

Inland dispersal of adult aquatic insects

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SUMMARY

1. Adult caddisflies (Trichoptera) and mayflies (Ephemeroptera) were light-trapped on summer evenings along the Detroit River and Lake St. Clair, near Windsor, Ontario, Canada. Light traps were located at the shore and at increasing distances inland up to 5 km, and were operated simultaneously for 2 h following sunset. Catches of five species of caddisflies of the family Hydropsychidae (*Cheumatopsyche campyla*, *Cheumatopsyche speciosa*, *Hydropsyche hageni*, *Hydropsyche phalerata*, *Macrostemum zebratum*) and the mayfly *Hexagenia* (Ephemeridae) were used to examine inland distribution.
2. Inland dispersal was limited: catches of caddisflies declined at a greater than exponential rate with increasing distance from shore. Mean dispersal distance from the shoreline ranged from 650 to 1845 m. Smaller caddisfly species dispersed shorter distances than larger caddisflies and *Hexagenia*.
3. Inland distribution of adult caddisflies exhibited considerable interspecific variation: distribution was inconsistent among trials for *Hexagenia*, possibly owing to timing of collections in relation to periods of peak emergence.
4. Sex ratios of caddisflies were female biased at most sites. No consistent bias was observed for *Hexagenia*. Different inland distribution patterns were observed for males and females. The differences appeared to reflect species-specific reproductive strategies.

Introduction

The primary purpose of the adult phase of the typical aquatic insect life cycle is mating and the deposition of eggs in habitats suitable for larval development. Adult aquatic insect dispersal has received considerable attention in connection with Müller's colonization cycle hypothesis (Müller, 1954, 1982). Adult females of many species of mayflies (Ephemeroptera) and caddisflies (Trichoptera) fly upstream prior to oviposition (Roos, 1957; Bird & Hynes, 1980; Flecker & Allen, 1988; Jones & Resh, 1988). Müller (1954, 1982) argued that such behaviour compensates for possible downstream drift by larvae, thereby completing a colonization cycle.

In contrast, the significance of flight perpendicular to the river channel (inland dispersal) has been largely unstudied. This type of movement has been observed for several mayfly and caddisfly species (Johnson, 1969; Svensson, 1974; Bird & Hynes, 1980; Jackson &

Resh, 1989), and was termed Type 3 flight movement by Svensson (1974). Inland dispersal may be of considerable importance in the colonization of new habitats (Johnson, 1969), in the entry of aquatic insects into terrestrial foodwebs (Menzie, 1980; Jackson & Resh, 1989), and/or may be associated with species-specific developmental or reproductive behaviour (Svensson, 1974).

Several factors may influence this type of dispersal. Proximal abiotic factors include environmental conditions (air temperature, wind, cloud cover, relative humidity) that may directly influence dispersal behaviour, and generally act by affecting take-off, and the timing and duration of flight (Johnson, 1969; Waringer, 1991). Ultimately, habitat characteristics (permanence, predictability, frequency and severity of disturbance) may influence the evolution of dispersal behaviour. Habitat characteristics may exert an indirect influence

through selective pressure as may geographical distance between suitable larval habitats. Large rivers are permanent and their discharge patterns are relatively predictable (Resh *et al.*, 1988); thus, the substratum may be less frequently disturbed by high flows than in small streams. Animals adapted to such habitats are believed to exhibit limited dispersal (Williams, 1988). Additionally, large rivers are distant from one another, and adults dispersing away from their larval habitat may not find another suitable river during their short lifespan, unless they are transported by favourable winds (Corkum, 1987). In summary, based on habitat characteristics, one might predict that inland dispersal by adults from large rivers and lakes may be limited and largely random (i.e. spatially undirected).

Inland dispersal patterns may also be influenced by reproductive behaviour. Emergence, reproduction and oviposition in mayflies and caddisflies occur near water, implying limited dispersal, especially considering that adults are short-lived (1 day to several weeks). However, some teneral (immature adult) caddisflies move inland, where they may rest until they become sexually mature (Ross, 1944). Although little information is available on flight behaviour of male caddisflies, females in different stages of reproductive development (immature, gravid, spent) in a Swedish stream exhibited non-random inland distribution (Svensson, 1974).

Light trap catches of adult aquatic insects are often used to infer species composition in adjacent aquatic habitats (e.g. Nimmo, 1966; Waringer, 1991 and references therein). Estimating likely recruitment area (the area from which the adults originate) is potentially valuable in assessing habitat characteristics. We and others have estimated contaminant burdens of emergent insects to assess degree of sediment contamination (Kovats & Ciborowski, 1989, 1993; Dukerschein *et al.*, 1992; Fairchild *et al.*, 1992). Knowledge of recruitment area is important in ascertaining the extent of the degree of contamination.

In this study, we used light traps to catch adult mayflies and caddisflies at the Detroit River and Lake St. Clair, in south-western Ontario, Canada. Our objectives were to examine inland distribution of hydroptychid caddisflies and the mayfly *Hexagenia*, to estimate mean dispersal distances and sizes of source areas of single-evening light trap catches, and to compare inland dispersal of male and female mayflies and caddisflies.

