



Original Article

Water temperature during winter may control striped bass recruitment during spring by affecting the development time of copepod nauplii

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Striped bass (*Morone saxatilis*) are anadromous fish that support an important fishery along the east coast of North America. In Chesapeake Bay, strong juvenile recruitment of striped bass can occur when larvae overlap with high concentrations of their zooplankton prey, but the mechanisms fostering the temporal overlap are unknown. Here, the influence of winter temperature on the peak abundances of a key prey, *Eurytemora carolleeae*, was estimated with a temperature-dependent developmental model. The role of these peaks in regulating striped bass recruitment was explored in three nursery areas: upper Chesapeake Bay, Choptank River, and Patuxent River. Model results indicated that cold winters delay the timing and increase the size of peak *E. carolleeae* spring abundance. When the model output was used in regression relationships with striped bass juvenile recruitment and freshwater discharge, the regression models explained up to 78% of annual recruitment variability. Results suggests that cold, wet winters could increase the chance of a match between striped bass larvae and high concentrations of their prey. This mechanistic link between winter temperatures and striped bass production, acting through prey dynamics, could further understanding of fish recruitment variability and indicates that warmer winters could negatively affect some striped bass populations.

Keywords: anadromous fish recruitment, copepod development, estuaries, winter temperature

Introduction

The match-mismatch hypothesis (Cushing, 1990) and the critical period hypothesis (Hjort, 1914) are fundamental theories, which have contributed our understanding of the factors underlying fish recruitment variability (Houde, 2008, 2016). While both point to the spatial and temporal coincidence of fish larvae with their prey, identifying the processes that cause this overlap requires knowledge of the complex interactions between the environment, prey, and fish larvae. Although challenging, this multifaceted understanding is important for predicting how climate change will

affect fish populations (Beaugrand *et al.*, 2002; Edwards and Richardson, 2004; Möllmann *et al.*, 2009; Staudinger *et al.*, 2019). Here, we focus on the match and mismatch between larvae of striped bass, *Morone saxatilis*, and the copepod, *Eurytemora carolleeae*. Specifically, we investigate the interaction between environmental conditions and copepod development rates that influence the temporal overlap of high abundances of *E. carolleeae* with striped bass larvae.

Copepods in the genus *Eurytemora* are an important prey of larval striped bass (Doroshev, 1970), a high-biomass fish species

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that is commercially and recreationally important in North America. The species *E. carolleae* (cf. *E. affinis*, Alekseev and Souissi, 2011) has been identified as the species inhabiting the Chesapeake Bay (Kimmel and Roman, 2004). The timing of the spring *E. carolleae* peak in abundance in Chesapeake Bay has been linked to striped bass recruitment variability (Martino and Houde, 2010). Building on the findings of Martino and Houde (2010), the objective of this research was to simulate the growth dynamics of *E. carolleae* that lead to the copepod's spring peak in abundance and to assess if these growth dynamics could explain a significant amount of the variability in striped bass recruitment.

Eurytemora carolleae is found in the oligohaline (0.5–5) and mesohaline (5–18) salinity zones of the Chesapeake Bay and its tributaries, and is a major component of the mesozooplankton community in winter and spring (Roman *et al.*, 2001; Kimmel and Roman, 2004). *Eurytemora carolleae* abundance peaks over a period of two months in spring (Kimmel and Roman, 2004; Martino and Houde, 2010), however understanding what factors affect the magnitude and timing of these peaks is not clear. It has been suggested that physical conditions in the Chesapeake Bay during winter could result in bottom-up control on spring *E. carolleae* populations (Kimmel *et al.*, 2006; Pierson *et al.*, 2016). Wet winters are associated with high abundance (Boynton *et al.*, 1997; North and Houde, 2003; Kimmel *et al.*, 2006) and wide distribution of *E. carolleae* populations in spring in Chesapeake Bay (Kimmel *et al.*, 2006). The wide distribution is most likely due to high river discharge that transports copepods farther down the Bay and lowers the salinity, providing ample suitable habitat for *E. carolleae* (Kimmel and Roman, 2004; Kimmel *et al.*, 2006).

In addition to freshwater discharge, water temperature during winter also may affect spring *E. carolleae* populations. The generation time of *Eurytemora* spp. is longer and has higher variability at lower temperatures than at higher temperatures (Heinle and Flemer, 1975; Heerkloss *et al.*, 1990; Lee *et al.*, 2007; Devreker *et al.*, 2012; Pierson *et al.*, 2016). Thus the inter- and intra-annual variability in winter water temperatures in Chesapeake Bay will affect the developmental rate of *E. carolleae* (Pierson *et al.*, 2016). However, the influence of winter temperature on the timing of peak *E. carolleae* abundances has not been quantified.

Understanding the factors that cause variability in the timing of peak *E. carolleae* abundance could help explain variability in striped bass recruitment. Extensive research has been conducted on striped bass early life history and recruitment (e.g. Bulak *et al.*, 1997 in the Santee–Cooper river system; Limburg *et al.*, 1999 in the Hudson River; Kimmerer *et al.*, 2009 in San Francisco Estuary). Striped bass typically spawn during April and May in Chesapeake Bay, which is one of the main nursery areas of this species (Rutherford and Houde, 1995; Secor and Houde, 1995). Once larvae begin feeding at 7–9 days old, one of their preferred prey is the copepod *Eurytemora* spp. (Doroshev, 1970; Setzler-Hamilton *et al.*, 1980 and references therein; Setzler-Hamilton and Hall, 1991; Shoji *et al.*, 2005; North and Houde, 2006; Shideler and Houde, 2014). When high *E. carolleae* abundances overlapped with striped bass larvae in space and time, striped bass recruitment was enhanced in upper Chesapeake Bay (Rutherford *et al.*, 1997; North and Houde, 2003; Martino and Houde, 2010), supporting the Match-Mismatch hypothesis (Cushing, 1990). Additionally, a delay in the timing of peak *E. carolleae* abundance was correlated with higher striped bass recruitment (Figure 8 in Martino and Houde, 2010). This

suggests that the best conditions for striped bass recruitment could occur when the peak in *E. carolleae* abundance occurs during late spring in upper Chesapeake Bay, and supports the idea that it is important to understand the factors that influence the population dynamics of a fish larvae's prey in order to understand the factors that affect a fish's juvenile recruitment (Rothschild, 2015). In the case of striped bass, this includes understanding what controls the timing of the peak in *E. carolleae* abundance each spring.

The goal of this research was to explore a mechanism that relates winter water temperature to striped bass recruitment variability through the influence of temperature on the development rate and timing of peaks in abundance of the copepod *E. carolleae*. To assess the potential link between winter temperature, peak copepod abundance, and striped bass recruitment, this research addressed two key questions: (i) How do winter water temperatures influence the timing and size of peak *E. carolleae* abundances during striped bass spawning season? (ii) Do inter-annual differences in these peaks account for a significant amount of variability in striped bass recruitment? To address these questions, a temperature-based developmental model was created to investigate how variations in winter water temperatures could affect the timing of and peaks in spring *E. carolleae* abundances. Additionally, historical monitoring data were used to explore the potential relationships between winter water temperatures, river discharge, and striped bass recruitment.

Methods

Model and data integration efforts focused on three important nursery areas for striped bass: upper Chesapeake Bay, Choptank River, and Patuxent River (Figure 1). These regions were selected based on availability of data on daily water temperature, river discharge and annual striped bass young of the year (YOY) recruitment index (Table 1). A large body of literature exists on striped bass in upper Chesapeake Bay (e.g. Dovel and Edmunds, 1971; Morgan *et al.*, 1973; Secor and Houde, 1995; Rutherford *et al.*, 1997; North and Houde, 2003; Martino and Houde, 2010), and the inclusion of the Choptank and Patuxent Rivers allowed for a comparison between other striped bass spawning areas in Chesapeake Bay. Temperature data from each region were used as the input for the *Eurytemora* spp. developmental model that predicted the timing and size of *E. carolleae* abundances in spring. Multiple linear regressions were used to identify whether water temperature, river discharge rates, and outputs from the developmental model could explain a significant amount of the variability in the annual striped bass recruitment indices for each region.

Water temperature data

Water temperature data during winter and spring was needed to drive the copepod developmental rate model. Hourly water temperature (°C) data measured between 1995 and 2016 was obtained for the period January 1 to May 31 from NOAA Tides and Currents (<https://tidesandcurrents.noaa.gov/>). Data were derived from weather monitoring stations in the upper Chesapeake Bay near Tolchester Beach, MD (station #8573364, 1996–2016), Choptank River near Cambridge, MD (station #8571892, 1998–2016), and Patuxent River near Solomons Island, MD (station #8577330, 1995–2016) (Figure 1). The hourly temperature data was averaged to daily data for use in the developmental model. In addition, these water temperatures were averaged by day across

all years in each region to create a climatology of daily water temperatures for each region.

