Timing of *Hexagenia* (Ephemeridae: Ephemeroptera) mayfly swarms

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Abstract: Although degree-days can be used to determine when insect emergence begins, peak swarming events in species that exhibit extended emergence periods are difficult to estimate. With the aid of logistic regression, we estimated the probability of adult mayfly swarms (≥50 individuals/m^2), occurring on any given night in western Lake Erie, using meteorological data. We sampled adult *Hexagenia* Walsh, 1863 from 2130 (sunset) to 2300 on 18 dates in 2000 (2 June – 18 July), with the largest numbers retrieved between 13 June and 2 July. Water temperature (20 °C) was the cue to the onset of swarming (subimagos). Highest mean (±SE) density of all *Hexagenia* adults (subimagos and imagos) was 24 740 ± 8 757 individuals/m^2. Overall, 10-fold more imagos (mostly females) than subimagos were attracted to lights. Of the factors examined (air and water temperature, Julian day, dew point, heat index, humidity, moon phase, wind chill, wind direction, wind speed), onshore wind speed (0–9.2 km/h) on calendar dates for which the water temperature exceeded 20 °C was the most significant factor to account for total adult swarms. Eighty-three percent of the 18 swarming events observed in 2000 were correctly predicted. Validity of the model was confirmed with data collected in 2002, during which 5 of 6 swarming events were correctly predicted from the logistic model. Wind promotes adult aggregation at the land–water interface, the effect of which facilitates mating success and predator swamping.

Résumé : Bien que les degrés-jours puissent servir à déterminer le début de l'émergence chez les insectes, il est difficile d'estimer les épisodes principaux de formation d'essaims chez les espèces qui ont une période d'émergence prolongée. À l'aide de la régression logistique, nous avons estimé la probabilité de la formation d'essaims d'éphémères adultes (≥50 individus/m^2) dans une soirée donnée dans la partie occidentale du lac Érié d'après les données météorologiques. Nous avons échantillonné les adultes d'*Hexagenia* Walsh, 1863 de 2130 (nuit tombante) à 2300 à 18 dates (2 juin au 18 juillet) en 2000 et nous avons obtenu les récoltes maximales entre le 13 juin et le 2 juillet. La température de l'eau (20 °C) sert de signal pour le début de la formation des essaims (subimagos). La densité moyenne (±ET) maximale de tous les *Hexagenia* adultes (subimagos et imagos) était de 24 740 ± 8 757 individus/m^2. Dans l'ensemble, 10-fois plus d'imagos (surtout des femelles) que d'imagos sont attirés par la lumière. De tous les facteurs examinés (température de l'air et de l'eau, jour julien, point de rosée, indice de chaleur, humidité, phase de la lune, refroidissement éolien, direction du vent, vitesse du vent), la vitesse du vent vers la rive (0–9,2 km/h) aux dates du calendrier quand la température de l'eau dépasse 20 °C est le facteur explicatif le plus significatif des essaims d'adultes totaux. Il a été possible de prédire correctement 83 % des 18 épisodes de formation d'essaims observés en 2000. La validité du modèle est confirmée par les données récoltées en 2002, puisque 5 de 6 formations d'essaims ont pu être prédites à partir du modèle logistique. Le vent provoque le rassemblement des adultes à l'interface eau–terre, ce qui favorise le succès de l'accouplement et la saturation des prédateurs.

[Traduit par la Rédaction]

Introduction

In contrast to many terrestrial insects, aquatic insects such as mayflies and stoneflies typically have a relatively short period to disperse, and exposure to meteorological conditions likely influences flight significantly (Briers et al. 2003). Air temperature, wind, cloud cover, relative humidity, and other factors may affect insect dispersal by influencing take-off (typically inhibited by high winds) and duration of flight (Johnson 1969). Lyman (1944) reported that onshore breezes resulted in the accumulation of adult *Hexagenia* Walsh, 1863 mayflies on the South Bass Islands in western Lake Erie. Waringer (1991) and Kovats et al. (1996) showed that night air temperature affected the daily catches of caddisflies, but precipitation and wind speed had minor effects on catches. Swarms of adult stoneflies were positively related to air temperature, but negatively related to wind speed (Briers et al. 2003). In wetlands, elevated temperatures, chlorophyll *a*, and low numbers of predators resulted in nuisance swarms of midges (Davis et al. 2002).

