

Published in final edited form as:

J Med Entomol. 2010 September; 47(5): 759–768.

Seasonal Abundance of Culex tarsalis and Culex pipiens Complex Mosquitoes (Diptera: Culicidae) in California

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Abstract

Large-scale patterns in the seasonal abundance profiles of the arboviral mosquito vectors *Culex* tarsalis Coquillett and the species of the Culex pipiens complex were described based on a decade of counts from 868 New Jersey light traps located throughout the urban and agricultural areas of California. Mean seasonal abundance profiles varied markedly among hydrologic regions. For all species, abundance increased earlier and declined later in drier, warmer southern regions, but variation could not be explained fully by latitude. The observed patterns may be driven by temperature, availability of larval habitats, and for the Cx. pipiens complex, the taxonomic composition of local populations.

Keywords

Culex tarsalis; Culex pipiens; Culex quinquefasciatus; seasonality; California

The mosquitoes Culex tarsalis Coquillett, Culex pipiens L., and Culex quinquefasciatus Say are important vectors of West Nile virus (WNV; Hayes et al. 2005) and other arboviruses (Reeves and Milby 1990) in North America, and prediction and monitoring of their abundance are central to arboviral surveillance and control programs (Centers for Disease Control and Prevention 2003). All three species are distributed broadly in western North America, and the complexity of arboviral transmission cycles and the impracticality of continuously monitoring vertebrate populations leave the abundance of these Culex vectors as an important and measurable determinant of the force of virus transmission (Reeves 1971, Olson et al. 1979). Operationally, abundance is estimated from trap counts (Eldridge 1987), and extensive datasets are necessary for establishing location- and time-specific baselines against which to measure anomalies.

Several publications have mapped or described the distributions of Cx. tarsalis and the species of the Cx. pipiens complex in California (Bohart and Washino 1978, Meyer and Durso 1998, Darsie and Ward 2005), and seasonal abundance patterns for Cx. tarsalis have been described broadly with respect to latitude (Nelson 1971, Reisen and Reeves 1990). In North America, the Cx. pipiens complex consists of two species—the diapausing Cx. pipiens in the north and the nondia-pausing Cx. quinquefasciatus in the south-separated by a zone of genetic introgression approximately between 36° and 39°N latitude (Barr 1957). California encompasses the entire Cx. pipiens-Cx. quinquefasciatus continuum, and population genetics throughout the state have been characterized (Iltis 1966, Tabachnick and Powell 1983, Urbanelli et al. 1997, Cornel et al. 2003). California's temperature regimes and land use

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patterns, both of which affect *Culex* abundance, are shaped by a variety of factors, including topography, marine influences, and elevation, in addition to latitude.

In the current study, we used an extensive surveillance dataset to describe the differences in the mean annual abundance patterns of *Cx. tarsalis* and the *Cx. pipiens* complex throughout the diverse ecological regions of California. This is a critical first step toward understanding the suite of factors modifying temporal patterns and building a statewide spatiotemporal forecasting model for these species.

Materials and Methods

Study Area

The area of study included most of the urban and agricultural regions of California served by mosquito control districts, ranging from the southeastern deserts near the Salton Sea through the northern agricultural regions of the Sacramento Valley. Many methods have been developed for dividing California into ecologically relevant zones for a variety of purposes, such as describing plant distributions (e.g., Hickman 1993) or conserving natural resources (California Department of Forestry and Fire Protection 2010). After considering the range of possibilities, we selected hydrologic regions (HRs; California Department of Water Resources 2005) because they represented a manageable number of total units (10), corresponded well with divisions where mosquito abundance patterns were expected to differ, and were large enough to include adequate sample sizes. The HRs included were North Coast, San Francisco Bay, Central Coast, South Coast, Sacramento River, San Joaquin River, Tulare Lake, South Lahontan, and Colorado River (Fig. 1). Because rice fields are important larval habitats for Cx. tarsalis (Wekesa et al. 1996), the Sacramento River HR was divided by the southern boundary of Tehama County into southern (Sacramento River) and northern (Shasta-Cascade) regions with and without rice, respectively. This division also was suitable for the Cx. pipiens complex because it divided areas with pure Cx. pipiens at the north end of the Central Valley (Cornel et al. 2003) from the zone of genetic introgression to the south (Urbanelli et al. 1997).

