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Estivation and Postestivation Development of Hemlock Woolly Adelgid (*Adelges tsugae*) (Hemiptera: Adelgidae) at Different Temperatures

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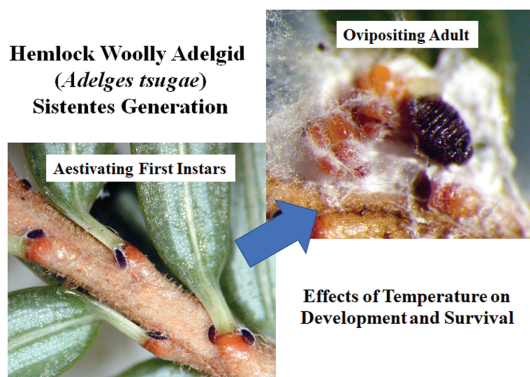
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Abstract

Hemlock woolly adelgid (*Adelges tsugae*) is the most important pest of hemlocks in the eastern United States, where it completes three generations a year. We investigated the impact of temperature (8, 12, 16, and 20°C) on the estivation and postaestivation stages of the *A. tsugae* sistens generation. Temperature significantly impacted development and survival of this generation. The highest mortality occurred at the coolest temperature (8°C). *Adelges tsugae* developed rapidly as the temperature increased and optimum temperatures for development ranged between 17 and 22°C for the different instars. The estimated lower temperature threshold was 0°C for second instar nymphs and 3 –5°C for the other instars and the preoviposition period. Estivating first-instar sistentes resumed development (as evidenced by segments becoming visible) after 40–100 d at the constant temperatures (fastest at 16°C) then required only 105 degree-days (DD) for 50% of the individuals to molt. Subsequent instars developed rapidly (another 470 DD total to reach adult), and oviposition began at ~623 DD from the time the first instars resumed development. This study provides valuable data required to develop an annual phenology model for *A. tsugae* which will assist in timing monitoring and control treatments.

Key words: Hemlock woolly adelgid, temperature, development, degree-day

Graphical Abstract

Hemlock Woolly Adelgid (*Adelges tsugae*) Sistentes Generation

Aestivating First Instars

Ovipositing Adult

Effects of Temperature on Development and Survival

The hemlock woolly adelgid, *Adelges tsugae* Annand, is a serious pest of hemlock trees in eastern North America where it impacts two native species: eastern hemlock *Tsuga canadensis* (L.) Carriere (Pinales: Pinaceae) and Carolina hemlock *Tsuga caroliniana* Engelmann. Within its native range in Asia, *A. tsugae* leads a complex life cycle that can include up to seven generations per year alternating between primary (*Picea* spp.) and secondary host tree species (*Tsuga* spp.). However, in North America, populations of the adelgid include only three generations per year, all originating on the secondary hemlock hosts. These generations include a winter, spring, and sexual generation (called sistentes, progredientes, and sexupara, respectively), and this three-generation life history is found among both the native populations in the Pacific Northwest (Limbu et al. 2018) and the introduced populations in the northeast. Although the sexuparae have the potential to migrate to the primary host species, suitable hosts are missing from the landscape making this generation a population sink, as none of the sexuparae can successfully reproduce. The sistens generation is present throughout summer and lays its eggs the following spring. This generation undergoes estivation in mid to late summer, resuming its growth in the fall. The progrediens generation is active during the spring and lays its eggs in early summer. Both the sistens and progrediens generations go through four instars (McClure 1987).

Adelges tsugae populations in eastern North America originated in southern Japan (Havill et al. 2006). Although first observed in Richmond Virginia in 1951, it likely arrived in the early 1900s and is now present in 20 eastern states in the United States (Havill et al. 2006) and two Canadian provinces (Emilson et al. 2018). It has spread more rapidly in the southern than in the northern part of the hemlock range, suggesting temperature may play a role in variability in the insect's spread (Evans and Gregoire 2007). Cold temperature extremes and long exposure to cold temperatures are known to reduce *A. tsugae* survival in winter (Parker et al. 1998, Paradis et al. 2008, Trotter and Shields 2009). It is widely known that temperature

has a large impact on the developmental rate of ectotherms like insects. A previous study indicated that temperature significantly impacted development of progrediens generation (Salom et al. 2002). However, there has been no similar study of temperature impacts on the sistens generation.

