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The Life Cycle of Ephemeroptera in the Lower Part of Aurland River in Sogn and Fjordane, Western Norway

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Abstract: LARSEN, R. 1968 The Life Cycle of Ephemeroptera in the Lower Part of Aurland River in Sogn and Fjordane, Western Norway. *Norsk ent. Tidsskr.* **15**, 49-59. Collections of larvae of *Ephemerella aurivillii*, *Baetis rhodani*, and *Ameletus inopinatus* (Ephemeroptera) were made each month during 1966 in the Aurland River, Western Norway, and were used to get information about the life cycle of the species. *E. aurivillii* emerges mainly in June, July, August and September. The new generation begins to appear in August and growth proceeds throughout the winter with a drop in the growth rate through January and February. The animals complete a generation in one year. *B. rhodani* emerges from April to the beginning of November, and completes two generations in one year. These consist of a long overwintering and a short summer generation, the former emerging from April to July, the latter from July to the beginning of November. *A. inopinatus* emerges throughout May-August. No hatching is found from December to August the next year. There is only one generation in one year.

During 1966 the life cycle of the benthic species of Ephemeroptera was studied at two localities in the Aurland River. The positions of the localities are shown on Fig. 1, marked Loc. 1 and Loc. 2, and more detailed maps of the stations, called TR and A_4, at which this work was carried out, are shown on Fig. 2 and Fig. 3. The River is characterized by the criteria given by Brinck (1949) for Northern rivers. Variations in water-flow during the investigation period are shown on Fig. 4.

METHODS

On each sampling station 15 samples were taken every month, 5 on sand bottom (A), 5 on stony bottom without moss vegetation (B), and 5 on stony bottom with a compact layer of moss (C). Because of the great number of individuals only a part of the samples were examined, as shown in Table I. The substrata mentioned above are seen on Figs. 5, 6 and 7. Samples were taken partly with a Surber-Sampler and partly with a Neill's cylinder (Macan 1958), both covering an area of approximately 0.1 m^2.

The collecting apparatus was made of plankton net size 250 μ. Sand, stones and moss were placed in a bucket. Larger stones and finer materials were washed and thrown away. The remains were preserved in 80 per cent alcohol, and total macroscopic fauna was sorted out under a binocular. The larvae of Ephemeroptera were measured in mm on a microscope slide. Measurements were taken from the anterior edge of clypeus to the base of caudal cerci. All larvae more than 1 mm in length were measured. Some larvae below 1 mm passed through the collecting net and were therefore excluded from the quantitative analysis. Water current and depth were measured every month. Samples were taken from 0 to 80 cm depth, and in the current range of 50 cm/sec. to 130 cm/sec. Care was taken to sample each of the three categories of substrata each month under the same current and depth conditons.

