

Article

Modeling Climatic Influences on Three Parasitoids of Low-Density Spruce Budworm Populations. Part 2: *Meteorus trachynotus* (Hymenoptera: Braconidae)

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Abstract: This is the second article of a series of three where we develop temperature-driven models to describe the seasonal interactions between parasitoids and their hosts which we use to explore the impact of climate on their spatiotemporal biology. Here, we model the biology of *Meteorus trachynotus* (Hymenoptera: Braconidae) with an individual-based model of its daily interactions with two host species. This model predicts the performance of the parasitoid in response to temperature affecting its seasonal development and that of the two hosts. We compare model output with an extensive set of field observations from natural host populations. The predicted activity of the first adult parasitoid generation closely matches the seasonal pattern of attack on the spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) within the limitations of available data. The model predicts 1–4 full generations of *M. trachynotus* per year in eastern North America, with generations well synchronized with larvae of a known overwintering host, the obliquebanded leafroller *Choristoneura rosaceana*. The model predicts the observed density dependence of parasitism on spruce budworm. Predicted performance exhibits spatial variation caused by complex life-history interactions, especially synchrony with the overwintering host. This leads to a better performance in warm but not hot environments at middle latitudes and elevations. The model's predicted spatial patterns correspond closely to our field observations on the frequency of parasitism on spruce budworm. Under climate change, the model predicts that the performance of *M. trachynotus* populations will improve in the northern portion of its range.

Keywords: biodiversity; ecology; environment; forest; global change; insect; parasitoids; spruce budworm; obliquebanded leafroller; seasonal biology; host synchrony



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1. Introduction

The spruce budworm (SBW), *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is an eruptive tortricid that undergoes spectacular population cycles that last about 35–40 years [1] and is an important periodic source of perturbation in boreal forests [2]. Many factors interact to cause SBW outbreak cycles [3,4]. Parasitoids are important mortality factors in insect populations [5]. The parasitoids of SBW are numerous, diverse, and inscribed in a complex and dynamic food web [6]. Yet, the impact of parasitoids on the dynamics of its populations is difficult to quantify and put in perspective with respect to that of other sources of mortality [1,4]. We know that parasitoids play a key role in the decline of outbreaks [3,4,7] and during the prolonged period between outbreaks [8–10]. Most of those species are poorly understood, and we are just beginning to fill-in these knowledge gaps [11–14].

Meteorus trachynotus (Vier.) (Hymenoptera: Braconidae) is a koinobiont endoparasitoid of the late larval stages (mostly 6th instar) of SBW [15]. High incidence of this braconid has been repeatedly associated with collapsing SBW outbreaks [3,15–21]. Yet, SBW is a univoltine species that overwinters in the second instar without feeding, and is not known as an overwintering host of *M. trachynotus*. The parasitoid overwinters as a first larval instar inside diapausing host larvae, probably lepidoptera, in particular those of the obliquebanded leafroller (OBL) *Choristoneura rosaceana* (Harr.) [22]. In its third and final instar, it egresses from the host [23], and spins a silk cocoon on foliage, in the immediate vicinity of its moribund host, which may survive for several days or even weeks after parasitoid egression. Mating presumably takes place soon after adult emergence and females of the first generation attack fifth and sixth instar SBW, although this is more a question of timing than preference [24]. Immature development (inside the host and in the cocoon) is rather short [23,25] compared to the potential period of attack by *M. trachynotus* females, which peaks while most healthy SBW hosts are pupating [22]. In Quebec, a second generation of adults searches for alternate hosts throughout much of July and August, at a time when OBL larvae are actively feeding [22]. These observations indicate that most attacked larvae of the OBL were in the 2nd and 3rd instars and were induced into diapause. However, OBL undergoes at least a partial second generation in Quebec, which suggested the proportion of *C. rosaceana* larvae entering diapause in August may vary considerably from year to year [26]. A recently-developed model of OBL phenology confirms this convincingly [14].

The parasitoid's multivoltinism and the availability of alternate hosts in which to overwinter may be the main factor limiting the abundance of *M. trachynotus* in outbreak populations of the SBW [19,22,25]. Some suggested that poor synchrony between parasitoid adults and larvae of SBW larvae may be an additional limiting factor [24]. High frequency of infection by the microsporidian *Nosema fumiferanae* (Thomson) may explain in part the increase of parasitism frequency by *M. trachynotus* in collapsing outbreak SBW populations [27–29], as the disease slows the host's development [30]. The frequency of parasitism drops once SBW populations have declined to the so-called “endemic” level ([15], J.R. unpublished data). Later in the endemic period, as SBW population continue to drop, three other species cause increasing levels of mortality: *Actia interrupta* (Diptera: Tachinidae), *Tranosema rostrale* (Brischke) (Hymenoptera: Ichneumonidae) [31], and *Elachertus cacoeciae* (Hymenoptera: Eulophidae) [8,12].

In this paper, we report on the development of an individual-based simulation model of the seasonal biology of *M. trachynotus* and of its interaction with two of its hosts, SBW and OBL, which is based on data from Reference [25] on the relationships between temperature and development, and the existing seasonality models for SBW [32] and OBL [14]. This is the second of a series of articles using this methodology to study the response of trophic interactions to climate. Our objective is to study the impact of climate on *M. trachynotus* at the seasonal level, through its effect on development, reproduction and synchrony with the larval stages of two well-known tortricid hosts of the parasitoid. Here, we simulate the effects of temperature on phenological changes in the abundance of hosts, and on the population growth of the parasitoid as determined by oviposition activity and entry into diapause of its progeny. This model is applied to eastern North America, the range over which SBW outbreaks occur most often and cause the most damage. We also examine the probable impact of climate change on the performance of the parasitoid.

2. Materials and Methods

2.1. Model Description

This simulation model follows the general design of a model of interactions between *Tranosema rostrale* (Brischke) (Hymenoptera: Ichneumonidae) and the same two hosts [14]. It is an individual-based model, using the life-cycle modeling approach described by Reference [33]. The model divides each generation of *M. trachynotus* into three stages: immature (egg and larva) inside the host, pupa inside the cocoon (after egression from

the moribund host), and adult (Figure 1). For convenience, all parasitoids are assumed to be female. *Meteorus trachynotus* is not known to overwinter in SBW. At the onset of a simulation (1 January), the entire initial parasitoid population, N_0 , is initialized as immatures inside overwintering OBL larvae. Development of the parasitoid does not begin until its overwintering host emerges from the hibernaculum [25]. Model inputs are daily minimum and maximum air temperatures and time-series of abundances of SBW and OBL larvae provided by their respective seasonal biology models [14,32], used by the host-attack component. The model outputs daily, for each generation, the number of parasitoid individuals in each life stage, the number dead from various causes (freezing, adult in old age), as well as the number of host larvae of SBW and OBL (feeding or in diapause). The annual population growth rate R is determined from the total number of parasitoid individuals in diapause (inside overwintering OBL larvae) at the end of the 1-year simulation, relative to the initial 100. The complete code of this model is available under an open-source license [34,35].

