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Source: Northeastern Naturalist, 24(sp7):B90-B118.
Published By: Eagle Hill Institute
DOI: http://dx.doi.org/10.1656/045.024.s713
URL: http://www.bioone.org/doi/full/10.1656/045.024.s713

Winter Ecology: Insights from Biology and History
2017 *Northeastern Naturalist* 24(Special Issue 7):B90–B118

Predicting Hemlock Woolly Adelgid Winter Mortality in Connecticut Forests by Climate Divisions

Carole A.S.-J. Cheah*

Abstract - Hemlock Woolly Adelgid (HWA) is a devastating non-native pest of North American *Tsuga canadensis* (Eastern Hemlock) and *Tsuga caroliniana* (Carolina Hemlock). I analyzed 15 years of data collected during the period 2000–2015 to determine important winter variables influencing HWA mortality in the 3 Connecticut climatic divisions. Absolute minimum daily winter temperature, the number of subzero days (temperature drops below -17.8 °C [0 °F]), and a new interaction variable—negative degree days (NDD)—were identified as significant predictors of HWA winter mortality. The absolute minimum daily winter temperature was the most critical factor. Minimum daily winter temperatures of -24 °C, 5.5 subzero days, and -130 NDD in Division 1(Northwest); -22.4 °C, 6 subzero days, and -100 NDD in Division 2 (Central); and -21.2 °C, 2.6 subzero days, and -45 NDD in Division 3 (Coastal) resulted in 90% HWA mortality. Patterns of HWA winter mortality in coastal Division 3 were distinct from the interior and suggest cold adaptation in northern interior populations. Recent, consecutive, arctic cold air outbreaks associated with weak polar vortex events have greatly reduced HWA populations statewide, with implications for the survival, spread, and control of HWA in the northeastern US.

Introduction

Tsuga canadensis (L.) Carriere (Eastern Hemlock), a shade-tolerant and late-successional species, occupies a very significant and unique ecological niche (DeGraaf et al. 1992, Quimby 1996). Eastern Hemlock is a moisture-sensitive species, but it also occupies a variety of habitat types, ranging from mesic to subxeric sites (Kessell 1979). It is a dominant late-successional species at primary-forest sites that are wetter or drier than normal and is dominant in wetter locations (DeGraaf et al. 1992). Eastern Hemlock is predominant in 50–75% of mature, second-growth mixed-hardwood stands in New England where it is associated with several herbaceous plant species (DeGraaf et al. 1992) and numerous avian and mammal species (Yamasaki et al. 2000). This species' natural distribution ranges from Minnesota, Michigan, and Wisconsin through southern and coastal Canada, New England, New York, Pennsylvania, and into the southern Appalachian Mountains (Godman and Lancaster 1990). Stands with dense Eastern Hemlock canopies provide important watershed protection and thermoregulation of streams year-round for native *Salvelinus fontinalis* Mitchill (Brook Trout) (Snyder et al. 2002) and obligate breeding habitat for several avian species such as *Setophaga fusca* Müller (Blackburnian Warbler) and *Setophaga virens* Gmelin (Black-throated Green Warbler) (Benzinger

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Manuscript Editor: David Orwig

1994a, 1994b; DeGraaf et al. 1992; Tingley et al. 2002). Hemlock habitat and winter cover are important for diverse mammal species such as *Erethizon dorsatum* (L.) (North American Porcupine), *Glaucomys sabrinus* Shaw (Northern Flying Squirrel), *Lepus americanus* Erxleben (Snowshoe Hare), *Martes pennanti* Erxleben (Fisher), *Odocoileus virginianus* Zimmermann (White-tailed Deer), *Peromyscus* spp. Gloger (Deer Mouse), and *Ursus americanus* Pallas (American Black Bear) (DeGraaf et al. 1992, Reay 2000, Yamasaki et al. 2000).

Adelges tsugae Annand (Hemlock Woolly Adelgid, hereafter HWA; Homoptera:Adelgidae), is native to Asia (Havill et al. 2006, McClure 1987) and has become a serious pest of native Eastern Hemlock and *Tsuga caroliniana* Englemann (Carolina Hemlock). Since the first report of HWA in the eastern US, in Richmond, VA, in 1953–1954 (Souto et al. 1996), it has spread to 20 states—north to Maine, south to Georgia, the Carolinas, and Kentucky, and west to Michigan (by 2006) and Ohio (by 2012) (USDAFS 2016a, b). Heavy infestations have resulted in the decline and mortality of both hemlock species in forest stands through much of the middle and southeastern range in the eastern US (Elliot and Vose 2011) and in parts of southern New England (Orwig et al. 2002)

The spread of HWA northwards has occurred in the last decade, with detections in natural stands in New Hampshire (2000), Maine (2003), Vermont (2007) (USDAFS 2016a, b), and most recently in central Canada (2012, 2013; Fidgen et al. 2014). HWA now threatens a very significant portion (>45%) of forests within the northern and western range of Eastern Hemlock (Morin et al. 2011). The first report of HWA in Connecticut was in 1985 (McClure 1987); thus, Connecticut has experienced HWA infestations for >30 years. The first studies on the biology and morphology of HWA and its devastating potential for hemlock decline and mortality were done in Connecticut (McClure 1989, 1990, 1991). Eastern Hemlocks (hereafter, Hemlocks) in Connecticut have also been stressed by episodes of extreme or severe drought (NRCC 2016) in the past 2 decades (Cheah 2010), attacks by other non-native insect pests such as *Fiorinia externa* Ferris (Elongate Hemlock Scale) (McClure and Fergione 1977), *Lymantria dispar* (L.) (European Gypsy Moth; Anderson 1986, Stephens 1984), and an extensive outbreak in 1992–1994 of the native *Lambdina athasaria* (Walker) (Spring Hemlock Looper) (Maier et al. 1993). Since 2006, Hemlocks in Connecticut have also been occasionally infected with *Sirococcus tsugae* Rossman, Castlebury, D.F. Farr, & Stanosz, (Tip Blight) (C.A.S.-J. Cheah, unpubl. data). Thus, multiple stressors contributed to extensive mortality and decline of many Hemlock stands in southern Connecticut and the Connecticut River Valley in the 1990s.

The unusual winter-feeding activity and habit of HWA, during which the insects are sessile and exposed on hemlock twigs, makes it particularly vulnerable to winter extremes. HWA has 2 parthenogenetic generations that feed and damage hemlock: the shorter progrediens or summer generation (April–June) and the sistens generation, which spans 10 months from July to April in the Northeast (McClure 1989). Seasonal variations in timing of adelgid phenology of oviposition and hatch can vary widely with temperature (Cheah and McClure 2000). The sistens generation generally hatches in early summer but then remains dormant as first-instar nymphs through the hot summer. Development resumes in early fall, and nymphs continue to feed throughout the winter, especially in milder periods, into the early spring when adults begin oviposition. During mild winters, HWA sistens have minimal mortality, while high mortality rates have been recorded during extreme winters (Cheah 2016). The objectives of this study were to identify and investigate winter climatic variables that best predict HWA winter mortality patterns in Connecticut over multiple years. In this study, I used a new approach to analyze patterns of HWA winter mortality across historical climatic divisions in Connecticut in order to enhance understanding of differential winter survival by HWA. This perspective is somewhat analogous to the concept of USDA plant-hardiness zones, but these demarcations are based only on average annual minimum winter temperatures (USDA ARS 2012). Climate divisions are developed from daily records of minimum and maximum temperatures and precipitation, and thus represent a more comprehensive source of data and were of greater utility in this study.

Different climate patterns within a region are distinguished by separate climate divisions or sections within a state, giving rise to the computation of state divisional datasets for climate data since 1895 (Guttman and Quayle 1996). Although Connecticut is the 3rd-smallest state in the US, it has a varied climate due primarily to its north–south-sloping hilly topography, the Connecticut River Valley, and an extended coastline (407 km) that is protected by Long Island Sound (Brumbach 1965). The highest elevations are in the northwest hills (240–700 m), which are an extension of the Appalachian mountain range; the eastern highlands range from 150–335 m, while the southern hills are the lowest, ranging from 60 to 150 m (Brumbach 1965). The National Climate Data Center (NCDC), part of the National Oceanic and Atmospheric Administration, recognizes 3 climatic divisions within Connecticut: Division 1 in the northwest; Division 2 in the central region, and Division 3 in the coastal region (Fig. 1A; adapted from NOAA 2015a).

The climate of the coastal plain is markedly different from that of the interior and northern hills; the greatest contrast occurs in the winter when mean temperatures can differ by 6–7 °C (Brumbach 1965). The northwest hills generally have the lowest winter-temperatures and receive the highest snowfall (Brumbach 1965; Figs. 1B, C), compared to the coastal plain, which has much milder winters because its climate is moderated by warming from Long Island Sound and proximity to the Gulf Stream (Goldstein 2009). Connecticut's juxtaposition between the Mid-Atlantic states and northern New England is the ideal geographically and climatically diverse setting for this long-term study of the influence of winters on HWA populations. Winters in Connecticut reflect the overall trends experienced in the Northeast (Fig. 1D), and findings here are thus applicable to other northern states. Connecticut's northwest interior highlands, with more-extensive Hemlock forests, approximate the southern limit of northern forests in Vermont; the warmer coastal sections have conditions resembling coastal Maine; and the lower Connecticut River Valley and eastern hills are extensions of more northern New England states (Brumbach 1965).

The influence of winter temperatures on the rapidity of HWA spread in Connecticut is indicated in Fig. 1B. After its initial report in 1985, HWA spread quickly from 1986 to 1990, during which the species infested 85 towns in the lower coastal counties of Connecticut. This initial exponential expansion was correlated with a warmer than normal winter minimum temperature average of -5.6 °C, which occurred in 1983, a year ranked 105 of 121 warmest winters since 1895 (NRCC 2016). By 1997, ninety-seven percent of all 169 towns in Connecticut had reported HWA infestations (Cheah 2006), and HWA was found statewide by 2001. When years were ranked by average minimum winter temperatures (December–February) in Connecticut from 1980 to 2015 (Fig. 1D), during the 1980s, only 1983 (ranked 105) and 1985 (ranked 91) were among the top 30 warmest winters since 1895. In contrast, during the 1990s, 6 of 10 Connecticut winters ranked in the top 20 warmest

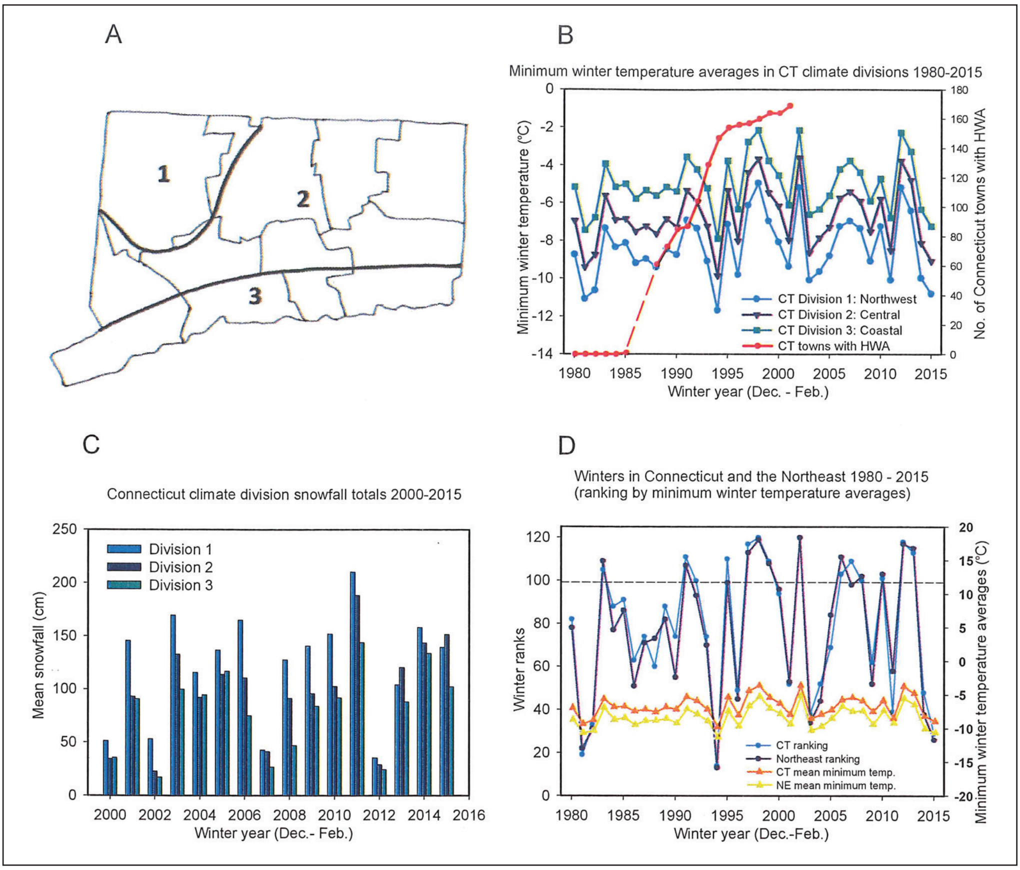

Figure 1. (A) Climate divisions of Connecticut from NOAA are illustrated: Division 1 (Northwest), Division 2 (Central), and Division 3 (Coastal). Graphs show the (B) divisional minimum winter-temperature averages from 1980 to– 2015 and the expansion of HWA in Connecticut since 1985; (C) annual winter snowfall from 2000 to 2015; and (D) winter rankings by minimum winter temperature averages since 1895 in Connecticut and from 1980 to 2015 for the entire Northeast region. The dashed line indicates the winter ranking of 100 since 1895. Data were obtained from the Northeast Regional Climate Center at Cornell University and from Climatological Data of New England, NOAA.