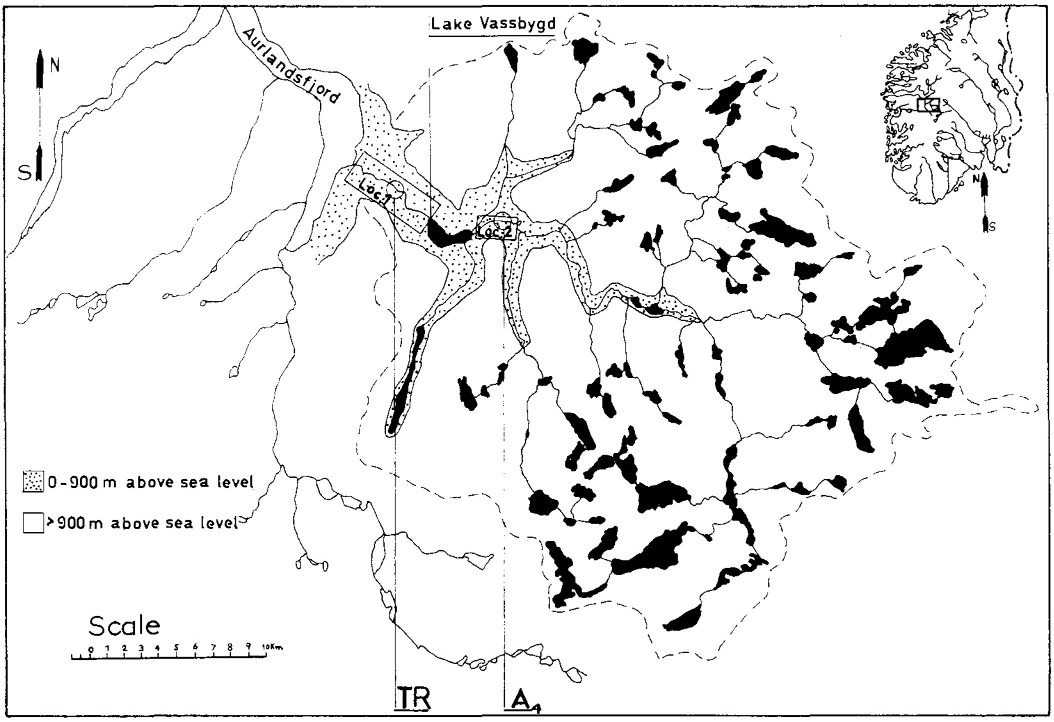

Fig. 1. The Aurland River system (within stippled line). The localities Loc. 1 and Loc. 2, and the stations TR and A_4

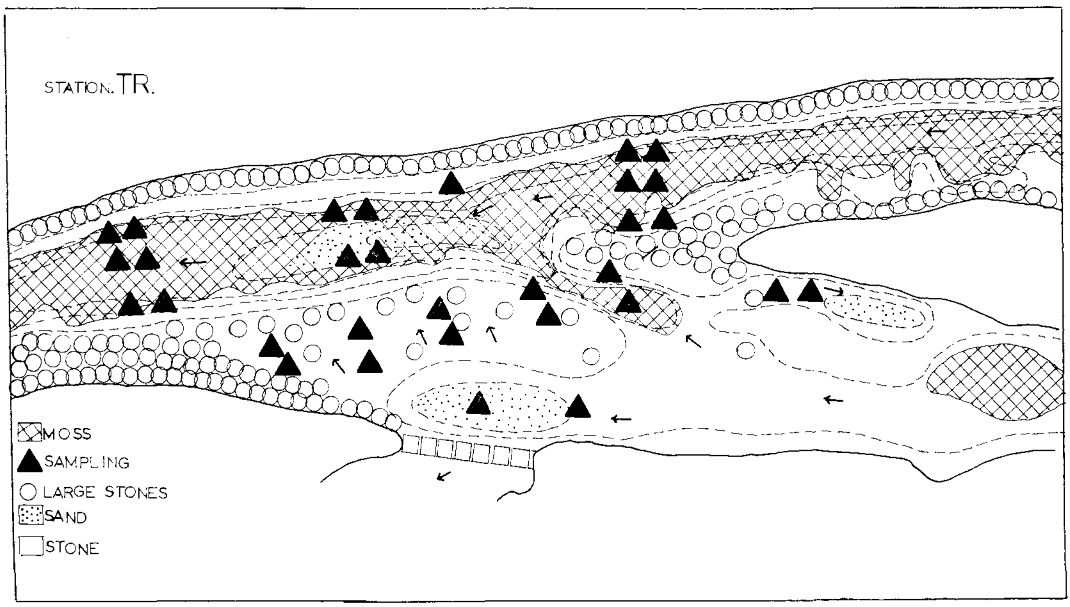

Fig. 2. Station TR, situated 30 m above sea level. Black arrows indicate direction of current flow. (Scale 1:2000)

