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CAUSES AND CONSEQUENCES OF LADYBUG WASHUPS IN THE FINGER LAKES REGION OF NEW YORK STATE (COLEOPTERA: COCCINELLIDAE)

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Abstract.—We searched for and collected data on a phenomenon known as ladybug washups, in which large numbers of coccinellids aggregate on the shores of major bodies of water. Our field season lasted from 5/23/2008 until 8/12/2008 in the Finger Lakes Region of New York, United States. Ladybug diversity and survival at washups, as well as washup size and frequency were studied to help understand why these events occur. Lab tests were conducted to determine how long ladybugs can survive afloat. This information was used to estimate the duration of floating in the washups we observed. The frequency, composition, and duration of washups in the Finger Lakes support the hypothesis that a weather condition known as a lake breeze forces coccinellids to fall into the water. These animals subsequently arrive on shore in large numbers. This study adds three new species to the growing list of coccinellids affected by this phenomenon.

Key words: Coccinellidae, ladybug, washup, Finger Lakes, Lake Breeze.

Introduction

Ladybug washups, a phenomenon in which sometimes massive numbers of Coccinellidae appear on the shores of major bodies of water, have been recorded from across North America and around the world (Bold, 1873; Needham, 1900; Marriner, 1939; Oliver, 1943; Hagen, 1962; Turnock and Turnock, 1979; Lee, 1980; Schaefer et al., 1987; Hodek et al., 1993; Hodek and Honek, 1996; Majerus and Majerus, 1996; Turnock, 1996; Nalepa et al., 1998; Acorn 2007). Possibly the first documentation of such an event was made by J. L. LeConte in 1850, who wrote "they [Coleoptera in general] were driven on shore, particularly on sand beaches, by the winds and waves after being drowned in the lake" (LeConte, 1850). The first author to recognize that Coccinellidae in particular were appearing *en masse* along a shoreline was Thomas J. Bold, who wrote in 1873, "Visitors to our local watering places must have noticed occasionally the sudden appearance of swarms of Lady-birds of various kinds. One of these, *Coccinella 11-punctata*, not rare generally, will some years appear in such profusion that every stone, brick, or clog of wood lying on the sandy bents will be reddened by congregated hundreds, but where they have come from, and why, is one of those perplexing questions which it is impossible to answer satisfactorily" (Bold, 1873).

A prerequisite to a massive washup is an equally large coccinellid flight. Hodek et al. (1993) provide two scenarios which can cause massive numbers of Coccinellidae to take flight. Commonly, coordinated movements to and from overwintering sites reach very large proportions. Also, when resources are super-abundant, coccinellid populations may explode, leading to a rapid decline in food availability. Coccinellidae are mainly diurnal fliers (Hagen, 1962; Acorn, 2007). On a warm day, massive numbers of hungry ladybugs may take flight (Hodek et al., 1993; Majerus and Majerus, 1996). Given the right conditions, either scenario could contribute to a ladybug washup.

A consensus as to what causes Coccinellidae to end up on water has not been reached in the literature. Hypotheses concerning ladybug washups fall into two categories: those that require the insects to travel by floating and those which suggest the insects are aggregating specifically at a shoreline. Several authors who noted this phenomenon would pass on hypothesizing as to what actually caused it (Oliver, 1943; Turnock and Turnock, 1979). Others pose that ladybugs are actually congregating at the shoreline because of a reluctance to cross major bodies of water, or are

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being brought together by wind on or near the shoreline, without having travelled by floating on the water for any significant length of time (Majerus and Majerus, 1996; Nalepa et al., 1998). Hodek et al. (1993) suggest that starving coccinellids may "actively move towards large bodies of water" after their food source becomes depleted, possibly to gather on the shore to drink.

In 1900 James G. Needham recovered 35 Coccinellidae of multiple species along a shoreline littered with an unusual diversity of insects, which he attributed to the very plausible cause of a massive thunderstorm that struck the previous day (Needham, 1900). The cause of Coccinellidae falling into the water has also been suggested to result from collision with waves (Marriner, 1939). The idea that coccinellid flights end spontaneously over water has been suggested (Hagen, 1962; Hodek and Honek, 1996). Lee (1980) and Schaefer et al. (1987) suggest a passing weather condition or wind may be blowing ladybugs into the water. Turnock also recognized a pattern in the wind flow, "whenever a northerly wind follows a warm, windy day," that seemed to coincide with ladybug washups (Turnock, 1996). The hypothesis that a weather condition known as a lake or sea breeze could be instrumental in creating a washup was suggested in 2001, but no empirical data were collected (Isard et al., 2001).

Although the cause of ladybug washups is still debatable, it is clear that the probability of finding a washup varies geographically. Acorn (2007) noted that ladybug washups appear with regularity in some regions, but are conspicuously absent from others. Our study is the first to consider this phenomenon in the Finger Lakes region of New York. We collected data on washup frequency, composition, and as a cause of beetle mortality. We performed experiments to test the length of time Coccinellidae survive while afloat in order to approximate the floating duration of the washups we encountered. This information was compared to the predictions of the competing hypotheses; whether coccinellids aggregate on shorelines specifically or are washed ashore after floating for some duration.

