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LIFE CYCLES OF LEUCTRA DUPLICATA AND OSTROCERCA PROLONGATA IN AN INTERMITTENT STREAMLET IN QUEBEC (PLECOPTERA: LEUCTRIDAE AND NEMOURIDAE)

P. P. Harper¹

ABSTRACT

Large populations of Ostrocerca prolongata and Leuctra duplicata developed in a small intermittent stream in the foothills of the Laurentian Highlands of Quebec. Both species were univoltine in 1974–1975. Ostrocerca prolongata started emerging in mid-to late May, followed by L. duplicata about 2 weeks later. The emergence periods lasted 3-4 weeks with similar patterns in both sexes. Ostrocerca prolongata laid its eggs before the stream dried up in early July, while L. duplicata oviposited just afterward. The eggs of both species did not hatch before October when flow had resumed; the prolonged incubation was due to a diapause in Ostrocerca, but to a depressed development rate in Leuctra. Nymphal growth continued through winter and accelerated considerably in May in both populations. Despite much overlap in timings of the life cycles and in size-frequency distributions of the nymphs, there appeared to be little competition between the two species, probably due to differing food habits.

Stoneflies (Plecoptera) are common inhabitants of headwater streams where they often develop into dense populations (Stewart and Stark 1988). Except when such streams are spring-fed and therefore offer relative stability, temperature and waterflow may vary considerably. Successful populations must therefore possess specialized traits in their cycle to allow them to colonize such marginal habitats.

The opportunity was taken to study the previously undescribed cycles of two species of stoneflies, *Leuctra duplicata* Claassen (Leuctridae) and Ostrocerca prolongata (Claassen) (Nemouridae), large populations of which inhabited a small intermittent stream in the Laurentian Highlands of Quebec. Emphasis was given to timing of adult emergence and nymphal growth.

STUDY SITE

The stream $(45^{\circ} 59' 40'' \text{ N}; 74^{\circ} 00' 17'' \text{ W})$ was situated on the Station de biologie (University of Montreal) at St. Hippolyte de Kilkenny, Terrebonne County (Quebec), about 75 km north of Montreal, in the foothills of the Laurentian Highlands, at an altitude of about 325 m.

The stream was very small and its width rarely exceeded 30 cm and its depth 10 cm. It arose in a small depression in a forested (second-growth mature white birch interspersed with young sugar maple) and hilly region where surface waters accumu-

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lated to form a boggy area of about 50 m in diameter. From there it flowed into Lac Croche, about 100 m away and 10 m below. Its flow was important in the spring due to snowmelt; however, by mid-July (13 July 1974; 4 July 1975) the stream had dried up and only damp substrate and occasional puddles remained. There was a heavy deposition of autumn-shed leaves on the bottom and the streambed was heavily shaded from mid-May to late September. Regular flow resumed in September-October. From early November to late April, snow accumulation was important (1-2 m) and flow was much reduced. Ice, however, did not form under the snow and water temperatures remained just above freezing. Water temperatures in May and June were generally less than or equal to 13° C, while most streams in the area, fed mainly from lakes and ponds, reached 25°C during this period. As the stream dried up, however, higher temperatures were recorded.

This stream is part of Ashby Creek drainage which has been described many times in the literature (Harper and Harper 1982, marked gc). The water was acidic (pH = 5.8-6.2), colored (80 Pt units), and soft (less than 30 mg CaCO₃/l).

MATERIALS AND METHODS

Adults were collected with a small emergence trap designed by Harper and Magnin (1971) and covering 0.25 m². It was emptied every 2-4 days, both in 1974 and 1975.

Nymphs were sampled approximately every month from April 1974 to June 1975 with a fine-meshed net (60μ mesh opening) using the "kick-sample" technique. This qualitative sample represented the relative composition of the population at a given date, but cannot be regarded as a measure of population density.

A few mature females were brought into the laboratory and allowed to oviposit in Petri dishes containing bottled water (Naya, Inc.) at approximately 15°C and simulated outdoor photoperiods. Their development was checked at irregular intervals, but not tallied in any quantitative manner.

