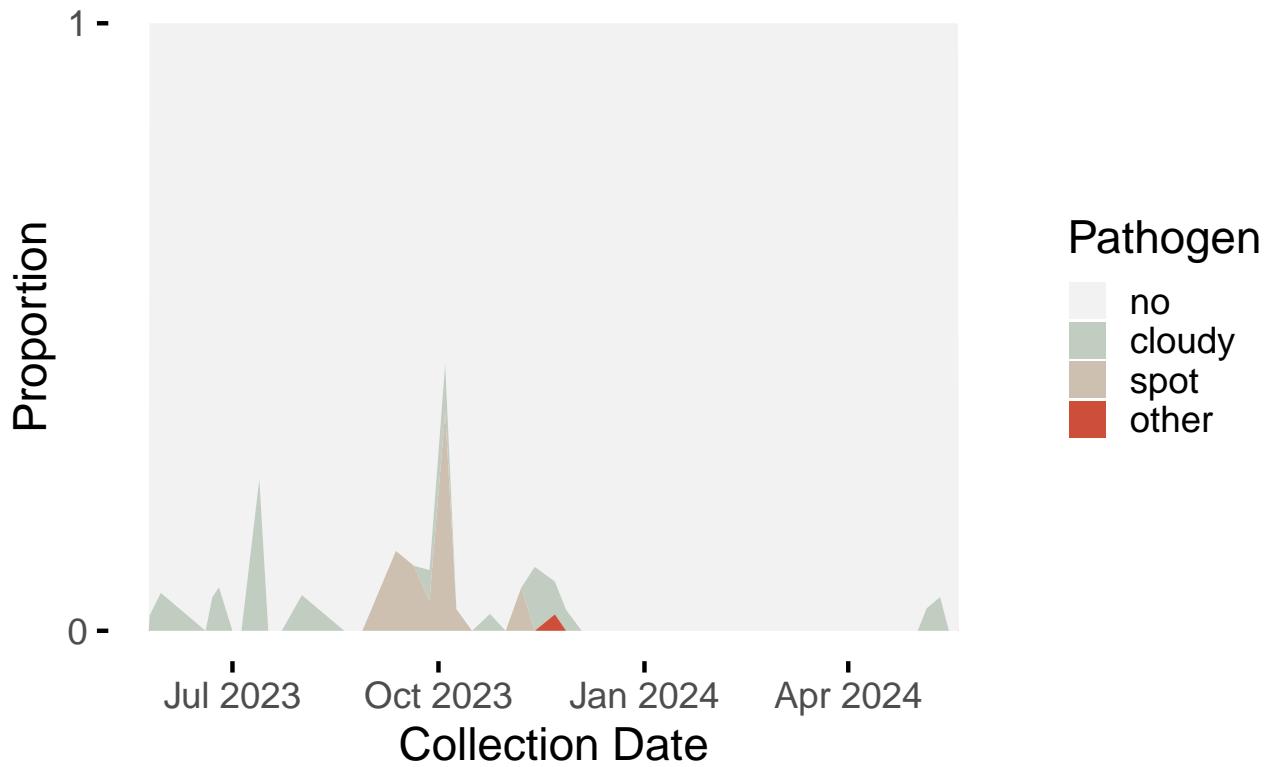


Size also varied, but primarily between rather than within species.

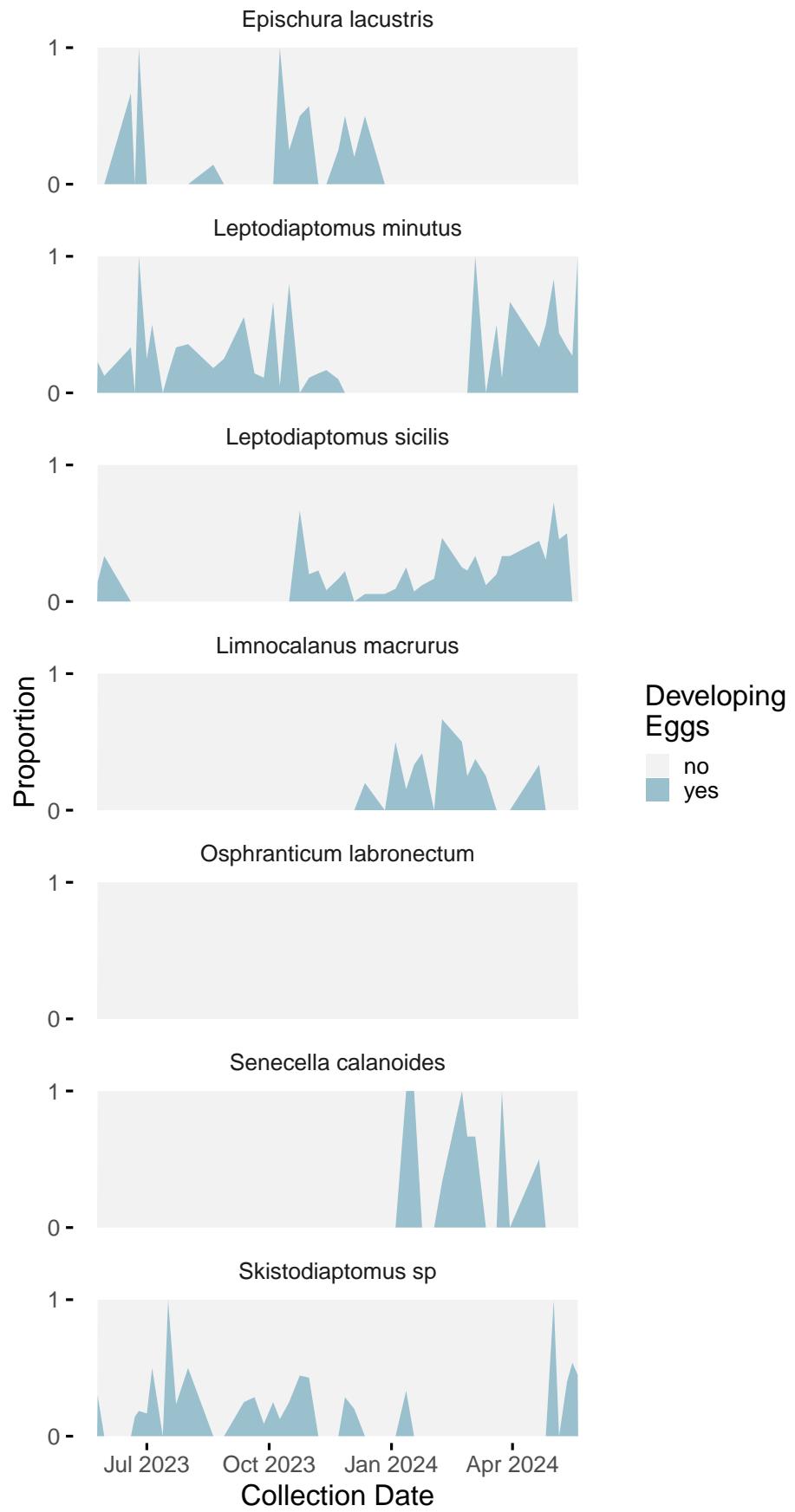


The samples captured the broad seasonal changes in calanoid copepod community composition in the lake. We note, however, that rare species (e.g. *Senecella* and *Limnocalanus*) were often preferentially sampled, so are over-represented in the data set.

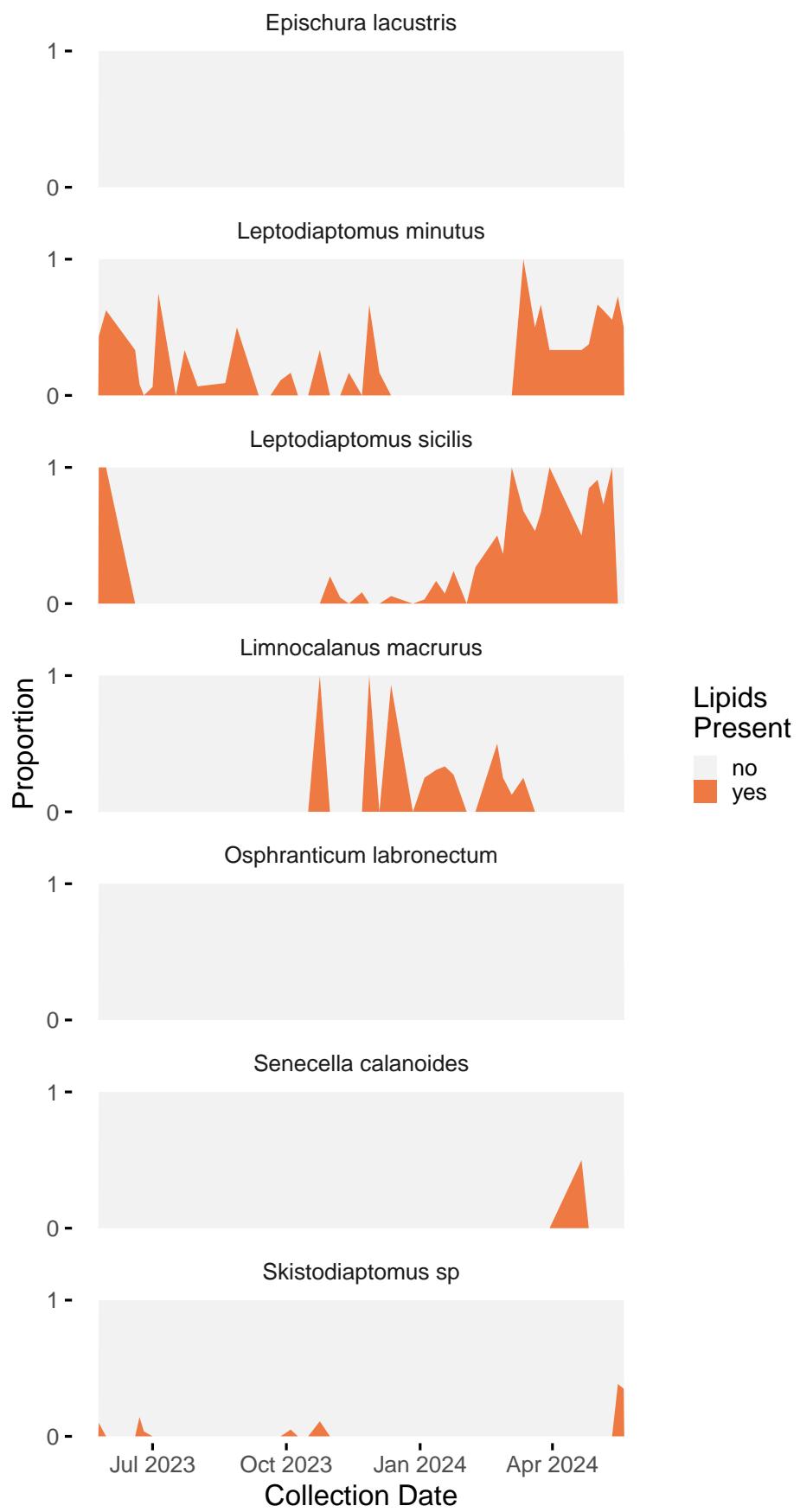
Throughout the season, the prevalence of various unidentified pathogens also varied, with very little infection observed during the Winter and Spring.



The transparent bodies of these copepods also allowed us to examine seasonal patterns in lipid reserves and in the production of eggs. Maturing oocytes are visible in female copepods before they are released. There was no strong seasonal cycle in the production of these eggs in any species, and instead, females were reproductively active throughout their respective seasons of occurrence.



The presence of lipids varied across species, with only *L. minutus*, *L. sicilis*, and *Limnocalanus* regularly possessing lipid stores.

