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ARTICLE

# Phenology and spatial distribution of spotted-wing drosophila (Diptera: Drosophilidae) in lowbush blueberry (Ericaceae) in Saguenay-Lac-Saint-Jean, Québec, Canada

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## Abstract

*Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), the spotted-wing drosophila, is an invasive pest of fruit crops, which appeared in eastern Canada in 2010. It represents a major threat to lowbush blueberry (*Vaccinium angustifolium* Aiton; Ericaceae) in the Saguenay-Lac-Saint-Jean region, Québec, Canada, at the northern limits of its distribution. The dynamics, overwintering capacity, population fluctuations, and damage to lowbush blueberry of *D. suzukii* are unknown in Saguenay-Lac-Saint-Jean. We aimed to 1) document *D. suzukii* abundance and phenology in lowbush blueberry in separate localities; 2) evaluate the potential of *D. suzukii* to overwinter and examine population dynamics over three seasons; and 3) study the spatial distribution of *D. suzukii* in lowbush blueberry fields with respect to forested borders. *Drosophila suzukii* is abundant in lowbush blueberry fields of Saguenay-Lac-Saint-Jean. In spring, *D. suzukii* were absent until late June, when few summer-morph females appeared. *Drosophila suzukii* densities started to increase regularly in August, with increasing male proportions, to culminate in fall at high levels with balanced sex ratios. Overwintering remains uncertain, *D. suzukii* being undetectable in spring despite intensive trapping. Appearance of diapausing winter morphs at high densities indicates that *D. suzukii* responds appropriately to local conditions preceding cold winter. Models of variation of *D. suzukii* densities and lowbush blueberry fruit infestation with distance from borders indicate that forest borders are favoured habitats over lowbush blueberry fields and the source of *D. suzukii* moving to some extent into lowbush blueberry fields.

## Résumé

*Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) est une espèce envahissante s'attaquant aux petits fruits apparue au Québec, Canada, vers 2010. Elle menace le bleuet nain (*Vaccinium angustifolium* Aiton; Ericaceae) au Saguenay-Lac-Saint-Jean, situé à la limite Nord de sa distribution. Sa dynamique, sa capacité d'hiverner, les fluctuations d'abondance et les dommages causés au bleuet sont inconnus au Saguenay-Lac-Saint-Jean. Les objectifs étaient : 1 : documenter son abondance et sa phénologie en bleuetières dans plusieurs localités du Saguenay-Lac-Saint-Jean; 2 : évaluer sa capacité d'hiverner et son cycle saisonnier; et 3 : examiner sa distribution spatiale en bleuetières par rapport aux bordures boisées. Sa présence dans les bleuetières du Saguenay-Lac-Saint-Jean est récurrente. Au printemps, les adultes de *D. suzukii* sont absents jusqu'à la mi-juin, alors qu'apparaissent des femelles du morphe d'été. La densité des adultes et la proportion de mâles augmentent en août pour finalement culminer en automne avec un rapport des sexes équilibré. L'hivernement au Saguenay-Lac-Saint-Jean reste incertain en l'absence de captures au printemps, même à forte intensité de piégeage. L'apparition de morphes d'hiver

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en diapause indique que *D. suzukii* répond aux conditions annonçant l'hiver. Des modèles prévisionnels des densités d'adultes et de fruits infestés en fonction de la distance à la bordure sont présentés. Les bordures boisées sont des habitats préférés par rapport aux bleuetières et la source des *D. suzukii* qui exploitent le bleuet à proximité des bordures.

## Introduction

*Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), also known as the spotted-wing drosophila, is a widely distributed invasive pest originating from Japan and attacking ripening soft-skinned fruits of many plants, including sweet cherry (*Prunus avium* Linnaeus; Rosaceae) and berries (raspberry (*Rubus* Linnaeus; Rosaceae), strawberry (*Fragaria* Linnaeus; Rosaceae), blueberry (*Vaccinium* Linnaeus; Ericaceae), *etc.*), and causing important economic damage (reviewed in, *e.g.*, Asplen *et al.* 2015; Bondi *et al.* 2016; Nikolouli *et al.* 2018). In the decade following its discovery in North America in 2008 (Hauser 2011; Walsh *et al.* 2011), *D. suzukii* invaded most fruit producing regions in North America, Europe, and South America and may continue to expand in regions of the world where climate is suitable (Gutierrez *et al.* 2016; Dos Santos *et al.* 2017).

Developmental plasticity and short-term acclimation (see Stockon *et al.* 2019 for a review) play important roles in *D. suzukii* survival to cold temperatures, and thus its capacity to persist and overwinter in northern climates. Winter morphs express enhanced cold tolerance and reproductive diapause (Stephens *et al.* 2015; Shearer *et al.* 2016; Wallingford and Loeb 2016; Enriquez *et al.* 2018). In addition to morphological and physiological plasticity, it is possible that adult *D. suzukii* could use behavioural frost avoidance expressed by shelter-seeking behaviour to survive in northern regions of its range. Stockon *et al.* (2019) studied the potential of *D. suzukii* to overwinter in leaf litter at different latitudes in northern (*e.g.*, New York State, United States of America) and southern states in the United States of America. They concluded that successful overwintering of acclimated winter morphs during winters with prolonged subzero freezing under leaf litter would be very low. Therefore, the question of overwintering of *D. suzukii* in cold regions such as Québec and elsewhere in eastern Canada remains open. All available research indicates that survival to the next season is unlikely and would depend on fall-acclimated *D. suzukii* being able to seek protected, natural (*e.g.*, forest debris buried under thick snow cover), or suitable artificial shelters associated with human activity (Stockon *et al.* 2019 and references therein).

However, it cannot be excluded that recurrent presence and abundance of *D. suzukii* in Québec are explained by migrating individuals from warmer regions to recolonise these northern parts of its range. This has frequently been suggested mainly based on its known migratory behaviour in Japan (Mitsui *et al.* 2010; Stockon *et al.* 2019). Long distance transport by wind or in relation to human activity (trade routes, grocery stores, fruit dumps) might explain its presence in regions that do not allow local overwintering (Kimura 2004; Dalton *et al.* 2011; Cini *et al.* 2012; Langille *et al.* 2016).

The Saguenay-Lac-Saint-Jean region of Québec is near the northeastern limits of the known distribution of *D. suzukii* in North America (Dos Santos *et al.* 2017; Centre for Agriculture and Bioscience 2019). Lowbush blueberry (*Vaccinium angustifolium* Aiton; Ericaceae) is a very important crop in Saguenay-Lac-Saint-Jean. Lowbush blueberry regularly supports high-density *D. suzukii* populations in Maine, United States of America (Drummond *et al.* 2019). Their long-term study indicates that *D. suzukii* abundance and first appearance in spring can be explained by winter temperature, population density (trap captures) in the past season, local abundance of suitable wild berry plants, and predation (Drummond *et al.* 2019). Langille *et al.* (2017) modelled the population dynamics of *D. suzukii* for different fruit producing regions of Canada and the United States of America and showed that Saguenay-Lac-Saint-Jean, which was represented in their model by climatic conditions in Saguenay (Québec, Canada), is marginally suitable to *D. suzukii* despite the presence of large lowbush blueberry fields. In the region, *D. suzukii* abundance, phenology, and risk of damage to lowbush blueberry are unknown.