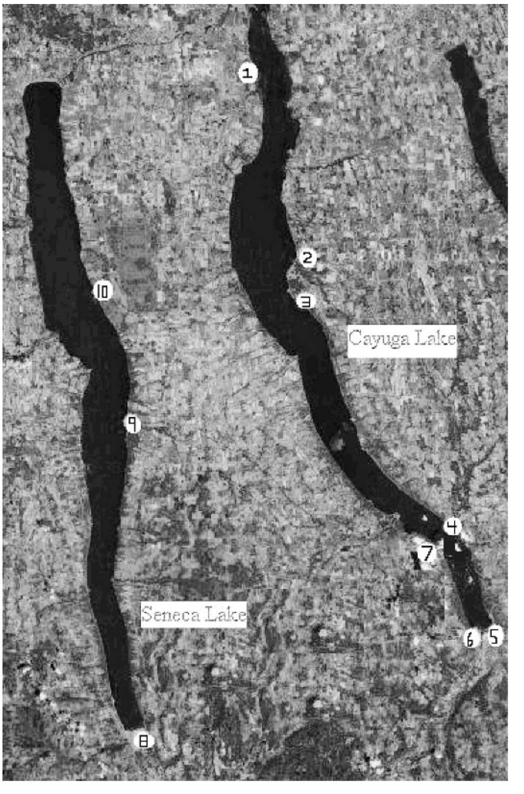

Fig. 1. Location of field sites on Cayuga and Seneca Lake indicated by white circles. 1: Cayuga Lake State Park. 2: Wells College. 3: Long Point State Park. 4: Myers Point. 5: Stewart Park. 6: Cass Park. 7: Taughannock Falls State Park. 8: Watkins Glen Park. 9: Lodi Point State Park. 10: Sampson State Park. Keuka Lake not shown.

Methods

Field collection

Washup data were collected in the Finger Lakes region of New York whenever weather conditions and resources allowed between 5/23/2008 and 8/12/2008. Field sites were limited to areas where expansive shoreline access was readily available. Locations on Cayuga Lake included Long Point State Park (42.71N, −76.70W), Wells College (42.74, −76.69), Stewart Park (42.46, −76.5), Myers Point (42.54, −76.66), Taughannock Falls State Park (42.54, −76.59), Cayuga Lake State Park (42.89, −76.85), and Cass Park (42.46, 76.51). Lodi Point State Park (42.61N, −76.87W), Sampson State Park (42.73, −76.91), and Watkins Glen Park (42.38, −76.85) were visited regularly on Seneca Lake, and Keuka Lake State Park (42.58, −77.12) on Keuka Lake was examined (Fig. 1). Air temperature was recorded and wind speed was designated categorically, low, medium, or high for every search. The specimens were brought back to the lab in a cooler to be counted, identified to species, and sorted by survival status. A reference collection was deposited in the Cornell University Insect Collection.

Washups were located by walking and visually scanning the shoreline. When a coccinellid was sited, a minute was dedicated to finding at least two more specimens. If this occurred, a ten meter by 1.5 m quadrat was established along the shoreline. Half an hour would then be dedicated to collecting as many coccinellids as possible from the site. After thoroughly searching the quadrat we would walk at least ten meters and then continue to look for coccinellids until we ran out of shoreline. On two occasions (5/27/08 Lodi Point State Park, 5/28/08 Wells College) three quadrats were collected and once (5/28/08 Long Point State Park) two quadrats were collected within 100 m of each other, so the beetle diversity and mortality percentage for those collections were combined in all later calculations.

Only one previous study (Lee, 1980) defined criteria for identifying a washup. Because Coccinellidae are not regular shoreline inhabitants, Lee designated 50 or more ladybugs on a shoreline a washup. We lowered this criterion for use in the Finger Lakes to ten specimens within our quadrat. On eight occasions we found between 3 and 9 ladybugs.

Aquatic survival experiments

To determine the ability of coccinellids to survive while floating, experiments were conducted in the laboratory in 2008. As in previous studies (Lee, 1980), single specimen survival was tested at 13°C with wild caught specimens of; *Coccinella septempuncata* (N = 5), *C. trifasciata* (N = 2), *Cycloneda munda* (N = 2), *Hippodamia variagata* (N = 2), *Harmonia axyridis* (N = 45) and IPM Laboratories *H. convergens* (N = 24). *H. convergens* (N = 24) and *H. axyridis* (N = 45) were also tested at 23°C. We used 29 ml plastic cups filled approximately halfway with distilled water and topped with a cardboard lid. Survival was checked approximately every twenty-four hours.