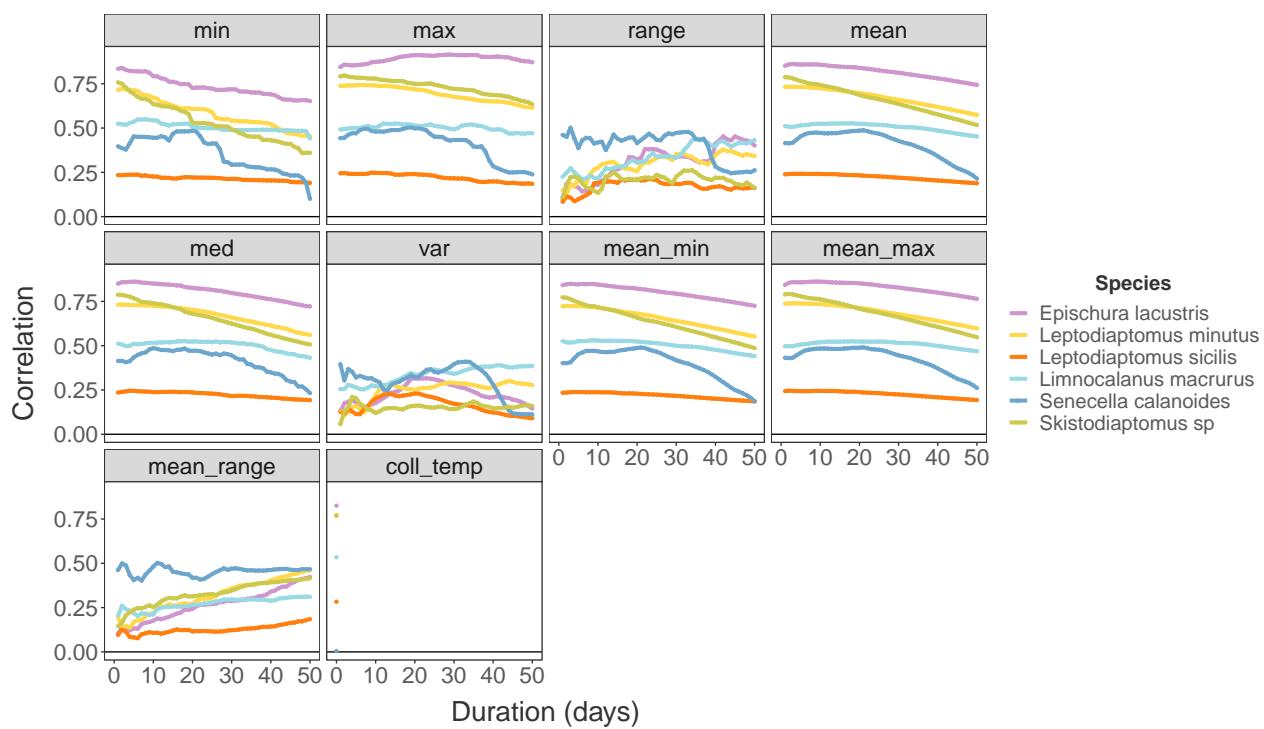


Temperature Variability

Lake Champlain is highly seasonal, with both average temperatures and temperature variability changing throughout the year. These patterns in the experienced thermal environment may drive the observed variation in copepod thermal limits. However, the time period affecting copepod thermal limits is unknown. Depending on the duration of time considered, there are large changes in the experienced environment, in particular regarding the temperature range and variance. Consider for example three time periods: the day of collection, one week prior to collection, and four weeks prior to collection. While the overall pattern is similar, we can see that, unsurprisingly, considering longer periods of time results in larger ranges and slightly changes the pattern of variance experienced.

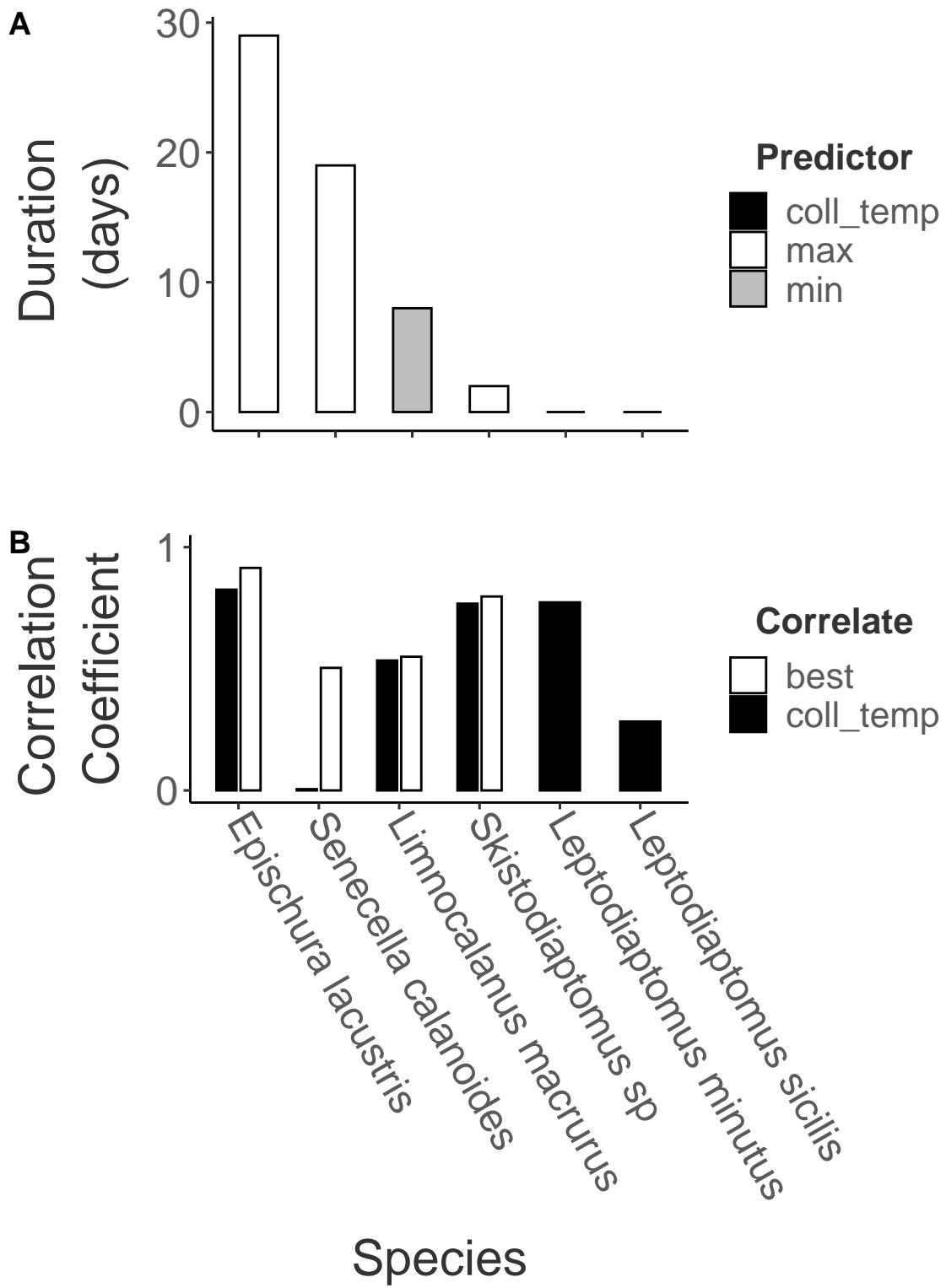
Organisms are unlikely to acclimate instantaneously to changes in temperature. To explore the potential temporal window these copepods are responding to, we examined the correlation between thermal limits and summaries of the thermal environment over different periods of time. For each species (inclusive of all sexes and stages), we examined the correlation between CTmax and one of nine representations of the thermal environment calculated for periods of time from 1 to 60 days before collection. These parameters include the overall maximum, minimum, median, and mean temperature for the period of time, the temperature range and variance during this time, and the mean daily temperature maximum, minimum, and range. We also examined the correlation between CTmax and the temperature recorded at the time of collection.

Shown below are the correlation coefficients for these relationships. Each facet shows the relationship for a different parameter, plotted against the duration of the time period before collection.



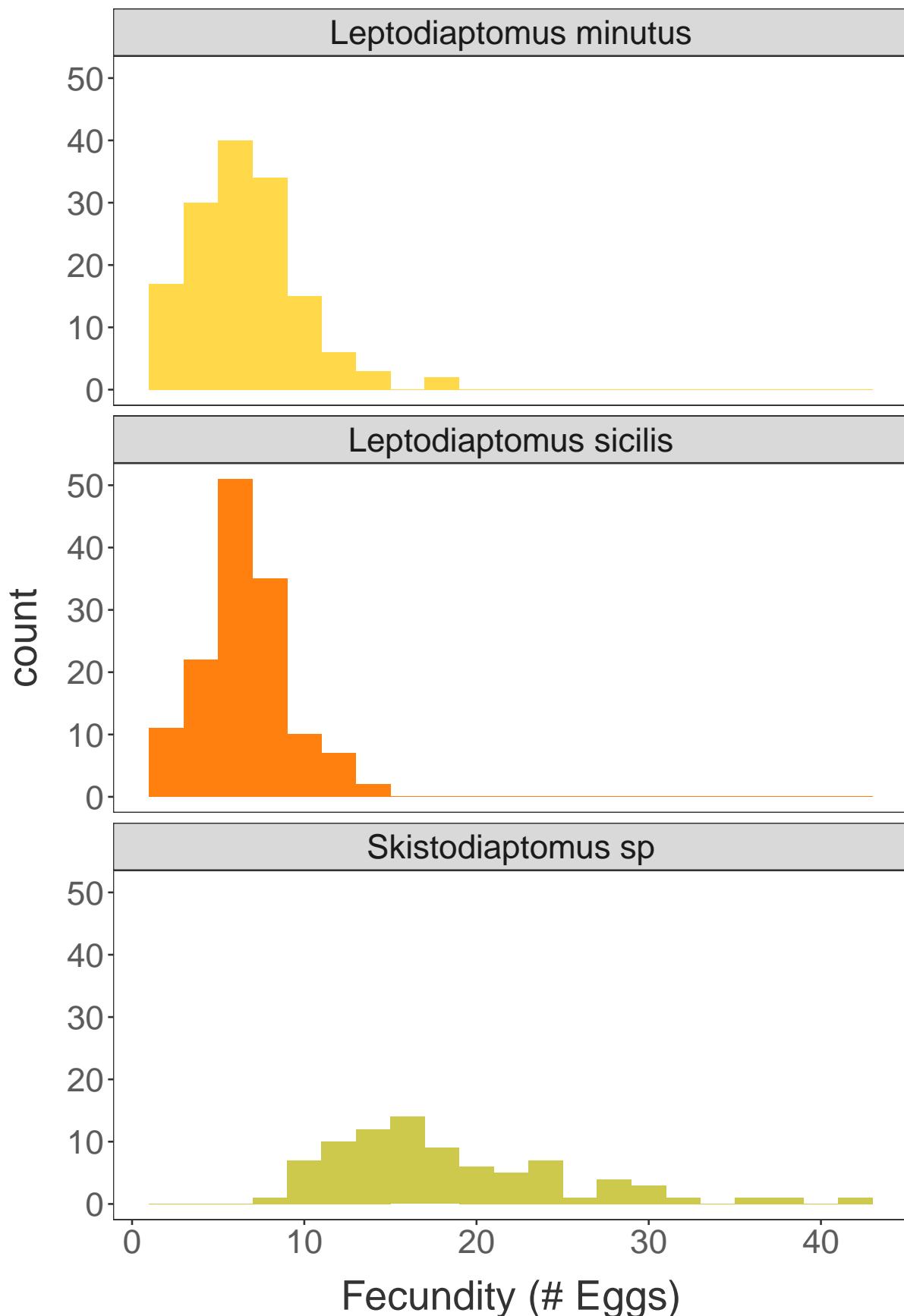
This table contains the top three factors for each species (based on correlation coefficient).

Shown here is a graphical summary of the duration of the best predictors for each species. Note that for the two Leptodiaptomids, collection temperature had the largest correlation coefficient so duration is zero. This representation highlights that there is variation across the community not only in the potential driver (e.g. minimum vs. maximum temperatures) but also in the duration of time. This variation is not grouped by season (the winter and summer communities both have representative species apparently responding to short and long durations).



Trait Variation

Shown below are the clutch size distributions for the three diaptomiid species, which produce egg sacs that allow for easy quantification of fecundity.



