LIFE HISTORIES OF *ENALLAGMA HAGENI* (WALSH) AND *E. ASPERSUM* (HAGEN) (ZYGOPTERA: *COENAGRIONIDAE*)

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The life histories of *E. hageni* and *E. aspersum* were studied in small ponds near Highlands in western North Carolina, United States. Both species over-wintered as larvae short of the final instar, *E. hageni* in instars F-6 to F-2 and *E. aspersum* in instars F-8 to F-1. The life cycle of *E. hageni* was completely univoltine with an early, relatively synchronized emergence. Although *E. aspersum* was primarily univoltine, about 8% of the new-year class was bivoltine, completing development and emerging within a single season. Emergence was temporally dispersed, but there was a distinct peak in early summer. The temporal separation of life cycle events is probably significant in enabling the two species to coexist.

INTRODUCTION

In North America, few life history studies have been made on members of the family *Coenagrionidae*, particularly representatives of the genus *Enallagma*, which has the largest number of species of any odonate genus in the American fauna, 19 species in North Carolina alone. Coenagrionid life histories were studied by GRIEVE (1937), JOHNSON (1964), KORMONDY & GOWER (1965), FERNET & PILON (1971), PAULSON & JENNER (1971), PROCTER (1973), and SAWCHYN & GILLOTT (1975), but only KORMONDY & GOWER (1965) employed the desirable approach of regularly sampling larval populations and exuviae over an annual cycle with a species of *Enallagma*.

Enallagma hageni (Walsh) and *Enallagma aspersum* (Hagen) coexist in small ponds in the mountains of western North Carolina. *E. aspersum* is recorded from extreme southern Canada and the eastern United States (WALKER, 1953) and extends southward into Georgia. *E. hageni* is found considerably further north, having a wide distribution in northern Canada and the northern United States (WALKER, 1953). *E. hageni* is near the southern limit of its range in North Carolina, where it is restricted to the higher elevations.

The abundance of *E. hageni* and *E. aspersum* in the vicinity of Highlands, North Carolina, provided an excellent opportunity for conducting comprehensive studies on the life histories of two closely related species. Because these two species were found together in large numbers and seemed to occupy similar niches, the study was designed as a comparative one to investigate the possibility that subtle temporal differences in their life cycles reduced competition between them. Particular attention was given to seasonal changes in larval composition, patterns of emergence, and adult population densities.

MATERIALS AND METHODS
LARVAL COLLECTIONS

All studies were conducted at Schroder's Pond near Highlands (35°5'N, 83°10'W) in southwestern North Carolina (cf. INGRAM, 1976). Larval collections (20 of *E. hageni*, 21 of *E. aspersum*) were made from September, 1968, to September, 1969, to determine changes in instar composition for both species. An effort was made to sample equally from all depths and from several areas in the pond. Larvae were usually collected with a standard long-handled dip net (mesh size = 1.0 mm). Nets with a fine mesh (0.1 mm) were used during the hatching periods so that younger larvae would be represented adequately in the samples. The samples were emptied into a white enameled pan with water and agitated, causing the larvae to move out of the vegetation and debris so that they could be collected with a Banta pipette. Larvae were generally returned to the pond within two days.

In the laboratory, a dissecting microscope with an ocular micrometer was used to measure head width (maximum across the eyes) and to determine relative wing-pad length (number of abdominal segments covered by the metathoracic wing-pads). By utilizing the distribution of these indices in field collections together with information on their dimensions from larvae reared in the laboratory until emergence, it was possible to recognize the advanced instars of both species. However, considerable difficulty was encountered in trying to separate the middle and smaller instars in many field collections as well as in the laboratory (INGRAM, 1971).

