SIMULATED MANAGEMENT OF AN HISTORICAL SPRUCE BUDWORM POPULATION USING INUNDATIVE PARASITE RELEASE

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Abstract

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Summary life table data of historical spruce budworm, *Choristoneura fumiferana* (Clemens), populations from the Green River Project in New Brunswick, Canada (1947–1958), provided information for developing a management strategy using annual inundative releases of the egg parasite *Trichogramma minutum* Riley. Three threshold levels (39, 169, and 201 budworm egg masses per 10 m^2 foliage) were assigned to the spruce budworm population and a simulation model employed to manage it at or below each level. Based on field data, the lowest threshold represented a light level of defoliation while the other two thresholds represented moderate defoliation levels. With the exception of 3 years at the low level, annual inundative releases of *T. minutum* successfully suppressed the spruce budworm population below the three thresholds in the model. Annual releases of *T. minutum* were also simulated during the inclining, plateau, and declining phases of one outbreak cycle of the spruce budworm. At the same rate (12×10^6 female *T. minutum* per hectare), inundative releases during the inclining phase were more effective than during either the plateau or declining phases. The results suggest that some low and moderate populations of spruce budworm can be effectively managed using annual inundative releases of an egg parasite, particularly toward the end of the inclining phase of an outbreak, but when populations reach severe levels, additional mortality agents probably will have to be considered in an integrated approach.

You, M., et S.M. Smith. 1990. Gestion simulée d'une population historique de la tordeuse de l'épinette en faisant l'utilisation d'un afflux de parasites. *Can. Ent.* **122**: 1167–1176.

Résumé

Les données en résumé d'un tableau vital des populations historiques de la tordeuse de l'épinette, *Choristoneura fumiferana* (Clemens), de l'Opération de Green River, Nouveau-Brunswick, Canada (1947 à 1958), ont fourni les renseignements nécessaires pour développer une stratégie de gestion en utilisant les afflux du parasite des oeufs, *Trichogramma minutum* Riley. Trois paliers (39, 169 et 201 masses d'oeufs de la tordeuse par 10 m^2 de feuillage) ont été attribués à la population de la tordeuse de l'épinette et un modèle simulé a été utilisé pour la gérer au niveau ou au-dessous de chaque palier. Selon les données des champs, le palier le plus bas a représenté un niveau de défoliation légère, pendant que les deux autres paliers ont représenté les niveaux de défoliation modérée. Sauf pendant 3 ans au niveau bas, les afflux de *T. minutum* ont réussi à supprimer la population de la tordeuse de l'épinette au-dessous des trois paliers du modèle. Les relâchements annuels de *T. minutum* ont été simulés également pendant les phases d'augmentation, de plateau et de déclin d'un cycle d'une épidémie de la tordeuse. Au même taux (12×10^6 femelles de *T. minutum* par hectare), les afflux pendant le phase d'augmentation ont été plus efficaces que celui de plateau ou de déclin. Les résultats suggèrent que quelques populations de grandeur légère et modérée pourraient être gérées efficacement en utilisant des afflux d'un parasite d'oeufs, surtout vers la fin d'une phase d'augmentation d'une épidémie. Cependant, quand les populations sont d'un niveau sévère, la considération d'autres agents nocifs serait probablement nécessaire pour une gestion intégrée.

Introduction

The intensive census of spruce budworm, *Choristoneura fumiferana* (Clemens), populations (the Green River Project) made between 1947 and 1958 in New Brunswick (47°N,

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68°W) provides an important historical record of one almost complete spruce budworm outbreak (Morris 1963). Royama (1984) criticized this pioneering work for its lack of understanding of the concept of density-dependence and reanalysed the data to propose a new interpretation for the population dynamics of spruce budworm. His interpretation supports the findings of Morris (1963) suggesting that long-term oscillations in budworm populations depend primarily on changes in large larval survival whereas short-term fluctuations are determined by the ratio of all eggs laid to the number of locally emerged moths (the E/M ratio) (Royama 1984).

A clear understanding of the population dynamics of spruce budworm is necessary for the efficient and economical management of this species. Smith and You (1990) developed a life system model incorporating all the information available to date on spruce budworm population dynamics. This model accurately described short-term budworm population changes and allowed the impact of annual strategies for suppressing budworm outbreaks to be examined. To predict the long-term outcome of such measures for managing the spruce budworm, however, life table data over a complete budworm outbreak cycle must be incorporated. Unfortunately, only the Green River Project currently provides any long-term data on generational survival in the spruce budworm.