Lowbush blueberry production areas in Saguenay-Lac-Saint-Jean (and presumably also in other regions in eastern Canada) consist of large semi-natural agroecosystems generally surrounded by forested landscapes. Here, lowbush blueberries are not planted crops, they have grown naturally over very long periods of time. Natural borders surrounding blueberries affect the abundance of *D. suzukii* in fruit crops due to the presence of shelters, alternative resources, and generalist natural enemies (Haro-Barchin *et al.* 2018; Santoiemma *et al.* 2018; Tonina *et al.* 2018; Drummond *et al.* 2019). In invaded territories such as North America, specialised natural enemies are rare or absent, thus biological control by natural enemies has relatively low impact on *D. suzukii*. In addition to alternative host fruit resources, the semi-natural field borders of berry crop agroecosystems are highly favourable to *D. suzukii* populations by reducing extrinsic mortality and allowing for the growth of population sizes (Santoiemma *et al.* 2018).

*Drosophila suzukii* is an opportunistic exploiter of fruit plants and has a wide range of wild fruit hosts, even in Canadian boreal climates (Ontario Ministry of Agriculture, Food, and Rural Affairs 2015; Little *et al.* 2017). Wild berry hosts can provide adequate resources for early season reproduction of winter morph *D. suzukii* females, which indeed use them as hosts (Panel *et al.* 2018). In this case, infestation of cherry (*Prunus* Linnaeus; Rosaceae) crops in early summer involved the winter morphs, not the first generation of summer morph *D. suzukii* emerged in the new season. *Drosophila suzukii* are also long lived, very mobile, and can express seasonal migration to locate abiotic conditions, resources, and shelter most suitable for reproduction and survival (Mitsui *et al.* 2010; Walsh *et al.* 2011; Stockon *et al.* 2019).

In this study, we investigated the phenology and spatial distribution of *D. suzukii* in the Saguenay-Lac-Saint-Jean region over three years, 2016–2018. *Drosophila suzukii* had been observed in this region since 2012, but it remained unknown whether it was established and can overwinter locally, or if the species colonised the region every year from the southern regions of Québec or the northeastern United States of America.

Our specific objectives were 1) measure *D. suzukii* abundance and phenology on lowbush blueberry in different years over the whole season of activity and in lowbush blueberry fields covering a large part of the Saguenay-Lac-Saint-Jean region; 2) search for evidence that *D. suzukii* is established in lowbush blueberry field ecosystems of the region and has potential for overwintering based on early and late season abundance and presence of winter morphs; and 3) model the spatial distribution of captures of *D. suzukii* and of lowbush blueberry fruit infestation by larvae in the fields, in relation to the lowbush blueberry harvest period to predict the risk of damage to the fruit crop.

## Materials and methods

### Sampling locations

In order to study *D. suzukii* phenology, sampling for adult *D. suzukii* and infested fruit was performed in widely distributed fields across the entire Saguenay-Lac-Saint-Jean region. In 2016, three fields were sampled (Saint-David-de-Falardeau, Labrecque, Dolbeau-Mistassini), four fields in 2017 (Saint-David-de-Falardeau, Sainte-Monique, Saint-Thomas-Didyme, Dolbeau-Mistassini), and three fields in 2018 (Albanel, Saint-Thomas-Didyme, La Doré) (see Table 1 for details).

Generally, lowbush blueberry fields in Saguenay-Lac-Saint-Jean are in production every two years, and sites were chosen according to this rotation regime. Selected fields also had to be surrounded mainly by wooded borders. The forested borders were generally dominated by grey pine (*Pinus banksiana* Lamb; Pinaceae), with substantial arbustive and herbaceous plant diversity. Only fields in production respecting these criteria were considered, which explains why sampling sites differed to some extent between years.

**Table 1.** Location and geographic coordinates of lowbush blueberry field sites sampled for *Drosophila suzukii* in three-year study of its phenology and distribution in Saguenay-La-Saint-Jean, Québec, Canada.

| Locality | Field | Year | Geographic coordinates |
|---|---|---|---|
| Albanel | 1 | 2018 | 48.846405°N, 72.347427°W |
| Dolbeau-Mistassini | 1 | 2016 | 48.842246°N, 72.157922°W |
|  | 2 | 2017 | 48.782673°N, 72.301986°W |
|  | 3 | 2018 | 48.780317°N, 72.306621°W |
| La Doré | 1 | 2018 | 48.741525°N, 72.567253°W |
| Labrecque | 1 | 2016 | 48.714528°N, 71.548654°W |
| Saint-David-de-Falardeau | 1 | 2016 | 48.671487°N, 71.229623°W |
|  | 2 | 2017 | 48.632483°N, 71.227936°W |
| Saint-Thomas-Didyme | 1 | 2017 | 48.863961°N, 72.702513°W |
|  | 2 | 2018 | 48.855713°N, 72.736084°W |
| Sainte-Monique | 1 | 2017 | 48.804525°N, 71.849597°W |

## Seasonal phenology of *Drosophila suzukii*

**Adult *Drosophila suzukii* captures.** In 2016 and 2017, adult *D. suzukii* were trapped with 500-mL drinking-type plastic containers with seven 2.5-cm openings each and coloured in red and black (Ministère de l'Agriculture, des Pêcheries et de l' Alimentation du Québec 2013). Traps were baited with 200 mL of commercial apple cider vinegar as attractant and a drop of liquid soap to break surface tension. Traps were placed near the border of each lowbush blueberry field (0 m) and were deployed from the beginning of May to mid-November in 2016–2017. Traps were collected on a weekly basis, except in July (2016) and August (2016 and 2017) where traps were collected twice a week to better follow rapid changes in *D. suzukii* abundance at peak density. Captures were sorted to count and sex *D. suzukii*. Samples evidently containing too many *D. suzukii* to be processed within reasonable time with available resources were fractioned once or more as needed by pouring trap content in a marked white tray. The total number of *D. suzukii* in each sample was thus estimated by multiplying each count by the appropriate number of subsamples. During sample processing in early season (May to July) and fall (September to October), *D. suzukii* cuticle melanisation and relative wing length were checked for evidence of presence or absence of the winter morphs (Shearer *et al.* 2016) in samples (we did not measure their proportions). Voucher specimens were deposited in the Collection d'insectes du Québec (Ville de Québec, Québec, Canada).

To increase the probability of *D. suzukii* capture in spring and early summer in 2017 and 2018, a larger trap set-up was put in place in the Dolbeau-Mistassini site, based on *D. suzukii* abundance in this site in 2016. This set-up consisted of 20 (2017) or 40 traps (2018) that were randomly placed 10 m within the wooded periphery of the lowbush blueberry field at a distance of 50 m from each other. Traps in this site were collected weekly from early May until spring detection of *D. suzukii* was no longer necessary, or as captures occurred also in the other sites.

