SOME ASPECTS OF THE LIFE HISTORY AND REPRODUCTIVE BIOLOGY OF **GERRIS REMIGIS** SAY AND **GERRIS BUENOI** KIRKALDY (HETEROPTERA) ON THE AVALON PENINSULA OF NEWFOUNDLAND

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Some aspects of the life history and reproductive biology of *Gerris remigis* Say and *Gerris buenoi* Kirkaldy (Heteroptera) on the Avalon Peninsula of Newfoundland

by

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Specimens of Gerris remigis Say and Gerris buenoi Kirkaldy were studied in the field and laboratory. Life history, ovarian cycle and changes in weight were studied in the field or from field specimens while egg and nymphal development, reproductive diapause and winter inactivity were studied in the laboratory.

Adults of both species emerged the first week of August 1974, entered obligatory reproductive diapause and inactivity in the fall and resumed activity in the spring. Copulation took place from April on, oviposition occurred for the first time 19. - 20. June in G. remigis and G. buenoi and a second time 28. - 29. June for G. buenoi. Nymphs of both species appeared 1. July 1974, and moulted five times in about 5 weeks in the field.

Both species follow a yearly ovarian cycle. Rudiments appear and develop serially from posterior to anterior in each of 4 ovarioles in 2 ovaries. G. remigis develops 6 eggs per ovariole without a break while G. buenoi develops 3 per ovariole, ovulates and oviposits these and repeats the process. G. remigis starts ovarian development in the fall while G. buenoi starts in the spring.

Changes in weight throughout the summer can be accounted for in part by changes in the ovarian cycle, appearance of new adults and, in late

summer deposition of fat reserves.

Exposure to 5^{o} C, 10^{o} C, 15^{o} C and 20^{o} C at 8 hours light to 16 hours dark (8L : 16D), 12L : 12D and 16L : 8D failed to break reproductive diapause or inactivity.

Higher temperatures and longer photoperiods inhibited the limited amount of ovarian development that is carried out in the fall. None of the regimes had any effect on the ovaries of G. buenoi. The lower the temperature and the shorter the photoperiod the more of both species survived the regimes.

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INTRODUCTION

Gerris remigis Say is the commonest and most widely distributed of the larger gerrids in North America ranging from Canada to Mexico. Gerris buenoi Kirkaldy is a transcontinental species ranging throughout the northern part of the United States and southern Canada, (Drake & Harris, 1934). Apterous and fully winged specimens of both species exist, however apterous G. buenoi were never recorded in this study and only 4 or 5 winged males of G. remigis were ever seen, but no winged females. The two species were determined by the key in Drake & Harris (1934).

G. remigis and G. buenoi live in different types of habitats and the two are never seen together. G. remigis is found at the edge of fast moving streams and rivers or at the edge of ponds or lakes where there is considerable wave action. G. buenoi is found in small, often stagnant pools and at the edge of ponds which have a large amount of submerged and/or emergent vegetation along the edges.

Although both species are widely distributed very little is known of their life histories. Bueno (1917) made an incomplete study of the life history of G. remigis in an undescribed area which must have been south of Newfoundland. There appears to have been no work on the ovarian development of either species.

This study attempted to work out the general life history and the yearly ovarian cycle of both species on the Avalon Peninsula. Some details

from the life history were studied in further detail in the field and in the laboratory. These included inactivity over the winter months, average body weight changes throughout activity, oviposition, copulation and nymphal development.

METHODS AND MATERIALS

Sample collecting

During 1973 samples of Gerris remigis were collected from a stream at Logy Bay in an area described by Pickavance et al. (1970). During 1974 the species was collected from Manuels River, just below the bridge (IN/10 535,646). G. buenoi was collected from pools at Logy Bay (IN/10 748 755) (Pickavance et al. 1970) and Gloria's Pond (IN/10 744 753). In 1973 large numbers for laboratory experiments were collected from Kents Pond (IN/10 700716).

Both nymphs and adults were caught with a standard dip net and retained in damp containers.

Samples of both species were collected at least three times a week except during the weeks of July 8. - 14., and September 19. - 25., 1974.

Field collections started 1. May in 1973, after the insects became active, and on 7. March 1974, before they became active.

Collections ceased 7. October in both years for G. buenoi and 15. November in both years for G. remigis.

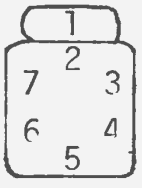
Dissections and weighing.

Except when insects were needed for laboratory experiments gerrids were dissected the day they were collected. Before dissection each was weighed on a Mettler H 34 balance to an accuracy of 0.1 mg. As far as could be ascertained collected gerrids carried no water so it was not considered necessary to blot dry before weighing.

Dissections were made in .08 % saline. Insects were pinned through the mesothorax into wax. The abdominal plate was lifted and the ovaries removed. In 1974 photographs were taken with a Zeiss camera / Zeiss dissecting microscope system. The state of the fat body and gut contents were recorded. The dissected insects and ovaries were fixed in Bouins fluid.

Marking

All gerrids used in laboratory experiments were marked with "Practa'namel" paint. Spots of colored paint were placed according to the following scheme :



Thorax

Any gerrids that accidentally received paint on the sense organs or joints were discarded. 25 specimens were weighed before and after marking. No difference in weight was detectable on the balance used.

Care of nymphs and adults.

Adult gerrids to be used in laboratory experiments were marked and placed in 20 cm by 30 cm aluminum dissecting trays. The trays contained sand, green plastic plants and dechlorinated water and were covered by a sheet of glass. Adequate ventilation was provided by the irregular junction of the tray lip and glass. The pans were cleaned twice a week when gerrids were active but not when they were inactive. Dechlorinated water was added when necessary. Nymphs and adults when active were fed flightless Drosophila; adults were fed an occasional Tenebrio larva.

Weight changes of adults of known age experiment.

Final instar nymphs were collected from several field sites in late July and early August 1973 and reared in the laboratory in Sherer environmental cabinets under 14 hours light : 10 hours dark (14L : 10D) at 20° C. Weights of individual gerrids were recorded daily for 2½ months starting 8. August, 1973. Initially 25 of each species were used but only 15 G. remigis and 14 G. buenoi survived the full experimental period.

Light and photoperiod experiments.

Sherer environmental chambers and Hotpack incubators were modified to obtain required conditions. The Sherer units were divided into 3 sections with a fluorescent light and a thermometer in each. General Electric timers were installed to regulate the photoperiod in 2 sections, the

third was controlled by the Sherer unit. The Hotpack units were divided into 2 sections with incandescent refrigerator bulbs for light. The compartments were separated by black cardboard and black tape. Four 12 cm holes were cut around the edges of the shelf to allow ventilation. Eighteen cm squares of the same cardboard were hung 10 - 13 cm below the holes by black wire to prevent light transfer. This arrangement produced a difference of 5^{+}_{-} 1.5° C between the shelves.

In the fall 1973 20 specimens of each species were maintained at 5° C, 10° C, 15° C and 20° C with photoperiods 8L : 16D, 12L : 12D and 16L : 8D at each temperature except 20° C where 16L : 8D was omitted. Of these, 5° C, 8L : 16D, 10° C, 12L : 12D and 20° C, 16L : 8D were repeated in 1974. Gerrids remained in these conditions for 3 months or until they died.

Obtaining eggs and hatching nymphs in the laboratory.

Adults collected in the field in April were placed in Hotpack incubators and exposed to 14L : 10D at 15° C. Some pairs were placed separately in glass dishes. Eggs were laid under these conditions. As the eggs were laid they and their substrate were removed to marked petri dishes kept at 14L : 10D at 20° C. About 700 G. buenoi and 1300 G. remigis eggs were obtained. An additional 300 ovulated eggs of each species were removed from the females and placed under the same conditions.

As the eggs hatched, the nymphs were removed and placed in glass petri dishes with a small amount of dechlorinated water under 16L : 8D at 20° C. As they moulted they were transferred to larger glass dishes with covers. The water was changed twice weekly; all nymphs were provided with excess food. Moulting was indicated by the presence of exuviae, which were removed and discarded. During rearing approximately 25 nymphs of various instars of each species were preserved.

Determining instars of field nymphs.

Nymphs were collected and preserved as they were found in the field. Length of the following were measured with an eyepiece micrometer: head, thorax and abdomen, individual antennal segments, femur, tibia of each leg and each tarsus of each leg. The results were then statistically analysed and compared with those from specimens of known instars.

Maintaining outdoor winter colony.

G. remigis and G. buenoi were collected in the fall and kept outdoors at Oxen Pond during winter 1973 - 1974. Unfortunately many of these specimens had to be used to replace laboratory specimens killed by equipment failures. Specimens were housed in a 2 m diameter by 0.33 m high blue plastic swimming pool with rocks and sand on the bottom. Their natural diet was occasionally supplemented with Drosophila. Specimens left from this collection in February and April were dissected and weighed, half at each time.

RESULTS

General life history.

Both species studied were univoltine. New adults were first seen in the field on 5. August, 1973 and 7. August, 1974 for G. remigis; 4. August, 1973 and 7. August, 1974 for G. buenoi. Adults were seen in the field until the fall; G. buenoi disappeared between 20. and 25. September 1973 and 1974; G. remigis disappeared later between 15. and 25. October 1973 and 1974. Very occasionally an adult or nymph was collected after this time.

In the winter G. remigis was found beneath and between the rocks at the edge of Manuels River and the Logy Bay stream. G. buenoi was not found even after careful searches of vegetation at all accessible levels near Gloria's Pond and the Logy Bay pools where it had been present during the summer.

During the winter both species are in a state called here inactivity. This means they are motionless, unless disturbed, with the legs close to the sides of the body, the first and second pair of legs pointing anteriorly and the other pair pointing posteriorly. In the active state they are not in this position.

After the winter inactivity they were first recorded in early spring; G. remigis on 15. April, 1974; G. buenoi on 22. April, 1974.

Copulation was first observed in the field on 19. April 1974 in G. remigis and 25. May 1974 in G. buenoi. Copulation often occurred more than once. In the laboratory a number of both species copulated twice or three times before laying. For example a G. remigis copulated on 3., 7. and 21. May before laying on 25. May 1974. Both species also copulated after laying, but infrequently.

Oviposition took place 19. - 20. June 1974 for both species and again between 28. and 29. June 1974 for G. buenoi. Following oviposition female G. remigis died. Following their 28. - 29. June oviposition G. buenoi died. The males of both species died at the same time as their respective females.

Nymphs of both species were first recorded on 1. July 1974. The nymphs moulted 5 times and the resulting adults overwintered.

Oviposition

Judging from the state of the ovaries of dissected field collected specimens, oviposition occurred once in G. remigis and twice in G. buenoi. Both G. remigis and G. buenoi oviposited 19. - 20. June and G. buenoi laid the second batch of eggs 28. - 29. June 1974.

In the laboratory eggs were laid on the underside of floating material, under submerged and exposed (up to 5 cm above the water) leaves

and directly on the bottom or sides of the container. The eggs adhered to the substratum by a colorless adhesive material. When laid on the bottom of the container they rarely adhered.

G. buenoi laid eggs singly, in pairs or in groups up to 20, usually in groups of 3 to 5. The largest number laid by one female at one time in the laboratory was 21. Eggs of a number of females were in groups of as many as 49. G. remigis laid eggs singly, in pairs and in groups up to 40. Eggs of a number of females were laid in groups as large as 96.

Copulation

A few G. remigis were first observed copulating at Manuels River 19. April and 5. May 1974. Every female caught was copulating between 27. May and 12. June 1974. In G. buenoi copulation was observed later at Logy Bay on 24. May 1974, but the main period of copulation was the same as in G. remigis. New adults which appeared in the field in August copulated neither in the field nor under any of the laboratory conditions to which they were exposed. Old female adults could be distinguished by the state of the ovaries.

Field and laboratory specimens of both species were seen copulating during the day while swimming or resting. At night copulation occurred while resting on nearby objects.

When about to copulate the male approached the female from behind, leaped on her back and held her prothorax with the first pair of legs, the other legs extended laterally as if still on water. The female then sometimes reared up on the third pair of legs sometimes dislodging the male. If not dislodged, the male then bent the tip of his abdomen into the female. The female seemed undisturbed by the presence of the male after the initial rearing and continued to feed and move freely.

Once a pair started copulating it was difficult to separate them. Major disturbances of the water, picking them up or transporting them back to the laboratory did not cause them to separate. Once in the laboratory they often continued in copula for up to 12 hours.

Eggs

Eggs of G. buenoi were 1.025 - 1.3 mm long and white when oviposited. 600 eggs laid in the laboratory during May and June hatched in 9 - 11 days, a few taking 12 days. The first hatched on 4. May. The eggs developed under water or in the air. Eggs laid in the air did not develop if they dried up.

Eggs known to have been laid within minutes by the same female did not always hatch at the same time; some hatched 4 days later than others. Of the approximately 300 eggs which had been ovulated and were removed by dissection and placed in incubators, none developed.

Eggs of G. remigis were 1.5 - 1.65 mm long and a bright yellow color when oviposited. 1000 eggs laid in the laboratory during May and June hatched in 11 - 13 days; a few took 14 days. These eggs developed in water and air as for G. buenoi. The first nymphs hatched in the laboratory on 7. May. Eggs known to have been laid within minutes by the same female hatched as much as 4 days apart.

In both species when the nymph hatched the egg split longitudinally, from the nymph's anterior end.

Nymphs

Nymphs of G. remigis were first recorded 1. July 1974 at Manuels River. The last nymphs of any instar were seen 18. October 1974. None of these late nymphs overwintered.

Nymphs of G. buenoi were also seen 1. July 1974 at Logy Bay, Pool 13. A nymph was seen at Gloria's Pond on 10. October 1974. No nymphs overwintered. Dissections of the late occurring nymphs showed no fat body and so no reserve to overwinter.

Both species had 5 nymphal instars. This agrees with Bueno (1917) for G. remigis. No previous records of this nature were found for G. buenoi.