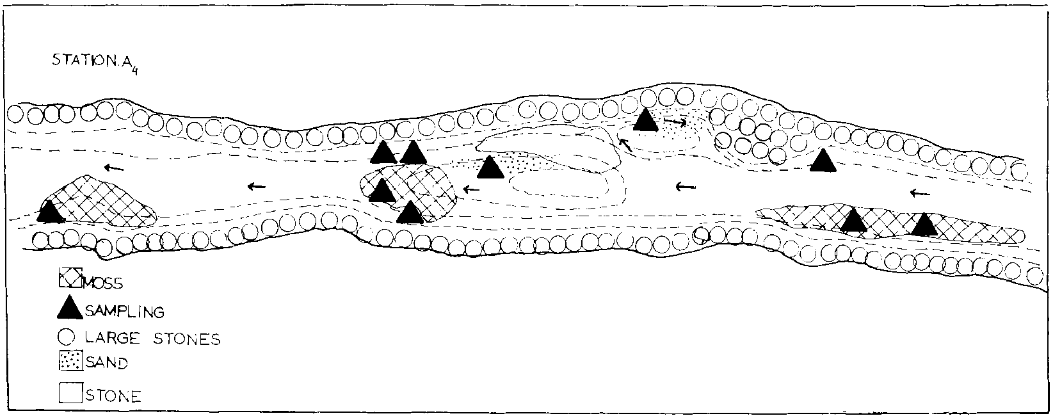

Fig. 3. Station A_4 situated 110 m above sea level. (Scale 1:2000)

The homogeneity of the sampling units will not be considered here.

THE SPECIES

Five species were found, *Leptophlebia marginata* (L.), *Leptophlebia vespertina* (L.), *Ephemerella aurivillii* Bengtsson, *Ameletus inopinatus* Eaton, and *Baetis rhodani* (Pictet). The first two species are not considered here, because they did not belong to the benthic species of the river.

The distribution of Ephemeroptera so far known for Norway is found in Brekke (1938, 1943, 1965), Grimeland (1963, 1965), Økland (1964) and Illies (1967). Regarding the species found by the author, only *A. inopinatus* have not previously been reported from Western Norway.

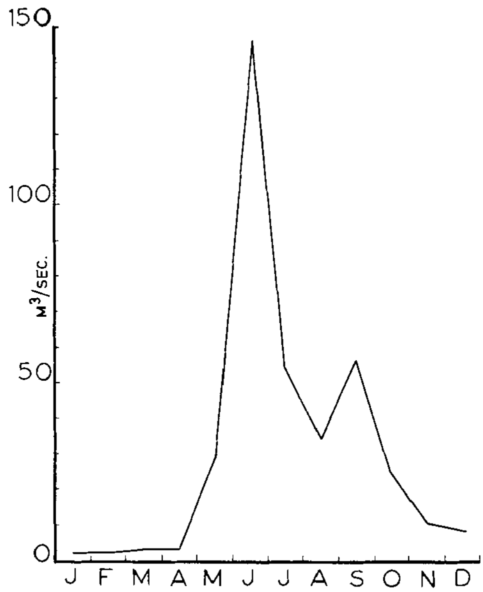

Fig. 4. The average water-flow every month during 1966 in m³/sec. measured at the outlet of lake Vassbygd.

THE LIFE HISTORY OF EPHEMEROPTERA

The life history of Ephemeroptera has been studied by Moon (1939), who estimated the growth-rate of two species of *Leptophlebia* and *Caenis horaria* (L.), and showed that there is a single brood each year in all three species. Rawlinson (1939) found two broods of *Ecdyonurus venosus* (Fabricius) a year, and found a marked seasonal variation in the growth-rate too. Harker (1952, 1953) studied the life cycle and growth-rates of four species, *Ecdyonurus torrentis* Kimmins, *Heptagenia lateralis* (Curtis), *Rithrogena semicolorata* (Curtis), and *Baetis rhodani* (Pictet), in a stream near Bolten. Because of the long period of emergence for *B. rhodani* and appearance of small larvae throughout the year he failed to determine the life cycle of this species. Macan (1957) examined *B. rhodani, Baetis pumiulus* (Burm.), *Ephe-*

Table I. *Number of samples examined and dates of sampling every month during* 1966 *at TR and* A_4