Mayflies can increase their fitness by emerging en masse, which facilitates mating and reduces predation (Sweeney and Vannote 1982). In mayflies, all growth occurs during the nymphal stage. Final-instar nymphs leave the substrate, swim to the water surface, and moult into a subimago. Subimagos emerge from the water and fly or are carried by wind to land where they rest for a day and then moult into a sexually mature imago. If prevailing winds affect flight

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direction, adult tallies can indicate the ultimate direction of dispersal from a site of emergence (but see Macneale et al. 2004).

The number of degree-days accumulated over the life cycle can be used to predict approximately when *Hexagenia* emergence from nymphs to subimagos begins (Giberson and Rosenberg 1994). However, we analysed abiotic factors to determine which ones were best correlated with swarming activity, i.e., those nights within the extended emergence period when peak swarms occurred. *Hexagenia* flight activity may function in (*i*) nighttime dispersal of subimagos from surface waters to shore, (*ii*) maneuverability peculiar to male mating swarms that occur prior to sunset, but are seldom recorded (Brodskiy 1973), and (*iii*) swarms that occur when females are attracted to oviposition sites after sunset. From 1994 to the present, episodic massive nighttime swarms of adult *Hexagenia* occurred anywhere within a 4-week period between June and July at Colchester Harbour, Ontario (northwest Lake Erie), but adult mayflies can be seen flying from late May until late August; stragglers are seen until October (L.D. Corkum, personal observation). Mayflies are relatively poor fliers (Corkum 1987), but *Hexagenia* adults fly or are carried inland by wind an average of 1.2 km (Kovats et al. 1996).

We estimated the probability of nighttime mayfly (non-mating) swarms forming at Colchester Harbour, using density estimates of adult *Hexagenia* and concurrently measured meteorological data. We expected that wind would likely account for the swarms of subimagos, but that other meteorological factors might account for the presence of sexually mature imagos. Consequently, wind direction was expected to be potentially important in determining relative proportions of subimagos and imagos in swarms. For example, onshore winds may cause females headed offshore for oviposition to bunch up along the shoreline where they are attracted to lights. Forecasting when massive swarms of *Hexagenia* species occur will aid fisheries managers, who need to estimate fish recruitment to enhance stocks, and managers of power-plant facilities, who want to avoid power outages that can be caused by the accumulation of massive numbers of insects on and around nocturnally illuminated power transformers. Additionally, estimates of flight activity have significant consequences for population dynamics and gene flow (Briers et al. 2003).

Materials and methods

Hexagenia natural history

In the Laurentian Great Lakes, *Hexagenia* species normally spend 1–2 years in the nymphal stage (Corkum et al. 1997). However, life-history interpretation is difficult because populations have a protracted emergence (Corkum et al. 1997) and often show multiple cohorts (Heise et al. 1987), delayed hatching of eggs (Gerlofsma 1999), differential growth of males and females (Wright et al. 1982), and wide variability in growth rates of individuals from the same egg mass (Hunt 1953; Hanes and Ciborowski 1992). *Hexagenia limbata* (Serville, 1829) and *Hexagenia rigida* McDunnough, 1924 (Ephemeroptera: Ephemeridae) frequently co-occur, contributing to the complexity of life-history analysis.

For centuries up until the mid-1950*s*, burrowing mayfly nymphs, *Hexagenia*, occupied the clay–mud sediments of the western basin and shoreline areas of the deeper basins of Lake Erie (Reynoldson and Hamilton 1993). However, accelerated eutrophication in the 1950s and 1960s induced episodic hypoxia at the sediment–water interface (Britt 1955; Winter et al. 1996) and resulted in the near extirpation of burrowing mayflies from the western basin of Lake Erie and their replacement with pollution-tolerant organisms (Carr and Hiltunen 1965).

