The Life-Cycles of *Simulium vittatum* Zett. in Iceland Lake-Outlets.

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VMST-R/87008

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Introduction

This paper on the life cycles of Simulium vittatum Zett. in Iceland is part of a investigation that concerns the life history events of blackflies in Iceland in relation to both biotic and abiotic factors (Jóhannsson 1986). As background, a comprehensive picture of the distribution and habitat preferences was sought by collecting blackflies from full range of habitat types. S. vittatum is common and widespread species, found throughout North America, including Alaska and extending north and east into Iceland and the Faroe Island (Peterson 1977). The taxonomy and geographical distribution of Icelandic blackflies have been dealt with in a number of papers. All this information is summarized in a paper by Peterson (1977).

Study Area

The main part of the fieldwork was directed on two outlets, River Bugda SW-Iceland and River Laxá NE-Iceland. Other outlets included in this study are all located in SW-Iceland. The R. Laxá flows from an euthrophic lake, Lake Mývatn (65^{o} 40' N, 17^{o} 00' W; altitude 277 m a.s.l.), with one of the highest levels of production of blackflies ever measured (Gíslason 1985, Gíslason and Jóhannsson 1985). The L. Mývatn area has been under intensive biological investigations for more than 15 years (see Jónasson 1979). Since research started there around 1970, biological changes have occurred in the area (Gardarsson 1979, 1980, Gíslason and Jóhannsson 1985). R. Laxá flows from the southwest part of the lake in 3 channels. At the outlet from L. Mývatn a mean flow of 32 m^3 sec^{-1} was recorded (Rist 1979). The water flow in R. Laxá is extremely stable and almost no floods occur (Rist 1979). Three sampling sites were selected in the upper part of the R. Laxá; station 1 (Midkvisl) near the river outlet from L. Mývatn; station 2 (Helluvad) about 4 km below the outlet; station 3 (Thverá) about 22 km downstream from the outlet. These sites are similar in terms of maximum water depth (1-1.2 m), water velocity (1 m sec^{-1}) and water temperature. The bottom consists mainly of porous lava rocks. S. vittatum is the dominant benthic invertebrate of the river, about 1/2 of the numbers and 2/3 of the biomass (Gíslason 1985). The numbers and biomass of S. vittatum changed rapidly during the study period 1977-1984 (Gíslason 1985, Gíslason and Jóhannsson 1985).

The R. Bugda is the outlet of L. Medalfellsvatn SW-Iceland (60^{o} 20' N, 21^{o} 35' W; altitude 46 m a.s.l.) and runs about 2.7 km into R. Laxá in Kjós. Additional flow in the R. Bugda is the R. Daelisá. Fluctuation in flow are great, discharge generally being greatest in the spring and in the autumn. For 1982 the flow rate ranged from 1.0 m^3 in March to 22 m^3 in February (Jóhannsson 1986). The river never freezes near its sources, but is often covered with ice further downstream, usually from November to March. Samples were taken at four stations in R. Bugda. Station 1 is just below the L. Medalfellsvatn; station 2 is 0.7 km below the lake; station 3 is 1 km below the outlet from L. Medalfellsvatn and station 4 is 2.4 km downstream from the lake. The stream bed in the upper part of the river consists of boulders, sand and gravel in between but in the lower part the stream bed is very uniform, mainly small stones and gravel. Difference in water temperature between the four sampling stations was small. In 1982-1983, the annual production of S. vittatum was about 1655 g wet weight m^{-2} at station 1. The production at the lower sampling sites was considerably lower than at station 1; down to 69.9 g wet weight m^{-2} yr^{-1} at station 4 (Jóhannsson 1986).

Methods

To obtain quantitative samples of blackfly larvae, 6-10 stones were removed at random from the bottom of the river and their surface being washed in the river water with a soft brush (Carlsson et al. 1977, Gíslason 1985). Window traps were used to catch adults. The traps were made of transparent plexiglass with windows facing both upstream and downstream (Jónsson et al. 1986). The trays were emptied every 7-15 days, from early May until October. Adult females were dissected and their ovaries removed for egg counting. Body size was estimated from measurements of wing length with a micrometer eyepiece in a binocular microscope. By observing the distribution and quantity of fat-body in the adult females, it is possible to achieve some degree of "age determination" in the blackflies (Davies 1955). Females caught in the window traps were divided into four main groups on dissection, namely, those with visible fat-body, those containing mature eggs, and those with no fat-body (or small amount in the posterior abdominal segments) and those containing blood. Flies in the first group i.e. those with fat-body are newly emerged flies (less than 4-5 days old). Flies with no fat-body (or small amounts) have already laid their eggs and are probably searching for a blood meal.
Water samples were collected following the method of Egglishaw and Shackley (1971). A measured volume of water from each sampling site (3-5 replicates) was filtered on to 0.45 um Millepore membrane filters. The filters were cleared in immersion oil and mounted in euparal. The relative proportion by area of constitute particles was estimated microscopically along randomly chosen transect across the filter, with the aid of a graticule eyepice. A phase contrast microscope was used. Larvae were removed qualitatively for gut-contents analysis from stones and vegetation and preserved immediately in 70% alchol. The guts of preserved larvae were dissected individually out in Petri dishes containing distilled water. The sample was then shaken vigorously to separate the constituent particles. Wotton (1977) has shown that there

is no significant difference in the particle size between this procedure and the fashionable use of sonification. Samples were filtered through membrane filters (0.45 um), cleared in immersion oil and mounted in Euparal.
Juvenile salmon was collected by electrofishing. The stomach contents were analyzed by visual estimation of area of the food items spread in a shallow dish under a binocular microscope. Only stomachs that were well filled or contained freshly ingested food were used.

