

Seasonal frequency and positioning of parasitic midges (Chironomidae) on *Pteronarcys biloba* nymphs (Plecoptera:Pteronarcyidae)

DONNA J. GIBERSON, ANDREW J. MACINNIS¹, AND MATTHEW BLANCHARD

Department of Biology, University of Prince Edward Island, 550 University Avenue, Charlottetown,
Prince Edward Island, Canada C1A 4P3

Abstract. Mature nymphs of *Pteronarcys biloba* collected from Catamaran Brook, New Brunswick, between October 1994 and October 1995, were hosts to high numbers of parasitic chironomid larvae [*Nanocladius* (*Plecopteracoluthus*) undescribed sp., nr. *branchicolus*]. *Nanocladius* (*P.*) sp. has a univoltine life cycle in Catamaran Brook, with emergence occurring nearly simultaneously with the stonefly host in late May and early June. The chironomid larva constructs a silken case on the stonefly nymphs and feeds on hemolymph by piercing the gill tissue or the intersegmental membranes. Stoneflies were collected from different habitat types in 4 stream reaches from the headwaters to the mouth, and the position and number of attached chironomids was recorded for each nymph. The frequency and density of parasitic chironomids was not related to habitat type, but was related to reach; significantly more larvae/host were found in mid-catchment reaches than at the headwaters or mouth ($p < 0.05$). No parasitized stoneflies were found in the headwater reach, but between 80 and 100% of mature stonefly nymphs collected from the mid-catchment and mouth reaches were parasitized. Mean chironomid densities ($\bar{x} \pm 1$ SE) were 6.7 ± 0.4 chironomids/mature host in the fall of 1994 and 3.5 ± 0.44 in the summer and fall of 1995. Both frequency and density of chironomids were highest on the oldest stonefly age class present; younger stoneflies were also parasitized, but at significantly lower levels. Larval positioning on stoneflies differed with age of larvae; early instar chironomids attached mainly to the thoracic pleura, just under the wingpads, but most migrated to femora by early fall (September), and overwintered on the femora.

Key words: Diptera, parasitic chironomids, *Nanocladius* (*Plecopteracoluthus*), stoneflies, *Pteronarcys biloba*, New Brunswick stream.

Chironomids have been reported in associations with many aquatic insect orders including Plecoptera, Ephemeroptera, Trichoptera, Odonata, and Megaloptera (e.g., Corbet 1961, Steffan 1965, 1967a, 1967b, White et al. 1980, Dosedall et al. 1986, de la Rosa 1992, Jacobsen 1993, Epler and de la Rosa 1995). In the Plecoptera, most reports have been confined to the Perlidae (Steffan 1965, 1967b, Dosedall and Mason 1981) and some species of *Pteronarcys* (Pteronarcyidae; Dosedall et al. 1986, R.E. Jacobsen, University of Pittsburgh, personal communication). Associations may range from simple phoresy (a symbiotic relationship where an organism uses its host as a means of transportation; de la Torre-Bueno 1978) to parasitism (feeding on the host hemolymph; Steffan 1967a, Jacobsen 1993). Parasitic relationships may be identified by the presence of feeding scars on the hosts and by the lack of sediment or detritus in the guts of

the midges (Jacobsen 1993). Phoretic associations are often facultative (midges found free-living as well as in association; de la Rosa 1992), but parasitic associations tend to be obligate, with the life cycle of the parasite closely tuned to the host (Jacobsen 1993).

High numbers of attached chironomid larvae were noted on *Pteronarcys biloba* nymphs in Catamaran Brook, New Brunswick during surveys in the fall of 1993. Little is known about the relationships of chironomids and their aquatic insect hosts other than the frequencies of occurrence and the identities of the species involved; information on habitat preferences, especially relative to the host, seasonality, and on mechanisms of colonization is generally lacking. However, substrate and food availability, predation, competition, and evolutionary history are all thought to influence symbiotic associations (Steffan 1967b, Svensson 1976, Gotceitas and Mackay 1980, Jacobsen 1993). The objective of this study was to determine the nature of the symbiotic association and to document the density, frequency, and positioning of attached chi-

¹ Present address: Department of Biological Sciences, University of Windsor, Windsor, Ontario, Canada N9B 3P4.

ronomids on their stonefly hosts over a 1-y period.

