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Patterns of Egg Laying, Overwintering Survival, and Spring Hatch in the Green Apple Aphid (*Aphis pomi*) on Apple Trees

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ABSTRACT

The green apple aphid, *Aphis pomi* De Geer (Hemiptera: Aphididae) is a major pest of apple, with early-season infestations mainly driven by the success of overwintered eggs. To characterize its overwintering biology, a 2-year study was conducted to quantify the timing and pattern of oviposition, egg distribution along shoots, overwintering survival, and hatch dynamics. Oviposition began in early October and lasted 11–12 weeks, peaking between late October and mid-November. Cumulative egg numbers averaged (mean ± SE) 384.96 ± 15.85 per 30-cm shoot on bearing plants in 2022, and 453.66 ± 16.49 on bearing plants and 461.84 ± 14.33 on non-bearing plants in 2023. During the early oviposition phase, eggs were strongly concentrated in the second to fifth 10-cm shoot segments. However, this spatial gradient weakened over time, with later-laid eggs more evenly dispersed along the shoot. Three overwintering conditions were compared: intact shoots on trees, excised shoots placed on the ground, and shoots stored under laboratory conditions. Egg survival was highest in the lab (63.6% ± 2.72%), moderate on intact shoots (42.6%–49.6%), and lowest on ground-excised shoots (23.9%–33.4%). Kaplan–Meier survival analysis indicated a 73% higher hazard of egg mortality in ground shoots compared to intact ones. Egg hatch began in early March and was complete by early April, with median hatch dates around March 20–21 (green tip to half-inch green tip). Cumulative hatch emerged as a more sensitive parameter than hatch timing alone for detecting treatment effects. These findings establish precise phenological benchmarks and show that oviposition behavior and overwintering success are influenced by shoot microhabitat and condition. This study provides the first large-scale, data-driven analysis of *A. pomi* overwintering and offers key parameters for temperature-based forecasting and integrated aphid management in apple orchards.

1 | Introduction

The green apple aphid, *Aphis pomi* De Geer (Hemiptera: Aphididae) is a dominant early-season pest of apple orchards where its rapid clonal multiplication from overwintered eggs enables it to colonize developing buds and shoots soon after budburst (Baker and Turner 1916; Sutton et al. 2014; Gupta and Tara 2015; Rakauskas et al. 2015; Alford 2016; Shah, Rehman, Tramboo, Rasool, et al. 2025; Shah, Rehman, and Tramboo 2025). Like many aphids in temperate climates, *A. pomi* exhibits a holocyclic life cycle, overwintering exclusively in the egg stage (Graf et al. 1985; Blackman and Eastop 2000; Rakauskas et al. 2015). The success of this overwintering phase is critical for population buildup in spring and is influenced by a suite of environmental and physiological factors, including microhabitat conditions and climatic variability.

The studies on overwintering biology of *A. pomi* were attempted very early due to its implications for early-season population establishment. The earliest detailed study on the general biology of *A. pomi* including overwintering strategy was conducted by Baker and Turner (1916) in their opus magnum report followed by numerous other studies including Lathrop (1928) and Cutright (1928, 1930) among others. Current understanding of the overwintering biology of *A. pomi* indicates that the cycle begins with the emergence of sexual forms in early autumn. Oviparous females and wingless males appear mainly in September (Baker and Turner 1916; Woolhouse and Harmsen 1991; Gautam and Kumari 2004; Khan and Shah 2018; Vasyliev 2022), driven by shortening day length and cooling temperature. Oviposition occurs from late September through November, peaking in October, when females deposit small, black, shiny eggs singly or in small groups on smooth young vegetative shoots and bud scales (Westigard and Madsen 1964; Beers et al. 1993; Alston et al. 2010; Walgenbach 2015; van Zoeren and Guedot 2017; Vasyliev 2022). Preferred oviposition sites are vigorously growing water sprouts and the upper portions of 1-year-old shoots rather than fruiting wood (Vasyliev 2022; UC IPM 2015). Fecundity is relatively low, with each oviparous female laying 3–6 overwintering eggs (Baker and Turner 1916), while earlier viviparous generations can produce 40–80 nymphs each (Vasyliev 2022). After deposition, embryonic development begins promptly, with blastoderm and segmentation forming within a week, followed by diapause—a dormant stage characterized by a dorsally flexed embryo encircling the yolk (Baker and Turner 1916).

This diapause persists until late winter when temperatures consistently rise above 4°C–5°C, usually in early March (Vasyliev 2022). Hatching occurs in mid- to late April, coinciding precisely with apple budburst from "green tip" to "mouse ear" stages (Beers et al. 1993; Alston et al. 2010; Walgenbach 2015; van Zoeren and Guedot 2017), requiring approximately 35°C–39°C accumulated effective temperatures (Vasyliev 2022). Reported overwintering egg mortality ranges from 50% to over 70%, caused by cold stress, desiccation, and predation (Leather 1992; Carroll and Hoyt 1984). Carroll and Hoyt (1984) further demonstrated that in Washington orchards, predators such as *Deraeocoris brevis* (Uhler), lacewings (*Chrysopa* spp.), syrphid fly larvae, and earwigs contributed up to 22% additional mortality compared to protected eggs. Mass hatching yields stem mothers (fundatrices), which reproduce parthenogenetically through spring and summer (Carroll and Hoyt 1984; Gautam and Kumari 2004; Khan and Shah 2018). This life cycle—tight synchrony with bud development, a prolonged diapause requiring chilling, and adaptation to survive extreme winter temperatures—underlies the persistent importance of *A. pomi* as an apple pest across temperate regions (Baker and Turner 1916; Beers et al. 1993; Alford 2016; UC IPM 2021; Vasyliev 2022).

The green apple aphid is recognized as a pest of significance affecting apple orchards across Europe, North America, and parts of the Middle East (Blackman and Eastop 2000; Stoeckli et al. 2008; Sutton et al. 2014; Rakauskas et al. 2015; Alford 2016). In India (Kashmir region which accounts for the majority of the country's apple production), populations of this species have recently increased to levels that frequently cause localized outbreaks, representing a significant shift in its economic importance (Shah, Rehman, Tramboo, Rasool, et al. 2025). To address this emerging challenge, systematic investigations have been conducted to characterize the pest's biological traits and ecological interactions, with the objective of developing effective management strategies suited to regional production systems. While classical studies have described the morphology and embryogenesis of *A. pomi* eggs, quantitative understanding of seasonal oviposition schedules, spatial patterns of egg deposition, and the survival and hatch outcomes under field conditions remains limited. Most prior work has either been descriptive, conducted at limited spatial or temporal scales, or has not quantitatively integrated ecological contexts such as tree bearing status and shoot-level oviposition patterns. In the context of increasing climatic variability, there is a need for updated, high-resolution biological benchmarks of oviposition, diapause, overwinter survival, and hatch dynamics, which can subsequently inform climate-linked and phenology-based forecasting efforts.

To address these gaps, a 2-year field study was conducted in apple orchards of Srinagar, Jammu and Kashmir, focusing on four core aspects of *A. pomi* overwintering biology: (1) temporal patterns of oviposition and how they vary between bearing and non-bearing apple trees, (2) spatial dispersion of eggs along terminal shoots, (3) survival of overwintered eggs under different conditions including intact shoots, excised shoots on ground, and laboratory cages, and (4) timing and progression of egg hatch in spring under different orchard blocks. These insights are not only fundamental to understanding aphid overwintering ecology but also critical for developing temperature- and phenology-based forecasting systems for early-season pest emergence.