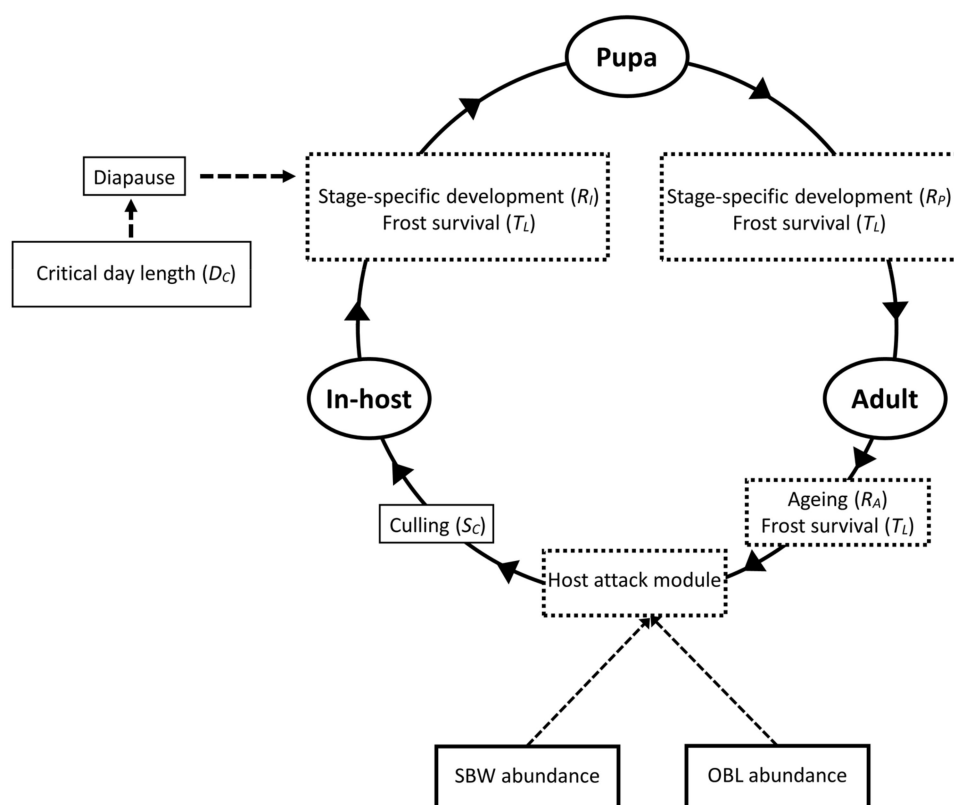


Figure 1. Flow chart illustrating the logical structure of the model for the development and reproduction of *Meteorus trachynotus* on its two hosts *Choristoneura fumiferana* (SBW) and *C. rosaceana* (OBL).

Feeding larvae of SBW are available for about six weeks each year, starting in May. There are no strong preferences by *M. trachynotus* for specific instars of SBW [24]. Development is computed and summed at intervals $\Delta t = 4$ h (0.1667 d) based on air temperature (T , in $^{\circ}\text{C}$). The simulation ends on 31 December. Hourly temperature is interpolated between input daily minima, T_{min} , and maxima, T_{max} , as described by Reference [36].

The first life stage of the overwintering generation does not start developing until emergence of the host OBL larvae once their post-diapause development is complete. At that moment, the parasitoid individual undertakes its spring immature development inside the host. Once the parasitoid egresses from the moribund host, it pupates inside a cocoon and undergoes pupal development, after which it enters the adult stage. Adult development ends when the individual has reached its longevity. Recruitment into the first stage of the second and subsequent generations is generated by the host-attack component

(Figure 1). The model assumes that all available hosts (active larvae of both OBL and SBW) are available to every single parasitoid female. Culling ($0 < S_c < 1$) is applied prior to the creation of new parasitoid individuals. This mortality rate is a constant used to limit the parasitoid's population growth rate. It was adjusted (see Section 2.4 below) so that the annual growth rate of the parasitoid averages close to 1. Besides from death of old age in the adults, frost is the only other source of parasitoid mortality in our model. Individuals of all three species not in diapause (or inside a diapausing host) are killed at temperature below $-5\text{ }^{\circ}\text{C}$ [32].

BioSIM [37] was used to provide the model with daily temperature data [38,39] specific to any simulation location. This open-source software, available at <ftp://ftp.cfl.forestry.ca/regniere/software/BioSIM/> as version 11, matches the four nearest weather stations to a simulation location, and compensates for differences in elevation, latitude, and longitude with regional thermal gradients. The daily minimum and maximum temperatures thus obtained are averaged using inverse distance as weight. Daily weather databases are compiled from all available North American station-based daily air temperature measurements. BioSIM also uses monthly normals from which it generates stochastic daily values of minimum and maximum temperatures; normals are monthly means, variances, and auto- and cross-correlation terms [38,40].

2.2. Parasitoid Development

The relationship between temperature T ($^{\circ}\text{C}$) and development rate r (in d^{-1}) in a given life stage (egg or larva in the host, or pupa in its cocoon outside the host, and adult longevity) is described by a non-linear thermal response equation:

$$r_i(T) = p_1 \left[e^{p_2 \tau} - e^{(p_2 - \frac{1-\tau}{p_3})} \right] \varepsilon_i \text{ with } \tau = \frac{T - T_b}{T_m - T_b}, \quad (1)$$

where ε_i is a lognormally-distributed term (mean 1, standard deviation σ_ε) representing each individual's deviation from the mean development rate in a given life stage. Values of parameters p_1 , p_2 , p_3 , and σ_ε were estimated by maximum likelihood [41] using the Excel Solver from individual development time or longevity data obtained at several constant temperatures [25]. Because the range of temperatures used in these experiments was insufficient to estimate lower and upper threshold temperatures, we retained the threshold values in Reference [25]: $T_b = 5$ for all stages, and $T_m = 35$ for immatures in the host and pupae. We also used $T_m = 40$ for adult longevity because there is no physiological reason for longevity to increase at high temperature, and $40\text{ }^{\circ}\text{C}$ is not encountered by *M. trachynotus* in its natural environment. Differences in the thermal responses of immature parasitoids were apparent between the spring (overwintered) and summer generations [25], and separate parameter values of p_1 and p_2 were estimated.

2.3. Parasitoid Reproduction

The pre-oviposition period of *M. trachynotus* is 1.6 d at $20\text{ }^{\circ}\text{C}$ [25]. In the model, oviposition by an adult occurs only once its development adult reaches $1.6\text{ }r_i(20)$, where $r_i(20)$ is the individual's adult aging rate at $20\text{ }^{\circ}\text{C}$.

The fecundity of female *M. trachynotus*, when provided with ample hosts for oviposition [25] is $F_{\max} = 194.2 \pm 91.1$ (standard deviation) and is normally distributed (Anderson-Darling (AD) = 0.218, $p = 0.828$ [42]). In the model, each individual adult is assigned a potential fecundity $F_{\max,i}$ that is drawn at random from this distribution. There does not seem to be strong discrimination against superparasitism, and contest competition inside host larvae leads to the emergence of a single parasitoid from each parasitized larva [23]. In this model, superparasitism is ignored. We also assume no competition between females for hosts, and all larval hosts are available to all females.

We modified the equation of Reference [25] describing the daily fecundity of *M. trachynotus* females n_a (eggs/day) by including Holling's disk equation [43] to describe the relationship between the attack rate of individual adult female i and total host density n_h :

$$n_{a,i} = \text{Min} \left[O_{\max} \left(\frac{a n_h}{1 + a t_h n_h} \right) \left(1 - \frac{F_{t,i}}{F_{\max,i}} \right) \right] \frac{r_{T,i}}{r_{20}}, \quad (2)$$

where $F_{t,i}$ is a female's cumulative oviposition up to time t , and $r_{T,i}/r_{20}$ is the individual's aging rate at temperature T relative to the average aging rate at 20 °C. This ratio yields attack rates that have the same temperature dependence as the aging of females. Thus, in this model, temperature itself does not affect realized fecundity. Cumulative oviposition is updated at the end of the time step ($F_{t+\Delta t,i} = F_{t,i} + n_{a,i}$). There are three estimatable parameters in Equation (2): $O_{\max}$ is the maximum oviposition rate, corresponding to the maximum rate at which a female can produce and mature new eggs (eggs/day), Holling's area of discovery a and handling time t_h . Because the total fecundity of each female in the original experiments of Reference [of Reference [25]] was unknown, a common value of the term $F_{\max}$ was also estimated. This value is specific to the females in this experiment. In the model, it is replaced by each individual females potential fecundity $F_{\max,i}$. Parameter estimates of Equation (2) were obtained by minimizing the residual sum of squared deviations between observed and predicted oviposition rates, using the Excel Solver.

