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# **Short Communication**

# Observation of key phenological stages of hemlock woolly adelgid (Hemiptera: Adelgidae): using citizen science as a tool to inform research and management

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Increasing efficiency of data gathering at the landscape scale on the growing number of pests and pathogens threatening forests worldwide has potential to improve management outcomes. Citizen science is expanding, with growing support and utility in environmental and conservation fields. We present a case study showing how citizen science observations can be used to inform research and management of a devastating forest pest. Hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), was introduced to eastern North America, leading to decline and mortality of eastern [*Tsuga canadensis* (L.) Carrière] (Pinales: Pinaceae) and Carolina hemlock (*Tsuga caroliniana* Engelmann) trees. Management activities, most notably biological control, rely on observations of *A. tsugae* phenology to inform the timing of releases and monitoring surveys of their highly synchronized specialist predators. In this article, we outline a citizen science program and report phenological observations on *A. tsugae*. Additionally, we report data comparing *A. tsugae* estivation break in Virginia (VA) and NewYork (NY) State, revealing that estivation break is synchronized between NY and VA. This observation is supported by 6 years of citizen scientist observations, showing similar patterns throughout NY, with egg laying shown to be much more variable than estivation break.

Key words: phenology, Adelges tsugae, forest health, estivation, life cycle

# Introduction

Understanding the ecological interactions of an invasive pest or pathogen requires an understanding of its basic life cycle. This is especially important when management activities are closely tied to discrete developmental stages. Researchers make management recommendations over broad geographic ranges and circumstances (Liebhold and Kean 2019), and citizen science programs have gained support as a method to solicit critical information for management outcomes (Crimmins et al. 2020) and contributions to research (Cooper et al. 2014, Ellwood et al. 2017). Citizen science refers to projects where members of the public work individually or in collaborative teams with professional scientists to collect data and advance scientific understanding (Bonney et al. 2016).

Adelges tsugae Annand (Hemiptera: Adelgidae) is a non-native invasive insect in eastern North America that feeds on eastern and

Carolina hemlock (*Tsuga canadensis* and *T. caroliniana*), causing widespread decline and mortality (Orwig et al. 2002). Introduction of *A. tsugae* likely occurred sometime in the early 1900s from southern Japan (Havill et al. 2006). It was first found in Richmond, VA, in 1951 (Stoetzel 2002) and has since spread throughout much of eastern hemlock's native range (https://hemlock-woolly-adelgid-national-initiative-gmsts.hub.arcgis.com/pages/distribution-maps). Eastern hemlock is a foundation species, creating unique forest communities critical for many organisms (Ellison et al. 2005). Hemlock conservation goals have prompted research on management approaches including silviculture, host tree resistance, chemical treatment, and biological control (Limbu et al. 2018). Biological control research began in the 1990s with species from *A. tsugae*'s native Asian and western North American ranges being investigated as potential agents (Mayfield et al. 2023). Three specialist predators

native to western North America, the predatory beetle *Laricobius nigrinus* (Fender) (Coleoptera: Derodontidae) and 2 fly species, *Leucotaraxis argenticollis* (Zetterstedt) and *Le. piniperda* (Malloch) (Diptera: Chamaemyiidae), have shown the most promise for management (Zilahi-Balogh et al. 2003, Kohler et al. 2008, Crandall et al. 2022), along with *La. osakensis* (Montgomery & Shiyake) from southern Japan (Vieira et al. 2013). In the introduced eastern North American range, *A. tsugae* undergoes 2 parthenogenic generations on hemlock: the summer–spring, overwintering sistens generation and the spring–summer progrediens generation (McClure 1989), with predation on both generations needed for effective control (Crandall et al. 2020).