A variety of climates are found in California, with the unifying feature being a paucity of precipitation during summer (Fig. 2). Climates are dictated by marine influences, latitude, and elevation. Air masses typically move from the ocean eastward, cooling and depositing precipitation as a result of the orographic effect as they cross mountain ranges (Dettinger et al. 2004). This results in rain shadows in the Central Valley and the Mojave and Colorado Deserts (Holland and Keil 1995). The amount of rainfall, particularly during winter, decreases from north to south, and coastal areas and inland mountain ranges receive greater precipitation than inland valleys. Marine influences and east—west elevational gradients have a stronger influence on temperature than latitude. Coastal HRs subject to the moderating influence of the Pacific Ocean have cooler summers, warmer winters, and smaller daily temperature ranges than inland valleys. Daily maximum temperatures generally increase from north to south, but the Sacramento Valley and Shasta-Cascade HRs deviate from this pattern during summer because of movement of cool marine air masses into the San Francisco Bay, through the Sacramento River delta, and northward into the Sacramento Valley, inverting the north—south temperature cline (Kesseli 1942,Iltis 1966).

Study Period

The period 1991–2000 was selected for study because it was 1) sufficiently long to include variation in environmental conditions, 2) short enough to reduce the influence of long-term trends in mosquito abundance, and 3) the period during which the largest number of trap sites was represented. The study period included a range of meteorologic conditions from the

prolonged drought during the early 1990s to the record El Niño event of 1997–1998, as well as more moderate periods.

Mosquito Counts

Abundance data for Cx. tarsalis and the Cx. pipiens complex were obtained from historical collection records from New Jersey light traps (NJLTs) (Mulhern 1942) operated by 34 vector control agencies (Table 1). NJLTs have been an important component of California's statewide mosquito surveillance program for >50 yr (Aarons et al. 1953), and until recent years, they were the only trap used for statewide abundance reporting. An advantage for long-term studies is their requirement for power from an electrical outlet, which means that moving these traps is inconvenient and occurs rarely. Their design has remained essentially unchanged and consistent among agencies since their adoption by California's mosquito abatement districts in 1953 (Longshore 1960, Loomis and Meyers 1960). Paper or electronic trap-by-trap mosquito collection records were obtained from each local mosquito control agency and entered into a Microsoft SQL Server 2000 database (Microsoft, Redmond, WA) before analysis. Relative abundance of *Culex* adult females (hereafter simply called abundance) was monitored weekly from April to October of the years 1991–2000. These months represent the period of highest abundance for the species studied. The months from November to March were excluded from analyses because collection effort was minimal and inconsistent among agencies and years. This was a result of staffing limitations and reduced mosquito abundance due largely to diapause in Cx. tarsalis and Cx. pipiens or the effects of cooler temperatures on mosquito reproductive rates.

Traps were operated continuously, and vector control personnel typically collected, morphologically identified, and counted mosquitoes weekly so that each trapping period covered seven trap nights. Sums of *Culex* females and trap nights were aggregated by the month within which the central date of the trapping period fell. Trapping periods longer than 15 nights for individual traps were excluded from analysis because such long periods may have resulted from an irregular collection schedule or overlapped 2 mo or more, making the trap counts less representative of the month to which they were assigned.

Analysis

Monthly counts were standardized to a 30-night trap month and natural log transformed ($log_e[count/trap\ nights \times 30+1]$) before calculations to reduce the skewness of count distributions. Analyses were based on geometric means back transformed to the scale of the original data, and all calculations were performed in R version 2.10.1 (R Development Core Team 2009).

Results

NJLTs were operated by local mosquito control districts at 868 sites (Fig. 1) during the 1991–2000 study period for a total of 35,908 trap months for Cx. tarsalis. The Cx. pipiens complex was not collected from NJLTs in two vector control agencies (Lake County and Burney Basin), so these agencies were excluded, resulting in a total of 857 sites and 35,450 trap months for the Cx. pipiens complex. Counts within each region and month were highly variable (Table 2) because of heterogeneity spatially among traps and temporally among years. Overall, fewer Cx. pipiens complex females were collected compared with Cx. tarsalis, and zero counts were common, frequently representing \geq 25% of counts within a region, particularly for the Cx. pipiens complex.