This study examined the effects of temperature (8, 12, 16, and 20°C) on estivation and the postaestivation development of the hemlock woolly adelgid sistens generation. The results of this study add to past work examining the development of the progrediens generation and provide a basis for the development of a model to predict the timing of critical life stages of *A. tsugae*. Model predictions would provide valuable information for monitoring and release of predators for biological control and strengthening *A. tsugae* monitoring and management efforts.

Materials and Methods

Hemlock Woolly Adelgid Population

Hemlock twigs containing first-instar estivating nymphs of the sistens generation of *A. tsugae* were collected in October 2017 and July 2018. The nymphs collected in July would have recently entered estivation, and those collected in October were close to breaking estivation. Both collections were made at a location near Taughannock Falls State Park, New York (42°32′35.6′N, 76°36′07.3′W). Insects used for the experiment were collected on hemlock trees in the same 0.5 ha stand. The trees in this stand were moderately infested with 2–4 *A. tsugae* per cm and were similar in health, age, and infestation level. One-meter-long branches infested with *A. tsugae* were collected from the bottom 5 m of the trees using pole and hand pruners. Collected branches were brought to the laboratory and placed in 19-liter buckets containing water. Buckets containing branches were then stored in an environmental chamber held at 3.5–4°C and 80% RH until processed for the experiment, usually within a day, and never longer than 36 h.

Table 1. Percentage (mean ± SE [*n*]) of *A. tsugae* mortality within each instar and by temperature

Instars/stage	Temperature (°C)				Statistics		
	8	12	16	20	*F*	df	*P*
I	84.4 ± 2.28a (52)	71.5 ± 3.41b (63)	51.8 ± 3.79c (81)	49.7 ± 4.24c (65)	22.23	3, 257	<0.0001
II	53.5 ± 6.12a (30)	33.3 ± 5.40ab (30)	29.6 ± 5.01b (30)	36.7 ± 5.67ab (30)	3.15	3, 116	0.0276
III	32.5 ± 5.31a (30)	31.5 ± 5.22a (30)	28.6 ± 4.91a (30)	38.5 ± 5.78a (30)	0.61	3, 116	0.6105
IV	78.7 ± 6.83a (10)	44.01 ± 9.93a (10)	14.7 ± 5.11b (10)	8.49 ± 3.13b (10)	12.34	3, 36	<0.0001
Ovipositing adult	68.7 ± 9.22a (10)	44.2 ± 10.75ab (10)	30.4 ± 9.04ab (10)	20.8 ± 6.82b (10)	4.07	3, 36	0.0137

There were three separate collections of individuals that were followed and summarized here: first instars, second to third instars, and fourth to adults. Means followed by different letters within each row are significantly different at *P* < 0.05 (Tukey–Kramer post hoc test). Sample size (*n*) is the number of twigs.

Table 2. Mean (± SE [*n*]) time spent (d) by *Adelges tsugae* at different temperatures and developmental stages

Parameter	Temperature (°C)				Statistics		
	8	12	16	20	*F*	df	*P*
I	58.83 ± 21.04a (5)	16.23 ± 1.56b (91)	12.22 ± 0.89bc (293)	11.82 ± 0.836c (466)	8.54	3, 95.7	<0.0001
II	23.3 ± 1.04a (208)	13.0 ± 1.04b (332)	10.8 ± 1.03c (530)	9.40 ± 1.04d (224)	146.4	3, 1261	<0.0001
III	34.7 ± 1.04a (119)	17.4 ± 1.03b (252)	15.9 ± 1.03c (416)	15.9 ± 1.04bc (132)	121.7	3, 874	<0.0001
IV	24.7 ± 0.93a (13)	15.3 ± 0.52b (44)	10.7 ± 0.48c (52)	8.30 ± 0.47d (56)	105.0	3, 152	<0.0001
Ovipositing adult	14.4 ± 1.13a (6)	8.60 ± 0.57b (28)	4.0 ± 0.49c (39)	4.50 ± 0.44c (51)	40.8	3, 111	<0.0001