More recently, trophic changes in Lake Erie occurred in response to phosphorus abatement programs initiated under the Great Lakes Water Quality Agreement of 1972 between Canada and the United States (Makarewicz and Bertram 1991). Subsequently, *Hexagenia* began to appear nearshore in the 1980s, but nymphal densities were low and populations isolated; nymphs were rarely encountered offshore (Schloesser et al. 2000). Zebra mussels, *Dreissena polymorpha* (Pallas, 1771), became established in western Lake Erie in 1989, possibly contributing to water-quality improvement beyond that realized by nutrient reduction from municipal and industrial discharges (Schloesser et al. 2000). By 1996, *Hexagenia* had re-colonized much of the western basin from nearshore Lake Erie locations and source populations in the Detroit River and Lake St. Clair (Krieger et al. 1996; Corkum et al. 1997). This recovery has important implications in the transfer of energy to forage, sport, and commercial fishes (Ludsin et al. 2001).

Sampling protocols

Hexagenia adults and meteorological variables at Colchester Harbour (41°59′N, 82°55′W) were monitored on the north-central shoreline of western Lake Erie, Ontario, Canada, during June and July 2000. Colchester Harbour has the highest mean density of *Hexagenia* adults of locations investigated along the shoreline of the western basin of Lake Erie (L.D. Corkum, unpublished data). The western basin of Lake Erie has a mean depth of 7.4 m and a surface area of 3284 km^2 (Bolsenga and Herdendorf 1993). The shallow waters of the western basin of Lake Erie are generally well mixed and do not form a permanent hypolimnion (Bridgeman et al. 2006). Western basin Lake Erie waters tend to become stratified in the early afternoon, but are well mixed at night (Ackerman et al. 2001).

Hexagenia mating swarms (dominated by males) occur from 2000 to 2030 EDT, i.e., prior to sunset (L.D. Corkum, personal observation). Mayflies often use landscape markers such as trees, tall crops (e.g., corn fields), lake shorelines, or roads for mating swarms (Brodskiy 1973; Savolainen 1978).

Our nighttime collections were made to avoid mating swarms, but to capture dispersing adults that result in mayfly swarms that are attracted to lights near shore. Swarms of mayfly adults around street lights in Lake Erie communities were common historically (Langlois 1951). The number of mayflies landing on the ground near the harbour lights was measured on (2130 EDT) and after sunset for 90 min. It was assumed that this number represented aerial adult *Hexagenia*, which were attracted to lights.

The sampling units (91 cm diameter hoops on white sheets placed on the ground) may have underestimated aerial density. For example, Kriska et al. (1998) reported that white matt-finished cloth, which reflects light diffusely, underestimates the number of some mayfly species, e.g., *Rhithrogena semicolorata* (Curtis, 1834) and *Epeorus sylvicola* (Pictet, 1865), whereas shiny black plastic sheets, with a high degree of polarization, serve as an attractant.

In 2000, adults were sampled on 18 dates in June (2, 6, 8, 13, 15, 18, 19, 21, 23, 27, and 30) and July (2, 4, 7, 9, 12, 16, and 18). On each sampling date, five plastic hoops (0.65 m^2 quadrats) were placed upon a white sheet on the ground within the sphere of a high-intensity mercury vapour street light and near the water's edge (a distance of about 6 m) to estimate density of adult *Hexagenia*. Following the identical sampling protocol, results of the 2000 model were used to determine if the same variables accounted for mayfly swarms in 2002. In 2002, adults were sampled on 13 dates in June (12, 19, 25, 28, 30), July (3, 9, 17, 29), and August (8, 14, 21, 28).

Adults were collected from each quadrat continuously from 2130 (near sunset) until 2300 EDT. Mayflies alighting within a quadrat were grasped by the wings and placed inside a glass jar with 70% ethanol. On evenings when massive swarms occurred, fractions of each hoop were sampled. Specimens were counted, sexed, and the males identified to species in the laboratory.