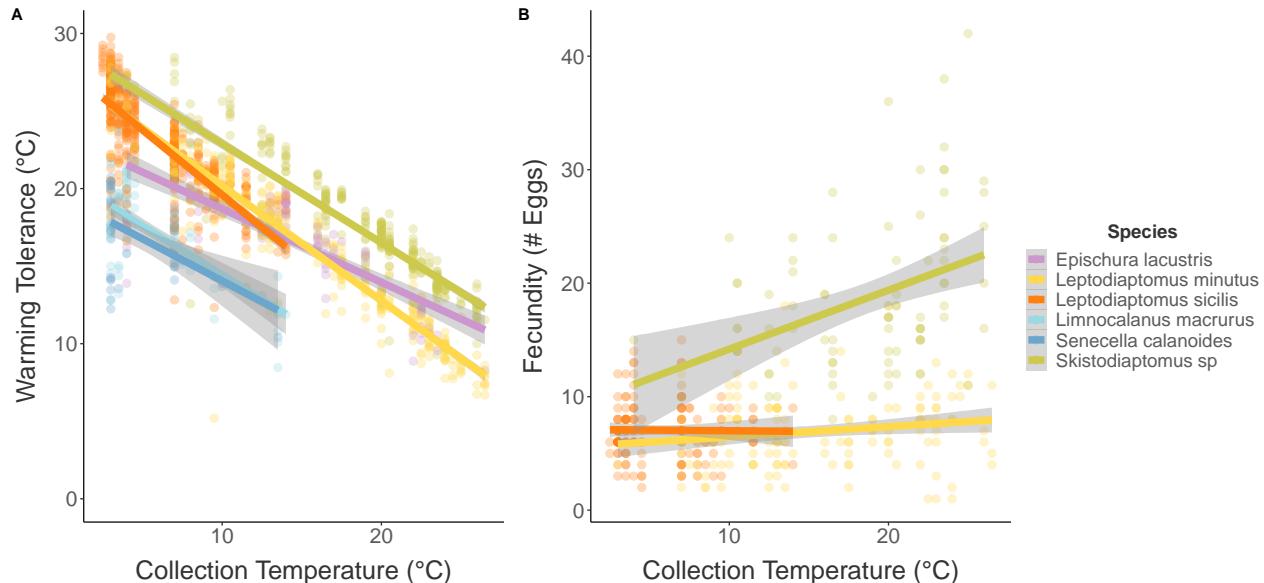
One of the main aims of this project is to examine the patterns and processes driving variation in upper thermal limits across these species of copepods.

Variation with temperature

We expect one of the primary drivers of copepod thermal limits to be temperature, as individuals acclimate to seasonal changes. Shown below are the seasonal patterns of when copepods were included in CTmax measurements (a proxy for the season of occurrence), and thermal limits for each species plotted against the temperature at the time of collection. We generally see an increase in thermal limits with increasing collection temperature.

The interaction between seasonal changes in temperature and the acclimation of thermal limits likely affects vulnerability of each species to warming. Shown below are warming tolerance values for each species, calculated as the difference between individual CTmax and the temperature at the time of collection. All species maintained some degree of buffer between environmental temperatures and upper thermal limits, but *L. minutus* appears to approach its upper thermal limit during the warmest collections during the summer.

Also shown below is the relationship between fecundity (the number of eggs contained in a clutch) for the three diaptomid species. For the two *Leptodiaptomus* species, there is no relationship between clutch size and temperature, while there appears to be a general increase in clutch size with temperature in the *Skistodiaptomus* species.

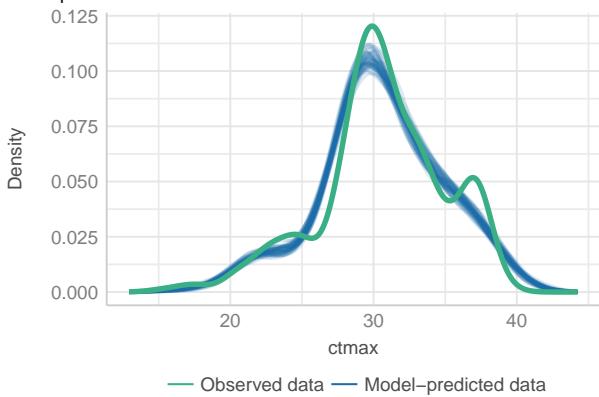


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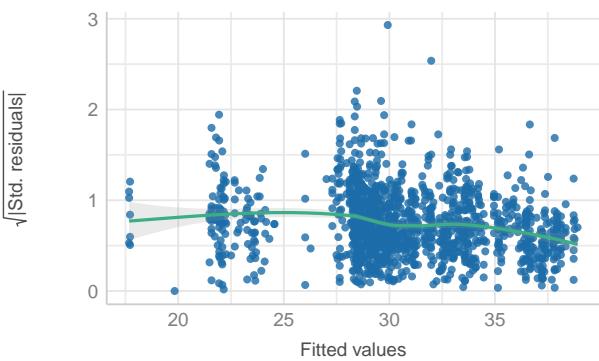
## Single term deletions
##
## Model:
## ctmax ~ sp_name * sex * temp_cent + (1 | days_in_lab)
##                      npar      AIC      LRT Pr(Chi)
## <none>                  5280.1
## sp_name:sex:temp_cent   10 5281.0 20.887  0.0219 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
## Name      | Model | BF | df | df_diff | Chi2 | p
## -----
## minimal.model | lmerMod |      | 11 |      |      |
## full.model    | lmerMod | 0.001 | 38 |  27.00 | 180.70 | < .001
## Models were detected as nested (in terms of fixed parameters) and are compared in sequential order.

```

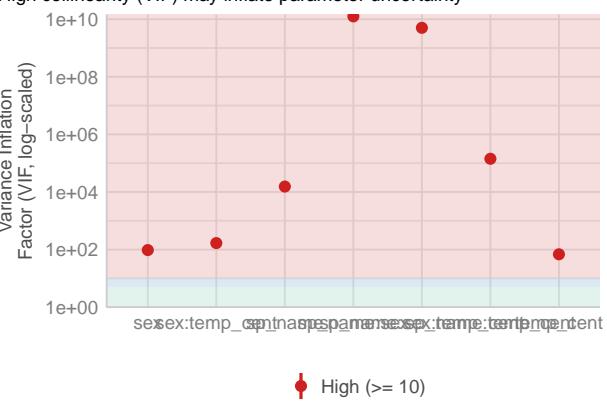
Posterior Predictive Check
Model-predicted lines should resemble observed data line



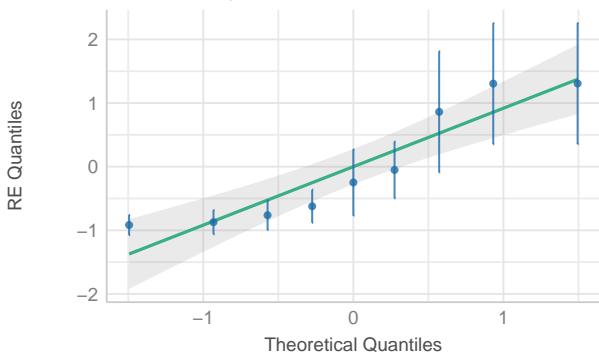
Homogeneity of Variance
Reference line should be flat and horizontal



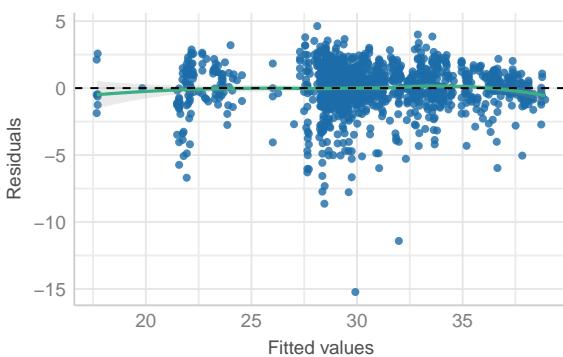
Collinearity
High collinearity (VIF) may inflate parameter uncertainty



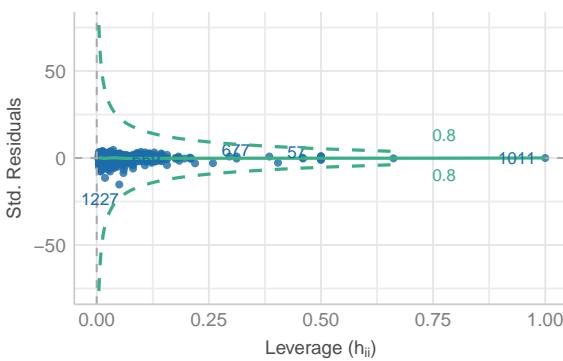
Normality of Random Effects (days_in_lab)
Dots should be plotted along the line



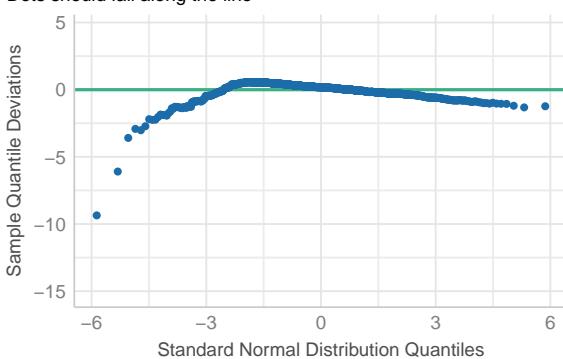
Linearity
Reference line should be flat and horizontal



Influential Observations
Points should be inside the contour lines



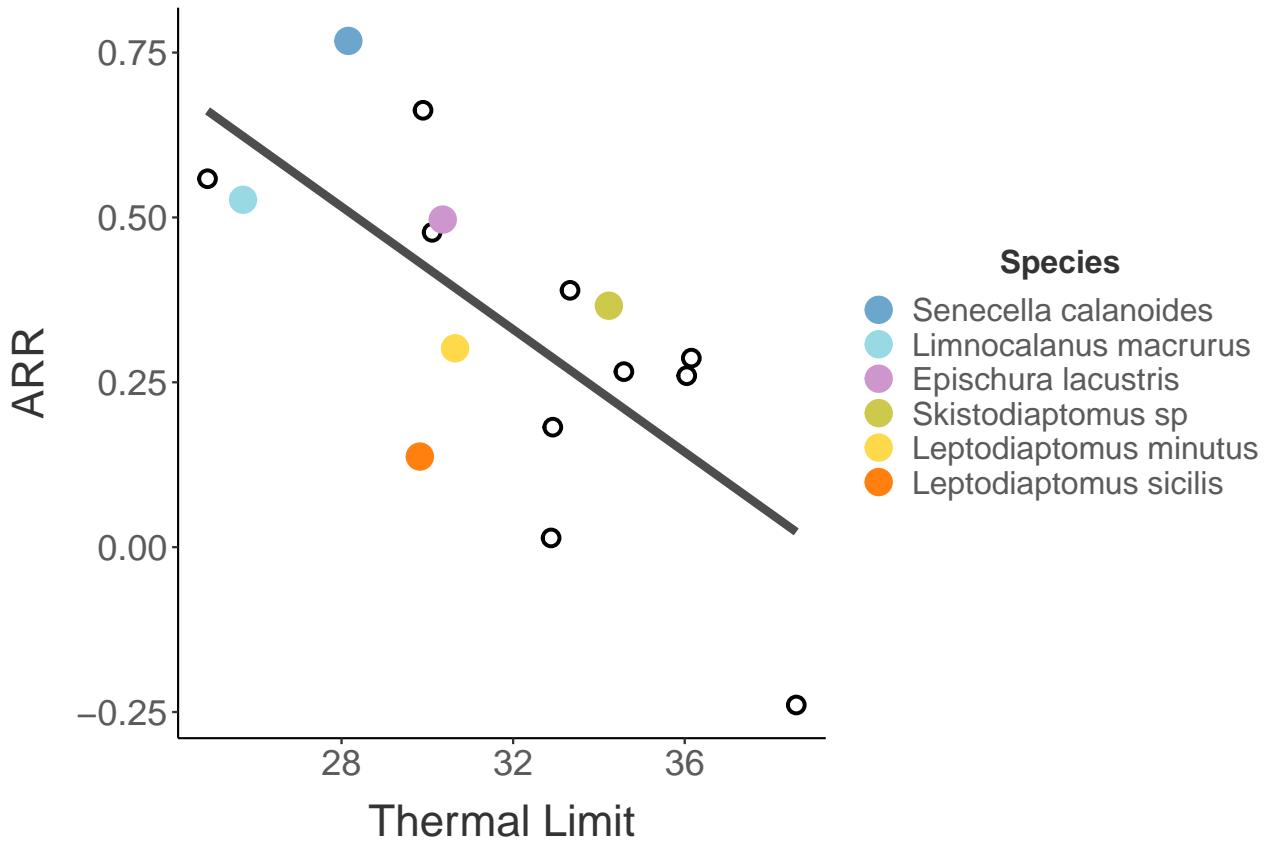
Normality of Residuals
Dots should fall along the line



```

## Analysis of Deviance Table (Type III Wald chisquare tests)
##
## Response: ctmax
##
##              Chisq Df Pr(>Chisq)
## (Intercept) 4619.014 1 < 2.2e-16 ***
## sp_name      344.724  5 < 2.2e-16 ***
## sex          51.233  2 7.495e-12 ***
## temp_cent    53.731  1 2.299e-13 ***
## sp_name:sex   10.611 10 0.38866
## sp_name:temp_cent 39.512  5 1.873e-07 ***
## sex:temp_cent 31.961  2 1.147e-07 ***
## sp_name:sex:temp_cent 20.616 10 0.02393 *
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```



Sex and stage variation in thermal limits

Previous sections have generally lumped juvenile, female, and male individuals together. There may be important stage- or sex-specific differences in CTmax though. For all species but *Osphranticum*, we have measurements for individuals in different stages and of different sexes.