Results and Discussion

Simulium vittatum is common all over Iceland (Fig. 1). This species is abundant in lake-outlets and usually the only blackfly species found in that habitat. It is difficult to demonstrate any habitat preferences in the case of S. vittatum. This species was collected right across Iceland, from many different types of streams, ranging from cold streams of all sizes to thermal rivers. S. vittatum larvae were found to tolerate temperature up to 30 °C. From this it is clear that among other factors, a wide range of temperature tolerance might explain the wide distribution of the species.

The form of life cycle, that is most common for S. vittatum in lake-outlets in Iceland is basically bivoltine. Eggs from the summer generation hatch in late autumn and the larvae develop slowly until late winter or early spring. Pupae are generally found in late April and May, adults begin to emerge in late May or early June (Fig. 2). The eggs from the winter generation hatch in June and the adults from that generation begin to emerge in August forming the major emerging period for the summer generation (Fig. 2).

The number of generations per year of S. vittatum can be different between localities in the same river and the numbers may vary between rivers. In R. Bugda SW-Iceland, S. vittatum had two generations or more per year (Fig. 2), but on the other hand within a short distance from R. Bugda, in R. Laxá in Kjós only small proportion of the S. vittatum population had two generations per year (Fig. 3). This difference is probably mainly due to low water temperature that resulted in shorter growing period of the larvae in R. Laxá in Kjós compared to the larvae in R. Bugda. In R. Laxá NE-Iceland there were at least two generations per year at station 1, at station 2 only small proportion of the population had two generations, but further downstream there was only one generation per year (Gíslason and Jóhannsson 1985). It was also found that the numbers of generations may vary in the upper part of the river between years in connection with food supply and possibly water temperature.

The proportion of material found in the guts of S. vittatum larvae (Fig. 4) tended to correspond to the proportion of material carried in the river water. After examining the food of blackfly larvae in the R. Laxá it is concluded that the blue-green alga A. flos-aquae provides a large proportion of the resource maintaining the huge larval population in the river. In 1977 and again in 1983-1984, the A. flos-aquae dominated the seston in the R. Laxá (Fig. 5), but 1979-1982 this alga was hardly found in the water samples from R. Laxá. During the years of low amount of A. flos-aquae, smaller proportion of the S. vittatum population in the upper part of R. Laxá had two generations per year and the summer generation produced smaller adults than during years when the A. flos-aquae was present in large quantities (Fig. 6). Small proportion of S. vittatum population at station 1 in R. Laxá might have up to three generations per year, mainly depending on the food availability. This can be seen in the numbers of newly emerged flies caught in the window traps at station 1 and 2 in R. Laxá (Fig. 6).

The most striking difference in the life history pattern of S. vittatum in Iceland is the difference that was found within the bivoltine groups, mainly due to difference in synchronization among populations of the species. The summer generation in R. Laxá NE-Iceland results from more synchronous hatch of larvae than that was found in the summer generation in the rivers in SW-Iceland, were continous hatching of larvae occurred through the summer (Fig. 7). The results from R. Laxá also show that this synchronization can be altered; this being especially noticeable in the cold summer of 1979. In this case low water temperature affected the synchronization of the population by prolonging the pupal stage i.e. most of the population had reached the pupal stage at the same time, resulting in more synchronous emergence of adults laying eggs forming the summer generation. Synchronization may also vary between species. Wotton (1982) showed that two species in the same river, Simulium noelleri and S. tuncatum showed different synchronization in larval hatching of the second summer generation. The second summer generation of S. noelleri resulted from a synchronous hatch of larvae and this was in contrast with the second summer generation of S. truncatum where continous hatching from eggs occurred. The way of overwintering may be an important factor determining the synchronization of a population and large variation in adult size may be the result of species having poorly synchronized life history (Corbet 1957). It is feasible to postulate that there is a difference in the rate of growth of larvae at a low temperature that results in greater synchronization of the spring emergence. S. vittatum overwinters in Icelandic rivers in several instars and size differences are reduced due to difference in growth rates of larvae of different size in the spring. However, there is usually an emergence delay of 3-4 weeks for adults of the winter generation, resulting in difference of adult sizes of the summer generation (Fig. 6), both due to difference in duration of the life cycle and difference in both biotic and abiotic factors, affecting the various cohorts of the summer generation.

Adult females of *S. vittatum* are able to mature a first batch of eggs without taking a blood meal (Chutter 1970). After they have laid the first egg batch, surviving females need to search for a blood meal if further clutch are to be produced. However, it was often found that small proportion of the females had considerable fat left in the abdomen after laying the first egg batch. These females were often starting to produce the second egg batch. It is therefore likely that small proportion of the *S. vittatum* females may produce a second batch without having a blood meal; the second egg batch being considerable smaller in egg numbers (Table 1). At station 1, in R. Bugda in June 1983, approximately 23% of the females found with mature eggs would fall into this group.

Blackflies are important food for juvenile salmon in R. Bugda (Fig. 8). High density and better growth of juvenile salmon may be correlated with the production of *S. vittatum* in the river (Einarsson 1986).

Acknowledgements

Many people have helped with this research. In particular, I thank Dr. G. M. Gíslason and Prof. A. Gardarsson, Dr. Á. Einarsson, Institute of Biology, University of Iceland and Mr. S. M. Einarsson, Mr. Á. Ísaksson and Mr. T. Gudjónsson, the Institute of Freshwater Fisheries for their assistance during different stages of the study. I wish to thank Dr. A. J. McLachlan, The University of Newcastle upon Tyne, for his advice and encouragement whilst I was working on my Ph.D. thesis under his supervision.

