

Persistence of *Dactylogyrus eucalius* (Monogenea: Dactylogyridae) on the Short-Lived Host *Culaea inconstans* (Pisces: Gasterosteiformes)

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ABSTRACT: The monogene *Dactylogyrus eucalius* Mizelle and Regensberger, 1945 and its ability to maintain a population from year to year on the annual fish *Culaea inconstans* Kirkland was examined in a small lake in central Ontario. Fish were sampled toward the end of their annual breeding season, at a time when the host population consisted of 2 cohorts, i.e., young-of-the-year (0+) and mature adults (1+). Prevalence of infection was 94%, with a mean intensity of 8.8 ± 9.6 ; neither measure varied significantly with host length or between cohorts ($P > 0.05$). At necropsy, parasites were characterized as juveniles that included postoncomiracidia (immature, with a ventrally directed haptor) as well as developing protandrous males (body with a near-complete haptor and with little or no pigmented vitellaria), or as adults (with testis, ovary, darkened vitellaria, and occasionally bearing a tanned egg). The proportion of juvenile to adult parasites differed significantly between cohorts ($P < 0.05$), with 0+ fish infected with a mixture of juveniles and adults, whereas 1+ fish had almost exclusively adult parasites. Since adult (1+) brook stickleback typically die after spawning, the increased frequency of juvenile parasites exploiting juvenile hosts may represent an evolutionary adaptation, maximizing the chances of parasites infecting hosts that will enter winter. It is suspected that 0+ fish can be infected in the nest within 2 wk of hatching and persist by effectively infecting new host recruits when they are sympatric with their parents.

Brook stickleback *C. inconstans* (Kirkland) is a gasterosteid, endemic to central North America, and is one of the region's smallest freshwater fishes, seldom exceeding 65 mm in length (Reisman and Cade, 1967). Summer populations typically consist of 2 cohorts including young-of-the-year (0+) and adults (1+) (Acere and Lindsey, 1986; Moodie, 1986). The fish grow rapidly during the first summer and reach sexual maturity the following spring. Spawning takes place midsummer, with males securing a territory, constructing a nest, and mating with several females. After spawning, the males tend to the eggs, guarding them and the newly hatched larvae (Scott and Crossman, 1973; Moodie and Moodie, 1996). Spawning, impaired by rising temperatures, ends around mid-July (Reisman and Cade, 1967; Moodie, 1986). Most adults die over the course of the breeding season or shortly thereafter, a fact that has led the brook stickleback to be considered an annual species (Acere and Lindsey, 1986; Moodie, 1986).

During a study of brook sticklebacks in Scott Lake, Ontario, the monogene *Dactylogyrus eucalius* Mizelle and Regensberger, 1945, was found infecting the gills. Infections of this host-specific parasite on brook stickleback are common throughout much of its North American range (Hoffman, 1999). The present study considers how this parasite persists on a fish, *C. inconstans*, with an annual life span.

Samples of brook stickleback from Scott Lake were collected on 16 and 17 July 2007, near the end of the spawning season of brook stickleback. Scott Lake is a small (28.9 ha) lake located in southwestern Algonquin Park (45°29'N, 78°44'W), with a maximum depth of 26 m. Under conditions of a scientific collection permit, discretion was shown in the number of fish collected from the spawning beds. The majority of fish were collected in traps, baited with bread, from shallow (1 m) spawning areas. The smallest fishes, <2 cm, were collected with butterfly nets while snorkeling near the shoreline. Both ripe and spent fishes were present in the collections and adults were observed guarding nests, facts that led us to believe that sampling took place toward the end of the spawning period. Dead adult fishes were also observed on the spawning grounds. The samples were returned live to the laboratory and necropsied, typically within 12 hr. The fish were killed by cervical cut, and the body surface, inner operculum, and gills were examined for monogenes. The gill arches were mounted in a temporary wet mount with a slightly compressed coverslip and examined microscopically. Samples of *D. eucalius* were categorized as juvenile, including postoncomiracidia (immature, with a ventrally directed haptor) and developing

protandrous males (body with near-complete haptor and with little or no pigmented vitellaria), or as adults (with testis, ovary, and darkened vitellaria, and often bearing an egg). The coverslip was removed from the slide and the parasites were placed into 1.5-ml eppendorfs containing 10% formalin and shaken vigorously to fix the parasites for appropriate microscopy. Prevalence and mean intensity of infection follow the definitions of Bush et al. (1997). A comparison of mean intensity between cohorts was done with the nonparametric Kruskal–Wallis test (Sokal and Rohlf, 1995), with confidence maintained at 95%. Host length frequency plots revealed the presence of 18 juveniles (0+) and 18 adults (1+) (Fig. 1).