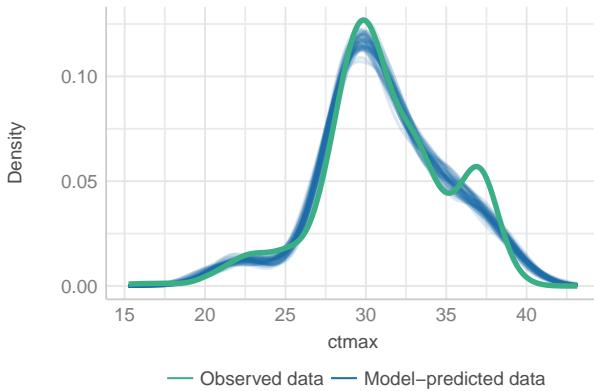
Species	Juvenile	Female	Male
Epischura lacustris	37	45	20
Leptodiaptomus minutus	12	273	39
Leptodiaptomus sicilis	31	356	95
Limnocalanus macrurus	4	43	39
<i>Osphranticum</i> labronectum	0	1	0

Species	Juvenile	Female	Male
Senecella calanoides	13	21	8
Skistodiaptomus sp	15	232	28

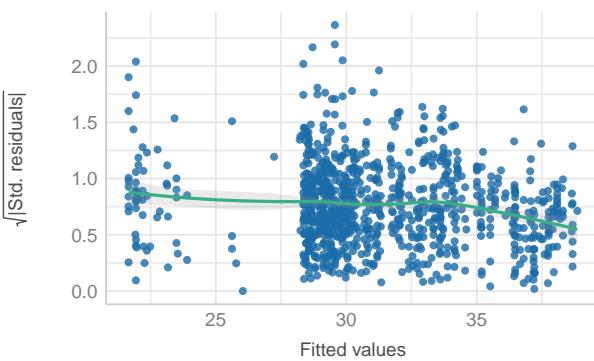
Across group comparisons show that there are generally no differences in thermal limits (represented here as the residuals from a $CT_{max} \sim collection_temp \times species$ linear regression), with the exception of *Senecella* males, which may have lower thermal limits (although sample sizes are very small in this group).

```
## Single term deletions
##
## Model:
## ctmax ~ sp_name * collection_temp + dev_eggs + pathogen + lipids +
##      (1 | days_in_lab)
##          npar     AIC      LRT   Pr(Chi)
## <none>           3601.6
## sp_name          5 3804.2 212.619 < 2.2e-16 ***
## collection_temp  0 3601.6   0.000
## dev_eggs         1 3602.0   2.391   0.1220
## pathogen          3 3629.4  33.832 2.149e-07 ***
## lipids            1 3600.0   0.416   0.5189
## sp_name:collection_temp  5 3635.7  44.139 2.171e-08 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

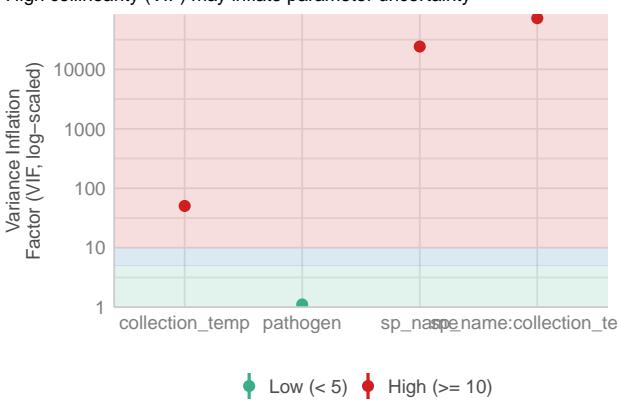
Posterior Predictive Check
Model-predicted lines should resemble observed data line



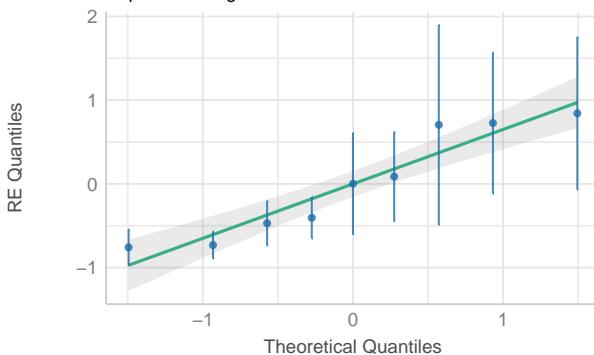
Homogeneity of Variance
Reference line should be flat and horizontal



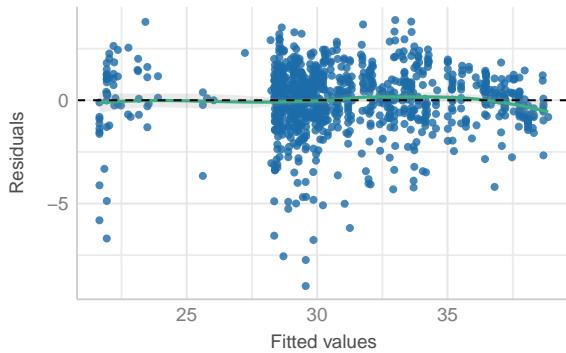
Collinearity
High collinearity (VIF) may inflate parameter uncertainty



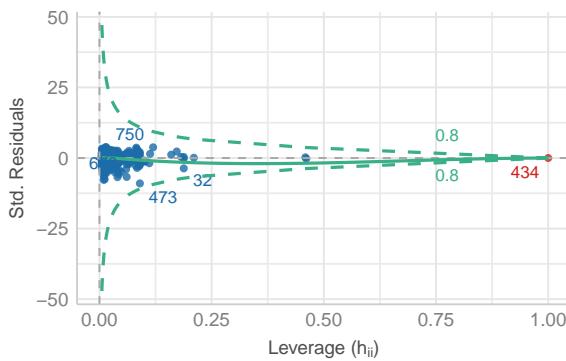
Normality of Random Effects (days_in_lab)
Dots should be plotted along the line



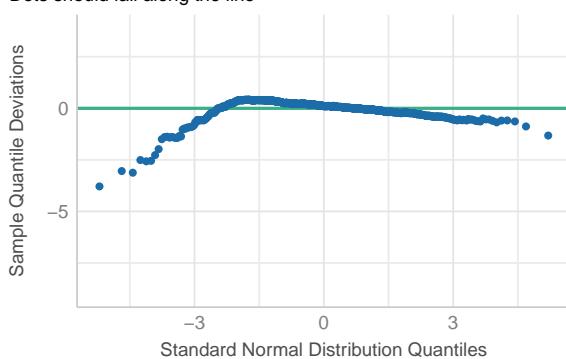
Linearity
Reference line should be flat and horizontal



Influential Observations
Points should be inside the contour lines



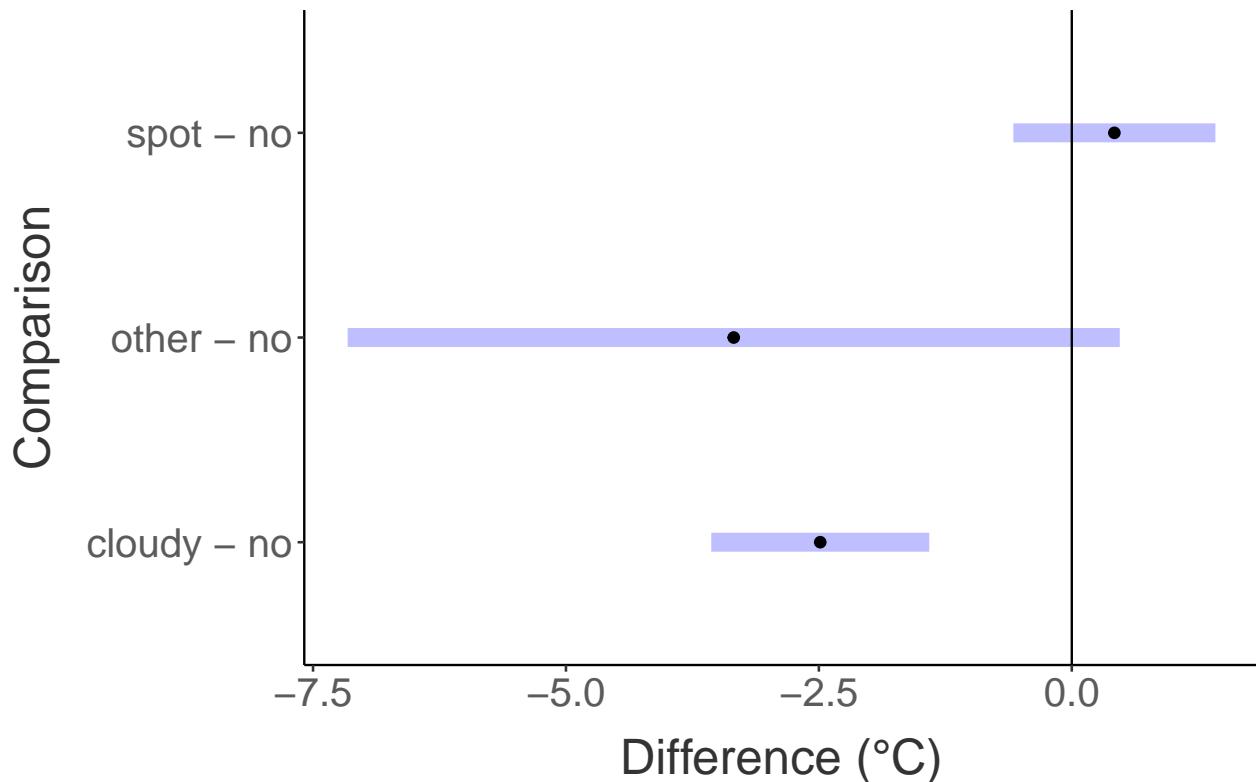