The difficulty in assigning individuals to an instar class was related to seasonal variation in the head width of larvae belonging to a particular instar. Seasonal

differences were significant in the head widths of F-1 (final instar minus one) and final instar larvae of *E. aspersum* (Tab. I). Seasonal variation in head width was less pronounced in both F-1 and final instar larvae of *E. hageni* (Tab. I). Presumably, similar variation occurred in the smaller larvae, causing overlap among adjacent instar classes. Despite these difficulties, the F-1 and final instars, which were of most value in determining seasonal cycles, could be recognized easily, often without head width measurement by noting the size of the wing-pads. For this reason, plus the inability to separate some of the smaller larvae distinctly, the histograms of seasonal development show only the F-1 and final instars as distinct groups. However, reference will often be made to other instar classes, since most of the middle instars could be recognized by considering both head widths and relative wing-pad lengths; also, many of the smaller larvae that were unassignable at the time of collection were retained and placed in instar classes when they molted to a larger size.

Table I

Seasonal changes in mean head width (mm) of final and F-1 instar larvae
of *Enallagma aspersum* and *E. hageni*

Species	Date	Final Instar		F-1 Instar	
		N	Head Width	N	Head Width
E. aspersum	30 October 1968	0	–	7	2.90
	12 December	0	–	2	2.82
	31 January 1969	0	–	3	2.88
	28 March	0	–	5	2.92
	15 April	0	–	37	2.82
	29 April	4	3.46	15	2.84
	20 May	24	3.46	14	2.80
	6 June	27	3.38	27	2.82
	18 June	–	–	28	2.78
	30 June	25	3.38	27	2.78
	14 July	25	3.36	3	2.68
	28 July	14	3.22	30	2.62
	4 August	12	3.24	28	2.62
	11 August	–	–	28	2.66
	18 August	28	3.24	8	2.70
E. hageni	15 April 1969	–	–	37	2.78
	29 April	–	–	48	2.76
	20 May	26	3.38	65	2.78
	6 June	27	3.36	31	2.72
	18 June	–	–	5	2.66
	30 June	19	3.30	–	–

COLLECTIONS OF EXUVIAE

Because of the dense marginal vegetation and the small size of the exuviae, exhaustive collections of these indicators of emergence were not possible. Instead, 100 dowels (0.5 cm diameter, 90 cm length) were placed around the periphery of the pond as artificial emergence sites as described by INGRAM (1976). Collected exuviae were carried to the laboratory for identification to species and sex. Daily exuvial collections were made throughout the emergence period from these artificial emergence sites and constituted the basis for an emergence curve.

The size of the year's total emergence was estimated by placing 20 strips of screen wire (0.5 m in length) at intervals of about 10 m around the margin of the pond (INGRAM, 1976). All exuviae collected either on the screens or on emergent objects in front of the screens were enumerated daily and converted into the mean number of emergences/m of shoreline. The mean daily emergence was then multiplied by the total shoreline length (465 m) and summed for the entire emergence period to estimate the total emergence.

EGGS AND HATCHING TIMES

Eggs were obtained by collecting adult females and transporting them to the laboratory, where they were allowed to oviposit endophytically on floating aquatic vegetation, usually *Juncus* sp., in finger bowls. Prior to its use, the vegetation was heated to kill any previously oviposited eggs. Daily inspection of the finger bowls for first instar larvae determined the time required for the eggs to hatch, which occurred over a period of 2-4 days in various batches of eggs. Hatching times were recorded at prevailing room temperatures (generally 17 to 22°C, range of 15 to 25°C) and at a constant temperature of 20°C.

ADULT POPULATION DENSITIES

Densities of adults along the margin of Schroder's Pond were monitored at intervals during the flight season in 1969. All mature adults (non-tenerals) were counted along a known length (43.5 m) of the dam. These observations were made between 1400 and 1600 h EST in full sunlight, and replicate counts (4 to 8) were made on each date.

