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Dimension and mortality in linear stage class models of *Acartia tonsa*

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Abstract

Zooplankton serve as an important link in marine ecosystem food webs, with accurate yet mathematically and computationally tractable models of zooplankton dynamics serving as an important component of large system models. Current models of zooplankton dynamics may have unnecessarily high dimensions resulting from tracking all stage classes or may lose accuracy due to neglected system characteristics such as non-predatory mortality from disease or starvation. Here we construct a six stage class model and compare it to the thirteen stage class model in Elliot and Tang (2011) of *Acartia tonsa* zooplankton in the Chesapeake Bay. We also incorporate both predatory and non-predatory zooplankton mortality in order to further study the mortality term. We use sensitivity and interval analysis to show that the six dimensional model retains the essential features of the thirteen dimensional model and that both models are most sensitive to error in the mortality term. Given the model sensitivity to error in the mortality terms, a nonlinear approach to zooplankton modeling that separates non-predatory mortality from predation by fish and intraguild predation is warranted to further improve current zooplankton models.

Keywords: Zooplankton, Acartia tonsa, Population Dynamics

1 Background

Accurate projections of zooplankton abundances are important for modeling natural populations in marine ecosystem food webs. In aquatic systems, understanding zooplankton dynamics is becoming increasingly important since zooplankton are the main grazers of phytoplankton and help in recycling materials. Zooplankton are also the main food source for several species higher in the food web, and therefore are considered to be an indicator species [5]. Zooplankton grazing also has a major impact on important ecological processes such as eutrophication and climate change. Because zooplankton are a critical component of aquatic ecosystems, it is imperative that they are modeled as accurately as possible.

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*These authors contributed equally to this work.

While most zooplankton rates, such as egg production rates and developmental rates, have been well-studied, mortality (both predatory and non-predatory) remains the least studied process [2]. Current models, such as Elliot and Tang's linear stage class model [2], set the mortality rates as constant or linear functions of temperature, which is often not biologically realistic as the mortality rate can reach zero at low temperatures. While knowledge of mortality rates in zooplankton populations is incomplete, mortality terms often play a critical role in zooplankton models. Many models use mortality as a "closure" or unconstrained term that is tuned to enforce stability in ecosystem models or field studies [7].

Motivated by the Elliott and Tang model, we here study linear population models of the dominant species of zooplankton in the Chesapeake Bay, *Acartia tonsa*, estimating the effects of dimension and mortality. We build a lower dimensional model by aggregating stages with similar life history traits using parameters from [2] and data on stage durations from [5]. The lower dimensional model shows similar results to the Elliott and Tang model in sensitivity and interval analyses, indicating that condensed models can be used in future analyses.

We also study the effects of mortality terms in the models, making an important distinction between predatory and non-predatory rates. The field study in [2] showed that a large proportion of total zooplankton biomass (approximately 30% in the Chesapeake Bay) consists of zooplankton carcasses, an indication of non-predatory mortality [2]. This recent improvement in the differentiation between live and dead zooplankton in samples can be used to improve estimates of predatory and non-predatory mortality rates. We show that the models are highly sensitive to error in mortality terms, suggesting that both improved model construction for mortality terms and increased data collection may offer a large payoff in improved model accuracy. Further studying the importance of the mortality term as well as the different types of mortality has the potential to improve our understanding of zooplankton dynamics and population models. Improved zooplankton models will also allow for more economically-relevant predictions of future coastal or oceanic ecosystems.

We begin by giving an overview of Elliott and Tang's linear, thirteen stage class model in Section 2. Section 3 describes our condensed, six stage class model that we construct through amalgamation of stages in the Elliott and Tang model and by using data to fit new rates. Sensitivity and interval analyses of both the full and condensed models are in Section 4. In Section 5 we discuss our results and briefly mention future research directions for this project.

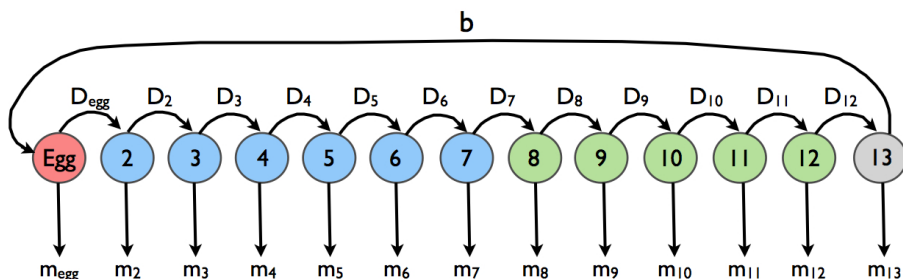## 2   Introduction to the Linear Zooplankton Model

Figure 1: *A life cycle diagram for Elliott and Tang's model [2]. The egg (red) represents the abundance of eggs, Stages 2-7 (blue) represent the abundance in each of the naupliar classes, Stages 8-12 (green) represent the abundances in each of the copepodite classes, and stage thirteen (gray) indicates the abundance of the adult class. The development rates are denoted by D_i, where i is the stage class. The mortality rates are denoted by m_i and the birth rate by b.*

Elliott and Tang's model has thirteen stages of development [2]. The stage classes group naturally

into six major stage groupings: eggs are stage class 1, nauplii I (NI) includes stage classes 2–4, nauplii II (NII) includes 5–7, copepod I (CI) includes 8–10, copepod II (CII) includes 11–12, and copepod adults (CA) are stage class 13. The stage classes are grouped in this way because the life history traits are nearly the same for individuals in each stage class aggregate. The naupliar and copepodite stages are the larval and adolescent stages of *Acartia tonsa*, respectively. The egg, nauplii, and copepod classes are immature (or non-reproducing) classes, and each class is affected by a mortality rate and a development rate. The mature class (adults) is also affected by mortality, but it is the only class that can reproduce (see Figure 1 for the life cycle diagram).

Coming from a fit to data, the governing differential equations for Elliott and Tang's model are

$$\begin{cases} \dfrac{dA_{egg}}{dt} &= 0.63\,b\,A_{13} - D_{egg}A_{egg} - m_{egg}A_{egg}, \\ \dfrac{dA_i}{dt} &= D_{i-1}A_{i-1} - D_iA_i - m_iA_i, \text{ where } i = 2 \text{ to } 12, \\ \dfrac{dA_{13}}{dt} &= D_{12}A_{12} - m_{13}A_{13}. \end{cases} \tag{1}$$

where where A_i is the abundance of individuals in stage i per cubic meter, t is time in days, b is the birth rate, or egg production rate, given in units of eggs produced per individual per day (63% of which survive), D_i is the development rate into the next stage class, and m_i is the mortality rate for individuals in stage class i. The mortality, development, and reproduction rates are functions of temperature, which in turn is a function of time. The mortality term not accounting for non-predatory mortality is referred to as "uncorrected", and the mortality term including non-predatory mortality is referred to as "corrected". See Appendix A and [2] for further details on the parameters in this model as well as the temperature function $T(t) = 16.133 - 11.132 \cos[2\pi(t + 28.076)/365]$.

Coming from a fit to data, the total development time S, as given in [5], is a Belehradek's function of temperature T (°C) given by

$$S(T) = 5491.85(T + 0.96)^{-2.05}. \tag{2}$$

Note that this function gives the development time for individuals from nauplii I to adult, and does not include the development time from egg to nauplii I. The stage duration of a class is the average length of time an individual stays in that particular class, with the following functional form

$$\begin{aligned} s_{egg}(T) &= 489(T - 1.8)^{-2.05}, \\ s_i(T) &= a_i S(T)/11, \; i = 2, \ldots, 12, \end{aligned} \tag{3}$$

where a_i are mean deviations from the isochronal [5] given by

$$a_i = \begin{cases} 1.0533, & \text{for } i = 2, 3, 4, \\ 0.8124, & \text{for } i = 5, 6, 7, \\ 0.9226, & \text{for } i = 8, 9, 10, \\ 1.3213, & \text{for } i = 11, 12. \end{cases} \tag{4}$$

This gives a very good approximate representation of the function S in (2) as a sum of functions s_i, given by

$$S(T) \approx \sum_{i=2}^{12} s_i(T), \tag{5}$$

with $||S - \sum s_i||_2 = 0.0781$.