There are 2 phenological events in the A. tsugae overwintering sistens generation that are critical for release and monitoring of biological control agents: estivation break in early fall and egg laying in late winter. Estivation is a period of dormancy occurring during summer months (Tauber et al. 1986). Laricobius nigrinus are released as adults in fall after estivation ends and monitored for establishment and dispersal as larvae in the spring during the A. tsugae sistens egg laying period (Zilahi-Balogh et al. 2003, Mausel et al. 2010, Jubb et al. 2021). Leucotaraxis spp. are released during late winter and spring during the A. tsugae sistens egg laying period (Dietschler et al. 2021). Adelges tsugae phenology has been documented throughout the introduced range, but the cues that terminate their summer estivation period are still unknown. Adelges tsugae has been shown to resume development between late September and late October in multiple studies documenting annual phenology at one or a few geographically related sites (see McClure 1987, Gray and Salom 1996, Zilahi-Balogh et al. 2003, Mausel et al. 2008, Joseph et al. 2011), and temperature had no significant effect on estivation break in laboratory studies (Limbu et al. 2022), suggesting another cue may terminate dormancy. Understanding the relevant cues and timing when A. tsugae terminate estivation and lay eggs would increase efficacy of predator release and monitoring in biological control.

This article represents the first report of *A. tsugae* phenological data collected by citizen scientists, professional land managers, and researchers over 6 years to inform *A. tsugae* research. These observations informed a subsequent field study exploring the timing of estivation break in 2 latitudinally distinct areas, Virginia (VA) and New York State (NY).

# Methods

#### **Citizen Science Observations**

In 2017, protocols were developed to observe A. tsugae phenology through the US National Phenology Network using their online and mobile interface, Nature's Notebook (https://www.usanpn.org/ natures\_notebook). The protocol was designed to observe phenological stages that were most informative for research and management. These stages include dormant sistens nymphs (estivating nymphs), postdormant nymphs (first-instar nymphs terminating estivation), sistens adults (grouping second through fourth instar), onset of progrediens egg laying, and crawlers (mobile first-instar nymphs). Observation periods were September through October to target sistens postdormant nymphs and late February through early April for sistens adult egg laying. These periods are critical to A. tsugae biological control research and management, and these observation windows were selected using previously published phenology research (see McClure 1987, Gray and Salom 1996, Zilahi-Balogh et al. 2003, Mausel et al. 2008, Joseph et al. 2011).

In late summer 2017 and 2018, a series of in-person short courses was held to train citizen science volunteers in *A. tsugae* 

biology, management, and phenology observation protocols. Training seminars consisted of a classroom lecture (covering *A. tsugae* biology, biological control, phenology monitoring, and using Nature's Notebook) and a field component, with hands-on experience identifying eastern hemlock and *A. tsugae*. In 2017 and 2018, 6 and 7 separate training events were held, respectively, throughout NY. From 2019 through 2022, citizen science volunteers were recruited through social media, organizational websites, and speaking engagements. Small group or individual training sessions were conducted in person or virtually. Volunteer training efforts were focused on the northeastern *A. tsugae* invaded range, with individuals trained to make observations in NY, Pennsylvania (PA), and Massachusetts (MA).

All observations reported here were made from 2017 to 2022, using hand lenses (7x-10x magnification) or dissecting microscopes. At most sites and years, observations were made on a weekly basis during targeted phenological periods, with occasional semiweekly observations. Sites were selected by each observer with observations being made on a minimum of 3 trees when possible, selecting 2 branches per tree, and recording A. tsugae development on 5 twigs. Postdormant nymphs (indicating estivation break) were defined as having visible elongation and sclerite separation with visible pink hemolymph through the sutures (Limbu et al. 2022) (Fig. 1), and egg laying was recorded at first appearance of eggs. The number of observation sites varied by year due to variation in volunteer retention. Data were collected on paper datasheets and later entered in the Nature's Notebook web interface, directly entered through the Nature's Notebook mobile app (USA National Phenology Network 2023) or sent directly to researchers.

#### NY and VA Estivation Break Study

In 2022, an observational study was conducted to compare timing of A. tsugae estivation break between sites in VA and NY. Beginning on 15 September, samples were collected daily from 2 sites in VA, Prices Fork Research Center (PFRC, Blacksburg, VA; 37.212385, -80.489560) and Eastview (Blacksburg, VA; 37.211783, -80.404424), and 1 site in NY, Ellis Hollow Preserve (Ithaca, NY; 42.442375, -76.408337). Observations were made until 14 October at the NY site and 17 October at the VA sites. The Eastview VA site missed observations on 24, 26, and 30 September-2 October. Adelges tsugae were monitored for the phenological stages of estivation (dormant nymphs), estivation break (postdormant nymphs), and second-instar nymphs (first molting). Eastern hemlock twigs infested with A. tsugae were collected and destructively sampled using a dissecting microscope on the same day of collection to assess phenological stage. The same characters used by citizen scientists to define estivation break were used in the NY and VA study. These characteristics were used by citizen science volunteers and in the A. tsugae development literature (Limbu et al. 2022). Data loggers were placed at each site and recorded temperature at 30-min intervals (Onset HOBO TidbiT MX Temp 400, Bourne, Massachusetts).