RESULTS
ENALLAGMA HAGENI

Changes in instar composition of the *E. hageni* population during 1968 and 1969 are shown as head-width frequency histograms in Figures 1A and 1B.
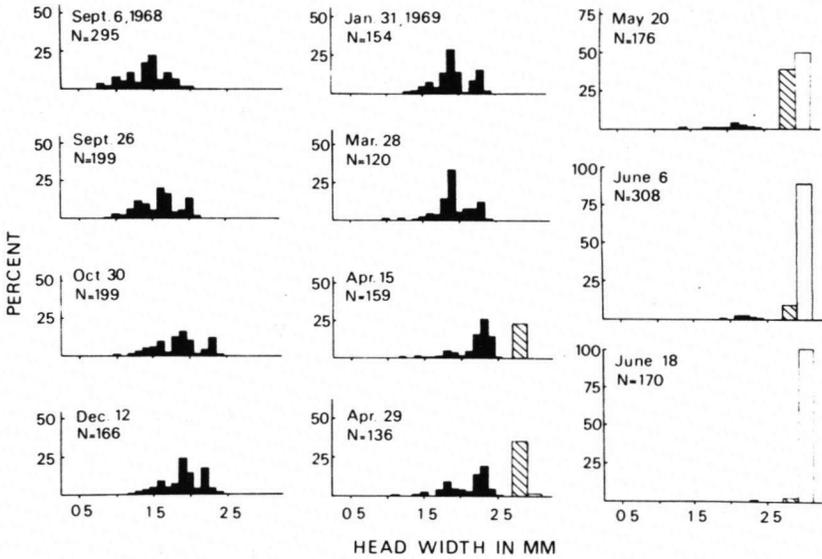
Fig. 1A. Head width frequency histograms of larvae of *Enallagma hageni* collected in 1968-1969. N = sample size. Head widths of the final (3.1-3.5 mm) (clear bars) and F-1 (2.6-2.9 mm) (hatched bars) instar classes are not drawn to scale. The other larvae are represented by class intervals of 0.1 mm and instar classes are not delimited (dark bars).
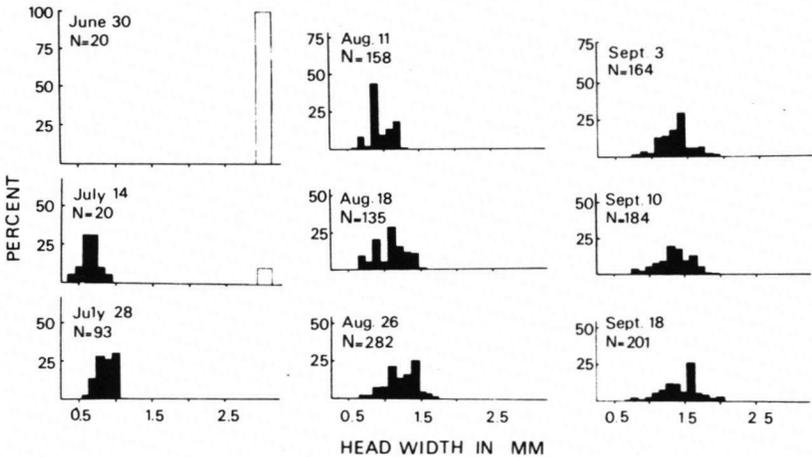

Fig. 1B. Continuation of Figure 1A.

Larvae overwintered in the F-6 to F-2 instars, and little change in the population occurred between 30 October 1968 and 28 March 1969. By 15 April many of the larvae had entered the F-1 instar, and by 29 April 1% of the larvae were in the final instar. Subsequent samples of the one-year class were dominated by the F-1 and final instars. The last collection of final instar larvae was made on 14 July, indicating that the emergence period was nearly ended. The first collection of members of the new-year class was also made on 14 July. Development of new-year larvae continued into fall to place eventually the population in the overwintering structure. *E. hageni* was thus a univoltine species with relatively synchronized growth throughout the year.