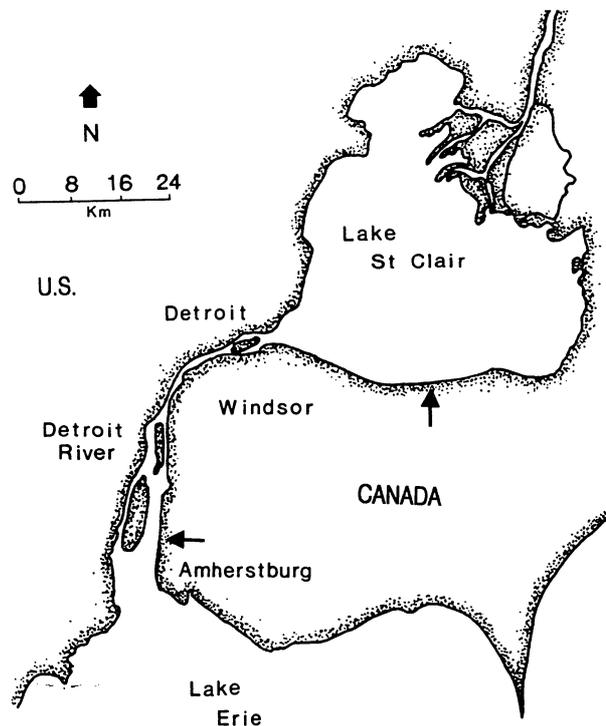


Fig. 1 Map of the study area. Sampling sites are indicated by arrows.

Materials and methods

Sample collection

Aquatic insects were collected at roadsides on calm evenings at two locations: the south shore of Lake St. Clair, Ontario (along Rochester Township Concession Road 4 in 1987; along Rochester Townline Road in 1988), and on the east bank of the Detroit River near Amherstburg, Ontario (along Essex County Road 10 in 1987) (Fig. 1, Table 1). The roads were selected because they ran perpendicular to the shoreline through very flat terrain dominated by cropland, and because they provided easy access to the waterbodies. The roads were bordered on both sides by fields, and most traps could be seen from several hundred metres in any direction. A line of shrubs and trees ≈ 120 m from the shore ran perpendicular to each road. A secondary road, illuminated by streetlights, intersected each road ≈ 300 m from shore.

The benthic fauna of the lower Detroit River is dominated by larvae of hydroptychid caddisflies and the mayfly *Hexagenia* (Ephemeroptera: Ephemeridae; Thornley & Hamdy, 1984; Hudson *et al.*, 1986). *Hexagenia* larvae are the most abundant aquatic insects

Table 1 Locations of dispersal distance study sites and sunset weather conditions

Date	Location	Latitude (north)	Longitude (west)	Taxa collected	Temp. (°C)	Wind velocity (km h ⁻¹)	Cloud cover (%)
17 July 1987	Lake St. Clair	42°08'39'	83°06'25'	<i>Hexagenia</i>	20	SSE 0–5	0
23 July 1987	Lake St. Clair	42°08'39'	83°06'25'	<i>Hexagenia</i>	24	SSW 0–5	60–80
29 July 1987	Lake St. Clair	42°08'39'	83°06'25'	<i>Hexagenia</i>	22	SE 0–5	0–20
31 July 1987	Detroit R.	42°17'54'	82°43'05'	Hydropsychidae <i>Hexagenia</i>	22	E 0–10	60–70
11 Aug. 1987	Detroit R.	42°17'54'	82°43'05'	Hydropsychidae <i>Hexagenia</i>	19	NE 0–5	10–20
13 Aug. 1987	Detroit R.	42°17'54'	82°43'05'	Hydropsychidae <i>Hexagenia</i>	23	E 0–5	0–20
13 July 1988	Lake St. Clair	42°09'05'	82°46'40'	<i>Hexagenia</i>	26	S 2–5	0
18 July 1988	Lake St. Clair	42°09'05'	82°46'40'	<i>Hexagenia</i>	24	S 0–5	100
20 July 1988	Lake St. Clair	42°09'05'	82°46'40'	<i>Hexagenia</i>	19	S 0–2	90

in fine sediments of Lake St. Clair (Hudson *et al.*, 1986). No other waterbodies (lakes, rivers or ditches) in the areas sampled support populations of *Hexagenia* or of the species of Hydropsychidae inhabiting the Detroit River.

Modified Pennsylvania-type light traps (Frost, 1957) were used for all collections (Kovats & Ciborowski, 1989). The light source was a 45-cm 12 V/15 W DC fluorescent long-wave ultraviolet lamp powered by two 6 V dry cell batteries connected in series. The lamp sat vertically at the central axis of three 45-cm tall, 15-cm wide, clear styrene vanes secured to a 30-cm diameter aluminium top-plate. The vanes rested on a 30-cm diameter plastic funnel that covered the mouth of a galvanized iron bucket. The bucket stood on a 1.2 × 1.2 m white cotton bed sheet spread on flat ground. Flying insects striking the vanes would fall through the mouth of the funnel into the bucket. Inside the bucket, dry ice was packed around a 12-cm diameter cylindrical aluminium hardware cloth reservoir, which retained the trapped insects. The dry ice anaesthetized and froze the insects. Mayflies tended to alight on the sheet rather than entering the trap. Such individuals were collected by hand.

Eight traps were set up, extending linearly away from the lake or river. Traps were located 0, 78, 156, 312, 625, 1250, 2500 and 5000 m from the shore. Traps were operated simultaneously for 2 h following sunset. This period corresponds to the time of greatest flight activity of adult aquatic insects (Hunt, 1953; Nimmo, 1966). Air temperature, cloud cover, wind direction and estimates of wind velocity were recorded during each collecting period.