Study Site

Catamaran Brook is a 3rd-order tributary of the Little Southwest Miramichi River in central New Brunswick, Canada (see Cunjak et al. 1990, 1993 for detailed habitat descriptions). The brook drains an area of 52 km² and has a total length of 20.5 km. Four reaches were chosen for study in the stream: the Upper Reach (headwaters), the Middle Reach (half-way down the length of the stream), the Gorge Reach (just downstream of the Middle), and the Lower Reach (at the mouth).

The Upper Reach had relatively high gradient, cobble-boulder substrate, and a stream width of only 1–2 m. The Middle and Lower Reaches were similar with respect to substrate and stream gradients; both reaches had relatively low gradient and primarily gravel/cobble substrates (with some boulder). Stream width varied from 4–5 m wide in the Middle Reach to 7–12 m wide in the Lower Reach. The Gorge Reach was a high gradient bedrock-controlled reach located between the Middle and Lower Reaches; substrates consisted mainly of bedrock outcrops, and stream width was 5–8 m. Riparian vegetation in all reaches consisted of alder near the brook, with a mixed forest of maple, pine, birch, balsam fir, cedar and spruce along the banks.

Replicated sites representing 4 habitat types were identified in each reach, consisting of 2 of each of the following: Riffle (characterized by shallow depths, fast water flow, a broken water surface, and large, heterogeneous substrate), Run (with deeper, slower water flow than the riffles, an unbroken water surface, and somewhat smaller substrates), Flat (slow but measurable water flow, an unbroken and glassy water surface, generally small sized and more homogeneous substrate than either the riffles or runs), and Pool (deep, depositional regions with zero or very slow flow, and silt-covered substrates).

Methods

Pteronarcys biloba nymphs were sampled from all sites in late October 1994, and every 2 wk from 18 May to 10 October 1995, by field-sorting leaf packs collected using a D-ring kick net with

a 200- μ m mesh. In October 1994, mature stoneflies were also picked off the barrier net and apron seine following electrofishing surveys to monitor fish populations. Stonefly nymphs were identified to species using the keys of Claassen (1931) and Smith (1917). Adult stoneflies were reared in the laboratory and confirmed as *P. biloba* using the keys of Hitchcock (1974). Identification of chironomid larvae and instar separation was done first by Bohdan Bilyj (BIOTAX Inc., Toronto, Ontario), then confirmed from lab-reared specimens (larvae, pupae, pre-pupae, and adults) by R.E. Jacobsen (Dept. of Biological Sciences, University of Pittsburgh), who is currently preparing a description of the species.

Total length (excluding antennae and cerci), head capsule width, and wing pad lengths of stonefly nymphs were measured using an ocular micrometer in a stereoscopic microscope and used to group the stoneflies into age classes. Number, position, and size of attached chironomids on stonefly hosts was recorded for each site and sample date. The total number of chironomids per late-instar host was statistically compared for Riffle and Run habitats only, for the Lower, Gorge and Middle Reaches, because stoneflies were too rare to provide a statistical sample in the other sites or reaches (i.e., Pools, Flats, Upper Reach sites). Comparisons were made among different habitat types and reaches on given sample dates, then for dates and reaches using a 2-way ANOVA.

Results

Life histories

We collected 465 *Pteronarcys* nymphs, all of which were *P. biloba*. Three separate stonefly cohorts were differentiated on most sample dates according to body length, head capsule width, and wing pad length, suggesting a 3-y life cycle. However, the field-sorting technique did not adequately sample very small nymphs, and a 4th cohort may have been present. Emergence of *P. biloba* occurred in mid to late June in 1994 and from early to mid June in 1995; no mature stonefly nymphs were found in the 13 June sample in 1995.

Only 1 species of midge [*Nanocladius* (*Plecoptera*) sp.] was found in association with *P. biloba*. All midge larvae collected in October and May were in the 4th instar, showing that

this instar is the overwintering stage. Prepupae were first noted in mid May, when numbers of chironomids per host were declining, and no midges were seen on any size of *Pteronarcys* nymph on the mid-June sample, suggesting that they emerged nearly simultaneously with their hosts in early June. Second-instar larvae were noted in small numbers in late June, and most larvae were in the 3rd instar by the end of July. Examination of gut contents of attached *Nanocladius* larvae collected throughout the season (R.E. Jacobsen, personal communication) revealed full guts with little sediment or detritus, suggesting that they were feeding parasitically on the stoneflies. In addition, feeding scars were noted on the gills (Fig. 1A) and thoracic intersegmental membranes of all stonefly hosts.