The general equation for the development rates in each class are thus

$$D_i(T) = \frac{1}{s_i(T)}. \tag{6}$$

The mortality rate equation for the eggs has the following exponential functional form

$$m_{egg}(T) = e^{0.0725T - 1.112}, \tag{7}$$

where T is temperature in $^\circ C$. The remaining mortality rates for the nauplii, copepods, and adults are all piecewise linear equations of the form

$$m_i(T) = \begin{cases} c_1 T - c_2, & \text{if } c_1 T - c_2 > 0, \\ 0, & \text{otherwise,} \end{cases} \tag{8}$$

with constants $c_1, c_2 > 0$ that depend on the stage class and whether the mortality estimates are corrected or uncorrected. The reproduction or birth rate b only directly affects the abundance of the egg class. The egg production equation is given by

$$b(T) = 50.9 \cdot ((34 - T)/9.22)^{3.95}) \cdot e^{3.95(T-24.78)/9.22}. \tag{9}$$

When the mortality term in this model does not account for non-predatory mortality, the population goes to extinction (see Figure 2a). However, when the mortality term does account for non-predatory mortality, the population is sustained (see Figure 2b), matching more closely the existing data from the Baywide CBP Plankton Database mesozooplankton monitoring project (`http://www.chesapeakebay.net/data/downloads/baywide_cbp_plankton_database`) from January 2000 to November 2002.
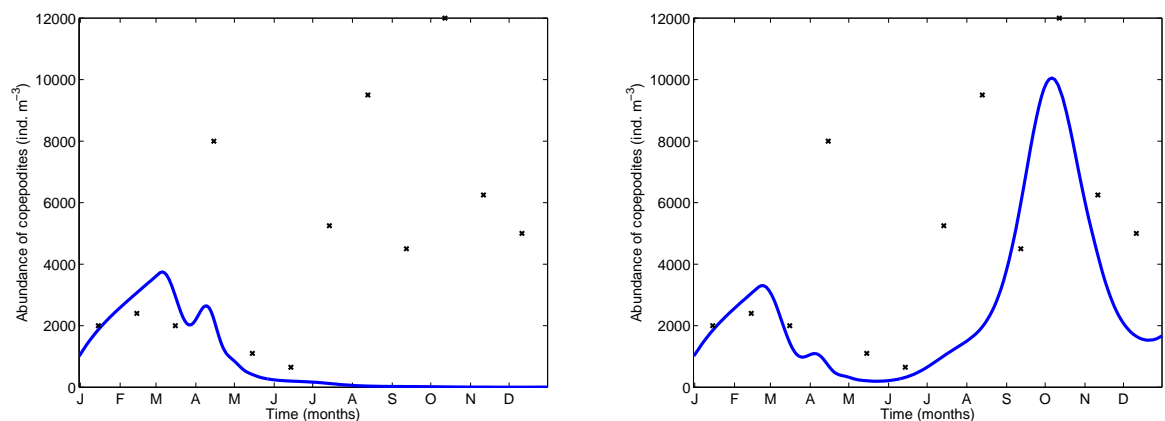
(a) The full zooplankton model using uncorrected mortality terms. The Day 0 abundances are 500 nauplii and 200 copepods per stage class. The total abundance of the copepods and adults are plotted.

(b) The full zooplankton model using corrected mortality terms. The Day 0 abundances are 500 nauplii and 200 copepods per stage class. The total abundance of the copepods and adults are plotted.

Figure 2: *Linear thirteen stage class model simulations. Data points are from the Baywide CBP Plankton Database mesozooplankton monitoring project from January 2000 to November 2002.*

3   Condensed Linear Model

We now reduce Elliott and Tang's thirteen dimensional model to a condensed, six dimensional model by combining stages with similar features. The six stage classes are egg, NI, NII, CI, CII, and adult (CA). This is a natural reduction to make since development and mortality rates are the same for each stage within each of these amalgamated states. In order to condense the model, new stage durations are calculated for NI, NII, CI, and CII as follows. Following (3), we represent the new stage durations by

$$s_\sigma(T) = a_\sigma S(T)/4, \ \sigma \in \{NI, NII, CI, CII\},$$

which shows we need to calculate the new mean deviations a_σ from the isochronal. To do this, notice that we need these new stage durations to sum to an approximation to $S(T)$, as in (3), giving

$$S(T) \approx \sum_{i=2}^{12} s_i = s_{NI} + s_{NII} + s_{CI} + s_{CII}.$$

By isolating portions of the sum in (3) that correspond to the appropriate condensed class, we have

$$
\begin{aligned}
s_{NI} &= a_{NI}S(T)/4 &\equiv& (a_2 + a_3 + a_4)S(T)/11, \\
s_{NII} &= a_{NII}S(T)/4 &\equiv& (a_5 + a_6 + a_7)S(T)/11, \\
s_{CI} &= a_{CI}S(T)/4 &\equiv& (a_8 + a_9 + a_{10})S(T)/11, \\
s_{CII} &= a_{CII}S(T)/4 &\equiv& (a_{11} + a_{12})S(T)/11.
\end{aligned}
$$

Solving for a_σ and using values of a_i in (4) gives

$$
a_\sigma = \begin{cases}
1.1491, & \text{for } \sigma = \text{NI}, \\
0.8863, & \text{for } \sigma = \text{NII}, \\
1.0064, & \text{for } \sigma = \text{CI}, \\
0.9609, & \text{for } \sigma = \text{CII}.
\end{cases}
$$

With these deviations and all other parameters for this condensed model the same as in Elliott and Tang's model [2], the zooplankton abundance blows up within one year. In order to correct for this and to do a proper comparison of the condensed with the full model, we use uncertainty in the estimates of the mortality terms and stage durations to constrain the relevant parameters for an optimization procedure to fit the condensed model output to the full model output (see Appendix C for details). The resulting optimized condensed stage durations are given by

$$
\hat{a}_\sigma = \begin{cases}
1.2764, & \text{for } \sigma = \text{NI}, \\
0.7671, & \text{for } \sigma = \text{NII}, \\
1.0811, & \text{for } \sigma = \text{CI}, \\
1.1339, & \text{for } \sigma = \text{CII},
\end{cases} \tag{10}
$$

with optimized coefficients c_j in modified corrected mortality terms m_σ (of the functional form (8)) given by

$$
\begin{cases}
c_1 = 0.0119, c_2 = 0.1610, & \text{for } \sigma \in \{\text{NI}, \text{NII}\}, \\
c_1 = 0.0461, c_2 = 0.2775, & \text{for } \sigma \in \{\text{CI}, \text{CII}\}.
\end{cases} \tag{11}
$$

These new deviations and mortality terms are within the 99% Bonferroni corrected confidence bounds for the parameters (see Figure 14).
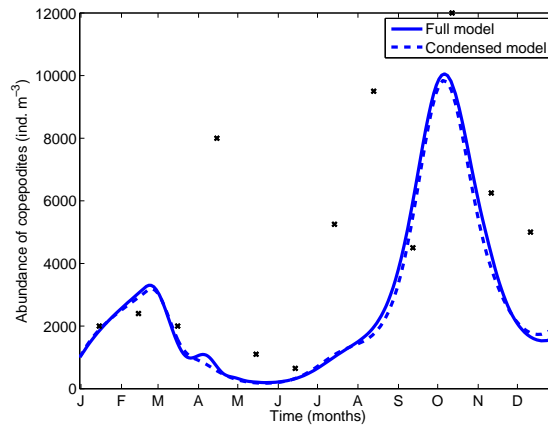

Figure 3: The full (solid line) and condensed (dashed line) zooplankton models using corrected mortality terms. Mean deviations and mortality functions are given in Table 1 (full model) and Eqs. (10)–(11) (condensed model). The Day 0 abundances are 1500 individuals in each of the two naupliar stage classes, 500 individuals in each of the two copepod stage classes. The total abundance of the copepods and adults are plotted.
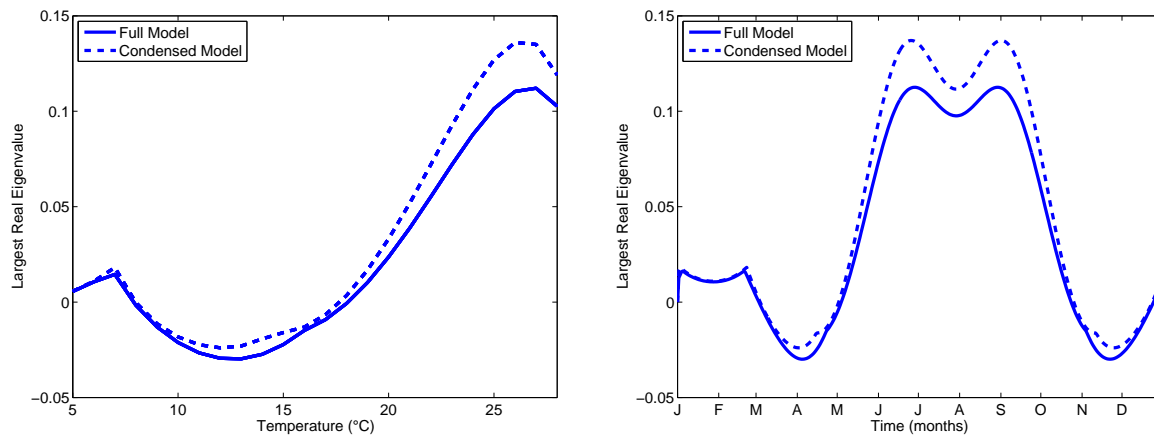
4   Analysis

We now analyze both the thirteen stage class, Elliott and Tang model and the six stage class, condensed model, both with corrected mortality terms. We use sensitivity and what we call *shift interval* analysis to determine which parameters influence the behavior of the models the most. We will show that the behavior of the linear model changes minimally when condensing the stage classes, indicating that the condensed model offers a good representation of the thirteen stage classes. We also find both the full (Elliot and Tang) and condensed models to be most sensitive to changes in mortality rates (as compared to all other system parameters). Considering that the mortality terms are the least known, this analysis shows that more data and further studies of zooplankton mortality should be conducted. For example, choosing corrected mortality rate functions from the 99% Bonferroni corrected confidence intervals in the full model, one can see either population crashes or population explosions. (See Figure 8.) Further refinement of the mortality terms is needed to make accurate predictions.