**Lowbush blueberry fruit infestation.** The phenology of lowbush blueberry fruit infestation by *D. suzukii* larvae was also studied in the 2016 and 2017 summer seasons. Fruits were collected at the border of the field in all sites sampled for *D. suzukii*, as listed above, from mid-July to mid-October. Up to 150 g of ripening lowbush blueberries were collected by hand near trapping positions every week at each site, brought to the laboratory, and incubated in meshed plastic containers lined with absorbent paper to avoid excess moisture and allow larvae to pupate. Fruits were incubated in Conviron E15 growth chambers (Controlled Environments, Winnipeg, Manitoba, Canada) under "standard" conditions (20 °C, 65% relative humidity, 16:8 light:dark hours), allowing to measure *D. suzukii* adult emergence from fruit up to three weeks after sampling. Emerged adults were counted and sexed, as well as any aborted pupae and larvae.

In order to follow late season reproductive and diapausing potential of *D. suzukii* (late August to mid-October) in 2016, live adults were sampled using a modified version of our trap at Dolbeau-Mistassini site. This new version contained a second compartment inside the conventional trap, lined with fine mesh above the liquid bait, which prevented *D. suzukii* from drowning. The modified trap was also fitted with small funnels around openings to prevent captured *D. suzukii* from escaping. Blueberry fruits from the supermarket were also placed in the trap to provide a food and water source until the *D. suzukii* samples were collected and brought to the laboratory. In any trapping event, live traps were deployed at the field border for a maximum of 24 hours. Captured *D. suzukii* were identified and individually maintained in 100-mL ventilated plastic vials under standard conditions (see above). Two blueberry fruits were placed in the vial as potential oviposition substrates for 48 hours, after which *D. suzukii* were discarded. The blueberries were then incubated under standard conditions for three weeks to allow development of any eggs laid, in order to count any emerging *D. suzukii* and any aborted larvae or pupae. Absence of egg laying could be interpreted as reproductive arrest in preparation for overwintering.

## Spatial distribution along transects

**Adult *Drosophila suzukii* captures.** To examine the spatial distribution of *D. suzukii* in lowbush blueberry fields and their wooded peripheries, transects of the usual unmodified traps were set up in three study sites in 2016 and 2017, from July to November (see Table 1). The single trapping transect in each site was perpendicular to the field border and consisted of four traps in 2016 and was extended to five traps in 2017 based on 2016 results. The first trap was positioned at 50 m from the field border into the woods, the second at the border (field-wood interface), and two (2016) or three (2017) other traps at distances of 50, 150, and 300 m (2017 only) into the lowbush blueberry field. Traps were collected weekly except during July (2016) and August (2016, 2017), during which traps were collected twice a week. Trap captures were screened for *D. suzukii* based on morphology, counted, and sexed.

**Fruit infestation in lowbush blueberry fields.** In parallel to *D. suzukii* capture distribution, the distribution of fruit infestation was followed in 2017 based on fruit sampling along a perpendicular transect, at 0, 50, 150, and 300-m intervals from the border in each site. Based on results of 2017 showing that fruit infestation away from border was very limited, fruits were sampled in 2018 along a finer scale transect for better resolution of fruit infestation density distribution close to the field border. Lowbush blueberry fruit samples were then collected at five points: 0, 12.5, 25, 37.5, and 50 m from the border. For each point, 150 g of blueberries were collected, brought to the laboratory and kept in growth chambers for a three-week period under standard conditions to monitor for *D. suzukii* emergence, and to count and sex *D. suzukii*, as well as record the number of aborted pupae or larvae.

## Statistical analyses

Statistical analyses were performed using SAS 9.4 (SAS institute, Cary, North Carolina, United States of America). Seasonal trends in sex ratio (female to male) of trapped *D. suzukii* and those emerging from collected fruits were obtained and tested for equality (1:1) using chi-square goodness of fit tests for three periods: the preharvest (July to mid-August), harvest (mid-August to mid-September), and postharvest (mid-September to October). Variation in total *D. suzukii* abundance between sites was compared using PROC GLIMMIX of SAS, for the harvest and postharvest periods with site as a fixed effect.

Spatial distribution of *D. suzukii* capture density and fruit infestation as a function of distance into the lowbush blueberry agroecosystem was modelled using SAS PROC NLIN. These analyses and modelling were done separately for the harvest period and postharvest period of 2017. Linear and exponential models ($y = ae^{xb}$, where y stands for density) were tested, and 95% confidence interval of model estimates was calculated. Model fitting and comparison based on $R^2$ were done using SAS PROC NLIN.

## Results

### Seasonal phenology of *Drosophila suzukii*

**Adult *Drosophila suzukii* captures.** In 2016, *D. suzukii* were captured in all traps placed at the wooded border/lowbush blueberry field interface (0 m), and significant captures occurred from August to November. During the preharvest season (May to August), no *D. suzukii* were captured in traps located at 0 m, but complementary traps located nearby 50 m into the woods (data not shown) had captured a few females in June. During the harvest period (August to September), low *D. suzukii* densities were recorded in all sites. Most catches during the harvest period were female *D. suzukii*, with an average highly female-biased sex ratio of 0.87 ($X^2$ (1, $n = 1055$) = 581.13, $P < 0.001$) (Fig. 1A). In all sites, a *D. suzukii* density peak occurred in October about four weeks after the lowbush blueberry harvest period. An average of up to 340 *D. suzukii* per day was captured in the Saint-David-de-Falardeau and Dolbeau-Mistassini sites (Fig. 1A). Males then were more abundant, and sex ratio tended to stabilise in late season, averaging 0.51, but being still slightly but significantly female biased ($X^2$ (1, $n = 12\ 502$) = 10.25, $P < 0.005$) (Fig. 1A). After peaking, *D. suzukii* density decreased until the end of the trapping season (20 November). During harvest and postharvest periods, *D. suzukii* density variation between sites was marginally insignificant ($F$ (2, 18) = 3.50, $P = 0.0521$ and $F$ (2, 6) = 4.91, $P = 0.0545$, respectively).

In 2017, the first *D. suzukii* catches occurred in July in traps located at the border of each lowbush blueberry fields (0 m); *i.e.*, slightly earlier than 2016, and all were female. However, as in 2016, traps in nearby wooded areas had already captured females earlier in June. During the harvest period, populations slowly increased and males appeared, with the overall sex ratio being strongly female biased at 0.77 ($X^2$ (1, $n = 2526$) = 732.22, $P < 0.001$) (Fig. 1B). During the postharvest period, male captures increased gradually and sex ratio finally came close to evenness (0.48), still being slightly but clearly male biased ($X^2$ (1, $n = 36\ 875$) = 58.20, $P < 0.001$) (2017) (Fig. 1B). *Drosophila suzukii* capture density variation between sites was marginally insignificant ($F$ (2, 15) = 3.62, $P = 0.0523$) during the harvest period. For the postharvest period in 2017, *D. suzukii* density variation between sites was highly significant ($F$ (2, 9) = 15.34, $P = 0.0013$), with the Sainte-Monique site having much higher densities of *D. suzukii* than the other sites.

