

Oviposition Site Preference and Factors Influencing Egg Mass Characteristics of the Saw-Combed Fishfly (Megaloptera: Corydalidae) in Southern Maine

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Abstract

We surveyed microsite conditions in the oviposition location used by female saw-combed fishflies (*Nigronia serricornis*) to investigate the relationship between egg hatching success and egg mass features and oviposition site selection. Egg-laying females showed a significant tree species preference at two of three sites sampled. Leaves used as oviposition sites differed in length, width, area, and height among sites, but differences in oviposition site characteristics were attributable to stream habitat conditions, not preference. Egg hatching rates were very high (ca. 95%) and did not differ between streams. Egg mass size was significantly different among sites, but average egg size was not. Egg size was not correlated with egg mass size, but hatching rate was significantly correlated with egg mass size. Recruitment estimates ranged from <25 to >95 hatchlings per m². Although leaf height, leaf length, and stream site were significant in predicting egg mass size, females showed great plasticity in selection of oviposition sites and no correlations were found between hatching success and microsite conditions.

Introduction

The Corydalidae (Megaloptera), commonly called hellgrammites or fishflies, are rather long-lived holometabolous insects common in streams and ponds throughout Maine. Being holometabolous, they have egg, larva, pupa, and adult stages, but only the larvae are aquatic. All members of the family are predators as larvae and many live up to three years in an aquatic habitat before crawling out to pupate in shallow chambers dug in nearshore soil or rotting logs (Magan 1994, Evans and Neunzig 1996). In Maine, Corydalidae emerge throughout June and July (Tarter *et al.* 1977). Once adults emerge and mate, females lay eggs on structures over water (generally leaves, docks, or bridges) and newly hatched larvae simply fall into the water below. Thus, the selection of a good oviposition site would seem paramount to ensuring successful completion of the life cycle.

Recruitment via the birth of new individuals is a significant occurrence maintaining the viability of animal populations. Organisms invest considerable energy to insure that their eggs/young will survive (see Stearns 1992 for review). For organisms that lay eggs and provide no parental care, selection of favorable oviposition sites is critical (*e.g.*, Price 1974, Butler 1984). Similarly, the importance of selecting good egg-laying sites is considerable for semelparous organisms that are unable to lay repeated masses in a variety of locations (*e.g.*,

Calow 1973, Sibly and Calow 1986). The Corydalidae are excellent model organisms to examine oviposition site selection because they provide no parental care, they are semelparous, their egg masses are easily identified, and the life history of several species has been well-studied (e.g., Baker and Neuzig 1968, Petersen 1974, Mangan 1992 and 1994, Contreras-Ramos 1999). In particular, Mangan (1992) suggested the dobsonfly, *Corydalus cornutus*, exhibited plasticity in oviposition site selection, but that egg masses were significantly clumped on a small number of available sites on the Susquehanna River in Pennsylvania. In contrast, Canterbury and Neff (1980) reported that *Sialis* sp. of eastern North America showed no preference for any plant species as oviposition sites.

In this study, we investigated oviposition site selection and egg hatching rates in three populations of the saw-combed fishfly, *Nigronia serricornis* (Say) (Megaloptera: Corydalidae), in streams of southern Maine to further our understanding of the life history of this important macroinvertebrate predator. Egg hatching success is a relatively unstudied, but important, life history parameters necessary for understanding secondary production in aquatic organisms (e.g., Calow 1973, Lewin 1986) and may provide insights into aspects of macroinvertebrate community ecology. Our laboratory has been investigating the dynamics of a *N. serricornis*/midge commensal symbiosis (Pennuto 1997, 1998, 2000) and required more extensive knowledge of host populations. Our specific objectives were to: 1) quantify oviposition site characteristics and 2) investigate the relationships between oviposition sites, egg hatching rate, and egg mass characteristics.

Methods and Materials

We investigated oviposition site selection and hatching success at three streams in southern Maine (Table 1). A 100-m reach was surveyed at each stream for all *N. serricornis* egg masses. Fishflies lay their eggs in late May/early June and eggs begin hatching within two-three weeks. We constrained our sampling reaches to exclude any docks or bridges. For each egg mass, we identified tree species, height above the stream surface, leaf area, egg mass area, egg count, egg size, and percent hatching. Leaves with egg masses were identified prior to hatching and all leaves were collected after larvae emerged. Hatched eggs were empty and translucent in appearance whereas unhatched eggs were generally brown or yellowish and contained remains of larvae, which made estimates of hatching success easy. Counting egg cases after hatching reduced negative impacts we might have had on local fishfly populations.

