Predicting the seasonal development of the yellowheaded spruce sawfly (Hymenoptera: Tenthredinidae) in eastern Canada

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Abstract—Degree-day phenology models for the yellowheaded spruce sawfly, *Pikonema alaskensis* (Rohwer), were developed from data sets collected in infested plantations of black spruce, *Picea mariana* (Mill.), and white spruce, *P. glauca* (Moench) Voss, in New Brunswick and Quebec, Canada, between 1995 and 1999. The models describe the relationships between degree-day accumulation (above –1 °C, from 1 April) and cumulative adult emergence, capture in pheromone traps, the dates of appearance of first adult, egg, and larva, and the relative frequency of successive larval stages. The models predict adult emergence with a precision of ±2 days and male catch in pheromone traps with a precision of ±1.6 days. The first adult, first egg, and first larva occurred after 527 ± 42, 660 ± 52, and 725 ± 18 degree-days above –1 °C, respectively, and the dates of these events are predicted within ±1.8 days. The dates of 50% occurrence of the successive instars are predicted within 4.5 days of observed dates, and the date of peak 2nd instar is predicted within ±3.6 days.

Résumé—Des modèles phénologiques de degrés-jours pour la tenthrède à tête jaune de l'épinette, *Pikonema alaskensis* (Rohwer), ont été ajustés à partir de données récoltées dans des plantations infestées d'épinette noire, *Picea mariana* (Mill.), et blanche, *P. glauca* (Moench) Voss, au Nouveau-Brunswick et au Québec (Canada) entre 1995 et 1999. Les modèles décrivent la relation entre l'accumulation de degrés-jours au dessus de –1 °C à partir du 1er avril, et l'émergence cumulative des adultes, la capture des mâles dans des pièges à phéromones, l'apparition du premier adulte, œuf ou larve, et la fréquence relative des stades successifs de développement larvaire. Les modèles permettent de prédire l'émergence des adultes avec une précision de ±2 jours, et la capture des mâles dans les pièges à phéromones avec une précision de ±1.6 jours. L'apparition du premier adulte, œuf et larve s'est produite après 527 ± 42, 660 ± 52 et 725 ± 18 degrés-jours au dessus de –1 °C, respectivement, et les dates de ces événements sont prédites à ±1.8 près. Les dates auxquelles 50 % des individus atteignent chaque stade larvaire successif sont prédites à ±4.5 jours des dates observées, et la date du pic du 2e stade larvaire est prédite avec une précision de ±3.6 jours.

Received 28 June 2006. Accepted 20 December 2006.

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Introduction

The yellowheaded spruce sawfly (YHSS), *Pikonema alaskensis* (Rohwer) (Hymenoptera: Tenthredinidae), is a pest of young, open-grown spruces (*Picea* spp.) across northern North America (Ross 1938; Nash 1939; Shenefelt and Benjamin 1955; Wilson 1962). Although it has been reported to occur in all species of spruce native to North America (Houseweart and Kulman 1976*a*), it is particularly harmful in plantations of black spruce, *P. mariana* (Mill.), white spruce, *P. glauca* (Moench) Voss, and Norway spruce, *P. abies* (L.) Karst., a widely planted exotic species. A bibliography of knowledge available on this insect was published by Katovich *et al.* (1995).

The YHSS is univoltine and overwinters as a diapausing prepupal larva (Eller *et al.* 1989) in a silk cocoon in the top 2 cm of soil (Schoenfelder *et al.* 1978), either immediately under or near the crown of host trees (Rau *et al.* 1979). Pupation occurs in late winter to early spring (Bartelt *et al.* 1981). Adult emergence in the spring is highly synchronous within a location (Bartelt *et al.* 1982), but its timing varies considerably across the insect's geographical range (Mitchener 1931; Morton 1948; Morse *et al.* 1984). Like many other sawflies, female YHSS need a pre-oviposition period of a few days before their ova are mature (Houseweart and Kulman 1976*b*). Eggs are laid in slits at the base of needles on the growing shoots of host trees. Oviposition preference is strongly linked to the development of the shoots as expressed by the proportion of needles covered by the bud cap or scales (Pointing 1957; Houseweart and Kulman 1976*a*). Females tend to lay all their eggs at once and prefer to lay them on host trees growing in full sunlight (Morse and Kulman 1984). Eggs hatch in 4–12 days, depending on temperature and exposure to sunlight (Pointing 1957). There are five instars in male larvae, and two thirds of females undergo a 6th instar (VanDerwerker and Kulman 1974). Larvae drop to the ground at the end of the feeding period, spin a cocoon, and enter diapause. The timing and duration of the various life stages vary drastically between years and between locations.

Host preference varies geographically, and Pointing (1957) suggested that synchrony between bud burst and emergence of YHSS females in the spring determines preference to some extent. The insect shows a marked preference for young, open-grown trees in sunny locations (de Groot 1995). In addition, stands growing on dry sites or on south-facing slopes (Bradley 1945; Daviault 1948; Morse and Kulman 1986) are more severely damaged by the insect. Life tables indicate that most larval mortality occurs in instars 5 and 6 and is mostly due to parasitism (Houseweart and Kulman 1976*a*).

Management of YHSS populations implies population monitoring by ground or aerial surveys for actively feeding larvae or defoliation (Morse and Kulman 1984) or by pheromone trapping combined with information on parasitism rates (Morse and Kulman 1985, 1986). When faced with population increases in the 1990s, the New Brunswick Department of Natural Resources (NBDNR) carried out sampling of all YHSS life stages. While the development of resistant varieties of black spruce to this insect is possible (le Cocq *et al.* 2005), pesticides remain the most immediate pest control approach. The Minnesota Department of Natural Resources (1992) recommends early pesticide applications (as soon as larvae are present). But aerial control trials conducted by the NBDNR in 1996 were aimed at the 2nd instar.