Means followed by different letters within each row are significantly different from each other at *P* < 0.05 using Tukey–Kramer post hoc test. Sample size (*n*) is the number of survivors.
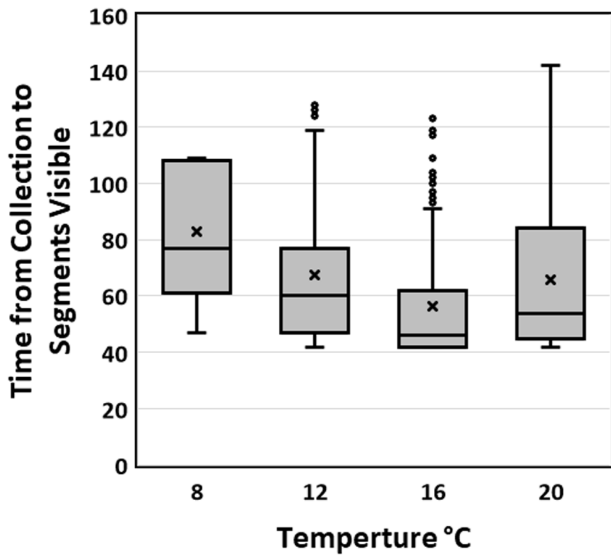
Fig. 1. Box plot of the time at each temperature from collection of estivating first instars to when segments became visible indicting that development had resumed. The line inside the box represents the median and the X is the mean.
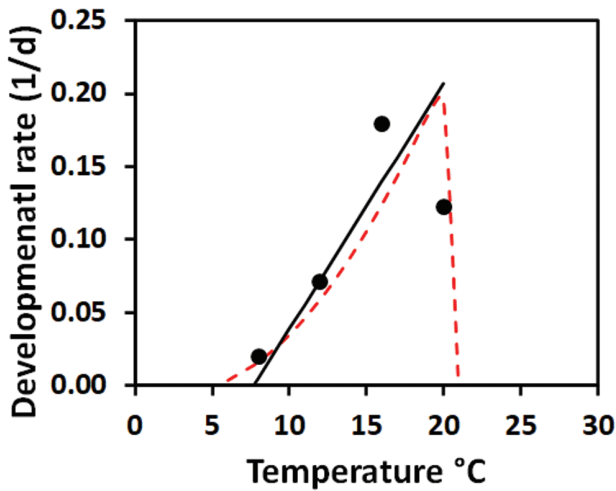

Fig. 2. Developmental rates (1/days) of estivating *A. tsugae* in response to constant temperatures. Developmental rates were fitted to linear regression (solid line) and Briere model (dashed line). Data points at each temperature represent median developmental rate.
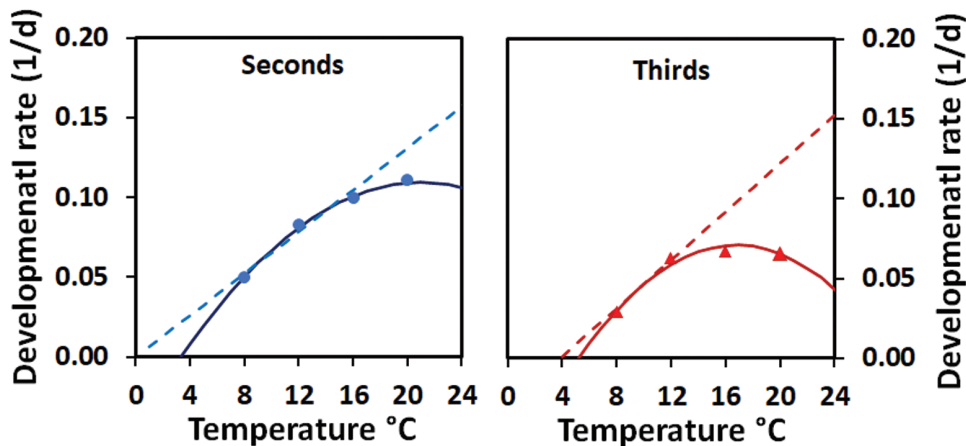
Estivating *A. tsugae* Development