winters, and 7 of 16 winters during the period 2000–2015 ranked among the top 20 warmest since 1895 (NRCC 2016). The winters of 2002 and 2012 were the warmest winters since 1895, but 2016 shattered this record and is the warmest winter on record (NRCC 2016). This extraordinary warming of Connecticut winters over time from 1895 to the present is shown in detail within the 3 climate divisions from 1895 to 2015 (Fig. 2; NOAA 2015b). These increases in average winter temperature over 120 years were all statistically significant within each climate division (Fig. 2). There is little doubt that the expansion of HWA in Connecticut has occurred in conjunction with warming winter trends in the last half-century, especially since 1990.

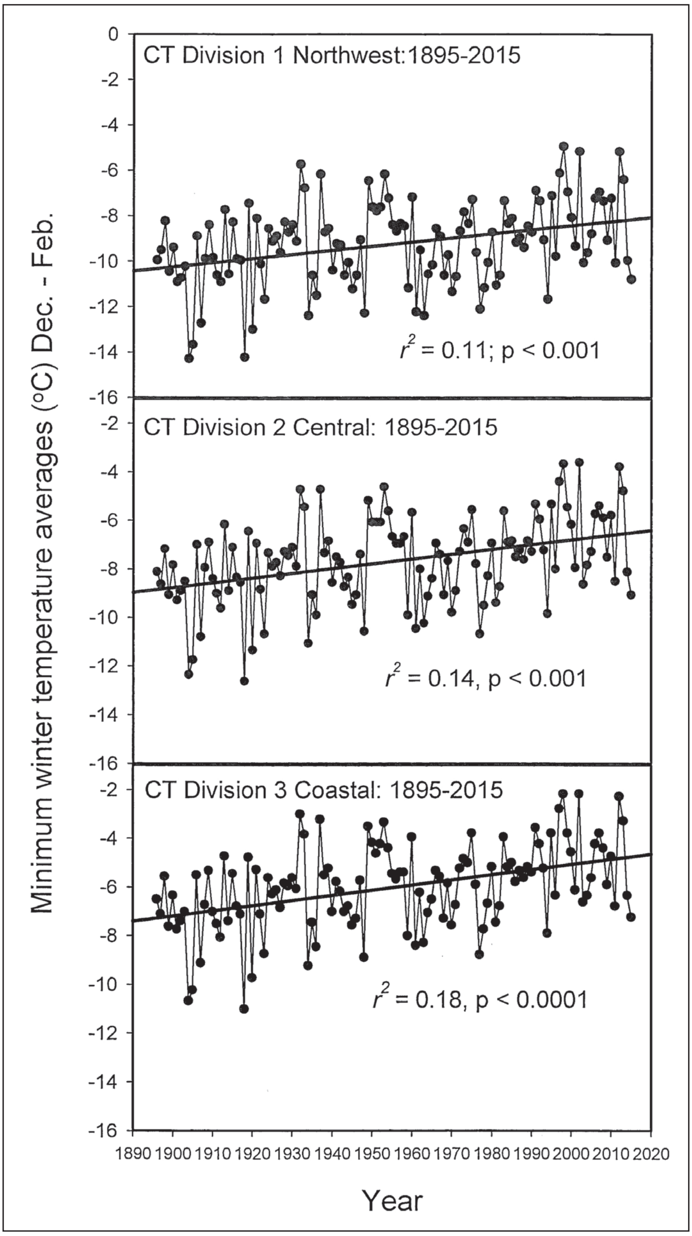

Figure 2. Minimum winter-temperature averages (obtained from Climate at a Glance, National Centers for Environmental Information (NCEI)) in the 3 climate divisions of Connecticut from 1895 to 2015. Significance of linear regressions and the regression coefficient (r^2) are shown.

In 2000, a significant and sudden cold snap in the latter half of January resulted in very high mortality (83–100%) of HWA in northern and central parts of Connecticut, in sharp contrast to coastal populations (11–28%) (McClure and Cheah 2002). This phenomenon was sampled widely and initiated the long-term annual field-monitoring of HWA winter mortality throughout Connecticut's 3 climate divisions for the next 15 years that is reported here. Earlier studies to assess the effects of winter temperatures on HWA mortality only spanned 1–3 years. Laboratory studies sampled 1–3 sites in 1 year (Parker et. al. 1998, 1999; Skinner et al. 2003), while field studies sampled more sites over 2 years (Shields and Cheah 2005) or 3 years (Paradis et al. 2007). In contrast, this Connecticut study has identified significant factors that accurately predict annual HWA winter-mortality patterns from a robust database with implications for the entire northeast region.

Long-term impacts of exotic pests like HWA on ecosystem processes and associated species are still largely unknown (Lovett et al. 2006). Optimal habitats of our northern tree species are under multiple stressors as the climate in the Northeast changes, with altered patterns of temperature and precipitation (Perschel et al. 2007). Understanding the implications of the changing climate on the spread and impact of invasive species, which threaten the ecology and biodiversity of native ecosystems, is of great importance (Ward and Masters 2007). This 15-year study in Connecticut combines 2 approaches: describing unpredictable fluctuations in winter patterns as the climate in the Northeast continues to warm, and documenting winter impacts on the abundance and persistence of populations of HWA in the Northeast. These findings are not just limited to the development of rational strategies for HWA control and management (Cheah 2016), but also contribute to understanding the potential for future spread and likely population trends, and may serve as a model for similar investigations for other invasive species.

Field-site Description

From 2000 to 2015, with the help of research assistants, I sampled a total of 208 Hemlock sites (10 trees per site) in Connecticut forests infested with HWA annually in late winter–early spring in each of the 3 Connecticut climate divisions (generally in mid-March–April). We visited 27 private and state forests in Division 1, 24 similar sites in Division 2, and 13 sites in Division 3 where HWA infestations were detected. Sample sites were natural pure Hemlock stands or mixed Hemlock stands of medium to good vigor at varying elevations and topography, and included some major release sites for *Sasajiscymnus tsugae* Sasaji and McClure (Coleoptera:Coccinellidae), a biological control agent from southern Japan (Sasaji and McClure 1997), reared and released throughout the state from 1995 to 2007 (Cheah 2010). *Sasajiscymnus tsugae* release sites represented 26% of sites sampled in Division 1, 50% in Division 2, and 31% in Division 3. Sampled forest areas had not been treated with chemicals and were rural in nature; thus, they were not affected by urban heat-islands. In most years, we also sampled planted Hemlock stands >30 years in age at the Connecticut Agricultural Experiment Station (CAES) Valley Laboratory research farm in Windsor and the Lockwood research farm in Hamden.

Methods

Temperature data

I obtained most of the winter temperature data used in the analyses from the official NOAA weather stations nearest the sample sites. To validate this method, we deployed temperature recorders (HOBO; Onset Computer Corporation, Bourne, MA) in the winter of 2010 on Hemlock boles at 14 sites and compared that data with minimum daily winter temperatures obtained from the nearest official weather station (9 in Division 1, 4 in Division 2, and 1 in Division 3).

For this study, climate data were generated for a period that corresponded to the meteorological definition of winter in the northern hemisphere (December, January, and February) (AMS 2016). I collected mean minimum winter temperatures for Connecticut as a whole, the Northeast as a region, and the 3 divisions of Connecticut from December through February, together with ranks since records began in 1895 from the summary tables of the Northeastern Climate Data Center at Cornell University (NRCC 2016) to show trends over the past 120 years. I downloaded time-series data on minimum winter temperatures for Connecticut from 1895 to 2015 from Climate at a Glance, National Centers for Environmental Information (NOAA 2015c). For each sampled site, I obtained daily minimum winter temperatures and snowfall depths from the nearest official weather station (NOAA 2015d; Climatological Data of New England), weather-underground airport stations, weather stations at the CAES research farms, or from Onset Computer HOBO temperature-recording devices (2010 only) to determine the lowest daily minimum winter temperature attained each winter. The minimum daily winter temperatures subsequently used in analyses refer to absolute minimum winter temperatures derived from daily weather records for each site. I utilized data from the Climatological Data of New England (NOAA 2015d) to generate mean snowfall per division per winter (Fig.1C) and to calculate subzero days, defined as the number of days during the winter when daily minimum temperatures fell below -17.8 °C (0°F). I derived a new composite interaction-statistic, herein called negative degree days (NDD), from the summation of the frequency of subzero days, multiplied by the respective minimum daily temperature. NDD were calculated for each site in every winter year sampled to capture the duration and cumulative intensity of extreme-cold events that occurred when daily minimum temperatures fell below -17.8 °C. I employed the Number Cruncher Statistical System (NCSS) (Hintze 1998) to perform non-parametric 1-way analyses of variance using the Kruskal-Wallis procedure to discern differences between divisions. All 3 variables were analyzed for their roles in influencing percent HWA winter mortality in the 3 Connecticut climate divisions.

HWA sampling

We selected Hemlock-branch tips with new growth from 10 intermediate or co-dominant trees with accessible foliage to ensure the healthiest growth conditions for HWA infestations. At each site, 10–12 infested but healthy branch tips, 0.3–0.38 m in length, were arbitrarily taken from the lower crown, 1 per tree, using hand pruners or pole-pruners, at a minimum of 1.3 m above ground to minimize the insulating effects of snow because snow cover has been shown to reduce the extent of winter kill of HWA (McClure and Cheah 2002). We usually collected samples in mid-March–April to ensure complete winter kill before assessments. The number of sites sampled each year varied due to heavy snowfall (Fig. 1B), which made some sites inaccessible, or the lack of HWA in some years, due to population reductions. However, sampling over 15 years of variable winters ensured that ample data were collected that spanned a wide range of daily minimum winter temperatures. Sampling was maximized for winters with extreme cold temperatures. In general, we sampled a mean of 14 sites annually (6–25 sites per winter); minimal sampling occurred in 2002 and 2013. The abnormally warm winter of 2012 was the only year not sampled.

To prevent HWA mortality due to desiccation of branch tips after collection, I kept samples hydrated by immediately immersing cut branch-ends in water in the laboratory. I placed samples in a Precision 818 low-temperature illuminated incubator (10–14 ºC) until processing at room temperature 1–2 weeks later. I assessed individual adelgids (≥ nymphal instar N2) infesting the underside of previous year's new growth as live or dead under a Zeiss dissecting microscope (x12). I readily distinguished dead adelgids from live adelgids by their dull, grey–black discoloration; desiccated state; and lack of turgor, leg movement, and fresh haemolymph when pierced with a probe. I then aggregated counts of all live and dead adelgids per branch sample (generally 1000–1500) to calculate a site mean percent HWA (%HWA) mortality per year, which I used in subsequent statistical analyses.

