

Spatial Analysis of Seasonal Dynamics and Overwintering of *Drosophila suzukii* (Diptera: Drosophilidae) in the Okanagan-Columbia Basin, 2010–2014

Howard M. A. Thistlewood,^{1,8} Paramjit Gill,² Elizabeth H. Beers,³
 Peter W. Shearer,^{3,4} Doug B. Walsh,⁵ Brigitte M. Rozema,¹ Susanna Acheampong,⁶
 Steve Castagnoli,⁴ Wee L. Yee,⁷ Peter Smytheman,³ and Alix B. Whitener³

¹Summerland Research and Development Centre, Agriculture and Agri-Food Canada, Summerland, BC V0H 1Z0, Canada,

²Department of Computer Science, Mathematics, Physics and Statistics, University of British Columbia Okanagan, 3187 University Way, Kelowna, BC V1V 1V7, Canada, ³Tree Fruit Research & Extension Center, Washington State University, 1100 N. Western Avenue, Wenatchee, WA 98801, ⁴Mid-Columbia Agricultural Research and Extension Center, Oregon State University, 3005 Experiment Station Drive, Hood River, OR 97031-9512, ⁵Irrigated Agriculture Research and Extension Center, Washington State University, Prosser, WA 99350, ⁶Plant and Animal Health Branch, BC Ministry of Agriculture, 200-1690 Powick Rd, Kelowna, BC V1X 7G5, Canada, ⁷USDA-ARS, Yakima Agricultural Research Laboratory, 5230 Konnowac Pass Road, Wapato, WA 98951, and

⁸Corresponding author, e-mail: howard.thistlewood@agr.gc.ca

Subject Editor: Darrell Ross

Received 20 July 2017; Editorial decision 19 October 2017

Abstract

Spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), was monitored from 2010 to 2014 in 314–828 sites located in interior fruit-growing regions of OR and WA, United States, and BC, Canada, using traps baited with apple cider vinegar or sugar-water-yeast. Seasonal population dynamics and sex ratios were summarized for berry, cherry, stone fruit, grape, non-crop host plants, non-host sites, and for conventional IPM, certified organic, backyard, and feral sites, by region and year. Overwintering was detected in all regions and years, despite winter temperatures below -17°C . A spatial analysis was conducted using a Geographic Information System (GIS), daily weather data, geomorphometric measures of terrain, distance to water, and other variables, at each site. Overwintering success at a site, measured as Julian week of first capture of *D. suzukii*, was significantly related ($R^2 = 0.49$) in cherry habitats to year, agronomic treatment, and number of winter days with temperatures $>-5^{\circ}\text{C}$. In berry, cherry, stone fruit and grape habitats, 2011–2014, it was significantly related ($R^2 = 0.42$) to year, agronomic treatment, the logarithm of peak population of *D. suzukii* in the prior autumn, latitude, elevation, and topographic wetness index. The results show that *D. suzukii* has adapted to exploit a succession of irrigated crops and feral habitats in mixed landscapes of a semi-arid region with cold winters and hot dry summers, and are shaping strategies for pest management and for biological control.

Key words: landscape, horticultural entomology, invasive species, population ecology, GIS

Spotted wing drosophila, *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), a vinegar fly, is associated with a wide range of plants and habitats in Asia and Hawaii as a seasonal migrant across landscapes (Beppu 2000, 2006, Leblanc et al. 2009, Mitsui et al. 2010), and in parts of Japan is a fruit pest (Kanzawa 1939). Following the detection of *D. suzukii* in North America after 2008 (Walsh et al. 2011), it very quickly spread and is now established throughout the fruit-growing regions of North America and Europe (Asplen et al. 2015, Gutierrez et al. 2016). Unlike other drosophilids, *D. suzukii* caused significant damage in the berry- and cherry-growing industries of western North America (Ioriatti et al. 2015, Steenwyk and

Bolda 2015, Walton et al. 2016). It forced great change in pest management programs (Beers et al. 2011, Walsh et al. 2011, Thistlewood et al. 2012, Steenwyk and Bolda 2015), as it did subsequently elsewhere (Asplen et al. 2015, Haye et al. 2016).

In this study, we monitored the seasonal dynamics of *D. suzukii* for the first 5 yr after detection across a large area (137,500 km²) of a major fruit-growing region in the Pacific Northwest of North America. This area comprises the lower elevations of a group of inland valleys, and plains, in the rain shadow of coastal mountains. The region has hot dry summer and cold winter climates, differing significantly from relatively well-studied mild winter coastal climates such

as in California (Harris et al. 2014, Caprile et al. 2016, Wang et al. 2016), or moderate summer and winter climates in Italy (Wiman et al. 2014, Ioriatti et al. 2015, Mazzetto et al. 2015) and coastal regions of British Columbia (BC), Oregon (OR), and Washington (WA) (Dalton et al. 2011, Wiman et al. 2014, Tochen et al. 2016). Much of our study area also differs from other regions by the landscape, i.e., semi-arid sagebrush steppe, sharing distinct ecosystems surrounding areas of irrigated crop production, including ponderosa pine, bunchgrass, and sagebrush ecosystems (Lyons and Merilees 1996).

When *D. suzukii* was detected in North America, it was suggested that cold winter and hot dry summer regions may not be suitable for it, according to temperature tolerance studies of an Asian population (Kimura 2004), a coastal OR population (Dalton et al. 2011), and from at least one niche model (Walsh et al. 2011). Consequently, the interior fruit-growing districts of OR and WA (east of the Cascade Mountains) and Canadian regions to the north were predicted to be unsuitable habitat for *D. suzukii* (Beers et al. 2011, Walsh et al. 2011). Previous Japanese studies suggested that populations of *D. suzukii* migrate seasonally and decline sharply in cold winter periods and regions, but that some overwintering flies may survive in sheltered locations (Beppu 2000, 2006; Mitsui et al. 2010). It was also thought possible that *D. suzukii* may annually infest areas along trade routes, or via wind, or be introduced via grocery stores, packing houses, or fruit dumps (Cini et al. 2012). Recent reviews noted that it remains unclear if and how *D. suzukii* overwinters in colder regions of North America or migrates seasonally from regions with benign climates (Asplen et al. 2015, Hamby et al. 2016). It has been suggested that such invasions may recur on a global basis and that it is still unknown if recurrent invasions are occurring (Adrian et al. 2014).

Locally within the Pacific Northwest, significant genetic differences were detected between populations from the dry interior fruit-growing region and from milder coastal habitats. Populations of *D. suzukii* from eastern Washington had much reduced genetic variation, as measured using microsatellite markers at six loci, than a coastal California population. Bahder et al. (2015) provide strong genetic evidence that *D. suzukii* of eastern Washington are from an established population that has undergone a significant genetic bottleneck, as opposed to one subject to annual reintroduction events. Consequently, results from our region may differ substantially from those of other regions, owing to well-defined climatic, terrain, habitat, or landscape differences.

The present study describes for the first time the seasonal dynamics of *D. suzukii* in various habitats of a key fruit- and grape-growing area with a distinct climate and landscape, and contributes to key research areas (Asplen et al. 2015) of biology at low temperatures, reproductive diapause, host plant effects and non-crop flora. The study had two objectives: to summarize seasonal population dynamics as determined from trap captures in a wide variety of situations in a semi-arid cold-winter region of irrigated agricultural crops, and to employ a spatially explicit analysis to relate climate, landscape, and agronomic features to overwintering survival.

Materials and Methods

Survey Area and Trap Locations

D. suzukii was first detected in pilot traps in the mid-Columbia region of OR, United States, and near Kelowna, BC, Canada, in the autumn of 2009 (Thistlewood et al. 2012). From March to May of 2010 and ending in September to December of 2014, traps were deployed in BC, WA, and OR and the contents collected at near weekly intervals (Supplementary Material and Supplementary Table S1). *D. suzukii* was detected in many different host plants or situations (Table 1) at 314–828 locations per year across 137,500 km² of the Okanagan and Columbia basins (Fig. 1 and Supplementary Table S2). Study sites were

initially chosen to examine seasonal trends in population dynamics, and to help predict risk to agricultural producers. Susceptible commercial crops were a priority in trap placement, together with sites of biological relevance (Table 1 and Supplementary Table S2) from the limited literature available. Sweet cherry, *Prunus avium* (L.) L., was the main crop monitored in all regions, in addition to likely host plants and sites of agricultural trading or tourism. Vineyards and berries were a priority in southern WA and OR, but monitored in all regions. After 2010, trap placement was reduced following experience, or increased as resources were made available (described in Supplementary Material and Supplementary Tables S1 and S2). Representative traps were retained at specific sites for the 5-yr study, and in some years large numbers of traps were deployed in BC and OR to find sites of overwintered flies.

Adult Trapping

We employed two attractants, commercially purchased apple cider vinegar (ACV) in all regions, or a yeast-sugar-water attractant in parts of WA only, within five trap bodies (Supplementary Materials and Supplementary Table S3), hung at a height of 1.5 m in all sites. Trap contents were removed in the field regularly, fresh attractants were added or the trap replaced, the contents examined under a binocular microscope for adult *Drosophila* spp., and any *D. suzukii* were separated and counted by sex. Details of trap bodies and attractants, total flies captured, and numbers of sites, trap-days per record, and observations by region and year, are given in Supplementary Materials (Supplementary Tables S1–S3).

Data Verification and Population Summaries

The trap location in each host plant or site was recorded annually using hand-held Global Positioning System (GPS) receivers (Garmin International Inc., Olathe, KS; Trimble Canada, North Vancouver, BC), then mapped and verified by inspection using Google Earth (Google Inc.). Prior to analysis, all locations and weekly records were again checked and verified spatially using Google Earth Pro (Google Inc.) and a Geographic Information System (GIS) described below. From 77,671 weekly trap counts, we discarded records from sites with multiple replicates, in close proximity unless in a different crop or habitat, trapped for only a few weeks, or if criteria below were not met.

To summarize population dynamics, trap capture was standardized by site and days per observation to mean catch of flies per trap day (ftd) for all sites, by Julian week, year, and region, and amongst groups as described below. Residence time was calculated to compare habitat use across groups of sites, being the number of weeks when *D. suzukii* adults were present during the 5-yr study. For apparent sex ratio, owing to low numbers of fly captures before week 25, we summed the males or females in all sites by Julian week, year, and region.