4.1   Eigenvalue Analysis

We now conduct an eigenvalue analysis on the Elliott and Tang model in order to determine at which fixed temperatures the population grows rather than declines. Writing the coefficients of the Elliott and Tang model (see Equation 1) in the 13×13 matrix-form, we have

$$C = \begin{pmatrix} -D_{egg} - m_{egg} & 0 & \cdots & 0 & 0.63\,b \\ D_{egg} & -D_2 - m_2 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & \cdots & D_{12} & -m_{13} \end{pmatrix} \tag{12}$$

If the maximum real eigenvalue of C is positive, then it is an indicator of growth of the population, while a negative eigenvalue is an indicator of population decline.

(a) The maximum real eigenvalue as a function of temperature in both the full and condensed models.

(b) The maximum real eigenvalue as a function of time in both the full and condensed models.

Figure 4: *Eigenvalue analysis with respect to temperature and time in both models.*

Figure 4a shows the maximum real eigenvalues at each temperature computed in MATLAB for both the Elliott and Tang model and the condensed model. The eigenvalue is positive at low temperatures because the mortality of nauplii and copepods are zero at those temperatures (see Figure 10a in Appendix A). This zero mortality rate leads to a positive maximum real eigenvalue in temperatures less than $8°C$, which is problematic for this linear model since it is not likely that

an organism's mortality rate would ever reach zero. The maximum real eigenvalue then decreases to below zero and remains negative until around 18°C when the population begins to experience growth again. The eigenvalue increases until a maximum is reached just after 25°C and then begins to decline as it approaches the maximum temperature in the system.

Figure 4b shows the maximum real eigenvalues of both models as a function of time. The maximum real eigenvalue is positive at the beginning of the year because of 0 mortality rates at low temperatures. The maximum real eigenvalue also has two minima that occur during the early spring and late fall and obtains two maxima at the beginning and end of summer. In the middle of summer, when the temperature maximum is reached, the eigenvalue has another local minimum. As with the comparison of leading eigenvalues as functions of temperature, the analysis with respect to time shows the two models to be similar. The slight differences in the computed leading eigenvalues can be attributed to model approximation error in the condensing process.

4.2   Sensitivity Analysis

Sensitivity analysis on the full and condensed models helps to estimate the effect of measurement error in the model parameters. We compute sensitivities for both the full (Elliott and Tang) model and the condensed model with respect to the development rates, the mortality rates, and the birth rate using corrected mortality rates that include both predatory and non-predatory mortality. Sensitivity estimates the change that occurs in the growth rate of the population when a parameter is perturbed slightly [1]. In what follows, we estimate the effects of small changes to mortality, development, and birth rates at fixed temperatures T, varying T over the feasible range of temperatures.

Sensitivity is more explicitly defined as the partial derivative of the maximum real eigenvalue with respect to a specific parameter. Positive sensitivity indicates that a small increase in the parameter leads to an increase in the maximum real eigenvalue, while negative sensitivity indicates that a small increase in the parameter leads to a decrease in the eigenvalue. The magnitude of the sensitivity indicates by how much the growth rate would increase or decrease given a unit of change in the specific parameter [1]. The general formula for sensitivity is thus given by

$$S\lambda(x) = \frac{\partial \lambda}{\partial x},$$

where λ is the masimum real eigenvalue and x is the parameter that is being tested for sensitivity. Sensitivity can be thought of as the linear multiplicative factor that maps a change in a parameter to the change in the growth rate

$$\Delta \lambda \approx \left[\frac{\partial \lambda}{\partial x}\right] \Delta x,$$

which leads to

$$\frac{\partial \lambda}{\partial x} \approx \frac{\Delta \lambda}{\Delta x}. \tag{13}$$

We use MATLAB to approximate the sensitivities of the parameters in both models. For this numerical approximation, we make a very small positive change ($\Delta x = 0.001$) to a specific parameter at a specific temperature and then compute the new eigenvalue. We consider this to be a good approximation of the partial derivative of the eigenvalue with respect to the parameter because as we decrease the small change in the parameter, the graphs of the sensitivities do not change significantly.

In the thirteen stage class model, the sensitivities of the stage classes line up with major groupings, given by: stages 2-4, which make up nauplii I; stages 5-7, which make up nauplii II; stages 8-10, which make up copepod I; and stages 11-12, which make up copepod II. Because the thirteen stage classes fall into a natural grouping of six stages, the sensitivities of the full model can be easily compared to the sensitivities of the condensed model.
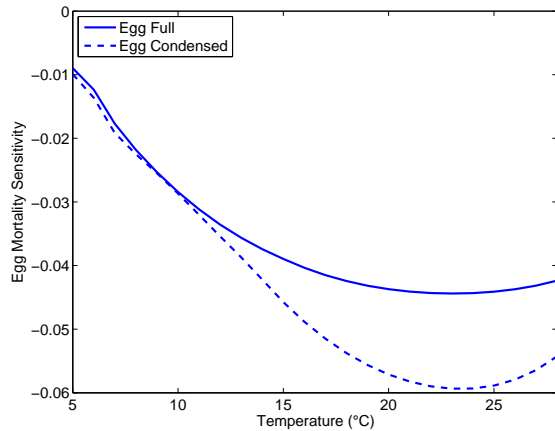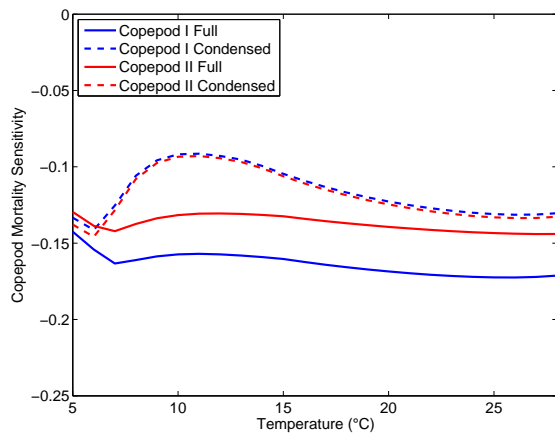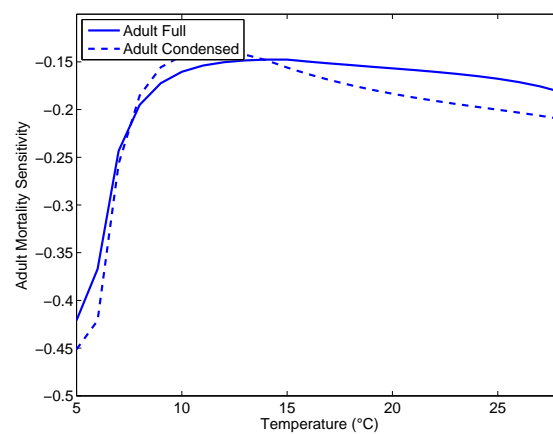
(a) The sensitivities of the full and condensed models with respect to egg mortality as a function of temperature.
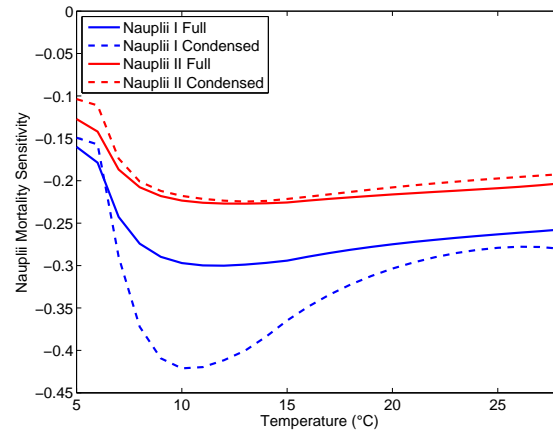
(b) The sensitivities of the full and condensed models with respect to nauplii mortality as a function of temperature.
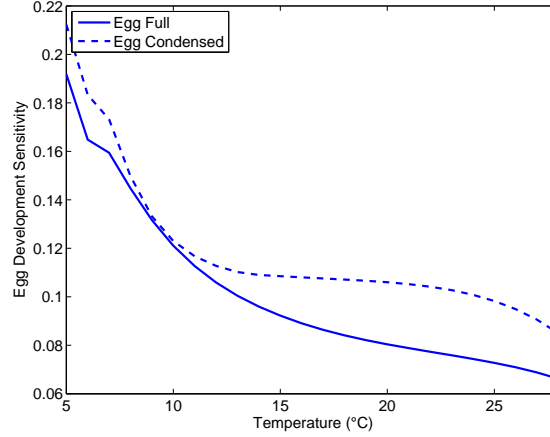
(c) The sensitivities of the full and condensed models with respect to copepod mortality as a function of temperature.