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Table 1.

Mean number of mature eggs per female S. vittatum caught in a window trap at station 1 in River Bugda 1982.

1 F= females producing their first batch of eggs
2 F= females producing their second batch of eggs.
n= number of flies

Date	1 F eggs (n)	2 F eggs (n)
10 June	221 (14)	91 (5)
19 June	293 (12)	73 (6)
9 July	292 (12)	92 (3)

Text to Figures

Fig. 1. Distribution of Simulium vittatum Zett. in Iceland. The map is based on 10 x 10 km squares.

Fig. 2. Mean number of S. vittatum caught per day in window traps at stations 1-4 in R. Bugda in 1983.

Dark areas: males

Open areas: females.

Fig. 3. Frequency histograms for overall length categories of larvae of S. vittatum and the proportion of pupae from R. Laxá in Kjós in 1982.
n= number of larvae measured. p= proportion of pupae (%)
Length categories: 1= < 1.0 mm overall length; 2= 1.1-2.0 mm etc.

Fig. 4. Average percentage composition of gut contents of S. vittatum larvae from station 1 in R. Laxá NE-Iceland for 1977, 1978 and 1984.

Fig. 5. Average numbers of A. flos-aquae and diatom cells per litre og river water from station 1 in R. Laxá NE-Iceland for May-October 1978-1984.

Fig. 6. A:"Age determination" of female adults of S. vittatum caught in window traps at station 1 (1977, 1978, 1982) and station 2 (1978) in R. Laxá NE-Iceland.
Group 1= newly emerged flies (with visible fat-body in the abdominal segments).
Group 2= flies containing mature eggs.
Group 3= flies with no or very little fat-body in the abdominal segments.
Group 4= flies containing blood.

B: Mean wing length of female adults of S. vittatum caught in window traps at station 1 (1977, 1978, 1982) and station 2 (1978) in R. Laxá NE-Iceland.
Vertical bars= 95% confidence limits. n= number of flies measured.

Fig. 7. Frequency histograms for overall length categories of larvae of S. vittatum and the proportion of pupae at station 1 in R. Bugda 1982.
n= number of larvae measured. p= proportion of pupae (%).
Length categories: 1= < 1.0 mm overall length; 2= 1.1-2.0 mm etc..

Fig. 8. Mean percentage volume of the stomach contents of juvenile salmon from R. Bugda SW-Iceland.
n= number of stomachs.
Ou= station just below L. Medalfellsvatn. 1-4= stations 1-4 in R. Bugda.