#### Data Analysis

Analysis of estivation break from the 2022 NY and VA field study was performed using a binomial Bayesian generalized linear model (GLM) with vaguely informative priors (Cauchy distribution with location = 0 and scale = 2.5), due to quasi-complete separation, with post hoc analysis and Tukey's correction using the emmeans package (Length 2022). Postdormant and second-instar nymphs were combined to represent post-estivation break when comparing with estivating nymphs (post-estivation = 1, estivating = 0), with date as



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**Fig. 1.** *Adelges tsugae* estivating sistens nymph (A), early signs of estivation break of a sistens nymph showing swelling and beginning of sclerite separation (B), and more advanced estivation break of first-instar sistens nymphs showing pigmented hemolymph between sutures (C). Photograph credits: C. Jubb and N. Dietschler.

a predictor and site as an interaction term. Dates were binned into 3-day intervals for Bayesian GLM analysis (Fig. 2A, Supplementary Table 1). Analysis and figures were completed using R Studio version 4.0.2 (R Core Team 2022), daylength was calculated using the "geosphere" package (Hijman 2022), and Bayesian GLM using the "arm" package (Gelman and Su 2022).

# Results

# **Citizen Science Observations**

In the first year, training seminars began in summer 2017 after the egg laying observation season, resulting in all egg laying observations being made by researchers. Citizen science observation sites were present in NY, PA, and MA (Table 1). Postdormancy development consistently started at the end of September from 2017 to 2022, while the onset of egg laying was highly variable (Table 1).

#### NY and VA Estivation Break Study

Mean *A. tsugae* individuals observed per day was 60.03 (SD: 37.68) at NY Ellis Hollow, 35.27 (SD: 7.67) at VA PFRC, and 69.46 (SD: 33.42) at VA Eastview. The onset of estivation break was observed on 20 September at the NY and VA Eastview sites and on 21 September at the VA PFRC site (Fig. 2B). The proportion of estivating nymphs steadily decreased throughout the study period with second-instar nymphs being observed first at VA PFRC on 7 October, followed by 12 October in NY and VA Eastview (Fig. 2B), with increasing probability of estivation break over time (Fig. 2A). The 2 VA sites had a significant difference in the probability of estivation break at 3 of the 10 comparisons: 24–26 September (P = 0.009), 6–8 October (P = 0.004), and 9–11 October ( $P \le 0.0001$ ). The NY site was significantly different to only VA PFRC on 30 September–3 October (P = 0.001) and to both VA Eastview and VA PFRC on 24–26 September ( $P \le 0.004$ ).



Fig. 2. Probability of *Adelges tsugae*-dormant nymphs breaking estivation at 3-day intervals (A) and the proportion of *A. tsugae* sistens estivating first-instar nymphs, first-instar postdormant nymphs, and second-instar nymphs (B). Comparison of 1 site in NY and 2 sites in Virginia from 15 September 2022 through 17 October 2022.

0.0001), and all comparison between 3 and 15 October ( $P \le 0.0001$ ) (Fig. 2A).

Locations selected represent a greater range of latitude and climate relative to sites in the citizen science program. The NY site represents a colder region of *A. tsugae*'s introduced range (5b), while the VA sites represent a warmer climate (7a; USDA Plant Hardiness Zones, average annual minimum winter temperatures, https:// planthardiness.ars.usda.gov/). The study regions have been shown to have significant differences in temperature (Preston et al. 2023), and temperatures were recorded during the observation period showing variation among sites (NY average of daily mean: 12.9 °C, min: 9.1 °C, max: 17.5 °C, VA Eastview average daily mean: 14.3 °C, min: 8.7 °C, max: 24.9 °C; and VA PFRC average daily mean: 14.8 °C, min: 8.1 °C, max: 23.6 °C) (Fig. 3). Average daylength during the study period between 15 September and 14 October was 11.9 h in NY and VA (Supplementary Fig. 1) (Forsythe et al. 1995, Hijmans 2022). Thus, across both studies, estivation break appears to be highly consistent, suggesting that daylength could be a cue.