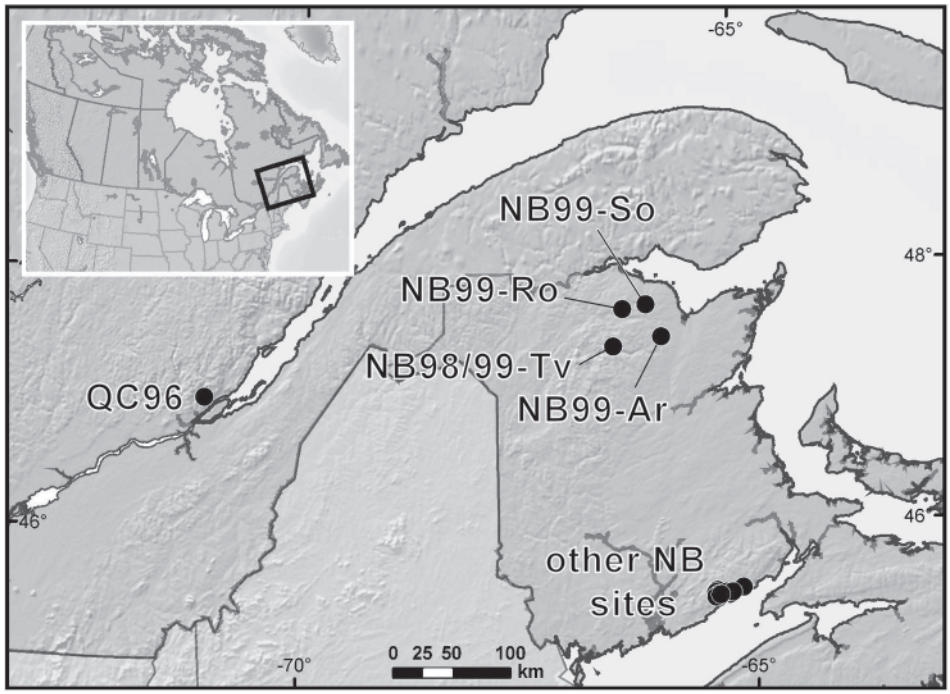
Population surveys and control operations against YHSS would greatly benefit from the availability of accurate phenology models. Morse *et al.* (1984) developed a degree-day model to predict adult emergence from the soil as a function of air temperature. However, their model required the use of a soil temperature sub-model, itself requiring as input the date of total snowmelt as well as initial soil temperature profiles. Other major aspects of this soil temperature sub-model are empirical and difficult to generalize. Katovich *et al.* (1995) noted that "More research to link adult emergence with conventional degree-day accumulations could provide a useful tool for prediction of adult activity and oviposition".

In this paper, we report on the development and validation of empirical degree-day models for first adult, egg, and larva, adult emergence and catch in pheromone traps, and relative frequency of the six feeding larval stages of the YHSS based on observations made in New Brunswick and Quebec.

Materials and methods

The data used in this study were obtained from 13 black spruce plantations in New

Fig. 1. Map of southeastern Quebec and New Brunswick showing the locations of study sites.



Brunswick (NB) between 1995 and 1999 and from a single white spruce plantation in Quebec in 1996 (Fig. 1; Table 1).

In most areas where YHSS is found, snow covers the ground until at least late March, so it is unlikely that much adult YHSS development can take place before early April. Daily minimum and maximum air temperatures were recorded on site, starting on 1 April, in many of the plots and years (Table 1). Estimates of daily minimum and maximum temperatures at sampling sites where on-site data were not available were obtained by applying the vertical thermal gradients of Gignac (2000) for NB to data recorded at the nearest Environment Canada or on-site weather station. On-site measurements for site QC96 started on 5 May 1996 and were completed back to 1 April from Environment Canada weather records from nearby Château Richer (46°58′N, –71°02′E, 15 m) using thermal gradients estimated for the area by Gignac (2000).

Degree-day summation was calculated by two methods: Allen's (1976) modified sine method and the simpler daily mean method:

$$d_t = \sum_{t_0}^{t} \max\left[\frac{T_{\min}(t) + T_{\max}(t)}{2} - \theta,\ 0\right] \qquad [1]$$

where $T_{\min}(t)$ and $T_{\max}(t)$ are daily minimum and maximum temperature on day t (t_0 = 1 April) and θ is the lower threshold temperature for summation.

Adult emergence and catch in pheromone traps

Emergence of adult sawflies in the spring was monitored with emergence cages in five NB plantations in 1995–1996 and in the Quebec site in 1996 (Table 1). The emergence cages were made of fine-mesh window screen (0.7 m × 0.7 m) topped with collecting jars (Rau 1976). Five to 15 traps were set on the soil surface under the crown of host trees in NB, and 30 were set in Quebec. To monitor adult male sawfly activity, Delta sticky traps or Multi-Pher® traps (Jobin and Coulombe 1988) baited with (*Z*)-10-nonadecanol and (*Z*)-5-tetradecanol (Bartelt *et al.* 1982) obtained from the New Brunswick Research and Productivity Council (921 College Hill Road, Fredericton, New Brunswick, Canada) were deployed. Five to 15 traps were set in each of five NB plantations in 1995 and 1996, and 24 traps were set in the Quebec site in 1996. Traps were inspected every 2–3 days throughout the flight period.

Table 1. Plantations sampled in this study and types of observations made in each.