Results are given as sample mean and standard error, $\bar{x} \pm \text{SE}$. Analyses were conducted using SAS/STAT v9.1 of SAS System for Windows, or JMP v12.2 (SAS Institute Inc., Cary, NC).

Climate at Trap Locations

The study area lies in a rain shadow to the east of coastal mountains and characterized by continental airstreams of dry air year-round, with hot and dry summers, especially at lower elevations and in southern WA and parts of OR. Convective rain often produces thunderstorms in summer, and winters are relatively cold and dry, as seen in representative climate data (Table 2). We assembled climate data at each trap site from a myriad of weather station networks but intermittent reporting and other difficulties (McMahan 2011) required a standardized National Oceanic & Atmospheric Administration (NOAA)/Daymet dataset (Thornton et al. 2014). Daymet data are

Table 1. Summary of trap locations (number positive for *D. sukuzii*) within consolidated *Habitat* groups, as assigned by host plant or situation

<i>Habitat</i> group	Family	Sites or plants with traps
Cherry ^a (<i>n</i> = 863)	Rosaceae	Sour cherry, <i>Prunus cerasus</i> L. Sweet cherry, <i>Prunus avium</i> (L.) L.
Stone fruit (<i>n</i> = 204)	Rosaceae	Apricot, <i>Prunus armeniaca</i> L. Nectarine, <i>Prunus persica</i> (L.) Batsch Peach, <i>Prunus persica</i> (L.) Batsch Plum pluot, <i>Prunus</i> spp. L.
Berry (<i>n</i> = 197)	Rosaceae	Raspberry, <i>Rubus idaeus</i> L. Thimbleberry, <i>Rubus parviflorus</i> Nuttall Blackberry, <i>Rubus plicatus</i> Weihe & Nees Himalayan blackberry, <i>Rubus bifrons</i> Vest
	Ericaceae ^b	Blueberry, <i>Vaccinium corymbosum</i> L. <i>Vaccinium</i> spp. L.
Grape ^c (<i>n</i> = 92)	Vitaceae	Table grape, <i>Vitis</i> spp. L. Wine grape, <i>Vitis vinifera</i> L.
Non-crop host ^{d,e,f} (<i>n</i> = 21) traps in host plants of <i>D. sukuzii</i> from the study region	Adoxaceae	Elderberry, <i>Sambucus</i> spp. L. Blue elderberry, <i>Sambucus nigra</i> ssp. <i>cerulea</i> (Raf.) R. Bolli
	Berberidaceae	Barberry, <i>Berberis</i> spp. L. Oregon-grape, <i>Berberis aquifolium</i> Pursh
	Caprifoliaceae	Snowberry, <i>Symphoricarpos</i> spp. Duhamel
	Cornaceae	Dogwood, <i>Cornus</i> spp. L.
	Grossulariaceae	Currant, <i>Ribes</i> spp. L. Golden currant, <i>Ribes aureum</i> Pursh
	Moraceae	Mulberry, <i>Morus</i> spp. L.
	Rosaceae	Chokecherry, <i>Prunus virginiana</i> L. Mahaleb cherry, <i>Prunus mahaleb</i> L.
Non-host ^{d,e} (<i>n</i> = 75) traps in plants not known as hosts of <i>D. sukuzii</i> from the study region	Grossulariaceae	Wax currant, <i>Ribes cereum</i> Douglas
	Rosaceae	Mountain-ash, <i>Sorbus</i> spp. L. Serviceberry, <i>Amelanchier</i> spp. Medikus Rose, <i>Rosa</i> spp. L. Hawthorn, <i>Crataegus</i> spp. L. Apple, <i>Malus pumila</i> Miller Crab apple, <i>Malus</i> spp. Miller Pear, <i>Pyrus communis</i> L.
	Ulmaceae	Siberian elm, <i>Ulmus pumila</i> L.
Structures and gardens ^g (<i>n</i> = 83) were located within or adjacent to:	Home gardens, ornamental gardens, parks, compost heaps, cull piles, commercial fruit stands, packinghouses, tourism stops, supermarket or produce handling rooms, cull piles, landfills or town dumps	

^aIn some OR sites, the trees were also near feral Himalayan blackberry bushes.^bFrom WA and OR only.^cWithin OR, were trapped in 2010–2012 only.^dNot monitored in WA in 2014.^eKnown regional hosts of *D. sukuzii* (Lee et al. 2015a,b; H.M.A. T., unpublished).^fNot monitored in WA in 2010, or OR from 2012 onwards.^gNot monitored in WA from 2012 onwards, or in OR in 2011 and 2014.

interpolated by NOAA over a 1 km × 1 km gridded surface for the conterminous United States and southern Canada, using a digital elevation model (DEM) and compiled ground observation data from official sources (Thornton et al. 2014). Daily data were accessed for each trap location, from 1 November 2009 onwards.

Spatial Description Using a GIS

Records by site of host plant or physical structure, habitat, agro-nomic treatment, trap attractant and body, location, trap deployment and collection dates, and fly captures, were entered in a GIS (ARC GIS 10.1, ESRI Canada, Toronto, ON), and matched to a National Elevation Dataset DEM from the US Geological Survey at resolutions of one arc-second (30 m) to 1/9 arc-second (3 m). Information layers were added for many measures of land cover, land use,

hydrography, transportation, soils, parks, and ecoregions, as described in Supplementary Material. To examine modifying effects of the highly variable terrain in our region upon micro-climates (Böhner and Antonić 2009, Gruber and Peckham 2009) and associated insect captures, we calculated 15 geomorphology layers at each site using ARC GIS functions and the System for Automated Geoscientific Analyses (SAGA) (Cimmery 2007–2010, Conrad et al. 2015). Values added to the GIS for each trap location are given in Supplementary Table S4.

Trap Locations Grouped by Habitat or Agronomic Treatment

In 2010 and 2011, little was known concerning the biology and hosts of *D. sukuzii*, and a wide variety of sites were monitored, with changes in number of some types of sites subsequently

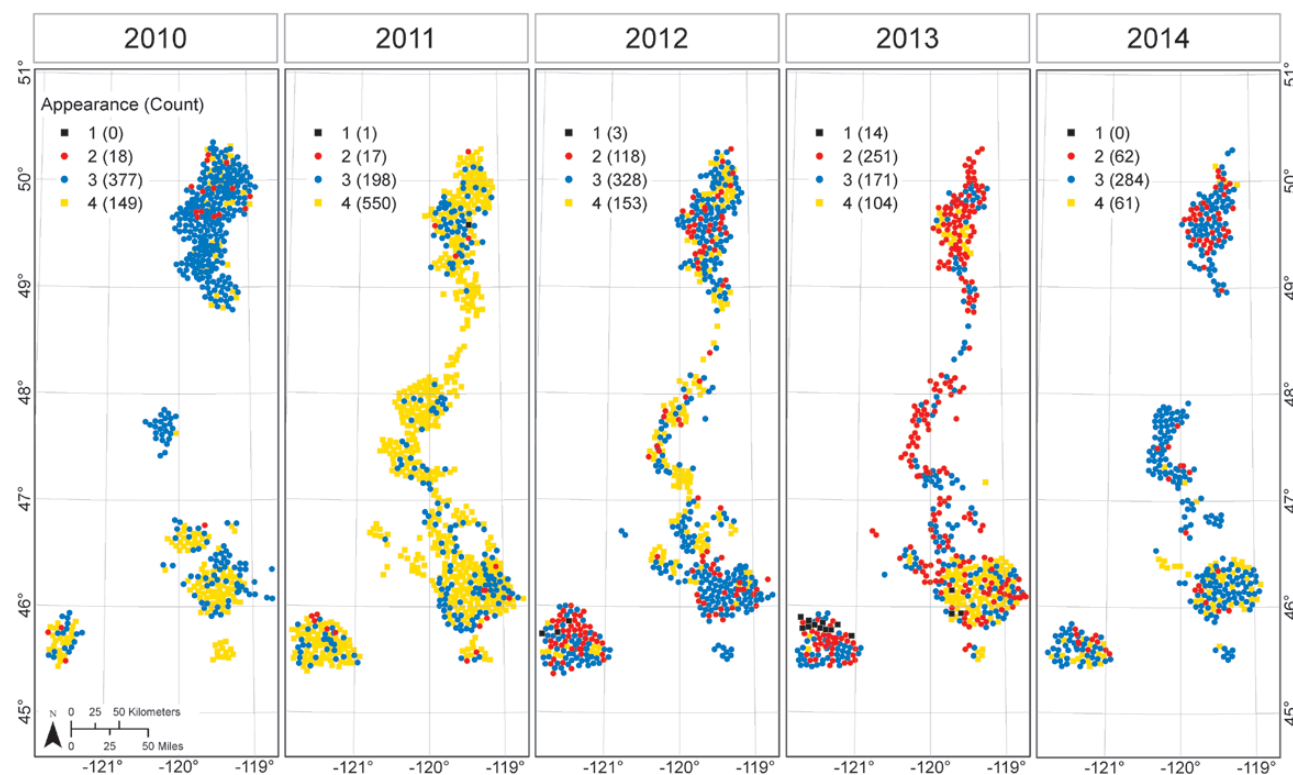


Fig. 1. Locations of sites trapped, showing the period of first catch of *D. suzukii* adults in 2010–2014 (black = January to April, red = May to June, blue = July to August, yellow = September to December), and as adjusted slightly (ArcGIS) to allow each point to appear. British Columbia sites are North of 49° latitude and Oregon sites are South of 46° latitude.