Normality of Residuals
Dots should fall along the line



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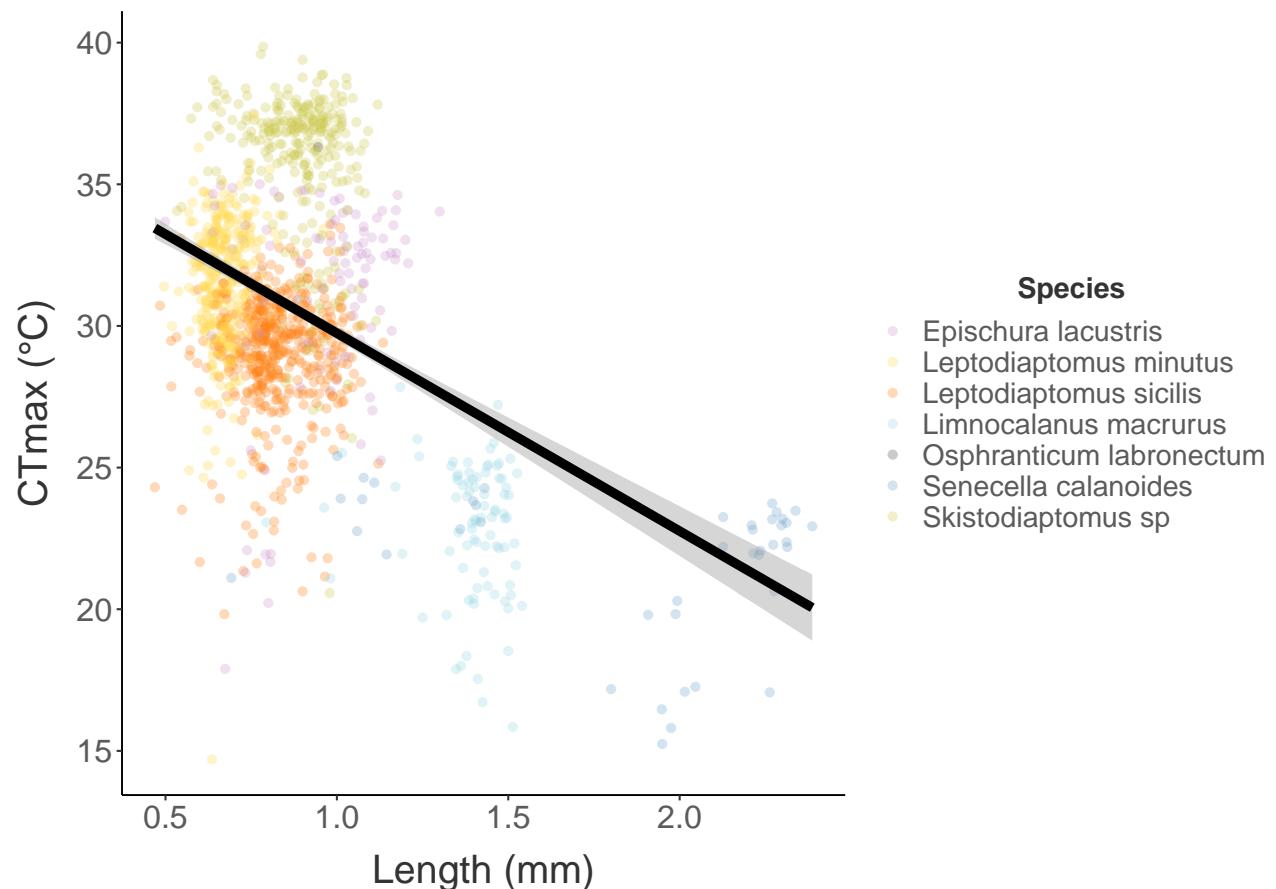
## Analysis of Deviance Table (Type III Wald chisquare tests)
##
## Response: ctmax
##              Chisq Df Pr(>Chisq)
## (Intercept) 570.328 1 < 2.2e-16 ***
## sp_name     234.027 5 < 2.2e-16 ***
## collection_temp    72.589 1 < 2.2e-16 ***
## pathogen      35.282 3 1.062e-07 ***
## sp_name:collection_temp 43.558 5 2.847e-08 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

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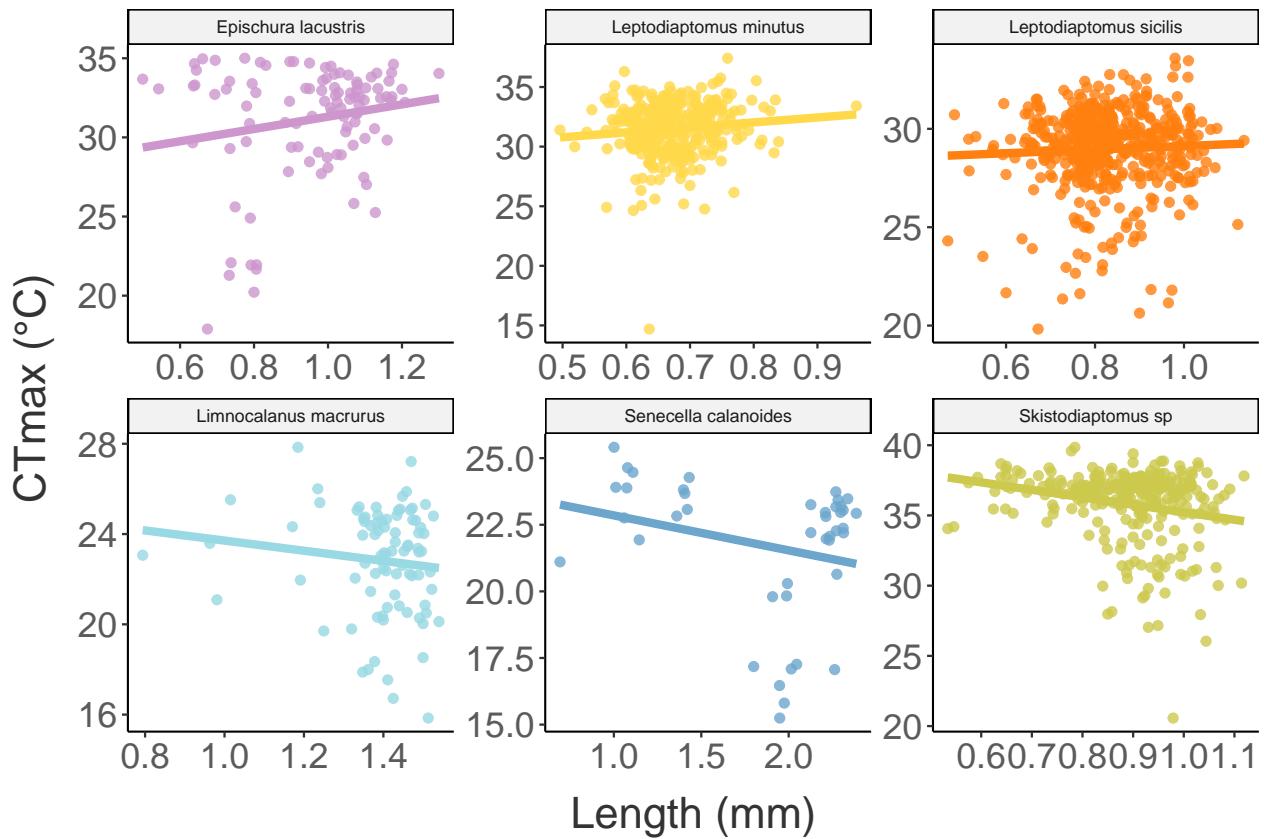


Trait Correlations and Trade-offs

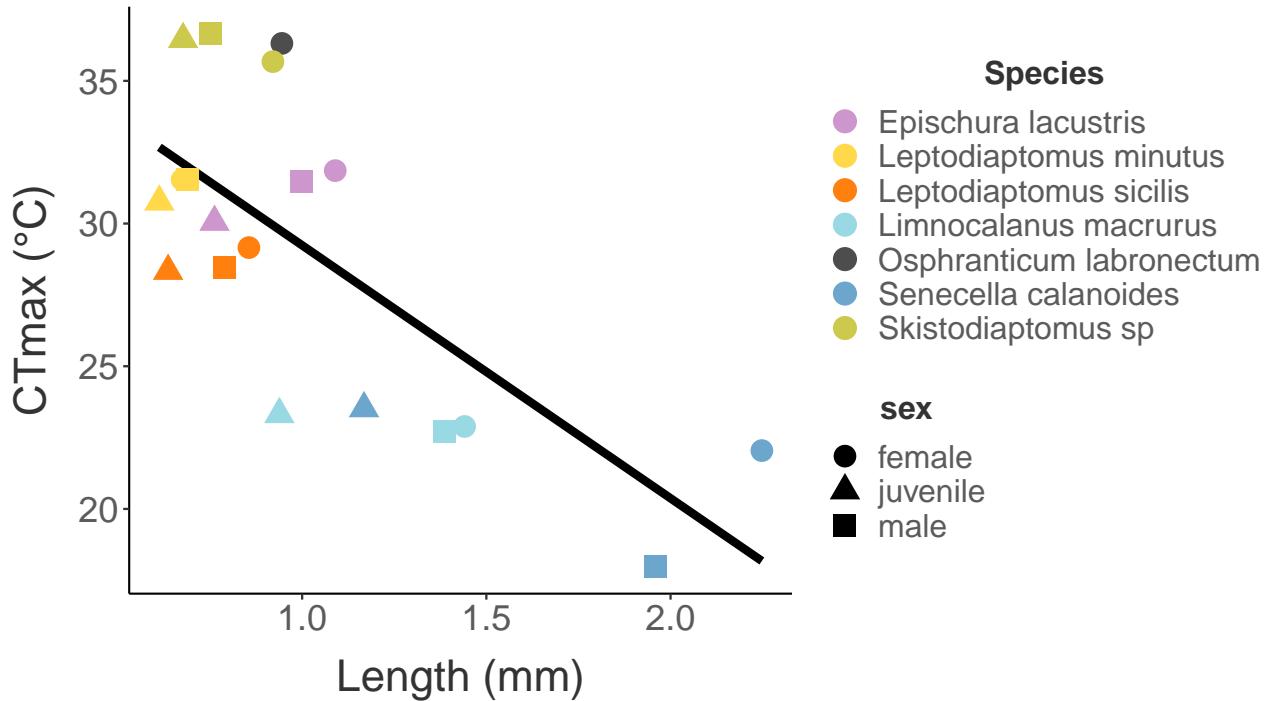
A relationship between size and upper thermal limits has been suggested in a wide range of other taxa. Shown below are the measured upper thermal limits plotted against prosome length. The overall relationship (inclusive of all species) is shown as the black line in the background. Regressions for each individual species are also shown. Across the entire assemblage, there is a strong decrease in thermal limits with increasing size.



Shown here is the relationship for each species individually.

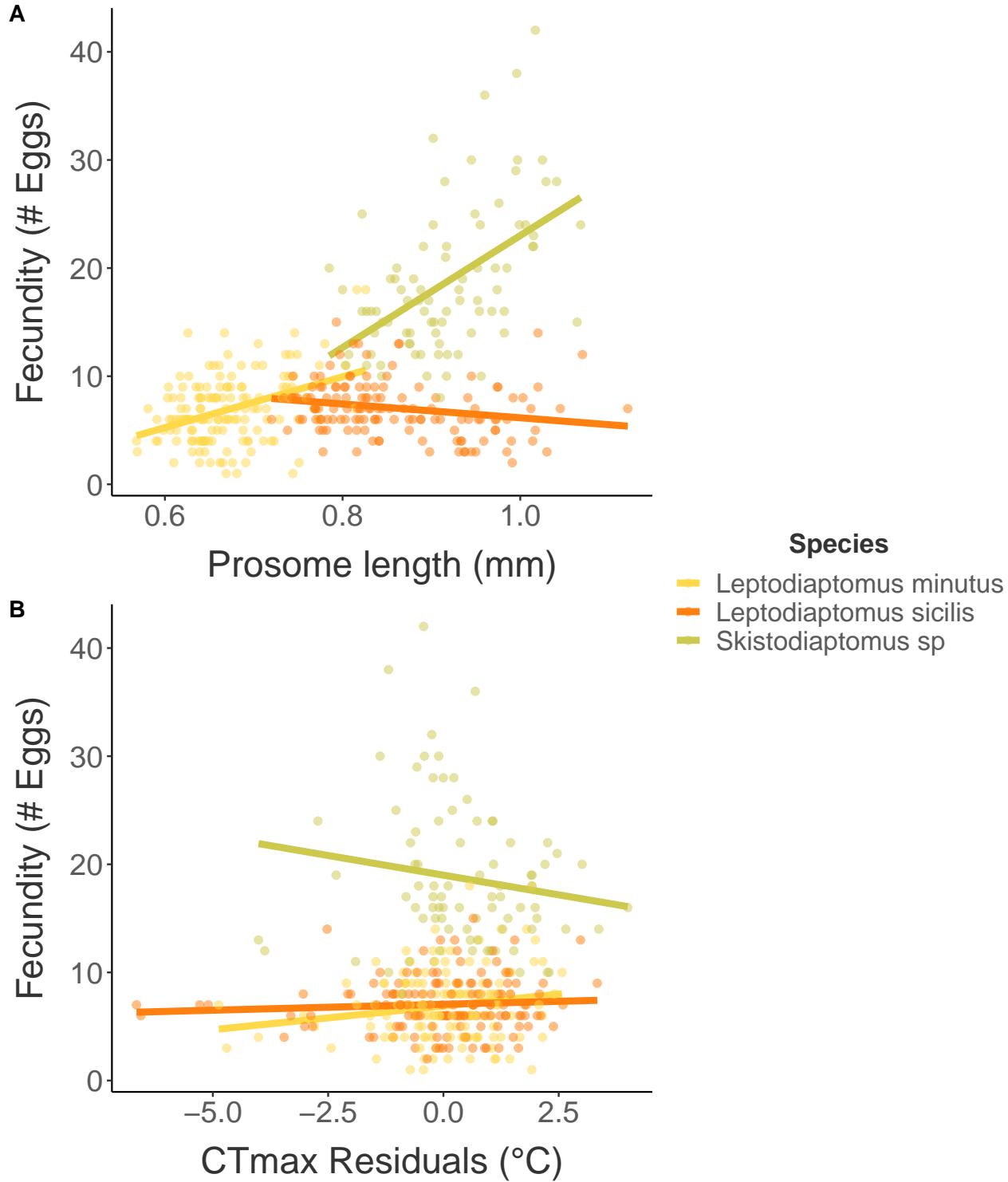


Shown below is the relationship between mean size and mean thermal limits for females of each species. We see that larger species within the community tend to have a lower thermal limit than smaller species.



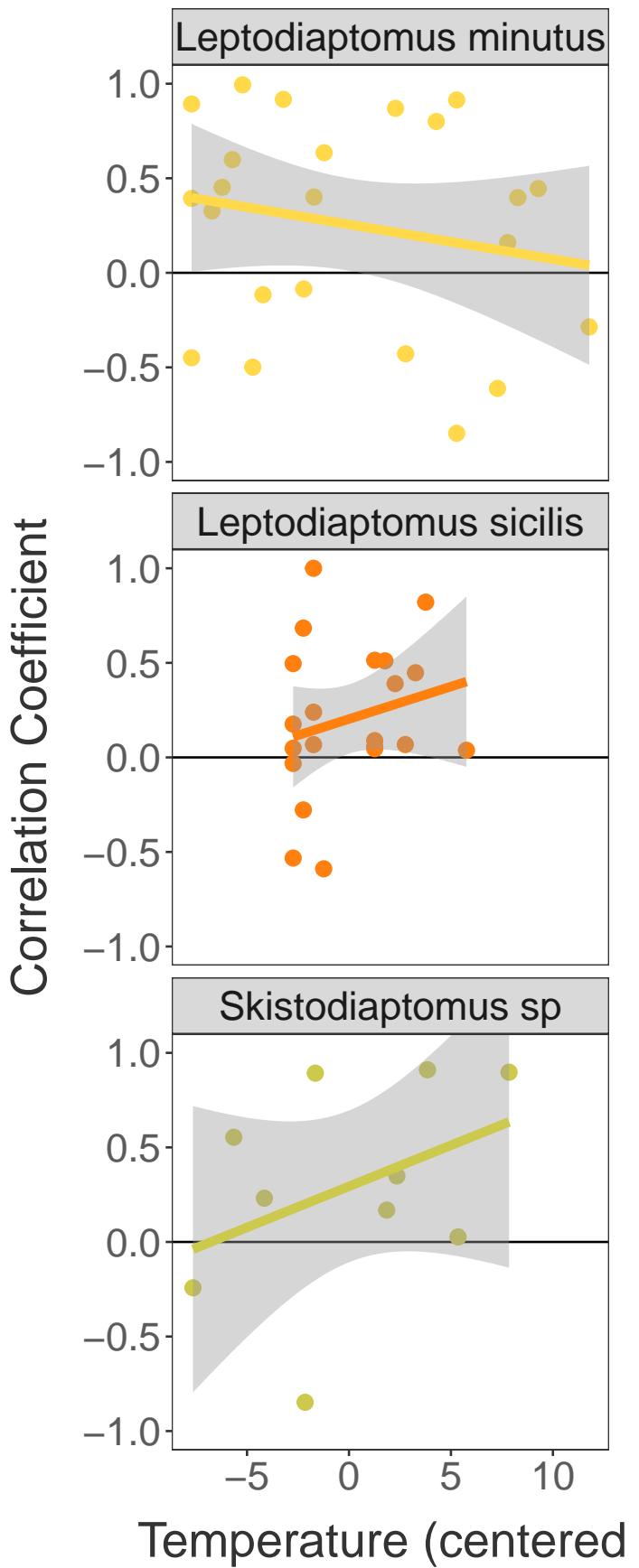
Shown here is the relationship between fecundity and size, showing the classic pattern of increasing egg production with increasing size.

Individuals may also allocate energy to different fitness related traits, prioritizing reproductive output over environmental tolerance, for example. Shown below is the relationship between CTmax residuals (again, controlling for the effects of collection temperature) against fecundity. We can see clearly that individuals with increased fecundity are not decreasing thermal limits, suggesting that there is no energetic trade-off between these traits.