2 | Materials and Methods

The study was conducted in two distinct apple orchard blocks located at the experimental farm of ICAR–Central Institute of Temperate Horticulture, Srinagar (Jammu and Kashmir, India). The non-bearing orchard covered approximately 0.8 ha, with its approximate centroid located at 33°59′05.8″ N, 74°47′47.3″ E, and consisted of newly planted apple trees that had not yet entered commercial bearing. The bearing orchard covered approximately 3.5 ha, with its approximate centroid located at 33°59′07.9″ N, 74°48′00.4″ E, and comprised approximately 15-year-old trees in regular bearing. Both orchards were planted at a uniform spacing of 3 × 2 m on MM106 rootstock and consisted of multiple apple cultivars. All experiments were conducted on the cultivar "Coe Red Fuji," which sustains high populations of *A. pomi*. The two orchard blocks were spatially separated, with a minimum distance of approximately 210 m between their closest edges. Both orchard blocks were located within the same agroclimatic zone and experienced comparable macroclimatic conditions. The orchard blocks were managed following standard cultural practices, including irrigation, fertilization, and pruning. No insecticidal applications were made against aphids during the study period to allow natural oviposition, overwintering, and egg hatch to occur. The study site has a known history of recurring green apple aphid infestations, and was therefore selected to ensure sufficient egg densities for detailed biological observations.

2.1 | Oviposition Schedule

The oviposition schedule of *A. pomi* was studied both in bearing and non-bearing trees. During the first season (2022–23), the oviposition schedule was studied only on bearing apple trees. Trees showing medium to high *A. pomi* infestation during the late summer period were identified, and 10 such trees were selected for detailed monitoring. The onset of oviposition on these trees was determined by the first appearance of green eggs, which served as the starting point for observations. On each selected tree, five terminal shoots were permanently tagged, giving a total of 50 shoots for the season. During the second season (2023–24), the study was expanded to include both bearing and non-bearing apple trees. Ten trees were selected from each block, and five terminal shoots were tagged on each tree, resulting in 50 shoots per block (100 shoots in total). In both seasons, due care was taken to select shoots from different cardinal directions and from both inner and outer canopy positions to minimize potential bias associated with shoot position within the tree. Tagged shoots were selected from current-season terminal growth and were representative of the range of shoot lengths present on each tree. The number of green eggs on terminal 30 cm of each shoot was counted at 5 days interval. The eggs when first laid are bright green but gradually turn dark and become shiny black in 3–4 days which enables to identify the newly laid eggs as compared to earlier laid ones. Observations started with the appearance of green eggs and ceased with the death of all adults of *A. pomi* including viviparae, oviparae, and males. Shriveled green eggs were not taken in to count as they represent the unfertilized eggs laid by unmated oviparae. Oviposition observations were conducted from 12th October to 3rd January during the first season (2022–23), and from 19 October to 3 January during the second season (2023–24), corresponding to the post-harvest and senescence period of apple, from the onset of leaf yellowing through leaf fall and entry into dormancy (approximately BBCH stages 91–00) (Meier 2001).

2.1.1 | Analysis

Oviposition data (number of freshly laid green eggs per shoot per sampling date) were analyzed using generalized linear models (GLMs) with a Poisson error distribution and log link, appropriate for count data. Sampling date was used as the primary explanatory variable to evaluate temporal trends in oviposition. For 2023–24, block (bearing vs. non-bearing) and the Date × Block interaction were included to test for differences in temporal oviposition patterns between tree types. Egg counts were pooled across shoot orientations because shoots were sampled in a balanced manner across cardinal directions and canopy positions, and orientation was not treated as an experimental factor. To compare oviposition dynamics between years for bearing trees, a model including a Date × Year interaction was fitted. Model diagnostics were examined to assess the adequacy of the Poisson error structure. Cumulative egg deposition per tree was calculated by summing egg counts across sampling dates and compared between bearing and non-bearing trees using a *t*-test. Differences in peak oviposition timing between blocks were evaluated using the Wilcoxon rank-sum test. All analyzes were performed in R version 4.3.1 (R Core Team 2023).

2.2 | Egg Dispersion

Relative egg dispersion on terminal shoots was studied during 2022–23 and 2023–24. The number of eggs was noted on shoots excised from the selected trees at each sampling and brought to the laboratory. Each shoot was divided into segments of 10 cm length and numbered from shoot tip downwards. During 2022–23, shoots from non-bearing trees were collected on October 27, 2022 representing the early phase of the oviposition period, and on October 27, 2022 representing the termination of oviposition. On each sampling date, 12 trees were selected with a medium to high number of *A. pomi* eggs, and four shoots were excised from each tree (96 in total). The number of eggs that were green and those that had turned black was counted on each segment of 10 cm length (1207 in total). In addition, the diameter of each shoot segment was also recorded at the top, bottom, and middle area. Further, the total shoot length and number of leaves were also recorded.

During 2023–24, shoots from both bearing and non-bearing trees were collected on one occasion (December 22, 2023) close to the termination of oviposition. Eight (8) trees were selected from the non-bearing block and 3–5 shoots were excised from each tree (30 in total) and brought to the laboratory. On the same date, six trees were selected from the bearing block and 3–4 shoots were excised from each tree (20 in total) and brought to the laboratory. A total of 349 and 169 shoot segments were studied, respectively, from the non-bearing and bearing blocks. The number of eggs and other parameters were recorded as described above. The number of shoots sampled per block varied according to shoot availability and length, but dispersion analyzes were conducted at the shoot-segment level, ensuring comparable analytical resolution across tree types.

2.2.1 | Analysis

The lateral surface area of shoot segments was calculated to determine the density of total number of eggs per square centimeter of the surface area of the segments. The difference in egg dispersion along the shoot segments was analyzed by a linear model. The effect of bearing status of the plants and the time of oviposition period (early and late) was tested as fixed effect using linear modeling with the *lm* function in R version 4.3.1 (R Core Team 2023).

2.3 | Egg Survival

The overwintering survival of the eggs of *A. pomi* was studied from the last week of December till the egg hatch started in the first fortnight of ensuing March for 2 years (2022–23 and 2023–24). This period corresponded to the dormant phase of apple development, from deep dormancy through the early stages of bud swelling (approximately BBCH stages 00–03), extending to about 2 weeks prior to the green tip stage (BBCH 53; Meier 2001). Shoots carrying a sufficient number of eggs were selected and areas were marked with a felt pen demarking a selected number of eggs. The number of intact eggs was counted along with shriveled and crumpled eggs on each sampling occasion roughly at 10 days' interval. The egg survival was studied on intact shoots on apple trees under actual field conditions. In addition, survival of eggs was also studied on pruned shoots stalked on the ground at the border of the orchard, and in laboratory conditions in insect cages.

During 2022–23, nine trees were selected with a high number of *A. pomi* eggs in an apple orchard consisting of *Coe Red Fuji* plants in the early bearing stage. On each tree, 2–3 shoots were tagged (20 in total), and three segments/areas were marked on each shoot. The number of intact eggs ranged from 38 to 150 on each marked segment at the beginning of the study.

For excised shoots stalked on ground, five bundles of 20–30 shoots were selected for the study. In each bundle, two shoots were tagged and three segments were marked on each tagged shoot. The number of intact eggs ranged from 55 to 330 on each marked segment at the beginning of the study. For laboratory study, shoot segments of 15 cm length were cut with a sufficient number of GAA eggs and brought to the laboratory and placed in ventilated insect-rearing cages under ambient laboratory conditions, with temperature, relative humidity, and photoperiod following natural winter fluctuations. In four cages, 24 shoot segments were placed, and out of these, 15 were tagged for the study, 3–6 in each cage. The total number of eggs on the whole shoot segment was counted. The number of intact eggs ranged from 125 to 460 on each marked shoot segment. The laboratory treatment was included during the first season to establish a reference condition representing minimal biotic and abiotic mortality and was not repeated in the second season, which focused on comparative survival under field-relevant overwintering conditions.