Since natural washups involve many ladybugs, we expanded on the traditional drowning experiments by also conducting group trials with *Coleomegilla maculata* (4 replicates), *Harmonia axyridis* (8 replicates), and *Hippodamia convergens* (14 replicates) Specimens were collected in the wild from fields, naturally occurring hibernating aggregations, or purchased from IPM Laboratories Inc. Locke, NY. The drowning experiments occurred in 15 liter Sterilite containers (42 cm l × 29 cm w × 17 cm h). These were filled with approximately 4 cm of water, and a 2.5 cm wide line of Vaseline was applied just above the water line to prevent escape. Only rarely were ladybugs found stuck in the Vaseline; they were always alive and returned to the water immediately.

Groups were designated by being either pulled directly from a hibernating cohort (N = 12) stored in refrigeration (1°C), or from underfed colonies (N = 14) which were kept at room temperature and supplied enough aphids for general survival, but not enough for reproduction (approximately 10 aphids per ladybug per day). These two groups were used to emulate specimen states under which coccinellid mass movement is known to occur, breaking of diapause (when coccinellids generally have enlarged fat bodies) or hunger/starvation (Hodek et al., 1993). Ladybugs from one physiological state were dropped into the water and a length of cloth was stretched beneath the plastic lid to prevent any flying escape before the container was placed in an environmental chamber.

Tests to determine the effect of density were conducted using *H. axyridis* (5, 10, and 20 specimens) and *H. convergens* (5, 10, and 40 specimens). Four containers were concurrently run in the same environmental chamber with 5, 10, 20, or 40 specimens (N = 2, 2, 4, 4 respectively), which corresponded to 0.0039, 0.0079, 0.0159, 0.0319 ladybugs/cm^2 respectively. The average density found on the shoreline washups in the Finger Lakes was 0.0373 ladybugs/cm^2 and the highest density found in the field was 0.0401 ladybugs/cm^2. Group sizes tested ranged from five (N = 4) to eighty specimens (N = 1), with most experiments containing thirty to forty individuals (N = 17). Evans or Percival environmental chambers were used to control temperature. A log-rank test was performed on the survival curves (time until 100% mortality) of these groups.

To observe the effect of floating debris on survival, flat pieces of Styrofoam covering 5% of the water surface area were added to two trials (one at 13°C, one at 23°C), each with 40 *H. convergens*. Five groups were removed from the water after 0, 24, or 48 hr (N = 1 for each time period) had elapsed or approximately 50% of the cohort had died (N = 2). These were kept in small colonies in order to test coccinellid survival post-washup. Survival was checked and recorded daily with only a few missed checkpoints due to life constraints. Special attention was given to noting the exact check time for group trials. Group trials were checked until all beetles had died, with the exception of the five trials used to investigate coccinellid survival after floating.

On three occasions controls were utilized for *H. convergens* (24 singletons, N = 3) and *C. maculata* (groups of 13, 26, 30) by concurrently testing survival of ladybugs not subjected to floating. These ladybugs were provided unlimited access to water in an attempt to replicate the conditions of their floating counterparts.

Estimation of floating time

Our aquatic survival experiments allowed us to determine the relationship between time spent afloat and mortality for different species under a variety of conditions. We found that a significant positive linear relationship ($r > 0.88$) exists between the time ladybugs spend floating and mortality. This information is useful because it allows us to estimate the time spent floating from an observed death proportion. We had data on death proportion per species for all of our washups. To ensure reliable results, we calculated a 95% confidence interval for the observed death proportion. The maximum and minimum of this interval correspond to a maximum and minimum amount of time spent floating. This defines the 'estimated time floating interval'. Because the aquatic survival experiments were conducted after the field season, we were able to target our lab work to temperature and specimen states applicable to our field data. Post-diapause status with enlarged fat bodies (Lee, 1980) was assumed for washups before June 1, 2008. This method requires the assumption that ladybugs in a washup arrive on the shore at the same time. Revisiting sites where washups were found resulted in no new coccinellids for up to three days after the event. This makes us confident that the assumption has minimal effects on our analysis.

The float interval estimation method only works for washups containing at least five specimens of a species used in the aquatic survival experiments (N = 17). This analysis could only be done for one species at a time. However, if death proportion data from multiple species were available for a washup, we used the overlap of derived intervals to calculate the 'estimated time floating interval'. The median of the 'estimated time floating' interval was used to compare washups.

Washup bioassay

We attempted to recreate the conditions of a washup in the laboratory using an artificial shoreline to find out what factors encourage ladybugs to stay at the shore. A 75 liter Zilla Turtle Tank with a screen lid and an AquaClear 30 Power Filter were used to construct the wave tank. Seven kilograms of pea gravel and potting soil comprised the land component of the tank. A slope of rock at approximately a 45° angle began at the midpoint of the bottom of the tank and abutted the shoreline, but only the top 5 cm were above water. Beyond this, soil and rock were contained in plastic boxes, creating a level beach area 15 cm long and as wide as the tank. Compressed air was delivered through 7mm internal diameter plastic tubing to create waves at the end of the tank near the external filter, which we ran at 570 liters per hour. The entire setup was placed inside of an Evans environmental chamber with glass doors and lit by multiple 25 watt household light bulbs located outside of the chamber. The lights were kept on a 12 hr light/dark cycle.