Table 1: Duration of nymphal instars in days

Instar	1	2	3	4	5	Total
G. remigis						
Mean ± S.D.	6.23 ± 1.93	6.47 ± 1.45	8.20 ± 2.30	9.67 ± 3.05	11.20 ± 1.10	41.77
G. buenoi						
Mean ± S.D.	6.48 ± 1.40	6.97 ± 1.67	8.06 ± 1.91	8.02 ± 1.58	12.60 ± 1.31	42.13

Table 2: Mortality in each instar of laboratory specimens

Instar		1	2	3	4	5	Adult
G. buenoi:	# in instar	86	77	69	55	39	15
	% mortality	10.5	9.3	16.3	18.6	27.9	
G. remigis:	# in instar	200	173	143	96	33	8
	% mortality	13.5	15.0	23.5	31.5	12.5	

Table 3: Mean percentage per day per instar of mortality

	1	2	3	4	5
G. buenoi	1.69	1.44	1.99	1.92	2.49
G. remigis	2.08	2.15	2.92	3.93	0.99

Nymphal development

Adults of both species appeared in the field for the first time 7. August 1974. This gave 38 days for development which involved five moults. This is in good agreement with the laboratory results which gave means of 41.77 days for G. remigis and 42.13 for G. buenoi (Table 1). However, the time taken in the laboratory was at constant photoperiod and temperature which on average was a little shorter and lower respectively than the field conditions during the time of development there.

The length of instars in the laboratory differed slightly between the two species. Instars 1, 2 and 3 differ in length only by a few hours while 4 and 5 are obviously different. Instar 4 in G. remigis is 1.65 days longer than in G. buenoi while instar 5 is 1.40 days longer in G. buenoi than in G. remigis (Table 1). The result is that total time is approximately the same in both species differing by 0.36 days (8.64 hours). According to Table 2 G. buenoi has a higher rate of nymphal survival than G. remigis, 17.44% surviving to adults compared with only 4% for G. remigis.

The mortality of G. remigis may be higher in the laboratory than in the field because they were in still water whereas in the field they live in flowing water. It was noted that G. remigis frequently died due to entanglement in its exuviae. In summer 1973 aerators were placed in a few containers to ascertain if this made any difference to G. remigis surviving moulting. Out of the 50 in this set up, 34 moulted successfully

Table 4: Means of measurement of G. remigis for nymphal instars

	Instar				
Measurements (MM)	1	2	3	4	5
Head	.34	.48	.61	.89	1.43
Thorax and abdomen	1.61	.30	4.14	6.22	8.32
1st antennal segment	.24	.35	.58	.91	1.50
2nd antennal segment	.15	.22	.34	.54	.75
3rd antennal segment	.22	.31	.45	.65	.88
4th antennal segment	.48	.62	.72	.93	1.11
Leg 1 femur	.53	.79	1.21	1.90	3.03
Leg 1 tebia	.55	.78	1.14	1.73	2.65
Leg 1 tarsus	.25	.31	.44	.59	.94
Leg 2 femur	1.18	2.03	3.19	4.82	6.95
Leg 2 tibia	1.41	2.13	3.02	4.39	6.02
Leg 2 tarsus	1.15	1.51	1.93	2.55	3.28
Leg 3 femur	1.14	1.87	2.92	4.35	6.20
Leg 3 tibia	.77	1.17	1.90	3.05	4.62
Leg 3 tarsus	.61	.74	1.04	1.41	1.93

Table 5: Least significant differences for mean measurements of *G. remigis*

Measurement (MM)	P 0.01
Head	.0395
Thorax and abdomen	.03595
1st antennal segment	.032
2nd antennal segment	.0215
3rd antennal segment	.0215
4th antennal segment	.1495
Leg 1 femur	.0555
Leg 1 tibia	.0630
Leg 1 tarsus	.0365
Leg 2 femur	.1010
Leg 2 tibia	.1145
Leg 2 tarsus	.0760
Leg 3 femur	.0765
Leg 3 tibia	.1175
Leg 3 tarsus	.0550

Table 6: Means of measurements of G. buenoi for nymphal instars

Measurements (MM)	1	2	3	4	5
Head	.13	.40	.54	.69	.85
Thorax and abdomen	1.40	1.88	2.87	3.97	5.39
1st antennal segment	.2	.25	.38	.60	.88
2nd antennal segment	.13	.19	.24	.37	.49
3rd antennal segment	.16	.25	.27	.41	.48
4th antennal segment	.45	.50	.62	.76	.84
Leg 1 femur	.37	.53	.72	1.13	1.63
Leg 1 tibia	.39	.50	.76	1.03	1.42
Leg 1 tarsus	.18	.21	.26	.41	.51
Leg 2 femur	.69	1.12	1.77	2.71	3.77
Leg 2 tibia	.88	1.26	1.76	2.46	3.29
Leg 2 tarsus	.74	1.03	1.41	2.02	2.70
Leg 3 femur	.66	1.05	1.69	2.53	3.49
Leg 3 tibia	.47	.66	.93	1.35	1.95
Leg 3 tarsus	.40	.52	.68	.93	1.21

Table 7: Least significant differences for mean measurements of *G. buenoi*

Measurements (MM)	P 0.01
Head	.0365
Thorax and abdomen	.1830
1st antennal segment	.0205
2nd antennal segment	.0160
3rd antennal segment	.0160
4th antennal segment	.0240
Leg 1 femur	.0450
Leg 1 tibia	.05
Leg 1 tarsus	.0265
Leg 2 femur	.0685
Leg 2 tibia	.0650
Leg 3 tarsus	.0995
Leg 3 femur	.0670
Leg 3 tibia	.0585
Leg 3 tarsus	.0315

as compared to 11 in the still water. It was impossible to provide aerators for all G. remigis containers so the experiments had to be run in still water. The figures for G. buenoi are probably more accurate since death due to being caught up in the exuviae was not as frequent as in G. remigis. Mortality was highest in the fifth instar of G. buenoi and the fourth instar of G. remigis. The fifth instar of G. buenoi is the longest for that species while the fourth instar is the second longest for G. remigis. Mortality might be expected to be higher in the longer instars but this is not the case with G. remigis. Even when we consider daily mortality (Table 3) the highest mortality is in the fifth instar (2.49%) for G. buenoi and the fourth instar (3.93%) for G. remigis.

In determining the number and size ranges of the instars 150 nymphs of each species were measured. Statistical analysis showed that 5 groups of measurements were highly significantly different from each other. This agrees with 5 instars found in laboratory material.

One-way analysis of variance was carried out on each measurement for the 5 groups. All F values were highly significant (Appendix A). The least significant difference for each measurement was then calculated (Tables 5 and 7). All measurements were significantly different between instars (Tables 4 and 6). Parameters used to build the key are thus highly significantly different between instars.

Key to nymphs of G. remigis and G. buenoi from material collected at Manuels River and Logy Bay.

1. Femur of leg one 0.35 - 0.40 mm long, femur of leg two 0.65 - 0.75 mm, femur of leg three 0.60 - 0.70 mm ....G.buenoi 1st instar
   Larger than this 2
2. Femur of leg one 0.50 - 0.60 mm; femur of leg two 1.1 - 1.25 mm; femur of leg three 0.9 - 1.2 mm 3
   Larger than this 4
3. Brown pigment patch on the metathorax with small central white spot (obvious under x 10 lens) .....G.buenoi 2nd instar
   No white spot on the metathorax .....G.remigis 1st instar
4. Femur of leg one 0.7 mm - 0.9 mm, leg two 1.7 - 2.2 mm, leg three 1.6 - 1.9 mm 5
   Corresponding femora larger than this 6
5. Fore-wing pads just starting to develop as crescent shapes. White spot on mesothorax easily visible with naked eye...G.buenoi 3rd instar
   No wing pads .....G.remigis 2nd instar
6. Femur of leg one 1.1 - 1.25 mm long, leg two 2.6 - 3.25 mm, leg three 2.4 - 2.9 mm 7
   Corresponding femora larger than this 8
7. Both fore and hind wing pads developed. In legs two and three femur longer than tibia or tarsus .....G.buenoi 4th instar
   No wing pads. Fourth antennal segment longest ....G.remigis 3rd instar
8. Femur of leg one 1.6 - 2.0 mm, leg two 3.7 - 4.9 mm, leg three 3.4 - 4.4 mm 9

Femur of leg one about 3.0 mm, leg two about 6.9 mm, leg three about 6.1 - 6.2 mm .....G.remigis 5th instar

9. Wing pads obvious. Pigment on thorax appears striped to the naked eye .....G.buenoi 5th instar

No wing pads. First antennal segment longest. G.remigis 4th instar

Description of nymphal instars of G. remigis.

First instar

Antennae moderately stout, joint 2 shortest, 1 next in length, then 3, 4 longest, longer than 1 and 3 together. All tarsi single jointed (true for all nymphs). Legs apparently far back due to marked shortness of abdomen. Leg 1 shortest, leg 2 longest (true for all instars). Femora of legs 1 and 2 shorter than tibia but longer than tarsus. Femur of leg 3 longer than tibia (true for all instars).

Second instar

Proportions of antennal segments as for first instar. Legs differ as follows : femur of leg 1 longest, then tibia, then tarsus; leg 2 tibia longest,then femur, then tarsus.

Third instar

Proportions of antennal segments as for first instar. Legs 1 and 2, femur and tibia subequal, tarsus shorter. Leg 3 femur longest, then tibia, then tarsus.

Fourth instar

Proportions of antennal segments same as 1. Legs same proportions as instar 3.

Fifth instar

First antennal segment longest, fourth next, second and third subequal. In all legs femur longest, then tibia, then tarsus.

Description of nymphal instars of G. buenoi.

First instar

Fourth antennal segment longest, then first, third, second. Leg 1 tibia longest, then tarsus, then femur. Leg 2 tibia longest, femur and tarsus subequal. Leg 3 femur longest, then tibia, then tarsus.

Second instar

Proportions of antennal segments as for 1. Leg proportions as for first instar except leg 2 femur longer than tarsus.

Third instar

Proportions of antennal segments same as 1. Leg proportions as first instar except leg 1 femur longest, tibia, then tarsus. Leg 2 femur longest, then tibia, then tarsus.

Fourth instar

Same as third instar but larger.

Fifth instar

Antennal segments as follows: first longest, then four, three two. Proportions of legs same as third instar.

Fat body of field specimens

The fat body of both species started to be deposited in September and reached maximum size about 1 month later before the gerrids become inactive for the winter. In February both species had similar amounts of fat (compared to body size), but it was reduced by approximately one half that in the fall. In the spring the first gerrids caught had very little fat body. Field specimens after 7. - 10. May 1974 had only traces. Very small traces, sufficient for identity of fat bodies, were visible all through the summer.

Moisture loss

A moisture loss was observed in both species kept at various photoperiod and temperature regimes before inactivity. This moisture appeared as droplets dorsally on the abdomen, more often in the region of the anus.

Description of ovaries

G. remigis and G. buenoi have similar ovarian structures. Both have 2 ovaries located postero-ventrally in the abdomen, often extending forward into the thorax when full of eggs. They are connected to the body wall by numerous tracheae. Each ovary consists of 4 ovarioles which join posteriorily to join a lateral oviduct. The 2 oviducts join to form a common median vagina. The ovaries undergo considerable size change during the year but they retain their initial structures.

Figure 1 Divisions of ovariole

Each ovariole is divided into 3 main regions, germarium, vitellarium and a posterior region as shown by Fig. 1.

Heteroptera typically possess telotrophic ovarioles characterized by having terminal nutritive tissue with connections to the rudiments (defined below) by a nutritive cord (Engelmann, 1970). The ovaries of G. remigis and G. buenoi are apparently of this type.

In both species rudiments start developing $\frac{1}{4}$ - $\frac{1}{3}$ the length of the ovariole anterior to the junction of ovarioles and lateral oviduct. In this region first rudiments develop simultaneously in each ovariole. In G. remigis there is a yellow spot on each ovariole immediately posterior to the first rudiments. These spots appear in the fall before the rudiments. In G. buenoi yellow spots appear in the same location but not until after ovulation. Ovulation here is taken as the movement of ripe eggs into the posterior $\frac{1}{3}$ - $\frac{1}{4}$ of each ovariole. In G. remigis only ripe eggs move past the yellow spots.

The ovarian cycle.

The ovaries of both species follow a one year cycle. The two differ a great deal despite their similar life histories. This section will outline the cycle for each species. It must be borne in mind that the process is continuous and that steps have been selected for convenience of illustration. Times given for each particular stage are the first time the changes were observed in the field material, but it must

Fig. 2. Stages of development of eggs in G. remigis.

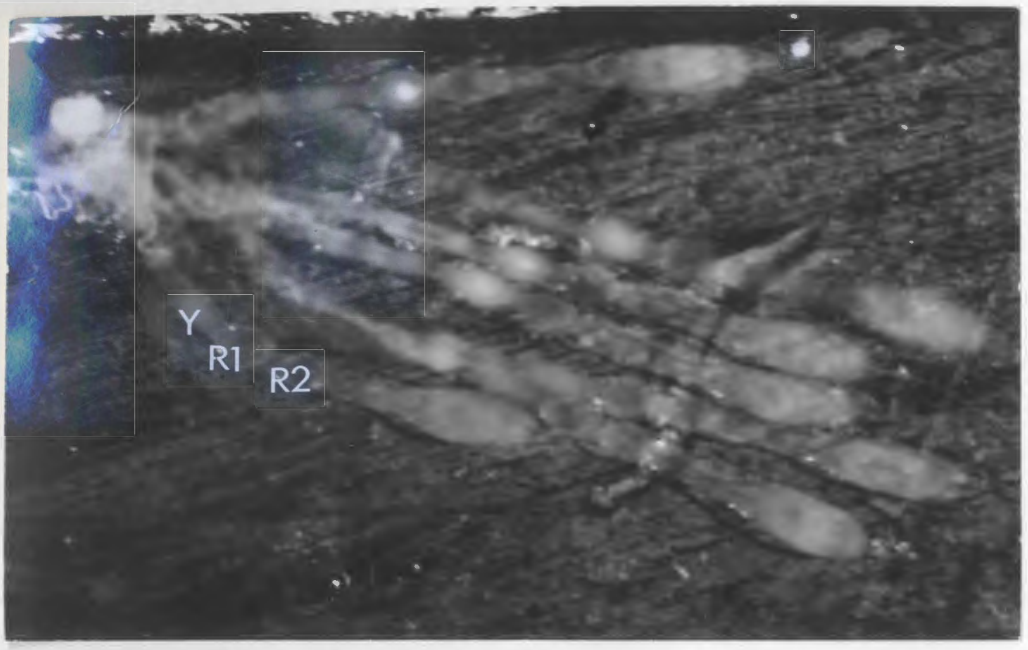


Fig. 2a. Two rudiments per ovariole. Y - yellow spots; R1 - rudiment 1; R2 - rudiment 2.