During 2023–24, the egg survival study was repeated on intact shoots on apple trees, and on pruned shoots stalked on the ground. Three shoots each were tagged on 10 selected trees (30 shoots in total), and three segments/areas were marked on each shoot. The number of intact eggs ranged from 15 to 47 on each marked segment at the beginning of the study. For excised shoots on the ground, five bundles of 20–30 shoots were selected again, and in each bundle, two shoots were tagged, and three segments were marked on each selected shoot. The number of intact eggs ranged from 22 to 55 on each marked segment at the beginning of the study.

2.3.1 | Analysis

Survival analysis was performed to evaluate the difference in egg viability over time for all the three sites of overwintering (treatments). The data were structured by individual egg units, with each replicate defined by a unique combination of tree, shoot, and segment. Survival time was calculated as the number of days from the initial observation until hatching or loss. Eggs that remained intact by the final observation date were treated as censored and death as the event (shriveled eggs and disappeared eggs marked as dead). Kaplan–Meier survival estimates were generated for each treatment group, and differences between survival curves were tested using the log-rank test. A Cox proportional hazards model was fitted to estimate relative risks associated with treatments. To account for multiple comparisons, Bonferroni correction was applied in pairwise tests. All statistical procedures were conducted in R version 4.3.1 using the *survival* and *survminer* packages. For the first year, egg survival on intact shoots, shoots stalked on ground, and those kept in laboratory were compared. For the second year, the intact and ground stalked shoots were compared. Survival on intact shoots over the two seasons was also compared. Survival analyzes were conducted at the individual egg level using time-to-event methods, which are robust to unequal sample sizes among treatments. Additionally, survival percentages were summarized at the replicate level to calculate means and standard errors across treatments. Because time was explicitly modeled as the survival response, sampling date was not included as a separate fixed effect.

2.4 | Egg Hatch

The hatching of overwintered *A. pomi* eggs was evaluated over two consecutive seasons (2022–23 and 2023–24) across two orchard management blocks (bearing and non-bearing). In each case, a number of shoots on a series of plants was identified carrying a sufficient number of eggs. On each shoot, segments containing multiple eggs were marked using a felt pen, and progressive egg hatch was monitored daily from the first week of March to the first week of April. The monitoring period was selected based on published phenological information for *A. pomi* (Beers et al. 1993; Alston et al. 2010; Walgenbach 2015; van Zoeren and Guedot 2017) and coincided with apple bud development from bud swelling through first flower opening (approximately BBCH stages 07–60; Meier 2001). Observations continued daily until no further egg hatch was recorded. In 2022–23, five plants each from bearing and non-bearing blocks were selected and two shoots were tagged on each tree. On each shoot, three segments were marked (totaling 30 segments each from bearing and non-bearing blocks). During 2023–24, 10 plants were selected from the bearing block and 2–4 shoots were tagged on each tree (20 in total). On each shoot, three segments were marked. In the non-bearing block, eight trees were selected and 2–4 shoots were selected on each tree (24 in total). Again on each shoot, three segments were marked. On each sampling date, the number of intact and hatched eggs was noted.

2.4.1 | Analysis

Daily and cumulative hatch percentages were derived from longitudinal observations on individual marked shoot segments nested within trees and shoots, and temporal progression of hatch was compared between blocks and years. Mixed-effects modeling was conducted to examine the effects of year and block on both daily and cumulative hatch percentages using *lmer* and *lmerTest* functions in R version 4.3.1. Year, block, and their interaction (year × block) were used as fixed effects and tree/shoot/marked segment as nested random effects, accounting for the experimental hierarchy: segments within shoots, within trees to account for repeated measurements and unequal sampling intensity. Total seasonal hatch and date of median hatch (50%) were also calculated.

3 | Results

3.1 | Oviposition

The oviposition activity of *A. pomi* exhibited a clear seasonal trend, with peak egg deposition occurring between late October and mid-December in both years. A total of 2340 oviposition records were

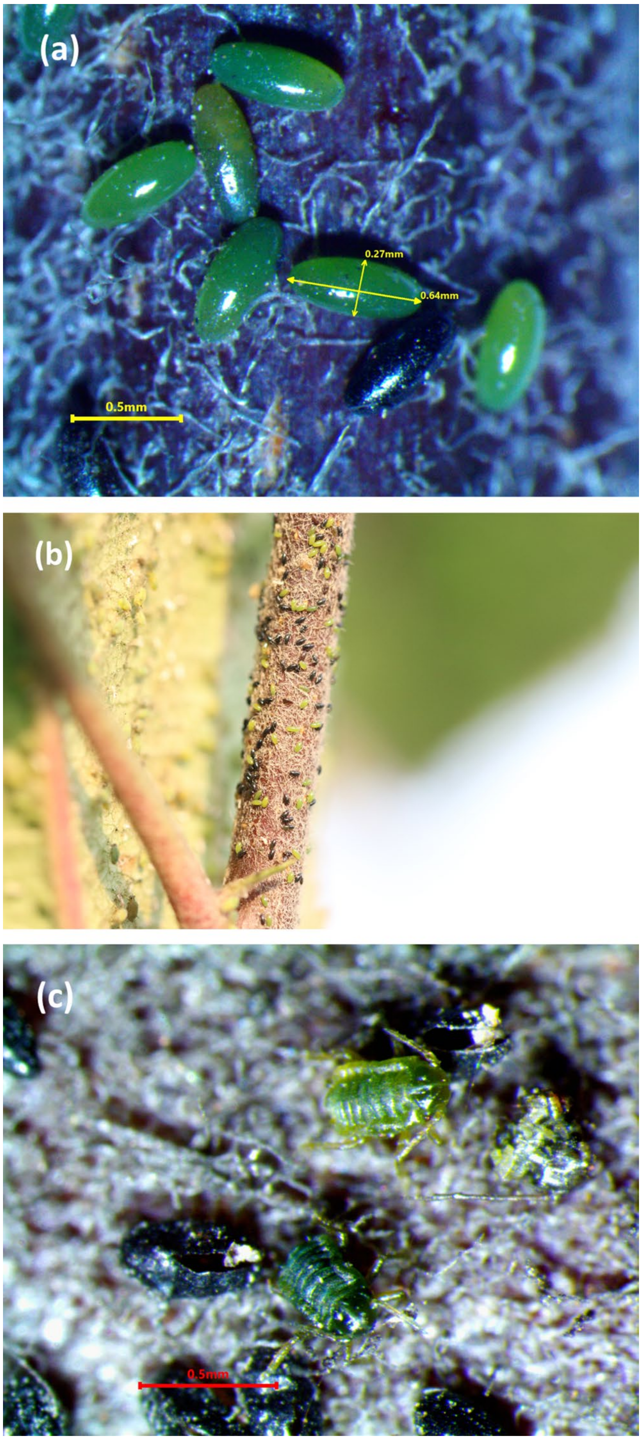

FIGURE 1 | Eggs of *Aphis pomi* on apple shoots (a), distribution of green and black eggs on apple shoots (b), and nymphs hatching from the overwintering eggs (c).

analyzed, spanning 2022–23 and 2023–24. In 2023–24, data were collected from both bearing and non-bearing apple trees, while only bearing trees were included in 2022–23. The green and black eggs, their distribution on the shoots and nymphs hatching from the overwintering eggs are depicted in Figure 1.

Weekly mean oviposition data revealed similar temporal trends across blocks, with *A. pomi* egg counts rising sharply during October, peaking October end to mid-November, and declining toward end of December (Figure 2). During 2022–23 on bearing plants, the mean number of green eggs laid per shoot was recorded as (mean ± SE) 29.6 ± 5.11 on the first date of observation (October 12, 2022). The number of eggs increased to 49.62 ± 6.45 on October 25, 2022, and declined gradually afterwards. During 2023 on bearing plants, the mean number of green eggs laid per shoot was recorded as 40.24 ± 5.74 on the first date of observation (October 19, 2023). The number of fresh eggs fluctuated over the next 5 weeks and the peak number of eggs (42.02 ± 4.21) was recorded on November 22, 2023. On non-bearing plants, the consistent number of eggs was laid (31.2–35.7) till November 7, 2023 and thereafter peaked on November 17, 2023 with 48.62 ± 5.86 eggs per shoot.