This approach to simulating attack rates generates an important effect of host abundance on realized fecundity of *M. trachynotus* females. The data of Reference [25] are composed of four sets, obtained under laboratory conditions at three host densities: 3, 6 and 12 hosts per petri-dish arena. At a density of 6 hosts per female, the experiment was repeated using first- and second-generation females. These observations allowed us to compare the observed lifetime fecundity of the experimental females to fecundity generated by Equation (2). This also allowed us to scale the range of densities of host larvae generated by the SBW and OBL modules to correspond to the range of experimental densities [25]. With a scaling factor of 16.67, the highest experimental density of 12 larvae per female corresponds to a model host density of 200 host larvae, the maximum density potentially available to the first generation of parasitoid females in the model. This scaling ensures that the model is realistically responsive to changes in abundance of hosts caused by variation of synchrony with adult females of the parasitoid.

2.4. Model Calibration and Validation

The "culling rate" S_c is the only calibrated parameter in the model. It is a constant applied to all simulations, and only serves to scale the predicted parasitoid population growth rate so it varies reasonably close to 1. This constant survival rate is applied to all parasitoid progeny prior to creating new individuals. To determine a likely value, S_c was varied over the range (0.008, 0.016) in 0.001 steps, for Armagh and Petit-lac-à-l'Épaulle (hereafter, Epaulle; Table 1; open circles in Figure 2). Populations of SBW and its parasitoids have been under study in these two sites since the mid 1980's [3,44]. Simulations were run for the period 1981–2010 (10 replicates). The parasitoid's annual population growth rate was averaged ($\bar{R}$, defined above) and regressed with a second-degree polynomial against S_c . The quadratic solution for $\bar{R} = 1$ was used in all subsequent simulations. Once an appropriate value of S_c was obtained, this constant was applied in all subsequent simulations so that the predicted population growth rates varied in response to climatic conditions but remained within a realistic range (i.e., near 1).

Table 1. Subset of thirty spruce budworm population sampling locations and years where parasitism by *Meteorus trachynotus* was highest (>8%), used for model validation.

Location	Coordinates			Observation Year						
	°N	°E	m	84	85	86	87	88	89	90
Armagh	46.7668	−70.6575	277	Y	Y	Y				
Laterriere	47.9688	−71.2205	815		Y					
Forestville	48.9814	−69.1938	250		Y					
Forestville 2	48.9257	−69.1078	130		Y					
Epaule	47.2997	−71.1940	789		Y	Y				
Tourville	47.1140	−69.9521	300		Y	Y				
Sainte Louise	47.2797	−70.1203	70		Y	Y				
Montmorency	47.3220	−71.1470	725			Y	Y			
Casapedia	48.4787	−65.9512	550			Y				
Bostonnais	47.8396	−72.4812	400			Y	Y			
Misticougeche	48.0198	−68.3508	440			Y	Y	Y	Y	
Reserve										
Rimouski	48.0630	−68.1263	350				Y	Y	Y	
Lac Normand	47.0135	−73.2025	335					Y		
Dunierie	48.4338	−66.7805	475					Y	Y	
Observation	48.5851	−65.1001	445						Y	
Lac Huit Milles	48.4607	−67.0853	345							Y
Allard	48.2217	−66.4153	306							Y

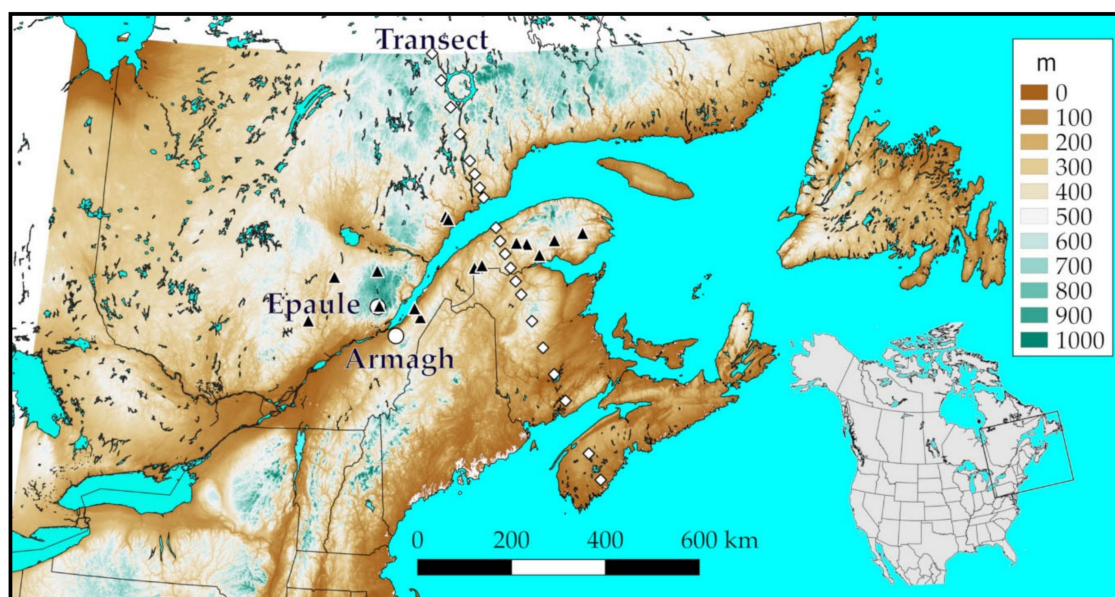


Figure 2. Elevation map of the portion of eastern North America considered in this study. Diamonds: Latitudinal transect locations. Circles: Armagh and Epaule locations. Triangles: Sampling locations in Table 1.

Model predictions of the timing of parasitoid attack on its spruce budworm host were compared to observations of SBW population density and *M. trachynotus* parasitism made between 1984 and 1993 in 23 locations in Quebec, Canada, during the collapse of the 1980's outbreak in eastern Canada. In total, 80 datasets (plot-years) were available for analysis. Foliage samples were taken from the mid-crown of co-dominant balsam fir, *Abies balsamea* (L.), and white spruce, *Picea glauca* (Moench.) Voss, at intervals of 2–7 days between peak 3rd instar in early June and >50% adult emergence in mid-July. Live SBW were extracted from the foliage and placed in individual rearing cups on artificial diet [45] until death or adult emergence. Sample sizes for each location and date averaged 101 (range 10 to 355). Parasitoids were identified from the cocoons or adults using taxonomic

keys [46] and reference collections. Observed parasitism rate was calculated from the proportion of SBW killed by *M. trachynotus* relative to the number placed in rearing on each sample date. A 3-day running average was applied to the parasitism time series to smooth-out the sampling error in each dataset.

We compared the observed relationship between maximum seasonal parasitism rate and SBW population density and parasitism rates predicted by the model. Initial overwintering SBW and OBL population densities in the model are set by default to 100 each, per parasitoid individual. The reality in the field is probably very different. We have no data on the abundance of either the parasitoid or the OBL larvae. We varied the initial density of overwintering SBW (n_{sbw}) between 1 and 100, while keeping that of OBL constant at 100 (n_{obl}) using factor $0 < p_{sbw} \leq 1$ applied to the SBW population exposed to parasitism. The number of hosts attacked, n_a , obtained from Equation (2) is distributed among available hosts according to their respective densities at time t , yielding the number of SBW attacked, $n_{a,sbw}$. Because there is intense intraspecific competition among *M. trachynotus* larvae inside the host, only one individual egresses from a parasitized host [23]. We used the Poisson distribution to express the probability of parasitism on SBW larvae:

$$p_{paras} = 1 - \exp \left[-k \left(\frac{n_{a,sbw}}{p_{sbw} n_{sbw}} \right) \right], \quad (3)$$

where $k > 0$ is a constant that sets the density of parasitoid adults relative to hosts, thus scaling predicted parasitism rates. The value of this constant was determined by establishing a linear relationship between k and the difference between average observed and predicted maximum seasonal parasitism rates, and solving for a zero difference. This was done using weather data from 1984–1993 in Armagh, replicating each model run 200 times to reduce output variation caused by the stochastic nature of the model.