(d) The sensitivities of the full and condensed models with respect to adult mortality as a function of temperature.

Figure 5: *The sensitivities of the full and condensed models with respect to mortality rates.*

The mortality sensitivities were found for each stage class for both the full and the condensed model (see Figure 5). While sensitivity for the condensed model is simply $\frac{\partial \lambda}{\partial m_\sigma}$, the reported sensitivities of the full model are given by

$$\sum_{i \in I_\sigma} \frac{\partial \lambda}{\partial m_i},$$

where I_σ is the set of stage classes amalgamated into class σ. This is the only fair comparison, as a small change in m_σ corresponds to a simultaneous change in all m_i for each $i \in I_\sigma$.

The results show that the sensitivity with respect to mortality is always negative, as a slight increase in the mortality rate should always lead to a decrease in the growth rate of the population (the maximum real eigenvalue). It is most strongly negative for the adult and nauplii stage classes in both models. When comparing the sensitivities of the full and condensed models, the biggest differences can be seen in the egg, nauplii I, and copepod classes.

(a) The sensitivities of the full and condensed models with respect to egg development as a function of temperature.
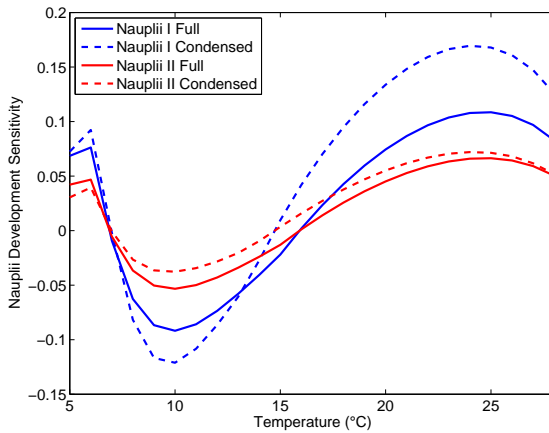
(b) The sensitivities of the full and condensed models with respect to nauplii development as a function of temperature.
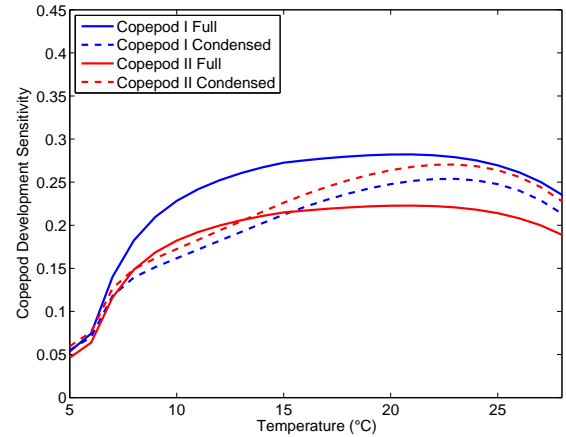
(c) The sensitivities of the full and condensed models with respect to copepod development as a function of temperature.

Figure 6: *The sensitivities of the full and condensed models with respect to development rates in both models.*

The development sensitivities were found for each stage class for both the full and the condensed model (see Figure 6). Similar to the mortality case, while sensitivity of the condensed model is given by $\frac{\partial \lambda}{\partial D_\sigma}$, the reported sensitivities of the full model are given by

$$|I_\sigma| \sum_{i \in I_\sigma} \frac{\partial \lambda}{\partial D_i},$$

where again I_σ is the indexing set of stage classes amalgamated into σ. This formula follows from the chain rule as follows. For the condensed development rate, we have

$$D_\sigma = \frac{1}{s_\sigma} \approx \frac{1}{\sum_{i \in I_\sigma} s_i} = \frac{1}{|I_\sigma|} D_i, \tag{14}$$

for each $i \in I_\sigma$ and with $|I_\sigma|$ the number of stage classes amalgamated into σ. (Note that $s_i = s_j$ and, therefore, $D_i = D_j$ for all $i, j \in I_\sigma$.) The approximation in the above chain of equalities comes

from the optimization procedure leading to modified stage durations for the condensed model. We now have

$$\frac{\partial \lambda}{\partial D_\sigma} = \sum_{i \in I_\sigma} \frac{\partial \lambda}{\partial D_i} \frac{\partial D_i}{\partial D_\sigma} \approx |I_\sigma| \sum_{i \in I_\sigma} \frac{\partial \lambda}{\partial D_i}.$$

The results in Figure 6 show that the sensitivity for the development is positive for eggs and copepods and is negative for the nauplii from around $7 - 17°$C. Since the mortality rate of nauplii is zero or near zero in this temperature range, developing into a copepod will increase those individuals' mortality rates and therefore will negatively affect the growth rate of the population. The sensitivity of the egg class in both the full and condensed models are slightly different but still comparable, and these differences can be attributed to the model approximation error incurred during the condensing process (see Figure 6a).

The sensitivities of the models with respect to birth rates appears sinusoidal over the possible temperature range in the Chesapeake Bay (see Figure 7a). It is always positive, but it is largest at low temperatures and smallest at high temperatures. The sensitivity range is very small meaning that a unit change in the birth rate at a fixed temperature in the considered range does not change the population's growth rate a significant amount. Since the birth rate can approach 50 eggs produced per day per individual (see Figure 10c), it is clear that the sensitivity of the birth rate should be much smaller than that of the mortality and development rates, as an absolute change in the large egg production rate would impact the growth rate less than the same absolute change would impact the significantly smaller mortality and development rates (see Table 1 in Appendix A for parameter values).
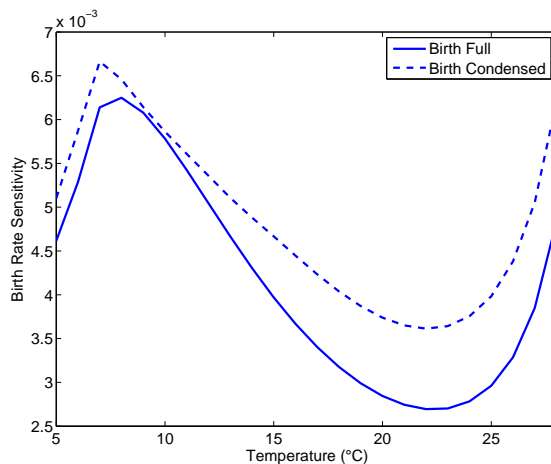

Figure 7: *The sensitivity of both the full and condensed models with respect to the birth rate as a function of temperature.*

The maximum sensitivity with respect to mortality of the adult class in both models has the largest magnitude of any of the sensitivities of the parameters, with a maximum sensitivity of -0.45 at low temperatures. The sensitivities of copepod I development rate in the full model and nauplii I mortality rate in the condensed model are the next largest in magnitude, reaching a maximum magnitude of 0.3 and -0.4 respectively. As the adults are the only stage class that can reproduce, it is logical that the models would be particularly sensitive to adult mortality rates. The models are sensitive to nauplii mortality rates as well as these rates are zero or near zero at low temperatures (see Figure 10a). In the next section we conduct further analysis which directly measures how far we can shift a given parameter (at fixed temperature) while maintaining growth (positive leading eigenvalue) in the model.

4.3 Parameter Shift Analysis

We now compute the largest distance, what we call the *shift distance*, that a parameter may be shifted while maintaining growth of the population. That is, for a parameter with value x we compute the maximal shift distance $\varepsilon \geq 0$ so that using a new, "shifted" parameter value $\hat{x} \in [x - \varepsilon, x + \varepsilon]$, the largest real eigenvalue for the model remains positive. As in the sensitivity analysis section, we treat the mortality rates (development rates) in stage classes I_σ of the full model as the same parameter, where σ corresponds to a condensed class. Thus, a parameter shift in a mortality rate (development rate) for a condensed class σ will be compared with a parameter shift in *all* mortality rates (development rates) of the corresponding full model classes in I_σ. Also note that, due to equation (14), there will be an expected multiplicative factor of $|I_\sigma|$ difference in the results from parameter shift analysis on the development rates between the full and condensed models. Any other difference can be attributed to the approximation scheme.

This analysis will give an indication of how precise we need to be when we measure certain parameters, and it shows that most of the parameters, and the mortality parameter in particular, cannot deviate much in this model without causing the model to predict a population crash (at fixed temperature). We numerically calculate the maximum possible ε for each parameter at fixed temperatures within the feasible range of temperatures. For the mortality rates (development/birth rates) we calculate the maximum mortality rate (minimum development/birth rate) for each stage class that still yields population growth. As only one parameter is changed at a time, these maximal shift distance values are computed assuming that all the other parameters in the model are accurate. Further computation is required for a more complete understanding of the parameter space in which parameters may be shifted simultaneously while maintaining overall population growth.