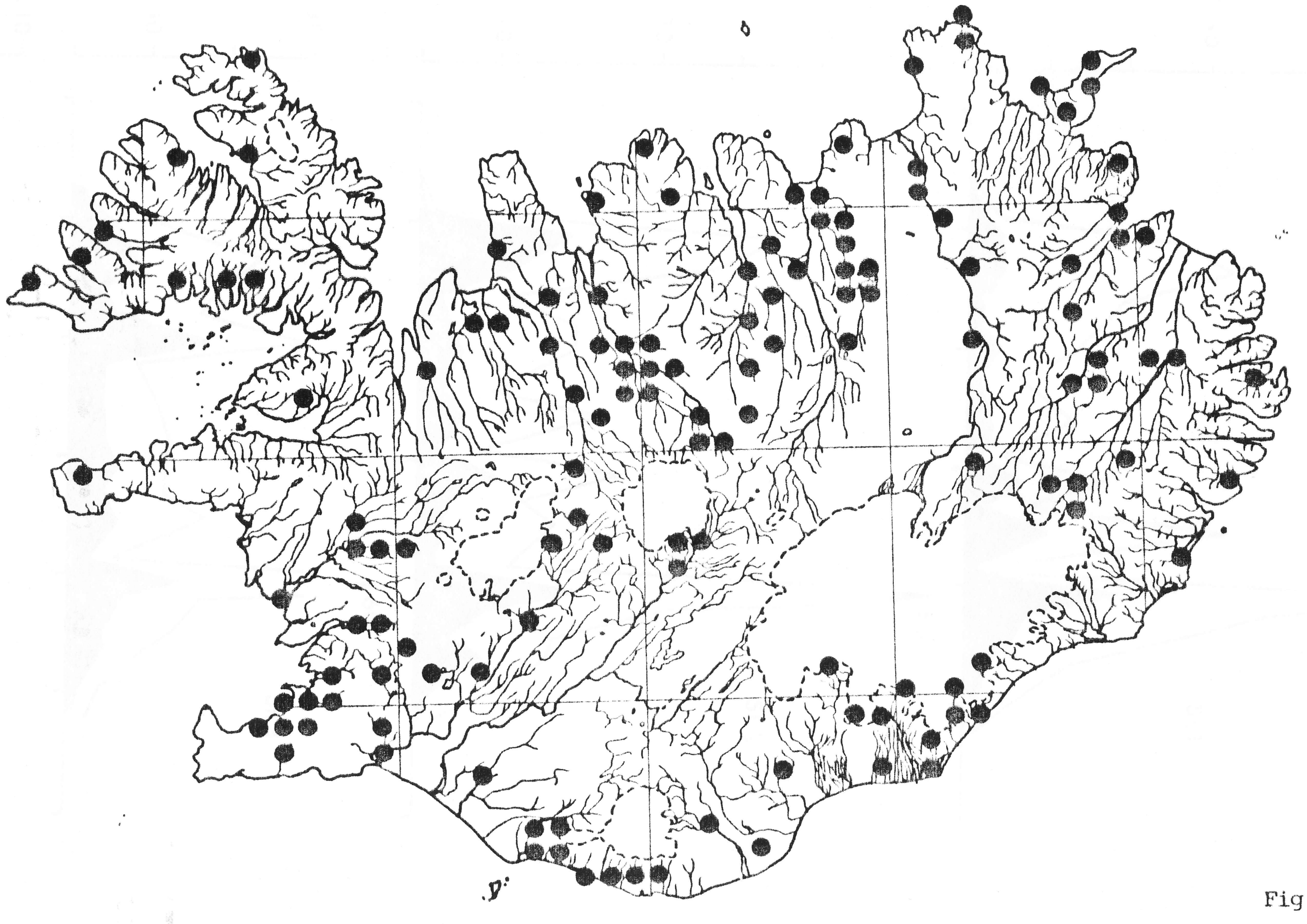
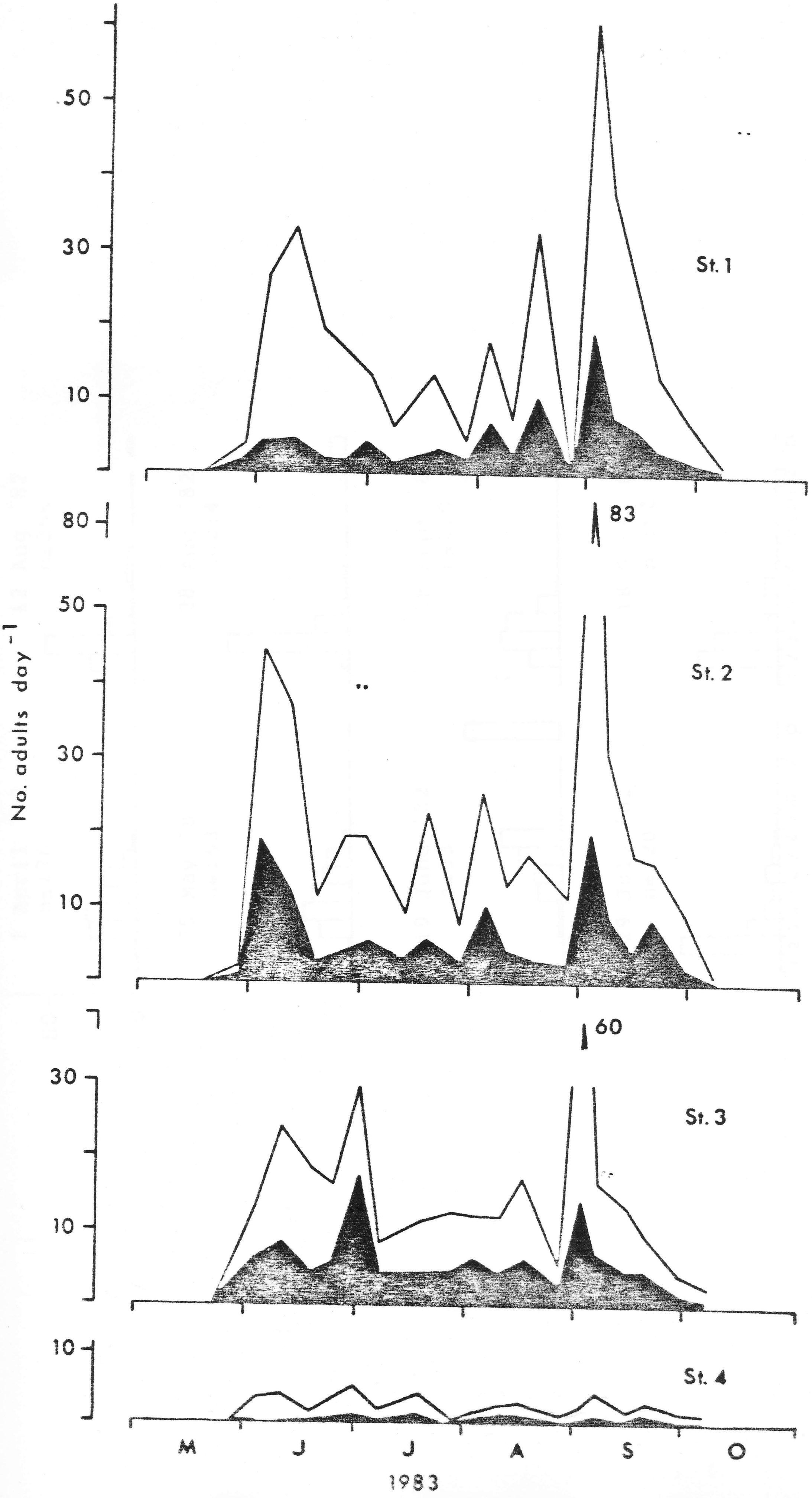
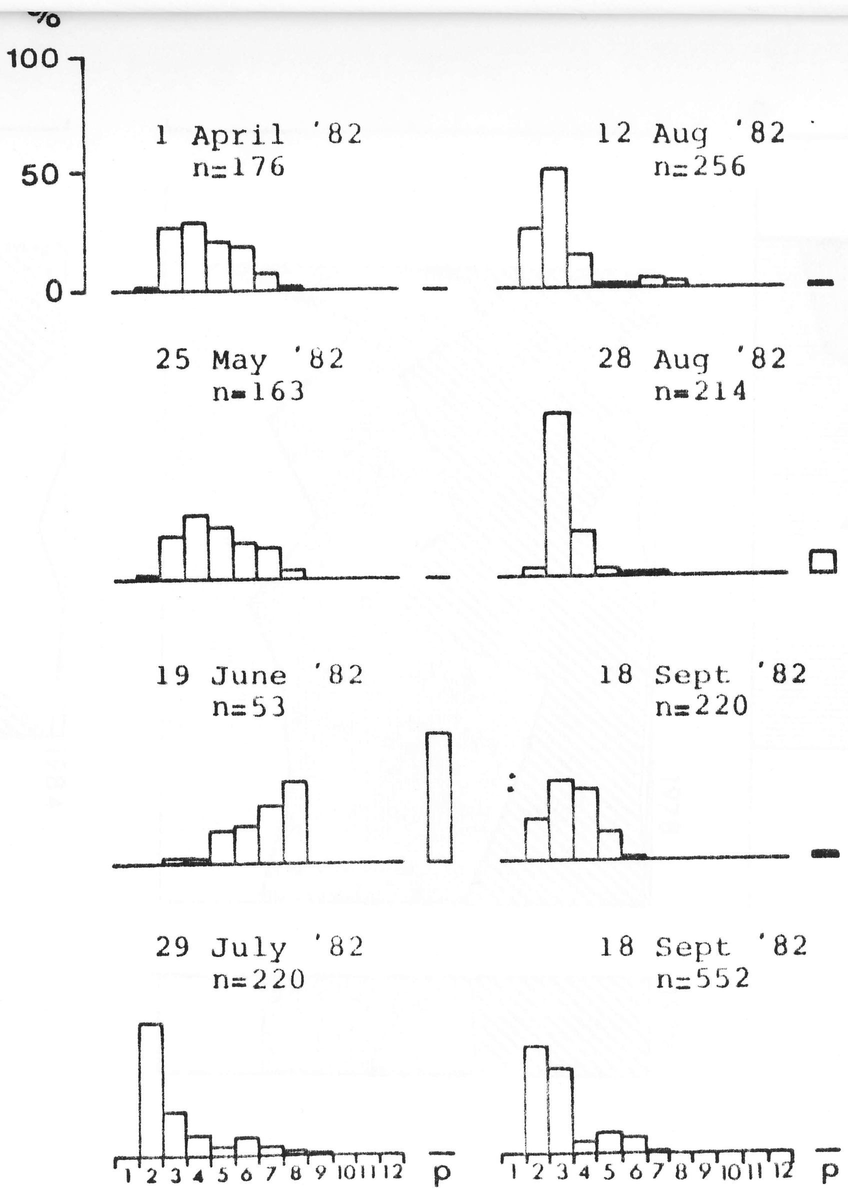