### Discussion

We report the first observations of key phenological stages of *A. tsugae* being recorded over a 6-year period and in multiple locations. *Adelges tsugae* egg laying phenology is variable based on geographic

 Table 1. Date ranges of Adelges tsugae phenological observations collected by citizen scientists, professional land managers, and researchers from 2017 to 2022. Ranges indicate the time frame in which phenological stage onset was observed for the first time. Observation sites were in NY, PA, and MA

Year	Observation sites			Estivation break	Observation sites			Egg laying
	NY	PA	МА		NY	PA	MA	
2017	12	_	_	21 September–11 October	3	_	_	23 February–24 March
2018	3	3	_	26 September–16 October	7	_	_	6 March–9 April
2019	2	_		27 September and 1 October	3	1	1	11–23 April
2020	4	_		21 September–2 October	3	_	_	13–27 March
2021	5	_	2	23 September–14 October	8	_	_	25 March-19 April
2022ª	1	_	—	29 September	3	—	—	7–18 April

<sup>a</sup>The 2022 season coincided with the NY and VA observational study, data not reported here.



Fig. 3. Average daily temperatures throughout the estivation break study at the NewYork and Virginia observation sites.

location (see McClure 1987, Gray and Salom 1996, Zilahi-Balogh et al. 2003, Mausel et al. 2008, Joseph et al. 2011). We provide additional evidence that the timing of A. tsugae egg laying can vary among sites and years in a geographic region (Table 1), highlighting the need for regular monitoring. The earliest onset of egg laying occurred in NY on 23 February 2017, similar to observations from more coastal and southern states (McClure 1987, Mausel et al. 2008, Joseph et al. 2011), but was not observed until 1 month later (24 March 2017) at another site, comparable to other annual observations reported here. Variability in egg laying onset is likely due to temperature influence on A. tsugae development (Salom et al. 2002, Tobin and Turcotte 2018, Limbu et al. 2022) and later seasonal egg laying reported for NY is consistent with colder northern winters. Estivation break is more challenging to observe than egg laying, yet it showed little variation in timing of onset (Table 1, Fig. 2B). Estivation break (i.e., appearance of postdormant nymphs) occurred in the last 2 weeks of September across observation years. Despite consistency in estivation break onset, there were differences in the probability of estivation break observed at each site (Fig. 2A), which could be due to differences in estivating nymph mortality driven by summer temperatures (Mech et al. 2018) or natural variation across sampled trees. The consistent nature of estivation break supports early release of Laricobius spp. at the end of September, before developing A. tsugae are visible to the naked eye. Variability in egg laying among sites and years highlights the need for detailed observations to inform predator release and survey in spring.

External cues are believed to trigger diapause termination in many insect species, with temperature and photoperiod being common influences (Tauber et al. 1986). Our observations along with those of Limbu et al. (2022) suggest that temperature may have little influence on termination of summer diapause in *A. tsugae*. Daily minimum temperatures were similar across sites, but laboratory observations exploring the influence of decreasing temperatures has shown little success in terminating *A. tsugae* estivation (Salom et al., unpublished data, Whitmore et al., unpublished data). Interestingly, occurrence of estivation break reported here coincides with the autumnal equinox, supplying an additional hypothesis for future research.

Determining a biofix, or biological point at which to begin development models, has been difficult with the *A. tsugae* overwintering generation due to the unknown cue(s) for resumption of development, with 1 January being used previously (Tobin and Turcotte 2018, Crimmins et al. 2020). Data presented here suggest that using an earlier biofix could increase accuracy of models, and we suggest 1 October for sistens generation development in eastern North America. This comparative study of estivation break between sites in VA and NY provides (i) a validation to observations collected by citizen scientists, land managers, and researchers in 2017–2022 and (ii) motivation for continued research into cues that influence the termination of *A. tsugae* estivation and its impacts on biological control predator synchrony.