Some curation and correction of the daily water temperature data was necessary. The equipment used to collect the water temperature data periodically malfunctioned, and years with large gaps in daily temperature measurements (>10 days) were excluded. Linear interpolation was used for smaller gaps (<10 days) in water temperature data for some years. In 2012, a large portion of daily temperature data were missing from the Cambridge, MD station and were filled with water temperature data collected weekly with a hand-held YSI-30 from a fishing pier within 0.8 km of the NOAA Choptank monitoring station (Millette, 2016). The weekly water temperature data was linearly interpolated between each of the sampling time points, for a total of 27 interpolated data points (13 February–10 March), or 23% of the data in 2012, a year with one of the warmest average winters in the Choptank River between 1998 and 2016. Water temperature data at the NOAA station and fishing pier in the three weeks prior to the

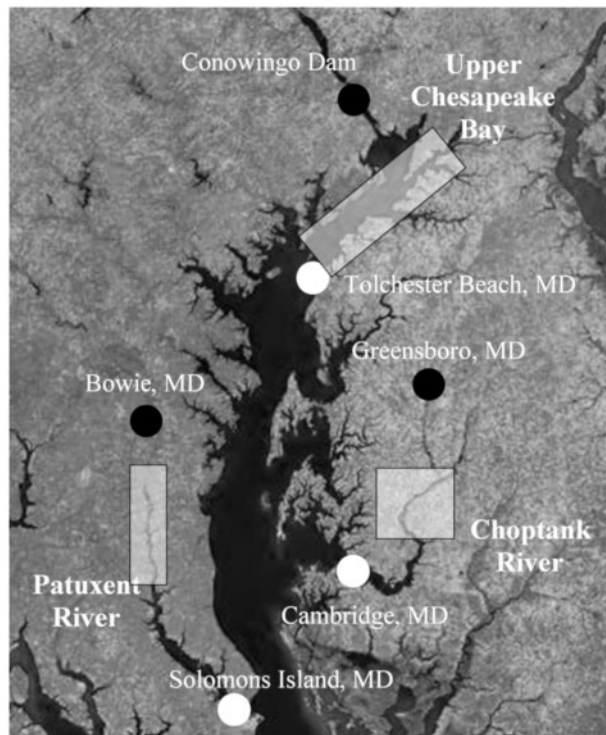


Figure 1. The location of the monitoring stations of the National Oceanic and Atmospheric Administration (NOAA) temperature data (white circles), CBP temperature data (grey circles), and United States Geological Survey (USGS) discharge data (black circles). The grey boxes indicate the regions where striped bass spawn in the Head of the Chesapeake Bay, the Patuxent River, and the Choptank River.

data gap (23 January–12 February) were significantly correlated ($r=0.85$, $p < 0.0001$, $n=20$), with the fishing pier temperatures slightly lower ($\sim 0.6^\circ\text{C}$) than water temperatures measured at the NOAA station. We did not apply an additional correction to this 3-week period because 2012 was the warmest average winter in the Choptank River, so an increase in temperature would have little impact on the output.

Because NOAA stations in the Patuxent and Choptank River were located significantly downriver from the regions where striped bass spawn (Figure 1), it was necessary to adjust the water temperatures measured at the NOAA stations to better reflect temperatures on the spawning grounds. To do so, bi-weekly or monthly water temperature data collected in the spawning areas by the Chesapeake Bay Program (CBP) in the Choptank (station ET5.1) and Patuxent (station TF1.7) Rivers were compared with water temperatures collected at the same time at the downriver NOAA stations (Figure 2). Water temperature upriver and downriver were significantly related for both rivers (Figure 2), but water temperatures were higher upriver compared with downriver. Therefore, the linear regression equations for the Choptank (inset of Figure 2a) and Patuxent River (inset of Figure 2b) were applied to adjust the daily temperature data at the NOAA stations to more accurately reflect temperatures where striped bass spawn.

Copepod developmental rate model

A temperature-dependent *Eurytemora* spp. developmental model was created to test how variations in winter temperature could have affected the timing and size of the spring peak in *E. carolleae*. This model focused on *E. carolleae* that hatched in winter and how they could have affected the spring peak in *E. carolleae* abundance; *E. carolleae* hatched in spring were not incorporated. The model was forced with daily water temperature data (described in the previous section) and had two sub-models: a generation time model and a relative abundance model.

In the generation time sub-model, one cohort of *E. carolleae* was set to hatch each day throughout winter (1 January–19 March, for a total of 78 cohorts) and the date that each of these cohorts reached the adult stage was calculated. Development of cohorts of nauplii in the sub-model was based on a fitted equation of generation time for *Eurytemora* spp. at a range of temperatures, compiled by Pierson et al. (2016):

$$G = a (T + \alpha)^{-2.05} \quad (1)$$

where G (days) is the number of days for *Eurytemora* spp. to develop from the first nauplii stage (N1) stage to the adult stage (C6) at a given water temperature (T , $^\circ\text{C}$), $a = 14\,185$, and $\alpha = 8.95$. *Eurytemora carolleae* have 12 distinct developmental stages, 6 nauplii and 6 copepodite, with the sixth copepodite stage being the adult stage. Equation (1) assumes that water temperature is constant during the entire developmental period of

Table 1. Study region, the name of the stations where water temperature ($^\circ\text{C}$) data were collected in each region, the number of years for which water temperature data were available in each system, and the years for which there were data.

Region	Location of temperature measurements	Number of years	Years
Upper Chesapeake Bay	Tolchester Beach	18	1996–1997, 1999–2003, 2005–2006, 2008–2016
Choptank River	Cambridge	15	1998–2004, 2006–2008, 2011–2012, 2014–2016
Patuxent River	Solomons Island	17	1995–1996, 1998–2003, 2007–2012, 2014–2016

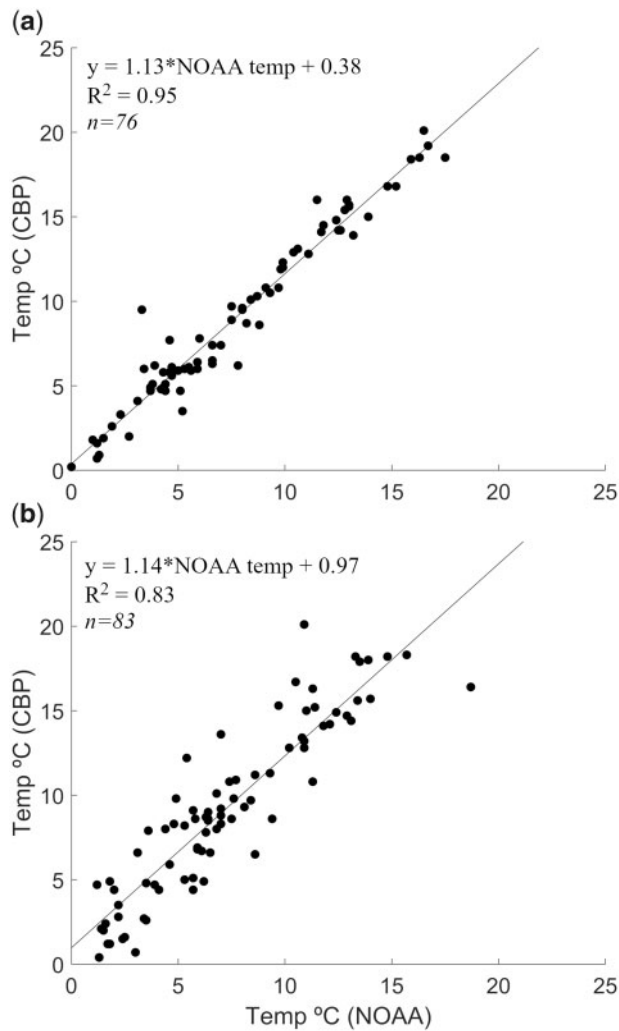


Figure 2. Water temperatures (°C) at downriver NOAA stations versus water temperatures measured at the same time at upriver CBP stations in the (a) Choptank River and (b) Patuxent River during January and March from 1998 to 2016 and 1995 to 2016, respectively. The linear regression equations derived from these data were used to correct daily temperature data from the NOAA stations to more closely match temperature data from upriver where striped bass spawn.

Eurytemora spp., which does not hold for Chesapeake Bay. To correct for this, the daily fractional development rate (D_i , d^{-1}) at each daily time step (i) was calculated based on the reciprocal of Equation (1):

$$D_i = \frac{1}{a(T + \alpha)^{-2.05}} \quad (2)$$

The cumulative sum (D_t) of the fractional developmental rates (D_i) was calculated for each cohort from the day the cohort was hatched until $D_t = 1$, the day when a cohort reached the adult stage. The total number of cohorts reaching the adult stage on each date was then calculated. See Table 2 for a visual representation of the generation time sub-model.