A Kestrel® 3000 Pocket Weather meter (Nielsen-Kellerman, Chester, Pennsylvania) was used to record meteorological variables that have been implicated as potential regulators of adult aquatic insect swarming behaviour. Air temperature (°C), dew point (°C), heat index (°C) (i.e., the temperature a body feels when heat and humidity are combined), relative humidity (%), wind chill (a combination of wind speed, km/h, and air temperature, °C), and wind speed were either directly recorded by the station instrumentation or calculated from the readings. The measurements, recorded at sunset, were used as independent variables in stepwise multiple analyses (see below). Wind direction (precise to the nearest 22.5° of the compass) was noted at the time of sampling. Calendar date and moon phase (obtained from the Lake Erie Charter Boat Association Web site, http://www.lecba.org) also were recorded. Lake Erie water temperature measurements (°C) were obtained from daily readings recorded from the intake pipe (within 500 m of the collection site) at the Harrow–Colchester South Water Plant in the town of Colchester. The intake pipe extends lakeward for 381 m and is buried 0.6 m below the lake bed until the end where it protrudes up into the water column for 1.6 m. Water temperature values were the average between mid-morning and mid-afternoon records. The water temperature at this depth was assumed to be representative of temperatures to which nymphs were exposed.

Statistical analyses

Flight patterns of adult *Hexagenia* species (total of all stages of mayflies, subimagos, imagos, females, and males) were examined over time. Relationships between density of subimagos and water temperature were analysed to determine cues regulating the onset of emergence.

Forward stepwise logistic regression analysis (SAS Institute Inc. 2002) was used to determine which meteorological variables (or combination of variables) were best able to forecast swarms of mayflies. The logistic equation is $\log\{p(y = 1|\mathbf{x})/[1 - p(y = 1|\mathbf{x})]\} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + ...$, where $p(y = 1)$ is the probability of success (i.e., a massive swarming date) and $\beta_0 + \beta_1 + \beta_2 + ...$ are regression coefficients associated with independent variables $X_1 + X_2 + ...$ Any variable that did not meet the 0.05 level of significance was removed from the model. The model was fitted to data collected in 2000. The resultant regression coefficients were used to predict the likelihood of a swarm occurring on each collection date in 2002.