			First					Traps	
Site name	Site coordinates	On-site weather	A	E	L	Larval stages	Peak L2	Em	Ph
NB95A	45°32′ –65°24′ 328 m							Y	
NB96A	45°32′ –65°24′ 328 m		Y	Y		Y	Y	Y	Y
NB95B	45°31′ –65°25′ 328 m	Y	Y		Y	Y	Y	Y	
NB96B	45°31′ –65°25′ 328 m	Y	Y	Y	Y		Y	Y	Y
NB95D	45°30′ –65°23′ 312 m							Y	
NB96D	45°30′ –65°23′ 312 m		Y	Y			Y	Y	Y
NB97D	45°30′ –65°23′ 312 m	Y	Y	Y	Y	Y	Y		
NB98D	45°30′ –65°23′ 312 m	Y	Y	Y		Y	Y		
NB95E	45°30′ –65°16′ 204 m							Y	
NB96E	45°31′ –65°18′ 219 m		Y	Y	Y		Y	Y	Y
NB95F	45°33′ –65°07′ 267 m							Y	
NB96F	45°31′ –65°14′ 274 m							Y	Y
NB96-2	45°29′ –65°25′ 317 m		Y	Y			Y		
NB96-4	45°30′ –65°22′ 183 m		Y	Y	Y		Y		
NB97-4	45°30′ –65°22′ 183 m	Y	Y	Y	Y	Y	Y		
NB98-So	47°45′ –66°05′ 296 m	Y	Y			Y	Y		
NB98-Tv	47°26′ –66°28′ 635 m	Y	Y			Y	Y		
NB99-Tv	47°26′ –66°28′ 635 m	Y	Y		Y	Y	Y		
NB99-Ro	47°43′ –66°21′ 450 m	Y			Y	Y	Y		
NB99-Ar	47°30′ –65°55′ 220 m	Y				Y	Y		
QC96	47°02′ –71°05′ 655 m	Y				Y	Y	Y	Y

Note: Site QC96 was in a white spruce plantation; all other sites were in black spruce plantations. Shaded cells indicate data sets used in parameter estimation. Y, observation made at site. A, adults; E, eggs; L, larvae. L2, second instar. Em, emergence; Ph, pheromone.

Larval development

The dates of appearance of the first adults, eggs, and larvae of YHSS were determined from emergence cages (first adult) when available and by visual examination of host tree foliage in many plantations in NB from 1995 to 1999 (Table 1). Observations in 1995–1997 were made daily except on weekends. In 1998 and 1999, observations were made twice weekly.

Host tree foliage was examined for YHSS larvae at intervals of 2–7 days from the adult stage to the end of the larval development period in several of the black spruce plantations in NB from 1995 to 1999 and in the white spruce plantation of Quebec in 1996 (Table 1). Branches from the upper third of the crown were examined from 6 (NB) or 10 (Quebec) randomly selected hosts on each sample date. YHSS larvae found on the foliage were placed in 70% alcohol. Instars were determined on the basis of head capsule width (Houseweart and Kulman 1976*a*). The number of larvae collected per sample date averaged 40 (range 10–87) in NB and 127 (range 59–225) in Quebec. In NB in 1996, pesticide application trials aimed at 2nd-instar larvae were carried out in four plantations (NB96B, NB96D, NB96E, and NB96F) where larval development was monitored only prior to treatment, at the peak of the 2nd instar. One nearby plantation (NB96A), used as an untreated control, was sampled throughout the summer (Table 1).

Models

A logistic regression model was used to describe the relationship between the cumulative proportion of adults caught in emergence cages (e_t) and degree-days accumulated to time t (d_t):

$$\hat{e}_t = h^{-1}(a_e + b_e d_t) \quad [2]$$

where a_e and b_e are parameters to be estimated by maximum likelihood and $h()$ is the logit link function

$$h(e_t) = \ln\left(\frac{e_t}{1 - e_t}\right) \quad [3]$$

so that

$$h^{-1}(a_e + b_e d_t) = \frac{\exp(a_e + b_e d_t)}{1 + \exp(a_e + b_e d_t)} \qquad [4]$$

From the cumulative adult emergence trend ($\hat{e}_t$), the accumulation of males in pheromone traps was simulated as follows. Assuming a constant adult longevity of δ days, the proportion of the total adult population that has emerged and is alive at time t is the cumulative proportion emerged at time t minus the cumulative proportion emerged at time $t - \delta$. Further, assuming that the probability of capture in pheromone traps is constant during an adult's life, the daily proportion of total capture is $(\hat{e}_t - \hat{e}_{t-\delta})/\delta$ and the cumulative proportion of total catch in pheromone traps can be simulated from simulated adult emergence using

$$\omega_t = \frac{1}{\delta}\sum_{t_0=t-\delta}^{t}(\hat{e}_t - \hat{e}_{t-\delta}) \qquad [5]$$

A second consequence of assuming that capture probability is constant is that, on average, individuals should be captured at midlife. This implies that the average difference (in days) between cumulative emergence and cumulative pheromone trap catch should be ½ δ. Thus, an estimate of δ can be obtained by doubling the difference in time between cumulative emergence and cumulative capture in pheromone traps. To estimate δ, we doubled the average differences in times at which these trends reached 10%, 25%, 50%, 75%, and 90% (by linear interpolation between sample dates) from the sites where both pheromone trap and emergence cage data were available.

The continuation-ratio model of Candy (1991, 2003) was used to describe the relationship between accumulated degree-days and the relative frequency of the six larval stages in the sampled populations. The probability of an individual being in instar j at time t was calculated as

$$p_{tj} = n_{tj} \Big/ \sum_{k=1}^{6} n_{tk} \qquad [6]$$

where n_{tj} is the number of larvae in instar j in the sample taken at time t. The conditional probability of an individual being in instar j, relative to the number of individuals in instar j or later, is given by

$$m_{tj} = n_{tj} \Big/ \sum_{k=j}^{6} n_{tk} \qquad [7]$$

The continuation-ratio model (using the notation of Candy 2003) expresses the relationship between degree-days d_t and these conditional probabilities:

$$\hat{m}_{tj} = h^{-1}(a_j + b_j d_t) \qquad [8]$$

where $\hat{m}_{tj}$ is the expected value of m_{tj}, a_j and b_j are parameters, and $h^{-1}()$ is the inverse logit link function (eq. [4]). This basic model was modified slightly to accommodate the sexual dimorphism of YHSS in the number of instars, because only a proportion c of females enter into a 6th instar (VanDerwerker and Kulman 1974):

$$\hat{m}_{tj} = \begin{cases} h^{-1}(a_j + b_j d_t) & j = 1, 2, 3, 4 \\ (1 - c) + c\,h^{-1}(a_j + b_j d_t) & j = 5 \end{cases} \qquad [9]$$