(Supplementary Materials and Supplementary Tables S1 and S2). For insight into effects of trap site or surrounding habitat on insect counts, we grouped sites that were trapped consistently for one or more complete seasons into six main types by host plant or feature (Table 1, Supplementary Table S2). The *Cherry* ($n = 863$) sites were in trees in cultivated orchards, abandoned orchards, wild or roadside sites, or on a fence between such orchards. In some OR sites, the trees were also near feral Himalayan blackberry (see *Berry*). *Stone Fruit* ($n = 204$) sites were placed in trees, *Berry* ($n = 197$) sites were located in bushes as described (Table 1) except blueberry was not monitored in BC. *Grape* ($n = 92$) sites were in vineyards, but only in OR from 2010 to 2012. *Non-Crop Host* ($n = 21$) sites were in known host plants, but not monitored in WA in 2010, or in OR from 2012 onwards. Prior to analysis, a better understanding of North American (Lee et al. 2015a,b) and regional (H.M.A.T., unpublished) hosts of *D. suzukii* resulted in reallocation of a few hosts. *Non-Host* ($n = 75$) sites were in plants not recorded as hosts of *D. suzukii* in our region during the study period, and were not monitored in WA in 2014. *Structures & Gardens* ($n = 83$) sites were within or adjacent to sites described (Table 1), but not monitored in OR in 2011 and 2014, or WA after 2011, and are discussed rarely.

For insight into differences between agronomic practices at feral sites, uncultivated sites, or cultivated sites, all were classified annually into five groups (Table 1 and Supplementary Table S2). The numbers varied annually, but the majority were in commercial crops receiving *Conventional* integrated pest management as a pesticide treatment ($n = 1,057$ sites; 200–585 per year). Roughly one quarter of all sites were certified *Organic* ($n = 222$ sites; 47–117 per year) in commercial crops, or were *Feral* ($n = 149$ sites; 54–88 per year), i.e., untreated plants in a setting not associated with

people, including abandoned sites, roadsides, or were wild seedlings. *Backyard* ($n = 39$ sites; 9–22 per year) sites were untreated, or received minimal pesticides, in home gardens, public parks or ornamental gardens, at compost heaps or untreated cull piles of commercial growers, or at sanitary landfills or ‘dumps’. *Structures* ($n = 58$ sites; 3–54 per year) sites were within a building, grocery store, packing-house or fruit stand, in a parking lot or tourism stop, and from 2011 onwards were collected in BC only. Amounts of pesticide use varied annually and regionally, but *Conventional* sites received the most insecticide and fungicide treatments, certified *Organic* sites received a limited range of insecticides and fungicides, *Backyard* sites received very little or no pesticides of any kind, and *Feral* sites were untreated.

Statistical Modeling of Insect Captures Following Winter

Insect counts were obtained weekly (Supplementary Table 1), so we examined the Julian week when *D. suzukii* was first detected in a site. We hypothesized that: small numbers of overwintered flies survive in relatively protected sites to populate each region annually; early trap capture (first week detected) results from an overwintered population at or near a site; and the likelihood of an overwintering site is a function of local climate (DAYMET data) as modified by unknown conditions. The latter include as predictor variables the host plant or habitat type, agronomic treatment, topography and geomorphological features, and other influences, from the GIS as described earlier. For each calendar year, we defined the winter season as 1 November of the prior year to 31 March of the current year and the spring season as 1 April to 30 June. To measure the degree of coldness or warmth of those seasons, we

Table 2. Representative climate data of temperature, precipitation, with number of days at two temperature thresholds and of minimum recorded during winter, from four representative weather stations (location and/or code, elevation above sea level) in three regions of the study area, for 2009–2014

Period	Climate variable	Year and location (station code, elevation above sea level)					
		2009	2010	2011	2012	2013	2014
Location: Kelowna, BC (MWSO, 456 m)							
Jan	Mean temp. (°C)	−3.2	0.9	−1.0	−2.4	−2.7	0
	Total precip. (mm)	28.2	25.2	37.6	22.5	29.4	21.6
July	Mean temp. (°C)	22.7	21.0	19.4	22.5	22.2	23.1
	Total precip. (mm)	22.4	11.6	26.4	35.4	6.0	43.8
Winter ^a	Days ≤ −5°C		30	49	43	23	44
	Days ≤ −10°C		12	14	9	2	19
	Min. temp (°C)		−17.9	−19.9	−19.1	−15.1	−18.1
Location: Bray's Landing, WA (405 m)							
Jan	Mean temp. (°C)	−3.7	0.5	−1.6	−2.2	−3.6	0.7
	Total precip. (mm)	11.9	56.4	25.2	20.3	12.2	12.9
July	Mean temp. (°C)	23.3	22.2	19.9	23	24.4	24.7
	Total precip. (mm)	6.1	9.1	12.7	32.5	2.3	4.3
Winter	Days ≤ −5°C		31	42	39	24	36
	Days ≤ −10°C		11	13	5	5	8
	Min temp. (°C)		−17.6	−21.3	−13.5	−14.6	−19.8
Location: Prosser, WA (WSU HQ, 264.6 m)							
Jan	Mean temp. (°C)	0.1	3.8	1.8	0.9	−0.7	1.2
	Total precip. (mm)	24.1	39.6	11.7	19.8	6.1	11.2
July	Mean temp (°C)	23.4	21.9	20.4	22.8	24	25
	Total precip. (mm)	0	6.1	6.1	7.4	0	4.3
Winter	Days ≤ −5°C		23	26	39	7	42
	Days ≤ −10°C		6	7	0	0	12
	Min temp. (°C)		−17.8	−17.3	−9.9	−8.9	−17.5
Location: Hood River, OR (HOXO, 155 m)							
Jan	Mean temp. (°C)	2.2	4.0	3.6	2.3	1.1	2.9
	Total precip. (mm)	148.3	121.2	95.3	170.9	35.1	79
July	Mean temp. (°C)	22.1	20	18.7	20.1	21.5	22.3
	Total precip. (mm)	0	0	8.6	22.6	0	13.7
Winter	Days ≤ −5°C		8	11	7	3	21
	Days ≤ −10°C		5	2	0	0	6
	Min temp. (°C)		−15.7	−13.2	−6.3	−8.6	−17.9

^aWinter is defined as 1 November of year prior to 31 March of year shown.

created 10 indices from DAYMET data for the numbers of days in winter and spring at various temperature thresholds from <−10°C to >25°C (Supplementary Table 6).

Two consecutive analyses were conducted with R v.3.3 (R Development Core Team 2017) using stepwise linear model selection by Akaike's AIC statistic as implemented in the R function step. Significance of terms was tested using *F*-tests and models were simplified iteratively by removing nonsignificant ($P = 0.05$ level) factors and interactions. We first examined *Cherry* sites, which had the best spatial and temporal representation in all regions, by regression analysis using 1,505 site-years of results from *Cherry* habitats, 2010–2014. We conducted a preliminary analysis of predictor variables using an extensive array of variables (Supplementary Material). After the preliminary analysis and discarding of non-significant measures, a smaller range of 33 predictor variables were tested (Supplementary Material). In a second analysis, we examined results from four major habitats of *Berry*, *Cherry*, *Stone Fruit*, and *Grapes*, comprising 1,135 site-years of observations during 2011–2014. This permitted addition of a between-season comparison of the prior population load (= peak number of *D. suzukii* ftd in autumn the year before) to the timing of first appearance in a year. The autumn population load of *D. suzukii* was highly skewed

in distribution and subjected to a logarithmic transformation prior to analysis.

Results and Discussion

Late in 2009, *D. suzukii* flies were first detected in the interior OR and BC regions of our study area, but no detection occurred in harvested fruit (Thistlewood et al. 2012). In 2010, traps were checked from weeks 18 (OR), 12 (WA), or 21 (BC), and any earlier fly activity was missed. Adult *D. suzukii* were detected throughout the study area by mid-summer of 2010, and thereafter (Figs. 1–3). From 2011, trapping began earlier in all years and regions, but trap effort varied in the winter (weeks 0 to 10 or 20) depending on resources available (Supplementary Tables 1 and 2). The final dataset resulted in 61,657 trap counts from 1,515 sites, comprising 1,824,547 adult *D. suzukii*, with annual totals between 59,101 flies in 2011 to 926,317 in 2013. Other *Drosophila* spp. were captured but are not discussed in the present study. In Washington State, assisted by molecular methods, Bahder et al. (2016) found that *D. suzukii* represented 8.7 to 38% of all drosophilids captured in traps when using ACV and yeast attractants from 2011 to 2013.

The trap bodies and attractants, numbers of observations, and flies captured by each trap body, are reported in the Supplementary Material and Supplementary Table S3. Most results (95.6% of observations and 97.3% of captured *D. suzukii*) were obtained with ACV attractants. The 4.4% of observations using yeast attractants captured 2.7% of flies; all in WA, mostly in grapes or nearby blueberry crops in the south of the state. Near 10- to 20-fold differences in populations of *D. suzukii* were recorded between 2010 and 2014 (Figs. 2 and 3), which influenced results much more by the year and other factors than by differences amongst traps. The latter were nonsignificant in preliminary analyses, so results for all attractants and bodies were combined and not separated further. The ACV and yeast attractants, and variants of the trap bodies deployed, were used in many recent studies of *D. suzukii*, and their relative strengths or weaknesses reviewed by Haye et al. (2016) and others (Supplementary Material).

Apparent Sex Ratio

From 856,513 male and 968,034 female adult *D. suzukii*, we calculated the apparent sex ratio (%female adults) in all traps by region and year (Fig. 4). The ratio cycled annually and was predominantly female-biased from the beginning of the year until weeks 25–35, depending upon region. However, early-season catches of males (only) or male-biased sex ratios occurred a few times in weeks 0–35 in all regions, and occasionally late in the year in OR (Fig. 4). After *circa* week 35, the ratio changed steeply and was male-biased with a peak in *ca.* weeks 35–45, when a decline towards female-biased captures was observed in most regions and years (Fig. 4). The overall sex ratio during the study was 53.1% female but differed across habitat groups (Supplementary Table S2), from 49.5% female in a preferred habitat (Berry) to 66.6% female in Grape, a less-preferred

crop (monitored using more yeast attractants than in other sites). Sites treated minimally or untreated with pesticides captured fewer females (Backyard 44.3%, Feral 47.4%, Structure 46.1%, of adults respectively) whereas Conventional (54%) and Organic (54.7%) sites showed a bias towards females (Supplementary Table S2).