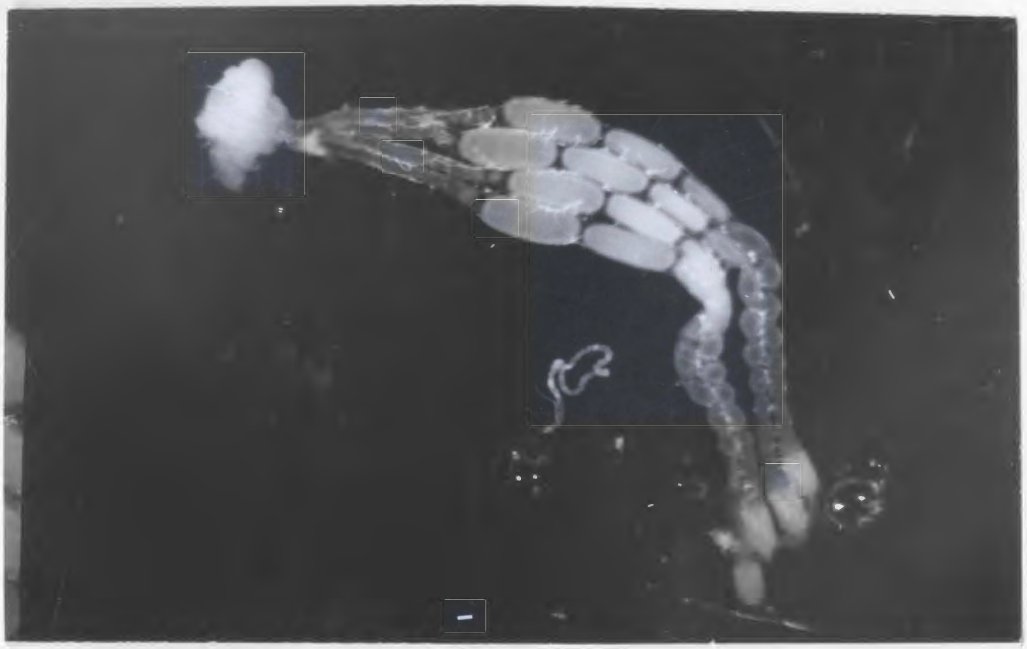


Fig. 2b. Second and third rudiments take on mature egg shape; yolk in rudiments 1 - 6.

Fig. 2c. One egg and 10 rudiments per ovariole. One egg ovulated.

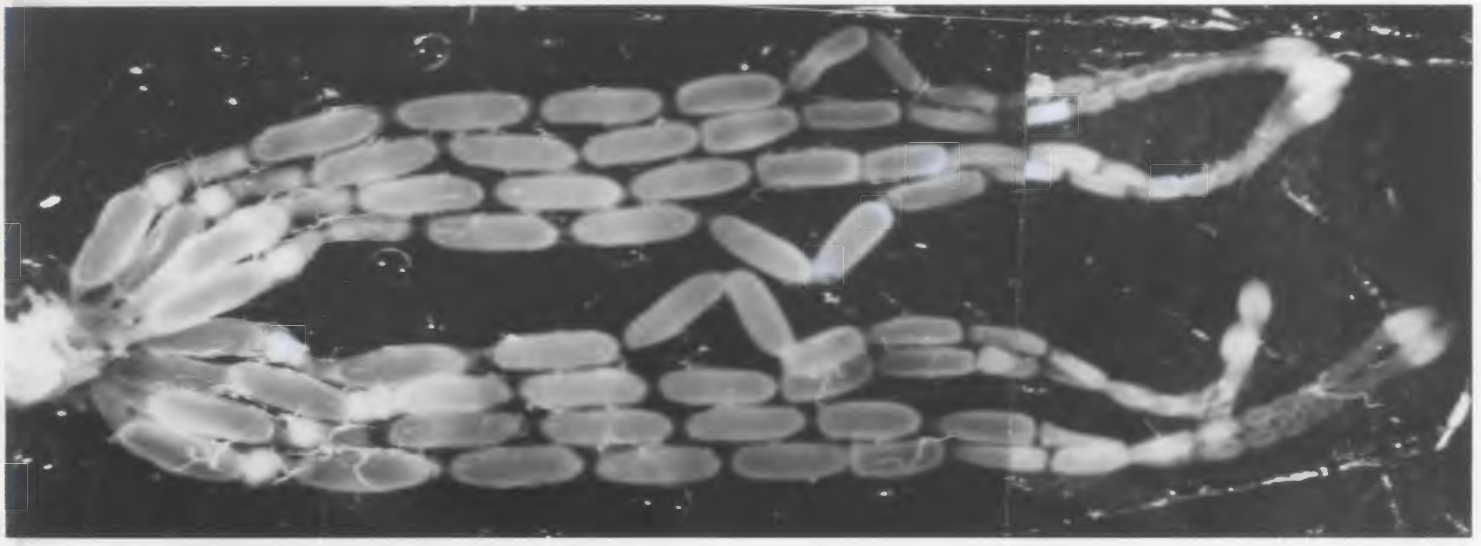


Fig. 2d. Two rows of eggs. One egg per ovariole ovulated.

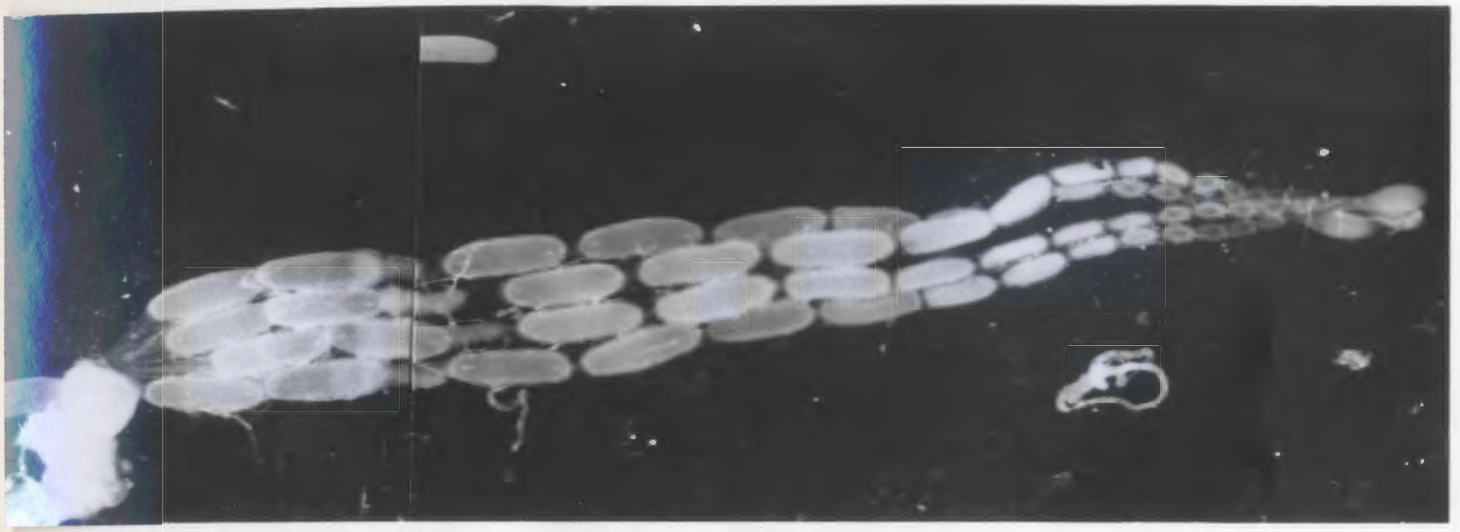


Fig. 2e. Three eggs per ovariole. Two eggs per ovariole ovulated.

2.4mm

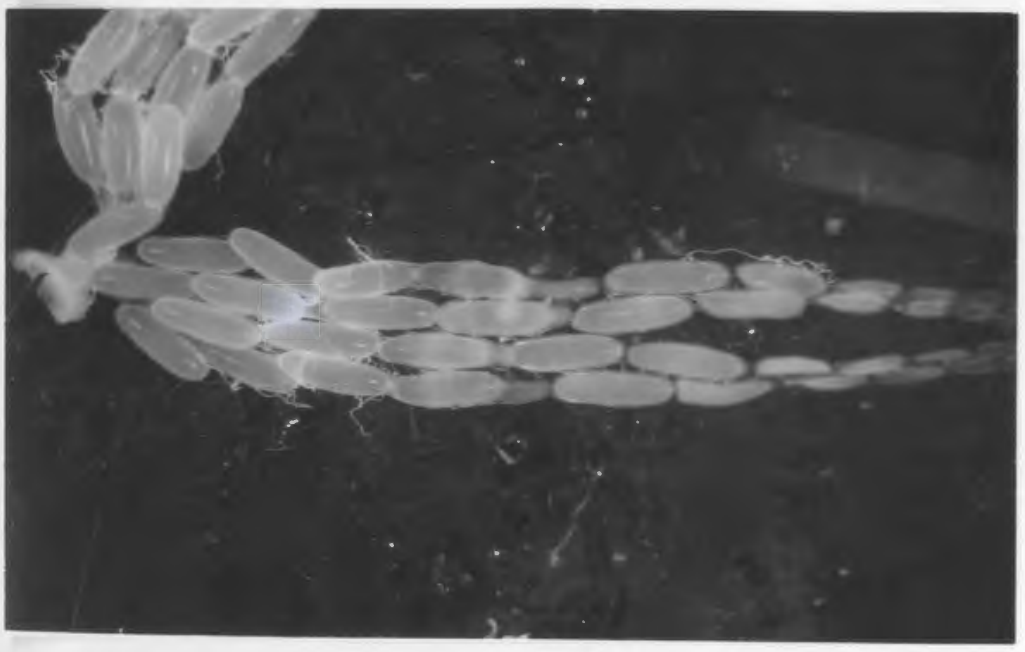


Fig. 2f. Four eggs per ovariole. Three eggs per ovariole ovulated, fourth under yellow spots.

2.4mm

2.4mm

Fig. 2g. Oviposition has begun with only 1 or 2 eggs remaining per ovariole.

2.4mm

Fig. 2h. Oviposition completed.

be remembered that there were several stages present in any one collection.

Several terms used in this section need clarification: rudiments, indicates developing eggs without shells; eggs, indicates that rudiments have developed shells; ovulation, the movement of eggs into the posterior $\frac{1}{3}$ - $\frac{1}{4}$ of each ovariole; oviposition, the elimination of the eggs through the oviducts and vagina out of the body; first egg or rudiment, the most posterior in an ovariole; eggs or rudiments are then numbered consecutively from posterior to anterior.

New adults of G. remigis that appeared in the first week of August 1973 and 1974 had no rudiments or germarium. The ovaries were small and the ovarioles hard to distinguish. Within 3 weeks there were traces of germarium but development of rudiments had not commenced. In early September the ovarioles started to show some development, when the germarium became distinguishable from the vitellarium. On 19. September 1974 yellow spots appeared, followed by 2 rudiments per ovariole on 1. October 1974 (Fig. 2a). On 15. October 1974, 5 rudiments per ovariole were present and traces of yolk were visible in the first rudiments, marking the start of vitellogenesis.

Because field specimens were not available due to snow etc., on 15. February 1974 a few specimens were taken from the Oxen Pond outdoor colony. At this time each ovariole had 6 rudiments, the germarium was larger than in October and the yellow spots were still present. There was yolk in the first and second rudiment in each ovariole. No picture is available but the first rudiment was at about the same stage as the second rudiment in April (Fig. 2b).

Field sampling resumed in the spring. On 15. April 1974 there was yolk in rudiments 1, 2 and 3 of 6 - 8 rudiments per ovariole. Through May, the second and third rudiments in each ovariole took on a mature egg shape while traces of yolk were deposited in the fourth, fifth and sixth (Fig. 2b). By the end of May the first rudiment in each ovariole had become an egg and the seventh to tenth or twelfth rudiment had appeared, (Fig. 2c).

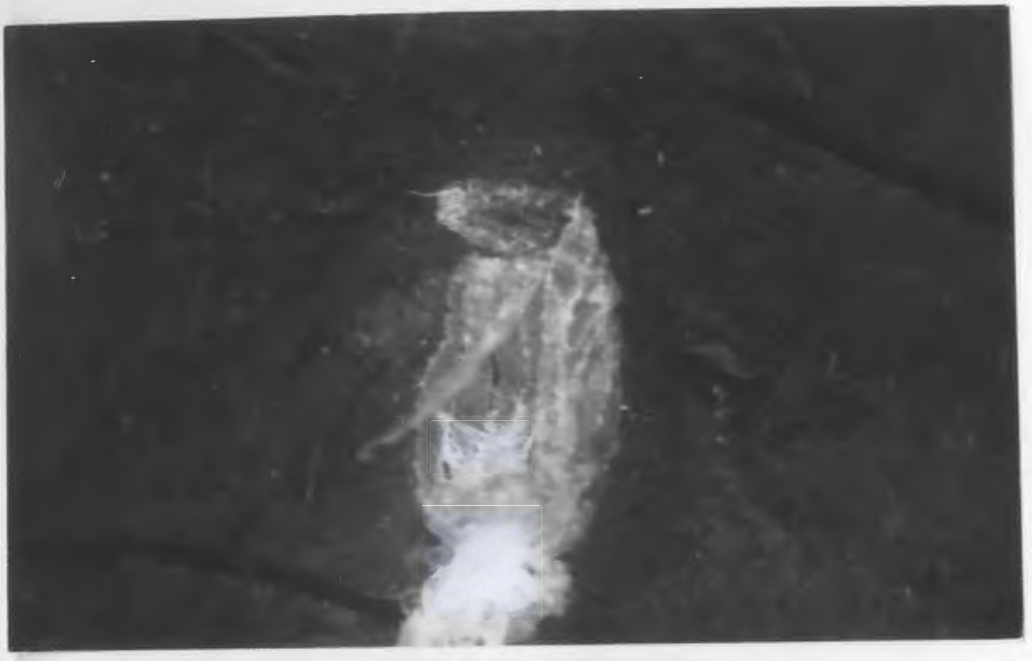
During the first few days in June rudiments 7 - 9 in each ovariole had at least traces of yolk in them. By 9. June 1974 the first egg in each ovariole had been ovulated, the second rudiments had become eggs and the sixth and seventh rudiments in each ovariole were further developed. Eggs plus rudiments had increased to 12 per ovariole (Fig. 2d). During the second week in June the second egg per ovariole was ovulated, the third rudiment became an egg and yolk was deposited as far back as the tenth rudiment and 14 eggs and rudiments were present (Fig. 2e). By 16. - 18. June the fourth rudiment became an egg. The third eggs ovulated and the fourth in each ovariole was level with the yellow spots (Fig. 2f). The

sixth and seventh rudiments were still developing.