Hemlock twigs collected in July 2018 were prepared by counting newly estivated *A. tsugae*, recutting the stem under water, and then placing them in a 266 ml clear cup containing 133 ml water and 64 g of play sand. The twigs were on average 15.64 cm in length and had 40 estivating *A. tsugae* on them. Any other adelgid stages were removed from the branches before use. In total, 120 cups were prepared and divided into four sets that were randomly assigned to a temperature treatment 8, 12, 16, and 20°C. The four environmental chamber temperatures were monitored using built-in temperature data loggers and maintained within 1 degree of the desired set temperature. Relative humidity was maintained at 70% and a photoperiod of 12:12 h (L:D) was used in all chambers. *Adelges tsugae* were carefully examined every day for segmentation, molt, and death. Segmentation was recorded when the nymph began to swell as it resumed development and the plates that make up the exoskeleton separated exposing the reddish colored skin between them. The separation of plates indicated the development of the insect had resumed and preceded molting. The time from the first observation of segmentation to the molt was considered to be the developmental time for each individual in the first instar. If an individual molted without segmentation being recorded or within 1 d of segmentation being recorded, then the individual was censored and not included in the analysis. The time from collection to segmentation was also calculated since it could provide information on the conditions need to break the estivation. Molted and dead individuals were removed to ensure no developing first instars were double counted. Water level in each cup was checked daily and was added as needed. Twigs were lightly misted with water every day.

Postestivating *A. tsugae* Development

Late estivation stage *A. tsugae* were collected in October 2017, and the twigs and cups were prepared similarly to those used in the estivation study. The twigs were on average 12.6 ± 2.9 cm in length and included 40 individual *A. tsugae*. In total, 120 sample cups were prepared to provide 30 for each temperature treatment (8, 12, 16, 20°C). Twigs/cups were randomly assigned to a temperature treatment and placed in their respective environmental chambers maintained at constant temperature treatments as described in the estivation study. *Adelges tsugae* were checked daily for changes including molts, becoming dislodged from the twig, and death. Ovipositing adults and dead individuals were removed as they occurred. Twigs that became dry and began to drop needles were replaced with extras kept for this purpose until they were exhausted.
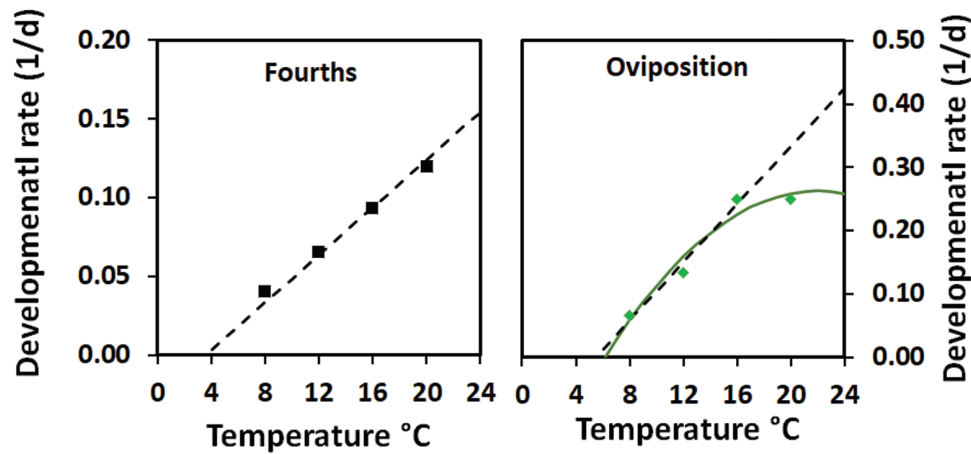

Fig. 3. Developmental rates (1/days) of *A. tsugae* second (left) and third (right) instars in response to constant temperatures. Developmental rates of second and third instars were fitted to polynomial model (solid line) and linear (dashed line) models. Symbols represent the median values for each temperature.

Fig. 4. Developmental rates (1/days) of *A. tsugae* fourths instars (left) and oviposition (right) in response to constant temperatures. Developmental rate oviposition were fitted to polynomial model (solid line), and both fourth instars and oviposition were also fitted to a linear (dashed line) model. Symbols represent the median values for each temperature.