Egg-mass collection began on June 30 and was completed by August 11, 1999. All trees with vegetation overhanging the stream were identified and the heights of their lowest leaves were estimated either by direct measurement with a meter tape or with a clinometer. Heights of leaf masses were estimated in a similar fashion. Leaf and egg mass dimensions were determined using a SummaSketch digitizing pad interfaced with a PC. Egg counts and estimates of hatching success were made under 10x magnification. To estimate the number of eggs per egg mass, we counted eggs in three random 0.25 cm² sections of each mass and multiplied the mean count by the mass area.

Table 1. Tree species presence and use by ovipositing *N. serricornis* from three streams in southern Maine.

Common name	Scientific name	Alden's Brook		Black Brook		Douglas Brook	
		No. Present	No. used	No. present	No. used	No. present	No. used
Eastern hemlock	<i>Tsuga canadensis</i>	14	0	1	0	28	0
Red maple	<i>Acer rubrum</i>	7	1	30	3	10	0
Striped maple	<i>A. pensylvanicum</i>	0	0	0	0	1	1
American elm	<i>Ulmus americana</i>	0	0	5	1	0	0
Slippery elm	<i>U. rubra</i>	0	0	0	0	1	1
Choke cherry	<i>Prunus virginiana</i>	0	0	1	0	0	0
Black cherry	<i>P. serotina</i>	1	0	0	0	0	0
White ash	<i>Fraxinus americana</i>	8	8	15	4	3	2
Beaked hazel	<i>Corylus rostrata</i>	0	0	4	0	0	0
Witchhazel	<i>Hamamelis virginiana</i>	0	0	0	0	4	0
American beech	<i>Fagus grandifolia</i>	2	0	6	0	5	5
Bigtooth aspen	<i>Populus grandidentata</i>	0	0	1	0	0	0
White oak	<i>Quercus alba</i>	0	0	2	0	0	0
Red oak	<i>Q. rubra</i>	1	1	0	0	0	0
Yellow birch	<i>Betula alleghaniensis</i>	12	0	1	0	10	3
Speckled alder	<i>Alnus incana rugosa</i>	1	0	0	0	0	0
Ironwood	<i>Ostrya virginiana</i>	1	0	0	0	0	0
Total no. trees		47	10	66	8	62	12
Total no. species		10	3	10	3	8	5

Oviposition height selection and tree species preference were examined using Chi-square goodness of fit tests with an alpha of 0.05. We examined site differences in egg mass characteristics and canopy conditions using ANOVA or Kruskal-Wallis procedures if no transformation brought the data into compliance with the normality and variance assumptions for ANOVA. Pearson product-moment correlations were used to investigate the relationship between egg hatching rate and oviposition site characteristics. Lastly, a multiple regression analysis was used to investigate whether oviposition site characteristics explained any variance in egg mass size. All analyses were performed using Statistix® 2.2 for Windows (Analytical Software, Tallahassee, FL).

Results

Riparian canopy conditions and oviposition preference

A total of 17 tree species occurred at the sites, but only seven were used as oviposition sites (Table 1). Stem density was lower at Alden's Brook than the other two sites and all sites were dominated by a few tree species. Birch (*Betula*

sp.) and eastern hemlock (*Tsuga canadensis*) represented 55% of the trees at Alden's Brook, ash (*Fraxinus* sp.) and maple (*Acer* sp.) comprised 68% of the trees at Black Brook, and hemlock, birch, and maple accounted for 77% of the trees at Douglas Brook. Female fishflies never oviposited on coniferous leaves, so these were excluded from subsequent analyses. Fishflies exhibited a tree species preference for oviposition at Alden's Brook and Douglas Brook (Table 2), using ash and beech, respectively, at frequencies greater than expected.