A second sub-model was used to track the relative abundance of copepods hatched during winter once they reached the adult

Table 2. An example of the matrix for each simulation run of the copepod developmental model.

	Day of the year						
	1	2	3	4	...	84	85
Date	1/1	1/2	1/3	1/4	...	3/25	3/26
Temp (°C)	3.0	2.9	2.8	2.7	...	7.3	7.5
Daily development	0.011	0.011	0.011	0.011	...	0.023	0.024
Cohort 1	0.011	0.022	0.033	0.044	...	1.01	–
Cohort 2	–	0.011	0.022	0.033	...	1.00	–
Cohort 3	–	–	0.011	0.022	...	0.99	1.01
Cohort 4	–	–	–	0.011	...	0.97	1.00
...
Cohort 78	–	–	–	–	–	0.144	0.166

The matrix was used to calculate the daily fractional development rate and estimate the date each cohort of *E. carolleae* would reach the adult stage. The model calculated the daily fractional developmental rate using the daily temperature input into the model and tracked the cumulative fractional development for each cohort in its row. Once the cumulative development reached 1.0 (bolded), the cohort was assumed to have reached the adult stage.

stage. The goal was to compare how differences in water temperatures between winters could affect the size of the spring peak in *E. carolleae* abundances, not to recreate *E. carolleae* abundances per se. In the sub-model, every cohort was assigned an initial abundance of $10l^{-1}$, the observed average abundance of *E. carolleae* between January and March in the Choptank River (Millette et al., 2015a), once they reached the adult stage. Each day, the abundance of cohorts that reached the adult stage that day and the abundance of copepods that were already in the adult stage were summed. A mortality rate of $0.4 d^{-1}$ also was applied each day to each adult cohort. This mortality rate was chosen because it reduced the maximum *E. carolleae* abundances output by the model to abundances typically seen in the upper Chesapeake Bay during March and April (Heinle and Flemer, 1975; Roman et al., 2001).

To test how altered temperature may affect the timing and magnitude of peaks in *E. carolleae* abundances, the full copepod development model was run in each region for each year with averaged daily water temperatures and with the climatologically averaged daily water temperatures. For each model run, the following metrics were calculated: average generation time of cohorts (average of time from N1 to C6), the first and last day that cohorts reached the adult stage, the number of days it took for all winter cohorts to reach the adult stage once the first cohort reached the adult stage, and the maximum number of daily cohorts to reach the adult stage on a single day. For each region, analysis of model results focused on comparing results between the climatologically averaged daily water temperature data and those based on the years with highest and lowest average winter water temperatures.

The sensitivity of the copepod developmental model to uncertainty in the a and α parameters of Equations (1) and (2) was assessed. The model was run with the parameters' upper confidence intervals (UCI, $a = 18\ 635$, $\alpha = 11.83$) and lower confidence intervals (LCI, $a = 9735$, $\alpha = 6.07$) (Pierson et al., 2016) and with the climatologically averaged daily water temperature data and the highest and lowest average winter water temperatures years in the upper Chesapeake Bay. The difference between

the timing and magnitude of peaks in *E. carolleae* abundances of the base model described above (with $a=14\ 185$, and $\alpha=8.95$) was compared with the model run with UCI and LCI parameter estimates to determine the influence of uncertainty in these parameters.

Striped bass recruitment analysis

To investigate whether variations in the timing and abundance of copepods could have influenced striped bass YOY recruitment, annual YOY recruitment data for striped bass collected by the Maryland Department of Natural Resources was compared with the average winter water temperature, average river discharge, and outputs from the copepod developmental model. The annual Maryland Department of Natural Resources YOY index for striped bass is based on the geometric mean catch per haul of YOY fish caught in seine surveys conducted between July and September (<http://dnr.maryland.gov/fisheries/Pages/striped-bass/juvenile-index.aspx>; Durell and Weedon, 2011). The number of years included in the analysis varied from 15 to 18 among the three regions, depending on data availability (Table 1).

Hourly river discharge rates ($\text{m}^3 \text{sec}^{-1}$) were downloaded from the USGS website (<https://waterdata.usgs.gov/md/nwis/sw>) and averaged over 1 January–31 March to calculate a mean “winter” discharge rate for each year, and from 1 March to 31 May to calculate a mean “spring” discharge rate for each year. Mean discharge rates were calculated with streamflow data collected at stations near Greensboro, MD (station #01491000), Bowie, MD (stations #01594440), and the Conowingo Dam (stations #01578310) (Figure 1).

The daily water temperature ($^{\circ}\text{C}$) data used in the copepod developmental model above were averaged over 1 January–19 March to calculate a mean “winter” water temperature for each year, and from 1 March to 31 May to calculate a mean “spring” temperature for each year. Martino and Houde (2010) identified a strong relationship between annual striped bass YOY recruitment and average air temperature and river discharge from the Susquehanna River between March and May upper Chesapeake Bay, which we attempted to recreate with water temperatures instead of air temperatures using data from the same USGS Conowingo Dam station (#01578310) as Martino and Houde (2010).

Multiple linear regression analyses were conducted for each region with average water temperature and river discharge data from March to May (“Spring Model”) as the independent variables and striped bass YOY recruitment index as the dependent variable. The same analyses were repeated with data from January to March (“Winter Model”) because water temperatures during these months were the most influential in the copepod developmental model.

To determine if the additional information on copepod development would account for as much variability in striped bass YOY recruitment as temperature, another set of multiple linear regression analyses were conducted for each region using outputs from the copepod developmental model instead of winter water temperature (“Winter Copepod Model”). The model outputs were: the day of the year that the first and last winter cohort reached the adult stage (“First Day” and “Last Day”), the number of days it took all winter cohorts to reach the adult stage once the

first cohort reached the adult stage (“Total Days”), the maximum number of daily cohorts to reach the adult stage on a single day (“Peak”), and the sum of the relative copepod abundance two weeks before and after the water temperature reached 12°C (“Sum”). 12°C is the temperature when striped bass begin to spawn (Rutherford and Houde, 1995) and the adult copepods present at that time would either directly become or would produce prey for striped bass larvae.

Two criteria were used to determine which combination of factors resulted in regression equations that accounted for the most variability in striped bass YOY recruitment. First, the Bayesian information criterion (BIC) of all possible combinations of factors was calculated and compared among all models. The BIC takes into account how well the model fits the data and how many parameters are in the model, penalizing models for every additional parameter (Findley, 1991). The model with the lowest BIC was considered to be the strongest descriptor of the recruitment index. Second, the factors included in the selected model were tested for collinearity using the “car” package in R with the variance inflation factor (VIF) function (Fox and Weisberg, 2016). The VIF function tests for variation-inflation in linear models. Any model that had a collinearity VIF value of three or greater (Zuur et al., 2010) was rejected and then the model with the next lowest BIC was selected until the model with the lowest BIC and collinear factor values <3 was found.

All of the multiple linear regressions were conducted with R using the built-in linear regression (“lm”) function (<http://r-statistics.co/Linear-Regression.html>). The “rsq” package in R was used to calculate the partial R^2 value for each variable included in the multiple linear regressions that were selected as described in the previous paragraph (Zhang, 2018). YOY index data for all locations were tested for normality (Lilliefors normality test), which suggested that the Choptank and Patuxent River YOY index data were non-normal ($p=0.009$ and $p=0.001$, respectively), while the upper Chesapeake Bay data were normal ($p=0.15$). These data were subsequently \log_{10} transformed to achieve normal distribution before calculating the multiple linear regression statistics. Although the YOY index was not transformed by Martino and Houde (2010), a \log_{10} transformation has been used with this striped bass YOY index (Wood and Austin, 2009).

Results

Winter water temperatures and discharge rates

The average daily water temperatures from 1 January to 19 March were significantly different in the three different regions (one-way ANOVA, $p<0.0001$) (Figure 3). Average winter temperatures ($\pm\text{SE}$) were significantly lower at the upper Chesapeake Bay ($3.0 \pm 0.2^{\circ}\text{C}$, $n=78$) than the Choptank River ($4.8 \pm 0.2^{\circ}\text{C}$, Tukey-test, $p<0.0001$, $n=78$) and Patuxent River ($5.8 \pm 0.1^{\circ}\text{C}$, Tukey-test, $p<0.0001$, $n=78$). There was no significant difference between average winter temperatures in the Choptank River and Patuxent River (Tukey-test, $p=0.39$, $n=78$). Average winter temperatures ranged from 0.2 to 5.4°C at the upper Chesapeake Bay, 1.8 – 7.0°C in the Choptank River, and 1.9 – 8.9°C in the Patuxent River (Table 3).