Dispersal trials were conducted on three dates at the Detroit River and on six dates over two summers at Lake St. Clair (Table 1). Each trial consisted of simultaneous 2-h collections by the eight light traps in one study area. *Hexagenia* and Hydropsychidae were collected at the Detroit River, and *Hexagenia* only were trapped at Lake St. Clair (Table 1). An observer at each trap recorded the time and general direction of arrival for all *Hexagenia* captured. Samples were frozen and stored at –20 °C prior to sorting and taxonomic identification.

Estimates of dispersal distance were made from light trap catches of representatives of six taxa common in the Detroit River. These included the mayfly genus *Hexagenia* (*H. limbata* Serville and *H. rigida* McDunnough, combined because females are indistinguishable (Ephemeroptera: Ephemeridae)), and the caddisflies *Cheumatopsyche campyla* Ross, *Cheumatopsyche speciosa* (Banks), *Hydropsyche hageni* Banks, *Hydropsyche phalerata* Hagen and *Macrostemum zebratum* (Hagen) (Trichoptera: Hydropsychidae). Only occasional representatives of other mayflies were caught. Leptocerid caddisflies (various genera) were collected in moderate numbers, but since larvae of these animals may also develop in small lakes and ponds near the collecting areas, they were excluded from analyses.

Sample sorting

Samples were sorted to species (Hydropsychidae) or genus (*Hexagenia*). Males and females were tabulated separately. Due to the large numbers of caddisflies

collected (up to 6.5×10^4 insects per light trap sample), only subsamples were identified. All individuals were identified in samples consisting of 1000 or less animals. Larger collections of caddisflies were thoroughly mixed and subsampled by transferring groups of 50–100 animals (the approximate number that could be lifted at once with a pair of forceps) randomly taken from the sample into a Petri dish until 6–8 g fresh mass (800–1000 animals) of material had been selected. Total number of animals per sample was then estimated by multiplying the number of animals in a combined subsample by the ratio of total sample fresh mass to subsample fresh mass. All specimens were preserved in 70% ethanol following sorting. Voucher specimens are stored in the University of Windsor entomological collection.

Size determination

We wished to determine if overall differences in mean dispersal distance among taxa were possibly related to body size or relative wing size, which might reflect flight ability. To determine mean individual biomass, twenty individuals of each species were dried at 60 °C for 24 h and singly weighed to the nearest 0.1 mg. We also removed the right forewing of fifty individuals of each species and measured wing length (base of the subcostal vein to the wing tip) to the nearest 0.1 mm using an ocular micrometer at $\times 6$ magnification and a dissection microscope. Additionally, five forewings from randomly selected specimens of each species were mounted on transparent 25 mm photographic slides, and the projected images were traced on paper to facilitate measurements of other wing dimensions. Forewing lengths were measured, and forewing areas were determined using a polar planimeter. There was a very strong linear relationship between forewing length and forewing area for each species ($R^2 \geq 0.97$; Kovats, 1990). Mean forewing areas were calculated for each species by substituting mean forewing lengths ($n = 50$) into the appropriate species-specific regression equation. Wing loading for each species was calculated by dividing mean body mass (g) by forewing area (cm^2) (Greenewalt, 1962).

Data analysis

Data from trials (single evening collections at all eight traps) with < 100 animals of a taxon were excluded

from analyses. Thus, results for five replicate trials for *Hexagenia* (of nine possible trials) and two replicate trials for *Macrostemum* (of three possible trials) were discarded, resulting in four replicates of *Hexagenia* and a single replicate of *Macrostemum* dispersal data being analysed. For all other taxa, data for three replicate collecting periods were analysed.

Mean number of Hydropsychidae, and their relative species composition in light traps, was examined in relation to distance from the shore.

Total numbers of insects of a species caught per evening varied greatly with sample date, primarily due to differences among emergence periods of the species collected (Kovats, 1990). *Hexagenia*, *Hydropsyche phalerata* and *Macrostemum zebratum* emerged synchronously over 2–3 weeks in late June or July, whereas *Cheumatopsyche campyla*, *Cheumatopsyche speciosa* and *Hydropsyche hageni* emerged continuously throughout the summer. As a result, samples collected as little as 10 days apart contained varying numbers of the former species. To account for this variability, numbers of animals of a species caught in a trap on a particular date were expressed as relative proportions of the maximum catch of that species on that date.

To estimate dispersal parameters (mean and median inland distance travelled) for each date, we plotted the relative proportion of individuals of a species captured (see above) against distance from the shore. When relative abundance declined monotonically with increasing distance from the shore, a least-squares regression line was fitted to the data following application of the most appropriate linearizing transformations of the variables (those giving the highest possible coefficient of determination (R^2)). Mean inland dispersal distance (m) was then estimated from the indefinite integral of the regression equation. Additionally, estimated distance travelled by 50% (D_{50} , i.e. median distance) and by 10% (D_{10}) of the animals was calculated from the integral of the regression equation.

Some species exhibited distinct inland maxima in relative abundances. In such cases, mean dispersal distance was calculated by summing the products of the number of animals captured at each trap times distance from shore of a trap (animals \times m), and dividing by the total number of animals (animals) caught in all traps in that trial. Values for D_{50} and D_{10} were estimated by interpolation between the two most appropriate trap distances for a trial.