The 1969 emergence of *E. hageni* began on 28 May and lasted until 17 July, a total of 50 days (Fig. 2). The early season emergence of this species was relatively synchronized, 50% of the population having emerged by 14 June, the 18th day of emergence. Emergence was at its peak from 7 June to 21 June, over 75% of the year's emergence having occurred by the end of this period. Exuviae from males were slightly more abundant, comprising 51.9% of the 626 exuviae examined. The total emerging population was estimated to be 22,901, an average of 49.2 emergences/m of shoreline for the entire emergence period.
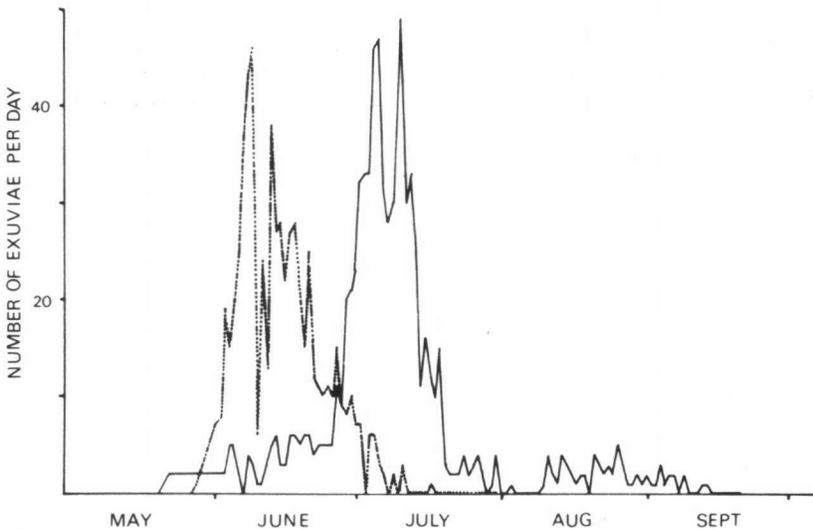

Fig. 2. Emergence curves based on daily collections of exuviae. Dotted line = *Enallagma hageni*; solid line = *E. aspersum*.

The flight season of *E. hageni* lasted from early June until the second week in August (Fig. 3). Adults reached their greatest density, 2.2/m of shoreline, on 28 June, approximately 2 weeks after the peak emergence period. After June the
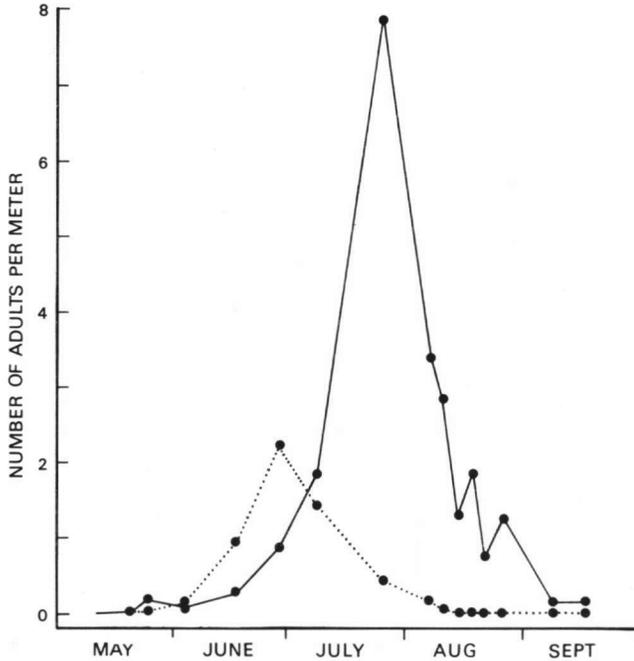
Fig. 3. Mean densities of adult populations per meter of shoreline. Dotted line = *Enallagma hageni*; solid line = *E. aspersum*.

density gradually dropped, and adults were last seen on 10 August. Oviposition occurred through most of the flight period. Laboratory studies of hatching time showed that eggs did not enter diapause. At room temperature, eggs from several females hatched between 17 and 22 days after oviposition.

ENALLAGMA ASPERSUM

Seasonal changes in instar composition are shown in Figures 4A and 4B. Larvae overwintered in the F-8 to F-1 instars, a wider range than in *E. hageni*, and a few larvae attained the F-1 instar in the fall, considerably earlier than *E. hageni* (Fig. 4A). Few changes in population structure occurred between 30 October and 28 March. During this time the mean head width of the population was 1.68 mm (F-4), compared to a mean of 1.89 (F-3) in *E. hageni* over the same interval. The first larvae of *E. aspersum* entered the final instar by 15 April, slightly earlier than *E. hageni*. Thereafter, a steady change occurred in the instar composition as larvae proceeded toward the final instar and emergence.