Fig. 1. V. Jóhannsson

Fig. 2.   V. Jóhannsson





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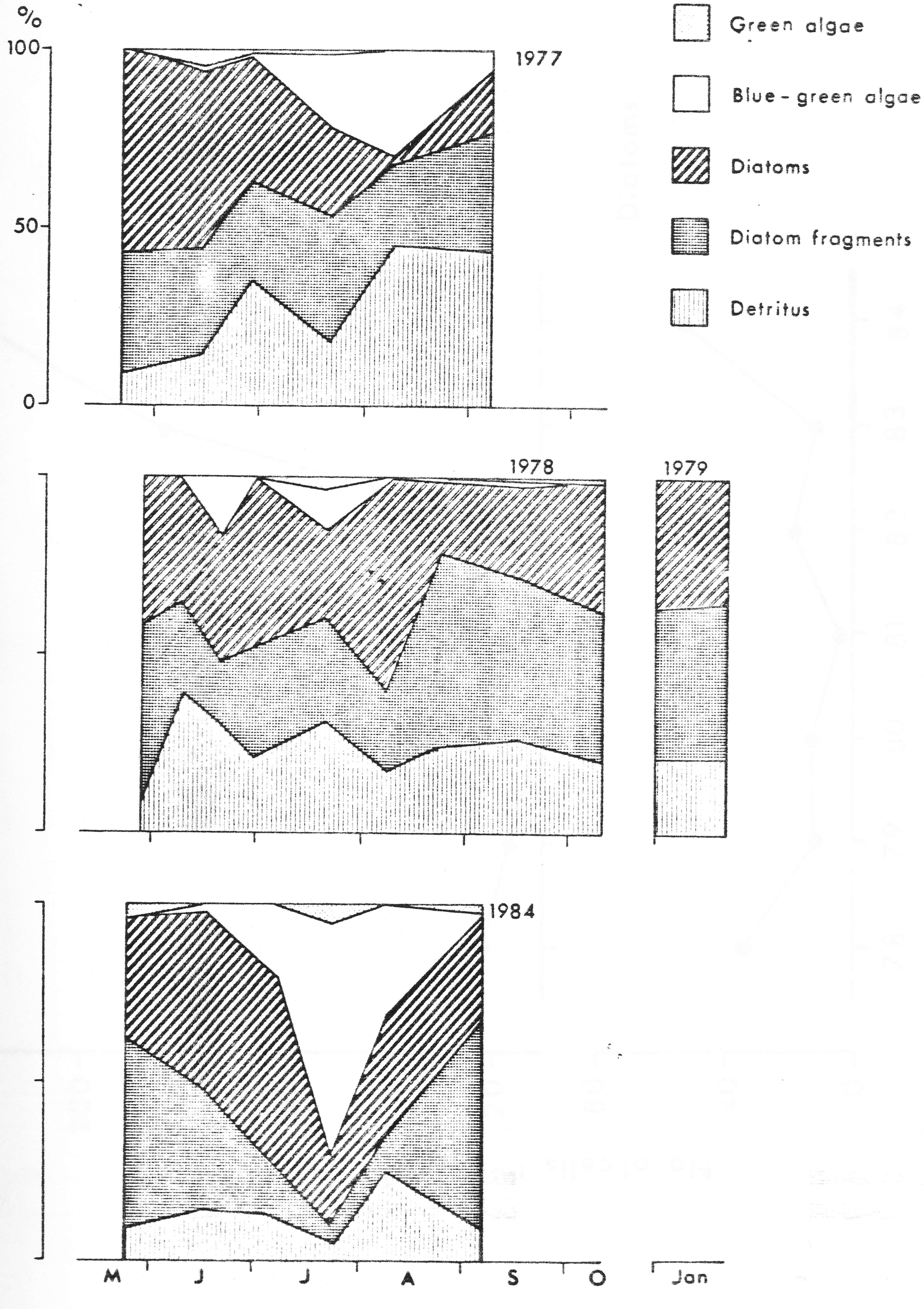

