Life history and abundance of the predaceous psammophilous mayfly *Pseudiron centralis* McDunnough (Ephemeroptera: Heptageniidae)

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Aspects of the life history and abundance of *Pseudiron centralis* McDunnough were examined in the Sand River in east central Alberta. The population exhibited a univoltine summer life cycle, spending 9 to 10 months of the year in the egg stage. Eggs were large (0.33 × 0.41 mm; mean dry weight, 0.005 mg). Larvae were associated with three types of substrate in the river bed: shifting sand, marginal sand, and gravelly sand. Larvae were active epibenthic predators, feeding primarily on psammophilous chironomid larvae. Larval density was low (<4 larvae/m^2); however, larval mortality also appeared to be low. Stage III and IV larvae exhibited a random dispersion pattern. Annual production (instantaneous growth method) was estimated to be 28.70 and 11.24 mg$\cdot$m$^{-2}\cdot$year^{-1} in 1980 and 1981, respectively. The relatively large size of first-instar larvae may allow them to cope with the dynamics of sandy substrates, or may be the minimum size that can effectively capture and consume chironomid larvae. Although chironomid abundance in sandy substrates remains high throughout the year, *P. centralis* larvae exploit this resource for only a short period.

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Certain aspects du cycle biologique et de l'abondance ont fait l'objet d'une étude chez l'Ephéméroptère *Pseudiron centralis* McDunnough, dans la rivière Sand du centre est de l'Alberta. La population semble avoir un cycle univoltin qui se déroule durant l'été puisque l'espèce passe 9 à 10 mois de l'année au stade oeuf. Les oeufs sont de grande taille (0,33 × 0,41 mm; masse sèche moyenne 0,005 mg). Les larves sont associées à trois types de substrat: sable en déplacement, sable riparin et sable mêlé de gravier. Les larves sont des prédateurs épibenthiques actifs et se nourrissent surtout de larves de chironomides psammophiles. La densité des larves est faible (<4 larves/m^2), mais la mortalité larvaire semble faible également. Les larves des stades III et IV se dispersent au hasard. La production annuelle (calculée par la méthode de croissance instantanée) a été estimée à 28,70 mg$\cdot$m$^{-2}\cdot$an^{-1} en 1980 et à 11,24 mg$\cdot$m$^{-2}\cdot$an^{-1} en 1981. Les larves néonates ont une taille relativement grande et il est possible que cette caractéristique les aide à s'adapter à la dynamique des substrats sablonneux; il est possible aussi que ce soit là la taille minimale requise pour la capture efficace et la consommation de larves de chironomides. Bien que les larves de chironomides soient abondantes durant toute l'année dans les substrats sablonneux, les larves de *P. centralis* n'exploitent cette ressource que durant une courte période.

[Traduit par le journal]

Introduction

Sand is a dominant component in the bed of most large rivers. However, very little is known of the ecology of organisms and the nature of communities found in sandy habitats in large rivers.

Several species of Ephemeroptera are associated with the sandy substrates of large rivers. These species have been of interest to systematists because many exhibit aberrant morphologies. Behaviorally, the larvae of many of these species differ from most Ephemeroptera in being predaceous. One species (*Dolania americana* Edmunds and Traver) has been studied in detail (Tsui and Hubbard 1979; Harvey *et al.* 1980; Sweeney and Vannote 1982), but knowledge of most sand-dwelling mayflies is restricted to anecdotal comments by collectors. Knowledge of these species should contribute toward an increased understanding of important ecological processes in one of the dominant habitat types in the lower reaches of most river systems.

Pseudiron larvae are associated with sandy river beds in medium to large rivers over much of North America (Edmunds *et al.* 1976). The carnivorous behavior of larval *Pseudiron* was discussed by Edmunds *et al.* (1976). Tsui and Hubbard (1979) suggested that habitat partitioning may occur between *Pseudiron meridionalis* Traver and another predaceous mayfly, *Dolania americana* (*P. meridionalis* occupies the surface of the sand while *D. americana* burrows beneath it).