A subset of thirty plot-years with highest maximum moving-average parasitism (>8%) was retained (from 17 locations; Table 1, Figure 2) to compare with the simulated time trends of parasitoid frequency in SBW hosts. The model was run for each location and year where data were available, and each model run was replicated 10 times. For this graphical comparison, parasitism rates output by the model were scaled so that maximum observed and predicted rates matched. Using the same subset, where numbers of parasitoid attacks were sufficiently high to provide good timing estimates, the observed dates at which first, maximum and latest parasitism occurred were compared by linear regression to the corresponding events (earliest 1%, maximum, latest 1%) in simulated SBW parasitism. Normality of regression residuals was tested with the Anderson-Darling statistic [42]. Mean observed and predicted dates of first and peak occurrence were compared by paired t -tests.

2.5. Performance of the Parasitoid over Northeastern North America, Present and Future

The potential annual population growth rate of *M. trachynotus* predicted by the model was mapped over the geographical extent depicted in Figure 2. Two maps were generated, one with daily air temperature records for 1981–2010 as input, and a second using 30 daily time series minimum and maximum air temperature generated from normals [38,40] for the period 2011–2040. To obtain normals for the latter period, we used the output of the Canadian Center for Climate Modeling and Analysis, Canadian Regional Model 4 [47], Canadian Earth System Model 2 [48], Representative Concentration Pathway (RCP) 4.5 climate change scenario [49], with 25-km spatial resolution [50]. We chose this moderate climate change scenario to maintain consistency with the first paper in our series [14]. The model was run for 20,000 randomly-located simulation points over the spatial extent depicted in Figure 2. Each run was replicated only once, given the high number of distinct locations used. For each simulation point, BioSIM provided daily air temperature inputs obtained from a large database of station records (1981–2000) or from gridded output of the climate models (2011–2040). Annual population growth rate at each location was then averaged over the 30 years for each period. The mapping interpolation of annual growth rates was done by universal kriging with elevation as external drift variable [51], based

on 250-m resolution Digital Elevation Model (Figure 2). We also calculated the average summer temperature (May to September) for each simulation point in each period, and the relationships between summer temperature and average annual population growth rate were graphed for the periods 1981–2010 and 2011–2040.

Two simulation series along a north-south transect of 20 evenly spaced locations (diamonds, Figure 2) were also run between 50° N, 69.57° W (Manicouagan Reservoir, Quebec) and 44° N, 65° W (Little Lake NS) using daily records for 1981–2010 and 2011–2040 as described above. Model output was averaged, by generation, for each location along this transect.

3. Results

3.1. Development and Reproduction of *M. trachynotus*

Parasitoid development times, rates, and the distribution of the individual variation term ε are very precisely described by Equation (1) (Table 2; Figure 3). There was a significant difference in the thermal response of the immatures in their host between the spring (overwintered) and summer generations (Table 2). The upper threshold temperature of 35 °C used for larval and pupal development is probably fairly well estimated, judging from the pupal development data. It is possible that the lower development threshold for pupae is actually lower than the assigned value of 5 °C (Figure 3e). However, pupae are present from June to August in most locations, during the warmest months of the year, and are probably not exposed to temperatures below 5 °C very often in nature. The lognormal distribution described quite well the observed distribution of individual deviations from the mean development time (Figure 3c,f,i).

Table 2. Parameter estimates of Equation (1) describing the developmental response of *Meteorus trachynotus* to temperature, obtained from SAS procedure NLMIXED (method of Reference [41]).

Parameter	Immatures		Pupa	Adult
	Spring	Summer		
p_1	0.0166 ± 0.0015	0.0222 ± 0.0009	0.0323 ± 0.0012	0.0124 ± 0.0010
p_2	2.9072 ± 0.2253	1.9227 ± 0.0878	2.7270 ± 0.1533	3.0574 ± 0.1567
p_3	0.0117 ± 0.5777	0.0117 ± 0.5777	0.1285 ± 0.0122	0.001 *
T_b *	5	5	5	5
T_m *	35	35	35	40
s_ε	0.3608	0.2929	0.1328 ± 0.0066	0.4317 ± 0.0208
Log likelihood		−1008.3	−372.3	−755.5

* Parameter value fixed.

The parameter values of Equation (2) that minimized the residual sum of squares between observed and predicted oviposition rates of *M. trachynotus* females as a function of female age and host density were $O_{max} = 13.86$ eggs/day, $a = 2.813$, $t_h = 1.1 \times 10^{-5}$ d and $F_{max} = 233.3$ eggs/female ($R^2 = 0.7$; Figure 4a–c). This value of F_{max} applies to the females in the experiments, and is higher than the average fecundity of 194.2 ± 91.1 eggs/female [25] used to assign the fecundity of individual females in the model. Predicted lifetime fecundity, calculated by summing oviposition rates given by Equation (2) over female longevity, corresponds very well with the experimental results (Figure 4d). With a scaling factor of 16.67, the highest experimental density of 12 larvae per female corresponds to a maximum model total host density of 200 overwintering host larvae (blue abscissa in Figure 4d).

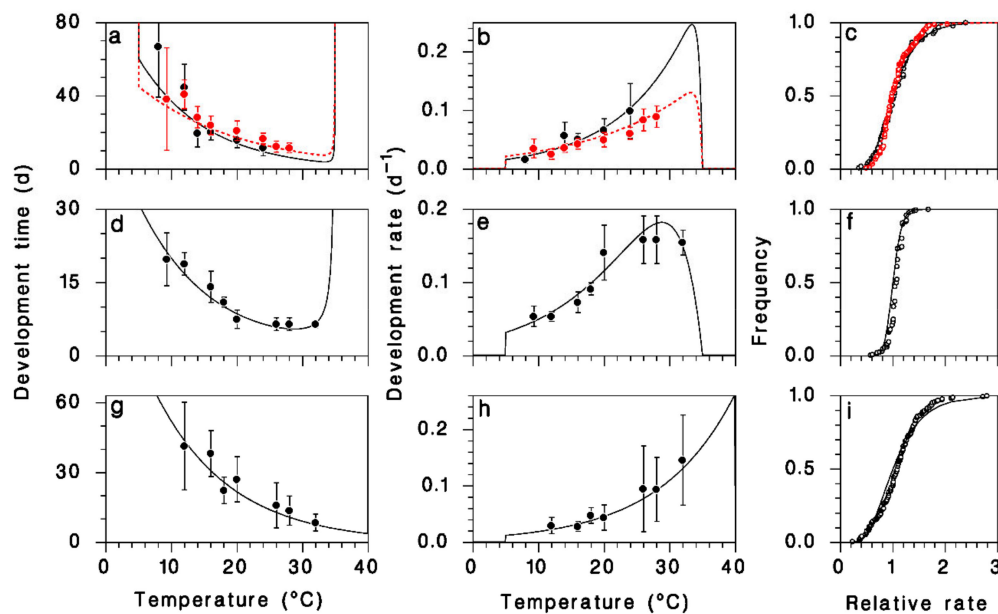


Figure 3. Developmental responses of *Meteorus trachynotus* to temperature. (a–c): Immatures in the host, spring (●) and summer generations (●); (d–f): pupa in its cocoon; (g–i) adult (longevity). (a,d,g): development time ($\pm$ STD); (b,e,h): development rate ($\pm$ STD) (lines: Equation (1)); (c,f,i): distribution of ε (lines: lognormal distribution). Data from Reference [25].