Station			TR			A_4			
Date		Substratum: A	B	C	A	B	C	Number of samples examined	Tested area in m²
Jan.	4.	5	2	2				9	0.9
	5.				5	5	5	15	1.5
Feb.	5.	5	5	5	5	5	5	30	3.0
Mar.	5.				5	5	5	15	1.5
	7.	5	5	5				15	1.5
Apr.	1.	5	5	5				15	1.5
	3.				5	5	5	15	1.5
May	4.	5	5	5				15	1.5
	5.				5	5	5	15	1.5
June	4.	5	5	5				15	1.5
	6.				5	5	5	15	1.5
July	4.	5	5	5				15	1.5
	5.				5	5	5	15	1.5
Aug.	4.	5	5	5				15	1.5
	5.				5	5	5	15	1.5
Sept.	3.	5	2	2				9	0.9
	5.				5	5	5	15	1.5
Oct.	1.	5	2	2				9	0.9
	3.				5	5	5	15	1.5
Nov.	4.	6	2	2				9	0.9
	6.				5	5	5	15	1.5
Dec.	20.	5	5	2				12	1.2
	21.				5			5	0.5
	22.					5	5	10	1.0

merella ignita (Poda), and *Paraleptophlebia submarginata* (Stephens). The life history of *A. inopinatus* has been studied by Gledhill (1959) in a little stream in the Lake District in England. As far as I know, nobody has studied the life cycle of *Ephemerella aurivillii*, but some knowledge about this species can be obtained from Bengtsson (1930), Tiensuu (1939), Södergren (1963), Ulfstrand (1967) and Illies (1967).

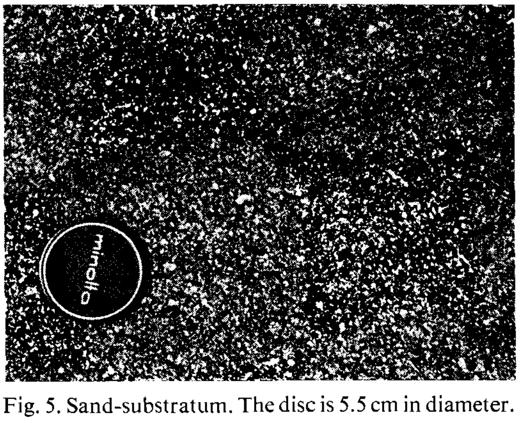

Fig. 5. Sand-substratum. The disc is 5.5 cm in diameter.

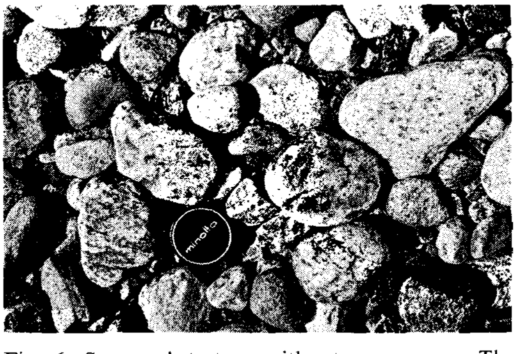

Fig. 6. Stone-substratum without moss-cover. The disc is 5.5 cm in diameter.

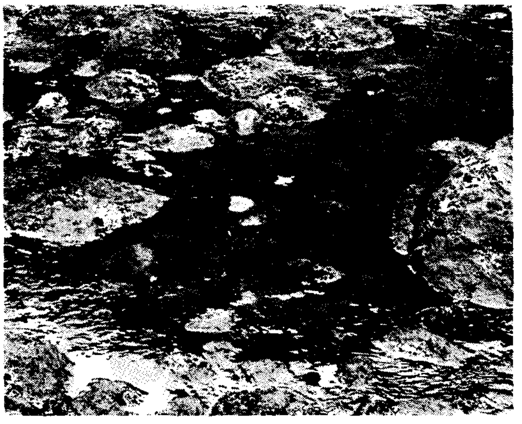

Fig. 7. Stone-substratum with moss-cover.

EPHEMERELLA AURIVILLII BENGTSSON 1908

A number of larvae and a few imagines and subimagines were collected on Station TR. It was not found in Loc. 2.