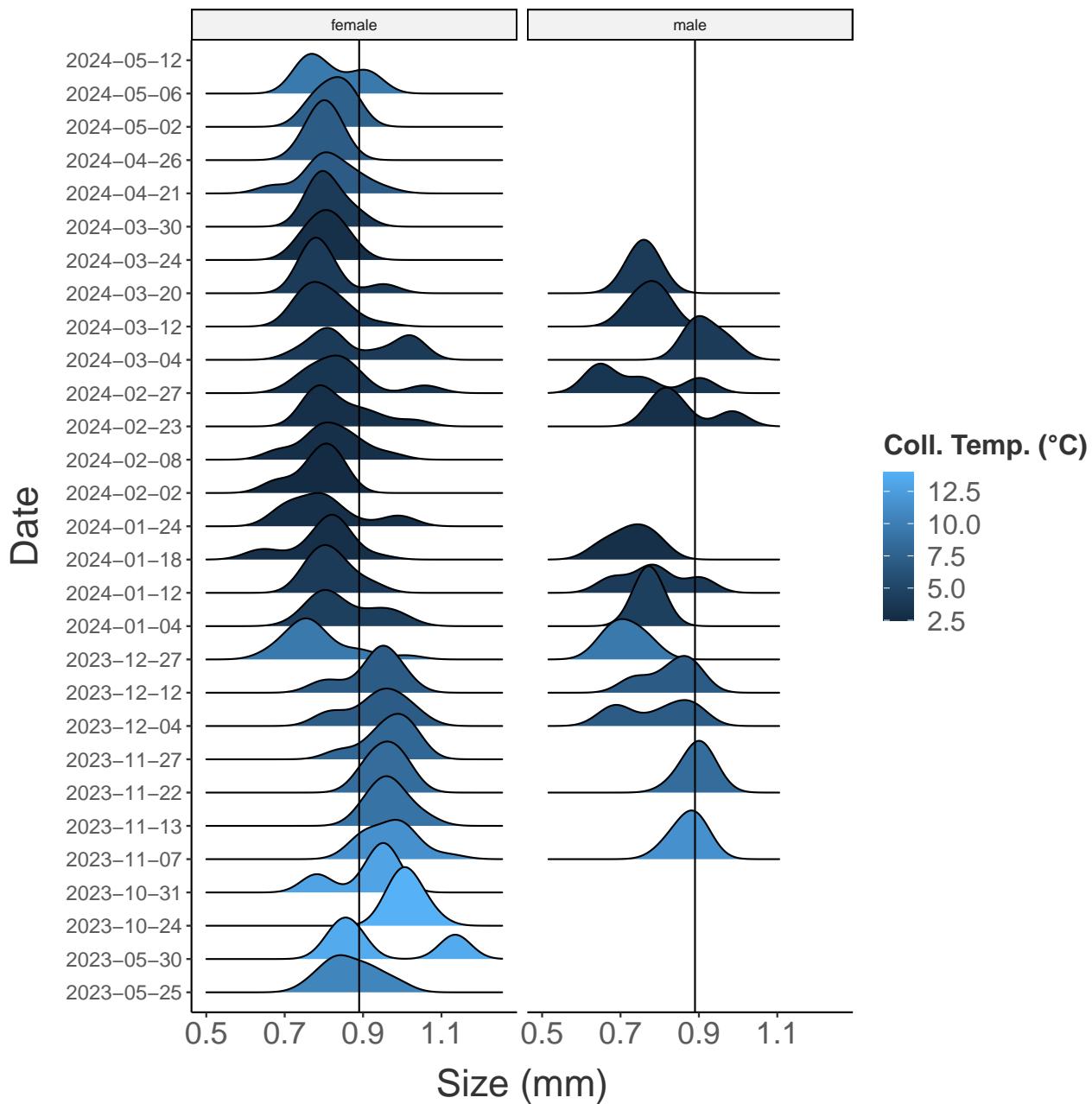
Previous studies have shown that the magnitude of the size-fecundity correlation may be environmentally-

dependent. This is not visible in the data from these collections.

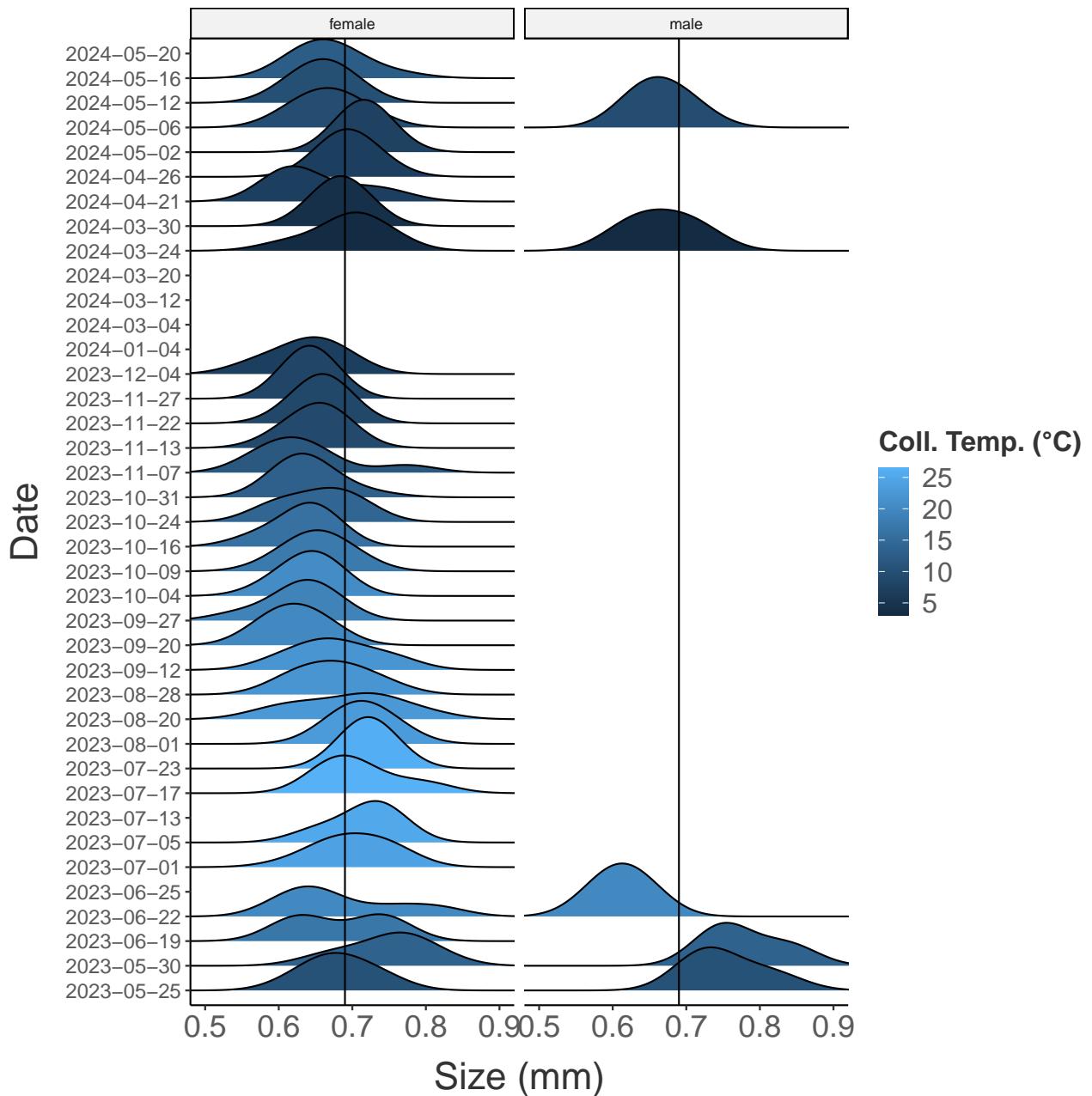


Other patterns in variation

Leptodiaptomus sicilis is the most abundant species during the winter. There was a large shift in the size of mature females towards the end of December. These large and small individuals are the same species (confirmed via COI sequencing), suggesting this shift may instead reflect a transition from one generation to another. This size difference may be caused by differences in the developmental environments. For example, individuals developing in January grow up at very low temperatures, and therefore may reach larger sizes. These individuals over-summer in deep waters, then re-emerge in October and produce a new generation. Water temperatures are still fairly high through November, which results in a generation of smaller individuals. These individuals mature in time to produce a new generation in January.

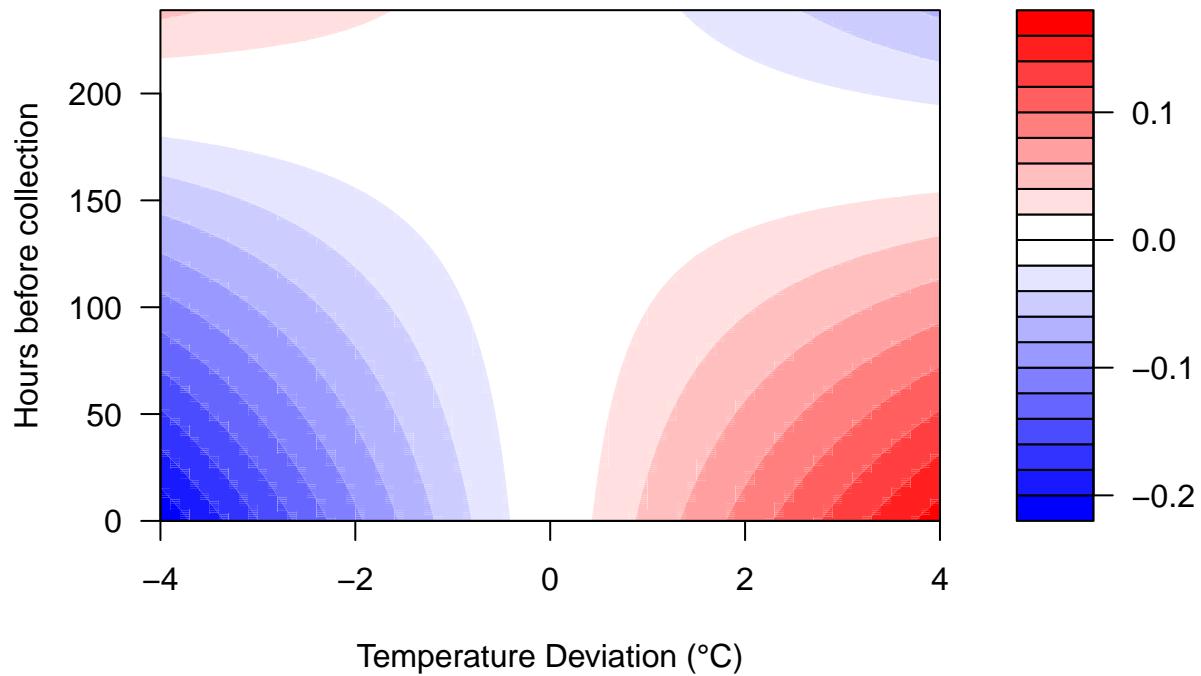
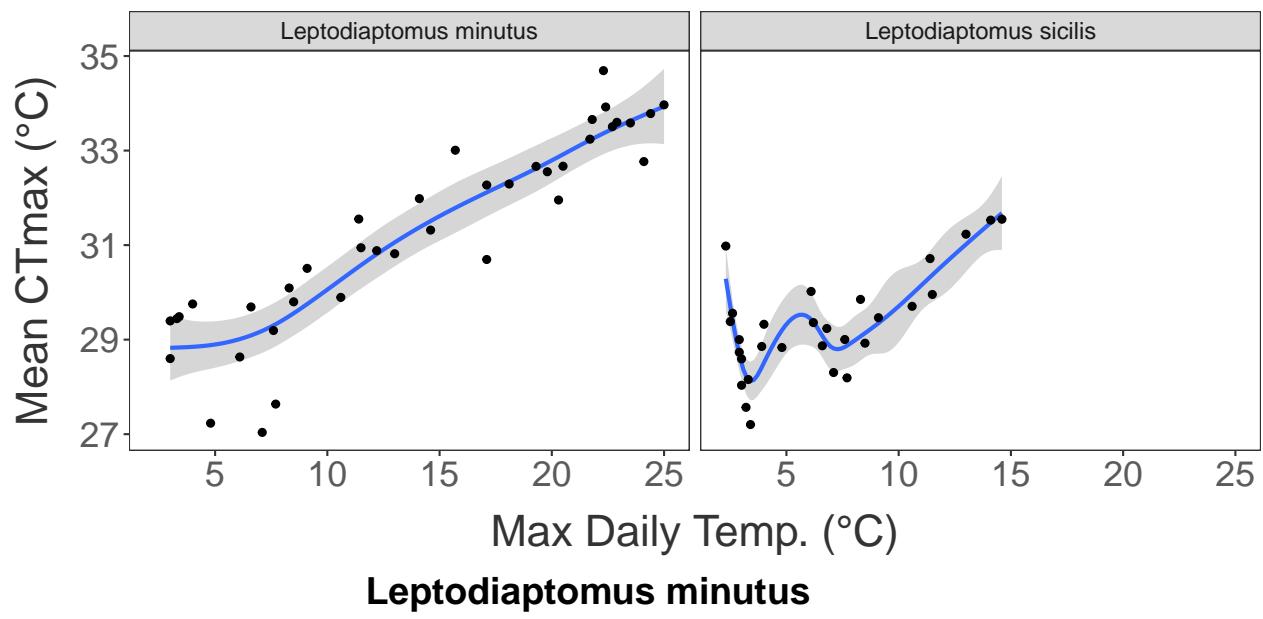


A similar, but less distinct pattern can be observed in *L. minutus* individuals as well.

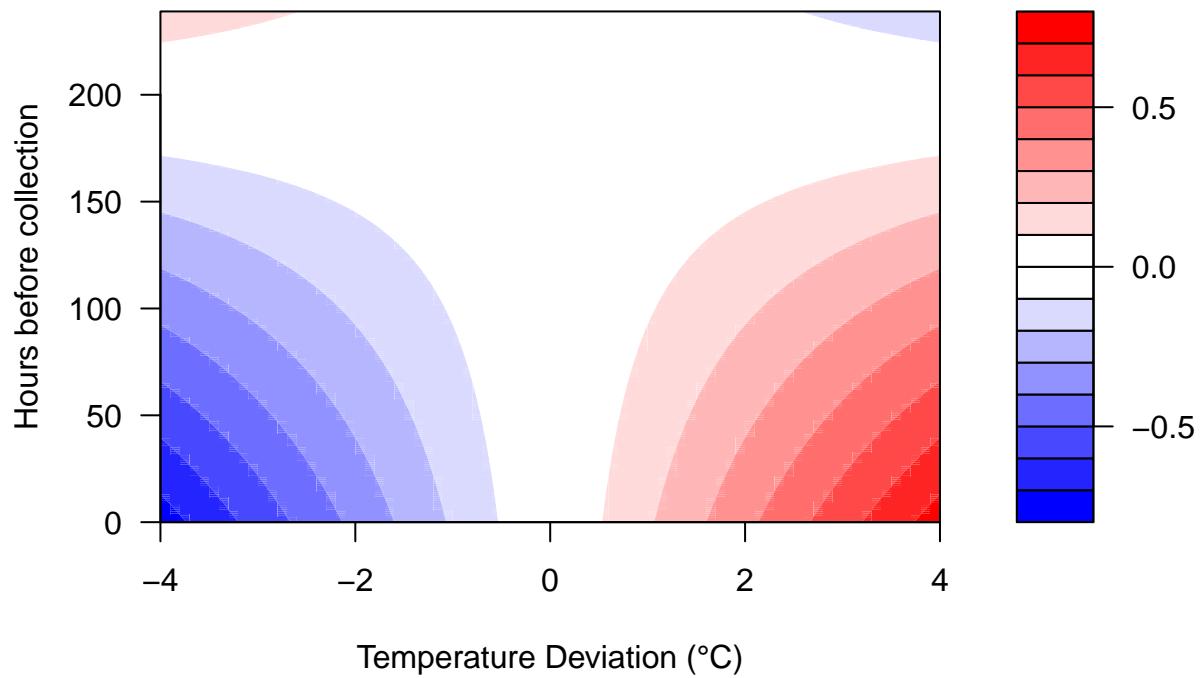


Distribution Lag Non-Linear Model (DLNM approach)

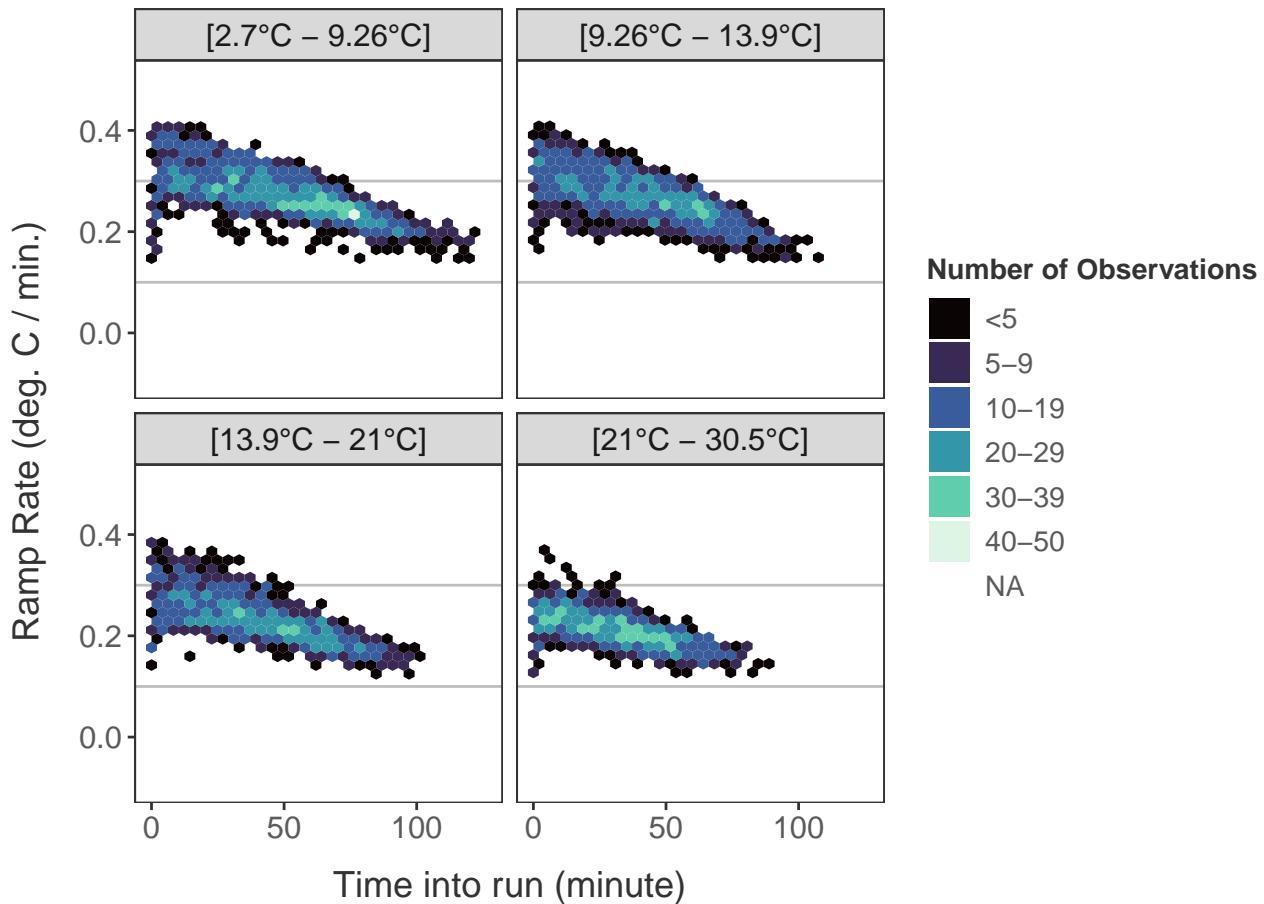
Distributed lag models examine a response variable, measured at multiple time points, as a function of the lagged occurrence of some predictor variable (response y at time t as a function of predictor $x(t\text{-lag})$). This method utilizes a bi-dimensional dose-lag-response function, which essentially examines not only the dose effect, but the effect of the timing of the dose.