Cumulative egg deposition was higher in 2023–24 (453.66 ± 16.49 on bearing plants, and 461.84 ± 14.33 on non-bearing plants) than in 2022–23 (384.96 ± 15.85). Although non-bearing trees in 2023 appeared to receive slightly higher total egg loads, a *t*-test comparing the total eggs per tree showed no significant difference between bearing and non-bearing trees ($t = -0.093$, df = 14.6, $p = 0.92$).

A Poisson GLM showed a strong temporal decline in egg numbers (green eggs) over time (Date: $\beta = -0.02$, $p < 0.01$), for bearing trees during 2022–23 indicating that oviposition decreased steadily as the season progressed. Modeling with a Poisson GLM including an interaction term between Date and Block revealed no significant difference in oviposition trends between bearing and non-bearing trees. The interaction term (Date × Block) was non-significant ($\beta = -6.3\text{e}{-}05$, $p = 0.88$), suggesting a similar temporal trend across tree types. The main effect of date remained strongly significant ($\beta = -0.013$, $p < 0.01$), reinforcing a general seasonal decline.

A Wilcoxon rank-sum test comparing peak dates between bearing and non-bearing blocks in 2023–24 showed no significant difference ($W = 1$, $p = 1.0$). To evaluate differences between years in case of bearing trees, a GLM with an interaction between Date and Year was used. The interaction term was highly significant ($\beta = 0.0072$, $p < 0.01$), indicating that while oviposition decreased over time in both years, the rate of decline was significantly slower in 2023–24, suggesting more sustained oviposition during the latter part of the season. However, oviposition duration—measured as the number of days from first to last observed oviposition activity—did not differ significantly between years for bearing trees ($W = 1$, $p = 1.0$), indicating a consistent oviposition window across seasons and plant conditions.

3.2 | Egg Dispersion

A total of 1657 shoot segments were assessed across bearing and non-bearing apple plants over two consecutive seasons (2022–23 and 2023–24). Eggs were counted and standardized as density per unit surface area (eggs/cm^2), using segment-specific diameters and lengths to calculate the lateral surface area of each segment. The average shoot length varied from 91 to 184 (129.86 ± 2.84) cm for non-bearing plants during 2022–23 and 84–146 cm (119.73 ± 3.34) cm during 2023–24. For bearing plants, average shoot length varied from 45 to 82 cm (62.35 ± 2.47).

The mean number of total eggs per segment was highest on segments 2 to 5 and gradually decreased downwards. The topmost segments also carried a lower number of eggs as compared to the adjacent segments. In the early part of oviposition, the number of eggs on the first segment was recorded as 187.1 ± 16.0 which increased to 261.1 ± 20.4 on the second segment. Toward the termination of oviposition, 75.6 ± 8.5 eggs were found on the top segment which increased to 143.3 ± 13.1 on the 4th segment.

During 2023–24, the average number of eggs on the top segment was recorded as 139.9 ± 16.4 on non-bearing plants which increased to 158.5 ± 17.5 on the 2nd segment. In case of bearing plants, 82.7 ± 9.5 eggs were recorded on the top segment which increased to 131.7 ± 16.6 on the 4th segment. In Figures 3 and 4, the egg dispersion is indicated as density per square centimeter of the lateral surface area of shoot segments. There was a distinct decrease in eggs from tip to base, more pronounced early in the season. Further, there is considerable overall reduction in the number of eggs on all segments toward the termination of oviposition period. Bearing and non-bearing plants show comparable

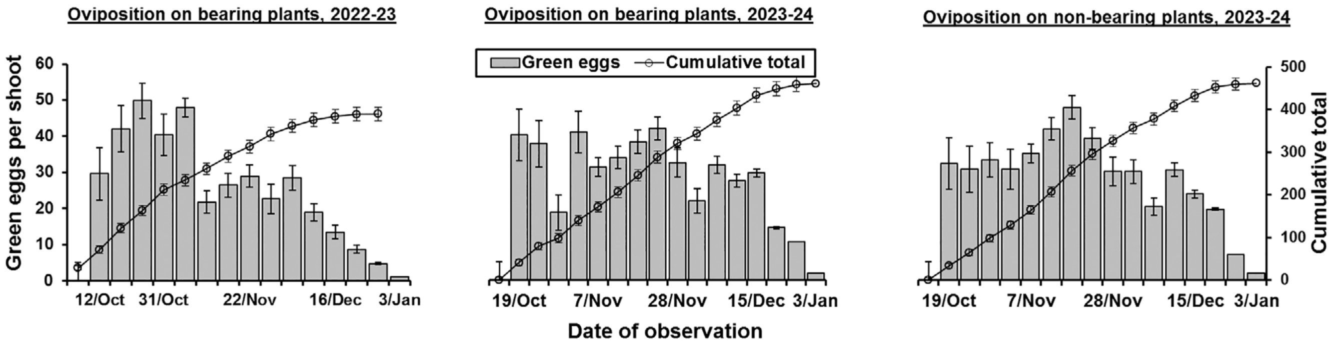

FIGURE 2 | Seasonal dynamics of oviposition by *Aphis pomi* oviparae on apple shots.

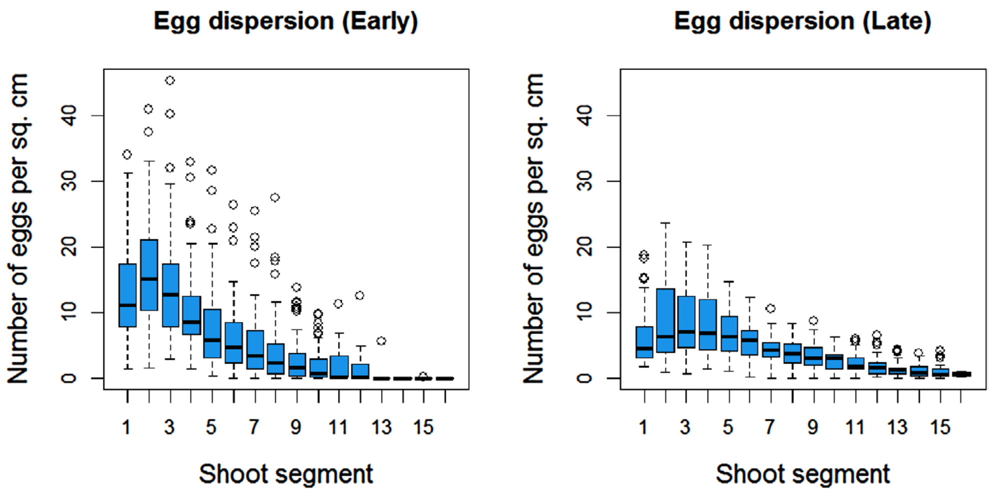

FIGURE 3 | Boxplots of egg density per segment for early versus late part of oviposition period (2022–23).