Equation [9] was fitted by logistic regression (maximum likelihood) to the frequencies of instars 1 to 6 in samples (note that in this model, no parameters are needed for instar 6 for which conditional probabilities $m \equiv 1$). The relative frequencies of the six larval stages in the simulated population can be calculated with

$$\hat{p}_{tj} = \begin{cases} h^{-1}(a_j + b_j d_t) & j = 1 \\ (1 - \sum_{k=1}^{j-1} \hat{p}_{tk})\,h^{-1}(a_j + b_j d_t) & j = 2, 3, 4 \\ (1 - c) + c\left(1 - \sum_{k=1}^{j-1} \hat{p}_{tk}\right)h^{-1}(a_j + b_j d_t) & j = 5 \\ \left(1 - \sum_{k=1}^{j-1} \hat{p}_{tk}\right) & j = 6 \end{cases} \qquad [10]$$

A reduced model with $b_j = b$, equivalent to the common-variance model of Candy (1991), was also fitted to the data. This reduced the number of parameters from 11 to 7. The improvement in fit provided by the more complex but flexible eq. [9] relative to the simpler common-

variance version was tested by the likelihood ratio test, where 2 × difference in log likelihoods is distributed as a χ^2_4 statistic.

The progression of population age structure was also summarized by calculating observed and simulated average instar (A_t, $\hat{A}_t$):

$$A_t = \sum_{j=1}^{6} (jp_{tj}) \text{ and } \hat{A}_t = \sum_{j=1}^{6} (j\hat{p}_{tj}) \qquad [11]$$

Parameter estimation and model validation

The best lower temperature threshold (θ) for degree-day summation was determined by fitting eq. [9] to life-stage frequency data, with accumulated degree-days calculated using values of θ ranging from –5 to 5 °C in 1 °C increments, comparing the two methods of degree-day calculation described earlier. The best combination of degree-day summation method and threshold temperature was selected on the basis of the logistic regression log likelihood. The optimal summation method and threshold found in this analysis were used in all other degree-day models.

Throughout, a random subset of about half of the data sets available was used for parameter estimation, and the other half was used for model validation. The adult emergence model (eq. [2]) was fitted to 5 of the 11 data sets available (Table 1). Observed emergence and pheromone trap catch information from the 6 available data sets were used to calculate the value of δ in eq. [5] to obtain simulated pheromone trap catch trends from simulated adult emergence. Model outputs were compared with observed 10%, 50%, and 90% emergence and pheromone trap catch (estimated by linear interpolation between sample dates) by analysis of covariance (general linear models, or GLM), using simulated dates as covariate and data set as factor. Common regression parameter estimates were tested for bias (H_0: intercept = 0, covariate slope = 1) with *t* tests. One-way analysis of variance (ANOVA) was used to test differences in model precision (absolute differences between observed and simulated dates) at these three points of the emergence and flight periods.

The number of degree-days accumulated until the observed appearance of first adult, first egg, and first larva was calculated for 7 of the 14 data sets that contained such observations (Table 1). The simulated dates of appearance of first adult, first egg, and first larva corresponding to these degree-day accumulations in the remaining 7 data sets were compared with the observed dates by GLM, using simulated date as covariate and data set as factor. Common regression parameter estimates were tested for bias (H_0: intercept = 0, covariate slope = 1) with *t* tests. Absolute deviations between simulated and observed dates of appearance of first adult, first egg, and first larva were tested by ANOVA to detect stage-specific differences in model precision.

Parameter estimates for larval development were obtained by fitting eq. [9] to the instar frequencies from 5 of the 11 available data sets (Table 1). The remaining 6 data sets were used to test the precision and accuracy of the model. The observed and simulated dates at which the cumulative frequency of instars j = 2 to 6 reached 50% (estimated by linear interpolation between sample dates) were calculated with

$$P_{tj} = \sum_{k=j}^{6} p_{tk} \text{ and } \hat{P}_{tj} = \sum_{k=j}^{6} \hat{p}_{tk} \qquad [12]$$

where $\hat{p}$ values were obtained from eq. [10]. These cumulative proportions can be interpreted as the proportion of the larval population that is in instar j or later at time t. Observed and simulated dates of 50% cumulative frequencies of instars 2 to 6 were compared by GLM, using simulated dates as covariate and data set as factor. Common regression parameters were tested for bias (H_0: intercept = 0, slope = 1) with *t* tests. Absolute deviations between simulated and observed dates of 50% cumulative frequencies of instars 2 to 6 were compared by ANOVA to detect instar-specific variation in model precision.

Because of the particular importance of the 2nd instar as a target for pesticide applications, the observed and simulated dates at which average instar (A_t, $\hat{A}_t$) reached 2.0 were determined and compared by regression analysis, using all available data sets. Parameter estimates were tested for bias (H_0: intercept = 0, slope = 1) with *t* tests, and absolute deviations were calculated to estimate model precision.

Results

The highest likelihood obtained by fitting eq. [9] to the conditional instar frequencies from the five NB data sets used in parameter estimation was obtained with a lower threshold temperature of θ = –1 °C (Fig. 2). There was very little difference between the daily mean method and Allen's (1976) modified sine

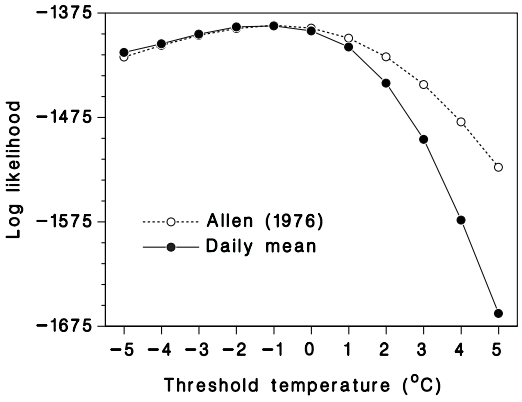
summation method, except at $\theta \geq 2$ °C. Therefore, the simpler method (eq. [1]) and a threshold temperature of –1 °C were used in all further model fitting.