Prevalence of *D. eucalius* was 94% (89% in the young-of-the-year fish [16 of 18] and 100% in the adults [18 of 18]). Mean intensity was 8.8 ± 9.6 , which was not significantly different between cohorts (Kruskal–Wallis test, $P > 0.05$) (Table I). The 2 cohorts differed in the proportion of juveniles and adults, with the young-of-the-year hosts carrying a summed parasite ratio of over 2:1 (adult:juvenile), while the adult hosts carried a summed parasite ratio of almost 44:1. Mean intensity of juvenile parasites was significantly higher on 0+ fish versus 1+ fish ($P = 0.009$). In contrast, mean intensity of adult parasites was significantly higher on 1+ fish versus 0+ fish ($P = 0.002$) (Table I).

Postoncomiracidia were found attached to the inner wall of the operculum and the flat surfaces of the gill arches. Protandrous males (Fig. 2) and adults (Fig. 3), however, were firmly embedded within an interlamellar space. There was no obvious gill pathology associated with infection.

The life cycle of *D. eucalius* is not known, but one can assume that it is similar to that of related species that infect the gills of temperate fishes (Prost, 1963; Cone and Burt, 1981, 1985). Eggs laid by the parasite will leave the host via the respiratory currents and sink. Short-lived, ciliated oncomiracidia will emerge and, when in contact with a

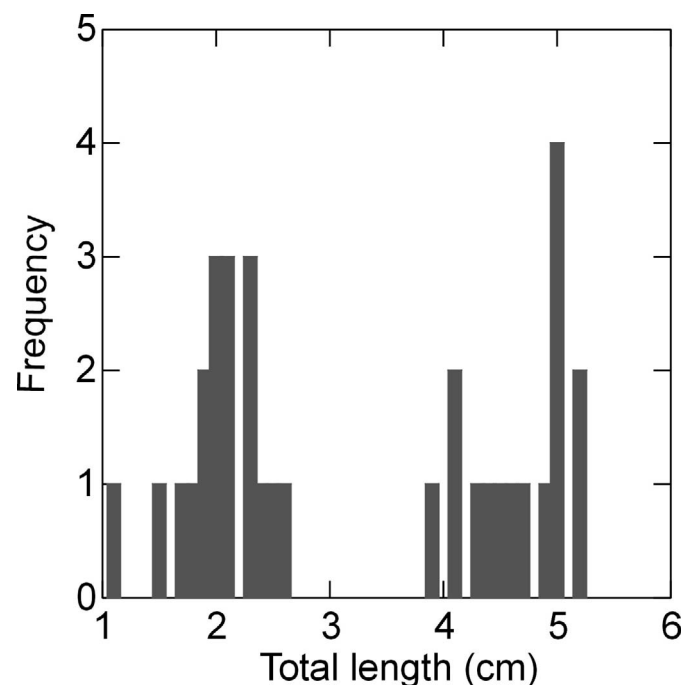


FIGURE 1. Length frequency plot for total length of 33 *C. inconstans* collected from Scott Lake, Algonquin Park, Ontario, 16 and 17 July 2007.

TABLE I. Summary statistics of host age, sample size, prevalence, mean intensity of juveniles and adults, and total mean intensity of *D. eucalius* parasitizing *C. inconstans* in Scott Lake, Algonquin Park, mid-July 2007.

Age	Sample size	Prevalence	Mean intensity juveniles	Mean intensity adults	Total mean intensity
0+	18	87 (16/18)	2.9 ± 1.4	4.2 ± 3.6	5.1 ± 4.3
1+	18	100 (18/18)	1.7 ± 0.6	12.3 ± 11.8	12.5 ± 11.9