Sex ratio may truly vary in nature seasonally, or trap captures may be an artifact of trap attractants or competitiveness thereof, or of other factors. Thus, male *D. suzukii* are more susceptible than females to insecticides (Beers et al. 2011, Bruck et al. 2011), used primarily in Conventional and Organic sites. Few reports exist for *D. suzukii* on a seasonal basis with ACV or yeast attractants, but some are similar: sex ratio varied with month of the year (Hamby et al. 2014), was female-biased in the first 26 wk annually (Arnó et al. 2016), or female-biased in winter and male-biased in summer (Zerulla et al. 2015, Rossi-Stacconi et al. 2016). Others differ from the present study: in 2 yr of monitoring a mosaic of fruit crops, Mazzetto et al. (2015) reported a sex ratio consistently near 50% female, except for fewer females (42.9%) in berry crops, as found in the present study. Similarly, the sex ratio was generally 50% female in California citrus, but in nearby sweet cherry was highly female-biased, at 73–86.7% of adults (Caprile et al. 2016).

Annual Pattern of Adult Captures and Influences of Habitat or Agronomic Treatment

Comparing all years, *D. suzukii* populations were relatively high in 2010, decreased in 2011, and then increased in all regions by 10- to 20-fold during 2012–2014 (Figs. 2 and 3). Such increases over time were reported in its recent invasion of northern Italy (Mazzetto et al., 2015, Arnó et al., 2016).

We observed an annual pattern that was modified by latitude and local climate (Table 2); the major variations in annual captures

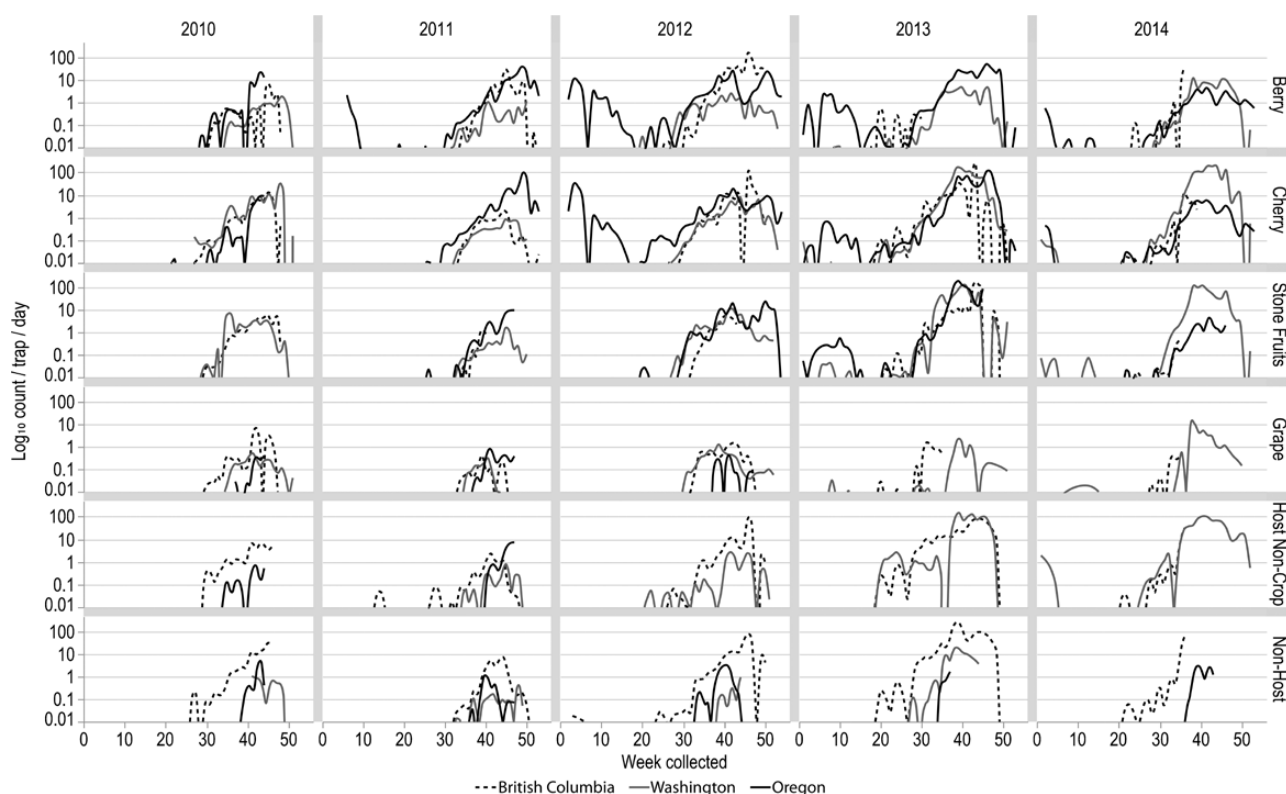


Fig. 2. Mean population density per trap day (\log scale) of *D. suzukii* in sites grouped by habitat, region (British Columbia, Washington State, Oregon), Julian week, and year, from 2010 to 2014 (week 20 is 7–15 May).

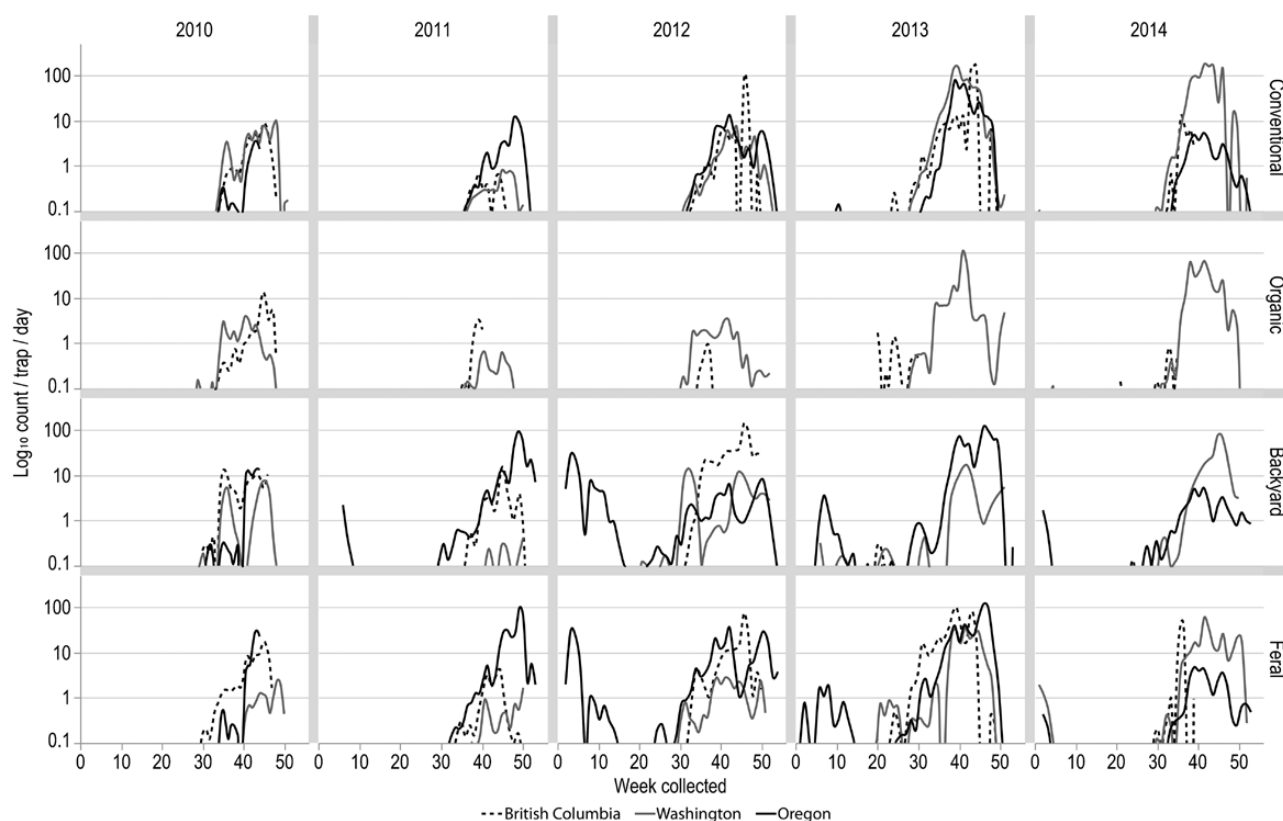


Fig. 3. Mean population density per trap day (log scale) of *D. suzukii* in sites grouped by agronomic treatment, region (British Columbia, Washington State, Oregon), Julian week, and year, from 2010 to 2014 (week 20 is 7–15 May).

are described in the Supplementary Material. To summarize, in most years, during the first part of winter (Julian weeks 0 to 10), we captured some flies in OR, very few flies in WA, and on one occasion only in BC (Figs. 1–3). In the coldest region (Kelowna, BC Table 2), or during cold winter and spring seasons in warmer regions, there was insufficient adult activity for detection in traps, i.e., from weeks 0 to 20 in BC in most years, in WA 2010–2012, and in OR 2010–2011 (Figs. 2 and 3). After week 20, steady and marked increases in number of infested sites and of within-site fly populations occurred to *ca.* week 40, or until the onset of winter (Figs. 2 and 3). Very high counts of *D. suzukii* occurred from October to December annually, as noted by Harris et al. (2014) in California. Such ‘autumn flushes’ of sudden and large increases in numbers of adult drosophilids were first reported from deciduous woods in Scotland (Basden 1953). In relatively mild districts or winters, a slow decline of adults occurred from *ca.* week 40 until zero catch in weeks 10–16 of the following year (WA in 2013, 2014 and OR in 2011–2014). In all regions, *D. suzukii* populations declined quickly after a significant cold weather event, below -5°C . Prior to such an event, or otherwise to the end of the year (week 52), adult flight activity occurred on days $>5^{\circ}\text{C}$ in all regions, and in OR year-round. Field observations of adult activity in winter can be contradictory even from warm areas with air temperatures rarely $<0^{\circ}\text{C}$: adults were active in winter in northern Spain (Arnó et al. 2016), but in northern Italy were reportedly inactive (Mazzetto et al. 2015) or active even when mean daily minima were $<0^{\circ}\text{C}$ (Rossi-Stacconi et al. 2016). We infer that, in winter months, trap capture is a combined measure of variable survival and/or frequency of temperatures suitable for flight. In years with a mild winter, flies were found in many sites shortly after the summer build-up began (Figs. 2 and 3), and subsequently reached

population densities higher than in other years, seen in all regions in 2013 (Figs. 2 and 3).