Leptodiaptomus sicilis



Miscellany



Hindcasting vulnerability with different acclimation scenarios

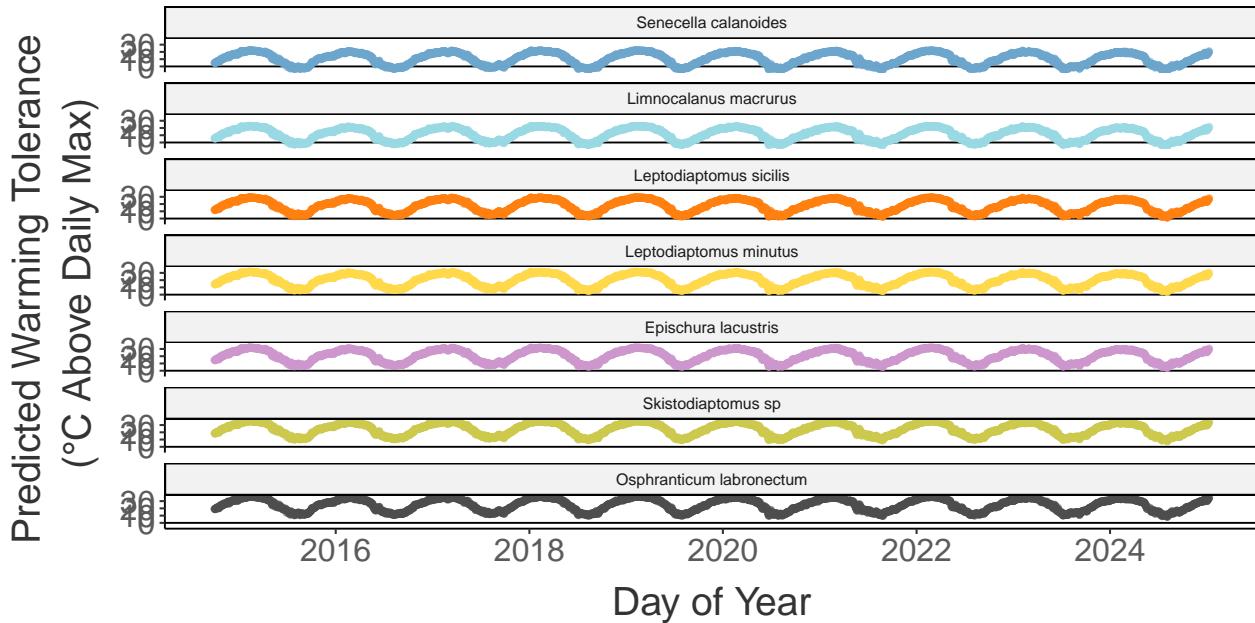
Using the observed thermal limit data, we can produce a hindcast of thermal stress for Lake Champlain copepods. We will use three different scenarios: 1) each species has a unique but fixed thermal limit (average female CTmax), 2) species have unique thermal limits and are able to acclimate (constant ARR across all species used to predict CTmax based on average daily temperatures), and 3) species have unique thermal limits and species-specific acclimation (CTmax predicted using whichever environmental factor and duration is the strongest candidate for driving acclimation from the correlation analysis).

Temperature data spans from 2014-10-01 to 2025-01-09.

Scenario 1

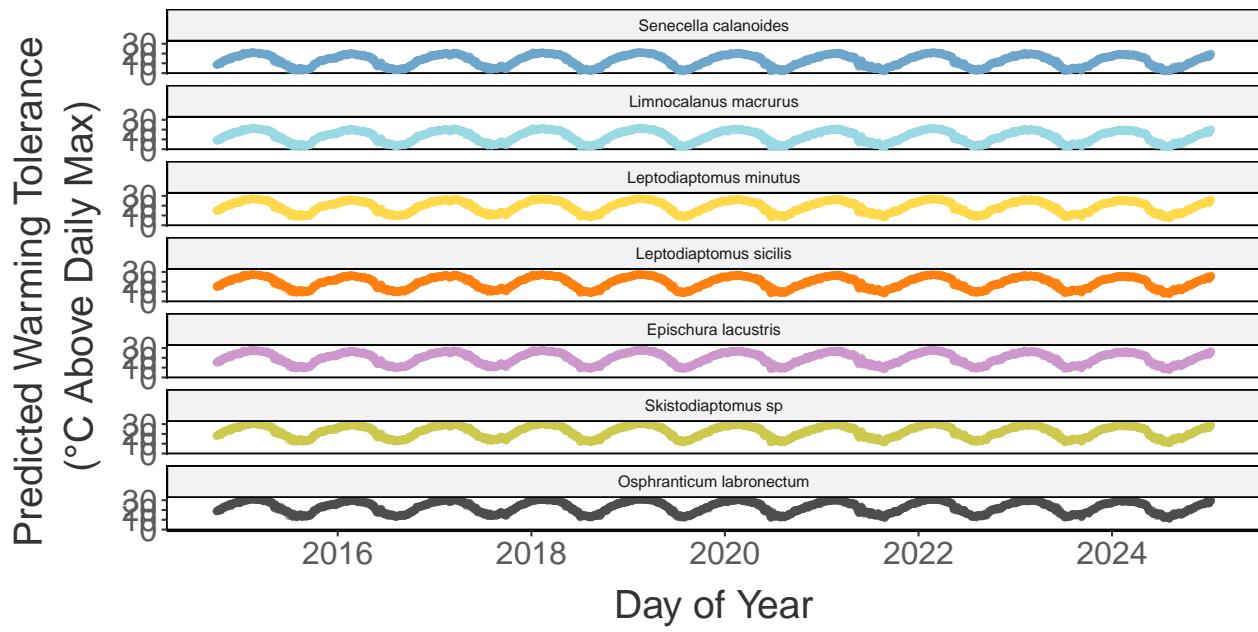
sp_name	mean_ctmax
Senecella calanoides	22.04
Limnocalanus macrurus	22.89
Leptodiaptomus sicilis	29.16
Leptodiaptomus minutus	31.54
Epischura lacustris	31.85
Skistodiaptomus sp	35.67
Osphranticum labronectum	36.31

In the simplest scenario, species thermal limits are static through time, represented by the average CTmax of adult female copepods. Temperatures approached the thermal limit of *Leptodiaptomus sicilis* on a handful of days. By contrast, *Senecella calanoides* and *Limnocalanus macrurus* were both exposed to substantial thermal stress throughout a large portion of the year, likely explaining why these species are absent from the community for the summer and fall periods.



Scenario 2

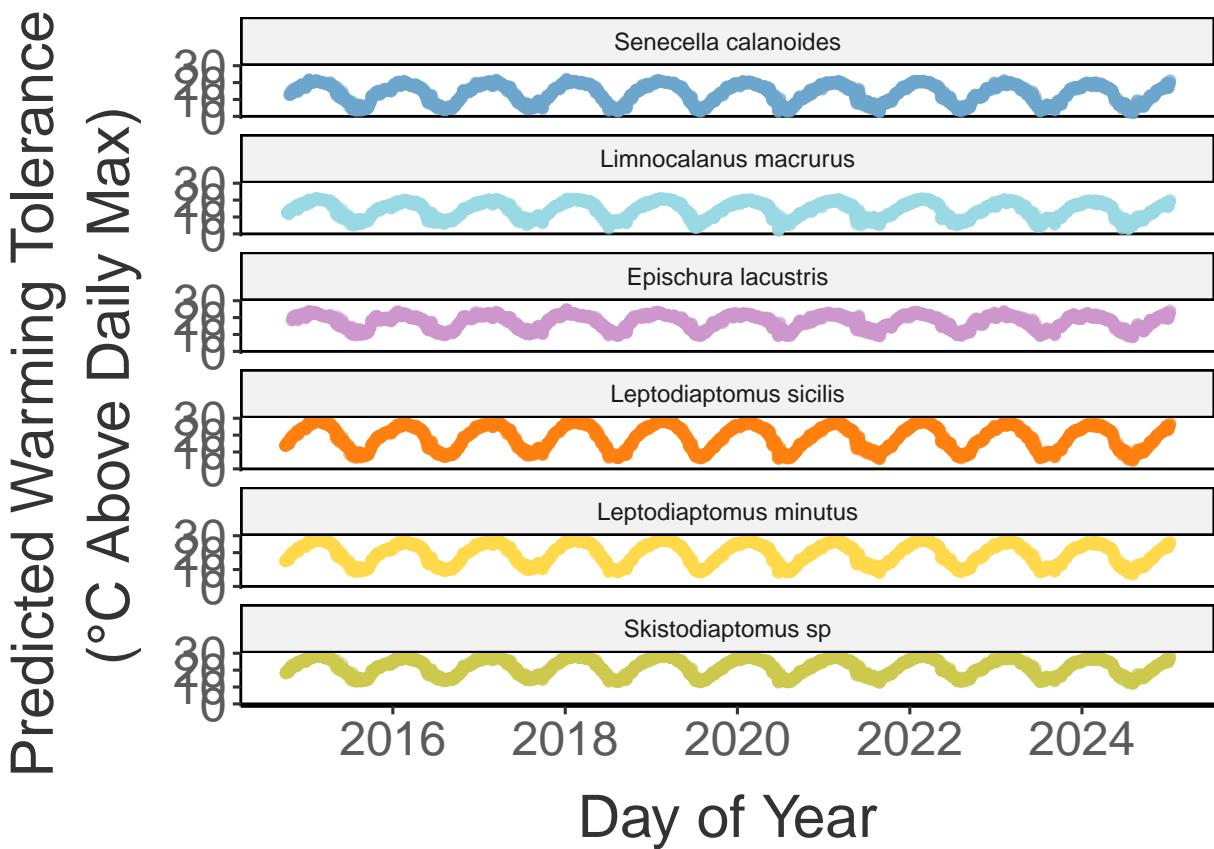