Density and frequency of midges

Chironomid density on *P. biloba* was dependent upon stream reach and sample date (Fig. 2, 2-way ANOVA, $p < 0.05$), but not on habitat. Midge density was generally lower on stoneflies collected from the Lower Reach than in the Middle and Gorge Reaches (Fig. 2), although stonefly densities were similar in all 3 reaches. Very few stoneflies were collected from the Upper Reach, and none of these carried parasitic chironomids. Chironomid densities (averaged over the entire sampling period) were highest in the Middle Reach, followed by the Gorge Reach and the Lower Reach. The parasite load was more than twice as high in fall 1994 than for the same period during 1995 (Fig. 2). No significant differences were found in numbers of attached chironomids among stoneflies collected from Riffle and Run habitats (ANOVA, $p > 0.05$); and although nymphs collected from Pools and Flats were too few for statistical analysis, they carried numbers of chironomids similar to those on stoneflies from Riffles and Runs.

Density and frequency of chironomids on host stoneflies were strongly dependent upon the age and size of the host. A comparison of chironomid density and frequency on the 2 largest stonefly size classes present on each sampling date showed that 80–100% of the largest stoneflies carried chironomid parasites for most of the year (Fig. 3A). In contrast, less than 40% of the next stonefly size-class had attached chironomids on summer sampling dates, and densities were considerably lower than on the larg-

est size class (Fig. 3B). No chironomids were found on stoneflies that were <12 mm in length. Seasonally, frequency of occurrence was highest in fall and early spring, with nearly 100% of mature nymphs and 75–100% of the next age-class carrying parasites.

Positioning of chironomids on stonefly nymphs

The chironomids attached to the stoneflies by constructing silken cases (Fig. 1). The most common attachment sites were the femora and thoracic pleura, just under the wingpads or the prothoracic terga (Figs. 1, 4), although some larvae attached to the abdominal or thoracic sterna, coxae, bases of the gills, back of the head capsule, tarsi, and—on one occasion—at the base of an antenna. Early instar chironomids (in June and July) attached preferentially to the thorax, just under the meso- and meta-thoracic wingpads; but as they grew larger they migrated to the femora, so that by late September, the majority of chironomids were attached to the legs of their stonefly hosts (Fig. 4).

Discussion

Earlier studies of associations between chironomids and stoneflies have inferred phoretic relationships, with the chironomids attaching to the stoneflies and feeding on detritus rather than directly on the host (Steffan 1965, 1967a and b, Dossdall and Mason 1981, Dossdall et al. 1986). The lack of sediment and detritus in the guts of the attached chironomids in this study, and the presence of feeding scars on the stoneflies, strongly suggest that *Nanocladius* (*Plecopteracoluthus*) sp. larvae are parasitic on *P. biloba*. The chironomid is believed to be the same species as one that is parasitic on nymphs of *P. proteus* and *P. scotti* in Maryland and Pennsylvania, feeding primarily on hemolymph obtained by piercing the gills (R.E. Jacobsen, personal communication).

Nanocladius (*Plecopteracoluthus*) sp. is univoltine in Catamaran Brook. Chironomids apparently emerged around the end of May in 1995, slightly in advance of the emergence period of the stonefly host, which occurred from the end of May to the first week or so of June. By mid-July, most of the older *P. biloba* were parasitized, and chironomid larvae grew steadily through the summer and fall, to overwinter as 4th-instar