Considering differences among habitats, populations of *D. suzukii* reached high densities most often in *Cherry*, followed in decreasing order by *Stone Fruit*, *Non-crop host plants*, *Non-host plants*, *Berry*, *Structures & Gardens*, and *Grape* (Fig. 2). The relative differences among habitat groups were broadly similar in each region across years, as reflected in Grand means ($\pm\text{SE}$) of male and female *D. suzukii* per trap day (Supplementary Table S2). The observed sequence of arrival of *D. suzukii* in the crops corresponded to their ripening and harvest periods in the study area. An initial hypothesis of annual reinfestation via trade routes was dismissed in 2010, when very few flies were found in such sites and only after field infestation. After 2010, we trapped only 3–5 retail or warehouse sites annually, with the same result.

Flies were present in *Non-crop host* sites for many weeks, in high populations (Fig. 2), and in some years, appeared earliest in *Non-crop host* sites, suggesting that they are refugia for overwintered adults. Fly populations also built up in a succession of *Non-crop hosts* after passing through fruit crops (Fig. 2). In *Structures & Gardens*, we noted that private gardens with high counts late in the year were often diverse habitats with many plant hosts. Most landscape level research on *D. suzukii*, including the present study, has been conducted using a biased distribution of traps but similar patterns across habitats, and seasonal changes, were reported from smaller studies using ACV baited traps in western North America (Harris et al. 2014, Caprile et al. 2016, Wang et al. 2016). However, definitive data are lacking on their importance in relation to neighboring cultivated plantings (Klick et al. 2016), and have been only rarely collected in semi-arid environments (Wang et al. 2016) or

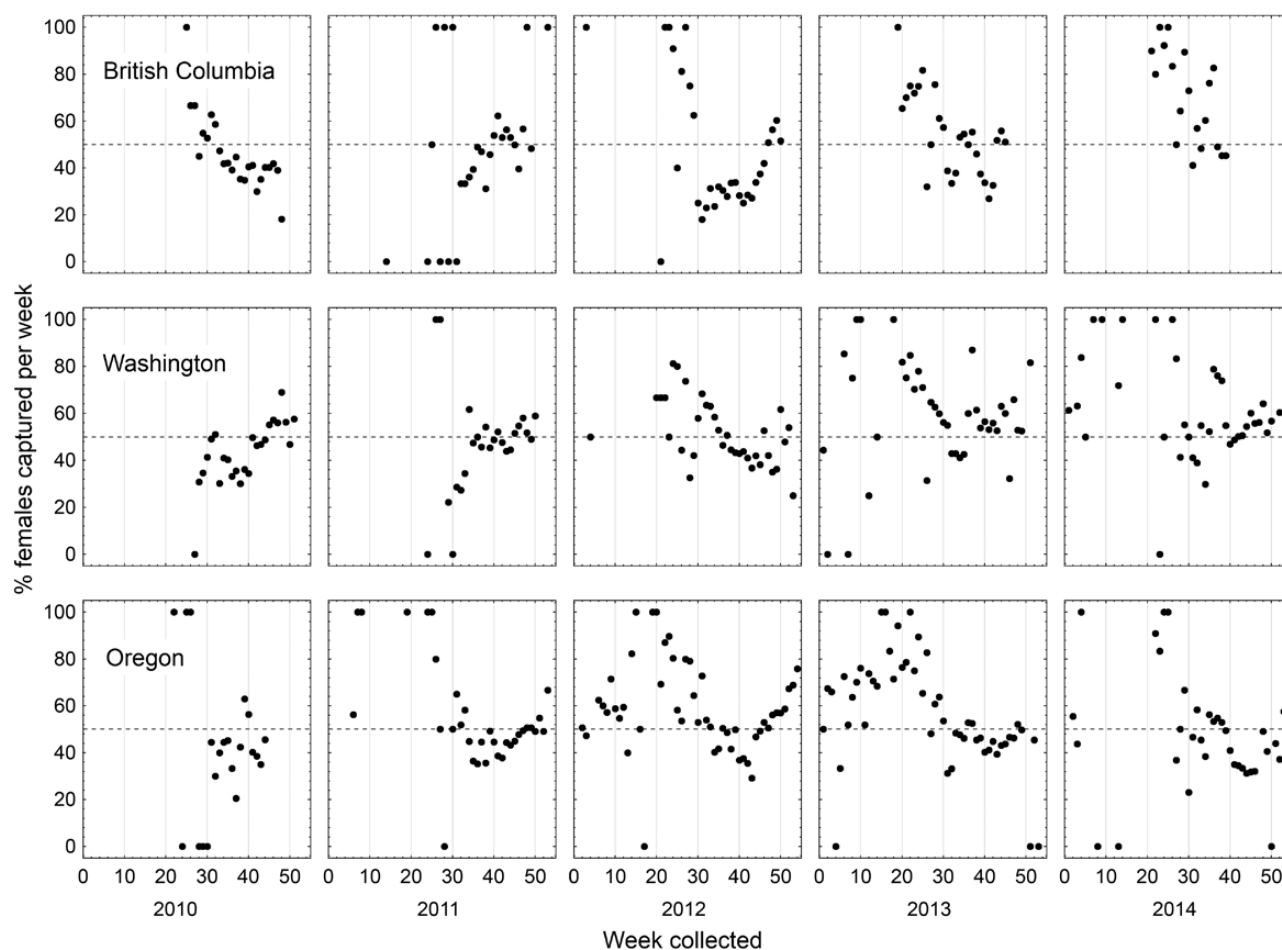


Fig. 4. Sex ratios (% female adults) of 1.8 million *D. suzukii* in 367–686 traps, as collected by week of year (2010–2014) in three regions (British Columbia, Washington State, Oregon State). Female-bias weeks are above and male-bias weeks are below a reference line of 50% on Y axis.

from cold winter regions (Pelton et al. 2016). In resource-restricted environments, where crop hosts are not available year-round, non-crop hosts or adjacent crops may play important roles as refugia, for seasonal biology, and in persistence or invasion success.

With regard to agronomic *Treatment* groups, trap captures were similar across regions and years, and ranked in decreasing order of population densities as *Conventional*, *Feral*, *Backyard*, and *Organic* (Fig. 3), as reflected in the Grand mean adult catch ftd (Supplementary Table S2). *D. suzukii* often appeared relatively early in *Feral* and *Backyard* sites (Fig. 3), and both had population levels equivalent to or exceeding those in *Conventional* sites, except in 2014 (Fig. 3). *Conventional* sites experienced very high trap counts in one or more years, typically by weeks 40–50 after cessation of harvest, but flight activity in winter was much less than in other agronomic categories (Fig. 3). *Organic* sites also showed much reduced captures in winter compared with *Backyard* and *Feral* groups, except for WA in 2013 to winter of 2014 (Fig. 3). In practice, *Berry* and *Cherry* crops were extensively treated with insecticides for *D. suzukii* for a short period until harvest (Beers et al. 2011), but large numbers of *D. suzukii* were tolerated postharvest in commercial sweet cherry and other susceptible plant hosts, and at times pre-harvest in the *Grape* habitat.

The repeated observation of periods of low to zero adult catch in landscape-level studies is of critical importance to understanding population survival, as a genetic bottleneck, and for exploitation in pest management. Seasonal periods of very low or zero catch were

found in the present study and in other regions where *D. suzukii* overwinter as adults; in California (Hamby et al. 2014, Harris et al. 2014) and in northern Italy (Mazzetto et al. 2015, Zerulla et al. 2015). After a few specimens were caught in early spring, adults were no longer found in our study area until week 20 (mid-May), or until June (Mazzetto et al. 2015), or from mid-April to late July (Zerulla et al. 2015). It has been suggested that this absence may arise from a great reduction in populations during overwintering leading to densities below the trap threshold, or that traps may lose attractiveness, or that *D. suzukii* may be active in other habitats or situations. If, as appears the case, the populations are at their lowest level at that time, vegetative management, or the targeted use of insecticides, sterile insect release, or augmentative release of natural enemies, requires the least effort. However, the optimal timing of control treatments differs across growing regions. In California, *D. suzukii* populations peaked in spring (early May) and declined as harvest approached in June (Harris et al. 2014, Caprile et al. 2016, Wang et al. 2016), whereas populations in the present study were non-existent or low in the early part of the season and peak populations occurred from mid-August to November, after most crops were harvested.

Overwintering and Climate

As each growing season began, low numbers of *D. suzukii* were captured in some sites across the study area before other, relatively nearby, sites (Fig. 1). The first detection of *D. suzukii* in

2,859 site-years of results occurred on 18 occasions in January–April (by region, OR = 14, WA = 3, BC = 1), 466 occasions in May and June (OR = 100, WA = 195, BC = 171), 1,358 occasions in July and August, and 1,017 occasions in September–December, with a spatial distribution as shown (Fig. 1). Early sites were detected in all years in complex terrain (steeply sloped valleys to >2,000m, with agriculture on benchlands) of BC and OR; in most years in relatively flat terrain of southern WA, and in some years in the intermediate sloped valleys of central and northern WA. After detection in the earliest sites (Fig. 1), detection continued at low levels in increasing numbers of sites, followed by population increases in all sites, and subsequent local spread to new sites, followed by population build-up therein (Figs. 2 and 3; H.M.A.T., unpublished results). This did not fit suggested patterns of reinfestation via fruit imports or recurrent invasions via passive long-distance dispersal by wind from southern situations (Cini et al. 2012, Stephens et al. 2015).