Oviposition started 19. June and continued in the population until all adults were dead. When oviposition started there were 4 or 5 ovulated eggs in each ovariole. Oviposition started with the first egg in every ovariole and then one from each in sequence until 6 eggs from each ovariole had been laid. By the time the fourth egg in each ovariole had been oviposited the fifth and sixth were completed and oviposition continued (Fig. 2 g). The time between laying of the first and last eggs (i.e. number1 - 6) was about 2 days. Rudiments that had not developed remained after all the ripe eggs had been laid (Fig. 2h) and were present at death, thus each female lays a total of 48 eggs, 6 per ovariole.

The cycle ended at this point. There is no evidence that any G. remigis in Newfoundland oviposited twice in the field. However, in the laboratory one female did not die upon completion of oviposition. This female took 2 weeks to develop and oviposit a second batch of eggs. There were only 16 eggs in this second batch.

Fig. 3. Stages in development of eggs in G. buenoi.



1.0 mm

Fig. 3a. Ovaries of new G. buenoi.

1.0 mm

Fig. 3b. Distended ovaries of fall and winter.

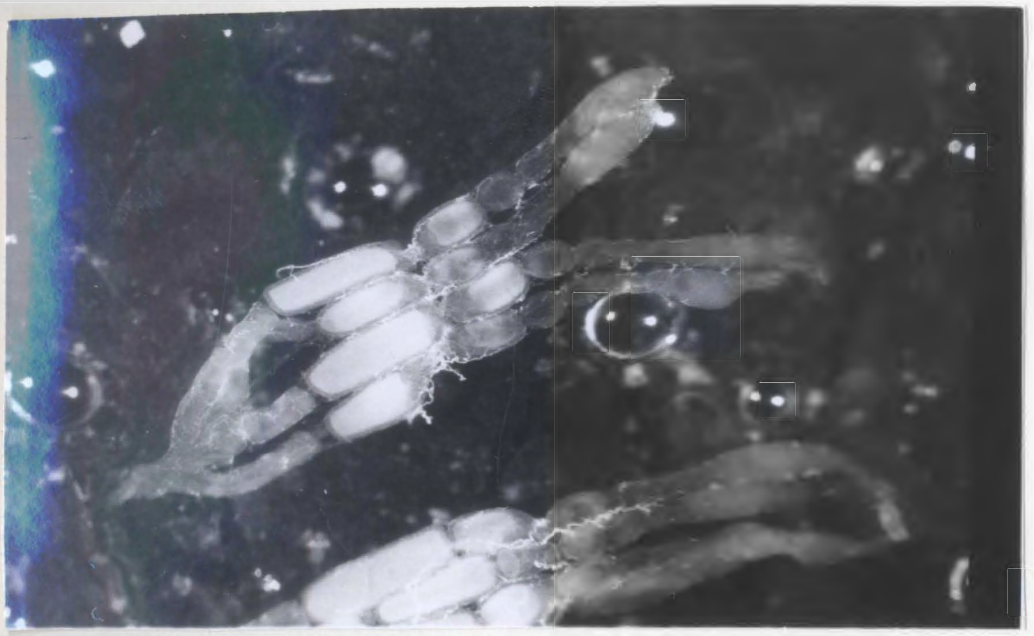
Fig. 3c. One rudiment and germarium per ovariole.

1.6 mm

Fig. 3d. Two rudiments per ovariole.

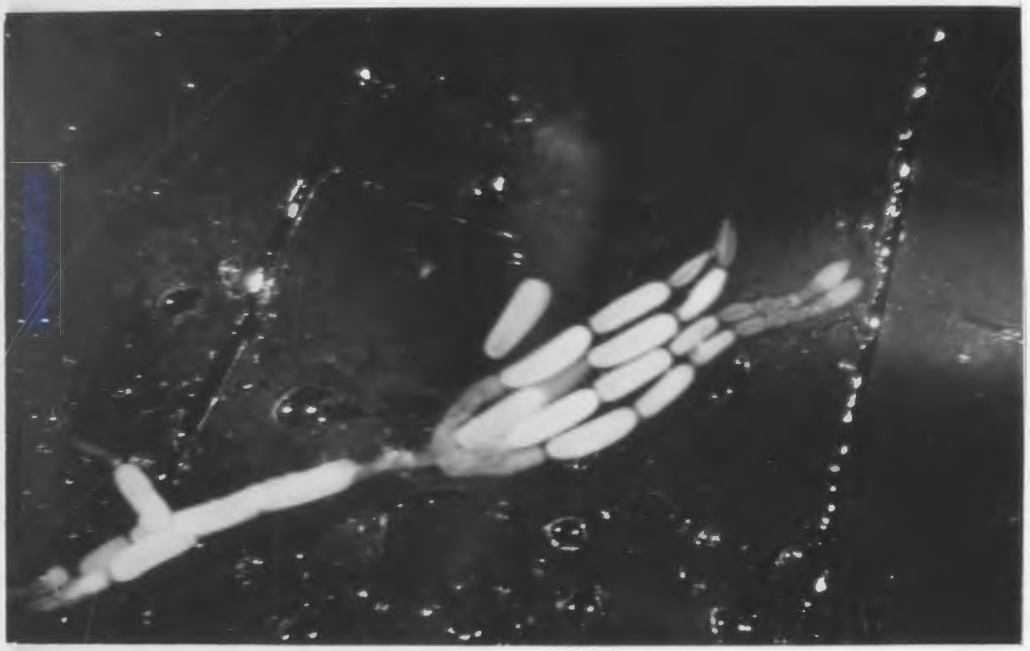
No vitellogenesis.

1.6 mm



1.6 mm

Fig. 3e. Yolk deposited in rudiment 1 and 2.



2.4 mm

Fig. 3f. One egg and 5 rudiments per ovariole.

1.0 mm

Fig. 3g. Development continuing behind yellow spots. One egg still in one ovariole.

1.6 mm

Fig. 3h. Three eggs in 2 ovarioles, two in other 2. Second oviposition under way. Egg in oviduct displaced in dissection.

The ovaries of new adults of G. buenoi were similar to those of G. remigis in that ovaries were small with individual ovarioles indistinguishable (Fig. 3a). Insignificant development occurred during the fall and winter; the ovarioles in February appeared slightly larger than in the fall but rudiments and germaria were not visible (Fig. 3b).

During the last 10 days in April 1974 one rudiment per ovariole and the germarium became visible. No yellow spots were present but the rudiments were located similarly to G. remigis (Fig. 3c).

During the first 2 weeks in May the next rudiment in each ovariole appeared, but vitellogenesis had not begun (Fig. 3d). In the middle of May vitellogenesis began in the first rudiments in each ovariole. The following week the first rudiments developed further, yolk appeared in the second, the third became more obvious and the fourth appeared (Fig.3e). Rudiments continued to develop proportionally from posterior to anterior until by 21. May 1974 the first rudiment in each ovariole had become an egg and the third and fourth had yolk (Fig. 3f).

Development continued until the second rudiment in each ovariole was almost completed, the fifth and sixth rudiments appeared. By the middle of June there were 2 eggs per ovariole, the third rudiment was near completion and the sixth and seventh egg in each ovariole appeared.

On approximately 18. June one egg per ovariole had ovulated and yellow spots appeared. Development continued until there were 3 eggs in each ovariole.

Oviposition started 19. - 20. June 1974 and continued until 24 eggs had been laid by each gerrid. Oviposition started with the laying of the first egg in each ovariole and continued in sequence up to the third (Fig. 3g). After oviposition rudiments 4 - 6 moved posteriorly up to the yellow spots (Fig. 3g). Development of these continued until they became eggs (Fig. 3h) and they were laid 28. - 29. June 1974. More rudiments appeared at the anterior end of the ovarioles as ovulation and oviposition occurred. Germaria were relatively small at this point. The second oviposition continued in the field until the population died.

It is interesting to note that G. buenoi collected on the Northern Peninsula of Newfoundland were later starting their ovarian development. Those collected there in June had ovaries at the same stage as those on the Avalon Peninsula in April.

Average weights of females of both species.

Most of the weight changes in field material throughout the summer can be explained by changes that occurred in the ovarian cycle, the appearance of new adults or changes in fat body content. Two graphs have been constructed for each species. The first is of the average weekly weights throughout the summer based on 15 - 20 specimens collected on at

List of dates corresponding to the weeks in Figures 4 and 6

Figure 4		Figure 6	
Week	Dates	Week	Dates
1	22-28.4.74	1	15-21.4.74
2	29.4-5.5.74	2	22-28.4.74
3	6-12.5.74	3	29.4-5.5.74
4	13-19.5.74	4	6-12.5.74
5	20-26.5.74	5	13-19.5.74
6	27.5-2.6.74	6	20-26.5.74
7	3-9.6.74	7	27.5-2.6.74
8	10-16.6.74	8	3-9.6.74
9	17-23.6.74	9	10-16.6.74
10	24-30.6.74	10	17-23.6.74
11	1-7.7.74	11	24-30.6.74
12	8-14.7.74	12	1-7.7.74
13	15-21.7.74	13	8-14.7.74
14	22-28.7.74	14	15-21.7.74
15	29.7-4.8.74	15	22-28.7.74
16	5-11.8.74	16	29-7.4.8.74
17	12-18.8.74	17	5.8-11.8.74
18	19-25.8.74	18	12-18.8.74
19	26.8-1.9.74	19	19-25.8.74
20	2-8.9.74	20	26.8-1.9.74
21	9-15.9.74	21	2-8.9.74
22	16-22.9.74	22	9-15.9.74
		23	16-22.9.74
		24	23-29.9.74
		25	30.9-6.10.74
		26	7-13.10.74

List of stages of ovarian cycle corresponding to numbers on Figures 5 and 7

Figure 5

1. Nothing in ovariols; no food in gut
2. One rudiment per ovariole; food in gut
3. Rudiments numerous
4. One egg in each ovariole
5. Two eggs in each ovariole
6. Three eggs in each ovariole
7. Oviposited
8. One egg in each ovariole anterior to yellow spots
9. Two eggs in each ovariole anterior to yellow spots
10. Three eggs in each ovariole anterior to yellow spots
11. Oviposited second time
12. New adults without fat body
13. New adults with fat body
14. New adults with fat body which have lost water

Figure 7

1. Ovaries in early spring; no food in gut
2. Ovaries in early spring; food in gut
3. One egg in each ovariole
4. Two eggs in each ovariole
5. Three eggs in each ovariole
6. Four eggs in each ovariole
7. Five eggs in each ovariole
8. Oviposited
9. New adults without fat body or ovarian development
10. New adults no fat body; no ovarian development
11. New adults September fat body
12. New adults October fat body and ovarian development
13. New adults with October fat body which have lost water

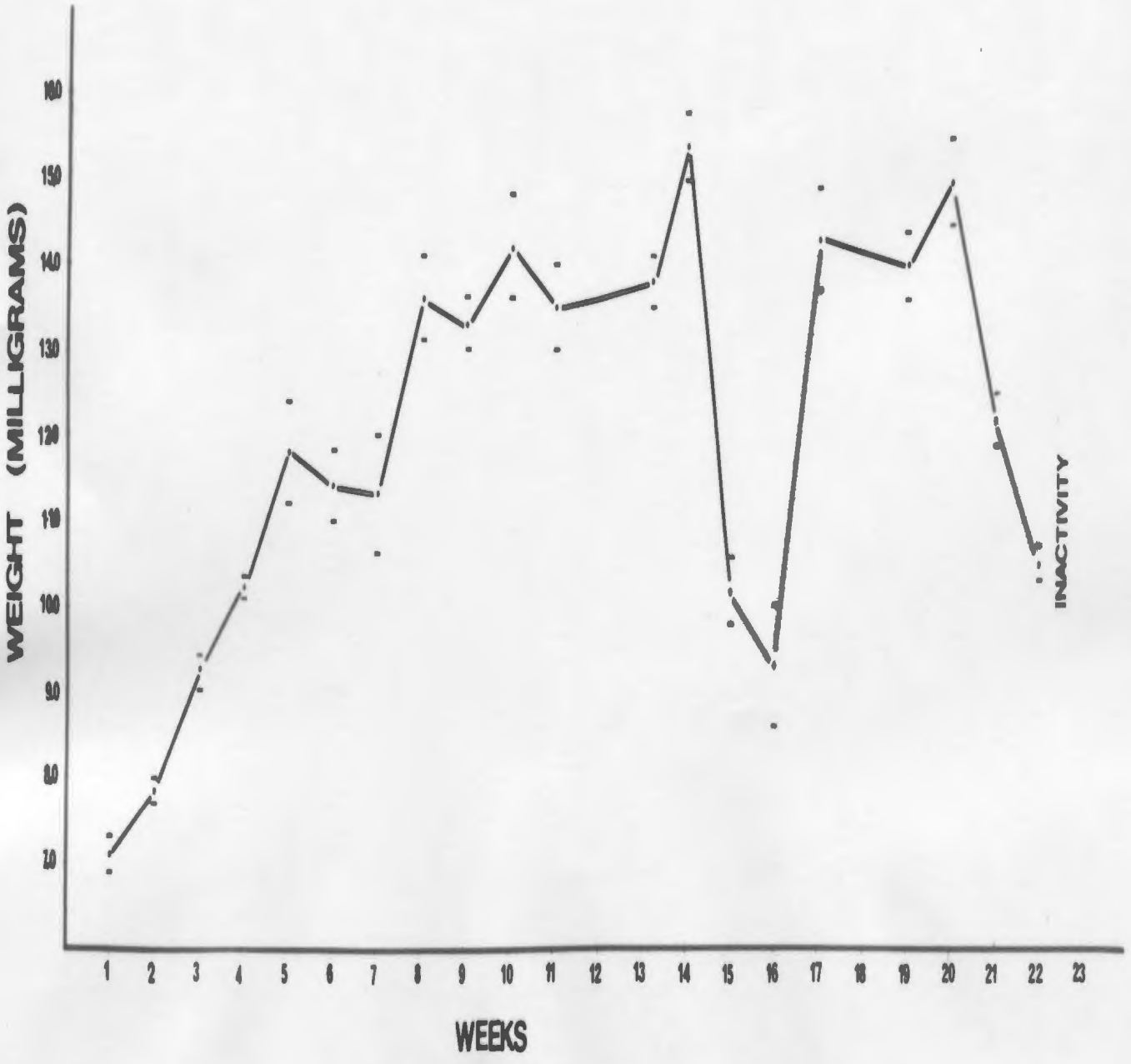


Figure 4 Average weekly weights of female G. buenoi throughout activity

least 3 different days throughout the week and of unknown ovarian stage. The second is the weights of gerrids selected according to ovarian stage thus eliminating distortion of the graph due to the presence of more than one stage of development in the sample.