Figures 12e-f show that the maximal shift distance allowed for the mortality rate that will still allow growth is the smallest for the adult class when compared with the other stage classes in both the full and condensed models. This conclusion is in line with our previous result that the adult mortality term is the most sensitive mortality parameter and among the most sensitive of all the parameters in the model (See Figure 5d). Figures 11 and 13 show the maximal shift distances for the (minimum) birth rates and development rates at different temperatures, respectively. The birth term, which we found was by far the least sensitive parameter in the model (see Figure 7), also allows the largest shift distance. At certain temperatures, the maximal shift distance allowed for the birth term is more than 25. The maximal shift distances for the development terms are the same magnitude as those for the mortality terms (see interval analysis figures in Appendix B).

While calculating the maximal shift distances corresponds to analyzing error in absolute terms rather than relative terms, looking at how large these shifts can be gives us an indication of how precise our tools need to be when we measure these parameters.

4.4 Mortality Confidence Bounds and Cumulative Effects

The previous techniques of sensitivity and parameter shift analysis measure how changes in the parameters affect the population growth rate *at fixed temperatures*. We now use the uncertainty in the estimate of the linear mortality functions calculated in [2] to test what effect a more global (in time) modification of mortality would have on the population dynamics. For the linear mortality fits, there is a 99% Bonferroni corrected confidence interval associated with the linear regression coefficients (see Figure 14 and Appendix C). The lower and upper bounds of the slope interval are used to test the lower and upper bounds on mortality (simultaneously for both the nauplii and copepods). With each slope, a new linear equation through the mean mortality and temperature will be found. These bounds correspond to the points on the confidence ellipse at each end of the major axis.

As expected, the zooplankton in the thirteen stage class model crashes with all uncorrected mortalities (see Figure 8). The population persists, however, using the lower bound and estimate of the slope for the corrected mortalities. Note, however, that the population becomes unbounded

using the mortality upper bound. Interestingly, the population crashes using the lower bound of the slope for the corrected mortality. With upper bound mortalities in both uncorrected and corrected versions, the model has higher abundances early in the year (at low temperatures), as the linear mortality becomes negative and is set to be zero for a larger temperature range than for the models using lower bound mortalities. Therefore, this follows from the inverse relationship between the slope and intercept of the regression line. Like the previous analyses, this analysis indicates how sensitive and important the mortality term is, as using the lower bound of the 99% Bonferroni corrected confidence interval for the slope of the corrected mortality causes the population of zooplankton to crash.
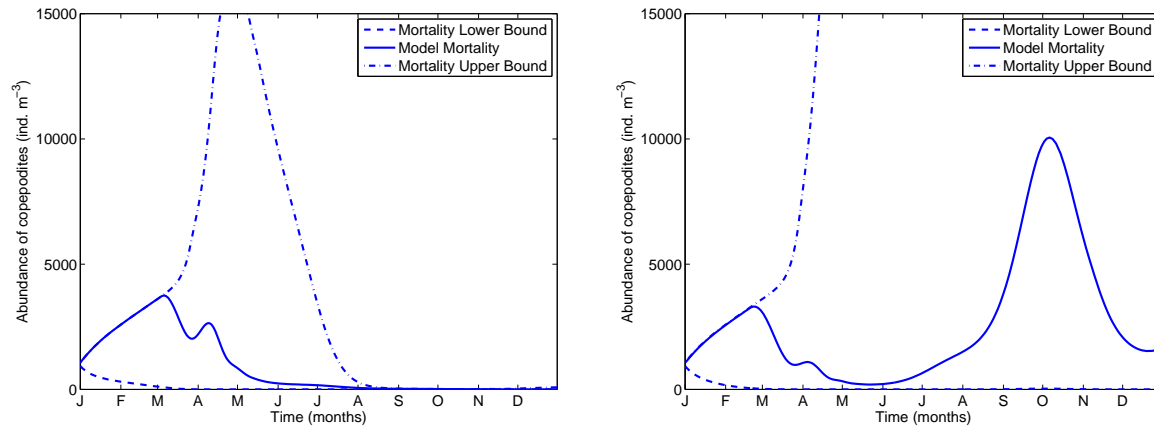
(a) The full model with uncorrected mortality and lower and upper mortality bounds. The Day 0 abundances are 500 nauplii and 200 copepods per stage class. The total abundance of the copepods and adults are plotted.

(b) The full model with corrected mortality and lower and upper mortality bounds. The Day 0 abundances are 500 nauplii and 200 copepods per stage class. The total abundance of the copepods and adults are plotted.

Figure 8: *The linear thirteen stage class model with mortality bounds.*

5 Discussion

Overall, the condensed six stage class model behaves similarly to the full thirteen stage class model from Elliott and Tang. The condensed and the full models have similar sensitivity and parameter shift analyses. The differences between the two models is generally slight and can be attributed to the model approximation error accrued during the condensing process, especially for the copepod classes which are associated with the most error in the condensed model (see Section 3). Since the condensed model behaves similarly to the full model in both overall fit to time-series data (due to simulations of the two models being close) and expected dynamics under small perturbations of parameters, larger end-to-end models incorporating zooplankton as just one component in a food web may take advantage of the lower dimension of this condensed model.

In addition to the good fit of the condensed model to the data, the sensitivity analysis, parameter shift analysis, and the mortality confidence bounds indicate that the models are most sensitive to error in the mortality term. Population crashes occur in both the full and the condensed models at corrected mortality rates within the confidence region determined by the data. In fact, even the highest resolution (thirteen stage) model with relatively low (uncorrected) mortality rates within the confidence region shows population crashes. These results suggest the importance of accounting for non-predatory mortality and indicate that better estimates for mortality are desired. This outcome is significant because mortality is the least studied rate and has not been as precisely measured in previous studies, as compared with the birth rate and development rates. Further data collection and including nonlinear terms in the model may improve model accuracy by separating non-predatory and predatory mortality. One promising avenue is to study intraguild predation, in particular

zooplankton cannibalism, which has been shown to account for up to 60% of total zooplankton mortality [3].

Acknowledgements

A Elliott and Tang Model Parameters

This appendix contains the equations and parameters used to run simulations of Elliott and Tang's thirteen-stage class model (Equation 1).

	Symbol	Value	Source
Day in model (t)	day	1 to 365	
Temperature (T)	$^\circ$ C	$16.133 - 11.132 \cdot \cos[2\pi(t+28.076)/365]$	[2]
Developmental stage (i)		eggs (egg), nauplii (2-7), copepods (8-12), adults (13)	
Stage duration (s_{egg})	day	$489(T-1.8)^{-2.05}$	[6]
Stage duration (s_i)	day	$(a \cdot 5491.85/11) \cdot (T+0.96)^{-2.05}$	[5]
Mean deviation of stage durations from isochronal (a)		1.0533 for Nauplii I (2-4), 0.8124 for Nauplii II (5-7), 0.9226 for Copepod I (8-10), 1.3213 for Copepod II (11-12)	Derived from Table 1 in [5]
Development rate (i =egg to 12)	day^{-1}	$1/s_i$	
Egg production rate (b)	day^{-1}	$50.9 \cdot ((34-T)/9.22)^{3.95} \cdot e^{(3.95 \cdot (T-24.78))/9.22}$	[4]
Mortality rate (i =egg)	day^{-1}	$e^{0.0725T-1.112}$	[3]
Uncorrected mortality rate ($i = $ 2 to 13)	day^{-1}	$0.0187T - 0.223$ ($i = 2$ to 7), $0.0392T - 0.224$ ($i = 8$ to 13)	[2]
Corrected mortality rate ($i = 2$ to 13)	day^{-1}	$0.0096T - 0.143$ ($i = 2$ to 7), $0.0412T - 0.243$ ($i = 8$ to 13)	[2]