A second set of twigs was collected in December 2018 when hemlock woolly adelgid were primarily late third instars. This second set was collected to supplement the samples, as many of the 2017 twigs began to lose needles indicating they had become too dry to support the development of the adelgid through the fourth instar and into oviposition. The twigs averaged 12.6 cm in length and cups were prepared using the methods previously described. All adelgids in other stages were removed before use. In total, 40 sample cups were prepared, 10 for each temperature treatment (8, 12, 16, 20°C). Twigs had varying numbers of third instars (4–10) on them and were randomly assigned temperature treatments. The number of adelgid per cm of twig was kept constant as much as possible by using longer twigs when more adelgids were present. Daily checks of the adelgids were made, recording molts, and removing dead nymphs. When adults began to oviposit, the date was recorded and the individual was removed.

Statistical Analyses

Statistical analyses were performed using SAS 9.4 (SAS Institute 2015). The Shapiro–Wilk tests were used to evaluate the normality of the data. When the data were not normally distributed PROC UNIVARIATE was used to assess the fit of the data to a lognormal and a gamma distribution which can handle data with long right tails. PROC GLIMMIX (a generalized linear mixed model) was used to evaluate the effects of temperature treatments on days in instar and time to first oviposition. The twig the adelgids were on was used as a random effect in each model. Days in the first instar (time from segmentation to the molt) were analyzed using a gamma distribution with a log link, days in the second and third instars used a lognormal distribution with an identity link, and days in the fourth instar and time to first oviposition used a normal distribution with an identity link. The percentage mortality was determined for each twig and fitted to a beta distribution with a logit link function. Proportion mortality values of zero and 1, which cannot be fit in a Beta distribution, were replaced with 0.00001 and 0.99999 before analyses. The Tukey–Kramer post hoc analysis at $\alpha = 0.05$ was used to determine whether means were significantly different in pairwise comparisons among temperature treatments. The residuals for each model were evaluated for normality and homogeneity of variance for each temperature treatment using a Levene's test.

To determine whether a linear or nonlinear model provided the best fit for each of the following relationships, we selected the model with both the best visual fit and adjusted r^2 value among those evaluated. The relationship between developmental rates and temperature was fitted to a linear ($Y = a + bT$), quadratic equation ($Y = a + bT + cT^2$) and Briere model ($Y = a \times T \times (T - T_{min}) \times ((T_{max} - T)^{(1 \div b)})$; Briere et al. 1999) using PROC NLIN and the Marquardt convergence method (SAS Institute 2015). Several other models not mentioned here (all those found in Rebaudo and Rabhi 2018) were preliminarily assessed but did not provide a good fit or convergence was not achieved. The quadratic equation was a good fit for some of the data, despite not being the standard shape for developmental rate curves, so was included to provide more information about the data. For each model, Y represents the rate of development, T represents holding temperature, and T_{min} and T_{max} represent minimum and maximum temperature thresholds, respectively. In each case, the points at which the fitted model crossed the *x*-axis were determined by solving for *y* = 0.

The number of degree-days (DD) required to complete each instar and to first oviposition (all temperature treatments) were calculated using the lower thresholds estimated based on the relationship between developmental rate and temperature (only the Briere or linear model estimates were used). The DD assumes the relationship is linear when most are nonlinear but is the accepted standard method used for this type of data. The relationship between cumulative proportion of individuals completing an instar (or first oviposition) and accumulated DD was modeled using the Gompertz function, $P = \exp[-\exp(-b * DD + a)]$ with PROC NLIN and the Marquardt convergence method.

Results

Mortality

Adelges tsugae mortality was significantly impacted by temperature. Mortality of first instars was significantly higher at 8°C than all the other temperatures and mortality at 12°C was higher than that at 16 or 20°C (Table 1). There was no significant difference in mortality between 16 and 20°C. Mortality of second instars was higher at 8°C than at 16°C but not significantly different over the 12–20°C temperature range. Third-instar mortality was not significantly different across the temperatures evaluated. Fourth-instar mortality was

Table 3. Parameter values for models used to describe the relationship between temperature (°C) and developmental rate of Hemlock woolly adelgid by developmental stages