Adult emergence and catch in pheromone traps

Equation [2] fitted well ($R^2 = 0.865$) the progression of adult emergence recorded in the five NB data sets used to estimate parameters (Table 2), with predictions falling within 2 days of observations (left column, Fig. 3). The fit was satisfactory when model output was compared with emergence in the remaining six data sets, except in QC96 (right column, Fig. 3). There was a significant correlation between observed and simulated dates of 10%, 50%, and 90% emergence ($F_{1,11} = 256.9$, $P < 0.001$), and significant site-related differences in model accuracy existed ($F_{5,11} = 25.6$, $P < 0.001$) owing to observations in the QC96 data set that were 6.5 ± 1.3 days earlier than model output (Fig. 4*a*). Overall, there was no significant bias in model output (common intercept = –1.9 ± 10.6, $P = 0.860$; common slope = 1.01 ± 0.08, $P = 0.937$). The average absolute deviation between observed and simulated emergence dates was 2.06 ± 2.04 days ($n = 18$), and no significant differences in model precision were found between 10%, 50%, and 90% cumulative emergence (ANOVA: $F_{2,15} = 0.02$, $P = 0.98$).

Cumulative pheromone trap catches in the six data sets available for analysis occurred 4.1 ± 2.2 days (SD) later than adult emergence, yielding an estimate of adult longevity (δ) of 8.2 days. The male flight season simulated by the model was close to observations in the three validation data sets where pheromone trap catch was monitored, including the QC96 data set (right column, Fig. 3). Observed and simulated dates of 10%, 50%, and 90% cumulative catch were highly correlated ($F_{1,5} = 81.5$, $P < 0.001$), and there were no significant differences in model accuracy between validation data sets ($F_{2,5} = 2.37$, $P = 0.189$; Fig. 4*b*). There was no significant bias in model output (common intercept = –26.2 ± 21.9, $P = 0.286$; common slope = 1.15 ± 0.13, $P = 0.302$). On average, simulated and observed dates of catch differed by only 1.6 ± 1.3 days, and no significant differences in model precision were found between 10%, 50%, and 90% cumulative emergence (ANOVA: $F_{2,6} = 0.11$, $P = 0.895$).

Fig. 2. Log maximum likelihood of eq. [10] fitted to conditional probabilities of being in instars 1–5 in yellowheaded spruce sawfly (*Pikonema alaskensis*) stage-frequency tables from 5 estimation data sets, using two methods of degree-day accumulation (●, daily mean; ○, Allen's (1976) method) over a range of lower threshold temperatures.



First adult, first egg, and first larva

Among the seven data sets used to estimate degree-day requirements, the first adult occurred after 526.9 ± 41.7 degree-days (SD, $n = 6$) above –1 °C, the first egg after 659.7 ± 51.5 degree-days ($n = 4$), and the first larva after 725.4 ± 18.4 degree-days ($n = 4$), on average. Among the seven validation data sets, observed dates of these three events were highly correlated with simulated dates ($F_{1,8} = 89.5$, $P < 0.001$), and there were no differences in model accuracy between data sets ($F_{6,8} = 2.15$, $P = 0.156$). However, there was a slight but significant bias in simulated dates (common intercept = 38.2 ± 13.4, $P = 0.022$; common slope = 0.77 ± 0.08, $P = 0.022$). The model predicted first adult appearance 1.0 ± 2.3 days (SD, $n = 7$) earlier than observed. First egg and first larva appearance were predicted 0.3 ± 2.3 days ($n = 5$) and 1.1 ± 2.2 days later than observed, differences that were smaller than the observation interval (Fig. 4*c*). Absolute deviations between observed and predicted dates of appearance of first adult, first egg, and first larva averaged 1.8 ± 1.3 days, with no significant differences in precision between stages (ANOVA: $F_{2,13} = 0.29$, $P = 0.753$).

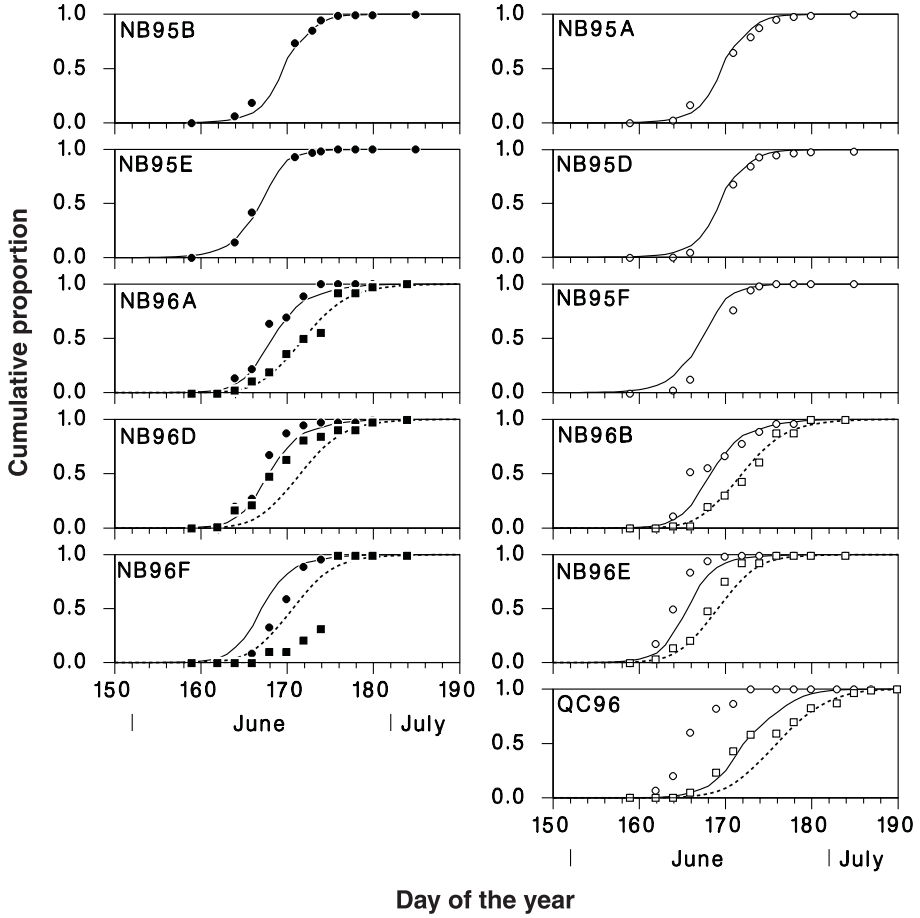
Larval development

Equation [10] fitted well the relative instar frequencies from the five data sets reserved for parameter estimation ($R^2 = 0.938$). The resulting