Table 1: *Parameter values and equations modified from Elliott and Tang [2].*

The temperature function was derived from water temperature readings in the Chesapeake Bay. The highest temperatures occur in mid-summer, between July and August. The temperature function varies between $5 - 28^\circ$C (see Figure 9).
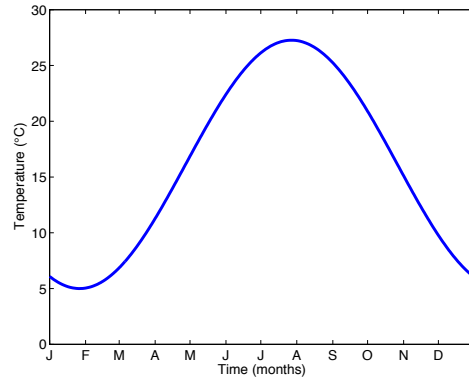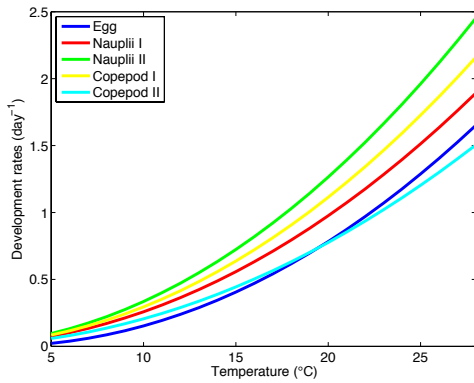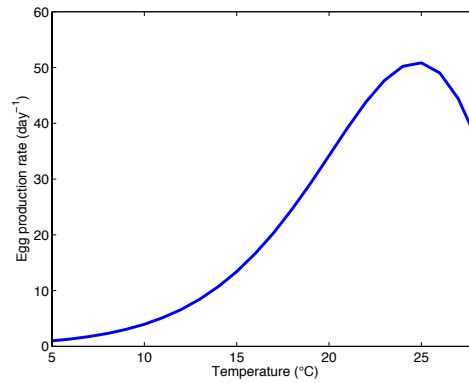
Figure 9: *Temperature as a function of time, as given in Table 1.*
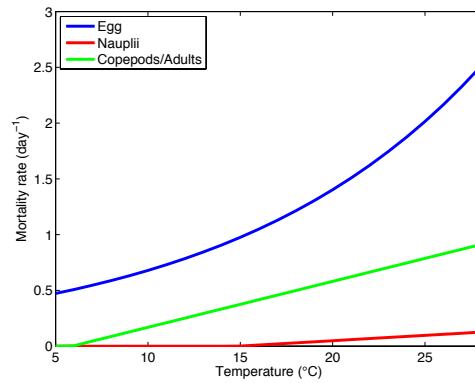
(a) The corrected mortality rates in the thirteen stage class model as functions of temperature.

(b) The development rates in the thirteen stage class model as functions of temperature.

(c) The birth rate in the thirteen stage class model as a function of temperature.

Figure 10: *Mortality, development, and birth rates of the linear model as a function of temperature.*

The only mortality rate that is nonlinear is the egg mortality rate, which increases exponentially as temperature increases. The mortality rates for the nauplii, copepods, and adults increase linearly as temperature increases. Because the mortality rates for the nauplii, copepods, and adults are

linear, the mortality equations–especially for the nauplii, but also for the copepods–give mortality rates that are less than zero at low temperatures. In these cases, mortality at those temperatures is taken to be zero (see Figure 10a).

The stage duration of a class is the average length of time an individual stays in that particular class. The development rate of a particular stage class is the rate at which individuals move from that stage class to the next stage class. The development rates of all the stage classes increase as temperature increases. The rate at which the development rates increases also increases with temperature. As the nauplii II and copepods I classes have the lowest a values and the smallest stage durations (see Table 1), they have the highest development rates (see Figure 10b). Each of the mean deviation a values are calculated from Table 1 in [5] as follows. We will illustrate how to derive a for Nauplii I, i.e. $a_2 = a_3 = a_4$, and the others follow similarly. For each Nauplii I stage class i, where $i = 2, \ldots, 4$, and for four different temperatures T_j, $j = 1, \ldots, 4$, there is a mean measured stage duration given by δ_{ij} (averaged over 2 replicates). We have

$$a_2 = a_3 = a_4 = \frac{1}{12} \sum_{i=2}^{4} \sum_{j=1}^{4} \frac{\delta_{ij}}{S(T_j)/11}, \tag{15}$$

which, by definition, is the mean deviation from the isochronal $S(T)/11$, where 11 represents the total number of stage classes.

The birth rate increases as temperature increases, and peaks around $25°$C before decreasing until the maximum temperature is reached (see Figure 10c).

B   Parameter Shift Analysis

Since the population is already in decline (the maximal real eigenvalue is negative) at low temperatures the maximal allowed parameter shift to maintain population growth is 0. Looking at Figure 4a, we can see that the eigenvalue is negative between $7 - 17°$C, which lines up with when all the max mortalities are equal to the actual mortality rates in Figure 12. The maximal mortality rates, however, initially spike at about 5 or $6°$C. This is because the eigenvalue is positive at the lowest temperatures, which may be because the mortality of the nauplii and copepods is zero at those temperatures.
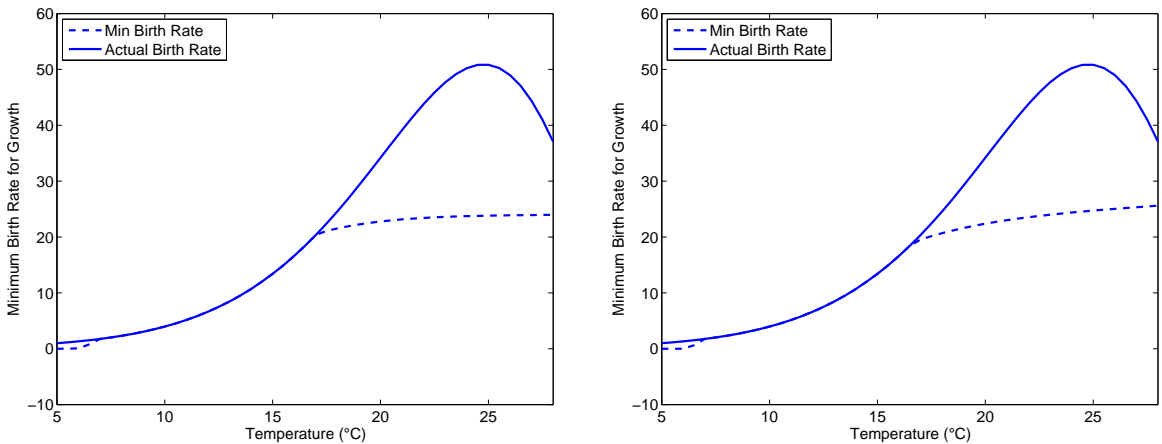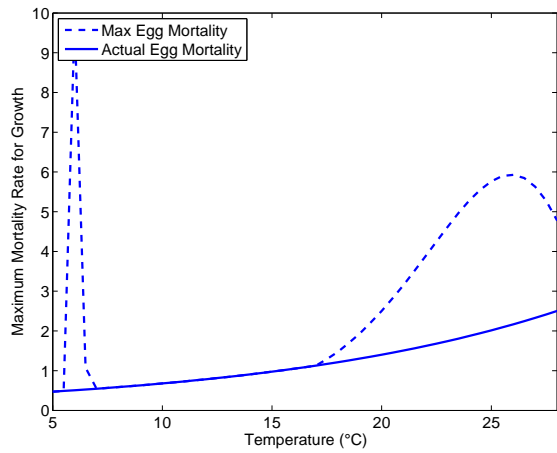

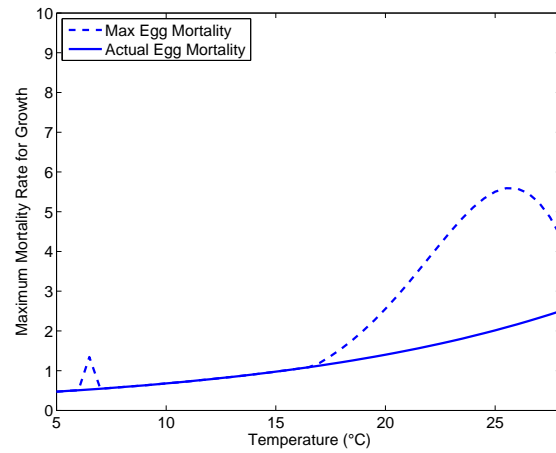(a) The minimal birth rate in the full model that will still allow growth.

(b) The minimal birth rate in the condensed model that will still allow population growth.