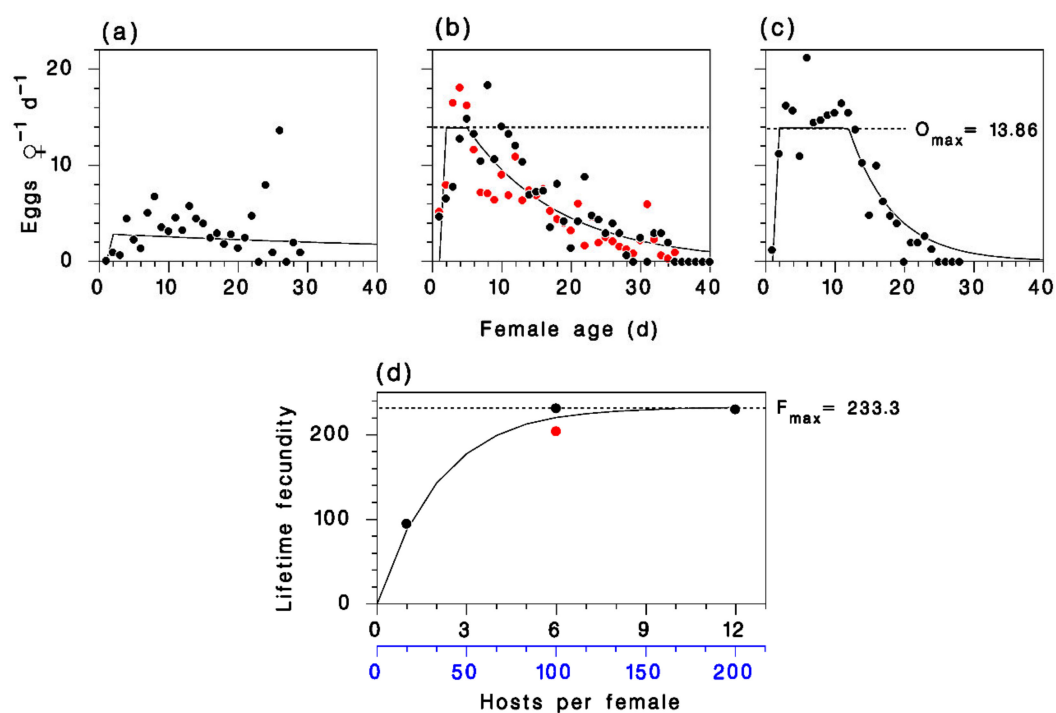


Figure 4. Daily oviposition rate of *Meteorus trachynotus* females, presented with (a) one, (b) six, and (c) twelve SBW larvae in petri dishes. (d): total lifetime fecundity. (●) summer generation; (●): spring generation. Lines: Equation (2). Secondary abscissa in (a): response rescaled ($16.67\times$) to host densities encountered by female parasitoids in the model. Data from Reference [25].

3.2. Model Calibration and Validation

A near-perfect regression ($R^2 = 0.9996$) was obtained between the average annual population growth rate $\bar{R}$ predicted by the model for Armagh and Epaule, and the culling survival term S_c , $\bar{R} = 8360S_c^2 - 53.51S_c - 0.768$. The quadratic solution of this relationship for $\bar{R} = 1$ yielded $S_c = 0.0125$, which was the value used in all subsequent simulations.

Equation (3), using the value $k = 0.114$, predicted a negative density-dependent relationship between parasitism rate and SBW host density over the observed range $n_{sbw} = 0.1$ to 100 of initial overwintering SBW larvae (the model assumes that the initial number of overwintering OBL hosts remains constant at 100). The trend in the observed proportion of SBW larvae parasitized over this range of SBW densities is very similar to model predictions: there was no significant difference between the slopes of predicted and observed parasitism rates against SBW density ($F_{1,71} = 2.4$, $p = 0.126$). However, at SBW density > 5 larvae per 100 shoots, observations suggest a drop in parasitism rate, although the sample sizes in the lower SBW density range are small (Figure 5).

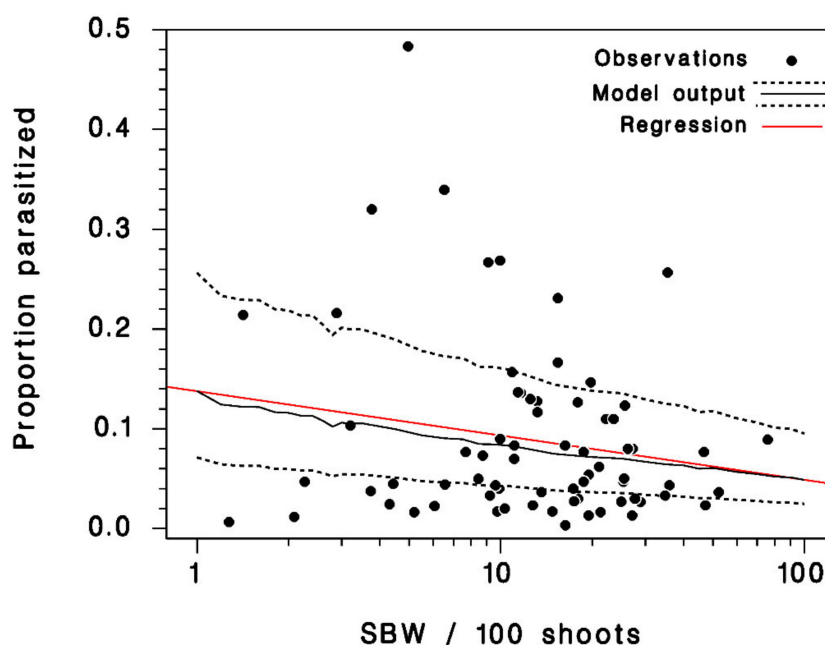


Figure 5. Relationship between SBW density and maximum seasonal parasitism rate observed in 77 plot-years (●). Lines: regression (red line), Equation (3) for Armagh, $k = 0.114$ (solid black line), $k = 0.114/2$ (lower dotted line), or $k = 2 \times 0.114$ (higher dotted line).

The timing of simulated seasonal parasitism of SBW larvae was compared to observations collected from wild SBW populations using a subset of 30 plot-years where maximum parasitism exceeded 8% (Table 1). Overall, there was no significant difference between average observed and predicted dates of earliest parasitism (observed: 170.4 ± 10.0 , simulated 168.9 ± 9.2 , difference 1.5 days, paired $t = 0.92$, $df = 29$, $p = 0.36$). Maximum parasitism occurred 3.7 days earlier than predicted, a biologically small difference (observed: 191.0 ± 8.1 , simulated 194.7 ± 10.4 , paired $t = -3.68$, $df = 29$, $p = 0.001$). However, the last observed attack occurred 15.5 days earlier than expected (observed: 199.1 ± 8.1 , simulated 214.6 ± 11.2 , $t = -14.7$, $df = 29$, $p < 0.001$). The correlations between observed and predicted dates of earliest, peak and latest parasitism were $r = 0.57$, $r = 0.84$ and $r = 0.87$, respectively (Figure 6). The slopes of observed versus predicted date regressions were significantly lower than 1 in all three cases ($F_{1,28} = 5.1$, $p = 0.03$; $F_{1,28} = 18.4$, $p < 0.001$; $F_{1,28} = 29.4$, $p < 0.001$; for earliest, maximum and latest parasitism, respectively). Regression residuals were normally-distributed (earliest: $AD = 0.24$, $p = 0.77$; peak: $AD = 0.3$, $p = 0.55$; latest: $AD = 0.41$, $p = 0.32$). These results indicate that the model predicts the beginning of the parasitoid's attack season on SBW accurately, but that it tends to be somewhat late at

predicting the peak of attack, and predicts a decidedly longer attack period on this host than is observed. These differences between observed and predicted dates also increase as the observed attack season occurs later in summer (Figure 6b,c).