In 2014, I investigated the extent and timing of HWA winter mortality following an early January extreme polar vortex event. As defined by the National Oceanic and Atmospheric Association, the polar vortex is a persistent large area of cold, low-pressure air circling around the Earth's poles. During some winters, when the polar vortex is weak, large masses of Arctic air move southward and alter the amplitude of the jet stream to cause a period of extreme, colder than normal winter temperatures in the mid-latitudes (NOAA 2015e). In 2014, I collected HWA samples in mid- to late January within 2–3 weeks of the polar vortex outbreak for comparison with HWA samples taken later in the winter, from February through April. In Division 1, I sampled 4 sites in January, after the polar vortex event, and 4 sites between late February and April. In Division 2, I sampled 5 sites in January after the polar vortex event and 2 in late February. In Division 3, I sampled 2 sites in January and 1 in April. I compared sample means for timing of sampling and elevation effects using 2-sample t-tests. I also collected samples from all 3 climate divisions in March and April to assess the effects of the polar vortex events of 2015.

Statistical methods

I first performed regression analyses in Sigmaplot 2000 and NCSS 2000 (Hintze 1998). Linear regressions were employed, where appropriate, as:

$$y = ax + b,$$

where y = %HWA mortality, x = the variable investigated, a = the slope, and b = the y-intercept. When data were not linearly distributed, I conducted and fitted nonlinear regressions for a standard sigmoid 3-parameter logistic model using

Sigmaplot 2000, which utilized the Marquardt-Levenberg algorithm:

$$y = a/(1 + e[-(x-x_0)/b]),$$

where y = percent HWA mortality and x = the variable investigated (explained below), e = the natural logarithm base, x_o = the value of the sigmoid's midpoint, a = the curve's maximum value, and b = the width of the transition (Sigmaplot 2000). I tested data for normality and constant variance, and determined goodness of fit by the regression coefficient (r^2). Sigmaplot 2000 and NCSS 2000 (Hintze 1998) were employed to conduct analyses of variance and obtain significance levels.

I then calculated grand means for each division for each variable (%HWA mortality, minimum daily temperature, subzero days, NDD) in order to determine the predictive values of the climate conditions that would result in 90% and 99% HWA winter mortality. Statisticians and I used a probit-analysis approach (Bliss1934a, 1934b) to linearize percentage data to test for significant differences between divisional sigmoid-curve models describing the relationship between mean minimum daily temperature and grand mean %HWA winter mortality per division per year. Linearization of sigmoid-distributed data (mean %HWA mortality per division per year) was achieved by the NORMSINV function in Excel 2013 to generate normal equivalent deviates of proportional HWA mortality. Subsequent linear regressions on mean minimum daily temperature, number of subzero days, and NDD for all divisions were performed on transformed data followed by individual climate-division regressions. We compared slopes and elevations (y-intercepts) of division regressions for significance using the homogeneity of slopes test in Statistix 9 (Analytical Software, Tallahasee, FL). to determine if the divisional regressions were significantly different. I calculated the minimum daily temperatures that generated 90% and 99% HWA mortality for each division using the respective linear-regression equations and compared them with visual extrapolations from sigmoid curves. For comparison, I also employed visual extrapolations to estimate the number of subzero days and the total NDD that would result in 90% and 99% HWA winter mortality in Connecticut's 3 climate divisions.

In addition, we analyzed the combined data from all 3 divisions as general linear mixed models with a binomial variance and logit-link function for model selection. We performed these analyses in SYSTAT 13 (using the REML, restricted maximum likelihood approach; Systat Software, San Jose, CA) and with the R statistical package (R core Team 2013). The variables minimum winter temperature, number of subzero days, and NDD were tested separately with "Site" and Year" as random effects to account for geographical and seasonal variability. The Akaike information criterion for model selection (AIC) values generated were used to identify the variable that best explained HWA winter mortality.

Results

Minimum daily winter temperatures

I compared minimum daily temperatures from 14 sites in winter 2010 from HOBO temperature recorders and data obtained from the nearest official NOAA weather stations (NOAA 2015c). Both sets of data were in very good agreement, differing at most by 1–2 °C, except for readings from the Valley Laboratory research farm in Windsor (site 14), which differed by about 5 °C. In this instance, the minimum daily temperatures obtained from a HOBO temperature recorder mounted in a dense Hemlock stand 94 m from a major interstate highway was warmer than that of the weather station 217 m away in an open field at the research farm. However, a 2-sample *t*-test showed that in spite of that large deviation, temperature data in general did not significantly differ between HOBO temperature recorders and the nearest official weather station, which was often located several to many miles away (Mann Whitney *U* Test, Z = 1.0634, *P* = 0.298), thus validating the use of the nearest weather station data in the analyses. When minimum winter temperature data from the nearest weather stations were substituted for HOBO temperature data in the analyses, regression coefficient values did not change significantly, validating the use of weather-station data.

HWA winter mortality in Connecticut climate divisions

All climate divisions. The total number of sites analyzed was 208, with a total of 244,313 HWA assessed from 2000–2015 in all divisions: 90,524 in Division 1, 99,247 in Division 2, and 54,542 in Division 3. Data comparisons showed that the type of site sampled (*S. tsugae* release and non-release sites) did not influence HWA winter mortality (Mann Whitney *U* Test, Z = 1.2420, *P* = 0.215). When I analyzed data per site for the 3 Connecticut climate divisions together for all years, a linear regression for mean %HWA mortality on minimum daily winter temperature (°C) provided a good fit (Fig. 3A), although a sigmoid curve was a better fit even though variances were not constant (Fig 3B). Scatter diagrams (Figs. 3C, D) indicated that maximal limits of %HWA mortality were approached at upper levels of total NDD and the number of subzero days, and that linear regression analyses were not appropriate.

I also analyzed the combined data for HWA winter mortality from all 3 divisions in general linear mixed-models; results from the REML approach indicated that the best fit was provided by the absolute minimum winter temperature. The corrected AIC value was 722.1886 ($P < 0.00001$) for the minimum winter temperature variable, 738.0701 ($P = 0.001$) for NDD, and 732.7687 ($P = 0.015$) for subzero days.

However, the graphs also clearly indicated regional differences in annual winter data among the 3 divisions (Fig. 4). A Kruskal-Wallis one-way ANOVA indicated divisional differences in %HWA mortality ($\chi^2 = 9.6553$, $P = 0.008$). Hence, I analyzed %HWA winter-mortality data separately for each climate division.

Climate division 1: Northwest. A scatter diagram for %HWA mortality in Division 1 plotted against the total NDD indicated that the data fell into 2 distinct sections, which accounted for the wide variance. From a visual inspection of the data, HWA winter mortality in Division 1 reached maximum threshold values at about -100 NDD, and greater values of NDD did not result in higher mortality (Fig. 5A). Thus, the subset of data with NDD < -100 was used for non-linear regression analysis. A sigmoid curve that graphed minimum daily temperature and %HWA mortality provided the best fit (Fig. 5B). Percent HWA mortality was also significantly related to the number of subzero days (Fig. 5C), and total NDD (Fig. 5D).

All assumptions of normality and variance were met and regressions were all significant at $P < 0.0001$.

Climate division 2: Central. I adopted a similar approach to analysis for %HWA mortality in Division 2. A scatter diagram for %HWA mortality in Division 2 plotted against the total NDD indicated that the data also fell into 2 distinct sections. The same maximum threshold value of -100 NDD was used to partition the data because greater NDD values in Division 2 did not result in higher HWA mortality (Fig. 6A). For data with NDD < -100, minimum daily temperature was significant in determining %HWA mortality (Fig. 6B). Percent HWA mortality was also significantly related to the number of subzero days (Fig. 6C) and to the total NDD (Fig. 6D). All assumptions of normality and variance were met and regressions were all significant at $P< 0.0001$.

Climate division 3: Coastal. Percent HWA mortality in Division 3 showed more variation than in Divisions 1 and 2, but because there were relatively few days that dipped below -17.8 °C, all data (NDD <-100) were analyzed together. A sigmoid model had the best fit (Fig. 7A). As in the other divisions, the number of subzero

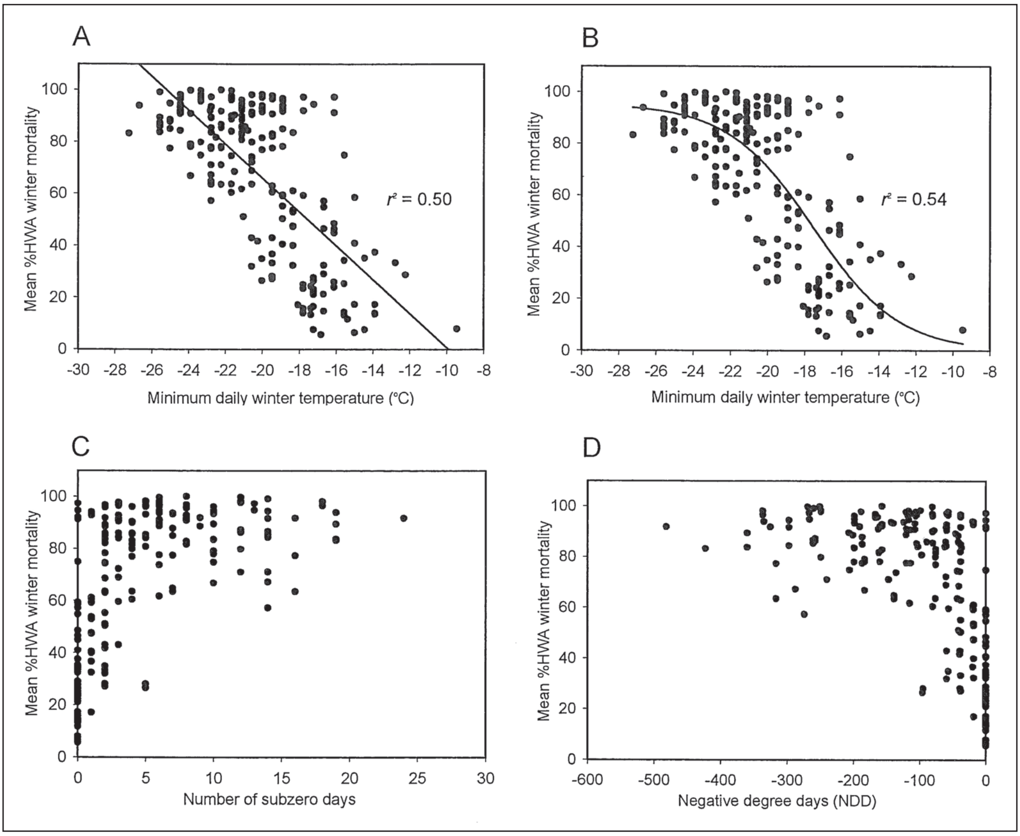

Figure 3. Relationships between %HWA winter mortality and minimum daily winter temperature (°C) are shown in (A) linear regression and (B) nonlinear regression ($P < 0.0001$). Also shown are %HWA relative to (C) the number of subzero days and (D) total negative degree days (NDD) for all Connecticut data from 2000 to 2015.

days (Fig. 7B) and total NDD (Fig. 7C) were also significant factors in determining HWA mortality. All assumptions of normality and variance were met, and regressions were all significant at $P < 0.0001$.

Polar vortex of 2014. A polar vortex outbreak brought extreme cold air from the Arctic Circle into the lower latitudes of North America on 4 and 5 January 2014.