Data of the historical population of spruce budworm in the Green River Project between 1947 and 1958 enabled Royama (1984) to identify changes in egg density (the E/M ratio) as the prime cause of yearly density fluctuations in the population dynamics of any given spruce budworm generation. In the present study, therefore, we considered that short-term savings in forests attacked by spruce budworm would be achieved best by reducing the E/M ratio through inundative releases of the egg parasite, *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae).

To date, few studies have used historical outbreak records to examine possible management strategies (Holling 1978; Clark *et al*. 1979; Baskerville 1982; Stedinger 1984). Such work could improve measures of control for the spruce budworm by providing information on the extent to which various control measures can suppress pest populations when applied at different population densities and at different stages in population fluctuation. Based on Royama's analyses (1981, 1984) of the Green River data, the results of our own simulation model (Smith and You 1990), and assuming exact knowledge of budworm population dynamics in the immediate future, the objectives in the present paper were as follows: (1) to determine whether inundative parasite release aimed at the egg stage of spruce budworm could manage populations from year to year around a given threshold level; and (2) to assess the impact of such a management strategy when applied over the three different phases of a spruce budworm outbreak (the inclining, plateau, and declining phases).

Methods

Simulated Management of Spruce Budworm Below a Threshold Level. Before performing our simulation, log values for the stage-specific survival rates of spruce budworm on Plot G4 in the Green River Project were obtained from Royama (1984). Inverse logs of these data were calculated to obtain the original values for our study (Table 1).

The initial step in using these historical data was to assign a threshold level at which spruce budworm populations were to be managed. According to current entomological surveys and assessment techniques, the intensity of the budworm infestations in New Brunswick can be classified by the number of eggs per 10 m^2 of conifer foliage: (1) a light infestation being 1–108 egg masses; (2) a moderate infestation being 109–260 egg masses; and (3) a severe infestation being ⩾260 egg masses (Dorais and Kettela 1982). Because spruce budworm populations never reached severe infestation levels (⩾260 budworm egg masses per 10 m^2) on Plot G4 in the Green River Project, we assigned the egg densities of 1949, 1953, and 1956 as three different threshold levels so that the population in 1949

Table 1. Data from spruce budworm (SBW) life tables for Plot G4 from the Green River Project in New Brunswick, 1947–1958 (taken from Royama 1984)

	SBW survival rate (S_{ij})†				
Year (i)*	S_{i1} (E)	S_{i2} (S)	S_{i3} (L)	S_{i4} (P)	S_{i5} (E/M)
1947 (1)	0.9490	0.1653	0.2400	0.8958	180.2312
1948 (2)	0.9484	0.2143	0.1619	0.6667	115.5873
1949 (3)	0.7201	0.1322	0.3690	0.6304	413.7900
1950 (4)	0.6306	0.2419	0.1985	0.6873	60.2629
1951 (5)	0.7489	0.1490	0.2505	0.7499	20.2083
1952 (6)	0.8711	0.2615	0.1088	0.7900	44.4734
1953 (7)	0.9172	0.1594	0.0518	0.6404	701.2131
1954 (8)	0.8209	0.1295	0.1244	0.4605	43.9997
1955 (9)	0.7597	0.1000	0.1325	0.4000	324.1903
1956 (10)	0.9602	0.0323	0.1878	0.5214	670.4864
1957 (11)	0.8313	0.0603	0.0483	0.5152	34.0589
1958 (12)	0.9102	0.1341	0.0189	0.4500	94.9992

*i = year of study (i = 1, 2, ..., 12).
†S_{ij} represents the survival rate of SBW where i is the study year (i = 1, 2,..., 12), j is the different SBW life stages with j = 1 representing the egg stage (E), j = 2 represents the small larvae (S), j = 3 represents the large larvae (L), j = 4 represents pupae (P), and j = 5 represents the ratio of all eggs laid to the number of locally emerged moths (E/M).

(39.3 egg masses per 10 m^2) represented a light level of infestation and the populations in both 1953 and 1956 represented two different moderate levels (169.0 and 201.0 egg masses per 10 m^2, respectively).