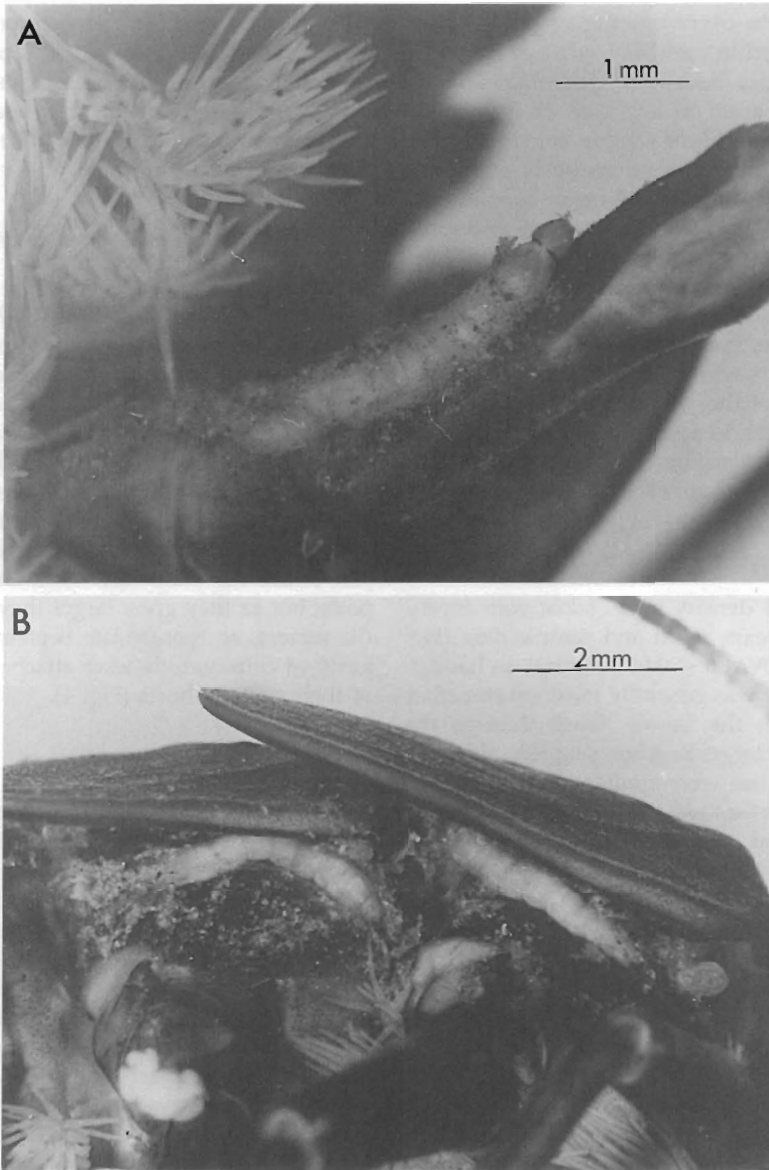


FIG. 1. *Pteronarcys biloba* nymph showing attachment sites of *Nanocladius* (*P.*) sp. larvae. A.—Ventral view; attachment along the meta-femur (metasternum is at the bottom left of the picture, and chironomid head is pointing toward the tibia). Note the feeding scars (dark spots) on the tips of the gills. B.—Lateral view, showing attachment under the mesothoracic and metathoracic wingpads (prothorax is to the right of the picture).

larvae. In Maryland, this species is bivoltine on *Pteronarcys proteus*, with emergence in May and August (R.E. Jacobsen, personal communication). Chironomids parasitizing mayflies attach to their hosts as early instar larvae and remain until emergence, which is timed to coincide with the emergence of the hosts (Jacobsen 1993); this

pattern is similar to that seen for the stoneflies in our study.

Pteronarcys biloba probably has a 3-y life cycle in Catamaran Brook, because 3 size classes of stonefly nymphs were present on any sampling date. Most studies of *Pteronarcys* populations suggest 2–4-y life cycles (Stewart and Stark