Cx. tarsalis

Mean annual abundance patterns of *Cx. tarsalis* varied among regions in both the amplitude of abundance peaks and the shape of the abundance profiles (Fig. 3A). In coastal HRs, abundance increased to a peak during July, followed by a steepening decline through October, except in the San Francisco Bay HR, where abundance was steady from August to October. Abundance in the northern Central Valley's Shasta-Cascade and Sacramento River HRs remained relatively low through May before a sharp increase to a July peak and subsequent rapid decline. The San Joaquin River and Tulare Lake HRs had abundance increases during spring, and abundance in the San Joaquin River HR remained relatively high through September, when a second slight peak occurred. In the Tulare Lake HR, abundance declined markedly from June to August before a second peak in September. The same pattern of midsummer decline was evident in the Colorado River HR, where abundance was highest during spring, with a second increase at the end of the collection season. The South Lahontan HR, which reaches summer maximum temperatures similar to those of the Tulare Lake HR, reached a single broad peak in June and July.

Like temperatures, the abundance in coastal HRs was more evenly distributed among months than that of inland HRs in the Central Valley or deserts (Fig. 4A). Inland HRs could be broadly divided between those that had single abundance peaks in summer and those that had two abundance peaks separated by a mid-season decline. The greatest abundance in the three northernmost HRs occurred during July, and these three regions also had the sharpest declines in abundance by the end of the collection season (Fig. 4C).

Cx. pipiens Complex

The abundance patterns for the *Cx. pipiens* complex also varied among regions in both amplitude and shape (Fig. 3B). Nearly all regions had relatively low abundance at the start of the collection season (Fig. 4B), followed by a steady increase (Fig. 4D) to a peak during late spring or summer. The Colorado River and South Coast HRs, which had warm temperatures during late winter–spring (Fig. 2) and populations comprised predominantly of *Cx. quinquefasciatus*, had relatively high abundance during spring and subsequent declines through late summer. In the Shasta-Cascade, North Coast, San Francisco Bay, and Central Coast HRs, all areas known from previous studies to have populations that are predominantly *Cx. pipiens* (Iltis 1966, Tabachnick and Powell 1983), abundance was low in April, then increased steadily to a single summer peak. A similar pattern also characterized the South Lahontan HR population south of the Tehachapi Mountains. Populations in Central Valley regions from the Sacramento River HR southward showed some evidence of a bimodal abundance pattern that appeared similar to a combination of the northern and coastal "*pipiens*" curves and the southern "*quinquefasciatus*" curves. Among coastal and Central Valley HRs north of the Transverse Ranges, abundance began to decline earlier in the northernmost HRs.

Discussion

Large-scale spatial variation in mean annual *Culex* abundance patterns, particularly with respect to latitude, has been described previously (e.g., Nelson 1971, Bohart and Washino 1978, Reisen and Reeves 1990, Vinogradova 2000). Instead of considering a single gradient, we divided California into 10 hydrologic regions that represented a diverse range of precipitation, temperature, and other environmental variables and used a 10-yr, 868-site dataset to describe seasonal abundance patterns of *Culex* within each region. In general, abundance increased earlier and declined later in southern regions that were drier and warmer than those to the north, but variation in the seasonal abundance patterns among regions was not explained entirely by latitude. Differences in abundance patterns probably were driven also by the

availability of larval habitats or the specific composition of *Cx. pipiens* complex populations, in addition to other local factors.

We chose NJLTs because they were used extensively by mosquito control agencies to monitor abundance during the study period, have a consistent design, and are operated for 7-d trapping periods that reduce the effects of night-to-night variation related to weather. Direct comparisons of trap counts among regions or species were complicated by relative differences in trap sensitivity because of competing background illumination from urban sources (Milby and Reeves 1989). In addition, NJLTs and other trap types differ in their sensitivity for the *Culex* species studied (Bidlingmayer 1985, Reisen et al. 1999), precluding direct comparisons of trap counts. Therefore, our inferences are based on comparisons of seasonal patterns in relative abundance rather than direct numerical comparisons of females per trap night.

NJLTs collect adult female mosquitoes of various ages and reproductive states, from newly emerged to senescing individuals, that vary in their potential for transmitting viruses. As a result of the additional potential for virus infection acquired with each blood meal and the extrinsic incubation period required for transmission, the proportion of infective females is expected to increase as the population ages during years when arboviruses are circulating. Therefore, it is likely that the abundance of infective females (and therefore the risk of virus transmission) would peak later than the overall female abundance observed in this study. This has been observed for WNV in the Colorado River HR (Reisen et al. 2008), Tulare Lake HR (Reisen et al. 2009), South Coast HR (Kwan et al. 2010), and northern Colorado (Bolling et al. 2009), and for other arboviruses in central and southern California (Barker et al. 2010; Reisen et al. 1990, 1992a, 1992b). Although these selected areas have been investigated, a broader comparative study of the period since the arrival of WNV is needed to determine how abundance patterns affect WNV dynamics.