The second step in the analysis was to identify the annual population level of the spruce budworm at which the management strategy should be implemented. This was based on the population "trend" index (I_{ik}), which represented the ratio of egg density in the study year (i) to that density in the assigned threshold year (k). Inundative releases of *T. minutum* were implemented when the annual budworm population exceeded the assigned threshold population (I_{ik} >1) (Table 2).

The third step in the analysis was to determine the level of mortality required to achieve the assigned threshold level. Thus, for each inundative release, that mortality for the egg population of spruce budworm (D_{ik}) required above the natural mortality already

Table 2. Population "trend" index (I_{ik}) between each study year and the assigned threshold level for spruce budworm (SBW) populations in the Green River Project, 1947–1958

Year (i)*	Density of SBW eggs (no. per 10 m^2 foliage)	Population "trend" index (I_{ik})† I_{i3}	I_{i7}	I_{i10}
1947 (1)	2.55	0.0649	0.0151	0.0127
1948 (2)	15.50	0.3944	0.0917	0.0771
1949 (3)	39.30†	1.0000	0.2325	0.1955
1950 (4)	360.00	9.1603	2.1302	1.7910
1951 (5)	458.00	11.6539	2.7101	2.2786
1952 (6)	194.00	4.9364	1.1479	0.9652
1953 (7)	169.00†	4.3003	1.0000	0.8408
1954 (8)	575.00	14.6310	3.4024	2.8607
1955 (9)	154.00	3.9186	0.9112	0.7662
1956 (10)	201.00†	5.1145	1.1893	1.0000
1957 (11)	409.00	10.4071	2.4201	2.0348
1958 (12)	17.37	0.4420	0.1028	0.0864

*Represents each study year i where i = 1, 2, ..., 12.
†Represents the year of an assigned threshold level where k = 3, 7, and 10. SBW densities that were assigned as one of the threshold levels are denoted individually by a dagger (†).

present was calculated with respect to the corresponding population "trend" index (I_{ik}). The required mortality was established such that the budworm population fluctuated around the assigned threshold level. To stabilize the population dynamics of each study year (i = 1, 2, ..., 12) at the assigned threshold level (k = 3, 7, 10), the population "trend" index had to be unity ($I_{ik} = 1$) or the populations in both years had to be equal ($N_i = N_k$). In other words, the survival rate of the egg stage in the study year, i, had to equal $1/I_{ik}$ after the release of *T. minutum*. Therefore:

$$S_i(\mathrm{E}) - D_{ik} = 1/I_{ik}$$
$$\text{or} \qquad D_{ik} = S_i(\mathrm{E}) - 1/I_{ik} \qquad [1]$$

where $S_i(\mathrm{E})$ = the survival rate of the egg stage in study year i under natural conditions.

The fourth step was to determine the number of *T. minutum* per hectare needed to achieve the desired egg mortality (D_{ik}). This was derived from the relationship between the rate of *Trichogramma* release (in females per hectare) and budworm egg parasitism established in a 5-year study in northern Ontario (Smith *et al.* 1990). The study predicted that, in balsam fir and spruce stands (ca. 20 years old) with severe populations of spruce budworm (>216 egg masses per 10 m^2), at release rates of 4.2, 4.8, 8.4, 9.6, 16.9, 19.2, and 28.8 × 10^6 females per hectare, daily maximum parasitism on susceptible budworm eggs would be 34, 45, 47, 56, 64, 66, and 69%, respectively. The strategy selected for parasite release was that which achieved the highest level of budworm mortality identified by Smith and You (1990): a "single staggered release" of *T. minutum*, where the proportion of spruce budworm eggs killed each day increased by 10, 15, 20, 25, and 30% per day for 5 days following release.

Finally, once the necessary release rate was determined, this rate was incorporated into the simulation model of spruce budworm developed by Smith and You (1990). This model was based on life table and daily temperature data from the Green River Project (1947 through 1958), as well as data on the relationship between temperature and spruce budworm development from Cameron *et al.* (1968) and Régnière (1987). Once the model was started, the simulation proceeded from day to day, outputting the daily number of budworm eggs present during the oviposition period according to the accumulation of degree-days (Smith and You 1990). The required number of parasites were released during the oviposition period according to the optimal strategy described previously, and the level of population suppression recorded in terms of the number of budworm eggs present after losses due to egg parasitism.