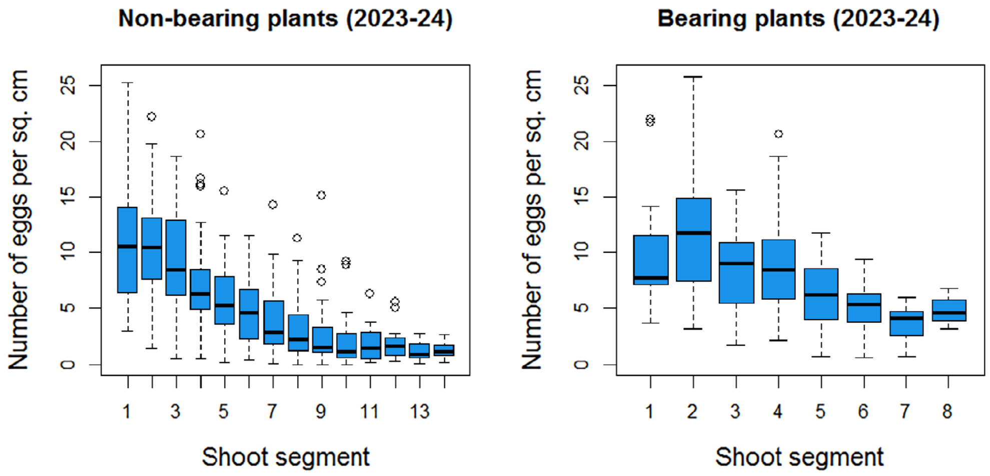

FIGURE 4 | Boxplots of egg density per segment for bearing vs non-bearing plants (2023–24). Survival of overwintering eggs.

TABLE 1 | Mean percent survival (±standard error) of the overwintering eggs of *Aphis pomi* under different treatments across two winter seasons (2022–23 and 2023–24).

Season	Treatment[a]	Total eggs observed	Replicates	Mean percent survival (±SE)
2022–23	Intact	4383	60	49.6 ± 2.34
	Ground	4253	30	33.4 ± 2.61
	Lab	3878	15	63.6 ± 2.72
2023–24	Intact	1902	60	42.6 ± 2.44
	Ground	1146	30	23.9 ± 2.72

[a] Treatments included intact shoots on trees; excised shoots placed on the ground, and excised shoots maintained in laboratory cages. Values represent means calculated across replicate units (tree–shoot–segment combinations).

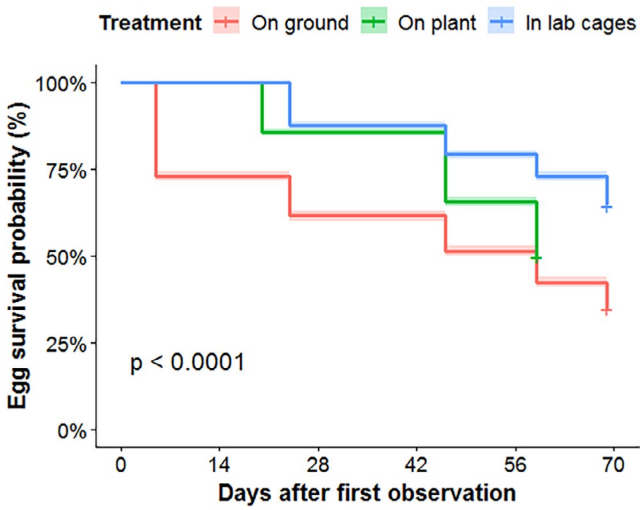

FIGURE 5 | Kaplan–Meier survival analysis of overwintering eggs of *Aphis pomi* across three treatments during winter 2022–23: Intact shoots on trees, excised shoots placed on the ground, and excised shoots maintained in laboratory cages. Eggs kept in the laboratory showed the highest survival, followed by those on trees and on the ground (log-rank test, $p < 0.001$).

oviposition gradients, although the number of eggs per segment and total egg complement is lower for bearing plants.

The distribution of eggs along shoot segments was significantly influenced by the position of the segment and the time of oviposition. A linear model assessing average egg density per sq. cm as a function of segment number, sampling date representative of beginning and termination of oviposition revealed that segment position was highly significant ($F = 597.5$; df = 1, 1185; $p < 0.001$), with egg density decreasing along the shoot from tip to base, and the difference between the sampling dates was also significant ($F = 36.67$; df = 1, 1185; $p < 0.001$), with higher densities observed during early oviposition. The interaction between segment position and date was significant ($F = 93.62$; df = 1, 1185; $p < 0.001$), indicating that the rate of decline in egg density along the shoot was less steep later in the season.

Notable effect of shoot position was also noted for both bearing and non-bearing plants ($F = 312.0$; df = 1, 464; $p < 0.001$ during 2023–24) but limited influence of plant bearing status on egg density was recorded. Bearing status (bearing vs. non-bearing plants) was not significant as a main effect ($F = 0.91$; df = 1, 464; $p = 0.34$), nor was the interaction term ($F = 1.14$; df = 1, 464; $p = 0.29$), indicating that oviposition pattern along shoots was similar between the two plant types. However, in a separate analysis comparing overall egg density pooled across shoot segments, bearing status had a significant effect, with non-bearing plants supporting higher egg densities than bearing plants ($F = 33.85$; df = 1, 466; $p < 0.01$).

3.3 | Egg Survival

Over two consecutive winters, the survival of *A. pomi* eggs was examined under different overwintering conditions to offer varying degrees of protection from mortality factors. The three treatment conditions included intact shoots on the tree (Intact), shoots excised and placed on the orchard floor (Ground), and shoots excised and stored in mesh cages under laboratory conditions (Lab). The intact eggs were tracked from the last week of December to the first fortnight of March. The mean survival percentages across all treatment combinations are given in Table 1.

During the 2022–23 season, a total of 12 514 eggs were included in the study: 4383 from intact tree shoots, 4253 from ground-excised shoots, and 3878 from excised shoots kept in laboratory cages. Eggs on intact shoots had a median survival of 59 days, similar to the ground treatment; however, survival probability dropped more sharply for the ground condition beyond the midpoint of the winter (Figure 5). Eggs in the Lab treatment showed superior survival, with the survival curve never reaching 50% mortality within the study duration. On day 30, survival probabilities were 87.8% for Lab, 85.7% for Intact, and 61.6% for Ground. By day 60, survival in the Ground treatment had dropped to 42.4%, while the Lab and Intact curves remained significantly higher.

Log-rank test for comparisons showed statistically significant differences between all treatments ($\chi^2 = 991$; df = 2; $p = 0.03$). Eggs on ground-excised shoots had significantly lower survival than those on intact shoots, and lab-stored shoots had significantly better survival outcomes than both field treatments. The Cox model estimated a 39.61% increased hazard of egg death for the eggs on shoots stalked on ground as compared to intact shoots (HR = 1.39, $p \leq 0.01$), and eggs on shoots inside laboratory experience 48.64% less hazard of death as compared to the intact shoots (HR = 0.51, $p \leq 0.01$). The shape of the survival curve and the greater cumulative mortality for ground-excised shoots confirmed significantly higher mortality for eggs on shoots stalked on ground.

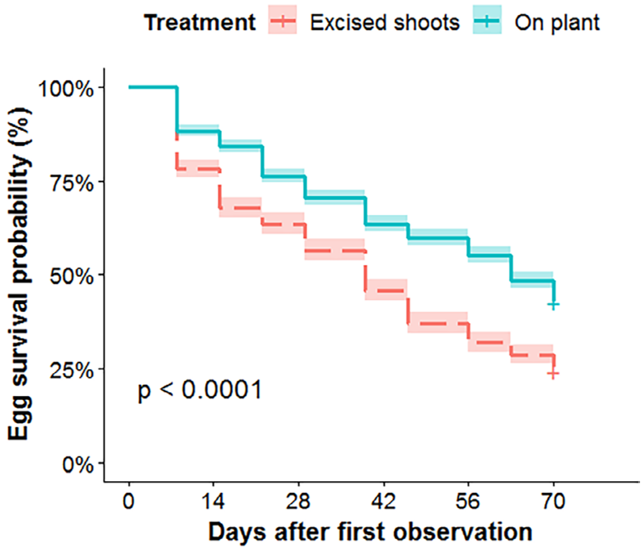

FIGURE 6 | Kaplan–Meier survival curves showing the probability of *Aphis pomi* egg survival over time during winter 2023–24 under two treatments: Intact shoots on trees and excised shoots placed on the ground. Eggs on intact shoots exhibited significantly higher survival rates compared to those on ground shoots (log-rank test, $p < 0.001$).