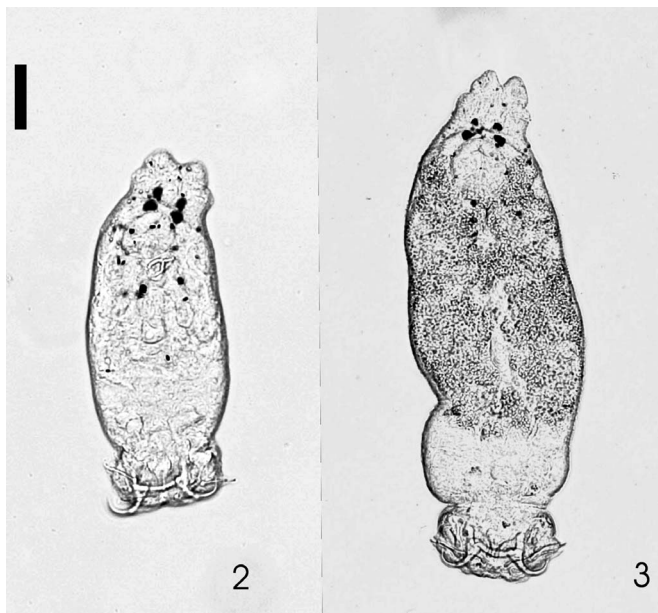
host, shed their cilia and subsequently migrate to the gills. During migration to the gills, the ventrally directed haptor is transformed into a complex structure suitable for attachment within an interlamellar space (Cone, 1979).

The present study reveals that *D. eucalius* persists on *C. inconstans* in Scott Lake by achieving almost complete success of transmission to new host recruits relatively early in the summer, during the spawning period, long before these fish enter their first winter of life. Part of this success must be related to a short prepatent period at summer water temperatures, which for related dactylogyrids is 6–10 days at or near 20 °C, with most species completing the entire life cycle in about 2 wk (Probst, 1963; Kollmann, 1972; Lambert, 1977; Imada and Muroga, 1978; Cone and Burt, 1981, 1985). If this holds true, *D. eucalius* in all likelihood can have several generations already completed by early summer. The overlap in habitat of the 2 cohorts during the extended spawning must also contribute to the success of *D. eucalius*.

We know that monogeneans do not infect fish eggs (Bakke et al., 2007); however, it is likely that new recruits may be infected shortly after hatching. After spawning, the male brook stickleback guards the nest from predators. As eggs hatch and the young start to wander away from the nest, the adult male collects the new recruits in his mouth and deposits them back into the safety of the nest (Winn, 1960). The male guarding behavior could give *D. eucalius* the opportunity to effectively infect newly hatched recruits. This guarding behavior maintains the presence of an infected host swimming over the nest and thus allows *D. eucalius* eggs to fall inside the nest. In all likelihood, young-of-the-year hosts hatch to waiting oncomiracidia.

The smallest fish (1.1–1.9 cm), and presumably the youngest, were caught schooling with cyprinids over the spawning beds. Based on growth data described for *C. inconstans* from a comparable habitat in Manitoba (Acere and Lindsey, 1986), the fishes that were <2 cm in length were probably <1 mo old. Our data show that these young fishes are already infected with adult parasites, which means they would have had to acquire infections at the latest within 2 wk of hatching. This further supports the idea that fish acquire infections near the nest. While studying 3-spined stickleback, *Gasterosteus aculeatus*, Chappell (1969) also surmised that ectoparasites must be transferred to the new 0+ cohort within a relatively short period based on the depletion of the 1+ cohort after spawning.

Given the abundance of *D. eucalius* at the study site, it is not immediately apparent why juvenile parasites were more abundant on young-of-the-year (0+) fish and relatively rare on the adult (1+). Studies on other monogeneans (Kearns, 1967; Cone and Burt, 1982) indicate that host specificity typically involves choice by oncomiracidia, which can discriminate between host species. If such discrimination extends to the level of the cohort, it has never been reported. The differential infection rates of juvenile and adult parasites begs the question: Are preferences in cohorts a factor in infection or do differences in host immune status come into play? Whichever the case, it is beneficial for *D. eucalius* to infect the 0+ cohort, since these fish have greater odds of surviving the winter and will allow parasite populations to be carried into the following spring. We suspect that *D. eucalius* has a seasonal cycle similar to that described for *Urocleidus adspersus* Mueller, 1936, on the gills of *Perca flavescens* in New Brunswick. This monogenean passes the winter as adults that resume laying eggs when water temperature rises in the spring, thus beginning a series of several summer generations (Cone and Burt, 1985). The situation is likely similar for *D. eucalius*, but more acute because the brook stickleback is an annual



FIGURES 2–3. Whole mounts of *D. eucalius* from the gills of *C. inconstans*. Scale bar = 20 µm and applies to both photomicrographs. (2) Juvenile with a developed male copulatory complex, fully developed haptor, but no pigmented vitellaria. (3) Adult with pigmented vitellaria, a male copulatory complex, and female ovary.

fish species, and transmission must occur sometime after the young-of-the-year hatch (0+), but before adults (1+) die.

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