Coupled with the patterns of captures before and after winter (Figs. 2 and 3), these are the first evidence of overwintering of *D. suzukii* under cold winter conditions, with as many as 44 d of <−5°C and 19 d with <−10°C (Table 2). The study area experienced greater extremes in summer and winter temperatures than any other reported to date, yet the activity pattern resembles that of *D. suzukii* in many other areas: a carry-over of populations by some form of overwintering, a short period between winter disappearance and spring reappearance in warm regions or years, and a long period in cold regions or years. Earlier field studies reported periods of winter drop-off to low or zero trap capture of other *Drosophila* spp. (Pipkin 1952, Basden 1954), and of *D. suzukii* in Japan (Beppu 2006). In some, *D. suzukii* was described as a seasonal migrant that reinfested areas, and in others as undergoing in the local area a reproductive arrest, followed by immediate reproduction when subjected to warmer temperatures. Reproductive arrest was described recently in laboratory studies of *D. suzukii* (Toxopeus et al. 2016, Wallingford and Loeb 2016).

Our results demonstrate sufficient survival of overwintered adults for high population levels to build up pre-harvest in 4 of 5 yr (exception 2011, Figs. 2 and 3) in three regions, each experiencing winters with daily maxima below the flight threshold and daily minima of −17.8°C or below (Table 2). The status of overwintering in cold winter regions was previously unclear. *D. suzukii* was reported as relatively cold intolerant when compared with other *Drosophilids* by Kimura (2004), who recorded mean lethal temperatures (LT₅₀) of −0.3°C to −0.1°C for males, and −1.6°C to −1.2°C for females, in strains from warm and cold regions of Japan. Overwintering under the conditions of our study area was also not anticipated from laboratory studies on cold tolerance, by niche distribution modeling, or by extrapolation from field or laboratory studies elsewhere (Dalton et al. 2011, Walsh et al. 2011, Jakobs et al. 2015, Stephens et al. 2015, Hamby et al. 2016, Langille et al. 2016, Ryan et al. 2016, Toxopeus et al. 2016). However, it was apparent early in the present study that a ‘winter morph’ of *D. suzukii* was present (Shearer et al. 2016), with biological features that are only now being described (Stephens et al. 2015, Shearer et al. 2016, Wallingford and Loeb 2016). Consequently, we retained sites that were important for comparison of overwintering populations. Additional physical evidence came from an overwintered adult male (winter morph) collected in BC in week 23 (2014) from ground emergence cages, in the week when the first flies were captured in traps in nearby trees (H.M.A.T., unpublished results). Zerulla et al. (2015) also found winter morphs of *D. suzukii* in a warm winter region of northern Italy.

Statistical Modeling of Measured Factors on Overwintering

By 2012, field results in BC suggested that some early sites (periods 1 and 2 in Fig. 1) had common characteristics. Using the GIS, six clusters were identified with three or more early sites within 1 km of each other (H.M.A.T., unpublished results). Building an explanatory linear regression model was challenging because of many possible explanatory variables: sites were chosen for ecological or crop monitoring reasons and not by a balanced experimental design across regions, years, crops, nor agronomic factors. Locations were spread over a large area or clustered together and associated geomorphometric factors were static, but meteorological and population variables varied greatly by year.

Extensive preliminary analyses of 1,505 site-years of data from *Cherry* habitat showed no significant contribution of any landscape or terrain variable to a regression model of first catch date of *D. suzukii*. In practice, much variability was due to uncontrolled, random, or confounded factors. Nonetheless, three factors (year, agronomic treatment, winter warmth) explained a significant portion ($R^2 = 49\%$) of the variation in date (Tables 2 and 3), and validated the general hypothesis. A second analysis used results from four major habitats of *Berry*, *Cherry*, *Stone Fruit*, and *Grapes*, in order to add between-season comparisons of the population load in the autumn of the previous year, for 1,135 site-years of data, 2011–2014. Using step-wise analysis, we reduced the set of predictor variables to 18 and to a regression model which was highly significant ($R^2 = 43.7\%$) for the first week of trap captures. On further examination, many of the variables did not contribute (5% significance level) to the model. Subsequently, a smaller and highly significant model ($R^2 = 42.2\%$; Tables 5 and 6) was fitted with five predictive factors (agronomic treatment, year, *log* population load, elevation, latitude, and topographic wetness index, TWI). The complexity of results is such that the exact proportion explained by each depends upon the order in which they are entered in the model, but in view of the large variance associated with insect populations, a predictive model explaining significant portions of variance is valuable in understanding key factors.

For both analyses, annual variability (year) is an expected main factor, well known from studies in horticulture and other integrative systems where variable environmental conditions affect an entire plant or cropping system and variously across seasons. These were also first observations of an invasive pest that varied many-fold in population densities across years and that may have undergone adaptation to novel habitats or climatic conditions. A general trend was of earlier appearance of flies throughout 2010–2014, in analyses of *Cherry* habitats and of four major habitats (Factor estimates, Tables 4 and 6). The exception is 2011, a very cool year with consequent late emergence; 2013 was the earliest in the study, at 7.5 wk earlier than in 2010 or 2011 (Tables 4 and 6), as a result of the warmest winter (e.g., Days ≤−5°C in Table 2). The trend to earlier appearance continued into 2014 (Table 6) despite a relatively cold winter (Table 2), and has continued in all three regions since 2014 (unpublished results).

The week of first catch did not differ significantly among four *Habitat* groups from 2011 to 2014, so *Habitat* is not a factor in the regression model (Table 5). This result is expected if *D. suzukii* overwinters in the wide variety of natural or cropping systems and sites in which it was detected. However, the timing of first catch differed significantly between sites by agronomic treatment in both analyses of *Cherry* and of multiple habitats (Tables 3–6). In *Cherry* habitats, using *Backyard* sites as the earliest and baseline value, no significant differences were found between *Backyard* and *Feral* ($P = 0.38$) or

Structure sites ($P = 0.88$), but flies appeared significantly later (4.8 to 5.2 wk, Table 4) in *Conventional* ($P = 0.01$) and *Organic* sites ($P = 0.01$). In multiple habitats, 2011–2014, agronomic treatments were similarly related to a lag of 4.6 to 7.9 wk in first catch behind baseline *Backyard* sites (Table 6). Some factor may have led to suppression of overwintered populations for relatively lengthy periods in *Conventional* and *Organic* sites; perhaps management practices of cultivation or pesticide treatment. Alternatively, overwintering success was relatively high within *Backyard* sites for unknown reasons.

One climatic factor was separated from annual variability in *Cherry* habitats: winter.warm2, when daily minimum temperature was $>-5^{\circ}\text{C}$ (Supplementary Table S5; measured at 44 to 148 d per site-year ($x = 116.2 \pm 0.39$)). It was related significantly ($P < 0.001$) to first capture date, the latter moving earlier in the year with increasing warmth. The result is significant as a first statistical link between winter weather and a measure of overwintering success, and from a field study in cold winter regions. In warmer regions, with temperatures rarely $<0^{\circ}\text{C}$, Zerulla et al. (2015) suggested that temperatures $\leq 5^{\circ}\text{C}$, with occasional periods of $\geq 10^{\circ}\text{C}$ for very short periods, caused increased mortality in winter. Rossi-Stacconi et al. (2016) significantly correlated winter trap catch with mean winter minima in the range -4°C to $+1^{\circ}\text{C}$, from 15 observations at 11 sites.

No other temperature thresholds or time periods were significant factors, and the unbalanced design of the dataset may have resulted in problems of scale. We regularly monitored sites with different habitats, pesticide treatments, and population levels in any week, within a unique cell of DAYMET climate data of 1 km \times 1 km. Gutierrez et al. (2016) recently reviewed temperature relations, overwintering, and mathematical modeling of *D. suzukii* populations, and recognized problems of scale for mountainous areas (using spatial resolution of 25 km \times 25 km), that were also identified by Zerulla et al. (2015), as in the present study.

Table 3. Analysis of variance table for regression analysis of week of first trap capture of *D. suzukii* in the *Habitat* group of *Cherry*, from 2010 to 2014

Factor	df	Sum of squares	Mean squares	F values
Year	4	22428.0	5607.2	313.01
Agronomic treatment	4	2119.3	529.8	29.58
Winter Warmth2	1	383.5	383.5	21.41
Residuals	1,495	26781.3	17.9	
Total	1,504	51712.1		

Table 4. Estimates of effects of factors on the value for the week of first trap capture of *D. suzukii* in the *Habitat* group of *Cherry*, from 2010 to 2014

Factor or coefficient	Estimate	SE	t value	P value
Treatments (with Backyard as the baseline group)				
Conventional	5.16	1.898	2.72	0.01
Organic	4.78	1.938	2.47	0.01
Feral	1.69	1.946	0.872	0.38
Structure	0.33	2.301	0.145	0.88
Years (with year 2010 as the baseline)				
2011	3.51	0.348	10.07	<0.001
2012	-1.49	0.375	-3.98	<0.001
2013	-7.48	0.366	-20.4	<0.001
2014	-2.55	0.409	-6.24	<0.001
Winter warmth	-0.042	0.009	-4.63	<0.001

From the analysis of multiple habitats, a statistically significant effect ($P < 0.001$) of autumn population load of *D. suzukii* (0 to 3,360 per trap count; $x = 104.3 \pm 18.8$) was related to date of first catch (Tables 5 and 6); the latter was earlier as the population increased at sites. Although intuitively sensible, this is the first study to link population parameters of *D. suzukii* across a prolonged period of very low or zero catch, such as winter, and has implications for management strategies. Three other factors also contributed significantly to the model in multiple habitats, 2011–2014 (Table 5): decreasing latitude (range 45.49°N – 50.30°N) significantly advanced the date, increases in topographic wetness index (range -15.8 to -4.9) and elevation (range 26.8–1921.8 m) significantly retarded the date. Topographic Wetness Index (TWI, Supplementary Table S4) is a topographic measure that is related to the movement of moisture or cold air. By contrast, climate measures should incorporate some effects of elevation and latitude, so the meaning of the latter two results is unclear.