Eight groups of one hundred *Hippodamia convergens* from moderately fed colonies were tested in the washup assay. Trials were conducted at 25°C and 13°C. Half of the groups were subjected to floating in a 15 liter container for twenty-four hours before being placed in the washup tank; the others were placed directly into the tank. Experiments began in the afternoon or after dark and were checked every six hours. The location of each specimen (water, shoreline, beach, glass, or lid) and the number and location of dead ladybugs were recorded at each check. Individuals who were found on the screen lid were considered 'dispersed', and were recorded before being removed from the trial.

Results

Field collection

Between 5/23/2008 and 8/12/2008, we made 57 attempts to find ladybug washups in New York's Finger Lakes region, and were successful 36.8% of the time (Fig. 2). The probability of success was

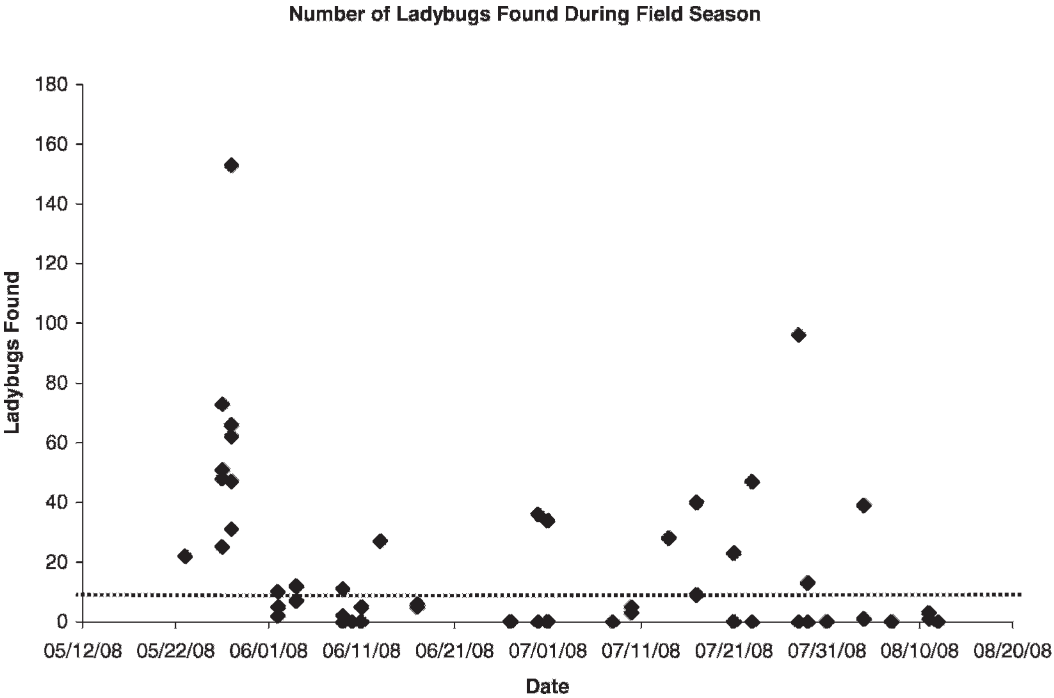

Fig. 2. Each point represents the number of ladybugs found at each attempt to locate a washup over the course of the field season. The dashed line indicates our washup minimum. No ladybugs were collected on 36 occasions.

not correlated with air temperature or wind speed/direction data obtained from the RUSS sensor for 0, 24, or 48 hr previous to the time of the washup discovery. We collected 1,053 specimens from washups, which represented 14 species in 11 genera (Table 1). The average number of species found per washup was 6.2, with a maximum of 10 and a minimum of 2. The most specimens collected from a single quadrat was 153, considerably less than what a similar sized search area could yield in the Great Lakes Region (Lee, 1980). *Harmonia axyridis* constituted 36.5% of specimens collected, followed by *C. septempunctata* (17.2%) and *Coleomegilla maculata* (16%), all of which were found throughout the field season. *Chilocorus stigma* represented 14.3% of specimens collected, but only two individuals were collected after 6/4/2008. *Anatis labiculata* was also only collected twice after 6/4/2008, and all 38 specimens found exhibited the dark purple coloration that individuals of this species turn as they age. *Hippodamia*, with four species, was the most diverse genus contributing to washups in the Finger Lakes. *Hippodamia parenthesis* was collected throughout the season. *Hippodamia convergens* appeared only before 7/8/2008, *H. glacialis* was collected between 6/13/2008 and 7/8/2008, and *H. variagata* was found only after 7/17/2008. Ten other species accounted for 16.1% of coccinellids collected. *Hippodamia glacialis* and *Neoharmonia venusta* were the rarest species found at washups in this region; only four specimens of each were collected. No washups were recovered from Keuka Lake.