Both larvae and imagines agree with the descriptions of Bengtsson (1930). The number of specimens in each size group throughout the year is shown in Table II, and Fig. 8 shows the groups: small, half-grown and full-grown. The flight period is indicated by the black horizontal line, deduced from findings of larvae ready for emergence, subimagines and imagines. The results can be summarized as follows.

1) The flight period of *E. aurivillii* starts in the beginning of June and lasts to the middle of September with no clear peaks of emergence.

2) The first newly-hatched larvae are found from the beginning of August and the larvae are growing rapidly throughout the autumn.

3) Apparently there is a cessation of growth or a drop in the growth rate in December, January, February and March. Then the larvae grow rapidly again and reach the time of emergence towards the beginning of June. However, this can only partly be deduced from the data given, because they belong to two following generations, and it must be mentioned that nothing is known about the yearly fluctuation of the population density.

4) The natural death rate of the young larvae is high, reducing the population to half or less during one or two months.

5) The animals complete a generation in one year.

6) The subimagines are found early in the morning and the imaginal stage is reached 2 or 3 hours later. In the afternoon an upstream flying activity begins. The females are flying low over the water and eggs are dropped on the surface mostly in the middle of the river. Copulation has never been observed.

Discussion

The flight period of *E.aurivillii* is long, lasting for almost 4 months, compared with the two and a half months of *E.ignita*, and the 20 days of *E.notata*.

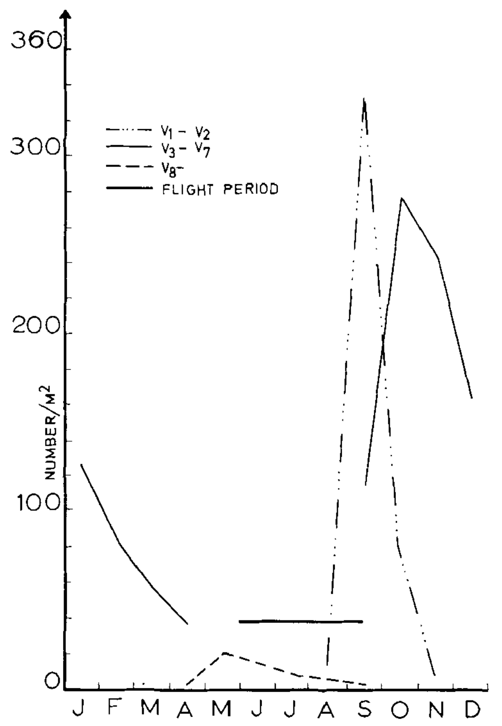

Fig. 8. Variation in number of *E. aurivillii* per m^2 at TR in the groups: small (V_1–V_2), half-grown (V_3–V_7), and full-grown (V_8–), based on monthly samples.

Table II. *Average number of* E. aurivillii *at station TR on substrata A, B, and C per m², and average number in each size group per m² based on the mean of the numbers on B and C. Size V of specimens in mm*

st. TR.		Average number per. m²						
Month	Subst.	A	B	C	$\frac{B+C}{2}$	$1 \leq V_1 < 2$	$2 \leq V_2 < 3$	$3 \leq V_3 < 4$
Jan.		2	0	250	125			
Feb.		2	0	164	82			
Mar.		4	0	112	56			
Apr.		4	2	74	38			
May		2	4	36	20			
June		0	18	12	15			
July		0	12	6	9			
Aug.		0	12	28	20	10	3	
Sept.		0	15	905	460	265	73	45
Oct.		2	0	710	355		78	85
Nov.		2	0	505	253		8	23
Dec.		4	0	326	163			
						$1 \leq$ small < 3		

Sawyer (1953) has shown that the flight period varies from place to place for the same species. This may be due to temperature differences. Brinck (1949) has shown that the emergence of many species of Plecoptera takes place progressively later and often the flight period becomes shorter in colder zones in Sweden.

This may be the case for Ephemeroptera too. But there is no reason to believe that temperature is the only factor regulating the flight period. Weather, water-flow and biotic factors as well as endogenous factors have to be considered regarding this question, see Remmert (1962) and Aschoff (1965).