Development period	Temperature range	Model	a	b	c or T_{max}	T_{min}	Optima	n	$_{Adj}R^2$	Statistics
First instar	8–20	Briere	0.00071 ± 0.00026	9.58 ± 84.0	20.00 ± 0.19	5.23 ± 10.95	20.0	855	0.052	$F = 385.9$; df 4, 851; $P > 0.0001$
First instar	8–16	Linear	−0.129 ± 0.0419	0.0168 ± 0.00278	NA	−7.702 ± 0.123	NA	388	0.0.0866	$F = 36.68$; df 1, 387; $P > 0.0001$
Second instar	8–20	Polynomial	−0.0450 ± 0.0141	0.0147 ± 0.0022	−0.004 ± 0.0001	3.32	21.2	4	0.9915	$F = 175.47$; df 1, 3; $P = 0.0533$
Second instar	8–16	Linear	−0.0003 ± 0.0056	0.00656 ± 0.000413		0.040 ± 8.76		1070	0.1902	$F = 252.03$; df 1, 1068; $P < 0.0001$
Third instar	8–20	Polynomial	−0.0787 ± 0.0327	0.0178 ± 0.0050	−0.0005 ± 0.0002	5.23	16.7	4	0.9046	$F = 15.22$; df 1, 3; $P = 0.1784$
Third instar	8–12	Linear	−0.0295 ± 0.00592	0.00758 ± 0.00054		3.89 ± 1.09		371	0.3427	$F = 193.94$; df 1, 369; $P < 0.0001$
Fourth instar	8–20	Linear	−0.0027 ± 0.0052	0.0076 ± 0.0004	NA	3.58 ± 0.49	NA	4	0.9934	$F = 451.89$; df 1, 3; $P = 0.0022$
First oviposition	8–20	Polynomial	−0.2430 ± 0.2114	0.0461 ± 0.0012	−0.0011 ± 0.0012	6.13	22.1	4	0.835	$F = 8.59$; df 1, 3; $P = 0.2345$
First oviposition	8–16	Linear	−0.1247 ± 0.0437	0.0229 ± 0.0035	NA	5.44 ± 1.01	NA	3	0.954	$F = 42.5$; df 1, 2; $P = 0.0969$

See Methods for details of the analysis.

Table 4. Estimated accumulated degree-days (± SE) required to reach each instar for 10, 50, and 90% of the population

Parameter	First	Second	Third	Fourth	Oviposition onset
a	0.0169 ± 0.000276	0.0157 ± 0.000359	0.0155 ± 0.000132	0.00486 ± 0.000149	0.0481 ± 0.00132
b	1.402 ± 0.027	2.256 ± 0.060	2.362 ± 0.023	5.798 ± 0.188	1.962 ± 0.062
10%	33.6 (32.5–34.6)	90.6 (88.8–92.3)	98.6 (97.9–99.2)	102.1 (101.4–1024–102.8)	23.4 (22.8–248–24.0)
50%	104.6 (104.8–104.5)	167.0 (167.0–167.1)	176.06 (176.05–176.07)	126.84 (126.81–126.87)	48.4 (48.36–48.44)
90%	216.1 (218.1–214.2)	287.0 (284.4–289.8)	297.6 (296.6–298.7)	165.6 (164.4–166.9)	87.6 (86.5–88.7)
Base temperature	7.70 ± 1.23	0.040 ± 8.76	3.89 ± 1.09	3.58 ± 0.49	5.44 ± 1.25
Statistics	$F = 39{,}574$; df 2, 106; $P > 0.0001$	$F = 32{,}923.6$; df 2, 160; $P > 0.0001$	$F = 12{,}5573$; df 2, 154; $P > 0.0001$	$F = 9{,}052.0$; df 2, 38; $P > 0.0001$	$F = 11{,}9997.2$; df 2, 34; $P > 0.0005$
R^2_{Adj}	0.995	0.985	0.997	0.995	0.994

R^2_{Adj} value is based on the relationship between degree-days and cumulative proportion to reach each instar using the Gompertz function, $P = \exp[-\exp(-b * DD + a)]$.
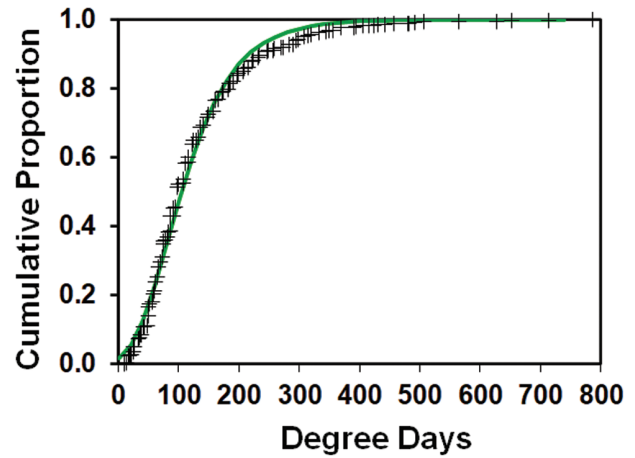