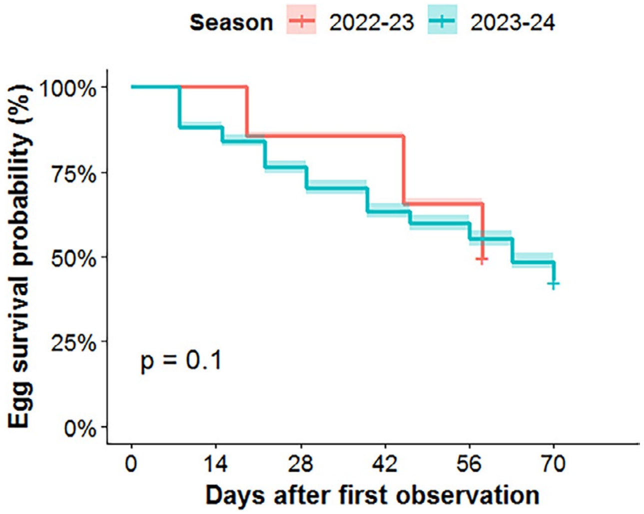

FIGURE 7 | Comparison of Kaplan–Meier survival curves showing the probability of *Aphis pomi* egg survival over time on intact shoots over two seasons.

In the winter of 2023–24, survival was compared between the Intact and Ground treatments. A total of 3048 eggs were monitored: 1902 on intact tree shoots and 1146 on excised shoots laid on the orchard ground. Eggs on intact shoots had a final survival rate of 42.6%, while those on ground-excised shoots had only 24.3% survival. Kaplan–Meier analysis revealed a clear separation between survival curves (Figure 6). The median survival time was 63 days for intact shoots and 39 days for ground shoots. A log-rank test confirmed that this difference was highly significant ($\chi^2 = 144$; df = 1; $p \leq 0.01$). The Cox proportional hazards model further supported this outcome, indicating a hazard ratio of 1.73, meaning that eggs on ground shoots were 73% more likely to die during the observation period compared to those on intact shoots.

When comparing survival on intact shoots across both winters, results were remarkably consistent. The final survival rate for intact shoots was around 49.8% in 2022–23 and 42.6% in 2023–24, with only a slight increase in median survival time in the latter year (63 vs. 59 days) (Figure 7).

3.4 | Egg Hatch

Egg hatch dynamics of *A. pomi* were evaluated over two consecutive seasons (2022–23 and 2023–24) across two orchard management blocks (bearing and non-bearing). The initiation of hatching occurred in early March in both seasons, with no hatch recorded on the first few observation dates. Hatch activity intensified rapidly thereafter, reaching peak rates between March 20 and 23 in both years. The date of median (50%) hatch occurred consistently around the third week of March for all treatments. Specifically, in the bearing block, median hatch occurred on March 21 in 2023 and March 20 in 2024. In the non-bearing block, median hatch was observed 1 day earlier in 2024 (March 19) compared to March 21 in the previous season.

The final percent hatch, calculated as the cumulative hatch at the end of each season, showed modest inter-annual variation and block-wise differences. In the bearing block, mean total hatch was 39.49% ± 3.61% ($n = 28$) in 2022–23, increasing to 43.78% ± 2.38% ($n = 30$) in 2023–24. The non-bearing block recorded higher overall hatch in both years, with means of 43.95% ± 2.04% ($n = 56$) and 45.72% ± 1.34% ($n = 72$) for 2022–23 and 2023–24, respectively.

Mean daily hatch percentages revealed a pronounced increase during the mid-March period (Figure 8). In 2022–23, daily hatch in the bearing block peaked at 8.85% on March 20, while the non-bearing block showed its highest daily hatch of 14.36% on March 21. A similar pattern emerged in 2023–24, with the bearing block peaking at 7.45% on March 20 and the non-bearing block at 10.25% on March 19. Earlier and more intense daily hatch in the non-bearing block was consistent across both years. Daily hatch values during early March were uniformly low across all treatments, with most days from March 5 to 13 registering less than 2% hatch.

Cumulative hatch percentages increased progressively from early March and plateaued by the end of the month (Figure 9). In 2022–23, the cumulative hatch reached 100% by March 31 in the bearing block and April 3 in the non-bearing block. In 2023–24, 100% cumulative hatch was achieved by April 1 in both blocks. The cumulative hatch curve was steeper in the non-bearing block, reflecting an accelerated hatching process. On March 21, 2023, cumulative hatch was 52.5% in the bearing block and 51.3% in the non-bearing block; however, by March 24, the non-bearing block had reached 79.8% compared to 96.1% in the bearing block, suggesting slight variation in the tapering phase of hatch between blocks.

Mixed-effects modeling was conducted to examine the effects of Year and Block on both daily and cumulative hatch percentages. For daily hatch, the linear mixed model showed no statistically significant fixed effects, although the year effect approached significance (Year: $t = 1.71$, df = 3364.99; $p = 0.08$). Neither the block effect ($p = 0.84$) nor the interaction between year and block

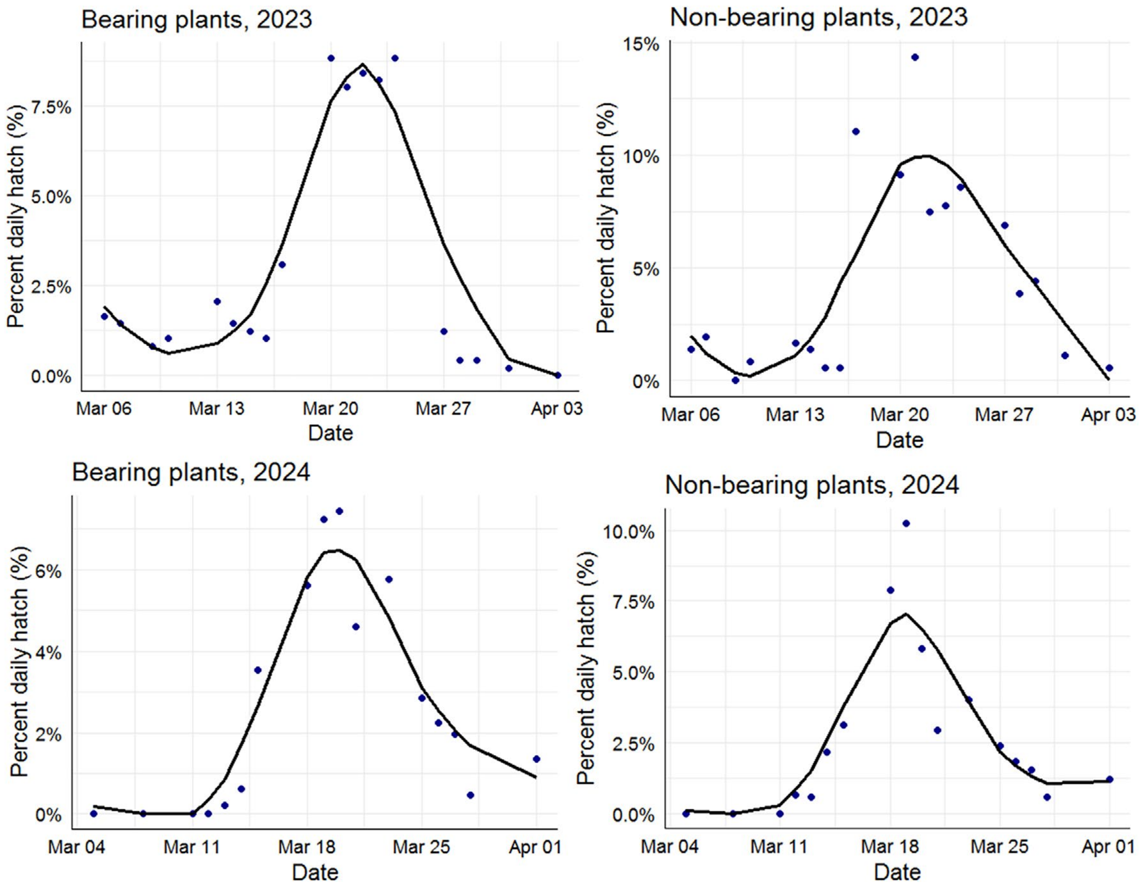

FIGURE 8 | Seasonal trend of daily hatch (%) of *Aphis pomi* eggs across different years and apple block types. Mean percent daily hatch is plotted over time for each Year × Block combination, with LOESS smoothing applied to highlight temporal patterns. Points represent mean values on each sampling date.