There was no significant difference in the mean minimum available canopy height of deciduous trees between sites ($F_{2, 117} = 1.75, p = 0.177$), but a significant site difference was observed in egg mass height (Table 3). Tree species differed in minimum canopy height among sites. At Alden's Brook, maple and ash provided the lowest canopy branches ($F_{4,29} = 5.23, p < 0.001$), whereas at Black Brook elm and maple were lowest ($F_{3,46} = 2.73, p = 0.054$), and at Douglas Brook birch and ash were the lowest available trees ($F_{4,30} = 3.63, p = 0.016$). Chi-square analyses suggested that fishflies oviposited at heights in proportion to their availability at each site (Table 2).

Table 2. Chi-square results determining whether *N. serricornis* egg masses are evenly distributed among the available deciduous tree species and lowest available leaf heights in a study reach. Eastern hemlock was excluded from analyses because its leaves are not large enough for oviposition sites and remaining species were combined such that $<20\%$ of expected frequencies ≤ 1 .

	Tree species			Canopy height		
	X ²	df	p	X ²	df	p
Alden's Brook	81.07	5	< 0.001	2.34	6	n.s.
Black Brook	3.71	6	n.s.	0.29	6	n.s.
Douglas Brook	57.15	5	< 0.001	11.17	7	n.s.

All measurements of leaf characteristics for leaves with egg masses were significantly different among sites (all ANOVA $p < 0.05$, Table 3), but not all contributed important information in explaining the variation in egg mass size. Although a three-variable regression model using leaf height, leaf length, and stream site was significant in predicting egg mass size ($F_{3, 80} = 5.40, p = 0.002$), it only explained 12% of the variation. Leaf area and leaf width were eliminated from consideration because of their high co-linearity with leaf length.

Egg mass characteristics

A total of 84 egg masses was sampled (Table 3) and all masses except one occurred singly on a leaf. However, some trees had more than one leaf with an

egg mass (range 0 to 5). There was a significant difference in the size of egg masses among sites ($F_{2,81} = 4.01$; $p = 0.022$; Figure 1), but no significant difference in the number of eggs per cm^2 ($H = 0.259$, $p = 0.878$), suggesting that egg size did not differ between streams. Similarly, there was no difference in hatching rate between site with over 95% of eggs hatching, and hatching rate did not correlate with any oviposition site characteristics (all $p < 0.05$). However, hatching rate was significantly correlated with egg mass size at Alden's Brook ($r = 0.575$, $df = 31$, $p < 0.01$) and Black Brook ($r = 0.651$, $df = 10$, $p < 0.05$), but not at Douglas Brook ($r = -0.011$, $df = 37$, $p > 0.05$). When pooled, there was a significant positive correlation (Figure 2). The number of fishflies hatched per mass differed significantly among sites, due to the difference in egg mass size (Table 3). Egg masses at Douglas Brook were the smallest, containing an average of 483 eggs per mass whereas egg masses at Black Brook were about 1.5x as large (mean = 766 eggs). The pooled mean number of eggs per mass was 573 (range = 51-1225, st. dev. = 294, $n = 84$), translating into recruitment estimates ranging from 25 to 99 hatchlings per m^2 (Table 3).

Table 3. *N. serricornis* egg mass characteristics from three streams sampled in southern Maine and results of tests for significant differences among sites. For all comparisons, ANOVA $df = 2, 81$.

	Alden's Brook	Black Brook	Douglas Brook	F	<i>p</i>
No. egg masses observed	33	12	39		
Mean height (m)	2.13	3.27	3.40	9.34	0.0002
Mean leaf width (cm)	7.3	8.3	6.1	5.02	0.009
Mean leaf length (cm)	14.1	10.7	11.8	7.39	0.001
Mean leaf area (cm^2)	7.3	6.6	5.2	3.37	0.039
Mean egg mass size (cm^2)	3.1	3.8	2.6	4.01	0.022
Mean no. eggs $\cdot \text{cm}^{-2}$	193.3	185.3	192.5	0.275	n.s.
Percent hatch	97.4	98.2	96.5	1.75	n.s.
Mean no. hatch $\cdot \text{mass}^{-1}$	597.0	823.8	467.3	7.12 ^a	0.028
Recruitment estimate (no. hatch $\cdot \text{m}^{-2}$)	98.5	24.7	36.4		
> 1 YR old nymph density (no. $\cdot \text{m}^{-2}$)	1.0	1.8	5.8		
Mortality estimate in YR 1 (%)	98.9	92.7	84.1		

^a Kruskal-Wallis one-way ANOVA used as no transformation alleviated variance heterogeneity or lack of normality.