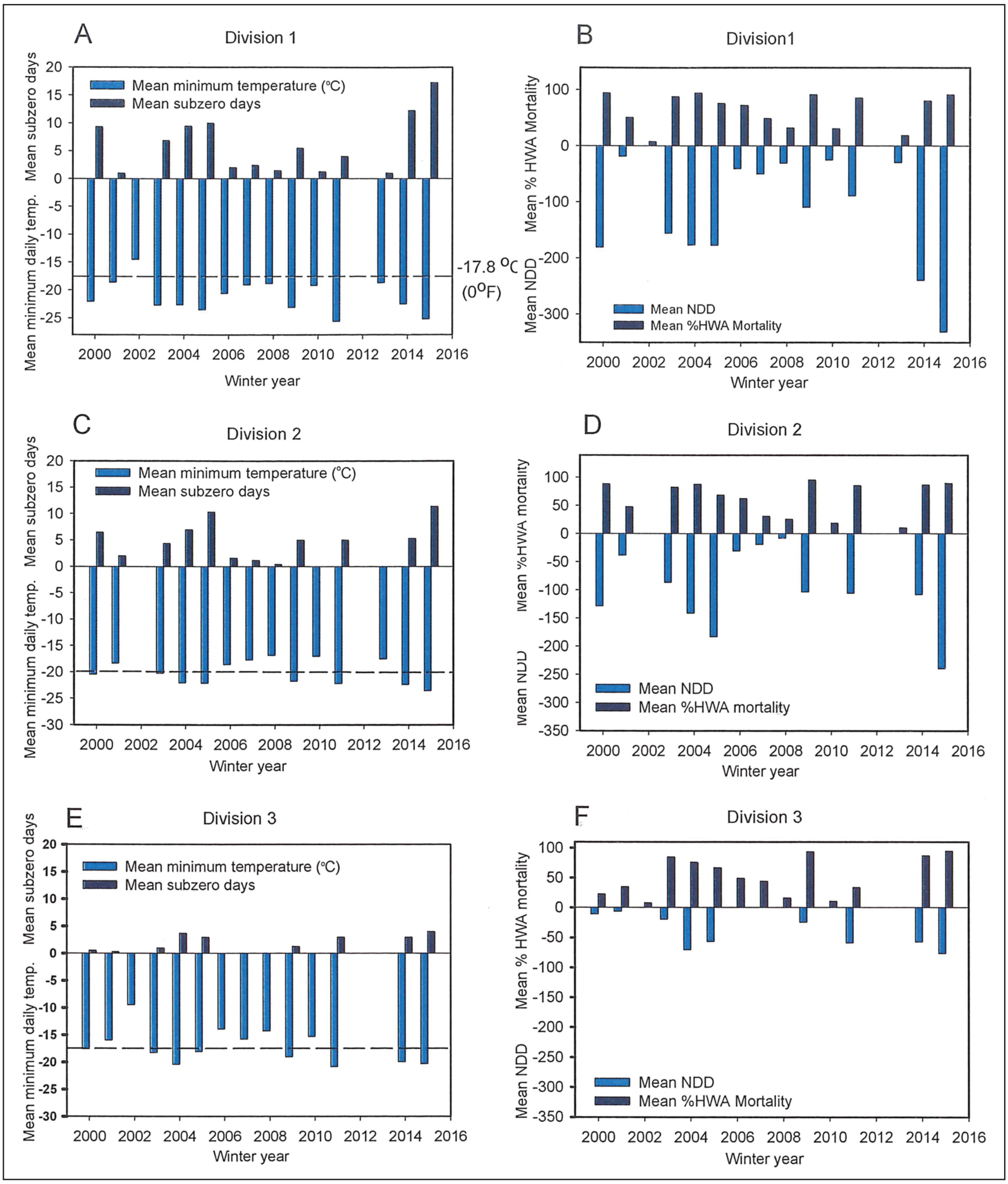

Figure 4. Differences in mean winter-climate trends and %HWA mortality in the 3 climate divisions of Connecticut from 2000 to 2015. The dashed line indicates -17.8 °C (0 °F). Variables shown are the mean minimum daily temperature, mean number of subzero days and mean NDD for (A and B) Division 1 Northwest, (C and D) Division 2 Central, and (E and F) Division 3 Coastal.

In Connecticut, mean minimum daily temperatures plummeted to -22.1 °C in Division 1, -22.0 °C in Division 2, and -22.6 °C in Division 3. Mean %HWA mortality was 79.3 ± 13.6, 86.91 ± 11.0, and 89.5 ± 5.5, respectively. However, HWA winter mortality did not differ significantly between Divisions 1 and 2 (t = -1.1739, P = 0.131), between Divisions 1 and 3 (t = -1.2260, P = 0.056), or between Division 2 and 3 (t = -0.3769, P = 0.318). Mean statewide HWA winter mortality in 2014 was 84.0 ± 11.9%. There were additional days in February when daily minimum temperatures in Division 1 dipped below -17.8 °C, especially at lower elevations and near the Massachusetts border in Division 2 (NOAA 2015c). However, 89–96% of all HWA winter mortality was due to the January polar vortex event alone. Subsequent minimum temperatures that dropped below -17.8 °C contributed minimally to additional HWA mortality. Percent HWA mortality from January samples was not different from mortality in samples collected in late February to April (t = -1.1069, P = 0.142). Site elevation (range = 21–483 m) also did not affect percent %HWA mortality (r^2 = 0.061, P = 0.323). In Connecticut, the winter of 2014 was ranked

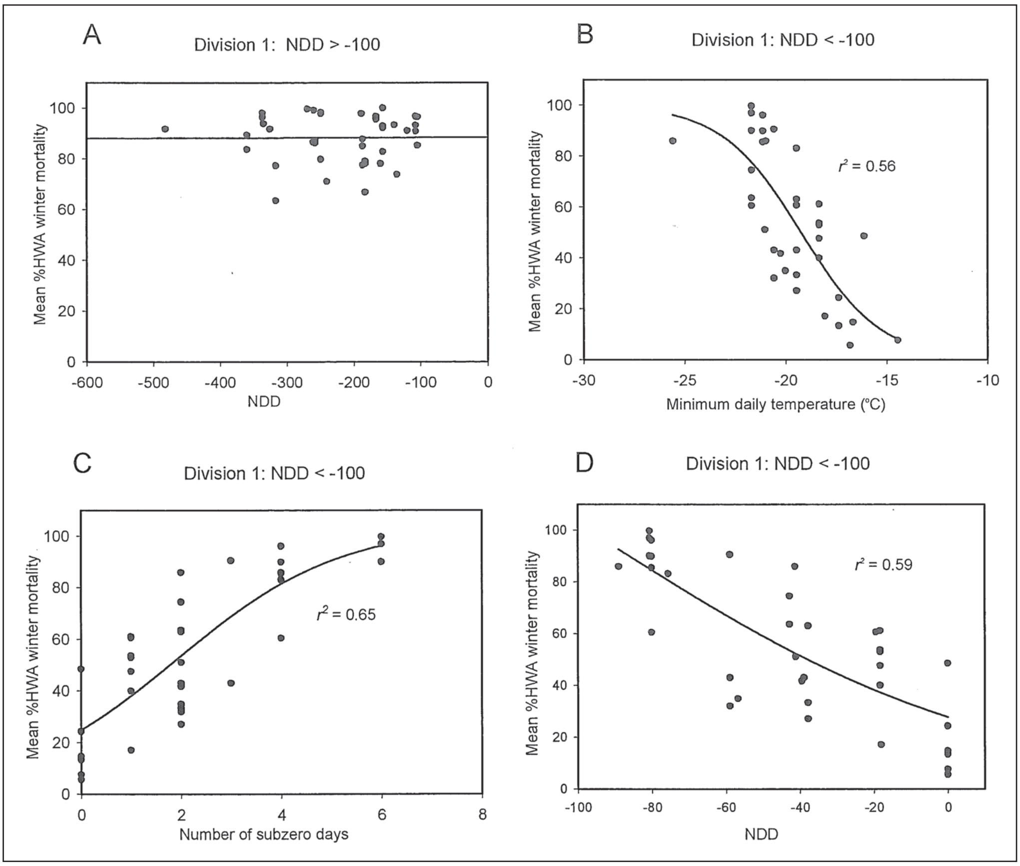

Figure 5. Division 1 relationships between mean %HWA winter mortality and (A) minimum daily temperature where NDD > -100, (B) minimum daily temperature where NDD < -100, (C) number of subzero days, and (D) NDD for NDD < -100. Regressions B, C, and D were significant at $P < 0.0001$.

48th coolest of the last 120 years, with a winter minimum temperature average of -8.1 °C (NRCC 2016).

Polar vortex of 2015. The winter of 2015 was notable in having the 2nd-coldest February since 1895 in Connecticut, with a minimum winter temperature average of -15.6 °C (NRCC 2016). In spite of the extended severity of February temperatures, the 2015 winter in Connecticut was ranked only 23rd with an overall minimum winter temperature average of -9.1 °C (NRCC 2016). Although minimum January daily temperatures fell to between -20 °C and -22.8 °C in northern areas of Divisions 1 and 2, the extended extreme cold did not occur until mid-February, when high levels of HWA mortality were recorded statewide. The polar vortex in mid-February was combined with a Siberian Express, which brought extreme arctic-cold across New England and beyond. In Division 3, the extended cold was of much shorter duration at 2–4 days (NOAA 2015d). Minimum daily temperatures dipped to some of their lowest levels in 120 years for an extended period of time (12 days) in Divisions 1 and 2. The minimum daily temperatures ranged between -24.4 and -26.7°C, -20.6 and -27.2 °C, and -18.9 and -20.6 °C in Divisions 1,2, and 3,

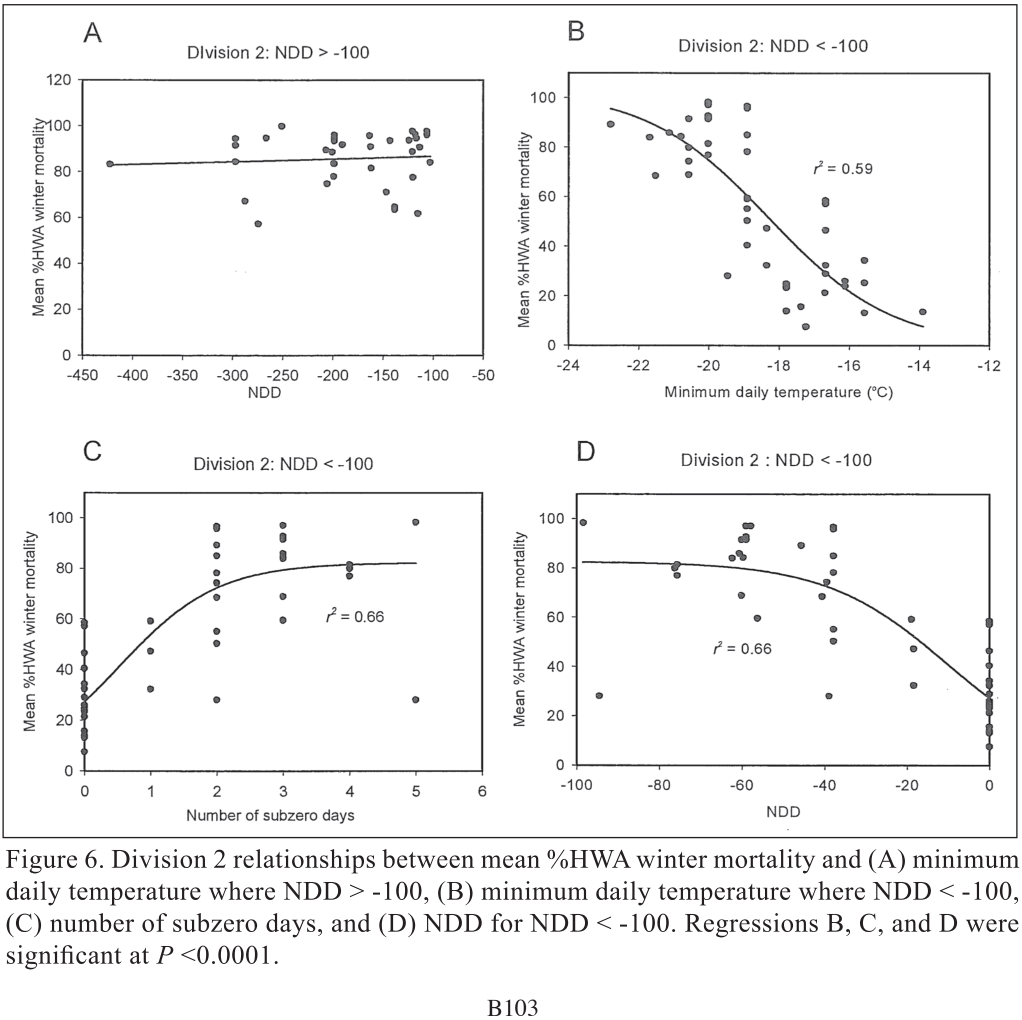

Figure 6. Division 2 relationships between mean %HWA winter mortality and (A) minimum daily temperature where NDD > -100, (B) minimum daily temperature where NDD < -100, (C) number of subzero days, and (D) NDD for NDD < -100. Regressions B, C, and D were significant at $P < 0.0001$.

respectively (NOAA 2015d). Analyses showed that in 2015, mean %HWA mortality in Division 1 (91.8 ± 5.48), Division 2 (89.46 ± 5.70), and Division 3 (94.2 ± 2.74) did not differ significantly (Division 1 vs 2: $t = 0.8534$, $P = 0.407$; Division 1 vs 3: $t = -0.8245$, $P = 0.427$; Division 2 vs 3 $t = -1.5482$, $P = 0.153$) . Winter mortality of HWA caused by the polar vortex of 2015 was high throughout Connecticut (average = 91.4 ± 5.26%).