Washup frequencies at sites surveyed on more than five occasions are shown in Figure 3. The 95% confidence intervals show that Sampson State Park (100% success) had a higher washup frequency than all sites except for Long Point State Park (75%). Long Point had a higher success rate than Myers Point (0%) and Wells College (11%). Washups do not appear to be dependent on thunderstorms, only three of which occurred during our field season according to NOAA Storm Data. Coccinellid mortality on shore was variable, averaging 14.95% across the season, with a minimum of 0% and a maximum of 72.73%. Washup mortality rates also varied among species (Table 1).

Table 1. Collection data for species found in washups in the Finger Lakes Region in order of abundance.

Species	Date range collected	Total collected	Percent of total collection	Total mortality
Harmonia axyridis	5/23–8/11/2008	384	36.47%	27.47%
Coccinella septempunctata	5/23–8/11/2008	181	17.19%	13.17%
Coleomegilla maculata	5/27–8/04/2008	168	15.95%	5.23%
Chilorus stigma	5/23–7/1/2008	150	14.25%	4.79%
*Propylea quatuordecimpunctata***	5/23–7/28/2008	46	4.37%	2.27%
Anatis labiculata	5/23–6/13/2008	38	3.61%	37.84%
H. parenthesis	5/27–7/28/2008	28	2.66%	0%
Hippodamia convergens	5/27–7/14/2008	15	1.42%	0%
Epilancha varivestis	7/17–7/28/2008	11	1.04%	0%
Cycloneda munda	5/28–7/29/2008	11	1.04%	0%
Hyperapsis undulata	5/28–6/4/2008	8	0.76%	0%
*H. variagata**	7/17–7/28/2008	5	0.47%	0%
*Neoharmonia venusta***	5/27–7/1/2008	4	0.38%	0%
H. glacialis	6/13–7/1/2008	4	0.38%	75.00%
Total	5/23–8/11/2008	1,053	100%	

* First record of species in a washup
** First record of genus in a washup

Aquatic survival experiments

Ladybugs died more slowly in singleton experiments than in groups. A two sample t-test shows no significant difference between the mean survival days of single *H. convergens* specimens in control (not floating) and test (floating) trials at the same temperature (23°C, $P = 0.16$, df = 20;

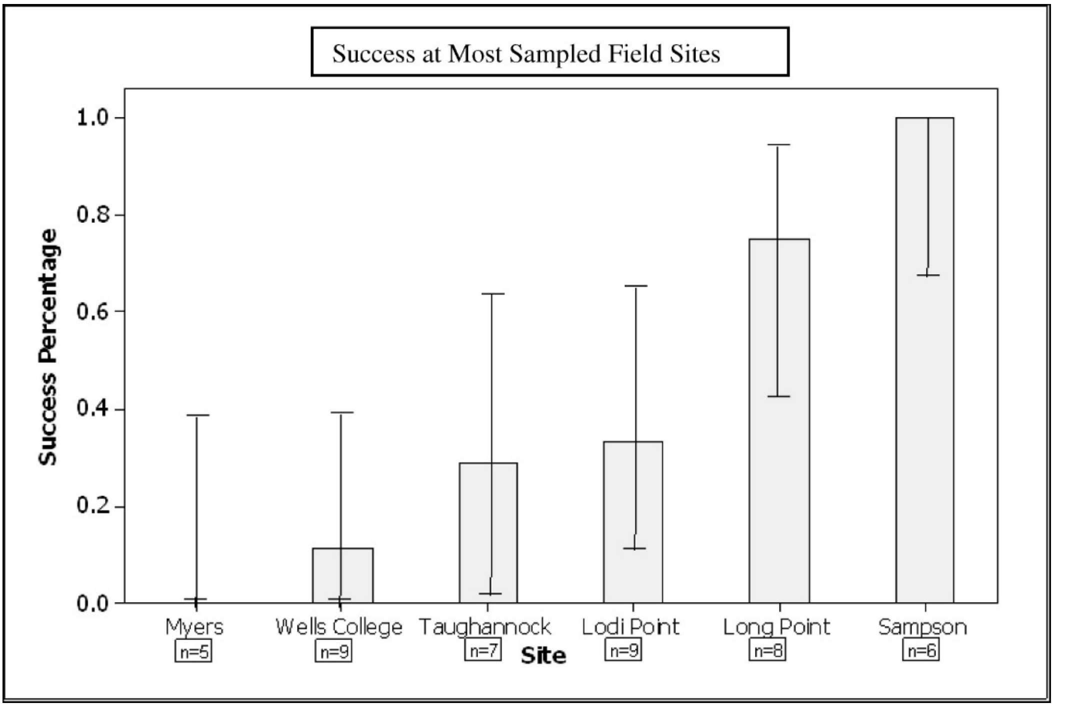

Fig. 3. Proportion of success in finding a washup at sites visited more than 5 times, with 95% confidence intervals displayed.

Table 2. Equations for the number of hours spent floating where x = hours spent floating and d = the observed death proportion.