In the more intensive trapping set-up employed in 2017 at the Dolbeau-Mistassini site to improve early *D. suzukii* detection, exclusively female *D. suzukii* were captured and at very low density (1–2 *D. suzukii* per week) for six weeks, from 18 June to mid-August. Populations started to increase rapidly in early August, concurring with similar increases in other sites (Fig. 1B). Males appeared and grew in numbers in mid-August, when intensive trapping ceased. In 2018, the intensive trapping set-up was operational for a shorter period (from May to late June), and first captures were recorded on 17 June.

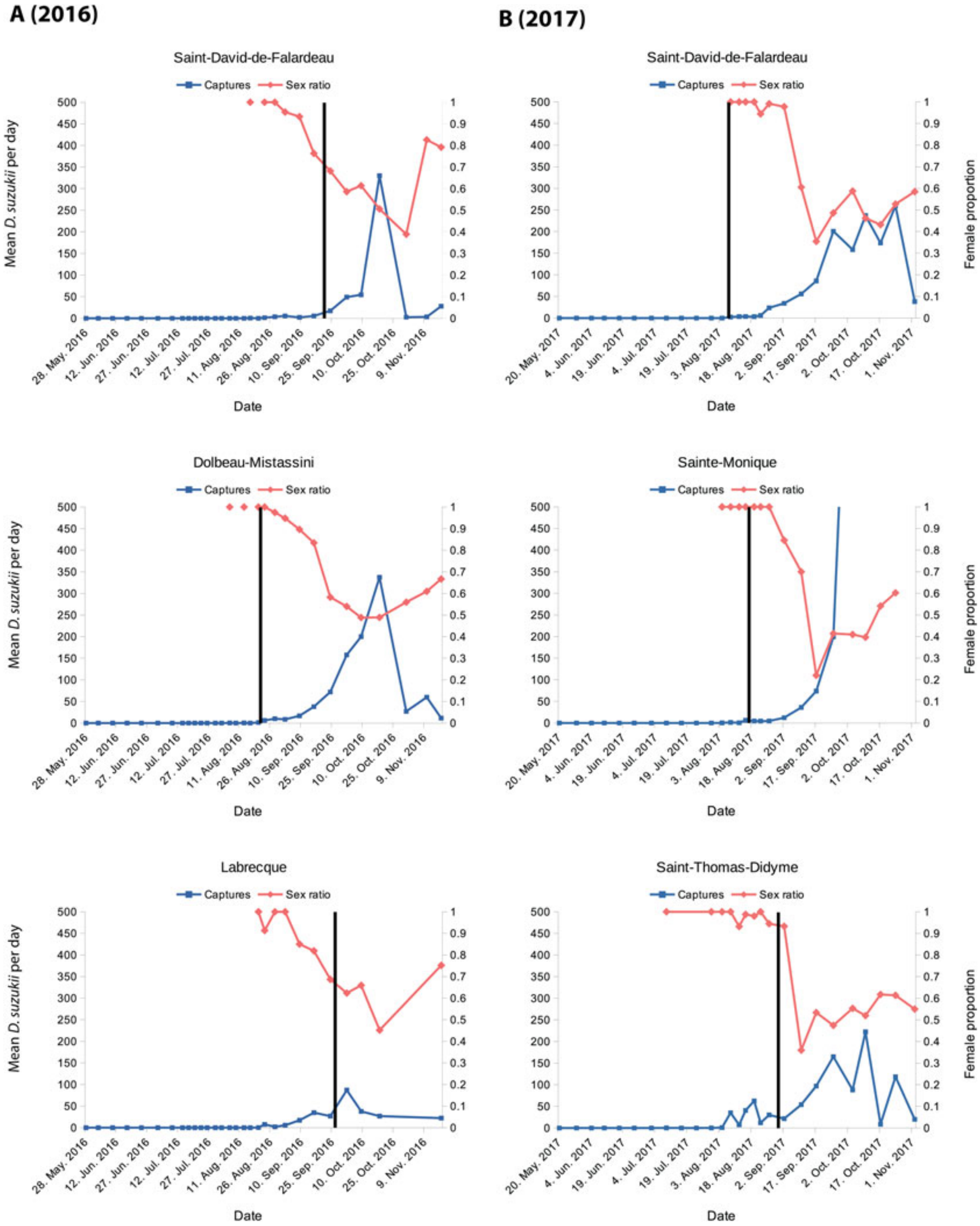

**Fig. 1.** Capture density and female sex ratio of *Drosophila suzukii* in three lowbush blueberry production sites. **A**, 2016 at Saint-David-de-Falardeau, Dolbeau-Mistassini, and Labrecque; **B**, 2017 at Saint-David-de-Falardeau, Sainte-Monique, and Saint-Thomas-Didyme. The vertical line indicates date of harvesting.

**Lowbush blueberry fruit infestation.** In 2016, mature lowbush blueberry fruits close to the field border were infested with *D. suzukii* larvae from mid-August until late September (Fig. 2A). Fruit infestation peaked in the third week of September, reaching up to 90 *D. suzukii* emerged per 100 g of fruits at the Labrecque site. The overall sex ratio of emerged *D. suzukii* was 0.51 ($X^2$ (1, $n = 766$) $= 0.63$, $0.25 < P < 0.50$), not being significantly different from a 1:1 ratio. In October, no berries remained on lowbush blueberry bushes and sampling ceased.

In 2017, lowbush blueberry fruit infestations occurred from early August to late September, thus starting one week earlier than 2016 (Fig. 2B). Peak infestation dates varied according to site in late season, from 29 August at Sainte-Monique to 28 September at Saint-Thomas-Didyme, mostly occurring long after harvest. The maximum recorded fruit infestation density was 75 emerged *D. suzukii* per 100 g of blueberries, with an overall sex ratio of 0.56 ($X^2$ (1, $n = 342$) $= 5.16$, $P < 0.025$); *i.e.*, a small but significant bias towards females. As in 2016, there were no intact lowbush blueberry fruits that were still suitable for sampling in early October.

Based on data from live *D. suzukii* brought back to the laboratory and tested for ability of females to lay eggs in commercial blueberries from the supermarket, mean daily fecundity decreased rapidly during September 2016, from an average of two *D. suzukii* produced per individual per day to complete arrest in October (Fig. 3), with high variation between individuals (0–4 eggs per day). The sex ratio of emerged *D. suzukii* born from field capture individuals also varied (see Fig. 3), as expected with estimates based on the low numbers obtained.