Simulated Management of the Spruce Budworm Over Different Outbreak Phases. Based on Royama's (1981, 1984) density-dependent concept, hypothetical releases of *T. minutum* were made over each of the three different phases of a budworm outbreak and their impact on budworm populations assessed to determine the optimal phase for release. As in Royama's (1981, 1984) studies, we treated one whole generation as a single stage for analysis.

Initially, a linear, second-order, autoregressive model which approximated the non-linear population dynamics in the simulation was used as a simplified description of the density-dependent processes within the spruce budworm population (Royama 1984). Thus:

$$Rt = a_0 N_t + a_1 N_{t-1} + Z_t \qquad [2]$$

where a_0 and a_1 were constants (a_0 = 0.80; a_1 = 0.89 [Royama 1984]; Z = the net effect of all density-independent factors involved; R = the log (natural logarithms are identified with "log" throughout this paper) rate of change in egg density; N = log egg density; and t = the generation year, which spans from the fall of the previous year ($t-1$) to that of the present year (t).

When an inundative release of *T. minutum* was made in a given year, say t, the budworm population density in that year (N_t) was re-calculated in terms of the mortality caused by *T. minutum* (Smith *et al.* 1990). Using this new budworm density as the initial condition, simulations were run based on Eq. [2] where the Z's were random numbers generated by the computer and distributed uniformly in the interval -0.5 to 0.5 (Royama 1984). The spruce budworm population dynamics and rate of change then fluctuated away from the original (or natural) dynamic pattern, and the autoregressive model of Eq. [2] gave the new oscillation for the population during the remaining years.

In the next step, the population trends in spruce budworm densities for Plot G4 from 1946 to 1959 were divided into three outbreak phases: inclining, plateau, and declining (areas A, B, and C, respectively, in Fig. 2*a*). Because the declining phase had a limited number of years of data, a set of hypothetical data from 1960 to 1965 was employed. Finally, a release rate of 12×10^6 female *T. minutum* per hectare was applied in the simulation model for each year and phase of the budworm outbreak. Emergence of these parasites was staggered over 5 days because our previous study had shown this to be optimal for reducing populations of spruce budworm (Smith and You 1990). Based on this simulation, it was assumed that 69.9% of the susceptible spruce budworm eggs would be parasitized using this strategy. The annual results, in terms of log density of spruce budworm, were examined and compared within each phase. For simplicity, emphasis was placed on the results of only two release years in each phase, one in the early part and one in the latter part of the same phase.

Results and Analysis

Simulated Management of Spruce Budworm Below a Threshold Level. The population "trend" indices between each study year (i = 1, 2, ..., 12) and each assigned threshold year (k = 3, 7, 10) were calculated according to the designated threshold levels (Table 2). Table 3 shows the level of egg mortality necessary for each I_{ik} as well as the corresponding rate of parasite release (R_{ik}). No management action (R_{ik} = 0) was needed if the egg mortality of spruce budworm (D_{ik}) was zero or negative because the population was low or stable. The release rate (R_{ik}) generally increased as the anticipated need for higher

Table 3. Level of egg mortality and corresponding release rate of *Trichogramma minutum* necessary to suppress spruce budworm populations from the Green River Project below three assigned threshold levels

	Assigned threshold level					
	I_{i3}		I_{i7}		I_{i10}	
Year (i)*	Egg mortality, D_{i3}	Release rate, R_{i3} (10^6 ♀♀/ha)	Egg mortality, D_{i7}	Release rate, R_{i7} (10^6 ♀♀/ha)	Egg mortality, D_{i10}	Release rate, R_{i10} (10^6 ♀♀/ha)
1947 (1)	−14.4628	0	−65.3255	0	−77.8745	0
1948 (2)	−1.5871	0	−9.9548	0	−12.0193	0
1949 (3)	−0.2799†	0	−3.5802	0	−4.3944	0
1950 (4)	0.5214	10	0.1612	4	0.0723	2
1951 (5)	0.6631	12	0.3799	8	0.3100	6
1952 (6)	0.6685	12	0.0000	0	−0.1650	0
1953 (7)	0.6847†	12	−0.0828	0	−0.2721	0
1954 (8)	0.7526	12	0.5270	10	0.4713	8
1955 (9)	0.5045	12	−0.3377	0	−0.5455	0
1956 (10)	0.7647†	12	0.0050	2	−0.0398	0
1957 (11)	0.7352	12	0.3570	6	0.3399	6
1958 (12)	−1.3523	0	−8.8192	0	−10.6615	0

*Represents each study year i where i = 1, 2, ..., 12.
†Represents the year of an assigned threshold level where k = 3, 7, and 10. SBW densities that were assigned as one of the threshold levels are denoted individually by a dagger (†).