Recruits to the new-year class were first collected on 14 July, although they were likely present earlier and were missed because of their small size and low density (Fig. 4B). In the 14 July collection, and in several subsequent ones, the largest new-year larvae were indistinguishable from the smallest larvae of the

previous year class. The fate of the new-year larvae was resolved by the following observations. First, in collections made between 6 June and 18 September, the percentage of the population in the final and F-1 instars decreased from a late June maximum to a low level in July, increased in August, and decreased again shortly afterwards (Figs. 4A, 4B). Second, since the compound eyes increased in width as metamorphosis progressed, measurement of this index of intermolt development provided a good estimate of the length of time a larva had been in the final instar. Eye width measurements of final instar larvae from the 28 July and 4 August collections showed a peak in the number of larvae that had recently entered that instar; no other summer collections contained such a large percentage of these new final instar larvae (INGRAM, 1971). These observations indicated that a group of new-year larvae reached the two terminal instars in late summer and proceeded to emerge. Thus, a small percentage of the new-year individuals completed their development within a single season and emerged just after the last members of the one-year class.
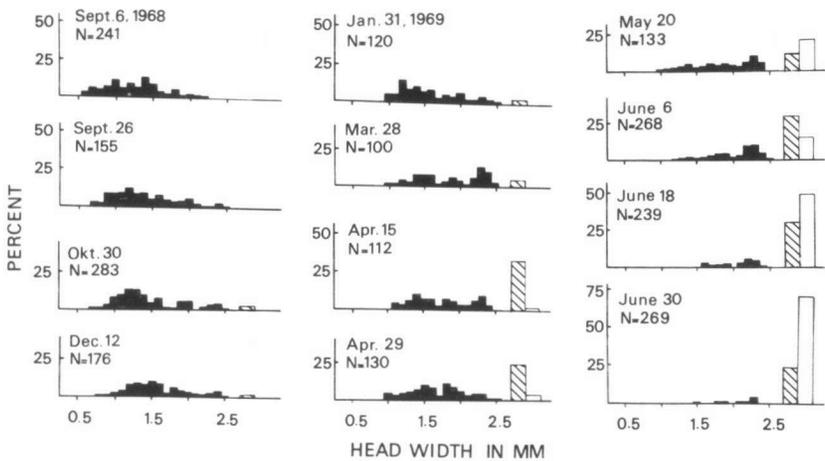

Fig. 4A. Head width frequency histograms of larvae of *Enallagma aspersum* collected in 1968-1969. N = sample size. Head widths of the final (3.1-3.5 mm) (clear bars) and F-1 (2.6-2.9 mm) (hatched bars) instar classes are not drawn to scale. The other larvae are represented by class intervals of 0.1 mm and instar classes are not delimited (dark bars).

The possibility existed that the small larvae that appeared in midsummer were not new-year recruits, but were representatives of the overwintering, one-year class that had been in deeper, colder water and had grown more slowly than the other members of their year class. However, extensive collections by boat from deeper offshore areas during the summer revealed no offshore concentration of larvae.

While rapid growth continued in the few individuals that would emerge, a developmental slowdown occurred in the other members of the new-year class,