($p = 0.84$) was significant. The model exhibited a singular fit, indicating limited variance among nested random effects (Tree/Shoot/Segment), with nearly all variance attributed to the residual error ($\sigma^2 = 58.31$). In contrast, the cumulative hatch model indicated significant effects for all fixed terms. Cumulative hatch percentage was significantly influenced by Year ($t = -2.681$, df = 1226.59, $p = 0.007$), Block ($t = -2.744$, df = 3144.19; $p = 0.006$), and their interaction ($t = 2.745$, df = 3143.89, $p = 0.006$). These results suggest that cumulative hatch dynamics are sensitive to both temporal and spatial orchard management factors. Notably, while residual variance remained high ($\sigma^2 = 1398.0$), tree-level random effects contributed meaningful variance ($\sigma^2 = 5.08$), supporting the inclusion of hierarchical structure in the model.

4 | Discussion

We investigated the oviposition schedule of *A. pomi* in terms of how the timing, intensity, and duration of oviposition varied between seasons and between bearing and non-bearing apple trees. The fact that oviparae that are unmated lay eggs which remain green and shrivel up, in contrast to fertilized eggs which turn black 2–4 days allowed counting of the freshly laid eggs sampled at roughly 5 days interval. As remarked by Baker and Turner (1916), this period (green eggs) corresponds to the active growth of embryos inside the eggs once laid and onset of dormancy within 5–6 days as the eggs turn black. Despite some year-to-year variation in egg numbers, the timing and duration of oviposition were remarkably consistent across both bearing and non-bearing trees during the 2 years of observation. Peak oviposition occurred in late November, and the seasonal window spanned approximately 11–12 weeks in both years. The oviposition biology of *A. pomi* has historically been described in general terms, with earlier studies noting that oviposition typically occurs from October to early December, peaking in late October or early November (Westigard and Madsen 1964; Rakauskas and Rupais 1983). Specht (1970) reported that egg deposition occurred after the photoperiod became shorter than 11.8/24 h and temperatures less than 12°C during the light period, and 8°C during darkness in controlled laboratory conditions. In the current study, for the first time, oviposition patterns were monitored at regular five-day intervals over 2 years, allowing precise characterization of the onset, peak, and decline of egg laying activity. Moreover, the study uniquely compared oviposition on bearing and non-bearing trees, revealing that the temporal dynamics and duration of oviposition were remarkably consistent across both orchard blocks.

Although it is observed that the incidence of viviparous population of *A. pomi* is higher on the non-bearing plants during the active season when the aphid multiplies parthenogenetically, the difference in the egg complement on bearing and non-bearing plants was non-significant. This indicates that when the plants are no longer in active growth and not producing succulent new

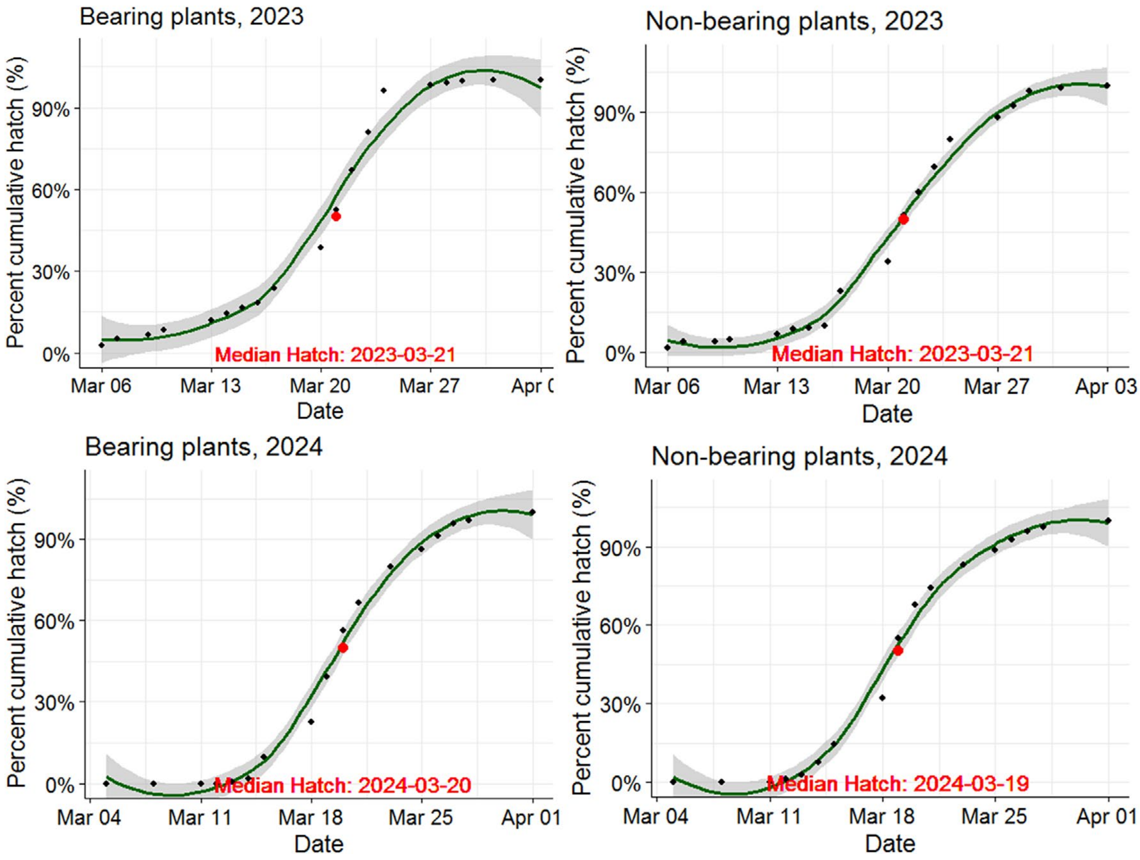

FIGURE 9 | Cumulative hatch (%) of *Aphis pomi* eggs over time across years and apple block types. Mean percent cumulative hatch is shown by sampling date for each Year × Block combination, with LOESS curves fitted to illustrate temporal progression. Data points represent observed means.

leaves and growing shoots, the preference for such tissues to feed on disappears or probably the sexual forms do not have a preference for such tissues. Specht (1970) reported that aphids left the apex of the tree after vegetative growth ceased and became distributed more or less evenly over the older leaves.

The rate of egg deposition peaks 2–4 weeks after commencement and declines thereafter. It might indicate a strong effect of declining daily temperature on the survival, mating, and hence egg laying capacity of the sexuals. Baker and Turner (1916) reported that some of the oviparous females could tolerate temperatures as low as 6°C with multiple exposures to sub-zero temperatures. The average monthly daily maximum/minimum temperature was recorded as 23.47°C/7.17°C during October, 15.55°C/2.13°C during November, and 10.26°C/−2.1°C during December during 2023. We also found that while oviposition decreased over time in both years, the rate of decline was significantly slower in 2023–24, suggesting more sustained oviposition during the latter part of the season. This could be related to slightly warmer temperatures during 2023 (23.43°C/7.02°C during October and 14.14°C/2.26°C during November 2022).