Average daily freshwater discharge rates ($\pm\text{SE}$) from 1 January to 31 March into the upper Chesapeake Bay ($1518.6 \pm 116.8 \text{m}^3$

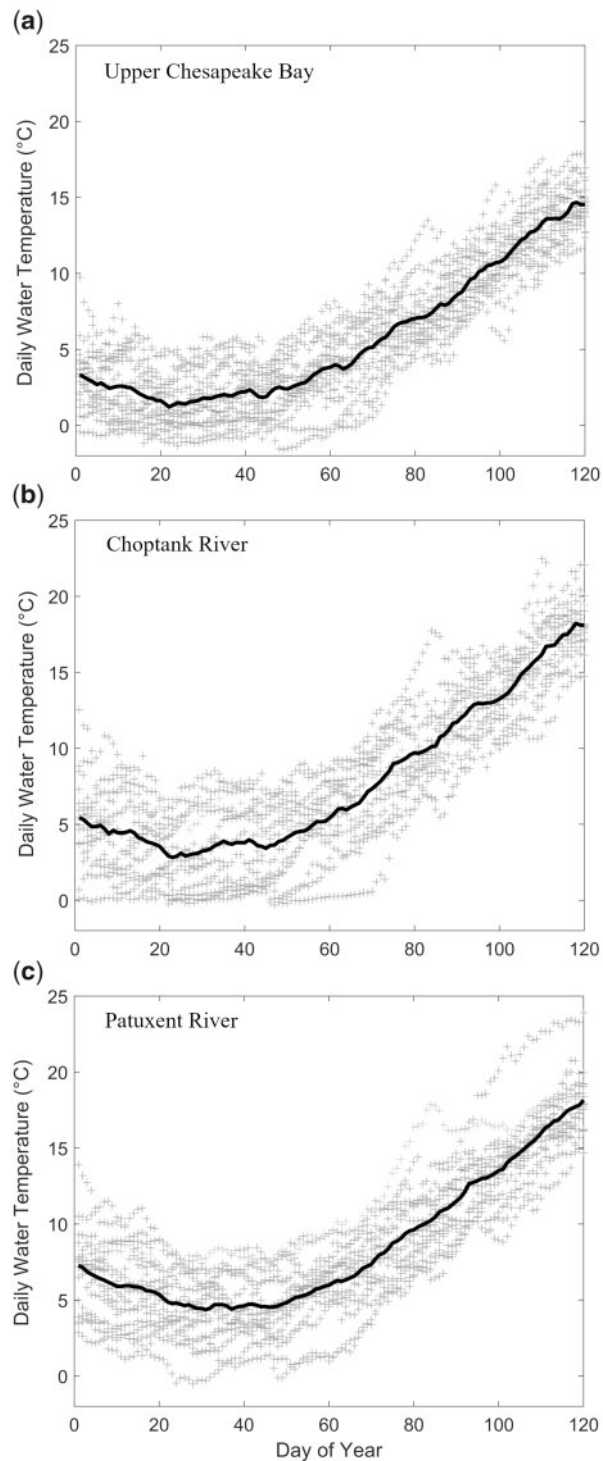


Figure 3. The daily water temperature ($^{\circ}\text{C}$) for the first 4 months of the year in the (a) upper Chesapeake Bay for 18 different years, (b) Choptank River for 15 different years, and (c) Patuxent River for 17 different years (see Table 1 for years). The black line is the climatologically averaged daily water temperature calculated using the daily temperature data for all years in each system.

sec^{-1}) were 200 and 100 times higher than those in the Choptank ($6.9 \pm 0.9 \text{ m}^3 \text{ sec}^{-1}$) and Patuxent Rivers ($14.0 \pm 1.4 \text{ m}^3 \text{ sec}^{-1}$), respectively.

Copepod developmental model

The daily fractional developmental rate of *E. carolleae* calculated using the model varied throughout each winter and between winters in each system (Figure 4). As a result, the timing and magnitude of the spring peaks in relative abundances predicted by the model varied between winters and regions (Figure 5).

Differences in winter water temperatures influenced the timing when the first cohort reached the adult stage (Figure 5, intersection of the left side of each peak with the X-axis). On average, the first daily cohort of *E. carolleae* reached the adult stage on day 83 (24 March) in the upper Chesapeake Bay, day 70 (11 March) in the Choptank River, and day 62 (3 March) in the Patuxent River (Table 3). The first daily cohort reached the adult stage as early as day 43 (12 February) during the warmest winter (Patuxent River, 2012) and as late as day 100 (10 April) during the coldest winter (upper Chesapeake Bay, 2003) (Table 3).

Winter water temperatures also affected the time period during which all cohorts reached the adult stage (Figure 5, duration between the two intersections of each peak with the X-axis). Based on the climatological average model run for each region, the time period to reach the adult stage once the first cohort reached the adult stage was between 29 and 43 d for all 78 daily cohorts hatched in winter (Table 3, Figure 5). The longest time period for all cohorts to reach the adult stage was over two months during a warm winter (65 d), while the shortest time period for all cohorts to reach the adult stage was under three weeks during a cold winter (18 d) (Table 3, Figure 5). After cold winters, it was possible for 7 or 8 cohorts hatched in winter to reach the adult stage on the same day in spring (Table 3). The large peaks in abundance of copepods after cold winters occurred just before or soon after water temperatures were high enough for striped bass to spawn (Figure 5, see arrows indicating 12°C).

Generation times also were influenced by winter water temperatures and differed between regions. The average ($\pm\text{SE}$) generation time for *E. carolleae* calculated using the model was 58 ± 2 d in the upper Chesapeake Bay, 49 ± 2 d in the Choptank River, and 47 ± 1 d in the Patuxent River (Table 3). Depending upon the average winter water temperature, the average generation time for cohorts hatched in winter could differ by up to 36 d, ranging from 34 to 70 d in the warmest and coldest winters, respectively (Table 3).

The copepod development model had the most uncertainty at low temperatures based on the sensitivity analysis, which used the UCI and LCI of parameters a and α . At the high temperature, there was minimal difference in relative copepod abundance between the model runs (Figure 6a). The difference between the average relative copepod abundance was 7.6% and -8.7% for the UCI and LCI models, respectively, compared with the base model. At the low temperature, there was a noticeable difference between the model runs (Figure 6c). The difference between the average relative copepod abundance was 39.4% and -30.9% for the UCI and LCI models, respectively, compared with the base model. When comparing base, UCI and LCI model runs between the climatological mean temperature and the coldest year, the coldest winter produced distinct peaks in relative *Eurytemora* spp. abundance that occurred over a shorter period and later in the year (Figure 6c) than the corresponding peaks produced with the climatologically averaged daily winter water temperatures (Figure 6a). Thus, distinct peaks in relative abundance during

Table 3. Climatologically averaged daily water temperature ($^{\circ}\text{C} \pm \text{SE}$) during winter (1 January–19 March) and copepod developmental model predictions for each region.