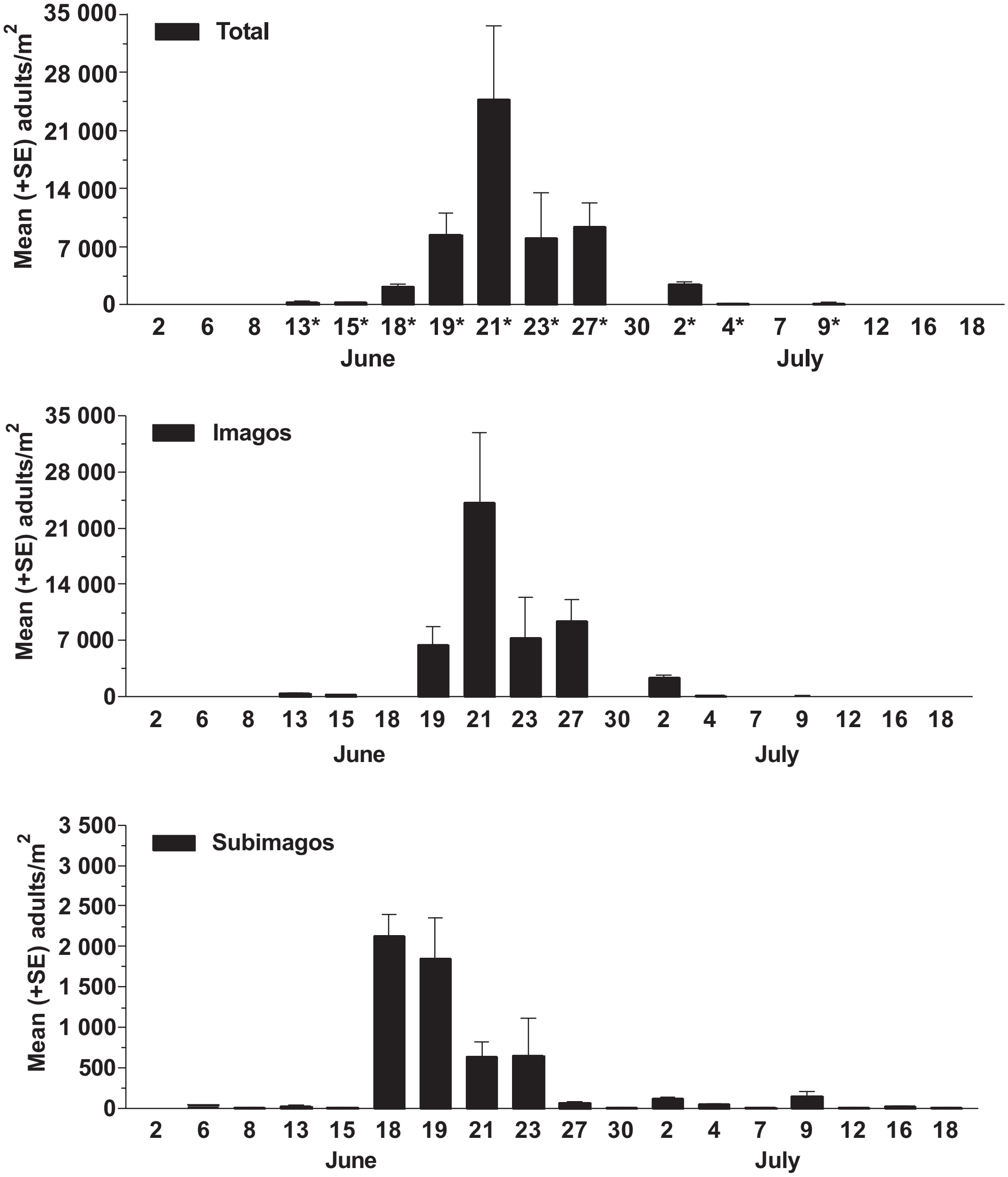
Results

Hexagenia adults were collected at Colchester Harbour from 2 June until 18 July 2000, with the largest numbers observed between 18 and 27 June (Fig. 1). Highest mean (±SE) density of all *Hexagenia* adults (24 740 ± 8 757 individuals/m^2) occurred on 21 June (Fig. 1). About 10 times more imagos than subimagos (Fig. 1) and many more females than males were collected (Fig. 2). After examining the frequency-abundance data (Fig. 1), we operationally defined a swarming date as one on which mean density of adults obtained from the quadrats was ≥50 individuals/m^2. Accordingly, the following calendar dates were designated as those on which mass emergence events (i.e., swarms) occurred: 13, 15, 18, 19, 21, 23, 27 June; 2, 4, 9 July. The remaining sample dates (2, 6, 8, 30 June; 7, 12, 16, 18 July) were designated as nonswarming dates.

Subimagos were most prevalent at the beginning of the mass emergence period (18–23 June) and declined in relative abundance as the season progressed (Fig. 1). The first mass appearance of subimagos is a function of water temperature (Fig. 3). Large numbers of subimagos were only collected once water temperature reached 20 °C. Consequently, we assigned onshore wind direction a value of 1 when the water temperature was ≥20 °C and when the wind direction was from any southerly direction (between 90° and 270° from north); otherwise, a value of 0 was assigned.

Results from the multiple logistic regression analysis indicated that only one variable, onshore wind speed (onshore wind × wind speed on dates after which water temperature reached 20 °C) correctly identified when swarms would occur. The regression model correctly predicted 83% (15/18) of the swarming events that occurred over the 2000 sampling period for total adults, imagos, and females (Table 1). Identical results were obtained for these designated groups of mayflies because swarms of each group occurred on the same dates. We observed many female imagos ovipositing eggs on the ground under the lights. Unpredicted swarms occurred on two dates (swarms were observed on two calm evenings early in the summer), and a swarm failed to occur as predicted on one evening early in the summer (Fig. 4). The probability of a swarm occurring was given by the equation $p(y = 1) = \exp(-0.981 + 6.629X)/(1 + \exp(-0.981 + 6.629X))$, where X is onshore wind speed (Fig. 4). Although onshore wind speed correctly predicted 10 of the 11 cases when neither subimago nor male swarms occurred, it predicted only 2 of 6 nights when subimagos swarmed and 2 of 7 nights when males swarmed (i.e., the insects were not present in sufficient numbers to meet the "swarm" criterion). Of the males collected, most