Citizen science programing has led to community engagement with *A. tsugae* management, and the phenological observation

program discussed here represents just one aspect of A. tsugae citizen science (other programs include A. tsugae survey and assessment, hemlock health assessments, and lingering hemlock surveys, see https://blogs.cornell.edu/nyshemlockinitiative/community-science/, Ingwell and Preisser 2011, https://holdenfg.org/great-lakes-basinforest-health-collaborative/). Without question, increased observation efforts by citizen scientists led to insights about the nuances of A. tsugae development and influenced management and research programs. These observations supported biological control release and establishment survey efforts in NY, resulting in release of over 51,000 La. nigrinus and 32,800 Leucotaraxis spp. (Virginia Tech 2023). Being able to release predators into the wild as soon as possible is important to reducing laboratory mortality (Foley et al. 2021). While there is still uncertainty about the cue(s) triggering estivation break, this work provides a path forward to understanding potential cue(s) that terminate dormancy, which would greatly benefit research efforts and biological control programs by improving predictive models (Crimmins et al. 2020) and timing of predator release. This case study highlights the importance of integrated research programs and demonstrates how citizen scientists and researchers can work together to inform research and management activities.

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#### **Author Contributions**

Nicholas Dietschler (Conceptualization [Lead], Data curation [Lead], Formal analysis [Lead], Investigation [Equal], Methodology [Equal], Project administration [Lead], Visualization [Lead], Writing original draft [Lead]), Tonya Bittner (Investigation [Supporting], Methodology [Supporting], Writing—review & editing [Lead]), Marshall Lefebvre (Data curation [Supporting], Methodology [Supporting], Writing—review & editing [Equal]), Jasmine Schmidt (Data curation [Supporting], Investigation [Supporting], Writing review & editing [Supporting]), Carrie Jubb (Data curation [Supporting], Investigation [supporting], Writing—review & editing [Equal]), Aryanna James (Data curation [Supporting], Investigation [Supporting], Writing—review & editing [Equal]), Scott Salom (Methodology [Supporting], Writing—review & editing [Equal]), and Mark Whitmore (Conceptualization [Equal], Funding acquisition [Lead], Methodology [Equal], Writing—review & editing [Equal])

#### **Supplementary Material**

Supplementary material is available at *Journal of Economic Entomology* online.

## References

- Bonney R, Cooper C, Ballard H. The theory and practice of citizen science: launching a new journal. Citiz Sci: Theory Pract. 2016:1:1. https://doi. org/10.5334/cstp.65
- Cooper CB, Shirk J, Zuckerberg B. The invisible prevalence of citizen science in global research: migratory birds and climate change. PLoS One. 2014:9(9):e106508. https://doi.org/10.1371/journal.pone.0106508
- Crandall RS, Jubb CS, Mayfield AE, Thompson B, McAvoy TJ, Salom SM, Elkinton JS. Rebound of Adelges tsugae spring generation following predation on overwintering generation ovisacs by the introduced predator Laricobius nigrinus in the eastern United States. Biol Control. 2020:145:104264. https://doi.org/10.1016/j.biocontrol.2020.104264
- Crandall RS, Lombardo JA, Elkinton JS. Top-down regulation of hemlock woolly adelgid (*Adelges tsugae*) in its native range in the Pacific Northwest of North America. Oecologia. 2022:199(3):599–609. https:// doi.org/10.1007/s00442-022-05214-8
- Crimmins TM, Gerst KL, Huerta DG, Marsh RL, Posthumus EE, Rosemartin AH, Switzer J, Weltzin JF, Coop L, Dietschler N, et al. Short-term forecasts of insect phenology inform pest management. Ann Entomol Soc Am. 2020:113(2):139–148. https://doi.org/10.1093/aesa/saz026
- Dietschler NJ, Bittner TD, Trotter RT, Fahey TJ, Whitmore MC. Biological control of hemlock woolly adelgid: implications of adult emergence patterns of two *Leucopis* spp. (Diptera: Chamaemyiidae) and *Laricobius nigrinus* (Coleoptera: Derodontidae) larval drop. Environ Entomol. 2021:50(4):803–813. https://doi.org/10.1093/ee/nvab037
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, et al. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ. 2005;3(9):479–486. https://doi. org/10.1890/1540-9295(2005)003[0479:lofscf]2.0.co;2
- Ellwood ER, Crimmins TM, Miller-Rushing AJ. Citizen science and conservation: recommendations for a rapidly moving field. Biol Conserv. 2017:208:1–4. https://doi.org/10.1016/j.biocon.2016.10.014
- Foley JR, Jubb CS, Cole DA, Mausel D, Galloway AL, Brooks R, Salom SM. Historic assessment and analysis of the mass production of *Laricobius* spp. (Coleoptera: Derodontidae), biological control agents for the hemlock woolly adelgid, at Virginia Tech. J Insect Sci. 2021:21(1):12. https:// doi.org/10.1093/jisesa/ieab005
- Forsythe WC, Rykiel EJ, Stahl RS, Wu H, Schoolfield RM. A model comparison for daylength as a function of latitude and day of year. Ecol Model. 1995:80(1):87–95. https://doi.org/10.1016/0304-3800(94)00034-f
- Gelman A, Su Y. arm: data analysis using regression and multilevel/hierarchical models. R package version 1.13-1. 2022. https://CRAN.R-project. org/package=arm.
- Gray DR, Salom SM. Biology of the hemlock woolly adelgid in the Southern Appalachians. In: Salom SM, Tigner TC, Reardon RC, editors. Proceedings of the First Hemlock Woolly Adelgid Review, 12 October 1995, Charlottesville, VA. FHTET-1996-10. Morgantown (WV): USDA Forest Service Forest Health Technology Enterprise Team; 1996. p. 26–35.
- Havill NP, Montgomery ME, Yu G, Shiyake S, Caccone A. Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to Eastern North America. Ann Entomol Soc Am. 2006:99(2):195–203. https://doi. org/10.1603/0013-8746(2006)099[0195:mdfhwa]2.0.co;2