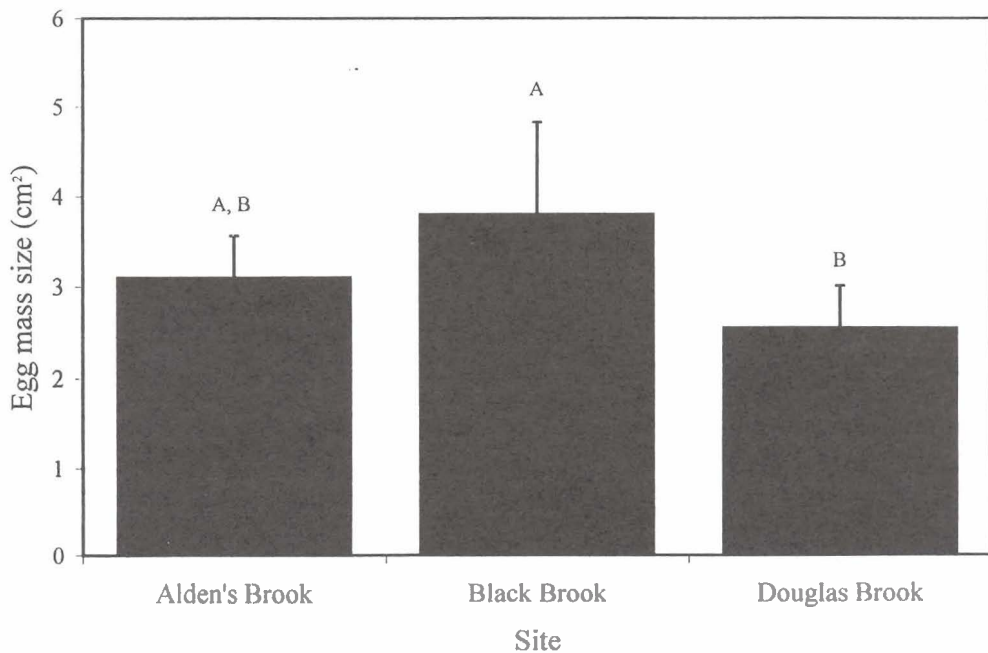


Figure 1. Mean (+ 95% C.I.) egg mass size of the fishfly, *N. serricornis*, at three stream sites in southern Maine. Similar letters indicate no significant difference.

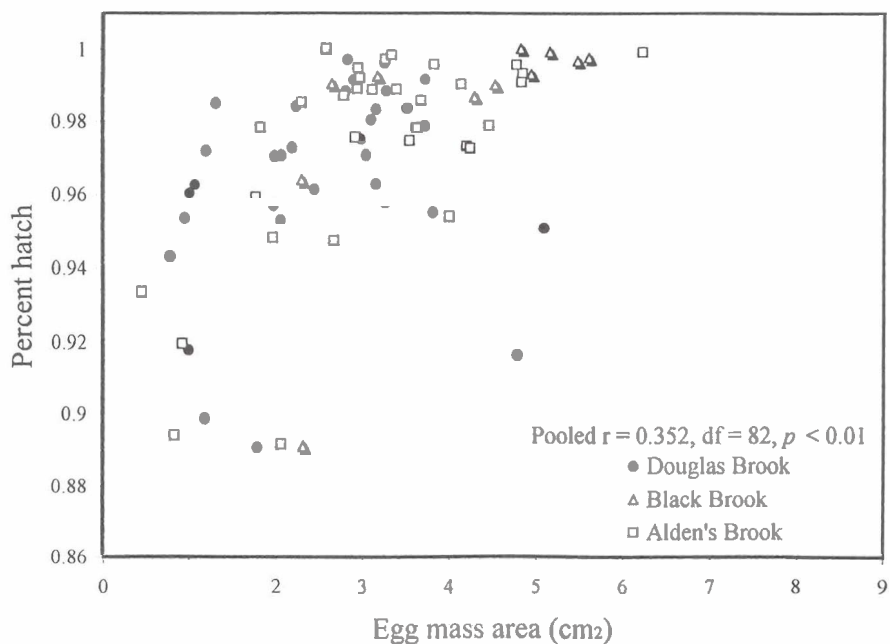


Figure 2. Relationship between egg mass size and egg hatching rate at three stream sites in southern Maine.