Fig. 1. Mean (+SE) density (individuals/m^2) of total *Hexagenia* adults, imagos, and subimagos collected at Colchester Harbour, Ontario, throughout the emergent period in 2000. The scale for subimagos (up to 3500 adults/m^2) is one-tenth the value for imagos and total *Hexagenia* species (35 000 adults/m^2). Numbers on the *x* axis with an asterisk in the upper panel (total *Hexagenia*) indicate dates with mayfly swarms.



were subimagos. Imaginal males reached the “swarming” criterion of 50 individuals/m^2 on 5 nights (19, 21, 23, and 27 June; 2 July) during the sampling period.

In 2002, swarming events of total *Hexagenia* occurred on 6 (25, 28, 30 June; 3, 17, 29 July) of the 13 sampling dates over the emergence period (12 June – 28 August). Five of 6 swarming dates occurred after lake water temperature reached 20 °C when wind direction was onshore.

Discussion

Although *Hexagenia* has an extended emergence period, most nymphs transform into adults during June and early July in temperate North America (Giberson and Rosenberg 1994; Corkum et al. 1997). It is advantageous for insects that have such a short adult life to emerge synchronously, as it increases their chance of finding a mate (Corbet 1964). In addition, an individual maximizes its chance to reproduce by emerging synchronously with enough others to satiate predators (Sweeney and Vannote 1982).

Our sampling protocol detected several variations in emergence patterns related to the stage and sex of mayflies. Onshore winds appear to blow newly emerged subimagos to the shoreline. Onshore winds also push adult female imagos shoreward, where, attracted to lights, they oviposit on cement rather than on water. It is unknown if most male

Fig. 2. Mean (+SE) density of female and male *Hexagenia* adults collected at Colchester Harbour, Ontario, throughout the emergent period in 2000.