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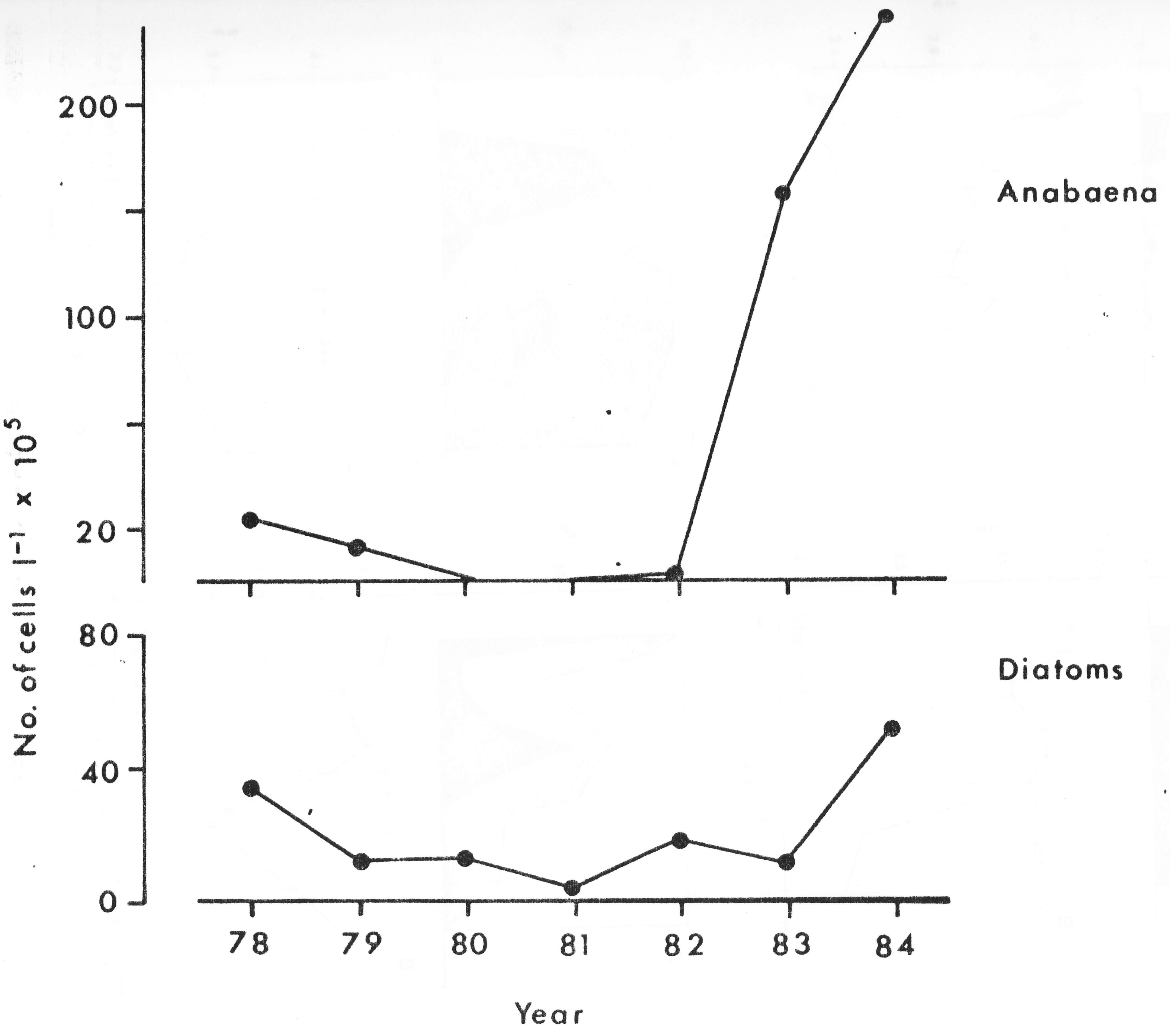