There are two described species of *Pseudiron*: *P. meridionalis* Traver occurs in the southeastern United States and *P. centralis* McDunnough is found in western and central North America (Edmunds *et al.* 1976). *Pseudiron centralis* is found in all major drainage systems in Alberta.

In this paper we examine aspects of the life history, abundance, and production of *P. centralis* in a medium-sized river in central Alberta, Canada.

Study site

The Sand River is located on the southern edge of the mixed boreal forest region in Alberta (Fig. 1) and drains approximately 5000 km^2 of largely forested land. It is the major tributary of the Beaver River system in Alberta and supplies approximately 75% of the total discharge. The Beaver River is a tributary of the Churchill River, which drains into Hudson Bay.

During the study, mean discharge of the Sand River was approximately 12 m$^3\cdot$s^{-1}, ranging from 1.5 to 42.9 m$^3\cdot$s^{-1} (Anonymous 1981; Environment Canada, Water Survey of Canada, unpublished data).

The bed of the Sand River is composed primarily of sand derived from the extensive deposits of this material found in northeastern Alberta. In the mainstream channel, sand forms moving dunes 6–15 cm in height, which usually are riding on larger dunes with very long wavelengths and heights of over 50 cm. Gravel bars occur at irregular intervals in the bed and there is a narrow (<1.0 m) marginal band of silty deposits.

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FIG. 1. Aerial view of the mouth of the Sand River (A, Sand River; B, Beaver River). Study area lies between the two arrows. Insert indicates location in Alberta.

The study area (54°23′ N, 111°02′ W) was at the mouth of the Sand River (Fig. 1). Thalweg current velocities ranged from 40 to 150 $cm \cdot s^{-1}$ at the study site, but were usually about 60 $cm \cdot s^{-1}$. Immediately upstream of its mouth, the Sand River is 30–50 m wide with a maximum depth of 1.5–2 m; below its mouth the channel widens and the mean depth decreases to between 1 and 1.5 m.

At the study site, the Sand River had an average summer temperature (June to September) of approximately 20°C; the maximum temperature recorded was 27°C.

Methods

Four major substrate types were recognized based on visual and tactile criteria: silt (SI) was characterized by a soft sticky texture, abundant visible silt, and dark grey or black colour; marginal sand (MS) had a firm fine-grained texture, some visible silt, and only a few sand particles in active motion; gravelly sand (GS) had a firm coarse texture, abundant apparent gravel, and few sand particles in active motion; and shifting sand (SS) had a soft loose texture, no apparent silt, and actively moving sand dunes.

Data on distribution and abundance of *P. centralis* larvae were obtained from samples taken along 10 transects established at 5-m intervals along a 50-m reach at the mouth of the Sand River. Along each transect samples were obtained from the middle area of those substrates (SI, MS, and GS) that occurred in narrow bands parallel to the banks, and at intervals of approximately 5, 10, 20, and 30 m from the bank in SS areas. The number of samples obtained from a particular transect depended upon the occurrence of the various substrate types along it.

Sampling was primarily biweekly throughout the open-water season (April–November) in 1980, from April to the end of July in 1981, and on one date (June 15) in 1982.

A Surber sampler (0.243-mm mesh) modified with a handle and an extra-long net bag (0.8 m) was the chief sampling device used throughout the study. The depths and current velocities encountered precluded the use of closed cylinder samplers. Samples were collected by disturbing the substrate, within the 930-cm^2 area defined by the sampler, with the foot for 30 s. Samples were placed in jars and preserved with 95% ethanol.

In the laboratory, organic material was separated from inorganic material by elutriation, examined under a dissecting microscope at 12× magnification, and the *P. centralis* larvae were removed. A standard D-frame dip net (0.5-mm mesh size) was used to collect additional larvae for life history determination and behavioral observation.

Larval stages were designated using the criteria of Clifford (1970): stage I larvae lacked wing pads, stage II larvae possessed wing pads whose length was less than the distance between them, stage III larvae had wing pads longer than the distance between them, and stage IV larvae had the darkened wing pads characteristic of the last larval instar. Head capsule width was measured at the widest point (just posterior to the eyes). All measurements were made at 25 or 50× magnification using an eyepiece micrometer on a dissecting microscope.