Changes in average weights of female G. buenoi throughout activity are shown in Fig. 4 and reference will be made to particular weeks. Overwintered G. buenoi were light in the spring. They contained very little or no fat body and they had not resumed feeding (week 1). Weight increased steadily over weeks 2 - 5, while they were feeding and while ovarian development, described above, was going on. Between weeks 1 and 2 there was 1 rudiment per ovariole, at week 3 there were 2 rudiments per ovariole but yolk was not present, at week 5 there was 1 egg per ovariole and the third and fourth rudiments had yolk. There was a drop in weight in week 6. Development continued until the second rudiment in each ovariole was completed and yolk was deposited in more rudiments. Since the food and fat body remained constant from the spring a further increase in weight would be expected, and the drop is inexplicable by the recorded data. As development of rudiments continued, weight increased again (week 8). Two eggs in each ovariole were now ovulated. Oviposition in week 9 was accompanied by a drop in average weight. Development of 3 more eggs per ovariole was accompanied by another rise (week 10). There is no explanation from available information for the drop at week 11.

From week 9 to 14 there is an overall increase in weight. This is due to the fact that gerrids that had oviposited were developing the second batch of eggs and those that had not oviposited contained ripe eggs

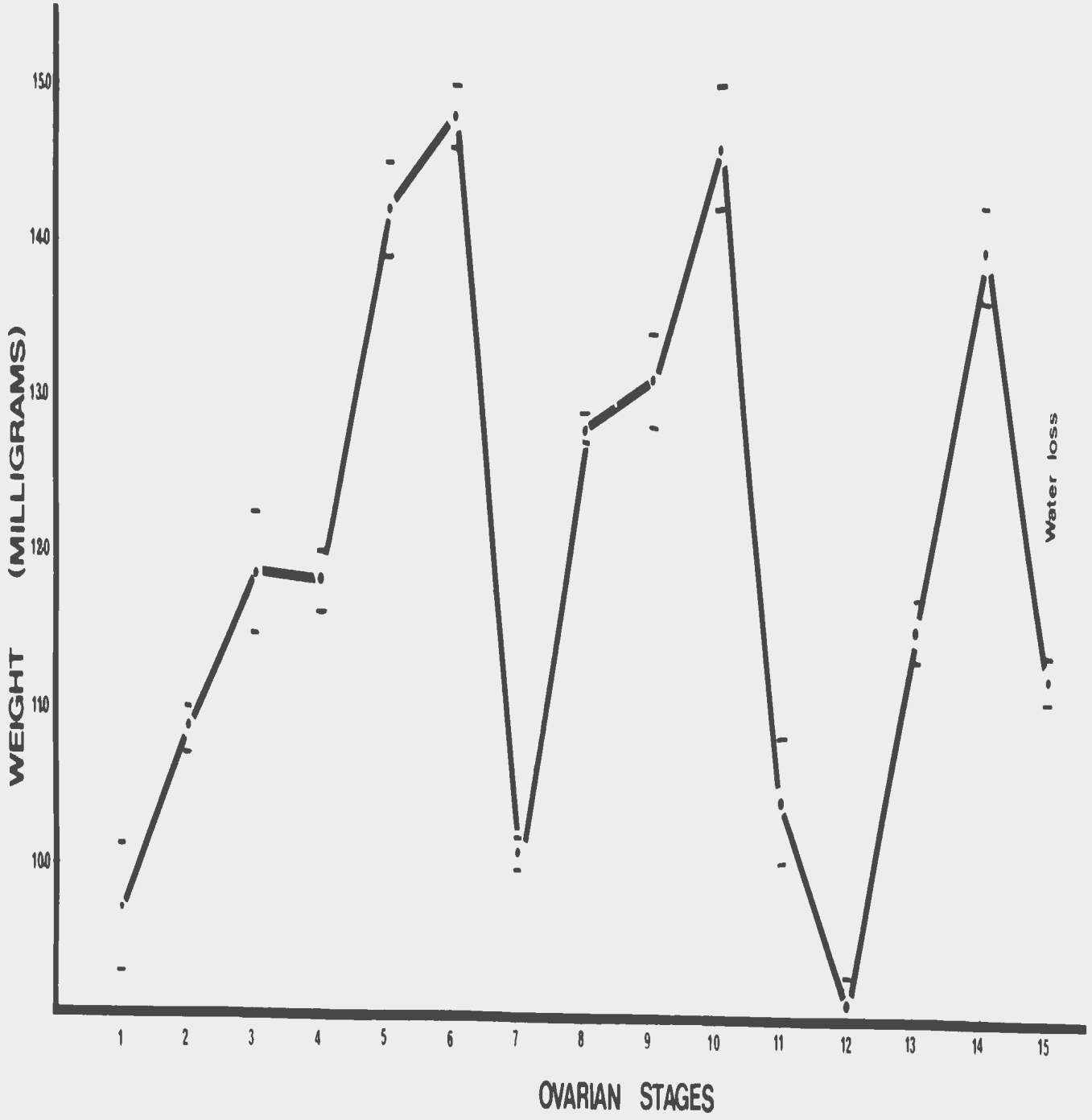


Figure 5 Average weights of female G. buenoi at known ovarian stages

and as a result there was an increase in average weight. Several gerrids which had oviposited and had not yet started developing again were collected but were not enough to cancel out the apparent increase in weight. At week 15 there is a decrease in weight because gerrids collected had ovaries from which some of the second batch of eggs had been laid. Empty ovaries were never found after this oviposition since it was followed by death. The appearance of new adults caused a considerable drop in average weight at week 16.

New adults increased in weight over weeks 16 to 17 but fat was not being deposited and there was no ovarian development. Fat body was laid down rapidly between weeks 17 and 20 resulting in an overall increase in weight. The drop at week 19 is inexplicable in terms of fat body. A moisture loss by gerrids of both species was recorded in the laboratory before they become inactive there. Presumably this also happened in the field for just before the gerrids became inactive for the winter there was a relatively large drop in weight (weeks 21 and 22).

Changes in average body weight of female G. buenoi of known ovarian stage based on field and laboratory specimens are shown in Fig. 5. Reference will be made to points which correspond to stages of the ovarian cycle already described. As a result of the manner in which the data for this graph were selected, the increase in weight from early spring until they lay for the first time is more gradual than in Fig. 4. The first laying is more obvious and is indicated by a sharp weight reduction at week 7.

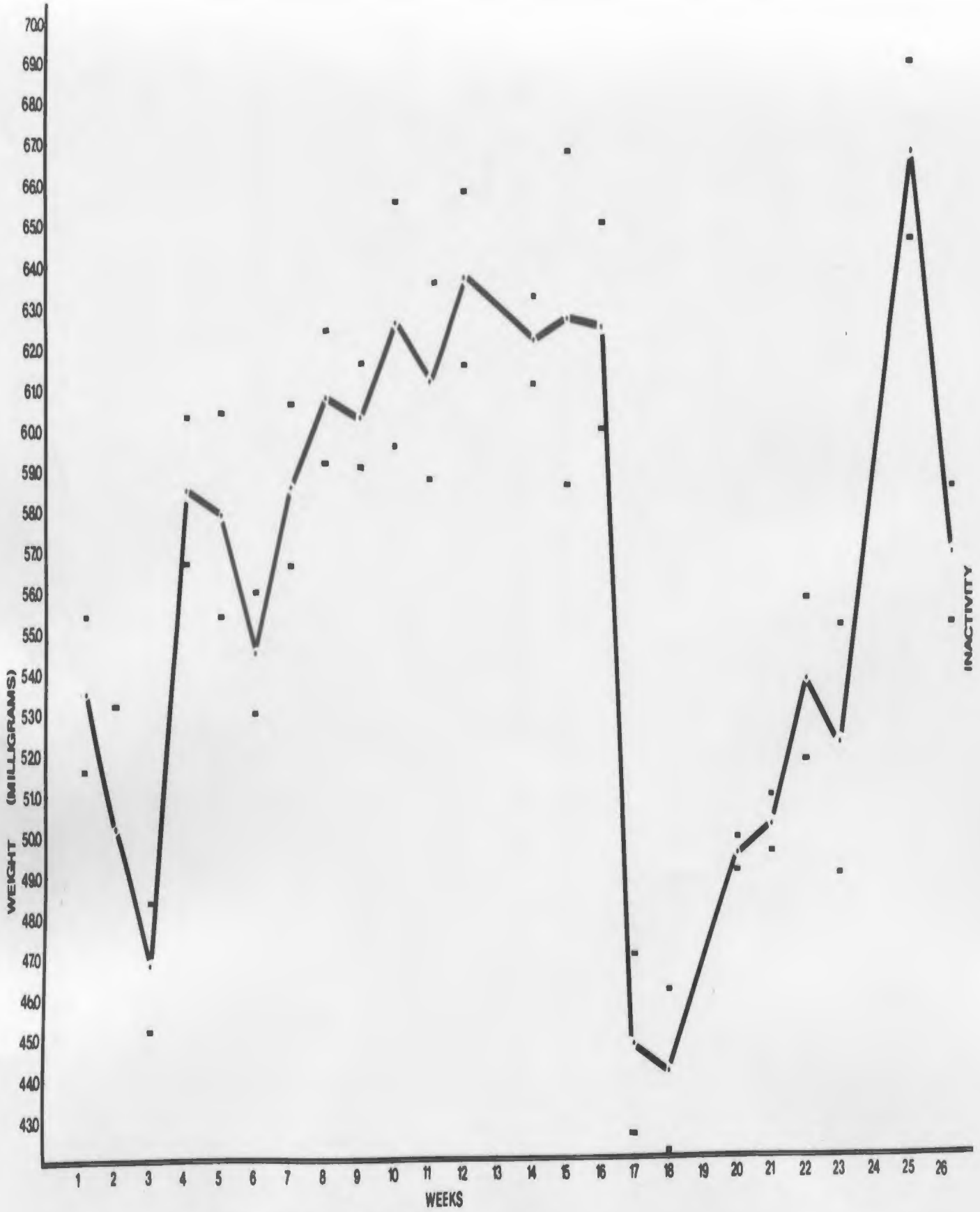


Figure 6 Average weekly weights of female G. remigis throughout activity

In points 7 - 10 more developing rudiments were near completion and caused an increase in weight. The second laying is indicated by a drop at point 11. Since death follows the second oviposition records for point 11 are made up of gerrids that had not completed oviposition. New adults are very light (point 13). Weight increases after emergence as adults are seen at points 12 and 13. The increase due to fat deposition is seen at points 13 and 14. Gerrids which gave off moisture and subsequently became inactive within a couple of days were lighter than those with equal fat body but which were still active (points 14 and 15).

Changes in average weights of female G. remigis throughout activity in the field are shown in Fig. 6. During week 1 gerrids had a large amount of food in their guts and this inflated the average weight. Ovaries continued development. During week 1 the first 3 rudiments of the 6 - 8 visible per ovariole had yolk. However, the amount of food found in the gut of each gerrid decreased and after 3 similar amounts were found in each gerrid. The drop in weight stopped at week 3 when the second and third rudiments in each ovariole had taken egg shape and the fourth, fifth and sixth had yolk present.

Further ovarian development is usually accompanied by an increase in weight. This was not the case at week 3. Besides the decrease in food content a small amount of the drop could be accounted for by the loss of traces of fat body. After this the development of rudiments continued but apparently not fast enough to account for such an increase as

was recorded at week 4. During weeks 4 - 5 the fourth rudiment in each ovariole developed more and the fifth and sixth followed them. From this an increase in weight might be expected but in fact a drop in average weight was recorded (week 5). As development continued the first rudiment in each ovariole became an egg and the other rudiments progressed correspondingly, up to week 6. At week 6 the average weight is further reduced, not as expected increased. After week 7 the average weight increased again. At week 8 the second egg in each ovariole had ovulated. Yolk was present as far back as the tenth rudiment. There was a weight reduction on the graph at this point which cannot be accounted for by any event in the ovarian cycle.