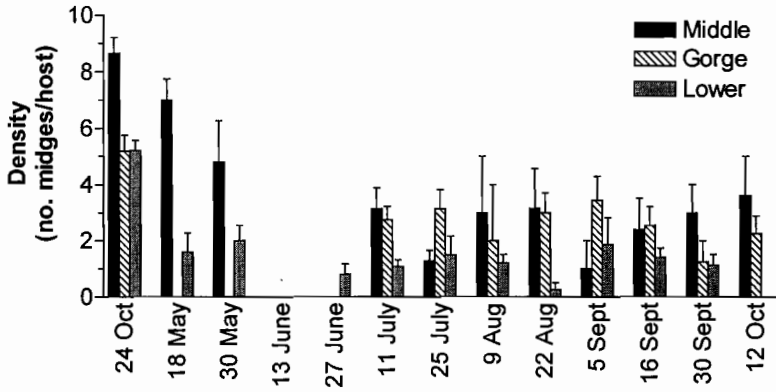
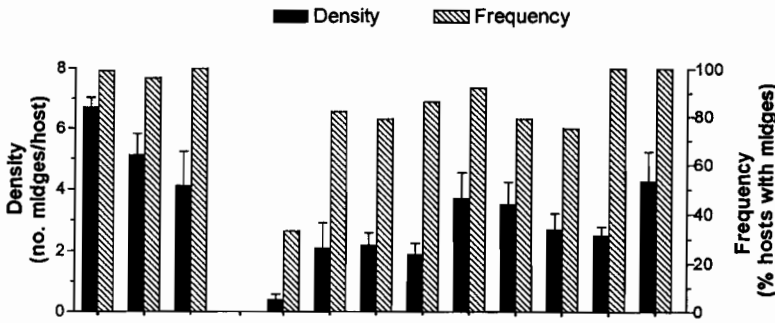


FIG. 2. Mean (\pm SE) numbers of *Nanocladius* (*P.*) sp. larvae per *Pteronarcys* host (>12 mm length) in Middle, Gorge, and Lower Reaches of Catamaran Brook, October 1994 to October 1995. Note: high discharge prevented sampling in the Gorge Reach on 18 May and 30 May.

A - Oldest Cohort



B - Middle Cohort

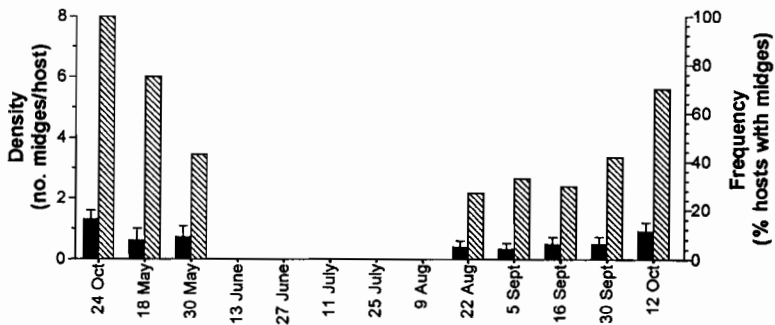


FIG. 3. Chironomid density (mean no. per host \pm SE) and frequency of parasitism (% of hosts carrying chironomids) for the 2 oldest cohorts of *P. biloba* nymphs on any sampling date in Catamaran Brook, October 1994 to October 1995. A.—Oldest cohort (those collected October 1994 to May 1995 emerged June 1995; the remainder emerged June 1996). B.—Middle cohort (those collected October 1994 to May 1995 emerged June 1996; the remainder emerged June 1997). Note: no chironomids were found on the youngest stonefly cohort, and nymphs were collected on all sampling dates; zero values indicate times when no chironomids were found associated with a particular size-class of stonefly.