The food habits of *P. centralis* larvae were determined by examination of the foreguts of 20 individuals in stage II, III, or IV. Contents were quantified by direct counts of the type and number of organisms.

To determine fecundity, female subimagoes (reared from larvae kept for a short period in the laboratory) were dissected, and all eggs were removed and counted. These eggs were then placed in dechlorinated water and their dimensions were measured at irregular intervals over a 24-h period to determine egg size.

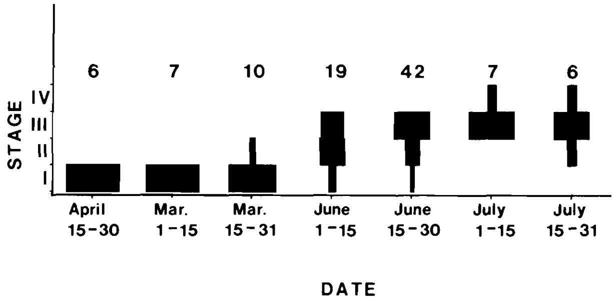

FIG. 2. Larval development of *P. centralis* based on larval stage. Horizontal width of bars represents proportion of larvae in each stage. Data is a composite based upon larvae collected 1977–1981. Values above bars are the no. of larvae collected.

Larvae and eggs were dried at 60°C for 24 h before weights were determined to the nearest 0.002 mg on a microbalance.

Observations of the behavior of *P. centralis* larvae were carried out in various types of artificial streams.

In addition to data collected during the study, qualitative collections made at the study site from 1977 to 1981 were used in the life history analysis.

Results

Life history

Pseudiron centralis was univoltine in the Sand River (Fig. 2). The relatively large first-instar larvae (head width approximately 0.24 mm, body length approximately 0.90 mm) appeared in late April and were easy to distinguish because compound eyes, ocelli, and gills were not apparent. Although no larvae were reared directly from eggs, identification of first-instar larvae was possible because one almost fully developed larva was removed from an egg collected in the field (see below). After hatching, development was rapid, with stage IV larvae appearing in the population in less than 8 weeks. The low number of stage IV larvae collected is probably due to the relatively short duration (2–3 days under laboratory conditions) of this stage. Adult emergence was not observed at the study site, but the presence of stage IV larvae indicated emergence from late June to late July. Neither quantitative nor intense qualitative collecting yielded larvae in late autumn before the formation of ice, indicating overwintering in the egg stage. Thus, it appears that *P. centralis* spends most of the year in the egg stage, its life cycle being best described as a univoltine summer cycle (*sensu* Clifford 1982).

Each of the designated larval stages except for III and IV represented discrete ranges of head capsule widths (millimetres): stage I, 0.23–0.94; stage II, 1.01–1.66; stage III, 1.67–2.66; stage IV, 2.29–2.66.

Swarming behavior of adult *Pseudiron* spp. has never been reported, and we were unable to find swarming adults. However, emerging subimagoes and spent imagoes have been collected from the surface of the Milk River in southern Alberta from midmorning to late morning (D. A. Soluk, personal observation).

The number of eggs in the two females we dissected was low (624 and 467) relative to values recorded for other large mayflies (Brittain 1982). The mean dry weight of an egg was 0.005 mg (SD = 0.001) based on the weights of five groups of 10 eggs.

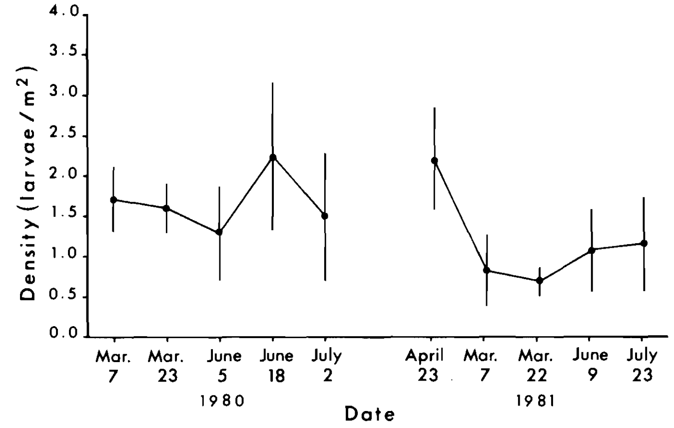

FIG. 3. Mean larval density (±SE) of *P. centralis* in the Sand River based on weighted estimates from the three types of sandy substrate.