Initially, we observed in BC that clusters of early sites occurred near water bodies or streams. However, for the entire study area and landscape elements (land cover types, distance to water bodies, etc.) commonly associated with levels of moisture, only TWI contributed

Table 5. Analysis of variance table for regression analysis of week of first trap capture of *D. suzukii* in the four *Habitat* groups of *Berry*, *Cherry*, *Stone fruit* and *Grapes*, from 2011 to 2014

Factor	df	Sum of squares	Mean squares	F value
Agronomic treatment	4	3673.5	918.4	41.75
Years	3	10675.7	3558.6	161.76
Log (prior population load of <i>D. suzukii</i>)	1	2867.0	2867.0	130.32
Elevation	1	362.4	362.4	16.47
Latitude	1	348.2	348.2	15.83
Topographic Wetness Index	1	103.5	103.5	4.70
Residuals	1,124	24727.0	22.0	
Total	1,135	42757.3		

Table 6. Estimates of effects of factors on the value for the week of first capture of *D. suzukii* in the four *Habitat* groups of *Berry*, *Cherry*, *Stone fruit*, and *Grapes*, from 2011 to 2014

Factor or coefficient	Estimate	SE	t value	P value
Treatments (Backyard as the baseline group)				
Conventional	6.71	0.98	2.72	0.01
Organic	7.93	1.03	7.70	<0.001
Feral	4.60	1.02	4.48	<0.001
Structure	4.85	1.30	3.74	<0.001
Years (year 2011 as the baseline)				
2012	-5.26	0.41	-12.76	<0.001
2013	-7.45	0.40	-18.44	<0.001
2014	-1.50	0.52	-2.87	<0.001
Log autumn (highest <i>D. suzukii</i> count in prior year)	-1.66	0.17	-6.24	<0.001
Latitude	-0.42	0.09	-4.55	<0.001
Elevation	0.0054	0.0013	4.20	<0.001
Topographic Wetness Index	0.18	0.082	2.17	0.03

significantly to the model. In our arid environment, a delay in first catch may as likely be due to cold air flow at sites with high TWI values, rather than moist air or water flow. Nonetheless, adult *Drosophila* are highly dependent on water resources, having a relatively low tolerance to desiccation, and moisture levels are critical for reproduction, survival, and even rate of dispersal (David et al. 1983). Winter rains and sudden drops in autumn temperatures were critical in seasonal population dynamics of nine species of drosophilids in the mountains of Lebanon (Pipkin 1952). Avondet et al. (2003) linked five variables including saturation deficit and maximum temperature to abundance and diversity of eight *Drosophila* spp. in six types of site. Recently, population parameters of *D. suzukii* were related significantly to moisture levels, and population pressure was greater in fields with high relative humidity, or in close proximity to water bodies, than in others (Tochen et al. 2016).

In conclusion, the results show that *D. suzukii* is well adapted to conditions of cold winters, hot summers, and fluctuating temperatures, within a semi-arid landscape of irrigated crops and feral plant hosts. Its activity as a seasonal migrant across habitats resemble those in warm conditions in Japan (Beppu 2000, 2006; Mitsui et al. 2010), northern Italy (Tonina et al. 2016), and extend to remote locations of WA and OR (Murray et al. 2017). The new understanding of *D. suzukii* as overwintering within our region and of its presence year-round in a succession of habitats is shaping the development of strategies for pest management and for biological control.

Supplementary Material

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

We thank Paul Couch, Grace Frank, Naomi DeLury, Sukhdeep Brar, Jill Goulet (AAFC, Summerland, BC), Joel Therrien (University of BC, Kelowna, BC), Chey Temple and Dana Jones (USDA-ARS, Wapato, WA), for technical assistance, Bradley Sinclair (Canadian Food Inspection Agency, Ottawa, ON) for Dipteran identifications, Denise Neilsen (AAFC, Summerland, BC) for advice on climate data, Laura Monteiro Torres and José Aranha (University of Trás-os-Montes and Alto Douro, Vila Real, Portugal) for sabbatical support to HMAT and GIS advice, Washington State University and the AgWeatherNet project for climate data. Invaluable trapping and site coordination was provided by Charlotte Leaming, Molly Thurston, Duane Holder, and Amanpreet Gill, (BC Tree Fruit Co-operative, Kelowna, BC), Gayle Krahn (Jealous Fruits, Lake Country, BC), Diane Thomas (Okanagan Clean Harvest Consulting, Lake Country, BC), Tamara Richardson (Cornucopia Crop Consulting Ltd., Cawston, BC), Amanda Borel and Tuck Contreras (MCAREC, Oregon State University, Hood River, OR), advisory staff of Cascade IPM, Dovex, Northwest IPM, and Stemilt, in Wenatchee, WA, as well as Northwest Wholesale (Brewster, WA), Quincy Fruit Company (Quincy, WA), Wilbur Ellis (Chelan and Mattawa, WA), and Zirkle (Mattawa, WA). Funding was provided in part by AAFC Growing Forward 1 and 2, BC Agriculture, Environment, and Wildlife Fund, BC Cherry Growers Assoc., BC Fruit Growers Assoc., BCFGA Tree Fruit Industry Development Fund, BC Table Grape Association, BC Investment Agriculture Foundation, Columbia Gorge Fruit Growers Association, Concord Research Council, USDA Specialty Crop Research Initiative Award number 2010-51181-21167, Washington Department of Agriculture Specialty Crop Block Grant, Washington State Commission on Pesticide Registration, Washington Tree Fruit Research Commission, and the Washington Wine Advisory Committee. H.M.A.T. was partially supported by a fellowship from the OECD Co-operative Research Programme, 2011–2012.

References Cited

Adrian, J. R., A. Kousathanas, M. Pascual, H. J. Burrack, N. M. Haddad, A. O. Bergland, H. Machado, T. B. Sackton, T. A. Schlenke, M. Watada,

- D. Wegmann, and N. D. Singh. 2014. *Drosophila suzukii*: the genetic footprint of a recent, worldwide invasion. *Mol. Biol. Evol.* 31: 3148–3163.
- Arnó, J., M. Solà, J. Riudavets, and R. Gabarra. 2016. Population dynamics, non-crop hosts, and fruit susceptibility of *Drosophila suzukii* in Northeast Spain. *J. Pest Science* 89: 713–723.
- Asplen, M. K., G. Anfora, A. Biondi, D. S. Choi, D. Chu, K. M. Daane, P. Gibert, A. P. Gutierrez, K. A. Hoelmer, W. D. Hutchison, et al. 2015. Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*): a global perspective and future priorities. *J. Pest Science* 88: 469–494.
- Avondet, J. L., R. B. Blair, D. J. Berg, and M. A. Ebbert. 2003. *Drosophila* (Diptera: Drosophilidae) response to changes in ecological parameters across an urban gradient. *Environ. Entomol.* 32: 347–358.
- Bahder, B. W., L. D. Bahder, K. A. Hamby, D. B. Walsh, and F. G. Zalom. 2015. Microsatellite variation of two Pacific Coast *Drosophila suzukii* (Diptera: Drosophilidae) populations. *Environ. Entomol.* 44: 1449–1453.
- Bahder, B. W., L. D. Bahder, M. Hauser, E. Beers, and D. B. Walsh. 2016. Relative abundance and phenology of *Drosophila* Fallén, 1815 (Diptera: Drosophilidae) species in south-central Washington State. *Pan-Pac. Entomol.* 92: 92–99.
- Basden, E. B. 1953. The autumn flush of drosophila (diptera). *Nature* 172: 1155–1156.
- Basden, E. B. 1954. Diapause in *Drosophila* (Diptera: Drosophilidae). *Proc. R. Ent. Soc. London (A)* 29: 114–118.
- Beers, E. H., R. A. Van Steenwyk, P. W. Shearer, W. W. Coates, and J. A. Grant. 2011. Developing *Drosophila suzukii* management programs for sweet cherry in the western United States. *Pest Manag. Sci.* 67: 1386–1395.
- Beppu, K. 2000. Faunal and ecological surveys on Drosophilid flies in the Imperial Palace, Tokyo. *Mem. Natn. Sci. Mus., Tokyo* 36: 409–435.
- Beppu, K. 2006. Seasonal change of Drosophilid assemblage and adult age structure of the common Drosophilid species in the Imperial Palace Grounds, Tokyo. *Mem. Natn. Sci. Mus., Tokyo* 43: 295–334.
- Böhner, J., and O. Antonić. 2009. Chapter 8: Land-surface parameters specific to topography, pp. 195–226. In H. Tomislav and I. R. Hannes (eds.), *Geomorphometry. Developments in soil science*, Vol. 33. Elsevier, Oxford, United Kingdom.
- Bruck, D. J., M. Bolda, L. Tanigoshi, J. Klick, J. Kleiber, J. DeFrancesco, B. Gerdeman, and H. Spitler. 2011. Laboratory and field comparisons of insecticides to reduce infestation of *Drosophila suzukii* in berry crops. *Pest Manag. Sci.* 67: 1375–1385.
- Caprile, J., J. A. Grant, K. Hamby, D. R. Haviland, and S. Rill. 2016. Phenology of spotted wing drosophila in the San Joaquin Valley varies by season, crop and nearby vegetation. *Calif. Agric.* 70: 24–31.
- Cimmery, V. 2007–2010. SAGA User Guide, updated for SAGA version 2.0.5. (<http://www.saga-gis.org/en/index.html>) (accessed 29 January 2018).
- Cini, A., C. Ioriatti, and G. Anfora. 2012. A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management. *Bull. Insectol.* 65: 149–160.
- Conrad, O., B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, and J. Böhner. 2015. System for automated geoscientific analyses (SAGA) v. 2.1.4. *Geosci. Model Dev.* 8: 1991–2007.
- Dalton, D. T., V. M. Walton, P. W. Shearer, D. B. Walsh, J. Caprile, and R. Isaacs. 2011. Laboratory survival of *Drosophila suzukii* under simulated winter conditions of the Pacific Northwest and seasonal field trapping in five primary regions of small and stone fruit production in the United States. *Pest Manag. Sci.* 67: 1368–1374.
- David, J. R., R. Allemand, J. V. Herrewewe, and Y. Cohet. 1983. Ecophysiology: abiotic factors, pp. 105–170. In M. Ashburner, H. L. Carson and J. N. Thompson Jr. (eds.), *The genetics and biology of Drosophila*, Vol. 3a. Academic Press, London, United Kingdom.
- Gruber, S., and S. Peckham. 2009. Chapter 7: Land-surface parameters and objects in hydrology, pp. 171–194. In H. Tomislav and I. R. Hannes (eds.), *Geomorphometry. Developments in soil science*, Vol. 33. Elsevier, Oxford, United Kingdom.
- Gutierrez, A. P., L. Ponti, and D. T. Dalton. 2016. Analysis of the invasiveness of spotted wing *Drosophila* (*Drosophila suzukii*) in North America, Europe, and the Mediterranean Basin. *Biol. Invasions* 18: 3647–3663.