General predictions from grand means. Using graphs of the grand means of the variables enabled more-precise extrapolations. The absolute minimum daily winter temperature, the number of subzero days, and the cumulative NDD were again validated as major factors determining the levels of %HWA winter mortality in each division (Fig. 8). Extrapolations in Figure 8 predicted that 90% HWA winter kill would occur at minimum winter daily temperatures of approximately -24 °C (Division 1), -22 °C (Division 2) and -20 °C (Division 3). Extrapolations produced the following subzero-day predictors for 90% HWA mortality: 5.5 (Division 1), 6 (Division 2) and 2.6 subzero days (Division 3) (Fig. 8). Similarly, extrapolations for 90% HWA mortality produced NDD predictors of -130 (Division 1), -100 (Division

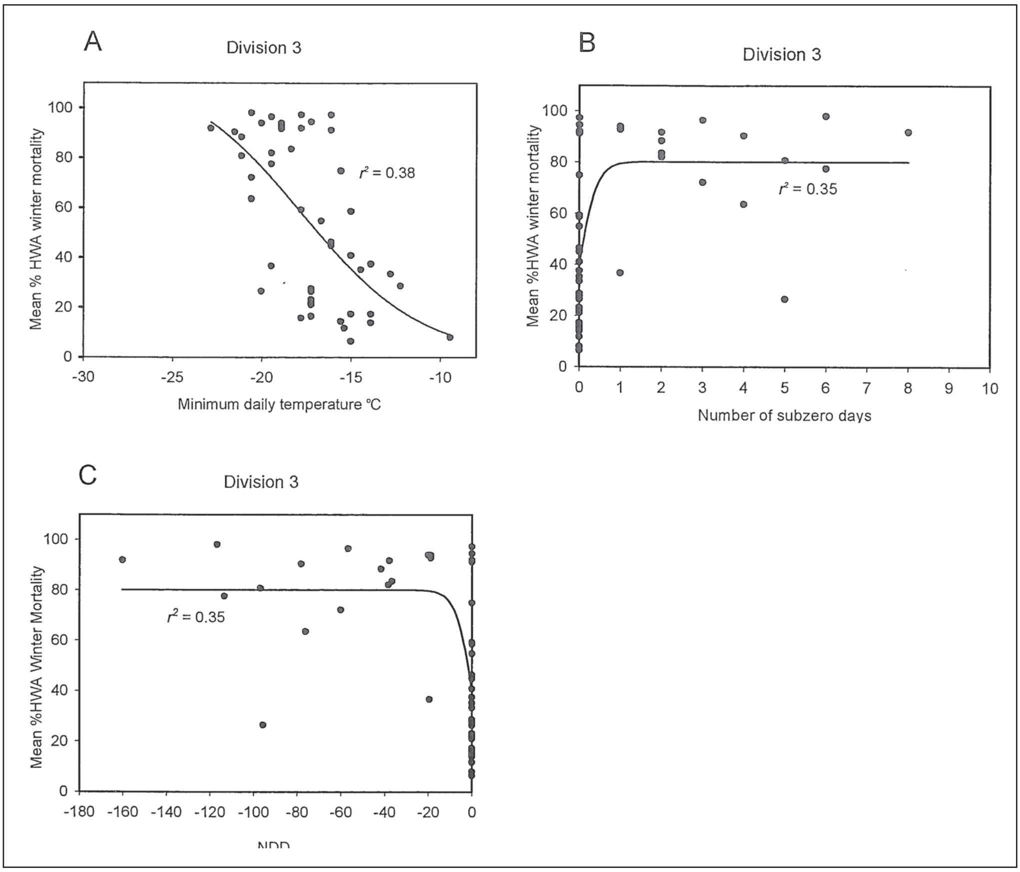

Figure 7. Division 3 relationships between mean %HWA winter mortality and (A) minimum daily temperature, (B) number of subzero days, and (C) NDD. All regressions were significant at $P < 0.0001$.

2), and -45 NDD (Division 3). Asymptotic levels of %HWA mortality in the sigmoid graphs did not allow for extrapolations of subzero days and NDD for 99% mortality because such high mortalities were not achieved in the period studied.

Division 1. Years in which mean HWA winter mortality >90% was observed in Division 1 were 2000, 2004, 2009, and 2015 (Table 1). The coldest winter in Division 1 during the study period, was 2015, with an average minimum winter temperature of -10.7 °C. In 2015, a mean (absolute) minimum daily temperature of -25.2 °C, 17.2 subzero days and -331.4 NDD resulted in 91.8% HWA mortality. The highest mean HWA mortality observed was 94.4% in 2004, when the mean minimum daily temperature was -22.6 °C , with 5.4 subzero days and -109 NDD. Higher

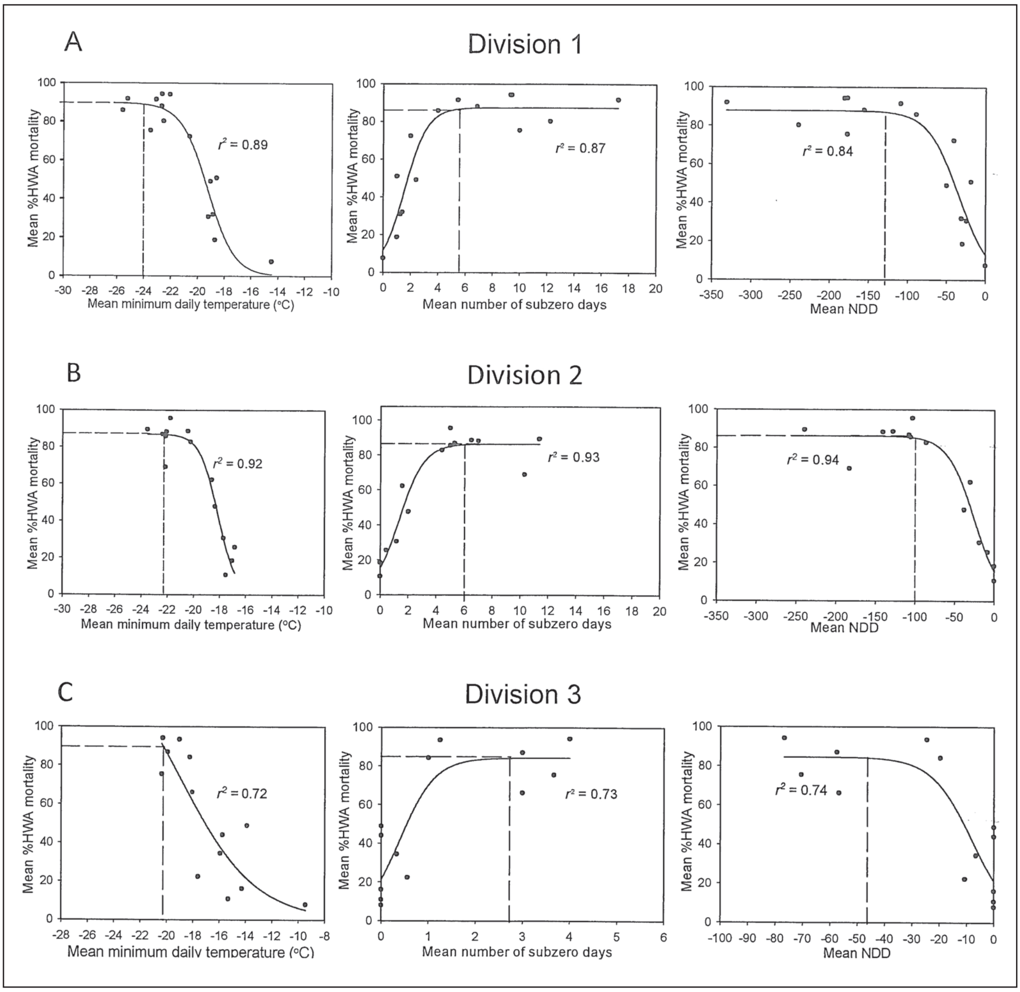

Figure 8. Nonlinear regressions are shown for grand means of %HWA winter mortality from 2000 to 2015 on mean minimum (absolute) daily temperature, mean number of subzero days, and mean NDD for (A) Division 1 (Northwest), (B) Division 2 (Central), and (C) Division 3 (Coastal). All regressions in all climate divisions were significant at $P < 0.0001$ (Divisions 1 and 2) and $P < 0.01$ (Division 3). Extrapolations for 90% HWA mortality in the 3 divisions are shown for the 3 variables.

Table 1. Major years for HWA winter mortality in most of the 3 climate divisions of Connecticut 2000–2015, where n = number of sites sampled and * denotes outlier data not included in analyses due to high probability of snow cover.

	Number of HWA counted at (n) sites			Total sites	Total HWA assessed	Grand mean %HWA mortality ± SEM and absolute minimum daily winter temperature (°C) reported as means					
Year	Division 1	Division 2	Division 3			Division 1		Division 2		Division 3	
2000	6497(6)	8705 (8)	8730 (9)	23	23,932	94.2 ± 4.9	-22.0	88.6 ± 9.9	-20.4	22.4 ± 10.8	-17.6
2003	9663 (8)	7899 (5)	7764 (6)	19	25,326	88.1 ± 7.1	-22.7	82.8 ± 8.6	-20.2	84.2 ± 7.6	-18.3
2004	8486 (7)	15,421 (10)	4765 (3)	20	28,672	94.4 ± 4.7	-22.6	88.3 ± 7.6	-22.1	75.5 ± 15.7	-20.4
2009	10,550 (9)	7051 (6)	4438 (4)	19	22,039	91.5 ± 6.7	-23.1	95.6 ± 3.2	-21.8	93.5 ± 4.9	-19.0
2011	1200 (1)	5116 (4)	1019 (1)	6	7335	85.9 ± 13.2	-25.6	85.7 ± 16.7	-22.2	$33.5 \pm 19.2^{*}$	-20.8
2014	9263 (8)	7855 (7)	2849 (3)	18	19,967	80.3 ± 7.6	-22.5	86.9 ± 8.8	-22.4	87.0 ± 9.7	-19.9
2015	10,728 (9)	9071 (8)	4776 (4)	21	24,575	91.8 ± 6.6	-25.2	89.4 ± 9.4	-23.5	94.2 ± 5.2	-20.3

HWA winter mortalities occurred in the first half of study compared to the second half, despite colder minimum daily temperatures in the latter (Table 1). For the period of the study, the mean minimum daily temperature reached its lowest value in 2011 at -25.6 °C, with 4 subzero days but only -89 NDD. In spite of this, the winter of 2011 was warmer than 2015 and had an average minimum winter temperature of -10.1 °C. The highest snowfall (Fig. 1C) and the greatest variability in adelgid mortality were also recorded in 2011 (Table 1). The average absolute minimum daily subzero temperature for the 7 coldest winters in Division 1 was -23.4 °C.

Division 2. Major HWA winter mortality in Division 2 (83–96%) occurred in 2000, 2003, 2004, 2009, 2011, 2014, and 2015 (Table 1). Mean winter mortality of HWA exceeded 90% only once in Division 2, when the absolute minimum daily temperature reached -21.8 °C in late January 2009. Minimum daily temperatures of approximately -22 °C in Division 2 killed almost 90% of HWA. The coldest winter in Division 2 was also 2015, with a mean minimum daily temperature of -23.5 °C, 11.4 subzero days and -239.6 NDD, which resulted in 89.4% mortality. During the study period, snowfall was greatest in 2011 in Division 2 (Fig. 1C). The average minimum daily subzero temperature for the 7 coldest winters in Division 2 was -21.8 °C.