which were destined to overwinter and emerge the following year. Although smaller larvae continued to molt, this developmental delay resulted in the almost complete cessation of growth by the most advanced larvae through most of August, with no larva proceeding out of the F-2 instar (Fig. 4B). In September 1969 those larvae that had been delayed in August resumed development and presumably would have undergone the molts that would eventually place the population in its overwintering structure, as indicated by the growth of the population in the fall of 1968 and in previous years. Therefore, although there was a small bivoltine element in the population, the life cycle of *E. aspersum* was primarily univoltine.
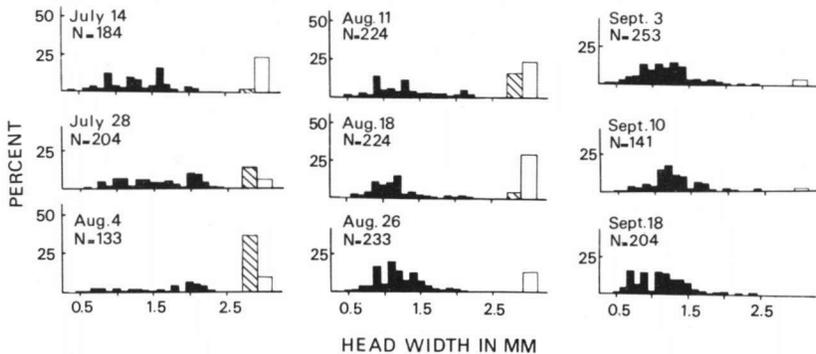

Fig. 4B. Continuation of Figure 4A.

Emergence of *E. aspersum* was temporally dispersed (Fig. 2). The emergence period began on 21 May and lasted until 15 September, an interval of 117 days. Over 50% of the population had emerged by 7 July, the 47th day of emergence. The peak emergence period was between 29 June and 19 July. After this, emergence declined abruptly. From 4 August to 9 August no exuviae were collected. On 10 August emergence resumed at a very low level, where it continued until the end of the season. Approximately equal numbers of exuviae were collected from each sex; 50.2% of 804 exuviae were from males. The total emerging population was estimated at 24,939, an average of 53.6 emergences/m of shoreline over the entire emergence period.

The cessation of emergence in August, followed by its resumption, points to two distinct emergence groups and offers additional evidence of a small bivoltine group of larvae. The first and larger emergence group consisted of larvae that hatched the previous summer, overwintered, and emerged approximately one year after hatching. The second group, comprising approximately 8% of the year's emerging larvae, consisted of those individuals that hatched in spring from eggs laid by the earliest emerging adults and, within a single season, completed development and emerged.

Adults were first sighted on 24 May, and they were still on the wing 16 September, the last observation date (Fig. 3). Adults reached a maximum density of 7.9/m of shoreline on 25 July, about 2 weeks after the peak emergence period. This peak was considerably larger than that of *E. hageni*. From August through September adults became progressively less abundant, and densities dropped below 0.2/m of shoreline in September. Oviposition occurred through most of the flight season. Laboratory observations showed that diapause was not entered in the egg stage. Eggs kept at a constant temperature of 20°C hatched in 21 to 24 days, and those maintained at room temperature required from 16 to 27 days to hatch.

DISCUSSION

PAULSON & JENNER (1971) studied 55 species of Odonata in North Carolina and concluded that, except at northern latitudes similar to those in England, CORBET's (1954, 1962) "spring" (overwinter in final instar, synchronized emergence) and "summer" (overwinter in several instars short of final, unsynchronized emergence) species categories are not meaningful and that they represent only the extremes in a continuum of emergence patterns and life cycle types. The results of the present study are in accord with that conclusion. Neither species overwintered in the final instar. But, *E. hageni* had a univoltine life cycle with an emergence that was less temporally dispersed than that of many summer species. *E. aspersum*, on the other hand, had the temporally dispersed emergence characteristic of Corbet's univoltine summer species, but there was a distinct early season peak, and a small portion of the population was bivoltine. These life history features, including the presence of a bivoltine element in the *E. aspersum* population, were also indicated by observations in 3 other years and at several additional ponds in the area (INGRAM, 1971). Thus, although both *E. hageni* and *E. aspersum* would be classified as summer species based on overwintering mode and emergence patterns, such a designation indicates nothing of the great differences between their life histories.