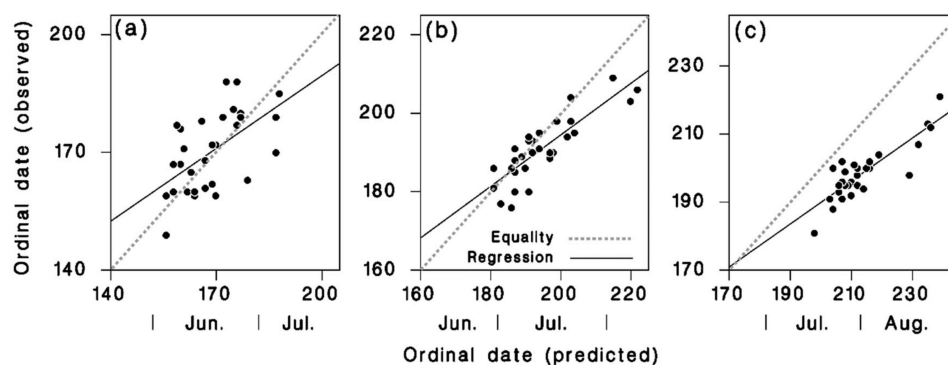


Figure 6. Regression between observed and predicted dates of (a) earliest, (b) maximum, and (c) latest parasitism by *Meteorus trachynotus* on SBW larvae for 30 plot-years in Table 1 (• observations;: equality; —: regression).

Nevertheless, the timing of simulated seasonal parasitism of SBW larvae was very similar to observations (Figure 7). In this graphical presentation, expected parasitism was scaled so that its maximum matched the observed maximum exactly. The model predicted parasitoid attack earlier than observed in a few cases, most notably in Epaule in 1986. The early decline of observed parasitism compared to model predictions is clearly apparent in most sites and years. Sampling of SBW populations usually stopped once most unparasitized SBW had reached the end of the pupal stage. In sites where parasitism occurred earlier, this provided a long enough sampling period for the entire attack pattern to be observed (e.g., Sainte-Louise in 1985, Armagh, Bostonnais, and Epaule in 1986). But in most cases, sampling stopped because of SBW pupation, well short of the end of the parasitoid's attack period (e.g., Armagh in 1984, Armagh, Epaule, and Forestville in 1985). This explains why the model's predicted end of the attack period is so much later than observed.

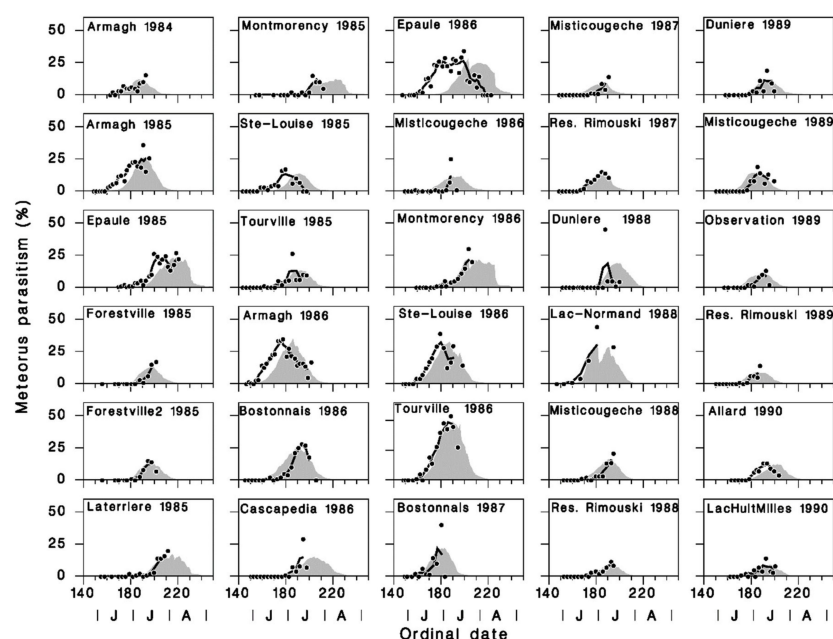


Figure 7. Comparison of the seasonal trends of parasitism by *Meteorus trachynotus* on SBW larvae in 30 datasets with maximum parasitism > 8%. •: observations. —: 3-day running average observed parasitism. Shaded: predicted parasitism. For location details, see Table 1.

3.3. Seasonal Biology of *Meteorus trachynotus* and Its Hosts

Three complete generations of *M. trachynotus* adults are predicted in Armagh (Figure 8b), with a fourth generation all entering into diapause and adding to the overwintering population. Only two complete adult generations are expected in Epaulé (Figure 8e). The late larval stages of both SBW and feeding OBL larvae are available simultaneously for attack by adult parasitoids of the first generation (g_1) in both locations (Figure 8a,d). In Armagh, very few of the g_1 adult parasitoids encounter OBL larvae that have been induced into diapause. Therefore, this generation does not contribute to the overwintering parasitoid population (Figure 8c). In Epaulé, however, many g_1 adults are still active while OBL larvae are entering diapause, thus contributing significantly to the overwintering parasitoid population (Figure 8f). In both locations, second-generation (g_2) adults are well timed with early larval stages of second-generation OBL and contribute considerable numbers of progeny to the overwintering parasitoid population (Figure 8c,f). In Armagh, the last generation of adults (g_3) overlaps with the last OBL larvae still feeding in late summer, thus also contributing to the overwintering parasitoid population (Figure 8c). This does not occur in Epaulé (Figure 8f).

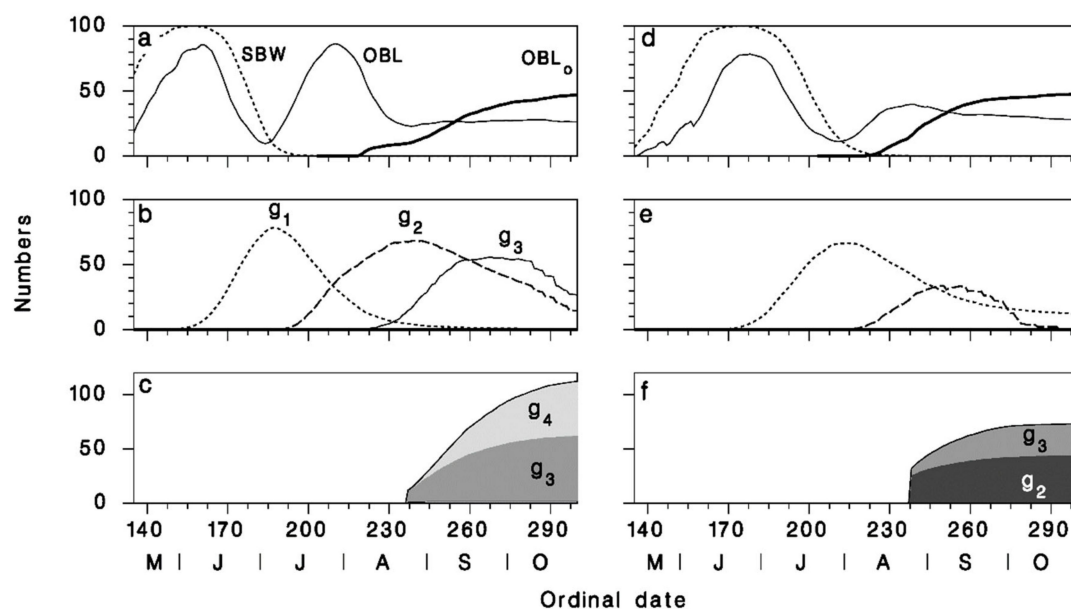


Figure 8. *Meteorus trachynotus* model output, averaged over the period 1984–2000 in (a–c) Armagh and (d–f) Epaulé. (a,d) Abundance host larvae (SBW:; feeding OBL: – –; overwintering OBL: —). (b,e) Abundance of parasitoid adults of successive generations (initial g_1 ; g_2 : – –; g_3 : —). (c,f): cumulative abundance of overwintering parasitoids in each generation.