Division 3. Years with high HWA winter mortality in Division 3 (84–94%) were 2003, 2009, 2014, and 2015 (Table 1), indicating that there were fewer severe HWA-killing winters in Division 3 (n = 4) than in Divisions 1 and 2 (n =7). Mean winter mortality of HWA exceeded 90% only twice (2009, 2015) in Division 3. In 2009, a mean minimum daily temperature of -19 °C, 1.25 subzero days, and -24.6 NDD resulted in 93.5% HWA mortality. The coldest mean minimum daily temperature included in our analysis was -20.4 °C in 2004 (2011 data was excluded because it was compromised by heavy snow cover), and together with 3.6 subzero days and -70.4 NDD, resulted in only 75.5% HWA mortality for that year. However, in 2015, during the 2nd-coldest February on record, a minimum daily temperature of -20.3 °C, 4 subzero days, and -76.7 NDD killed 94.2% of HWA, the highest mean mortality recorded during this study (Fig. 8C). As in Divisions 1 and 2, Division 3 had a record-breaking snowfall during the winter of 2011 (Fig. 1C). The average minimum daily subzero temperature for the 6 coldest winters in Division 3 was -19.8 °C.

Predictors of HWA winter mortality. Linearized normal deviates of proportional mean HWA mortality were regressed successfully on minimum daily temperature. Table 2 shows the linear regressions of normalized equivalent deviates which were all significant at $P < 0.0001$ (Divisions 1 and 2) and $P < 0.001$ (Division 3). Data plots indicated that linear regressions of mean %HWA mortality on NDD and subzero days were not appropriate. From Table 2A, regression equations, where y = normal equivalent deviate for the proportion of dead HWA, are formulated below:

Division 1: $y = -0.28383\,(x) - 5.52039$

Division 2: $y = -0.35727\,(x) - 6.73891$

Division 3: $y = -0.26909\,(x) - 4.41260$

Solving for x (using the normal equivalent deviate for 90% = 1.281552), the minimum daily temperature that would result in 90% HWA winter mortality (Table 2) in each of the division regression equations was -24 °C (Division 1), -22.4 °C (Division 2), and -21.2 °C (Division 3). Solving for *x* to produce 99% HWA mortality (normal equivalent deviate = 2.326348), the projected minimum daily temperature that would result in 99% HWA winter mortality was -27.6 °C (Division 1), -25.4 °C (Division 2), and -25.0 °C (Division 3). Regression coefficients for all nonlinear regressions were highly significant, explaining 73–94% of the variation and validating the importance of other factors such as NDD and the number of subzero days. The homogeneity of slopes test showed that the regression slopes were equivalent for all divisions and that there were no significant differences in the *x*-intercepts between Divisions 1 and 2 (Table 2B), but the *x*-intercept for Division 3 was significantly different from that of Divisions 1 and 2 (Table 2B), predicting zero HWA mortality at around -8 °C, compared to approximately -11 °C for Division 1 and -12.5°C for Division 2.

There was good agreement between the 2 approaches: extrapolations of minimum daily temperatures in each division required to kill 90% of HWA were similar to temperatures calculated from linear regressions of linearized normal deviates of proportional mean HWA mortality. Using generalized linear mixed models, AIC values were minimized for minimum winter temperature, which indicated that this was the most important variable in predicting HWA winter mortality, followed by the number of subzero days and NDD.

Table 2. Results for statistical comparisons of slopes and *y*-intercepts using the homogeneity of slopes test (Statistix 9) for (A) all Connecticut-division linear regressions and (B) pairwise division comparisons. Grand means of %HWA mortality from 2000–2015 were transformed by the Normsinv function (Excel 2013) for regressions on mean absolute minimum daily temperatures. Predicted minimum daily temperatures in each division resulting in 90% and 99% HWA mortality were calculated from the linear regressions.

(A)

								Predicted minimum temp. (°C)for %HWA mortality	
Div.	*n*	Intercept	Slope	MSE	Bartlett's test of equal variances	Comparison of slopes	Comparison of elevations	90%	99%
1	15	-5.52039	-0.28383	0.22493	χ^2 = 1.31, df = 2, *P* = 0.52	*F* = 0.67, df = 2, 36 *P* = 0.5172	*F* = 7.73, df = 2,38 *P* = 0.0015	-24.0	-27.6
2	14	-6.73891	-0.35727	0.21335				-22.4	-25.4
3	13	-4.41260	-0.26909	0.39086				-21.2	-25.0

(B)

Comparison of regression lines	Comparison of slopes			Comparison of elevations		
	F	df	*P*	*F*	df	*P*
Division 1 vs. 2	1.10	1, 25	0.3048	2.51	1, 26	0.1254
Division 1 vs. 3	0.04	1, 24	0.8367	10.75	1, 25	0.0031
Division 2 vs. 3	1.14	1, 23	0.2962	7.19	1, 24	0.0130

Discussion

The 15 years of HWA winter-mortality data in Connecticut indicate that there are 3 important variables that strongly influence the degree of HWA winter mortality: (1) the absolute minimum daily temperature, (2) the number of subzero days, and (3) the cumulative negative degree days or NDD. The variable that best explained HWA winter mortality in each climatic division was the lowest minimum daily winter temperature, or the absolute minimum winter temperature (December to February). Although minimum winter temperature averages are typically used to rank winters, they do not always reflect the coldest daily winter temperatures experienced, which this study indicated is the most critical factor in determining HWA mortality (Table 1). For example, the lowest minimum daily temperature in Division 1 during the study period was recorded in 2011 (-25.6 °C, Table 1), but the coldest winter overall was in 2015, with a higher minimum daily temperature of -25.2 °C. This outcome was due to the fact that the minimum winter temperature average in Division 1 in 2011 was -10.1 °C and it was -10.7 °C in 2015 (NRCC 2016). Similarly, in Division 3, the lowest daily minimum winter temperature of -20.8 °C was recorded in 2011, compared to -20.3 °C in 2015. However, the average minimum winter temperature for winter 2011 was -6.8 °C, which was warmer than that for winter 2015 at -7.3 °C.

Negative degree days is a new measure that combines temperature exposure, magnitude, and duration. Field data showed that critical minimum daily temperatures of -21 to -24 °C are presently sufficient to kill 90% of the overwintering sistens generation of HWA in the different climatic divisions of Connecticut. In Division 1, a minimum daily temperature of -24 °C, 5.5 subzero days and -130 NDD are predicted to kill 90% of HWA. In Division 2, a minimum daily temperature of -22.4 °C, 6 subzero days, and -100 NDD are predicted to kill 90% of HWA. In Division 3, a minimum daily temperature of -21.2 °C, 2.6 subzero days, and -45 NDD is predicted to kill 90% of HWA sistens. The data also suggest that during less-severe winters, when minimum daily winter temperatures are less extreme, the number of subzero days and NDD may be more relevant, contributing incrementally to cumulative HWA winter mortality over time. Results also showed that HWA populations in Connecticut differed in winter susceptibility between the 3 climate divisions, possibly due to selection.

This study differs from earlier published studies in that it is based on a robust dataset of HWA winter mortality measurements spanning 15 years of variable winters. The accuracy of predicted values of HWA winter mortality is based on nonlinear-regression analyses; other studies have employed linear regression. The approach used in this study enables the prediction of mean HWA winter mortality in any of the climatic divisions based on the absolute minimum daily winter temperature recorded at the nearest weather station. The use of the nearest weather-station data greatly expands the utility of the approach for a wide range of stakeholders, from foresters to land managers to homeowners, without the requirement for on-site temperature-data recorders. This study demonstrated that data from the nearest weather station could be used to accurately predict resulting levels of HWA mortality. The simple predictors developed for 90% and 99% HWA mortality in the 3 CT climate divisions could be easily estimated in any winter season, and methods developed here are applicable to other regions and states. Climate data on winter minimum-temperature averages for winter 2015 in the northeast (NRCC 2016) indicate that Division 1 in CT is comparable to central MA (warmer), the Hudson Valley in NY (warmer), and the northern tier of PA (similar).

Earlier small-scale laboratory studies (Parker et. al 1998, 1999; Skinner et al. 2003) investigated the consecutive response of 1-year field collections of HWA to cold temperatures from January to March at 1–3 sites in southern MA and in central and southern CT during 1996, 1997, and 1998. These laboratory studies showed that %HWA survival and cold hardiness declined at subzero temperature exposures. Adelgids sampled in January in their studies had greater survival at subzero temperatures in the laboratory than those sampled in February, and March samples had the least survival at -20 °C and -25 °C. No HWA survival was recorded at -35 °C or -40 °C (Parker et al. 1999). In 2014, the brief but early January polar vortex event with minimum daily temperatures of -20 °C to -22.8 °C (which were also the absolute minimums for winter 2014) accounted for 89–96% of the overall HWA mortality in CT, showing that HWA were less cold-hardy than would have been expected. Moreover, a cold snap in early winter (e.g., in December) can also kill high numbers of HWA, as happened in the winter of 2005–2006 in Divisions 1 and 3. The warmest winter until 2016 (ranked 122) was 1998 (ranked 121); 1997 was ranked 117 and is also among the warmest winters in CT since 1895 (NRCC 2016). HWA sampled for the laboratory studies may have lacked cold-temperature conditioning. Extrapolations from these laboratory studies should be made with caution. A recent laboratory study showed that northern HWA exposed to -12 °C for 3 days subsequently developed lower-supercooling points (Elkinton et al. 2016). In Japan, minimum daily temperatures at high elevations of 1500–1650 m often reached -35 °C, and HWA mortality there was only 25% (McClure 1996). It is uncertain if current HWA populations in the eastern US could achieve such cold hardiness. It also suggests that the source of the HWA introduction into the eastern US may have been from a lower elevation, perhaps a coastal and hence, warmer region in its native homeland of Honshu, Japan.

Ellison (2014) indicated that the minimum winter temperature at which 50% HWA mortality is expected is -25 °C. CT field studies have shown that at -25 °C, HWA populations experience >90% mortality, or at least, >80% mortality near the MA border. Shields and Cheah (2005) sampled 36 sites in New England and the Mid-Atlantic in 2003 and 2004, which were some of the coldest winters in the past 2 decades, and could only correlate latitude with %HWA mortality, while the relationship with minimum daily temperature was weakly significant. When the same dataset was reanalyzed, landscape-level estimates of absolute minimum winter temperatures explained only 9% of variation in 2003 and 46.4% in 2004 (Trotter and Shields 2009). Paradis et al. (2007) sampled from 2004 to 2006 at 12 Hemlock stands in MA and CT, and used a linear mixed model to analyze 8 measures of winter temperature (December to March) for effects on HWA winter mortality. They found that average daily mean winter temperature was the most significant factor in determining mortality level, and they projected that all HWA would likely die at -40 °C (= -40 °F), or at 93 days when the average daily minimum temperature was below -10 °C, or if exposed to a mean winter temperature of -5 °C (Paradis et al. 2007). However, using the average daily mean winter temperature fails to account for the potential effects of any sudden and brief extreme temperature fluctuations on HWA winter survival (C. Cheah, unpubl. data). Data from the NRCC (2016) showed that the mean winter temperature in 2015 in the climate divisions in the Northeast fell below -5 °C or 23 °F in much of northwestern CT, central and western MA, coastal and interior ME, southern NH, the Hudson Valley and central lakes of NY, the Pocono Mountains, and the Upper Susquehanna and Central Mountains of PA. However, in CT, HWA survived and even thrived in 2015 in pockets of the northwestern and northeastern part of the state (C. Cheah, unpubl. data). Despite a cold winter in 2014 and contrary to projections, HWA continued to spread in NY, PA, VT, NH (USDAFS 2016a, b), and Maine (Maine Forest Service 2016). The current study confined analyses to the meteorological definition of winter (December to February), which is the basis of climate data reported at NOAA and NRCC. By employing this approach I found regional or divisional differences in HWA mortality, hence validating my analytical method.