The incubation period is variable, varying from 10 days in *Ephemera vulgata* (Schoenemund 1930) to 10 months in *E. ignita* (Macan 1961 and Pleskot 1958). The time spent in the egg stage cannot be determined exactly for *E. aurivillii*. But it may be about one month, as only one month elapses from the time the first larva is ready for emergence until newly-hatched larvae appear, unless the newly-hatched larvae are from diapause eggs laid in the autumn the year before. This is shown by Gledhill (1959) to be the case for *A. nopinatus*. But the diapause eggs of *A. nopinatus* hatched early in the spring, those of *E.aurivillii* in August. Why should the diapause last till August for the eggs of *E. aurivillii?* So it is possible that my suggestion of no diapause eggs for *E. aurivillii* is correct in this case. The exact death and growth rates cannot be estimated from the average of monthly catches and measurements as done by Harker (1952) and Illies (1952), because a) drifting of the specimens is not considered, b) the specimens below 1 mm are excluded from the material, and c) a delayed hatching or growth in the small stage invalidates the calculations. Therefore I think that the calculations of Illies and Harker are doubtful, because they have not taken into account these factors. Considering the death and growth rates of *E. aurivillii* it is therefore not possible to do more than gain an idea of these two.

Regarding copulation in other *Ephemerella* species, it takes place on land up to two hundred metres from the water edge (Kimmins and Frost 1943). This can be the case for *E. aurivillii* too. I was prevented from making observations that far from the water because

Table II *(Contd.)*

Average number in each size group per. m²							
$4 \leq V_4 < 5$	$5 \leq V_5 < 6$	$6 \leq_6 < 7$	$7 \leq_7 < 8$	$8 \leq_8 < 9$	$9 \leq V_9 < 10$	$10 \leq V_{10} < 11$	$V_{11} \geq 11$
43	70	13					
36	27	19					
11	28	17					
	5	28	3	2			
				2	3	15	
					5	7	3
						3	6
						4	3
60	13					3	3
105	48	40					
78	40	105					
57	34	72					
3≤ half grown <8					full grown ≥8		

of the cultivated land in the area. The same mode of egg depositing is also found in American and other European *Ephemerella* species (Smith, 1935, Jensen 1961).

BAETIS RHODANI (PICTET) 1844

This is the most abundant species in the Aurland River both in Loc. 1 and Loc. 2. The larvae agreed completely with the discriptions by Müller-Liebenau (1965), and the imagines with that of Kimmins (1954). The number of specimens in each size group throughout the year is shown in Table III, and Fig. 9 shows the groups: small, half-grown and full-grown. The flight period is indicated as for *E. aurivillii.* This result is based on collections from TR, but for comparison some data for *B. rhodani* on A_4 are shown in Table III. The results can be summarized as follows.

1) The flight period of *B. rhodani* starts at the beginning of April and lasts to the begin-

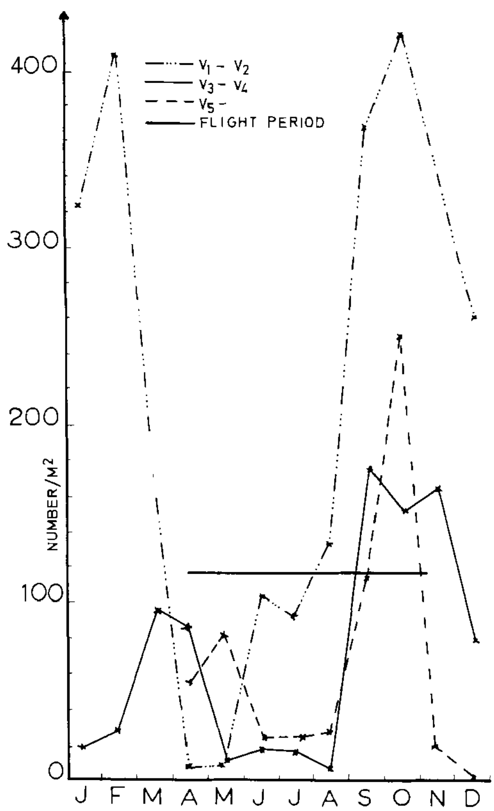

Fig. 9. Variation in number of *B. rhodani* per m² at TR in the groups: small (V_1–V_2), half-grown (V_3–V_4), and full-grown (V_5–), based on monthly samples.