## Spatial distribution along transects

**Adult *Drosophila suzukii* captures.** During the harvest period in 2017, the exponential model best fitted the *D. suzukii* capture data as a function of distance into the lowbush blueberry agroecosystem, with an $R^2$ value of 0.63 ($R^2 = 0.42$ for linear), showing a sharp decrease in *D. suzukii* density with distance from the 50-m position within woods, up to 300 m in the field (Fig. 4A). The model predicts that *D. suzukii* capture density right at the border (0-m trapping position) is only about half as high as 50 m into the woods. Model parameters indicate that *D. suzukii* density decreased by 1.31% per m with distance from the woods into the field. Data from 2016 trapping were added to Fig. 4A for comparison to predictions of the model based on 2017 data. As already mentioned, the 2016 data were not used in modelling because the trapping transect then consisted of only four rather than five traps (see above). Note that independent prediction of the 2016 data by the 2017 distance model is reasonably accurate (Fig. 4A).

For the postharvest period, it is also an exponential model that best fitted to *D. suzukii* capture density data, with an $R^2$ of 0.48 ($R^2 = 0.38$ for linear). This model also predicts that captures decrease exponentially with distance into the field from the woods (Fig. 4B) at a rate of 2% per metre. Right at the border (0 m), 62.66% fewer *D. suzukii* were caught on average, as compared to 50 m into the woods. Note that most variability in *D. suzukii* capture density is attributable to the Sainte-Monique site during postharvest when captures averaged 1000 *D. suzukii* per day, which is 5–10 times more than the two other sites. The Sainte-Monique field site was a relatively small enclosed area on humid terrain, but more work would be needed to explain exceptional *D. suzukii* densities here. Data for 2016 were also added to Fig. 4B although not being used for model fitting, as independent validation.

**Fruit infestation in lowbush blueberry fields.** In 2017, lowbush blueberry samples were collected at 0, 50, 150, and 300 m from the border into the field. However, only blueberries that were collected at the 0-m position were actually infested by *D. suzukii*, thus no model can be fitted to 2017 data on fruit infestation.

In 2018, finer scale spatial sampling closer to the border allowed modelling *D. suzukii* fruit infestation (*D. suzukii* emerged per 100 g of fruits) as a function of distance into the field; *i.e.*, up to 50 m from border. As for *D. suzukii* capture data, an exponential model of the effect of distance on fruit infestation best fitted the data ($R^2 = 0.88$ compared to $R^2 = 0.60$ for a linear regression) (Fig. 5). At the border (0 m) 8.80 *D. suzukii* emerged per 100 g of lowbush blueberry

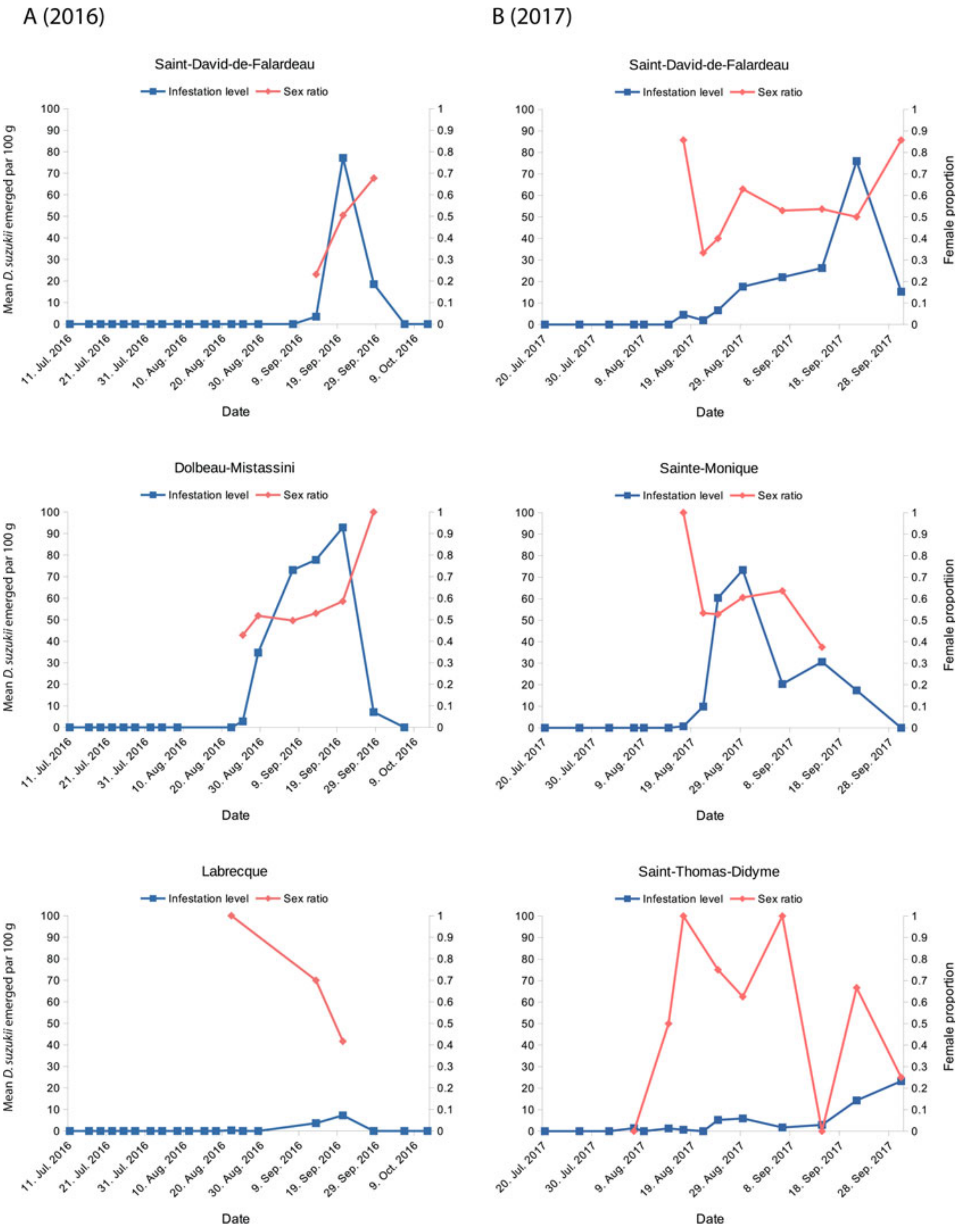

**Fig. 2.** Lowbush blueberry fruit infestation by *Drosophila suzukii* larvae as measured by number and sex ratio of flies emerged from 100 g of fruit collected at the field border in the Saguenay-Lac-Saint-Jean region of Québec. **A**, Summer 2016 at Saint-David-de-Falardeau, Dolbeau-Mistassini, and Labrecque; **B**, summer 2017 at Saint-David-de-Falardeau, Sainte-Monique, and Saint-Thomas-Didyme.