Coastal HWA populations in Connecticut's Division 3 remained vulnerable to >90% winter mortality at higher minimum daily temperatures than occur in the interior and do not appear to have developed substantially greater cold tolerance in the past 16 years. Perhaps this susceptibility is also because extreme winters are less frequent along the coast. Results suggest that by 2015, minimum daily temperatures required to achieve >90% HWA mortality were 1.3 °C colder than in 2009. The winter of 1994 was a very severe one, and in CT, it was ranked 15th-coldest in terms of its minimum temperature average as compared to the winter of 2015, which was ranked 23rd (NRCC 2016). January 1994 was ranked 9th coldest (NRCC 2016), and yet the ability of HWA progrediens populations to rebound after severe winters presents a challenge, as was shown by the continued expansion throughout interior regions of CT in the mid- to late 1990s. Minimum daily temperatures of that magnitude in 1994 and perhaps colder have only just recurred during 14–15 February 2016, with the 3rd weak polar vortex outbreak in succession that affected HWA populations.

An alternative explanation for the relative susceptibility of HWA populations in Division 3 to higher minimum daily temperatures may lie in the possibility of the recurrent spread or immigration of HWA from lower latitudes through migratory birds (Russo et al. 2015) and wind currents. More-southerly HWA source populations might be expected to have lower cold tolerance, and, thus be susceptible to high winter-kill rates even at these moderately low daily minimum temperatures in maritime areas along the CT shore. Results indicated that comparatively less-frequent severe winters occur along the coast in CT than in the interior (Fig. 4). This temperature regime may explain why initial HWA spread was so rapid along the coast. A closely related species, *Adelges piceae* Ratz. (Balsam Woolly Adelgid [BWA]), was introduced from Europe into eastern North America in the early 1900s and has been limited in its distribution and spread in the Maritime provinces of Canada by colder temperatures in the interior (Greenbank 1970). There was no survival of BWA at -37.2 °C (Greenbank 1970). Greenbank's seminal 1970 study recognized the importance of distinct bioclimatic regions in the Maritime Provinces of Canada, and postulated that regional differences in environmental conditions could lead to the development of genetically distinct races of BWA. However, he concluded from his study that there was no evidence for that hypothesis because BWA mortality was similar between the regions. Unlike HWA, BWA overwinters as 1st-instar nymphs which do not feed in the winter and can be more protected by snow cover on the bole and base of *Abies* (Fir) than HWA, which infests outer foliage throughout the Hemlock crown and is more exposed to winter extremes. The role of snow cover as insulating protection for HWA was not studied directly here but should be investigated further. Mean HWA mortality from 1 site in southern CT (Division 3) in 2011 was unusually low in spite of extreme minimum temperatures (Table 1). These samples came from trees on a roadside slope, which in retrospect, had a high probability of being covered by cumulative snow from snowplow throw in addition to record snowfall (155 cm by early March 2011) during the snowiest winter in the period studied (Fig. 1C). In the conifer forest, snow interception, adhesion, and subsequent removal is a complex science and is affected by numerous factors such as wind velocity and pattern, air temperature, solar radiation, and forest canopy (Miller 1964). Snow-to-liquid ratios also affect adhesion of snow to foliage. Under certain conditions, such as lack of wind and/or wet sticky snow, I have observed that snow continues to adhere to Hemlock foliage for several days after snowstorms that are followed by extreme low temperatures. Such instances of snow insulation have the potential of protecting random patches of HWA infestations from extreme cold and will be investigated further.

In this study, HWA mortality patterns were not the same throughout CT, and Division 3 patterns were distinct from Divisions 1 and 2. This result suggests that coastal populations of HWA in CT might represent a different HWA biotype. A key question remains as to whether greater cold adaptation is occurring in the interior and more northerly parts of CT, where HWA populations are experiencing much colder and more widely fluctuating winter extremes, as compared to milder, coastal regions. The data seems to suggest that this possibility should be investigated further. In Division 1, some cold tolerance may have developed since 2000. The minimum daily temperature required to achieve >90% HWA mortality in 2015 was approximately 3 °C colder than in 2000 and 2004 (Table 1). The central region of Division 2 encompasses widely varying terrain (Brumbach 1965) and would thus be expected to have more variable patterns of HWA winter mortality. However, the annual patterns generally mirrored those observed in the colder Division 1. In Division 2, the minimum daily temperature required to kill 88–89% HWA in 2015 was 3 °C colder than in 2000, when the minimum daily temperature was -20.4 °C. Much higher HWA mortality (>95%) occurred in 2004 at -21.8 °C. The CT predictors for 90% and 99% HWA mortality—minimum daily temperature, number of subzero days, and NDD—were developed from data collected during 2000–2015 and represent invaluable baseline data for future studies on HWA cold adaptation. Field-collected HWA from the species' southern range had higher supercooling-points and were less cold-hardy than HWA collected from northern and interior portions of its range (Elkinton et al. 2016). However, my results show that even within an area as small as CT, interior populations appear to have developed greater cold-hardiness than coastal populations.

The results of this study show that, during the 15-year sampling period, extreme winters were punctuated by record warm winters in a changing climate, and that consecutive severe winters dramatically reduced HWA sistens populations. Extreme cold air events during the winter season in the mid-latitudes of North America (Cellitti et al. 2006, Walsh et al. 2001) are, therefore, of great importance in limiting HWA populations, especially in the Northeast. The winters of 2014 and 2015 were very severe but also notable for the increased media attention focused on the phenomenon of the polar vortex, one of several underlying mechanisms for such extreme winter events (NWS 2016). The northern polar vortex is typically centered near Baffin Island during the winter months (Overland et al. 1997) and cold arctic outbreaks which affect the mid-latitudes of North America can sometimes be the result of a weakened polar vortex. Occasionally, weak polar vortex events in winter can extend very cold air into the lower latitudes, producing abnormal and extreme arctic temperature lows. Both extreme cold events in 2014 and 2015 were the result of weak and unstable Arctic Oscillations in the northern polar vortex that enabled Arctic air to escape and push down with the jet stream into the lower latitudes of the North American continent (Fischetti 2014). For the period studied, earlier notable polar vortex outbreaks also occurred in 2000, 2004, and 2009, which are coincident with the majority of >90% HWA winter mortalities (Table 1). The frequency of extreme cold air outbreaks may not have diminished in spite of warming climate trends (Walsh et al. 2001). Polar vortex incursions into the lower mid-latitudes may become more frequent, as was witnessed in back-to-back events in 2014 and 2015, which resulted in great reductions in overall HWA populations. The effects of the brief polar vortex in February 2016 were extremely devastating on HWA (Cheah 2016). Recent analyses indicate that weakening of the polar vortex and shifts in its position from North America toward Europe and Asia could result in more and later arctic outbreaks of extreme cold in North America (Zhang et al. 2016). The impact of severe winters on winter populations of HWA also affect introduced predator species which specialize on the HWA sistens generation. Thus, the results of this study have extended implications for current HWA biological control management strategies. An alternative is to deploy HWA predators such as *S. tsugae*, which is active later in spring, has 2 generations, feeds continuously from spring to fall (Cheah 2011, Cheah and McClure 2000, Cheah et al. 2005), and is readily available to the public through a commercial supplier (Cheah 2016).

Acknowledgments

I am most grateful to R. Cowles and F. Ferrandino (CAES) and M. Wininger (Yale University) for expert statistical advice, J. LaMondia (CAES) for pertinent review and insights, and to 2 anonymous reviewers for suggestions. I also thank X. Asbridge, B. Beebe, J. Fengler, M.K. Frost, R. Hiskes, S. Lamoureux, J. Preste, P. Trenchard, S. Sandrey, E. Varricchio, L. Young, and J. Winiarski (CAES) for valuable technical assistance, and M. McClure for the initial opportunity to conduct HWA research. I am grateful to J. Bronson, R. Russ, and H. Carlson (Great Mountain Forest Corporation); C. Rand and S. Gilman (Mt. Riga, Inc.); C. Youell, A. Hubbard, and S. Rogers (Metropolitan District Commission); and the foresters of the Connecticut Division of Forestry, State Parks and Forests of the Connecticut Department of Energy and Environmental Protection for their support and permission for property access. Special thanks to Dr. L. Magnarelli (CAES) for his unwavering support and encouragement. Funding for this research was from the USDA Forest Service, Northeastern Area State and Private Forestry 2000–2009, and the National Institute for Food and Agriculture, McIntire-Stennis Cooperative Forestry Research Program 2013–2016.

Literature Cited

American Meteorological Society (AMS). 2015. Glossary of American Meteorological Society. Available online at http://glossary.ametsoc.org/wiki/Winter. Accessed 28 January 2016.

Anderson, J.F. 1986. Gypsy Moth outbreaks in Connecticut in the 1980s. Frontiers of Plant Science 39(1):7–8.

Benzinger, J. 1994a. Hemlock decline and breeding birds. I. Hemlock ecology. Records of New Jersey Birds 20:2–12.

Benzinger, J. 1994b. Hemlock decline and breeding birds. II. Effects of habitat change. Records of New Jersey Birds 20:34–51.

Bliss, C.I. 1934a. The method of probits. Science 79:38–39.

Bliss, C I. 1934b. The method of probits. Science 79:409–410.

Brumbach, J.J. 1965. The Climate of Connecticut. Bulletin 99. State Geological and Natural History Survey of Connecticut, Hartford, CT. 215 pp.

Cellitti, M.P., J.E. Walsh, R.M. Rauber, and D.H. Portis, 2006. Extreme cold air outbreaks over the United States, the polar vortex, and the large-scale circulation. Journal of Geophysical Research: Atmospheres 111: Issue D2. doi:10.1029/2005JD006273.

Cheah, C. 2006. Hope for hemlocks. Connecticut Woodlands. Fall 2006:13–15.

Cheah, C. 2010. Connecticut's threatened landscape: Natural enemies of biological control of invasive species. Frontiers of Plant Science 57:5–16.

Cheah, C. 2011. Chapter 4. *Sasajiscymnus* (=*Pseudoscymnus*) *tsugae*, a ladybeetle from Japan. Pp. 43–52, *In* Implementation and Status of Biological Control of Hemlock Woolly Adelgid. B. Onken and R. Reardon. (Technical .Coordinators.). US Department of Agriculture Forest Service FHTET- 2011-04 Publication. Forest Health Technology Enterprise Team, Morgantown, WV. 230 pp.

Cheah, C. 2016. HWA winter mortality in Connecticut and implications for management and control. Connecticut Agricultural Experiment Station Factsheet. Available online at http://www.ct.gov/caes/lib/caes/documents/publications/fact_sheets/plant_pathology_and_ecology/hemlock_woolly_adelgid_winter_mortality__7.12.16.pdf. Accessed 25 July 2016.

Cheah, C.A.S.-J., and M.S. McClure. 2000. Seasonal synchrony of life cycles between the exotic predator *Pseudoscymnus tsugae* (Coleoptera,Coccinellidae) and its prey, the Hemlock Woolly Adelgid, *Adelges tsugae* (Homoptera,Adelgidae). Agricultural and Forest Entomology 4:1–11.

Cheah, C.A.S-J., M.A. Mayer, D. Palmer, T. Scudder, and R. Chianese, 2005. Assessments of biological control of Hemlock Woolly Adelgid with *Sasajiscymnus tsugae* in Connecticut and New Jersey. Pp. 116–130, *In* B. Onken and R. Reardon (Compilers). Proceedings of the 3rd Symposium on the Hemlock Woolly Adelgid in the Eastern United States, 1–3 February 2005. United States Department of Agriculture FHTET 2005-01. Asheville, NC. 384 pp.

Degraaf, R.M., M. Yamasaki, W.B. Leak, and J.W. Lanier. 1992. New England wildlife: Management of forested habitats. General Technical Report. NE-144. US Department of Agriculture Forest Service, Northeastern Forest Experiment Station. Radnor, PA. 271 pp.

Elkinton, J.S., J.A. Lombardo, A.D. Roehrig, T.J. McAvoy, A. Mayfield, and M. Whitmore. 2016. Induction of cold hardiness in an invasive herbivore: The case of Hemlock Woolly Adelgid (Hemiptera:Adelgidae). Environmental Entomology 46:118–124. Available online at doi.org/10.1093/ee/nvw143.