RESULTS

Ostrocerca prolongata

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The emergence began on 30 May in 1974, about three weeks after the icemelt on Lac Croche (Fig. 1). Males appeared earlier than females, but the emergence patterns of both sexes were generally similar. The emergence period lasted about two weeks. In 1975, the emergence started on 23 May, a week earlier than the previous year, and it also extended into mid-June. The protandry was more pronounced. The density of emergence was 819 and 416 individuals / m^2 respectively in 1974 and 1975.

By the third week of June, the females collected in the field were all mature and ready to oviposit. The eggs were thus deposited while the stream was still flowing. Eggs incubated in the laboratory showed no sign of development during the first two months of incubation and were presumed to have entered diapause.

The first nymphs, many of them still hatchlings, were collected in mid-October (Fig. 2), which suggests the existence of an egg incubation of nearly 4 months. Despite the low temperatures, growth proceeded throughout the winter, though the rate declined, particularly in March. By the time snow melted in late April, the nymphs had a mean length of about 2 mm. Growth then accelerated considerably and within a month total lengths had more than doubled and the nymphs were ready to emerge. There was little or no size differences between the sexes.

The size-frequency distribution of nymphs observed in May 1974 was comparable with data in the spring of 1975, so the earlier emergence in 1975 was probably not

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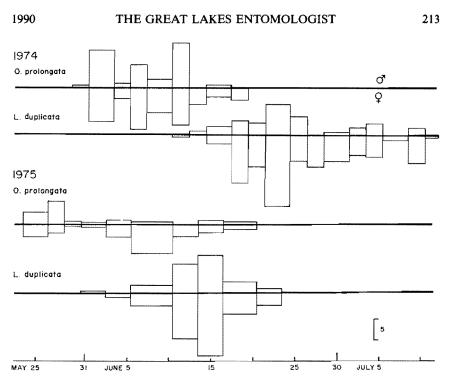


Figure 1. Emergence patterns (N/0,25 m^2/day) of adult Ostrocerca prolongata and Leuctra duplicata in 1974 and 1975. Males are illustrated on the upper graphs, and females on the lower graphs.

due to differences in the cycle between years, except in the last weeks of nymphal growth.

Leuctra duplicata

Adults started emerging about 10 days later than those of *O. prolongata* in 1974 (Fig. 1), but peak emergence did not occur before yet another week. The emergence period lasted about one month. In 1975, emergence began about a week earlier and lasted only three weeks. There appeared to have been little difference between the emergence times of males and females. Emergence density was 932 individuals / m^2 in 1974 and 1052 / m^2 in 1975.

By early July, females collected in the field were mature and oviposited readily in the laboratory. Such females were collected until late-July. Eggs were therefore deposited in the stream at about the time it dried up. Eggs kept in the laboratory did not undergo diapause, as in the preceding species, but developed directly, albeit very slowly. They did not start hatching before October. By contrast, eggs of *Leuctra tenuis* Pictet, an inhabitant of permanent streams, hatched within 3–4 weeks. These were collected at the same time and kept in the same conditions.

The first nymphs (n = 2) were collected in mid-October (Fig. 3), but they were not hatchlings; for some reason, these were not collected. In December, a more representative sample was secured and the mean length was 1.0-1.25 mm. Growth then proceeded through the winter, though there appeared to be a lull in March. It resumed and accelerated in April and May and by mid-June the nymphs were mature and ready to emerge.

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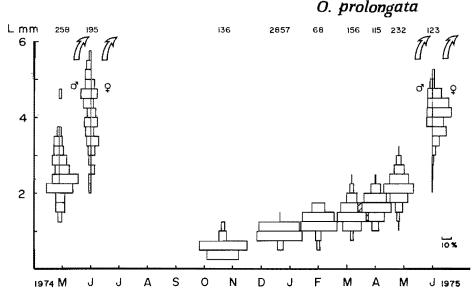


Figure 2. Growth pattern of nymphs of Ostrocerca prolongata in 1974–1975, based on relative distribution of size (total length, in 0.25 mm classes) frequencies. Sexes are separated in larger nymphs, males on the left, females on the right. Arrows indicate emergence times. Numbers on top row give sample size.

The samples in May 1974 and April 1975 had similar size distributions, but the June 1974 sample indicates an important delay in growth, which probably accounts for the later onset of the emergence.