Discussion

Female fishflies exhibited significant plasticity in oviposition site selection among the three stream sites sampled in this study. Although there were significant differences in all measured characteristics of oviposition sites, those differences probably represent site differences in the availability of oviposition habitat because fishflies used canopy heights in proportion to their frequency. These results are in agreement with observations of Mangan (1992) and Canterbury and Neff (1980) for related Corydalidae. Mangan also suggested that some sites were used more heavily than others as evidenced by a clumped distribution of egg masses. Although we did not measure spatial distribution *per se*, we observed multiple egg masses on a given tree on several occasions, which supports Mangan's interpretation.

It does not appear that oviposition sites were limiting because all egg masses except one occurred singly on leaves. We would expect to observe much higher egg mass densities if oviposition sites were limiting. The occurrence of all single egg masses suggests that female fishflies were either not numerous enough to require overlap in oviposition sites or that *N. serricornis* females somehow select unoccupied sites (or are deterred from occupied sites). Canterbury and Neff (1980) indicated that *Sialis* species tend to deposit all of their eggs at once, and Mangan (1992) observed *Corydalus cornutus* females laying a single egg mass unless disturbed. Further, the average number of eggs counted per egg mass was very close to that reported by Petersen (1974), suggesting that females were depositing all their eggs in one oviposition event. However, as we did not observe ovipositing females, we cannot rule out multiple egg masses by individuals. If females did lay a second or third egg mass, we would expect them to be laid in close proximity to the first, potentially inflating our results on tree species or leaf height preference.

The characteristics of oviposition microsites only explained about 17% of the variation in egg mass size, probably because condition factors inherent to female fishflies (*e.g.*, size or nutritional status) play a more important role. For example, Tarter *et al.* (1975) found a significant positive correlation between female fishfly size and number of eggs laid. Egg masses at Douglas Brook were the smallest among the sites, and egg masses were also most abundant at this site. Potentially, females oviposit fewer eggs as density of masses increases. Further investigations are warranted to determine whether ovipositing fishflies influence, either directly or indirectly, oviposition behavior of conspecifics.

Hatching rates at all sites were very high, generally in excess of 95% of eggs laid. Several reports suggest that egg predation by hemipterans, *Trichogramma* sp. (Hemiptera: Trichogrammatidae), can be extensive among Megaloptera (Needham and Betten 1901, Kimmins 1962, Prichard and Leischner 1973). In a study of *Chauliodes rastricornis* (Corydalidae), Needham and Betten (1901) reported 70% of the eggs observed were parasitized by *T. minutum*. Petersen (1974) also suggested that egg mass damage due to leaf-cutting or leaf-feeding insects might result in significant mortality to *N. serricornis* eggs. He documented nearly 50% of the egg masses at one sampling location in Michigan were consumed or destroyed by leaf harvesting activities. We observed one unidentified hemipteran

preying upon a single egg mass at Alden's Brook but found no other evidence of significant egg predation or parasitism.

None of the oviposition microsite features measured in this study correlated with egg hatching rates. However, there was an overall positive correlation between hatching rate and egg mass size. Although we believe *N. serricornis* females generally deposit a single egg mass, others have reported corydalids are capable of laying multiple egg masses but that subsequent masses are smaller in size (Petersen 1974, Tarter *et al.* 1977). Potentially, later eggs do not contain as large a food store as early eggs or fertilization of later eggs is incomplete, thus leading to a depression in the hatching rate of later eggs.

Recruitment of new individuals is critical for the maintenance of viable animal populations. We estimated recruitment rates of nearly 100 hatchlings per m² based on egg mass abundance, fecundity, and hatching rates. By coupling recruitment estimates with density estimates for larvae, we will be able to determine age-specific survival rates for these macroinvertebrate predators. For example, our benthic estimates of 2-yr old larvae (head capsule width > 3.0 mm) indicate that all sites experience >80% mortality in the first year (range 84 to 99%). Mortality rates of this magnitude are common among aquatic insects (*e.g.*, see refs in Benke 1984) and this knowledge can provide much insight into community ecology.

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