TABLE 1. Number of samples (collected 15 June 1982) from shifting sand areas containing particular numbers (*N*) of *P. centralis* larvae

No. of larvae (*N*)	No. of samples with *N* larvae
0	8
1	6
2	7
3	2
4	0
5	1

Needham *et al.* (1935) described the egg of a *Pseudiron* sp. removed from a preserved specimen of an unspecified stage (presumably subimago or imago). The egg was ellipsoid in shape with dimensions of approximately 0.19 × 0.31 mm. The size and shape of this egg was similar to that of the compressed eggs found within the bodies of female subimagoes of *P. centralis* from the Sand River. However, when we exposed these eggs to water, they rapidly became more rotund, attaining their maximum dimensions of approximately 0.33 × 0.41 mm after 1 h.

One egg was collected from the shifting sand area of the Sand River (17 October 1981). This egg had approximate dimensions of 0.35 × 0.41 mm, and a number of sand grains were firmly attached to it.

Larval distribution and abundance

Larvae exhibited a shift in their association with the types of sandy substrate during development: stage I larvae were primarily associated with MS areas, and stage III and IV larvae were mainly associated with SS areas. The significance of this shift is discussed by Soluk (1983).

Pseudiron centralis larvae occurred at low densities which remained relatively constant throughout the period of larval development, suggesting relatively low rates of larval mortality. Mean larval densities (Fig. 3) were obtained by averaging density estimates of larvae on GS, MS, and SS areas (no larvae were ever collected from SI areas), weighted with respect to the proportion of river bed occupied by the particular substrate type. At the study site, proportions were estimated to be approximately 70% SS and 15% MS and GS (SI areas were considered insignificant), based on the occurrence of these substrates along the transects. The study site was generally representative of the bed of the Sand River, except that the GS area was somewhat overrepresented.

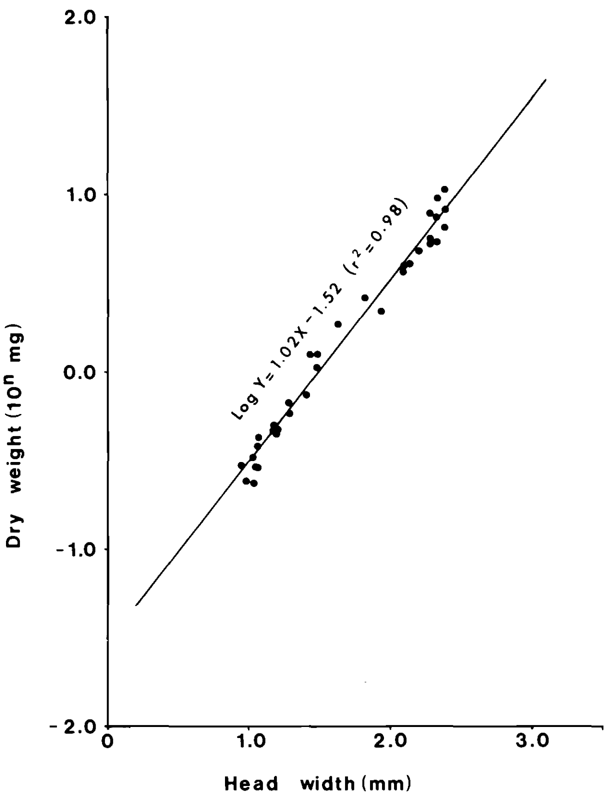

FIG. 4. Relationship between head width and dry weight in *P. centralis* larvae.

Despite the low density of larvae, individuals were collected with a high degree of regularity on a per sample or per unit effort basis. To determine the dispersion pattern of *P. centralis* larvae, we collected a series of 24 samples in 1982 from SS areas. Numbers of larvae in each sample (Table 1) were compared with values expected from a Poisson distribution utilizing an index of dispersion (Southwood 1978). The analysis indicated that *P. centralis* larvae were randomly distributed ($\chi^2 = 28.70$, $p > 0.10$) over shifting sand areas.