Cx. tarsalis

Cx. tarsalis females complete diapause after the winter solstice (Mitchell 1981, Reisen and Reeves 1990, Reisen et al. 1995a) and emerge from overwintering hibernacula and seek blood meals once temperatures increase. Winter day lengths are longer and temperatures generally are warmer at southern latitudes, which results in an earlier emergence and subsequent population increase. For the inland regions of California, our results indicated earlier increases in Cx. tarsalis abundance in southern regions. The South Lahontan HR was an exception, and its delayed abundance increase probably was attributable to higher elevation and colder winters compared with the other HRs studied (Fig. 2). Along the coast of California, both temperatures and Cx. tarsalis abundance were more uniform than those of inland regions, possibly because of the moderating influence of the ocean. Cx. tarsalis counts from traps near wildlife areas typically remained higher during September and October because of flooding of wetlands for migratory waterfowl management (Barker et al. 2007). In HRs with many such traps, the lateseason increase is evident in the regional means (e.g., the San Francisco Bay and Colorado River HRs). Associations between land use patterns and abundance are being evaluated as part of ongoing modeling efforts.

The shift from a unimodal abundance pattern at northern latitudes to a bimodal pattern at southern latitudes has been reported previously (Nelson 1971, Reisen and Reeves 1990). The bimodal pattern in the southeastern deserts of the Colorado River HR has been attributed to the negative effect of hot, desiccating conditions on abundance (Reisen and Reeves 1990, Reisen et al. 1992a), presumably caused by a reduction in adult survival. However, reductions in summer survival measured by reproductive age structure have been modest or inapparent (Reisen and Lothrop 1995, Reisen et al. 1995b), and the temperatures of the microhabitats to which adult mosquitoes are exposed are cooler than daytime maximum air temperatures (Meyer et al. 1990). Nelson (1971) pointed out that midsummer declines in abundance could not be

explained entirely by extreme temperatures based on a comparison of the Rio Grande Valley in Texas and the Imperial Valley in California where both midsummer *Cx. tarsalis* abundance and temperatures were higher in the latter. Our results also suggest that the explanation involves more than temperature alone. Abundance in the South Lahontan HR was unimodal, despite having summer temperatures almost identical to those of the Tulare Lake HR where abundance was bimodal. Peaks in *Cx. tarsalis* abundance follow crop-specific agricultural irrigation (Reisen et al. 1990, 1992c) or other increases in surface water (e.g., flooding of wildlife refuges in late summer; Reisen et al. 1992a), and it is likely that midsummer declines are caused by the contraction of available larval habitats in the driest areas rather than high temperatures per se.

Cx. pipiens Complex

At similar temperatures, diapause in *Cx. pipiens* may delay abundance increases compared with *Cx. quinquefasciatus*, which increases earlier after a brief winter quiescence. From the results of our study, it seems plausible that average abundance patterns were associated with the genetic composition of local *Cx. pipiens* populations. In warm southern HRs with pure *Cx. quinquefasciatus* populations, relative abundance was higher at the start of the trapping season and peaked earlier than in cool northern HRs. In contrast, in cool HRs with only *Cx. pipiens*, the trapping season started with low abundance and then gradually increased to a peak late in the season. Abundance of the *Cx. pipiens* complex in the HRs in the Central Valley hybrid zone exhibited both early and late peaks, perhaps consistent with a combination of *Cx. quinquefasciatus* and *Cx. pipiens* abundance patterns. This may provide indirect evidence that these populations include pure *Cx. pipiens* and *Cx. quinque-fasciatus* in sympatry or that hybrid populations consist of both diapausing and quiescent females, a condition that has been documented for *Cx. tarsalis* and the *Cx. pipiens* complex in Kern County, CA (Reisen et al. 1986). Further studies on the reproductive status of overwintering females in the *Cx. pipiens* complex would be necessary to confirm or refute these hypotheses.