The differences between *E. hageni* and *E. aspersum* in the timing of seasonal events was most clearly revealed by their contrasting emergence patterns. However, there were also differences in the temporal patterns and developmental rates of larvae of the two species; as a result, the two larval populations were not composed of individuals of the same sizes. This temporal separation of life cycle events may be important in enabling the two species to exist sympatrically, since some segregating mechanism is critical for the coexistence in abundance of two populations with similar niches. Laboratory observations (INGRAM, 1971) indicated that competition between larvae of the two *Enallagma* species for food and other resources is minimized in the same way that it is reduced between different size classes of *Pseudagrion salisburyense* Selys, which feed on prey

proportional to their own size (CHUTTER, 1961). The important role of seasonal timing in the separation of niches has been postulated by BENKE (1970) for two anisopterans, *Ladona deplanata* (Rambur) and *Libellula incesta* Hagen. BENKE & BENKE (1975) noted that congeneric species of Odonata in the same habitat generally had almost identical life cycles and suggested that coexistence was possible because of the inability of a dominant species to fully exploit a rarer ecological homologue due to environmental unpredictability, as proposed for ecologically similar species of waterboatmen (*Corixidae*) by ISTOCK (1973). The degree of life cycle similarity may also be significant, and subtle differences such as shown for the two *Enallagma* species (e.g., time of emergence, univoltine vs. bivoltine element, etc.) may provide sufficient temporal separation for the coexistence of species with life cycles that are superficially similar.

Several factors suggest that temporal separation of the larvae may not have been the critical factor reducing competition between *E. hageni* and *E. aspersum*. Overlap in size of the larval populations was considerable on most dates, and the larger animals could have fed on the smaller ones in addition to other competitive interactions. Temporal separation of the adults may be more significant in these species, as indicated by the distinctly different peak times of both emergence and adult densities. BENKE & BENKE (1975) also found that *Celithemis fasciata* Kirby and *C. ornata* (Rambur), while having considerable overlap as larvae, tended to be more separated during emergence and as adults. Perhaps separation among larvae is important among some genera, but temporal separation among adults is a more important segregating mechanism within a genus.

The size of the maximum adult population of *E. aspersum* was considerably larger than that of *E. hageni* even though emergence records from both dowels and screens indicated that the populations were similar in size. This difference suggests that the longevity of *E. hageni* may be less than that of *E. aspersum*. CORBET (1964) postulated that spring or synchronized species have shorter adult lives than summer or temporally dispersed species. However, the evidence in the present study is limited because estimates were not made at short, regular intervals of time. Also, the influence of the relatively frequent rainfalls was difficult to evaluate. Rain did not appear to differ greatly during either the peak of post-emergence periods in the two *Enallagma* species. However, whether a given amount of rain within a short period of time is more or less detrimental to emerging, maturing, and adult damselflies than an equal amount of rain spread over a longer period must be answered before the relation between adult longevity and emergence synchrony is thoroughly evaluated.

Among the Odonata of temperate areas, the most common life cycles are univoltine or semivoltine. However, at a single locality the length of the life cycle may vary among members of one species. Such variations have been found

in the anisopterans *Anax imperator* Leach (CORBET, 1957c) in England and *Epitheca cynosura* (Say) (LUTZ, 1962) and *Pachydiplax longipennis* (Burmeister) (ELLER, 1963) in North America and in the British coenagrionid zygopterans *Coenagrion puella* (Linnaeus) and *Ischnura elegans* (Vander Linden) (PARR, 1970). *Pyrrhosoma nymphula* (Sulzer), another British coenagrionid, usually has a semivoltine life cycle (MACAN, 1964; CORBET, 1957b; LAWTON, 1970). But in one study (MACAN, 1964), larvae in one part of a pond required two years to complete development while those in another part of the pond required three years. *Enallagma cyathigerum* (Charpentier) at the same site showed a similar variation in life cycle (MACAN, 1964). The coenagrionids *Coenagrion mercuriale* (Charpentier) and *Ceriagrion tenellum* (Villers) were semivoltine in England (CORBET, 1957a). Much less information is available on the life cycles of North American coenagrionids. *Enallagma ebrium* (Hagen) and *Ischnura verticalis* (Say) in Pennsylvania were completely univoltine (KOR-MONDY & GOWER, 1965), as were *Enallagma vernale* Gloyd, *E. boreale* Selys, *E. hageni* (FERNET & PILON, 1971; PROCTER, 1973), *Coenagrion angulatum* Walker and *C. resolutum* Hagen (SAWCHYN & GILLOTT, 1975) in Canada. Primarily univoltine life cycles were also found in all of the 27 species of coenagrionids studied by PAULSON & JENNER (1971). These included 12 of the 19 species of *Enallagma* found in North Carolina, indicating that a univoltine life cycle is typical for the genus in North Carolina. However, the techniques used by PAULSON & JENNER (1971) in determining life cycles would not have revealed subtle modifications such as the emergence of a small, second generation. But the long flight seasons and wide range of overwintering instars in some species suggested that, in fact, a bivoltine element might be present.