Larval density on 15 June 1982 was higher (10.16 larvae$\cdot$m^{-2} for all sandy substrates) than during the previous 2 years (Fig. 3), but this change was not considered large enough to affect the dispersion pattern of larvae.

Larval biomass and production

The regression (Fig. 4) based on the dry weights of larvae collected on 15 and 23 June 1982 (weight of first-instar larvae estimated from mean weight of eggs) was used to interpolate the weights of all larvae collected. These weights were in turn used with the mean larval densities (Fig. 3) to estimate standing crop (Table 2). Larval production (Table 2) was estimated, using the instantaneous growth method, to be 28.70 and 11.24 mg$\cdot$m$^{-2}\cdot$year^{-1} in 1980 and 1981, respectively.

Larval behavior

Pseudiron centralis larvae preyed primarily on chironomid larvae associated with the sandy habitats of the Sand River (Table 3). The only other prey items found in the guts of larvae were small larvae of other species of Ephemeroptera (early instars of *Baetis*, *Centroptilum*, and *Ephoron*). Accurate identification of material in the foreguts of *P. centralis* was possible because prey items were consumed whole, with little or no maceration.

In laboratory streams, *P. centralis* larvae foraged principally along the upstream face of actively moving sand dunes. Larvae moved in a crablike manner and, when at rest, their legs were positioned in typical insect fashion; larvae were never observed in the unusual posture (all three legs directed posteriorly) reported by Edmunds *et al.* (1976), except when swimming. Although larvae did not actively burrow after chironomids, they were able to make shallow excavations in the sand by using body orientation to direct the force of the current. A more detailed description of this unique foraging behavior is provided by Soluk (1983).

Discussion

In the Sand River, *P. centralis* exhibited a summer-type life cycle, with a relatively short larval period and a long egg dormancy (approx. 9 months). This pattern is probably similar over the entire range of this species; all reported adult records are from June and July (McDunnough 1931; Burks 1953). Overwintering as a dormant egg appears to be a relatively common strategy in Ephemeroptera (Clifford 1982). Long egg dormancies have been reported for *Dolania americana* (Harvey *et al.* 1980), and have been suggested for *Analetris eximia* Edmunds (Lehmkuhl 1976), both of which are predaceous mayflies associated with sandy river beds.

Although the life cycle of *P. centralis* is not unusual, its significance is obscured when annual patterns in abundance of potential prey organisms in the sandy substrates of the Sand River are examined. Soluk (1983) determined that the abundance and biomass of chironomid larvae remained relatively high throughout the year, suggesting a high level of food availability. Since *P. centralis* was the only macroinvertebrate predator collected on shifting sand areas in the Sand River, it appears that the chironomid populations in this habitat remain unexploited for much of the year. Given the presence of a relatively constant availability of prey items, the *P. centralis* population might be expected to exhibit a more staggered or extended larval growth and emergence pattern (e.g., some individuals hatching in late May and emerging in August). The absence of this pattern suggests overriding factors making developmental synchrony advantageous to members of this population.

Sweeney and Vannote (1982) discussed the advantages of the highly synchronized mass-emergence patterns found in many species of mayflies; however, we were unable to find evidence indicating that *P. centralis* exhibits this type of emergence.

Clifford (1982) suggested that the summer cycle may be an adaptation to shorten the larval period and thereby minimize the impact of such factors as predation on this stage. *Pseudiron centralis* larvae did not seem to exhibit high mortality rates, based on the changes in larval density over time (Fig. 4). Also, the relatively low fecundity of females does not suggest high levels of larval or egg mortality. Thus it seems unlikely that the adaptive significance of the life cycle pattern of *P. centralis* is to minimize larval mortality.

Summer cycles in Ephemeroptera have usually been viewed as mechanisms for the avoidance of harsh or uncertain winter conditions (Clifford 1982), and it is possible that the egg stage of *P. centralis* is more resistant to stresses such as ice scour or freezing. However, *D. americana*, which exhibits a 2-year life cycle, spends the first winter as an egg in the relatively benign conditions of the southeastern United States (Harvey *et al.* 1980).