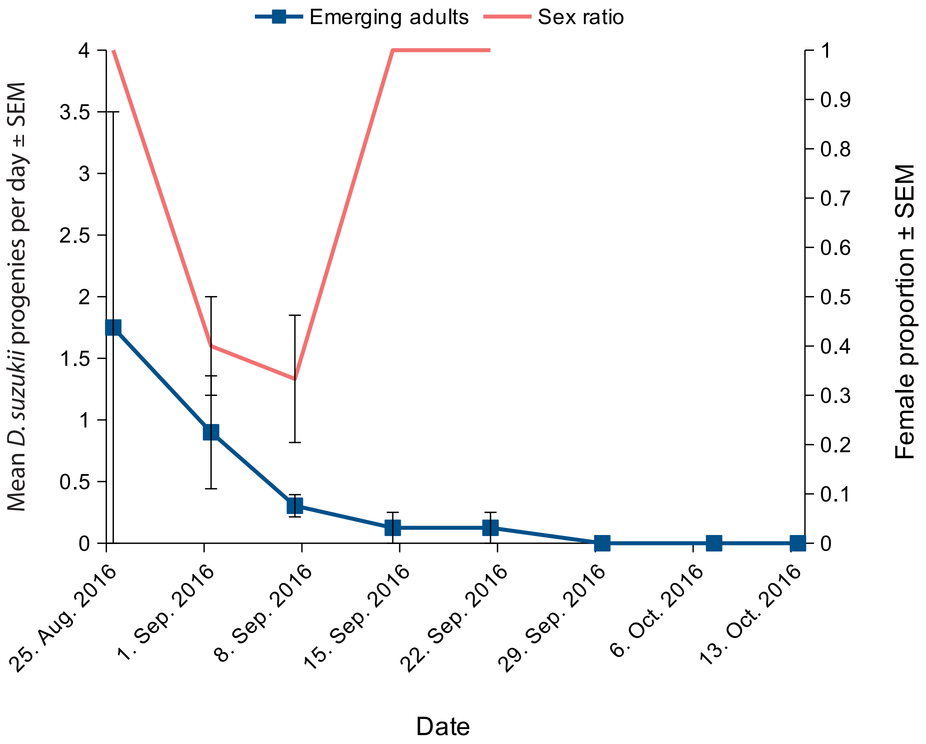

**Fig. 3.** Trends in egg laying frequency and sex ratio of progeny per day at 20 °C, for individually reared females *Drosophila suzukii* captured alive in late season in sampling site. Dolbeau-Mistassini in 2016. SEM, standard error of the mean.

fruits and infestation decreased with distance at the rate of 9.49% per metre into the field. The model predicts that 25 m from the border, fruit infestation would be reduced by 91.73% compared to the border (0 m); *i.e.*, to $\leq 1$ *D. suzukii* emerged per 100 g of fruit. Data for the two sampling points (0 and 50 m) in 2017 were also added in Fig. 5 for validation, as these data were not used in estimating model parameters.

## Discussion

The first objective of this study was to document the abundance and phenology of *D. suzukii* in lowbush blueberry of the Saguenay-Lac-Saint-Jean region over a wide area. We focussed on this region because it comprises most of the lowbush blueberry production in Québec and is likely to be close to the northern limits of the range of *D. suzukii* in eastern Canada. We found that *D. suzukii* was very abundant during summer seasons of 2016, 2017, and 2018 although sampling did not cover the whole 2018 season as the focus was on fruit infestation. Density of *D. suzukii* catches varied greatly among sites, as shown, for example, with peaks averaging from 100 to 1000 *D. suzukii* captured per day among sites. The seasonal changes in *D. suzukii* abundance and sex ratio remained similar across sites and varied only slightly between years (Fig. 1), even though global abundance sometimes differed across sites. Captures started with very low numbers of *D. suzukii* that were exclusively female in early summer, followed by a period of rising densities paralleled by growing proportions of males from mid-summer until early fall, when populations peaked more or less sharply. Then capture density declined in late October when the sex ratio tended towards near equality. The observed phenology might suggest the possibility of three or more generations per year in the region, although this could only be confirmed by more detailed field observations on local population dynamics.

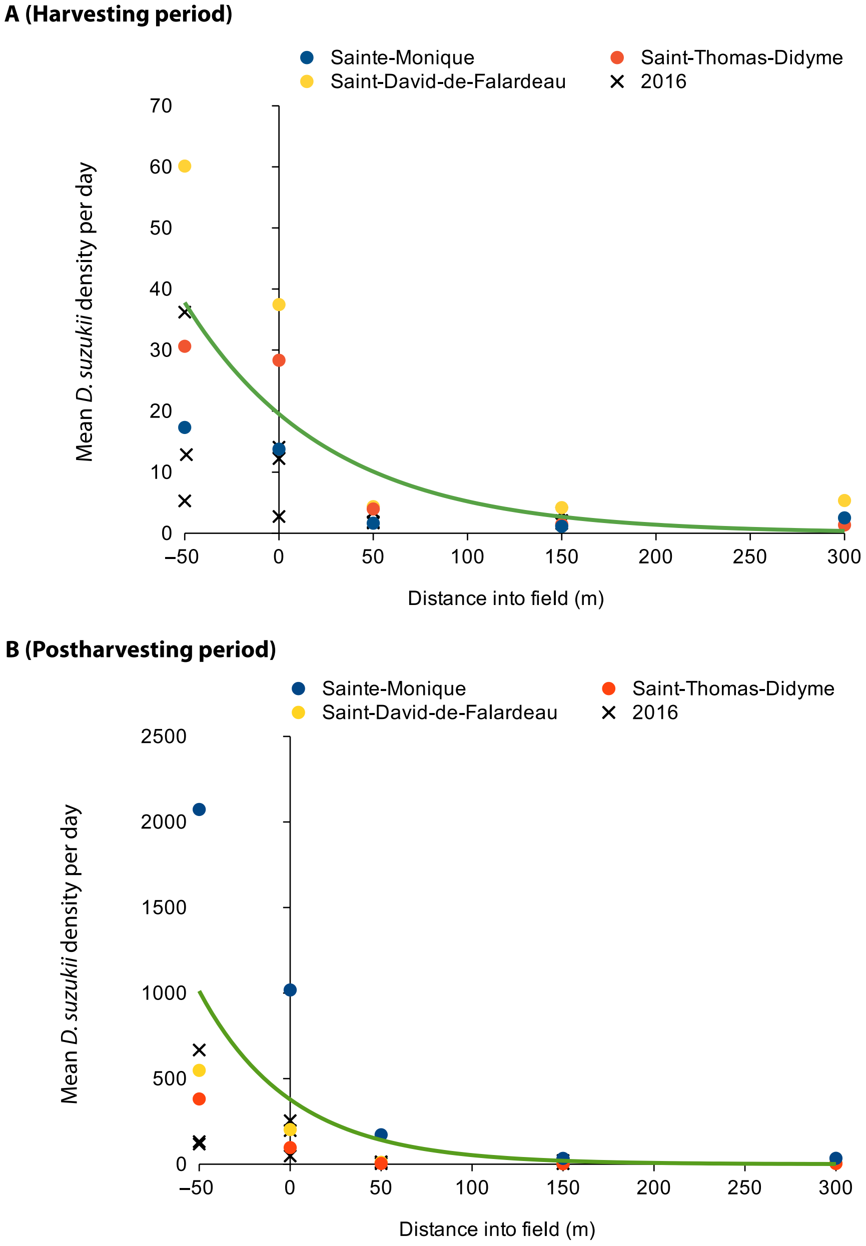

**Fig. 4.** Models of exponentially decreasing capture density of *Drosophila suzukii* as a function of distance into lowbush blueberry fields ($n = 3$). **A**, During the 2017 fruit harvesting period; **B**, during the 2017 postharvest period. The 2016 data (not used for model parametrisation) are also shown (x symbols) for independent model validation.