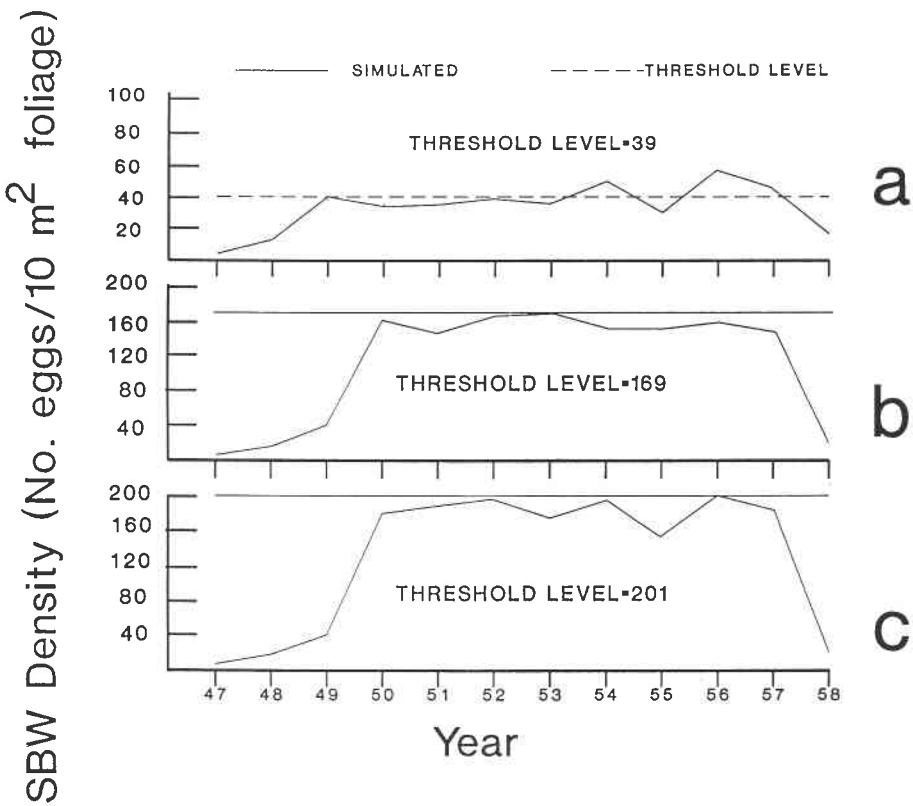

FIG. 1. Simulation results when the egg parasite, *Trichogramma minutum*, was hypothetically released at three threshold levels of spruce budworm (SBW) in the Green River Project (1947–1958). (*a*) Light defoliation, threshold level of 39.3 SBW eggs per 10 m^2 foliage; (*b*) moderate defoliation, threshold level of 169.0 SBW eggs per 10 m^2 foliage; (*c*) moderate defoliation, threshold level of 201.0 SBW eggs per 10 m^2 foliage.

mortality (D_{ik}) increased. As expected, when the assigned threshold level was lower, the necessary egg mortality (D_{ik}) was larger and the rate of parasite release increased.

Between 1947 and 1958, inundative releases of the egg parasite, *T. minutum*, suppressed the spruce budworm population in the model below both moderate infestation levels of 201.0 and 169.0 egg masses per 10 m^2 foliage (Fig. 1). The necessary application rates for release varied from year to year because the initial egg density of each year fluctuated.

For three of the study years (1954, 1956, and 1957) it was impossible to maintain the budworm population below the light infestation level of 39.3 egg masses per 10 m^2 foliage because the maximum egg mortality obtained with the parasite releases was 69.9% (at a release rate of 12 $\times$ 10^6 female *T. minutum* per hectare [Smith *et al.* 1990]). It may be possible to achieve higher egg mortality of spruce budworm if a greater number of parasites are released; however, continued research is needed in the field to determine the associated level of parasitism and whether this is a cost-effective alternative to current controls.