Table 2. Parameter estimates of the adult emergence model (eq. [2]) and the larval-stage frequency model (eq. [9]), ± their standard errors.

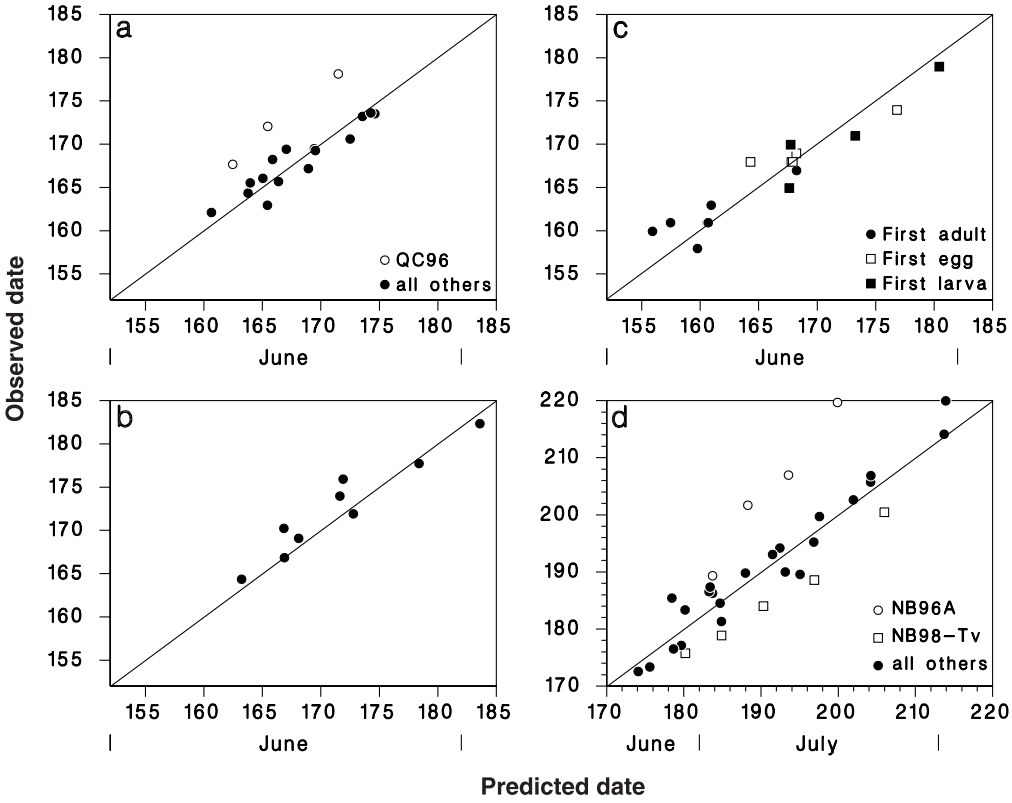
Stage	*a*	*b*	*c*
Adult emergence	–21.26±0.62	0.0320±0.0009	—
1st instar	30.69±2.12	–0.0353±0.0025	—
2nd instar	33.43±2.68	–0.0352±0.0028	—
3rd instar	30.40±2.21	–0.0292±0.0021	—
4th instar	25.16±1.84	–0.0216±0.0016	
5th instar	23.49±6.59	–0.0190±0.0055	0.603±0.042

Fig. 3. Comparison of observed and predicted cumulative yellowheaded spruce sawfly adult emergence and pheromone trap catch trends. Left column: five data sets used to estimate emergence model parameters (● and —, observed and simulated emergence; ■ and ····, observed and simulated catch in pheromone traps). Right column: six data sets kept for model validation (○ and —, observed and simulated emergence; □ and ····, observed and simulated catch in pheromone traps).



parameter values are given in Table 2. There was a clear increase in the variability of development times in YHSS populations from the 1st to the 6th instar, as reflected by the decreasing value of parameter b_j between instars 1 and 5 (Table 2; Fig. 5). The likelihood ratio test (χ^2_4 = 129.0, $P < 0.001$) indicated that the 11-parameter continuation-ratio model fitted significantly better than the simpler common-variance model with 7 parameters ($R^2 = 0.885$). The high variability and prolonged duration of the last two instars are due to the fact that individuals drop to

Fig. 4. Comparison of observed and predicted dates in the validation data sets for (*a*) 10%, 50%, and 90% emergence (○, QC96 data set; ●, all others); (*b*) 10%, 50%, and 90% catch in pheromone traps; (*c*) first adult (○), first egg (●), first larva (■); and (*d*) 50% cumulative frequencies of successive instars (○, NB96A data set; □, NB98-Tv data set; ●, all others). Line of equality: —.



the ground at the end of larval development, and thus the declining residual population on host foliage is composed mostly of slow-developing individuals, especially females. The value of parameter c (= 0.603 ± 0.042) corresponds well to the observation that two thirds of female YHSS larvae undergo a 6th instar (VanDerwerker and Kulman 1974).