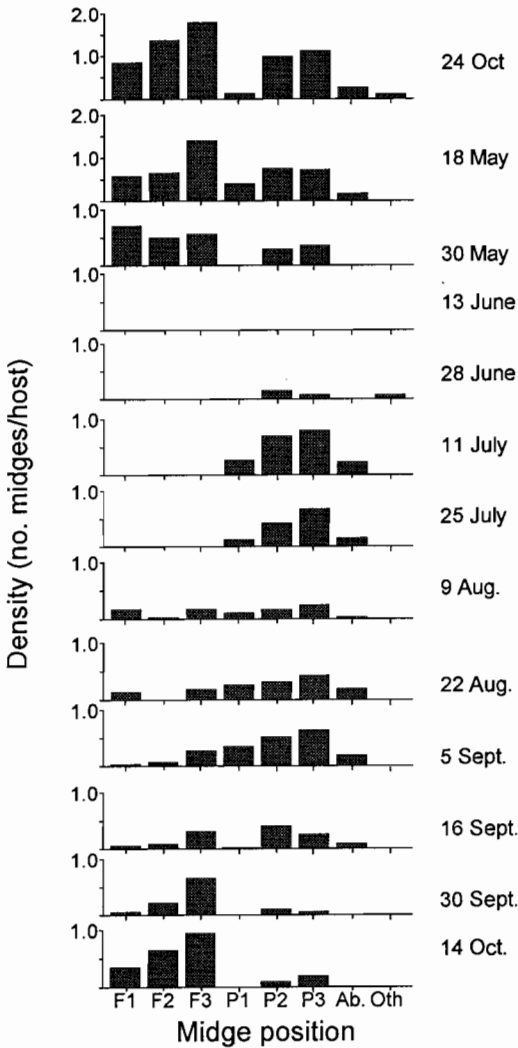


FIG. 4. Seasonal patterns in positioning of *Nanocladius* (*P.*) sp. larvae on *Pteronarcys biloba* from Catamaran Brook, October 1994 to October 1995. Key: F1 = prothoracic femur; F2 = mesothoracic femur; F3 = metathoracic femur; P1 = prothoracic pleuron; P2 = mesothoracic pleuron (under wingpad); P3 = metathoracic pleuron (under wingpad), Ab = first or second abdominal sternum, Oth. = other. Note that midges emerged in early June, were first noted as 2nd-instar larvae on 28 June, and grew to 4th instar by mid to late September.

1993). *Nanocladius* (*P.*) sp. preferentially attached to the oldest size class (2-y-old nymphs) of *P. biloba* present in the brook in the early summer following oviposition, and did not attach to younger nymphs (1-y old) until late August.

This pattern could relate to the size of the stonefly nymphs at that time; nymphs <12 mm long never carried chironomid parasites, and only the 2-y-old nymphs were >12 mm at the time that early instar chironomids were present. By late August, some 1-y-old nymphs reached 12 mm in length and began to show some parasitism, but always at a lower level than the older nymphs. This suggests that some of the older chironomid larvae may become displaced from their hosts and reattach to other suitable hosts, or that some may migrate from one host to another during development. An important result of this pattern, however, is that the stonefly hosts may spend most of their lives with no, or relatively low, parasitism levels, even where the parasite load for later instars is high.

The most commonly reported attachment sites for chironomids on aquatic insect hosts are the wingpads and thoracic sterna (Benedict and Fisher 1972, Dosdall and Mason 1981, Dosdall et al. 1986) although Steffan (1967b) and Dosdall and Mason (1981) reported phoretic chironomids on the tibiae of perlid stoneflies. In our study, early instar chironomid larvae attached preferentially to thoracic pleura, mainly under the meso- and metathoracic wing pads, but by early autumn, they began to migrate to the femora of the stoneflies. Steffan (1967b) and Bottorff and Knight (1987) also reported differential attachment sites of older and younger larvae of *N. (P.) downesi* on *Acroneuria* (Perlidae) nymphs, although in that case, the larvae moved from positions around the cerci and tibiae to the surface of the wingpads. Positioning on the thoracic pleura would give larvae easy access to the gills and intersegmental membranes for feeding, but attachment to the femora, especially in the fall, often resulted in the heads pointing away from the soft gill tissue. It is possible that the femurs provide a more favourable attachment site for overwintering, perhaps in a diapause or non-feeding stage. Results of laboratory rearing (Giberson, unpublished data) support the possibility of a diapause stage for the midges, because fall-collected chironomids showed little or no development after 8 wk at 20°C in lab aquaria, although stoneflies began emerging after 4 wk.

Steffan (1967a) and Corbet (1961) have suggested that ectosymbiotic associations in aquatic insects resulted from the need for protection from drifting or damage in fast-flowing, unstable watercourses. A host insect is thought to

represent a more stable substrate and decreases a chironomid's risk of being dislodged in fast flowing streams. Further, White et al. (1980) hypothesized that phoretic chironomids were more common in sand-bottomed streams where other hard substrates suitable for attachment are unavailable. Steffan (1965) and Jacobsen (1993) proposed that commensal and parasitic orthocladiine midges represent distinct and independently derived life strategies, with commensal forms evolving from herbivorous or detritivorous ancestors and parasitic forms arising from predacious forms. However, Jacobsen (1993) points to the discovery of parasitic species in genera that were previously believed to be entirely commensal as proof that some parasitic species may have evolved from commensals.