Fig. 5 Cumulative proportion of *A. tsugae* individual breaking diapause at 8, 12, 16, 20°C over accumulated degree-days. Solid line was fitted to cumulative proportion of individuals using Gompertz function, $P = \exp[-\exp(-b * DD + a)]$.
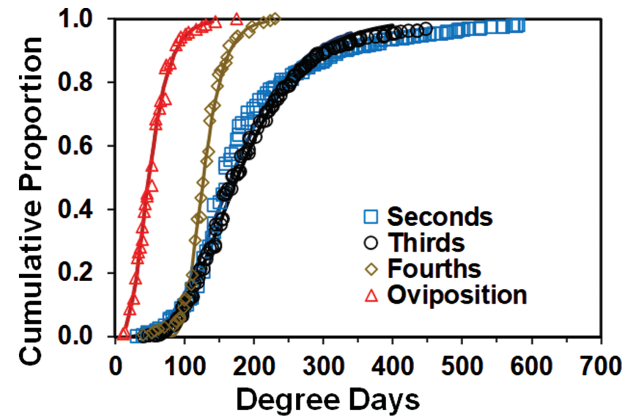

Fig. 6. Cumulative proportion of *A. tsugae* individual reaching second, third, fourth, and oviposition stage reared at 8, 12, 16, 20°C over accumulated degree-days. Solid lines were fitted to cumulative proportion of individuals using Gompertz function, $P = \exp[-\exp(-b * DD + a)]$.

higher at 8 and 12°C than 16 and 20°C. Ovipositing adult mortality at 8°C was higher than that at 20°C, but there was no difference in mortality between individuals held at 12–20°C.

Development Time at Different Temperatures

Temperature had a significant impact on *A. tsugae* developmental time. Mean developmental time spent in each instar generally decreased as the temperature increased (Table 2). For example, the individuals required 14 more days to complete the second instar at 8°C than at 20°C. There were also differences in the time nymphs took to complete the different instars. As expected, *A. tsugae* sistentes spent a long time as first instars before segmentation was observed (Fig. 1) but then time from segmentation to the molt (time in first instar in Table 2) was more comparable to the time spent in the other instars at the various temperatures. Although the time from when estivating first instars were collected to visible segmentation did not significantly differ between temperatures ($F = 2.27$; df 3, 86.9; $P = 0.0861$), the mean number of days decreased from 8 to 16°C and then increased slightly at 20°C (Fig. 1). At warmer temperatures, *A. tsugae* oviposited within 5 d of reaching the adult stage (Table 2).

Rate of Development and Estimated DD Requirements

Development rate of *A. tsugae* increases as the temperature increases until it reaches the estimated optimum temperature of around 17–22°C, depending on instar (Figs. 2–4). The parameters for the model fit to the developmental rate versus temperature for each instar and time to first oviposition are given in Table 3. The T_{min} for the first, third, and fourth instars were all estimated to be between 3 and 5°C, while the T_{min} for the second instars was close to 0°C. The estimated degree days for each instar and time to first oviposition are given in Table 4. Results show that 50% of the nymphs of *A. tsugae* in each instar required 105–176 DD to complete development and molt (Figs. 5 and 6).

Discussion

Temperature had a significant impact on survival of the *A. tsugae* sistens generation. Mortality of *A. tsugae* was highest at the coolest temperature (8°C) and was lower at the higher temperatures (16 and 20°C) for most instars. At higher temperatures (16 and 20°C) *A. tsugae* was able to complete development faster than at cooler temperatures (8 and 12°C). Optimum temperature for development of sistentes nymphs was estimated to range from 17 to 22°C. This follows a similar pattern to that reported for the progrediens generation of *A. tsugae* (Salom et al. 2002).