Hijmans R. geosphere: spherical trigonometry. R package version 1.5-18. 2022. https://CRAN.R-project.org/package=geosphere.

- Ingwell LL, Preisser EL. Using citizen science programs to identify host resistance in pest-invaded forests. Conserv Biol. 2011:25(1):182–188. https:// doi.org/10.1111/j.1523-1739.2010.01567.x
- Joseph SV, Mayfield AE, Dalusky MJ, Asaro C, Berisford CW. Phenology of the hemlock woolly adelgid (Hemiptera: Adelgidae) in northern Georgia. J Entomol Sci. 2011:46(4):315–324. https://doi. org/10.18474/0749-8004-46.4.315
- Jubb CS, McAvoy TJ, Stanley KE, Heminger AR, Salom SM. Establishment of the predator *Laricobius nigrinus*, introduced as a biological control agent for hemlock woolly adelgid in Virginia, USA. BioControl. 2021:66(3):367– 379. https://doi.org/10.1007/s10526-020-10072-5
- Kohler GR, Stiefel VL, Wallin KF, Ross DW. Predators associated with the hemlock woolly adelgid (Hemiptera: Adelgidae) in the Pacific Northwest. Environ Entomol. 2008;37(2):494–504. https://doi. org/10.1603/0046-225x(2008)37[494:pawthw]2.0.co;2
- Length RV. emmeans: estimated marginal means, aka least-squares means. R package version 1 (7), 5. 2022. https://cran.r-project.org/web/packages/ emmeans/index.html
- Liebhold AM, Kean JM. Eradication and containment of non-native forest insects: successes and failures. J Pest Sci. 2019:92(1):83–91. https://doi. org/10.1007/s10340-018-1056-z
- Limbu S, Keena MA, Dietschler N, O'Connor K, Whitmore MC. Estivation and post-estivation development of hemlock woolly adelgid (Adelges tsugae) (Hemiptera: Adelgidae) at different temperatures. Environ Entomol. 2022:51(6):1210–1217. https://doi.org/10.1093/ee/nvac089
- Limbu S, Keena MA, Whitmore MC. Hemlock woolly adelgid (Hemiptera: Adelgidae): a non-native pest of hemlocks in Eastern North America. J Integr Pest Manag. 2018:9(1):1–16. https://doi.org/10.1093/jipm/ pmy018
- Mausel DL, Salom SM, Kok LT, Davis GA. Establishment of the hemlock woolly adelgid predator, *Laricobius nigrinus* (Coleoptera: Derodontidae), in the Eastern United States. Environ Entomol. 2010:39(2):440–448. https://doi.org/10.1603/EN09088
- Mausel DL, Salom SM, Kok LT, Fidgen JG. Propagation, synchrony, and impact of introduced and native *Laricobius* spp. (Coleoptera: Derodontidae) on hemlock woolly adelgid in Virginia. Environ Entomol. 2008:37(6):1498– 1507. https://doi.org/10.1603/0046-225x-37.6.1498
- Mayfield AE III, Bittner TD, Dietschler NJ, Elkinton JS, Havill NP, Keena MA, Mausel DL, Rhea JR, Salom SM, Whitmore MC. Biological control of hemlock woolly adelgid in North America: history, status, and outlook. Biol Control. 2023:185:105308. https://doi.org/10.1016/j. biocontrol.2023.105308
- McClure MS. Biology and control of hemlock woolly adelgid. Bulletin 851. New Haven (CT): Connecticut Agricultural Experiment Station; 1987.