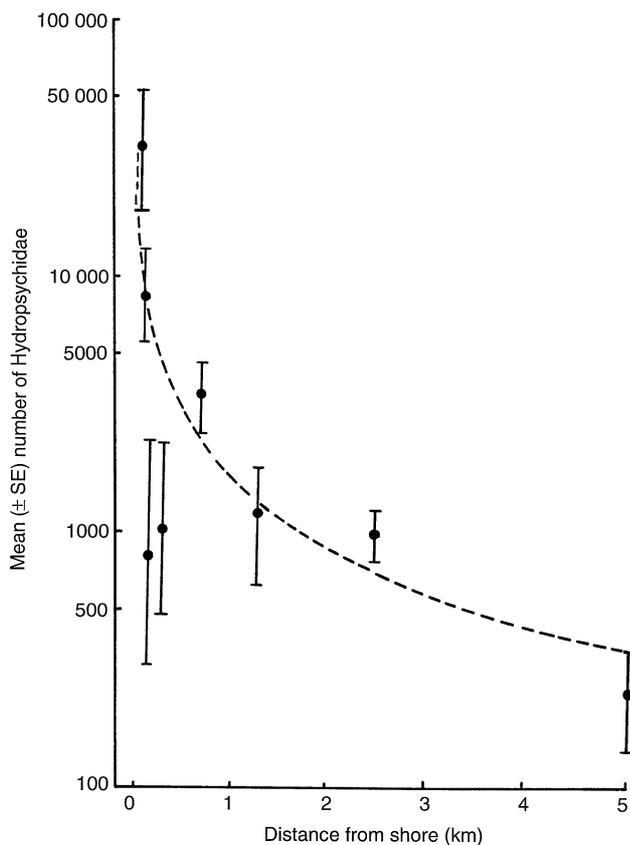


Fig. 2 Relationship between mean (± 1 SE) total catch of adult Hydropsychidae in light traps and distance inland from waterbody. The dotted line corresponds to the regression equation $\ln(\text{total catch}) = 10.436 - 0.063 \times (\ln \text{distance})^2$. Data points from sites 3 and 4 were not included in the regression analysis.

The values of D_{50} and D_{10} were used to estimate the area of aquatic habitat from which 50% and 90% of shoreline-collected insects might be recruited. These distances were each treated as the radius of a semicircle extending from the shore into the waterbody. Recruitment area for a hypothetical shoreline trap was then calculated from the formula for area of a semicircle, $0.5\pi r^2$. The assumption of this procedure is that large-waterbody insects disperse equal distances in all directions over water and that a dispersing insect will fly an equivalent distance over land as over water.

Mean dispersal distances of four caddisfly species and *Hexagenia* were compared by one-way analysis of variance, followed by Tukey's test (Tukey-Kramer method; Sokal & Rohlf, 1981), as recommended by Day & Quinn (1989). Data were logarithmically transformed prior to statistical analysis.

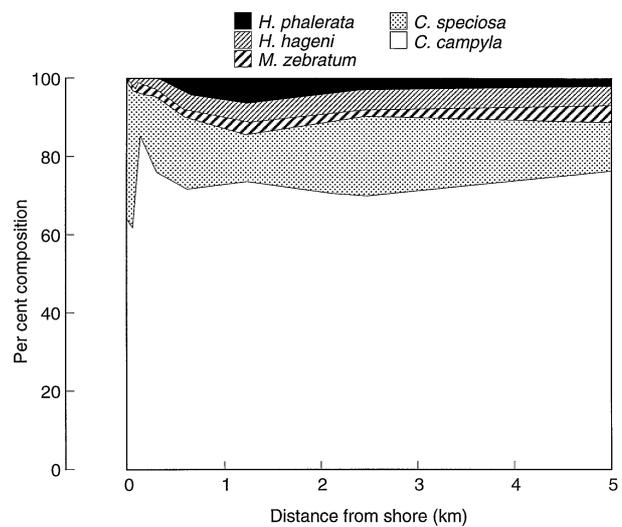


Fig. 3 Relationship between species composition of samples of Detroit River Hydropsychidae and distance from waterbody.

To determine whether the sex of dispersing insects affected dispersal patterns, the proportion of catch composed of females was plotted for each species at each site. Replicated tests of goodness of fit (G -statistic; Sokal & Rohlf, 1981) were used to determine whether significant heterogeneity in proportion of females existed among replicate samples, and whether significant deviation from a 1 : 1 sex ratio occurred.

Results

Meteorological conditions were similar during all sampling periods (Table 1), with a mean (± 1 SE) sunset air temperature of 22.1 ± 0.81 °C ($n = 9$) and wind velocities below 10 km h^{-1} . Although estimated cloud cover was variable (0–100%), the effect of cloud cover on adult insect activity is relatively minor (Kovats, 1990). The high consistency of weather conditions during sampling periods suggests that relatively little of the variation in insect dispersal observed among sampling periods was due to environmental variation.