TABLE 2. Production calculation for *P. centralis* larvae, determined by the instantaneous growth method

Date	Density (no./m^2)	Mean weight (mg)	Standing crop (mg/m^2)	G	B (mg/m^2)	P (mg/m^2)
1980						
May 7	1.72	0.065	0.112	0.65	0.16	0.10
May 21	1.61	0.124	0.200	1.36	0.41	0.56
June 5	1.30	0.484	0.629	2.87	9.88	28.30
June 18	2.25	8.499	19.123	−0.02	15.83	−0.27
July 2	1.50	8.352	12.528			
Total						28.70
1981						
April 23	2.22	0.056	0.124	−0.04	0.08	0.00
May 7	0.83	0.054	0.045	1.42	0.10	0.14
May 22	0.69	0.224	0.154	3.59	4.46	15.99
June 9	1.08	8.110	8.759	−0.74	6.63	−4.89
June 23	1.16	3.880	4.501			
Total						11.24

NOTE: G, instantaneous growth rate; B, mean standing crop; P, production.

TABLE 3. Proportion by number of prey types found in the foregut of 20 *P. centralis* larvae

Organism type	Proportion in foregut (%)
Robackia demeijerei	1.4(3.7)
Rheosmittia sp.	79.0(26.6)
Other chironomids	14.4(24.5)
Ephemeroptera	5.2(7.3)

NOTE: Values are means with SD in parentheses.

The eggs of *P. centralis* are larger than the maximums reported for most large Ephemeroptera (0.20 × 0.30 mm; Elliott and Humpesch 1980). The large size of these eggs was probably not simply a function of the duration of the dormancy period and the food requirements of the embryo, since most other Ephemeroptera with similar egg dormancy periods do not possess such large eggs. The large egg size may be a consequence of the fact that first-instar *P. centralis* larvae are larger than those of most other mayflies studied (e.g., Needham *et al.* 1935). Larvae may be large at hatching because of their predaceous habits (chironomid larvae were found in the guts of even the smallest stage I larvae examined), which may impose a minimum size constraint, below which larvae cannot prey effectively on chironomids. Alternatively, *P. centralis* larvae might be constrained to a certain minimum size to cope effectively with the dynamic nature of the sandy beds on which they are found. It is perhaps significant that the only other species of predaceous psammophilous mayfly for which egg size is reported (*Dolania americana*) has the largest eggs known in the Ephemeroptera (1 mm diameter; Edmunds *et al.* 1976).

The random dispersion pattern of stage III and IV *P. centralis* larvae on shifting sand areas greatly facilitated accurate population estimates. Random dispersion patterns have seldom been reported for lotic benthic invertebrates, although they have been found in populations of species frequenting areas of relatively uniform substrate composition (Resh 1979). The presence of a random dispersion pattern on shifting sands suggests that larvae may be perceiving this area as a relatively uniform patch, at least at the population level; this supports the designation of shifting sand areas as a distinctive habitat type for *P. centralis*.

Although *P. centralis* larvae and adults are rarely collected, the species is probably not rare. The low densities at which it occurs and the difficulties involved in sampling the invertebrate fauna near and in the mainstream of larger rivers have probably combined to give this impression. This is probably true for the genus *Pseudiron* as a whole. Specimens of *Pseudiron* have been collected in sandy reaches of all major river systems in North America, with the exception of the St. Lawrence River and some drainages west of the Rocky Mountains.

Barton (1980) commented on the generalized invertebrate assemblages associated with the sandy beds of larger rivers over wide geographic areas. Mayflies of the genus *Pseudiron* appear to be consistent members of these assemblages in North America.

In the Sand River, and probably in other rivers, *Pseudiron* larvae are the only epibenthic predators that occupy areas of actively shifting sand. They are highly specialized predators on the chironomid fauna of these areas, and as such may play an important role in the biological communities associated with shifting sand areas. Further examination of the biology and ecology of *Pseudiron* is likely to increase our understanding of one of the dominant habitat types in river ecosystems.

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