- Hamby, K. A., M. P. Bolda, M. E. Sheehan, and F. G. Zalom. 2014. Seasonal monitoring for *Drosophila suzukii* (Diptera: Drosophilidae) in California commercial raspberries. *Environ. Entomol.* 43: 1008–1018.
- Hamby, K. A., D. E. Bellamy, J. C. Chiu, J. C. Lee, V. M. Walton, N. G. Wiman, R. M. York, and A. Biondi. 2016. Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*. *J. Pest Sci.* 89: 605–619.
- Harris, D. W., K. A. Hamby, H. E. Wilson, and F. G. Zalom. 2014. Seasonal monitoring of *Drosophila suzukii* (Diptera: Drosophilidae) in a mixed fruit production system. *J. Asia Pac. Entomol.* 17: 857–864.
- Haye, T., P. Girod, A. G. S. Cuthbertson, X. G. Wang, K. M. Daane, K. A. Hoelmer, C. Baroffio, J. P. Zhang, and N. Desneux. 2016. Current SWD IPM tactics and their practical implementation in fruit crops across different regions around the world. *J. Pest Sci.* 89: 643–651.
- Ioriatti, C., V. Walton, D. Dalton, G. Anfora, A. Grassi, S. Maistri, and V. Mazzoni. 2015. *Drosophila suzukii* (Diptera: Drosophilidae) and its potential impact to wine grapes during harvest in two cool climate wine grape production regions. *J. Econ. Entomol.* 108: 1148–1155.
- Jakobs, R., T. D. Gariepy, and B. J. Sinclair. 2015. Adult plasticity of cold tolerance in a continental-temperate population of *Drosophila suzukii*. *J. Insect Physiol.* 79: 1–9.
- Kanzawa, T. 1939. Studies on *Drosophila suzukii* Mats, pp. 49. Yamanashi Prefecture Agricultural Experiment Station, Kofu, Japan.
- Kimura, M. T. 2004. Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia*. 140: 442–449.
- Klick, J., W. Q. Yang, V. M. Walton, D. T. Dalton, J. R. Hagler, A. J. Dreves, J. C. Lee, and D. J. Bruck. 2016. Distribution and activity of *Drosophila suzukii* in cultivated raspberry and surrounding vegetation. *J. Appl. Entomol.* 140: 37–46.
- Langille, A. B., E. M. Arteca, G. D. Ryan, L. M. Emiljanowicz, and J. A. Newman. 2016. North American invasion of Spotted-Wing *Drosophila* (*Drosophila suzukii*): a mechanistic model of population dynamics. *Ecol. Modelling* 336: 70–81.
- Leblanc, L., D. Rubinoff, and R. I. Vargas. 2009. Attraction of nontarget species to fruit fly (Diptera: Tephritidae) male lures and decaying fruit flies in traps in hawaii. *Environ. Entomol.* 38: 1446–1461.
- Lee, J. C., A. J. Dreves, R. Isaacs, G. Loeb, H. Thistlewood, and L. J. Brewer. 2015a. Noncrop host plants of Spotted Wing *Drosophila* in North America, pp. 3. E. E. S. Communications, Oregon State University, Corvallis, OR. (<https://catalog.extension.oregonstate.edu/em9113>) (accessed 29 January 2018).
- Lee, J. C., A. J. Dreves, A. M. Cave, S. Kawai, R. Isaacs, J. C. Miller, S. V. Timmeren, and D. J. Bruck. 2015b. Infestation of wild and ornamental noncrop fruits by *Drosophila suzukii* (Diptera: Drosophilidae). *Ann. Entomol. Soc. Am.* 108: 117–129.
- Lyons, C. P., and B. Merilees. 1996. Trees, shrubs and flowers to know in Washington and British Columbia, Lone Pine, Vancouver, BC.
- Mazzetto, F., M. G. Pansa, B. L. Ingegno, L. Tavella, and A. Alma. 2015. Monitoring of the exotic fly *Drosophila suzukii* in stone, pome and soft fruit orchards in NW Italy. *J. Asia-Pac. Entomol.* 18: 321–329.
- McMahan, H. 2011. Climate and precipitation of Hood River County WPG Document 4. Hood River County Water Planning Group (HRCWPG) documents, Hood River, OR.
- Mitsui, H., K. Beppu, and M. T. Kimura. 2010. Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. *Entomol. Sci.* 13: 60–67.
- Murray, T. A., N. C. Afritto, P. W. Shearer, and S. P. Castagnoli. 2017. Spotted wing drosophila in high elevation and culturally significant *Vaccinium* species in southwest Washington State and northwest Oregon. *Acta Hort.* 1180: 479–484.
- Pelton, E., C. Gratton, R. Isaacs, S. Van Timmeren, A. Blanton, and C. Guédot. 2016. Earlier activity of *Drosophila suzukii* in high woodland landscapes but relative abundance is unaffected. *J. Pest Sci.* 89: 725–733.
- Pipkin, S. B. 1952. Seasonal fluctuations in *Drosophila* populations at different altitudes in the Lebanon Mountains. *Zeit. Indukt. Abst.- und Vererb.* 84: 270–305.
- R Development Core Team 2017. R: A Language and Environment for Statistical Computing computer program, version. R Development Core Team, Vienna, Austria.
- Rossi-Stacconi, M. V., R. Kaur, V. Mazzoni, L. Ometto, A. Grassi, A. Gottardello, O. Rota-Stabelli, and G. Anfora. 2016. Multiple lines of evidence for reproductive winter diapause in the invasive pest *Drosophila suzukii*: useful clues for control strategies. *J. Pest Sci.* 89: 689–700.
- Ryan, G. D., L. Emiljanowicz, F. Wilkinson, M. Kornya, and J. A. Newman. 2016. Thermal tolerances of the spotted-wing *Drosophila* *Drosophila suzukii* (Diptera: Drosophilidae). *J. Econ. Entomol.* 109: 746–752.
- Shearer, P. W., J. D. West, V. M. Walton, P. H. Brown, N. Svetec, and J. C. Chiu. 2016. Seasonal cues induce phenotypic plasticity of *Drosophila suzukii* to enhance winter survival. *BMC Ecol.* 16: 11.
- Steenwyk, R. A. V., and M. P. Bolda. 2015. Spotted wing drosophila: devastating effects on cherry and berry pest management. *Acta Hort.* 1105: 11–17.
- Stephens, A. R., M. K. Asplen, W. D. Hutchison, and R. C. Venette. 2015. Cold hardiness of winter-acclimated *Drosophila suzukii* (Diptera: Drosophilidae) adults. *Environ. Entomol.* 44: 1619–1626.
- Thistlewood, H., P. W. Shearer, B. V. Steenwyk, V. Walton, and S. Acheampong. 2012. *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae), a new pest of stone fruits in western North America. *IOBC WPRS Bulletin* 74: 133–137.
- Thornton, P. E., M. M. Thornton, B. W. Mayer, N. Wilhelm, Y. Wei, R. Devarakonda, and R. B. Cook. 2014. Daymet: daily surface weather data on a 1-km grid for North America, Version 2. ORNL Distributed Active Archive Center, Oak Ridge, TN. (<https://doi.org/10.3334/ORNLDAAC/1219>) (accessed 8 June 2015).
- Tochen, S., J. M. Woltz, D. T. Dalton, J. C. Lee, N. G. Wiman, and V. M. Walton. 2016. Humidity affects populations of *Drosophila suzukii* (Diptera: Drosophilidae) in blueberry. *J. Appl. Entomol.* 140: 47–57.
- Tonina, L., N. Mori, F. Giomi, and A. Battisti. 2016. Development of *Drosophila suzukii* at low temperatures in mountain areas. *J. Pest Sci.* 89: 667–678.
- Toxopeus, J., R. Jakobs, L. V. Ferguson, T. D. Gariepy, and B. J. Sinclair. 2016. Reproductive arrest and stress resistance in winter-acclimated *Drosophila suzukii*. *J. Insect Physiol.* 89: 37–51.
- Wallingford, A. K., and G. M. Loeb. 2016. Developmental acclimation of *Drosophila suzukii* (Diptera: Drosophilidae) and its effect on diapause and winter stress tolerance. *Environ. Entomol.* 45: 1081–1089.
- Walsh, D. B., M. P. Bolda, R. E. Goodhue, A. J. Dreves, J. Lee, D. J. Bruck, V. M. Walton, S. D. O'Neal, and F. G. Zalom. 2011. *Drosophila suzukii* (Diptera: Drosophilidae): invasive pest of ripening soft fruit expanding its geographic range and damage potential. *J. Intl. Pest Manage.* 2: 1–7.
- Walton, V. M., H. J. Burrack, D. T. Dalton, R. Isaacs, N. Wiman, and C. Ioriatti. 2016. Past, present and future of *Drosophila suzukii*: Distribution, impact and management in United States berry fruits. *Acta Hort.* 1117: 87–93.
- Wang, X.-G., T. J. Stewart, A. Biondi, B. A. Chavez, C. Ingels, J. Caprile, J. A. Grant, V. M. Walton, and K. M. Daane. 2016. Population dynamics and ecology of *Drosophila suzukii* in Central California. *J. Pest Sci.* 89: 701–712.
- Wiman, N. G., V. M. Walton, D. T. Dalton, G. Anfora, H. J. Burrack, J. C. Chiu, K. M. Daane, A. Grassi, B. Miller, S. Tochen, et al. 2014. Integrating temperature-dependent life table data into a matrix projection model for *Drosophila suzukii* population estimation. *Plos One*. 9: e106909.
- Zerulla, F. N., S. Schmidt, M. Streitberger, C. P. W. Zebitz, and R. Zelger. 2015. On the overwintering ability of *Drosophila suzukii* in South Tyrol. *J. Berry Res.* 5: 41–48.