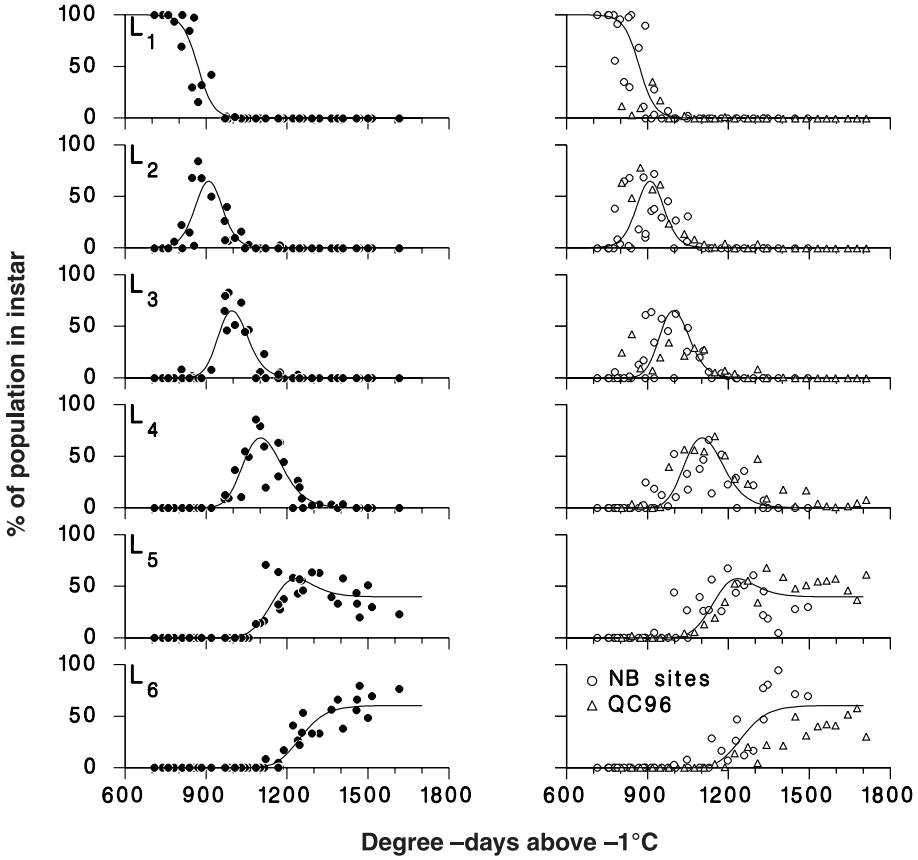
There was a significant correlation between observed and simulated dates of 50% cumulative frequencies of instars 2 to 6 among the six validation data sets ($F_{1,20}$ = 291.8, $P < 0.001$), and a significant effect of data set ($F_{10,20}$ = 13.1, $P < 0.001$). The intercept of the common regression line did not differ significantly from 0 (–10.3 ± 11.7, P = 0.392), and the slope did not differ significantly from 1 (1.065 ± 0.063, P = 0.313). Absolute deviations between observed and predicted dates did not vary significantly between instars ($F_{4,27}$ = 0.43, P = 0.785) and averaged 4.5 ± 4.2 days (SD). The differences in model accuracy between data sets were caused by two aberrant sets out of the 11 for which complete larval development data were available (Fig. 6). In data set NB96A, observed development was >10 days slower than predicted. In data set NB-98-Tv, it was >5 days faster than predicted (Fig. 4*d*).

The average observed date at which average instar reached 2.0 was 185.2 ± 7.8 (SD), whereas the average predicted date was 183.5 ± 5.2, a mere 1.7 day difference. The intercept of the observed–predicted date regression line (R^2 = 0.768) did not differ significantly from 0 (–56.9 ± 44.4, P = 0.232), and the slope did not differ significantly from 1 (1.32 ± 0.24, P = 0.219). The mean absolute deviation was 3.6 ± 2.3 days.

Discussion and conclusions

A sufficient amount of data from a number of years and locations allowed us to parameterize and validate degree-day models for several important points in the life cycle of YHSS in

Fig. 5. Observed and simulated relative frequencies of instars 1 to 6 of yellowheaded spruce sawfly as a function of accumulated degree-days above –1 °C. Left column: five data sets used in model parameter estimation (●, observed; —, simulated). Right column: validation data sets (○, △, observed; —, simulated).