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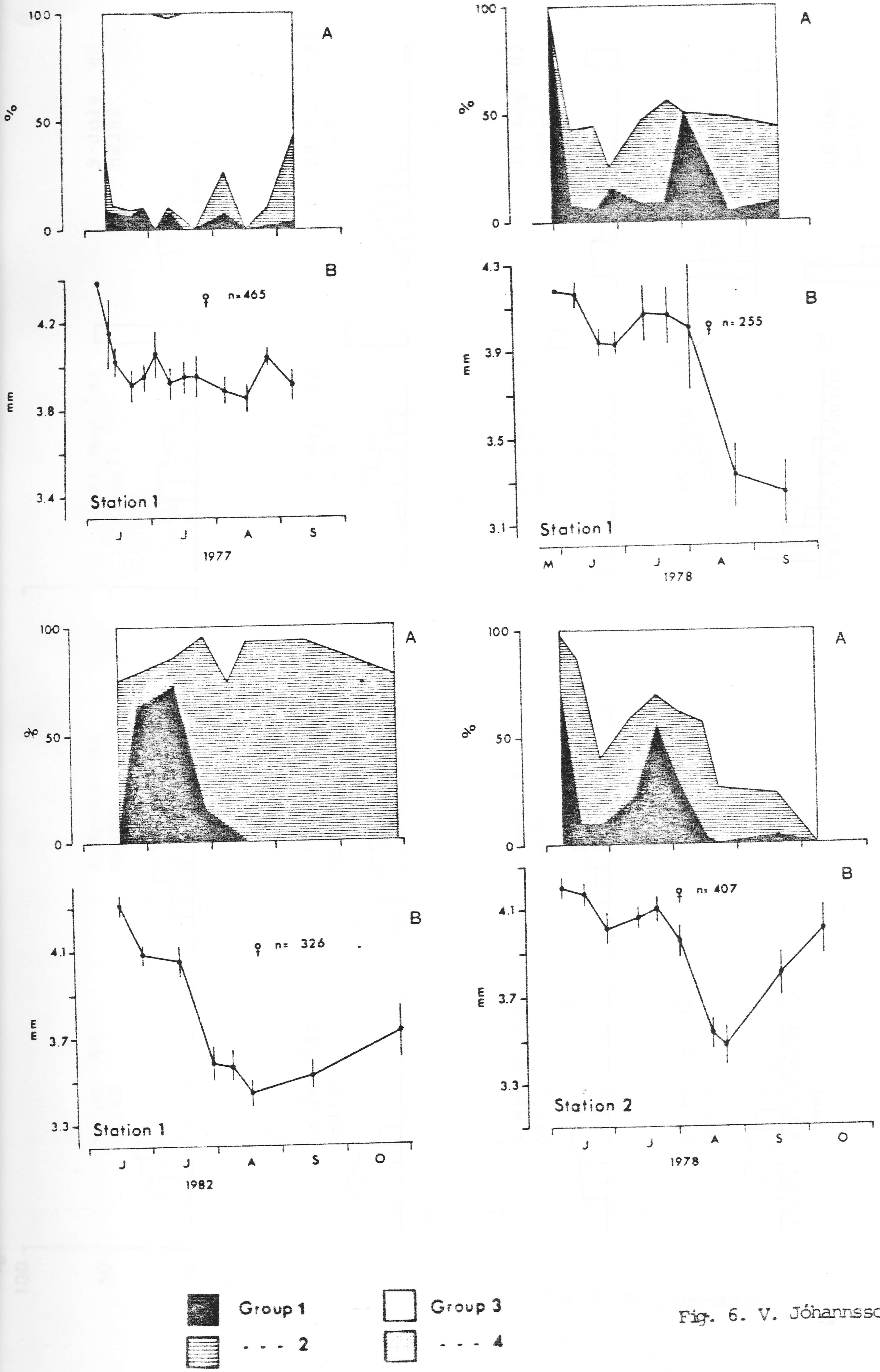

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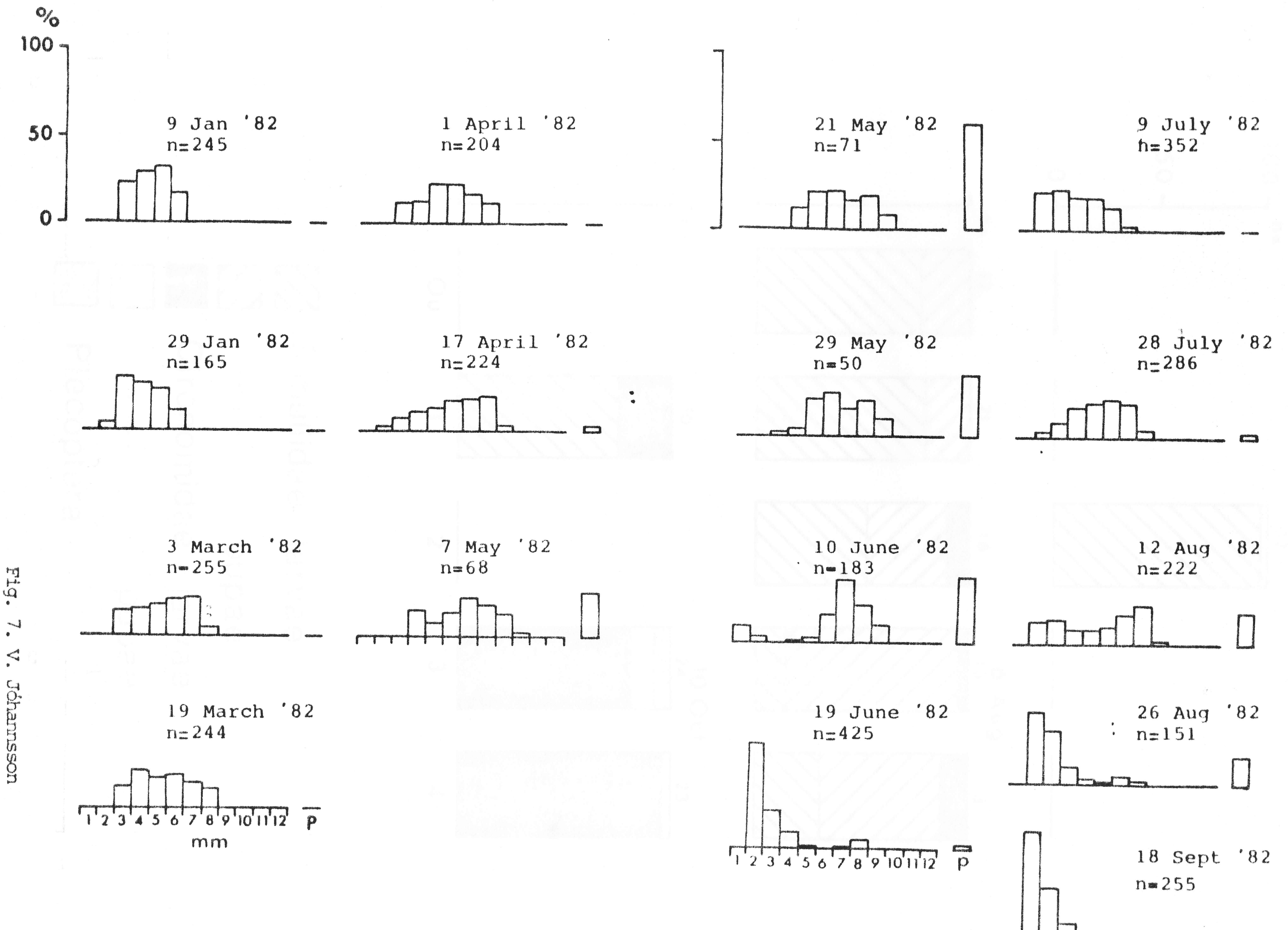