	Year	Temperature ($^{\circ}\text{C}$)	Mean generation time	First Day	Last Day	Total Days	Peak	Sum
Upper Chesapeake Bay	1996	1.7 \pm 0.2	64 \pm 2	93	115	22	5	1815
	1997	3.9 \pm 0.3	53 \pm 1	75	111	36	4	1623
	1999	3.2 \pm 0.2	57 \pm 2	82	111	29	4	1771
	2000	3.0 \pm 0.4	55 \pm 2	80	111	31	7	1800
	2001	2.2 \pm 0.2	62 \pm 2	90	115	25	4	1916
	2002	4.0 \pm 0.2	54 \pm 1	75	110	35	4	1344
	2003	0.2 \pm 0.2	70 \pm 2	100	118	18	7	1851
	2005	2.7 \pm 0.2	61 \pm 2	86	112	26	6	1691
	2006	4.5 \pm 0.2	53 \pm 1	72	110	38	3	1403
	2008	3.8 \pm 0.2	56 \pm 1	76	111	35	3	1510
	2009	2.1 \pm 0.2	61 \pm 2	89	114	25	5	1718
	2010	2.7 \pm 0.2	54 \pm 2	83	105	22	6	1934
	2011	2.8 \pm 0.3	56 \pm 2	82	112	30	4	1634
	2012	5.4 \pm 0.2	45 \pm 1	66	105	39	3	1433
	2013	3.8 \pm 0.2	58 \pm 2	77	112	35	4	1645
	2014	1.6 \pm 0.2	65 \pm 2	95	114	19	7	1878
2015	1.2 \pm 0.2	68 \pm 2	97	115	18	7	1924	
2016	4.4 \pm 0.3	51 \pm 2	72	109	37	4	1623	
	Average	3.0 \pm 0.2	58 \pm 2	83	112	29	4	1636
Choptank River	1998	7.2 \pm 0.2	41 \pm 1	52	104	52	3	1075
	1999	5.5 \pm 0.2	46 \pm 1	59	107	48	3	1244
	2000	4.8 \pm 0.5	45 \pm 2	70	103	33	5	923
	2001	4.0 \pm 0.3	50 \pm 1	75	108	33	4	1191
	2002	6.4 \pm 0.3	41 \pm 1	59	104	45	3	1163
	2003	2.4 \pm 0.2	57 \pm 2	85	108	23	6	1475
	2004	3.4 \pm 0.4	53 \pm 2	78	110	32	5	1006
	2006	6.0 \pm 0.2	46 \pm 1	59	106	47	3	1345
	2007	4.6 \pm 0.4	52 \pm 2	66	107	41	7	1479
	2008	6.4 \pm 0.3	42 \pm 1	59	104	45	4	1339
	2011	4.1 \pm 0.4	46 \pm 2	74	104	30	5	1424
	2012	7.0 \pm 0.3	39 \pm 1	56	97	41	4	1363
	2014	2.9 \pm 0.2	60 \pm 2	84	110	26	5	1889
	2015	1.8 \pm 0.2	63 \pm 2	91	109	18	8	1822
2016	5.8 \pm 0.4	44 \pm 2	63	101	38	5	1366	
	Average	4.8 \pm 0.2	49 \pm 2	70	105	35	3	1635
Patuxent River	1995	6.6 \pm 0.2	44 \pm 1	53	104	51	3	1312
	1996	3.3 \pm 0.2	57 \pm 2	81	111	30	4	1491
	1998	8.0 \pm 0.1	38 \pm 1	46	104	58	2	1002
	1999	6.8 \pm 0.1	43 \pm 1	50	106	56	3	1138
	2000	6.4 \pm 0.4	43 \pm 1	60	103	43	4	1475
	2001	5.2 \pm 0.2	47 \pm 1	67	106	39	3	1121
	2002	4.7 \pm 0.1	52 \pm 1	69	110	41	3	1175
	2003	1.9 \pm 0.2	61 \pm 2	89	112	23	5	1500
	2007	6.5 \pm 0.3	47 \pm 1	42	107	65	3	1257
	2008	7.7 \pm 0.2	39 \pm 1	47	104	57	2	1156
	2009	5.7 \pm 0.2	47 \pm 1	61	106	45	3	1472
	2010	6.2 \pm 0.2	42 \pm 1	62	98	36	3	1398
	2011	4.8 \pm 0.3	47 \pm 1	71	105	34	4	1376
	2012	8.9 \pm 0.2	34 \pm 1	43	96	53	3	1173
	2014	4.4 \pm 0.2	56 \pm 1	71	110	39	4	1595
	2015	3.9 \pm 0.2	58 \pm 2	76	109	33	6	1670
2016	7.6 \pm 0.3	41 \pm 1	44	102	58	3	1165	
	Average	5.8 \pm 0.1	47 \pm 1	62	105	43	3	1451

Model results include average (day \pm SE) generation time for *E. carollaeae* cohorts, the first (First Day) and last (Last Day) day of the year that the winter cohort reached the adult stage, the number of days that it took all winter cohorts to reach the adult stage once the first cohort reached the adult stage (Total Days), the maximum number of daily cohorts to reach the adult stage on a single day (Peak), and the sum of the relative copepod abundance two weeks before and after the water temperature reached 12 $^{\circ}\text{C}$ (Sum).

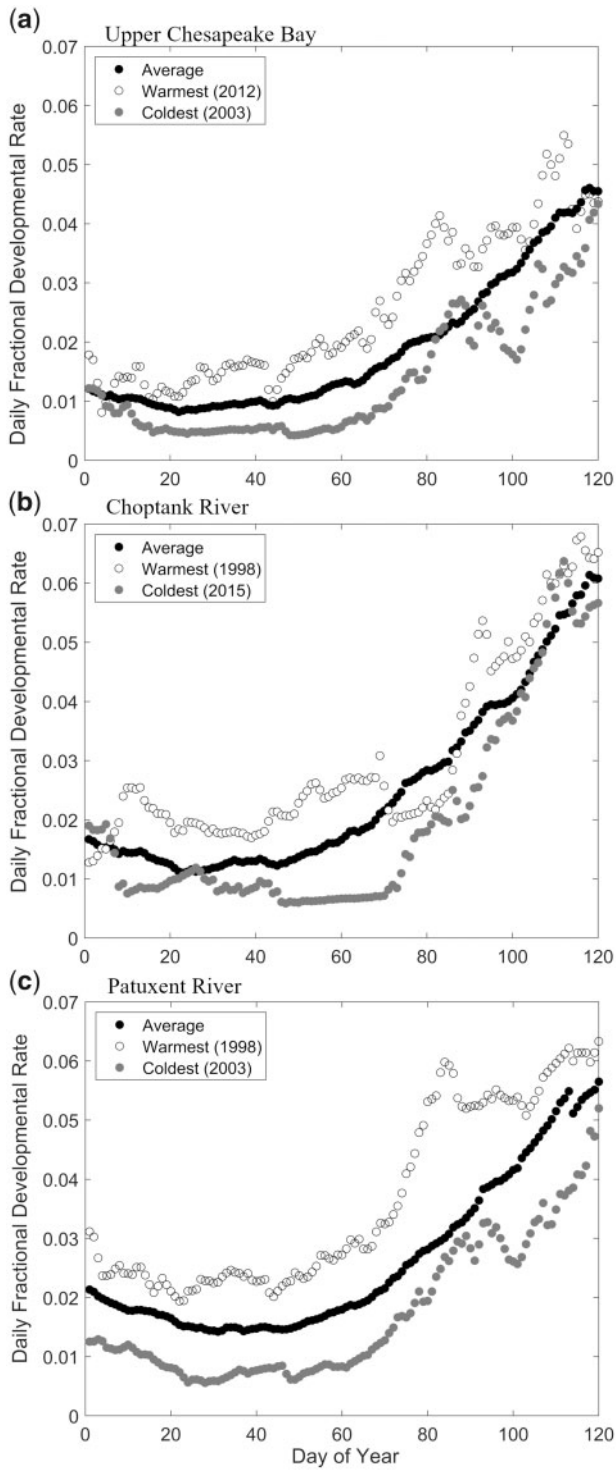


Figure 4. Fractional developmental rates (d^{-1}) calculated using daily temperature during the coldest winter (open circle), warmest winter (black circle), and the climatologically averaged daily temperature (grey circle) in the (a) upper Chesapeake Bay, (b) Choptank River, and (c) Patuxent River.

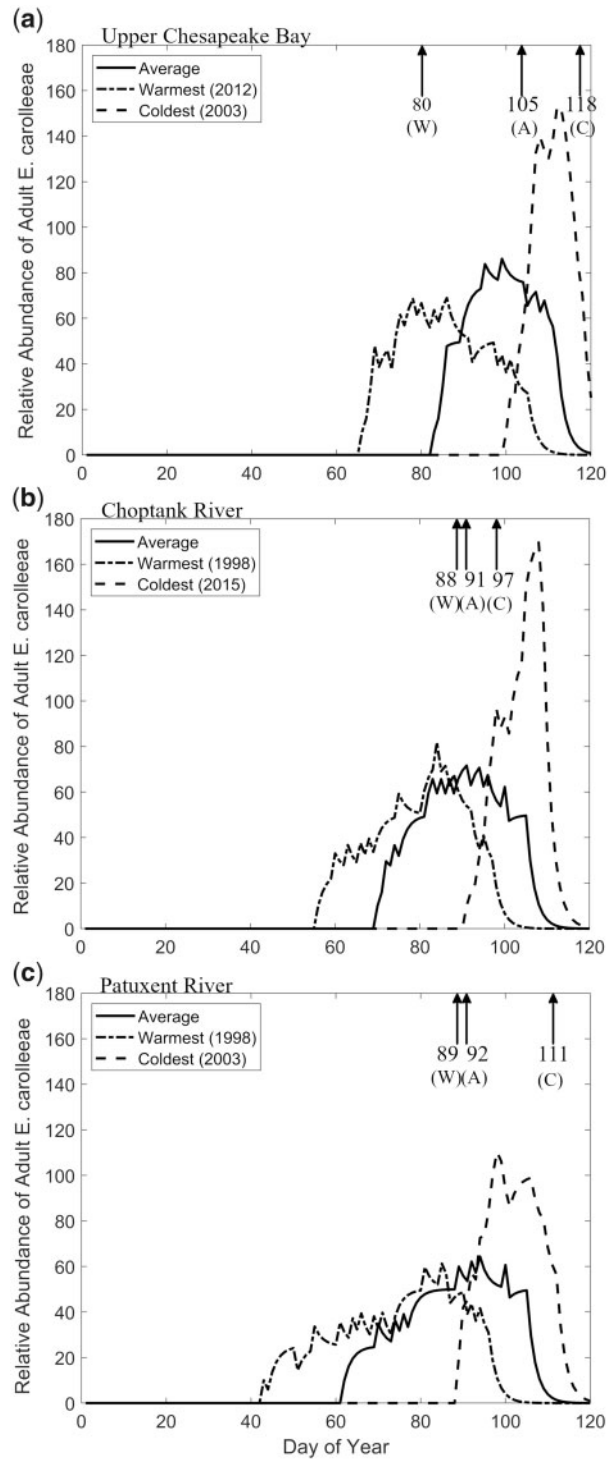


Figure 5. The relative abundance of stage C6 (adult) *E. carolleae* in spring based on the predictions of the copepod developmental model during the coldest winter (dashed line), warmest winter (long dash dot line), and the climatologically averaged daily temperature (solid line) in the (a) upper Chesapeake Bay, (b) Choptank River, and (c) Patuxent River. This accounts for 78 cohorts of *E. carolleae* that hatched during the winter, and not any hatched during the spring. The arrows refer to the day on which water temperature reached $12^{\circ}C$, a temperature threshold for striped bass spawning. Under the arrows, the day of the year and the corresponding model is listed, with W being warmest, A being average, and C being coldest.