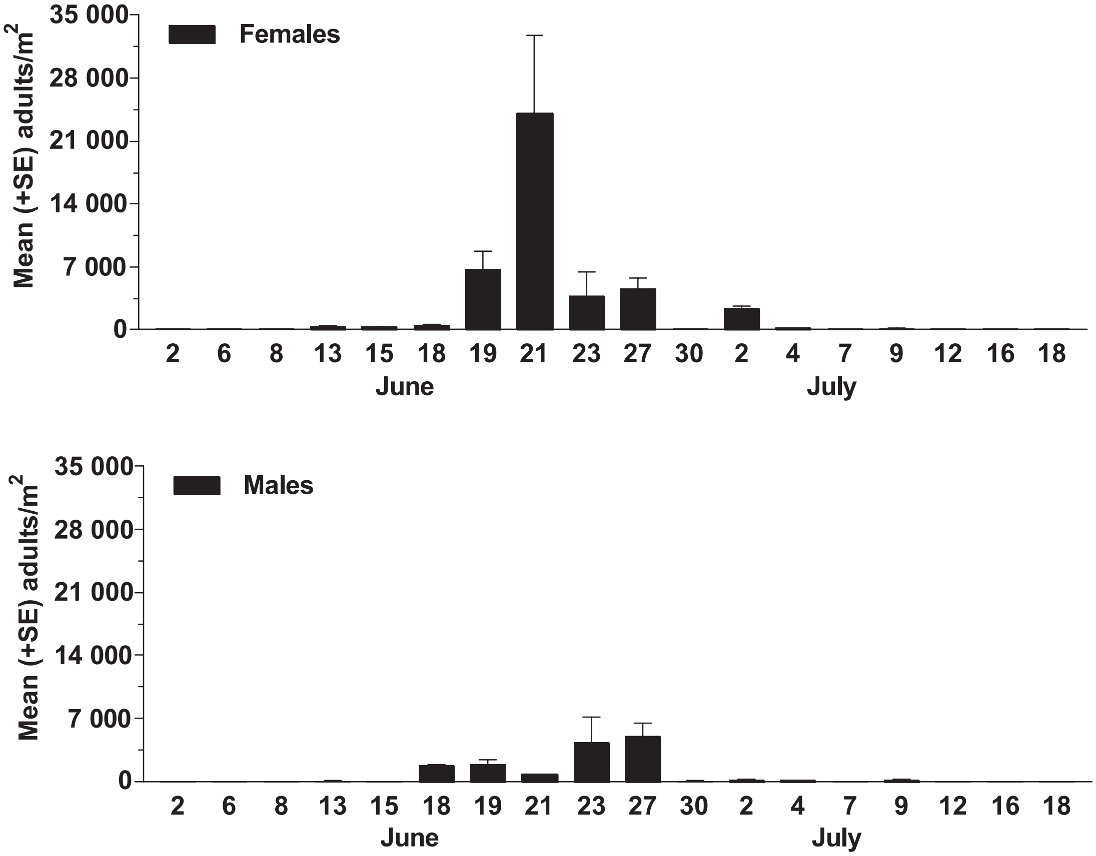


Table 1. Summary of the logistic models that predicted the swarms of total adult–imago–female, male, and subimago *Hexagenia* on 18 dates in 2000 (SE, standard error; *P*, probability).

Dependent swarming	Independent variable	Estimate	SE	Likelihood ratio (χ^2)	*P*	Percentage of swarms predicted
Total–imago–female	Intercept	–0.981	0.677			
	Onshore wind	6.629	61.656	11.838	0.001	83.3
Male	Intercept	–0.889	0.604			
	Onshore wind	0.227	0.176	1.910	0.167	66.7
Subimago	Intercept	–1.285	0.659			
	Onshore wind	0.289	0.184	2.930	0.087	72.2

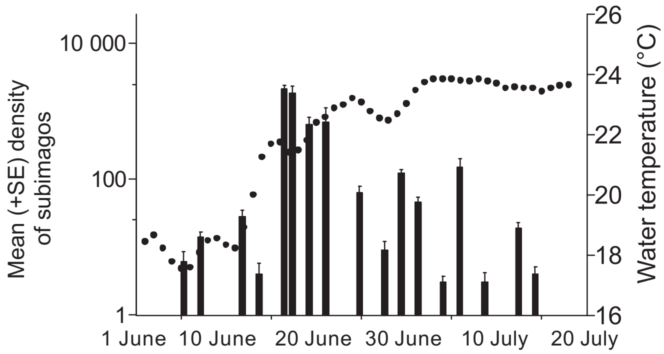
imagos die after mating swarms before sunset, but far fewer males than females are attracted to lights after sunset.

Density of subimagos collected in quadrats was one-tenth the density of imagos collected (Fig. 1). This imbalance between stages collected likely occurred because once on land, most subimagos rest on vegetation until they moult to the sexually mature imago (Hunt 1953). Nevertheless, the largest swarms of subimagos appeared on 18 and 19 June and, as expected, the records for imagos peaked shortly thereafter (21 June). Moulting from subimago to imago was rarely seen during the sampling period, suggesting that the subimagos sampled were recent arrivals, i.e., individuals that flew or were carried by wind from water to land. Thus, the effect of synchronous subimaginal swarms may be an example of predator swamping.

Density of female imagos was about 10 times greater than that of male imagos. Most males likely died after forming mating swarms that occurred before sunset. The females, however, were likely attracted to the lights during their oviposition flight. Lights apparently mimic moonlight on the water, and females often mistakenly oviposit on asphalt (Kriska et al. 1998). Anglers frequently report that sport fish (especially smallmouth bass, *Micropterus dolomieu* Lacepède, 1802) do not "bite" during the full moon when mayflies are on the wing, suggesting that the fish are satiated with adult *Hexagenia*.

Brittain (1982) reported that mayflies as a group are notoriously weak fliers. On the basis of allometric relationships between body and wing lengths, small lentic and large riverine mayflies are more likely to disperse greater distances than other mayflies (Corkum 1987). Mayflies, such as *Hexagenia*, that occur in both lake and riverine habitats are more

Fig. 3. Mean (+SE) density of subimagos (bars) and water temperature (●) throughout the emergence period, June and July 2000. High densities (swarms) of subimagos on land appear once water temperatures reach 20 °C.