Simulated Management of the Spruce Budworm Over Different Outbreak Phases. Figure 2*b, c,* and *d* shows the results of releasing *T. minutum* during the inclining, plateau,

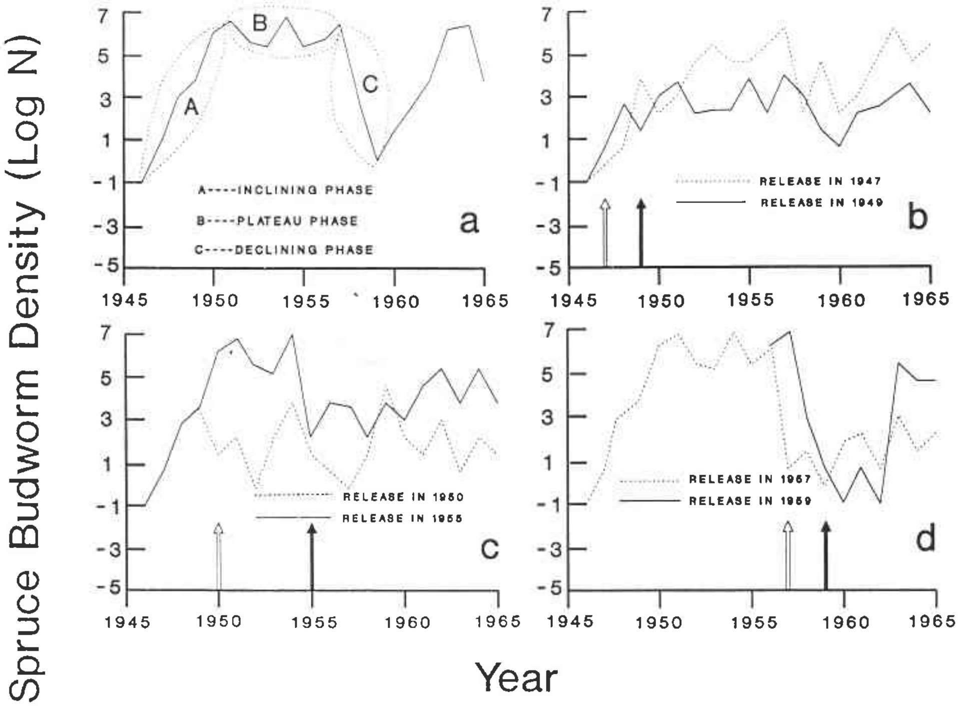

FIG. 2. Simulation results when the egg parasite, *Trichogramma minutum*, was hypothetically released during three different phases of a spruce budworm (SBW) outbreak in the Green River Project (1946–1965). (*a*) Three spruce budworm outbreak phases; (*b*) releases made during the inclining phase; (*c*) releases made during the plateau phase; (*d*) releases made during the declining phase.

and declining phases, respectively, of a spruce budworm outbreak. These results were generated by Eq. [2] with the same a_0 and a_1 values that had been chosen for the simulations. The density-independent Z's in each simulation are uncorrelated random numbers (Royama 1984). After each parasite release, relatively regular cycles were generated because the second-order density-dependent model yielded periodic autocorrelations. These oscillations varied, however, with the different phases and different release dates because the ''initial'' population (the simulation started when the releases were made) was different from phase to phase and from year to year. The amplitude of any given oscillation depended partially on the random nature of the density-independent Z term.

Our results suggest that, from the point of suppressing spruce budworm outbreaks and protecting foliage, releases of *T. minutum* will be most effective when made between the inclining and plateau phases. Based on our assumption that *T. minutum* operates independently of the net effect of other mortality factors and vice versa (Smith *et al.* 1990), the timing of the releases can be refined further in terms of the outbreak phase. During the inclining phase of the outbreak, we found that the later release (1949) provided better suppression than the early release (1947) (Fig. 2*b*). In contrast, for both the plateau and the declining phases, the early release (1950 for the plateau phase and 1957 for the declining phase) was better than the late release (1955 for the plateau phase and 1959 for the declining phase). This is probably due to the effect of budworm density on *T. minutum*. For the early stage of the inclining phase and later stage of the declining phase, the density of spruce budworm would be too low for *T. minutum* to suppress the budworm population.