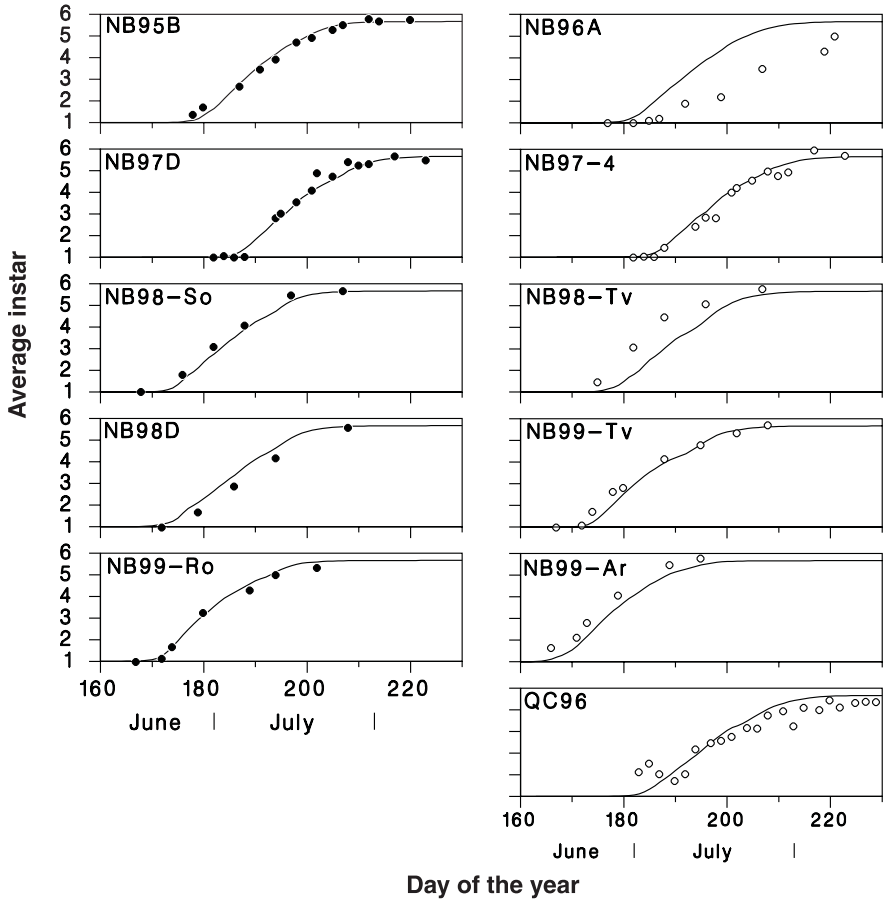


eastern Canada. We found that the best degree-day summation method was the simple daily mean method with a lower threshold temperature of –1 °C.

The first adult, first egg, and first larva were observed to occur at 526.9 ± 41.7, 659.7 ± 51.5, and 725.4 ± 18.4 degree-days above –1 °C, with a precision of ±1.8 days. The adult emergence model provided an accurate description of YHSS emergence from the soil in 10 of the 11 data sets in this study, with absolute deviations of ±2 days between observed and predicted dates. However, emergence recorded in 1996 in the Quebec site (data set QC96) occurred 6.5 days ahead of the model's prediction. The Quebec site had an 8% slope and southwest (228°) exposure and a very open stand structure. It is likely that daily maximum soil temperature in May and June was higher than air temperature on sunny days. This could explain why model predictions were late relative to observed emergence. Adaptation of YHSS to local host phenology is another possibility, as QC96 was a white spruce plantation, a host plant in which bud burst is earlier than in black spruce. However, the larval phenology data and model do not suggest that development was advanced in QC96 compared with that in other sites later in the season.

Our model of male YHSS capture in pheromone traps (eq. [5]) provided a good description of the temporal patterns of male YHSS flight, within ±1.6 days of observations among the three validation data sets. Pheromone traps measure male flight activity, rather than adult emergence, because they can catch males throughout their life span. Our data suggested an 8.2 day adult male life span. Pointing (1957) reported a 3–14 day adult YHSS longevity. Given that male YHSS emerge a few days earlier than females (Duda 1953), our result is probably an underestimate. While pheromone

Fig. 6. Comparison of observed and predicted trends in average instar of yellowheaded spruce sawfly in the five New Brunswick data sets used to estimate model parameters (left column: ●, observed; —, simulated) and the validation data sets (right column: ○, observed; —, simulated).



traps do not measure adult emergence *per se*, in practice it is simpler to base management decisions on pheromone trap catch rather than emergence cages because the former are far easier to use. In addition, should pheromones be used as a control tactic, the ability to predict the male flight season would become more critical. Thus, predictions of the timing of trap catch may be more useful than predictions of adult emergence.

The larval phenology model (eq. [10]) described well 9 of the 11 data sets in this study and can be considered well validated. Absolute deviations between predicted and observed dates of 50% cumulative frequency of successive instars averaged ±4.5 days. Yet a certain amount of variation in larval development remains unexplained, as illustrated by the NB96A and NB98-Tv data sets (Figs. 4*d*, 6). An air microclimate hypothesis cannot be invoked in the case of NV98-Tv, because model fit was excellent in the NB99-Tv data set from the same location (Fig. 6). A snow-cover or soil microclimate hypothesis is also untenable to explain the poor model fit in the NB96A data set, because the adult emergence and pheromone trap catch models fit quite well in both 1995 and 1996 at that location (Fig. 3). Therefore, the lack of fit in these two data sets suggests that factors other than temperature are involved in YHSS larval phenology. One attractive hypothesis is the possible influence of bud burst on hatch and subsequent development. It is known that previous YHSS defoliation delays bud break in black spruce (Pointing 1957) and affects the dynamics of the insect population in the following generation on both black and white spruce (Cook 1976; Johns *et al.* 2006). Past defoliation was particularly severe at NB96A. It is also possible that oviposition by

female YHSS is cued to the phenological development of host buds, which may explain part of the variation in resistance found among black spruce to YHSS (le Cocq *et al.* 2005). There is evidence of a strong correlation between bud burst, oviposition behaviour, egg hatch, and population dynamics in another spruce plantation defoliator, *Zeiraphera canadensis* Mutuura and Freeman (Lepidoptera: Tortricidae) (Turgeon 1986; Quiring 1994).

One key aspect of YHSS physiology that the model does not simulate at this point is control of the population's sex ratio through the proportion of females that undergo a 6th instar. While our data suggested that about 60% of females enter a 6th instar, this proportion seems quite variable, as evidenced by the wide scatter in 5th and 6th instar frequencies in late-summer samples (Fig. 5). It may be important to better understand this source of variation in late larval population age structure, as it is during this period that most of the mortality in YHSS populations occurs (Houseweart and Kulman 1976*a*). Most of this mortality has been assigned to the activity of several species of parasitoids (Bradley 1951; Rau 1976; Thompson and Kulman 1980; Houseweart *et al.* 1984), whose synchrony with susceptible host stages may be a critical factor determining their potential impact on populations (Régnière and Griffiths 1992). Although no YHSS-specific data are available, several species of the parasitoids that attack late-stage larvae may delay host development.

The second instar, once all eggs have hatched and the population is actively feeding, seems to be the most appropriate target for pesticide applications against YHSS. Our larval phenology model can be used to determine the proportion of the population that is in that sensitive stage. It can predict the date at which average instar reaches 2.0 (the peak of the 2nd instar) with a precision of ±3.6 days.

Acknowledgements

The data from New Brunswick were collected by a number of individuals supervised by Wilf Patterson and Greg Simpson. This research was funded in part by the New Brunswick Department of Natural Resources, Forest Protection Limited, the Ontario Ministry of Natural Resources, and the Société de protection des forêts contre les insectes et maladies (SOPFIM).

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