Our second objective was to examine the potential of *D. suzukii* to overwinter in the Saguenay-Lac-Saint-Jean region, which is likely to be relatively close to the northern limits of its range in eastern Canada, with a maximum of only about six months of warm enough conditions to allow its development and reproduction. Low-temperature thresholds from published work indicate that immatures cannot complete development below approximately 6 °C, and summer morph females cannot reproduce below approximately 10 °C (Dalton *et al.* 2011; Tochen *et al.* 2014; Jakobs *et al.* 2015; Stephens *et al.* 2015; Ryan *et al.* 2016).

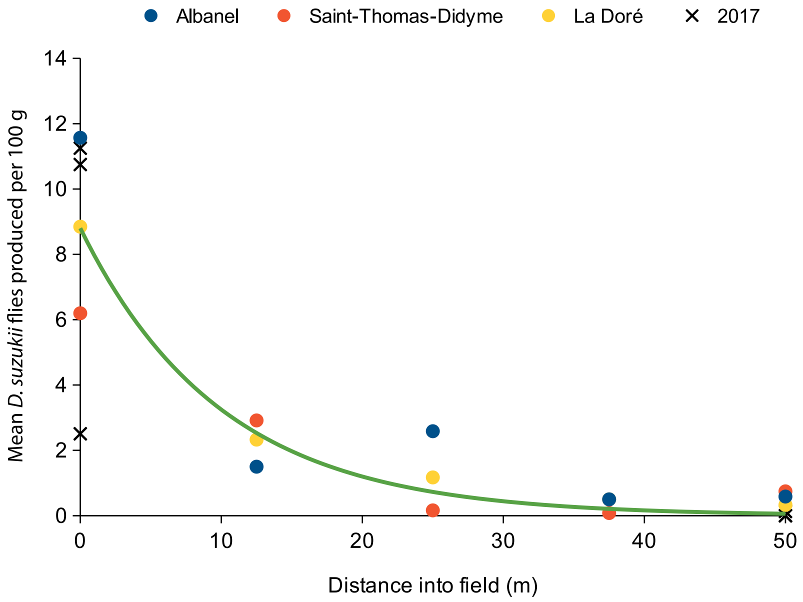

**Fig. 5.** Model of exponentially decreasing lowbush blueberry fruit infestation by *Drosophila suzukii* as a function of distance from field border, during the harvest season in 2018. The 2017 data for two corresponding fruit collection distances are added (x symbols, 0 and 50 m), showing that they are within predicted levels from independently parametrised model based on 2017 data.

The first catches of *D. suzukii* in Saguenay-Lac-Saint-Jean were all summer morph females, which were not continuously captured in our sites until mid to late August in 2016, and until late July-early August in 2017. The intensive trapping set-up that was operational from mid-May onwards in 2017 and 2018 at the Dolbeau-Mistassini site in the field border captured just a few individuals around 15–20 June, which were also summer morph females; *i.e.*, they could not be postdiapause winter morph *D. suzukii* that overwintered locally. This suggests that overwintered *D. suzukii* were either absent even in forest borders or they were so rare that they remained undetected even with intensive trapping effort.

The earliest summer morph female captures here could be migrants from another region to the south or, assuming that overwintered *D. suzukii* were present but remained undetected because they were not sufficiently abundant in spring to be detected, those early summer morphs could be the first current-year (new) generation of *D. suzukii* born from the rare overwintering *D. suzukii* that had survived winter locally. If indeed present, when resuming activity in spring overwintered *D. suzukii* may also have failed to respond to our apple cider vinegar baited traps, which were operational starting in mid or late May, as suggested by Thistlewood *et al.* (2018) to explain similar seasonal patterns of *D. suzukii*.

The all-female sex ratio of first-captured *D. suzukii* did not tend to stabilise near equality (1:1) until the postharvest period in late summer, suggesting that males first appeared in these Saguenay-Lac-Saint-Jean populations among progeny of the summer morph females that were first caught. By the end of season, the sex ratio had stabilised, but was still slightly biased either towards females (2016) or males (2017).

It is possible that winter survival did occur in microhabitats such as forest leaf litter (Zerulla *et al.* 2015), but with high mortality rate, especially among males. The idea that low numbers of *D. suzukii* indeed survived winter but remained undetected might find indirect support in data from our intensive trapping set-up in Dolbeau-Mistassini in 2017 and 2018, where the first *D. suzukii* were captured about one month earlier than in other sites. According to Kirkpatrick *et al.* (2018), the winter morph has reduced antennal response to volatiles, potentially limiting apple cider vinegar-baited trap effectiveness on postdiapause winter morph *D. suzukii* resuming flight activity in spring.

Overall, it is still unclear if *D. suzukii* can overwinter in the Saguenay-Lac-Saint-Jean region, as we can report no evidence of it at this stage. However, given the consistent presence of winter morphs *D. suzukii* in large numbers very late in fall in all sites (Figs. 1, 4), it is probable that many *D. suzukii* could find suitable overwintering microclimates in the protected forested borders before temperatures were finally too cold to sustain flight activity. Further experimental research on late-season behaviour of *D. suzukii* and potential overwintering microclimates in the forest borders would be required to better understand the low-season dynamics of these *D. suzukii* populations.

Concerning fruit infestation, it is very interesting that it started more than one month after the onset of lowbush blueberry harvesting in both the 2016 and 2017 seasons (Fig. 1). This latency to infest lowbush blueberry fruit in the fields could be explained by the exploitation of alternative wild berry hosts in the forest borders (or to some extent also within field margins) in early summer by *D. suzukii*, such as Canadian bunchberry (*Cornus canadensis* Linnaeus; Cornaceae) (J.-F.G., unpublished data). Early maturing wild fruits in the protected forest borders could serve as reproductive resources supporting early summer population growth to some extent. With increased *D. suzukii* density, reproductively mature adults would then spill over on the adjacent cultivated lowbush blueberry to start laying eggs as lowbush blueberry fruit maturation starts.

Whatever the precise dynamics, the observed pattern of late appearance of cultivated lowbush blueberry fruit infestation by larvae is reassuring for lowbush blueberry producers, since according to our data from all sites, fruit was harvested mainly before field infestations started. During the early season, appropriate management of wild berry hosts and a focus on early harvesting could therefore be a suitable pest management strategy to limit the impact *D. suzukii* on this culture by limiting early season alternative reproductive resources. That the new dynamics thus created in forested borders could indeed decrease crop infestation would need careful study.