In late summer—early fall, diapause induction results from the exposure of late larval instars and pupae to shortened day lengths (Eldridge 1968, Spielman and Wong 1973, Spielman 2001) and cool temperatures. In the northernmost HRs within the coastal and Central Valley provinces, abundance began to decline earlier compared with southern HRs. The earlier decline in trap counts at northern latitudes agrees with another study at a slightly higher latitude in Iowa (42.5°N) (Vandyk and Rowley 1995) that showed a similar decline starting in mid-August. The differences in the timing of declines may be related to the composition of *Cx. pipiens* complex populations (i.e., the degree to which nondiapausing *Cx. quinquefasciatus* are represented in each HR) and among HR variation in photoperiod and temperature. Earlier declines at northern latitudes seem consistent with an earlier induction of diapause, but this is hard to reconcile with photo-period and temperature data for the sites in our study (Figs. 2 and

4). Day lengths are longer at northern latitudes before the autumnal equinox in late September, and daily mean temperatures during August and September in the northernmost HRs are the second highest in their respective provinces. The rates of decline in day length and temperature are greater at northern latitudes, but whether these are cues for diapause induction and whether late-stage larvae and pupae are even capable of detecting the changes during these short stadia is unclear.

Our study has raised a number of questions regarding the causes of the observed variation in seasonal *Culex* abundance patterns. For both *Cx. tarsalis* and the *Cx. pipiens* complex, the observed regional patterns certainly were the result of many interacting factors that influence abundance at individual sites, including the composition and biology of local populations, meteorological conditions, and land use patterns. Our ongoing modeling efforts are evaluating these spatial and temporal relationships with the goal of developing forecasts to support decision making for mosquito control by vector control programs throughout California.

Acknowledgments

We thank the member agencies of the Mosquito and Vector Control Association of California and other local vector control agencies for providing mosquito collection records used in this study (see Table 1). This work was supported by National Aeronautics and Space Administration Earth-Sun Science Applied Sciences Program Research Opportunities in Space and Earth Science, Decision Support through Earth-Sun Science Research Results RM08-6044 for NNA06CN02A, and National Oceanic and Atmospheric Administration Office of Global Programs, Climate Variability and Human Health Grant 00-543. C.M.B. and W.K.R. also acknowledge funding support from the Research and Policy in Infectious Disease Dynamics program of the Science and Technology Directorate, Department of Homeland Security, and the Fogarty International Center, National Institutes of Health.

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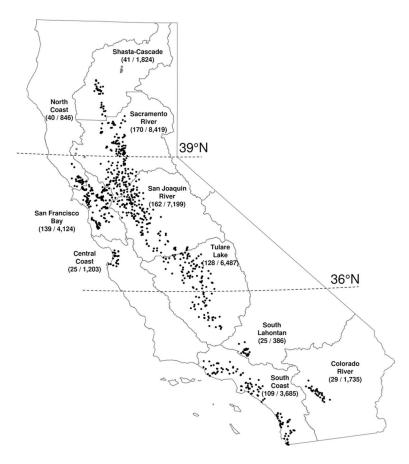


Fig. 1. Map showing the hydrologic regions of California, as applied in this study. Locations of NJLTs operated during the study period are shown as points on the map, and dashed lines at 36° and 39°N latitude represent the approximate boundaries of the hybrid zone between *Cx. quinquefasciatus* to the south and *Cx. pipiens* to the north (Barr 1957). The total traps/trap months analyzed for each region are indicated on the map. The traps represented by gray points in the Shasta-Cascade and Sacramento River HRs were included only in the analyses for *Cx. tarsalis* because the *Cx. pipiens* complex was not collected during the study period in these districts (Burney Basin Mosquito Abatement District and Lake County Vector Control District).

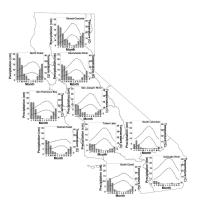


Fig. 2. Temperature and precipitation values from PRISM data (PRISM Group at Oregon State University 2009) for trap sites within each region during the 1991–2000 study period. Mean monthly high and low temperatures (°C) are represented by black lines, and precipitation (cm) is represented by vertical gray bars.