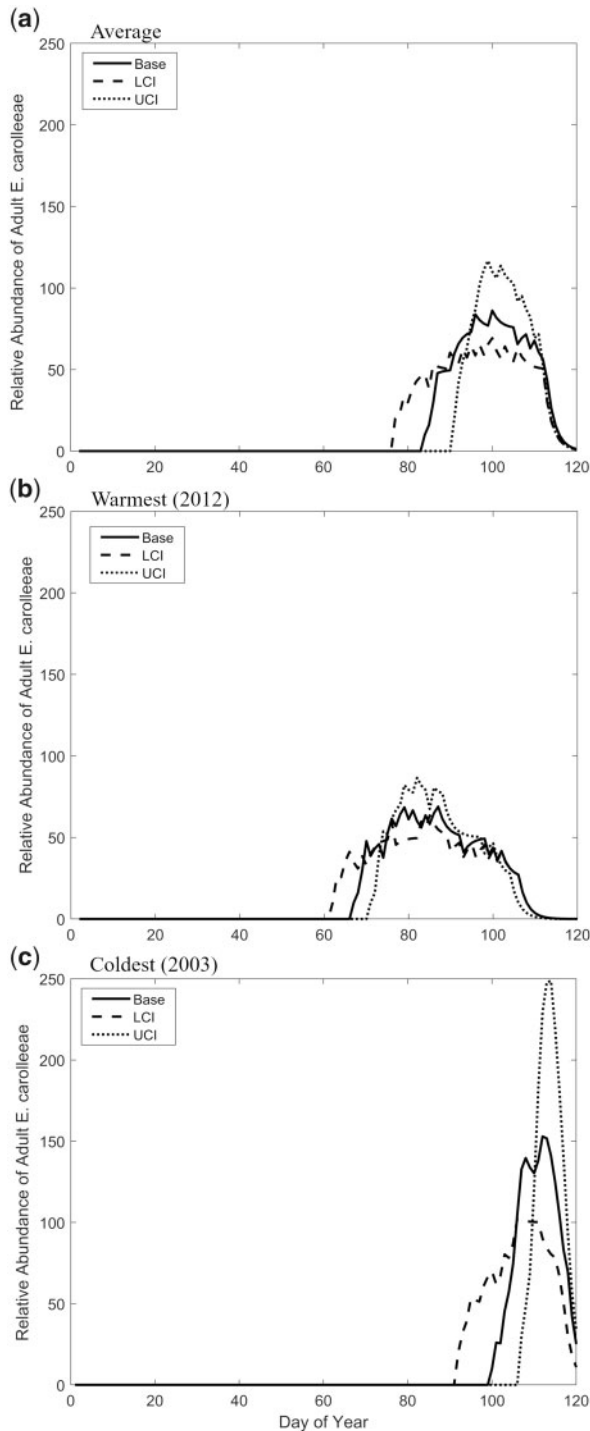


Figure 6. Results of sensitivity analysis to determine how uncertainty in the a - and α -parameters of the copepod development model could affect model results. The model was run with the UCI (dotted lines) and LCI (dashed lines) 95% confidence intervals of the a - and α -values (from Pierson et al., 2016) and used to predict the relative abundance of stage C6 (adult) *E. carolleae* in the upper Chesapeake Bay. Relative abundances are plotted with those from the base model (solid lines, from Figure 5a) when daily water temperatures from the (a) climatologically averaged, (b) warmest winter, and (c) coldest winter were used in the copepod development model. Note the difference in Y-axis scale between Figures 5 and 6.

cold winters were reproduced when uncertainty in model parameters was taken into account.

Striped bass recruitment

In upper Chesapeake Bay, the spring temperature model with water temperature and freshwater discharge accounted for 61% of the variability in the striped bass YOY recruitment index (Table 4), similar to the regression relationship of Martino and Houde (2010), which accounted for 65% of the variability. For the winter temperature model, the regression accounted for 67% of the variability in the striped bass YOY recruitment index (Table 4). For all of these models, temperature was negatively related to the YOY recruitment index, while river discharge was positively related (Table 4). When predictions from the copepod developmental model were substituted for winter water temperature in the winter copepod model, the best fitting model included average river discharge between January and March, the sum of the relative copepod abundance two weeks before and after the water temperature reached 12°C, the day that the last winter cohort reached the adult stage, and the maximum number of cohorts that reached the adult stage on a single day. This regression model described 78% of the variability in the striped bass YOY recruitment index (Table 4, Figure 7a). There was no collinearity between any of the factors in this model (Table 4).

In the Choptank River, the spring and winter temperature model accounted for 21 and 38%, respectively, of the variability in the striped bass YOY recruitment index (Table 4). Similar to the model for upper Chesapeake Bay, the best fitting model that incorporated predictions from the copepod developmental model for the Choptank River included average river discharge between January and March, the sum of the relative copepod abundance two weeks before and after the water temperature reached 12°C, and the day that the last winter cohort reached the adult stage. This regression model described 56% of the variability in the striped bass YOY recruitment index (Table 4, Figure 7b) and had no collinearity between independent variables (Table 4).

In the Patuxent River, spring temperature model accounted for 15% of the variability in the striped bass YOY recruitment index. Similar to models in the other regions, more variability in striped bass recruitment (45%) was accounted for by the winter temperature model, compared with the spring model (Table 4). When the output from the copepod developmental model was applied, the best fitting model included average river discharge between January and March and the day that the last winter cohort reached the adult stage. This model described 45% of the variability in the striped bass YOY recruitment index (Table 4, Figure 7c) and passed tests for collinearity (Table 4).

Discussion

Model results suggest that winter temperatures have a strong effect on the timing and magnitude of peak *E. carolleae* abundances in upper Chesapeake Bay and Choptank River during spring (Figure 5). Furthermore, metrics related to development of winter *E. carolleae* cohorts improved the fit of regression models and accounted for more variability in striped bass recruitment than models without copepod metrics in the upper Chesapeake Bay (R^2 increased from 0.67 to 0.79) and the Choptank River (R^2 increased from 0.38 to 0.56) (Table 4). Colder water temperatures delayed the time of the year when the last winter cohort of copepods matured (“Last Day”) and increased the magnitude of the