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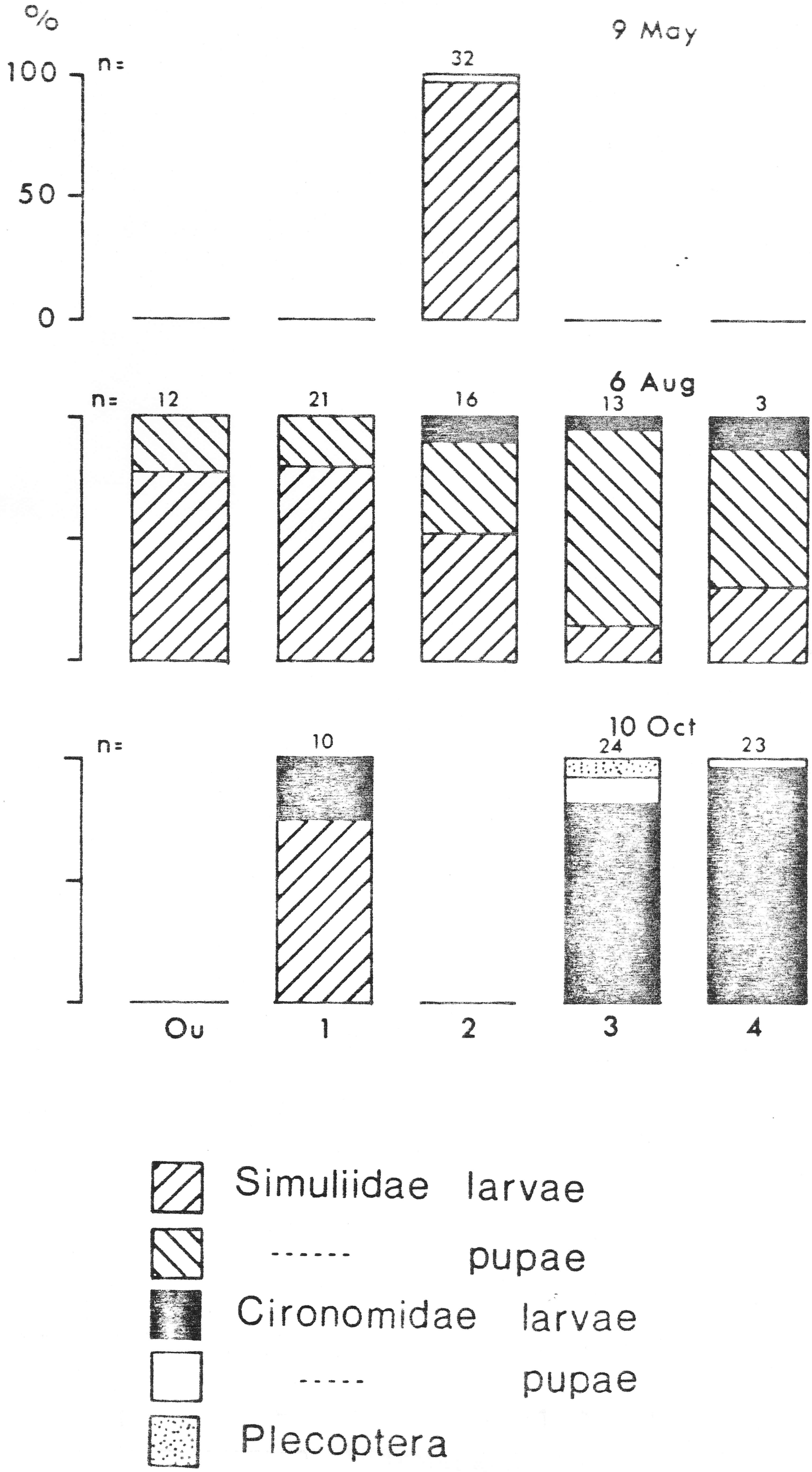

Fig. 8. V. Jóhannsson

E1