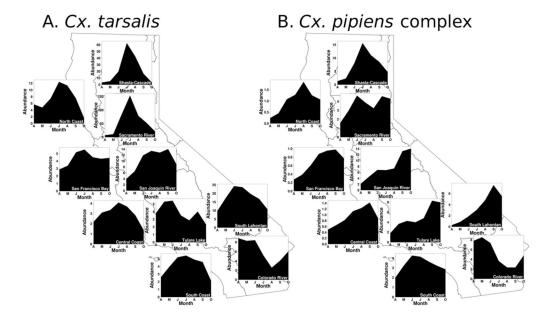


Fig. 3. Mean monthly female *Cx. tarsalis* (A) and *Cx. pipiens* complex (B) abundance by hydrologic region. Shaded black areas indicate geometric mean counts per trap month during the April–October collection season, 1991–2000. The ranges of the *y*-axes differ to reveal phenological differences among regions.

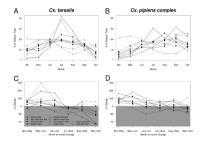


Fig. 4. Mean monthly female *Cx. tarsalis* (A) and *Cx. pipiens* complex (B) abundance expressed as a percentage of the total abundance over the season to aid comparisons of temporal distributions among hydrologic regions. (C and D) Present the percentage of change in abundance of the two species from each month to the next. The gray area within each plot indicates declines in abundance. The legend is consistent for all plots and is presented in C, with hydrologic regions listed from north to south within coastal, Central Valley, and desert provinces (left, middle, and right columns, respectively).

Table 1

California vector control agencies with mosquito collection records included in this study

Agency	Hydrologic region(s)	Trap months
Alameda County MAD	San Francisco Bay	566
Antelope Valley MVCD	South Lahontan	386
Butte County MVCD	Sacramento River	1,643
Burney Basin MAD	Shasta-Cascade	255
Colusa MAD	Sacramento River	185
Consolidated MAD	Tulare Lake, San Joaquin River	1,394
Contra Costa MVCD	San Francisco Bay, San Joaquin River	958
Coachella Valley MVCD	Colorado River	1,735
Delano MAD	Tulare Lake	574
Delta VCD	Tulare Lake	908
East Side MAD	San Joaquin River	727
Fresno MVCD	Tulare Lake	578
Fresno Westside MAD	Tulare Lake, San Joaquin River	923
Glenn County MVCD	Sacramento River	295
Greater Los Angeles County VCD	South Coast	1,617
Kern MVCD	Tulare Lake	1,182
Kings MAD	Tulare Lake	613
Lake County VCD	Sacramento River	203
Madera County MVCD	San Joaquin River	192
Marin-Sonoma MVCD	San Francisco Bay, North Coast	1,827
Merced County MAD	San Joaquin River	983
Northern Salinas Valley MAD	Central Coast	1,203
Orange County VCD	South Coast	430
San Diego County DEH	South Coast	751
San Mateo County MAD	San Francisco Bay	810
Sacramento-Yolo MVCD	Sacramento River, San Joaquin River	3,429
Shasta MVCD	Shasta-Cascade	1,069
San Joaquin County MVCD	San Joaquin River	2,934
Solano County MAD	San Francisco Bay, Sacramento River	1,621
Sutter-Yuba MVCD	Sacramento River	2,566
Tehama County MVCD	Shasta-Cascade	500
Tulare MAD	Tulare Lake	665
Turlock MAD	San Joaquin River	1,299
Ventura County DEH	South Coast	887

The hydrologic region(s) represented by each agency is indicated. Data and permission for their use were granted by individual agencies. MAD, Mosquito Abatement District; MVCD, Mosquito and Vector Control District; DEH, Department of Environmental Health; VCD, Vector Control District.

Table 2

Geometric means (25th, 75th percentiles) of NJLT counts for Cx. tarsalis and Cx. pipiens complex females per month (30 trap nights) by hydrologic region