Elliot, K.J., and J.M. Vose. 2011. The contribution of the Coweeta Hydrologic Laboratory to developing an understanding of long-term (1934–2008) changes in managed and unmanaged forests. Forest and Ecology Management 261:900–910.

Ellison, A.M. 2014. Experiments are revealing a foundation species: A case study of Eastern Hemlock (*Tsuga canadensis*). Advances in Ecology 2014:456209. Available online at doi:10.1155/2014/456904.

Fidgen, J.G., J.J. Turgeon, and J.D. Allison. 2014. Alien, invasive Hemlock Woolly Adelgid found in Ontario. Canadian Forest Service Great Lakes Forestry Centre. Frontline Technical Note No. 114.

Fischetti, M. 2014. What is this polar vortex that is freezing the US? Available online at http://blogs.scientificamerican.com/observations/what-is-this-polar-vortex-that-is-freezing-the-u-s/. Accessed 9 January 2014.

Godman, R.M., and K. Lancaster. 1990. *Tsuga canadensis* (L.) Carriere. Pp. 605–612, *In* R.M. Burns and B. Honkala (Eds.). Silvics of North America, Vol. 1. Conifers. Agriculture Handbook 654. US Department of Agriculture Forest Service, Washington, DC. 675 pp.

Goldstein, M. 2009. Dr. Mel's Connecticut Climate Book. Wesleyan University Press, Middletown, CT. 229 pp.

Greenbank, D.O. 1970. Climate and ecology of the Balsam Woolly Aphid. Canadian Entomologist 102:546–578.

Guttman, N.B., and R.G. Quayle. 1996. A historical perspective of US climate divisions. Bulletin of the American Meteorological Society 77:293–303.

Havill, N.P., M.E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006. Mitochondrial DNA from Hemlock Woolly Adelgid (Hemiptera:Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. Annals of the Entomological Society of America 99:195–203.

Hintze, J.L. 1998. User's Guide: NCSS 2000 Statistical System for Windows. Number Cruncher Statistical Systems Publication, Kaysville, UT. 91 pp.

Kessell, S.R. 1979. Adaptation and dimorphism in Eastern Hemlock, *Tsuga canadensis* (L.) Carriere. American Naturalist 113:333–349.

Lovett, G.M., C.D. Canham, M.A. Arthur, K.C. Weathers, and R.D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56:395–405.

Maier, C.T., C.R. Lemmon, R.M. Weseloh, and T.G. Andreadis. 1993. Spring Hemlock Looper returns to attack hemlock forests in Connecticut. Frontiers of Plant Science 45(2):6–8.

Maine Forest Service. 2016. Hemlock Woolly Adelgid overview. Available online at http://www.maine.gov/dacf/mfs/forest_health/insects/hemlock_woolly_adelgid_overview.htm#hwa2007. Accessed on 13 February 2016.

McClure, M.S. 1987. Biology and control of Hemlock Woolly Adelgid. Bulletin 851. Connecticut Agricultural Experiment Station, New Haven, CT. 8 pp. Available online at http://www.ct.gov/caes/lib/caes/documents/publications/bulletins/b851.pdf. Accessed 21 January 2016.

McClure, M.S. 1989. Evidence of a polymorphic life cycle in the Hemlock Woolly Adelgid, *Adelges tsugae* (Homoptera:Adelgidae). Annals of the Entomological Society of America 92:50–54.

McClure, M.S. 1990. Role of wind, birds, deer, and humans in the dispersal of Hemlock Woolly Adelgid (Homoptera:Adelgidae). Environmental Entomology 19:36–43.

McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera:Adelgidae) on *Tsuga canadensis*. Environmental Entomology 20:258–264.

McClure, M.S. 1996. Biology of *Adelges tsugae* and its potential for spread in the northeastern United States. Pp. 16–25, *In* S. Salom, T.C. Tigner, and R.C. Reardon (Eds.). Proceedings of the 1st Hemlock Woolly Adelgid Review), US Department of Agriculture Forest Service Forest Health Technology Enterprise Team, Morgantown, WV. 129 pp.

McClure, M.S., and C.A.S-J. Cheah. 2002. Important mortality factors in the life cycle of the Hemlock Woolly Adelgid, *Adelges tsugae* Annand (Homoptera:Adelgidae) in the Northeastern United States. Pp.13–22, *In* Proceedings of the Hemlock Woolly Adelgid Symposium, 5–7 February 2002. East Brunswick, NJ. 403 pp.

McClure, M.S., and M.B. Fergione. 1977. *Fiorinia externa* Ferris and *Tsugapidiotus tsugae* (Marlatt) (Homoptera:Diaspididae): Distribution, abundance, and new hosts of two destructive scale insects of Eastern Hemlock in Connecticut. Environmental Entomology 6:807–811.

Miller, D.H. 1964. Interception processes during snowstorms. US Forest Service Research Paper PSW-18. SW Pacific Forest and Range Experiment Station, Berkeley, CA. 24 pp.

Morin, R.S., S.N. Oswalt, R.T. Trotter III, and A. M. Liebhold. 2011. Status of hemlock in the Eastern United States. Forest Inventory Factsheet US Department of Agriculture Forest Service e-Science Update SRS-038. Available online at http://www.srs.fs.usda.gov/pubs/38492. Accessed 25 July 2016.

National Oceanic and Atmospheric Administration (NOAA). 2015a. US Climatic Divisions. Available online at http://www.ncdc.noaa.gov/monitoring-references/maps/us-climate-divisions.php. Accessed 8 December 2015.

NOAA. 2015b. National Centers for Environmental Information: Climate at a glance. Available online at: http://www.ncdc.noaa.gov/cag/. Accessed 11 December 2015.

NOAA. 2015c. National Centers for Environmental Information, (NCEI): Climatological rankings. Available online at http://www.ncdc.noaa.gov/temp-and-precip/climatological-rankings/. Accessed 23 November 23.

NOAA. 2015d. Climatological data publications. Available online at http://www.ncdc.noaa.gov/IPS/cd/cd.html. Accessed 1 December 2015.

NOAA. 2015e. What is the polar vortex? Available online at http://www.nws.noaa.gov/os/winter/polar_vortex.shtml. Accessed 6 December 2015.

National Weather Service (NWS). 2016. Winter weather basics: Cold air outbreaks. Available online at http://www.weather.gov/media/apx/spotter/Basics_Winter_Wx.pdf. Accessed 3 February 2016.

Northeast Regional Climate Center (NRCC). 2016. Summary tables. Available online at http://www.nrcc.cornell.edu/regional/tables/tables.html. Accessed 13 January and 19 April 2016

Orwig, D.A., D.R. Foster, and D.L. Mausel. 2002. Landscape patterns of decline in New England due to the introduced Hemlock Woolly Adelgid. Journal of Biogeography 29:1475–1487.

Overland, J.E., J.M. Adams, and N.A. Bond 1997. Regional variation of winter temperatures in the arctic. Journal of Climate 10:821–837.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the Hemlock Woolly Adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Parker, B.L., M. Skinner, S. Gouli, T. Ashikaga, and B.T. Teillon. 1998. Survival of Hemlock Woolly Adelgid at low temperatures. Forest Science 44:414–420.

Parker, B.L., M. Skinner, S. Gouli, T. Ashikaga, and B.T. Teillon. 1999. Low lethal temperature for Hemlock Woolly Adelgid. Environmental Entomology 28:1085–1091.

Perschel, R.T., A.M. Evans, and M.J. Summers. 2007. Climate change, carbon, and the forests of the Northeast. Available online at www.forestguild.org/publications/2007/ForestGuild_climate_carbon_forests.pdf. Accessed 20 November2016.

Quimby, J. 1996. Value and importance of hemlock ecosystems in the eastern United States. Pp 1–8, *In* S. Salom, T. Tigner, and R.C. Reardon Eds.).Proceedings of the 1st Hemlock Woolly Adelgid Review. US Department of Agriculture Forest Service Forest Health Technology Enterprise Team, Morgantown, WV.129 pp.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reay, R.S. 2000. Management of Eastern Hemlock for deer wintering areas. Pp. 144–147, *In* K.A. McManus, K.S., Shields, and D.R. Souto (Eds.). Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. General Technical Report NE-267. US Department of Agriculture Forest Service, Northeastern Research Station, Newton Square, PA. 237 pp.

Russo, N.J., C.A. S-J. Cheah, and M.W. Tingley. 2015**.** Experimental evidence for branch-to-bird transfer as a mechanism of avian dispersal of the Hemlock Woolly Adelgid (Hempitera:Adelgidae). Environmental Entomology 45:1107–1114.

Sasaji, H., and M.S. McClure. 1997. Description and distribution of *Pseudoscymnus tsugae* sp. nov. (Coleoptera: Coccinellidae), an important predator of Hemlock Woolly Adelgid in Japan. Annals of the Entomological Society of America 90:563–568.

Shields, K., and C. Cheah. 2005. Winter mortality in *Adelges tsugae* populations in 2003 and 2004. Pp. 354–356, *In* R. Reardon and B. Onken (Eds.). Proceedings of the 3rd Symposium on Hemlock Woolly Adelgid in the Eastern United States, Asheville, NC. US Department of Agriculture Forest Service Forest Health Technology Enterprise Team, Morgantown, WV. 384 pp.

Skinner, M., B.L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of Hemlock Woolly Adelgid (Homoptera:Adelgidae) to low temperatures. Environmental Entomology 32:523–528.

Snyder, C.D., J.A. Young, D.P. Lemarie, and D.R. Smith. 2002. Influence of Eastern Hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. Canadian Journal of Fisheries and Aquatic Sciences 59:262–275.

Souto, D., T. Luther, and B. Chianese. 1996. Past and current status of HWA in Eastern and Carolina Hemlock stands. Pp. 9-15, *In* S. Salom, T.C. Tigner, R.C. Reardon (Eds.). Proceedings of the 1st Hemlock Woolly Adelgid Review. US Department of Agriculture Forest Service Forest Health Technology Enterprise Team, Morgantown, WV. 129 pp.

Stephens, G.R. 1984. Heavily defoliated White Pine has lower mortality than hemlock. Frontiers of Plant Science 37(1):4–5. Available online at http://www.ct.gov/caes/lib/caes/documents/publications/frontiers/fps_37.1.pdf. Accessed 22 January 22 2016.

Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002. Avian response to removal of a forest dominant: Consequences of Hemlock Woolly Adelgid infestations. Journal of Biogeography 29:1505–1516.

Trotter, R.T. III, and K.S. Shields. 2009. Variation in winter survival of the invasive Hemlock Woolly Adelgid (Hemiptera:Adelgidae) across the eastern United States. Environmental Entomology 38:577–587.

United States Department of Agriculture, Agriculture Research Service. 2012. Plant hardiness zone map. Available online at http://planthardiness.ars.usda.gov/PHZMWeb/Default.aspx. Accessed 30 December 2016.

United States Department of Agriculture Forest Service (USDAFS). 2016a. Forest health highlights by state. Available online at http://www.fs.fed.us/foresthealth/fhm/fhh/neregion.shtml. Accessed 2 February 2016.

USDAFS. 2016b. Forest health highlights by state. Available online at http://www.fs.fed.us/foresthealth/fhm/fhh/ncregion.shtml. Accessed 2 February 2016.

Walsh, J.E., S.P. Adams, D.H. Portis, and W.L. Chapman. 2001. Extreme-cold outbreaks in the United States and Europe, 1948–99. Journal of Climate 14:2642–2658.

Ward, N.L., and G.J. Masters. 2007. Linking climate change and species invasion: An illustration using insect herbivores. Global Change Biology 13:1605–1615.

Yamasaki, M., R. DeGraaf, and J.W. Lanier. 2000. Wildlife-habitat associations in Eastern Hemlock: Birds, smaller mammals, and forest carnivores. Pp 135–143, *In* K.A. McManus, K.S., Shields, and D.R. Souto (Eds.). Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America. General Technical Report NE-267. US Department of Agriculture Forest Service, Northeastern Research Station, Newton, PA. 237 pp.

Zhang, J., W. Tian, M.P. Chipperfield, F. Xie,and J. Huang. 2016. Persistent shift of the Arctic polar vortex towards the Eurasian continent in recent decades. Nature Climate Change 6:1094–1099.