During week 9 there were as many as 4 eggs per ovariole and ovulated. The fifth and sixth rudiments were nearly completed and yolk was present back to rudiment 12. This development could account for some of the weight increase from week 9 to 10. Oviposition started in the middle of week 9 (19. June). Oviposition should have either reduced the average weight or prevented a further increase. Gerrids which had oviposited were much lighter than those which had not, approximately 48.3 mg as compared to 60.5 mg and more. Oviposition continued through week 10 and the rise in average weight is similarly inexplicable. After this time collections consisted of gerrids that were either fully developed or were half empty; this should have resulted in an apparent increase in average weight but weight dropped at point 11. During week 12 collections continued to include gerrids which had fully developed ovaries or those

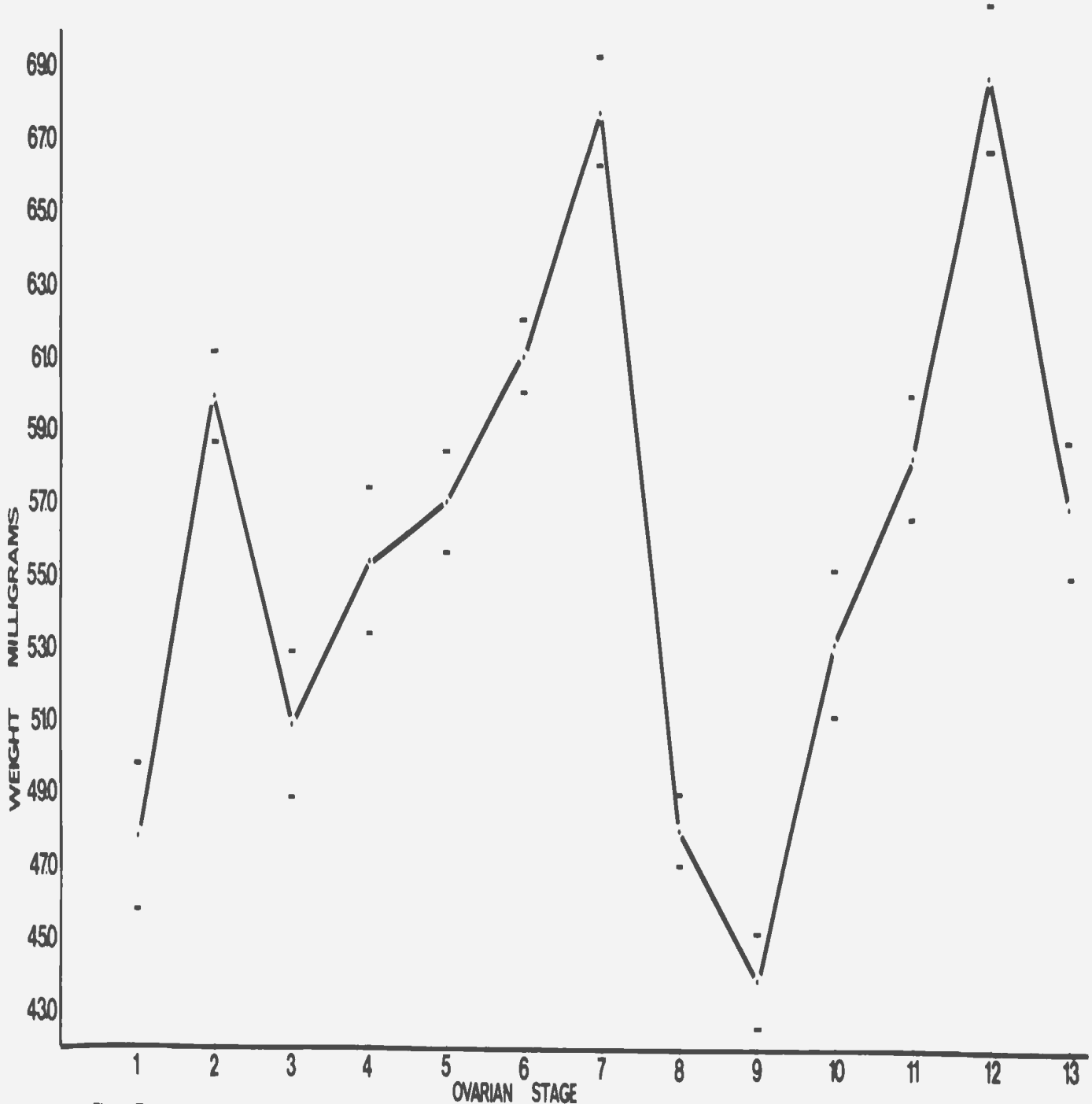


Figure 7 Average weights of female G.remigis at known ovarian stages

that had not completed oviposition. As a result an apparent increase in average weight is seen at week 12. In weeks 14, 15 and 16 the remaining gerrids were ovipositing and thus a drop in average weight can be seen at the corresponding weeks on the graph.

At week 17 there was a drastic decrease in average weight due to the appearance of very light new adults (week 17). Between weeks 18 and 25 there was an overall increase in average weight. This is also shown in Fig. 8. After the initial inexplicable weight gain of new adults (weeks 18 - 22), further gains were recorded (weeks 23 - 25) due to deposition of fat. A drop presumably due to water loss before inactivity is recorded at week 26.

Changes in average body weight of female G. remigis of known ovarian stage, based on laboratory and field observations, are shown in Fig. 7. Even though the ovarian stages are known there is an unusual rise in weight at the beginning at point 2. The only difference between gerrids used in calculating weights for points 1 and 2 was that those at point 2 had more food in the gut while those at 1 had none. Thus feeding led to a large weight increase. After this the average weight dropped (week 3). These gerrids and all after these had some food in their guts but never as much as at point 2. The drop may have represented a levelling off of the food content in the population and thus no further drastic difference in food content appeared after this. At point 1 and 2 the ovaries had resumed development after the winter. There was yolk present in rudiments 1, 2 and 3 of the 6 - 8 rudiments in each ovariole. This

increase in ovary content was not reflected in average weights due to the way the gerrids fed.

Between points 3 and 7 there was a steady increase in average weight. At point 3 there was one egg per ovariole plus 5 rudiments with yolk. At point 4 the ovaries had 2 eggs per ovariole often with 1 per ovariole ovulated. Eggs plus rudiments numbered 12 with yolk up to at least rudiment number 7. At point 5 there were 3 eggs per ovariole with corresponding increases in rudiment development. At point 6 there were 4 eggs per ovariole and at point 7 there were 5 eggs per ovariole. The increase is obviously due to ovarian development and is more clearly seen than in Fig. 6. Oviposition is obvious and is indicated by a sharp dip at point 8. New adults were very light and as a result there is a further reduction at point 9. Increases after emergence of adults are seen after point 9 - 10. The increase due to fat deposition is seen at point 11; 9 gerrids used in calculating this mean had deposited relatively large amounts of fat body, but no ovarian development had started. A further increase in the amount of fat deposited and the beginning of ovarian development is accompanied by another increase at point 12. At this point there were 5 rudiments per ovariole with traces of yolk in the first 2. Laboratory gerrids which gave off moisture and subsequently became inactive within a couple of days were lighter than those with equal fat body but which were still active (Point 13).

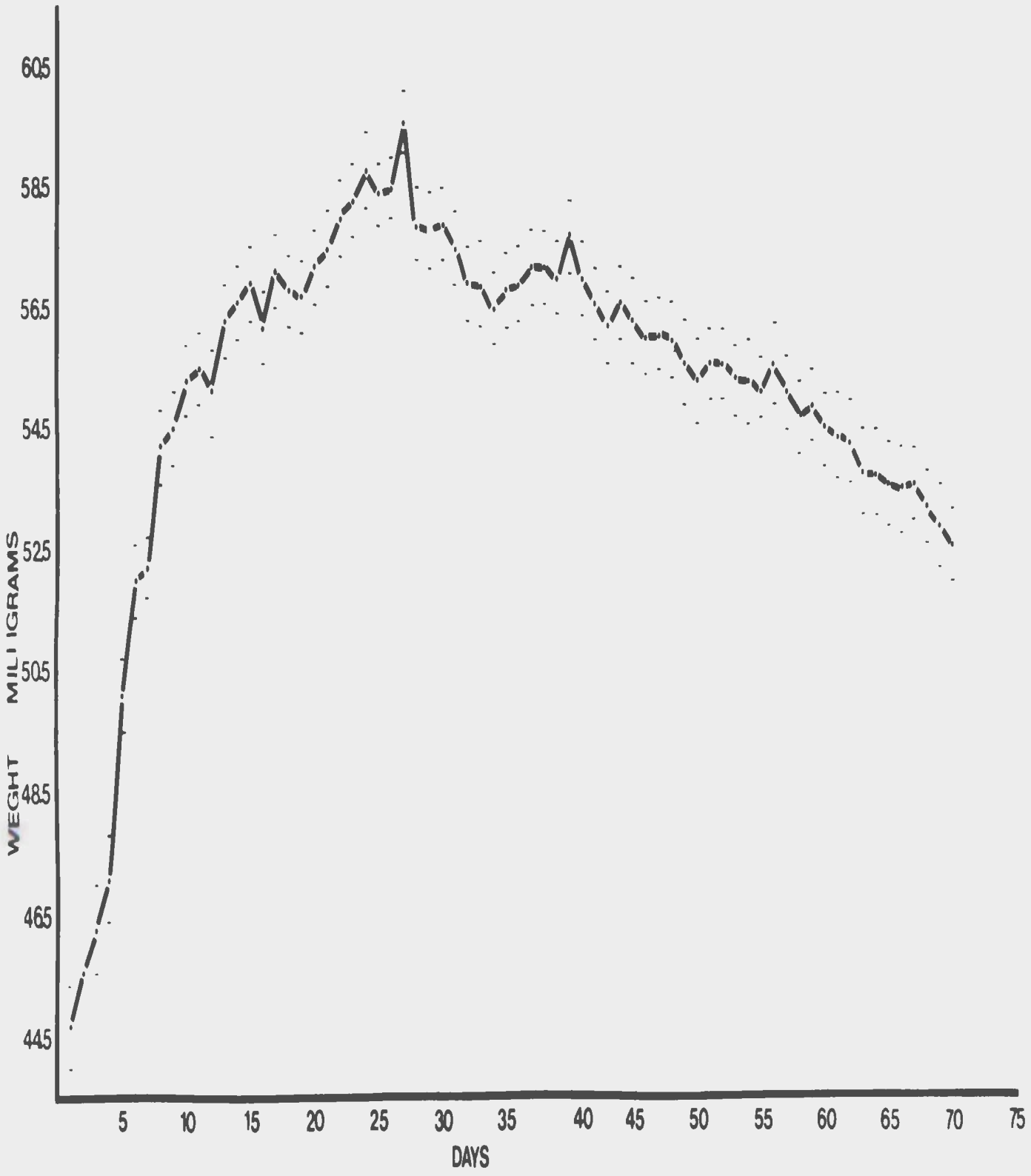


Figure 8 Average daily weights of G. remigis adults of known age

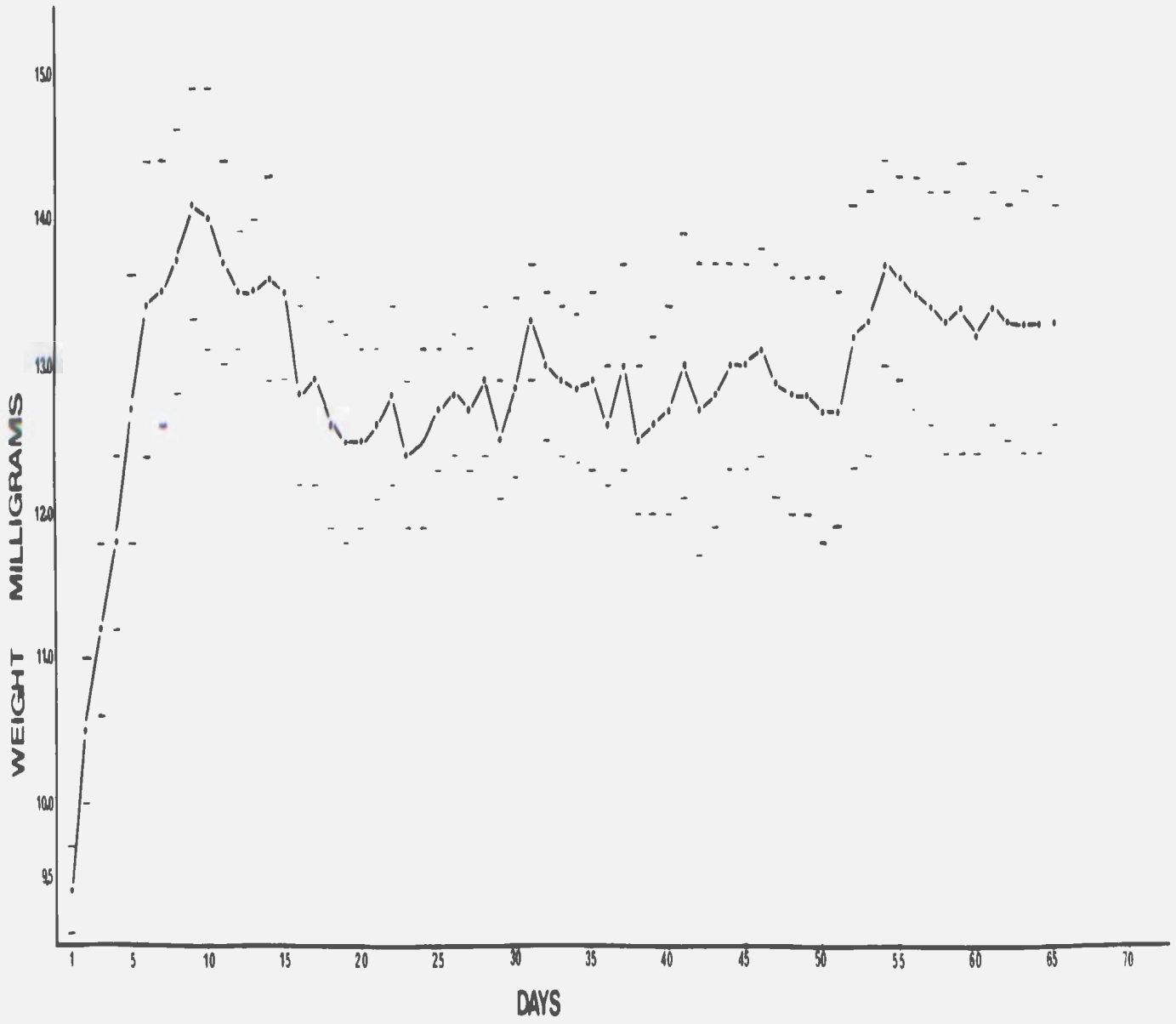


Figure 9 Average daily weights of G. buenoi adults of known age

Average daily weight changes of adults of known age.

Only the 15 G. remigis and 14 G. buenoi that survived the full experimental period were used to construct the graphs in Fig. 8 and Fig. 9. Short lived gerrids were not used because their early death distorted the average weights. These short lived gerrids were dissected when they died revealing no fat body or ovarian development. The rest of the gerrids were killed and dissected at the end of the experiment and the same results were obtained.

Fig. 8 shows results for G. remigis and Fig. 9 for G. buenoi. This experiment showed an initial increase in weight in both species. G. buenoi increased in weight until day 9, while G. remigis increased until day 24. After these initial increases both species gradually decreased in weight. Adequate food was provided as described in Methods and Materials.

Despite the fact that laboratory specimens did not prepare physiologically for inactivity and were exposed to summer conditions, both species became inactive. G. buenoi became inactive between 41 and 43 days after emergence as adults while G. remigis took about 70 days.