3.4. *Meteorus trachynotus* Performance Now and in the Future

Under current climatic conditions (1981–2010), our model predicts high annual population growth rates of *M. trachynotus* in the southern portion of the SBW’s distribution in eastern North America (Figure 9a). We expect the parasitoid’s distribution to shift northward and towards higher elevations in the near future (2011–2040) under the RPC 4.5 greenhouse gas emission scenario, a moderate climate change scenario. Lower population growth rates should occur at lower elevations in the south of its range, except along the maritime edges in New Brunswick and Nova Scotia (Figure 9b).

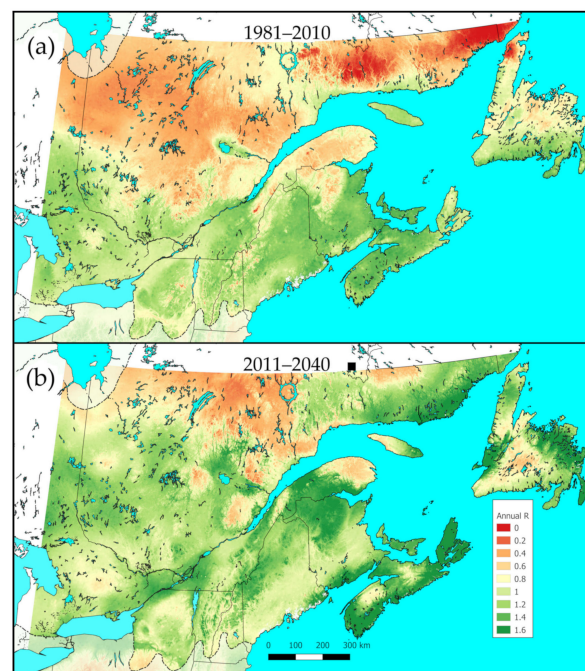


Figure 9. Maps of annual population growth rate of *Meteorus trachynotus* over northeastern North America overlaid on the distribution of SBW (dash-dotted wavy line). (a) From 1981–2010 daily minimum and maximum air temperature records. (b) From 2011–2040 normals disaggregated to stochastic daily minimum and maximum air temperature.

Much of the complexity of this spatial pattern in annual population growth rate of *M. trachynotus* resulted from its relationship with latitude (Figure 10a) and with mean May–September temperature (Figure 10b). Climate change in the near future is expected to shift the latitudinal distribution of growth rates northward (dotted line in Figure 10a), but the pattern of the relationship between annual growth rate and mean summer temperature is not expected to change (dotted line in Figure 10b).

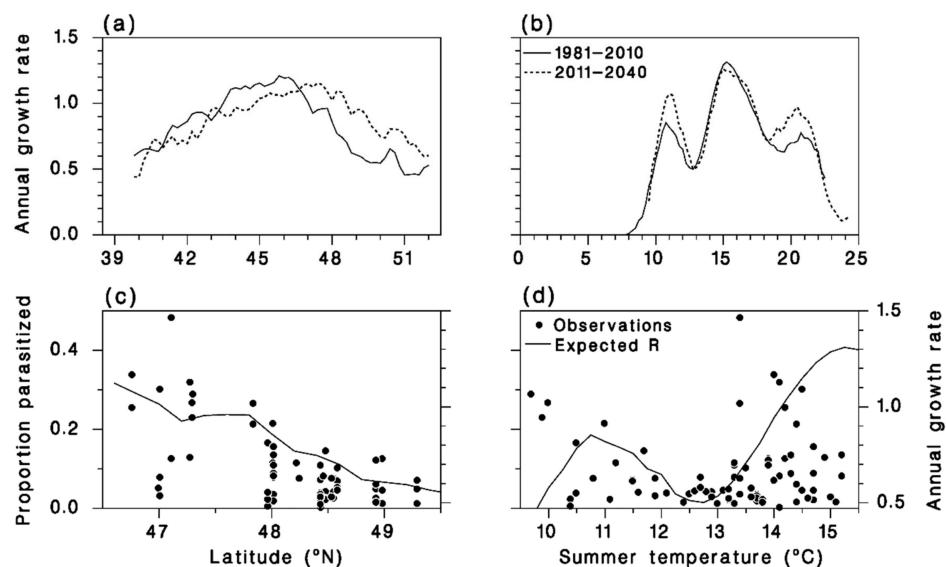


Figure 10. Expected relationship between annual population growth rate of *Meteorus trachynotus* and (a) latitude and (b) mean summer temperature from May to September (—: from daily air temperature records between 1981 and 2010;: from climate-changed disaggregated normals 2011–2040). Comparison between expected growth rate and maximum seasonal parasitism observed in 80 plot-years in Quebec with respect to (c) latitude and (d) means summer temperature.

3.5. Performance of *M. trachynotus* along a North-South Transect

Predicted population performance of the parasitoid (annual growth rate) displayed a complex spatial pattern along the north-south transect, as a result of interactions between survival, realized fecundity, and voltinism (Figure 11). Under current climate (1981–2010), the growth rate was lowest in the middle of the transect (solid line in Figure 11c), in northern New Brunswick and Quebec's Lower St. Lawrence region. Interaction between voltinism and timing of attack with the overwintering stage of the OBL host caused a drop in the survival of g_3 immatures, itself causing the growth rate at middle latitudes to drop (Figure 11a). The number of generations of the parasitoid decreased northward. In the south, most overwintering individuals belonged to generations g_2 , g_3 , and g_4 , but northern overwintering populations contained no individuals from generation g_4 (Figure 11d). Growth rates in the future (2011–2040) should decrease at the southern and northern ends of the transect but should increase considerably in the central portion along the St. Lawrence River valley (Figure 11g).