Table III. *Average number of* B. rhodani *at station TR and A_4 on substrata A, B, and C per m², and average number in each size group per m² at TR based on the mean of the numbers on B and C. Size V of specimens in mm*

st. TR.	Average number per m²				Average number in each size group per m²						st. A_4	Average number per m²		
Month	Substr. A	B	C	$\frac{B+C}{2}$	$1\leq V_1<2$	$2\leq V_2<3$	$3\leq_3<4$	$4\leq V_4<5$	$5\leq V_5<6$	$V_6\geq 6$	Subst.	A	B	C
Jan.	40	495	185	340	218	105	15	3			Jan.	20	242	104
Feb.	32	660	210	435	301	108	23	3			Feb.	16	374	118
Mar.	44	380	140	260	109	53	46	52			Mar.	16	146	50
Apr.	30	260	30	145		6	77	8	3	51	Apr.	10	136	16
May	64	180	20	100	1	8	5	2	20	64	May	14	136	22
June	4	200	86	143	101	3	14	2	6	17	June	4	88	42
July	2	155	105	130	73	20	10	5	8	15	July	0	94	68
Aug.	4	130	200	165	130	5	3	0	20	8	Aug.	0	80	74
Sept.	6	1200	110	655	300	68	85	90	78	35	Sept.	10	636	56
Oct.	48	1470	175	823	348	73	23	130	148	103	Oct.	26	946	108
Nov.	105	845	205	525	240	105	80	83	18		Nov.	82	530	164
Dec.	80	430	250	340	215	45	63	15	3		Dec.	64	260	144
					$1\leq$ small <3		$3\leq$ half grown <5		full grown ≥ 5					

Table IV. *Average number of* A. inopinatus *at station A_4 on substrata A, B, and C per m², and average number in each size group per m² based on the mean of the numbers on B and C. Size V of specimens in mm*

st. A_4	Average number per m².						
Month Substr.	A	B	C	$\frac{B+C}{2}$	$1\leq V_1<2$	$2\leq V_2<3$	$3\leq V_3<4$
Jan.	0	8	10	9		2	
Feb.	2	6	10	8		1	
Mar.	2	6	8	7			
Apr.	0	4	6	5			
May	0	8	4	6			
June	0	16	2	9			
July	0	26	8	17			
Aug.	0	32	4	18			
Sept.	0	4	2	3	3		
Oct.	0	10	12	11	6	2	3
Nov.	0	4	20	12	7	3	1
Dec.	0	8	2	5		3	
					$1\leq$ small <3		

ning of November. Two peaks appear, one in May and another in October.

2) Newly hatched larvae are found throughout the year, except in April and the beginning of May, and the larvae are growing rapidly during spring, summer and autumn.

3) As for *E. aurivillii* there is a drop in the growth rate in the winter.

4) As for *E. aurivillii* the death rate is high.

5) The animals complete two generations in one year.

6) The subimagines are found in the morning, and the imaginal stage is reached the same afternoon. Copulation takes place near the water edge or some distance from the water.

Discussion

The analyses made by Macan (1957), Pleskot (1958) and Harker (1953) on *B. rhodani* show almost the same pattern. But there are some differences. This species has a longer flight period in Great Britain than in Aurland. In England newly hatched larvae also are found in April, but this size group is extremely low in April, as only 3 specimens in the smallest group were found by Macan. In the preceding month he found 68 specimens and in the following 425. These differences can be explained by the longer flight period in Great Britain, which causes an overlapping of the two generations. Macan (1957) also says that there are two generations in one year for *B. rhodani*, but Illies (1959) has shown that eggs of *B. rhodani* remain unhatched for a long time. If some eggs laid in the autumn do not hatch before May of the next year, there could be reason to believe that there is only one generation in one year. But why should eggs not hatch in April, when they are hatching in January, February and March? I think that all the eggs laid in the autumn are hatched during October-March. Therefore no newly hatched larvae are to be found in April and the beginning of May. The peak of imagines in May give rise to a new generation that go through the larval stage during the summer and gives rise to a peak of imagines in October. Furthermore, these imagines produce a new generation of larvae that cannot complete the larval stage the same year, because of the decreasing temperature and food shortage. These larvae produce the imagines appearing in May.