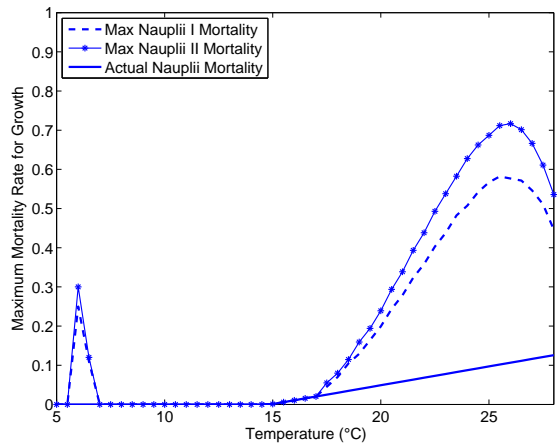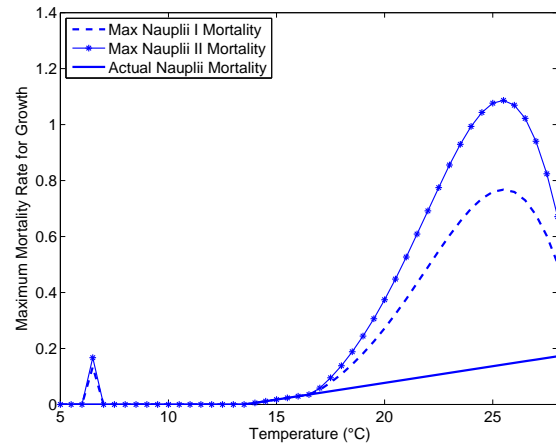Figure 11: *Parameter shift analysis of the birth term.*

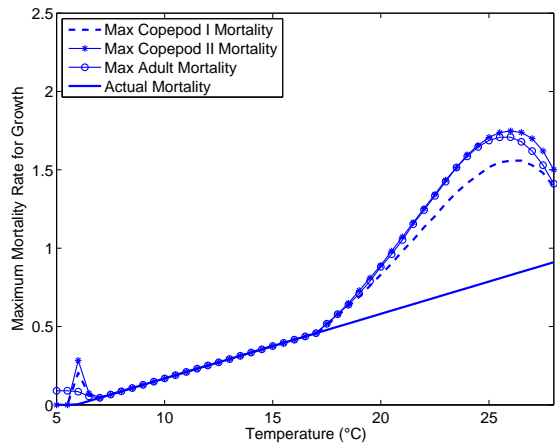(a) The maximal egg mortality rate in the full model that will still allow population growth.

(b) The maximal egg mortality rate in the condensed model that will still allow population growth.
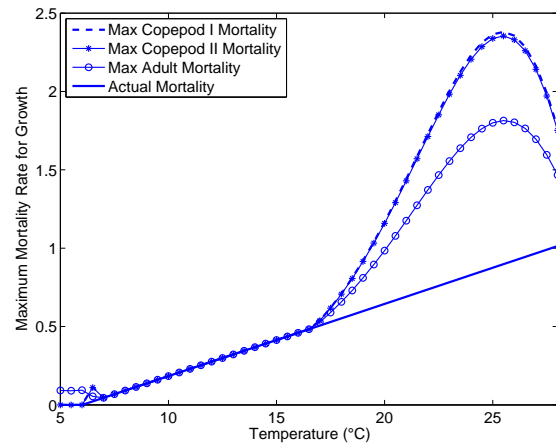
(c) The maximal nauplii mortality rates in the full model that will still allow population growth.

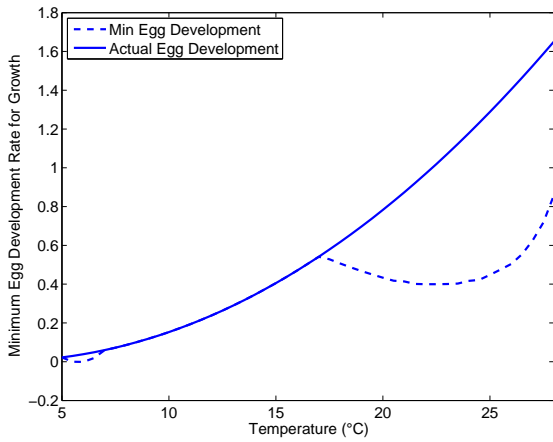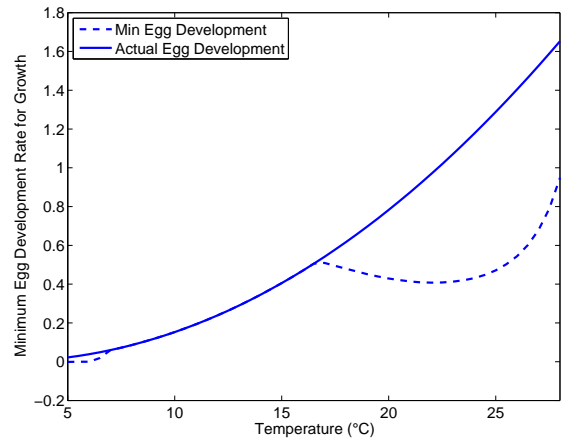(d) The maximal nauplii mortality rates in the condensed model that will still allow population growth.

(e) The maximal copepod and adult mortality rates in the full model that will still allow population growth.

(f) The maximal copepod and adult mortality rates in the condensed model that will still allow population growth.
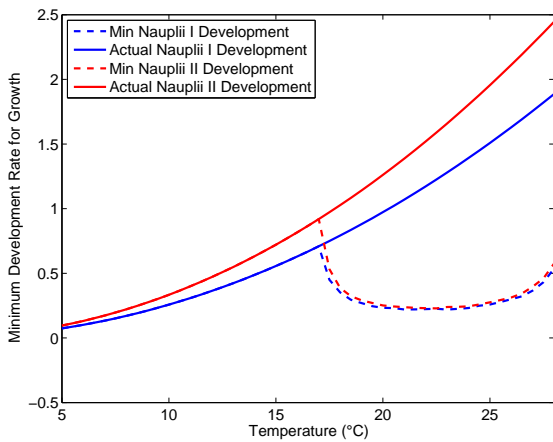
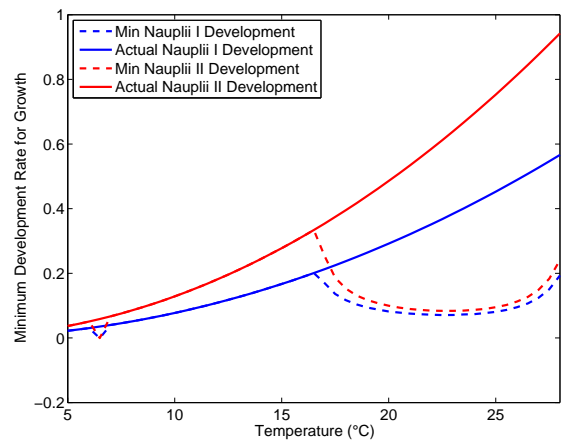Figure 12: *Parameter shift analysis of the mortality terms.*

(a) The minimal egg development rate in the full model that will still allow population growth.
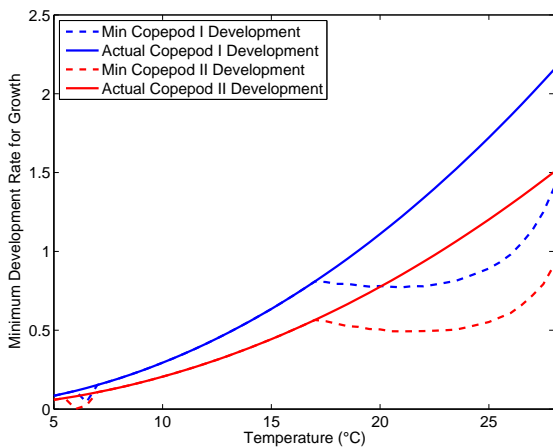
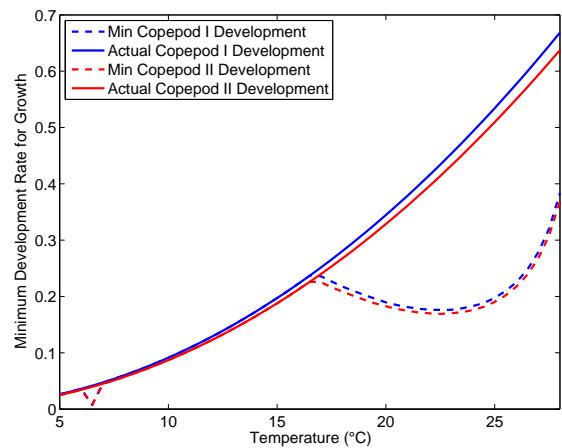(b) The minimal egg development rate in the condensed model that will still allow population growth.

(c) The minimal nauplii development rates in the full model that will still allow population growth.

(d) The minimal nauplii development rates in the condensed model that will still allow population growth.

(e) The minimal copepod development rates in the full model that will still allow population growth.

(f) The minimal copepod development rates in the condensed model that will still allow population growth.

Figure 13: *Parameter shift analysis of the development terms.*

C Data Analysis and Optimization

In order to compare the behavior of the condensed to the full model, optimization was performed while varying the mortality terms and stage durations, leaving all other parameters fixed and equal between the two models. Data were analyzed as follows:

- Mean deviations from the isochronal stage duration a_i were calculated as in (15), along with 99% Bonferroni corrected confidence intervals (Figure 14(c,d)) and standard errors SE_{a_i}.

- Zooplankton abundance data was taken from [2], which included live and dead counts for NI, NII, CI, CII, and adults (CA). Live counts are denoted by L_z^k, where $1 \leq k \leq 229$ for $z \in \{NI, NII\}$ and $1 \leq k \leq 127$ for $z \in \{CI, CII, CA\}$.