Catches at two sample distances (156 and 312 m) were consistently lower than catches at all but the most remote sites during most trapping periods. In both study areas, traps at 156 m were situated adjacent to a dense hedgerow and the 312 m traps were located near the intersection of crossroads illuminated by streetlights that were significantly brighter than our traps. Because we suspected that catches at these distances substantially underestimated local popula-

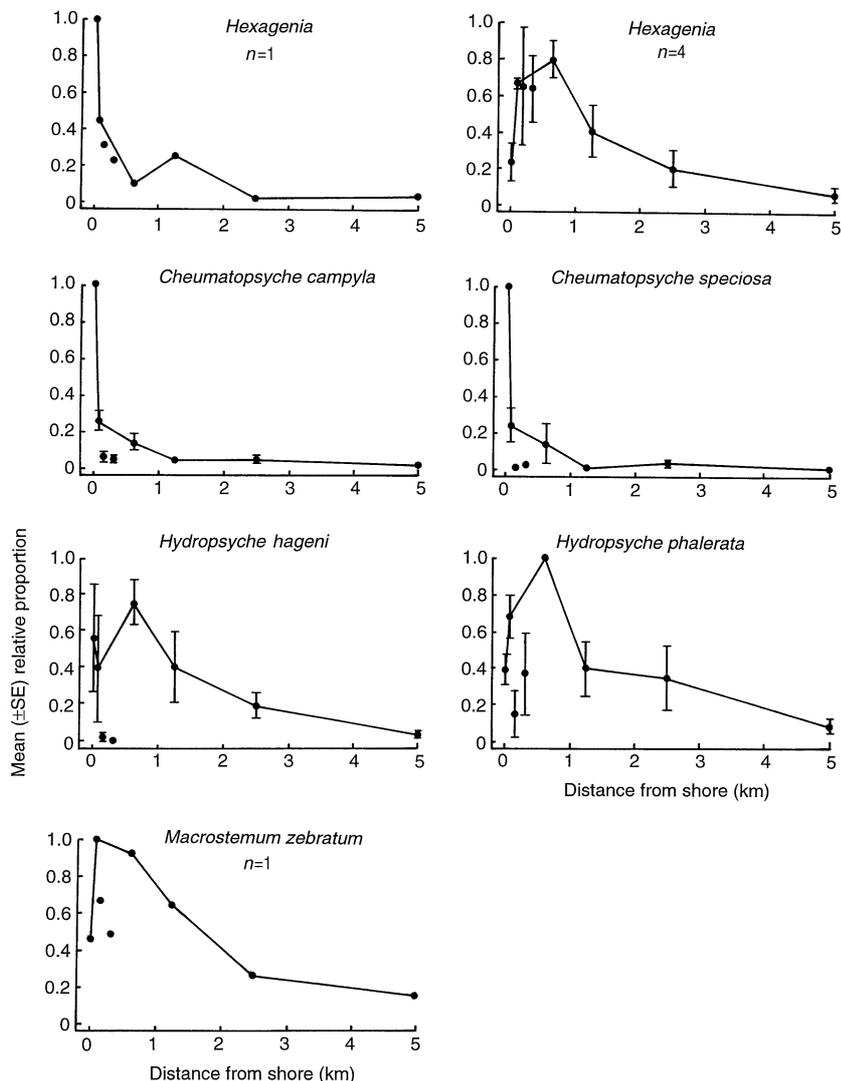


Fig. 4 Relationship between mean (± 1 SE) catch of adult insects in light traps and distance inland from waterbody. Each curve represents collections on three nights, except where otherwise indicated. For *Hexagenia*, left figure represents catch in July 1987 at Detroit River; right figure represents catches at Lake St. Clair. Data points from sites 3 and 4 were not included in calculation of dispersal parameters.

tion sizes we did not include these data points in our calculations of dispersal distance or recruitment area.

Total numbers of hydropsychid caddisflies in traps declined with increasing distance from the shore (Fig. 2). The pattern of decline was best approximated by a log–log² model (\ln number of animals v (\ln distance)²; replicated linear regression, $R^2 = 0.78$). Regression analysis of log-transformed data against distance explained a lower proportion of the variation in numbers of animals ($R^2 = 0.68$). The better fit obtained with the log–log² transformation suggests that total numbers of animals declined more rapidly with distance from the shoreline to 1250 m inland than a simple exponential model (implying random diffusion) would predict.

Relative species composition of Detroit River hydropsychid caddisflies varied with increasing distance from the river bank to 1000 m inland (Fig. 3), but was relatively constant from 1000 to 5000 m. *Cheumatopsyche campyla* was numerically dominant in all collections made along the Detroit River, constituting $\approx 70\%$ of total numbers of Hydropsychidae.

Three species (*Hydropsyche hageni*, *H. phalerata*, *Macrostemum zebratum*) exhibited inland maxima when means of standardized proportion of animals collected ($n = 3$) were plotted against distance from water (Fig. 4). *Cheumatopsyche campyla* and *C. speciosa* were most abundant at the riverbank, and numbers declined sharply with distance inland. Modal dispersal distances were consistent among collection dates for all

Table 2 Mean forewing dimensions (length, cm; area, cm²), body masses (g) and forewing loadings (g cm⁻²) of aquatic insect adults collected from the Detroit River and Lake St. Clair in August 1987. Standard errors are indicated in parentheses