Table IV *(Contd.)*

Average number in each size group per m²							
$4 \leq V_4 < 5$	$5 \leq V_5 < 6$	$6 \leq V_6 < 7$	$7 \leq V_7 < 8$	$8 \leq V_8 < 9$	$9 \leq V_9 < 10$	$10 \leq V_{10} < 11$	$V_{11} \geq 11$
5			2				
1		6					
	3		4				
	2	2	1				
			1	3		1	1
				2		2	5
							17
							18
		1					
	1		1				
3≤ half grown <8				full grown ≥8			

AMELETUS INOPINATUS EATON 1887

Many larvae and a few imagines were taken on station A4, the species was not found at Loc. 1. The larvae agreed closely with the description by Macan (1961), and the imagines with the description by Kimmins (1954). The number of specimens in each size group throughout the year is shown in Table IV, and Fig. 10 shows the groups, small, half-grown and full-grown. The material is small, due to the fact that *A. inopinatus* had a much denser population higher up along the River, and that the place where the samples were taken lay on the limit of the population range. This has caused some peculiarities in the results obtained. But some information may be drawn from the data.

1) The flight period of *A. inopinatus* starts at the beginning of May and lasts until the end of August.

2) No newly-hatched larvae are found from December to August the next year.

3) The growing periods are almost identical with those of *B. rhodani* and *E. aurivillii.*

4) Nothing can be said about the death rate, because the drifting of animals from places with higher population density gives an increasing number of animals per m^2 during the summer, and it is probable that the drift has a larger influence on the samples taken at the limit of the population range then on samples taken in places with a dense population.

5) The animals complete a generation in one year.

6) Copulation and oviposition were not observed.

Discussion

Gledhill (1959) found that *A. inopinatus* has an emergence period from May to late August, and grows throughout the winter. This agrees with my observation. He found two peaks of larvae in each size group, and said that they appear to be due to two bursts of hatching, one in the autumn and the other at the beginning of the year. This cannot be deduced from the data obtained by the author.

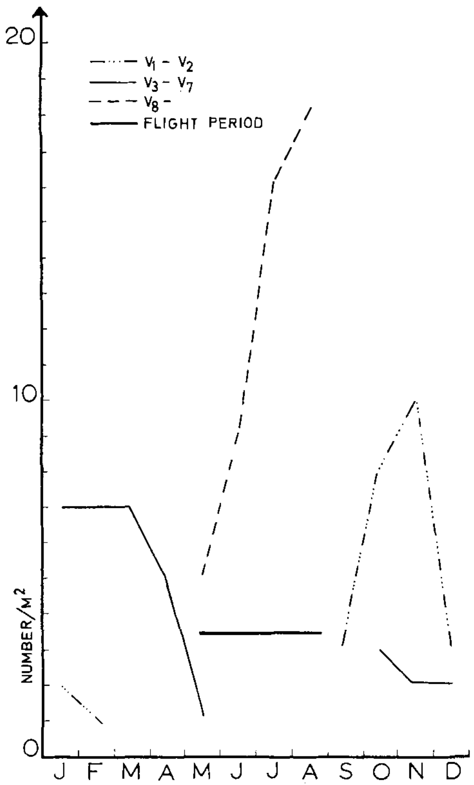

Fig. 10. Variation in number of *A. inopinatus* per m^2 at A_4 in the groups: small (V_1–V_2), half-grown (V_3–V_7), and full-grown (V_8–), based on monthly samples.

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