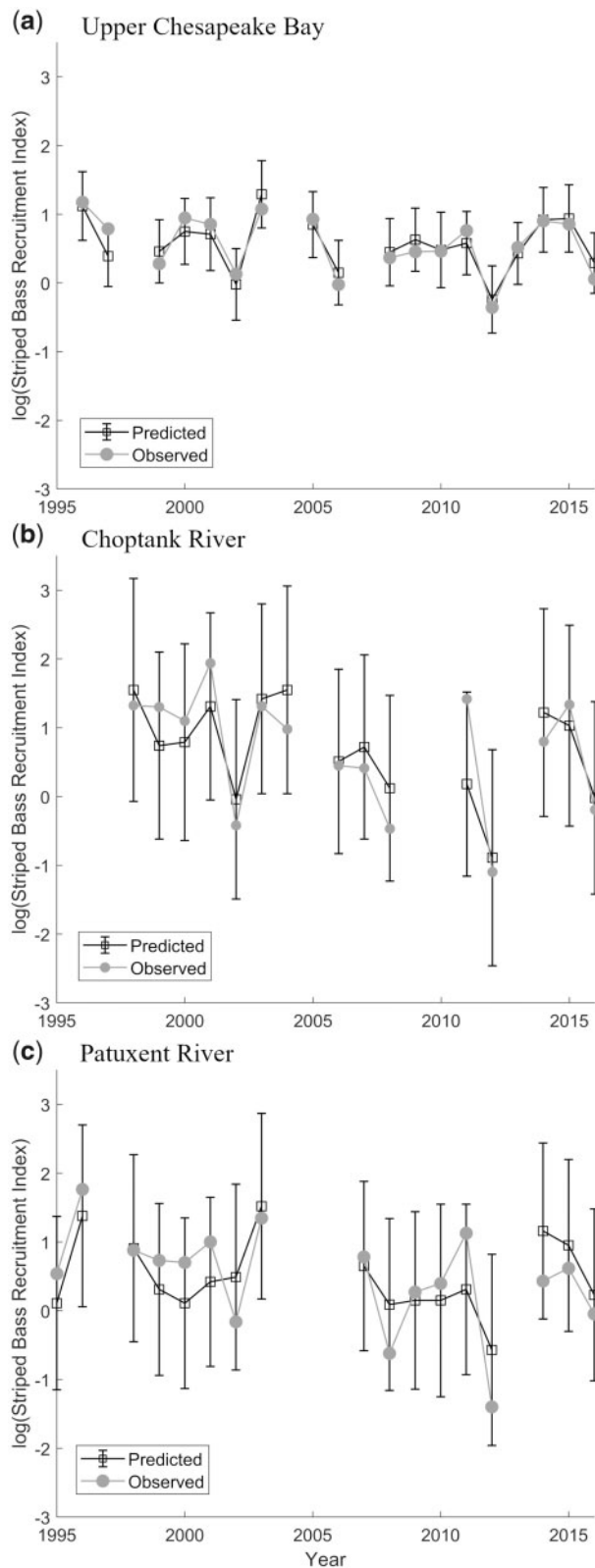


Figure 7. Comparison of observed (black circles) striped bass YOY recruitment indices to indices predicted by the “Winter Copepod Model” from Table 4 (open squares) in the (a) upper Chesapeake Bay, (b) Choptank River, and (c) Patuxent River. Error bars represent the 95% confidence intervals of the predicted values from the “Winter Copepod Model.”

peak in copepod abundance just before and during the initiation of striped bass spawning (“Sum”), both of which were positively associated with striped bass recruitment. In contrast, metrics associated with copepod development in winter did not account for more variability in striped bass recruitment in the Patuxent River, which had average winter water temperature that was at least 1°C warmer than the other regions. Based on these findings, we propose that winter water temperature could influence striped bass recruitment by affecting the match between high peaks in copepod abundance and fish larvae. In systems with average winter temperatures similar to or lower than the Choptank River (<5°C), winter water temperatures could exert a strong control on striped bass recruitment. The lower the average winter temperature, the larger the effect that winter temperature variations could have on copepod phenology and thus could have on striped bass recruitment.

The model developed for this study, based on the empirical relationship between temperature and *Eurytemora* spp. generation time, showed the strong control of winter water temperatures on the timing and relative abundance of the *E. carolleae* spring peak. Under warmer conditions in winter, *E. carolleae* cohorts produced over 1 or 2 days reached the adult stage on a single day in spring. Alternatively, under colder winter conditions, *E. carolleae* hatched over eight separate days in winter could reach the adult stage on a single day in spring. Our model results suggest that developmental rates during colder winters are so slow that cohorts hatched over several days could form a single, larger cohort that could proceed through the developmental stages at nearly the same time. Then, as temperatures increase in spring, the copepod developmental rates increase exponentially causing all *E. carolleae* nauplii to rapidly develop to the copepodite stages. Hence, the large peaks in *E. carolleae* abundance following colder winters could result from the combination of reduced development in winter combined with rapid and synchronous development in spring. The copepods hatched during these large peaks could either be consumed by striped bass larvae or produce nauplii and copepodites that could then be consumed by the larvae.

The copepod developmental model provides insight into how winter temperature influences the timing and size of the spring *E. carolleae* peak, but it is important to acknowledge that the model provides a simplified view of the mechanisms underlying the changes in *E. carolleae* abundances from year to year. Additional factors would need to be included for a more comprehensive understanding, such as the number of nauplii hatched in a cohort on each day, egg production rates, time-varying mortality rates, and prey concentration. The number of nauplii hatching each day in the winter depends on the abundance of adult female copepods and the egg production rate, which itself has been shown to be temperature-dependent for *E. carolleae* (Devreker *et al.*, 2012; Lloyd *et al.*, 2013). As temperature decreases, the egg production rate of a single *E. carolleae* female decreases (Devreker *et al.*, 2012), hence fewer eggs may be produced in cold winters compared with warm winters. In contrast, mortality of *E. carolleae* hatched in cold winters is likely to be lower compared with warm winters because of decreased metabolic rates and increased prey concentrations. It takes longer for *Eurytemora* spp. to die from starvation at lower temperatures (Devreker *et al.*, 2004) and winter blooms of *Heterocapsa rotundata*, an important prey of *E. carolleae* (Sellner *et al.*, 1991; Millette *et al.*, 2015a), decrease the mortality *E. carolleae* nauplii (Millette *et al.*, 2015b).

Table 4. A comparison of R², BIC, and collinearity values for different multiple linear regression models.

Location	Model	R ²	Factors	Partial R ²	Collinearity	BIC
Upper Chesapeake Bay	Martino and Houde (2010)	0.65	–Air Temp (Mar–May)	N/A	N/A	N/A
			+Discharge (Mar–May)	N/A	N/A	
	Spring Temperature Model	0.61*	–Water Temp (Mar–May)	0.54*	1.00	–10.76
			+Discharge (Mar–May)	0.45*	1.00	
	Winter Temperature Model	0.67*	–Water Temp (Jan–Mar)	0.70*	1.00	–13.70
			+Discharge (Jan–Mar)	0.13	1.00	
	Winter Copepod Model	0.78*	+Discharge (Jan–Mar)	0.23*	1.03	–17.93
			+Sum	0.22	2.30	
			+Last Day	0.50*	1.31	
			+Peak	0.19	2.24	
Choptank River	Spring Temperature Model	0.21	–Water Temp (Mar–May)	0.04	1.36	2.25
			+Discharge (Mar–May)	0.17	1.36	
	Winter Temperature Model	0.38*	–Water Temp (Jan–Mar)	0.26	1.15	–1.39
			+Discharge (Jan–Mar)	0.18	1.15	
	Winter Copepod Model	0.56*	+Discharge (Jan–Mar)	0.33*	1.13	–5.01
			+Sum	0.21	1.14	
Patuxent River	Spring Temperature Model	0.15	–Water Temp (Mar–May)	0.16	1.03	3.52
			+Discharge (Mar–May)	0.09	1.03	
	Winter Temperature Model	0.45*	–Water Temp (Jan–Mar)	0.41*	1.05	–3.86
			+Discharge (Jan–Mar)	0.15	1.05	
	Winter Copepod Model	0.45*	+Discharge (Jan–Mar)	0.24*	1.00	–3.88
			+Last Day	0.41*	1.00	

The analyses assessed how well average water temperature and river discharge between March to May (“Spring Temperature Model”) and January to March (“Winter Temperature Model”) accounted for the variation in the striped bass YOY recruitment index. The model “Martino and Houde (2010)” reports results of the analysis conducted by Martino and Houde (2010) which this work builds upon. The “Winter Copepod Model” substituted winter water temperature with variables from the copepod developmental model and is comprised of the combination of those variables with the lowest BIC. Last Day is the day of the year that the last winter cohort reached the adult stage. Sum is the sum of the daily relative abundances of C6 copepods 2 weeks before and after the water temperature reached 12°C. Peak is the maximum number of daily cohorts to reach the adult stage on a single day. Collinearity values above three indicate collinearity with other independent variables.

* $p < 0.05$.

Heterocapsa rotundata need a reduction in temperature for a prolonged period of time to form a bloom (Millette et al., 2015a), hence cold winters may enhance copepod nauplii growth, or at least prevent low prey concentrations from decreasing copepod developmental rates (Campbell et al., 2001; Millette et al., 2015b). *In situ* data on *E. carolleae* developmental stage composition, egg production, and mortality rates would enhance the copepod developmental model so that it could be used to track the actual, instead of relative, abundances of *E. carolleae* hatched each day in winter as they develop.

Measurements of copepod development rates at low temperatures also would improve the model. The equation that forces the copepod development model (from Pierson et al., 2016) was created with developmental rates published in a range of different papers using an established relationship for generation time (Bělehrádek, 1935). The lowest temperature for which developmental rates were measured for *Eurytemora* spp. was 5.0°C (Heerkloss et al., 1990); hence, the developmental rates that were employed in the model for temperatures below 5.0°C need to be confirmed for *E. carolleae* in Chesapeake Bay. However, the data used to fit the equation clearly show that developmental rates exponentially increase with temperature for *Eurytemora* spp. (Pierson et al., 2016) and for copepod in general (Forster et al., 2011). Our sensitivity analysis of the model showed that even with different parameterizations of the a - and α -values in the model, the conclusion that winters with below average temperatures could produce a large peak in *E. carolleae* abundance in

late spring is robust. Still, confirmation through observation of development rates across all relevant water temperatures is needed.