Species	Wing length (n = 50)	Wing area (n = 50)	Body mass (n = 20)	Wing loading
<i>Cheumatopsyche speciosa</i>	0.585 (0.00280)	0.0606 (0.00120)	0.00456 (0.000270)	0.0752
<i>Cheumatopsyche campyla</i>	0.685 (0.00316)	0.0992 (0.00139)	0.00831 (0.000666)	0.0838
<i>Hydropsyche phalerata</i>	0.812 (0.00367)	0.1371 (0.00175)	0.01336 (0.000478)	0.0975
<i>Hydropsyche hageni</i>	1.091 (0.00610)	0.2548 (0.00368)	0.02652 (0.001495)	0.1041
<i>Macrostemum zebratum</i>	1.187 (0.00914)	0.3643 (0.00517)	0.03517 (0.002825)	0.0965
<i>Hexagenia</i>	2.046 (0.02890)	1.1871 (0.03059)	0.06465 (0.004070)	0.0545

caddisfly species. Both of the above patterns (inland maximum *v* riverbank maximum) were observed for *Hexagenia*, depending on the sampling date: consequently, replicates were grouped accordingly for the plots (Fig. 4). Of the total number of animals caught, only $1.63 \pm 0.623\%$ were captured at 5000 m inland during all studies, indicating that the trap distances chosen were appropriate for the dispersal abilities of the animals studied.

There was no interspecific overlap in size of any of the taxa collected (Table 2). The *Cheumatopsyche* species were the smallest caddisflies, and *Macrostemum* was larger than the *Hydropsyche* species. *Hexagenia* adults were much larger than the caddisflies but had the lowest wing loading. Wing loadings for the *Cheumatopsyche* species were lower than wing loadings of the other two hydroptychid genera.

Mean dispersal distance and distance travelled by 50 and 10% of animals are listed in Table 3, along with estimates of the area of recruitment for each species collected. A one-way ANOVA revealed significant differences among mean dispersal distances calculated for the taxa studied ($P < 0.05$). Congeners exhibited very similar dispersal distances (Fig. 5). Mean dispersal distance corresponded more closely with body size (forewing length or biomass) than with wing loading. Because the power of the test comparing dispersal distances among individual species was relatively low, only the difference between the taxa displaying the greatest and smallest dispersal dis-

tances was statistically significant: the mean dispersal distance of *Cheumatopsyche speciosa* was significantly shorter than that of *Hydropsyche phalerata* (Tukey's test (Tukey-Kramer method), $P < 0.05$; Fig. 5).

Plots of the proportion of females at each distance sampled (Fig. 6) showed a significant female bias at all distances for *C. campyla*, *H. hageni* and *H. phalerata* (replicated *G*-statistic goodness-of-fit test (RGGFT), $P < 0.005$). Sex ratios of *C. speciosa* were also significantly female-biased with the exception of traps located at 625 m inland, where a significant male bias was found (RGGFT, $P < 0.005$). *Hexagenia* exhibited balanced sex ratios with the exception of one site (78 m), where a significant male bias was detected (RGGFT, $P < 0.05$). Significant heterogeneity among sample dates with respect to sex ratio was observed for all species at nearly all distances (RGGFT, $P < 0.005$). Exceptions were *C. campyla* at the shoreline and at 78 m inland, *C. speciosa* at 2500 m inland, and *H. phalerata* at 78 m inland. In summary, inland distribution of male and female insects was non-uniform with respect to distance from shore for two of the taxa collected (*C. speciosa*, *Hexagenia*), but sex ratios varied considerably with time. Since *M. zebratum* was collected in adequate numbers for analysis only during a single collecting period, our sex ratio data are not reliable for this species.

Discussion

Our study demonstrated limited inland dispersal by adult aquatic insects. Most adult Hydroptychidae by total numbers ($84.6 \pm 5.4\%$, all species pooled; Fig. 2), and more than half of *Hexagenia* specimens ($56.5 \pm 11.1\%$) were collected in the two sets of light traps situated within 100 m of the water's edge. We suspect that exponentially declining, but still large numbers of insects would have been collected up to 350 m from shore had bushes and/or streetlights not been located near these more remote trap locations. Short distance dispersal might be apparent because a number of activities associated with reproduction (mating swarms, oviposition) occur near the water's edge. Furthermore, freshly emerged adults would add to shoreline catches. Additionally, increased trap visibility of shoreline light traps to insects upstream and downstream along the water's edge cannot be ruled out. Our results do not allow evaluation of the relative importance of these variables.

Table 3 Dispersal parameters (mean \pm 1 SE) of aquatic insects collected during the dispersal studies. D_{50} , D_{10} , A_{50} and A_{90} represent distances travelled by 50 and 10% of collected animals and likely source areas of 50 and 90% of animals collected in single, shoreline light traps, respectively

Species	<i>n</i>	Mean distance (m)	D_{50} (m)	D_{10} (m)	A_{50} (km ²)	A_{90} (km ²)
<i>Cheumatopsyche campyla</i>	3	670.3 (142.3)	502.0 (106.3)	1573.2 (334.2)	0.43 (0.19)	4.24 (1.81)
<i>Cheumatopsyche speciosa</i>	3	650.3 (227.1)	487.7 (169.6)	1527.0 (533.7)	0.47 (0.30)	4.56 (2.96)
<i>Hydropsyche phalerata</i>	3	1685.7 (329.2)	1470.4 (348.1)	3386.4 (572.2)	3.78 (1.65)	19.40 (5.95)
<i>Hydropsyche hageni</i>	3	1499.1 (267.4)	1180.3 (338.7)	3261.7 (337.4)	2.55 (1.39)	17.07 (3.63)
<i>Macrostemum zebratum</i>	1	1845.5	1557.6	3984.4	3.81	24.93
<i>Hexagenia</i>	4	1213.3 (192.5)	900.4 (199.5)	2778.6 (371.2)	1.46 (0.66)	12.78 (3.50)