Our data on late season reproductive potential (female fecundity) clearly demonstrate a decrease in the number of viable eggs laid under controlled conditions by female *D. suzukii* from September to October, as indicated by *D. suzukii* emerging from fruit samples under similarly controlled conditions in the laboratory. This is consistent with previous studies and reflects *D. suzukii* acclimation to fall conditions in Saguenay-Lac-Saint-Jean; *i.e.*, colder temperatures and rapidly decreasing photoperiod, as previously documented (Stephens *et al.* 2015; Toxopeus *et al.* 2016; Everman *et al.* 2018). Decreasing female fecundity in late season can be interpreted as incipient reproductive diapause (Shearer *et al.* 2016; Wallingford and Loeb 2016), although the true diapause status of fall-acclimated *D. suzukii* has been debated (*e.g.*, Toxopeus *et al.* 2016). Based on experimental induction and termination of reproductive dormancy, Zhai *et al.* (2016) concluded that *D. suzukii* is a short-day diapausing species.

The last objective of this study was to examine the spatial distribution of *D. suzukii* and larvae in fruit of lowbush blueberry in relation to (forested) field borders in the Saguenay-Lac-Saint-Jean, based on *D. suzukii* capture density and fruit infestation frequency along transects perpendicular to the border. We found that much larger *D. suzukii* densities occurred in wooded borders than in fields and capture densities decreased exponentially as a function of distance from the woods during both the harvest and postharvest periods in 2017. This can be explained by the natural tendency of *D. suzukii* to use the forest landscape of the borders for physical protection and to use wild berry hosts for reproduction (*e.g.*, Santoiemma *et al.* 2018). In the Saguenay-Lac-Saint-Jean region, suitable fruit species include *Cornus canadensis,* and *Aralia hispida* Ventenat (Araliaceae), which were common in our sites (J.-F.G, unpublished data).

The marked decrease in *D. suzukii* densities in the lowbush blueberry fields compared to nearby forest borders suggests that the complex environment of the forest is more suitable to

**Table 2** Exponential model parameters and their 95% confidence interval predicting the spatial distribution of adult *Drosophila suzukii* density and fruit infestation (*D. suzukii* emerging from 100 g of fruit) as a function of distance from the wooded border in lowbush blueberry, Saguenay-Lac-Saint-Jean, Québec.

| Model | Parameter a (95% confidence interval) | Parameter b (95% confidence interval) | $F$ (2, 13) | $P$ value | $\Delta R^2$ versus linear |
|---|---|---|---|---|---|
| Adult flies (harvest) | 37.786<br>(24.391, 51.181) | −0.0132<br>(−0.0234, −0.00291) | 23.72 | $< 0.0001$ | 0.21 |
| Adult flies (postharvest) | 1021.1<br>491.6, 1532.7) | −0.0197<br>(−0.0431, 0.0371) | 10.09 | 0.0023 | 0.20 |
| Blueberry infestation | 8.8015<br>(7.225, 10.377) | −0.0997<br>(−0.1435, 0.0559) | 79.32 | $< 0.0001$ | 0.28 |

*D. suzukii* than open lowbush blueberry fields. Temperature, wind, and rainfall can be more extreme in the field than the forest borders, which could limit adult movement and survival (Enriquez and Colinet 2017). Furthermore, air humidity is an important physical factor for *D. suzukii* (Eben *et al.* 2018). Forested habitats are more humid than open fields (*e.g.*, Tochen *et al.* 2016), and lowbush blueberry field borders indeed support higher *D. suzukii* densities. According to Guédot *et al.* (2018), maximum humidity interacting with maximum temperature as abiotic factors best explained *D. suzukii* density variation during the season and between years.

Abiotic factors, wild berries, and shelter could also explain variability between sites, which needs further study. During the postharvest period, the largest numbers of *D. suzukii* were trapped in the forest borders. Based on laboratory studies, Wallingford *et al.* (2018) suggested that *D. suzukii* about to overwinter would prefer substrates with sufficient nutritional value. In late season, suitable feeding substrates are possibly more abundant in wooded borders than in lowbush blueberry fields, where much of the organic matter has been harvested or is in advanced state of decomposition. However, we caught adult *D. suzukii* in most traps along the field transects (Fig. 4). As Santoiemma *et al.* (2019) reported, *D. suzukii* move between different habitats in heterogeneous environments and thus use both fields and forests depending on time and seasons.

Spatial distribution of lowbush blueberry fruit infestation by larvae along perpendicular transects was also modelled for the 2018 season and the exponential decrease model with distance best fitted the data. Just like the spatial distribution of adult *D. suzukii* density, results show that fruit infestation occurs mostly close to the wooded border at the edge of the fields. Furthermore, the exponential model fit was better than for spatial distribution of adult *D. suzukii* (Table 2), with distance to the wooded border explaining 88% of the decrease in infestation (Fig. 5). Close similarity in the fruit infestation trends and that for *D. suzukii* captures is not surprising and suggest that female *D. suzukii* do not move very far from the edge to lay their eggs into cultivated lowbush blueberry fruit. Proximity to shelters and alternative wild berry resources in the woods for reproduction are key factors explaining this species presence and abundance in the lowbush blueberry agroecosystem. Our results on spatial distribution of *D. suzukii* and larvae in fruit could possibly be used in a pest management strategy, where, for example, early harvesting a 50-m strip of ripening lowbush blueberry adjacent to the borders could help prevent or limit *D. suzukii* from laying eggs further into the field as they tend to move to the crop, assuming that *D. suzukii* mainly inhabit the woods from where they disperse to lay eggs in lowbush blueberries.

## Conclusions

We found no evidence that *D. suzukii* overwinters in the Saguenay-Lac-Saint-Jean, but it was generally abundant in late summer and reached high densities in all our study sites. However, our data indicate that its recurrent presence in very high densities during late summer and fall in forest habitats bordering lowbush blueberry in Saguenay-Lac-Saint-Jean may represent considerable risk to the lowbush blueberry industry. We found clues in the seasonal pattern of abundance that the species might overwinter in the region, although this clearly requires further work. Its reproductive acclimation to fall conditions expressed as decreasing female fecundity from September with complete arrest in early October and the accumulation of very high densities of winter morphs before freezing, both are compatible with overwintering potential in protected microhabitats. We also developed quantitative predictive models of the spatial distribution of both *D. suzukii* density and concurrent lowbush blueberry fruit infestation, which decrease markedly with distance from the forested border of lowbush blueberry fields. We found that adult *D. suzukii* mostly inhabit the wooded borders of the lowbush blueberry fields and that annual growth in *D. suzukii* population density occurs relatively late in the summer. We also found that female *D. suzukii* lay the majority of their eggs in the first metres of the lowbush blueberry fields and mostly after the normal lowbush blueberry harvesting period. According to our findings, a pest management strategy adapted to the current situation should mainly focus on timing and location (near the borders) of harvesting. Eventually and based on results we present elsewhere, effective management of wild berry hosts in the lowbush blueberry environment should also be considered. Finally, further studies should be developed to better understand the population dynamics of *D. suzukii* in lowbush blueberry in the Saguenay-Lac-Saint-Jean region, and its behaviour and basic resources during the early season (May to early June) when *D. suzukii* is rare to absent or possibly unresponsive to the apple-cider baited traps currently used, and is very limited in terms of potential reproductive resources.

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