	April	May	June	July	Aug.	Sept.	Oct.
A. Cx. tarsalis							
Shasta-Cascade	3.1 (0, 7.9)	5.2 (1.7, 12.9)	19.6 (7.6, 53.8)	62.6 (28.9, 133.8)	42.7 (19.9, 97.4)	16.4 (6.4, 37.5)	3.2 (0, 7.7)
Sacramento River	7.1 (2.1, 18.6)	10.9 (3.2, 34.3)	83.4 (23.6, 320)	153.2 (41.5, 593.1)	78.7 (21.6, 293.8)	52.1 (15.6, 174.9)	21.2 (6.4, 63.2)
San Joaquin River	4 (0, 13.4)	6.5 (0.9, 24.3)	11.9 (2.1, 48.2)	13.4 (1.7, 63.5)	12.8 (1.1, 67.2)	14 (2.1, 64.3)	8.9 (1.1, 31.7)
Tulare Lake	3.8 (0, 11.7)	5.3 (0.9, 15)	5.4 (1.1, 15.5)	3.5 (0, 9.4)	2.9 (0, 7.5)	4 (0, 12.9)	2.3 (0, 5.7)
North Coast	5.7 (1.4, 15.3)	4.7 (1.1, 12)	7.4 (2.1, 17.1)	12.4 (4.3, 32.1)	11.3 (4.6, 27.3)	7.6 (2.3, 20.1)	1.6 (0, 4.3)
San Francisco Bay	2.9 (0, 9.6)	3.4 (0, 11.1)	5.2 (0, 16.2)	5.5 (1.1, 17.1)	4.5 (0, 13.9)	4.3 (0, 11.8)	4.4 (0, 12.9)
Central Coast	2.2 (0, 5.4)	3.1 (0, 7.6)	3.4 (0, 11)	4.1 (0, 10.9)	3.7 (0, 10.2)	2.8 (0, 7.5)	1.4 (0, 3.2)
South Coast	2.6 (0, 7.1)	3.9 (0, 10.8)	5.2 (1.1, 15.6)	5.4 (1.1, 14.6)	4.9 (0.9, 12.9)	4.6 (1, 11.8)	2.1 (0, 5.2)
South Lahontan	9.7 (2.5, 30.3)	17.3 (4.3, 89.9)	24.3 (7.3, 86.8)	23.6 (8.1, 66.5)	19.6 (10.7, 38.7)	16.8 (5.4, 46.1)	10.7 (2.6, 36)
Colorado River	8.8 (1.1, 44.3)	8.3 (1.1, 34.5)	8.4 (1.1, 34.3)	5.2 (0.9, 19.3)	2.6 (0, 7)	4 (0, 17.1)	6 (0, 18.7)
B. Cx. pipiens complex	<u>.</u>						
Shasta-Cascade	1.3 (0, 2.9)	2.3 (0, 5.4)	7.9 (2.1, 19.3)	15.6 (5.1, 36.3)	11 (2.1, 26.7)	8.5 (1.1, 23.6)	4.7 (0, 12.9)
Sacramento River	1.6 (0, 4.3)	3 (0, 8.6)	4.6 (0, 16.3)	3.9 (0, 14.6)	3.2 (0, 11.2)	4.6 (0, 17.1)	4.3 (0, 12.9)
San Joaquin River	2.2 (0, 5.5)	4.5 (0, 13.2)	6.8 (1.1, 23.6)	6.7 (1.1, 21.3)	7.3 (1.1, 23.6)	13.2 (2.1, 50.4)	14 (2.9, 55.4)
Tulare Lake	1.8 (0, 5.4)	3.7 (0, 11.8)	4.3 (0, 13.3)	4 (0.9, 11.8)	4.8 (0.9, 15)	8.3 (2, 26.8)	8 (1.4, 25.7)
North Coast	0.2 (0, 0)	0.5(0, 1.1)	1.1 (0, 2.9)	1.3 (0, 3.2)	1.8 (0, 4.3)	1.2 (0, 3.2)	1.1 (0, 2.1)
San Francisco Bay	0.3 (0, 0)	0.4 (0, 0.9)	0.6 (0, 1.1)	0.9 (0, 2.1)	1 (0, 2.1)	1 (0, 2.1)	0.8 (0, 1.7)
Central Coast	0.5(0, 1.1)	0.6 (0, 1.1)	0.8 (0, 2.1)	1.1 (0, 2.4)	1.2 (0, 3.2)	1.4 (0, 3.2)	0.9 (0, 1.1)
South Coast	2 (0, 5.8)	3.2 (0, 9.5)	4.3 (0, 14)	4.1 (0, 12.4)	3.6 (0, 10)	3.2 (0, 9.4)	2.9 (0, 9.3)
South Lahontan	0.3 (0, 0)	0.9 (0, 2.4)	1.9 (0, 8.6)	3.1 (0, 15.3)	4.8 (0, 18.6)	7.5 (2.1, 28.9)	5.5 (1.4, 15.4)
Colorado River	7.8 (2.1, 19.8)	8.5 (1.7, 26.9)	7.4 (1, 27.9)	3.7 (0, 9.6)	2.3 (0, 6.5)	2.3 (0, 6)	4.8 (0.9, 13.9)