The drop in weight due to water loss which occurs under natural conditions before inactivity was not seen here. At the time that this loss could have been expected to occur there was a very gradual drop, but not enough to suggest a water loss.

Table 8: State of ovaries after dissection of G. remigis females

Photoperiod L:D (hours)	5°C	10°C	15°C	20°C
8:16	Vitellogenesis started in 2 rudiments per ovariole of the 5 present. First rudiments in each ovariole egg shaped.	Small amount of yolk in first rudiment of each ovariole. Five rudiments per ovariole.	Traces of yolk in first rudiment. Four rudiments per ovariole.	Vitellogenesis not begun. Three rudiments per ovariole.
12:12	Small amount of yolk in first rudiment in each ovariole. Five egg rudiment per ovariole. No rudiments have mature egg shape.	Vitellogenesis not started. Three rudiments per ovariole.	Two rudiments per ovariole just visible.	All died before completion of experiment due to incubator failure.
16:8		All died due to incubator failure.	All died due to incubator failure.	All died before completion of experiment. Not due to incubator failure.

Table 9: State of ovaries after dissection of G. buenoi females

	5°C	10°C	15°C	20°C
Photoperiod L:D (hours) 8:16	Ovaries distended but no rudiments present in any ovariole.	Same as 5°C	Same as 5°C	Same as 5°C
12:12	Same as 5°C 8:16	Same as 5°C 8:16	Same as 5°C 8:16	All died due to incubator failure.
16:8		All died due to incubator failure.	All died due to incubator failure.	All died but not due to incubator failure.

Light and photoperiod experiments.

All gerrids used in these experiments were collected in late September and early October. A few from each collection were dissected to ensure that all experimental animals were at about the same stage of ovarian and fat body development. All gerrids were apparently ready for normal inactivity.

Gerrids that survived were dissected at the end of the experimental period and the results are shown in Tables 8 and 9. Throughout the experimental period gerrids were observed daily for the first 3 weeks and every 3 days for the remaining 13 weeks. Their activity throughout the experiment is recorded in Tables 10 and 11.

Ovaries

In G. remigis kept at constant short photoperiod (8L : 16D) lower temperatures were better for development of the ovaries. The most development at the time of dissection was at 5^{o} C while the least was at 20^{o} C. At constant low temperatures shorter photoperiods were better for ovarian development. The most development at the time of dissection was at 8L : 16D the least at 12D : 12D (16L : 8D was not used) (Table 8).

There was no effect on the ovaries at any light and photoperiod regime in G. buenoi (Table 9).

Table 10: Activity of G. remigis during exposure to various photoperiod and temperature regimes

Photoperiod L:D (hours)	5°C	10°C	15°C	20°C
8:16	All inactive in less than 24 hours of exposure and remained so throughout experiment.	All inactive in less than 6 hours. Second day 4-5 became active. Two of these active for 1 week, then all became inactive.	Three active initially. Ten sluggish and on water but legs not in customary inactive position. Twelve inactive after 2 weeks. Eight-10 active periodically throughout experiment.	Most active periodically throughout experiment. Usually each became active, then sluggish with most dying.
12:12	Four-5 active the first 2 weeks, but not the same one each time. All inactive after 2 weeks.	First 3½ weeks 7-8 were active, then all became inactive. Some died 10-14 days after incubation.	Very sluggish but not all died. Tended to bunch together and rarely in customary position.	Became sluggish after a week of activity. Majority were sluggish by 10th day. Started dying after 10th day. Only one alive when incubator failed at the 2 week point.
16:8		About ½ active from the beginning. Half were inactive and none had died when incubator failed at the two week point.	About ½ active from the beginning. Four dead in 7 days. Remainder very sluggish. When incubator failed (2 week point) 3 alive.	Majority very sluggish after 2 days of activity. Started dying third day. Fourteenth day 6 alive. All dead at seventeenth day.

Table 11: Activity of G. buenoi during exposure to various photoperiod and temperature regimes

Photoperiod L:D (hours)	5°C	10°C	15°C	20°C
8:16	All inactive within 24 hours and remained so.	All inactive within 2 days. Then 10 became active, some staying active 2 weeks. After this all inactive until death or end of experiment.	About ½ active from beginning. Some of these sluggish but not in characteristic position, not same ones all the time. All inactive after 2 weeks.	Three inactive first 2 days. Rest sluggish and not in characteristic position. Started dying 5th day. All inactive after 3 weeks of exposure. Some dying even though inactive.
12:12	Two inactive the first day of incubation. All inactive from second day on.	Five active for 2 weeks. Then all became inactive and stayed that way.	No records	No records
16:8		No records	No records	This group was never inactive. Started dying 4 days after exposure, all dead by 14th day.

Activity

At a fixed photoperiod higher temperatures caused fewer gerrids to become inactive. At fixed temperatures longer photoperiods caused fewer gerrids to become inactive. At high temperatures (20^{o} C) and long photoperiods (16L : 8D, 12L : 12D) all gerrids died (one *G. remigis* remained after 3 weeks at 12L : 12D at which time the incubator failed) (Tables 10 and 11).

D I S C U S S I O N

Life history

Both species have basically the same life history. The times of occurrence of events such as commencement of winter inactivity, copulation and oviposition are not identical but are very close.

Both species manage very well to synchronize their life cycle with our seasons presumably because both are responding to the same environmental conditions. From the time the first eggs are laid until the first adults emerge is approximately seven weeks. Since the summer in Newfoundland is short, about three months from June to August, there is no time for the insects to produce more than one generation in one year.

Both species became inactive in the fall. They laid down fat reserves, decreased in weight and then overwintered as adults. They became active as soon as the ice and snow were gone and G. buenoi immediately started egg production, while G. remigis continued with it.

Some work has been done on the life history of G. remigis by Bueno (1917). A number of his observations on the life history in the areas he studied differ from those noted on the Avalon. Bueno states that :

> "Breeding and oviposition begins as early as February ..... It is seemingly continuous all through the summer and it is not unusual to find nymphs of various stages in company with the adults."

Unfortunately he does not state where these observations were made.

At Manuels River adults surviving from the previous year do not start mating until April or May. Oviposition occurred 19. - 20. June 1974 and nymphs of various instars were found through July, with a few adults at the beginning of the month. The new generation of adults appeared in the first week of August, not continuously throughout the summer.

Bueno also states that the nymphs are numerous until October. At Manuels River and Logy Bay the majority of the nymphs are seen in July and the first two weeks of August. Some may occasionally be collected after these dates. Adults are rarely seen once the nymphs appear. This is probably due to the cannabalistic tendencies of the species, which led to adults eating nymphs in the laboratory. The differences in the two populations are due to climate, since Bueno's work was presumably done further south. This allowed time for development of more than one generation a year.

It appears then that G. remigis has adapted to the climate on the Avalon Peninsula by modifying its life history.

During the life history of G. buenoi there are two inexplicable decreases in weight shown in Fig. 4 at points 6, 7 and 11. In both cases the drops occurred before a rise that preceded a drop due to oviposition. The gerrids dissected at that time had not laid eggs, yet a drop in weight occurred.

Inactivity

Diapause is difficult to define. Early authors such as Henneguy (1904) used it to describe any period of arrest at any stage in the life history of an insect, including simple inhibition by cold. More recently Chapman (1969) defines it as a delay in development which although its effect is usually to facilitate survival during unfavorable conditions is not immediately referable to them; that is the unfavorable conditions do not trigger the diapause but rather cues received before the unfavorable conditions trigger it (facultative diapause) or it is genetically induced (obligatory diapause). Periods of diapause are usually accompanied by preparatory periods before inactivity, such as deposition of fat body and a water loss. Diapause is broken by the series of events that ensue after the onset of diapause or by specific environmental cues. These statements also apply to reproductive diapause except that the insect is not necessarily physically inactive.

Both species of Gerris lay down fat reserves during late summer and early fall and both species show a drop in weight before inactivity which has been attributed to moisture loss. None of the treatments used on the gerrids prepared for inactivity succeeded in breaking it in the fall. There is obviously something other than the conditions to which they were exposed that breaks the inactivity and this must occur in the spring or during the winter. These two considerations would allow the use of the term "diapause". Adults reared in the laboratory and exposed to summer conditions still became inactive despite no preparation.

Gerrids taken from the field after preparation for inactivity and subjected to summer conditions became inactive, or if they did not they died (tables 10 and 11). The fact that they became inactive regardless of this physiological state or the conditions to which they were exposed suggests that the diapause is obligatory.

Even though the gerrids enter an obligatory diapause in the laboratory both species can and do move about during diapause when they are touched or disturbed and will feed quickly if food is available. Also Mr. Alex Coombs of the Chemistry Department, Memorial University, has seen them active in his well near St. John's in February 1973. These, however, are probably adaptations to survival in winter, especially in the Newfoundland climate. When gerrids are in diapause they need to keep damp. G. remigis achieves this in two ways, first by staying close to the water's edge and secondly by bunching together in groups of 20 or more. The fact that they stay close to the water's edge endangers them since the water level can rise or fall quickly. They therefore must be able to move or they might die. The opportunistic feeding is advantageous since it could supplement fat reserves.

Besides entering an obligatory winter diapause both species enter a reproductive diapause. This is obligatory for the same reasons that the physical inactivity was, none of the light and photoperiod regimes offered the gerrids, would break it and summer conditions did not inhibit the diapause.

Neither species mates in the fall under any conditions. The ovaries do not develop at all in G. buenoi and very slowly through the winter in G. remigis. Despite the difference the overall result is the same, i.e. another generation is not produced until the following summer, which is an adaptation to climate since more than one generation a year is produced further south, at least in G. remigis (Bueno, 1917).

Copulation

Isolated G. remigis seen copulating at Manuels River early in the year, did so on exceptionally warm days, 13° C compared with 4.5° C before and after. At the same time G. buenoi was not copulating at Logy Bay where the temperature was 4.5 - 7° C. Since G. remigis mated in early spring only when temperatures were high and G. buenoi did not start until temperatures were higher than 9° C, copulation was probably induced by high temperatures provided other requirements were fulfilled.

Of approximately 300 eggs of each species that were removed from the females after ovulation and kept under favorable conditions none developed, probably because they were not fertilised. Gerrid eggs have the usual micropyle for the entry of sperm (Poisson, 1933). So since oviposition and fertilisation are approximately simultaneous, it appears that copulation began very much earlier than necessary. In the field G. buenoi started copulating 26 days before oviposition while G. remigis started 51 days before. These seem to be unnecessarily long periods of

time. Speculatively, this may be attributed fo filling spermathecae in case males are wiped out before oviposition. Copulation in the laboratory seemed to be indiscriminate and random, the female accepting as many as three different males.

Oviposition

Oviposition sites are similar for both species as mentioned in Results. However, the species differ in some ways in their oviposition. The greatest difference is in the number of times each lays. Judging from dissections, G. remigis in the field started laying 19 June and individual females took 1 - 2 days to complete oviposition. G. buenoi laid twice 19.-20. June and 28. - 29. June 1974.

G. buenoi eggs are usually found in groups of 3 - 5 but groups of up to 49 have been found. G. remigis eggs are usually found in groups of 14 - 20 with 96 eggs in the largest group recorded. The number of eggs laid at a particular time also differs between the two species. The dissection results show that G. remigis empties its ovaries when 32 eggs are fully developed and 16 more are almost completed. G. buenoi empties its ovaries when it has 24 eggs. G. remigis lays the other 16 in 2 lots of 8 within a couple of days of the initial oviposition. G. buenoi waits until it has another 24 eggs and lays these 7 - 9 days after the initial 24. Based on this evidence both species must move around, laying their eggs in small groups while the large groups are a result of communal

laying. It is, however, not clear whether these large groups are the result of a few females laying all their eggs or many females laying a few. Movement while laying can be advantageous especially to G. remigis since water levels in its habitat may vary as much as 30 - 40 cm in a couple of days. A perfectly adequate oviposition site one day could be high and dry the next. Spreading the eggs around and laying some directly in the water ensures that at least some will be kept moist.

Eggs

The eggs of G. remigis and G. buenoi differ in size and color. G. remigis eggs are larger and yellow while those of G. buenoi are smaller and white. According to Buenoi (1917) G. remigis has white eggs but all G. remigis eggs laid by this population were yellow.

In both species eggs laid within the same group by one female do not develop at the same rate. This is probably an adaptation to their habitats. Variation in water levels over short time periods have been mentioned. As a result, variation of a day or so in the length of development can ensure survival. Aside from the varying water levels daily changes in the weather could make conditions one day much more favorable than the next. Staggering hatching provides for the hatching of some eggs into satisfactory conditions.

The two species also differ in the length of time it takes their eggs to develop in the laboratory. Both species have ranges within which

they develop, G. remigis between 11 and 13 days, G. buenoi between 9 and 11 days. However, in the field the first eggs of both species are laid at the same time and the first nymphs of both species appear at the same time, so it appears that even though different ranges exist in the laboratory eggs require the same time for development in the field.

Nymphs

Death due to being caught up in exuviae is probably less frequent in G. buenoi than in G. remigis since G. buenoi is found in small, often stagnant pools and may be better able to survive the type of conditions experienced in the laboratory set-up.

The relative mortality values (Table 2) within each species may be valid between instars. The ability of a species to survive will be reflected in relative numbers surviving in each instar regardless of the severity of the conditions. For example if the fourth instar has the highest mortality rate then it will have the same mortality rate under any conditions even in the lack of moving water in the laboratory set-ups.

Both species used in this study developed in about the same time in the laboratory and the field.

Ovarian Development

There are a number of differences between the ovarian cycle of G. buenoi and G. remigis despite the similarity of their life histories.

The major difference is in the starting time of ovarian development. In G. remigis rudiments and germaria develop and vitellogenesis starts in the fall while in G. buenoi egg rudiments and germaria do not develop and vitellogenesis does not begin until spring.

Yellow spots appear in the same location in both species but at different times of the year. In G. remigis they appear in the fall before the appearance of any rudiments while in G. buenoi they appear after ovulation in the summer. These yellow spots are not corpora lutea. They also cannot be termed resorption bodies since when they appear in G. remigis they are the only thing in the ovarioles and when they appear in G. buenoi the eggs are ovulated not reabsorbed.