The reported frequency of symbiotic chironomids on their aquatic insect hosts is variable depending on the study and the host species involved. In some cases, nearly 100% of mature nymphs or larvae are occupied (Steffan 1967b, Hilsenhoff 1968, Benedict and Fisher 1972), whereas other studies report only a small percentage of hosts with attached chironomids (Dosdall et al. 1986, de al Rosa 1992). The number of chironomids found per host is also variable, but is generally low, with only one or two per host (e.g., Steffan 1967b, Gotceitas and Mackay 1980, White et al. 1980, Dosdall and Mason 1981, Dosdall et al. 1986). In Catamaran Brook, both the frequency and density of attached midges on stoneflies appears to be higher than in other studies of ectosymbiotic midges on stoneflies (e.g., Steffan 1967b, Dosdall et al. 1986, R.E. Jacobsen personal communication), although there was no shortage of stable substrates for natural attachment sites. In addition, there was no consistent pattern of abundance (number of chironomids per host) between slow and fast water habitats. The only density pattern that was noted was a reach effect; a higher level of parasitism was observed in the mid-catchment reaches (Middle and Gorge) than in the Lower Reach despite similar stonefly densities in the 3 reaches, and no consistent pattern was found between density and reach stability.

Although we present data on the presence and distribution of parasitic midges on *Pteronarcys*, the ultimate effect of this interaction remains to be investigated. The relatively high chironomid load on the stonefly hosts (1 stonefly carried 17 chironomids, and many carried >10)

might be expected to have a detrimental effect on the performance or fitness of the host. Some mayflies (e.g., Ephemeroidea) also carry high parasitic chironomid loads and show visible feeding damage with no apparent effects on development or emergence, although Jacobsen (1993) suggested that there could be overall effects on fitness. Presence of attached chironomids did not appear to have impeded emergence of stonefly hosts in the lab, but studies of overall survivorship, growth, and fecundity are required to determine the impact of parasitism in this species. In particular, it would be interesting to compare parasitism effects on *Pteronarcys*, where the parasitism is confined to the latter part of the life cycle, with those on other insects that are parasitized for most or all of their life cycle.

Acknowledgements

This research was funded partly through an internal research grant to DG from the University of Prince Edward Island, and partly by grants from the Natural Sciences and Engineering Research Council of Canada. Rick Cunjak first pointed out the parasitized stoneflies, and Rick Cunjak, Ben Hoteling, Rick Doucett, and Peter Hardie helped collect stonefly nymphs on various sampling dates. Bohdan Bilyj initially identified the chironomids as an undescribed species of *Nanocladius* (*Plecoptera*:*coluthus*), and was extremely helpful in determining to whom the specimens should be sent for confirmation. Richard Jacobsen confirmed the identification and the parasitic feeding mode, and very generously shared information from his research in the south and central Appalachians. Rosemary Mackay, John Jackson, and two anonymous reviewers provided insightful and helpful comments on an earlier version of the manuscript. This is contribution No. 21 of the Catamaran Brook Habitat Research Project.

Literature Cited

- BENEDICT, P. R., AND G. T. FISHER. 1972. Commensalistic relationships between *Plecoptera*:*coluthus downesi* (Diptera:Chironomidae) and *Chauliodes pectinicornus* (Megaloptera:Corydalidae). *Annals of the Entomological Society of America* 65:109-111.
- BOTTORFF, R. L., AND A. W. KNIGHT. 1987. Ectosymbiosis between *Nanocladius downesi* (Diptera:Chironomidae) and *Acroneuria abnormis* (Plecoptera:

- Perlidae) in a Michigan stream, U.S.A. *Entomologica Generalis* 12:97-113.
- CLAASEN, P. W. 1931. Plecoptera nymphs of North America (north of Mexico). Charles C. Thomas Publisher. Springfield, Illinois.
- CORBET, P. S. 1961. The biological significance of the attachment of the immature stages of *Simulium* to mayflies and crabs. *Bulletin of Entomological Research* 52:695-699.
- CUNJAK, R. A., D. CAISSIE, AND N. EL-JABI. 1990. The Catamaran Brook habitat research project: description and general design of the study. Canadian Technical Report of Fisheries and Aquatic Sciences, 1751.
- CUNJAK, R. A., D. CAISSIE, N. EL-JABI, P. HARDIE, J. H. CONLON, T. L. POLLOCK, D. J. GIBERSON, AND S. KOMADINA-DOUTHWRIGHT. 1993. The Catamaran Brook (New Brunswick) habitat research project: biological, physical, and chemical conditions (1990-1992). Canadian Technical Report of Fisheries and Aquatic Sciences 1914.
- DE LA ROSA, C. 1992. Phoretic associations of Chironomidae (Diptera) on Corydalidae (Megaloptera) in northwestern Costa Rican streams. *Journal of the North American Benthological Society* 11: 316-323.
- DE LA TORRE-BUENO, J. R. 1978. A glossary of entomology. New York Entomological Society. New York.
- DOSDALL, L. M., AND P. G. MASON. 1981. A chironomid (*Nanocladius* (*Plecoptera*) *branchicolus*: Diptera) phoretic on a stonefly (*Acroneuria lycorias*: Plecoptera) in Saskatchewan. *Canadian Entomologist* 113:141-147.
- DOSDALL, L. M., P. G. MASON, AND D. M. LEHMKUHL. 1986. First records of phoretic Chironomidae (Diptera) associated with nymphs of *Pteronarcys dorsata* (Say) (Plecoptera:Pteronarcyidae). *Canadian Entomologist* 118:511-515.
- EPLER, J. H., AND C. L. DE LA ROSA. 1995. *Tempisquitoneura*, a new genus of Neotropical Orthocladiinae (Diptera:Chironomidae) symphoretic on *Corydalus* (Megaloptera:Corydalidae). *Journal of the North American Benthological Society* 14:50-60.
- GOTCEITAS, V., AND R. J. MACKAY. 1980. The phoretic association of *Nanocladius* (*Nanocladius*) *rectinervis* (Kieffer)(Diptera:Chironomidae) on *Nigronia serricornis* Say (Megaloptera:Corydalidae). *Canadian Journal of Zoology* 58:2260-2263.
- HILSENHOFF, W. L. 1968. Phoresy by *Plecoptera* *downesi* on larvae of *Nigronia serricornis*. *Annals of the Entomological Society of America* 61:1622-1623.
- HITCHCOCK, S. W. 1974. Guide to the insects of Connecticut. Part VII. The Plecoptera or stoneflies of Connecticut. *Bulletin of the State Geological and Natural History Survey of Connecticut* 107.
- JACOBSEN, R. E. 1993. Symbiotic associations between Chironomidae (Diptera) and Ephemeroptera. Pages 317-332 in L.D. Corkum and J. J. H. Ciborowski (editors). *Current directions in research on Ephemeroptera*. Canadian Scholars Press, Toronto.
- SMITH, L. W. 1917. Studies of North American Plecoptera (Pteronarcinae and Perlodini). *Transactions of the Entomological Society of America* 43: 433-489.
- STEFFAN, A. W. 1965. *Plecoptera* *downesi* gen. et sp. nov. (Diptera:Chironomidae), a species whose larvae live phoretically on larvae of Plecoptera. *Canadian Entomologist* 97:1323-1344.
- STEFFAN, A. W. 1967a. Ectosymbiosis in aquatic insects. Pages 207-289 in M. S. Henry (editor). *Symbiosis*. Volume 2. Academic Press, New York.
- STEFFAN, A. W. 1967b. Larval phoresis of Chironomidae on Perlidae. *Nature* 213:846-847.
- STEWART, K. W., AND B. P. STARK. 1993. Nymphs of North American stonefly genera (Plecoptera). University of North Texas Press, Denton.
- SVENSSON, B. 1976. The association between *Epoicladius ephemerae* Kieffer (Diptera:Chironomidae) and *Ephemera danica* Muller (Ephemeroptera). *Archiv fur Hydrobiologie* 77:22-36.
- WHITE, T. R., J. S. WEAVER, AND R. C. FOX. 1980. Phoretic relationships between Chironomidae (Diptera) and benthic macroinvertebrates. *Entomological News* 91:69-74.

Received: 15 March 1996

Accepted: 19 June 1996