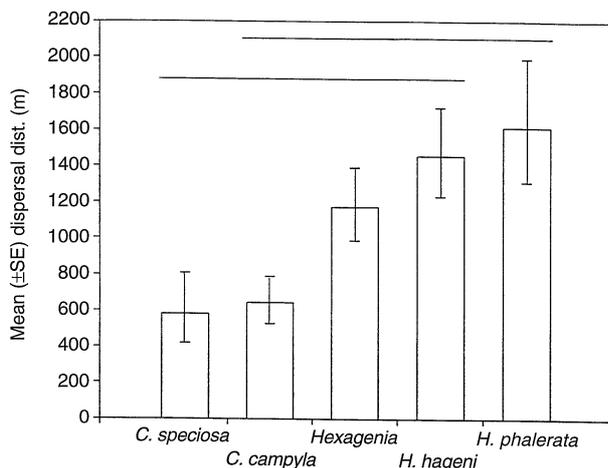


Fig. 5 Comparison of mean (geometric mean \pm 1 SE) dispersal distances of the four most abundant species of Detroit River Hydropsychidae and *Hexagenia*. Means not significantly different from one another are connected by horizontal bars ($P < 0.05$, Tukey's test).

Although most animals, even taxa displaying inland maxima, were captured at relatively short distances inland, numbers of adult *Hexagenia* (2–20 animals) and caddisflies (33–352 animals) caught in traps at 5 km inland suggest the potential for long-distance (> 5 km) dispersal by a small proportion of adults. Long-distance inland travel of mayfly and caddisfly adults by flight has not been studied directly. Although it has been suggested that the wings of some mayfly species that inhabit temporary habitats are adapted to utilize wind for long-distance dispersal (Corkum, 1987), mayflies and caddisflies have rarely been

observed flying at heights of 60–1525 m (Johnson, 1969), where wind may facilitate dispersal. Take-off is generally inhibited by high wind velocities (Johnson, 1969; Wolfenbarger, Cornell & Wolfenbarger, 1974). Thus, animals caught by light traps located at 5 km inland were probably displaced accidentally.

Inland distribution of adult caddisflies exhibited considerable interspecific variation. Maximum numbers of animals (modes) were observed both at the shore (*Cheumatopsyche campyla*, *C. speciosa*) and at some distance inland (*Hydropsyche phalerata*, *H. hageni*, *Macrostemum zebratum*). Freshly emerged female caddisflies frequently move inland following mating where they may rest until eggs mature (Ross, 1944). Following egg maturation, females return to the water to oviposit. Therefore, greatest densities might be expected either at the water's edge or some distance inland, depending on species-specific behaviour; inland maxima in numbers of animals caught may represent preferred resting places. In a study of caddisfly dispersal that used a similar study design to ours but shorter trap distances, J.C. Morse & J.D. Culin (Clemson University, unpublished) also found considerable interspecific variation in the location of peaks of caddisfly abundance, and suggested that inland distribution pattern may be species-specific.

In addition to insect flight behaviour, timing of emergence in relation to sampling periods may indirectly influence inland distribution. Since newly emerged animals tend to move inland (Ross, 1944), during times of little or no emergence animals already

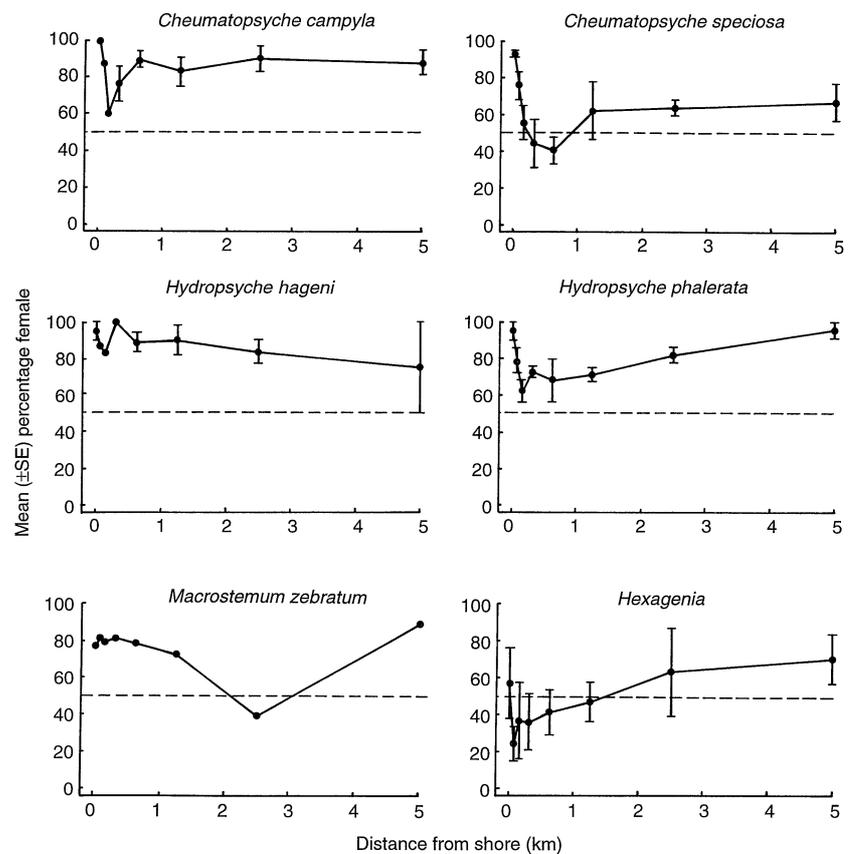


Fig. 6 Relationship between relative abundance of females (± 1 SE) and distance inland for five species of Hydropsychidae and *Hexagenia*. Dashed lines indicate even sex ratios.

inland will constitute the bulk of light trap samples. Thus, the observed differences in inland distribution may partially be a reflection of the timing of collections for those species that do not emerge continuously during the summer months (*Hydropsyche phalerata*, *Macrostemum zebratum*).