Species	Temperature	State	Equation	R^2	N
H. axyridis	13 C	Starved	0.0079(x) = d	0.958	30
H. axyridis	13 C	Hibernating	0.0053(x) = d	0.987	106
H. axyridis	23 C	Hibernating	0.0098(x) = d	0.773	71
H. axyridis	23 C	Starved	0.0233(x) = d	0.777	99
C. maculata	13 C	Hibernating	0.0012(x) = d	0.8786	32
C. maculata	23 C	Hibernating	0.0083(x) = d	0.9204	56
H. convergens	13 C	Hibernating	0.0053(x) = d	0.9244	135
H. convergens	23 C	Hibernating	0.0103(x) = d	0.8281	56

13°C, $P = 0.178$, df = 17). At 23°C, *H. axyridis* averaged 92 hr of survival when solitary and 51 hr in groups ($\alpha = 0.05$, $P < 0.001$, df = 85). Solitary *H. convergens* at 13°C survived 430% longer than individuals in groups, and 346% longer at 23°C. The survival of *H. axyridis* in 13°C water was significantly different, 151.5 hr on average in solo animals and 94.33 hr in groups ($\alpha = 0.05$, $P < 0.001$, df = 85). Singleton floating experiments are therefore not likely good indicators of survival while floating in the wild. The results of the singleton survival experiments do reveal a significant difference in survival time between temperatures seen in group trials. At 13°C we found longer survival than at 23°C in *H. convergens* ($\alpha = 0.05$, $P = 0.024$, df = 11) and *H. axyridis* ($\alpha = 0.05$, $P = 0.01$, df = 22).

Group survival was tested in *H. axyridis*, *C. maculata*, and *H. convergens*. A two sample t-test shows that for *C. maculata* at 23°C, control specimens (not floating) survived for significantly longer than their floating counterparts ($P < 0.001$, df = 2). Groups in cold water survived longer than those in warm, and well fed individuals from hibernating colonies generally lasted longer than underfed counterparts. Linear regression lines with intercepts fixed at zero (since no mortality was assured at the start of the trial) were fitted to the survival data for the three species (Table 2). The equations derived from the linear regressions represent the relationship between the proportion of beetle mortality and the number of hours spent floating. No significant differences were found using the log-rank test between densities of 5, 10, or 20 *H. axyridis* per container (5–10: $P = 0.85$, df = 1; 5–20: $P = 0.88$, df = 1; 10–20: $P = 0.56$, df = 1) or 5, 10, or 40 *H. convergens* (5–10: $P = 0.43$, df = 1; 5–40: $P = 0.55$, df = 1; 10–40: $P = 0.49$, df = 1). This allowed us to pool data from multiple trials when creating the survival curves.

Floating debris that covers 5% of the surface area slows the mortality rate of coccinellid groups floating in cold and warm water, but does not prevent it. The beetles appear to leave these sanctuaries on a regular basis. In the presence of floats, *H. convergens* survived an average of 132 hrs in cold water and 96 hrs in warm water. Without floats, they survived an average of 94.33 and 48.54 hr, respectively.

Estimation of floating time

The average 'estimated time floating' for washups in the Finger Lakes is 33.29 hr. The median of the 'estimated time floating interval' for each washup available was compared to the date it was discovered. A significant negative linear relationship ($P < 0.001$) was found (Fig. 4). No significant relationship was found between the proportion dead at a washup and the number of ladybugs recovered (n = 21, $R^2 = 0.048$), nor did the death proportion correlate with the date of washup discovery (n = 21, $R^2 = 0.03$).

Washup bioassay

We were unable to reproduce washup conditions in our bioassay that led to coccinellids staying at the shoreline. All trials experienced a similar 'fast rate' of ladybugs leaving the shore for the tank lid, despite variations in temperature, prewashup floating duration, or time of day the washup trial began.

Discussion

Thirty-two species of Coccinellidae representing 17 genera have been reported from washups

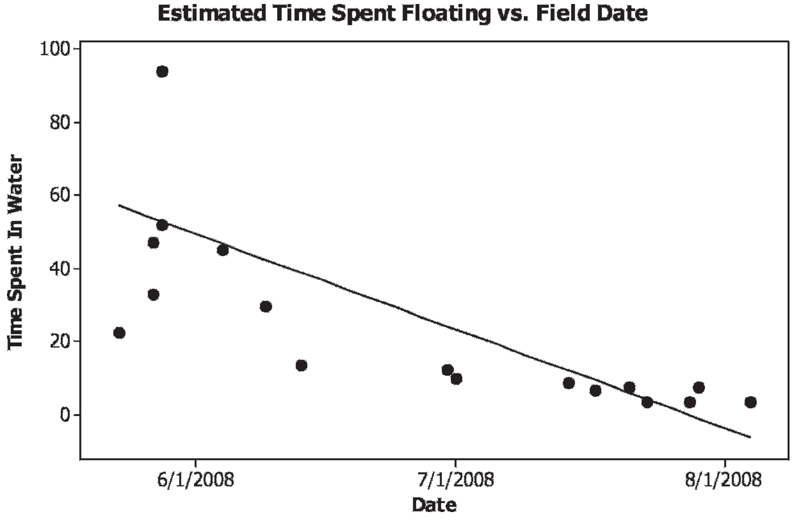

Fig. 4. Estimated time spent afloat compared to field day. Each point is the median of the 'estimated time floating interval' for a washup. Calculations controlled for temperature, species, and specimen state as much as possible. As the season progresses, the time a washup is predicted to have spent in the water decreases, $R^2 = 0.57$.