Both species develop and lay the same total number of eggs, 48, but differ in the length of time it takes to develop them. G. remigis starts development in the fall, continues slowly through the winter and oviposits 19. - 20. June while G. buenoi does not start until the middle of April and has laid 48 eggs by 28. - 29. June.

In G. remigis the eggs were stored in the ovarioles after ovulation while awaiting oviposition. However, in G. buenoi there was no storage, eggs were ovulated and immediately laid.

In both species rudiments remain in the ovarioles after ovulation and oviposition has been completed even though they do not develop. In both species the adults die after oviposition and ovulation. The remaining

rudiments are used in more southerly populations, where there is also more than one generation a year (Bueno, 1917). Possibly rudiments that do not develop in Newfoundland populations represent vestiges of this. Since both species would be capable of producing another generation if they did not die perhaps death is also a genetically controlled event limiting the number of generations a year. In the laboratory one G. remigis lived and produced a small second batch of eggs, showing that the ability persists in some of the population.

Gerrids in Newfoundland may be at the northern limit of their range. Further south they produce more than one generation a year. On the Great Northern Peninsula near Hawkes Bay (12-1/11 875 058) G. buenoi is slower developing its eggs than on the Avalon Peninsula. In late June the ovaries were at the same stage as they were on the Avalon in April. This may be the extreme limit since these eggs barely have time enough to develop and the nymphs to become adult and to prepare for diapause before the winter.

Average daily weight changes of adults of known age.

The fact that gerrids in this experiment did not deposit fat body or lose moisture in preparation for inactivity is perhaps because they missed environmental cues such as lower temperature or shorter photoperiod that the field specimens received. However, they did become inactive in the laboratory despite their lack of preparation.

In the field G. buenoi prepared and became inactive within 44 - 49 days after emergence as adults while G. remigis took 74 - 79 days. This agrees well with laboratory figures of 43 - 44 days for G. buenoi and 70 days for G. remigis.

In the field the gerrids prepare and become inactive in the same time as the laboratory specimens with no preparation. It appears then that the inactivity is genetically controlled but the preparation for it is environmentally controlled.

Light and photoperiod experiments, ovaries.

It appears that G. remigis requires the cold short days of winter for the development of its ovaries to the point they reach in the spring. Long warm days at this point in its life history impede ovarian development in regimes where some survived. Ovaries of gerrids under winter conditions (8L : 16D, 5^{o}C) were most developed, (Table 8).

The conditions to which G. buenoi was exposed did not affect the ovarian cycle. It appears that reproductive diapause is obligatory and ovarian development will not start until spring regardless of whether or not they were exposed to favorable conditions.

Activity

The main difference in activity between the two species is in the length of time is takes them to become inactive. G. buenoi becomes inactive in each regime earlier than G. remigis. G. buenoi also becomes

inactivity in one regime (8L : 16D 20° C) where G. remigis does not. This is a reflection of the field situation, where G. buenoi becomes inactive about one month before G. remigis.

Under all regimes both species of gerrids either became inactive or died. None of the experimental conditions broke the inactivity. At low temperatures or short photoperiods both species became inactive, while at more summer-like conditions of high temperature or long photoperiod they became sluggish and most eventually died. At 20° C 16L : 8D in both years, all specimens of both species died.

The low temperatures and short photoperiods were the most favorable conditions. This is expected since these are the conditions they would have had to face in the field.

The inability of Newfoundland populations of these two species to respond to a lengthened summer in the laboratory suggests that they must be genetically different from populations living further south.

It is interesting to compare egg production and diapause in G. remigis and G. buenoi with that in other insects, some of which have been intensively studied.

The ovaries of gerrids are telotrophic and the nomenclature used is that of Imms (1957) and Engelmann (1970) for the parts of such an ovary. According to Eschenberg (1966) the reduction division takes

place in the germarium so the developing eggs, here called rudiments, are in reality oocytes. The term "primordia" has been used by Detinova (1962) for these, but is open to the objection that "primordial germ cell" has been used many years synonymously with "oogonium" or "spermatogonium". Eschenberg (1966) gives a detailed histological and histochemical analysis of oocyte differentiation in G. remigis. The yellow spots mentioned in these two species have been referred to as fat bodies bu Eschenberg (1966) and follicular plugs by Woodward (1952).

The winter inactivity of G. remigis and G. buenoi is of a rather peculiar kind in that both species can be aroused by stimulation. As in most other insects these two species lay down fat reserves and lose water before becoming inactive (Chapman, 1969). Chapman (1969) also states

> "Sometimes every individual in every generation enters diapause. This is obligatory diapause and as a result there is usually only one generation a year."

This further supports the view that the inactivity of these two species is an obligatory diapause.

Adult diapause in insects may be reproductive, in which development of germ cells does not continue, though activity may. This is particularily well known in Nomadacris septemfasciata (Serv.) (Orthoptera) in which it lasts for 7 months in the Rukwa Valley, Zambia (Norris, 1964). Reproductive diapause is also exhibited in the life history of those insects with long lived overwintering adults including Cydnidae, Naucoridae, Nepidae, most Pentatomidae and Corixidae and about half the Nabidae

(Woodward, 1952). Either production of egg rudiments is completely inhibited (as in G. buenoi) or considerably retarded during winter when small rudiments have been formed in the autum (as in G. remigis).

The factor or factors that cause the breaking of the inactivity and reproductive diapause could be a series of events or a particular cue. For example in the beetle Pterostichus nigrita following long days in summer short days induced oocyte development to some extent but only after succeeding long day exposure was growth completed and eggs laid (Thiele, 1966). This may be the case with G. remigis since ovarian development does continue slowly through the winter (short days) but exposure to longer photoperiods in the fall inhibited instead of increasing the limited amount of development that normally took place.

In another beetle of the same genus Pterostichus oblongopunctatus successions of long and short photoperiods or vice versa did not cause egg maturation - but rather exposure to cold terminated the diapause (Thiele, 1968). This may be the case with G. buenoi. Exposure to long days and high temperatures in the fall had no effect on the ovarian development, the ovaries remained in the same state. It may be that this species has to experience a period of chilling before development is initiated.

It is interesting to note that these 2 beetles are of the same genus as are the bugs studied here. Even though the two gerrid species lay their eggs at about the same time of the year, it is obvious that they use different environmental cues in timing their reproductive season.

SUMMARY

Gerris remigis Say and *Gerris buenoi* Kirkaldy were observed in the field, specimens were brought into the laboratory where some were weighed and dissected and ovarian development noted while others were maintained in culture. Numbers of eggs laid, period of incubation and number and length of nymphal instars were recorded in the laboratory. Other specimens of both species were kept under controlled conditions of photoperiod and temperature in fall and winter to determine the effect of these on ovarian development and to break or inhibit reproductive diapause and inactivity. All laboratory specimens were weighed and dissected at the end of the experimental period.

The life histories of both species are similar; both are univoltine. Adults emerged the first week of August each year and entered obligatory diapause in the fall; *G. buenoi* 20. - 25. September and *G. remigis* 15. - 25. October. Activity resumed in the spring, *G. remigis* 15. April 1974 and *G. buenoi* 22. April 1974. Copulation was first observed 19. April 1974 in *G. remigis* and 25. May 1974 in *G. buenoi*. Oviposition took place for the first time in both species 19. - 20. June 1974 and again 28. - 29. June in *G. buenoi*. Eggs developed in and out of water; in *G. remigis* in 11 - 13 days, in *G. buenoi* in 9 - 11 days. Both species have five nymphal instars, the mean total nymphal period in the laboratory was 41.77 days in *G. remigis* and 43.13 days in *G. buenoi*. The first nymphs of each species appeared in the field 1. July 1974.

The ovaries of both species are structurally similar with four ovarioles per ovary, a lateral oviduct from each of two ovaries joined to form a common median vagina. The ovarian cycle occupies one year.

In both species the first rudiments appear simultaneously in each ovariole $\frac{1}{4}$ - $\frac{1}{3}$ the length of the ovariole anterior to the junction of the ovarioles and the lateral oviduct. Rudiments appear one behind the other, anterior to the first that appear and development takes place at the original location of each rudiment. Development occurs from posterior to anterior in each ovariole, the most posterior rudiment being the first to become an egg and ovulate (move into the first $\frac{1}{4}$ - $\frac{1}{3}$ of each ovariole). G. remigis develops 6 eggs per ovariole without a break while G. buenoi develops 3 eggs per ovariole, ovulates and oviposits these and then repeats the process.

The two species differ in a number of respects with regard to their ovarian cycle. G. remigis starts ovarian development in the fall and carries on slowly through the winter. G. buenoi does not start until the following spring. G. remigis stores most of its eggs after ovulation until ready to oviposit while G. buenoi lays as they are ovulated. Yellow spots appear in G. remigis in the fall but not in G. buenoi until ovulation of the first egg in each ovariole. There are also a number of similarities. Both species develop and lay 48 eggs; in both species rudiments remain after oviposition is completed. In both species eggs

develop from posterior to anterior in each ovariole and at the same location in the ovarioles.

Changes in weight throughout the summer can be accounted for, at least in part, by changes in the ovarian cycle, appearance of new adults, or deposition of fat. Increases in weight are seen with development of eggs and deposition of fat body. Decreases in weight occur with oviposition and a moisture loss prior to inactivity. Adults are lightest when they first emerge; they increase in weight without any increase in fat or ovarian development.

After exposure to 5^{o}C, 10^{o} C, 15^{o} c and 20^{o} C at 8L : 16D, 12L : 12D and 16L : 8D reproductive diapause and physical inactivity was not broken in either species. The higher temperatures and longer photoperiods inhibited the limited amount of ovarian development that normally occurs in G. remigis during the winter. None of the regimes had any effect on the ovarian development of G. buenoi, ovarian development did not commence in the fall. The lower the temperature and the shorter the photoperiod the more of both species survived the regimes. At 20^{o} C and 16L : 8D all of both species died in a short time.

In conclusion, although both species are similar in their overall life histories the details are often quite different.

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APPENDIX A

Analysis of Variance Tables for Measurements of *G. remigis* and *G. buenoi* nymphs

Analysis of variance tables for measurements of G. remigis nymphs

Source	d.f.	s.s.	m.s.	F
Head				
Total	149	353.25		
Instars	4	342.96	85.74	1207.60**
Error	145	10.292	.0710	
Thorax and Abdomen				
Total	149	17244.39		
Instars	4	16399.836	4099.959	704.4603**
Error	145	844.55	5.82	
Antennal segment 1				
Total	149	628.399		
Instars	4	621.779	155.44	3401.31**
Error	145	6.62	.0457	
Antennal segment 2				
Total	149	142.98		
Instars	4	140.022	35.00	1715.68**
Error	145	2.961	.0204	
Antennal segment 3				
Total	149	169.82		
Instars	4	166.87	41.717	2044.95**
Error	145	2.951	.0204	
Antennal segment 4				
Total	149	150.078		
Instars	4	146.214	36.553	1374.17**
Error	145	3.86	.0266	
Leg 1 femur				
Total	149	2457.61		
Instars	4	2437.55	609.387	4403.085**
Error	145	20.06	.1384	
Leg 1 tibia				
Total	149	1825.006		
Instars	4	1798.97	449.74	2502.72**
Error	145	26.06	.1797	
Leg 1 tarsus				
Total	149	196.37		
Instars	4	187.55	46.888	771.18**
Error	145	8.81	.0608	

Source	d.f.	s.s.	m.s.	F
Leg 2 femur				
Total	149	12716.928		
Instars	4	12650.05	162.5	6857.11**
Error	145	66.87	.4612	
Leg 2 tibia				
Total	149	7876.44		
Instars	4	7790.56	1947.64	3288.26**
Error	145	85.87	.5923	
Leg 2 tarsus				
Total	149	1796.161		
Instars	4	1758.35	439.58	1686.15**
Error	145	37.80	.2607	
Leg 3 femur				
Total	149	9820.09		
Instars	4	9781.61	244.54	921.40**
Error	145	38.483	.2654	
Leg 3 tibia				
Total	149	5542.54		
Instars	4	5452.24	1363.06	2188.95**
Error	145	90.29	.6227	
Leg 3 tarsus				
Total	149	702.61		
Instars	4	687.96	171.99	1702.87**
Error	145	14.651	.1010	

Analysis of variance tables for measurements of G. buenoi nymphs

Source	d.f.	s.s.	m.s.	F
Head				
Total	149	125.49		
Instars	4	116.88	29.22	491.91**
Error	145	8.61	.0594	
Thorax and Abdomen				
Total	149	6554.51		
Instars	4	6336.02	1584.01	1051.21**
Error	145	218.49	1.5068	
Antennal segment 1				
Total	149	184.97		
Instars	4	182.16	45.85	2363.40**
Error	145	2.81	.0194	
Antennal segment 2				
Total	149	51.02		
Instars	4	49.19	12.30	968.50**
Error	145	1.84	.0127	
Antennal segment 3				
Total	149	44.39		
Instars	4	42.656	10.66	895.7**
Error	145	1.73	.0119	
Antennal segment 4				
Total	149	64.69		
Instars	4	60.86	15.215	578.51**
Error	145	3.82	.0263	
Leg 1 femur				
Total	149	611.14		
Instars	4	597.898	149.47	1637.13**
Error	145	13.24	.0913	
Leg 1 tibia				
Total	149	479.166		
Instars	4	462.81	115.70	1026.61**
Error	145	16.34	.1127	

Source	d.f.	s.s.	m.s.	F
Leg 1 tarsus				
Total	149	55.27		
Instars	4	50.71	12.67	404.14**
Error	145	4.55	.0314	
Leg 2 femur				
Total	149	3676.968		
Instars	4	3646.42	911.605	4330.6651**
Error	145	30.52	.2105	
Leg 2 tibia				
Total	149	2250.416		
Instars	4	2222.84	555.71	2921.71**
Error	145	27.57	.1902	
Leg 2 tarsus				
Total	149	1510.407		
Instars	4	1445.91	361.477	812.67**
Error	145	64.49	.4448	
Leg 3 femur				
Total	149	3162.00		
Instars	4	3132.61	783.15	3863.59**
Error	145	29.38	.2027	
Leg 3 tibia				
Total	149	824.30		
Instars	4	802.09	200.52	1308.87**
Error	145	22.21	.1532	
Leg 3 tarsus				
Total	149	260.48		
Instars	4	254.07	63.517	1433.7923**
Error	145	6.41	.0443	