EVIDENCE FOR OBLIGATORY PARTHENOGENESIS AND ITS POSSIBLE EFFECT ON THE EMERGENCE PERIOD OF CLOEON TRIANGULIFER (EPHEMEROPTERA: BAETIDAE)

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Abstract

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The absence of males in 1000 adults examined over a 2 year period, the facility with which unmated females deposited eggs, and the high percentage (86%) of these eggs which hatched are presented as evidence for obligatory parthenogenesis in *Cloeon triangulifer* McDunnough. It is suggested that the unusually long (June to November) emergence period of the species is a result of parthenogenesis.

Introduction

Obligatory parthenogenesis, where parthenogenesis is the normal mode of reproduction, appears rare in Ephemeroptera but has been established for *Ameletus ludens* Needham (Clemens 1922; Burks 1953) and suggested for *Caenis cuniana* Froehlich (Froehlich 1969). Occasional or accidental parthenogenesis in normally bisexual species resulting from failure of a female to find a mate is more widespread (Degrange 1960; McCafferty and Huff 1974; Pescador and Peters 1974). The aptitude that these species display for this mode of reproduction varies with the ability of unmated females to deposit eggs and these eggs to hatch.

The effect of parthenogenesis on the seasonal emergence period and pattern of aquatic insects in temperate regions has not been studied. Synchronization of emergence occurs when members of the population emerge and are present for a short time, and it is logical to assume that this synchronization is associated with the need for the sexes to meet in sexually reproducing populations.

This paper presents evidence of obligatory parthenogenesis in *Cloeon triangulifer* McDunnough and discusses the possible effect of parthenogenesis on the emergence period of the species.

Study Area and Sampling Methods

The observations reported here are based on a study of the seasonal distribution of adults and nymphs of *C. triangulifer* in a pond at Rigaud, Que. A description of the study area and sampling techniques is given by Gibbs (1973).

Observations and Discussion

During 1967 and 1968 approximately 1000 female adults were collected from emergence traps and 3000 female nymphs by a standardized netting procedure. No males were seen. The absence of males was also reported by McDunnough (1931), who described the adult from female specimens collected in Ontario and Quebec, and Ide (1937), who described the nymph from female nymphs also collected in Ontario and Quebec.

Swarming, frequently associated with mating and pre-oviposition activity in mayflies, was never observed in this species. During the day females were frequently observed to fly from the vegetation to the surface of the pond where the eggs were released as soon as the abdomen came into contact with the water. In the laboratory, 24 h after the imaginal ecdysis, females would immediately release their eggs if their abdomens were brought into contact with water. Froehlich (1969) reported that unmated females of parthenogenetic *Caenis cuniana* readily oviposited when brought into

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contact with water. Degrange (1960) found considerable variation in the mayfly species that he studied, finding that some species would readily oviposit when their abdomens were brought into contact with water while other species would not. He concluded that in some species certain pre-oviposition activity, such as a special flight, is necessary and speculated that the muscular activity involved in this flight may favour the progression of eggs in the oviducts and their expulsion.

Hatching of eggs from females reared in isolation or from emergence traps was frequently observed. To study the percentage of eggs hatching, 1251 eggs were collected on 26 September 1969 from females taken from emergence traps. These were held at room temperature and hatching was recorded on the following days: 7 October, 488; 8 October, 224; 9 October, 152; 10 October, 12. Thus 1076, or 86%, of the eggs hatched over a 4 day period. The percentage hatch of eggs from unmated females recorded in the literature has varied from 0.18–4.46 for normally bisexual heptageniid genera (Degrange 1960; McCafferty and Huff 1974) to 79.4–99.0 for the normally parthenogenetic *Caenis cuniana* (Froehlich 1969).

Closon triangulifer, therefore, exhibits two of the characteristics that Suomalainen (1962) and Degrange (1960) have concluded are necessary for the change from reproduction by fertilization to parthenogenesis: (a) that the female be able to lay eggs without mating, (b) that a high proportion of the unfertilized eggs be able to hatch.

The evolution of parthenogenesis from bisexual reproduction in *C. triangulifer* is indicated by the presence of a well developed micropyle, as described by Koss and Edmunds (1974), in eggs taken from females collected during this study.

An aptitude for thelytokous (female-producing) parthenogenesis is shown by other species of *Cloeon*. Hirvenoja (1964) failed to collect any males from a population of *C. praetextum*. Degrange (1960) reared three successive thelytokous parthenogenetic generations from eggs from a single female of the normally bisexual *C. simile*.

The seasonal distribution of the nymphs and adults of *C. triangulifer* was reported by Gibbs (1973). It was found that adult emergence continued from the first week in June until the third week in October with the majority of the insects emerging in July, August, and September, and a reduced emergence in June and October (Fig. 1). Final instar nymphs approaching metamorphosis (as indicated by darkened wing pads) were present until early November so emergence may have continued until this time. This emergence period is unusually long when compared with other mayflies in the same

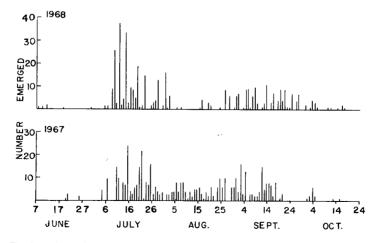


Fig. 1. Total numbers of C. triangulifer emerging into eight emergence traps during 1967 and 1968.

environment and other species of the same genus. Callibaetis ferrugenius and C. fluctuans, numerous in the Rigaud study pond, did not emerge after the end of August. Brown (1961) reported Cloeon dipterum as emerging from 23 June to 12 September in England. Hirvenoja (1964) reported emergence of C. dipterum during June, July, and August, and C. praetextum during June and July in Finland.