DISCUSSION

The life-cycle strategies of these two species are very similar in many respects. Growth is concentrated in both the fall and spring seasons, when the probabilities of the stream being flooded are very high. Growth is especially important in late April and May when temperatures are rapidly increasing. The timing is probably only secondarily related to the presence of allochthonous leaf litter, which is abundant in this stream throughout the year. Nevertheless, such life cycles in stoneflies probably evolved originally as adaptations to the seasonal availability of detritus in the form of leaf litter.

The summer months bring an interruption in the flow of the stream and both species evade this hazard because nymphs are not present at that time. Although O. prolongata manages to lay its eggs before the stream actually dries up, L. duplicata probably has to oviposit on the damp substrate or in the puddles (no oviposition was observed in the field). The eggs of both species, as inferred from laboratory observations, did not hatch until October when flow had resumed. This delayed hatching is brought about in O. prolongata by a diapause (complete cessation of growth after minor initial development), and this is the common strategy in the Nemouridae in such situations. Diapausing eggs have been described in many genera, such as Amphinemura (Khoo 1964, Harper 1973), Prostoia (Radford and Hartland-Rowe

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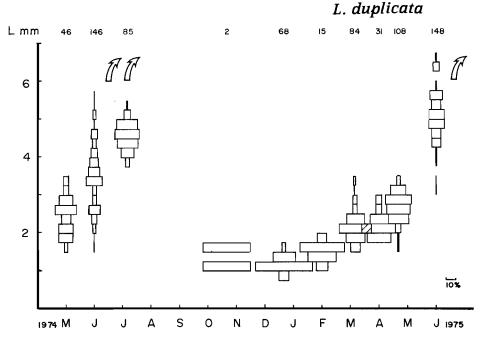


Figure 3. Growth pattern of nymphs of *Leuctra duplicata* in 1974-1975, based on relative distribution of size (total length, in 0.25 mm classes) frequencies. Arrows indicate emergence times. Numbers on top row give sample size.

1971, Harper 1973), *Protonemura* (Malicky 1982), and *Shipsa* (Harper 1973). The cycle of *O. prolongata* is very similar to that described for *Ostrocerca albidipennis* (Walker) from southern Quebec by Mackay (1969): the earliest nymphs were, however, collected only in December and no growth was reported from February to April. The growth patterns were nevertheless similar, with a maximum rate in April and May; the overwintering nymphs belonged to a larger size-class (3 mm) than is the case here.

In Leuctra duplicata, there is no evidence of an egg-diapause, but rather of a depressed developmental rate which extends the duration of the embryogenesis. Indeed, in all species of Leuctra whose life cycle has been studied until now, the development of the eggs is direct (Harper 1973, Lillehammer 1985, Elliott 1987) and it would seem that the mechanism of embryonic diapause may not be available in the family Leuctridae. The North African Tyrrhenoleuctra tangerina (Navas), which inhabits temporary streams, has no egg diapause, but has a nymphal diapause in its 6th instar (Berthélemy 1973). However, Berthelemy (1973) mentioned the existence of an egg diapause in an undescribed Leuctra ("sp. nov. A") from Tunisia and promised more details in a forthcoming paper, which never appeared; this was the only species among five he collected that colonized temporary streams is L. maria Hanson. Not surprisingly, it is a close relative of L. duplicata and can be expected to have a similar life-cycle.

Both species were affected by the lower temperatures in May 1974. Although ice on Lac Croche disappeared at the same time in both years (8 May 1974 and 10

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May 1975), stream temperatures were approximately 2-3°C lower throughout the later half of May in 1974 (9.5 vs 12°C). This lower temperature slowed growth much more in *L. duplicata* than in *O. prolongata*, probably because the former completed more of its growth later in May when conditions were less favorable, resulting in a delayed emergence.

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Both species achieved remarkable success and maintained very dense populations in this stream which supported no mayflies and only an occasional caddisfly. The two species did not seem to interfere with one another. Although the emergence and oviposition periods of the adults were separated in time, the eggs hatched at the same period and there was little difference in the size-frequency distributions of the nymphs until May. The species belong, however, to different families that differ in their general habitus, and presumably in their choice of microhabitat. Also, although both are detritus feeders, the Nemouridae are shredders of leaves, while the Leuctridae seem to feed on smaller particles (Merritt and Cummins 1984). This presumably minimizes competition between the two populations.

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