- For each k, a corrected nauplii mortality rate $m_N^k \equiv m_{NI}^k = m_{NII}^k$ was calculated by solving the following nonlinear equation [9]

$$\frac{e^{m_N^k \hat{s}_2^k} - 1}{1 - e^{-m_N^k \hat{s}_5^k}} = \frac{L_{\text{NI}}^k}{L_{\text{NII}}^k},$$

where $\hat{s}_i^k$ is similar to (3) and is given by

$$\hat{s}_i^k = 3\alpha_i^k S(T)/11, \quad i = 2, 5,$$

with random variable α_i^k drawn from a non-standardized t-distribution with 23 degrees of freedom, location a_i and scale SE_{a_i}. In other words, the α_i^k are drawn from the sampling distribution for a_i and account for the uncertainty in the estimate of the mean deviations. Linear regression was then performed on the resulting m_N^k, arriving at the linear functional form given in (8), with 99% Bonferroni corrected confidence region displayed in Figure 14(a).

- For each k, a corrected copepod mortality rates $m_C^k \equiv m_{CI}^k = m_{CII}^k = m_{CA}^k$ was calculated by solving the following nonlinear equation [9]

$$m_C^k = \frac{\ln\left(1 + \frac{L_{\text{CII}}^k}{L_{\text{CA}}^k}\right)}{\hat{s}_{11}^k},$$

where $\hat{s}_{11}^k$ is similar to (3) and is given by

$$\hat{s}_{11}^k = 2\alpha_{11}^k S(T)/11,$$

with random variable α_{11}^k drawn from a non-standardized t-distribution with 15 degrees of freedom, location parameter a_{11} and scale $\text{SE}_{a_{11}}$. Linear regression was then performed on the resulting m_C^k, arriving at the linear functional form given in (8), with 99% Bonferroni corrected confidence region displayed in Figure 14(b).

- Optimization was performed using a Sequential Quadratic Programming (SQP) procedure in MATLAB [8] with nonlinear constraints given by the ellipse corresponding to the 99% Bonferroni corrected confidence regions for the mortality coefficients, and linear constraints for the 99% Bonferroni corrected confidence intervals of the stage duration parameters (8 total free parameters). The 99% Bonferroni corrected confidence regions/intervals were used to arrive at simultaneous confidence bounds, corresponding to $(100 - 1/6)\% \approx 99.83\%$ confidence regions/intervals. The correction of six comes from: one each for the confidence regions of the two linear mortality fits, and one each for the confidence intervals for the four stage deviations. (see Figure 14).
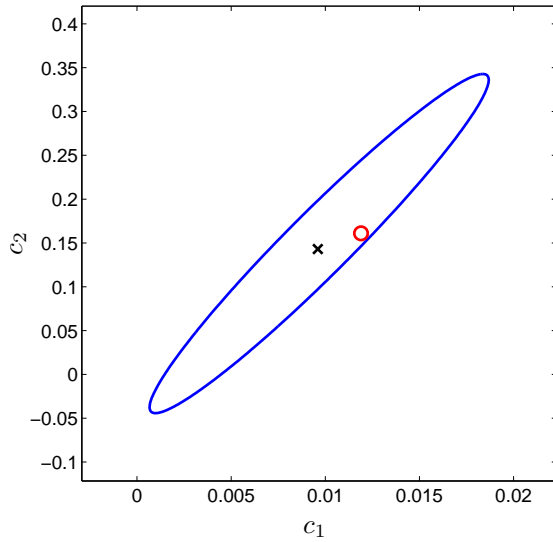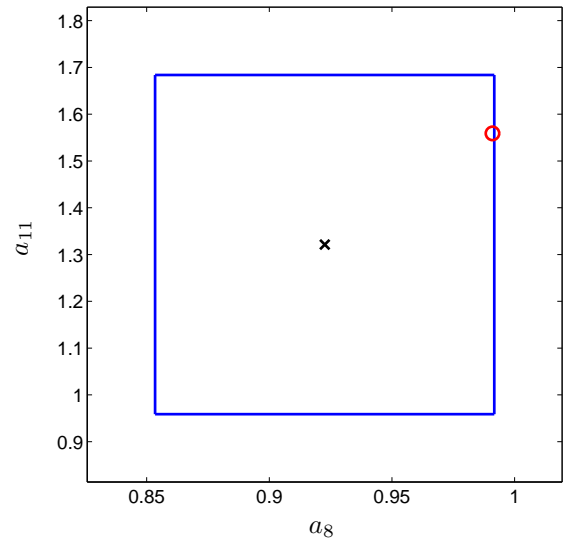
(a) Confidence region for the linear regression coefficients of the nauplii mortality term (see (8)).
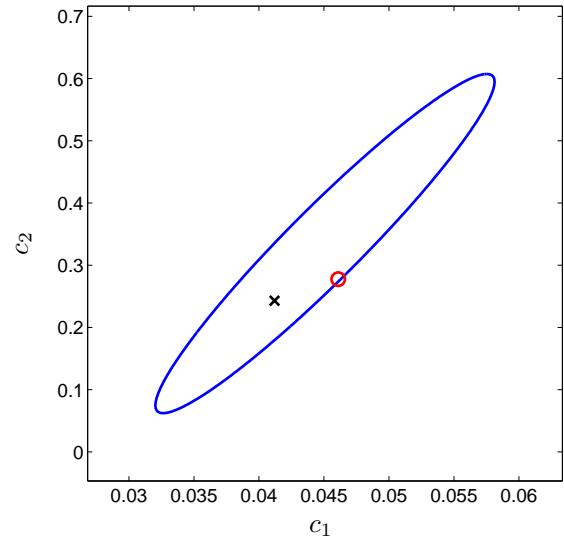
(b) Confidence region for the linear regression coefficients of the copepod mortality term (see (8)).
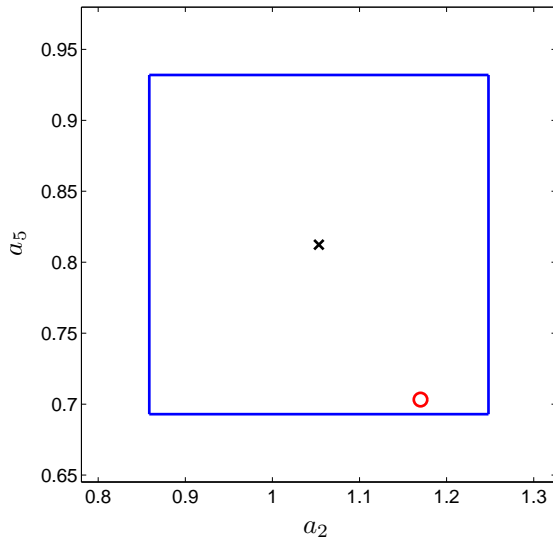
(c) Confidence region for the deviations from the isochronal stage durations [Nauplii I ($a_2 = a_3 = a_4$) versus Nauplii II ($a_5 = a_6 = a_7$)].

(d) Confidence region for the deviations from the isochronal stage durations [Copepod I ($a_8 = a_9 = a_{10}$) versus Copepod II ($a_{11} = a_{12}$)].

Figure 14: *99% Bonferroni corrected confidence regions for the nauplii and copepod mortality terms [(a) and (b), respectively] and the deviations from the isochronal stage durations for the nauplii and copepods [(c) and (d), respectively]. Black x's and red circles denote parameters used in the full and condensed models, respectively.*

References

[1] H. Caswell, 2001. *Matrix Population Models: Construction, Analysis, and Interpretation.* Sunderland: Sinauer Associates.

[2] D. T. Elliott and K. W. Tang, 2011. The influence of carcass abundance on estimates of mortality and assessment of population dynamics in *Acartia tonsa. Marine Ecology Progress Series*, **427**, 1–12.

[3] A. G. Hirst and T. Kiørobe, 2002. Mortality of marine planktonic copepods: global rates and patterns. *Marine Ecology Progress Series*, **240**, 189-205.

[4] L. Holste and M. A. Peck, 2005. The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. *Marine Biology*, **148**, 1061-1070.

[5] S. M. Leandro, P. Tiselius, and H. Queiroga, 2006. Growth and development of nauplii and copepodites of the estuarine copepod *Acartia tonsa* from southern Europe (Ria de Aveiro, Portugal) under saturating food conditions. *Marine Biology*, **150**, 121-129.

[6] J. A. McLaren, C. J. Corkett, and E. J. Zillious, 1969. Temperature adaptations of copepod eggs from the arctic to the tropics. *Biological Bulletin*, **137**, 486-493.

[7] A. Mitra, 2009. Are closure terms appropriate or necessary descriptors of zooplankton loss in nutrient-phytoplankton-zooplankton type models? *Ecological Modelling*, **220**, 611–620.

[8] R. Fletcher, 1987. *Practical Methods of Optimization.* John Wiley and Sons.

[9] D. L. Aksnes, C. B. Miller, M. D. Ohman, and S. N. Wood, 1997. Estimation techniques used in studies of copepod population dynamics. *Sarsia*, **82(4)**, 279-96.