The genetic stability that is associated with parthenogenesis is thought to act to the disadvantage of a species by limiting its adaptability. There must, therefore, be compensating advantages which can be exploited. One of these is the greater biotic potential which results from all individuals being able to produce offspring. Also, parthenogenetic species do not have to expend energy to bring the sexes together nor are they dependent on particular climatic conditions to allow mating to take place.

The exceptionally long emergence period of C. triangulifer may be associated with its parthenogenetic mode of reproduction. As Macan (1958) has pointed out, a short emergence period increases the ease with which the sexes find each other but it has never been proved that this is the basis for a short emergence period. It is obvious that if a population is scattered in time and if the adults are short-lived, the reproductive potential of many individuals which would be lost in a sexually reproducing species is exploited in the parthenogenetically reproducing populations and the species is thus able to avoid the disadvantages of synchronized emergence — competition for emergence sites, overcrowding of newly hatched larvae at oviposition sites, and increase in predation (Corbet 1964). Brown (1961) speculated on why the emergence period of C. dipterum did not extend beyond 12 September. He found that nymphs collected in the spring and kept at 10°C emerged successfully and temperatures in the field remained above this level until October. He suggested that a temperature-regulated mechanism which restricted the emergence of adults would have the value of restricting emergence to the season when air temperatures were high enough to allow successful flight and mating activity.

In the case of *C. triangulifer*, the necessity to restrict emergence to periods during which temperatures are favourable for mating flights to take place, is removed and emergence can and does continue until ice forms over the pond.

The eggs from *C. triangulifer* females hatched and contributed to the nymphal population until mid-September when hatching ceased. Eggs deposited after that time accumulated on the substrate, hatching the following June (Gibbs 1973). This restriction of hatching until environmental conditions were suitable for nymphal development allowed the realization of the reproductive potential of all individuals emerging late in the fall.

The suggestion that parthenogenesis may lead to a breakdown of synchronized emergence patterns is supported by evidence that obligatory parthenogenesis leads to a "decay" of diel flight activity patterns in tropical species of Trichoptera and Ephemeroptera (Tjønneland 1970). In insects with a restricted adult life the flight activity patterns may be closely associated with the emergence patterns.

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References

Brown, D. S. 1961. The life cycle of *Cloeon dipterum* L. (Ephemeroptera: Bactidae). *Entomologist* 94: 114-120.

Burks, B. D. 1953. The mayflies, or Ephemeroptera of Illinois. *Bull. Ill. St. nat. Hist. Surv.* **26**: 1–216. Clemens, W. A. 1922. A parthenogenetic mayfly *Ameletus ludens* Needham. *Can. Ent.* **54**: 77–78. Corbet, P. S. 1964. Temporal patterns of emergence in aquatic insects. *Can. Ent.* **96**: 264–279.

- Degrange, C. 1960. Recherches sur la reproduction des Ephéméroptères. Trav. Lab. Hydrobiol. piscic. Univ. Grenoble 51: 7-193.
- Froehlich, C. G. 1969. Caenis cuniana sp. n., a parthenogenetic mayfly. Beitr. neotrop. Fauna 6: 103-108.
- Gibbs, K. E. 1973. The seasonal distribution of *Cloeon triangulifer McDunnough* in a pond in eastern Canada. *Proc. First int. Conf. Ephemeroptera*, *Tallahassee*, *Fla.*, 1970, pp. 39-48.
- Hirvenoja, M. 1964. Studien über die Wasserinsekten in Rühimäki (Südfinnland). IV. Ephemeroptera, Odonata, Hemiptera, Lepidoptera and Coleoptera. *Ann. ent. fenn.* 30: 65-93.
- Ide, F. P. 1937. Descriptions of eastern North American species of baetine mayflies with particular reference to nymphal stages. Can. Ent. 69: 219-231, 235-243.
- Koss, R. W. and G. F. Edmunds, Jr. 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. J. Linn. Soc. (Zool.) 55: 267-349.
- Macan, T. T. 1958. Causes and effects of short emergence periods in insects. Verh. int. Verein. theor. angew. Limnol. 13: 845-849.
- McCafferty, W. P. and B. L. Huff, Jr. 1974. Parthenogenesis in the mayfly Stenonema fermoratum (Say) (Ephemeroptera: Heptageniidae). Ent. News 85: 76-80.
- McDunnough, J. 1931. New species of North American Ephemeroptera. Can. Ent. 63: 82-93.
- Pescador, M. L. and W. L. Peters. 1974. The life history and ecology of *Baetisca rogersi* Berner (Ephemeroptera: Baetiscidae). *Bull. Fla St. Mus. biol. Sci.* 17: 151-209.
- Suomalainen, E. 1962. Significance of parthenogenesis in the evolution of insects. A. Rev. Ent. 7: 349-366.
- Tjønneland, A. 1970. A possible effect of obligatory parthenogenesis on the flight activity of some tropical larvo-aquatic insects. Orb. Univ. Bergen. 1970. Mat. Naturv. Serie.: 1-7. (Received 30 January 1976)