Despite these caveats, the metrics related to copepod development improved regression models of striped bass recruitment in both the upper Chesapeake Bay and Choptank River, and these metrics, plus the freshwater discharge during winter, accounted for a large fraction of the variability in striped bass recruitment across all systems (45–78%, Table 4). Our research focused on the effect of winter temperature on the temporal overlap between peaks in *E. carolleae* abundances and striped bass larvae. The fact that freshwater discharge was a significant variable in the winter copepod model suggests that the spatial overlap of prey and larvae also may be important. In upper Chesapeake Bay, high discharge rates appear to enhance the convergence zone and concentrate *E. carolleae* at the estuarine turbidity maximum (ETM) in spring, resulting in high concentrations of *E. carolleae* where striped bass larvae can be found (Boynton et al., 1997; North and Houde, 2001, 2003; Roman et al., 2001). Fish larvae located near the ETM could encounter and track high concentrations of prey, thereby improving their chance of survival (North and Houde, 2003, 2006; Shoji et al., 2005; Martino and Houde, 2010). Hence, cold winters with high freshwater discharge rates may promote overlap of striped bass with *E. carolleae* in both time and space.

In this study, results of regression models with temperature and discharge indicated that the best years for striped bass

recruitment in upper Chesapeake Bay were those with cold water temperatures and high freshwater discharge rates (Table 4), similar to Martino and Houde (2010). A difference between the studies was the focus on air temperatures during spring (Martino and Houde, 2010) versus during winter (this study). Furthermore, this study suggests the relationship between winter water temperature and striped bass recruitment could be due to the effect of temperature on *E. carolleae* development. Although all upper Chesapeake Bay models with temperature accounted for more than 60% of the variance in the striped bass recruitment index, average winter temperature and average river discharge rates accounted for slightly more of the variability in striped bass recruitment ($R^2 = 0.67$ of the winter temperature model) compared with the regressions with spring conditions ($R^2 = 0.65$ and 0.61 of the Martino and Houde (2010) and spring temperature models, respectively). When temperature was replaced with metrics related to the relative abundances of copepods, the winter copepod model accounted for 78% of the variance in striped bass recruitment in upper Chesapeake Bay, an increase in the explanatory power of the model which was able to predict both high and low recruitment years. This would imply that during the months before striped bass spawn in Chesapeake Bay, the success of their recruitment for that year could be strongly influenced by the winter water temperature via its influence of copepod development rates.

Hence, we suggest that the process underlying the relationship between temperature and striped bass recruitment in the upper Chesapeake Bay is the effect of temperature on copepod development, and hypothesize that the coupling of cold and wet conditions during winter could enhance striped bass recruitment through two mechanisms: (i) cold temperatures that slow copepod development and create peaks in copepod abundances in spring and (ii) high freshwater flow rates that could concentrate copepods. When combined, the high flow and cold temperatures could create optimal feeding conditions for striped bass larvae by promoting high concentrations of copepods, a fundamental factor controlling contact rates of fish larvae with their prey (see N in Eq. (10) of Rothschild and Osborn, 1988). Alternatively, in years with warm temperatures and low freshwater flow, striped bass recruitment could be reduced because *E. carolleae* abundances do not have a sharp peak and the flow rates do not facilitate high concentrations of prey for larvae.

The relationship between the winter copepod model (with copepod metrics and river flow) and striped bass recruitment was strongest in the upper Chesapeake Bay, where average winter water temperatures were lowest and freshwater discharge rates were highest compared with those in the Choptank and Patuxent Rivers. River discharge and the effect of winter temperature on peaks in relative abundance of *E. carolleae* in spring still explained a substantial portion of the variability in striped bass recruitment in the Choptank River, but other unexplained factors are likely influential, especially in the Patuxent River. For example, other prey species could be more important: peak concentrations of the cladoceran *Bosmina longirostris* appear to be key for feeding and recruitment of striped bass in the Patuxent River (Campfield and Houde, 2011). In addition, winter temperature could have less of an effect on striped bass recruitment in the two river systems because average winter temperature was higher in these systems than in the upper Chesapeake Bay. In particular, the Patuxent River had the highest average temperature (Table 3) and, based on the model results for that system, *E. carolleae*

hatched in winter reached the adult stage earlier, over a longer period of time, and formed less of a distinct spring peak (Figure 5c). The effect of winter temperature on striped bass recruitment is likely the greatest in systems with similar to, or lower than, the average winter temperatures in upper Chesapeake Bay ($\leq 3^\circ\text{C}$), such as systems to the north of Chesapeake Bay with large striped bass spawning populations, like the Hudson, Miramichi, and Shubenacadie Rivers (Clark, 1968; Jessop, 1995; Robichaud-LeBlanc *et al.*, 1996).

Despite differences in responses between the regions in this study, all regression models predicted decreases in striped bass recruitment at higher winter temperatures (Table 4), which suggests that global warming will negatively affect striped bass. By the end of the twenty-first century, winter water temperatures are predicted to increase by $2\text{--}6^\circ\text{C}$ in the Chesapeake Bay (Najjar *et al.*, 2010). If our hypothesis is correct, warmer winters would result in *E. carolleae* reaching the adult stage earlier in spring and with lower peaks in abundances during striped bass spawning season, thereby reducing the chance of successful striped bass recruitment. In other words, the low indices of striped bass YOY recruitment in the present day would become more common. Similarly, other fish species for which recruitment is influenced by temperature [e.g. Atlantic herring in the Gulf of St. Lawrence (Brosset *et al.*, 2019) and silver hake on the Scotian Shelf (Reed *et al.*, 2019)] may be susceptible to changes in climate. In Chesapeake Bay, the mortality of juvenile Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic croaker (*Micropogonias undulatus*), species which spawn in the coastal ocean (Able and Fahay, 1998), is reduced during winters with above average temperature (Hare and Able, 2007; Atkinson and Secor, 2017).

There are numerous ways that climate change is predicted to directly or indirectly affect fisheries around the globe (Pörtner and Peck, 2010, and references therein; Hollowed *et al.*, 2013, and references therein). Our findings add to the mounting evidence that suggests that increases in average temperatures will disrupt the ability of fish larvae to match up with their prey in space and/or time (Beaugrand *et al.*, 2002; Edwards and Richardson, 2004; Möllmann *et al.*, 2009). This increase in mismatch between fish larvae and prey has been associated with regime shifts in the North Sea and Baltic Sea from cold water to warm water copepod species that are less nutritious to fish (Beaugrand *et al.*, 2002; Möllmann *et al.*, 2009). In the North Atlantic, the increases in water temperature has affected the timing of seasonal peak and the seasonal cycle for a range of plankton species, thus causing a mismatch between plankton and their predators (Edwards and Richardson, 2004). Similarly, our results suggest that warmer temperatures could both reduce the size of the seasonal peak of *E. carolleae* and cause a mismatch in the timing of the peak with striped bass larvae.

Since the critical period (Hjort, 1914) and match-mismatch (Cushing, 1990) hypotheses were proposed, understanding of the factors that affect the spatial and temporal overlap of fish with their prey has improved (e.g. Houde, 2008; Neuheimer *et al.*, 2018). Our findings add to this body of research by providing a potential mechanistic explanation for this overlap through the influence of water temperature on copepod generation times. Research has shown that survival of fish larvae can improve when larvae overlap with their prey (Illing *et al.*, 2018). In addition, findings of research in the North Sea on the copepod *Calanus helgolandicus* and the fish *Ammodytes marinus* (lesser sandeel) were similar to this study—that colder temperatures which delay

copepod development are beneficial to fish recruitment (Régnier *et al.*, 2017). However, Régnier *et al.* (2017) looked at the timing of peak *C. helgolandicus* egg production and lesser sandeel hatch dates, which overlap with each other. A key difference between our research and their work in the North Sea is that our results focus on environmental conditions 1–3 months before striped bass spawn. This indicates that assessing environmental conditions before fish larvae hatch may improve understanding of the factors that contribute to their survival.

The connection between winter water temperatures, prey production, and striped bass recruitment in upper Chesapeake Bay and the Choptank River suggests that striped bass recruitment could be determined months before striped bass spawn in some systems. This result has important implications for management of striped bass and other species of anadromous fish that have similar life histories and that spawn at a similar time. While future field research is necessary to confirm the direct mechanistic links between winter conditions and fish recruitment through the trophic interactions suggested here, the link between climate, temperature, prey, and striped bass production warrants further investigation to better understand striped bass population dynamics, inform ecosystem based management, and respond to climate change.

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