During the other periods, however, populations of spruce budworm would be high enough to allow the parasite to provide some controlling influence because of the importance of the E/M ratio in the host's population dynamics.

Discussion and Conclusions

In systems modelling, as in population management, ecological factors influence population processes in two ways: as density-dependent or density-independent components. With the spruce budworm, Royama (1981) analysed data from the Green River Project and considered generation survival (H_g) to behave as a density-dependent component. Morris's life table (1963) from the same area suggests that the high mortality (82%) of small budworm larvae (first to third instar), primarily caused by fall and spring dispersal and local climatic conditions, is a density-independent component. Obviously then, generation survival (H_g) in spruce budworm results from the combined effect of both density-dependent and density-independent components. In simulation modelling, it is often difficult to separate the action of these two components. Our model, therefore, has simplified the system by considering most factors as density-independent. This may have serious repercussions because in the real life system, increased mortality in the egg stage may be compensated for by reduced mortality in later stages (if this later mortality is dependent on spruce budworm density and, thus, not additive) and the model cannot take this into account. Although results obtained recently from 2 years of field studies (Smith *et al.* 1990) support our assumption of density-independent survival of late-instar budworm larvae following the release of an egg parasite, further field trials should be conducted to examine the predictions of the model and elucidate the density-dependent or -independent nature of spruce budworm mortality in the various life stages.

Another factor that may result in a discrepancy between the model's prediction and real events in the field may be the relative level of egg parasitism used in the model. The relationship between the rate of parasite release and subsequent parasitism of spruce budworm eggs was derived from field studies in Hearst, Ont. (Smith *et al.* 1990). Infestations of the spruce budworm at this site were always severe. Because the density of the host has been shown to influence the level of egg parasitism by *T. minutum* (Smith *et al.* 1986), the relationship of parasite release rate to egg parasitism at lower budworm densities (light infestations) may be different from that at higher densities (severe infestations). Until the functional response of *T. minutum* on the spruce budworm is elucidated, both in the laboratory and the field, it is not clear whether the results predicted by the model are completely accurate representations of field events.

The relationship between an insect population, such as the spruce budworm, and its environment is often very complex, and although the outbreak history of this species is well known, the causes of these periodic eruptions are still controversial (Fleming 1985). We have tried to avoid this debate surrounding the cause of eruption and, instead, concentrated on determining the potential of one specific management strategy to suppress annual populations of the spruce budworm. Because the extensive data required to analyse long-term oscillations in budworm populations are lacking, we have only dealt with management decisions based on short-term fluctuations. Results of our simulated management, however, do reveal that the oscillating trend in spruce budworm populations can be changed by proper implementation of inundative parasite release.

In the present paper, we have attempted to simulate the management of an historical spruce budworm population using inundative parasite release against the egg stage. Because summary life table data were obtained from the Green River Project (1947–1958), we did not have to estimate budworm egg density (N) or egg survival rate (S) to determine the egg mortality (D) required in Eq. [2]. In a field situation, however, these variables would have to be estimated in our model to derive D. Obviously, the survival rate of spruce budworm eggs is a complex function comprised of weather or natural enemies, or both, and further studies are needed before the projections of egg survival from a mechanistic model such as that developed by MacDonald (1963) can be reliably incorporated into our own model for meaningful predictions under field conditions.

One of the main purposes of any pest management program is to reduce the frequency of pest outbreaks so that the population dynamics of the pest fluctuate around an acceptable stable level. It is essential, therefore, that all strategies available for suppressing pest populations be investigated. Our results suggest that an historical population of spruce budworm can be most effectively managed when parasites are released at the end of the inclining phase or the beginning of the plateau phase and that this strategy will maintain an outbreak population at or below a moderate threshold level, but not at a low threshold level. Future studies should be aimed at integrating this strategy with control methods causing mortality in other life stages, either simultaneously (in the same generation) or sequentially (in consecutive generations). The consequences of changing spatial scale for applications, from small experimental plots, as used in the present study, to full-scale forest management units, must also be addressed to determine the feasibility of this approach. In the final analysis, the financial implications will determine the extent to which egg parasites will be used to manage budworm populations and further cost-benefit analysis will be needed to address this problem adequately.

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