Previous reports on *A. pomi* egg placement largely emphasized qualitative trends, such as preference for water sprouts and young shoots, with eggs concentrated near buds and bark crevices (Baker and Turner 1916; Leather 1992). However, there was no systematic quantification of vertical egg distribution along the shoot. The present study addresses this by segmenting terminal shoots into 10 cm intervals and standardizing egg counts by lateral surface area (eggs/cm^2), offering the first spatially explicit model of egg dispersion in *A. pomi*. The results showed a distinct pattern: peak egg density occurred between the second and fifth segments from the tip, with significantly fewer eggs at the shoot apex and base. Additionally, this vertical distribution pattern became more diffuse toward the end of the oviposition period, indicating a temporal shift in oviposition spatial pattern. In California, Westigard and Madsen (1964) found the greatest density of eggs at 15 cm from the tip of the limbs and 82% were found within 38 cm from the tip. Specht (1970) reported that at the time of the highest rate of oviposition in an environment, a larger concentration of aphid was found on the 6–10 leaf area than on the other leaves. Perdikis et al. (2008) reported that eggs were more commonly laid near the buds of the central part of the twigs. Our findings provide a new framework for understanding spatial egg placement and suggest that aphids modulate egg dispersion over time, likely in response to crowding, environmental cues or senescence of shoot tissues. The observed vertical egg distribution, with consistent concentration on sub-apical shoot segments, suggests that aphid oviposition is spatially structured rather than random. These findings suggest that routine winter pruning, when it removes distal portions of terminal shoots where egg densities are highest, may incidentally reduce overwintering egg loads without requiring changes to standard pruning practices. It is important to note that the shoot-segment–based approach used in this study differs from conventional in-season aphid sampling protocols, which typically focus on short (10–15 cm) fresh shoots in the outer canopy to monitor active populations (Alford 2016). In contrast, the present study intentionally examined longer terminal shoots to characterize spatial patterns of overwintering egg placement along the shoot during the sexual phase.

The rate of decline in egg density along the shoot was less steep later in the season. As noted by Baker and Turner (1916) and numerous others, the eggs tend to cluster around the buds and other rough areas on the shoots. This seems to be the case during the early part of oviposition when the number of eggs is lower. The preference for such locations may not be a factor when the number of eggs laid is higher (higher number of oviparae). Even the steepness of the gradient of egg dispersion along the shoot length, top to bottom, decreases toward the termination of the oviposition period possibly to avoid crowding of the eggs, as observed in the current study.

Significant overall reduction in the number of eggs on all segments toward the termination of oviposition period was noted as a rule. Carroll and Hoyt (1984) noted significant predation of oviparae and eggs during the period of oviposition to the extent of 34.2%. Westigard and Madsen (1964, 1965), Woolhouse and Harmsen (1991), and Stewart and Walde (1997) showed that predator activity were the most influential agents in lowering aphid populations toward the end of active crop growth. Further, they also noted that the late season predators were predominantly sucking insects. As such, the attacked aphid eggs are left in place but shriveled in appearance (Holdsworth 1970; Carroll and Hoyt 1984; Tracewski et al. 1984). Therefore, it seems like predation may have been a significant factor that may shape the dispersion pattern of the eggs during the oviposition period itself and may cause significant reduction in the number of eggs as well. The predatory activity on the eggs is reported to continue after the termination of the oviposition well in to winter albeit at much lower rate (Carroll and Hoyt 1984).

The relative risk of egg mortality was evaluated by comparing overwinter survival across three contrasting environments: intact shoots on trees, excised shoots placed on the orchard floor, and excised shoots maintained under laboratory conditions. These treatments represented different overwintering microhabitats associated with varying degrees of exposure. Survival analysis using Kaplan–Meier curves and Cox proportional hazards models showed that eggs maintained under laboratory conditions exhibited the highest survival (63.6%), eggs on ground-laid shoots the lowest (23.9%–33.4%), and eggs on intact shoots intermediate but consistently higher survival (42.6%–49.6%), with limited inter-annual variation. Among the mortality factors, the activity of predatory insects and spiders, birds, freezing injury, and physical abrasion and dislodgement by snow, etc., in addition to natural mortality differed significantly among the three tested environments (Leather 1992).

Previous assessments of *A. pomi* overwinter survival have largely relied on single-condition field estimates with broad mortality ranges. By explicitly comparing survival across multiple overwintering environments over two winters, the present study provides a quantitative assessment of how shoot condition and placement influence overwintering success. Notably, the persistence of viable eggs on pruned shoots placed on the orchard floor indicates that such material may contribute to early-season aphid emergence. Although the relative contribution of this source requires further evaluation, these findings support orchard sanitation practices, such as removal of pruned material, as a complementary cultural measure within integrated pest management programs.

Although it has long been known that *A. pomi* eggs hatch in spring shortly before budburst, with a correlation to rising temperatures (Baker and Turner 1916; Vasyliev 2022), detailed temporal resolution of hatch progression has been lacking. This study delivers the first fine-scale daily monitoring of egg hatch, revealing that hatch begins in early March, peaks between March 20 and 23, and concludes by early April, with consistent median hatch dates across years and blocks. The consistency of median hatch date for *A. pomi* eggs across both seasons and orchard blocks suggests a strong phenological synchrony with environmental cues, mostly temperature-dependent. The final percent hatch, calculated as the cumulative hatch at the end of each season, showed modest inter-annual variation and blockwise differences, ranging from 39.49% to 45.72%.

By applying mixed-effects modeling, the study also identified that daily hatch was highly variable and statistically nonsignificant; cumulative hatch showed significant effects of both year, block type, and their interaction—highlighting cumulative metrics as more robust indicators for assessing treatment or environmental effects on overwintering egg survival and hatch success. This might be a good indicator for study of annual variation in spring hatch and hence its modeling and forecasting, to the extent of understanding the impact of climate change on a long-term basis. The consistently earlier and more rapid egg hatch in non-bearing trees hints at a possible influence of host tree physiology or microclimate on diapause termination. Understanding whether these differences are driven by bud phenology, bark moisture, or temperature gradients may reveal new biological cues regulating aphid development. This could pave the way for more refined forecasting models or even novel behavioral or physiological targets for intervention. More vigorous studies might indicate the true nature of such observations.

Taken together, this research substantially enriches the understanding of *A. pomi* overwintering biology, highlighting how consistent oviposition schedules, overwintering mortality factors and survival, and abiotic factors and possibly the host plant factors interact to determine early-season egg hatch. By generating precise, high-resolution data across two seasons and diverse orchard conditions, the study lays a strong foundation for temperature-driven phenological models tailored to Himalayan apple systems. Such models, coupled with timely pruning, targeted shoot removal, and judicious use of oils or selective insecticides, can underpin integrated pest management strategies that are effective, cost-efficient, and environmentally sustainable. Ultimately, these findings bridge critical knowledge gaps and the phenological information generated in this study may serve as biological input for future decision-support or advisory tools.

Author Contributions

Mohd Abas Shah: conceptualization, methodology, funding acquisition, project administration, investigation, formal analysis, validation,

resources, data curation, software, visualization, writing – original draft, writing – review and editing. **Sheikh Aafreen Rehman:** investigation, validation, methodology, data curation, writing – original draft, writing – review and editing. **Hafsa Ajaz Tramboo:** investigation, validation, methodology, data curation, writing – original draft, writing – review and editing. **Maheen Khurshid:** investigation, resources, data curation, writing – review and editing. **Birjees Parvez:** investigation, data curation, writing – review and editing. **Shahid Yaqub:** investigation, data curation, writing – original draft, writing – review and editing. **Rifat Rasool:** investigation, resources, data curation, writing – original draft, writing – review and editing. **Akhtar Ali Khan:** conceptualization, writing – original draft, writing – review and editing.

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Ethics Statement

The authors have nothing to report.

Consent

All authors give their consent for publication.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Mendeley Data at https://data.mendeley.com/, reference number DOI: https://doi.org/10.17632/hpffm3tct5.1.

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