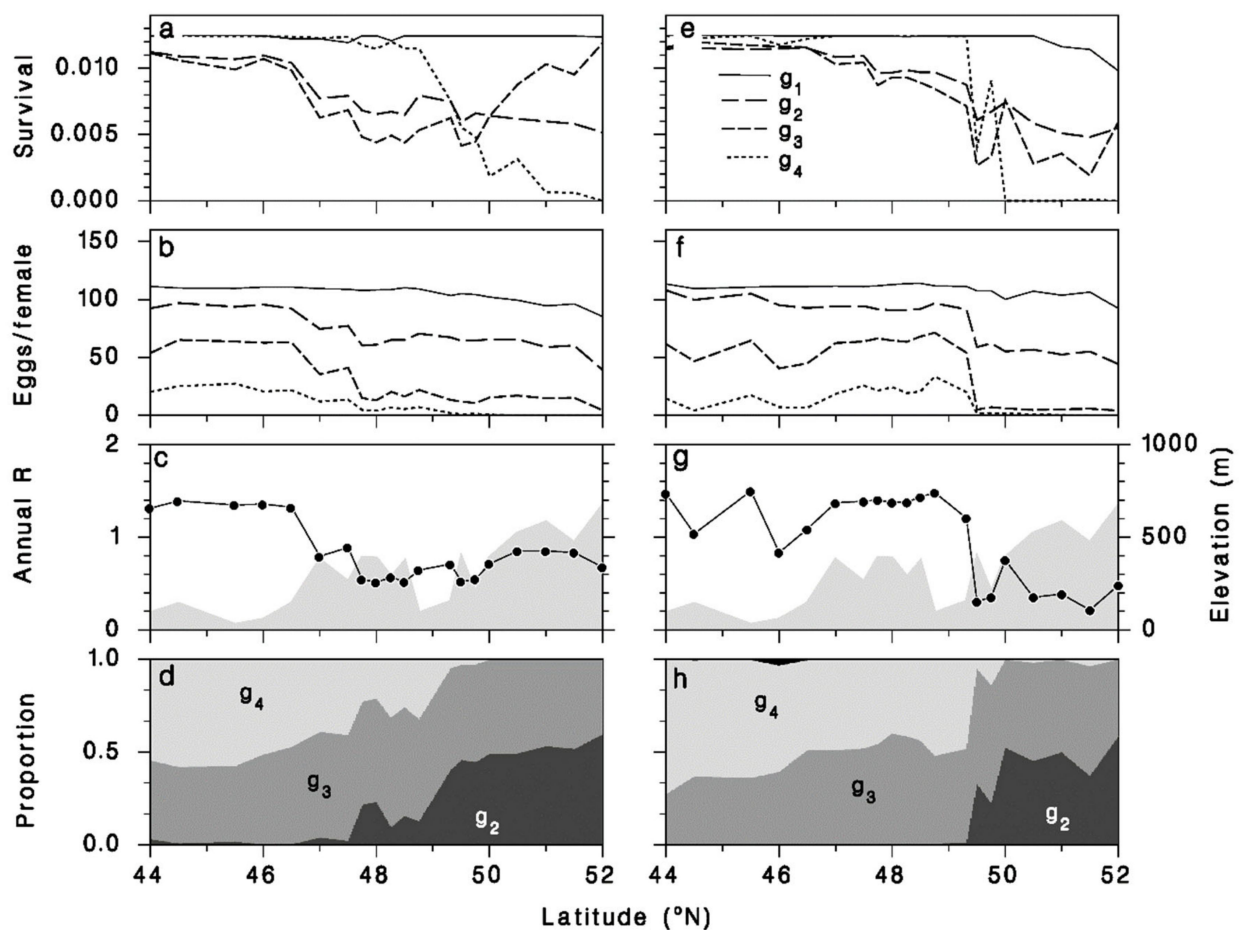


Figure 11. Summary of model output along the north-south transects under (a–d) 1981–2010 climate and (e–h) future climate (2011–2040). (a,e): Survival from egg to adult in each generation (g_1 to g_4 , where g_1 is the initial generation in overwintering hosts in January), including culling survival $S_c = 0.0125$. (b,f): Realized fecundity per female parasitoid. (c,g): Annual population growth rate R , from initial 100 to overwintering in L_{30} of OBL hosts at the end of the year; shaded curve: elevation along the transect. (d,h): Proportion of overwintering parasitoid population in each generation.

4. Discussion

This model of the seasonal interactions between *Meteorus trachynotus*, a parasitoid attacking two major tortricid hosts, the spruce budworm *Choristoneura fumiferana* (SBW) and the oblique-banded leafroller *C. rosaceana* (OBL), has allowed us to better understand the influence of climate on the performance of this parasitoid at the population level. In doing this, we were lucky to have at our disposal a large amount of data on its thermal responses [25] and on its impact on SBW, obtained during the decline period of the 1970–1990 outbreak in Quebec.

Our data indicate that there is no important difference in the optimal temperatures for development of *M. trachynotus* (either inside the host or as pupae) than that of either of its SBW or OBL hosts. Thus, our results do not support the hypothesis that host-parasitoid interactions are susceptible to climate change because of lower thermal optima in parasitoids [52].

We did not have access to data from which to relate survival of various life stages, nor fecundity of the parasitoid at different temperatures, such as were available to us to model those responses in *T. rostrale* [14]. However, we had a solid description of the effect of host density on realized fecundity which was not available to model the ecology of *T. rostrale* [14]. A simple rescaling of host densities between experimental conditions used by Reference [25] and model environment allowed us to calibrate a realistic host-density response.

The model required the calibration of a single constant through optimization: culling rate $S_c = 0.0125$, which allowed the model to generate realistic annual population growth rates (near 1). The fit to observed timing of parasitism on the primary summer host (SBW) was verified from a large dataset (a subset of 30 out of 80 plot years) obtained during the decline of the 1970–1990 outbreak in Quebec. The observed seasonal pattern of parasitism on SBW larvae was well predicted by the model, given that the parasitoid attacks the last larval instar while many of the SBW hosts are pupating [22], and given the limitations imposed by sampling low-density SBW at the end of the larval and pupal period. In those datasets, parasitism was measured on several occasions during the same season, allowing us to compare not only the timing of parasitoid attack but also the relationships between peak parasitism rate, population density, latitude, and summer temperature. The timing observations were favorably compared to model output, except in Epau. The Epau site is located in mountainous terrain, in the middle of a steep elevation gradient [44]. The two larval hosts of *M. trachynotus* exploit different host plants (SBW on conifer trees and OBL on deciduous trees), and their relative abundance can vary spatially in particular in topographically complex areas. Increased developmental variability of hosts and parasitoids may have resulted from this topographic heterogeneity, affecting the timing of parasitism on SBW. We hypothesize that parasitoid adults need to shift between the different habitats of their two main hosts, apportioning search time between those habitats in response to the relative densities of those hosts. This is a spatial factor not considered in this model. At low relative density of SBW, parasitoid adults may abandon the search for this host and focus more exclusively on the search for OBL larvae.

Close examination of the data (Figure 5) suggests that attack rates may drop at very low SBW density, which may indicate that *M. trachynotus* loses interest in SBW as a rare host and focuses on more abundant hosts, including OBL. While the model predicts an inverse density-dependence of attack on SBW larvae that closely reflects observations, the model does not contain a mechanism that would lead to a drop of impact at very low SBW density. Nevertheless, allocation of search time between two hosts that live in different habitats could explain this pattern, arising from a Type-III functional response [53–55]. This question may be amenable to further investigation under Charnov's Marginal Value Theorem [56,57].

The model predicts that voltinism in *M. trachynotus* varies between 2 and 4 adult generations per year, and depends on the entry into diapause by the overwintering host

(OBL). There is no apparent relationship between the number of generations achieved per year and annual population growth rate (compare Figure 10a to Figure 11c,d).

The spatial pattern of parasitoid population performance is complex, and results from intricate synchrony relationships between parasitoid adults and OBL host larvae entering into diapause. Fitness (expressed as population growth rate) peaks at latitude 45° N, with a 3° northward shift expected over the next 30 years in response to climate warming. The relationship is further modulated by mean summer temperature, with three optima at 11°C, 16°C, and 21 °C, a relationship unaffected by climate change. These spatial and environmental relationships are well reflected in our data.

5. Conclusions

Meteorus trachynotus is the dominant parasitoid during the decline of SBW outbreaks [3,15–21]. We have known for some time that it is multivoltine, polyphagous and overwinters in the larvae of alternate hosts, such as OBL [22–25]. In this paper, with the help of an individual-based model of the climate-mediated interactions between the parasitoid and two of its main hosts, we explain with some success the highly variable impact of this parasitoid on collapsing SBW populations. This “predictable variability” stems from geographical and topographical patterns of ambient temperature, as they influence the development and reproduction of the parasitoid in interaction with those two tortricid hosts. We know little about the geographical patterns of parasitoid abundance and diversity [58–61]. Given the paucity of available data for any given species, models may be the best short-term approach to understanding the effect of climate on the current and future distribution and performance of these elusive organisms [62–64], as well as to predict the impacts of climate change on the ecological relationships between parasitoids and their hosts [65,66].

Author Contributions: J.R. conceived and designed research, J.R., C.H., and P.T. collected field data. J.-C.T. contributed laboratory data. J.R. developed the model and did the analysis. R.S.-A. assisted in model development and implementation into BioSIM. J.R., V.M., and J.-C.T. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author. The data are not publicly available due to copyright issues.

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