- McClure MS. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, Adelges tsugae (Homoptera: Adelgidae). Ann Entomol Soc Am. 1989:82(1):50–54. https://doi.org/10.1093/aesa/82.1.50
- Mech AM, Tobin PC, Teskey RO, Rhea JR, Gandhi KJK. Increases in summer temperatures decrease the survival of an invasive forest insect. Biol Invasions. 2018:20(2):365–374. https://doi.org/10.1007/ s10530-017-1537-7
- Orwig DA, Foster DR, Mausel DL. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. J Biogeogr. 2002:29(10– 11):1475–1487. https://doi.org/10.1046/j.1365-2699.2002.00765.x
- Preston CE, Dietschler NJ, Whitmore MC, Salom SM. Phenology of *Leucotaraxis argenticollis*, a specialist predator of the invasive hemlock woolly adelgid, in the eastern United States. Environ Entomol. 2023;52(6):1008–1019. https://doi.org/10.1093/ee/nvad103
- R Core Team. R: a language and environment for statistical computing computer program. Vienna (Austria): R Foundation for Statistical Computing; 2022. https://www.Rproject.org/.
- Salom SM, Sharov AA, Mays W, Gray DR. Influence of temperature on development of hemlock woolly adelgid (Homoptera: Adelgidae) progrediens. J Entomol Sci. 2002:37(2):166–176.
- Stoetzel MB. History of the introduction of Adelges tsugae based on voucher specimens in the Smithsonian Institute National Collection of Insects. In: Onken B., Reardon R, Lashomb J, editors. In: Proceedings of the hemlock woolly adelgid in eastern North America symposium. East Brunswick (NJ): US Department of Agriculture Forest Service and State University of NJ Rutgers; 2002. p. 12.
- Tauber MJ, Tauber CA, Masaki S. Seasonal adaptations of insects. New York (NY, USA): Oxford University Press; 1986.
- Tobin PC, Turcotte RM. Phenology of hemlock woolly adelgid (Hemiptera: Adelgidae) in the Central Appalachian Mountains, USA. J Econ Entomol. 2018:111(5):2483–2487. https://doi.org/10.1093/jee/toy175
- USA National Phenology Network. Plant and animal phenology data from the NYS Hemlock Initiative hemlock woolly adelgid phenology project. Data type: Site Phenometrics. 1 Jan 2017–31 Dec 2022 for New York State, USA. Tucson (AZ): USA-NPN; 2023 [accessed 2023 Jul 27]. https://www. usanpn.org/data.
- Vieira LC, Lamb AB, Shiyake S, Salom SM, Kok LT. Seasonal abundance and synchrony between *Laricobius osakensis* (Coleoptera: Derodontidae) and its prey, *Adelges tsugae* (Hemiptera: Adelgidae), in Japan. Ann Entomol Soc Am. 2013;106(2):249–257. https://doi.org/10.1603/an12075
- Virginia Tech. HWA predator database. Virginia Tech; 2023 [accessed 2023 Jun 28]. http://hiro.ento.vt.edu/pdb/.
- Zilahi-Balogh G, Humble L, Lamb A, Salom S, Kok L. Seasonal abundance and synchrony between *Laricobius nigrinus* (Coleoptera: Derodontidae) and its prey, the hemlock woolly adelgid (Hemiptera: Adelgidae). Can Entomol. 2003:135(1):103–115. https://doi.org/10.4039/n02-059