Actual demonstrations of bivoltinism or multivoltinism in temperate zone Odonata are rare. AGUESSE-(1959) reported that the anisopteran *Sympetrum fonscolombei* Selys in southern France had a bivoltine life cycle. Although several authors have reported or predicted bivoltinism in North American zygopterans (GRIEVE, 1937; WALKER, 1953; JOHNSON, 1964), the present study on *E. aspersum* is the only demonstration of bivoltinism in North America that was based on seasonal changes in larval populations and emergence patterns. Preliminary observations of caged larvae of *E. aspersum* exposed to natural daylengths and temperatures indicated the subtle nature of the change from univoltinism to bivoltinism. Larvae that reached the F-3 instar by 4 August could emerge in one summer, whereas smaller larvae stopped development short of the F-1 instar (INGRAM, 1971). Larvae collected later in the summer showed a progressive decrease in the maximum instar that could be reached before winter. The advanced larvae that did not emerge entered diapause in late summer, as did all advanced members of the new-year class of *E. hageni* (INGRAM, 1971). The rapid larval growth that is necessary for a bivoltine element in *E. aspersum* is supported by limited laboratory data. Two larvae in

the F-7 instar completed development in 73 and 83 days at 21°C. Considering the usual rapid completion of the earliest instars and the high temperature (frequently above 21°C) in nature during summer and early fall, the completion of development in the field in about 70 days appears feasible. Even if some of the larvae emerging shortly after the temporary cessation in August were members of the one-year class, the evidence indicates that those emerging in late August and September were representatives of the new-year class.

AGUESSE (1955) reported that *Ischnura elegans* had three generations per year in southern France, although it was mainly univoltine in northern England (PARR, 1970) and semivoltine in northern Scotland (PARR, 1969). CHUTTER (1961) .demonstrated multivoltinism in *Pseudagrion salisburyense* in South Africa. Although these observations are too few to be conclusive, they do indicate that bivoltinism and multivoltinism may not be rare among the *Coenagrionidae*.

The seasonal changes in the head widths of *E. aspersum* were apparently related to the number of larval molts. Extra molts led to increases in size (head width) that were proportional to the number of molts. Extra molts were induced in the laboratory by relatively high temperatures combined with short daylengths, conditions similar to those existing in late summer and fall when extra molts likely occurred in nature (INGRAM, 1971). The growth during September apparently involved extra molts that often led to larvae of intermediate size between the F-2 and F-1 instars. Extra molts were absent or infrequent in the development of larvae under long daylengths and relatively high temperatures. Correspondingly, larvae entering the advanced instars in spring and early summer apparently had few or no extra molts. The lack of clear separation between some instar classes at certain times was presumably caused by extra molts resulting in invididuals of intermediate size. The reduced variation in the size of *E. hageni* compared to *E. aspersum* was also probably related to the absence of extra molts, since this species was more synchronized and all advanced instars were exposed only to late spring and summer environments when daylength-temperature conditions did not induce extra molts.

The present study has demonstrated the existence of subtle, but apparently significant, temporal differences in the life histories of *E. hageni* and *E. aspersum*. Because of the wide distribution of these two species, much information on possible variation in life histories and the timing of life history events could be obtained by comparing these populations with those from more northerly latitudes. Further, detailed studies with concurrent laboratory investigations are needed from populations over a wide geographic range before life history variation and the influence of environmental factors on the timing of seasonal events is understood in the Odonata.

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