In the second scenario, thermal limits vary within and between species. A simple model is used to predict species thermal limits based on mean daily temperature (CTmax as a function of species and collection temperature, but without the interaction between these two factors). These predicted thermal limits are then compared against the maximum daily temperature to estimate thermal stress, as in Scenario 1. Including this simple form of acclimation in the model reduced the degree of thermal stress for each species, eliminating it entirely for *Leptodiaptomus sicilis*. Note that the magnitude of the predicted stress is low enough that removing the 5°C buffer around the predicted thermal limits would actually limit predicted thermal stress to just a few days for *Senecella calanoides*.



Scenario 3

The final scenario allows the environmental variable used to predict CTmax to vary between species. For species observed in fewer than 5 collections, we use the same approach as in Scenario 2. For species observed in more than 5 collections, however, the factor with the strongest correlation with CTmax is used to predict thermal limits. These factors are included below.

Species	Predictor	Duration	Correlation	P-Value
Epischura lacustris	max	29	0.9147764	0.0000000
Leptodiaptomus minutus	coll_temp	0	0.7732711	0.0000000
Leptodiaptomus sicilis	coll_temp	0	0.2833554	0.0000001
Limnocalanus macrurus	min	8	0.5496742	0.0000000
Senecella calanoides	max	19	0.5038896	0.0006688
Skistodiaptomus sp	max	2	0.7972819	0.0000000



This third approach did not affect the predicted patterns in *Limnocalanus* or *Senecella* (neither species has been observed in enough collections to estimate the effects of different environmental factors). Changing the acclimation approach did affect patterns in thermal limits in the other species though. The figure below shows how predicted warming tolerance varies over the year in the seven species, based on the three different prediction methods. In general, constant thermal limits (the ‘no acclimation’ method) resulted in larger warming tolerance during the winter and lower warming tolerance during the summer, although this effect was small in most species.