(Oliver, 1943; Lee, 1980; Schaefer et al., 1987; Turnock, 1996; Nalepa et al., 1998). Our study adds three new species from two new genera to the growing list of Coccinellidae affected by this phenomenon. This includes one native species, *Neoharmonia venusta*, and the introduced *Hippodamia variegata* and *Propylea quatuordecimpunctata*. *Epilachna varivestis*, an increasingly common agricultural pest first reported from a washup by Schaefer et al. (1987), also appeared in small numbers in our sampling in mid-July. Lee (1980) found neither of the introduced species *C. septempuncata* nor *H. axyridis* in his Great Lakes region washup sampling. *Coccinella. septempuncata* is reported as abundant in coastal Delaware by 1987 (Schaefer et al., 1987) as is *H. axyridis* in a North Carolina washup by 1998 (Nalepa et al., 1998). Washups provide another method of examining coccinellid local diversity and identifying the range of both native and invasive species.

Species native to the Finger Lakes region that were collected in washups by other researchers but were conspicuously absent from our study include; *Anatis mali*, *Adalia bipunctata*, *Coccinella transversoguttata*, *C. trifasciata*, and *C. novemnotata*. *Coccinella. novemnotata* has not been reported from New York since the mid 1980's, so its absence from washups in the region is not unexpected (Losey et al., 2007). Given the broad range of ladybug species affected by washups, the dearth of the other five native coccinellids from our sampling garners concern.

The washups we found in the Finger Lakes provide evidence contradictory to the expectations of several hypotheses concerning the cause of this phenomenon. Although a thunderstorm could force ladybugs to land on water, the frequency of washups compared to the relative infrequency of sizeable storms suggest this is not a principle cause. Collision with waves seems unlikely given that many of the species found on shore fly well above the water and waves rarely exceed five centimeters in the Finger Lakes.

Cayuga Lake is now the smallest body of water from which a washup has been recorded. The hypothesis that ladybugs are landing on the shore because of a reticence to cross large bodies of water seems unlikely. Coccinellids regularly undergo long distance flights (Hodek et al., 1993) and probably can not distinguish between the 5.6 km maximum width of Cayuga Lake, the 257.5 km maximum width of Lake Superior, or the expanse of the Atlantic Ocean as they approach it. If a renitence to cross were causing washups, we would expect to find low mortality on the shoreline. Also, the phenomenon would be approximately the same size on any body of water over a minimum size threshold. This is not the case; washups in the Finger Lakes region are minute in comparison to those found on the Great Lakes, which in turn are small in comparison to reports from ocean coasts. Although a standard comparison is not available, available literature suggests a positive correlation between the number of ladybugs at a washup and the size of the body of water at which it occurred. A reticence to cross bodies of water would also leave coccinellids scattered broadly along the shoreline, not localized as washups tend to be. Localization could be caused if a migratory group encountered a shoreline together, but the diversity of species found at washups suggests this is not the case.

Hypotheses that suggest coccinellids are gathering at or close to the shoreline are not supported by our data. Because Coccinellidae seem quite capable of surviving afloat for a day or more, we would expect low mortality if beetles were aggregating at or near the shoreline. High mortality rates only occur in lab experiments after several days of floating, even for the most quickly dying species. At 13°C, 50% mortality was reached in groups of *H. axyridis*, *H. convergens*, and *C. maculata* at 94.3, 94.3, and 416.6 hr respectively. At 23°C, 50% mortality was reached earlier at 51, 48.5, and 60.2 hr. We suggest that if floating debris is available, survival time will be increased. High or complete mortality at washups has been reported in several studies (Lee, 1980; Nalepa et al., 1998; Oliver, 1943; Schaefer et al., 1987). The average mortality at washups recovered during this study was 14.9%. The average estimated floating interval for the 17 washups we were able to test was 33.29 hr. We reject the hypothesis that ladybugs are congregating at or near the shoreline in favor of the notion that they are traveling for a considerable distance while floating.

An unknown weather or wind condition has been invoked as the cause of washups by several authors (Lee, 1980; Schaefer et al., 1987; Turnock, 1996). Isard et al. (2001) suggest a specific phenomenon known as a lake or sea breeze and explain how this wind pattern could deposit insects flying over land into nearby water. This weather condition seems to fit the available data better than any other. Lake and sea breezes are caused by differential heating and cooling of water and land, but are affected by several local variables (Isard et al., 2001). This phenomenon can happen on a daily basis, or never, in some localities. The frequency of washups reported in this and other studies and the observation that washups are localized and occasionally completely absent from a region (Acorn, 2007) can be explained by the dynamics of lake and sea breezes. This explanation also accounts for the difference in size of washups compared to the size of the body of water, as larger bodies of water enhance coastal breezes. Given the phylogenetic diversity of coccinellids affected by washups and the lack of other taxa, it seems likely that ladybugs are flying at times or altitudes that make them particularly vulnerable to being relocated by lake or sea breezes. Unseasonably warm temperatures are known to be a favorable condition for the production of a lake or sea breezes (Isard et al., 2001), and for the mass movement of coccinellids (Hodek et al., 1993).