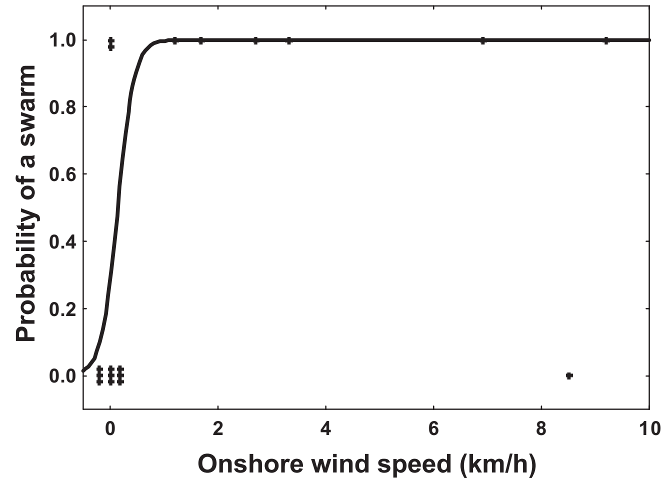
similar to the habits of riverine species in their ability to disperse (Corkum 1987).

Our study showed that adult mayflies are carried to shore by wind. This phenomenon could be a mechanism that promotes adult aggregation, facilitating mating success and predator swamping. Lyman (1944) noted that local concentrations of *Hexagenia* at the F.T. Stone Laboratory, Ohio State University (Gibralter Island, western Lake Erie), were dependent on wind direction. Emerging subimagos would be carried with onshore breezes and accumulate on the windward side of the island as our current study shows.

There is a difference between factors that initiate emergence and factors responsible for swarming behaviour in aquatic insects. Despite the tight diel synchrony of *Hexagenia* swarms (Fremling 1970), the calendar date of mayfly emergence varies considerably from year to year. Degree-day accumulation in the final year before emergence can be used to predict when adult *Hexagenia* were apt to occur (Giberson and Rosenberg 1994). Often, spring temperature can be related to the start of emergence in *Hexagenia* and other burrowing mayfly species (*Ephemera simulans* Walker, 1853 (Britt 1962); *Ephemera strigata* Eaton, 1892 (Takemon 1990)). Hunt (1953) reported that cold spring temperatures in 1947 delayed the onset of peak emergence from early June to August in three Michigan lakes compared with other years when spring temperatures were more moderate. In 1997, Lake Erie water temperature in the western basin did not reach 20 °C until 28 June (raw water temperature data obtained from the Harrow–Colchester South water plant); swarms were observed 30 June 1997 (L.D. Corkum, personal observation). These observations help to confirm the 20 °C temperature threshold for mayfly emergence in western Lake Erie.

Savolainen (1978) studied the swarming behaviour of seven species of Ephemeroptera (excluding *Hexagenia*, which is confined to the western hemisphere) in Finland. Both light intensity and air temperature affected the time of swarms. Wind speed between 1.5 and 2 m/s (5–7 km/h) and low and high temperatures inhibited mayfly swarming (Savolainen 1978). Other researchers also reported that mayfly adults typically avoid locations where wind is strong (Spieth 1940; Brodskiy1973; Whelan 1980; Kovats et al. 1996). Wind speed (up to 9.2 km/h) did not inhibit flight activity of *Hexagenia* at our study site.

Fig. 4. Relationship between the probability of a swarm occurring (i.e., adult mean density ≥50 individuals/m^2) and onshore wind speed (km/h) on dates after which water temperature had reached 20 °C in 2000.



In summary, adult *Hexagenia* (subimagos and imagos) tend to occur in swarms on the same date, so the mechanism producing swarming events is a function of abiotic factors. If swarms are the result of mechanical effects of wind acting on generalized and nondirected flight behaviour, then a knowledge of local meteorology is useful in our ability to forecast swarming events. Swarms can first be expected within a few days of water temperature reaching 20 °C and the period of maximum probability of swarming persists up to 10 days (swarms in our study were greatest between 18 and 27 June). Because the probability of swarming is correlated with the advent of onshore winds, regional weather forecasts of wind direction are not likely to be useful. Instead, factors that promote differential heating and cooling of land and of water that are related to onshore winds would be most beneficial in forecasting swarming events of *Hexagenia*.

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