Inland distribution of *Hexagenia* was variable, exhibiting either inland or shoreline maxima, depending on sampling date. As noted above, the relative contribution of freshly emerged adults to light trap catches may explain much of the variation observed. On the evening with the largest catch of *Hexagenia* (1020 animals total, 13 July 1988), numbers of animals in light traps declined exponentially with distance inland. Sample sizes were considerably smaller (117–242 animals) on other occasions, and inland maxima were noted in numbers of animals. Sequential differences of up to 10 min in times of first arrival of insects among adjacent traps (Z.E. Kovats & J.J.H. Ciborowski, unpublished) also suggest that at least in some cases, captured mayflies were returning from inland locations to the lake.

Sex ratios of the caddisfly species collected were significantly female-biased at most sites and on most dates (Fig. 6). Our results are in agreement with those of J.C. Morse & J.D. Culin (unpublished), who also found female-biased sex ratios in light trap samples of caddisflies. The overall female bias may reflect actual larval sex ratios, or may be attributed to light trap selectivity towards adults of different sexes. Sex ratios of emerging adult caddisflies may be balanced (Corbet, Schmid & Augustin, 1966), or variable and species-specific (Singh, Smith & Harrison, 1984). Variable larval sex ratios have been observed for mayflies in running waters (Corkum, 1978, 1979). We do not know the sex ratios of larval populations in the waterbodies sampled during our study.

Greater attraction of females by UV light has been reported for *Hexagenia* mayfly adults (Hunt, 1953), suggesting that, at least for some aquatic insects, adults of different sexes may respond differently to UV light. No consistent male or female bias (or species-related bias, based on collections of males) was detected for *Hexagenia* adults captured in our traps.

As was observed for caddisflies, the proportion of females exhibited considerable variation with distance. Contrary to the findings of Hunt (1953), our mayfly samples exhibited nearly balanced sex ratios.

Our finding of different inland distribution patterns of males and females suggests that inland dispersal patterns of aquatic insects may vary with the sex of the animal. With the exception of the single replicate of *Macrostemum*, the proportion of females declined from the water's edge to 156 m or more inland for all taxa collected. This pattern was most pronounced for *Hexagenia* and *C. speciosa*, with significantly male-biased sex ratios 78 m and up to 625 m inland, respectively. Further inland, the proportion of females increased with distance, in most cases returning to values similar to those at the shoreline.

Assuming that the large-scale spatial patterns of insect activity were not greatly influenced by the local, temporary influence of our light traps, the above results suggest that male and female animals have different preferred areas of activity. One may expect male dispersal to maximize encounters with females. Males are capable of multiple matings. Caddisfly females mate immediately following emergence, and subsequently move inland to rest on vegetation until eggs mature (Ross, 1944). We interpret the distribution patterns as follows. Females emerge and immediately move inland, and are intercepted by males at some distance inland, where mating occurs. Thus, males may aggregate in specific locations that maximize chances of encountering receptive females. Mating is followed by continued inland movement by females to resting places, where vegetation may provide refuge from flying insectivores (birds, bats). Following egg maturation, females return to the water to oviposit. Upstream flight to oviposition sites may occur at this point.

Inland dispersal pattern of *Hexagenia* may be interpreted similarly (inland dispersal followed by return). However, in the case of mayflies, the period of sexual maturation includes an additional moult from subimago to imago (reproductively mature life history stage; Edmunds, Jensen & Berner, 1976), and mating occurs following return to the water's edge, immediately preceding oviposition. This general type of inland dispersal pattern corresponds to Johnson's (1969) definition of Class II migration (emigration and return by the same, relatively short-lived individuals within a season).

Svensson (1974) conducted a similar study of aquatic insect dispersal at a small south Swedish stream, and found relatively uniform sex ratios at all inland distances sampled. In analysing the stage of ovarian maturation of females of *Potamophylax cingulatus* (Steph.) caught in light traps at increasing distances from the stream, Svensson (1974) noted that females at different stages of ovarian development were trapped at different distances from the stream. Immature females and mature females that had oviposited were captured at the stream, while mature females with fully developed eggs were trapped at distances of 50–1000 m inland. Although Svensson's sex ratio data differ from findings of the present study, the same general pattern of inland dispersal related to mating strategy is likely. Therefore, inland dispersal by adults appears to be influenced by reproductive behaviour, as suggested by life history characteristics of adult aquatic insects.

In summary, our results suggest that inland dispersal by adults of large river species of aquatic insects is limited, as may be predicted, based on the insects' life cycle and habitat characteristics. However, the possibility for relatively long distance dispersal (> 5 km) exists for a small proportion of emerging adults, particularly mated females. We also found that inland distribution of males and females was different, and appeared to reflect species-specific reproductive behaviour.

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