Because lake breezes depend on a higher air than water temperature, we would expect their effect to be strongest when water temperature is the lowest. In our data set, this occurs early in the season, when the air temperature is warming but the water is still cold from the long winter (RUSS 2008, Fig. 5). This could explain why we found a negative correlation between the estimated time spent floating and the washup collection date. Perhaps as the lake warms throughout the summer, the lake breeze becomes less intense, so washups float for shorter periods of time before reaching the shore.

The implications of ladybug washups for other members of the ecological community are intriguing. Fish consumption of ladybugs floating on the surface has been generally regarded as unimportant in the washup literature. Turnock (1996) concluded after interviews with fisheries biologists that fish predation was rare. However, a photograph submitted to the Lost Ladybug Project shows an *H. axyridis* found in the gut of a Rainbow Trout (*Oncorhynchus mykiss*). Another photograph depicts a ladybug being eaten by a shore bird (John Losey, pers. comm. 2009). Ladybugs may or may not play a regular role in the food web of these ecosystems.

Ladybug washups can occasionally cause massive loss of life, which raises conservation concerns. Oliver (1943) estimated the aggregation caused by the largest reported ladybug washup to contain 4.5 billion individuals spread over 20.92 km of shoreline, only a small proportion of which were still alive. All of these ladybugs were reported to be *Coccinella 11-punctata*.

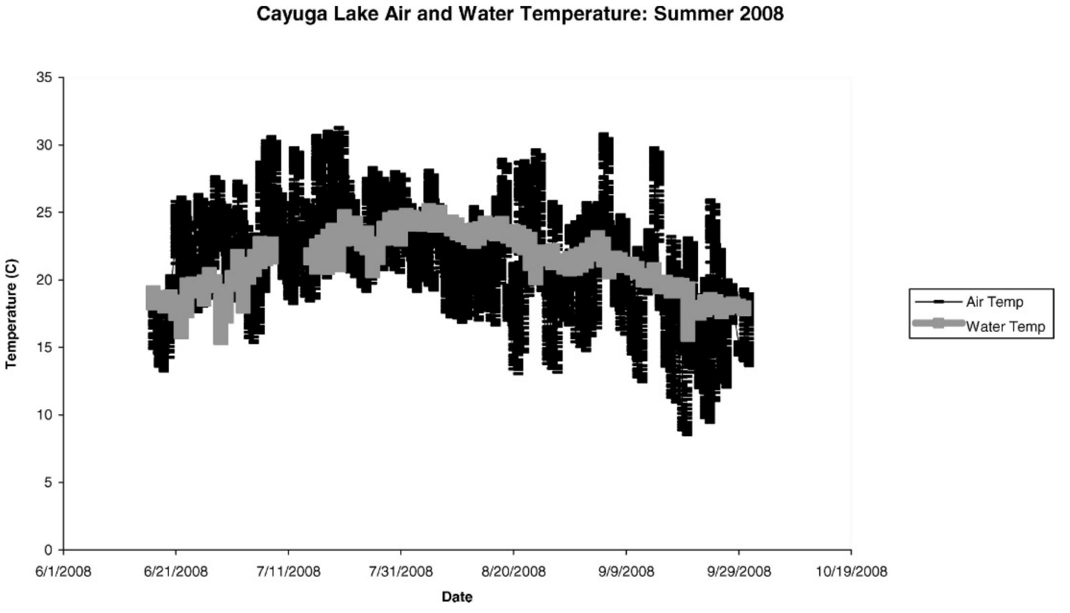

Fig. 5. Cayuga Lake air and water temperature data courtesy of RUSS shows that the air is generally warmer than the water earlier in the summer than later.

Previous studies have shown that the composition of a washup does not correspond with nearby coccinellid communities, causing shoreline aggregations to be labeled as "pseudo-communities" (Hodek and Honek, 1996). Turnock et al. (2003) present data to the contrary. The largest washups recorded are generally monotypic (Bold, 1873; Oliver, 1943; Schaefer et al., 1987; Majerus and Majerus, 1996). Some ladybugs aggregate conspecifically in enormous numbers to overwinter and massive migrations occur to and from hibernation locations (Hagen, 1962). If one of these migrations encountered a sea or lake breeze, it could precipitate a giant washup. Although a washup may cause massive mortality, it generally occurs to only one species. Washups that contain the greatest diversity of species tend to be smaller. This phenomenon is therefore not likely to affect the long term balance of species in a region.

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