Adelges tsugae sistentes undergo summer estivation as a first instar and typically break diapause around October (McClure 1987, Joseph et al. 2011). As expected, our results demonstrated *A. tsugae* sistentes spend a significantly longer total time (time from collection to the molt) as a first instar than it does in all the other instars combined. However, the time from segmentation (the visible sign that development had resumed) to the molt in the first instar was comparable to that of other instars for most temperatures. The sharp decline in developmental rates of first instars when temperatures go to 20°C or above is consistent with diapause induction by temperatures slightly above 20°C. This also fits with the finding that the progrediens generation first instars will diapause if spring temperatures spike to temperatures above 20°C (Weed et al. 2016). Diapause also seems to be broken (segmentation visible) by 40- to 100-d exposure to temperatures between 8 and 20°C: fastest at about 16°C. This cold cue has been found to be required for the adelgid predator *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) to break its diapause (Lamb et al. 2007). The variation among individuals in days at each temperature from collection to segmentation visible may have been due to the broad span of days over which first instars hatched and entered diapause since we did not track that, and they were all collected after the nymphs had already entered diapause. Further work is needed to fully understand this process.

The T_{min} for progrediens nymphs was previously estimated to be 3.9°C (Salom et al. 2002). Our estimated T_{min} for sistentes ranged from 3 to 5°C for all the instars except the second instar, which is only slightly higher than that estimated for the progrediens nymphs., The second-instar sistentes T_{min} was much lower (0°C), which would be the instar most likely to be developing during the winter so the lower T_{min} would be advantageous for exploiting even short warmups during the winter. Adelgid survival at lower temperatures has also been shown to decline from January to March which could also be connected with differences between the early and later instars in response to temperatures (Skinner et al. 2003). In nature, sistentes oviposition occurs in spring, which would be consistent with the ovipositing stage T_{min} estimated to be 5°C. Although the sistens generation has been shown to survive <10°C (Elkinton et al. 2017), its development halts at much warmer temperatures, which may help it conserve energy to survive the winter in more northern latitudes or delay production of dilute hemolymph in preparation for egg laying, which would be detrimental for survival of low winter temperatures.

The estivating first-instar T_{max} that was estimated to be close to 20°C suggests higher temperatures would be detrimental to this stage. Studies have found that estivating sistentes mortality increases exponentially above 20°C (Mech et al. 2018) and that full sunlight on these nymphs can be sufficient to increase temperatures to levels that would cause this mortality (Sussky and Elkinton 2015). This higher mortality with higher temperatures may be limiting the southern spread of hemlock woolly adelgid and provides the basis for silvicultural thinning to open the canopy, exposing estivating sistentes to increased light and help improve hemlock health (Brantley et al. 2017, Piatek et al. 2017).

The current study used adelgids from a northern population and only used constant temperature conditions. The insect has already been shown to adapt to survive colder temperatures in the north (Paradis et al. 2008), so the population used here may have different lower developmental threshold and optimum developmental temperatures than those in more southern populations. Further study is required to determine what regional differences among *A. tsugae* may exist. Care should also be taken in applying laboratory estimates to the field. First, because fluctuating temperatures have been shown to improve development and survival of insects over constant temperatures as long as temperatures remain within the acceptable range (Colinet et al. 2015). Second, we had to use cut twigs to do this work which results in declining host quality as the study progressed, creating a potential food × time × temperature interaction that could have affected the results.

The results of this study when combined with what is already known about the effects of temperature on the progrediens generation (Salom et al. 2002) contributes to the creation of a phenology model for hemlock woolly adelgid. The model could be used to predict the timing of different stages for monitoring, pesticide applications, and predator releases. Dietschler et al. (2021) found that native hemlock woolly adelgid predator adults in the Pacific Northwest emerged in a distinct pattern associated with the presence of different prey life stages. Considering the broad distribution of hemlock woolly adelgid in eastern North America, knowledge of the timing of prey development would be important when considering release of these predators in efforts to establish classical biological control. In addition, this model would improve our understanding of the potential range of hemlock woolly adelgid both under current and future climates.

Author Contributions

All authors conceived the study. S.L., N.D., and K.O. collected the data. M.W. and M.K. obtained the funding. M.K. analyzed the data and prepared the graphs. S.L. and M.K. wrote the first draft of

the paper. All authors provided corrections and comments on the paper. M.W. and M.K. dealt with reviewer comments and revisions.

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